

Understanding microfungal diversity – a critique

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Abstract – This paper reviews recent advances in understanding microfungal diversity. It questions the large amounts of funding given to molecular phylogenetics despite the fact that we barely know more than a small percentage of the global fungi. It also questions the practice of sequencing fungal strains from culture collections, as they may be wrongly identified and usually lack any herbarium specimens to check characters against. The need for epitypification with living specimens is vindicated. Host fungi relationships have been shown to be important to our knowledge of fungal numbers and research on fungi on various hosts are outlined. Data on the fungi from extreme environments, endophytes and aquatic fungi have advanced the knowledge of fungal diversity, while recommendations that funding bodies should fund basic research are expressed.

Biodiversity / current research / molecular phylogenetics / plant pathogens / species numbers

INTRODUCTION

Relatively massive amounts of funding have been spent over the past few years on improving and understanding the higher classification of fungi (e.g. AFTOL, 2007; Kodsueb *et al.*, 2006; Tang *et al.*, 2007) by sequencing an increasing number of fungi and genes. This culminated in an issue of *Mycologia* (Volume 98, 6) with all papers on molecular phylogeny, (e.g. Schoch *et al.*, 2006; Zhang *et al.*, 2006). In a provocative but pragmatic paper, Korf (2005) has questioned the use of such funds at the expense of basic research in fungal taxonomy and biodiversity research and one has to wonder if funding bodies are really getting value for their money? With less than 10% of the world's fungi known (Hawksworth, 1991) can we justify using large amounts of funding for sequencing a few, often poorly scrutinized taxa – or worse using sequencing to identify taxa that could be identified using the microscope. One of the greatest criticisms of the molecular approach is that type species are not being sequenced, while fungal strains without checkable herbarium specimens are thoughtlessly being used to represent genera (e.g. Tang *et al.*, 2007). This is akin to monographing a genus without actually examining the type species. Imagine the consequences of this – the authors could completely misinterpret a genus and exclude numerous taxa which were in fact similar to the type. Yet mycologists continue to sequence fungal strains loaned from culture collections, without any knowledge of whether these are correctly identified or that may even be contaminants! This is confounded by the fact that

taxonomic reliability of DNA sequences in public sequence databases (e.g. GenBank) are seriously flawed, with 20% or more taxa incorrectly identified (Nilsson *et al.*, 2006).

Despite this, however, there have been considerable advances in the understanding of fungal diversity and some well designed experiments using a molecular approach have helped to solve important problems with plant pathogenic and other fungi. This paper critiques these advances by reviewing recent publications in taxonomy and fungal diversity.

UNDERSTANDING SPECIES DIVERSITY

The definition of a taxonomic species has long been a matter of debate and it has mostly been the prerogative of the investigator whether one, two or several characters should define a new species. Previously, numerous species were described based on host-specificity, even though they exhibited similar characters (e.g. *Colletotrichum* – Photita *et al.*, 2005) and *Pestalotiopsis* – (Jeewon *et al.*, 2004; Lee *et al.*, 2006). Now with the advent of molecular data we now have more data that may provide a much better understanding of a species than previously known (Farr *et al.*, 2006). However, the significance of differences in nucleotide sequences in relation to species is still speculative. It is therefore imperative to check the morphological data and look for the differences that are backed up by molecular differences.

Species differentiation using molecular sequencing is also compounded by the fact that the type of the species has rarely been sequenced. Photita *et al.* (2005) sequenced 34 isolates of *Colletotrichum* from seven hosts. They found that the strains clustered in four clades that allied with morphological groupings and that these clades were likely to represent at least 3 distinct species. Endophytes isolated from the different hosts were probably the same species. This study is, however, flawed by the fact that no sequence data was obtained from the holotype and no sequence from a holotype of a *Colletotrichum* species can be found in GenBank. There are sequences of putative *Colletotrichum* species in GenBank. We cannot however, be certain that we have an archetypical strain of the species in question, no matter how many putative strains (or so-called authentic strains) we sequence, until we have a sequence from the holotype (or other type) or designate an epitype.

Many scientists would point out that in most cases a living culture is not available and that most types are so ancient that the DNA is not useful for sequencing purposes. There is however a practicable solution and this which is to loan the type and check it morphologically. Then an identical fresh collection can be sought after from a location and host as near as possible to that of the type collection. An isolate can be obtained from the fresh specimen, the latter which can be dried and distributed in as many international herbaria as possible. This specimen will be designated the epitype, while the living culture can be deposited in several international culture collections and designated the ex-epitype (see Alves *et al.*, 2006; Phillips *et al.*, 2006). The epitype can also be sequenced using various genes and this will represent the molecular type of the species which can be deposited in GenBank, and/or listed in a database and act as a starting point for all future studies of the species or genus.

FUNGAL DIVERSITY VERSUS HOST

One progressive way to establish data on fungal diversity is to examine the fungi on selected hosts and several studies have adopted this approach. Zhou & Hyde (2001) extensively discussed whether fungi were host-specific, host recurrent or generalists and concluded that far more data were needed before any conclusions could be drawn. A group of papers was published in 1991 which dealt with the biodiversity of fungi on several hosts (i.e. bamboo: Hyde & Zhou, 2002; palm fungi: Yanna *et al.*, 2001; fungi on Gramineae: Wong *et al.*, 2001). These papers provided a starting point for other studies to establish whether specific communities of fungi occur on different hosts.

In a series of papers Tanaka and coauthors are revisiting the microfungi from bamboo in Japan. In the latest of their papers Tanaka *et al.* (2005a) and Tanaka & Harada (2005a) describe and provide a new combinations for *Kalmusia scrabispora* and describe *Astrosphaeriella aggregata* with anamorph associations. They also redescribe three species of *Tetraploa* (Hatakeyama *et al.*, 2005c) and introduce a new genus, *Katumotoa* in the *Pleosporales* (Tanaka & Harada, 2005b). However considerable work is required before we can obtain a good understanding of these fungi.

Research on palm fungi (Fröhlich & Hyde, 1999; 2000; Taylor & Hyde, 2003) and fungi on Pandanaceae (Mckenzie *et al.*, 2002) showed that the fungi on these families were unique with little species overlap. In the case of palm fungi there was even little overlap between the fungal communities occurring on different palm species at the same site (Pinnoi *et al.*, 2006; Pinruan *et al.*, 2007). Palms support a rich diversity of microfungi (Taylor & Hyde, 2003; Hyde & Sarma, 2006) and Pinnoi *et al.* (2006) identified 112 taxa from a single host. Many of these taxa were new to science and are in the process of being described (Pinnoi *et al.*, 2003; Pinnoi *et al.*, 2004).

There continues to be an impressive body of literature being published on the fungi on *Eucalyptus* and other forest pathogens (Hunter *et al.*, 2006; Hyde *et al.*, 2007). *Eucalyptus* is an important forest plantation tree as the trees are hardy and relatively quick growing. New diseases or records include stem cankers caused by *Chrysosporthe doradensis* in Ecuador and the *Eucalyptus* microfungi known from culture are also being described in a beautifully illustrated series (Crous *et al.*, 2006; Summerell *et al.*, 2006; Crous *et al.*, 2007).

Grasses have been further studied although there is much more to do. Van-Ryckegem & Verbeke (2005a,b,c) have studied the fungi on *Phragmites australis* at the border of Belgium and the Netherlands. They identified 77 taxa and these are mostly illustrated in their professional webpage (see <http://intramar.ugent.be/nemys/fungi/web/>). There have however, been few other studies of saprobic microfungi on grasses.

There is very high tree diversity in rainforests, yet all trees contribute to the litter layer that accumulates on the forest floor. One important biodiversity issue which is yet to be resolved is whether a group of fungal generalists degrade this litter layer, or whether specific fungal communities degrade each species of litter. The conclusion will have considerable relevance to the fungal species number debate. Paulus *et al.* (2006) showed that there was very little overlap between the fungi on leaves of four host trees in a north Queensland rainforest. Since the leaves were from four different host families we now need to establish if these differences occur between the fungal communities on leaves of trees of the same genus/family. There are great differences and very little overlap between the

fungi occurring on different hosts and substrates in various habitats (Hyde *et al.*, 2007). We still however, have very few clues as to why fungi seem to be host-specific or exhibit host and tissue-recurrence. There is much research to be carried out to resolve these phenomena.

FUNGI FROM EXTREME ENVIRONMENTS

Fungi from extreme environments have received a renewed interest, because 1) of their potential use in biotechnology and 2) molecular techniques can reveal unculturable fungi. In the quest to discover fungal biodiversity some captivating extreme habitats have been investigated, with Selbmann *et al.* (2005) reporting on fungi from the Antarctic. Rock-inhabiting micro-organisms in the Antarctic live at the absolute edge of life under the most extreme conditions known on Earth. Selbmann *et al.* (2005) isolated 26 strains of black, mostly meristematic fungi from cryptoendolithic lichens and characterized them using light and scanning electron microscopy and sequencing of the ITS rDNA region. The taxa belonged to *Cryomyces* (gen. nov., 9 strains) and *Friedmanniomyces* (10 strains), while 7 strains could not be assigned to any taxonomic group within the *Dothideales*. All strains were psychrophiles or psychrotolerant and had very thick melanized walls and are thought to be well-adapted to the harsh Antarctic environment. Hoog *et al.* (2005) also sampled biomats from lakes in the Antarctic and the predominant taxa were psychrotolerant *Thelebolus* species and these were identified by culturing and sequencing. Hoog *et al.* (2005) proposed that the occasional birds droppings falling into an Antarctic lake was adequate to provide sufficient nutrients for growth of these microfungi.

There have also been several reports of new thermophilic fungi. Hambleton *et al.* (2005) isolated a new anamorphic genus *Leohumicola* with four new species from heat treated soil collected in Canada and elsewhere. Yaguchi *et al.* (2005) discovered that *Talaromyces eburneus* which was previously unregarded as a heat resistant fungus was found to cause spoilage of pineapple juice in Japan and sequence data (28S rDNA) showed the anamorph to be *Geosmithia argillacea*.

Because of the possible roles extreme fungi can play in biotechnological applications and the “compelling” aspect of these habitats, we can expect far more publications in this field.

ENDOPHYTES

There continues to be a number of publications on endophytes which document fungi from within living hosts, although unlike previous studies, recent research trends have tended to be more focused on a particular hypothesis, e.g. movement with insects: Devarajan & Suryanarayanan, 2006; effect of water stress: Gonthier *et al.*, 2006.

One main concern in endophyte studies is that the endophytes are isolated from surface sterilized living leaves onto artificial media (Ganley &

Newcombe, 2006; Koide *et al.*, 2005). Duong *et al.* (2006) used DGGE to isolate endophytes from living leaves of *Magnolia* and obtained 14 operational taxonomic units. Their approach was relatively successful and resulted in some endophyte OTUs not normally isolated by conventional methodology. The number of endophytes detected, was however, low (possibly because only 3 leaves were used in the study) and the effort was disproportionate to the results obtained. Duong *et al.* (2006) demonstrated that DGGE could be used to detect endophytes, but noted several drawbacks with the methodology.

Endophyte isolations usually result in a considerable number of sterile mycelia and recent studies have used molecular analysis to provide taxonomic placement of these sterile fungi (Promputtha *et al.*, 2005; Wang *et al.*, 2005). Hambleton & Sigler (2005) went one step further and used a rather spirited approach to describe a new genus with three new taxa based on sterile mycelia and gene sequence data. All are well illustrated in culture and with colour and halftone plates. Mandyam & Jumpponen (2005) bravely hypothesized on the function of dark septate root-colonising endophytic fungi, concluding however that information on possible functions is scant and that more work is needed. They proposed that, as with mycorrhizal symbioses, the dark septate endophyte symbioses are multifunctional and may include host nutrient acquisition, host water uptake, host drought and heat tolerance, protection from herbivores and plant pathogens and may drive plant community dynamics via differential host responses and resource capture. Several new endophyte species have also been introduced and include two new *Cryptosporiopsis* species (Sigler *et al.*, 2005).

Devarajan & Suryanarayanan (2006) provide an interesting perspective on the role of grasshoppers in the dispersal of non-grass endophytes. The insects neither preferred or avoided milkweed leaves covered in a *Colletotrichum* spore suspension, however the spores passed through the gut and retained their viability. They suggested that insects could act as vectors for non-grass endophytes. One of the problems with this point of view is that endophytes rarely sporulate on living leaves and it is unlikely that grasshoppers would eat dead leaves on which the endophyte is sporulating.

AQUATIC FUNGI

There has been relative few publications on marine fungi, while freshwater fungi are presently under investigation by several groups. Vijaykrishna *et al.* (2006) provided a review paper dealing with research on freshwater fungi, data on their diversity and roles, explanations on how taxa are adapted to freshwater and established their evolutionary origins. Freshwater ascomycetes were shown to have evolved from terrestrial fungi and occur in mainly three classes. The adaptation to populate freshwater has occurred in several lineages and it is estimated that fungi became adapted to freshwater habitation approximately 390 million years ago.

Shearer and coworkers continue to describe new species of freshwater fungi (*Aliquandostipite* - Raja *et al.*, 2005; *Arniium gigantisporum* - Raja & Shearer, 2006a; *Cyanoannulus* - Raja *et al.*, 2003; three new *Jahnnulla* species - Raja & Shearer, 2006b). Miller *et al.* (2006) described *Cuspidatispora xiphiago* gen et sp. nov. from a creek in north America, while Tanaka *et al.* (2005b) described

three new freshwater ascomycetes from Japanese rivers. One interesting ascomycete, *Ascoyunnania aquatica* with microcytic conidiation was described from China (Cai *et al.*, 2005). This species produces large hyaline ascospores which germinate with aging within the asci to form dark, warted secondary spores. The secondary spores may be an adaptation towards unfavourable conditions.

Aquatic hyphomycetes diversity has been studied in Portugal (Pascoal *et al.*, 2005). Gönczöl & Révay (2004; 2006) provided some interesting data on species diversity of conidia in rain from living trees and stemflow, throughfall and gutter conidial assemblages.

Freshwater ascomycetes are now relatively easy to study following the recent books of Tsui *et al.* (2003) and Cai *et al.* (2006). They are also ideal as streams rarely dry out and collections can be made throughout the year. It will also be intriguing to establish the effect of global warming on these micro-organisms. Methodology is also simple, while species diversity and new discoveries are rewarding. There are likely to be many more publications on freshwater fungi as the Asian Freshwater Mycology Research Group (www.fungaldiversity.org) start writing up their findings.

CONCLUSIONS

Despite the large amounts of funds being spent on molecular phylogenetics there have been several advances in our knowledge of fungal diversity. It is highly likely, however, that a large percentage of fungi remain undiscovered. Investigations of new habitats and new locations will result in discovery of new species and taxa from yet unknown lineages. A proportional amount of funding should therefore be allocated via funding bodies to investigate unexplored regions and search for the microfungi. At the same time mycologists from the developing countries should be trained in the skill of taxonomy, which in turn will benefit biotechnological research, plant pathology and quarantine.

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