
Phylogeographic examples of Asian biodiversity in mushrooms and their relatives

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Using characters from morphology, sexual recognition systems, DNA sequencing and RFLP patterns, geographic patterns and directions of geographic migration can be ascertained. In fungal groups such as *Artomyces* (*Clavicornia*), *Flammulina*, *Lentinus*, *Panellus* and *Pleurotus*, four principles can be elucidated: 1) for some sexually compatible groups, an obvious Eurasian cohesion can be identified, as opposed to a sister American population; 2) for certain groups, a strong Asian-western North American cohesion can be identified; 3) care must be taken to distinguish relatively ancient migration from recent events, the latter sometimes human-mediated; and 4) many sexually intercompatible ancestral populations existed before ultimate continental drift, later becoming allopatric but retaining sexual recognition. Sexual recognition among intercontinental populations appears to be a more reliable measure of relatedness than morphological characters and (to some extent) DNA sequence mutations.

Key words: Distribution patterns, mycogeography, Agaricales

Introduction

By the dawn of the 21st century, it has become clear that the word “species” means different things to different people. Traditionally, if two organisms looked alike, they were considered to be one species – which became known as the “morphological species concept.” About fifty years ago, another way to consider “species” was put forward. It was based on potential or actual interbreeding rather than morphological traits. If two individuals could interbreed, they were to be considered as one species – which became known as the “biological species concept,” revolving around “intersterility groups” – populations which were internally sexually interfertile, but inter-populationally sterile. More recently, once phylogenetic reconstructions were formulated based on DNA sequences, it became possible to trace monophyletic assemblages that could be considered as “species” – which became known as

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the “phylogenetic species concept.” While these three viewpoints of “species” have become established, albeit with some controversy, numerous other constructs have been proposed.

In the senior author’s career, after some years of involvement in morphological taxonomy mostly of clavarioid fungi, he was persuaded to try culturing higher basidiomycetes. The very first exercise took place in Jilin Province, China, in a rather dry mushroom season. Wu Qiu-xin, a student of RHP at the time, was attempting to culture from *Clavicornia* fruit bodies, and without many collections of coral fungi on hand, RHP decided to try his hand with *Pleurotus*, which seemed relative common in the nearby forests. And so it started.

Present research includes two laboratories: RHP collects basidiomata in nature to domesticate taxa through harvest of single-basidiospore isolates. KWH analyzes DNA sequences and RFLP patterns in order to prepare phylogenetic reconstructions and to understand population biology. Together with several graduate students over the last decade or more, we have attempted to apply three methodologies to systematics in selected groups of mushrooms and their relatives.

First; specimens from nature are preserved for morphological examination in order to judge the material in the morphological species concept. Second; single-basidiospore isolates from basidiospore germlings lead to sexual compatibility experiments, testing the biological species concept. Third; DNA from cultures or from basidiomata is utilized to construct phylogenies as an application of the phylogenetic species concept. This approach we term “the triangulation method.” From some phylogenetic reconstructions, however, phylogeographic signal can be read, and it is this work which forms the basis for this paper. Some of this work has been summarized elsewhere (Petersen and Hughes, 1999).

General considerations

Our early sexual compatibility experiments were naively simple. Our first intention was to reveal the mating systems (bipolar, tetrapolar, amphithallic, homothallic) of individual species. Luckily, these experiments proved straightforward, and several reports were offered on species whose mating systems had remained unknown (viz. Gordon and Petersen, 1991; Petersen and Gordon, 1994; Petersen, 1995, 1997; Johnson and Petersen, 1997). But as collecting and culturing continued, it became possible to conduct sexual compatibility experiments using collections of a single taxon made over long distances: long, overland distances [(i.e. Alaska-contiguous United States-

Costa Rica for *Phyllotopsis nidulans* (Petersen and McCleneghan, 1997); Japan-Europe for *Oudemansiella mucida*], or transoceanic intercontinental populations [i.e. Europe-North America for *Marasmius androsaceus*, *Pholiota spumosa*, *Mycena rosella*, *Pleurotus pulmonarius*, etc.; Antipodes-South America for *Conchomyces bursaeformis*, *Pleurotopsis longinqua*, etc.(Petersen and McCleneghan, 1997); trans-Pacific for *Xeromphalina brunneola* (Petersen, 1991) and *Artomyces* (as *Clavicornia*) *pyxidata* (Wu and Petersen, 1991)]. Although certain complications were encountered, it was clear that biological species could be very widespread. Equally clear, morphological characters and sexual compatibility were not necessarily linked and did not always evolve at the same rate.

But these early experiments opened a question asked many times previously. If sexual intercompatibility was retained over long distances and over formidable barriers – oceans, mountain ranges, etc. - was long-distance spore dispersal responsible, or was sexual compatibility retained even after prolonged populational separation? And if separation was prolonged, HOW long was the separation; measured in glacial eras or thousands of years, or measured by continental drift or many millions of years?

Along the way to some answers, we discovered some cautionary problems. We can summarize them quickly.

First; not all basidiospores are created equal. When collections of a single taxon from widespread locations are paired, some single-spore isolates (SBIs) are strong dikaryotizers, some moderately so, and still others appear unable to dikaryotize any mate (see Gordon and Petersen, 1992, for data on *Marasmius siccus*). Likewise, not all basidiospores are uninucleate. In some cases, all spores are binucleate, as in *Oudemansiella canarii* (Petersen and Halling, 1993), while in other instances, some spores are uninucleate and others are binucleate, as in *Pholiota spumosa* (McCleneghan, 1997) and *Agrocybe pediades* (Rehner, 1989). Such basic facts must be understood in order to explain some intercompatibility data.

Second; clamp connections are only an imperfect measure of dikaryotization. Basidiomata and cultures of some taxa, such as species of *Strobilurus*, are consistently clampless, so pairing experiments must be analyzed under epifluorescence microscopy (Petersen, 1995). In other cases, such as *Pseudohiatula ohshimae* (Petersen, 1995), basidiomata can be without clamps, but dikaryon cultures show common, normal clamp connections.

But more peculiarly, in some clamped species, clamp connection formation apparently is suppressed in long-distance pairing experiments. In *Oudemansiella mucida*, for example, normal clamps were formed in intercollection pairings between Japan and far eastern Russia, and similarly

between European collections. When eastern Asian collections are paired with European, however, dikaryotization took place more or less normally, but with no accompanying clamp connections (Petersen and Halling, 1993).

Third; care must be taken to correctly interpret mating data. Ginns (1974) furnished examples of reported bipolarity which could be interpreted as tetrapolar, while Arita and Mimura (1969) showed that some tetrapolar grids could be collapsed and read as bipolar.

For the rest of this paper, we wish to review some of the distribution patterns of mushrooms and their relatives which include Asia and Pacific Ocean landmasses. Some are well-known for green plants as well as fungi, while others may be somewhat novel.

Asia-Eastern North American similarities

The famous American botanist, Asa Gray, was able to examine herbarium material from Asia during his tour of European capitals in 1839-40. Later, after the “Opium Wars” in coastal China and after Admiral Perry opened Japan to international trade, resulting in the availability of Asian botanical specimens, Gray was struck by the similarity of many Asian taxa to eastern North American representatives. In fact, these data were part of the ammunition he used to rebut Louis Agassiz’s creationist construct. Only 3 decades ago, Radford *et al.* (1968) could point to 98 genera of higher plants whose distribution was disjunct from eastern North America to eastern Asia.

In passing, we note that numerous publications have appeared which putatively compare Asian-Pacific mycota with that of other geographic areas (i.e. Imai, 1961; Hongo, 1978; Hongo and Yokoyama, 1978; Mao *et al.*, 1986, Redhead, 1989; Wu and Mueller, 1997; Mueller *et al.*, 2001). Unfortunately, conclusions based on names used in literature are fraught with more inaccuracies than can be considered empirical. Even papers employing molecular evidence are open to doubt based on inaccurate use of names. We have subjected previous literature to our own analyses and find that some names used for North American taxa were incorrect, and that *eastern* North American taxa actually may show less similarity to Asian taxa than do taxa from *western* North America. Gray’s hypothesis remains to be proven for fungi.

Eurasian influence

Our experience reinforces the hypothesis that the Atlantic Ocean is and has been a major barrier to intercontinental sexual contact. Several experiments

have shown this graphically, including intercontinental laccase isozyme exclusivity in *Marasmius androsaceus* and *M. scorodonius* (Gordon and Petersen, 1997, 1998), and some complexes in *Pholiota* (McClenaghan, 1997). Just as graphic are preliminary data for *Lentinus tigrinus* (Grand, 2002). Phylogenetic reconstruction using ITS sequences from widespread collections clearly segregates the large Eurasian population from that in North America.

One of the most dramatic instances of basidiomatal pleomorphism **across** Eurasia is the case of *Pleurotus cornucopiae*. In Europe, extending to Turkey, fruitbodies of *P. cornucopiae* are formed in clusters, with brown pilei. Krisai-Greilhuber (Petersen and Krisai-Greilhuber, 1999) noted that occasional yellow basidiomata could be seen among the otherwise brown clusters.

Seemingly separately, in northern Asia a *Pleurotus* with lemon yellow pilei is sold commercially in mushroom markets, and has been described as *P. citrinopileatus*. The two entities, *P. cornucopiae* and *P. citrinopileatus*, are so different as to make them readily identifiable and their names acceptable. But Ohira (1990) showed that these disparate forms were sexually compatible. A single biological species is involved, presumably to be called *P. cornucopiae*, but recognition of the yellow *Pleurotus* at species rank is still common and understandable.

Another example in *Pleurotus*: Petersen collected a thin, brown *Pleurotus* on dead conifer logs in far eastern Russia in 1993. Sexual compatibility tests showed these two collections to be incompatible with all other species in our library, and it was described as *P. abieticola* (Petersen and Hughes, 1997). Only last year, in screening photos from a trip to northern China a decade previous, similar *Pleurotus* basidiomata were noted, and cultures from those collections proved compatible with the Russian organism. This might have been expected, for the Chinese and Russian locations were within a thousand kilometers of one another (Albertó *et al.*, 2002).

Then, in 2000, fieldwork north of St. Petersburg, Russia, included collections of *Pleurotus* basidiomata thought to be the ubiquitous *P. pulmonarius*. Even before compatibility tests were performed, however, molecular evidence showed these collections to be *P. abieticola*, fully 8000 miles away from its earlier stations. Surely this obscure species must be found across Russia in appropriate temperate forests.

Gondwana

The floristic link joining the Antipodes (Australia, New Guinea, New Caledonia, New Zealand) to southern and Patagonian South America is most conspicuously seen in *Nothofagus* – the southern beech. Horak (1983) explored

the less conspicuous but similar pattern of agarics, citing dozens of cases. Much less explored is southern Africa and Madagascar, although Roger Heim's herbarium may hold many wonders from this island. One of our early studies showed that *Conchomyces bursaeformis* showed sexual recognition compatibility from the Antipodes to Chile (Petersen and McCleneghan, 1997)

In our lab, Edgar Lickey took on the genus *Artomyces* (until recently called by the more familiar name, *Clavicornia*). We had numerous collections from New Zealand and Tasmania and Patagonia, secured in most cases by haploid, monokaryon cultures. It was possible, therefore, to test sexual intercompatibility and molecular phylogenetic placement of these fungi. The result showed several species pairs, in which one member resided on Pacific landmasses, the other in South or Central America (Lickey, 2001). Within *A. pyxidatus* (Lickey *et al.*, 2002), phylogeographic signal from ITS-sequence data suggested that a Eurasian population was sister to an American population, and that within North America (adding supplementary RFLP data) northeastern and southwestern populations could be identified.

In the poorly understood genus *Lentinellus*, one almost cosmopolitan species is *L. castoreus*. Years of indiscriminate collecting and culturing provided many isolates that could be subjected to intercollection pairing experiments and molecular analysis. All collections of the morphospecies and its infraspecific variants were sexually compatible, and the ITS sequence phylogenetic reconstruction clearly showed distributional populational clades. A relatively basal clade includes the Antipodes, South and Central America. Relatively derived is a European clade, and North American collections appear to be of two lineages.

A third member of the Auriscalpiaceae, *Auriscalpium vulgare*, also conforms to a distinctly Eurasian-American phylogeographic pattern (KWH, unpubl. data), but in this case, the strobili on which basidiomata are found differ with the continent, but include *Pinus*, *Picea*, *Pseudotsuga* and *Abies*.

Care is necessary, however, in ascertaining whether such distribution patterns are old, or if recent distribution might be involved. For example, *Pleurotopsis longinqua* exhibits a widely disjunct distribution of New Zealand/southern Australia, Chile/Andean Argentina, and northern Pacific coastal North America. Collections from all locations are morphologically indistinguishable and all are sexually intercompatible. But more revealing, almost no differences can be found in ITS DNA sequences. In other words, not enough time has elapsed in this wide distribution pattern to have allowed differences in even relatively variable DNA sequences. Conclusion: although we have no directionality to report, the distribution appears to be quite recent,

most probably human-mediated (Hughes *et al.*, 1998). More will be said about this under *Flammulina*.

The case of *Lentinula*

It is always interesting to superimpose taxonomic decisions on commercially important fungi. So it is with Shiitake.

The commercially popular shiitake has been tied to the northern Asian fungus, *Lentinula edodes*. Work now a decade old showed that other *Lentinula* morphological entities were present, described a century previous. *Lentinula novozelandiae* basidiomata were smaller than those of *L. edodes* and fruited on a different set of hosts. Likewise, *L. lateritia* of Australia and New Guinea showed another form and different colors from *L. edodes*. Shinomura *et al.* (1992), however, showed that all three recognized species were sexually intercompatible and that fertile hybrids could be produced among these forms. Here was a classic case of relatively fixed morphological variation not reflected in sexual isolation.

Subsequently, Hibbett *et al.* (1998) discovered that DNA phylogenetic reconstruction within *L. edodes* revealed more than three clades, and that in some geographic locales (notably Papua New Guinea) more than a single molecular entity existed.

In our lab, Juan Luis Mata executed compatibility tests across several *Lentinula* collections from southern United States, Mexico and Central America (now extended to South America). To that time, only the single species name, *L. boryana*, was recognized from the New World, but Mata's data clearly showed two biological species, which could also be recognized by subtle micromorphological characters of basidiomata. A meticulous examination of type specimens of names listed as synonyms under *L. boryana* by Pegler (1983; Mata and Petersen, 2001) furnished the name *Lentinula raphanica* for the second species (Mata *et al.*, 2001). Yet another species was added as new, *L. aciculospora* (Mata and Petersen, 2000). Not only are the three American species mutually sexually incompatible, but all are incompatible with *L. edodes* and its forms across the Pacific. Indeed, phylogenetically, *L. aciculospora* seems intermediate between the Pacific and American taxa.

Although the genus is obviously widely distributed, nothing is known about possible African taxa and their relation to known organisms.

The Trans-Beringian connection

Some years ago, RHP was able to collect and describe *Ramaria* taxa from Jilin Province in northern China (Petersen, 1989), and from southern and northern Yunnan Province (Petersen, 1988; Petersen and Zang, 1986, 1989, 1990). In several instances, these basidiomata were very similar to some collected and described from moist, western North America, mostly by Currie Marr (Marr and Stuntz, 1971). If only basidiomata were compared, one might conclude that single taxa spanned the considerable distance of this distribution pattern. Instead, micromorphological differences, especially in spore dimensions and ornamentation could be seen. In some cases, separate but similar taxa were described, in others, infraspecific ranks seemed more appropriate. But these surmises preceded the advent of DNA sequencing as a measure of similarity or relationship.

Subsequently in our lab, two major stories evolved, neither of them intended to test the trans-Beringian connection, but doing so anyway.

In our culture collection, we had numerous isolates of *Panellus stypticus*, a common wood-rotting mushroom in temperate climates around the North Temperate Zone and much less common in the Antipodes. Literature on this genus had already been established for many years (Macrae, 1937, 1942; Petersen and Bermudes, 1992a, b). Our student, Jianking Jin, was persuaded to examine the genus *Panellus*, which, depending on the literature consulted, included at least 6-7 species (Miller, 1970), and up to 30 (Corner, 1986). Moreover, it had been proposed by Miller (1970) and Burdsall and Miller (1975) that the closest relative of these small, gilled mushrooms was the tropical polypore genus *Dictyopanus*, presenting another hypothesis to be tested.

Jin established that there were certain morphological differences among the collections in hand, including lamellar interveining or forking and cheilocystidial size and structure. Moreover, we already knew that basidiomata of eastern North American collections were bioluminescent, while those from other parts of the world (including western North America) were not so (Macrae, 1942). But in the face of these differences, all worldwide collections were sexually intercompatible. Obviously, although sexual recognition systems had been maintained, geographical separation had occurred long enough ago to allow for morphological and biochemical mutations to become fixed, and contemporary contact among worldwide populations did not exist.

This premise was tested through molecular evidence (Jin *et al.*, 2001a). A phylogenetic reconstruction based on ITS sequences exhibited phylogeographic signal, in which one clade represented Australia/New

Zealand, another was trans-Beringian from far eastern Russia to Alaska and northern California, a third clade included Europe and Scandinavia, and a fourth clade represented eastern North America. Likewise, RFLP analysis of the ITS sequence, using three restriction enzymes, again showed distinct similarity of collections from Asia and western North America. Eastern North America, conversely, seemed relatively unique, as might have been expected considering bioluminescence data. Separately (Jin *et al.*, 2001b), *Dictyopanus* was shown to be closely related to *Panellus stypticus*, perhaps only a poroid form of the tropics.

A report by Yokoyama (1991) on sexual recognition systems in *Flammulina velutipes* concluded that more than one intersterility group was sheltered under this name. Lamoure (1989) had drawn the same conclusion, but had used cultures under additional species names. This led to a very small experiment, in which six collections of putative *F. velutipes* from Alaska, Scandinavia and eastern North America were paired in a round-robin. Three intersterility groups were revealed, leading, of course, to more interesting questions. Conversations about this experiment with Dr. Scott Redhead revealed that he had been studying this genus for a decade and had concluded that several morphotaxa could be segregated in addition to those already described. A project was undertaken using the triangulation methodology mentioned above. The following results were produced.

First; the new morphotaxa required description so their names could be used in subsequent papers. This was accomplished (Redhead and Petersen, 1999), but Redhead concluded that many intermediate micromorphological forms existed, and that the genus required further study.

Second; sexual recognition experiments revealed certain clusters of morphotaxa within which gene flow could occur. *Flammulina velutipes*, with its several infraspecific variants was partially sexually compatible with *F. ononidis*. *Flammulina rossica* and *F. elastica* showed significant sexual intercompatibility. These species pairs, however, were virtually sexually isolated from others, as were *Flammulina populicola* and *F. fenae*. But throughout all pairing experiments, low levels of apparent “interspecific” hybridization were recorded: taxa of this genus, already known to be morphologically plastic, also were not sexually clearcut (Petersen *et al.*, 1999). Moreover, dikaryon cultures that resulted from these putative “interspecific” crosses could be fruited, and viable basidiospores produced (A.S. Methven, pers. comm.). Most telling, however, was the discovery of an interspecific hybrid in nature (Hughes and Petersen, 2001), in which the ITS DNA sequence repeat was a combination of European *F. velutipes* and transBeringian *F.*

rossica. The hybrid, strangely, came from three collections from Argentine Patagonia.

Significantly, the most primitive form of *F. velutipes*, based on ITS DNA sequences, was a collection from Szechwan Province, China, made by D. Hibbett (KWH, unpubl. data)).

Third; RFLP patterns within *F. velutipes* showed rather clearcut geographic distributions (Methven *et al.*, 2000). Not surprisingly, one RFLP pattern dominated eastern North America, with another dominating Europe. But a third pattern clearly linked Asia with western North America, not really surprising, since the morphospecies *F. rossica* was known also to conform to a transBeringian pattern.

Collections from temperate South America, New Zealand and Tasmania exhibited an RFLP pattern identical to that from Europe, and we concluded that this organism was introduced to these far-off locations by recent human-mediated transport either through immigration or commerce or both.

Fourth; other species, geographically much more restricted, were identified. *Flammulina mexicana* seemed to be a relic left by the widely distributed *F. populicola* (Hughes *et al.*, 1999). The New Zealand *Flammulina stratosa*, with a gelatinous lateral stratum, appeared most similar to *F. similis* from Tierra del Fuego (Redhead *et al.*, 1998), an apparent Gondwanan distribution.

Tropical distribution

Perhaps the most difficult distributional pattern to untangle is that of tropical taxa. The empire-building imperative of the 19th century sent specimens from worldwide locations to the capitals of Europe. The earliest descriptions were not vouchered by specimens. Rumphius (1750) described both higher plants and fungi, with the fungi numbered but not named, although usually illustrated. Fries adopted some of Rumphius' more sensational taxa (including *Boletus secundus arboreus*), coining Latinized binomials for them. Thus Rumph's unnamed pleurotooid agaric became *Agaricus djamor* Fries. Over a century later, the great expeditions brought dried specimens back to their home ports, and Miles Joseph Berkeley redescribed this unassuming pleurotooid at least a dozen times. Almost every explored land, from Ceylon to Brazil, added its own epithet. In the 20th century, colored forms were emphasized: from India came *Pleurotus eous*, from eastern Russia *P. salmoneostramineus*, from Brazil *P. ostreatoroseus*. All three refer to pink basidiomatal forms of *P. djamor* (Albertó *et al.*, 2002). The species appears to be somewhat unique in "dimitic" hyphal construction of at least the stipe

(Albertó *et al.*, 2002). Most of the genetic bases for forms and colors were worked out by David Nicholl (Nicholl and Petersen, 2000) in our laboratory.

Even though each name is attached to a type specimen, the types are old – not fit for DNA extraction or spore germination. Sexual compatibility and molecular evidence, therefore, are no longer available, so only the thread of morphology links type specimens into a coherent taxon. Occasionally, re-collecting over topotype ground may provide new material, again linked to the older names through morphology.

In our lab, David Sime (Sime, 2000) examined relationships among taxa of *Melanotus* – small, pleurotoid forms of *Psilocybe*. Although not less than 40 species epithets were available, several names were found to represent a single taxon. A conspicuous example was that of *M. eccentricus* and *M. alpinae* from the New World tropics. Type specimens (and fresh collections) were only marginally distinguishable morphologically, and when cultured collections were paired, they were found to be sexually intercompatible. But even more surprising, a new collection of *M. bambusinus* from Vietnam was sent by Thomas Laessoe, and was found to be fully intercompatible with the New World species. Doubtless other names in this small genus will be subsumed into synonymy based on compatibility studies.

The already difficult biogeographical situation is often complicated by pleomorphism over widely scattered locations. Using only morphological characters, for example, *Sarcodon atroviridis* of the New World seems to be a luxuriant form of the same species from Asia. Likewise, *Ramaria grandis* is a large edition of *R. zippellii* from the tropics. *Clavaria aurantio-cinnabarina* comes in a plethora of color forms across the Pacific landmasses from Japan to New Zealand, but the largest basidiomata seem to fruit in southeastern North America.

Other tropical-subtropical distribution patterns extend from Asia and Southeast Asia to southeastern North America. *Gloeocantharellus* was based on *Cantharellus purpurascens* collected and named by Hesler from our southeastern mountains. Corner (1966) greatly expanded the genus through taxa found in Malayasia, Singapore and other tropical Asian locations, so the genus now appears relatively disjunct. This is not the only genus with such a Pacific-eastern North American distribution. Among others are *Ramaria* subg. *Echinospora* series *Dendrocladium*, with large, heavily ornamented spores, *Ramariopsis* with simple clubs for basidiomata, and spiny-spored *Clavaria* species (Petersen, 1976). *Neonothopanus* may represent another such, but it is not well enough understood to be categorically stated.

Conclusions

In the preceding discussion, we have tried to summarize some of the work from our lab which concerns biogeographic patterns for fleshy basidiomycetes, with Asia and the Pacific as cases-in-point. It is necessary to re-emphasize that all of the fungi discussed in detail have been subjected to the “triangulation methodology,” which assumes the ability to be domesticated into laboratory culture. To be sure, most of the euagarics (as propounded by Moncalvo *et al.*, 2002) will not pass this test, but today’s literature is full of molecular phylogenetic reconstructions linked to morphotaxonomy – two of the three requisites for our consideration. Depending on the fungus group to be considered, the inability to test long-distance sexual intercompatibility may be significant or not. But whether morphological similarity is matched by molecular evidence can be measured through DNA sequence comparison, especially if appropriate sequences are examined. One thing is for sure: if a single taxon segregates into intersterile entities, regardless of how fast or slow this occurs, these intersterile populations will be able eventually to express molecular and/or morphological changes without the damping effect of back-crossing with the parental taxon (*viz.* Petersen and Hughes, 1999).

Regardless of culturability, however, I think our work has shown Asia to sit astride a cross-roads of distribution patterns. Eurasian taxa are common, transBeringian distributions are often seen, and Gondwanan and tropical patterns abound. None of these patterns, however, addresses the significant number of endemic taxa, nor the enormous number of yet undescribed taxa. Current research on DNA characterization of ectomycorrhizae and of rhizosphere soil communities point to large numbers of undescribed fungi in the very groups I have addressed. We live on the brink of tremendous systematic, ecological and evolutionary discovery. There is much yet to be done.

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