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The Pursuit of Mycology in the Tropics: Recollections By: Dr. C.V. Subramanian

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The name of the journal KAVAKA *is a Sanskrit word which means Fungus.*

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From the Editor's Desk

The publication of dedicated 45th volume of journal Kavaka, being transactions of the Mycological Society of India, as memoirs of its founder Editor, Professor C.V. Subramanian is in recognition of his significant contributions to the development of Science of investigating fungi as an independent discipline on worldwide basis in general and India in particular. It is a must read document for the botanists in general and the mycologists in particular as it teaches us in unequivocal terms how good science can be done by adopting passionate approach without losing our ethical sense using bare minimum facilities. Going through the pages of the memoirs teaches us about how to search for truth with independent thinking and describe novelties with utmost honesty and accuracy. Driving names of several new genera and species of fungi discovered by him along with his students from Sanskrit roots instead of Latin was a noval and bold example of thinking independently and differently, which the Mycologists the world over supported. Despite achieving so much which no other mycologist has achieved so far, he has been a student and a learner all through his life as is evident from the contents of his memoirs. For doing good taxonomy, he has rightly stressed to complement the traditional systematic approach with the conclusions drawn from the need based molecular investigations. As a world of caution he has emphasized that the system should not become so highly sophisticated that it becomes impracticable and not easy to practice. If taxonomic methods for investigating these microbes remain simple and user friendly, more and more scholars will be in a position to contribute their bit towards investigating the complete biology of fungal organisms including their morphological, biochemical and phylogenetic aspects. Emulating his footsteps will be a real tribute to the efforts this great man has put in to bring recognition to the Indian Mycology at the International level.

31-12-2015

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FELICITATIONS : THANKSGIVING

Maathrudevo Bhavah! Pithrudevo Bhavah! Aaachaaryadevo Bhavah!

I am here from my parentage and upbringing, from my training, the head playing its part, and the heart. Life is a matter of being fit to play one's part well. Basically, I am a botanist, concerned with structural and functional beauty which is what makes a plant what it is. I am concerned with nature's way of making plants meaningful. Studying the wilt disease of cotton which is a soil-borne disease caused by a soil fungus, I was fascinated by the interactions of the fungus in the host root system and the interactions of the fungus with other microbes in the soil. Thus, I considered myself a plant pathologist. Fascinated by the fungi in the soil, I focused on the innumerable moulds, mildews and mushrooms, and came to do mycology. When a Chair in Plant Pathology, the first one in the country, was established in the country, I thought it was a great honour. When a Chair in Botany was established in the University of Rajasthan first in Jodhpur and later in Jaipur, again I felt happy about it. It was later that I came to hold a Chair in Mycology with all that was meaningful and significant in my pursuit of tropical mycology.

Life for me has been wonderful, with my great teachers, and my students, and the many friends and professionals, and my wife and my children who have enriched my life in a special way giving contentment and satisfaction in every way. I have been fortunate in having been able to dedicate my monograph on Hyphomycetes to my mother who brought me up and took care of me. I am happy I dedicated my second book on Hyphomycetes to my wife Lakshmi who has been a pillar of strength to me. I cannot ask for more. My life has been eventful, with its turns and twists, with kindness and courtesy marking achievements in my pursuit of tropical mycology. I have enjoyed exploring fungi and biodiversity, in hunting and inventorying fungi, limitless and perennial, in forest, river and sea. The extraordinary structural and functional beauty of fungi that came my way is what kept me engaged all along in my endless quest for novelties that abound in the tropics. Many of my new fungi were named using Sanskrit roots. I was fortunate to have been able to visit many countries worldwide collecting fungi and meeting and discussing fungi to learn more about them. What can be more edifying?

Many are those who helped me in my pursuit and I remember them and their many kindnesses. I value and cherish their friendship. In my Recollections, I have recorded them as part of my pursuit of mycology. Many are the associations and institutions to which I was exposed, and many the Conferences and Symposia, national and International, wherein I played my part. I had two innings in the University of Madras, and stints at the IARI in Delhi, and in the University of Rajasthan. In general, I received warm support from colleagues in these institutions. Indeed, some of these institutions, notably the University of Madras and the University Grants Commission, the Botany School, Cambridge, the Commonwealth Mycological Institute, Kew, the British Council and the Jawaharlal Nehru Memorial Fund played a significant part in my studies of fungi in general and plant pathogenic fungi in particular. Recognition and awards have come to me unasked as I find myself being with you today. My wife, my children and I wish all of you all the best in life. May God bless you.

C V Subramanian

11 August 2014, Chennai

The Pursuit of Mycology in the Tropics:

Recollections

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PART ONE

MY LIFE WITH FUNGI AND FUNGOLOGISTS

Studying fungi in the tropics has been for me a wonderful, exciting experience. Excitement and fascination came from a sense of wonder at the beauty of form, function, or 'natural fit' of fungi, of interdependence among the biota. Excitement is part of the experience of probing the mysterious, the unknown as James Hopwood Jeans (1930) wrote in "*The Mysterious Universe*". With all our Science, and Philosophy I am sure, there will always remain, at least a moiety of the mysterious, to evoke a sense of awe and wonder, and excite us. There is still so much that we do not know. Amidst all the beautiful and wonderful things around us, we feel small; indeed, we are small. Such a feeling of smallness reduces one to a speck in an ocean! Yes, a speck in an ocean.

I began studying fungi well over sixty years ago - by accident, rather than by design. It just happened. As a student, I was attracted to the algae, and wanted to study them as I was fascinated by their beauty of form. An alga like the chlorophycean *Fritschiella* with its heterotrichous habit, was believed to have given rise to the first land plants by Frederick Orpen Bower (1935) in his *Primitive Land Plants*. *Fritschiella* typically has a creeping plant body with erect filaments and rhizoids fixing it to the soil which is its normal habitat. Indeed, there are so many beautiful algae such as the *Volvocales* and the desmids, besides green, red and brown seaweeds, that are marine.

On a visit to the Krusadai Islands near Rameswaram in southern India, in 1941, to collect algae, I had seen the beauty and diversity of these marine algae. Such beauty is beyond description, and must be seen to be enjoyed. M. O. P. Iyengar, who discovered and described *Fritschiella* (Iyengar, 1932) was not merely a great algologist but a great botanist of the last century, I should say, one of the greatest. I had wanted to study algae with him, but he retired from the Madras University Botany Laboratory (UBL) at the time I graduated and wanted to study the algae… it was as if I was not destined to study the algae.

I Fungi, Plants and Soil:

Instead, I was ushered into doing soil mycology, the study of the countless fungi involved in varied activities in soil and in



Dr. C.V. Subramanian

Interactions with other biota. Iyengar's successor was T. S. Sadasivan, a young botanist, who had specialized in soil mycology and plant virology working at the Rothamsted Agricultural Experiment Station at Harpenden in England and had a Ph.D. in Plant Pathology from the University, London. I wanted to pursue research, but the need for financial support to do so, was a constraint. When I saw the new Director of the UBL and presented my credentials, I was readily accepted as his first research student. I was given a University scholarship on the strength of my First Class Honours Degree in Botany from the Presidency College, University of Madras. The problem I was to study had to be fitted into the broad title, 'Soil conditions and *Fusarium* wilt in cotton', but I hardly knew what exactly I would be doing.

Two great books, one published in early 1944, the year I began my research, and another in the following year, had a profound effect on me and virtually guided the course of my research and even defined it. The first of these was *Root Disease Fungi* by S. D. Garrett. This book inspired me to study the autecology of the *Fusarium* that caused the wilt disease in cotton plants in southern India. Cotton wilt was primarily soil-borne, because the pathogen, a species of the [anamorphic] fungal genus *Fusarium*, dwelt in the soil or at least infected the root system of the plant through the soil.

Garrett's book introduced me to the exciting world of soil-borne fungal pathogens and the 'root diseases' they cause. It evoked an enormous amount of research on soil-borne fungal diseases of plants worldwide. A good book has infinite power to do good for science and for humanity. The second book published in 1945, which inspired me was Selman A. Waksman's *Microbial Antagonisms and Antibiotic Substances*. If Garrett's book focused my attention on interactions between soil-borne fungal pathogens and root systems of plants, Waksman's book introduced me to the interactions between the microbes themselves.

Thus, taken together, these two works converged towards a holistic view of soils, microbes, and plants, and their root systems. My approach to studying the problem had to be based on this holistic view. Sadasivan did nothing to curb my enthusiasm and freedom to do what I wanted to do, and encouraged and guided me. It is this freedom that I valued most in my search for beauty, for truth, and for goodness.

Seeing is believing. It was imperative that I saw for myself the disease in the field and collected diseased plant material and soils with a view to isolating the pathogen and establishing its ability to infect cotton plants and cause disease. Problems of plant disease arise in the field.

Visiting wilt-prone areas of cotton in Udamalpet and adjacent areas around Coimbatore, with the help which generously came from K. M. Thomas, the then Government Mycologist at the Agricultural College and Research Institute at Coimbatore, I saw for myself the extensive damage to the crop from the incidence of severe wilt. Indeed, on a visit to our laboratory soon after I joined it, it was Thomas who suggested to my mentor that I work on this problem. With a Carl Zeiss bellows camera in the field, I took photographs of diseased and healthy plants as a record of what I saw, and collected diseased material and samples of 'wilt-sick' soil for isolating the pathogen. The farmer who cultivated the crop where I found the disease was courteous and helpful, and I thought he knew a lot about cotton varieties and their resistance or susceptibility to wilt and about soil and environmental conditions conducive to the disease. Nothing matched the learning that came from experience.

Though I knew nothing about the fungus called *Fusarium*, from diseased material I isolated many fungi, presumably fusaria, of which I made single-spore (pure) cultures for study. The identification of fungi posed a serious problem. Anyone who works with an organism must know precisely what that organism is, in order to be able to communicate his findings. There was no specialist taxonomist around to help me. Wading through the pages and the volumes of the celebrated *Review of Applied Mycology* (RAM), I found there was extensive work on wilt diseases of plants and on *Fusarium*.

The foremost authority on *Fusarium*, H. W. Wollenweber, worked in Berlin. His *Die Fusarien*, *ihre Beschreibung, Schadwirkung und Bekaempfung* written jointly with Otto A. Reinking and published in 1935, was then not only the first, but the most recent and definitive monograph of the genus. As evident from the title, the text was in German. No copy of this classic was around and so I had to borrow the book from the University at Lucknow. And, since it was needed for constant reference, I made my own handwritten copy of the entire taxonomic part of the text, with tracings of all line drawings on thin paper. Since I had made an effort in learning German, it was possible for me to have some idea about *Fusarium*. A reprint of the book appeared sometime later, and we then procured a copy.

Indeed, after detailed study, the cotton wilt *Fusarium* turned out to be indistinct from *Fusarium vasinfectum* described by G. F. Atkinson in 1892 from wilted cotton plants in Alabama in the U.S.A. Atkinson, who was the first ever to describe the disease and the pathogen, and had also the distinction of having been President of the Botanical Society of America, noted that the pathogen infected root systems of cotton plants and established a close connection with the vascular system of the plant. It is this feature that he wanted to preserve in the specific epithet, “vasinfectum”. The disease itself was designated a 'vascular wilt.' The prediliction of these 'wilt fungi' to colonization of the vasculature of plants is mysterious and we do not have a satisfactory explanation for it. Though these fungi are known to have the enzyme systems to break down plant cell walls, we do not know why no cell walls or tissues seem to be broken down at the site of entry. Such behaviour is apparently peculiar to fusaria that cause vascular wilts.

Following Atkinson's work, an Egyptian, Tewfik Fahmy, reported the disease from Egypt. Whereas wilt in the U. S. A. occurred in sandy, acidic soils, in Egypt wilt occurred in heavy, alkaline soils. Similarly, in India too, wilt occurred only in clayey, alkaline soils. What could be the reason for this? My tests for pathogenicity of the *Fusarium* on cotton plants were initially negative. The tests were conducted on the susceptible Karunganni cultivar in pots with soil collected from wilt-sick cotton fields, satisfying optimum conditions for infection and disease development. At least I thought so.

One of our early plant pathologists, J. F. Dastur (1924; 1931) had studied the disease and carried out pathogenicity tests, but the plants remained healthy. He had then attributed the wilt of cotton in India to aluminium toxicity of the soil, and to accumulation of aluminium and iron in cotton plants, somewhat on the lines of Hoffer and Carr's (1923) attribution of a disease of corn in the U. S. A., to aluminium toxicity. There had been no confirmation of this.

Among the early workers on cotton wilt in India, S. L. Ajrekar (1926), G. S. Kulkarni (1931; 1934) and B. B. Mundkur (Kulkarni and Mundkur, 1931a; b) showed that wilt was due to a *Fusarium*. [The “Ajrekar Mycological Herbarium” at the Maharashtra Association for Cultivation of Science (MACS) at Pune commemorates Ajrekar's contributions to mycology]. Mundkur (1936) showed further that the Indian strains of the *Fusarium* infected only Indian cottons (*Gossypium arboreum*) but not American cotton. Conversely, the American strain of the *Fusarium* infected only American cotton (*G. barbadense, G. hirsutum*), but not Indian cotton. Such specificity was remarkable. The beauty of this finding lay not merely in its confirmation, but in the thought of its extension in terms of a global picture of fungal strains with prediliction to specific host genomes.

A series of cross-inoculation experiments were carried out during 1948-50 in South Carolina in the USA by G. M. Armstrong and Mrs Armstrong (Armstrong and Armstrong, 1950) on a range of cotton cultivars with a range of strains of the cotton wilt *Fusarium* of different regional origins (also other Fusaria of Section *Elegans* and their respective hosts). The Armstrongs had used several of my strains of the cotton wilt *Fusarium* from southern India and seeds of different Indian cultivars of cotton which I had sent them for their study. The specificity of strains to particular host cultivars

was thereby established (Armstrong and Armstrong, 1960; 1975).

On the basis of these studies and those of others, five Races of the cotton wilt *Fusarium* were recognized: Races 1 and 2 from the USA, Race 3 from Egypt, Race 4 from India and Race 5 from Sudan. Race 4 from India was unique as it caused wilt only on *Gossypium arboreum*. Conversely, Races 1 and 2 from the USA induced wilt only on *G. barbadense* and *G. hirsutum*, but not on *G. arboreum*. Thus, it seemed that host resistance or susceptibility was important and would determine pathogenicity. Viewed from another angle, it was host-specificity of the pathogen that mattered. Host specificity, however, was one of the unanswered questions in plant pathology.

Currently, eight races have been identified which appear to be nonmonophyletic with at least two independent, or polyphyletic, evolutionary origins. Races 3 and 5 embraced a clade distinct from the other six races. Based on geographical origin, four lineages are recognized: Lineage I Race 3 from Egypt and Race 5 from Sudan; Lineage II comprising Races 1, 2 and 6 from North and South America, and Africa; Lineage III with Race 8 from China; and Lineage IV comprising Race 4 from India and Race 7 from China (Skovgaard *et al*., 2001).

Since my tests for pathogenicity were done on the highly susceptible Karunganni cultivar, I wondered what might have been the reason for the negative results I had in my pathogenicity tests.

The puzzle of pathogenicity must have an answer. Perhaps, I thought, I should study the behaviour of the pathogen in the soil, what the fungus did in the soil, its interactions with the microbes resident in soil; i.e. its autecology. This I tried to do, using the Rossi-Cholodny-slide technique which involved ordinary microscope slides with the fungus aseptically grown on them being buried in natural soil, removed periodically, and examined microscopically after suitable staining to observe what happened to the fungus - especially the microbial interactions *in situ* as seen on the slide. Microscopic examination of the Cholodny slides buried in unsterilized soil showed that the fungus was wiped out sooner or later and disappeared. Actinomycetes and bacteria which, unfortunately, could not be identified precisely, crowded around and on the fungal hyphae and on micro- and macroconidia, and ultimately lysed their cell walls. Though chlamydospores were relatively resistant to microbial attack, their walls also were lysed in due course.

I was thrilled to see on the slides these interactions between microbes in the soil, something I had not seen before and I was really excited about. For me it served as proof of microbial antagonisms to the pathogen in the soil. I did not know then that actinomycetes had chitinase enzyme systems capable of lysing fungal cell walls. I did some experiments in which the soil was amended with inorganic and organic supplements to ascertain if the disappearance of the fungus (as seen on the Cholodny slides) could be speeded up by such treatment. I then observed that organic manure did, indeed, hasten the disappearance of the fungus. Some of the photomicrographs I then took of these interactions on the Rossi-Cholodny slides were included in two of my early publications (Subramanian 1946a; 1950). In sterilized soil, the fungus flourished, obviously free from microbial assault. However, with further work, it became clear that this was only part of the story.

It was known that the pathogen persisted in 'wilt-sick' soils planted with cotton year after year and it was not easy to eradicate it from such soils. If the pathogen was very susceptible to microbial antagonism in soil, how then did the fungus persist? Some experiments were carried out to elucidate this. When surface-sterilized cotton root pieces were buried in moist wilt-sick soil for periods of a few days to some weeks and periodically removed, surface-sterilized and plated out on agar media on Petri dishes, the *Fusarium* grew out of the root pieces. Such experiments were repeated to confirm the observation. In all cases, I maintained proper controls.

Cotton root pieces and stubble collected from wilt-sick soils also yielded the fungus when surface-sterilized and plated out on agar media in Petri plates. There was now no doubt that the fungus perennated as a saprophytic colonizer in root pieces and organic debris in wilt-sick soils. It also survived in tissues of the host infected during its parasitic phase. When the fields lay fallow without a crop and with the soils dried up, the pathogen remained secure on the stubble it colonized. As a colonizer of stubble, the pathogen enjoyed relative safety from microbial antagonism. Such competitive saprophytic colonization was the hallmark of what S. D. Garrett designated as a soil inhabitant.

In later work, it was noted that the cotton wilt *Fusarium* could colonize roots of a range of plants other than cotton saprophytically. It was thus clear that continued persistence in soils was a function of competitive saprophytic colonization. Yet another interesting aspect of the behaviour of the cotton wilt *Fusarium* was that it had the ability to infect root systems of several plant species in which it induced no symptoms. Such plants then became symptomless carriers. These findings were intriguing, in fact exciting, and raised questions about specificity not easily answered.

Fascinated as I was by these findings, it seemed worthwhile looking at another wilt-causing *Fusarium, F. udum*, described by E. J. Butler (1910) as causing a wilt of *Cajanus cajan*, arhar or pigeon pea, in India. One of my colleagues, T. S. Sarojini (1951) studied this problem and it turned out that *F. udum* was unlike *F. vasinfectum* on many counts. From further study of the autecology of *F. udum* it became clear that the saprophytic ability of this fungus was limited to tissues invaded as a pathogen. It had to be reckoned as a typical root inhabitant, to use Garrett's terminology.

And yet, *Fusarium* wilt of pigeon-pea could be devastating. On diseased plants, especially the stems, there was a late-disease phase where the pathogen expressed its presence by profuse sporulation all over the stem producing millions and millions of conidia in sporodochia and pionnotes that were conspicuous by their characteristic salmon colour. Here then was a source of inoculum that was rich and difficult to eradicate. McRae and Shaw's (1933) field trials at Pusa had shown that effective control of pigeon pea wilt was possible

by green manuring. There was wisdom in this farming method. The farmers knew their soils and their crops. The basis of this control could well have been increased microbial antagonism to the pathogen, although building up of plant resistance to disease cannot be ruled out. *Fusarium udum* f. sp. *crotalariae* preferentially infects species of another legume, *Crotalaria*, in which it causes a vascular wilt.

The concept of 'suppressive' soils is an offshoot of observations on the positive role of antagonistic microbes in direct or indirect suppression of pathogenicity of fusaria causing soil-borne plant disease. One aspect of such suppression is soil fungistasis (Lockwood, 1977). The control of soil-borne pathogens such as the fusaria by solar-heating of soils in arid regions which has been experimentally tried and proven in Israel and Iran, also hinges on suppression of the pathogen, or pathogenicity, or both.

Fusaria cause vascular wilts in a range of crops, besides cotton, pigeon-pea and *Crotalaria* tomato, tobacco, watermelon, flax, banana, and oil palm, among many others. At the turn of the nineteenth century, many studies were carried out on the relation of soil conditions to wilt in several crop plants, notably by L. R. Jones (Jones, 1922; Jones *et al*., 1926) and his students at the University of Wisconsin at Madison in the U.S.A. Studies were also initiated on plant resistance to wilt. Jones devised his famous 'soil temperature tanks' to study the effect of soil temperature on wilts. E. W. Brandes (1919) evolved special methods for pathogenicity tests on banana, a plantation crop. What was important, Jones held, was "being at the right place, at the right time, for the right reasons."

At the University of Minnesota, studies focused on fusaria and other plant pathogenic fungi, especially the cereal rusts, their virulence and their variability, and their genetics, thanks to the initiative and leadership of E. C. Stakman (1936). The studies on epidemiology and genetics of rusts led to H. H. Flor's work on flax rust and his 'gene-for-gene' concept: for every gene that conferred resistance in the plant, there was a corresponding gene that conferred avirulence in the pathogen (Flor, 1947; 1956). [Currently, in such a system, the products of resistant genes are considered to serve as receptors for specific ligands produced by the fungus (Lamb, 1996).] Some of the work on fusaria appeared as *Bulletins of the Minnesota Agricultural Experiment Station* such as, for example, the study on saltation in *Fusarium* and *Helminthosporium* by S. Dickinson (1932) and on *Fusarium lini* (causing flax wilt) by Norman E. Borlaug (1945). Dickinson's cytological study of these fungi predated studies on heterokaryosis by H. N. Hansen and R. E. Smith (1932) that were to follow some years later.

Fusaria causing rots of fruits and vegetables were a distinct group.

Species causing root rots and foot rots, especially of cereals, were yet another group, and the subject of study by soil microbiologists and plant pathologists, especially in Europe, Canada and Australia. A few of these fusaria, but notably, *F. culmorum* that caused foot rot in wheat, were soil inhabitants and known to invariably follow the take-all pathogen (*Gaeumannomyces graminis* var. *tritici*) on wheat roots as secondary invaders or colonizers. Working at the Rothamsted Experiment Station in Britain, T. S. Sadasivan (1939) had described the fungal succession on wheat roots and noted that *F. culmorum* was a primary colonizer on wheat straw in a range of soils. Some fusaria were also known to cause head blights in cereals.

Fusarium decemcellulare produced galls on cacao (*Theobroma cacao)* in Africa. A curious disease of mango (*Mangifera indica*) widespread in India and known as mango malformation had defied understanding of a cause for many years, but when, following a great deal of research, it was finally demonstrated that it was due to *Fusarium subglutinans* (*F. moniliforme* var. *subglutinans*); there was a sense of achievement in having identified the cause of the malady (Varma *et al*., 1974). A comprehensive compendium of *Fusarium* and fusariose diseases was provided by Nelson *et al*. (1981). Later work on fusaria associated with mango malformation led Britz *et al*. (2002) to conclude that the cause of mango malformation throughout the world is not *F. subglutinans*, but a distinct species, *Fusarium mangiferae* sp. nov. Yet another species, distinct from *F. mangiferae* and christened *F. sterilihyphosum*, was isolated from malformed mango tissue only from Africa.

No story of *Fusarium* would be complete without mention of the Panama Disease of bananas, so-called from its prominence in Panama early in the history of the disease.

The *Fusarium* that caused the wilt was named *F. cubense* by Erwin F. Smith (1910) from material collected in Cuba (Currently, Cuban fungi, especially hyphomycetes, are being collected and described by Cubans themselves, and calls for emulation from mycologists elsewhere in the tropics). In his Diseases of the Banana published in 1935, C. W. Wardlaw gave an excellent account of the disease with insights into the anatomical manifestations of vascular wilt on this economically important monocot. Banana seemed exceptional to me in having received such detailed study demonstrating structural stress during pathogenesis and disease.

Wardlaw had his training from Bower, equipping him admirably for such anatomical study. In addition, he was trained in mycology at Imperial College and was plant pathologist at the Imperial College of Tropical Agriculture in Trinidad. The disease, in its fury, appeared in a severe form in many parts of the tropics where banana was grown, including India, but especially in Central America and the West Indies where banana was a major crop. The susceptible Gros Michel cultivar was virtually wiped out in many areas; a crisis in banana cultivation and production resulted. Deeply concerned, the United Fruit Company, with headquarters in Guatemala, initiated a study of the taxonomy and distribution of fusaria in tropical soils, both virgin and those cropped to banana. Wollenweber, Reinking and other specialists were closely associated with these studies. A group of *Fusarium* taxonomists met in Washington, D.C. under the aegis of the USDA and finalized fundamentals for *Fusarium* taxonomy (Wollenweber *et al*., 1925). These studies also led to a most significant paper carrying descriptions and illustrations of the

many *Fusarium* species encountered in the study (Reinking and Wollenweber, 1927).

One major question asked was: did the banana wilt *Fusarium* occur in virgin and cultivated soils, irrespective of the planting of banana, or was it confined to soils on which banana was grown? Reinking and Manns (1933; 1934) and Reinking (1934) made extensive isolations of fusaria from tropical soils in Honduras, Colombia, and other parts of Central America, and concluded that fusaria could be classified into two groups according to their occurrence and distribution. They designated those with a general distribution in soils 'soil-inhabitants' and those that were confined to soils which were continuously cropped to specific crops 'soil-invaders.'

Garrett's designations for such behaviour, already mentioned, stemmed from the work of Reinking and Manns on fusaria, or rather that of Waksman (1917) on soil fungi, but were more refined. The term 'soil invader' somehow seemed to imply some kind of invasion of the soil, whereas the alternative term 'root inhabitant' reflected the close association of the fungus with roots of the host plant. And this is of the essence of the behaviour of the fungus in its micro-habitat in relation to its perennation in soil. Nevertheless, when one considered some fungi as "native" to the soil (soil-inhabitants), it was logical to recognize a category, "aliens" (soil-invaders).

In the case of *Fusarium cubense*, working in Jamaica, John Rishbeth (1955) concluded that it was not as abundant in soils as it was thought to be, as it could not be easily isolated. Its presence in soils was closely linked with the disease. Somewhat similar results were reported by Stover and Waite (1954) working in Honduras. Stover (1959) discussed growth and survival of root disease fungi in soil. Rishbeth (1955) noted that dead roots or rootlets were not colonized by *F. cubense*, but living roots and rootlets were. Thus, *F. cubense* fitted the definition of a root inhabitant.

The presence of the pathogen in banana trash and debris and its spread thereby was, however, well documented, and here one had to presume that the occurrence in banana trash was a consequence of colonization during the parasitic phase. Indeed, E. W. Brandes (1919) had reported that sporodochia of the fungus appeared in abundance on the surface of petioles and leaves in infected plants in the final phase of the disease. In the wake of the Panama Disease of bananas, there was consequently a strengthening of the taxonomy of *Fusarium* coupled with a new wave of interest in the ecology and distribution of these important fungi.

A significant contribution of the period was C. G. Hansford's (1926) paper on Fusaria of Jamaica, published in Kew Bulletin. In the case of the banana wilt *Fusarium* and other vascular wilt fusaria, it was not easy to distinguish the pathogenic strains and non-pathogenic strains on the basis of morphological or cultural characters alone. Pathogenicity was the only guide. Hansford isolated from banana plants, banana debris and soils, numerous strains of fusaria belonging to the section *Elegans* (the equivalent of *F. oxysporum* in current usage), morphologically indistinguishable from each other. Despite the variation noted among the strains, it was seen that many caused the disease in banana, and Hansford concluded that they belonged to *F. cubense*. It was also noted that most of the species of the section *Elegans* were indistinguishable from each other except on the basis of their pathogenicity to specific hosts. Hansford was perhaps one of the earliest to make such a significant observation.

Several years later, W. C. Snyder and H. N. Hansen came to the same conclusion. Snyder and Hansen (1940) combined all forms, varieties and species that are typical wilt-inducing fungi under the single name *F. oxysporum*, within which they recognized many special forms on the basis of their pathogenicity to specific hosts. However, host specificity is applicable to only some but not all special forms. Thus, f. sp. *lini* is restricted to flax (*Linum usitatissimum* [*Linaceae*]) and f.sp. *lycopersici* to *Lycopersicum* [*Solanaceae*], and f.sp. *conglutinans* to *Cruciferae*. *Fusarium oxysporum* f. sp. *vasinfectum* (*F. vasinfectum*) infected, besides cotton (*Gossypium*) and *Hibiscus* [*Malvaceae*], *Cajanus, Glycine, Medicago* and *Vigna* [*Fabaceae*], *Coffea* [*Rubiaceae*], *Hevea* and *Ricinus* [*Euphorbiaceae*], and *Solanum* [*Solanaceae*]. It is not easy to explain the basis of such behaviour.

Heterocaryosis and parasexual recombination (Pontecorvo, 1956; Burnett, 1984) have been reported in *formae speciales* such as *cubense* causing wilt in banana (Buxton, 1962), a situation that would contribute to variability in host/cultivar preference and virulence or otherwise of these pathogens. In a discussion of the evolutionary biology of *Fusarium oxysporum*, Gordon and Martyn (1997) observed that many *formae speciales* represented multiple clonal lineages, a pathogenic race often being associated with more than one clonal lineage, indicative of independent origins. One pathogenic race may give rise to another pathogenic race, but derivation of a pathogenic race from a non-pathogenic one is apparently not documented. The geography of races in the tropics is an important area for study.

I have often wondered why *F. oxysporum* causes tracheomycotic wilting primarily only on dicotyledonous plants but not on monocots except the *Musaceae* and woody members such as the palms. The main factor here could be structural.

As part of my post-doctoral work, I continued my study of fusaria of black cotton soils of southern India (and of some crop plants). I wrote to Wollenweber in Berlin and to Reinking in the U. S. A., for their publications, help and advice. Wollenweber had died in 1949, as I learnt from his successor, H. Richter, who was generous in responding to my letter to Wollenweber by sending me reprints of Wollenweber's original publications (1913; 1916-1935) including the two parts of his invaluable *Fusarium*-Monographie (Wollenweber, 1931; 1943). He also offered help and assistance in my endeavour. Reinking replied to me, in his beautiful handwriting, giving me useful suggestions and advice about how to go about the serious pursuit of *Fusarium* taxonomy.

Another specialist, C. D. Sherbakoff, whom I had also written to, was equally kind and encouraging. He not only gave me

much technical and taxonomic advice, but sent me a number of photomicrographs of micro- and macroconidia of a range of species from his collection as aids to identification, besides his publications. He also sent me United States Department of Agriculture (USDA) tags to serve as permits for quarantine clearance to be used to send him live cultures, if I chose to, so that they could be examined and commented on. With such help I had to build my own expertise in dealing with fusaria. And that was what I tried to do. I procured a copy of F. Bugnicourt's (1939) splendid book on Fusaria and *Cylindrocarpon* of Indo-China which had beautiful photomicrographs of these fungi, and I gathered other important literature on the genus, most of which was not readily available in India.

Using a root-burial technique (Subramanian, 1946b) I was able to isolate from soils several fusaria belonging to sections *Sporotrichiella, Roseum, Gibbosum, Elegans,* and *Martiella*. A brief summary of my work appeared in *Nature* (Subramanian, 1951b). I also isolated many strains of *F. vasinfectum* from diseased cotton plants and carried out comparative taxonomic study of these with cultures of the various forms and varieties of *F. vasinfectum* obtained from the Centraalbureau voor Schimmelcultures, then located in Baarn, in the Netherlands (Subramanian, 1952a). This study showed that most of the forms and varieties of *F. vasinfectum* under the Wollenweber-Reinking system were not easily distinguishable from each other. This was partly in line with the Snyder and Hansen theme for a new system of classification for the genus *Fusarium* which appeared in a series of papers in the American Journal of Botany during 1940-45.

G. Watts Padwick, the last of the Imperial Mycologists at the Indian Agricultural Research Institute at New Delhi, called the Snyder-Hansen system a “mass revision” (Padwick, 1941). Padwick, before he departed from India, had, along with two of his able Indian colleagues, M. Mitra and P. R. Mehta, reviewed the genus *Fusarium* in India in a series of papers in the Indian Journal of Agricultural Science (Padwick, 1939; 1940a;b; 1941; Padwick *et al*., 1940) and crowned it with a candid appraisal of the Snyder and Hansen system. I had no difficulty in accepting Snyder and Hansen's treatment of section *Elegans* which included most of the wilt-inducing fusaria under the single binomial, *F. oxysporum*, but could not agree with their treatment of the other 15 sections, or their disposition of *F. redolens*.

All Snyder and Hansen's cultures were single-spored and maintained that way. The nuclear condition of the spores, I thought, determined the nature of the resulting cultures. Under these conditions the characteristics of progeny overlapped in many cases. For this reason, many cultures had to be clubbed for taxonomic purposes. This might seem quite simple. If so, the Snyder and Hansen System was rooted in this logic. The Wollenweber-Reinking System, on the other hand, had too many infraspecific entities such as varieties and forms that were virtually not recognizable morphologically. That was the dilemma of the time. But between these two extremes, there seemed to be a middle path.

W. L. Gordon, originally trained in rust epidemiology at Minnesota, but then working with the Department of Agriculture in Canada, chose that middle path. Taking the best from the two systems, that of Wollenweber-Reinking, and the other, of Snyder-Hansen, he proposed a scheme that generally was welcomed (Gordon, 1944; 1952; 1954a;b; 1956; 1959; 1960). The sixteen sections of Wollenweber and Reinking were retained and many of the species as well. Indeed, W. Gerlach, successor to H. Richter in Berlin and heir to the Wollenweber heritage, later came up with a revision of the genus incorporating some of the new thinking. (Later, jointly with his younger colleague, H. Nirenberg, he brought out an Atlas of the Genus *Fusarium* in 1982. Gerlach spoke on his revision of the genus at the International Symposium on Taxonomy of Fungi in Madras in 1973).

Indeed, *Fusarium* was always around. Its importance showed up here, there or anywhere, arresting our attention and arousing our curiosity. What the Japanese called the 'bakanae' phenomenon is an example. 'Bakanae' in Japanese meant 'foolish', and referred to rice plants in the field growing unusually tall, a condition that was thought to be caused by a mould of the genus *Fusarium* by Shotaro Hori (1898) of the Agricultural Experiment Station of the Ministry of Agriculture, Tokyo. Hori thought that a mould, *F. heterosporum*, was involved. In 1917 the Japanese mycologist Kenkichi Sawada, working in Formosa (now Taiwan), discovered the sexual state or teleomorph of the *Fusarium* and christened it *Lisea fujikuroi*. The specific epithet was in memory of Yosaburo Fujikuro who had first recognized the disease locally. In 1931 Wollenweber noted that the sexual stage was a *Gibberella*, and accordingly reclassified Sawada's fungus in the genus *Gibberella*. Thus, it came to be known as *Gibberella fujikuroi*.

In a paper published in 1912, Sawada had suggested that the elongation of infected rice seedlings might be due to the stimulus of the fungal hyphae. The discovery of how the *Fusarium* caused the rice plants to grow tall was made in 1926 in what seemed an obscure laboratory in Formosa, then under Japanese occupation, by a Japanese scientist, Eiichi Kurosawa (1926b). Kurosawa's preliminary report appeared in the *Transactions of the Natural History Society of Formosa* in 1926. Some years ago, on a visit to Taiwan, I was shown the laboratory and I recalled C. V. Raman's oft-repeated observation that great work was often done in small places. Kurosawa studied the effect of culture filtrates of the fungus on growth of rice plants, and was astonished to note that something in the culture filtrate induced internodal elongation. Moulds do remarkable things. Kurosawa graduated from Chiba Prefectural High School of Horticulture and later moved to Sawada's laboratory in Taiwan to work on the bakanae disease.

Though he had no training in chemistry, he thought that there must be some chemical action involved in the elongation of rice plants. Orchestration is often vital for success in research, and the concerted efforts of plant pathologists, mycologists, plant physiologists and organic chemists in the University of Tokyo finally led to the isolation of a substance considered to be growth-stimulating by Teijiro Yabuta and Yusuke Sumiki (1938), forty years after Hori's original

discovery of the 'bakanae' phenomenon. Yabuta was an organic chemist and he, along with two of his co-workers, K. Kambe and T. Hayashi, had published a paper four years earlier, naming the substance "gibberellin." In his efforts to obtain gibberellin in a pure crystalline form, Yabuta also stumbled on an inhibitory substance excreted by the fungus which he named fusaric acid and whose structure was eventually determined as 5-n-butylpicolinic acid. This is part of the early exciting story of the 'plant hormone' gibberellin and its discovery.

The war years prevented research on gibberellin by scientists in the West. On my first visit abroad, in 1950, I spent a few months in Britain working in Cambridge and at Kew. In July of that year, I had met and befriended, among many others, Percy W. Brian, at the VII International Botanical Congress at Stockholm, Sweden. I had been aware of Brian's work at the Imperial Chemical Industries (ICI) Butterwick Research Laboratories at Welwyn in England, and was keen to know about it first hand. Brian set apart a whole day to show me round and tell me about the work of his group. Quite interestingly, that was the time ICI was embarking on an intensive study of fusaria in their collection with a view to finding a strain that could be used for the production of gibberellin on a commercial scale (Brian *et al.,* 1954). It was this group which identified gibberellic acid as another metabolite in culture filtrates of the rice *Fusarium* (Curtis and Cross, 1954).

Padwick, who had retired as Imperial Mycologist at the Indian Agricultural Research Institute (IARI) in Delhi, was now the Scientific Consultant to ICI. IARI had been built on Butlerian traditions when it was located at Pusa in Bihar and that was where many were trained to deal with the enormous plant disease problems of India. However, after the Institute building was destroyed in the vicious earthquake in Bihar in January 1934 and moved to a new location in the Indian capital, *Fusarium* apparently occupied a back seat until Padwick gave it a push. I was keen to meet Padwick primarily because of our common interest in *Fusarium*. At that time I was thoroughly absorbed in work on *Fusarium* and was the beneficiary of an ICI Research Fellowship awarded to me by the National Institute of Sciences of India (now Indian National Science Academy) to pursue my study of *Fusarium*. Padwick welcomed me at his office at 12, Upper Belgrave Street, London and we discussed *Fusarium*, and its importance in plant pathology and soil mycology. I believe Padwick's tropical experience in India, especially with *Fusarium*, helped in strengthening the hunt for efficient gibberellin-producing *Fusarium* strains at ICI.

Coincidentally, a group in the US, under J. E. Mitchell (Mitchell and Angel, 1951) at a research unit at Camp Dietrick, Maryland, and another group under Frank H. Stodola at the Northern USDA Regional Research Laboratories at Peoria, Illinois, were also working on similar lines and with similar objectives on fusaria and gibberellin (Stodola *et al*., 1955; Stodola, 1958). Following the work of these two groups, there had been a great deal of research on gibberellins.

Being in Britain, and having read Harold Raistrick's Bakerian Lecture of 1949 to the Royal Society on "A region of biosynthesis", I made it a point to go to the Institute of Tropical Medicine and Hygiene in London where Raistrick worked and learn first hand from him about the secondary metabolites of fungi on which he had done pioneering work. There I met George Smith, the mycologist who ensured that all Raistrick's moulds were correctly identified and named, something unusual with chemists in general, something that vitiated their otherwise important contributions. Raistrick had discovered many secondary metabolites from diverse moulds and characterized and named them, including the antifungal antibiotic griseofulvin from *Penicillium griseofulvum* (Oxford *et al*.,1939). Secondary metabolism (Turner, 1971) is an exciting area not only for organic chemists but for fungal taxonomists, as I believe fungal metabolism is part and parcel of fungal form. Form and function are inseparable.

Though we have had in India many who were distinguished in organic chemistry, few of them took up fungal secondary metabolites for serious study. An exception was T. R. Seshadri who contributed significantly to our knowledge of the chemistry of tropical lichens. Seshadri delivered a Special Evening Lecture on the chemistry of lichens at the International Symposium on Taxonomy of Fungi which I had the privilege of organizing at the University of Madras in 1973 (Seshadri, 1984).

The Japanese organic chemists, Yasuhiko Asahina and Shoji Shibata also made very important contributions to our knowledge of lichen chemistry, and it was a disappointment to me that they could not join our congregation. (On a visit to their laboratory in the University of Tokyo in 1969, Asahina and Shibata had shared with me the highlights of their work. Shibata worked with Asahina, and later with Raistrick in London in 1950, but I had no knowledge then about this. Asahina passed away in 1975. I met Shibata again at a symposium organized by Tadashi Arai in Chiba, soon after IMC3 in 1983, where Shibata spoke on the chemistry of bioactive fungal products [Asahina and Shibata, 1954; Shibata, 1985]). Other than lichen natural products, aflatoxins, toxins from *Fusarium*, and ergot alkaloids have, of course, received study from Indian organic chemists.

Let me return to the bakanae story. If the first part of the bakanae story was exciting, the second part also turned out to be exciting, being a surprise package. Once again, the unexpected happened. First, screening many fungal and other microbial taxa to identify gibberellin production showed that *Gibberella fujikuroi* alone had this property among the many moulds that were screened. But, was there a limit to the number of fungi to be screened to be able to get a firm answer to the question? What turned out to be interesting is that gibberellins were found to occur naturally in flowering plants by C. A. West and B. O. Phinney (1956) working in the U. S. A., and independently by M. Radley (1956), working with ICI in Britain (see Phinney *et al*., 1957). This seemed to be a startling discovery, and one wondered why it had to await the discovery of the 'bakanae' disease in rice plants.

The discovery stimulated much work in plant physiology, especially the role of gibberellins in plant growth and

development (Takahashi *et al*., 1991; Mander, 1991). For example, the dwarf varieties of rice and wheat that played an important part in the "green revolution" were found to carry mutant genes that, in the case of rice, interfered with the synthesis of their gibberellins, and, in the case of wheat, reduced the ability to respond to their own gibberellins. (There is also a view that gibberellins were possibly involved in the genetic differences between the tall and dwarf pea varieties used by Gregor Mendel in his original studies on inheritance.)

However, the further study of the gibberellins and bakanae disease then declined, at least in part because it was difficult to pin down the cause to endogenous gibberellin and/or gibberellin produced by the pathogen *in-vivo*. Did the fungus produce gibberellin *in vivo* in rice plants? Or, did the fungus induce increased levels of endogenous gibberellin in infected plants? As far as I am aware, the issue has not yet been resolved, but I may be wrong. Could it be that the ability to produce endogenous gibberellin arose by horizontal gene transfer (Pirozynski, 1981; 1988) from an ancient plant-fungus association? There are many such questions awaiting answers.

On the other hand, work on gibberellins was on the agenda and at least fifty-seven different gibberellins came to be recognized, thirty-one of which were produced only by flowering plants, sixteen only by the rice fungus and ten by both. (Currently, over a hundred and thirty gibberellins are known!). And the last word is yet to be. Gibberellin biosynthesis now turned up in a most unexpected place. The new discovery was an offshoot of the study of another tropical plant disease, super elongation of cassava (tapioca, i.e. *Manihot esculenta* of the *Euphorbiaceae*) in which the causal fungus, *Sphaceloma manihoticola*, described by A. Bitancourt and A. E. Jenkins (1950) was shown to produce gibberellin A4 by Rademacher and Graebe (1979). This was confirmed by Zeigler *et al.* (1980). In further work on 28 species of *Sphaceloma* and *Elsinoe*, Rademacher (1992; 2005) showed that four other species of *Sphaceloma* also produced gibberellins: *S. bidentis*, *S. menthae, S. perseae*, and *S. rhois*. The list of microorganisms producing gibberellins expanded further to include other fungi such as *Neurospora crassa* (Kawanabe *et al.*, 1988), and *Phaeosphaeria* spp., besides bacteria such as *Rhizobium phaseoli, Azospirillum lipoferum* and *A. brasiliense* (Rademacher, 1994; Bottini *et al.*, 1991). That biosynthetic properties may lurk in unexpected quarters is a perennial theme with me, and this is something that continues to excite. In a study of head smut of sorghum, Matheussen, *et al.* (1991) presented data implicating gibberellins from the pathogen, *Sporisorium reilianum*, in the disease.

Further, there have been several reports of gibberellin-like substances (GLS). For example, G. F. Pegg (1973a) described production of free and bound GLS in sporophores of the common button mushroom, *Agaricus bisporus*. The major component of the "free" extract was found in the stipe, pileus and lamella. Further study widened the list of basidiomycetes in which GLS were identified to include *Boletus elegans, Phallus impudicus, Grifola frondosa*, and the pathogen *Phellinus pomaceus* (Pegg,1973b). *Boletus elegans* is a mycorrhizal symbiont that stimulates growth of its host (*Larix*) and one might speculate involvement of fungal GLS, though positive evidence for this seems lacking. Now there is also evidence for production of GLS by some bacteria such as *Azotobacter chroococcum* and *Pseudomonas* species.

The gibberellin story never ends. Gibberellins continue to turn up in new places and situations. Several endophytic fungi have now been shown to produce gibberellins and are believed to be involved in growth stimulation of their host plants. Hamayun *et al*. (2010) tested nineteen endophytic fungi isolated from roots of cucumber (*Cucumis sativus* L.) grown on soil from barren paddy fields collected from outskirts of Daegu city in Korea for gibberellin production. Several isolates stimulated shoot elongation in Waito-C rice, a dwarf bioactive GA-deficient cultivar. A strain, MH6, of an isolate identified as *Cladosporium* sp. produced nine different gibberellins. Culture filtrates of this strain had higher amounts of bioactive GA3, GA4 and GA7 than wild type *Gibberella fujikuroi.*

Gibberellin synthesis has also been reported in several endophytes and soil fungal species: *Cladosporium sphaerospermum* (Hamayun *et al*., 2009a), *Phoma herbarum* (Hamayun *et al*., 2009b), *Chrysosporium pseudomerdarium* (Hamayun *et al*., 2009c), *Scolecobasidium tshawytschae* (Hamayun *et al*., 2009d), *Arthrinium phaeospermum* (Khan *et al*., 2009a), and *Gliomastix murorum* [*Sagrahamala murorum*] (Khan *et al*., 2009b). The original thinking that gibberellin synthesis is unique to *Gibberella fujikuroi* has eroded away. The ubiquity of gibberellin synthesis in so many fungal species from diverse ecological niches once again raises the question of the source of gibberellins shown to occur in higher plants. Are they truly endogenous and, if so, are they *in-vivo* fungal products or stimulated by fungal associates, endophytes or whatever?

Unlike the vascular wilt fusaria discussed earlier, the rice *Fusarium* became systemic within the host. Some strains remained localized in root tissue causing foot rot. Evidently, the bakanae fungus was a root inhabitant with poor competitive colonizing ability. Apparently also, it did not survive for long periods in the soil except on tissues colonized during the parasitic phase. However, the occurrence of a sexual phase in nature was noteworthy, although only about 50% of infected plants in the field usually produced the sexual state. In my collecting in southern India I did not find the sexual state despite persistent search.

Also, on a visit to Madras and the UBL in 1971, W. C. Snyder looked for the *Gibberella* state on rice crops around Madras, but did not find any. On the other hand, on his visits to Taiwan, he regularly collected the *Gibberella* on rice crops around Taichung. In the case of self-sterile strains, perithecia would occur only where both mating types occurred in the same region. As Snyder noted, complementary strains were often separated geographically. The microconidia of the fungus are produced in basipetal 'chains' and are considered to be dry and wind-disseminated. Whether the rice *Fusarium* is a typical soil fungus is arguable, though it is generally

considered to be one. From a phylogenetic study of *F. oxysporum* f. sp. *cubense* (Foc), O'Donnell *et al.* (1998) recognized at least three independent origins for it. Different clades of the fungus were distantly related. One of them was found to be more closely related to *F. oxysporum* f. sp. *melonis* than to other clades of Foc.

The bakanae fungus is not merely a plant pathogen; involvement in animal disease from infected animal feed such as corn is documented. Such disease has now been traced to carcinogenic mycotoxins, the fumonisins, from the fungus. Two fumonisins, B1 and B2, have been identified and these are produced by *Fusarium vertcillioides* and the closely related *F. proliferatum*, besides *F. nygami*, strains of *F. anthophilum*, *F. dlamini* and *F. napiforme*, all belonging in section *Moniliforme* (*Liseola*). However, they are not produced by *F. subglutinans* and *F. beomiforme*. Carcinogenicity to test animals (rats) has been demonstrated, and there is a likelihood of carcinogenicity to humans. Apart from these, Fusaria are known to produce a host of other toxins involved in both plant and animal disease.

Fusarium plagued plant pathologists the world over with its variability. Variability was reflected in cultural characteristics, conidial morphology, specificity to particular host species or cultivars, even patterns of conidiogenesis. Every problem had its inherent essence of excitement and challenge. It was not unusual for plant pathologists to hold cultures unidentified in cold storage for extended periods and then to find that the cultures did not sporulate. What could be the reason for this? At the Imperial College of Science and Technology in London, William Brown and his students had carried out studies on saltation in the genus *Fusarium*, and provided data on variation and variability of fusaria in culture. Two Indians, Manoranjan Mitra and Julian H. Mitter who were trained by Brown were associated with these studies.

Wollenweber recognized that cultures would show one of two growth and culture patterns: what he called the *ankultur* and *hochkultur* states. *Ankultur* was the condition where the fungus showed subnormal features with mycelium and microconidia only, and often the characteristic macroconidia were not produced at all. A culture required to be in the *hochkultur* state for its proper identification, producing macroconidia and with the characteristics of the *Fusarium* best expressed. These difficulties led to the question of whether there was a 'wild type' in the genus *Fusarium*. Working in Canada, J. J. Miller made a study of fresh isolates of fusaria from muskmelon (*Cucumis melo* [*Cucurbitaceae*]) plants. The 'wild type', as conceived by Miller, was that which usually occurred in nature as a form or forms that, when cultured on most artificial media, produced abundant aerial mycelium and a few non-septate microconidia. In prolonged culture they tended to produce abundant 0-3- or more-septate conidia.

However, this was not the experience of many students of *Fusarium* who have time and again affirmed that isolates of *Fusarium* maintained in culture over long periods lost their ability to sporulate and turned mycelial. I isolated a large number of fusaria from diverse hosts and from soil and made a study of the cultural characters and morphology of each of them in first cultures. When first isolated almost all of them were in a state of *hochkultur* and produced an abundance of conidia including sporodochial macroconidia. Thus, the 'wild type' of these tropical fusaria was typically conidial and sporodochial, not mycelial as observed by Miller for his muskmelon fusaria (Subramanian, 1951a). In a further study, now of the 'wild type' in *F. udum*, it was seen that there was no fixed wild type. For, first cultures isolated from diseased host plants (*Cajanus cajan*) were mycelial or conidial or intermediate in character (Subramanian, 1955b).

These observations must be read along with Hansen and Smith's experimental work with cultures of several conidial fungi wherein they showed that cultures fell into two groups, the non-sporulating mycelial [M], and the sporulating conidial [C]; they called this the 'dual phenomenon', and also recognized an intermediate [MC] type. We now know that the MC type was a product of 'heterokaryosis', a term that seems to have been used for the first time by W. B. Brierley in 1920, presented at the Ithaca Congress of Plant Sciences in 1926, and elaborated on in a paper in the *Annals of applied Biology* in 1931. Brierley wrote: "I would suggest that the function of sexuality with its genetic consequences is, in many fungi, taken by hyphal fusion of a somatic nature. This would not result in heterozygotic but in heterokaryotic and heteroplasmic states whose degree of complexity would depend on the nature and number of the contributing elements. The permutations and combinations inherent in this type of fusion…provide a basis for most of the phenomenon of variation which has been observed." Thus, the role of heterokaryons and heteroplasmons in fungal variation was explicitly noted by Brierley. (Brierley's candid reviews of books in the *Annals of Applied Biology* always amused and delighted me and it is a matter of regret that I never had an opportunity to meet him.)

II Doing Mycology: The British and European Experience

At this stage in my narration I must digress to give further details of my visit to Britain and Europe, with the twin objectives of obtaining training and guidance in *Fusarium* taxonomy, and attending the VII International Botanical Congress at Stockholm. The Congress, interrupted by the War, was meeting after a gap of fifteen years and had been looked forward to by many scientists. For me, a novice in science, it was a way of getting to know the great ones and their work first hand. Sailing from Bombay on the 15 June 1950, I disembarked at Tilbury docks in London on the 2nd July 1950.

II-1 The Sycamore Disease and Forest Pathology

The first scientist I met after I set foot on British soil was Philip H. Gregory, then Head of the Department of Plant Pathology, Rothamsted Experiment Station, Harpenden. Gregory happened to be one of three Examiners from Britain who had commended my thesis for award of the Ph.D. degree by the University of Madras in 1947. At the time we met, Gregory was investigating a new but devastating disease of sycamore trees (*Acer pseudoplatanus* [*Aceraceae*]), the sooty bark disease, in Britain. Characteristic of the sycamore disease was the formation of a profusion of conidia of the

pathogen beneath the bark which now appeared sooty with the massive, powdery accumulation of its dry conidia overlying a stroma. The conidia got easily disseminated by wind.

There have been reports of a "conidiosporosis" of timber workers who develop a severe bronchial asthma after inhaling spores of the fungus. In trying to identify the disease and the pathogen, Gregory came across the description of what seemed a tantalizingly similar disease of *Casuarina* [*Casuarinaceae*] trees in India described by E. J. Butler (1905). On a request from Gregory, before my departure to England, we had sent him specimens of the *Casuarina* disease collected in Madras. From King's Cross where we met in London, Gregory took me by the Underground train to Wanstead Park to show me the sycamore disease. This, my first outing in Britain, with Gregory, remains unforgettable to this day, because we both surveyed the area and the disease in incessant, pouring rain. We came out of the 'jungle' of sycamore trees completely drenched and yet wondering how the two diseases, one of sycamore and the other of *Casuarina*, the former in Britain and the latter in India, could be so like each other in their symptomatology. We pondered over the issue.

Gregory pursued the problem. The *Casuarina* fungus appeared quite distinct from the sycamore fungus and was not taken up for study. And then came an unexpected discovery. A fungus answering to the description of the sycamore fungus had been described in North America by J. B. Ellis and B. M. Everhart under the name, *Coniosporium corticale*. A study of type material of the North American fungus convinced Gregory that the sycamore fungus was indeed conspecific with the American fungus. However, Ellis and Everhart's disposition of their fungus in the genus *Coniosporium* seemed inappropriate. The conidia in the sycamore fungus were produced from characteristic phialides and were dry. The phialides lined an underlying stroma, the whole being concealed under the bark.

The conidia in *Coniosporium* were holoblastic and muriform (with transverse and longitudinal septa) and were produced in infinite basipetal succession. Thus, both conidiogenesis and conidial morphology in *Coniosporium* appeared different from that in the North American fungus and the sycamore pathogen. The sycamore fungus had therefore to be placed in a new genus. Gregory and Waller (1951) published their study of the sycamore disease and classified *Coniosporium corticale* in a new genus for which they chose the very appropriate name, *Cryptostroma* (from crypto= hidden, + stroma). The sycamore fungus came to be known as *Cryptostroma corticale*.

The resolution of the taxonomy of the *Casuarina* fungus came fifty years later. As already noted, the disease had been described by Butler from India in 1905. Butler assigned the fungal pathogen to the genus *Trichosporium* and named it *T. vesiculosum*. *Trichosporium* was a variant spelling of *Trichosporum*. The generic name *Trichosporum* of Fries turned out to be a later homonym and also a nomen confusum and, being illegitimate, could not be used. Accordingly, *Trichosporum vesiculosum* required renaming. The disease was now widespread: it has been reported from Sri Lanka, Thailand, Vietnam, China, Mauritius, and Kenya.

J. K. Sharma, Forest Pathologist at the Kerala Forest Research Institute (Kerala State in southern India), as part of his in-depth study of the disease, published a paper on the taxonomy of the *Casuarina* fungus, jointly with his student, C. Narayanan, and David Minter of the then International Mycological Institute, Kew. From a study of Butler's type material and other collections, they redescribed the fungus. They showed that the fungus was unique in a number of features. It had two kinds of conidiogenous cells: simple, doliiform to ampulliform, hyaline conidiogenous cells that were enteroblastic with one or two apertures, and penicilloid, hyaline, holoblastic cells, often 3-4 on apices of secondary or tertiary branches of conidiophores. The conidia formed chains and were non-septate, and light brown at maturity, often with a longitudinal germ slit and a faintly visible germ pore; they were blackish in mass and powdery and dry as in *Cryptostroma.* On the basis of such unique features, Narayanan *et al.* (2003) introduced the new generic name *Subramanianospora* to accommodate *Trichosporum vesiculosum*. The honour in the name hid the beauty within. Had I known what Narayanan *et al*. were up to, I would have suggested a better name for the beautiful *Casuarina* fungus suggestive of some of its unique features.

I might recall here my efforts to pursue research in mycology soon after I obtained my Ph.D. in the course of which I was interviewed for a post of Assistant Forest Mycologist at the Forest Research Institute (FRI), Dehra Dun where E. J. Butler was stationed when he first came to India in 1901. I was interviewed by the Union Public Service Commission in Simla (now Shimla) in the summer of 1948. Among other things, K. D. Bagchee, the then Forest Mycologist at FRI and expert on the Selection Committee, tested my knowledge of German and ability to read the language. Soon after, I received a letter from the Commission appointing me and B. K. Bakshi, one among the other applicants interviewed, to the post. The Commission, however, did not grant me the higher starting salary I had asked for, and so I wrote to the Commission regretting my inability to accept the appointment. Had I accepted it, I might have been a forest pathologist working on tree diseases.

Perhaps, I might have prospered in the forest environment and would have seen and described many more fungi than I could have. I do not know. Bagchee was a distinguished mycologist who contributed to our knowledge of Himalayan tree rusts, notably those on conifers, besides the diseases of Himalayan trees (Bagchee, 1939). Bakshi accepted the offer, eventually succeeded Bagchee and made valuable contributions to our knowledge of polypores (Bakshi, 1971), having worked with S. R. Bose in Calcutta for his doctorate. I knew Bakshi from the day of our interview at Simla and found him a quiet, unassuming person wholly devoted to his work, confined to the FRI and Dehra Dun. He had training in Britain and even published on *Ceratocystis* species causing sap stain (Bakshi, 1951).

II-2 The Stockholm Botanical Congress and After

After Wanstead Park and the sycamore disease, I flew from

London into Goteborg in Sweden to participate in a pre-Congress Lichenological Expedition to the island of Skafto in Bohuslan. The expedition led by Gunnar Degelius was perhaps the smallest ever. Besides Degelius, it had A. H. Magnuson, Ove Almborn, Rolf Santesson, Eilif Dahl, R. A. Maas Geesteranus, T. S. Sadasivan, Per-Olaf Lindahl and myself. There was also Santesson's six-or-seven year old son Johan who had lost his mother early and so accompanied his father on expeditions. He seemed as active as any of us in the group in collecting and I recollect his calling Degelius loudly to bring his attention to what he thought to be a *Lecanora* and another, a *Parmelia*! Many years later when I saw Rolf Santesson at one of the International Congresses I enquired about his son and he then told me he was doing biochemistry of lichens! It was remarkable how tradition lingered in families. Magnuson knew India from collections of lichens sent to him for identification from Kodaikanal in southern India. Thus, he was keen to know more about southern India.

Sailing from Goteborg, we made Lysekil our headquarters. The expedition was aimed at collecting marine and maritime lichens and learning about lichen communities and, equipped with hammer and chisel, we collected lichens on rocks and bark of trees along the coasts and fjords. Many lichens were readily named for us by one of the lichenologists in our group. The expedition gave me a glimpse of the diversity of Swedish lichens and I wondered how much more diverse tropical lichens would be. I was lucky to have been exposed to such an expedition early in my career.

The expedition over, we all moved to Stockholm by train to attend the Botanical Congress. As expected, many leading botanists were there. Truly, the Congress was a meeting of minds. There was A. F. Blakeslee, discoverer of heterothallism in the *Mucorales*; 2004 marked the centenary of Blakeslee's discovery (Blakeslee, 1904). Blakeslee had come to India soon after independence at the invitation of the Government of India. The University of Delhi conferred an honorary doctorate on him. He had then visited our laboratory at Madras along with W. F. Hanna from Winnipeg, Canada, who had also been invited by the Government, and they had been shown round. At the Congress, in his late seventies, and yet a super-active scientist, Blakeslee moved from one session to another at the Congress energetically. Now his primary interest was in genetics of *Datura* [*Solanaceae*]. At the Congress he distributed small samples of a white powder to participants and wanted our response of taste and smell of the sample. (I learnt later that he showed from his studies that the ability to perceive certain tastes and smells is inherited!)

There was Ernst Gaeumann whose original and brilliant ideas in the twin fields of mycology and plant pathology made him a leading figure in Europe. Though physically handicapped by polio, he radiated an air of confidence. When a participant at the Congress put it to him that fusaria could be identified solely on the basis of their biochemistry, he showed his disdain for the idea with a stroke of his hand and an 'Uh!' Gaeumann was at that time deeply involved in studies on the physiology of *Fusarium* wilts, particularly fungal toxins such as fusaric acid and lycomarasmin and their role in the wilt syndrome. W. B. Brierley's (1950) English translation of his Pflanzlische Infektionslehre had just been published in Britain with the title, Principles of Plant Infection, a volume at once remarkably original and stimulating (See Gaeumann, 1950).

There was Selman A. Waksman, pioneer and the leading light in soil microbiology. There was F. E. Fritsch whose "The Structure and Reproduction of the Algae" had kindled my love and fascination for the algae. I had often wondered if a comparable text could ever be written by someone for the fungi. Gilbert M. Smith and William Randolph Taylor are the other algologists whom we met. I met several mycologists and plant pathologists from different parts of the world, notably G. M. Armstrong, F. C. Bawden, William Brown, S. D. Garrett, Mary D. Glynne, Oscar Hagem, Lilian E. Hawker, H. L. Jensen, Ivar Jorstad, E. W. Mason, J. T. Middleton, J. A. Nannfeldt, D. J. D. Nicholas, A. J. P. Oort, John Ramsbottom, Harald Richter, D. P. Rogers, E. C. Stakman, Elsie M. Wakefield and H Zycha.

Armstrong spoke on his work on host specificity and host range of the cotton wilt *Fusarium*, to which I referred earlier in this account. I had corresponded with Mason before my departure from Madras to ask him if he would have me work with him on *Fusarium*. He now made it clear that there was no one at the Commonwealth Mycological Institute (CMI) to help me with *Fusarium*, and that I may look at the hyphos if I liked. My response was a quick 'Yes.' With that 'yes,' came a new turn in my pursuit of tropical mycology, a pursuit full of excitement.

A Reception was organized by the Indian ambassador to Sweden, R. K. Nehru and his wife, Rajan Nehru, to welcome botanists from India attending the Congress. Nehru was an uncle of the Prime Minister, and was the first ever Ambassador of India to Sweden. The Reception at the Chancery on the 19th July brought together several of us, all of them my seniors, notably F. R. Bharucha, K. A. Chowdhury, E. K. Janaki Ammal, Panchanan Maheshwari, Vishwambar Puri, T. S. Sadasivan, Savitri Sahni and J. Venkateswarlu.

I visited Uppsala, the home and Garden of the great Carl von Linne, and the University in Uppsala. The University, the first of its kind in northern Europe, was founded in 1477, but grew only gradually to what it was in 1950. Ramsbottom led some of us and placed a wreath at the tomb of Linne in Uppsala Cathedral on behalf of the Linnean Society and the British Mycological Society. When the Swedish Linnean Society was founded in 1917, the Society took over the Garden and restored and preserved it. The Garden, with the plants arranged on Linne's Sexual system, was kept just as it was during his time.

In the Garden I met John S. Niederhauser, who was then in Mexico with the Rockefeller Foundation, and his wife, both of whom evinced interest in talking to me about India. In later years, having identified Mexico as the centre of origin of late blight of potato and having located *Solanum demissum* germplasm as a source of resistance locally (Niederhauser and Mills, 1953; Niederhauser *et al.*, 1954), Niederhauser

spearheaded a global programme of breeding potatoes for resistance to the disease that benefitted several developing countries including India.

At the University in Uppsala, I recall meeting Nils Svedelius, the distinguished algologist, whose papers I had read as a student. Svedelius, who knew M. O. P. Iyengar, made kind enquiries about him. I saw Elias Melin who explained to me his work on mycorrhizas. Showing me round his laboratory, he introduced me to two of his associates, Nils Fries and Lizbeth Fries who, over the years, became life-long friends and we had the pleasure of having them as guests of my University in India many years later (1981). For some years I had the privilege of working with Nils on a Committee entrusted with the task of selecting candidates for the award of the prestigious Jakob Eriksson Medal, presented at International Botanical Congress. My visit to Uppsala kindled my interest in mycorrhiza and on my return to Britain I procured a copy of Melin's (1936) *Methoden der experimentellen Untersuchung mykotropher Pflanzen* from Heffer's at Cambridge.

It was at the Stockholm Congress that it was resolved to establish an International Association for Plant Taxonomy (IAPT) and a Bureau for Plant Nomenclature. The Congress was a great event and was opened by H. R. H. the Crown Prince of Sweden. At the Reception at the Royal Palace of Drottningholm, the Crown Prince shook hands with every member of the Congress. The Congress was prominently covered in the local newspapers. Someone brought to my notice a picture of the Chinese mycologist Lee Ling with his Indian counterpart (me) in one of the papers. This made me the cynosure of the public eye! Of course, that was the first and last time my picture appeared in a foreign daily. Ling had studied Chinese fungi, especially *Ustilaginales*, and was with the FAO.

Giving his impressions of the Congress several years later, Selman Waksman (1958) wrote: “The congress was accompanied by several receptions that did not quite compare with those we had attended on previous occasions, especially in 1929. Gone were the luxurious collections of smorgas dishes that preceded each dinner. But, then, the world had changed. The war had had its effect even upon prosperous Sweden. But, perhaps, it is really our own fault. We have grown up, have been around a lot, and are quite different from the young innocents who travelled all over Europe in 1924 and in 1929, with a rather meagre purse”, very true. Indeed, in 1950 I was a young innocent with a rather meagre purse travelling in Europe. And I found the Congress a great experience.

From Stockholm I travelled by train to Copenhagen, Brussels, Amsterdam and Paris and took the boat from Calais to Dover. In Copenhagen I visited the Danish algologist, F. Boergesen in his palatial residence. Boergesen visited Madras in 1928 and he and Iyengar had then collected algae together on the Coromandel coast, and Boergesen described many algae collected by them from southern India in a series of papers. I also visited Paul Neergaard who had authored a monograph (1945) on the Danish species of *Alternaria* and *Stemphylium*. Neergaard (1977) later stimulated a great deal of work on seed-borne fungi and seed pathology and his leadership in this area was appreciated worldwide, but especially in many developing countries in the tropics. Neergaard came to India several times and had close links with his Indian counterparts. He spearheaded launching of Courses in Seed Pathology in several universities in India and other countries in the tropics.

The journey from Copenhagen to Brussels through Germany opened my eyes to the horrors of the War. All I could see around were long stretches of desolate land with no vegetation, no human dwellings and no inhabitants. It was a painful experience. On arrival at Brussels, I found to my dismay there was a general strike, an expression of the peoples' disapproval of the return of the King, and, in consequence, I had to walk it out with my baggage, rucksack and all, to find the hotel where I had made a reservation. My short stay enabled me to take a guided tour to Waterloo where the battle was fought in 1815 and Napoleon was defeated. On the route our attention was drawn to Victor Hugo's house. That reminded me of Hugo's Notre Dame de Paris (1831), immortalized by Charles Laughton's superb portrayal as Quasimodo, the hunchbacked bell-ringer, in the movie, Hunchback of Notre Dame.

(Twenty-eight years later, in 1978, I was in Brussels, by invitation, for the celebration of the Jubilee of the Belgian Royal Academy of Overseas Sciences where I was introduced to the King of Belgium by my esteemed friend, Raymond Vanbreuseghem, and I recalled to the King the incident of the return of the exiled King to the city on that day in August 1950 when I was first in Brussels. The King, in return, greeting me, recounted the Belgian connection with Madras where they had a few important projects. Of course, Brussels always reminded me of my dear friend Gregoire Hennebert whom I had the pleasure of meeting on this trip also. As on this occasion of the Jubilee of the Academie, I felt highly honoured by Gregoire's invitation to me to attend the Centenary of the Belgian Culture Collection (MUCL) in 1994. It was, indeed, a memorable event in the history of mycology).

Back to 1950, from Brussels I reached Amsterdam. In the Netherlands I worked at the CBS (Centraalbureau voor Schimmelcultures), then in Baarn, examining herbarium material and cultures of fusaria in their collection, thanks to the generosity of Johanna Westerdijk, then Director of the CBS. I had met Westerdijk at the Congress in Stockholm and had been aware of her dynamic role in building the culture collection at the CBS. Both Westerdijk and her colleagues, van Beverwijk and G E Bunschoten were most kind in giving me facilities to study fusaria in their collection. Van Beverwijk's primary interest then was in *Fusarium*, and almost all herbarium material of *Fusarium* at the CBS had been seen by Wollenweber and some collections carried notes or comments by him.

The year 2004 marked the centenary of the establishment of the CBS. The founding of a culture collection was a recommendation of the “Association Internationale des Botanistes” which met at Leiden in 1903 and accepted at the Botanical Congress in Vienna in 1904. The task was assigned to F. A. F. C. Went, Professor at Utrecht, with a nucleus of a

few cultures. Went had training from Anton de Bary, and later worked as a plant pathologist in Buitenzorg (now Bogor) in Java (now Indonesia). Went's name is permanently attached to the hyphomycete genus *Thielaviopsis* and its type species *T. basicola* which he described while working in Java. *T. basicola* is a conspicuous and universal colonizer of coconut kernels in the tropics. Yet another Went's epochal discovery was the mould, *Monilia sitophila*, later on of its teleomorph, *Neurospora*, the mould that led to many significant discoveries in genetics and molecular biology. Westerdijk was Director of the CBS from 1907 to 1959 when she retired. From 1917 she was also Professor of Plant Pathology at the University at Utrecht. The Phytopathological Laboratory "Willie Commelin Scholten"was adjacent and closely associated with the CBS. I went to nearby Bussum from where Oudemans and Koning did their pioneering work on soil fungi in the beginning of the twentieth century.

I visited the great Agricultural University at Wageningen, and Groeningen as well, where I was shown round the work in plant pathology and mycology. The Institute in Wageningen was founded in 1918 and had distinguished men like H. M. Quanjer, van Slogteren, and A. J. P. Oort who was then the Director. Quanjer was its first Director and held office from 1918 to 1949. I met T. H. Thung, the plant virologist, a most hospitable and dear friend, and other plant pathologists. Thung had just been appointed Professor of Virology and initiated the important work in this area that was to follow. Thung is credited with the idea of an international centre for phytovirology information.

I also took the opportunity to visit the laboratory of the distinguished plant physiologist, F. W. Went in Utrecht. The laboratory was established by his father, F. A. F. C. Went on his return from Java. Utrecht, Leiden and Amsterdam were intellectual centres, being alive with leaders in physiology, medicine and botany. During the War, F. W. Went continued to do his experiments on hormones and plant growth in an underground cellar which served as a laboratory. It was in the underground cellar that *Avena* coleoptile and other tests were carried out by Went. I had the opportunity to see this laboratory which I found was being maintained just as it was during his time. It was inspiring to be in a place where great work was done in the midst of the horrors of a War, an example of ecstacy amidst agony!

In Paris I visited R. J. Gautheret's laboratory in Versailles to see his work on plant tissue culture which I thought could prove useful in studies in mycology and plant pathology. A pioneer in tissue culture, Gautheret had demonstrated the multiplication of salix cells with addition of auxin to the culture medium in 1937; in 1939 he succeeded in maintaining carrot tissue in continued culture (Gautheret, 1942). He spoke at the Stockholm Congress (see Gautheret, 1983). The visit was further enriched by the experience of seeing the beauty of the palace at Versailles and its garden. On the boat from Calais to Dover, I happened to meet and got to know A. J. Mix, who worked in Kansas in the USA and was an authority on the genus *Taphrina*. Like me, he was returning from the Stockholm Congress. His monograph on *Taphrina* had appeared in 1949.

II-3 Cambridge: Soil Mycology, Root-infecting Fungi

From Dover I went to Cambridge and reported to S. D. Garrett at the Botany School on Downing Street.

Cambridge had an early historical connection with mycology in the tropics. That connection began with Marshall Ward who took his Natural Science Tripos with a First Class in 1879. Later, he had training from Anton de Bary in Germany. The British Government chose to send him as Government Cryptogamist to Ceylon to investigate the rust disease which was devastating coffee plantations there. First reported on coffee growing in the wild in Kenya in Africa in 1861, the rust fungus (*Hemileia vastatrix*) appeared in Ceylon on cultivated coffee in 1869. Unfortunately, the fungal enemy had its day and an immediate solution to the problem eluded Marshall Ward; he submitted his final Report to the Ceylon Government in 1881 and returned to Britain.

Coffee was given up and instead, tea was introduced for cultivation in Ceylon. The pathogen spread to coffee in India, Malaya, Java, Madagascar and Africa by 1920. In 1970 the fungus showed up in Brazil and thereafter quickly spread to other coffee-growing states in South and Central America. *Hemileia* is a tropical genus of about 40 species infecting *Rubiaceae* and *Apocynaceae* (A. Ritschel, 2005). The aecial and spermogonial states are not known. Thirty-two races of coffee rust are known and there is no arabica cultivar (the preferred one) resistant to all races. *Coffea canephora* is the main source of resistant genes not found in *C. arabica*. Though cultivation of coffee had to be given up in Ceylon, the gain to our science from Marshall Ward's (1882) elucidation of fundamental aspects of the coffee disease was significant.

Despite this, recognition came to him late, in 1895, when he was appointed to the Chair of Botany in Cambridge. The Botany School building on Downing Street was the direct result of the vision and powers of persuasion of Marshall Ward (Ayres, 2004; Raven, 2004). "The enthusiasm that brought him to the front tended also to shorten his days" (Bower, 1938, p. 56). His health was not robust, and he overworked himself. Marshall Ward died early and, though his work, particularly on plant rusts, was continued by F. T. Brooks, the history of plant pathology in Britain would, I believe, have been different had he lived longer to continue the great work he initiated at Cambridge. An Indian, Karam Chand Mehta, worked with Brooks and, on his return to India, initiated research on the epidemiology of wheat rust at Agra College in Agra, Uttar Pradesh (Mehta, 1929; 1933; 1940). That was an early Cambridge-India mycological connection.

At the time I reached Cambridge, Brooks had just retired, but still came to the Department occasionally. A second revised edition of his *Plant Diseases* appeared in 1953, a masterpiece of brevity and very authoritative. The Botany School was headed by Harry Godwin whose special interest was in Quaternary Biology. The Department of Genetics had David G. Catcheside doing fungal genetics at that time. One of my compatriots, J. Venkateswarlu of the Andhra University, Waltair, Andhra Pradesh, was working with Catcheside on genetics of maize. Our friendship grew over the years, and yet Venkateswarlu did not yield to my appeals to him to take

up and pursue fungal genetics on his return to India.

The distinguished algologist E. G. Pringsheim's collection of pure cultures of algae was located in the Botany School. M. O. P. Iyengar had written to me to see Pringsheim and try to learn from him the methods of making pure cultures of algae. Pringsheim and his Assistant were courteous in showing me round the culture collection at my mention of Iyengar's name and they explained to me the techniques of obtaining pure cultures of algae. Pringsheim's (1949) book on pure culture, and preparation and maintenance of algae had just then appeared.

The sub-Division of Mycology in the Botany School was headed by W. J. Dowson, who had authored a book on bacteria and bacterial diseases of plants (Dowson, 1949). I had dialogues with him in trying to learn about bacteria and their interactions with plants and fungi. I found him a very kind and understanding person. He posed the question of my future on my return to India, and when I told him I planned to go to my old laboratory where I hoped to secure a lecturership, he quickly warned me by saying, "a seedling will not grow under a big tree. You must seek a position away from the tree!"

I carried with me from Madras about 200 cultures of fusaria I had isolated from soils and from different crop plants in southern India. I reported bringing the cultures into Britain to the Plant Quarantine authorities located at Harpenden, and was given permission to use them for my study in a letter from W. C. Moore who headed the Plant Quarantine authority. However, there was no '*Fusarium* specialist' in Cambridge, nor any special *Fusarium* collection. The Cambridge laboratory under Garrett represented one of the world's most active and most reputed, and was known for its work in the twin fields of soil mycology and soil-borne diseases of plants.

In August 1950 when I joined there, J. H. Warcup from Australia had just completed his first major and innovative work on soil fungi. Warcup continued to do more on soil fungi later. He explained his soil plate technique, by which he could isolate basidiomycetous fungi from soils, something not possible by the well established soil dilution plate technique. His soil-steaming technique enabled him to isolate several interesting ascomycetes which also would not normally appear on soil dilution plates. Warcup's work opened up a whole spectrum of soil fungal diversity. Identification of some of these fungi was not always easy and depended on the production of fruit bodies by them. Fortunately for Warcup, the Department had E. J. H. Corner on its staff.

Corner had spent many years (1929-1946) in Singapore at the Botanical Garden, had collected widely in the tropics, and was an expert not only on fungi but also on tropical plants. His monograph on *Clavaria* and related fungi had just been published as an Annals of Botany Memoir (Corner, 1950). His analysis of hyphal systems in polypores (bracket fungi) and other basidiomycetes was to be one of his most significant contributions to basidiomycete taxonomy (Corner, 1953). I was fortunate that I could meet and learn from him. It occurred to me that he was a thinker, very original in his approach to everything. He had, for example, mathematical ideas of representing basidial morphology. In our discussions on *Fusarium* he suggested that I give thought to the idea of representing conidial shape in *Fusarium* with greater precision than what was usually followed in descriptions.

What is more, he had first hand and intimate knowledge of the tropics and its fungal biota, not to mention the plants and even the fauna (Corner, 1935; 1968). He had trained monkeys to fetch him inaccessible specimens from tree tops. During the Japanese occupation of Malaya, Corner (along with R. E. Holttum and C. X. Furtado) was allowed to remain in Singapore and continue his research on plants and fungi. My dialogues with Corner enriched my knowledge of tropical fungi. On my return to India, we had corresponded whenever there was need for consultation and once, seeing my report of *Actiniceps cocos* from India, he promptly wrote: "I was very interested to see *Actiniceps cocos* in one of the papers you so kindly sent me recently. I think it must be the conidial state of *Chaetotyphula hyalina* (Jungh.) Corner, described in my monograph on "*Clavaria* and Allied Genera"…" (letter dated 20 September, 1955).

Denis Garrett was undoubtedly the recognized leader in the twin fields of soil fungal ecology and soil- borne diseases of plants. Self-effacing and kind by nature, he wielded his preeminence lightly. Garrett's original contributions were on the ecology of *Gaeumannomyces graminis* var. *tritici*, in relation to the epidemiology and control of take-all disease in wheat. Originally begun with G. Samuel in Australia, he continued the study at Rothamsted, and made a most significant contribution to our understanding of take-all epidemiology. He gave a new meaning to the science of fungal ecology in relation to soil-borne diseases of plants (Garrett, 1944; 1950; 1956; 1970). The evolution of parasitism and of symbiosis in soil fungi was a focus on which he analyzed the interaction of parasites, pathogens and symbionts, with root systems and the soil environment. 2006 marked the centenary of his birth.

I had many fruitful discussions with him on the ecology of root-infecting fungal pathogens as well as symbionts. I saw for the first time some of the simple experimental layouts and glassware he used in his studies. He was still working on various facets of take-all, besides studies on *Armillaria mellea*. The rhizomorph literally a bundle of fungal hyphae growing like a root, hence the term, rhizomorph is typical of *Armillaria mellea* and its allies. Some species of *Marasmius* produce conspicuous black rhizomorphs and are common on tropical forest litter. Rhizomorphs have the ability to grow freely in natural soils and thus reach trees around and infect them. Indeed, the mycelium survived in root systems of tree hosts for decades, and infected root systems afresh. *Fomes annosus* was another soil-borne pathogen that infected root systems of rubber and other trees in the tropics.

R. P. N. Napper's (1939) investigations on the control of spread of *Fomes annosus* from an infection focus to adjacent trees in rubber plantations in Malaya through free growth in soils highlighted the role of rhizomorphs in free spread of pathogens in tropical soils and their relevance in disease control. (Napper was killed early in 1942 as a result of enemy action in Malaya; he pioneered studies on root diseases of

rubber and their control). Take-all, of course, was a lifetime-study with Garrett and even when enough was known, so it seemed, enough was not known. I had always looked at it as a model to be followed by those wanting to study soil-borne fungal diseases of plants.

Garrett introduced me to S. Dickinson at the School of Agriculture. I have referred earlier to Dickinson's work on *Fusarium* with Stakman in Minnesota. He was now working on the physiology of obligate parasitism. My discussions with him on *Fusarium* enriched my knowledge of variation and variability in the genus. Dickinson had also made cytological studies on *Helminthosporium sativum*, the wheat foot rot fungus, particularly of the conidia in relation to the variability seen in this pathogen.

Dickinson took me to K. O. Mueller who was then working in the School of Agriculture, having migrated there from Germany during the War. Mueller had propounded his famous 'phytoalexin theory' of resistance of potato varieties to late blight due to *Phytophthora infestans* (Mueller and Boerger, 1940; Mueller, 1956). In his own characteristic English, punctuated by mannerisms, he spoke to me about his work on resistance of potato to late blight, of which I knew little then. I listened to him with the greatest interest as late blight had been one of the world's major problems. (Late blight was the cause of the Irish famine in 1843-45 and is cited as the first example of a plant disease in which proof of fungal complicity was experimentally established. However, *Phytophthora* and other related 'phycomycetes' (or 'algal fungi') are no true fungi. They resemble the algae in many features and are placed in the kingdom *Chromista* or *Straminopila* along with the water moulds and downy mildews. The placement of these plant pathogens apart from the fungal kingdom is yet another long story of discoveries and surprises which is very much a part of tropical mycology and plant pathology.

One of the youngest on the faculty in Cambridge was Noel F. Robertson, who was working on mycorrhizas of pines. I learnt from him a good deal about what he was doing and about the techniques he was using to induce mycorrhizal development. Mycorrhizal fungi and root disease fungi are but part of the soil mycobiota and had relevance in plant health. Learning of my interest in *Fusarium*, Noel suggested I study gladiolus wilt which was known to be caused by a *Fusarium*. I isolated from diseased gladiolus plants a number of fusaria and studied them in first cultures. This study confirmed my earlier findings on the 'wild type' in *Fusarium*. Without exception my isolates conformed to the vigorously sporulating 'wild type' which I had described for many fusaria in India. Constraints of time prevented me from continuing my study of gladiolus *Fusarium* and I left the cultures with Noel. These cultures were later taken up for study by E. W. Buxton at Rothamsted (Buxton and Robertson, 1953; Buxton, 1955). Noel later moved to Hull, where I visited him in 1965, and thereafter to Edinburgh where he finally settled. For a time he studied the fungal hypha and morphogenesis in fungi, which formed the subject of his Presidential Address to the BMS in 1965. Noel was a great friend and I had occasion to visit him thrice during 1975-1984.

II-4 Oxford: Ecology of Larger Fungi

While at Cambridge, I made a short trip to Oxford to meet W. H. Wilkins and J. L. Harley in the School of Forestry. Wilkins, Harley and co-workers had published a series of papers on the ecology of larger fungi in the Annals of Applied Biology and their work evoked special interest in me (Wilkins *et al.*, 1937; Wilkins *et al.*, 1938; Wilkins and Harris, 1946). Their systematic and well-planned studies threw light on the ecology of the larger fungi in Britain. Data were given on the various fungal species, their monthly frequency and abundance in fruiting over a period of five years, together with data on temperature, rainfall, soil type, etc. obtained from several different locations around Oxford and Haslemere.

After talking to Wilkins and Harley, I was further impressed with what they were doing and their approach to studying fungal ecology in the open. The occurrence of specific fungi under oak or birch or beech or conifer observed in the study was a pointer to specific mycorrhizal associations. Thus, my visit to Oxford kindled my interest in the larger fungi, a great many of which were dwellers in the soil. Compendiums on soil fungi such as that of J. C. Gilman (1945), which were available then, dealt with fungi caught on soil dilution plates, but not the innumerable basidiomycetous components of the soil that showed up in their conspicuous fruit bodies such as were noted by Wilkins and others, though some were isolated by Warcup by his soil plate technique. Be that as it may, it is a wondrous step from Gilman (1945) to Domsch, Gams and Anderson (2007). Our knowledge of soil fungi has expanded enormously.

II-5 Kew: Hyphomycetes and the Masonian Tradition

From Cambridge I moved to Kew to work at the Commonwealth Mycological Institute (CMI), (cf. Aitchison and Hawksworth, 1993, pp.96-99), then housed in a small building on the west side of Ferry Lane on the banks of the river Thames, and reached by walking across Kew Green. I was given the room on the ground floor on the left of the entrance and close to the Director's room. The then Director, S. P. Wiltshire, was a kind and soft-spoken person. His work on the taxonomy of *Stemphylium* was well known (Wiltshire, 1938). His organizational ability, editorial skills and affable nature all combined in enabling him to develop and expand the activities of the Institute on sound lines. Wiltshire gave his Zeiss microscope for my use as there was a shortage of microscopes.

On the very first day, I was introduced to H. A. Dade, Deputy Director, and mycologists, G. R. Bisby, S. J. Hughes and M. B. Ellis. 'Major' Dade was in charge of the Culture Collection and he had rare technical skills and interest in the development of techniques for studying fungi. Bisby had been one of the three from Britain who had examined my Ph. D. thesis. Greeting me, Bisby introduced me to a former Canadian colleague of his, M. I. Timonin who was then visiting CMI. I was aware of Timonin's work on root exudates and soil fungi and was very pleased to meet him. Bisby had worked on soil fungi in Manitoba, Canada, and had jointly authored with John Dearness and A. H. R. Buller

(1929), *The Fungi of Manitoba*. He had also co-authored with E. J. Butler, the first Director of the Institute, *The Fungi of India*, an authoritative compilation of remarkable accuracy and precision (Butler and Bisby, 1931). He was also co-author of *The Fungi of Ceylon* with T. Petch (Petch and Bisby, 1950). With G.C. Ainsworth, he co-authored the indispensable *Dictionary of Fungi* which first appeared in 1943.

The Dictionary was perhaps one of the earliest works to be written in C. K. Ogden's Basic English, a venture in which Ogden himself was known to have taken keen interest. My doubts and queries on entries in the Dictionary were readily cleared by Bisby whenever I wanted a clarification. Additionally, he also helped in understanding or solving nomenclatural problems and interpretation of the Code. He was ever friendly and, on my return to India, whenever I sent him reprints of my publications, he responded with a compliment in his own beautiful handwriting.

Hyphomycetes were the concern of S. J. Hughes and M. B. Ellis. Mason had initiated the study of classical genera based on their types, chiefly of the *Hyphomycetes*, and specimens poured in from all parts of the world for Mason to find a name for. The only way to do that was to try and match each with another authentic one which had a name already. But this required a good deal of research. Mason gathered the type specimens of the type species of many genera from scattered collections worldwide, studied them and published a series of annotated accounts on them over a period of years (Mason, 1933; 1937; 1941).

This important basic taxonomic work was being continued by Hughes and Ellis. In the process, Mason, Hughes and Ellis retrieved many classical genera from the confusion and obscurity in which they lay submerged, which they rediscovered and redescribed. Many new genera and species were also discovered and described, especially from the tropics. It was a unique experience to have been in the midst of such activity. The arrangement of specimens in the Herbarium at the CMI reflected the then current taxonomy of taxa at various levels in a system. Changes in generic or species concepts were reflected in the placement of specimens in the genus and species folders, a situation then unique to the CMI. Specimens had IMI accession numbers, were indexed in ledgers, and so could be traced and examined and types had special labels. Types are important, and essential for the circumscription of genera and species.

Stan Hughes had collected widely in the Gold Coast of Africa (Ghana), and was describing many beautiful novelties (Hughes, 1952a;b). His work on these tropical fungi was at its peak at this time. I found Stan soft-spoken, kind and helpful in guiding me to genus folders which he thought I should look at, for example, *Curvularia* and *Podoconis*, both genera, described originally from Java by Boedijn (1933), *Helminthosporium*, and many others common in the tropics. This way I came face to face with the beauty and diversity of hyphos that abound in the tropics. As a diversion from the microscope and the herbarium, he drew me out one afternoon to the Linnean Society in London to listen to G. C. Ainsworth's Presidential Address to the British Mycological Society. It was there that I met and was introduced to Geoffrey Ainsworth for the first time. Ainsworth's Presidential Address (Ainsworth, 1951) was on Medical Mycology, and impressed on me the relevance of fungi in medicine and public health. That the tropics held problems in this area also dawned on me.

Ellis had been in India with the British Army during the War and had travelled all over the country. Ellis drew my attention to several genera, notably *Papularia* and *Arthrinium,* and several others which were not known to me. These enriched my knowledge further.

A visitor like me working at the Institute at the same time was A. Chaves Batista from Brazil. I did not know what exactly he was working on. It was my guess that he was already a senior scientist and, though friendly and courteous, he seemed to me a somewhat reticent or shy person who could perhaps not understand my English with its Indian accent, or felt that his English might not be understood by me! Whatever that might have been, on my return to India, I regularly received his publications and outpourings on Brazilian fungi, which showed that the CMI played a significant role in the development of mycology in Brazil. Indeed, Batista was prodigious and did great work on Brazilian fungi (see Da Silva and Minter, 1995).

The introductions over, I plunged into my work. I went to Mason to have instructions. He asked me to go along the Thames and bring him some specimens. When I brought him a bagful of twigs and leaves of different plants with fungi and placed them before him, he bid me take them away and bring them back to him named! Having studied them and found names for several of them, I took them back to him again, but now with names. He looked at them and exclaimed, “you have 'eyes,' you can 'see'.” Did not the great Goethe, writing to Frau von Stein in 1785, say of himself that the eye was the organ with which he investigated the world, and that he felt himself “born to see, appointed to look”? and, did not Teilhard de Chardin begin his *Phenomenon of Man* with the words: “*Seeing*. We might say that the whole of life lies in that verb”?

I was then put on training in various techniques imparted to me by the technicians. I was told the way I should handle material of foliicolous and other fungi. Material of the *Meliolineae* from Africa was pouring in at that time from Hansford, and I was asked to prepare 'Necol mounts' (Hopkins, 1960) of each specimen. These would be examined by Mason and with his approval would be kept in the appropriate folders along with the material. This explained why slides of fungi stored with the herbarium specimens at the CMI were perfect in every way and of immense use in studies of these fungi.

Now the entire collection was open to me. The library had all important classical works and monographs on fungi, besides a fantastic collection of reprints of papers painstakingly collected by Butler and others. There was the British Mycological Society's library on the first floor where everyone met for tea in the afternoon. The atmosphere was peaceful, everyone doing with enthusiasm whatever he or she wanted to do. I enjoyed working there. I looked at many

fungi, some known to me by name, many not known to me at all. I was struck by the beauty and variety that I saw. Every Genus Folder had a story to tell virtually a history of the genus and of the species, including locations and habitats of occurrence, names of collectors, and dates of collection, information unavailable from other sources.

Specimens were not just filed as they were received, but carefully examined and filed under what the CMI specialists considered to be the correct names, a procedure that ensured order in arrangement of specimens in place of mere heaping of specimens. I made camera lucida sketches of the key features of many, primarily tropical, species and noted the literature citation for each. Many specimens carried annotations in Mason's own handwriting which, with some familiarity, I could decipher. Mason himself would not speak much, but the annotations spoke for him. He knew the power of silence. There was no need for a discourse. Look at the fungi; they will speak to you. The experience and knowledge I gained thereby, more particularly, the approach to study, what I have called the Masonian tradition, was my most important acquisition.

It was around this time that the Conference of Prime Ministers of the Commonwealth was held in London to which Jawaharlal Nehru, Prime Minister of India, had come. There was a Reception on Monday the 8th January, 1951 at India House in Aldwych to which I and others like me had been invited. At the reception I saw my Prime Minister for the first time. Here I renewed my acquaintance with Janaki Ammal, the Indian botanist, whom I had met in Stockholm and who was working with C. D. Darlington at the John Innes. Janaki Ammal was joint author, with Darlington, of the *Chromosome Atlas of Cultivated Plants* which was published in 1945. She introduced me to the Prime Minister. It was great to greet one who had a memorable Cambridge connection and particularly, the Botany School, like the Prime Minister who was also a great supporter of Science.

Janaki Ammal returned to India soon after, at the invitation of the Prime Minister, was appointed Officer on Special Duty, and assigned the work of re-organization of the Botanical Survey of India which she did. On her retirement, she continued to work and around 1970 or so we had her with us in the UBL at Madras as an Emeritus scientist working on the cytogenetics of a variety of plants, especially medicinal plants, and ethnobotany of tribals, until her demise in 1984. The Government of India instituted a National Award for Taxonomy in her name.

During my stay at Kew, I called on William Brown at the Imperial College of the University of London; I had been introduced to him in Stockholm by Philip Gregory. Brown was Chairman of the committee of Examiners who commended my thesis for the award of a Ph.D. Despite being extremely busy at that time, he saw me briefly and made kind enquiries about my work and my future plans. I thought his apparent reticence was a cloak for a large and kindly heart that had an all-embracing aura. I saw him again at the First International Congress of Plant Pathology at Imperial College in 1968, where he was surrounded by his students, his colleagues and his many friends…

I also visited the Research Station at East Malling in Maidstone in Kent to see W. G. Keyworth and his work on *Verticillium* wilts, which interested me because *Fusarium* and *Verticillium*, I thought, had much in common, though, admittedly, I knew very little about them. *Verticillium albo-atrum* caused wilt in several crops, in temperate as well as tropical parts of the world and was considered a root-inhabitant. Work at East Malling concerned various crops, notably hops [*Humulus lupulus* (*Cannabaceae*)].

(Many years later, in 1971, Keyworth visited the UBL and participated in the International Symposium on Pathological Wilting in Plants which brought together other mycologists that included F. Grossman, A. C. Hastie, Ivor Isaac, R. M. Jackson, G. F. Pegg, N. Prasad, W. A. Sackston, W. C. Snyder, R. K. S. Wood and others. Later in the year, the International *Verticillium* Symposium at Wye College in England, which I attended, brought many of us together again , notably Ivor Isaac, W.G. Keyworth, P.W. Talboys, G.F. Pegg, W.E. Sackston, C.D. Mckeen and A.C. Hastie. The meeting contributed to a meaningful understanding of the status of *Verticillium* as a soil-borne pathogen, and its taxonomy and biology.)

I visited Rothamsted to see Bawden, Gregory, Mary Glynne, and the entire plant pathology and plant virology groups, B. Kassanis, and the Watsons, besides B. N. Singh, from India. Indeed, several scientists from India had been trained there. Rothamsted with its history and record of work in soil science and field trials fascinated me from my interest in soil mycology, soil science, and soil-borne plant disease. I was introduced to the Ministry of Agriculture fraternity located in Harpenden: W. C. Moore, Joan Moore, and E. C. Large, the author of the celebrated *The Advance of the Fungi* (1940).

A brief visit to W. H. Pearsall at the Botany Department, University of London was prompted by my love for algae. Pearsall was a much respected senior botanist. He introduced me to his student and associate, G. E. Fogg who showed me round the Department and explained the work on algae. Here I met a compatriot, M. R. Suxena, who was then working with Pearsall. On his return to India, Suxena continued his work on algae at the Osmania University, Hyderabad.

And then my time was up. I took leave of all my good friends, and finally, went up to Mason. He asked me, 'What would you do on your return?' I told him I would be teaching plant pathology and mycology. He then exclaimed, 'Viruses, plant diseases…?'. I said, 'Yes'. He then wished me well, but added, 'if ever you send me specimens,' and as he was speaking, he took out from one of the cupboards a packet of leaves with spots and spread them on his table, and continued, 'if ever you send me specimens, do not send such material as this plant pathologist has done, and ask me to name the fungus which is not there!'

It was now time to leave the shores of Britain. I took the boat sailing from Southampton to Bombay on the 13th January1951, and was back at Madras by the end of the month.

III The Excitement of Exploration

Back at Madras and the UBL late in January 1951, I joined the university as Senior Lecturer, a post for which I had applied and was appointed. On the voyage back to Bombay, I had made my plans. I was excited. I must explore.

III-1 The Known, the Little Known, and the Unknown

To begin with, I started collecting around the laboratory. 'Recognosce notum, inspice ignotum' Recognize the known, inspect the unknown, the motto of the British Mycological Society, became my motto. In just a day of collecting, I picked up quite a few interesting finds, just the kind of hyphomycetous fungi I was looking for. And I could name them easily from my experience at the CMI: for example, some of my earliest finds included *Corynespora cassiicola*, *Memnoniella echinata, Stachybotrys atra*, *Torula herbarum,* and *Zygosporium oscheoides*, surprisingly, none of which had previously been recorded from the country. We know that they are some of the commonest hyphomycetous fungi in the tropics. *Torula* had been a genus much misunderstood, and only someone who knew Mason's work on *Torula* could have identified *T. herbarum* correctly at that time.

Excitement ran high when I picked up for the first time *Wiesneriomyces javanicus,* which I found had not been reported till then by anyone since it was first described from Java by S. H. Koorders (1907). How exciting! What appeared to be a synnematous hyphomycetous fungi which I repeatedly collected on twigs of *Thevetia peruviana* (*Apocynaceae*) and which baffled me for some years finally turned out to be *Tretopileus sphaerophorus*, a sterile mycelial fungus, originally described by Berkeley and Curtis in 1868 on *Cajanus* from Cuba under the binomial *Monotospora sphaerophora*. I came across many more such fungi which were until then known only from the type collections in the tropics. Virtually, a beauty pageant of fungi! I gave a number to each collection with details of locality, host or substrate, collector's name and other details. I also kept a register of the specimens. These formed the nucleus of a Herbarium at MUBL.

Many common fungi had not then been recorded from India, and in the course of a month I had added about 50-60 new records to the list of Indian fungi. There was an equal number which could not be named so easily. The known, along with the unknown, came to give me strength and joy. Treasures came by the untrodden path. Specimens collected and identified by me were sent to Mason for confirmation. I continued this procedure until after a year and a half or so, I felt I could confidently go on on my own and not trouble Mason any further except when I faced special problems. And, he was of immense help, always. Assignment of a large number of collections which turned out to be *Periconia*s had to await the publication of the *Mycological Paper* on *Periconia* by Mason and Ellis (1953). And, when my paper on *Periconi*a appeared (Subramanian, 1955c), Ellis had a kind word for it.

It was always excitement, exploration, excitement, in a never-ending continuum. Indeed, the excitement persists in this recounting of my excitement. I derived pleasure in collecting anything I had not seen before. In the process, I also came across many a novelty hitherto not known to science. It was not always easy to affirm that a specimen was really a novelty. Only time could show the truth and the genuineness of newly named species. It was important therefore for the truth seeker to assess the status of novelties periodically. Naturally, this exercise generated great excitement.

For example, a new hyphomycete genus, *Beltraniella*, was established by me (Subramanian, 1952e) for a fungus we collected on dead and dying leaves of *Lannea grandis (Odina wodier)* [*Anacardiaceae*] in the backyard of my laboratory in Madras. After so many years, I still vividly remember the precise location where this fungus was collected, though the place has changed and the *Lannea* tree might have been cut down and disappeared. I collected it on a morning when the dew drops were still to be seen on the fallen leaves, along with fungus colonies thereon. It then seemed to me that it was an early colonizer on the fallen leaves; they were freshly fallen leaves, so I did not think the fungus had colonized from the soil and I did not know where else it came from.

I saw in it some similarities with *Beltrania rhombica*, a very beautiful fungus for which the genus *Beltrania* had been established by the Italian mycologist, Penzig in 1882, from a collection on the undersurface of leaves of *Citrus limon* (*Rutaceae*) from Sicily. The characteristic conidia were solitary and biconic with a hyaline transverse band in the region of the broadest part. The conidiophores were interspersed with sterile, stiff setae, both of which arose, each from a radially lobed basal cell. *Beltrania rhombica* was also later collected and had been described from Java by Penzig and Saccardo (1904).

My fungus also had setae and biconic one-celled conidia, each with a median transverse hyaline band. However, the conidia were borne on branches arising from the setae, the setae being sterile towards the apex. There were also conidiophores distinct from the setae. Further, the setae as well as the conidiophores arising independently arose from radially lobed basal cells, a feature seen in a few other foliicolous genera allied to *Beltrania,* and grouped together for this reason in a tribe, '*Beltraniae*'. Having collected a specimen of *B. rhombica* myself from Madras, and having seen a slide of the type specimen at CMI, I knew my fungus was not the same as *B. rhombica*. I then took the risk of naming what then apparently had no name.

Both fungi were later shown to have a wide distribution in the tropics. K. A. Pirozynski and S. D. Patil described in 1970 two new species of *Beltrania*: *B. mundkurii* (honouring B. B. Mundkur) on fallen leaves of *Syzygium cuminii* (*Myrtaceae*) and *B. santapaui* (honouring H. Santapau) on rotting fallen leaves of *Ochrocarpus longifolius* (*Guttiferae*) from western India. They also described three new species of *Beltraniella*: *B. spiralis* on fallen deaying leaves of *Ochrocarpus longifolius* (Pirozynski and Patil, 1966), *B. nilgirica* on fallen leaves of *Ilex denticulata* (*Aquifoliaceae*) and *B. porosa* on fallen decaying leaves of *Diospyros* (*Ebenaceae*) (Pirozynski and Patil, 1970).

During the 50 or more years since the genus *Beltraniella* was

established, at least 17 more species were described by mycologists working in different parts of the world, from India to Japan to Europe to Ethiopia to Cuba! Granting that all these species were congeneric, I wondered how speciation occurred in a genus with such a wide geographical scattering of species that was predominantly tropical. Surely, we knew nothing about speciation in these or many of the other fungi which we had been collecting. In this scenario, Fernando and Gusmao (2004), in a reappraisal of these fungi, proposed a new genus, *Porobeltraniella,* to accommodate *Beltraniella porosa* Pirozynski & Patil, and *B. patilii* Karandikar & Patwardhan (Karandikar and Patwardhan, 1992), both from India, primarily because the biconic condia of both species had equatorial pores instead of a continuous band. This is a measure of the continuing excitement, although here also the last word is yet to be.

A fungus I collected on living leaves of a *Crataeva* species (*Capparidaceae*) which keyed down to the genus *Camptomeris* using the Clements and Shear (1931) *Genera of Fungi* keys was described by me as a new species, *C. crataevae* (Subramanian, 1952d). Very soon, writing from Michigan, E. A. Bessey brought to my notice my error and sent me a copy of his paper on *Camptomeris* in the *Papers of the Michigan Academy of Science* (Bessey, 1955). This, coupled with a later more detailed study of the genus by Stan Hughes, underlined the importance of hidden structures and host prediliction in the study of foliicolous fungi in particular. Indeed, I felt grateful to Bessey for his timely correction and the message behind his letter to me. *Camptomeris* species, I now noted, were restricted to leguminous hosts (*Acacia, Albizzia, Astragalus, Calliandra, Desmanthus, Leucaena*, *Pithecellobium*) that are tropical.

The generic name *Lacellinopsis* was proposed by me (Subramanian, 1953a) for a fungus (*L. sacchari*) I collected on dead and decaying sugarcane (*Saccharum officinarum*). A second species, *L. levispora* (on dead leaf of an unidentified plant) was described by me the following year. A third species, *L. spiralis* on dead leaves of *Pennisetum purpureum* (*Gramineae*) from Ghana was described by M. B. Ellis in 1957. Stan Hughes (1958) added a fourth species, *L. glomerulosa* that was originally collected on decaying culms of a grass at Tjibodas in Java and described by Penzig and Saccardo as *Torula glomerulosa* in 1904. Since then, two more species have been described, both from India: *L. desmostachyae* Roy & Dwivedi on dead leaves of *Desmostachya bipinnata* (*Gramineae*) and *L. osmaniae* on dead leaves of *Typha elephantina* (*Typhaceae*). Thus, *Lacellinopsis* seemed to prefer monocot substrates in the tropics.

There were other novelties. I collected a beautiful sporodochial fungus on dead culms of rice plants from Madras. The conidia of this dematiaceous fungus were produced singly from phialides and were one-celled and fusiform, each with an apical brush-like appendage. The new generic name, *Koorchaloma* that I chose to accommodate it was derived from the Sanskrit koorcha (brush), and loma (hair), an obvious reference to the brush-like appendage of the conidium. I named the fungus *Koorchaloma madreeya*, the specific epithet being suggestive of Madras where it was collected (Subramanian, 1953c). The fungus was reported as causing cotyledonary infections and on leaves of *Gossypium arboreum* (cultivar AKH-4) at a Farm in Nagpur (Mukevar *et al.*, 2006).

During the past five decades and more since it was described, at least twelve other species have been added to the genus. An addition from a marine environment, on decaying leaf blades of *Spartina alterniflora* from Georgia, USA, was described by Sarma *et al.* (2001) and named *Koochaloma spartinicola*. The fungus was collected not only on naturally decaying leaves subject to submergence in saline water, but also leaf blades and leaf sheaths infrequently submerged. Sarma *et al.* (2001) therefore consider it a facultative marine fungus. It is noteworthy that the fungus colonized only *Spartina*, but not the closely ecologically associated *Juncus*. *Koorchaloma galateae* Kohlm. & Vollk-Kohlm. is another marine species. Later additions include: *K. bambusae* Nag Raj, *K. dimorpha* Matsushima, *K. novo-journalis* Yanna, K.D. Hyde & Goh, *K. occidentale* Nag Raj, *K. okamurae* I. Hino & Katum. and *K. okamurae* var. *assamica* Agnihothr.

More recently, Alleguchi *et al.*(2011) described a new species, *K. scutiae* on leaf litter on *Scutia buxifolia* from Magdalena in Buenos Aires, Argentina. That *Koorchaloma* enjoyed a distribution beyond the tropics became clear by the discovery of a new species, *K. europaea* and its teleomorph *Kananascus europaeus* collected from Lithuania on *Acorus calamus, Carex panicea, Equisetum* sp., and *Scirpus sylvaticus* (Treigiene, 2006). Discovery of a sexual state for *Koorchaloma* in the pyrenomycetes was made in 1984 by Nag Raj who christened it *Kananascus* (*Sordariomycetes*) of which he described two new species, *K. koorchalomagnatus* (anamorph *Koorchaloma madreeya*) and *K. verruccisporus* (anamorph *Koorchaloma jamaicense* Nag Raj) from Jamaica, West Indies. Nag Raj noted that the conidiomata in *K. madreeya* were cupulate with excipulum, and so must belong in the *Coelomycetes*. *Koorchaloma*, like *Beltraniella,* continues to excite.

A beautiful find I collected on dead spathe of coconut (*Cocos nucifera*) turned up on a collection trip to Kerala. The blackish powdery colonies carried branched chains of deep brown phragmoconidia individually connected by isthmi or distinct one or two separating cells, a noteworthy feature. The conidial chains of darkly pigmented phragmoconidia of *Torula herbarum* are without separating cells and quite distinct. From these features, the collection on coconut spathe was disposed by me in a new genus, *Bahusandhika*. A congeneric species on orchids described by Cash and Watson was transferred to *Bahusandhika* as *B. intercalaris* (Cash & Watson) Subram. Rao and Rao (1972) described *B. sundara*, collected on identified twigs from Andhra Pradesh in 1972. A fourth species, *B. compacta* Ricky, Mukerji & Malhotra was described in 1975 (Ricky *et al*., 1975). A recent study by Prathibha *et al*. (2014) has shed light on the taxonomy of *Bahusandhika indica*. The fungus was recollected, brought into culture, and the ITS and LSU gene regions sequenced. The affinities of *Bahusandhika* was shown to be with the *Pleosporales* (subclass *Pleosporomecetidae*,

Dothideomycetes).

It was important to communicate the beauty of my novelties. Though I had been trained to do drawings of vascular anatomy and structural features of plants by my great teachers, I knew I lacked the artistic talents to depict the beauty of my finds which included many novelties at the level of species and, in many cases, genus. Nevertheless, I always drew camera lucida sketches of my fungi. The attempt to do this brought into my focus the key features of my fungi. I therefore argued the case for line drawings as an essential part of study and description. The Rev. Father H. Santapau of the St Xavier's College, Bombay helped me generously over a period of many years with Latin translations of diagnoses of my new genera and species and words are inadequate for expression of my gratitude to him. A 'son of Jesus', he lived a life of service in the country he chose as his own. His lofty figure held a large heart within. The Reverend Father once advised me to have photomicrographs of my fungi showing their key features as one might err in making a drawing, whereas a photomicrograph cannot 'lie'.

R. W. G. Dennis, successor to Elsie Wakefield, and then Mycologist at the Royal Botanic Gardens, Kew, while acknowledging receipt of a packet of reprints of my papers I sent him, wrote to me: “I have derived much pleasure from scanning them and admiring your beautiful and very clear drawings. It is obvious you have an appreciation of line derived beauty which seems to be very seldom developed in students of microfungi! I think one cannot repeat too often how valuable it is to publish clear figures like these of all our critical collections. How much easier it is to know what you are talking about than with Petrak's interminable descriptions of new species and new genera, usually without a recognizable figure in pages.” (letter dated 25 September 1956). There was always another point of view, one that gave a new vision, a new discernment.

Finding names for new genera was not always easy as, under the Code, a name once used was unavailable for use for any other taxon. Thus, sometimes names proposed turned out to be homonyms and, having no legitimacy, had to be replaced by fresh new names. I got over this potential problem by using names coined from Sanskrit roots for my new genera and new species. Once again, R. W. G. Dennis, in the same letter, thought it was wise to draw on Sanskrit instead of from Greek or Latin, both of which, according to him, had been overworked. Dennis wrote: “I like, too, your idea of deriving names from Sanskrit roots, which overcomes the difficulty now becoming acute, of finding new and still descriptive names from latin or greek roots. It is possible you may be criticized for doing this but I do not think there is any objection to it. Latin itself is full of loan words already, as any living language is, and there are innumerable precedents for deriving generic names from non-classical (so-called 'barbarous') sources much less euphonius than yours. One of the worst of these I think is the well known genus *Menziesia* (*Ericaceae*) based on the Scotch name Menzies which is pronounced 'Mingis' by the natives!” Perhaps, I need to add that Sanskrit is a classical language like Latin and Greek with much in common and all three belong to a common stock.

The beauty and diversity of the fungi being described attracted the attention of Franz Petrak, who wrote to me from Vienna asking me to arrange to issue Exsiccatae of Indian fungi and promising to send me Exsiccatae in exchange. Petrak would virtually fill an aerogramme with lengthy (interminable!) instructions in German in his own beautiful handwriting about the preparation of the Exsiccatae; such was the interest of European mycologists like Petrak in tropical fungi at the time. At the Botanical Congress in Stockholm, Nannfeldt had similarly asked me if I could exchange Exsiccatae of Indian fungi in return for Exsiccatae of Swedish fungi.

Perhaps I should have responded positively to Petrak's repeated requests to me. Perhaps, yes, but only one like Petrak could have done it. His patience and his incessant enthusiasm were amazing. Not only did he describe numerous fungi from the tropics, but in addition he issued Exsiccatae of fungi and also was chief Editor of *Sydowia,* a continuation of *Annales Mycologici* which was founded and edited by the Sydows. As if this was not enough, all by himself, Petrak courageously brought out (Petrak's) Lists of fungal genera and species described after the appearance of the last Volume (Vol.25) of Saccardo's "*Sylloge Fungorum*", at a time when we had nothing like information technology! The Sydows, father and son, and Petrak published most of their work in their journals and so there is a great deal of tropical mycology in the pages of *Annales Mycologici* and *Sydowia*.

III-2 Specimens, Species, Names

When my friend K. Ramakrishnan joined us on the staff in Madras, I knew that his expertise in fungal systematics gained at the Mycology Section of the Agricultural Research Institute in Coimbatore would strengthen the UBL. Ramakrishnan knew most of the common plants of southern India and could name them and this is a basic requirement in a mycologist. In an effort to study the fungi of southern India, we agreed on a joint plan whereby I would take up the hyphomycetes, and he the ascomycetes, and coelomycetes and other groups, jointly by the two of us.

I had then collected a coelomycete which produced characteristic appendaged phragmoconidia within dimidiate pycnidia. The dorsiventral, subcylindrical, hyaline conidia had an appendage each at the apex and at the base, the basal one arising on the concave side. In trying to find a name for the fungus, we first made a list of all pycnidial fungi known from India that had appendaged conidia. We also looked at the descriptions of these fungi and tried to match our fungus with known descriptions of all such fungi. Our limited search into the literature gave us no clue to the identity of this beautiful find. The pycnidia of the fungus were found on dead leaves of a few dicotyledonous plant species. I sent a set of these specimens together with descriptions and drawings to Mason for his opinion.

Mason wrote several letters to me about this fungus. In one letter he said: “No one at the C.M.I. has made any special study of the *Coelomycetes*, nor have any of the collectors who send us their stuff.” (6 November, 1951). Earlier, he had

written: "I see from your last letter to the Director that you are rolling up your sleeves, preparatory to doing *Coelomycetes* in a big way: and I am afraid that we shall not be of much direct assistance." No one was working on coelomycetes at the CMI then. Following a search of Petrak's Lists and other literature, Mason replied that he had not found a name for our fungus. In the meantime, we had made further collections of it on other hosts and from other localities which were also sent to Mason in successive batches as and when these new ones turned up.

Mason then wrote that the fact that the fungus was turning up on different hosts and from different locations was a clear indication that it must already have been described, and so would have a name. And yet, a further year's search did not give any clue and Mason now concurred with us that we could describe the fungus and propose a new genus for it. We then wrote a paper describing the fungus and proposing the generic name *Lateronema* for it. While approving the manuscript, Mason wrote: "If the worst comes to the worst, and a new genus has to be, let it not be a horrid hybrid, *Lateronema* [*latero* (Latin)+ *nema* (Greek)]. *Plagio* (Greek) + *nema*, *Plagionema* would be appropriate." Following Mason's advice we used the generic name *Plagionema* (Subramanian and Ramakrishnan ,1953c). But the story did not end there.

As part of our study of coelomycetous fungi with appendaged conidia, we now wanted to see type or authentic specimens of all such taxa known from India, and wrote to various collectors for the loan of specimens. The Sydows had described some fungi from India in the 1930s, jointly with J. H. Mitter and R. N. Tandon of the Botany Department, University of Allahabad, but we were told that the types of these fungi, including *Ciliochorella mangiferae*, a pycnidial fungus with appendaged conidia, were in Berlin. However, writing to Berlin, we learnt that many Sydow specimens were lost during World War II. Then, one fine morning, though I did not then know him personally, I received a packet from R. N. Tandon who now said he was happy to have found the type of *Ciliochorella mangiferae* which he was sending on loan!

When we examined it we found that it matched our *Plagionema indicum* (as *indica*) perfectly - in every detail. The type was on leaves of *Mangifera indica* (mango) and we had also collected our fungus on leaves of *Mangifera indica* [*Anacardiaceae*] (and many other hosts). We now realized how prophetic Mason was when he said the fungus would already have a name! The problem arose because Sydow did not correctly describe the fungus, and so our fungus did not match Sydow's description. Sydow represented the conidia of his fungus as one-celled with two divergent apical appendages and a persistent tail-like conidiophore. The Sydows seldom illustrated their fungi! When a description was inaccurate, the inaccurate description persisted in all literature and was then accepted and copied *ad nauseum*; the inaccuracies persisted in keys to genera, everywhere. M. O. P. Iyengar once told me: 'Subramanian, it does not matter if your name for a fungus is wrong, but your description of the fungus must be accurate in every detail.' His advice still rings in my ears.

We now redescribed Sydow's fungus from the type specimen and reduced *Plagionema indica* to synonymy with *Ciliochorella mangiferae*. I sent the manuscript of the paper to Mason to be forwarded for publication in the *Transactions of the British Mycological Society* where it eventually appeared (Subramanian and Ramakrishnan, 1956e). B. L. Chona and R. L. Munjal (1955) of the Indian Agricultural Research Institute, New Delhi, independently came to the same conclusion after examining the type of *Ciliochorella mangiferae*.

Brian Sutton (1980) reviewed the status of *Ciliochorella*, projecting it as being monotypic, with several synonyms, and confirming Mason's uncanny prediction and its widespread occurrence in the tropics. He also showed that conidiogenesis in this fungus is phialidic. R. L. Munjal (1966) described a second species, *C. castaneae* on leaves of *Castanea europaea* from India. Sutton (1980) considered *C. castaneae* indistinct from *C. mangiferae*. A third species was collected on leaves of *Quercus oleoides* var. *sagraeana* in Cuba and described and named *C. splendida* by Nag Raj and Castaneda (in Nag Raj, 1993, pp. 213-215). More recently, Alleguchi *et al.* (2011) described yet another species, *C. buxifolia* on dead leaves and litter from Argentina (Buenos Aires). So far as we know, *Ciliochorella* is foliicolous, and tropical and subtropical.

As part of the study of coelomycetes with appendaged conidia, we took up several classical but neglected genera such as *Neottiospora* Desm., and *Cryptostictis* Fuckel. In our study of *Neottiospora* (type species*, N. caricum*), we noted that, during the development of the conidium, its outermost wall layer, being inelastic, split transversely along a line just below the middle of the conidium due to the elongation of the body of the conidium. The conidium itself then got detached from the conidiogenous cell and the upper part of the outer wall which had split was now carried as a cap enclosing the conidium down to more than half its length. This thin cap later got everted and then appeared as a hyaline, very thin-walled, inverted hollow cone above (Subramanian and Ramakrishnan, 1953b). We thought that this was interesting. The inspiration for this interpretation came from discussions with M. O. P. Iyengar.

Once again, it was Dennis from RBG who, after seeing my *Neottiospora* and other papers, wrote: "It is good, too, to see someone taking the *Sphaeropsidales* seriously and I look forward to many more valuable contributions from your laboratory in this very productive field." It was in the course of this study that I proposed in 1961 the new generic name *Neottiosporina* to accommodate *Cryptostictis apoda* Speg.which I thought, from a study of the type (collected by Spegazzini in Argentina, South America in November 1909), was not a *Cryptostictis*, and needed to be placed in a new genus (Subramanian, 1961a).

Later, Brian Sutton described some, and added several, species in *Neottiosporina*, some under joint authorship (Sutton, 1976; 1980; Sutton and Alcorn, 1974; 1985; Sutton and Marasas, 1976; Sutton and Wu, 1995). Indeed, Brian wrote a massive tome on coelomycetes which was published by the CMI in 1980. The study of coelomycetes with appendaged conidia was pursued vigorously by Nag Raj in

Canada, culminating in the publication of a magnificent monograph of these fungi in 1993. He described (and re-described) and illustrated numerous beautiful coelomycetes with appendaged conidia with meticulous care and dedication. He recognized six species in *Neottiosporina*. The type species was collected on a composite, *Achyrocline*; however, of the other species, each was restricted to one of the following host genera: *Cyperus* [*Cyperaceae*], *Phragmites* and *Paspalum* [*Poaceae*], all monocots. The known distribution is tropical.

We gave priority to studying the types of novelties already described from India. It was part of the Masonian tradition. Apart from collecting in uncharted territory, I began borrowing types from various collections and studying fungi already described and listed in Butler and Bisby's (1931) *Fungi of India*. I made a list of species already recorded from India but not known to me, and tried to find these on the hosts on which they had been collected and the likely locales where they were or could have been collected.

Among these, for example, there was a fungus collected in Madras on *Gloriosa superba* [*Liliaceae*] and sent to the British mycologist, M. C. Cooke who described and illustrated the fungus, and placed it in the new genus, *Basidiella*, as *B. sphaerocarpa* (Cooke, 1878; 1885). I looked for this fungus on *Gloriosa superba* in Madras and elsewhere, but without success; all I could collect on *G. superba* in Madras was a black *Aspergillus*, possibly the ubiquitous *A. niger*. Though the types of most Indian fungi could be found in the CMI, there was none of *Basidiella*, which had remained monotypic. Apparently, no species had been added to the genus since it was described by Cooke in 1878.

During a visit to the CMI in the summer of 1965, I stepped into the Herbarium of the Royal Botanic Gardens, Kew where, greeting me, R. W. G. Dennis asked me if he could be of help to me in any way. I told him that I had been on the hunt for the type of *Basidiella sphaerocarpa* Cooke, described from India, and wondered if he could help me to find it. Dennis straightaway stationed a ladder below a Herbarium rack and, climbing up and opening a rack, brought out a folder. And then he exclaimed, “Here you have the type you wanted!” The type was a collection of dead roots of *G. superba* covered with black powdery spores. I was allowed to make two slides of the fungus. On examination under the microscope I saw a typical black *Aspergillus*! I thanked Dennis for his courtesy and straightaway went to Ellis at the CMI.

When I announced my discovery of the type of *Basidiella* to Ellis, he stood up like an officer in the Army would do before a superior and immediately placed one of my slides under the microscope and examined it. He concurred with me that it was a black *Aspergillus*. We checked Cooke's (1885) original illustrations and the accompanying brief description. Cooke's reference to flocci “collected in bundles” probably referred to the cluster of phialides at the apex of the mononematous conidiophore. Saccardo's disposition of the fungus in the *Stilbaceae-Phaeosporae* (copied by Clements & Shear in their *Genera of Fungi*) added to the confusion. I took my slides to J. J. Elphick who specialized in *Aspergillus* at the CMI and, after seeing it, he further confirmed our conclusion. I left the slides at the CMI where they now reside for anyone to see. There is a philosophy behind the openness that the CMI practised, the philosophy of perennial search for the truth.

Almost a decade of such exploration and description of hyphomycetes brought forth many beautiful novelties. I collected a great deal in the Nilgiris at different elevations of up to 8000 ft above sea level. The Nilgiris flora was well-known from the pioneering work of J. D. Hooker (Hooker *et al*., 1872-1897); J. S. Gamble and C.E.C. Fisher (1915-1936); Richard Henry Beddome (1863; 1869-1873; 1873; 1868-1874); P. F. Fyson (1932), and others. Beddome and Gamble were foresters who contributed significantly to our knowledge of the flora. Beddome spent twenty five years in southern India and used every opportunity to collect and describe plants and illustrating his works with accurate drawings done by draughts men specially trained by him. Fyson was Professor of Botany in the Presidency College, Madras and drew up an illustrated flora of the Nilgiris and the Pulneys, a great seminal work. The flora of much of the erstwhile Madras Presidency has been beautifully updated by my friend K. M. Mathew (1978/1981; 1983; 1991; 1999), working at the Rapinat Herbarium, St Joseph's College, Tiruchirapalli (Trichy, for short).

A unique flora must harbour unique fungi. The two Ramakrishnans, T. S. and K., had described many fungi from this region, with living foliage as their focus. For me not only the living foliage, but the litter of fallen leaves and twigs demanded attention. With experience, I learnt that the number of fungi one collected was inversely proportional to the area one covered. The more carefully one looked for fungi in a single location and on different kinds of leaves and twigs, and these in different states of decomposition, the greater the chance of new discoveries. Mason carried a lens hung from his neck wherever he went, and when someone asked him about it, he said he would be naked without it! In like manner, I carried a lens too. And yet, I know I missed many fungi, for example, those on insects which required a special 'eye' like that of a Thaxter, a Petch, or a Kobayasi. I would also have missed the many small colonies of fungi growing on lichens on the bark of trees. Areas ridden with leeches are often rich in fungal diversity, but leeches could be a real distraction and threat to good collecting. Collecting fungi is an art.

My trips to the Nilgiris were part of my taking students to get them to know fungi and plant diseases of tropical and sub-tropical as well as temperate crops. These trips incidentally enabled me to collect material for my study. I enjoyed these trips immensely, chiefly from the chance discovery of novelties of extraordinary beauty turning up here and there. Moreover, I learnt a great deal about fungi and plant diseases on such trips. Large areas of natural vegetation were being replaced by cultivation of various crops, partly to meet the needs of the local people and partly to fill the pockets of the greedy. *Exobasidium vexans* (blister blight) always showed up on tea, as did *Plasmodiophora brassicae* (club root) on cabbage. I can cite many other examples of plant pathogens

which flourished on the crops of their choice, something unthinkable in a natural forest.

But leaving these aside, something that appeared remarkable to me was the discovery of several common European hyphomycetes and other fungi in the Nilgiris. I had thought that some species could have come with material imported by the British when they were in India, but apart from these, there used to be a *Rhododendron* tree [*Ericaceae*] in the Botanical Garden at Ooty which had flower buds studded with the synnemata of a little-known but beautiful fungus, *Pycnostysanus azaleae*, redescribed by Mason in his Annotated Account of fungi in 1941. Year after year I used to visit this tree, and it always had the inevitable synnemata. I could match these with those from a specimen of the same fungus (on *Rhododendron*) from Herb. IMI.

I wondered how the tree could bear perennial crops of synnemata. It occurred to me that the fungus itself might have been perennial and even systemic within the tree without, of course, killing it and, remaining perennially within, producing synnemata year after year. Partridge and Morgan-Jones (2002) argued why *Pycnostysanus* would not do for this fungus and proposed a new genus, *Seifertia* for its disposition and called it *S. azaleae*. There is still need to probe old names and old specimens.

Another beautiful synnematous fungus fastidious in its choice of host is *Trochophora fasciculatum*, also seen in the higher elevations in the Nilgiris on living leaves of *Daphniphyllum neilgherense* [*Euphorbiaceae*]. Originally described by Berkeley and Curtis from tropical America under the name *Helicoma fasciculatum* in 1856 [U.S.North Pacific Expedition, No. 142, 1853-1856], it was reported by T. Petch from Ceylon as *Helicostilbe simplex*. The Japanese mycologist, Sawada recorded it from Taiwan. On a visit to Taiwan in 1995, I collected this fungus again and I found the Taiwan fungus exactly the same as the one from the Nilgiris. Here again I found it on the same host genus.

There was a peach tree (*Prunus persica* [*Rosaceae*]) in the Sim's Park in Coonoor, also in the Nilgiris, to which we used to take our students to show them the peach leaf curl disease. How did the leaf curl fungus (*Taphrina deformans*) appear year after year on the same lone tree with no other (infected) peach trees around? Did the pathogen live perennially within the host? *Pleiochaeta setosa* was another beautiful foliicolous fungus with appendaged conidia and was redescribed by Stan Hughes from its type collection on lupin leaves (Hughes, 1951). I once collected this fungus in the Ooty garden, again on the same host. Such host specificity is amazing, and much more so when one finds it across continents. The curious thing is that *P. setosa* colonized leaves of plants other than lupins too (*Crotalaria*, *Cytisus*, and *Ornithopus*), but all of them are legumes. The plant recognized the fungus, and the fungus recognized the plant, a real test of good taxonomy! In Australia, *P. setosa* has been found to cause not only leaf spots but a root rot on lupins. Thus this fungus had a dual personality!

Even a casual analysis of the occurrence of fungi on diferent substrates would immediately suggest either their indifference or their preference for specific substrates. There are many fungi that prefer palms, especially their leaf sheaths, often forming conspicuous, blackish, powdery colonies which cannot be missed. I like the palms not only for their majesty, but for their utility, and for their hospitality to beautiful fungi. *Arthrinium* species prefer the *Cyperaceae* to colonize, but once *Arthrinium* colonized bamboo, there was no room for other fungi, so it seemed to me. It is one of the most aggressive saprophytes that I know. Likewise, *Deightoniella torulosa* is almost always a colonist on banana leaves and leaf sheaths throughout the tropics. D. S. Meredith's (1962) study of fungi on living leaves and litter of the banana plant in the West Indies offered an eye-view of the richness and diversity of fungi in a typical tropical niche. I gained the impression that monocot plants for some reason were excellent substrates for certain kinds of fungi. If true, there must be a reason for this. I wonder if the reason is structural or chemical, or both.

III-3 The Beauty of Conidial Fungi

Developmental Morphology and Morphogenesis

The beauty of what fungi do is matched by the beauty of their form and the processes leading to attainment of form. The way fungi develop and reproduce, and the sequence of structural changes that characterize and contribute to fungal diversity always fascinated me and formed part of my endeavour to understand phylogenetic relationships among these organisms. Developmental morphology and morphogenesis naturally contributed to excitement.

It is in this context that I must refer to my visit to Britain in 1964 to participate in the International Botanical Congress at Edinburgh, where I had been invited to chair a session on Taxonomy of Fungi Imperfecti. Taxonomy is a continuing endeavour. For the Fungi imperfecti (conidial fungi), Mason had initiated the process which culminated in two epochal contributions from Stan Hughes in the *Canadian Journal of Botany*, one in 1953 and the other in 1958. Hughes had moved from the CMI to the Biosystematics Research Institute of the Department of Agriculture at Ottawa in 1952.

The first of Hughes' contributions was entitled 'Conidiophores, conidia, and classification' and described in detail conidium ontogeny in many hyphomycetous fungi, including type species of many classical genera originally described by the pioneers of mycology, and he outlined a tentative classification into eight sections representing distinct modes of conidiophore behaviour and conidium ontogeny (Hughes, 1953). The observations and line drawings depicting conidiogenesis, were made with the ordinary light microscope, a truly remarkable achievement. Extending the conidiogenesis theme of the French mycologists, J. Costantin (1888) and P. Vuillemin (1910a; b; 1911), and of Mason, Hughes gave a comprehensive and convincing picture of a conidiogenesis-based taxonomy as the answer to the unsatisfactory Saccardoan system, based mainly on conidium morphology, colour and septation, then in vogue.

Hughes recognized eight sections representing eight modes of conidium ontogeny and/or conidiophore behaviour. For

the first time, conidium origin through pores on a conidiophore or conidiogenous cell was recognized; the conidia produced in this way were called porospores. Production of a succession of conidia from a conidiophore following sympodial or percurrent proliferation was noted in many fungi, and so was considered a feature of taxonomic value. Repeated percurrent proliferations from a conidiogenous cell gave rise to characteristic annellations which in hyaline or subhyaline fungi would be recognizable only with some difficulty. A not so common feature, but a feature peculiar to some fungi, was what Hughes called the 'basauxic' nature of the conidiophore. In contrast to normal conidiophores that grew by apical growth, basauxic conidiophores elongated by growth at the base, and not at the apex. A very curious feature, indeed!

There were also conidiophores or conidiogenous cells that produced a basipetal succession of an infinite number of conidia at the apex (somewhat like the infinite number of cells that a 'meristem' would give rise to in plants); Hughes called these 'meristem spores'. An infinite number of spores could be produced from a single conidiogenous cell (or locus) in this way, a feature that was, in fact, quite common. Saccardoan divisions into sporodochial and coremial (synnematal) forms and into moniliaceous (hyaline) and dematiaceous (dark) categories were demolished. This was in conformity with Mason's arguments for treating all these forms and even the pycnidial forms (*Coelomycetes sensu* Grove, 1935) as a continuum.

Indeed, in a monographic study of the coelomycetous genus *Discosia* which I wrote jointly with one of my students (Subramanian and Reddy, 1974b), we found that when we brought the fungus into pure culture, it first produced conidia on independent, discrete conidiophores, thereby simulating a member of *Moniliaceae*. Later, in the same culture we noted an organization of the conidiophores to form a sporodochium, suggestive of a placement in *Tuberculariaceae*. With further incubation, the same culture produced synnemata so that it now could be placed in the *Stilbellaceae* (*Stilbaceae*). Thus, here we had a range in the organizational pattern of conidiophores that lent full support to Mason's argument of a continuum of forms. It is pertinent here to draw attention to Lodha and Reddy's (1971) genus *Hyphodiscosia,* which they proposed to accommodate a fungus collected on dead bark from Jaipur, Rajasthan, India. *Hyphodiscosia*, as the name was suggestive, approximated a depauperate *Discosia* in hyphomycetous guise.

Referring again to my correspondence with Mason on the identification of the coelomycete which we called *Plagionema indica*, in an effort to arrive at a correct identification of the fungus, Mason wrote to me specifically: "I expect that you are familiar with the fact that the same species can produce pycnidia on the dead host and acervuli with similar spores on the living host, e.g. *Heteropatella antirrhini* Wakef. & Buddin, and have been alert to ensure that your fungus does nothing of the sort." In *H. antirrhini*, we had an example of the dual forms a fungus took on the living leaf and the dead leaf as it occurred in nature of which what we observed in culture in the case of *Discosia* was a parallel.

I must mention here that many fungi produce more than one anamorph state, and for such an additional state, Hughes suggested the term, 'synanamorph.' Species of genera such as *Acremoniella* that produce solitary gangliar conidia apically on simple conidiophores also have phialoconidial states producing slimy conidia, though the phialoconidial state is seldom named. In the case of *Fusarium*, by definition, all species should produce sporodochial conidia, besides a microconidial state almost indistinguishable from *Acremonium*. Thus, there is an *Acremonium*-like state for *Fusarium*. In other fungi where the synanamorphs are distinctive, they are sometimes designated by separate names appropriate to them. Synanamorphs thus pose a problem in nomenclature. When a conidial fungus has synanamorphs with names attached to them, we then have to choose one of those names; but, how do we decide which one to choose? In many cases the name of the more common or first recognized synanamorph is used, but perhaps it should be the earliest published name.

Many taxonomic categories that we recognize are part of the practice of taxonomy. The kind of integration of the two major divisions, hyphomycetes and coelomycetes, advocated by Mason, is of great import, but requires a great deal of further study, especially of the latter group which has not kept pace with studies on hyphomycetes. On the other hand, doing away with all hierarchy and formal nomenclatural recognition of conidial fungi seems inadvisable for the present, especially when there is so much enthusiasm and interest in the establishment of anamorph-teleomorph connections which is going on fast on a global scale. Further, despite the continuing discovery of anamorph-teleomorph connections, we shall have to contend with innumerable anamorph names that will lack a teleomorph connection. And yet, our ideal and objective of "one fungus, one name' will continue and will be aided by molecular studies whose potential in understanding relationships between taxa is currently being explored vigorously. [Indeed, since I wrote this, the 'one fungus one name' has been accepted and integrated into the Code. See Hawksworth, 2011]

The second major contribution by Hughes (1958) was a superb summation of taxonomic revisions of classical hyphomycete taxa arrived at by him from a study of types extant in European and other collections, a great many described by the early pioneers in the field. This was a Herculean task fulfilled with enthusiasm, courage and conviction. While the 1953 paper stimulated an immense amount of work throughout the world on conidiogenesis, the second served as a new testament of generic concepts stregthened by the studies of classical types embodied therein. Indeed, these two contributions must be rated as two of the most significant in our science in the last century.

In the wake of the first of these contributions, Keisuke Tubaki (1958) adopted a modified version of the Hughesian System in his study of Japanese hyphomyctes on leaves and leaf litter. My own study of hyphomycetes from India and those known to me at the CMI led to yet another variation of the Hughesian System. While both Hughes and Tubaki had proposed divisions into sections or groups, I preferred the recognition

of families instead. My paper on the classification of hyphomycetes appeared in *Current Science* in1962, and an expanded version in the *Bulletin of the Botanical Survey of India* in the same year (Subramanian, 1962b;c).

The Edinburgh Symposium was a meeting of minds of differing perceptions but common objectives. The participants included Hughes, Ellis, Tubaki, Sutton, W. Bryce Kendrick, F. L. Howard, and myself. Discussion at the Symposium highlighted differences in opinion, but did not serve to iron out differences. We dispersed, so it seemed, a motley group with self-approved convictions. Chatting, immediately after the meeting, with me and G. W. Martin, Bryce Kendrick held out promise of a meeting to resolve the problems. For me, meeting Hughes and Ellis after fourteen years gave me immense pleasure. During these years we had kept in touch with each other and were fully aware of each other's work.

The Congress was presided over by Harry Godwin of Cambridge. At the Congress I met many old friends, and others for the first time. Those whom I met for the first time included S. Bartnicki-Garcia, E. C. Cantino, R. Emerson, T. W. Johnson, J. Kohlmeyer, G. W. Martin and F. K. Sparrow from the USA, Kendrick and A. G. Lochhead from Canada, M. A. Donk from the Netherlands, G. L. Hennebert from Belgium, G. Turian from Switzerland, A. Gaertner and A. M. Henssen from Germany, Tubaki from Japan, and E. B. Gareth Jones, C. J. Hickman, G. Morgan-Jones, John Rishbeth, Eva Sansome, and John Webster from Britain.

Both mycology and plant pathology were well represented. I was attracted by the majestic presence of M. A. Donk and his indisputable scholarship. He worked at the Rijksherbarium at Leiden. The Rijksherbarium was established by a Royal Decree in 1829 and completed 185 years of its existence in 2014. A National Museum of Natural History had been founded in Leiden earlier in 1820. (On a visit to Leiden two or three years later I had the opportunity to spend a whole day with Donk and hear from him more about tropical fungi and his work in the Indonesian tropics). Of special interest to me was Percy Brian's lecture on gibberellins (Brian, 1964). This was my first visit to Scotland and I was fascinated not only by the beauty of the city of Edinburgh, but by its history seen in the monuments to Robert Burns and Walter Scott.

IV A Mixed Bag

IV-1 Europe and Britain Again

On my way back from Britain in 1964, I visited The Netherlands, Switzerland, and both sectors of the then divided Germany. I stopped at Amsterdam to visit the CBS at Baarn where I met J. A. von Arx and several of his colleagues. Van Beverwijk, whom I had met in 1950, had succeeded Johanna Westerdijk, but van Beverwijk died in 1963 and was then succeeded by von Arx. Van Beverwijk had described several beautiful aero-aquatic fungi from the Netherlands, thereby drawing attention to a fascinating ecological group, previously virtually unknown. What was unique about these fungi was that the mycelium developed submerged in water, but the spores were always produced above the water surface. I met G. A. de Vries whose monograph on *Cladosporium* I had used with profit, and A. C. Stolk.

A highlight of my short visit to the Netherlands was my meeting with the Dutch mycologist, Karel Bernard Boedijn who had collected and described many fungi from Java and other parts of what is now Indonesia, working in Buitenzorg (Bogor). Boedijn was a collaborator of the geneticist Hugo de Vries, and later of the mycologist C. van Overeem. Boedijn had retired from Buitenzorg and now worked as a guest of the Rijksherbarium at Leiden; he was kind enough to have me visit him in his home in The Hague. Boedijn recounted to me his memorable experiences with fungi in the tropics. We talked about a new genus and species of hyphomycetous fungi, *Circinoconis paradoxa*, which he had collected in Java and Sumatra and described in 1938 in the 150th anniversary volume of the *Royal Botanical Garden, Calcutta* (Boedijn, 1942). The characteristic solitary conidia were circinate but conical in aspect, septate and brown. I had examined the type specimen of this beautiful fungus at the CMI, and had been on the hunt for it in India, but without success.

(Many years later, by sheer luck, this beauty of a fungus turned up in my collections from North-eastern Thailand, something that I treasured. Why are such fungi not so readily found, unlike many others that turn up on continents far apart? And, why are some genera, like *Circinoconis*, monotypic?) Apart from *Circinoconis* and his papers on *Curvularia* and *Podoconis*, Boedijn had published sporadically, but never extensively, on fungi in different groups which reflected his wide interests and competence in dealing with them. Jointly with J. Reitsma, in 1950 he had written a valuable paper on the hyphomycetous genus *Cylindrocladium* which is an important component of the tropical mycota. It was my good fortune that I could meet him, for later in the same year he passed away.

Early during our studies, we had collected on dead twigs from the Madras Christian College Campus in Tambaram, not far from Madras, a fungus which turned out to be a basidiomycete. The basidia in the fungus formed a linear basipetal series, each basidium with one to two oblique septa. We tracked the fungus to the genus *Sirobasidium,* described by Lagerheim and Patouillard in 1923. Boedijn (1934) had described a *Sirobasidium*, *S. magnum*, from Java in the *Bulletin of the Botanical Garden, Buitenzorg* and reference to his paper confirmed that our fungus was indeed a *Sirobasidium*, but one that differed from species that were known until then; K. Ramakrishnan and I described our fungus as a new species, *S. indicum*. This is the only species of the genus so far known from India..

Is it a rare fungus? Could it be that no one had looked for it? The fruit body was not more than 5 mm across and with its waxy-gelatinous nature typical of jelly fungi, and its reddish brown colour, I am certain, with some familiarity, one can find it if one looks for it. It is all a matter of seeing. Often, I have wondered why I did not care for this and related fungi more. I should have. These objects of neglect are part of nature, and ring beauty in their form, and yet we do not know what they do where they dwell! So far, only around fifteen species are known in this genus and they are mostly tropical. On the one hand, the underexplored tropics may hold a

plethora of novelties awaiting an observer. It might also be that they are on the road to extinction and extant forms are relicts of an ancient past.

My stay in the Netherlands was further enriched from a visit to Rijksherbarium in Leiden where I met Donk and van Brummelen and their colleagues. Apart from talking to van Brummelen, I spent the whole day with Donk lunching with him and learning about polypores, especially their taxonomy. He was master not only of European species, but those of the tropics as well, having collected and worked in Buitenzorg in Java. Though I had seen some of his publications, our meeting at the Edinburgh Congress and now in Leiden clearly showed his scholarship and scientific acumen as a taxonomist. His magnificent *Check-list of European Polypores* appeared posthumously in 1974. It is a landmark in the global advance of mycology.

From Amsterdam I now flew into Zurich. My sole purpose: to see Emil Mueller and learn about his work. Emil worked at the Technische Hochschule, and had made significant contributions to our science. The two volumes on amerosporen und didymosporen Ascomyzeten he jointly wrote with von Arx are, by themselves, monumental contributions. He not only described his work to me but showed me around part of beautiful Zurich. I also used the visit to acquaint myself with the work of H. Kern and his colleagues on the biochemistry of *Fusarium* wilts in plants at the Technische Hochschule, being the continuation of the work of Ernst Gaeumann…

From Zurich I flew to Berlin and, crossing Checkpoint Charlie, went to Aschersleben in East Germany to participate in an International Symposium on 'The Biochemistry of the Sick Plant' to which I had been invited and which was organized by H. Klinkowski. I presented some of the results of our work on the interaction between *Bipolaris sorokiniana* (*Helminthosporium sativum*) and root systems of wheat in relation to foot rot, reporting the findings of our group in Rajasthan in which several of my students (P. D. Tyagi, B. L. Jain, N. G. Nair, and H. C. Sharma) contributed. The symposium brought together plant pathologists, biochemists and mycologists with the focus on biochemistry and disease in plants.

The biochemistry of resistance to disease in plants was central to the main theme. Besides K. O. Mueller, whom I had met in Cambridge in 1950, and James G. Horsfall who had visited me in Rajasthan in 1962, there were several whom I met for the first time, notably, M. A. Stahmann and C. E. Yarwood from the USA, T. Hirai, I. Uritani, and H. Yamamoto from Japan, B. A. Rubin from the USSR, R. Heitefuss from Germany, G. L. Farkas from Hungary, and I. A. M. Cruickshank from Australia. Together, they formed a formidable world group working on the biochemistry of resistance to disease in plants. Mueller's 'phytoalexin' hypothesis of disease resistance in plants was discussed avidly. The debates at the symposium were a sign of the times and of the rise of biochemical plant pathology, but I was left with a feeling that biochemists working on plant disease could not perhaps think in terms of a plant as a whole; their focus seemed to be on just one or another of the enzymes or proteins or other molecules and their interaction. Focus is important, but not to the exclusion of a wider comprehension of the plant as a whole.

Apart from the Symposium, what I enjoyed most was a visit to Leipzig, to the laboratory of Kurt Mothes at Halle. In 1935 at the age of 35, Mothes was appointed Professor of Botany at Konigsberg from where he moved to Halle in 1950. His work is the basis for modern phytochemical research. Mothes explained his work on alkaloids, notably ergot alkaloids. Ergot conjured up in my mind the beauty and power of the fungus, the beauty in what it was, and the power in what it did. That is why it was good to talk to Mothes.

In India, the earliest to initiate cultivation of ergot on a commercial scale was K. M. Thomas, Government Mycologist at the Agricultural Research Institute at Coimbatore during the 1940s.Though pursued with vigour and purpose, cultivation of ergot on rye in the Nilgiris in southern India seemed commercially unviable at that time. However, artificial cultivation of ergot was initiated at the Regional Research Laboratory (RRL), Jammu-Tawi by L. D .Kapoor, D. Ganguly and co-workers, following which Akhtar Hussain, the founder Director of the Central Institute of Medicinal and Aromatic Plants (CIMAP), Lucknow intensified the work. With further work in the RRL by K. S. M. Sastry, large scale production of ergot was attained (Sastry *et al.*, 1985.)

Mothes had visited India and the UBL at Madras in 1957, the centenary year of my University, and it was a joy to see him again. Mothes trained many students of which at least twenty-four became Professors. What I realized when Mothes spoke to us was not merely the importance of ergot in medicine, but the remarkable way in which progress in alkaloid chemistry and organic chemistry had come from studies of ergot and many other fungi. In a flash, for me, ergot symbolized nature, science, mysticism, and philosophy, all in one. Tropical mycology was not mere mycology. There was something more and beyond, and exciting.

From Aschersleben I went to Berlin-Dahlem where I was to spend a week with Wolfgang Gerlach at the Biologische Bundesanstalt fur Land- und Forstwirtschaft, Institut fur Mikrobiologie to study fusaria. As mentioned already, Gerlach was part of the Wollenweber lineage. The Institute was founded in 1898, and housed Wollenweber's collection of *Fusarium* cultures,exsiccata, etc., which was the most authentic for the genus. The study of *Fusarium* was initiated here by Otto Appel in the beginning of the 20th century, and he was joined by Wollenweber (Appel and Wollenweber, 1910). For those wanting to study *Fusarium*, this was the place. The American W.C. Snyder had his training here with Wollenweber.

This was my first visit to the Institute and I had a wonderful time examining cultures of fusaria I had not seen before, besides discussion on some species such as *F. udum.* Gerlach showed me the methods used for the maintenance of cultures, and of photomicrography to bring out diagnostic microscopic features of the macro- and microconidia. We had a full discussion of all the sections and species not known to me

from cultures, and had no difficulty in agreeing on a modified Wollenweber-Reinking approach to *Fusarium* taxonomy. I met other scientists in the Institute, notably R. Schneider who was studying the genus *Pyrenochaeta* and H. Kroeber who was working on potato diseases. As a finale to this visit, I was taken to a magnificent performance of Beethoven's *Fidelio*.

A year later, in the summer of 1965, I visited the CMI a second time for two months. I met Mason this time, although he had retired and had been succeeded by Merton Ellis as Principal Mycologist. I saw a great deal of Ellis during this and many later visits and was struck by his methodical approach to the study of his beloved Dematiaceous hyphomycetes. While the Institute and the CAB were concerned with the time-consuming volume of material pouring into the Institute for identification from countries like India, Ellis always stood against special levies for identifications on member countries as he believed material from most countries in the tropics would bring in valuable novelties or new finds. What came in from these countries, so Ellis thought, were rich sources for building up the CMI herbarium and culture collection. He had very cordial relations with fellow mycologists from overseas. Bisby also had retired, and J. C. F. Hopkins was now the Director, to be soon succeeded by Geoffrey Ainsworth.

Everyone welcomed me just as I had been welcomed there 15 years earlier. The Institute now had additional space in a new building facing the old one on the eastern side of Ferry Lane, and additional staff and facilities. Among the new staff was Colin Booth who was now fully involved with *Fusarium*; he later wrote a book on *The Genus Fusarium* (1971), essentially reflecting the scheme suggested by Gordon. By now it was recognized that a few species of *Fusarium* produced dry blastoconidia, besides the phialidic norm that was considered typical, a fact given recognition by Booth in his book. (Ian Pascoe from Australia, who later worked with Colin on *Fusarium*, and whom I had met at the CMI, eventually proposed the term 'mesoconidia' for such blastic conidia. See Pascoe, 1990a; b).

There was Kris A. Pirozynski, another newcomer to the Institute. Our friendship grew over the years. Kris was a great friend to talk to, and great company during collecting trips. He had an eye for fungi and a fine hand to write and draw. Two other newcomers were E. Punithalingam (Puni) and A. Sivanesan (Siv), both from Sri Lanka and now long-time friends. J. E. M. Mordue was in charge of the smuts and the rusts, besides *Colletotrichum*. She had her training with Lilian Hawker in Bristol before she joined the CMI. F. C. Deighton (with his pipe always on hand!) devoted his time to sorting out the foliicolous *Cercospora* complex, a difficult group. The tropics are full of them. Crous, Kang and Braun (2001) provided an overview of the diversity of known mitosporic taxa which should help in the resolution of problems of their taxonomy and phylogeny. Phyllis M Stockdale studied dermatophytes and related fungal pathogens, besides her involvment in the editing of the *Review of Medical and Veterinary Mycology*. A. H. S. Onions was in charge of the Culture Collection since she left George Smith who had collaborated with him at the London School of Hygiene and Tropical Medicine. Grace M. Waterhouse came to the Institute two or three days a week, continuing her work on *Pythium* and *Phytophthora*. Her expertise on these genera was much sought after.

A Polish mycologist, Bronislaw Zyska was also at the CMI as a visiting scientist studying fungi causing damage to paintings and other art works. It was during this stay at the CMI that the *Basidiella* puzzle, to which I have already referred, was solved. I also tried to resolve many other unresolved taxonomic problems and puzzles, besides updating my knowledge, from a study of type and other material, of the numerous new hyphomycetous taxa that had been described during the period. As before, I made drawings and notes of the fungi I saw.

During the visit, Mason drove up to the CMI to invite me to supper with him. He had invited, among others, Elsie Wakefield, John Ramsbottom with his daughter Mary, and Peter K. C. Austwick. It was a quiet but wonderful evening, a very memorable meeting where Mason tried to hear of my 'doings' on *Hyphomycetes* since I first learnt about them from him fifteen years earlier.

IV-2 Plant Pathology: An Interlude

I must digress here to speak of the period 1958-1964 that turned out to be a significant interlude in my pursuit of tropical mycology. My stay at the UBL during 1951-58, first as Senior Lecturer and then as Reader was a period not only of teaching and research in mycology and plant pathology but one of assisting my mentor in supervising research in plant pathology. I gained experience in planning, guiding and executing research, besides imbibing qualities for leadership. I was now familiar with plant diseases of various crops and specially the plant disease systems such as cotton and pigeon pea wilt, *Pyricularia* blast of rice, *Rhizoctonia* root rot of cotton, and koleroga of coffee that were being studied intensively at the UBL. I enjoyed doing my work immensely.

IV-2-i The IARI Experience

It was with reluctance that I moved to Delhi in 1958 to occupy the first ever Chair in Plant Pathology in the country, leaving the UBL where I had enjoyed doing the work I had been doing on conidial fungi. My new assignment called for attention primarily to plant pathology as part of the broad spectrum of Indian agriculture. It was a challenging assignment. I took pride in the fact that I was now in the Division of Mycology, originally the creation of E. J. Butler, at the Indian Agricultural Research Institute (IARI), then at Pusa in Bihar. At one time Balachandra Bhavanishankar Mundkur worked and lectured to the students here. Mundkur's careful and thorough studies of types of Indian smuts paved the way for a monograph of the *Ustilaginales* of India (Mundkur and Thirumalachar, 1952). Mundkur had, in addition, contributed enormously to the mapping of the rust fungi (*Uredinales*) of India. He founded the Indian Phytopathological Society in 1946 and his *Fungi and plant disease* appeared in 1949.

The IARI was thus a seat of traditional mycology as much as plant pathology in India. Among others, Philip Gregory and Denis Garrett from Britain wrote congratulating me on my

new assignment and wishing me well. There was reason to believe that I had been chosen for the post primarily from an expectation that fungal taxonomy in the Institute could be strengthened. However, my efforts to strengthen taxonomy and pathology did not materialise. I had proposed that I might take up the taxonomy of '*Helminthosporium*' and the diseases the species of this genus caused in cereal crops for detailed study, as such a study seemed to have topical relevance in Indian agriculture. The 1943 Bengal famine had been ascribed to the blight of rice caused by *H. oryzae* (Padmanabhan, 1973; Padmanabhan *et al.*, 1948). The most authoritative monograph on graminicolous *Helminthosporium* species was that by Charles Drechsler published in 1923, and, although it would have been difficult to replace it in essentials, there was a need to update information, terminology, and nomenclature. There was only half-hearted support for my proposal.

On the other hand, the Director of the Institute, and the Rockefeller Foundation which sponsored the Post- Graduate School, wanted me to be Chairman of the Committee to formulate Regulations and Curricula for the Institute as a whole. Here was a great experiment in agricultural education and research, of developing programmes and curricula on the pattern of what obtains in American colleges and universities. Though I first declined the onerous responsibility, I was finally persuaded to accept it and the Rockefeller Foundation nominated two distinguished Professors from the University of Minnesota, E. C. Stakman, and W. M. Myers, to help me on the Committee.

I had met Stakman at the Stockholm Botanical Congress in 1950. Apart from the Committee's deliberations, my association with Stakman sharpened my taste for plant pathology; Stakman was not merely a great plant pathologist, but a great teacher and gifted speaker who could keep audiences spellbound. As mentioned earlier, he was a pioneer who guided much research on *Fusarium* as a plant pathogen (see Kommedahl *et al.*, 1970), besides *Helminthosporium*, and the epidemiology of wheat rust in the U. S. A. (Stakman and Levine, 1922; Stakman, *et al.* 1930). Fighting hunger, and fighting plant disease, were a passion with him. I enjoyed working with Stakman, and with Myers, and greatly benefited from my association and discussions with them. Stakman fondly inscribed a copy of his *Principles of Plant Pathology*, written jointly with J.G. Harrar, for me.

Besides Committee work, I had my share of teaching courses in Mycology and Plant Pathology, now on the pattern of Universities in the U. S. A. I fully enjoyed the new experience which broadened my outlook as a mycologist and teacher. Here I had the unique opportunity to impart training and knowledge to young and enthusiastic students drawn from the entire country. While at the Institute, I attended the Annual Meeting of the Indian Science Congress in Bombay where I was elected to the Fellowship of the National Institute of Sciences of India and where I met Prankrushna Parija, President of the Congress Session and H Santapau. Year 2005 marked the centenary of the founding of the Institute.

I tried to use my stay at the Institute in the best way possible, and gathered and arranged in broad outline the materials for a monograph of Indian hyphomycetes. The Institute was rich in its collection of classical treatises and monographs on fungi that were essential for that purpose. Nowhere else in India could I have found such a treasure of information and valuable historical data. They were largely Butler's legacy to the Institute. To my advantage, I was assigned the duties of Officer in charge of the Institute Library which made it easy for me to delve into the Library's most prized-possessions and use them in the writing of my monograph. Luck played a part in all this. The Institute with its many Divisions had on its faculty some of the best minds in disciplines ranging from cytogenetics and plant breeding, to soil science and microbiology, entomology and nematology, and agronomy. Interaction with these minds contributed to broadening my approach to problems of tropical agriculture. However, I found too much of Committee work forbidding, leaving not much time for research.

IV-2-ii The Rajasthan Experience

In 1960 when I was at the IARI, an invitation came to me from Mohan Sinha Mehta, Vice-Chancellor, University of Rajasthan to organize its new Department of Botany in Jodhpur and head it. Mehta was a dynamic person looking for men with leadership qualities from all over India to head the University's new science departments. He was a diplomat and had been India's ambassador to the Hague. Some of my peers thought that here was an opportunity for me to organize a new Department and to establish an active school in plant sciences and in my own special field. Accordingly, I felt inclined to accept the assignment, though there was much reluctance on the part of the Director of the Institute, the distinguished plant geneticist, Benjamin Peary Pal, to permit me to leave. There were also colleagues and friends in the Institute who did not want me to leave, but I had my reasons…

The new Department to be organized would undertake teaching and research in plant sciences at the post-graduate level with a number of specializations for which there would be specialists on the faculty. The Botany and the Zoology Departments functioned at Jodhpur. My counterpart in the Zoology Department, L.S. Ramaswamy, was appointed and joined at the same time as myself. He was some years senior to me and was an endocrinologist of repute. We teamed up very well in the University. As for Botany, the faculty grew in size gradually and we had competent colleagues: B.D. Tyagi, H.S. Narayana, G.S. Nathwat, Dalbir Singh, Pushpa Khanna, Shiv Sharma, Sudhakar Misra, Uma Kant Sharma and P. D. Sharma. In the area of Mycology and Plant Pathology, my students included B.C. Lodha, B.L. Jain, C.G. Prakasha Rao, N.G. Nair, P.D. Tyagi, H.C. Sharma and A.K. Garg.

Besides organizing the new Department with the necessary infrastructure, I continued my work on conidial fungi, and took up studies on *Helminthosporium* and also coprophilous fungi in which several of my research students were involved. One of my students (B. L. Jain) studied the graminicolous 'Helminthosporia,' in continuation of the work of my first student (R. N. Prasad from Bihar) at the IARI. The genus *Helminthosporium* (originally spelt '*Helmisporium*') had been misunderstood for many years until Stan Hughes noted that the type species, *H. velutinum* was a saprophytic,

lignicolous fungus in which the conidia were borne apically and laterally on an erect, simple, dark, determinate conidiophore. The conidia were produced through pores at the tip and on the sides of the conidiophore. The mature conidium virtually sat and pressed on the conidiophore. In a picture of a pore taken with a scanning electron microscope, is a vivid image of the pore and the impression the sitting conidium left around the pore, following its dispersal.

In graminicolous species which are facultative parasites on grasses, on the other hand, the solitary conidia were produced at the apex and at the apices of successive sympodial proliferations of the conidiophore. Further, though conidiogenesis was through a pore in both cases, conidia in *Helminthosporium* were euseptate, but distoseptate in graminicolous 'Helminthosporia.' When all this was understood, it seemed prudent to accept the segregate genus *Drechslera* established by the Japanese plant pathologist Seiya Ito for all 'graminicolous Helminthosporia' in place of *Helminthosporium*. We had considered the desirability of establishment of two or three additional genera, besides *Bipolaris* which had been proposed by R. A. Shoemaker (1959), to take in this somewhat heterogeneous assemblage, but finally we decided against it. Our conclusions appeared in *Current Science* (Subramanian and Jain, 1966) and, though they were immediately accepted by Ellis at the CMI, our 'lumping' these fungi in a single genus evoked a mixed reaction.

We had, nevertheless, the satisfaction that our conclusions generated discussion and led to reappraisal of the taxonomy of these fungi which have great relevance in tropical plant pathology. Taxonomy evolves through 'lumpers' and 'splitters.' For species with conidia, each with a protruding hilum, a new genus, *Exserohilum* , was proposed by Leonard and Snuggs (1974). Shoemaker (1998) placed the few-septate, small-spored species in a new genus, *Marielliotia*. As (Sir) James Jeans (1930) observed, science advanced by approximations to the truth.

One of my students, V. Ramesh Bhat, continued the work on graminicolous 'Helminthosporia' at Madras. He studied a large number of isolates of the rice pathogen, *Drechslera oryzae* (syn. *Helminthosporium oryzae*) from different sources and geographical locations. On the basis of a study of several morphological parameters, the isolates could be classified into three groups: namely, one with fusiform conidia, a second with obclavate conidia, and a third with clavate conidia (Subramanian and V. Ramesh Bhat, 1978).

Further in-depth study of the host-pathogen interactions between host cultivars and the three groups would throw more light on the differences, if any, in the reaction of the host to the fungus, and the nature of the leaf spots induced by the three groups. We believed, from studies of past workers and of our own, that the rice pathogen existed as three subspecies equivalent to these three groups. Selection of host cultivars in south-east Asia, where rice is a major crop, had apparently led to the evolution of these groups. The evolution of subspecies and of races of various pathogens provides an example of cospeciation steered by domestication of plants and of agriculture.

Organization of the new Department in Jodhpur and relocation in Jaipur occupied a good deal of my time. But we did collect in my new location and we described some interesting fungi and a few new genera such as *Phragmospathula*, *Panchanania*, *Angulimaya* and *Neottiosporina*.

During my tenure in Rajasthan, I completed the manuscript of the monograph on *Hyphomycetes*, publication of which was sponsored by the Indian Council of Agricultural Research, New Delhi. Apart from this, one of the most memorable episodes of the Rajasthan interlude was the visit of John N. Couch of the University of North Carolina to the Department in Jodhpur in 1961. He came on a visit to India at the invitation of the University Grants Commission to assess the work of Botany Departments in universities in the country. During his visit to my Department in Jodhpur, I had the opportunity of accompanying him on trips to collect soil samples from which he wanted to isolate *Actinoplanes* and allied organisms from tropical soils for study. Couch was one of the most distinguished mycologists of the 20th century. His work on various aquatic 'phycomycetes,' and *Actinoplanes*, his monograph on *Septobasdium* (1938), and on *Coelomomyces* (jointly with Bland, 1985), are a few of his great contributions. While in India, Couch found time to read through the Introductory Chapter of my monograph in manuscript form, and the response he left behind served as a source of strength for me.

The Department moved to Jaipur, the capital of Rajasthan, when the University of Jodhpur was established in Jodhpur in 1962. Fortunately, there was support from my University and funding agencies around to equip the new laboratories and organize and develop a good library. We had several distinguished visitors, notably plant morphologist, Adriance S. Foster (Berkeley, USA), microbiologists, W. D. Gray (Ohio, USA) and Academician N. A. Krassilnikov from the USSR, and plant pathologists, James G. Horsfall (Connecticut, USA) and Mary D. Glynne (Harpenden, U.K). All of them delivered lectures on topics of their speciality which was attended and appreciated by our faculty and students.

Though I did not continue in Rajasthan for long, and returned to the UBL at Madras to occupy a newly created Chair in Mycology, I had the satisfaction of having organized the Department at Jaipur which now had several young and active mycologists and plant pathologists, among several other disciplines in the plant sciences.

V The Fruits of Orchestration

I returned to the UBL in late December 1964 for a second innings, soon after my second visit to Britain. Along with a team of very dedicated and enthusiastic students and colleagues, we now focused attention on fungal exploration, description and taxonomy, studies on the taxonomy and biology of ecological groups of fungi, and developmental studies of conidial fungi and their sexual states with particular reference to their taxonomy. My first innings entirely depended on my own efforts as an opener, and now appeared to be a preparation for my second innings which was a team

effort and not a solo performance. What sustained me throughout was the excitement of discovering novelties, a sense of wonder in studying the remarkable process of conidiogenesis in diverse fungi, studying the marvel of development of the ascoma in teleomorphs of conidial fungi that were supposedly closely related, and a fascination in investigating the succession of fungi on living, senescing, dying or dead leaves or other substrates. Within the canvas of this account, I can only briefly touch on a few of these areas.

Following my 1964 visit to Britain and the aftermath of the Aschersleben Symposium, Professor Hirai arranged a visit to a few phytopathological centres in Japan sponsored by the Japanese Society for the Promotion of Science in August 1969. Starting in Tokyo, I visited the University in Tokyo and the National Musuem at Ueno Park in Tokyo. Junta Sugiyama showed me round the Instutute of Microbiology even though the visit was vitiated by a general students' unrest and strike. I did gather a general picture of the mycological work being pursued by Sugiyama and his associates. Sugiyama introduced me to Asahina and Shibata, well known for their work in lichen chemistry and about which I have already referred in this narration.

At Ueno Park, where Sugiyama had arranged a meeting with members of the Mycological Society of Japan, I met Yosio Kobayasi, the President of the Society and several members that included Hirohara Indoh, Hiroshi Kurata, Shin-ichi Udagawa, and Junta Sugiyama. Indoh briefed me on his work on aquatic phycomycetes of which he had described several genera and species from Japan. Yosio Kobayasi explained to me his work on freshwater phycomycetes, besides entomogenous fungi. That he had wide ranging interests was obvious to me. Udagawa is an authority on microfungi of Japan of which he had described many new and interesting species and genera. Sugiyama worked with S. J. Hughes in Canada and his interests are in microbiology. Kurata is an expert on mycotoxins.

At Kyoto I was accommodated by the Takeda Foundation and I found the medicinal plant garden of great interest. In the Kyoto University, plant pathologist S. Akai received me and showed me round the laboratory and introduced me to his colleague S. Ouchi. Of special interest was the ongoing work on host-parasite interactions and diseases of a number of crops. We discussed fusarioses in particular. It was a fruitful visit and a most friendly experience. From Kyoto we moved to Osaka for a visit to the Instittute for Fermentation and Culture Collection where we were received by T. Hasegawa and K.Tubaki. They showed us round the work and facilities. Since our first meeting in Edinburgh, this was the first time we were meeting: Tubaki explained his recent work on fungal taxonomy especially of the hyphos. It was a most enjoyable meeting. The final stop was in Nagoya and the Nagoya University which represented the strong group on the biochemistry of plant disease. Here we were received by T. Hirai, joined by I. Uritani who showed their recent work on disease resistance, phytoalexins and host-pathogen interactions. Fungal, bacterial and viral disease systems were being investigated.

V-1 Fungal Diversity of the Silent Valley and the Western Ghats

Exploration of fungal diversity was extended to regions not yet explored such as the Western Ghats, especially the Silent Valley. There was also exploration with the focus on specific fungal groups, primarily the *Ascomycota* and, of course, *Hyphomycetes* and *Coelomycetes*. Studies on the ecology of soil, litter, and coprophilous fungi, and fungi in marine and mangrove ecosystems, and in freshwater, further contributed to knowledge of fungal diversity. The contribution of my students in adding to this corpus of data is significant.

The exploration of the Silent Valley in the Western Ghats threw up several novelties at the level of the genus and species. Thus, in the *Hyphomycetes*, in all, 255 species belonging to 152 genera were recorded. Of these, 142 species (accounting for 55.4%) belonging to 95 genera (accounting for 62.5% of the total) were recorded from the Silent Valley. Of the 255 species in 152 genera, 43 species (16.7% of the total) and of the 152 genera, 13 (8.4%) appeared to be new. Of the new taxa, 22 species (51.1%) and 7 genera (53.8%) were from the Silent Valley. In the other groups that we paid special attention to, namely, the *Coronophorales*, the *Diatrypaceae* and the *Diaporthaceae* in the *Ascomycota*, many novelties were found and were identified and described. And yet, we knew we had only scratched the surface. There was so much more to explore. It was thus imperative that the forest with its rich flora, fauna and mycota be protected and conserved as a national bioreserve.

At the time, Silent Valley and its conservation was a political issue not easily resolved. All the same, in view of its importance, I made bold to address the then Prime Minister of India (Indira Gandhi) on the urgent need to protect and conserve the Silent Valley; I sent her my data on its fungal diversity and an appeal to her to focus her attention on this issue. She responded quickly, positively and favourably by appointing a Committee to make recommendations; as a result, the area was declared a national bioreserve by the Government of India in 1980. When there was darkness all round, the light that trickled in brought hope. Unfortunately, enforcing protection and conservation is never easy. Continued vigilance is needed. Conservation of our resources must become part of our mental attitude.

That we could collect a great deal of material belonging to the *Coronophorales* (*Ascomycota*) from the Western Ghats was a matter of joy for me and to my student G. Sekar. Sekar had an eye for these beautiful fungi, and spent several weeks at the CMI studying them with help from Sivanesan. Our luck in finding them led to the publication of a monograph of the *Coronophorales*, and a statement of the status of their taxonomy which continued to elicit debate. On the road to doing this monograph we drew inspiration and courage from the work of pioneers like von Hoehnel, H. M. Fitzpatrick, J. A. Nannfeldt, and E. S. Luttrell. (In 1944 when I passed the Honours examination with distinction and I was given the choice of a Prize book, I chose *The Lower Fungi* by Fitzpatrick (1930). To me it was a model textbook, and I often wondered why he did not write a companion to The Higher Fungi!)

Nannfeldt (1932) placed the *Coronophorales* in the *Ascohymeniles* in which he recognized two Families, the *Nitschkiaceae* and the *Coronophoraceae*. From study of *Coronophora angustata*, Petrak (1921) had noted that the asci in *C. angustata* were produced in a locule in a stroma, an important observation. J. H. Miller (1949) placed the Coronophoralean fungi in a single Family (*Nitschkiaceae*) in the *Pseudosphaeriales* alongside the *Pleosporaceae*. And yet, Nannfeldt (1975a;b) in later work, stuck to his original stance and placed these fungi in the *Ascohymeniales*. From our studies (Subramanian and Sekar, 1990), and that of Luc (1952) on *Bertia moriformis*, and of Parguey-Leduc (1967), the asci in these fungi were seen to be produced in locules in a stroma.

The *Coronophorales* are ascostromatic, but unitunicate, a strange combination of features, from the Nannfeldt-Luttrell perspective. Reynolds (1989) reviewed and discussed the bitunicate ascus paradigm in detail. With our disenchantment with the Nannfeldt-Luttrell concepts, the combination of features in the *Coronophorales* seemed no longer strange. Two families were recognized, *Coronophoraceae* for genera with ascostromata that were cupulate, and *Bertiaceae* for genera with ascostromata that were non-cupulate. The "Quellkorper", a peculiar structure hanging from the apex of the ascomal cavity, first noticed by von Hoehnel, occurs in some species in the *Coronophoraceae* as circumscribed here. Thus, two groups, one with "Quellkoerper" and the other without "Quellkoerper" are recognized within this Family.

Eight genera (*Biciliosporina, Cryptosphaerella, Janannfeldtia, Euacanthe, Neotrotteria, Scortechinia, Biciliospora* and *Fracchiaea*) belong in the group with "Quellkoerper" and four genera (*Acanthinischkea, Nischkia, Gaillardiella* and *Schizocapnodium*) in the group without "Quellkoerper." Two genera, *Bertia* and *Spinulosphaeria* belong in the *Bertiaceae*. Twenty-three species belonging to 12 genera were described from the Western Ghats by us, of which two genera and ten species turned out to be new.The two new genera, *Biciliosporina* and *Janannfeldia* both have ascospores, each with a simple appendage at either end, the asci being 8-spored in the former and multispored in the latter. From our study of material from various collections worldwide, a few species such as *Fracchiaea broomeiana* appeared to have a wide distribution not only in India but throughout the tropics.

In a study of the molecular systematics of the *Sordariales*, Huhndorf *et al*. (2004a) placed the *Nitschkiaceae* in the *Coronophorales*. Elucidation of molecular systematics of the *Coronophorales* by Huhndorf *et al.* (2004b) lent support to recognition of two families, *Nitschkiaceae* (syn.*Coronophoraceae*) and *Bertiaceae* in the Order. The *Coronophorales* are held to be monophyletic. Huhndorf *et al*. concurred with Subramanian and Sekar's placement of *Thaxteria* and *Spinulosphaeria* in the *Coronophorales*. They described two additional Families, namely, *Chaetosphaerellaceae* and *Scortechiniaceae* to take in the clades embracing *Chaetosphaerella* and *Crassochaeta*, and the taxa having a quellkoerper (*Euacanthe, Neofracchiaea* and *Scortechiniia*), respectively. Zhang *et al*. (2006) reconfirmed the placement of *Coronophorales* in the *Sordariomycetes*.

The case of the tropical and subtropical genus *Xylobotryum* is somewhat similar and its taxonomic placement in the ascomycetes has been under speculation.Yu-Ming Ju and J. D. Rogers (1994) studied development in *Xylobotryum andinum*. They noted that the ascoma is stromatic and the asci are functionally bitunicate. The ascal base that simulates the legs of a pair of trousers and the absence of a coiled ascogonium also suggest a loculoascomycete connection. However, the occurrence of true paraphyses was an ascohymenial feature. There is the possibility of finding functionally bitunicate asci in other taxa and new knowledge on this would pave the way to settle the taxonomy of these fungi. Confirmation might emerge from molecular studies.

V-2 The Whole Fungus

V-2-i The Phialide Beautiful but Enigmatic

Conidiogenesis was then central to any scheme of classifying conidial fungi, but there were disputes and discussions of concepts, terminology and usage which had to be resolved. Bryce Kendrick kept his promise made at Edinburgh and organized a meeting of the specialists in the area worldwide at Kananaskis in the Canadian Rockies in the autumn of 1969, close on the heels of the International Botanical Congress at Seattle. Bryce had briefed us about the meeting well in advance, and had assigned various topics for the participants to speak on. I had been asked if I could speak on "The Phialide," and had agreed. I thought I knew the phialide and phialidic fungi. When I began organizing my thoughts and ideas on the phialide, however, it became clear that I knew very little, and it was not an easy topic to deal with. And yet, here was a good opportunity to discuss the phialide with supporting data from published records and from observations based on original study. And that was what I tried to do.

Though the term 'phialide' was originally intended to convey the aspect of a conidiogenous cell shaped like the Greek 'phial,' with deeper understanding of conidiogenesis and the characteristics of conidia that were produced from it, our concept of the phialide took a new meaning. One of my students (M. Pushkaran) investigated several phialidic fungi in slide culture and elucidated conidium ontogeny under the ordinary light microscope. (One might disapprove of this method as unnatural and I would not try to defend the procedure, except to say that there was no alternative method. When a fungus grew in pure culture, as Mason used to say, it was not what it was, but what it was not. This may sound paradoxical, but I must stress that if you want to know what a fungus is, you must see it in its natural habitat.) Type or authentic cultures of many taxa were studied. Authenticity is of prime importance not only in taxonomy but in the application of names, and the evolution of taxonomy.

Many phialidic taxa (ex CMI) were examined by me during an extended visit to Britain as a Visiting Professor at the University of Bristol in 1968. Lilian E. Hawker of the Botany Department at Bristol had been a great friend since we met in Stockholm at the Botanical Congress in 1950. During this

visit I tried to get some insights into conidiogenesis using their scanning electron microscope, which was then a great novelty, and I did get some fairly decent pictures though certainly not of the highest quality. Richard Campbell (1968) had done an excellent transmission electron microscope study of conidiogenesis in *Alternaria* and he and Alan Beckett were very helpful to me in studies with the scanning electron microscope.

The Kananaskis meeting brought together Hughes, Ellis, Tubaki, Pirozynski, Hennebert, Roger D. Goos, Emil Mueller, J. W. Carmichael, M. Nicot, J. Leland Crane, G. C. Carroll, W. Bridge Cooke, F. Pollack, Gary T. Cole, G. C. Hughes, Nag Raj, Kendrick and myself in an effort to dissolve differences. Here was a fraternity holding diverse views, but there was a genuine effort to redefine concepts of conidiogenesis and a reconsideration of terminology in defence of unambiguity. Gary Cole introduced us to time-lapse photomicrography which he used to great advantage to elucidate conidiogenesis.

Listening to and seeing Gary's presentation, I recalled to myself how the great M. O. P. Iyengar, in his passion for the algae, used to sit through the night waiting to view under the microscope the liberation of zoospores or motile gametes and their fusion or otherwise; Iyengar would then and there fix the various stages on microscope slides and even make camera lucida drawings of his material! In those days there was no other way to study live organisms and their development and reproduction. Now technology did all that for us.

The use of transmission electron microscopy in the elucidation of conidiogenesis had only just begun. Therefore, the discussions centred on data from studies using the ordinary light microscope. The use of adjectives to distinguish modes of conidiogenesis seemed a step forward and we agreed on some adjectives as our choice. These included: arthric, blastic, tretic (poric), and phialidic, besides holoblastic and enteroblastic. Hughes had recognized arthrospores, chlamydospores (aleuriospores), blastospores, porospores, and phialospores, besides a number of other categories such as meristem arthrospores. The terms holoblastic and enteroblastic that were accepted at Kananaskis, were in part products of a better appreciation of cell wall participation in conidiogenesis, understanding of which was catalyzed by studies of conidiogenesis using transmission electron microscopy. Fluorescent antibody staining had also been harnessed in the study of conidiogenesis (Goos and Summers, 1964). The conference proceedings were edited by Kendrick and appeared in print with the discussions recorded in full in 1971. The meeting paved the way for a second more conclusive meeting at a future date.

En route to Calgary from the Seattle Botanical Congress, well attended by many mycologists, I had visited beautiful Vancouver and talked to and seen the work of R. J. Bandoni, and G. C. Hughes. Bandoni carved out a niche for himself by his dedicated studies of tremellaceous and related fungi. 'Gill' Hughes had contributed significantly to our understanding of marine mycology, especially ecology and geographical distribution. Following Kananaskis, I visited Ottawa and the strong mycological group at the Biosystematics Research Institute: J. Walton Groves, D. B. O. Savile, S. J. Hughes, R. A. Shoemaker, D. J. S. Barr, Kris A. Pirozynski, Luella Weresub, C. Madhosingh, and one of my students at the IARI, Yogesh Paliwal. There was so much to discuss and learn from them. I visited Bryce Kendrick's laboratory, and then Toronto to meet Roy F. Cain and his colleagues at the University there. Then on to Montreal to see W. E. Sackston and his work on *Verticillium* and *Verticillium* wilts; I had met Sackston at the Commonwealth Plant Pathology Conference in London in 1968. Later, Sackston participated in the symposium on pathological wilting in plants at the UBL in Madras in 1971.

A second meeting was organized in the same venue at Kananaskis by Bryce Kendrick in the autumn of 1977, in the wake of the second International Mycological Congress at Tampa, Florida. The theme was 'The Whole Fungus' and discussion now was not limited to conidial fungi but was extended to their sexual states with a view to arriving at correlations between the two. This was an old theme ushered into our science by the French brothers Tulasne in their *Selecta Fungorum Carpologia* (1861-1865). Indeed, the French had always been in the forefront of the pursuit of mycology, and the theme of the Tulasne brothers had been kept alive all along. But now, with so much data on developmental morphology of a diversity of fungi and with improved techniques of study, the accumulated knowledge needed consolidation.

Once again Bryce Kendrick asked me to update information on the phialide and attempt a correlation between phialidic fungi and their sexual states. In keeping with the theme of the meeting, we now had with us specialists on *Ascomycota* and *Basidiomycota*, besides other groups. Thus, we had the benefit of the views of von Arx, Emil Mueller, E. S. Luttrell, Mrs von Arx, John Webster, David Malloch, Mike F. Madelin, Luella Weresub, Roy Watling and Richard K. Benjamin, besides several who had participated in Kananaskis I.

Along with my students, I had been studying conidiogenesis in several taxa with phialides, basically of two kinds those that produced a basipetal succession of discrete, slimy conidia that adhered in heads at the tip of the phialide or formed loose (unconnected) chains (e.g. *Acremonium, Gliocladium, Gliomastix*, *Stachybotrys,* and *Trichoderma*), and those that produced a basipetal succession of dry conidia that formed true or persistent (connected) chains (e.g. *Aspergillus*, *Memnoniella*, *Paecilomyces, Penicillium,* and *Sagrahamala*). A further subdivision of the first group into hyaline (moniliaceous) and dark-coloured (dematiaceous) forms had also been recognized.

We also took up for detailed developmental study sexual states of representative species of these two groups of phialidic fungi with the aim of arriving at possible correlations in an effort to identifying features of predictive value in both the states. The concept of dry and slimy conidia is an old one, and its biological significance is immense. As Mason used to stress, conidia are intended for dispersal and propagation, not for the pleasure or luxury of observation! The conidia of *Penicillium* are dry and so are easily air-borne and disseminated by wind; indeed, the conidial wall is

impregnated with hydrophobic materials. Most conidia in airspora are naturally of the dry category.

One of the earliest studies on the air spora in India was carried out by D. D. Cunningham, commissioned into the Indian Medical Service in 1867, and stationed in Calcutta from 1869. The results of his work were published by the Government of India in the form of a book, *Microscopic examination of air,* in 1873, which incorporated a great deal of original data along with many Plates illustrating fungal and other spores from the air. Many diverse dry spores from air catches were illustrated by Cunningham. (On one of my several trips to P. H. Gregory, he made me a gift of Cunningham's priceless book of which I had not seen a copy.)

Importantly, the dry nature of the spore in *Penicillium* mattered in the discovery of penicillin. That discovery was quite clearly incidental to a dry conidium of a *Penicillium* fortuitously settling on a Petri plate in Fleming's laboratory in the hospital at Paddington in London and growing on the plate as a contaminant (Fleming, 1929). If ever a dry spore hit the headlines, it was that. Slimy conidia are not so abundant in the air spora, though, when the slime dried up, they would also be air-borne. However, slimy spores are usually dispersed by insects or by water. Mason (1937) had stressed the importance of this biological distinction in his Annotated Papers, and Wakefield and Bisby (1941) had applied this distinction in listing the 'British *Hyphomycetes*'. From considerations such as these, I drew a line between these two categories of phialide in an effort to ascertain their value in predicting their teleomorphs.

I must draw attention to a further distinction between these two modes of conidiogenesis typified by *Trichoderma* on the one hand, and *Penicillium* on the other. Transmission electron micrographs of conidiogenesis (which appeared after the Symposium meeting and were later incorporated in my paper) suggested that the basipetal, persistent chains of conidia in *Penicillium* were a product of synechidic ('mersitem') behaviour of the phialide. On the other hand, the *Trichoderma* phialide was in truth an annellide in which annellations were concealed within the collarette of the phialide, the annellations collectively forming something like a lamella. In other words, the conidia were not products of synechidic behaviour of the conidiogenous cell, but resulted from repeated percurrent proliferations as in an annelide. There was no doubt now that structurally and ontogenetically these two types of phialide were not the same. There could be many variations of the theme.

Two other kinds of phialides were also recognized. These were: the *Thielaviopsis* type in which the conidia were cleaved out from the cytoplasm and were then endowed with a wall, the conidia being formed in basipetal succession (Delvecchio, *et al.*, 1969); and the *Chloridium* type in which conidia were delimited sympodially (not percurrently as in *Trichoderma*) within the collarette. Terrence Hammil's (1972; 1974) transmission electron micrographs of conidiogenesis in these fungi were crucial in these studies. It was truly amazing to see heterogeneity in what looked like such a simple structure as the phialide. Heterogeneity is part of complexity. The distinct modes contributing to the heterogeneity of the phialide called for a descriptive terminology in terms of the new understanding of cell wall relationships and other parameters in conidiogenesis and I proposed such a terminology to be used for understanding the process in 1972 in *Current Science* (Subramanian, 1972c).

In this analysis it is important to note that a basipetal succession of conidia due to synechidic ('meristematic') growth of the conidiogenous cell occurred only in the *Penicillium* and the *Thielaviopsis* types of phialide. In the *Trichoderma* type, the conidiogenous cell produced solitary conidia from successive *percurrent* proliferations. In the *Chloridium* type too, the conidiogenous cell produced only solitary conidia but from successive *sympodial* proliferations. Neither of these were truly synechidic, but were pseudosynechidic (appearing synechidic). Viewed this way, the term phialide would apply *sensu stricto* only to the *Penicillium* and the *Thielaviopsis* types!

On the other hand, I have drawn attention elsewhere to the similarity in conidiogenesis in the *Oidium* states of powdery mildews, and in *Wallemia sebi*, to the *Penicillium* type. Minter *et al.* (1982), in a discussion of 'holoblastic' phialides, used the term 'holoblastic phialides' for the conidiogenous cells in *Oidium*. We must also note here that Langeron and Vanbreuseghem (1965), following Langeron (1945), called the conidiogenous cells in *Oidium* 'phialides.' El. Foex (1912) described and illustrated the development of conidia in *Oidium alphitoides* (Oidium des chenes) which conforms to the description of a holoblastic phialide as currently understood. He also reported and described a similar pattern in the development of conidia in *Sphaerotheca humuli* (Foex, 1913) and *Erysiphe graminis* (Foex, 1924). [see also Vuillemin, 1910a;b;1911]. On some of these problems which have been debated for long, the last word is yet to be. Perhaps, I need to remind myself that the variety and diversity in ontogeny are simply the unfolding of an essentially homogeneous formative power.

Within the ambit of our study, it was seen that moniliaceous slime-spored phialidic taxa had teleomorphs primarily in the *Hypocreales*, and the dematiaceous slime-spored taxa had teleomorphs distributed primarily in the *Xylariales*, but also in the *Pleosporales*, *Capnodiales*, *Meliolales*, *Eurotiales*, *Microascales* and *Helotiales* in the *Ascomycota*, and in the *Septobasidiales* in the *Basidiomycota*; it was obvious that the latter is a heterogeneous assemblage. The ontogenetic mode could have evolved independently in diverse fungal groups. The dry-spored phialidic taxa with conidia in true chains had teleomorphs primarily in *Eurotiales*. This holistic approach appeared to strengthen the validity of the distinction between the two kinds of phialides I have referred to.

These observations also lent support to the Saccardoan distinction into moniliaceous and dematiaceous hyphomycetes, erasure of which was suggested by Mason, by Hughes, and most of us, their followers. We know 'melanins' protect fungi from high levels of ultra-violet radiation especially on exposed substrates and such protection helps in survival and perennation, but how does the presence or absence of a dark pigment (melanin) make for such large differences between taxa? Did colour really count for

separation? What could be the linkage between pigmentation and development? It will be exciting to find answers to such questions.When we looked at the teleomorphs of these two categories, the teleomorphs of moniliaceous, slimy- spored phialidic taxa in the *Hypocreales* were all similar and had the same ontogenetic pattern. Any lack of correlation would be suggestive of errors in the identity or taxonomic placement of one or both morphs.

With the teleomorphs of the second category, traditionally placed in the *Eurotiales*, the situation was quite different and intriguing. The teleomorphs of species of the ubiquitous genus *Aspergillus* which C. Rajendran and I studied had a long story behind them, a story replete with excitement and surprises. The generic name *Aspergillus* was established by Pier Antonio Micheli in 1729 in his *Nova Plantarum Genera*. Born twenty-eight years before Linnaeus, he was truly the father of mycology. Linnaeus commemorated him by establishing the tropical plant genus *Michelia* (*Magnoliaceae*). It was not until 1926 that the first definitive monograph of the genus, *The Aspergilli* by C. Thom and M. B. Church appeared. The work of Pasteur and his students on the chemistry of these moulds, their ubiquitous occurrence in soils, and their role in spoilage of fruits and vegetables all served to highlight their importance, and Charles Thom played a pioneering role in developing the culture collections of aspergilli and the equally important penicillia at the USDA Laboratories in Peoria, Illinois.

Thom had examined specimens and cultures in evolving a classification with description of cultural characters and microscopic features for each species. Though he described the sexual states of species known to have one, he would not use a separate generic name for the sexual state as required under the Code. Kenneth B. Raper, who joined him in this endeavour, was a convinced follower of Thom. Both were great scientists whose contributions to our science are immeasureable and in their approach to nomenclature they were ahead of their time in using a 'one name for one fungus' ideal (Raper and Thom, 1944; Raper, 1957; Raper and Fennell, 1965). C. R. Benjamin drew attention to the impropriety in the use of the generic name *Aspergillus* for the perfect state in a paper published in *Mycologia* in 1955. Though I had been convinced of the strength of Benjamin's argument, I kept away from the problem as I did not wish to step in where angels feared to tread.

However, one morning in 1972 I woke up to take the step which I had resisted for years, of putting my thoughts on the sexual states of *Aspergillus* on paper. I had been looking at these fungi, authentic cultures of which had been made available to me by Dorothy Fennell, Kenneth Raper's successor at the USDA laboratory in Peoria, and that was what triggered me suddenly to prepare the paper. What had smouldered imperceptibly for a long time now became visible. On the basis of my study I concurred with Benjamin on the need to use teleomorph generic names such as *Eurotium* and *Emericella*. I also proposed generic names for teleomorphs of some species of *Aspergillus* for which teleomorph names did not exist: *Chaetosartorya, Edyuillia, Sclerocleista*, *Warcupiella,* and *Syncleistostroma*. *Warcupiella* was proposed for the sexual state of *Aspergillus spinulosus* originally described by Warcup, whose work with Garrett in Cambridge was mentioned by me earlier. My paper on the sexual states of *Aspergillus* appeared in *Current Science* in 1972 (Subramanian,1972e).

Almost at the same time, David Malloch and Roy F. Cain (1972), working independently, published a paper in *Canadian Journal of Botany*, in which they also proposed new names for the teleomorphs of aspergilli for which new names were needed under the Code almost on the same lines as I had done. Their paper, however, appeared in print after mine. Malloch and Cain (1973) followed up with a second paper in the same journal in which they acknowledged priority for several of the new generic names I had proposed, but rejected *Syncleistostroma* for nomenclatural reasons and argued that the name *Petromyces* proposed by them for the same taxon was correct. That Malloch and Cain had come to almost the same conclusions as I had was both interesting and satisfying. They were justified in their rejection of *Syncleistostroma,* and I acknowledged the error in turn.

Dorothy Fennell herself was reconciled now to the view I had taken, and accepted it in a paper she published early in 1977. Hoping to see her I visited Peoria on the same trip in 1977, but she was no more and had passed away some weeks earlier. I gave a talk on Phialidic fungi and their Teleomorphs a repeat of my talk at Kananaskis II which was dedicated to Dorothy Fennell. C. W. Hesseltine who presided over the talk told me later that my lecture (mycology) was attended by organic chemists and biochemists according to him, something unusual!

J. A. von Arx, whom I had visited at Baarn in 1975, thought I had been lucky to have had the paper on *Aspergillus* in print before the Malloch and Cain paper appeared. For, he said, he himself had come to the same conclusions and had wanted to publish a paper, but did not, because Malloch and Cain had sent the manuscript of their paper to him for comments before publication! As in life, so in science, we should not lose our ethical sense. I had known von Arx for over a decade, since my visit to CBS in 1964. I admired his scholarship and dedication, reflected in the monumental two volumes on the 'Amerosporen und didymosporen Ascomyzeten' co-authored with Emil Mueller [“Ascus”] (both students of Ernst Gaeumann) in 1954 and 1962, and his varied other contributions to our science. And so it was that I felt gratified to know that he viewed with favour my conclusions on the sexual states of *Aspergillus*.

I had great respect for R. F. Cain, a senior mycologist of repute, and David Malloch, a valued friend. Questions of priority apart, what is really vital is the search for the truth and, when minds thinking independently converge to a common point of view, such convergence gives strength to a given point of view. It is also a reflection of the universality of the problems that are so much a concern in tropical mycology. The proper test is not that of finality, but of advance.

The surprising part of our study of *Aspergillus* purported to the sexual states whose nomenclature now came to be properly recognized according to the Code then in force.

With the authentic cultures we had from Dorothy Fennell, Rajendran made a study of the developmental morphology of all the anamorph-teleomorph pairs we had. To our surprise, we found that the teleomorphs were themselves heterogeneous. Heterogeneity precedes speciation and we found a whole range of forms from ones with just naked clusters of asci (*Edyuillia*) to others with typical closed ascomata/cleistothecia (*Eurotium, Chaetosartorya*) to stromatic forms, the stroma being plectenchymatous or pseudoparenchymatous. The so-called cleistothecium in *Warcupiella* was shown to be an ascostroma in which several non-peridiate ascomata developed. Indeed, the asci were produced in 'locules' in a stroma. In the case of *Fennellia*, discrete, walled ascomata developed within a prosenchymatous stroma. As in *Emericella*, hulle cells surrounded the ascomata. *Petromyces* resembled *Fennellia* in having walled ascomata embedded in a stroma, but the stroma was not prosenchymatous but pseudoparenchymatous from the beginning.

Such heterogeneity among the teleomorphs of a single anamorph genus was hardly expected and was a surprise. The recognition of separate generic names for some of these teleomorphs now seemed in order. With the data we had, it was possible to visualize hypothetical lines of evolution in this group, and derive the simpler forms from the complex ones by reduction or *vice versa*. In any system of classification of the *Ascomycota* in which patterns of ascomal development were accorded primary importance, such as, for example, the Luttrelian System, some of these teleomorphs would occupy widely separate positions.

However, all of them had in common some features such as globose or subglobose asci with no apical apparatus, the asci developing from croziers, ascospores that are typically rigid or of the bivalve type, and a phialoconidial anamorph of the *Penicillium* type with dry conidia in true chains. On this basis, then, it seemed logical to keep them all in a single basket. Luttrell, who was at the meeting, concurred in this thought, but by then would have already been aware of the problems in his 'system' as well. Classifications are, in fact, dictated by the organisms themselves.

At the conclusion of Kananaskis II, I thought my points were well taken. After all, the fruit or sequel of the general effervescence of minds was to cast new light on conidiogenesis and new shadows on some ideas, just as the ebb and flow of tides leave some things on the shore, and wash others away.

Having accorded due importance to morphology and developmental morphology, we now wanted to check if correlations suggested here would have support from approaches other than morphological. Secondary metabolism immediately suggested itself as a potentially useful parameter. Could there be a correlation between the distinct patterns of conidiogenesis seen in *Penicillium* and *Acremonium* and the pathways to biosynthesis of penicillins and cephalosporins in these two distinct phialidic taxa? Both penicillins and cephalosporins are ß-lactam antibiotics. That we had in penicillin G and cephalosporin C two of the most thoroughly worked out biosynthetic pathways is a matter of pride for our science.

Noting the specificity in the synthesis of penicillins and cephalosporins, and the distinct taxonomic niches *Penicillium* and *Acremonium* occupied in current systems of classification, and the distinct positions their sexual states within the *Ascomycota*, it seemed that all this was perfectly in tune with the differences in biosynthetic steps species of the two genera exhibited, following synthesis of isopenicillin, as far as our present knowledge went. Although isopenicillin was produced by both species (*Penicillium chrysogenum* and *Acremonium chrysogenum* (see Lemke and Brannon, 1972 [? *A. strictum*]) and the steps leading to isopenicillin synthesis were the same, the chemical similarity seemed to end there.

The biosynthesis of penicillin N (cephalosporin N) and thereafter cephalosporin C occurred only in *Acremonium*. On the other hand, synthesis of 6-amino penicillanic acid from isopenicillin preceded synthesis of penicillin G in *Penicillium* (Abraham, 1974; 1977; Bycroft and Shute, 1987; Chain *et al*., 1940; Elks, 1977; G. L. Gregory, 1981; Haslam, 1985; Hostettman and Lea, 1987). Thus, the evidence from biosynthetic pathways supported the distinction between the two genera, the two distinct phialidic modes they represented, and all that went with them. But one can never be sure; an 'ugly' fact might turn up and demolish the distinction!

Secondary metabolism and metabolites can also be a guide to evolution and relationships between apparently closely similar phialidic fungi. Having considered the contrasting behaviour of *Acremonium* and *Penicillium*, we shall consider the species of the *Aspergillus flavus* group that are also phialidic. The four species that comprise this group are: *A. flavus* and *A. parasiticus* that habitually infect insects, produce aflatoxins known for their carcinogenicity, and *A. oryzae* and *A. sojae*, both widely used in Oriental fermentations in the production of sake, miso, and soy sauce, but do not produce aflatoxins. That *A. oryzae* might have arisen as a variant from *A. flavus* by long-term cultivation was suggested by Blochwitz in 1929, and by Saito in 1943. It is not unlikely that domestication of 'wild' strains might lead to the loss of the ability to generate aflatoxins.

C. P. Kurtzman and D. T. Wicklow of the Northern Regional Centre of the USDA in Peoria whom I had befriended several years earlier, along with their colleagues, M. J. Smiley and C. J. Robnett, made a study of DNA- relatedness of these species (Kurtzman *et al*., 1986). They concluded that all four species were merely variants of a single species, *A. flavus*. And yet, morphological differences between them would be adequate for recognition on this basis. From their data, the authors recognized two subspecies, *flavus* and *parasiticus* (both supposed to be the 'wild' strains) and two varieties, *flavus* and *oryzae* for subspecies *flavus*, and two varieties, *parasiticus* and *sojae,* for the subspecies *parasiticus*. Thus, domestication led to derivation of *A. oryzae* from *A. flavus*, and *A. sojae* from *A. parasiticus*. The value of molecular data in such studies is obvious. But there was still more to the excitement in our pursuit of the truth and beauty of the phialide.

Let me focus once again on anamorphs with the *Trichoderma* type of phialide which had teleomorphs in *Hypocreales*. *Fusarium* is an important member of this group, and Wollenweber and Reinking (1935) in their monograph of the genus attached importance to the nomenclature of sexual states of the species known and always linked the conidial 'form generic' names to the names of the sexual states. Along with our studies of perfect states of *Aspergillus*, one of my students (D. J. Bhat) studied the developmental morphology of several teleomorphs and their respective anamorphs belonging to *Hypocreales*, including *Calonectria nivalis, C. rigidiuscula, Nectria humicola, N. kera,* and *Thyronectria pseudotrichia*. A *Nectria*-type centrum was typical of all of them in their ascomal development, except in *C. nivalis*. Additionally, in *C. nivalis* the ascus had an amyloid apical apparatus, again not a hypocrealean feature.

Indeed, the taxonomic position of this fungus, which caused the well-known snow mould disease in cereals in temperate climes had been in doubt for a long time. It had even been placed in the genus *Griphosphaeria* Hoehnel. K. Walter Gams and Emil Mueller, recognizing its sphaerialean features, placed it in the genus *Monographella* as *M. nivalis*. While our study confirmed its placement outside the *Hypocreales*, a moniliaceous phialidic anamorph with slimy conidia was inconceivable on present knowledge. When I presented these results at the International *Fusarium* Conference in Berlin in 1978, Walter Gams came up and said that the anamorph of *Monographella nivalis* was not phialidic, but annellidic! The anamorph was, after all, not a *Fusarium* and Gams and Mueller (1980) established a new genus, *Gerlachia* (honouring W. Gerlach) for the anamorph. However, *Microdochium* Sydow was later shown to be an earlier validly published name so that the anamorph was now redisposed as *M. nivale* v. *nivale* by Samuels and Hallett (1983). Here then, we had yet another example of a fairly well tested anamorph-teleomorph correlation, one which strengthened predictability.

The predictability of correlations could well be a test of their validity. If that be true, we might now have another look at *Fusarium udum*, the fungus that cause vascular wilt in pigeon pea. The most distinctive feature of this species is the characteristic macroconidia with an apical cell that is uncinate. It was on the basis of this feature that Wollenweber and Reinking (1935) placed it in the section *Lateritium*. Snyder and Hansen (1940) considered this species a synonym of *F. oxysporum*, although as already noted, the macroconidia of *F. udum* are unique and unlike those of *F. oxysporum* in their morphology. I had placed it in the section *Elegans* on the basis of it being a vascular wilt pathogen, like most members of the section (Subramanian, 1971a).

However, the discovery of a *Gibberella* sexual state by Bharath Rai and Upadhyay (1982), disclosed the error and reinforced the validity of Wollenweber and Reinking's placement in section *Lateritium*. I thought that this was a correlation that one could not be challenged, and one could have predicted; it was a beautiful correlation. In this scenario, it is difficult to imagine *Fusarium udum* being reshuffled. While there could well be a case for a realignment of all species with *Gibberella* sexual states, realignment would have to be on the basis of a comparative assessment of affinities between all extant species within *Gibberella*.

I refer here to some of the recent taxonomic work on *Fusarium* with an emphasis on molecular data. Any effort aimed at improving our taxonomy must be welcomed, but it is imperative that traditional approaches and boundaries and hierarchies are not totally abandoned and replaced by molecular ones. We need to balance these two as complementary strategies. It is also vital that a system does not become so highly sophisticated to the extent it ceases to be practicable and not easily usable by plant pathologists and other clientele who require a simple method of identification.

One of the most significant contributions on conidiogenesis to appear in the post-Kananaskis II scenario was by Cole and Samson (1979) who joined hands to produce a lovely eye-view of patterns of conidiogenesis elucidated using scanning electron microscopy. Transmission electron microscopy doubtless will reveal much more that lies hidden from view and so there is much more to do and to be excited about.

V-2-i-a The Sagrahamala Story

The Sagrahamala story is an offshoot of my obsession with the phialide and the search for features of taxonomic value in classifying monophialidic fungi. It is part of the 'phialide theme'. The focus on the genesis of conidial chains, their nature and significance in the taxonomy of the hyphomycetes served to clarify some issues and was a prelude to a better appraisal of monophialidic genera: *Acremonium, Monocillium*, *Gliomastix, Torulomyces*, and monophialidic species of *Paecilomyces*. Brown and Smith's (1957) monograph of the genus *Paecilomyces* provided a definition of that genus. Onions and Barron (1967) segregated monophialidic species of *Paecilomyces*. The account of *Cephalosporium* and *Cephalosporium*-like fungi by Walter Gams (1971) was a courageous attempt to monograph a diffificult genus that was much needed. And yet, the last word is yet to be.

In my life with fungi and their taxonomy, the guiding lights were E. W. Mason who always insisted on circumscription of genera based on the type specimen or type material, and M. O. P. Iyengar who insisted on accuracy in descriptions of taxa. Accordingly, during my visits to the CMI I looked at type or authentic material of a number of these taxa in an effort to understand them. I also tried to arrive at accurate descriptions of conidium ontogeny.

First, about *Gliomastix*, a beautiful but much misconstrued or misunderstood taxon for no fault of its own, except that no type material was on hand to protect it. From the description and illustrations of its author Gueguen, *G. chartarum* on which the genus was based, produced one-celled conidia in basipetal chains from the tips of simple conidiophores, conidia that eventually slimed down from the tip downwards. Mason studied three isolates that he considered congeneric and interpreted the conidiophores as phialides. He also confirmed the sliming down of conidial chains. Mason's isolates were considered by him to be conspecific with *Torula convoluta* described by Harz, though we are not sure if he

examined type material of this species.

Hughes (1958) accepted the synonymy, but noted that *T. murorum* (of Corda), of which he examined type material, provided an earlier name for the fungus. In describing species of *Gliomastix* from New Zealand, Hughes and Dickinson (1968) described *G. novae-zealandiae* as a new species. In this species as well as in *Gliomastix luzulae* (*Torula luzulae*), the phialidic conidia were produced in true chains and did not slime down. The very name *Gliomastix* signified slime and the sliming of the conidial chain (from apex downwards), a feature Mason observed in his three isolates. *Gliomastix*, then, would seem to be a dematiaceous *Cephalosporium* (*Acremonium*). If this is correct, *Gliomastix luzulae* and other similar fungi that produce true chains of conidia cannot be kept in *Gliomastix.* As for *Torula murorum*, I examined type material [ex Herb.IMI 87344] and found that the conidia were produced in true chains, and were dry.

Arnaud (1952) described many beautiful hyphomycetes of which *Basitorula*, I thought, might be a suitable repository for *Torula luzulae, T. murorum* and other similar fungi. The two species Arnaud compiled in the genus did not seem congeneric one producing conidia in true chains and the other producing conidia that slime down. Moreover, *Basitorula* would need validation. Thus, there was need for a generic name to take in these fungi. The generic name *Sagrahamala* was proposed in this context. Walter Gams (1978) came up with a refined terminology for the two kinds of chain I recognized. In place of "true chains" and "false or fragile chains", he proposed the terms "connected" and "disconnected" chains, respectively. However, his views on the taxa disposed by me in *Sagrahamala* need review. In any case, errors in description must be viewed more seriously than errors in names.

I like to highlight the importance of accurate description from observations on a study of conidiogenesis in *Sagrahamala striatispora* (*Paecilomyces striatisporus*). Typically, phialoconidia are 'enteroblastic', an interpretation established at Kananaskis I. However, in *S. striatispora*, the striate conidia from the so-called phialide appeared to develop by wall extension and growth without a break in the wall of the conidiogenous cell, the conidia being produced 'holoblastically' in Kananaskis terminology. There are two types of conidia in *S. striatispora*, the striate and the smooth that are produced on different phialides. The smooth conidia are produced by the enteroblastic mode as on typical phialides (Subramanian and Pushkaran, 1975). If these observations made under the ordinary light microscope are correct, conidiogenesis of the striate conidia could well fit into Section V of Hughes (1953). There is more to be learnt about the phialide and phialidic fungi. As for *Paecilomyces sensu lato*, we have moved beyond Brown and Smith's (1957) definition, with the elucidation of its polyphyletic nature by Luangsa-ard, Hywel-Jones and Samson (2004) based on 18S-generated rDNA phylogeny.

V-2-i-b The Genus Nalanthamala

I introduced the generic name *Nalanthamala* for a phialidic fungus collected on a dead twig in Madras which I named *N. madreeya* (Subramanian, 1956b). After nearly fifty years, I find that the name is being brought up as a suitable repository for a few phialidic fungi with names in diverse genera. Schroers *et al*. (2005) reported on an exciting study of three different plant pathogenic fungi, all phialidic, which they have redisposed in *Nalanthamala* after careful scrutiny of various parameters. Their study focuses on three fungi: *Myxosporium psidii* on *Psidium guajava*, originally described from Taiwan by Sawada and Kurosawa (Kurosawa, 1926a) but now widespread, *Penicillium vermoesenii* on *Areca* described by Biourge in 1923 (location not known), and *Cephalosporium diospyri* on *Diospyros virginiana* from Tennessee, USA, described by Crandall (1945). On the basis of their study, the authors reclassified these fungi in *Nalanthamala*. Apparently, the genus has a subtropical to tropical distribution. Also, the species seem host-specific.

From partial nuclear large subunit ribosomal DNA (LSU rDNA) analyses of Hypocrealean and related taxa, *Rubrinectria* is considered the teleomorph of *Nalanthamala* which is held to be monophyletic. The excitement from the study is heightened by the inclusion of a large number of live cultures of *Nalanthamala* species from tropical and subtropical regions, notably from Africa.

V-2-ii The Genus Basifimbria

Among the many fungi that turned up in studies of coprophilous fungi by B. C. Lodha working with me in Rajasthan was a beautiful one that we described and named *Basifimbria aurea* in a new genus, *Basifimbria* (Subramanian and Lodha, 1968). *Basifimbria* is yet another novelty that continues to excite. In their study of *Rhinocladiella* and related genera, de Hoog and Hermanides-Nijhof (1977) focused on *Basifimbria* as a repository for *Rhinocladiella peruviana* described by Matsushima (1975) from soil in Peru; they redisposed Matsushima's fungus in *Basifimbria* as *B. peruviana*. On the other hand, von Arx (1982) considered *Basifimbria* indistinct from *Dicyma* and reduced the former to synonymy with the latter. *Dicyma*, however, has characteristic sterile hairs, besides branching, and stands far apart. From her study of collections of *Rhinotrichum subalutaceum* from Czechoslovakia, Holubova-Jechova (1982) affirmed its identity with *Basifimbria aurea* and proposed the combination, *Basifimbria subalutacea*. *Basifimbria* came up again in a study of *Cephalosporium succineum* by Seifert *et al.*(1983). Massee and Salmon (1902) described *C. succineum* from sheep dung in England. Seifert *et al.(*1983) redisposed the *Cephalosporium* as *Basifimbria succineum* [*succinea*] and considered it the same as *B. aurea*.

In 1985 Buffin and Hennebert described a fungus on horse dung from Belgium which they placed in *Basifimbria* as a new species, *B. spinosa*. If *B. aurea* was unique, *B. spinosa* was still more so. If conidial secession was rhexolytic in *B. aurea*, in *B. spinosa*, secession was not invariable and could be rhexolytic or schizolytic. Thus, *B.spinosa* threw up questions of possible pleoanamorphy. In this scenario, it is not surprising that my friend Gregoire Hennebert reverted to *Basifimbria aurea* with determined enthusiasm to unearth the true nature of this beautiful fungus, now with an isolate of *B. aurea* brought into culture from horse dung in Belgium in

1984 and matching the type material. The results on "Diagnosis and variability of coprophilous *Basifimbria aurea*" (Hennebert, 2005) form an important contribution and the paper was appropriately dedicated to another long-time friend, John Webster, himself an authority on coprophilous fungal successions. The variability of *B. aurea* was established and conidiogenesis in *B. aurea* and *B. spinosa* were shown to be similar. In summary, besides *B. aurea*, three species were accepted: *B. succinea*, *B. peruviana* and *B. spinosa*. Since the conidia are larger in *B. succinea*, Hennebert favoured its retention as a distinct species for the present. Admittedly, species lurk in places not yet explored!

V-2-iii The Basauxic Conidiophore

I had always believed that the basauxic conidiophore was an extraordinary phenomenon. Given the diversity of conidial fungi, only a keen observer could have recognized the basauxic nature of a conidiophore. This feature is seen in only about 45-50 mainly tropical species distributed in six genera (*Arthrinium, Cordella, Dictyoarthrinium, Endocalyx, Pteroconium*, and *Spegazzinia*) of the countless hyphomycetes we know.

Typically, the basauxic conidiophore develops enteroblastically from a conidiophore mother cell and elongates by growth at the base. Taking *Spegazzinia* as an example, if the conidiophore mother cell is viewed as the equivalent of the phialide, the solitary ornamented conidium at the apex of the conidiophore would be the equivalent of the first (distal) conidium in *Penicillium*. Basipetal delimitation and conversion of the basauxic conidiophore to form a succession of conidia would then constitute the equivalent of a *Penicillium* phialide. No further conidia to form a basipetal succession of such conidia are produced in *Spegazzinia*, as in *Penicillium*; instead, the conidiophore continues to elongate by basauxic growth.

We can thus postulate an origin for the *Penicillium* type phialide from the conidiophore mother cell that gives rise to the basauxic conidiophore. In the case of *Arthrinium* also, the conidiophore arises enteroblastically from the conidiophore mother cell. The simple conidiophore has many characteristic dark bands and, apart from a first terminal holoblastic conidium, solitary conidia arise laterally on the conidiophore blastically in basipetal sequence. Further, the conidia in *Arthrinium* are one-celled, and usually lenticular with a pale rim or germ slit. One could theoretically derive *Arthrinium* from *Spegazzinia*, but that would require endowing it with a number of features not seen in *Spegazzinia*. *Dictyoarthrinium* is close to *Arthrinium* in most features except for its muriform conidia. The conidia in *Cordella, Pteroconium* and *Arthrinium* are similar.

Comparison of conidiophores exhibiting basauxic growth with 'holoblastic' phialides (*Oidium*) and phialides of the *Penicillium* type (synechidic) assumes a new relevance from some unique features seen in a new genus and species of a hyphomycete which Shun-ichi Udagawa and Tokio Iwatsu (1990) described and christened *Phaeohiratsukaea expansa* from Japan. As the authors note, their fungus is unique among phialidic hyphomycetes because it produces conidia with a longitudinal germ slit similar to those of *Arthrinium*. The conidia are produced in basipetal succession, forming chains, and are dry. Conidiogenous cells are mono- or polyphialidic, and integrated. To begin with, conidia are produced from polyphialides. However, what is curious is that, in further development, the conidiophore proliferates enteroblastically through the collarette of the first conidium, simulating the basauxic mode reminiscent of *Arthrinium*. Novelties continue to emerge and excite us.

On an assignment as Visiting Scientist to the University of Western Australia (UWA) in 1987, I had the benefit of collecting many beautiful fungi in that part of the country. In the UWA, K. Sivasithamparam (Siva) is an old friend and colleague (his having been at the UBL for a short spell in the 1950s) and I had help from Siva and his student Giles Hardy, whose interest in the fungi on eucalypt-compost endeared him to my hunt for fungi. Giles was of real help in the field as well as in the laboratory. On this visit I was looking for the hyphomycete *Herposira velutina,* described by Sydow on dead leaves of *Xanthorrhoea* from Australia (Sydow, 1938). Thus, the focus of my attention primarily was the 'black boy', *Xanthorrhoea preissii* in the *Xanthorrhoeaceae*, a family endemic to Australia. As far as I know, this fungus has not been collected again. I was not successful in finding Sydow's fungus, but collected several others.

Among these there was a dematiaceous hyphomycete that produced large dictyoconidia linked by 'connectives' of variable length. A study of the fungus in culture showed that it was unique in several features, notably in producing conidia on basauxic conidiophores arising from conidiophore mother cells. The conidia were produced acrogenously on basauxic conidiophores and on 'connectives' arising from one or more cells of the primary conidium, with successive conidia similarly produced on connectives, in an infinite sequence, the whole constituting a complex network or system of solitary muriform conidia linked by connectives. The connectives simulated basauxic conidiophores in all aspects although they were relatively shorter than usual, and possessed the characteristic circumscissile break in the outer wall. Being potentially basauxic, they are the equivalent of basauxic conidiophores.

Close study of single spore cultures showed that there were two different species that were congeneric. Thus my hunt for Sydow's *Herposira* led to the unexpected discovery of two congeneric but unique fungi for which a new genus had to be proposed: *Catenospegazzinia* I introduced in 1991. I was, of course, disappointed that I could not locate *Herposira* in western Australia on *Xanthorrhoea preissii*, or other species or on other members of the family such as *Kingia australis* and *Dasypogon hookeri*. Is *Herposira* one of those rare genera on the road to extinction? Or extinct, already?

Yet another beautiful find came my way on a brief early morning collecting trip in the Cameroon Highlands in Malaysia in 1987. It was on the rachis of an unidentified palm, growing on moribund conidiophores of an unidentified fungus. The solitary, basauxic conidiophores arose from conidiophore mother cells. A single holoblastic conidium was borne terminally on the conidiophore. The conidium was

short-clavate, 3-5-euseptate, dry, and conspicuously tuberculate. These features were not seen in any of the fungi known to have basauxic conidiophores, and I therefore proposed the new genus, *Basauxia* for it, and called it *B. pulchra*; my paper appeared in the *Korean Journal of Mycology* (Subramanian,1992g). Collecting in Singapore, we described several beautiful fungi: *Dwibeeja sundara, Javonarxia triseptata, J. quadriseptata, Tretocephala decidua*, *Blastophragma subulata, B. rostrata, Nusia scheeleae*, and *N. collariata*

The discovery of a novel fungal metabolite, arundifungin, from species of *Arthrinium* (Cabello *et al*., 2001) has further excited interest in fungi with basauxic conidiophores. Arundifungin, first isolated from a tropical isolate of *A. arundinis*, inhibits the synthesis of glucan which thus endows it with antifungal properties. In further tests the metabolite was identified in isolates of *A. phaeospermum* and at least six sterile mycelial strains, mostly from litter. Whether these sterile mycelial strains bear a relationship to fungi with basauxic conidiophores remains to be answered. Special interest also surrounds the discovery of terpestacin produced by a strain of *Arthrinium* sp. Terpestacin is a bicyclic sesterterpene that inhibits the formation of syncitia by HIV-infected T4 cells, and so is a potential anti-HIV agent (Oka *et al*., 1993).

V-2-iv The Sporidesmium Complex

Sporidesmium was virtually unknown to me when I began my work on hyphomycetes in 1950. In restoring this name from the obscurity and confusion in which it remained submerged, M. B. Ellis redefined the genus and built a commendable and generally accepted taxonomy of the genus with its many species that are so common in the tropics.

I was familiar with the genus *Podoconis* established by Boedijn (to accommodate several phragmospored dematiaceous fungi he collected in Java), from collections I had examined at the CMI in 1950. Indeed, on my return to Madras, I made many collections of these and other congeneric fungi from southern India which I then placed in the genus *Podoconis* in Herb.MUBL. Hughes (1958) reduced *Podoconis* to synonymy with *Sporidesmium* and the *Podoconis* specimens in the CMI were now redisposed suitably in *Sporidesmium*. I had a fascination for the beauty and diversity of these fungi and, during a period spanning several years, on my several visits to the CMI, I had the opportunity of examining the many collections, including Types of the species disposed in *Sporidesmium* and related genera..

My familiarity with the CMI collections coupled with my study of my own collections gradually left me to wonder if the assemblage in *Sporidesmium* so clearly and so beautifully illustrated by Ellis in his two magnificent books on dematiaceous hyphomycetes was truly homogeneous. And it took me several years of collection and study to conclude that, with continued study and description of new species from many parts of the world, the assemblage had become heterogeneous and now needed careful revision. Such a revision, of course, could not have been possible without the circumscription of the genus by Ellis and his bringing together what he considered species congeneric with *Sporidesmium ehrenbergii* M .B. Ellis held to be congeneric with the type species *S. atrum* Link.

Several important criteria of diagnostic value were considered in the re-appraisal of the taxonomy of these fungi. These included: euseptation/pseudoseptation of conidia, the nature, regularity and other features of percurrent proliferation of conidiophores, and the presence or absence of conidiophores. Species congeneric with the type species have non-hyphopodiate mycelium, simple non-proliferating conidiophores or conidiophores with irregular percurrent proliferations, and conidia that are solitary, gangliar, acrogenous and euseptate. Species with the same features but with pseudoseptate conidia were placed in a new genus, *Ellisembia*. Many species have conidiophores with terminal annellate conidiogenous cells. Species in this group with euseptate conidia were placed in a new genus, *Repetophragma*, and those with pseudoseptate conidia in the genus *Sporidesmiella* Kirk. A number of species have conidiophores with characteristic lageniform, doliiform or nodose percurrent proliferations. In this group, species with euseptate conidia were placed in a new genus, *Penzigomyces*. For species in this group with pseudoseptate conidia the genus *Polydesmus* Mont. was suggested as a possible repository, but no formal dispositions were proposed, pending further study.

A few species in *Sporidesmium* in which conidiophores appear to be absent and the conidia that are euseptate are produced directly on simple conidiogenous cells were redisposed in a new genus, *Stanjehughesia*. In all, 26 species were accepted in *Sporidesmium*, 12 in *Ellisembia*, 5 in *Stanjehughesia*, 9 in *Repetophragma*, one in *Sporidesmiella*, 13 in *Penzigomyces*, and 3, tentatively, in *Polydesmus*. Five other *Sporidesmium* species described by Matsushima were also reclassified on similar or other criteria: *Sporidesmium arengae* in a new genus *Acarocybellina*, *S. casuarinae* in a new genus, *Gangliophora*, and *S. guadalcanalense* in a new genus, *Hemicorynesporella*. Two *Sporidesmium* species unnamed by Matsushima were given names: *S. matsutakashiae* and *S. takashiae*. A third unnamed species was assigned to the genus *Janetia* as *J. matsushimae*.

Following the revision, there has been renewed interest in the *Sporidesmium* complex (McKenzie, 1995; Hernandez-Gutierrez and Sutton, 1997; Reblova, 1999; Shoemaker and Hambleton, 2001; Mercado-Sierra *et al.*, 2004; Wu and Zhuang, 2005). Hernandez-Gutierrez and Sutton (1997) proposed as segregates from *Sporidesmium sensu lato* two new genera, *Imimyces* and *Linkosia* and redescribed *Polydesmus elegans* from the type specimen. They introduced the new generic name *Imimyces* to accommodate *Helminthosporium densum* (*Sporidesmium densum*). Following my reassessment of *Sporidesmium*, Stan Hughes wrote to me and to David Hawksworth on the confusion about *Sporidesmium densum*. It was clear that I was in error about *Polydesmus*. In their discussion of *Polydesmus elegans*, the type species of the genus, and related taxa, Shoemaker and Hambleton noted that *Helminthosporium densum* (*Sporidesmium densum*) and *Polydesmus elegans* are

conspecific. The resulting exclusion of its type species from *Imimyces* necessitated proposal of a new name, *Imicles* (with *Helminthosporium leptosporum* as the type) in which the remaining species in *Imimyces* were placed.

McKenzie (1995) recorded several species of the *Sporidesmium* complex on *Pandanaceae* from the tropics. He described three new species in *Ellisembia* (*E. palauensis, E. vaginata* and *E. paravaginata*) and one new species in *Sporidesmium* (*S.freycinetiae*). In describing a new species of *Penzigomyces* from Spain, Mercado-Sierra *et al.* (2004) provided a key to the species of this genus. Currently, there are 42 names in *Ellisembia*, 22 in *Penzigomyces*, 19 in *Repetophragma*, and 7 in *Stanjehughesia* (Index fungorum). However, Reblova (1999) argued against the segregation on the basis of conidia being borne on simple conidiogenous cells (as in *Stanjehughesia*) and the kind of septation (eu- or pseudo-). "Nothing is completed, but ever completing!" The last word is yet to be.

The excitement continues. Ribosomal and RPB2 DNA sequence analyses of representatives of the *Sporidesmium* complex were carried out by Shenoy *et al.* (2006) to determine the possible familial placement of *Ellisembia, Linkosia, Repetophragma, Sporidesmiella, Sporidesmium* and *Stanjehughesia*. Shenoy *et al.* (2006) concluded that *Sporidesmium* is not monophyletic and the species are phylogenetically distributed in two major ascomycete classes, *Dothideomycetes* and *Sordariomycetes*. I foresee that, in the future, we will learn more about the *Sporidesmium* complex.

V-2-v Connecting Conidial Fungi to their Sexual States

Apart from work on phialidic fungi and their teleomorphs, one of my students (G. Sekar) tried to grow some ascomycetous fungi from single ascospores and establish anamorph connections wherever possible. In the effort, he was able to establish some important connections. A fungus collected on unidentified wood and bark from Naduvattam, close to Ootacamund in the Nilgiri Hills, turned out to be a new lasiosphaeriaceous fungus for which a new genus, *Pseudocercophora* was proposed, with *P. ingoldii* as the type species (Subramanian and Sekar, 1986). Single ascospore cultures produced a hyphomycetous anamorph indistinguishable from *Mammaria echinobotryoides*, the type species of *Mammaria*.

Connections were likewise established between some bitunicate ascomycetes and their tretic anamorphs (Subramanian and Sekar, 1987). Single ascospore cultures of a new *S. planchnonema, S. kalakadense*, produced an anamorph indistinguishable from *Helminthosporium velutinum*, the type species of the genus. The *Helminthosporium* state was associated with the teleomorph in the natural material also. [The molecular phylogeny of *Helminthosporium* s.s. was investigated by Olivier *et al.* (2000) with special focus on *H. solani*. *H. solani* and *H. chloropheora* grouped tightly with *H. velutinum*, but *H. asterinum* stood apart. Shoemaker and Hambleton (2001) chose *Ellisembia* as the most suitable genus for its disposition.] A new *Otthia, O. pulneyensis,* grown from single ascospores, gave rise to a *Diplococcium* state we named *D. pulneyense*.

Among several interesting and new finds, one I collected many years ago on a short visit to the Narsapur forest near Hyderabad in Andhra Pradesh was a beautiful fungus I assigned to *Excipularia* as a new species, *E. narsapurensis*. Many years later, B. M. Spooner and P. M. Kirk (1982) placed it in a new genus, *Excipulariopsis*, and in 1989, A. Sivanesan and W. H. Hsieh collected and described what turned out to be the teleomorph of this fungus in Taiwan, for which they proposed the new generic name, *Kentingia,* and called it *K. corticola*. In their study of the genus *Bombardioidea*, Krug and Scott (1994) described an *Angulimaya* state of *Bombardioidea bombardioides*. *Angulimaya* was established for *A. sundara* isolated from cow dung (Subramanian and Lodha, 1964b). *Lindquistia* (Subramanian and Chandrashekara, 1977b) is also coprophilous and has teleomorphs in *Podosordaria* and *Poronia* (Whalley, 1996).

The generic name *Dwayaangam* was proposed to accommodate *Triposporina quadridens* described by Charles Drechsler from a collection of herbaceous material taken from a grassy area near Lake Alfred in Florida (Subramanian, 1977c). Since the generic name was introduced, seven more species have been described from different parts of the world: *D. yakuensis, D. cornuta, D. dichotoma, D. heterospora, D. gamundiae, D. junci* and *D. colodena*. Of these, *D. junci* is known to have an *Orbilia* teleomorph. However, molecular study points to an *Arachnopeziza* teleomorph for *Dwayaangam colodena* (Sokolski *et al.,* 2006). Sokolski *et al.* suggested that the genus *Dwayaangam* may have teleomorphs in unrelated genera. Many other examples can be cited of the establishment of anamorph-teleomorph connections in this way from the literature. The biogeography of these tropical fungi and their connections are intriguing.

Mention must also be made here of a beautiful synnematous hyphomycete I collected in Madras (Subramanian, 1954c) on dead wood: the conspicuous, stout, white synnematous stipe was capped by a subglobose blackish mass of slimy conidia. It keyed to *Antromycopsis* Patouillard & Trabut (Patouillard, 1897), proposed for a synnematous fungus found within the trunk of *Broussonetia* (*Moraceae*) in Algeria and named *A. broussonetiae*. Penzig and Saccardo (1904) described a variety of this species, var. *minor,* from Java in their *Icones fungorum Javanicorum*. It was easy to pin down the identity of my fungus to *A. broussonetiae* var. *minor*. My study showed that the conidia were produced in basipetal chains in infinite succession from the apices of synnematal hyphae. Accordingly, many years after I collected and described this fungus from India, I proposed a new family, the *Antromycopsidaceae*, to accommodate the genus (Subramanian, 1983).

Interest in this genus was revived with the description of the basidiomycete, *Pleurotus cystidiosus* from the U.S.A. by O. K .Miller (1969), followed by the demonstration by F. G. Pollack and O. K. Miller (1976) that *Antromycopsis broussonetiae* was the conidial state of *P. cystidiosus. Antromycopsis* states are now known for several species of

Pleurotus. Currently, about 16 species of *Antromycopsis* are known and the taxonomy of these and the various *Pleurotus* species is in the melting pot. Significant contributions on this have come from Royall T. Moore (1977; 1984); R. H. Petersen (1993); J. A. Stalpers *et al.* (1991), G. Guzman *et al.*(1991) ; Vilgalys and Sun (1994) and Zervakis *et al*.(2004). For the first time, O. Hilber (1982) segregated *Pleurotus* spp. with synnematous anamorphs in a subgenus which he named *Coremiopleurotus*, of which *P. cystidiosus* was designated the type.

In a study of the *P. cystidiosus* complex, using interfertility tests, phylogenetic species concepts and geographical evidence, Zervakis *et al*. (2004) recognized five species: *P. australis* Cooke & Massee (New Zealand, Australasia), *P. abalonus* Han, Chen & Cheng (Asia, Hawaii), *P. fuscosquamulosus* Reid & Eicker (Africa, Europe), *P. smithii* Guzman (Mexico) and *P. cystidiosus* sensu stricto (North America). Zervakis *et al*.(2004) studied a range of isolates from Greece, South Africa, India, Thailand, the Philippines, Taiwan, China, Korea, Japan, Hawaii, and the U.S.A. What is noteworthy is that these species are distinguishable morphologically only on minor differences, or not at all, and yet data primarily from molecular phylogeny, and secondarily from biogeography, dictate their recognition as distinct taxa. The predicament, I imagine, far from being an isolated example, might well be more general than meets the eye and would in that case have major implications in taxonomy, speciation and nomenclature.

VI Life-styles and Habitats of Tropical Fungi

Fungal ecology is undoubtedly one of the most fascinating facets of tropical mycology. It is fascinating because it concerns what fungi are, what fungi do, what sustains them, their life-style, their interactions amongst themselves and with other biota, their impact on and role in the environment, the impact of the environment on them, their history and distribution in the great tropics. The discovery of a great many fungal taxa in the last century came in the wake of a mighty wave of interest in ecology and distribution of fungi in terrestrial, freshwater and marine environments, and interest in special ecological groups such as entomogenous fungi, predacious fungi, and fungal pathogens of plants, animals, and human, to mention some.

John Couch's (1938) study of the unique fungal genus *Septobasdium* contributed to understanding the taxonomy and biology of the genus in the tradition of the studies of *Laboulbeniales* and other entomogenous fungi by Roland Thaxter (1895-1931). Charles Drechsler combed habitats for predacious fungi and, with remarkable dexterity, brought them alive in all their diversity in his beautiful sketches and descriptions, with meticulous and thorough attention to the minutest detail. Drechsler's was work of a life-time that stimulated many important studies on the taxonomy, ecology and interactions of these fungi with their hosts so that we now know a great deal about them. C. Terrence Ingold combed British freshwater streams for aquatic hyphomycetes with their queer and bizarre conidia of diverse shapes and origin and, in his pioneering study, he drew our attention to what was then a little known ecological group (Ingold, 1942; 1975a;b). If only one I knew where to look and how to look for them, they would become visible as a dominant component of freshwater streams throughout the tropics. They abound in flowing freshwaters of streams pure and serene. On their trip to Madras in 1973, Ingold and John Webster collected and recorded aquatic hyphomycetes from a freshwater stream in the Kambakkam Hills, north of Madras. Ingold's students in Africa and Asia followed the trail, and worldwide interest in Ingoldian fungi has led to accumulation of a voluminous literature on them (Nawawi, 1985; Marvanova, 1997; 2007; Descals, 2005; Schoenlein-Crusius and Malosso, 2007).

Working at the Freshwater Research Station at Ambleside in north-west England, Hilda Canter-Lund brought forth from her studies many interesting fungal parasites of algae (see Canter-Lund and J.W.G. Lund, 1995). The Lunds quite appropriately dedicated their book to three great botanists, C. T. Ingold, F. E. Fritsch and W. H. Pearsall. M. O. P. Iyengar also studied fungal parasites of algae in southern India and had left behind in the UBL camera lucida sketches and notes on them, which remain unpublished. (They are in the Iyengar Collection at the CAS in Botany, University of Madras.) His kindness and affection were such that I had the benefit of being shown some of these beautiful fungi by him.

The pioneering work of E. S. Barghoorn and D. H. Linder (1944) on marine fungi, and that of D. G. Cooney and R. Emerson (1964) on thermophilic fungi are other examples of the flowering of fungal ecology at the time. There is now a great corpus of data on the taxonomy and biology of marine fungi, fungi of oceans, estuaries, and mangroves from the work of T. W. Johnson and F. K. Sparrow (1961), of W. Hoehnk, Alwin Gaertner and Annemarie ulken, of Jan Kohlmeyer and Erika Kohlmeyer (1964; 1964-1969; 1979), of E. B. Gareth Jones (1976) and S. T. Moss (1986), and all this was part of the great rise of fungal ecology of the last century. In 1985, UNESCO arranged a Workshop on Mangrove Microbiology in the Philippines with participants from countries in Asia and the Far East. Gareth Jones and I were closely involved in imparting knowledge and training in marine mycology to the participants. The impact of the workshop could be seen in the enthusiasm it evoked in the participants for doing mangrove microbiology in their respective countries. Jointly with M. Vannucci of the UNESCO in Delhi and A.D. Agate of the Maharashtra Association for Cultivation of Science (MACS), Pune, I edited a booklet on mangrove microbiology which was published by UNESCO (Agate *et al*., 1988; Subramanian, 1988b).

One of my students (S. Raghukumar) studied marine fungi of the Adyar estuary in Madras with me, and later did post-doctoral work with Alwin Gaertner at the Institut fur Meeresforschung in Bremerhaven in Germany for a few years. He and his wife Chandralatha Raghukumar have made notable contributions to our knowledge of marine mycota, particularly the thraustochytrids, their taxonomy and biology, at the National Institute of Oceanography (NIO), Goa, India.

C.G.Hansford devoted a lifetime to studying African fungi and his accounts of foliicolous ascomycetes (Hansford, 1946) and, especially meliolines (Hansford, 1961; 1963), brought

out the beauty and diversity of this ecological group vividly. The fungi that colonize fallen leaves form another group. Keisuke Tubaki (1958) reported on a detailed study of litter fungi in Japan. B. P. R. Vittal worked with me on fungal succession in dicotyledonous leaf litter, and an active group worked with him at the UBL on fungi and fungal succession on mangrove litter in the mangroves of our eastern coast. Their work has brought out the beauty and diversity of the mycota associated with the mangroves (Vittal and Sarma, 2005). The sooty moulds with their unique features and unique niche are better known to us from the sustained work of Stanley J. Hughes (1976). Stan continues to be active on the mycological front (Hughes, 1993). The *Trichomycetes* are yet another special group which has come into its own from the work of R. W. Lichtwardt (1986) and others.

Lichenized fungi have been studied by several students, as already mentioned. Apart from his work on North American lichens, and his book on biology of lichens (1967), Mason Ellsworth Hale travelled widely and collected in the tropics including south-east Asia. He visited India several times and we had his participation in one of our annual meetings of the Mycological Society of India. (I had a very warm welcome from him on a visit to the Smithsonian where I was exposed to his scholarship and enjoyed his hospitality). Lichens and the specialized fungi that grow on them are the love of David L. Hawksworth who is continually, and with conspicuous dedication, unearthing novelties (see Hawksworth, 2004).

Raymond Vanbreuseghem from Antwerp devoted a lifetime to studying tropical mycoses, and his interest in them was such that he visited India several times. His enthusiasm in studying tropical mycoses is seen in the rich culture collection of dermatophytes and of *Cryptococcus* he left behind at the Institute of Tropical Medicine in Antwerp and the treatises he wrote on mycoses (Vanbreuseghem, 1958; Vanbreuseghem and DeVroey, 1981). Important contributions to our knowledge of tropical mycoses came also from Libero Ajello, M. McGinnis, F. Staib, E. Drouhet and others. And yet, there is so much more to do. For example, we still do not know enough about *Rhinosporidium* and *Rhinosporidiosis* (Arseculeratne, 2002).

The discovery of obligately anaerobic fungi, which turned out to be chytrids, in the rumen of sheep, by C. G. Orpin in 1975, showed how limited our knowledge of the fungi had been prior to that discovery. There are perhaps other such unique organisms awaiting discovery (Orpin, 1975; Orpin and Joblin, 1988; Barr, 1988; Barr *et al*.,1989; Ho and Barr, 1995). The fungi of 'extreme' environments are yet another group, diverse in their own way. A great many fungi are involved in biodeterioration and the breakdown of a variety of substrates in a range of habitats.

No one working in soil mycology and on the ecology of rhizoplane fungi would miss the hyaline and dark mycelial forms that are so common in this microhabitat. With no clue to their identity, most of these had been labelled sterile forms, and set aside from further consideration in numerous studies in the last century. This neglect has been an irrecoverable loss. Their universal presence in soils and on root systems clearly indicates that they have a role in plant health or soil fertility. The perennial mycelium of *Marasmius oreades* is known to live for as many as 400 years. As Philip Gregory stressed, "biologically the vegetative mycelium is the most important part of the fungus…We write about fungi like those old-fashioned historians who treat history in terms of the Napoleons and Cleopatras, but ignore Tom, Dick and Sally" (Gregory, 1984, p. 1).

The discovery by Dewan and Sivasithamparam (1990) of a sterile red fungus on root systems of wheat and ryegrass in Western Australia and its potential in the biological control of take-all in wheat illustrated the point strikingly. It is in the identification of such sterile fungi that molecular taxonomy can really help dramatically. There are innumerable hyaline fungi in soil many of which appear on dilution plates and are easily brought into pure culture and then sporulate. And yet, many of these moniliaceous fungi are not easily identified since their hyphae may be thin, and their spores small, thus defying precise identification. Even trained mycologists find their identification a difficult task as few authoritative monographs deal with them.

I have often wondered why porospores (tretic conidia) are virtually unknown in the moniliaceous hyphomycetes. That could be because pores do not show up in moniliaceous species as they do in dematiaceous ones. Nevertheless, we have seen pores and porospores in an albino (hyaline) mutant of the common *Drechslera sorokiniana*. There is a clear paucity of studies on hyaline fungi. There are two delightful lovingly illustrated volumes, *Dematiaceous Hyphomycetes* (1971) and *More Dematiaceous Hyphomycetes* (1976) by M. B. Ellis, but there is no comparable work on moniliaceous hyphomycetes. There is an urgent need to give attention to some of these difficult fungi that are so common in diverse habitats.

We now have also the fungal endophytes many of which seem to be sterile. Only relatively recently have they been given serious study. That some endophytes produce, *in vivo*, metabolites that play a role in the development of resistance to pests or pathogens in the host is a theme that has emerged from recent studies. Endophytes invite comparison with biotrophic pathogens in so far as both seem to live in a balanced association with their respective hosts. However, the biotrophic parasite lives at the expense of the host, but apparently this is not the case with endophytes. I am not sure. Barbara Schulz & Christine Boyle (2005) discussed non-balansiaceous fungi involved in asymptomatic colonizations of plants and viewed them as an 'endophytic continuum' exhibiting interactions ranging from asymptomatic to pathogenic to saprobic, depending on the balance between the defences of the host and the aggressiveness of the colonizer. This is a logical and perfectly justifiable stance of what we know about these organisms. Endophytic fungi have also been shown to produce novel secondary metabolites (Schulz *et al*., 2002). Azevodo and Araujo (2007) reviewed tropical endophyte diversity.

In the 1930s, E. J. Butler drew attention to the vesicular arbuscular fungi and their close association with root systems of a variety of plants in India and elsewhere in the tropics. That they are of ancient lineage going back to the Devonian, is

well known. During the past thirty or forty years they have come to be increasingly studied worldwide. But the life of these fungi is absolutely linked to the life of their hosts. The distinction between so-called 'fungal endophytes' and vesicular arbuscular mycorrhizal endophytes seems to be *prima facie* valid. Many vesicular arbuscular fungi appear to exhibit little host specificity, and a relatively small number of species of these fungi are associated with a range of host plant species which are not necessarily closely related. They do not grow in axenic culture.

The recent discovery of a free-living sterile fungus, *Piriformospora indica*, from soils from Rajasthan in India and its purported symbiotic association with root systems of a variety of plants, if correct, would seem to further substantiate our expectation of finding novelties in soils. The authors of this discovery used molecular and other techniques to elucidate its taxonomy, and the most that they could do was to establish its basidiomycete affinities. Both examples of sterile soil fungi I have cited, the one from Australia and the other from India, evoked immediate interest, from their potential use in agriculture.

But these are unusual examples. More examples are known where novelties received little attention when discovered and were even forgotten, until suddenly interest arose from some unexpected new discovery. Westling's *Penicillium notatum* (*P. chrysogenum*) is a well known example. Though described by Westling in 1911, its importance was recognized only in 1929, from the discovery of its antibacterial properties by Alexander Fleming that year. *Olpidium brassicae* is a lowly fungus that infected root systems of *Brassica* species. Though the Japanese mycologist Shunsuke Kusano had published a study of the life-cycle of this species in 1912, and it had a place in some text-books, few had any interest in it. However, when it was discovered that tobacco necrosis virus was transmitted by this fungus (Teakle, 1960; Cadman, 1963), plant virologists and pathologists combed the literature avidly to obtain all available information on the fungus and even initiated further studies!

The early studies on soil fungi were linked to their role in improving soil fertility, and later studies came from their importance as plant pathogens or even as pathogens of domesticated animals and humans (Waksman, 1916; 1927; 1944). Definition of some of these ecological categories, such as soil fungi or litter fungi, is not always easy as one can find a given fungus both in the soil and in litter. The soil is remarkable for what it holds, an immense diversity of moulds and other fungi, not to mention bacteria, protozoa, nematodes and numerous other microscopic animals and their predators.

Novelties are turning up continually, many from root systems and others from soil. *Rhynchogastrema coronata* isolated from farmland loess soil near Braunschweig in Germany (Metzler *et al*., 1989) is one such beautiful basidiomycetous mycoparasite. Poeder and Scheuer (1994) described a new hypogeous fungus, *Moserella radicicola* (*Helotiales*) on ectomycorrhizas of *Picea abies* from Austria. The discovery of a new species of *Penicillium, P. nodositatum*, that induced myconodules in *Alnus* roots (Valla *et al.*, 1989) highlights the diverse ways in which soil fungi might interact with live root systems.

Mycorrhizas

When we consider the soil mycobiota as a whole, and the diversity that makes the whole, it becomes evident that they all collectively present a picture of synergistic, antagonistic, or other interactions. In natural soils, for example, soils in a forest, soil-borne disease in epidemic form is rare. This is also true of infections of aerial parts of a plant such as the leaves. Epidemic diseases and the rapid evolution of pathogens are a direct result of crop monocultures in agriculture. On the other hand, interactions between the soil biota and, say, root systems, as already noted, seem to have developed from the time land plants evolved as, for example, is evident from the occurrence of vesicular-arbuscular fungi in the Devonian (see above). Mutualism and other types of symbiosis evolved early on our planet long before the emergence of humans.

Ectomycorrhizas are especially common in forest soils where a variety of forest trees serve as suitable symbionts. I referred earlier to the pioneering work of W. H. Wilkins on the ecology of the larger fungi in the Oxford area in England. Among his collaborators was Jack L. Harley who later made great contributions to our knowledge of mycorrhizas. His book on *The Biology of Mycorrhiza* (1959) stimulated a great deal of work on the physiology and biology of mycorrhiza. Jointly with his daughter Sally Smith, who had her early training with S. D. Garrett at Cambridge, he later wrote *Mycorrhizal Symbiosis* (1983), a beautiful synthesis of ideas and facts on an exciting subject. Following his visit to the UBL in the early 1970s, I enjoyed his hospitality at Oxford on several occasions and learning from him about mycorrhiza.

The Institute of Terrestrial Ecology in Midlothian in Scotland is known for its research on the role of mycorrhiza in afforestation under the leadership of Fred T. Last. I had known Fred (and the family) from the days he was at the Glasshouse Crops Research Institute at Littlehampton, Hampshire in the late 1960s. Fred is a versatile scientist who did so many things so well in different places along the way and radiated friendliness around. During a visit to Midlothian and the Institute, he wanted to know from me if the fly agaric, *Amanita muscaria*, was known from India. When I answered in the affirmative, he was surprised. He had looked up Butler and Bisby's *Fungi of India* (1931) and had not found *Amanita muscaria* listed there. And there can be no error in that list. But I had observed fruit bodies of the *Amanita* around pine trees in the Sim's Park in Coonoor in the Nilgiri Hills on visits from the 1950s and later in the 1970s in the Pulneys, in Kodaikanal under pines, a point I made in my Birbal Sahni Lecture in Lucknow (Subramanian, 1976) with reference to the identity of Soma and Gordon Wasson's theory that the Soma of the Vedas is the fly agaric.

In his valuable 'history of Ootacamund,' Frederick Price (1908) mentions early plant and tree introductions by the British beginning the mid-1840s, notably by John Sullivan, the founder of Ootacamund, but gives no clear or specific details about native or exotic pines. No large-scale

introductions these, but isolated ones of two or three saplings, may be. Also, occurrence of the *Amanita* in northern India, in the Himalayas, for example, was in doubt. I had it from the Dutch mycologist, Maass Geesteranus, who led an expedition to the Himalayas, that he had not found it in the areas he had been to. On the other hand, if Gordon Wasson's thesis that *Amanita muscaria* is the Soma plant of the Vedas be true, *Amanita muscaria*, the fly agaric must occur in India. Somehow, I had thought such a common fungus must have been recorded. But I could be wrong.

On my return to Madras, I went on a hunt for the *Amanita* in Kodaikanal in the Pulneys which had good stands of *Pinus patula*. And I found what I thought was *Amanita muscaria* under pines fruit bodies in many stages of development. As a prelude to taking up studies on agarics and related fungi, one of my students (K. Natarajan) spent a year as a post-doctoral with Ron H. Petersen at Knoxville in Tennessee USA during 1972-73. Ron graciously took him in and imparted training that was invaluable. In the following year, we had with us as a Visiting Scientist David Pegler, well-known for his work on tropical agarics, from the Royal Botanic Gardens, Kew. Pegler confirmed the identity of the *Amanita muscaria* from Kodaikanal.

Fred Last also came and, having found the *Amanita* himself, was now fully convinced that *A. muscaria* did occur in the high elevantions in the Pulney Hills under pines. The exercise led to collaborative research between us towards understanding the ecological and afforestation aspects of this mycorrhizal relationship (Last *et al*. 1992). I have stressed elsewhere the relevance of mycorrhizas in afforestation programmes. Though my initial interest in mycorrhiza began with my visit to Elias Melin's laboratory in Uppsala in Sweden in 1950, and my subsequent association with Noel Robertson at Cambridge in the same year, it was only now that I plunged into this area.

The urgent need to check and verify records of Indian agarics was obvious. But who would do that? We had a young and enthusiastic lady, B. Manjula, who worked with Natarajan on agarics in the UBL, and I asked David Pegler if he could help her with the types at the RBG and also offer guidance so that the lacuna could be filled. David Pegler and the RBG, Kew readily agreed with the proposal. Accordingly, Manjula spent a few weeks working at the RBG, examining the types of agarics described from India. That this study was totally self-supported by a young, keen and enthusiastic student reinforces the hope that tropical mycology will grow and develop even without (monetary) support. A great deal of good science can be done in our country with simple and not very expensive equipment as long as there is the passion to do good science and we ourselves do not look down on small science (in comparison with so-called 'big science').

We have also the example of Takashi Matsushima in Kobe, Japan, and his quest for micro-fungi, all on his own!. Manjula's taxonomic study of Indian *Agaricales* appeared in the *Proceedings of the Indian Academy of Sciences* (Plant Sciences) in 1983, filling a long-felt need and now an important work of reference. In addition, K. Natarajan and N. Raman published *South Indian Agaricales* in 1983. More recently, Natarajan *et al*.(2005) updated Manjula's work.

The collaborative work with Fred Last begun by me was continued by Natarajan and led to better understanding of the ectomycorrhizal symbionts of *Pinus patula* in the Nilgiris. Records show that some pines, specifically *Pinus patula*, were introduced in the Pulneys from South America (date not known, but possibly in early 1940s), from Brazil, and one might presume *Amanita muscaria* came in along with *P. patula*. There seems to be no other way of explaining the occurrence of *A. muscaria* in the Pulneys and the Nilgiris. If this is true, the occurrence of *Amanita muscaria* in southern India is recent. Plant introductions have a bearing on geographical distribution of mycobionts, an aspect of global study that has great relevance in fungus and plant sociology.

Several ectomycorrhizal symbionts were identified, including *Amanita muscaria, Laccaria laccata*, *Suillus breviceps, S. subluteus* and others. An exciting part of the study pertained to observations on mycorrhizal fungal succession on *Pinus patula* in plantations of different ages: trees 3-7 years old had *Thelephora terrestris*, *Laccaria laccata* and *Rhizopogon luteolus* as symbionts, and on trees 7-11 years old, these were replaced by *Amanita muscaria* and *Scleroderma citrinum*. Knowledge of fungal succession is useful in establishing mycorrhizal association with fungal symbionts appropriate to the age of a plantation or of seedlings. Change is written in bold letters on the face of nature and the recognition of early mycorrhizal colonizers and late comers might find a partial explanation in the accumulation of recalcitrant leaf litter in soils.

Amanita muscaria and other amanitas, and agarics in general, have many other dimensions. Their chemistry, their history, their tribal links and use in religion and mysticism, and their biogeography make an exciting world of their own. The discovery by Weiss *et al*. (2004) of mycorrhizal heterobasidiomycetes which form ecto-, ericoid, and jungermannoid mycorrhizas opens new vistas of probing the life styles and ecology of these fungi which have been accommodated in a new order, the *Sebacinales*.

Fungi and Termites

Termites and termite mounds abound in the tropics, presenting a unique scenario in mutualistic symbiosis. Termite mounds may be up to 6 m tall and 3 m wide at the base in Africa, but are smaller in Asia. Basically, the mounds comprise two parts: (1) a subterranean living part habited by the termite, and (2) the conspicuous structure above, studded with tunnels and with a seemingly purposeful architecture. Fungi play a key role in the life of termites. Wood and timber, lignin and cellulose, which are primary sources of food for termites, need to be degraded at least partially before termites can feed on them. Such preliminary degradation of wood occurs especially from the activity of basidiomycetous fungi. Apparently, there is no direct mutualistic association between termites and such wood degraders.

However, symbiosis between the termite group known as the *Macrotermitinae* and the basidiomycete *Termitomyces* is one of the most fascinating among biotic interactions in the tropics, and there are many vivid accounts of this. Quite

interestingly, the first discovery of the sponge-like 'fungus-gardens' of the *Macrotermitinae*, with their mycelium, conidiophores and conidia, came from Koenig (1779), working at Tranquebar (Tarangambadi) in southern India. Koenig intuitively thought that the fungus formed the food of the young termites. Johann Gerhard Koenig was a Baltic-German pharmacist and physician who, as missionary and plant collector visited India, Siam (Thailand), Malacca and Ceylon, beginning 1767. From 1773 to 1785 he worked as a naturalist for the Nawab of Arcot in the then Madras Presidency. Similar fungus gardens were discovered by Smeathman (1791) in West Africa; he thought the gardens were nurseries. What is more, he observed food 'magazines' of stored plant fragments in the upper parts of the nest.

The real nature of the fungus gardens came from the work of Holtermann (1898; 1899) in the Malay Archipelago. The British mycologists, M. J. Berkeley and C. E. Broome pioneered the study of the fungi making up the gardens. Tom Petch, who studied these fungi in Ceylon (Sri Lanka) contributed a great deal to our understanding of them, which were previously known by different names; he synonymised several names under *Collybia albuminosa*, the name suggested by him for the fungus growing from the nests of species of *Odontotermes* in Ceylon (Petch, 1906; 1913). Since these early discoveries, termite fungus gardens have been described from several parts of the tropics, including Africa, Asia, and the Far East.

However, specific data on the fungal species and the termite species that were associated were not always available. It was Roger Heim of the Natural History Museum in Paris who provided the much needed taxonomic treatment in a series of papers he published from 1940 to 1963; *Termites et champingnons* (1977) was the last among several books he wrote. From a study of the fungi from termite nests, Heim established the genus *Termitomyces* for the basidiomycete mutualist of the *Macrotermitinae* (Heim, 1942).

Among the several species recognized by Heim, the majority had caps at the tips of long stipes or 'pseudorrhiza' that emerged from the fungus combs, through the mounds or soil above the nest. What was interesting was that the central portion of the cap of some of the larger species was conspicuously thickened or hardened, or even pointed, which might be an adaptation for easy penetration through the soil. Heim called this structure a 'perforatorium'. The form and development of this structure varied from species to species, and therefore is considered to be of importance in taxonomy. As in other fungi, variations were common in these fungi also. The size and position of the combs from which they grew might be factors important here. *Termitomyces microcarpus,* alone among a host of other species, was disposed by Heim in subgenus *Praetermitomyces*.

Originally named *Entolomola microcarpum* by Berkeley and Broome from their pioneering studies of material from Ceylon, what was characteristic of this species was that it was associated with species of *Odontotermes* and, fructifications, that were relatively small, developed on fragments of the comb brought up out of the nests by the termite during the rainy season. All other species of *Termitomyces* were assigned to subgenus, *Eutermitomyces*, of which *T. albuminosa* (*Collybia albuminosa*) was considered a good example. However, it later turned out that the specific epithet *albuminosa* was a misapplication for the fungal symbiont of *Odontotermes* described by Heim, and could not be used for it.

On the other hand, a *Termitomyces* collected from a termite nest in Madras and described by Natarajan (1979) as *T. heimii,* matched the description of Heim's fungus and came to be accepted as the correct name for this common tropical agaric. *T. heimii* has a global distribution in the tropics. From the work of students working in the states of Tamil Nadu, Kerala and the Punjab, over fifteen species of *Termitomyces* have been described or reported from India (Natarajan, in litt.), but precise linking with a termite species is wanting.

Despite the vast literature on termites and termite fungi, many questions about them such as specificity, remain unanswered. *Odontotermes badius* occurred in association with one or the other of the two widely separated *Termitomyces* species, *T. microcarpus* and *T. heimii*. With the former, *Odontotermes*, it seemed, had adapted as, in the rainy season, just as the fungus was about to produce its fructifications, the termite had the habit of shaving away the outer layers of its fungus combs and spreading them on the soil surface above the nest. We have no idea of the basis of this behaviour.

What seemed most remarkable about the termite-fungus symbiosis was the way the termites raised the fungus garden, keeping out all contaminants in the soil which teemed with microbes and little animals. How did the termites grow and maintain pure cultures of the fungus of their choice? What is the secret of pure cultures? What is the technique of pure cultures? We need to learn. How did the symbionts recognize each other? An interesting aspect of the symbiosis was the way fruiting by the fungus was held in check by constant foraging so that fruit bodies came up only in nests and mounds deserted by the termite. Was there some mechanism by which the fungus was held in a vegetative phase? Were secretions or chemicals involved in the maintenance of the fungus in a vegetative phase? Secretions might have a role in warding off contaminants. It is likely that oral secretions from the soldier caste and workers might be (selectively) fungistatic to fungi other than *Termitomyces*.

The true nature of the comb material had been debated for long in the past. A fecal origin had been suggested quite early, in keeping with the internal lining and shelving that characterized termites in general. J. Bathellier (1927) came up with the view that the fungus combs were constructed from undigested plant material that had been fully masticated. Working on the termite, *Ancistrotermes guineenis*, W. A. Sands (1969) observed and photographed the process of fungus comb construction. The combs were built from deposition of fecal pellets from the workers. Repeated observation gave no evidence of chewed wood being deposited in the construction of combs. P. P. Grasse and C. Noirot (1957) argued against this theory and drew attention to the fact that the green-coloured combs seen in the nests of *Macrotermes* that foraged on green grass indicated that passage through the gut had not taken place. It is important to

note here that termites habitually did not use undigested food as building material. Fecal material was used to plug holes in wood by wood-inhabiting termites that lived entirely within wood.

The comb and nest were dynamic structures and resulted from the mutualism between termite and fungus involving recycling of fecal material - a beautiful mutualism! The fungus served as food for the termite, but also played a key role in the degradation of lignin, besides supplying nitrogen and possibly vitamins. Cellulose in wood underwent decomposition by resident protozoa within the gut of the termite. While the termite got its share from the fungus, the fungus was ensured a very secure environment and benefactor in the termite. That *Termitomyces* did not occur in the free mycelial state apart from the termite nests is noteworthy. Introduction of the fungus into new combs must then come from basidiospores. This fitted well with the physical advantages of a long stipe capable of emergence from within the comb to the outside and the conspicuous gills of the species in *Eutermitomyces*.

The mound was not a mere heap of sand or soil. It had a complicated internal architecture with a network of tunnels, but no termites; the termites lived in a subterranean cavity below the base of the mound. Most termites are soft and delicate-bodied and exposure to sunlight for any length of time would dry them out and they would die. They live in darkness and, with no need for vision, are totally blind. The mound was no static structure, but was a dynamic one, with annual accretions concurrent with erosion of material.

The incessant changes in the internal conditions within the termite galleries suggest manipulation of conditions to suit the development of *Termitomyces*, and suppression of competing microbes. Air-conditioning is crucial for the dwellers. The primary role here is considered to be that of the termite, but could well be that of the fungus. The heightened carbon dioxide content resulting from respiration of the fungus, it has been suggested, might be inimical to growth of competing microbes. In any case, maintenance of the mound's internal atmosphere and its continuous adjustment ensures a condition of homoeostasis comparable to what we find in a live organism (Scott-Turner, 2000; 2007).

Termitomyces species continue to be described, and many are edible by humans and are sold in the markets. Termite fecal material carried not merely *Termitomyces*, but spores of several other fungi and bacteria too, and one should expect competition for food from the component microbes. The frequently mentioned among these are *Podaxis*, and the ascomycete, *Xylaria* (*Xylariales*). *Podaxis pistllaris* is believed to have been the first ever fungus recorded from India. Linnaeus described the fungus from a collection made from Tranquebar in Southern India in the1750s. I am not certain if this collection was associated with a termite nest. But it is known that *Podaxis* occurs in mounds of *Nasutitermitinae* in the tropics; it appears that the association is with *Trinervitermes* in India, Sri Lanka, Africa, and Malayasia. The probable host genera seem to be *Coarctotermes* in Madagascar, and *Tumulitermes* in Australia.

As for *Xylaria*, Petch (1913) recognized two species associated with termite mounds, *X. nigripes* and *X. furcata*. Their fructifications have been known to emerge from abandoned nests of *Odontotermes*. Characteristic of *X. nigripes* were its grey mycelium and cylindrical stromata. As the name suggests, *X. furcata* produces dichotomously branched stromata. *X. nigripes* is known to occur in association with several species of *Macrotermitinae* from Africa to China. Heim recognized a third species, *X. obovata*, from Congo, which he thought was a rare and obligately saprophytic fungus.

Xylaria furcata was once thought to have a conidial state. P. A. Dixon (1965) described in detail the development of the conidia and their liberation. He noted that the conidia were discharged by a sudden rounding off of the cell walls between conidium and conidiophore. Apart from the violent discharge of the conidia, the development of a pair of conidia at the tip of the conidiophore was unique. It was then considered fitting to give conidial states separate anamorph names and, accordingly, I proposed a new generic name, *Padixonia* (anagram P. A. Dixon) for it (Subramanian, 1972b). Further elucidation of conidiogenesis in the fungus by Dixon (1985) showed that the conidia produced in tandem terminally on the branches of the conidiophore made an acropetal pair of which the first was holoblastic and the younger enteroblastic, a feature not seen in any other conidial state in *Xylariales*. In his discussion of anamorphs of *Xylaria*, Rogers stressed the uniqueness of conidiogenesis in *Padixonia* and classified the *Xylaria furcata* group in a separate Section in the genus. Dixon (1985) who described conidiogenesis in the fungus from scanning and transmission electron micrographs, was uncertain if *Padixonia* was conidial *Xylaria*. The identity of the *X. furcata* was itself called into question. Rogers *et al.* (2005) concurred with this view.

They discussed *Xylaria* species (*X. arenicola, X. brasiliensis, X. escharoidea, X. furcata, X. nigripes, X. piperiformis* and *X. rhizomorpha*) known to inhabit abandoned termite nests. *Xylaria piperiformis*, originally described by Berkeley from India is known mostly from India. According to them, *X. furcata* is more common than *X. nigripes*. Rogers *et al*.(2005) described two new species *X. tanganykaensis* and *X. readeri* thought to be associated with termite nests. Ju and Hsieh (2007) listed and described *Xylaria* species associated with nests of *Odontotermes formosanus* from Taiwan. They described six new species: *X. acuminatilongissima, X. atrodivaricata, X. brunneovinosa, X. griseosepiacea, X. intraflava* and *X. ochraceostroma*; they also described *X. cirrata, X. escharoidea* and *X. nigripes*. Anamorphs were described for eight of the species.

A number of other fungi have also been reported from time to time as being saprophytic in the combs. A small reddish-brown ascomycete, *Neoskofitzia termitum* was reported by Petch (1913) to have been found in a termite specimen sent from Jaffna in Ceylon, but he was not sure if there was an association with the termite in Ceylon; it was originally described on a termite comb lying on the ground in Java by von Hoehnel. Batra and Batra (1966) found this fungus again in association with mounds of *Odontotermes gurdaspurensis*

in the Punjab in India (see also Roonwal, 1962). Other fungi reported as saprophytic in termite mounds include *Psalliota termitum*, *Gyrophragmium delilei* and species of *Leucocoprinus* and *Xerocomus*.

An interesting find from termite nests in Cuba is *Bahusakala niditermitae* described by Castaneda *et al.* (1996). The genus *Bahusakala* was established to accommodate *Septonema olivaceo-nigrum* originally described by Berkeley & Broome in 1873 for a collection on *Agave* from Ceylon (Subramanian, 1958a). *Hyphomycetes* such as species of *Termitaria* and *Mattirolella* are ectoparasites on termites. These fungi develop intracuticular haustoria but do not penetrate further. The host is hardly affected. Roger Heim (1951) described *Antennopsis gallica*, an interesting ectoparasite on termites from France and suggested the Ordinal name *Gloeohaustoriales* for such fungi.

What could be the possible origins of termite-fungus interactions and mutualism? We have noted earlier that mutualism is an ancient game of life. Considering the lignolytic function of the fungal symbiont in the nutrition of the termite, and the role of termite feacal material in comb construction and fungal nutrition, I imagine a coprophilous origin not unlikely. Coprophilous fungi that occur in dung and excreta of animals are a special ecological group in which *Zygomycetes*, *Ascomycetes*, *Basidiomycetes* and conidial fungi are major components. Termite fecal material had all these components except the *Zygomycetes*, though in much smaller measure in both numbers and diversity. This could be a reflection of the special nature of termite fecal material.

The coprophilous fungal domain is a sequel to herbivory in animals for which vegetable matter such as leaves and litter are primary sources of nutrition. Herbivorous animals act as sieves in the development of coprophily for fungi that originally dwelt on vegetation in its living and decaying states. From a welter of coprophilous fungi which now preferentially colonize termite faeces, a lignolytic fungus would fit in as the natural partner in a mutualistic association with the termite. This can come by only if the termites' presence led to conditions favourable for the fungus. The arrangement succeeded primarily from the fact that fecal material had the dual function of being part of the architecture of the comb as well as being part of the nutrition of the fungus. Further, the fungus itself formed the food of the termite. Termites that were part of such mutualism ended up with one or another species of *Termitomyces*.

The occurrence of agarics such as species of *Coprinus* (e.g. *C. cinerius*), and of *Xylariaceae* (e.g. *Poronia*, *Hypocopra*, *Podosordaria* spp.) in dung of animals, parallels that of *Termitomyces* and *Xylaria* in termite nests. The *Xylariaceae* are widespread in litter and are known to be endophytes of a range of plant species throughout the world (Whalley, 1996). To reach coprophily, of course, they have to traverse the gut of the animal. The endophytes may not come through as they seem to stand in the way of herbivory from their powers of secondary metabolism. But all this is in the region of imagination and speculation, with, of course, some facts to back the thought. There is much more to be done in this fascinating study of termite-fungus mutualism in the tropics.

The Lowly and the Beautiful

Having dealt with soil-borne pathogens and symbionts infecting root systems of plants, I shall now consider a few lowly but beautiful fungi from the vast array that occur in soils and waters in the tropics and have excited those who discovered and studied them, and continue to excite us.

Allomyces

Allomyces was established by E. J. Butler (1911) for *A. arbuscula* (as '*arbusculus*'), a fungus he isolated from soil from Pusa in Bihar, India. Butler's paper describing the fungus appeared in the *Annals of Botany*. Like many such discoveries, this one apparently had little impact on science or botanists in India. After all, it was a lowly fungus from soil, and was not a plant pathogen potentially dangerous to our crops. As an undergraduate student, I had no knowledge about this fungus and it surprises me now that it would not have been difficult for me then to have isolated this fungus from soil and known something about it first hand. Be that as it may, following Butler's discovery, there had been descriptions of a few additional species.

Notably, Kniep, working in the Treub Laboratory at Buitenzorg in Java (now Bogor, Indonesia), collected and described in 1929 a new species he called *A. javanicus*. Karl Johann ('Hans') Kniep succeeded von Haberlandt as Professor of Plant Physiology at the University of Berlin in 1924 and authored *Die Sexualitat der niederen Pflanzen* (1928). Kniep noted that the male and female gametes in *A. arbuscula* were similar (isogamous), but dissimilar or unequal in size (anisogamous) in *A. javanicus*. A year later, in 1930, he crowned his work with a paper on alternation of generations in these fungi which, in fact, was what made these fungi unique; these two papers were his last ones as he died the same year when only 49.

The peak in excitement with *Allomyces* came with the publication of a monograph of the genus by Ralph Emerson (1941). Emerson's work was carried out for his Ph. D. under the supervision of W. H. Weston at Harvard, completed on a sojourn at the Botany School in Cambridge in England, and appeared in *Lloydia* in 1941. He presented in that paper the distilled essence of his discoveries. At one stroke, Emerson brought into one frame several dimensions of his object, a model for emulation: life cycle, speciation, taxonomy, occurrence, and geographic distribution. Emerson found *Allomyces* exciting. He now made it exciting for us. Though isolated from soil, *A. arbuscula* was a fungus that must be considered amphibian from its predominantly aquatic features, such as reproduction by swarm spores (planospores). In fact, it is a chytrid with its cell wall composed of chitin, and its swarmers posteriorly uniflagellate.

However, what made *Allomyces* unique was the discovery that, alone among known aquatic fungi, it produced two kinds of thalli, which were seen to alternate in a regular cycle: a gametophyte bearing gametangia, and a sporophyte bearing sporangia. The general aspect of both thalli was the same, so that we had here an isomorphic alternation of generations, a situation quite common in the algae, but rare in the fungi. The

gametophyte produced pairs of male and female gametangia, with the male gametangium in a hypogynous position in *A. arbuscula*. Posteriorly uniflagellate male and female gametes from the gametangia fused to form a zygote. The zygote gave rise to the sporophyte thallus, and the sporophyte produced characteristic thick-walled sporangia, planospores from which re-established the gametophyte. Planospores from the thick-walled sporangium were products of meiosis resulting in the re-establishment of the haploid phase. Such a life-cycle was unique to this lowly amphibian.

Emerson dealt with a whole spectrum of species known until then using type or authentic material, besides many collections from different parts of the tropics, and gave data on occurrence and distribution. Apart from some new species, he also described a variety of *A. arbuscula* (var. *minor*) and three varieties of *A. javanicus* (var. *japonensis*, var. *macrogynus*, and var. *perandrus*). What was noteworthy about *A. javanicus* var. *macrogynus* was that, though it resembled *A. javanicus* in its life-cycle and general aspect, and the gametangia were produced in pairs; the male gametangium was always epigynous, whereas in *A. javanicus* it was variable, being hypogynous or epigynous. The constancy of hypogyny of the male gametangium in *A. arbuscula* and of its epigyny in *A. javanicus* var. *macrogynus*, viewed alongside the inconstancy and variability of this feature in *A. javanicus* (var. *javanicus*), clearly showed that *A. javanicus* had features intermediate between *A. arbuscula* and *A. javanicus* var. *macrogynus*, suggesting the possibility that *A. javanicus* could be a natural hybrid of *A. arbuscula* and *A. javanicus* var. *macrogynous*.

Crosses were now made between *A. arbuscula* and *A. javanicus* var. *macrogynus* by Emerson and Wilson (1954). When this was done, the resulting hybrid, as suspected, combined features of *A. javanicus* var. *macrogynus* and *A. arbuscula*, the gametophytes being characterized by epigyny and hypogyny on the same thallus. This observation was further rigorously tested by a cytological study of the chromosome numbers of the parents, of the hybrid, and of *A. javanicus*. Thus, it now became clear that *A. javanicus* was a natural hybrid, *A. arbuscula*. x *A javanicus* var. *macrogynus.*

Further, it was shown that the hybrid was analogous to hybrid plants in their tendency to form a polyploid series. Emerson and Wilson (1954) postulated that natural *Allomyces* hybrid species accounted for at least some of the polyploid series in this genus. They raised the status of *A. javanicus* var. *macrogynus* to that of a species, *A. macrogynus*. This is a beautiful example of speciation by hybridization in nature. *Allomyces* obviously would not toe the line of Ernst Mayr and his biological species concept! On the other hand, *Allomyces* embraced Hofmeister's theory of alternation of generations. Both cytology and genetics played their role in the *Allomyces javanicus* story.

Despite the early fillip given to studies of simple aquatic and amphibian fungi by E. J. Butler, whose classic monograph on the genus *Pythium* was published in India in 1907, it is a pity that such fungi did not receive the attention they deserve. Rachel John studied aquatic fungi in and around Lucknow with guidance from S. N. Das Gupta in the 1950s. Das Gupta was trained by William Brown at Imperial College in London, while Rachel later worked with W. C. Snyder at Berkeley and finally, with the UNESCO in Paris (and generously gave financial support for a Meeting of Asian Mycologists which I organized in Singapore in 1985). It is a coincidence that Das Gupta himself was with the UNESCO in Paris in 1950; indeed, that is where I was first introduced to him. Part of Rachel's work appeared in the joint names of Das Gupta and Rachel John in 1953, which was supplemented by Das Gupta in 1982; they described many novelties. There is little doubt that there are many more such fungi to be discovered in India and elsewhere in the tropics. In 1958 Das Gupta contributed a most useful review of work in Mycology and Plant Pathology, being part of the History of botanical researches in India, Burma and Ceylon brought out by the Indian Botanical Society.

Emerson's work stimulated further research on sexuality and morphogenesis in *Allomyces* and related blastocladialean fungi, notably by E. C. Cantino, G. Turian, L. Machlis, J. S. Lovett, and M. J. Carlile. The observation that male gametes were attracted to female gametangia, even when they were separated by a dialysing membrane from a liquid culture medium, led to the postulate of a diffusible sexual hormone, sirenin (Machlis, 1958a;b; Carlile and Machlis, 1965a;b). The structure and formula of sirenin have since been elucidated. The synthesis and activity of sirenin is specific to *Allomyces*. It is synthesized by female motile gametes and it acts chemotactically on male gametes.

Coelomomyces

If *Allomyces* arrested our attention, *Coelomomyces* did no less. This fungus was described by Keilin (1921) from a pickled specimen inhabiting the coelome of a single larva of a mosquito (*Stegomyia scutellaris*, possibly a misidentification, *fide* Laird), collected in Malaya (Malayasia). It is a typically tropical genus with many species now known. Two species, *C. anophelesicus* and *C. indicus* from larval anophelines were described from India (M. O. T. Iyengar, 1935). Two other species, *C. sulcatus* on *Culex vishnui* and *C. iyengarii* on *Anopheles vagus*, both from Tamil Nadu, were described by Couch (in Couch and Bland, 1985, pp.263, 185, respectively). During the visit of Mike Madelin from the University, Bristol to the UBL, he and I called on M. O. T. Iyengar who was living in Bangalore and had discussions with him on *Coelomomyces* and his work with the World Health Organization (WHO).

A great deal of our present knowledge of the morphology, taxonomy, biology, occurrence and distribution of this genus comes from the work of J. N. Couch whose visit to India and my Department in Jodhpur I mentioned earlier. Couch made extensive collections of many species of *Coelomomyces* from diverse locations in the tropics, and maintained them in his laboratory in the University of North Carolina at Chapel Hill. Way back in 1968, Couch succeeded in maintaining in the laboratory, larvae of *Anopheles quadrimaculatus* infected with *C. punctatus*. The development of a successful method for *in vivo* laboratory culture of *Coelomomyces* species by Couch helped in the maintenance of a large world collection of *Coelomomyces*.

When I visited Couch for a few days in 1977, he was Professor Emeritus and still active in research. Indeed, he was at the peak of his work on *Coelomomyces* and near-completion of a monograph of the genus. Though he did not now have the funding and assistance he had earlier, his enthusiasm was as high as ever. During my stay at Chapel Hill, he made a point of taking me to his laboratory and showing me his work on this remarkable genus. He had in his collection many species of the fungus on live larvae of the respective mosquito hosts. The mosquito larvae had to be reared and maintained to keep the fungi going on in them. During the days I was there, his assistant was on leave and he then fed the larvae and maintained the live collection himself. He spoke to me with feeling and joy.

For, *Coelomomyces*, which until then was known only on mosquito larvae in which it produced a thallus that produced thick- walled sporangia, was now (1975) shown to infect an entirely unrelated host, a copepod (*Cyclops vernalis*), a discovery by Howard Whisler *et al.* (1975), one of Emerson's students. The planospores (meiospores) produced in the thick-walled sporangia, encysted when they encountered the alternate host, infected it, and re-established the haplophase (gametophyte) in the hemocoel of the animal. In a few days, gamete formation was initiated, triggered by darkness, the events precipitating apparent paralysis and death of the host. The gametes and zygotes swarmed within the copepod, before they finally burst through the cuticle of the cadaver. The zygote infected the mosquito host in which it established the sporophyte.

This was a remarkable discovery which now brought *Coelomomyces* in line with *Allomyces* in its life-cycle pattern. Here, in *Coelomomyces*, then, was a life cycle characterized by an alternation of a gametophyte and a sporophyte, as in *Allomyces*. However, the gametophyte was on a copepod, and the sporophyte on the mosquito larva. The situation can be likened to that in a heteroecious rust fungus such as the black rust (*Puccinia graminis* f. sp. *tritici*) on wheat (*Triticum*) which has a separate aecial host, barberry (*Berberis*). I was thrilled to see through the microscope *Coelomomyces punctatus* with the gametophyte thallus with gametangia within the copepod, and the sporophyte thallus with sporangia within the mosquito larva. Seeing my face light up, Couch made me a gift of two kodachrome transparencies, labelled in his own handwriting, of what I saw; a permanent memento of my visit to him.

He now wanted me to leave behind conidial fungi and embrace *Coelomomyces* instead, in an effort to complete what still remained to be done. What he had in mind was best done in India with its great rice fields which were an ideal environment for both *Coelomomyces* and its mosquito host. Assuring me assistance in procuring taxonomic expertise to identify mosquito hosts, he prompted me to devote time to *Coelomomyces*. Not long afterwards there was a WHO proposal under Whisler's leadership to carry out studies on *Coelomomyces* in southern India which I had occasion to support strongly. Unfortunately, at some level, I do not know what or where, the proposal seemed to have been aborted. To me it seemed as though the wings of a beautiful butterfly had been cut off.

It is pertinent to mention here that one of the two species described from India, *C. indicus*, was a pathogen of medically important anophelines (e,g. *Anopheles gambiae*), known to transmit malaria. Naturally, the potential use of *Coelomomyces indicus* in the biological control of these insect vectors merited study. Following Whisler's discovery of a copepod as the host for the gametophyte of *Coelomomyces*, further studies brought to light copepod hosts other than *Cyclops, Acanthocyclops, Microcyclops, Eucyclops, Mesocyclops, Tigriopus, Harpaticus* and *Elaphoidella*. A further significant discovery was that ostracods were found to serve as hosts for the gametophyte states of two species, *Coelomomyces chironomi* and *C. utahensis*. Beautiful and diverse are the interactions between biota.

During the eight decades of the last century following the discovery of *Coelomomyces* by Keilin, a large number of species of the genus have been described from many parts of the world, many restricted to particular species of mosquitoes, and thus to particular areas of the tropics. An analysis of the distribution of these species shows that they form a number of small or large clusters of species. How these species-clusters evolved is a question that intrigues me. The coevolution and biogeography of *Coelomomyces* are exciting areas for further navigation. Couch's great work found fruition in the monograph on *Coelomomyces* published in 1985, under the joint authorship with one of his students C. E. Bland.

Caulochytrium

Two years later, in 1979 I was again in North Carolina for the Marine Mycology Symposium organized by Jan Kohlmeyer in Morehead City, and took the opportunity to visit Chapel Hill. I could not meet Couch then, but I did meet his successor, Lindsay S. Olive. I had met him earlier, was aware of his work on mycetozoans, and more particularly of his discovery of an interesting chytrid, *Caulochytrium gloeosporioides*, collected in Miami, Florida and parasitic on a conidial fungus, *Gloeosporium*, a plant pathogen! A few years earlier, while preparing lectures for my students, I had come across this interesting chytrid which had several unique features and could not be placed in one of the existing families; I therefore proposed the family, *Caulochytriaceae* (Subramanian, 1974) to accommodate this strikingly interesting chytrid. I had always been fascinated by chytrids, but this was my first affair with one.

When I met Olive he spoke to me about his discovery of a second species of *Caulochytrium, C. protostelioides*, on which he had written a paper; this was collected in St Vincent, in the Caribbean and was parasitic on another fungus, *Cladosporium cladosporioides*. He independently decided to establish a family for *Caulochytrium*, but when he sent the paper for publication, Olive said, it was returned with the comment that a new family had already been proposed. When my paper appeared, I sent a reprint of it to Olive, but he evidently had not received it. Olive then resubmitted his paper making mention of the family I had proposed and placing his new species in it.

After tea I was to give a seminar on the "Phialide" in the Department and, before the seminar, Olive treated me to a dish of *Amanita caesarea*, the *Amanita* that Caesar loved, and some tea. I had never tasted this tasty dish before and had little hesitation in going at it when Olive assured me that it was not one of the hallucinogenic amanitas and that my seminar should go on well! Two years later a paper appeared in the *American Journal of Botany* on zoospore structure of the mycoparasitic chytrid *Caulochytrium protostelioides* by Martha J. Powell (1981). This brought out the ultrastructure of the zoospores, which appeared to be unique among the chytrids so that the status of the family *Caulochytriaceae* now seemed secure, at least for now!

Karling and Tropical Chytrids

The work of John S. Karling is testimony to the beauty and diversity of tropical chytrids. Karling's contributions to our knowledge of a range of so-called lowly organisms is well known and is enshrined in numerous original papers and monographs. He published a series of papers on Brazilian chytrids (Karling, 1945;1946;1947), on Indian chytrids (Karling, 1965; 1966), besides zoosporic fungi from the USA and other regions (Karling, 1932; 1937). Karling came to India at least twice and studied Indian chytrids and related fungi. A great part of our knowledge of Indian chytrids stems from his work. He worked at the Central Marine Fisheries Research Institute at Mandapam near Rameswaram in southern India during 1963-64.

Let me cite here the exciting facts about one of the several chytrids he found in our country. For us the story begins in 1946 when Karling described and named a fungus he isolated from soil and grew on snake skin and other keratinic substrata. He called it *Perirhiza endogena*, but without a valid diagnosis. Following the establishment of a new generic name, *Phlyctorhiza* and the species, *endogena* by A. M. Hanson (1946) in 1947 Karling described his fungus as *Phlyctorhiza variabilis*. It was considered to be a eucarpic, monocentric (i.e. with a single centre of reproduction in the thallus) chytrid that occasionally produced polycentric (i.e. with several centres of reproduction) thalli. Four years later, he found that about 20% of the thalli of the fungus isolated from soil from Israel and Alaska on snake skin were polycentric. It was now necessary to check if planospores from monocentric thalli would perpetuate monocentric thalli only, or a mixture of the mono- and polycentric ones.

Results from six successive generations with monocentric and polycentric thalli showed that both were totipotent for both types of thallus organization. However, the monocentric thalli yielded a preponderance of like progeny, and the polycentric a preponderance of polycentric offspring. From further work on isolates from Brazil, and from New York, New Jersey, Massachusetts, Lousiana, and Indiana, Karling concluded that purely monocentric, purely polycentric, and totipotent strains might be found in nature. The abundant development of polycentric thalli suggested a similarity to the genus *Catenaria*, a blastocladialean fungus close to *Allomyces*. In 1963, W.W. Scott, R. Seymour and C. Warren, finding polycentric thalli in *Phlyctorhiza variabilis,* suggested that both this species and *P. peltata*, another species which had been described by F. K. Sparrow, needed to be removed from *Phlyctorhiza* and reclassified.

In the same year, Karling isolated this fungus from 68 soil samples from Bengal, Kerala, Madras (Tamil Nadu), Panjab, and Rajasthan. Karling concluded that the fungus enjoyed a wide distribution in India, and was a soil inhabitant. When the fungus was grown on human fibrin film and other substrates, the structure, development and growth of the thalli showed that the fungus cannot be retained in the genus *Phlyctorhiza.* Karling now erected the new genus, *Catenophlyctis* for it. But was it a chytrid or a blasocladiad?

Karling concluded his paper in the *American Journal of Botany* in 1965: "Thus, *Catenophlyctis variabilis* is both chytrid- and *Catenaria*-like in thallus organization and may be both monocentric and polycentric. No other species has been found so far which exhibits such a wide and frequent range in organization, and it shows that the categories of monocentricity and polycentricity are not always clear-cut and hardfast criteria for separating genera, families, and orders of zoosporic fungi. It demonstrates also that the lines of demarcation between the *Chytridiales* and *Blastocladiales* are not as sharp as they were formerly believed to be." The focus here is only on thallus organization and not on other parameters on which the two Orders are delimited. Later, in a contribution on the taxonomy of the *Chytridiomycetes* and *Hyphochytriomycetes* presented at the International Symposium on Taxonomy of Fungi at Madras, Karling (1978) placed *Catenophlyctis* in the family *Catenariaceae* in the *Blastocladiales*.

Karling's studies on Brazilian chytrids from the Amazon Valley are a model for anyone wanting to study chytrids in the tropics as they throw light on the beauty and diversity of these fungi and provide information on baits and baiting techniques used by Karling to isolate these fungi. He discovered, described and illustrated many monocentric and polycentric chytrids from the Amazon Valley some of which were found by him in locations in the U.S.A. also. These include species of *Nowakowskiella, Nephrochytrium, Karlingia, Rozella, Rhopalophlyctis*, *Chytriomyces*, and *Siphonaria*, several of them new to science. For most species he described the development and life cycle, unlike in standard descriptions of so-called higher fungi. The genus *Karlingia* was established in 1944 by A. E. Johanson to accommodate a monocentric chytrid, *Rhizophlyctis rosea* which had endo-operculate sporangia instead of inoperculate sporangia that characterize *Rhizophlyctis*. Karling described three new species, *K. granulata, K. spinosa* and *K. hyalina*, besides *K. rosea* from the Amazon Valley.

Though all these species are basically monocentric, occasional polycentric thalli have been observed, an aspect of the development of chytrids already referred to in the discussion on *Catenophlyctis*. Polycentric chytrids such as *Nowakowskiella* develop rhizoid-like extensions from the primary centre that results from germination of a resting spore and often there are several such extensions. They cannot be viewed as a mycelium *sensu stricto* and the term "rhizomycelium" describes what they are. When a nucleus migrated from a centre in what was now a monocentric

thallus, and located itself at some point in the rhizomycelium, a new centre developed at the point. A repetition of this process led to more than one centre leading to polycentricity. Karling's study of the cytology of the *Chytridiales* with special reference to *Cladochytrium replicatum* which appeared in the Memoirs of the Torrey botanical Club in 1937 is basic to understanding the development of rhizomycelium and polycentricity. In *C. replicatum*, sporangia and resting spores developed only in regions of the rhizomycelium where the nuclei became localized and multiplied.

A factor that contributed to success in such studies was the use of innovative techniques and diverse baits by Karling. The use of chitin as a bait is described by Karling (1945) in his paper on two new genera of Brazilian chytrids, *Rhopalophlyctis* and *Chytriomyces*. The predilection of chytrids to specific substrates is reflected in their classification as chitinophilic, keratinophilic and cellulosophilic. Such predilection is an indicator of the nature of the food sources or substrates that such chytrids colonized and degraded. This threw partial light on their life style in the habitat. While many are aquatic, some at least would be amphibian if one considered them as dwellers in the soil. Freshwater chytrids that inhabit the chitinous exuviae of insects seem to be common in nature. Many chytrids in soil seem to be saprophytic, subsisting on their preferred substrate. There are also those that are omnivorous, with no preference to any particular substrate. Some are hyperparasites, and still others parasitic on algae and other aquatic organisms.

Karling came again to India, this time as Raman Visiting Professor of the University of Madras working at the UBL with us in 1965. I accompanied him for collection in the Nilgiris. We both had a ride on an elephant in the Gudalur forest, which reminded me of Aldous Huxley's remark about his elephant ride in Jaipur as “a minor earthquake” in *Jesting Pilate* in 1926. Karling obtained many isolates of his beloved fungi, and his studies were published as a monograph in *Sydowia* in 1966. Karling's two later publications (1977; 1981) reflect his continued and sustained study of these beautiful organisms.

Anaerobic Chytrids

Orpin's discovery, in 1975, of obligately anaerobic fungi in the rumen of sheep set in motion studies on them worldwide. The elucidation of their taxonomy and biology led to several exciting findings. Thus, they were shown to be chytrids, but chytrids that lacked mitochondria, possessed hydrogenomes, and produced formate, acetate, lactate, succinate, ethanol and hydrogen. Orpin's discovery was momentous in the sense that it cut at the age-old view that the fungi are, by definition, aerobes.

Sapromyces

I recollect a collection trip over 50 years ago to the Kambakkam Hills north of Madras, which used to be a favourite collection spot for us in the UBL. M. O. P. Iyengar who was on this trip had an eye for microscopic algae of freshwaters and puddles, and among the many common and rare algae he collected was what he recognized under the microscope as a fungus. Having studied this interesting find and made camera lucida sketches in his characteristic way, he called me and Ramakrishnan, and after showing us the fungus, passed on the material to us for study. We tracked the fungus down to the genus *Sapromyces* of *Rhipidiaceae,* of which four species were then known (Thaxter, 1896; Sparrow, 1943).. But the Iyengar collection was distinct from those.

At this stage we got back to Iyengar and suggested that he publish a paper on the new find. But he was quite firm that he was no mycologist and a paper must go in our joint names alone, and without his name. However, following persistent appeals, he finally agreed, and a paper on the new species, *S. indicus* appeared under the authorship of our three names (Iyengar, Ramakrishnan and Subramanian, 1955). Currently, *Sapromyces* is classified in the *Chromista* along with other water moulds and algae. Thus, my dream of working with Iyengar on algae, albeit ones with no chlorophyll, was fulfilled. That only five species of the genus were known since the genus was established in 1893 might seem to suggest that it is a genus possibly on the road to extinction, but it might also be that exploration of water moulds in nature is on the decline!

Saksenaea

As already mentioned, the soil is a great reservoir of fungi in which novelties abound, and the temptation to cite yet more examples persists. One of the most lovable and respected among my friends was S. B. Saksena who led an active school of research in the Saugor University at Sagar in Madhya Pradesh in India. Saksena worked on soil fungi, and one of his early discoveries was a most interesting zygomycete, the group to which the common bread mould, *Rhizopus* belongs. Saksena's fungus was beautiful, and was unique. It had solitary, flask-shaped sporangia, each with a long neck and a columella and rhizoids subtending each sporangium. It could not be accommodated in any of the known genera, and Saksena erected the new genus, *Saksenaea* for it in honour of his teacher, Ram Kumar Saksena of the Allahabad University, and the fungus itself was called *S. vasiformis*, from the flask-shaped sporangia (Saksena,1953).

Saksena once narrated how the culture remained sterile for months and, in his hopelessness, it dawned on him to bait it in water and the fungus dramatically produced the vesicular sporangia. Later work showed that it had a worldwide distribution, and yet a sexual stage is not yet known. On the other hand, it has been shown to be a pathogen and the cause of disease in humans (Ajello, Dean and Irwin, 1976). Infection could be rhinocerebral, cutaneous or subcutaneous, or disseminated (osteoarticular or pulmonary). Infection from contaminated catheters has also been reported. In addition, *S. vasiformis* has been reported to infect the killer whale (*Orcinus orca*), Pacific white sided dolphins (*Lagenorhynchus obliquidens*) and bottlenose dolphins (*Tursiops truncatus*) in captivity (Robeck and Dalton, 2002). Infection in some cases has been fatal and fairly speedy, death occurring about three weeks after the first clinical symptoms. In all cases, the fungus became systemic, even occupying the central nervous system. Its medical importance has prompted continued study, and the uniqueness of the fungus in the

zygomycetes won for it placement in a separate family, *Saksenaeaceae* (Ellis and Hesseltine, 1974).

Fungal Successions

Colonization and succession are part of the life-style of fungi. Be it the leaf, young or senescent, or stem or bark, or subterranean root system of the plant or tree, there was a fungus already there on the surface or within. Many plants harbour endophytes invisible outside, and such endophytes could well be the primary colonizers of the living plant. In some trees, the endophytic mycelium could be perennial. The living root, the living leaf, and the living stem, each of them is a microhabitat for specific fungi. Many apparently 'sterile' fungi are closely tied to the rhizoplane, the root surface, which is colonized by pathogens, mutualists, and saprophytes. Here there is a fungal succession that represents stages in the decadence, followed by decomposition of the root when it no longer serves the needs of the plant.

Similar colonization and succession processes occur on leaves and twigs, and in the litter of which they form a part. The patterns of succession in terrestrial, aquatic and marine habitats differ not only from differences in the physical, chemical and biological conditions, but also from the differences in the component mycobiota peculiar to each habitat. The coprophilous fungal succession has been studied by many, and two of my students, B. C. Lodha and K. V. Chandrashekara have described the fungal succession on dung and excreta of animals and beautifully illustrated the many novelties that appeared in the coprophilous fungal succession. In most successions, sugar was first utilized by 'sugar fungi' followed by ones which utilized cellulose, hemicellulose, and lignin, in that order. Thus, in most successions, the lignin-decomposing basidiomycetes were the last to appear. The rate of decomposition depended on many factors. For example, nitrogen in soil was often a limiting factor in the decomposition of cellulose.

In his study of fungal succession on wheat roots, Sadasivan (1939) noted that the addition of nitrogen to soil hastened decomposition, whereby *Fusarium culmorum* was soon replaced in the succession by fungi such as *Trichoderma* and *Penicillium* species. There are many imponderables in nature, so that patterns of succession vary. Even in litter, specific fungi preferentially colonized leaves of different plant species. The relationships of the various fungi to the variety of substrates available in litter are really complex when you come to think of the many kinds of interactions and arrangements that would seem likely. Both B. P. R. Vittal and K. Sudha who studied with me fungal succession in different plant species over time, provided confirmation of this. They described several novelties, including new species and new genera, and showed how the primary fungal colonizers showed marked specificity, whereas late entrants in the succession had little or no specificity. In many cases, the 'primary colonizers' may be endophytes fruiting. I have discussed these and other fascinating aspects of fungal succession in detail elsewhere (Subramanian, 1983).

Fungal successions in cooling towers and in industrial effluents such as those from factories producing fertilizers or oil refineries are very different from successions in natural ecosystems. My students, M. Udayan, S. Sankaran, and J. Savitha have contributed to these studies and described the nature of the fungal species in the fungal succession in cooling towers and industrial effluents. An analysis of such data as are now available from such studies would show the rather poor spectrum of fungal species involved compared to litter or soil. Such studies demonstrate the inhospitality of some of these technology-driven environments to fungi, as distinct from the natural environment. They also demonstrate that some fungi manage to thrive even in the face of inhospitality. They serve to highlight the importance of a healthy environment for healthy life, a life of quality.

Fungal Speciation

During the past 60 years, I have been concerned with species, names, and concepts linked to taxa and taxonomy. I have been excited about their diversity, their form and their life-style, of which we know a great deal. But we know little about their evolution, of their speciation. John H. Burnett stressed the fact that "there is, as yet, no comprehensive and systematic corpus of ideas concerning the origins of species in fungi." (Burnett, 1983, p. 1). I shall touch on just a few examples.

The genus *Amanita* seems to have diversified, for example, along at least three lines represented by the edible (*A. caesarea*), the poisonous (*A. phalloides*) and the hallucinogenic (*A. muscaria*) kinds, which also represent distinct features in secondary metabolism. Could there not be other lineages here, on this or other criteria, such as those that are mycorrhizal and those that are not? Oda *et al.* (2004) probed the molecular phylogeny and biogeography of two *Amanita* species (*A. muscaria* and *A. pantherina*) from diverse localities. *A. muscaria* fell into three biogeographical regions, Eurasian, Eurasian-subalpine, and North American. Speciation of *A. muscaria* seems to have occurred in Eurasia followed by migration to North America along land bridges. Future studies would give us a better understanding of these issues.

Consider, for example, host preference in parasitic fungi such as *Claviceps*, species of which primarily colonize *Poaceae* (rarely *Cyperaceae*). They have co-evolved with their hosts (Clay, 1988; White *et al*., 2003). The *Ephelis* anamorphs of *Balansia* colonize grasses (rarely sedges also), mostly in the tropics (Diehl, 1950; Govindu and Thirumalachar, 1984). How does speciation proceed in these fungi? There are also many other fungi preferentially colonizing grasses such as the 'graminicolous' Helminthosporia which have been referred to earlier. The genus *Taphrina* has species that cause leaf-curl or witches brooms in dicotyledonous hosts that are primarily temperate, with the exception of *T. maculans* (Butler, 1918; Butler and Bisby, 1931) which is tropical and causes, not leaf-curl but leaf- spots, on species of *Curcuma*, *Hedychium* and *Zingiber*, all monocots (*Zingiberaceae*). *Taphrina maculans* has intrigued me for a long time from its uniqueness in host preference, and its propensity to cause leaf spots (justifying the epithet 'maculans').

The genus *Kordyana*, established by Raciborski (1900) for

Exobasidium tradescantiae Pat., of which five species are known, parasitizes *Commelinaceae* in which it induces leaf-spots. The genus *Brachybasidium* was proposed by Gaeumann in 1922 for *Kordyana pinangae*, collected and described by Raciborski on *Pinanga* (*Palmae*) from Java. It is tropical, monotypic, and does not appear to have been reported again. *Graphiola* (*Graphiolales*, *Ustomycetes*) occurs on *Palmae* in the tropics; *G. phoenicis* is ever present on *Phoenix* and is very common.

Extending consideration further to genera belonging to the *Exobasidiomycetidae*, from present knowledge, we note that the host spectrum of *Botryoconis* is limited to the *Lauraceae*, *Coniodictyum* to the *Rhamnaceae*, *Georgefischeria* to the *Convolvulaceae* and *Tilletia* to the *Poaceae*. *Ustilago esculenta* preferentially infects *Zizania latifolia* (Manchurian wild rice), widespread in south-east Asia. *Entyloma* and *Exobasidium* infect only dicots, whereas *Doassansia* infects both dicots and monocots. Even within a preferred host spectrum, some of these fungi preferentially infect ovaries, anthers, or heads. The evolution of host-specialization of these fungi needs further scrutiny and we need to explore the tropics specifically for them to understand the pattern and modus of evolution. Host preference and specialization occurs in all fungal groups and at all levels. In the rust fungi, *Sphaerophragmium* is a small genus of about 16 species that are tropical, mostly on *Leguminosae* (Lohsomboon *et al*., 1994). About 200 species of *Ravenelia* are known, which are autoecious on legumes and are also tropical. Species of the rust genus *Kernkampella* are widespread and infect *Euphorbiaceae*.

Several tropical genera have remained monotypic of which some examples have been noted already. *Trichocoma* (Junghuhn, 1838), originally described from Java, has remained monotypic, despite its wide distribution in the tropics. Boedijn (1935a) recorded collecting the fungus, only occasionally, and then on erect, standing wood, but not on fallen, decaying wood. *Penicilliopsis* (Solms-Laubach, 1886), also originally described from Java, and again a member of the *Trichocomaceae*, now accommodates at least three species (Samson and Seifert, 1985; Hsieh and Ju, 2002) and is also tropical. *Dendrosphaera* Pat. (Boedijn, 1935b) is yet another closely related, tropical, monotypic genus whose distribution appears to be limited to south-east Asia.

Large species assemblages such as what we have in *Fusarium*, *Penicillium,* and *Aspergillus* are other examples which have intrigued me. They reflect so much diversity in life-style, habitat, and metabolism that I have always wondered how speciation could have occurred. At the other end of the spectrum, as we have noted, we have small species assemblages and monotypic genera. This may be a reflection of incomplete inventory, or poor speciation, or a sign of extinction. While fungal enumeration must continue before extinction overtakes enumeration, it is also important to pay attention to questions of speciation.

In a recent study on the *Gibberella fujikuroi* complex, but specifically on *Fusarium subglutinans*, Steenkamp *et al*.(2002) identified two major groups representing cryptic species further divided into a number of subgroups that appeared to be reproductively isolated in nature. They believe that extant populations of this taxon are in the process of divergence and also that each of the resulting lineages is undergoing separation into a distinct taxon. In drawing these conclusions, the authors are refreshingly cautious and hold that we are still in the learning phase in respect to methodologies and interpretation of results, and more important, we are still in the process of developing a definition for a fungal species and how to recognize this unit. The morphological, the biological and the phylogenetic concepts of species are facets of one and the same thing and, I believe, cannot be other than complementary. The application of concepts and their interpretation is, of course, important.

Early in this account, I referred to my meeting J.S. Niederhauser in the Linne garden in Uppsala, his discovery of the origin of *Solanum demissum* and his work on disease resistance to combat late blight caused by *Phytophthora infestans*. The importance of *Phytophthora* species as plant pathogens worldwide has led to special focus on origins and speciation of *P. infestans* and allied species. A contribution from Gomez-Alpizar *et al.*(2008) reports recent findings on the origins and speciation in *P. infestans*. The Andean highlands of South America are home to three clonal lineages, US-1, EC-1 and EC-3, besides EC-2, a heterogeneous assemblage. They have a host spectrum of different species of *Solanum*. Two mitochondrial (mtDNA) haplotypes 1a and 1c are recognized in the EC2 lineage. From molecular studies Gomez-Alpizar *et al.*(2008) have arrived at important conclusions.

The EC-2 assemblage associated with section *Anarrichomenum* of *Solanum* has a lineage divergent from *Phytophthora infestans* and must be considered distinct, from molecular parameters, though this assemblage answers to the morphological description of *P. infestans*, a situation I have referred to earlier as likely to become more common. Besides *P. infestans*, *P. phaseoli, P. mirabilis* and *P. ipomoeae* belong here. These species are host-specific, with *P. infestans* on *Solanum tuberosum* (potato) and wild *Solanum* spp. (*Solanaceae*), *P. phaseoli* on *Phaseolus* (*Leguminosae*), *P. mirabilis* on *Mirabilis jalapa* (*Nyctagineae*) and *P. ipomoeae* on *Ipomoea longipedunculata* (*Convolvulaceae*).

These species are believed to have undergone sympatric speciation in the Toluca valley in central Mexico. A new species, christened *Phytophthora andina* is considered a natural hybrid between *P. infestans* and *P. mirabilis*, from a consideration of their biology and phylogeny using different methodologies. The hypothesis that the central highlands of South America are the centre of origin of *Phytophthora infestans* and allied species (Niederhauser 1991; Brasier and Hansen 1992; Goodwin *et al*., 1992; Flier *et al*., 2003) receives support from these findings. That the population in the region is sexual with both mating types, A1 and A2, further strengthens this view.

Part Two

ORGANIZATION OF MYCOLOGY IN THE TROPICS

I now turn to the organization of mycology which is central to the development of mycology itself mycology in its broadest sense.

Mycology in India

We owe the early development of mycology in India to sporadic collections of fungi by foreign missionaries and naturalists, and the naming of these collections by naturalists and mycologists primarily from Europe and especially the United Kingdom. The organization of mycology came later, with the arrival of E. J. Butler in India in 1901 as Cryptogamic Botanist stationed at Calcutta. Butler was Imperial Mycologist at the Agricultural Research Institute at Pusa, in what is now Bihar, from 1905-20. Early mycological work was confined to the Institute at Pusa. The first Province to have a Government Mycologist was Madras where W. McRae began mycological research during 1909-1910, working at the Agricultural College and Research Institute at Coimbatore.

Besides initiating research in mycology and plant pathology, Butler trained a number of colleagues who made important contributions. Butler's *Fungi and Disease in Plants* (1918) and *The Fungi of India* (1931, jointly with G. R. Bisby), are major contributions. Butler also issued Exsiccatae of Indian fungi, jointly with H. and P. Sydow, and also established a Herbarium of Indian fungi, the "Herb. Cryptogamie indiae orientalis" (HCIO) at the Institute at Pusa. He brought together mycological workers in a common forum to discuss problems and benefit by mutual discussion. He organized two such meetings, of which the second was held in Pusa on 20 February 1919 and subsequent days, prior to his departure from India the following year. The meeting was attended by all leading mycologists in the country, 22 in number, including F. J. F. Shaw, J. F. Dastur, Froilano de Mello, W. McRae, A. C. Tunstall, S.L. Ajrekar, G. S. Kulkarni, S. Sundararaman, L.S. Subramaniam, and K. F. Kheswalla. It was at this meeting that a resolution recommending establishment of an Imperial Bureau of Mycology in London on the pattern of the Imperial Bureau of Entomology was passed after thorough discussion (see Stuart, 1919).

The recommendation was accepted by the Governments of India and of Britain, and the Imperial Bureau of Mycology was established in London in 1920. Butler was appointed its Director in the same year. In passing, I should mention that the idea of a Bureau of Mycology first came from W B Brierley, speaking at the meeting of the British Association for the Advancement of Science at Newcastle in 1916. The proposal was considered and accepted by the Imperial War Conference in 1918. Overseas governments concurred and even came forward to finance the project for a period of three years to begin with. The UK, Canada and India contributed 250 pounds sterling each, Australia and South Africa 150 pounds sterling each, New Zealand 100 pounds sterling and the balance of 850 pounds sterling by Sudan, Egypt and other Colonies. The Bureau functioned at 17-19 Kew Green. The Bureau, later named the Commonwealth Mycological Institute, moved into a new building within the boundary of the Royal Botanic Garden (RBG), Kew on Ferry Lane in July 1930. The cost of the building was met from a grant of 8000 pounds sterling from the Empire Marketing Board.

Butler was a man with a vision, a man with a mission. During his stay in India, he initiated and fostered research in mycology and fungal diseases of plants in relation to agriculture and forestry. As a result, such research came to be centred in the Departments of Mycology in agricultural colleges and institutes in the country. In the traditional universities, mycology was taught as part of courses in botany and, in consequence, the emphasis on mycology was generally inadequate. As taught in the traditional colleges and universities, mycology had mainly a morphology-taxonomy content. On the other hand, courses in the agricultural colleges and institutes had a strong emphasis on fungi as pathogens of plants. Only in the beginning of the last century did mycology receive better emphasis in curricula with the appointment of teachers specially trained in mycology in well-known centres abroad. Thus, mycology came to receive special attention in a few Indian centres such as Agra College (K. C. Mehta), the University of Allahabad (Julian H. Mitter, R. N. Tandon, R. K. Saksena), the University of Lucknow (S. N. Das Gupta), and the R. K. Kar Medical College, Calcutta (S. R. Bose). At the turn of the last century, then, the major contributions in the twin disciplines of mycology and plant pathology came from agricultural institutions. Since then, the leadership of teachers trained in mycology led to further development of the subject in several traditional university centres all over the country. In the Punjab University at Chandigarh, for example, K. S. Thind and his students surveyed and described the larger fungi, especially of the Himalayan region *Aphyllophorales*, *Clavariaceae, Discomycetes, Xylariaceae*. Thind authored a monograph on the *Clavariaceae* and another on *Myxomycetes*. He was a great contributor to our science and a dear friend (Thind, 1961). He had his training in Plant Pathology at Wisconsin in the USA but devoted a lifetime to taxonomic mycology. At the Maharashtra Association for Cultivation of Science (MACS), Poona (Pune), M. N. Kamat and his students pioneered exploration and study of fungi and lichens of Maharashtra. In Agra College, plant pathology continued to flourish, now under the leadership of Shaligram Sinha, with additional inputs in seed pathology with the active collaboration of Paul Neergaard. In the University, Allahabad too, the mycological tradition continued, now with commendable inputs from B. S. Mehrotra and his colleagues. In the Saugor University in Madhya Pradesh, soil mycology and fungal diseases of plants were the focus of vigorous study by S.B. Saksena and his students. In the University at Gorakhpur in Uttar Pradesh foliicolous fungi (the *Cercospora* complex) were collected and studied critically by Kamal and his co-workers. In the Rajasthan University at Jaipur seed pathology grew from the initiative of B. L. Jain with support from Paul Neergaard.

With training from P.H. Gregory at Rothamsted, T. Sreeramulu initiated researches in aeromycology in the Andhra University at Waltair. In the University at Mysore K. M. Safeeulla organized studies on downy mildews

culminating in the publication of a monograph of this important group. In the University of Delhi mycology developed led by K.G. Mukerji who made important contributions to fungal taxonomy and biology. An active group in lichenology grew around D. D. Awasthi and around J. N. Rai in general mycology in the University, Lucknow. In the University at Madras, freshwater fungal parasites of algae received special study from M. O. P. Iyengar as part of study of algae. Research in mycology and plant pathology came to be initiated by Iyengar's successor, T. S. Sadasivan. An active mycological research group grew around C. V. Subramanian in the late 1950s. Many students trained in the various centres mentioned above are currently inheritors of the legacy. These developments centred in Departments of Botany in Universities and Colleges in the country. The Indian Botanical Society and its Journal fostered the development of mycology alongside other botanical disciplines.

Fungal exploration and description during the past six decades led to fungal enumeration on a modest scale, although several fungal groups and several potentially rich areas in the country have hardly been touched. In a vast country like India with its varied biota, it would be unwise to allow the emphasis on molecular approaches to thwart the development of descriptive biology which, in the final analysis, is basic not only to biology but to science itself. Science must be a judicious combination of description, experiment, and theory. The application of science to human needs is also an imperative.

In laying a foundation for mycology, E. J. Butler took note of these requirements, and tried to meet them. His discovery of *Allomyces* highlighted the importance of exploration, study and description. By his study of the genus *Pythium*, and publication of a monograph of this genus in 1907, Butler focused on the need to monograph fungal genera. In another contribution, he highlighted the importance of vesicular arbuscular fungi in agriculture and forestry (Butler, 1939). In yet another contribution, he dwelt at length on the relevance of what he called “economic mycology” to human needs and welfare (Butler, 1929). In fact, the relevance of fungi touched numerous facets of human acivity and human needs that called for a comprehensive coverage and application of mycology appropriate to each facet. In founding the *Review of Applied Mycology* in 1921, Butler provided a source of information on all aspects of mycology and the application of mycological knowledge in the fulfilment of human needs, gleaned from the world's scattered literature in several languages, a stupendous effort considering the conditions that obtained then (I was unhappy when the name of the journal was changed to the *Review of Plant Pathology* by the CAB the change narrowed the scope and coverage and went against the very spirit and objective of the founder!).

There are several questions that we have to address. How can we harness fungal power to our needs? How can we identify the fungal power that lies hidden in nature and is therefore not available to us? And how can we share the fruits of research for the benefit of humankind globally? We need to strengthen the pipeline of information and its network. Early in the development of the Imperial Bureau of Mycology, the Bureau provided support in the form of information and bibliographic facilities to the authors of works on plant diseases of the tropics: for example, to Briton-Jones for writing the books on diseases of cacao (1934), and diseases of the coconut palm (1940), to Wardlaw for writing on the diseases of the banana (1935), and to Sharples for writing on the diseases of the rubber tree (1936). The publication of the *Bibliography of Systematic Mycology*, the *Index of Fungi*, and of *Mycological Papers* and *Phytopathological Papers* by the CMI were part of this broad objective. A basic requirement to do all this is the strengthening of teaching and training in mycology and mycology-related other skills and disciplines.

The induction of faculty trained in mycology in traditional universities into agricultural colleges and institutes in the country led to strengthening the mycological base in agricultural institutions. B. B. Mundkur, one of India's most respected mycologists, took his honours degree in Botany from the Presidency College, Madras (a student of M. O. P. Iyengar), and after doing field and laboratory research on plant diseases, taught mycology to students taking the Associateship at the Indian Agricultural Research Institute, New Delhi. After retirement, Mundkur organized the Botany Department at the University of Poona at Poona. Mundkur wanted to build his Department into a centre for fungal taxonomy and medical mycology, but he died in 1952 before his dream could be realized.

My first encounter with Mundkur was unanticipated and in unexpected circumstances. In the summer of 1948, while on a short holiday at my native Ernakulam, in what is now Kerala State, my maternal uncle who lived in a bungalow on the banks of the river Alwaye, informed me that, at the request of the Fertilizer Company (Fertilizers and Chemicals of Travancore, FACT for short) in Alwaye, he was entertaining at tea a group of agricultural scientists from the Indian Council of Agricultural Research, Delhi, and he wanted me to meet them as I had by then obtained my doctorate in botany. My uncle introduced me to the scientists saying I had a PhD in plant pathology. When I mentioned soil conditions and *Fusarium* wilt of cotton as the topic of my research to the group, one of them wanted to know where I worked and, given the information, showed surprise and unbelief at a doctorate having been awarded to one who (he assumed) had little training or expertise to identify Fusaria. The gentleman was excited and, giving his name as 'Mundkur', asked me “who gave you the PhD degree?” I was surprised. I knew about Mundkur's work and his reputation as a scientist. I merely said, “the University, on the recommendation of the examiners of the thesis.” Mundkur's concern seemed to be that there was no expert fungal taxonomist who could help a novice like me at Madras.

I mentioned this episode to my mentor on my return to Madras, but there was no reaction from him. Three or four years later, at one of the meetings of the Indian Science Congress, which my mentor attended, Mundkur reportedly walked up to him to say that he (Mundkur) happened to be the referee for a series of papers on *Fusarium* which were being considered for publication in the *Proceedings of the National Institute of Sciences of India*, and he was happy to see the

good work of the young scientist (referring to me) from Madras. This was reported to me by my mentor. I felt very happy. Around this time (1952) the publication of a *Supplement* to the *Fungi of India* by K. Ramakrishnan and I attracted Mundkur's attention and, as one who knew the difficulties involved in bringing out an authoritative list, he wrote to my mentor applauding our effort.

Later, in his Presidential Address to the Botany Section of the Indian Science Congress in Bangalore, Mundkur surveyed the "Study of Systematic Mycology in India" and wrote: "Many fungi belonging to the Fungi Imperfecti group await discovery of their perfect states. I understand that in one University the study of Fusaria has been recently taken up. I hope that a school will soon develop there so that we can turn to that University for identifying our cultures of these ubiquitous organisms. May I plead that this genus and the allied genera be mastered there, leaving alone the problems of control of diseases to the Agricultural Departments?" (Mundkur, 1951, p. 167).The reference was to the UBL. Finally, when he retired and began organizing the Botany Department in Poona University, he became a friend and regular correspondent, writing to seek suggestions for organizing the new Department.

Benjamin P. Pal, one of India's leading lights in plant genetics and plant breeding, and a former Director of the I.A.R.I., earned his Master's degree in botany from the University of Rangoon in Burma. At the Post-Graduate School established in 1958 following the granting of university-status to I.A.R.I. by the University Grants Commission, students were selected for admission from both the traditional and the agricultural streams. The complementary benefit of these two streams is obvious. In the UBL in Madras where I began my research over 60 years ago, students were admitted from the traditional stream to begin with, but with the recognition it gained in mycology and plant pathology, agricultural graduates were attracted to join the UBL for research. And we took them in.

Here then was a beautiful fusion of the two streams. A direct result of this was a clear strengthening of the teaching of mycology and plant pathology. The post-MSc one-year Diploma Course that we organized in the UBL for students joining us (something like the Diploma of Imperial College in the University of London) was in Mycology & Plant Pathology. (There was another, in Algology). In the post-Independence scenario in the country, mycology figured prominently in several Departments of Botany in the traditional Universities.

Following my first visit to Britain in 1950, my contacts with mycologists overseas had grown from friendship and correspondence, and they grew further following my second visit in 1964. During my visit to the CMI at Kew in the summer of 1965, I envisaged the possibility of some kind of an exchange programme between our Centre in Madras and the CMI whereby there could be mutual visits on a short-term basis, something that would benefit both institutions. The opportunity came soon after, when Lilian Hawker from the University of Bristol visited the Centre. Her visit was sponsored by the British Council. I had by then suggested the idea to my mentor, the Director of the Centre, T. S. Sadasivan. He supported the idea with gusto and we put forth the same to Lilian Hawker. Lilian liked the work and the atmosphere of the Centre. On her return to Britain, she gained the support of the British Council for the idea in principle, but the modalities had still to be worked out.

Following in the wake of Lilian Hawker's visit, came a visit from Geoffrey Ainsworth who had suceeded John C. F. Hopkins as Director of the CMI in 1964. Though Ainsworth had examined a couple of Ph.D. theses from our Centre, this was his first visit to us. When I mentioned to him the idea of a possible exchange programme between our Centre and the CMI, he concurred. Now we put forward a proposal to the University Grants Commission where we envisaged an exchange programme between our Centre and various institutions in the UK whereby travel costs could be met by the guest institution and hospitality by the host institution, reciprocally. When the UGC gave its approval, the British Council had no difficulty in accepting the proposal.

The first of a series of exchange visits began with that of Kris Pirozynski of the CMI to our Centre in 1965. CMI was happy to send Kris to Madras to work with us. The interaction with Kris was wonderful, and he made many collections of fungi especially in the Nilgiris and, I suppose, that there are many collections yet to be named. My colleagues and students and I benefited from our interactions and discussions with him. Once begun, well done! We had many visits from Britain, and many visits to Britain, enriching mycology, plant pathology and algology in both countries.

The first visit to Britain under the programme was mine, and I worked in Lilian Hawker's Department in the University of Bristol for some months in 1968. I was honoured by the University of Bristol with a Visiting Professorship. The focus of my work was on conidiogenesis, and I tried to use scanning electron microscopy to solve some of the problems, besides lecturing to the students. I received much help from Mike Madelin, Richard Campbell and Alan Beckett in this effort. The trio formed a dynamic research and teaching group. I had many discussions with Mike Madelin, often over lunch or dinner, on topics of special interest and we often agreed to disagree, parting as friends and remaining friends. Criticism is often the prelude to agreement.

The British Council arranged visits to several centres including the CMI, and the Freshwater Biological Station at Ambleside in north-west England where I saw L. G. Willoughby's work on chytrids and related aquatic fungi, and also got to know methods of collection and study of freshwater aquatic fungi. I saw work on freshwater algae and fungal parasites of algae by the Lunds, J. W. G. and Hilda-Canter, husband and wife. I spent a pleasant evening with them at their home talking about algae, fungi, and Iyengar. Algae and aquatic fungi that go with them are a fascinating group. Visiting Edinburgh, I spent time with Mary Noble to learn and talk about seed-borne fungi and seed pathology. The laboratory at East Craigs had a team with M. J. Richardson who enlightened me about cereal and seed pathology and related problems.

The 1968 autumn Foray of the BMS at Kindrogan which I attended with Lilian Hawker introduced me to British larger

fungi and micro-fungi, and mycologists whom I had not met before. (At an International Symposium in Thailand some years ago, Anthony J. S. Whalley from Liverpool John Moore's University recollected and reminded me of our first meeting at the Kindrogan Foray). It was also during this visit that I met Terrence Ingold for the first time when I called on him at Birkbeck College by prior appointment. Ingold spoke to me about aquatic hyphomycetes and gave me a copy of his little book on these fungi which was published by the Freshwater Biological Station at Ambleside. Canter-Lund's early work was with Ingold. My visit to Manchester and to John Colhoun revived interest in *Fusarium*, and a visit to Swansea and to Ivor Isaac revived interest in *Verticillium*. I visited Charles G. C. Chesters again and saw the work of the active group of his colleagues (Apinis *et al.)* and students in Nottingham. I dined with Geoffrey and Bridgett Pugh in their home where we discussed not only mycology but D. H. Lawrence and 'Lawrence country'.

I combined a visit to Fred Last (then at the Glasshouse Crops Research Institute, Littlehampton) and to Gareth Jones, Steve Moss and others at Portsmouth. At Liverpool, G. N. Greenhalgh and I talked about *Hypoxylon* and its conidial states and taxonomy. There was a fruitful meeting with Eggins to learn about biodeterioration and fungal relevance which is very much a global issue. At Hull my long-time friend N. F. Robertson and I recollected our days in Cambridge. Noel was now concerned with problems of fungal morphogenesis, a theme that fascinated me. My visit to Sheffield to see John Webster was, as always, most rewarding. John is a true mycologist, one who combined field studies and laboratory work in a judicious way and spent a good deal of time and effort to achieve the best results in teaching and learning. We went out collecting around the University campus and John assured me that one could get much of what was needed for classroom study and instruction in the campus itself. .

I also attended the Commonwealth Plant Pathology Conference organized by the Commonwealth Agricultural Bureau, and the First International Congress of Plant Pathology in London in August 1968 where I had the opportunity to see many old friends and make new friendships. I saw E. C. Stakman again, and the *Fusarium* specialist W. C. Snyder for the first time. It had not been possible for me to attend the Symposium on Soil-borne Plant Disease which Snyder organized at Berkeley in 1964. His joviality and friendliness marked his uniqueness as a great teacher and scientist and drew me to him ever closer. Three years later he visited us at Madras. I saw him last at the *Fusarium* Conference in Berlin-Dahlem in 1978. He hoped then to have the next *Fusarium* Conference in Honolulu in Hawaii where one of his students was then working and said he expected me to join. That, however, was not to be! Mycology and Plant Pathology are so closely linked that one can never think of the one without the other. Each of these disciplines has contributed in no small measure to the other, a fact that was reflected in the proceedings of the Congress. On my way back to India I visited Gregoire Hennebert again, in Louvain, Belgium. I recollect his arranging my visit to the Institut J. B. Carnoy and meeting P. Martens, whose classic contribution to sexuality in *Ascomycetes* in *La Cellule* (1946) was well known.

During 1975-1985 I sought and succeeded in getting support from my University, the UGC, and the British Council for a proposal whereby we could have relatively long visits to the CMI from pre-Doctoral research Fellows who could pursue part of their research for a doctoral degree at the CMI, benefitting from the expertise and other facilities available there. Three of my students (G. Sekar, J. Muthumary and D. Ananthapadmanabhan) who were beneficiaries of this scheme did excellent work. Initially there was objection from the UGC for the proposal on the count that the CMI was not a teaching institution. But I told them that I myself had been trained at the CMI.

The First International Mycological Congress: The International Mycological Association (IMA)

From an early beginning the development of mycology was linked to Departments of Botany in traditional Colleges or Universities in the West as well as the East. Botanical Societies fostered the development of mycology as part of the larger development of Botany. As we have noted, George F. Atkinson who described *Fusarium* wilt in cotton for the first time was the first President of the Botanical Society of America (1907). In its formative years the Society had as Presidents Roland Thaxter (1909), Erwin F. Smith (1910), William G. Farlow (1911) and Lewis R. Jones (1912), all distinguished for their contributions to mycology and plant pathology. Since then, several mycologists and plant pathologists have been elected to the august office. Many landmark papers in mycology have appeared in the American Journal of Botany and continue to do so. There is the parallel in India of the Indian Botanical Society and its Journal, the Journal of the Indian Botanical Society in which many mycological papers have appeared.

Successive International Botanical Congresses embraced mycology and plant pathology in their fold and continue to do so. The attendance and active participation of mycologists and plant pathologists at the International Botanical Congresses at Stockholm (1950), Edinburgh (1964), Seattle (1969), Leningrad (1975) and Sydney (1981), which I attended, were overwhelming. Each Congress had a flavour of its own and reflected the status of our science at a given time. At the Seattle Congress, Stafleu (1969) gave a factual account of the proceedings and trends of past Congresses, at least partly from his own experience of successive Congresses. He noted the all-inclusive character of the 1926 Ithaca Congress which was called the International Congress of Plant Sciences. As Faegri (1975) noted, the Congresses helped effective exchange of ideas beyond disciplines and subdisciplines, transgressing boundaries that separate narrow specialities. I have already written about the Stockholm and Edinburgh Congresses in this account.

For many reasons, the Leningrad Congress was an attraction for many, especially in the West, and we had a very well attended Congress. And Leningrad is a city with a character. Armen Takhtajan was President of the Congress. There was the opportunity to meet our Russian counterparts. Thus, I met

M. A. Litvinov, V. I. Bilai, M. P. Cherapanova, I. A. Dudka and others. Communication in English with them was not easy, but with younger mycologists like Dudka it was easy to converse. Dudka's work centred on Ingoldian fungi and her monograph of Ukrainian Ingoldian fungi of which she gave me a copy is an important contribution. Bilai's work on the taxonomy of *Fusarium* is well-known and I was happy to meet her. It was also good to see E. J. H. Corner again. Though aware of her work, it was at the Leningrad Congress that I met Vera Holubova-Jechova for the first time and established a friendship that cannot be erased. She had collaborated actively with colleagues in the tropics on tropical fungi with commendable friendship. During the Congress there was a mycologists' banquet one evening at which I was invited to be the Chief Guest, a signal honour and friendly gesture. Those who could, danced to the music of mycology in a friendly way, symbolic of a coming together!

At Seattle and Sydney too, mycology was amply represented. The Seattle Congress at the University of Washington was memorable in many ways. For example, we had at the Congress 'the giants of the *Blastocladiales'*: Couch, Emerson, Cantino, Machlis, Lovett, and Turian. There was special focus on fungal ultrastructure and on palaeobiology. Kenneth Thimann was President of the Congress. Stan Hughes was honoured with the award of the prestigious Jakob Eriksson Medal for his epochal work on *Hyphomycetes*. During the Sydney Congress there were several symposia in mycology and plant pathology: taxonomy of fungi, Pacific mycogeography, Recognition and specificity in plant-pathogen interactions, Physiological and ecological aspects of mycorrhizal plants, and lichen taxonomy and ecology. Rutherford Robertson was President of Congress. I had the honour of being one among the twelve Vice-Presidents. A business meeting of the IMA was held. Referring to the next Botanical Congress to be held in Berlin, Karl Esser from Germany suggested holding of the next IMC along with the Botanical Congress in Berlin. I mention this to emphasize the continuing close link between Botany and Mycology.

All this has been just as it should have been. And yet, noting the ever-increasing attention to plant diseases and their control in the global scenario, a step was taken at the Botanical Congress in Edinburgh in 1964 by a Committee headed by Frederick Bawden to launch the first International Congress of Plant Pathology in London in 1968. The Congress, presided over by Bawden, was held at Imperial College in South Kensington and attracted plant pathologists, mycologists, bacteriologists, virologists, geneticists, biochemists, epidemiologists and specialists in related disciplines contributing to its success.

The organization of the First International Mycological Congress at Exeter in England in 1971 was a follow-up and is a landmark in the history of mycology. The driving force behind the organization of the first Congress was Geoffrey Ainsworth. Mycologists from many countries congregated at the Congress, including several from India. Terrence Ingold was President of the Congress and John Webster its Secretary. At the opening ceremony, besides the Officers of the Congress, representatives of the various Mycological Societies from around the world were seated on the dais. Richard ('Dick'). P. Korf from the USA spoke on behalf of all the Mycological Societies. India was not formally represented. No, this cannot be, I thought to myself. It was imperative that India established a Mycological Society to represent its community of mycologists. Accordingly, mycologists from India met at Exeter during the Congress and set up a Committee under my stewardship to take steps to establish a national Mycological Society in consultation with mycologists in the country.

At the Congress, the International Mycological Association (IMA) came into being, and Constantine J. Alexopoulos from Texas was unanimously elected first President of the IMA. My nomination as a Vice-President came as a surprise to me, but it was encouraging, and I thought it was in recognition of India's'contribution to mycology. Given the responsibility of bringing mycologists of the country together to a common forum of a Mycological Society, to me it seemed appropriate to bring them together at an international symposium in which mycologists from overseas could participate. The idea appealed to everyone, to my University, the funding agencies, and mycologists in India and abroad. I received warm support from the entire mycological community in India, from my colleagues and students, besides the University, the UGC, other funding bodies and science academies.

The theme of the symposium was “Taxonomy of Fungi.” Forty mycologists from abroad and an equal number from India participated. It was also attended by many students from different parts of India. Two Special Lectures were delivered, one by C. T. Ingold on “How a Toadstool Works” and a second by T. R. Seshadri on “Lichen Chemistry.”There were no concurrent sessions, and no clash in the choice of programmes. The Symposium had, I believe, a tremendous impact on the further development of mycology in India and there was a spurt in mycological research in the country as a whole. It was at this Symposium that the Mycological Society of India was formally launched by me on the 16th January, 1973 on the mandate given to me by mycologists from India at Exeter.

The Society's journal *Kavaka* began appearing in the same year; it was edited by me with assistance from an Editorial Board. It was a modest beginning, and yet, seemed promising as it was chosen for citation in *Current Contents* from the very first issue. A set back to publication of the journal after fifteen years of publication and regular appearance led to discontinuation of citation in *Current Contents,* but the journal is catching up and, I believe, would, in time, get cited. Since its inception, the Society has organized annual meetings in different locations in the country. This has helped bringing together mycologists effectively from different parts of the country and spread the message of mycological relevance to a wide audience.

A visit to Sri Lanka with David Pegler of the Royal Botanic Gardens and K. Natarajan was aimed at exploring fungi. We visited the Peradeniya Botanical Garden known for its rich vegetation and its mycota. The Flora of Ceylon attracted many botanists Linnaeus downwards and the list of eminent scientists who visited and worked on algae, fungi and plants

include K. Goebel, G. Haberlandt, G. Karsten, W. and G.S. West, C. Penzig, A.G. Tansley, F.E. Fritsch, Nils Svedelius and several others. C. Holtermann wrote his "Mykologische Untersuchungen aus der Tropen" and "Fungus cultures in Tropics" while working in Peradeniya. Likewise, several works were authored by T. Petch when he was the Director of the Gardens. During the Directorship of J.C. Willis, Willis studied the *Podostemaceae* and expounded the Age and Area hypothesis. Both are important contributions.

The leading light that guided the development of botany and the Garden was, of course, George Henry Hendrick Thwaites. This introduction is relevant to know the history of mycological research in Ceylon. Pegler's exploration of the agaric flora extended to the Hagkala Botanic Garden which is noted for its temperate climate, its elevation to about 7000 ft. and the exquisite flora. It was a rewarding trip. And yet, there is a great deal to explore the larger fungi, not to mention microfungi. But where do we find the students and amateur botanists?

The Tampa Mycological Congress

The second International Mycological Congress (IMC2) was held at the University of South Florida in Tampa, Florida in 1977. Encouraged by the cooperation I had from mycologists in India and abroad, and from academies and funding agencies in holding the 1973 Symposium, I was keen to invite IMC3 to India. First, it required clearance from the Indian National Science Academy (INSA) which is the recommending body for the Government of India. India would have to agree to the guidelines of the International Union of Biological Sciences (IUBS) in the matter of allowing participation from all countries, notwithstanding difficulties arising for political reasons. I wrote to the then President, INSA (B. R. Seshachar) setting forth the need to invite IMC3 to India, giving him some idea of financial inputs and other commitments. I had every reason to believe I would have an encouraging reply, though I had none. However, some weeks before the Congress, the Academy sent me its approval to invite IMC3 to India which I forwarded to the then Secretary of the IMA (Colin Booth). I wrote to the INSA and the UGC on the need to send an official delegation to the Tampa Congress. The Academy and the UGC jointly sponsored a strong delegation to the Congress. The Indian participation at the Congress was notable: a reflection of mycological progress in the country.

The Congress was itself a great event. There were many more participants than at the first Congress. Frederick K. Sparrow was President of the Congress. The organization of the Congress owed a great deal to Emory G. Simmons as Secretary-General, and his able colleagues. It was good to see so many friends, particularly Constantine and Mrs Alexopoulos who had been with us at Madras for the symposium four years earlier. Besides the Presidential address on Professor Anton de Bary, the two Congress Lectures were both stimulating and scintillating: "What can lichens tell us about real fungi?" by D. C. Smith, and "Bugging the molds" by Howard Whisler. The announcement of my election to the Presidentship of the IMA at the Plenary Session of the Congress on the 3 September touched my heart with gratitude. I took my election as a mandate to me to play my role and forge ahead with all that can be done to promote mycology globally, and in the broadest sense.

There was so much more to be done, and so much more to learn. From Tampa I wanted to go round the country and see the mycological work underway in the US. There was the constraint of time and of funds, but I did visit a few centres. I was holding a Jawaharlal Nehru Fellowship at the time and the Nehru Memorial Fund was gracious in allowing me to visit the centres. At the University at Ann Arbor, Michigan, I had the pleasure of meeting Frederick Sparrow and Alexander Smith, and giving a seminar at the invitation of Alfred S. Sussman. I first met Sparrow at the Exeter Congress in 1971 and then at the International Symposium on Marine Mycology organized by Alwin Gaertner at Bremerhaven in 1972, and had been an ardent admirer of his contributions to our knowledge of aquatic phycomycetes and his massive tome with that title (1960). Incidentally, the Bremerhaven Symposium brought together a number of paticipants which included W. Hoehnk, Gareth Jones, Geoffrey Pugh, and H.J. Swart. The creativity in Swart provided us a taste of his cartoons elegantly presented by him during the sessions.

Back to what I was saying, I visited Harvard to see Richard Evan Schultes with whom I discussed his work in ethnobotany and ethnomycology. Schultes shared with me his thoughts on mushrooms, Soma, and hallucinogenic plants. He was keen to have my thoughts on the enigma of Soma. To complete the thread, I visited Gordon Wasson who welcomed me as his guest in Connecticut. Jointly with Roger Heim, he had authored a monograph on hallucinogenic fungi of Mexico (Heim and Wasson, 1958). His identification of Vedic "Soma" with the fly-agaric *Amanita muscaria* (Wasson, 1968) was original and opened the gate for debate. He showed me his collection of mushroom stones which fascinated me. He was kind and generous in letting me into his collection of oriental inscriptions and books which had a wealth of information on the Soma of the Vedas, on Hinduism and India, and on lingchi (*Ganoderma lucidum*) of Chinese lore. I entreated him to pose for me with the mushroom stones and he readily agreed. There was no doubt, it seemed to me, about the genuineness of his quest to unearth the mystery of Soma.

At Harvard, I met E. S. Barghoorn who had left marine mycology behind and embraced paleobiology in which he had made significant contributions. Barghoorn brought out a painting by my friend, the distinguished plant scientist and thinker, B. G. L. Swamy which he (Barghoorn) treasured and he let me take a picture of him with the treasure. Swamy worked with I. W. Bailey at Harvard during 1947-50. He was an exceptional plant morphologist, thinker, teacher and friend. Incidentally, Swamy criticised Gordon Wasson's identification of Soma, from strong reasons and firm conviction, in a paper on the subject in 1976! I visited the Farlow Herbarium at Harvard and was happy to meet Donald Pfister who very kindly showed me around.

My visit to the School of Forestry at Syracuse was really memorable from the saintly generosity and kindness of Josiah

and Mrs Lowe in having me stay with them, despite Mrs Lowe's indisposition at the time. Such humaneness as the Lowes radiated is indeed rare. It was wonderful going round with Josiah Lowe to see mushrooms and fairy rings. The Wangs, C. J. Wang and her husband, were a charming couple and I was delighted to be shown the many fungi on wood and pulp by C. J. Wang. She even sent me photomicrographs of many of her interesting lignicolous fungi. In Syracuse I had a fruitful meeting with Terrence Hammill whose elucidation of phialoconidiogenesis in several taxa using transmission electron microscopy helped significantly in formulating my views on phialoconidiogenesis.

Visiting Rhode Island, I saw Roger D. Goos on his home ground. I learnt a great deal from him about fungi, especially helicosporous hyphomycetes (Goos, 1987). Roger took me to dine at a vegetarian restaurant, "The Merciful Lion," where I was told that the vegetables and fruits served came from the restaurant's backyard garden. I then mentioned to him, the lion being fed purely on vegetables, had become merciful! A few years later, Roger visited and worked with us for a few weeks at Madras, making collections in Madras and other locations in the Kerala State, making additional contributions to the fungi of southern India (Goos and Hosagoudar, 1998).

In New York I went and saw the beautiful monument to the author of *Alice in the wonderland* in the Central Park. I visited the Botanical Garden in Bronx Park and the mycological herbarium where Clark T. Rogerson talked to me about the work there and the NYBG herbarium. At Beltsville, besides meeting Amy Rossman and her colleagues, Lekh R. Batra took me to see Charles Drechsler at his home. This was a great meeting as I admired Drechsler's monumental contributions to our science and his beautiful illustrations of his fungi. I found him agile and pleased to talk to me, despite his age. He even posed so I could take a picture.

The Tampa Congress adopted two resolutions:

First,

That international scientific organizations consider allocating significant financial support to projects designed to strengthen mycological training, research, and service in countries and regions where such activities now were inadequate; for specialist mycologists to visit tropical countries and other areas requesting such expertise, and to hold workshops and seminars in their own specialities on subjects of regional significance; also to improve facilities for exchange of scientific materials, including cultures, exsiccatae, and bibliographic information.

That international funding agencies support international centers of excellence in fungal identification, and strengthen involvement of the mycological community in the UNEP/UNESCO Microbiological Resource Center programmes.

Second,

That the IMA expand its responsibilities to:

Establish special committees for the development of mycology in Latin America, Tropical Africa, the Middle East, and Tropical Far-East Asia, with activities to include establishment of directories of institutions, herbaria, living collections, and research staff in mycology for all countries of each area, as well as informational material on national regulations governing the collection and transport of fungal materials; establish a liaison office to improve cooperation and coordination in the work of regional Committees; and establish a mechanism to explore the possibility of transfer of funds between countries to support identification services and other international mycological activities.

The Resolutions defined the vision for the role of the IMA in the development and organizaion of mycology worldwide.

The Status of Mycology: Looking Ahead

The IUBS to which the IMA was affiliated took note of these Resolutions and reported them in their Newsletter (No13, June 1978, p. 13). The XX General Assembly of the IUBS held in the University of Helsinki, Finland in August 1979 is historic for the support it gave to Mycology. The meeting was attended by me in my capacity as President of the IMA and Leader of the Indian delegation to the General Assembly, and David L. Hawksworth as Secretary-General of the IMA. A Working Paper on "THE STATUS OF MYCOLOGY IN IUBS" submitted by us was considered by the General Assembly at Helsinki. Notably, there was a Resolution on Support for Mycology which read:

RESOLUTION 11: Support for Mycology

Resolves to endorse the resolution of the 2nd International Mycological Congress (Tampa, 1977), given in detail in IUBS Newsletter No.13, p.13, requesting international organisations to consider allocating financial support for projects designed to strengthen mycological training, research, and service in countries and regions where such activities are now inadequate.

The IMA had requested the IUBS to take steps to establish an Institute of Tropical Mycology which was considered along with proposals from past Presidents of the IUBS to establish an Institute of Biological Taxonomy.

We had sought for the IMA the status of an independent Section in the framework of the IUBS. Representing the Section of Botany, it was argued that mycology had traditionally been with Botany and, advisedly, should not sever the connection. David Hawksworth and I agreed with this view which was then given effect to by renaming the Division of Botany as the "Division of Botany and Mycology". The IMA became the basis of the Section of General Mycology. At this same General Assembly, the Division of Microbiology decided to leave IUBS and form a separate Union, the International Union of Microbiological Sciences (IUMS). J. Heslop-Harrison from the UK and Karl Esser from Germany further arranged on the spot nomination of my name representing Mycology to the membership of the IUBS Executive Committee, although I had not sought nomination, and had not been nominated until then. And, I was duly elected a member of the IUBS Executive Committee.

On all counts then, we were satisfied with the progress we made for securing Mycology its rightful independent place in the IUBS. I wrote about these developments to our good friend Emory Simmons who organized IMC2 at Tampa and he expressed, in reply, his joy at the happenings at the General Assembly at Helsinki. Constantine Alexopoulos responded likewise to a similar letter I had written to him about the happenings in Helsinki. A highlight of the visit to Helsinki was a visit to the Ruotsinkyla Experimental Area and the Forest Research Institute about 25 km north of Helsinki. We were shown round the Institute and the area where the area with its vegetation rich in species.

At the Plenary Session of the Tampa Congress, after taking over the Presidentship of the IMA, I had said that the choice of venue of IMC3 would rest with the Executive Committee of the IMA and I would stay neutral on the matter. The Committee met and was unanimous in agreeing to hold IMC3 in Japan in 1983. In the IMA, I received warm support from the entire Executive Committee and, in the day to day activities and actions, from the Secretary-General, David Hawksworth, and the Treasurer, J. A. von Arx. An early blow to the IMA was the demise of Ralph Emerson, a member of the Executive Committee, a good friend, and one of world's most distinguished mycologists. At Tampa, Ralph had advised me in private that I desist from taking the onerous responsibility of holding the Congress in India as that would sap my energies and render me unfit for mycological work! Ralph was a wonderful human being and his demise is a loss to science and philosophy and to me.

The IMA had a business meeting at the International Botanical Congress in Sydney, Australia in August, 1981 which was attended by Hawksworth, some members of the Executive Committee, mycologists attending the Congress and myself. Arrangements for IMC3 were discussed with Keisuke Tubaki, Secretary of the Organizing Committee of IMC3. The new status of Mycology in the IUBS set-up was explained. This was a prelude to the Congress in Tokyo (see the report in *Mycotaxon* **16**:335-39, 1982).

At Tampa a group of students from the University of Wisconsin at Madison came to me with greetings from their teacher, M(arion) P. Backus. They mentioned to me how the introductory part of my book on *Hyphomycetes* (1971) was being used by them as a text on the recommendation of their teacher. Coming from students, this was most encouraging, as I was then engaged in expanding the introductory part referred to into an updated version of a new book, which finally appeared in print only in early 1983 with the title, *Hyphomycetes: Taxonomy and Biology*.

At the request of the Publisher (Academic Press, London), the book was released by the then Prime Minister of India, Indira Gandhi on the 20 April 1983 at her residence in Delhi. It was on this occasion that she asked me about the genesis of the book and what it dealt with. I knew this was a great opportunity, and I must focus on mycological relevance. And I did exactly that in a brief, passionate and spontaneous way that, I thought, impressed the Prime Minister. For, she seemed to have asked the Department of Science & Technology (DST) to ascertain what needed to be done to foster the development of mycology in the country. The DST wanted a proposal from me, perhaps a sequel to the Prime Minister's interest, and I submitted to the DST a modest proposal for the establishment of an Institute of Tropical Mycology in a suitable location in India.

Early in 1984 Indira Gandhi had called a meeting of a Committee of the Jawaharlal Nehru Memorial Fund of which I was then a member. It was an important meeting to discuss matters of policy. The meeting was held in her room and, in the course of the meeting, she mentioned to me how there was so much jealousy among 'friends' and 'scientists' so that proposals got torpedoed. She did not elaborate, nor did I want her to, as I had always thought I had only friends. Be that as it may, had not the Prime Minister tragically fallen victim to an assassin a few months later, my dream of an Institute of Tropical Mycology might, I believe, have been realized. However, in the wake of my proposal, a Culture Collection was set up at the Institute of Microbial Technology at Chandigarh by the Government of India, but this hardly met the prime need of building inventories and mapping mycodiversity in diverse regions and ecological habitats and niches, and of critical taxonomic studies (in the broadest sense) and preparation of monographs.

As the world knows, C. V. Raman, the Indian physicist and Nobel Laureate, detested seeking aid from Governments as aid came with strings attached. At one of the annual meetings of the Indian Academy of Sciences at Bangalore which I attended, in his opening Address Raman referred to the derecognition of the princes which struck the headlines of the newspaper that morning and asked “Do you want Science and scientists to be derecognized?” The audience knew the answer. Science must develop unhampered by strings. Mycology's best support is Mycology.

The Visitors' Laboratory in Buitenzorg (Bogor) in Java (Indonesia) has for long been a model for me. My visit there in 1986 was the fulfilment of a long-standing wish. The Curator of the Herbarium at Bogor was M. A. Rifai whom I had met and known since his Sheffield days with John Webster. Rifai's work on the taxonomy of *Trichoderma* is well-known, and his monograph on the Australasian *Pezizales* is a significant contribution to the mycobiota of the tropics. Another special attraction was Kostermans, the distinguished plant taxonomist who had visited me at Madras some years earlier and had even collected in the vicinity of Madras in my company. Following his visit to me and my good friend B. G. L. Swamy, the distinguished botanist and thinker, our friendship had grown and, being at Bogor at the time, he welcomed me (and my wife) most warmly. We both had met him in 1975 on a visit to Leiden and the Rijksherbarium where he was then working. Kostermans had been Curator of the Bogor Herbarium and continued to be active and was in the process of completing a monograph of the Mango (*Mangifera*).

The Botanical Garden in Buitenzorg founded in 1817 had a succession of distinguished Directors, but it was during the Directorship of Melchior Treub that the Garden enjoyed a glorious period of development. Treub was not only a great botanist but a great organizer with a commanding presence. It

was on 14 November 1884 that the building of the Military Medical Service was handed over to the Botanical Garden in Buitenzorg and the Laboratory began functioning in the hospital room. The Laboratory was opened for visitors on 10 January 1885. Thus, it was perhaps the oldest botanical station in the eastern tropics. In 1890 there was an extension to the lab "to investigate the conditions of life, anatomy, and diseases of tropical economic plants." In 1889 the botanical garden in Tjbodas came to have a laboratory, and working and sleeping accommodation for a small number of visitors. This laboratory, often known as 'phytopathological laboratory,' was opened in August 1920. (The Imperial Bureau of Mycology was also founded in 1920 what a coincidence!)

The Laboratory had a small core of botanists and naturalists, but primarily functioned as a Visitors' Laboratory to which some of the most distinguished botanists and naturalists were attracted to come and study the plant life of the Indonesian tropics. Treub wanted Dutch botanists to benefit from visits of scientists from other countries to the Garden and its laboratories. With this in view Treub raised, during his stay in Holland, a fund (the 'Buitenzorg foundation' as it was called) that was to be used to pay for regular trips by botanists to Buitenzorg. The very first to work in the laboratory was S. H. Koorders of the Netherlands Indian Forest Service. Among the three foreign visitors in the first year was K. von Goebel, Professor of Botany in the University of Rostock (Germany) and author of *Organographie der Pflanzen.* As Dammerman (1935) has noted, if one took note of the conditions under which the early visitors worked, one cannot but admire the great perseverence of these scientists and the work they did in the tropics.

Several distinguished botanists from all over the world came and worked here : H. B. Guppy (Britain), W. Schimper, G. Haberlandt, P. Knuth, E. Haeckel, Adolph Engler, M. Koernicke, G. Tischler, G. Klebs (Germany), N. E. Svedelius (Sweden), D. H. Campbell (U.S.A.), G. Senn (Switzerland), Franz Verdoorn, A. J. P. Oort (the Netherlands), to mention a few. The list of visiting scientists who studied fungi during the period 1883-1934 is itself impressive **(See table**).

In May 1914, the Visitors' Laboratory was christened Treub Laboratory honouring the man who did so much to make it the great centre of tropical research it became.

My idea of a Centre for Tropical Mycology was something on the Treub pattern that would draw the great ones globally together to the Centre toward fulfilling our objectives.

Following the deliberations at Helsinki, there was great enthusiasm in fostering the development of mycolgy, in initiating inventorying, and conserving fungi for the good of humankind.

The Tokyo Congress (IMC3)

The Tokyo Congress (IMC3) had Naohide Hiratsuka as its President who, in keeping with his speciality, addressed the Congress on the past, present and future of studies on the rust fungi. Though not customary, as President of the IMA, I thought it pertinent to highlight the global aspect of the pursuit of mycology in the face of threats to mankind from the use of atomic and other forces of destruction. And so I chose

Table: List of visiting scientists to Botanical Garden Laboratory in Buitenzorg (1883-1934)

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to speak on "Mycology A Global View." Geoffrey Ainsworth and Constantine Alexopoulos were honoured with Honorary Presidentships of the IMA to the unanimous acclamation of everyone present. A special event to mark Stan Hughes' sixty-fifth birthday hosted by the Sugiyamas brought together his many friends worldwide. Several of us including myself spoke briefly with our association with Stan. A group photograph taken then is a worthy reminder of this memorable event.

The Congress was well attended and paved the way for another Congress seven years later in 1990 in beautiful Regensburg in Germany, the cradle of great Science. The Regensburg Congress was reviewed by me in *Current Science* in 1990. IMC5, IMC6, IMC7, IMC8 and IMC9 followed, an indication of the health of the IMA as the world body responsible for the development and organization of mycology.

Following in the wake of IMC3 at Tokyo, the Research Institute for Chemobiodynamics, Chiba University organized the First International Symposium on Chemobiodynamics : Filamentous Microorganisms Current Topics of Infection, Toxicosis and Control on September 5-6, 1983. The proceedings of the Symposium edited by T. Arai *et al.*, with the title, FILAMENTOUS MICROORGANISMS: Biomedical Aspects, was published in 1985. Professor Arai requested me to write an OVERVIEW for the volume. Of special interest was the participation of Hughes, Yokoyama, Malloch, Onions, McGinnis, Udagawa, Samson, Kurata, Hanlin and Shibata in several aspects of taxonomy and biology of fungi.

The establishment of IMA Regional Committees for Asia, Africa and Latin America, a follow-up of the recommendations made at the Tampa Congress, led to strengthening mycological expertise and mycological awareness to a commendable level in these regions. Several meetings, symposia and congresses were held, bringing together mycologists in each of these regions for dialogue and discussion. The First Regional Conference on Mycology in Africa was held in Mauritius in June 1990, the Proceedings of which, edited by Gregoire L. Hennebert, have been published. Mycological Societies became active in the so-called developing regions and are currently spearheading efforts in inventorying and conservation of mycodiversity. The Mycological Societies in Japan, China, and Korea have been active. A Mycological Society has been formed in Thailand. The IMA Committee for Asia (IMACA) had its first meeting in the Genting Highlands, Malaysia in 1985, and later organized well-attended meetings in Thailand, Korea, Taiwan, India (twice), Hongkong, China, and Iran.

The Asian Mycological Symposium on "Role of Fungi as Frontier of Biosciences" was organized jointly by the Korean Mycological Society and the IMA Committee for Asia (October 1-4, 1992) to mark the 20th Anniversary of the Society. My programme of visits and lectures were coordinated by Hoo-Sup Chung, Chairman, Organizing Committee of the Symposium. Plenary Lectures were delivered by C.P. Kurtzman, S.C. Jong, H. Oku and myself. Presentations reflected the high level scholarship and interest in taxonomy as the one on Korean *Laboulbeniales* by Yong-Bo Lee and Dong-Su Choi and the monograph of the Section Difformia of the genus *Lyophyllum* (*Agaricales*) by J. M. Montcalvo. There was a taxonomic study of freshwater chytrids from a volcanic area of Taiwan by Mei-Lien Hsu and Chiu-Yuan Chien.

I visited several scientists who showed me round and explained their work: Min-Woong Lee, Dongkuk University; Hack Sung Jung, Dept. of Microbiology, Seoul National University; taxonomists, Kwang-Poh Kim and Young Hee Lee, Dept. of Mycology and Phytopathology, Seoul National University, Suwon Campus; Hoo-Sup Chung, Seoul National University; Seung-Hun Yu, Chungnam National University, Thejon; Bong-Koo Chung, Chungbuk National University; and Hyeon-Dong Shin, Kangreung National University, Kangnam. These visits were highly rewarding, and friendly, and the lectures at all centres were very well attended and evoked immense interest.

On a brief visit to Taipei and the National University of Taiwan I was shown round by Z. C. Chen whom I had met in National University of Singapore in 1985 at the Asian Mycological Symposium. The visit turned out to be a good introduction to mycological studies in Taiwan. I was met by Wu and her husband on arrival. We began with a visit to the Culture collection and thence to Taichung for a meeting with mycologists and plant pathologists. The meeting at Taichung was a memorable event that focused on a number of problems and areas of special interest to the development of tropical mycology. We were happy to get to know all those who were at the meeting. There was a fabulous lunch which we enjoyed. Peng took me to the Mushroom Laboratory the next day and in the afternoon we discussed with Hsieh *Fusarium* and Snyder. At the National Museum of Science, I discussed with Wu the *Corticiaceae* of Taiwan and the *Discomycetes* with Yei-Zing Wang.

The International Mycological Association Committee for Asia and the Mycological Society of India jointly organized a Symposium on "Ecology of Fungi" at Goa University on 19-21 January, 1998. The Symposium was well attended by several delegates from India and abroad : Z. C. Chen, John Webster, T. K. Tan, K. D. Hyde, R. S. Mehrotra, B. C. Lodha, B. P. R. Vittal, S. Raghu Kumar, and myself. The President of the MSI, R. S. Mehrotra delivered his Presidential Address, "On certain aspects of *Trichoderma* taxonomy, ecology, biology and biocontrol". Two Pleanary Lectures were delivered, by John Webster on "Coprophilous Fungi" and the other by me on "The Excitement of Doing Mycology in the Tropics" The lectures and the poster sessions were stimulating, besides mutual discussions.

The Asian Mycological Congress was held in the University of Madras during 20-22 January, 1999 along with the Silver Jubilee of the Mycological Society of India with a Symposium on "Tropical Mycology". It was presided over by me and I delivered the Presidential Address on "Mycology at the turn of the century." Special lectures were delivered by J. F. White on "Biology of the plant-infecting *Clavicipitaceae*" and by F. T. Last on "Fungi : Forester's Friends?". Overseas delegates who participated in the Symposium included: F. T. Last, S. Z. Chen, K. D. Hyde, J. A. Johnson, J. F. White, T. K. Tan, Quimio, J. A. Buswell, M. M. Tschen, C. Novotny, and E. J. M. Florence. Several leading delegates also attended including V. Ramesh Bhat, M. C. Srinivasan, C. Rajendran, A. K. Sarbhoy, S. Raghu Kumar, V. Agnihotrudu, S. B. Sullia, D. Ananthapadmanabhan, D. J. Bhat, and B. P. R. Vittal.

The Proceedings of several of these meetings have also appeared in print. Similar well-attended meetings have been organized by the Committees for Africa and for Latin America. Mycologists from the west have continued to visit, collect and describe fungi from the far-eastern tropics. The coming together of mycologists at IMCs and their interaction has undoubtedly been a direct result of the initiative taken by the IMA and its affiliated societies. Both teaching and research in mycology are thus currently seen as enjoying a global uplift despite the paucity of funding for traditional approaches in the inventorying and mapping of the mycota throughout the world.

During my visits to Taiwan, Thailand, the Philippines, and Korea I had the pleasure of meeting scientists in these countries and I found great enthusiasm which was reflected in systematic studies on fungi. The judicious use of traditional and molecular approaches has led to important contributions. Thus, studies on the systematics, phytopathology and pharmacology of *Ganoderma* led to the publication of a significant contribution on the genus by Buchanan, Hseu and Montcalvo (1995). We need more such studies on tropical taxa. The launching of *Mycotaxon* devoted to fungal taxonomy in 1974 was a significant event and its sustenance augurs well for our science. While fashions and fads invite public attention, the silent and dedicated work in systematic and taxonomic mycology might remain obscure, but will, I am sure, continue as long as there is the sense of wonder at the mystery and the beauty of biodiversity and all that it signifies.

Epilogue

The excitement and the enjoyment I derived from my life with fungi in the tropics which I have tried to share with you have been possible primarily because my efforts and endeavour have been in the region of what is desirable but also what is possible. Though we know a lot about our flora, our fauna, and our mycobiota, enough is not enough. The flame of discovery of novelties is perpetual, whether a novelty is a star in a galaxy or a tiny fungus in a tropical forest. Each is beautiful (and important) in its own light. It will be erroneous to think that our planet is for us alone and the future is only for machines and man, technology and development. Interaction and interdependence and homoeostasis are of the essence of life.

The perpetual novelty of fungi that gave me joy also aroused my sense of wonder about their place in our planet. Every organism, big and small, has its place and its role, a role reflecting an inner power fashioned by interdependence, of complemetarity. Our agriculture, our forestry, our medicine and public health, our biotechnology and industry all derive from the huge potential of our plants, animals, fungi and microbes which are what make our forests, our grasslands and savannah, our river systems, and our oceans what we might designate, our resources. But we know only a fraction of our biota. And yet, we are crazy about engineering superorganisms tailored to our crazy needs! As we have noted in what I have written, the exploration of fungi in the vast tropics in the past was an endeavour to which many from many countries contributed. It was truly a global effort. The quest for novelties continues but currently, in some places, with the questionable motive of greed and making a fortune out of these great resources. The destruction of our resources must stop. The theme is not new. But truly, no scientist in his search for truth mixed his endeavour with personal monetary gain. There is an urgent need to inventorying our resources. Such inventorying can be done with minimal equipment and cost, but will need encouragement and patronage from us, the scientists, and the people, the tax payers who sustain science, Big and Small.

Beginning without knowing the path to be travelled, I was engaged in the pursuit of mycology in the tropics. I have narrated some facets of the story of my pursuit. The path was littered with beautiful fungi, “God's creations”, as the brothers Tulasne would have it, and the journey has been wonderful and exciting. Alas, life is short.

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APPENDICES

I. PUBLICATIONS OF C. V. SUBRAMANIAN

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