

Benefactors' Lecture¹

Thoughts and musings on tropical *Xylariaceae*

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The following topics are addressed: the interfaces of the *Xylariaceae* with related groups and the 'essence of xylariaceousness'; speciation of *Xylariaceae* in the tropics; the distribution of *Xylariaceae* in the tropics; xylariaceous fungi categorized into ecological groups based on substrate type and timing of colonization and on modes of water conservation; xylariaceous fungi as latent pathogens and endophytes; novel morphological features of xylariaceous fungi and their roles under tropical conditions.

INTRODUCTION

It is particularly appropriate to discuss the tropical *Xylariaceae* here because British workers have contributed so much to understanding them. M. J. Berkeley and associates and correspondents made many of the early descriptions and collections of these fungi. M. C. Cooke was among the first to try to organize and categorize them. Thomas Petch's (Fig. 1) studies of a variety of xylariaceous fungi – particularly those associated with insect nests and root decays – are classics, as relevant today as yesterday (Petch 1924, 1928). Dennis' (Fig. 2) many contributions toward clarifying the taxonomic and nomenclatural status of *Xylariaceae* of Africa, South America, and other tropical areas are the foundations of modern studies (Dennis 1958, 1961, 1970). The great resources of the Royal Botanic Gardens, Kew, to which Dennis contributed so much in terms of identifications, annotations, illustrations, and specimens, are consulted constantly by those of us who aim to understand tropical *Xylariaceae*. The British tradition of leadership on studies of tropical *Xylariaceae* continues under the Whalley's, Anthony and Margaret, and others.

Among those non-British pioneers of tropical *Xylariaceae* must be mentioned P. Hennings, J. H. Miller, C. Montagne, H. Rehm, R. A. Toro and F. Theissen. With the exceptions of the workers mentioned above and a few others, most collectors or students of tropical xylariaceous fungi have done so in the course of other interests. In recent years there have been concentrated efforts to collect and investigate the *Xylariaceae* of particular regions. The collections of G. J. Samuels have

contributed greatly to the understanding of the *Xylariaceae* of South America and Sulawesi (Rogers, Callan & Samuels 1987, Rogers *et al.* 1988). Læssøe has made substantial contributions to our knowledge of the *Xylariaceae* of South America, and, with Lodge, to the mycobiota of Puerto Rico. Kathleen van der Gucht has greatly increased our understanding of the *Xylariaceae* of Papua New Guinea (van der Gucht 1995). Felipe



Fig. 1. Thomas Petch.

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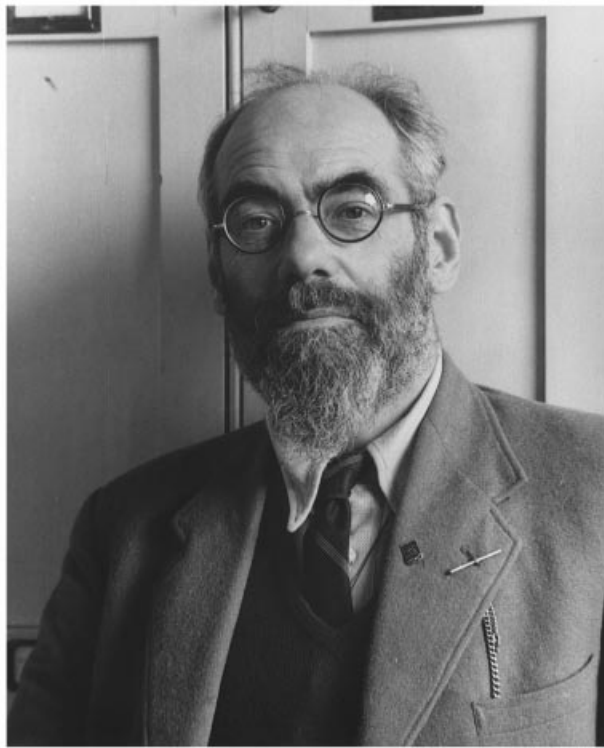


Fig. 2. R. W. G. Dennis.

San Martín has led the effort to collect and investigate the *Xylariaceae* in Mexico (San Martín Gonzalez & Rogers 1989). The incomparable Yu-Ming Ju is a pioneer in describing the *Xylariaceae* of Taiwan and has made many other indispensable contributions toward understanding tropical fungi through many publications, including a number of monographs (Ju & Rogers 1999, and other papers cited later). To all of these workers, past and contemporary, I express my admiration and thanks. They have all provided inspiration and, some of them, companionship and friendship during my 40-year love affair with the *Xylariaceae*.

XYLARIACEOUSNESS: WHENCE AND WHITHER?

The cardinal features of the *Xylariaceae* are widely known: perithecial ascomata embedded in more or less well-developed dark-coloured stromata; cylindrical asci with an amyloid apical ring; ascospores with dark coloured complex multilayered walls with a germ slit; and an anamorph producing conidia holoblastically from a sympodially, or occasionally percurrently, proliferating conidiogenous region. The complexity of such structures as the ascospore would lead to the belief that, once acquired by gradual accretion and integration of a regulatory system, reversion to a former, morphologically simpler state would be unlikely. I became aware that the germ slit might be lacking or, indeed, be eliminated during a study of *Collodiscula japonica* with Samuels and Nagasawa (Samuels, Rogers & Nagasawa 1987) and subsequent studies. *Collodiscula* is a *Rosellinia*-like taxon with two-celled ascospores that are devoid of a definite germination site. We hypothesized that the genus represents a stage along the road to becoming

‘truly xylariaceous’, i.e. having a single-celled mature ascospore with a germ slit. Later, Ju and I re-examined two taxa often placed in *Astrocystis* concluding that they represent *Rosellinia* species that have become structurally adapted to the hard surface of bamboo (Ju & Rogers 1990). Ascospores of *R. bambusae* are two-celled when immature, becoming one-celled at maturity via a disintegration of one of the cells and having a germ slit; it is suspected that those of *R. mirabilis* are likewise two-celled when immature (Ju & Rogers 1990). *Collodiscula* and these *Rosellinia* species are essentially identical in habitat and structure of stromata, in the *Acanthodochium* anamorph, and in their bamboo hosts in subtropical and tropical environments. We were thus even more convinced that *Collodiscula* ascospores represent the ancestral type, i.e. dark coloured two-celled ascospores devoid of a germ slit. We elected to continue to consider *Collodiscula* as a genus that had not made it to ‘true xylariaceousness’ (Ju & Rogers 1990). This view seemed strengthened by the fact that many undoubted xylariaceous taxa have ascospores with a vestigial cell that is lost prior to maturity (development of full ascospore colour) or that persists as a hyaline cellular appendage (Ju & Rogers 1990).

Our view of the fixity of the typical xylariaceous ascospore was challenged by our study of *Biscogniauxia anceps* (Rogers, Ju & Candoussau 1996). This fungus features unequally two-celled hyaline ascospores with the sporadic occurrence in a few asci of two-celled ascospores with a dark body, a typical germ slit, and a hyaline cellular appendage. I first collected *B. anceps* in Honduras, but did not describe it because I believed it to be immature. Many years later Françoise Candoussau began systematically collecting the fungus in France and it became evident that most of the ascospores of this fungus never develop a coloured cell with a germ slit. It was astounding to discover that both cells of the hyaline ascospores germinated in very high percentages (Rogers *et al.* 1996). It appeared that most of the ascospores had reverted to an ancestral state, i.e. two-celled hyaline ascospores devoid of a complex multilayered wall with a germ slit. The fact that ‘normal’ ascospores were produced, albeit in small numbers and in no apparent pattern, showed that the fungus has the genetic tools to produce them. One question that arose is this: can taxa with permanently hyaline ascospores devoid of a germ slit – but showing other cardinal features of the *Xylariaceae* such as stromatal, ascial and anamorphic characteristics – be included in the *Xylariaceae*? *Vivantia* and *Induratia* have permanently hyaline ascospores. Læssøe included the latter, alone with *Collodiscula*, in the *Xylariaceae* (*Vivantia* was erected after the publication of Læssøe’s paper) (Læssøe 1994). How far should the limits of the family be extended?

Another genus with ascospores atypical of the *Xylariaceae* *s. str.* is *Camillea*. I discovered that the light-coloured ascospores of *Camillea* are variously ornamented with pits, spines or much more complicated structures and seem universally devoid of germ slits (Rogers 1977). *Camillea* has bipartite stromata like *Biscogniauxia*, but the anamorph produces the conidiogenous apparatus on ampullae and is referable to *Xylocladium* (Læssøe, Rogers & Whalley 1989). In culture, however, conidial structures devoid of ampullae and assignable to *Nodulisporium* are produced (Jong & Rogers

1972). Moreover, a taxon with dark reticulated ascospores, *B. reticulospora*, was collected in Thailand by Bandoni & Bandoni Flegel. This is the only known *Biscogniauxia* with ornamentation approaching *Camillea* (Ju *et al.* 1998) and our failure to obtain cultures (and perhaps the anamorph) was highly disappointing. Nonetheless, there are clearly relationships between *Biscogniauxia* and *Camillea*, but we do not presently understand them.

Two genera that have been accepted in the Xylariaceae lack most of the cardinal features of the family. *Phylacia* features clavate to globose asci devoid of an apical apparatus containing subhyaline to brown ascospores devoid of germ slits borne in cleistocarpous stromata; the anamorph is reported to be *Geniculosporium* (Rodrigues & Samuels 1989). *Thuemenella*, a genus with cuboid hyaline ascospores devoid of germ slits, borne in asci devoid of amyloid apices and featuring soft, light-coloured stromata, was placed in the Xylariaceae primarily on the *Nodulisporium* anamorph (Samuels & Rossman 1992). If it is indeed xylariaceous, its nearest kin would appear to be *Stromatoneurospora*, *Podosordaria* and *Sarcoxydon*, genera with light-coloured and fairly soft stromata.

Examples cited here, and others that could have been cited, raise serious questions about the limits and boundaries of the Xylariaceae. Evolution in the group is surely more akin to a much-branched shrub than to a tree.

MODES OF WATER CONSERVATION IN THE XYLARIACEAE

I hypothesized many years ago that the initial impetus for the various relationships of xylariaceous fungi with their hosts and substrates was water conservation, i.e. various xylariaceous lifestyles developed on periodically dry sites (Rogers 1979). These types of adaptations are summarized in Table 1.

It is perhaps paradoxical that xylariaceous taxa are often strongly represented in large numbers and kinds in rain forests and cloud forests, as well as seasonally dry environments. That is, taxa with water conservation adaptations are often represented in areas where such adaptations seem unnecessary. It is known that some tropical climates have changed dramatically, perhaps repeatedly, over more or less lengthy periods, e.g. Bolivia over 25 000 years (Thompson *et al.* 1998)

and Africa (Goldblatt 1993). Hosts and substrates have undoubtedly changed along with climatic shifts. Contemporary distributions of tropical Xylariaceae are undoubtedly complex interactions among climates and hosts and might tell us little about the forces that drove various structural adaptations and life history features in the past. Tropical rain forests have sometimes been considered as 'museums', for diversity, but, if so, they are probably largely short-term 'repositories' or refugia.

XYLARIACEAE AS COMPONENTS OF ECOSYSTEMS

Most xylariaceous fungi that have been assessed have a strong capacity to degrade cellulose and lignin, causing physiological white rots, and the most efficient of them rival basidiomycetes in substrate degradation (Nilsson *et al.* 1989). With the exception of endophytic Xylariaceae or the endophytic phase of some taxa, the enzymatic capacity for decay is widely exploited. The Xylariaceae can be roughly categorized by the part or position of a host or substrate invaded and by the timing of the invasion.

1. **Species that invade living leaves and stems, often fruiting on living host material.** Many species of *Anthostomella* invade and kill limited areas of host tissue, fruiting on dead islands in living tissue. On death of the whole organ fruiting is often greatly enhanced.

2. **Species that invade living stems, remaining dormant until the host is stressed and then rapidly and widely colonizing the host and fruiting on it.** Many species of *Daldinia*, *Biscogniauxia*, *Camillea*, and *Hypoxylon* are associated with their hosts in this way. In some cases hosts are stressed by insufficient water, a concept put forward by Bier (1961). In Hawaii, for example, *B. capnodes* is encountered on dying or recently killed branches of a variety of hosts. This fungus, like others of this group, does not appear to colonize host material on the ground. Another example is the widespread *C. tinctor*. This is the most widely distributed *Camillea*, being found in the north temperate zone, subtropics, and both the American and Asian tropics on a variety of angiospermous hosts. These fungi are basically facultative parasites, i.e. opportunistic and generally weak pathogens. During a study of the mamane-naio vegetation zone of the Hawaiian Islands, Gilbertson

Table 1. Relationship of perithecial stromata to substrate.

Type of relationship	Genera
Stromata embedded in decayed wood	<i>Lopadostoma</i> <i>Eupeixylon</i>
Stromata more or less superficial, but borne in a subiculum	<i>Rosellina</i>
Stromata embedded in dung	<i>Hypocopra</i>
Stromata erumpent from bark via dehiscent outer stroma	<i>Biscogniauxia</i> , <i>Camillea</i> pro parte
Stromata with gelatinous tissue in form of rings	<i>Daldinia</i>
Stromata with gelatinous tissue and free water under pressure	<i>Entonaema</i>
Stromata massive, lacking conspicuous gelatinous tissue; usually superficial on substrate	<i>Hypoxylon</i> , <i>Kretzschmaria</i> , <i>Podosordaria</i> , <i>Poronia</i> , <i>Rhopalostroma</i> , <i>Xylaria</i> , and others

(unpubl. data) recognized 46 species of wood-rotting basidiomycetes. I recognized seven xylariaceous species from the same substrates and most of them had probably invaded the standing tree and continued their activities on material on the ground. This ratio of 7 basidiomycetes: 1 *Xylariaceae* seems similar to what is encountered in other vegetation zones in the Hawaiian Islands.

3. **Species that decay living roots and wood, moving to living material from dead material.** Species such as *Kretzschmaria clavus*, *Rosellinia necatrix*, and various *Xylaria*'s are primarily saprophytes – facultative parasites – that can become serous root pathogens when allowed to build up on debris. These fungi are competitive with wood-rotting basidiomycetes in invading and destroying dead wood on the ground.

4. **Species that often fruit on decayed material, but are isolated as endophytes from living hosts.** Species of *Xylaria* and *Nemania* are frequently in this category. They are discussed below under endophytes.

5. **Species that fruit on seeds and fruits.** These fungi, mostly *Xylaria* species, have specific and discrete relationships with their hosts. Examples include *Xylaria magnoliae* on *Magnolia* fruits; *X. ianthino-velutina* on leguminous pods; *X. carpophila* on *Fagus* fruits; *X. persicaria* on *Liquidambar* fruits; and others. None of these fungi has been thoroughly investigated, but some of them probably invade *via* the floral parts. Alternatively, they would appear to be exceedingly selective and successful in invading specific substrates on the soil, i.e. the substrates act as very specific baits. Whalley (1996) categorized some of these fungi as litter inhabitants. If this is the case, taxa such as *X. magnoliae* must be almost universally present in the spheres of their hosts and have a great competitive advantage over other litter fungi in colonizing specific substrates. Because of their great specificity they must be constantly available, with adequate inoculum, on debris or living material of their particular hosts. Alternatively, they might persist as endophytes on other hosts. Until and unless endophytic relationships are proven, however, such fungi are not to be considered as endophytes, but as highly selective saprophytes or as latent pathogens.

6. **Species that invade dung.** These fungi, mostly species of *Hypocopra*, *Podosordaria*, and *Poronia*, have special relationships with animals. Many taxa have dormant ascospores that seem to be achieved *via* passage through a mammalian digestive tract. In general morphology and cytology, including dark walls, sticky sheaths, and multinucleate condition, ascospores of these fungi resemble their sordariaceous counterparts and probably are examples of convergent evolution.

7. **Species that are associated with ant and termite nests.** A number of *Xylaria* species, including *X. melanaxis* and *X. nigripes*, are associated with dead or dying insect nests. It is possible that such fungi are cultivated by the insects for food, fruiting being inhibited until the nest is abandoned. In any case, there are a number undescribed insect nest associates and the systematics of described taxa need attention. For example, a number of taxa have been equated with *X. nigripes* that undoubtedly are distinct species. One of the features of many *Xylaria* species associated with insects is the small size of their

ascospores, a feature among others that led Boedijn (1959) to erect *Pseudoxylaria*. It seems likely that small ascospores are advantageous in that they could be easily ingested or otherwise transported by insects to nests for cultivation or other purposes.

8. **Species that inhabit litter and organic soils.** Xylariaceous fungi are often isolated as their anamorphs, such as *Nodulisporium* and *Geniculosporium* species from soil litter. Most of these fungi do not form the teleomorph in culture and, thus, have not been identified. *Nemania* spp. are involved and several do produce the teleomorph in culture (Petrini & Rogers 1986). Whalley (1996) gives examples of xylariaceous litter inhabitants. Some of these are likely to have other activities, as well.

9. **Species that are damaging pathogens.** The most widespread and damaging category of tropical pathogens is the root-rotters (discussed above). Species that destroy living bark and continue to decay the underlying wood are likewise commonly encountered. Examples include *Camillea tinctor*, *Biscogniauxia capnodes*, *B. mediterranea* and probably most of the tropical representatives of these two genera. These appear to be latent pathogens, invading living hosts and remaining quiescent until stress, thought to be most commonly drought, allows the pathogen to rapidly and widely colonize the host.

XYLARIACEAE AS ENDOPHYTES

Much has been written about the *Xylariaceae* as endophytes and the literature has been well-summarized by Petrini & Petrini (1985) and Whalley (1996). My definition of 'endophyte' is more circumscribed than some. I do not consider fungi that have a cryptic or latent phase on a specific host, on which they eventually fruit, to be endophytes. I consider them to be latent pathogens. Such temperate species are *Hypoxylon fragiforme* on *Fagus* spp. and *H. fuscum* on *Alnus* spp. To me, an endophyte is a fungus that leads a cryptic life that does not normally disrupt the host, i.e. a parasite that is not pathogenic or not highly so. Both of the above-cited taxa are known endophytes, also. Endophytic relationships are usually proven by careful culturing techniques (Whalley 1996 and references therein).

At first examination, the *Xylariaceae* would seem to be an unlikely group to contain a large number of endophytes. Their widespread capacity to destroy lignocellulosic substrates and to cause various types of diseases largely based on extensive tissue degradation would tend to lead to the conclusion that the general lifestyle of the *Xylariaceae* is that of a facultative parasite or facultative saprophyte. In fact, the *Xylariaceae* seem to be rivaled only by the *Clavicipitaceae* in their numbers and distribution of endophytes *s. neo*. I believe that the success of the *Xylariaceae* as endophytes can be explained by my 'sneaky' hypothesis. Pathogens such as *H. fragiforme* apparently invade the living host without profoundly disturbing it (Chapela, Petrini, & Petrini 1990). This capacity to 'sneak' into a host without initiating symptoms seems widespread among the *Xylariaceae* and probably originated, or was at least exploited, during the Cretaceous radiation of angiosperms. Indeed, the first host-specific associations were probably initiated in this way (see below). Thus, the parasite

would invade the host and remain quiescent until a change in host status allowed it to destroy bark and wood, i.e. until a signal allowed the enzymatic machinery to destroy cellulose and lignin. This capacity to 'sneak' past host defence apparently allowed many xylariaceous fungi into other hosts where the signal to initiate destruction of the lignocellulosic complex did not occur. These are the true endophytes, in my opinion. They probably persist primarily on predictable substrates where inoculum is formed, i.e. inoculum that is available to set up truly endophytic associations as well as those with a latent pathogenic state or even a truly saprophytic state.

An example of a 'sneaky' fungus is *Xylaria cubensis* along with *X. pannosa* and *X. laevis* which are usually confused with it. These fungi are often implicated as endophytes because the *Xylocoremium* states are easily identifiable in culture. Both the anamorphs and teleomorphs of these fungi, which occur on different and separate stromata, are encountered on decayed wood. The abundant inoculum from both anamorph and teleomorph is widely available to initiate associations in plants as unrelated as Atlantic cedar and pecan! Many other *Xylaria* species that are more difficult to identify undoubtedly operate in this manner. Judging from the frequency of isolations of the *Geniculosporium* anamorph from plants as varied as conifers and grasses, *Nemania* species are especially active as endophytes. *Nemania* species are usually encountered as perithecial stromata on decayed wood. It is assumed that at least some of the inoculum to establish endophytes would come from ascospores and conidia from such saprophytic colonies. Attempts to induce perithecial formation in *Nemania* species from decayed wood or from endophytic *Geniculosporium* isolates have largely failed. Curiously, several teleomorphic fruiting cultures of *Nemania* have originated from litter isolations; these are related to, but distinct from, *Nemania serpens* and its named allies (Petrini & Rogers 1986). Carroll (1999), in his Presidential address to Mycological Society of America, has shown that *Nemania serpens*, a common inhabitant of *Acer* wood, cryptically occurs in the foliage of nearby *Pseudotsuga menziesii*. He has categorized this and other fungi with similar life cycles as 'foraging ascomycetes' and interprets the strategy as one that permits dispersal and persistence when a primary host is unavailable (Carroll 1999). Polishook *et al.* (1999) have reported that endophytic *Nodulisporium* spp. from seven tropical countries belong to the same species, but from more or less distinct populations. At the time of the presentation the isolates had not been connected to specific xylariaceous teleomorphs.

One of the frustrating aspects of endophytic studies in the tropics and elsewhere involves the identification of isolates. *Xylaria* species are often isolated, but usually cannot be equated with known taxa. There are several reasons for this. First, most *Xylaria*'s have not been cultured from ascospores, and, thus, their cultural morphologies are unknown. Second, many *Xylaria* species in culture are very similar to each other. Third, a substantial number of isolates probably represent taxa that seldom or never occur outside of the endophytic relationship. If such fungi are to be identified to any practical level and made available for comparative purposes, cultures should be preserved and gene sequences deposited in GenBank

or elsewhere. The ultimate understanding of xylariaceous endophytes will involve identifications made in large part by way of molecular techniques.

SPECIATION AND GEOGRAPHICAL DISTRIBUTION OF XYLARIACEOUS FUNGI IN THE TROPICS

There is little question that the *Xylariaceae* diversified explosively on the rapidly radiating angiosperms. This angiosperm radiation, based upon the fossil record, occurred during the Mid- to Upper Cretaceous, with the major evolution of modern taxonomic groups occurring in the Lower Cretaceous (Sun *et al.* 1998). The beginning of this radiation has been pushed back into at least the Upper Jurassic by the discovery of *Archaeofructus*, an angiosperm with both primitive and advanced features (Sun *et al.* 1988). The relationships of the *Xylariaceae* with their hosts could represent ancient associations. For example, *Xylaria magnoliae* on *Magnolia* fruits, and *X. clusiae* on *Clusia* leaves, have probably been associated with these ancient genera from the earliest times. Moreover, these *Xylaria*'s seem to be rather advanced, based on their general morphology, and, especially, their discrete relationships with their hosts. It is suspected that these relationships originated from even earlier-occurring, less-specialized species. It is tempting to speculate that a taxon, or complex of taxa, that seems rather unspecialized, such as *X. hypoxylon*, first became associated with a specific host by 'sneaking' past the host defence system (see under endophytes above). Regardless of the manners in which they occurred, many associations, speciation events, apparently took place early in the radiation of angiosperms. Following the initial explosive radiation of angiosperms, at least in part on seasonally dry sites, and the radiation of xylariaceous associates on them further speciation probably occurred *via* opportunities of host distribution and isolation. Like the beetles (Farrell 1998), the *Xylariaceae* are most numerous in terms of taxa and individuals in the American and Asian tropics. This is apparently the result of the large number of tree and shrub species per hectare in tropical *vs* temperate forests. For example, 700 species of trees were identified in 10 individuals one-hectare plots in Borneo, approximating the tree species count for all of North America (Lewin 1986). Such mixtures of arboreal taxa have certainly provided speciation opportunities for specialized saprophytes, facultative parasites, and endophytic relationships, perhaps by a species on one host species 'sneaking' into one or more hosts in the vicinity. Burger (1992) remarked on the altitudinal parapatry among phanerogams on the Caribbean slope of Costa Rica. Congeneric species occurring together on the same slope are usually not related sister species. Burger (1992) hypothesized that, for some species, the interaction of host, environment, and pathogens can create sharp limits to survivorship on a gradual altitudinal gradient, i.e. could be the result of temperature and moisture on host resistance, pathogen presence or absence, pathogen virulence, or the restricted range of pathogen vectors. As a corollary to Burger's hypothesis, it might be that the occurrence of a pathogen at the edge of a host range could likewise contribute to endemic

Table 2. Pairs of taxa and their geographical occurrences.

Small-spored taxa	Location	Large-spored taxa	Location
<i>Hypoxyylon aeruginosum</i>	Mexico, S. America, Jamaica	var. <i>macrosporum</i>	Louisiana
<i>H. bovei</i> var. <i>microspora</i>	China, Japan, Philippines, Taiwan	<i>H. bovei</i>	Australia, Indonesia, S. Am., NZ
<i>Nemania chestersii</i> var. <i>microsporum</i>	Brazil	<i>N. chestersii</i>	British Isles, continental Europe
<i>Biscogniauxia atropunctata</i> var. <i>maritima</i>	Maritime East Russia	<i>B. atropunctata</i>	Mexico, USA
<i>B. atropunctata</i> var. <i>intermedia</i>	Mexico		
<i>B. weldenii</i> var. <i>microsporum</i>	Honduras	<i>B. weldenii</i>	Louisiana
<i>Xylaria magnoliae</i> 'small-spored'	Thailand	<i>X. magnoliae</i>	Mexico, USA

speciation of the pathogen, such as a *Hypoxyylon* (Ju & Rogers 1996).

Stanley (1975) concluded that the main function of sexual reproduction is in promoting speciation itself, rather than causing evolutionary change in established species. This certainly appears to be true in large genera such as *Hypoxyylon* that have many species and varieties which, in spite of obvious close relationships with other taxa, appear to be going their separate directions (Rogers 1999). In general, where taxa are separable primarily on ascospore size, those with smaller spores are usually found in more tropical environments (Table 2). This probably roughly reflects a correlation between food reserves of larger ascospores and longer periods of dormancy in cooler environments requiring greater endogenous reserves.

Another interesting phenomenon of certain taxon pairs is that the member of the pair with smaller ascospores has the larger geographic and host range. For example, *Hypoxyylon fragiforme* is found most commonly on *Fagus* in temperate regions (Ju & Rogers 1996). *Hypoxyylon howeianum*, usually regarded as a small-spored sister species of *H. fragiforme*, has a cosmopolitan distribution on a variety of hosts (Ju & Rogers 1996). *Hypoxyylon cohaerens* is likewise commonly encountered on *Fagus* in temperate regions, whereas *H. cohaerens* var. *microsporum* has a wide geographic and host range (Ju & Rogers 1996).

The geographic distribution of xylariaceous taxa is of great interest and probably largely unexplainable at this time. It was a shock to learn of a small-spored variant of *Nemania chestersii* from Brazil (Rogers & Samuels 1985), whereas the typical variety was described from Wales (Rogers & Whalley 1978) and has since been found in various parts of Europe. *Nemania immersidiscus* was first described from Papua New Guinea and the Hawaiian Islands (van der Gucht Ju & Rogers 1995), but is now known from Guyana. *Hypoxyylon aeneum* var. *aureoluteum*, actually a *Nemania*, has been considered a European fungus, but has recently been collected in the Hawaiian Islands. *H. vandervekenii* was described from Papua New Guinea (van der Gucht, Ju & Rogers 1997), but has been collected in the Hawaiian Islands. *Biscogniauxia anceps* was originally described from Italy; it is widespread in France, has been found in the British Isles, and in Honduras (Rogers *et al.* 1996), and most recently amongst Mexican collections (Ju *et al.* 1998). *Xylaria moelleroclavus*, which has been widely misidentified as *X. scruposa*, is known from South America, Hawaiian Islands, and Taiwan (Rogers, Ju & Hemmes 1997).

H. bovei was originally described from Argentina, but is now known from Australia, Indonesia, and New Zealand as well, probably largely associated with *Nothofagus* species (Ju & Rogers 1996). *X. castorea* is likewise known from both South America and New Zealand. It seems likely that both of these species have been distributed along with *Nothofagus* in part by repositioning of land masses. *Camillea* has long been considered to be a genus principally of the Americas, excepting *C. tinctor* which occurs also in Africa and Asia (Laessøe, Rogers & Whalley 1989). The recently described species, *C. selangorensis*, from Malaysia and Thailand (Whalley, Whalley & Jones 1996) and *C. malaysianensis* from Malaysia (Whalley *et al.* 1999), have extended the general range of the genus to southeast Asia and it is expected that additional species will be revealed in Asia and elsewhere. Molecular studies of taxa from different geographic areas holds promise in explaining some current distributional mysteries.

ELUCIDATION OF CONFUSED OR MISUNDERSTOOD TAXA

One of the most satisfying aspects of the studies of my colleagues and me has been the clarification of ancient taxonomic problems. A highly significant one with pantropical ramifications involved *Moelleroclavus*. Hennings (1902) erected *M. penicilliopsis* on the basis of a curious immature *Xylaria* originally described and figured by Moeller (1901). Don Hemmes began sending from the Hawaiian Islands material that exactly matched Moeller's figure and additional collections by R. L. Gilbertson and me provided a developmental sequence from the anamorphic stroma to the mature stroma. It was shown that *M. penicilliopsis* is the anamorph of a *Xylaria* that, although common in Asian and American tropics, had not been properly understood or named; it was thus named *X. moelleroclavus* (Rogers *et al.* 1997). One of the more important spinoffs of this work is that *X. moelleroclavus* has long been identified, among other taxa, as *X. scruposa*; the latter name is untypified and has been applied to various taxa with ascospores a bit shorter than those of *X. polymorpha*. The clarification of additional taxa that are too often identified as *X. scruposa* should allow the latter to be either rejected as of uncertain application or neotypified so that it can be applied more rationally and precisely.

Another significant taxonomic problem involving Hennings and Moeller is *Stilbohypoxyylon*. Hennings (1902) created

Stilbohypoxyton on the basis of Moeller's drawing (Moeller 1901) and (probably) his material. Both Hennings and Moeller misinterpreted the synnemata of the fungus and Laessøe (1994) accordingly considered *Stilbohypoxyton* to be of uncertain status. I had long been suspicious that the flat wart-like structures on stromata of taxa such as *Hypoxyton cyclopicum* were, in fact, the bases of broken spines or synnemata. Ju and I showed by examination of numerous collections from the tropics and by culturing that *Stilbohypoxyton* is, indeed, a xylariaceous genus based on *S. moelleri* (Rogers & Ju 1997) and a number of species in addition to the three currently recognized will eventually be described. Ironically, it still remains to be proven that *H. cyclopicum* is, in fact, a *Stilbohypoxyton*. My former student and imminent Mexican mycologist, Felipe San Martín, has furnished material and participated in the solution of several old taxonomic problems. Hennings (1897) described the anamorphic genus *Hypocreodendron* on material collected in Argentina. He believed it to be a hypocreaceous fungus. Lindquist & Wright (1964) described *Discoxyllaria myrmecophila* and believed it to be the teleomorphic state of *H. sanguineum*. We initiated cultures from ascospores of Mexican material and proved the anamorph-teleomorph connection by inducing the *Hypocreodendron* state (Rogers, Ju & San Martín Gonzalez 1995). As far as we know, *D. myrmecophila* is the sole member of this ant nest-associated genus.

Felipe San Martín, Y.-M. Ju and myself have been involved in another problem of more far-reaching taxonomic consequences. *Podosordaria* was erected on material collected from cow dung in Mexico and is separated from *Poronia* by most workers on the basis of more rounded fertile parts and more conspicuous perithecial contours (Rogers, Ju & San Martín 1998). Some investigators were uncomfortable with separating *Podosordaria* and *Poronia* on potentially trivial stromatic characteristics. It was known that *Poronia punctata*, the type species, has a disarticulating anamorph now assigned to *Lindquistia* (Rogers *et al.* 1998). No anamorph was known, however, for *Podosordaria mexicana*, the type species of its genus. Because anamorphs are considered to be highly important in delimiting genera in the *Xylariaceae*, and because *Lindquistia* is unique in its disarticulating propensity, it was critical to establish the anamorphic differences between *Poronia* and *Podosordaria*, if any. Fortunately, we were able to culture material collected by San Martín and to obtain both the anamorph and teleomorph. We showed that the anamorph of *Podosordaria mexicana* does not disarticulate and, thus, to put the concept of *Podosordaria* on a much more solid foundation (Rogers *et al.* 1998).

Numerous other examples of taxonomic detective work involving tropical material could be cited. There are some specific problems that I would like to investigate, should material fortuitously become available. For example, what is *Xylocrea piriformis* (Moeller 1901)? Is it a *Sarcoxyton* or something unique? What is *Squamotubera* (Rogers 1981)? Is it a xylarioid *Sarcoxyton* or does it represent a 'good' genus? What is *Xylariodiscus*? In any case, Laessøe's 1994 assessment of generic names (Laessøe 1994) contained a number of xylariaceous names of uncertain status. A number of these have been clarified, including *Entoleuca* (Rogers & Ju 1996),

Kretzschmariella (Ju & Rogers 1994), *Stilbohypoxyton*, and *Moelleroclavus*. These can now be comfortably accepted as xylariaceous. But, to modify and paraphrase the joyous and excited comment of Sherlock Holmes to Dr Watson, 'the game is still afoot'!

FUTURE STUDIES IN TROPICAL XYLARIACEAE

Many of the future investigations of tropical xylariaceous fungi, and other fungi, for that matter, should be by resident tropical mycologists. As discussed eloquently by Corner (1993), much of importance is missed by the casual or short-term collector. Workshops on tropical mycology in tropical environments, where specialists interact with students, help to introduce problems and build relationships among interested mycologists. Two notably successful workshops in which I participated were held in Puerto Rico and in Venezuela in 1998 and 1999, respectively. Both workshops were supported by the USA National Science Foundation. More such workshops should further strengthen and enhance tropical mycological activities.

Intensive purposeful collecting must continue in the tropics, worldwide. Most groups of fungi have been inadequately and unsystematically collected in most tropical areas. Almost every collecting expedition or box of specimens from correspondents reveals new taxa and other surprises. Although I have not collected in India or Thailand, *Xylaria* collections from both areas contain a high percentage of taxa unknown to me. Along with more intensive collecting should be an increased effort to identify hosts and substrates. This, of course, is a problem in tropical forests with their diversity of taxa. When possible, competent phanerogamic systematists should be involved in collecting expeditions and, in some cases, grants should be sought to compensate for their aid.

One of the most critical needs in tropical mycology is the elucidation of the life histories and activities of tropical fungi. Without the frequent collecting of Don Hemmes, for example, the life history and taxonomic status of *Xylaria moelleroclavus* (discussed above) would still be unknown. What do we know about the development and activities of any member of the curious genus *Camillea* in the tropics? Do the curious depressions into which ostioles empty in *C. cyclops*, for example, act as splash cups, as repositories for ascospores that will be collected by insects, or function in some other way? What is the developmental sequence? What is the status of the host when invaded by the fungus and what is the extent of the invasion? Seed- and fruit-inhabiting fungi mostly seem to be highly host-specific. Are invasions *via* flowers or are the seeds and fruits remarkably efficient baits for certain fungi? *Xylaria magnoliae* seems specific to *Magnolia* fruits in southern USA, but virtually identical fungi have been found on wood in several tropical locations. Does this represent a host shift in this species? Are we dealing with a species complex? Molecular data will probably be required to arrive at an answer.

Xylaria species are frequently associated with ant and termite nests in the tropics, usually producing stromata on old nests. Are the insects, in fact, cultivating *Xylaria* and

suppressing fruiting on active nests? Or are nests acting as bait for specific *Xylaria* species?

Xylaria and *Entonaema* species in dried collections are often shrunken, wizened corpses, bearing little resemblance to the stromata in nature. Moreover, *Xylaria* stromata frequently pass through developmental stages that can make newly mature and overmature collections appear to be separate taxa. Such taxa should be observed and photographed throughout their development and, in most cases, resident mycologists will have to do it.

Endophytic *Xylariaceae* are common in the tropics. As mentioned earlier herein, a molecular component should be included in investigations of such fungi.

Xylariaceous fungi, particularly species of *Kretzschmaria* and *Rosellinia*, are often of great importance as root-rooters of woody cultivated plants. Life history studies are required in order to formulate control measures toward some of them.

A major gap in the understanding of the biology of xylariaceous fungi is the total lack of formal genetic information. The comparatively few taxa that produce mature perithecia in culture are homothallic. Attempts in my laboratory to create genetic markers and to make crosses have failed. New and innovative approaches to this problem seem necessary.

Xylariaceous fungi produce abundant secondary metabolites of potentially great taxonomic and economic significance. Whalley (1996) has reviewed the subject well. Judging from the inquiries that I receive, pharmaceutical companies worldwide are highly interested in metabolites of *Xylariaceae*. The great diversity of tropical *Xylariaceae* makes me believe that there is a wealth of metabolites to be exploited in various ways.

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REFERENCES

- Bier, J. E. (1961) The relationship of bark moisture to the development of canker diseases caused by native, facultative parasites. VI. Pathogenicity studies of *Hypoxylon pruinautum* (Klotzsch) Cke., and *Septoria musiva* Pk. on species of *Acer*, *Populus*, and *Salix*. *Canadian Journal of Botany* **39**: 1555–1561.
- Boedijn, K. B. (1959) On a new family of the *Sphaeriales*. *Persoonia* **1**: 15–19.
- Burger, W. (1992) Parapatric close-congeners in Costa Rica: hypotheses for pathogen-mediated plant distribution and speciation. *Biotropica* **24**: 567–570.
- Carroll, G. C. (1999) The foraging ascomycete. *16th International Botanical Congress, Abstracts*: 309. International Botanical Congress, St Louis, MO.
- Chapela, I. H., Petrini, O., & Petrini, L. E. (1990) Unusual ascospore germination in *Hypoxylon fragiforme*: first steps in the establishment of an endophytic symbiosis. *Canadian Journal of Botany* **68**: 2571–2575.
- Corner, E. J. H. (1953) 'I am part of all that I have met' (Tennyson's Ulysses). In *Aspects of Tropical Mycology* (S. Isaac, J. C. Frankland, R. Watling, & A. J. S. Whalley, ed): 1–13. Cambridge University Press, Cambridge, UK.
- Dennis, R. W. G. (1958) Some Xylosphearas of tropical Africa. *Revista de Biologia. Lisboa* **1**: 175–208.
- Dennis, R. W. G. (1961) *Xylarioideae* and *Thamnomycetoideae* of Congo. *Bulletin du Jardin Botanique de l'Etat, Bruxelles* **31**: 109–154.
- Dennis, R. W. G. (1970) Fungus flora of Venezuela and adjacent countries. *Kevo Bulletin, Additional Series* **3**: i–xxxiv, 1–531.
- Farrell, B. D. (1998) 'Inordinate fondness' explained: why are there so many beetles? *Science* **281**: 555–559.
- Goldblatt, P. (ed.) (1993) *Biological Relationships between Africa and South America*. Yale University Press, New Haven.
- Hennings, P. (1897) Beitrage zur Pilzflora Sudamerikas. II. *Hedwigia* **36**: 190–246.
- Hennings, P. (1902) Fungi blumenaviensens. II. A. cl. Alf. Möller lecti. *Hedwigia* **41**: 1–33.
- Jong, S. C. & Rogers, J. D. (1972) *Illustrations and Descriptions of Conidial States of some Hypoxylon Species*. [Washington State Agricultural Experiment Station Technical Bulletin No. 71.] Pullman, Washington.
- Ju, Y.-M. & Rogers, J. D. (1990) *Astrocystis* reconsidered. *Mycologia* **82**: 342–349.
- Ju, Y.-M. & Rogers, J. D. (1994) *Kretzschmariella culmorum* (Cooke) comb. nov. and notes on some other monocot-inhabiting fungi. *Mycotaxon* **51**: 241–255.
- Ju, Y.-M. & Rogers, J. D. (1996) *A Revision of the Genus Hypoxylon*. American Phytopathological Society Press, St Paul, MN.
- Ju, Y.-M. & Rogers, J. D. (1999) The *Xylariaceae* of Taiwan (excluding *Anthostomella*). *Mycotaxon* **73**: 343–440.
- Ju, Y.-M., Rogers, J. D., San Martin, F., & Grammo, A. (1998) The genus *Biscogniauxia*. *Mycotaxon* **66**: 1–98.
- Laessoe, T. (1994) Index ascomycetum 1. *Xylariaceae*. *Systema Ascomycetum* **13**: 43–112.
- Laessoe, T., Rogers, J. D. & Whalley, A. J. S. (1989) *Camillea*, *Jongiella*, and light-spored species of *Hypoxylon*. *Mycological Research* **93**: 121–155.
- Lewin, R. (1986) Damage to tropical forests, why were there so many kinds of animals? *Science* **234**: 149–150.
- Lindquist, J. C. & Wright, J. E. (1964) *Discoxyllaria* genero nuevo la forma perfecta de *Hypocreadendron*. *Darwiniana* **13**: 138–145.
- Möller, A. (1901) *Phycomyceten und Ascomyceten. Untersuchungen aus Brasilien*. G. Fischer, Jena.
- Nilsson, T., Daniel, G., Kirk, T. K. & Obst, J. R. (1989) Chemistry and microscopy of wood decay by some higher ascomycetes. *Holzforschung* **43**: 11–18.
- Petch, T. (1924) *Xylariaceae* Zeylanicae. *Annals of the Royal Botanic Gardens, Perideniya* **8**: 119–166.
- Petch, T. (1928) Tropical root disease fungi. *Transactions of the British Mycological Society* **13**: 238–253.
- Petrini, L. E. & Petrini, O. (1985) Xylariaceous fungi as endophytes. *Sydowia* **38**: 216–234.
- Petrini, L. E. & Rogers, J. D. (1986) A summary of the *Hypoxylon serpens* complex. *Mycotaxon* **26**: 401–436.
- Polishook, J., Pelez, F., Platas, G., Ondeyka, J., Dombrowski, A. & Teran, A. (1999) Biogeography and relatedness of *Nodulisporium* sp. producing nodulisporic acid. *16th International Botanical Congress, Abstracts*: 305. International Botanical Congress, St Louis.
- Rodrigues, K. F. & Samuels, G. J. (1989) Studies in the genus *Phylacia* (*Xylariaceae*). *Memoirs of the New York Botanical Garden* **49**: 290–297.
- Rogers, J. D. (1977) Surface features of the light-colored ascospores of some applanate *Hypoxylon* species. *Canadian Journal of Botany* **55**: 2394–2398.
- Rogers, J. D. (1979) The *Xylariaceae*: systematic, biological and evolutionary aspects. *Mycologia* **71**: 1–42.
- Rogers, J. D. (1981) *Sarcoxyllon* and *Entonaema* (*Xylariaceae*). *Mycologia* **73**: 28–61.
- Rogers, J. D. (1999) The genus concept in ascomycetes. *16th International Botanical Congress, Abstracts*: 121. International Botanical Congress, St Louis.
- Rogers, J. D., Callan, B. E., Rossman, A. Y. & Samuels, G. J. (1988) *Xylaria* (*Sphaeriales*, *Xylariaceae*) from Cerro de la Neblina, Venezuela. *Mycotaxon* **31**: 103–153.

- Rogers, J. D., Callan, B. E. & Samuels, G. J. (1987) The *Xylariaceae* of the rain forests of North Sulawesi (Indonesia). *Mycotaxon* **29**: 113–172.
- Rogers, J. D. & Ju, Y.-M. (1996) *Entoleuca mammata* comb. nov. for *Hypoxylon mammatum* and the genus *Entoleuca*. *Mycotaxon* **59**: 441–448.
- Rogers, J. D. & Ju, Y.-M. (1997) The genus *Stilbohypoxyton*. *Mycological Research* **101**: 135–138.
- Rogers, J. D., Ju, Y. M. & Candoussau, F. (1996) *Biscogniauxia anceps* comb. nov. and *Vivantia guadalupensis* gen. et sp. nov. *Mycological Research* **100**: 669–674.
- Rogers, J. D., Ju, Y.-M. & Hemmes, D. E. (1997) *Xylaria moelleroclavus* sp. nov. and its *Moelleroclavus* anamorphic state. *Mycological Research* **101**: 345–348.
- Rogers, J. D., Ju, Y.-M. & San Martín Gonzalez, F. (1995) *Discoxyllaria myrmecophila* and its *Hypocreadendron* anamorph. *Mycologia* **87**: 41–45.
- Rogers, J. D., Ju, Y.-M. & San Martín, F. (1998) *Podosordaria*: a redefinition based on cultural studies of the type species, *P. mexicana*, and two new species. *Mycotaxon* **67**: 61–72.
- Rogers, J. D. & Samuels, G. J. (1985) New taxa of *Hypoxylon*. *Mycotaxon* **22**: 367–373.
- Rogers, J. D. & Whalley, A. J. S. (1978) A new *Hypoxylon* species from Wales. *Canadian Journal of Botany* **56**: 1346–1348.
- Samuels, G. J., Rogers, J. D. & Nagasawa, E. (1987) Studies in the *Amphisphaeriaceae* (sensu lato). 1. *Collodiscula japonica* and its anamorph, *Acanthodochium collodisculae*. *Mycotaxon* **28**: 453–459.
- Samuels, G. J. & Rossman, A. Y. (1992) *Thuemenella* and *Sarawakus*. *Mycologia* **84**: 26–40.
- San Martín Gonzalez, F. & Rogers, J. D. (1989) A preliminary account of *Xylaria* of Mexico. *Mycotaxon* **34**: 283–373.
- Stanley, S. M. (1975) Clades versus clones in evolution: why we have sex. *Science* **190**: 382–383.
- Sun, G., Dilcher, D. L., Zheng, S. & Zhou, Z. (1998) In search for the first flower; a Jurassic angiosperm, *Archaeofructus*, from northeast China. *Science* **282**: 1692–1695.
- Thompson, L. G., Davis, M. E., Mosley-Thompson, E., Sowers, T. A., Henderson, K. A., Zagorodnov, V. S., Lin, P.-N., Mikhaleiko, V. N., Campen, R. K., Bolzan, J. F., Cole-Dai, J. & Francou, B. (1998) A 25,000-year tropical climate history from Bolivia ice cores. *Science* **282**: 1858–1864.
- van der Gucht, K. (1995) Illustrations and descriptions of xylariaceous fungi collected in Papua New Guinea. *Bulletin du Jardin Botanique National de Belgique* **64**: 219–403.
- van der Gucht, K., Ju, Y.-M., & Rogers, J. D. (1995) *Hypoxylon ravidoroseum* and *Nemania immersidicus*, two new species from the Hawaiian Islands and Papua New Guinea. *Mycotaxon* **55**: 547–555.
- van der Gucht, K., Ju, Y.-M., & Rogers, J. D. (1997) New *Hypoxylon* species from Papua New Guinea and notes on some other taxa. *Mycologia* **89**: 503–511.
- Whalley, A. J. S. (1996) The xylariaceous way of life. *Mycological Research* **100**: 897–922.
- Whalley, M. A., Whalley, A. J. S., & Jones, E. B. G. (1996) *Camillea selangorensis* sp. nov. from Malaysia. *Sydowia* **48**: 145–151.
- Whalley, M. A., Whalley, A. J. S., Thienhirun, S. & Sihanonth, P. (1999) *Camillea malaysianensis* sp. nov. and the distribution of *Camillea* in southeast Asia. *Kew Bulletin* **54**: 715–722.

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