REVIEW

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Some agaric distribution patterns involving Pacific landmasses and Pacific Rim

Abstract The Pacific Ocean and the "Pacific Rim" include a vast geographic area and most categories of the earth's ecological niches. As could be expected, macrofungi conform to many distribution patterns, some of which are discussed in this article. An introduction to species concepts and some other ancillary methodological considerations is followed by examples of some distributional patterns: Gondwanan, Transberingian, and island biogeographic. Some considerations of changing distributional patterns are also discussed: widening distributions, probable human mediation, and some unique cases that seem not to conform to accepted patterns. Not surprisingly, we conclude that concerted future collecting and comparison of specimens using multiple methodologies offer the only hope for understanding mushroom distributions, regardless of the geographic area of interest.

Key words Fungal distribution · Gondwana · Island biogeography · Phylogeography · Transberingian distribution

Introduction

The Pacific Rim extends from Australia and New Zealand, north through New Guinea, Malaysia, Indonesia, the Philippines, Southeast Asia, coastal China, the Korean Peninsula, Japan, far eastern Russia, Sakhalin, and Kamchatka, then east across the Aleutian Islands to Alaska, western Canada, and the western coast of North, Central, and South America. Within this circle lie the myriad islands of Micronesia, Melanesia, and the Hawaiian group. The temperate rain forests of New Zealand, northwestern North America, and southern South America can be contrasted to the deserts of Pacific-central South America. The hot, humid environment of New Guinea and Southeast Asia is opposed by the near-Arctic tundra conditions of Kamchatka, the Aleutians and Alaska. In short, almost all the array of climatological and ecological niches on earth are supported within the range of the Pacific and its Rim. The spectrum of forest types and the fungi supported by them are still in the descriptive stage of knowledge.

The land masses of the Pacific Rim harbor a number of unique biogeographic domains. The Pacific is rich in islands, including the Malay/Indonesian archipelago and Japan, providing possible characteristic evolutionary patterns of endemism and local adaptation. The Pacific coastal regions of North and South America are partially isolated from their remaining continental masses by the Cascades, the Rocky Mountains, and the Sierra Madre Occidental chain in the north and the Andes in the South. In Indo-Asia, the Himalaya and Hengduan Mountains separate India and China from Tibet. Eastern China and far eastern Russia are vast terrestrial regions with numerous microclimates.

Widespread collecting, including that on Pacific landmasses, has collided with unfortunate obstacles in this modern, dangerous world, including permit restrictions and inability to borrow herbarium specimens. Political unrest and terrorism make access to some areas extremely difficult. For example, the search in East Timor for topotype material of Rumphius's *Lentinus sajor-caju* (Rumph. *apud* Fr.) Fr. and *Pleurotus djamor* (Rumph. *apud* Fr.) Boedijn must be delayed indefinitely in the face of internal violence. Equally, recollection of Petch's fungi from Ceylon (Sri Lanka) is out of the question at this time. Obviously, collection of mushroom specimens is not the most earthshaking endeavor, but it is symptomatic of the scientific loss resulting from the turmoil so common these days.

The most significant inhibition to our knowledge of agaric distribution is time. A decade ago we (the authors) thought we understood the distribution pattern of a particular mushroom, but 10 years later we find that our earlier conclusions, although accurate, were too limited. A mushroom thought to occur only in far eastern Russia (i.e., *Pleurotus abieticola* R.H. Petersen & K.W. Hughes) is now

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known from a circum-North Temperate distribution. A group of traditionally morphologically definable mushroom "species" [i.e., *Gymnopus* subg. *Levipedes* (Fr.) Halling] is now known to be a large, molecularly nearly indistinguishable complex. Molecular analyses have fractured old genera (e.g., *Coprinus* Pers. per Gray; *Lentinus* Fr.) while merging others into larger entities (e.g., *Rozites* P. Karst. into *Cortinarius* Pers. per Gray; *Micromphale* Gray into *Gymnopus* Gray). In short, every publication is written at a particular time (even the time "in the press" can produce additional data), and the efficacy of its data should not be judged from the vantage of hindsight. This caveat is particularly true of the following discussion.

Species concepts and methodology

Although some of the examples outlined below are based on the morphological species concept, increasing work has employed more than one methodology. In order to judge investigations of distribution patterns, it is necessary to understand the stringency of the work itself. Some general considerations follow.

A species concept must be considered

Numerous "species concepts" are current in the biological marketplace. The oldest and probably still most widely accepted is a morphological species concept: if two specimens sufficiently resemble each other, they are contaxic (Smith 1968; Singer 1952a, 1986). To traditional macromorphology have been added layers of higher resolution, from unadulterated microscopy to electron microscopy of various types. Nonoptic characters such as production of unique secondary metabolites may be in this category. Mushrooms have structures, and structures can be compared to arrive at a "morphological species concept." The accuracy of morphotaxonomy depends on the skill of the observer and the calibration of his or her microscope (see Clemençon 1977). The "art" of just how similar specimens must be to be considered contaxic, however, remains somewhat subjective, begging for some more statistical or empirical measurement of "similarity."

For one of us (R.H.P.), early mycotaxonomic training dealt exclusively with morphological species concepts, mostly in clavarioid fungi (e.g., Petersen 1974, 1975, 1978a, 1981).

A second "species concept" centers in sexual compatibility and interfertility (Mayr 1942, 1974). If two organisms can mate and produce viable offspring, they are considered contaxic. This concept is fraught with arguable problems: for how many generations must viability be measured?; what if the individuals refuse to mate for behavioral reasons?; what manner of barriers can be construed as valid to measure inability to mate?; can in vitro sexual compatibility be substituted for in vivo interbreeding?; what percentage of spores must be viable to qualify for the "biological species concept?" Again, the parameters of the biological species concept are open to discussion. Comparative investigations of "morphological" versus "biological" species concepts were summarized by Petersen (1995a,b). In our laboratory, theses and dissertations began to include data from both concepts (Johnson 1997; McCleneghan 1996). Sexual compatibility of multiple collections strengthened the internal cohesion of "species," but required additional time, effort, and experience for positive identification. Sexual compatibility experiments demand haploid, monokaryotic cultures for mating purposes. Establishment of such cultures requires either spore germination (whether basidiospores or asexual spores may depend on the organism involved) or "neohaploidization" techniques (see Petersen 1992a; Petersen et al. 1999). This requirement disqualifies huge segments of the mushroom spectrum: *Cortinarius*, *Russula* Pers., *Lactarius* Pers., *Amanita* Pers., *Cantharellus* Fr., and others, spores of which have not been germinated in vitro. Moreover, the result of sexual compatibility is usually obvious (clamp-connection formation or at least establishment of dikaryotic state), but sexual incompatibility could be caused by multiple factors, some of which remain unidentified.

To answer any question about Pacific Rim organisms and their relationships, some sampling of the Pacific Rim is necessary. For our studies, this has meant carrying Petri dishes with agar across the world (or making spore prints for transportation to our laboratory, these days a questionable practice through plant quarantine and "homeland security" screens). We consider essential a well-maintained herbarium of voucher specimens with documentation (photographs, notes, etc.) so when the sexual compatibility system of a named organism is questioned, the underlying specimen is available for examination and comparison, with cultures of its mating types so pairing experiments can be duplicated. As our collection of haploid, monokaryon cultures grew, it became possible to examine sexual intercompatibility across collections or populations over wider geographic areas (Johnson and Petersen 1997; Petersen and McCleneghan 1995, 1996; Gordon and Petersen 1997, 1998; Sime and Petersen 1999). Additional evidence for genetic relatedness can be based on biochemical analyses including isozymes (Wu 1991; Wu and Petersen 1991; Gordon 1994; Gordon and Petersen 1997; Johnson and Petersen 1997; Lickey et al. 2004).

Third, the new innovation in biological systematics has been a DNA-based "phylogenetic species concept," in which sequences of DNA are compared. Because DNA is considered basic to life and not a derivative (as, for example, whole structures or tissues such as cystidia, pileipellis, spores and their color), it should serve as a highly empirical data set. But even this concept leaves room for conjecture: must "contaxic" intercontinental specimens have exactly the same sequence?; how many base-pair differences dictate separate taxa?; must taxa be monophyletic or might they be paraphyletic? All these questions remain open, but at least various sequences of DNA seem to be providing scaffolds around which many surprising alliances are being revealed. It is common these days to see phylogenetic re-

constructions based on more than 3000 base pairs of DNA composed of several genes.

Most agaricologists would agree that the use of morphological characters alone, when molecular suites are available, draws an incomplete picture, not only for fastidious descriptions of organisms, but especially for their relationships. Older literature commonly used the word "related" when comparing basidiomata (Smith 1968), when the more accurate term was "resembles." If molecular analyses have shown anything, it is that apomorphies, and especially synapomorphies (as the search for uniting morphological characters could be termed), can be misleading. The value of spore print color, lamellar trama construction, and presence or absence of clamp connections have all been questioned in light of clades revealed by molecular means.

Recently, some criticism has been written about workers who deposit incorrectly named sequences in public databases. All too often there is no herbarium voucher, or if there is such, it is not available for examination or comparison. It would be ideal if a holotype specimen were supported by cultures of its mating types and sequences of several genes and/or spacers, so multiple comparisons could be made, but that time will never come.

In our laboratory in recent years, such studies have involved whole or parts of genera worldwide (*Pleurotus* Kummer: Petersen 1992a; Petersen and Krisai-Greilhuber 1996, 1999; Petersen and Ridley 1996; Petersen and Hughes 1993; Petersen et al. 1997; Nicholl and Petersen 2000; Albertó et al. 2002; Lechner et al. 2003, 2004; Badalyan and Hughes 2004; etc.; *Flammulina* P. Karst.: Redhead et al. 1998; Redhead and Petersen 1999; Hughes et al. 1999; Petersen et al. 1999; Psurtseva and Petersen 1999; Methven et al. 2000; Hughes and Petersen 2001; *Panellus* P. Karst.: Petersen and Bermudes 1992a,b; Jin et al. 2001a,b; and numerous others, including *Omphalotus* Fayod, *Lentinellus* P. Karst., *Lentinus*, stipitate polypores, *Gymnopus*, and *Artomyces* Jülich/*Clavicorona* Doty). Distribution patterns of individual taxa or of supraspecific complexes were only incidental to more monographic pursuits. Syntheses of this work have been published (Petersen 1995a,b; Petersen and Hughes 1999). Numerous dissertations added such analyses to morphological and biological species concepts (Johnson 1997; Jin 1999; Sime 2000; Mata 2002; Krüger 2002; Lickey 2002; Grand 2004).

The links among the "species concepts"

So long as mycology operates under the International Code of Botanical Nomenclature and therefore accepts the principle of type specimens, basidiome comparison, especially to type specimens, remains the foundation of systematics. The principle of epitypification, lately added to the Code, allows an additional specimen to be designated when the type specimen is inadequate for one or more characters (e.g., DNA sequences, single-basidiospore isolates). If a specimen of putative *Tetrapyrgos nigripes* (Schwein.) E. Horak is collected in Southeast Asia, however, a DNA sequence or a tetrapolar mating system will not suffice for identification unless an "authentic" specimen exists (topotype = South Carolina) and the new collection compares favorably to it. Thus, morphotaxonomy remains the bedrock under all systematics, including geographic studies.

The age of empires

In what native English-speakers know as the Victorian era (early to late 19th century) and in post-Victorian eras (early 20th century), Eurocentric national empires were worldwide. England's empire was the most far flung and populated (from Canada to various African colonies, to Guyana to Australia/New Zealand and Hong Kong), but France (French Guiana, French Equatorial Africa, French Indochina), Holland [later The Netherlands; Surinam, Dutch East Indies (largely Indonesia), Caribbean islands], and Portugal (Angola, Macao, Brazil) owned and controlled scattered colonies. Under governmental and nongovernmental auspices, civil servants, priests, military personnel, and merchants fanned out far from home. Once colonists were established abroad, hobbies were started or resumed, and specimens were collected. In the fungi there was very little guiding literature, and specimens were commonly dispatched to the experts of the governing country. Thus, the likes of Berkeley (1877, 1878, 1885), Hennings (1891, 1893, 1894, 1896), Overeem (1923a,b), and Patouillard (1886, 1887, 1891) examined specimens of fungi they could only dream about. As the mycota of the tropics was posted homeward, descriptions appeared and plates were published. Often the same fungus was described more than once in different languages. A glance at the nomenclator for *Pleurotus djamor* (Nicholl and Petersen 2000; Albertó et al. 2002) shows how a single mushroom species could take the fancy of multiple workers. However, such redundancy may have been necessary as part of the process of describing the world's higher fungi. Specimens from strange places often arrived at their destination, the expert's table, in such poor condition that even the same author described the same fungus more than once. In the rush to maintain nationalistic pride, general principles were rarely sketched: some forms seemed to occur within but not outside the tropic zone; rarely was the same fungus recognized from widely scattered locations; and macrofungi differed in their preference for certain tree associations. Such ideas remained for a succeeding generation. To be sure, Japan was closed to such exploration until the midpoint of the 19th century, but when plants were recovered there, the Grayan disjunct was uncovered.

Grayan distribution

More than 150 years ago, Asa Gray (1846) pointed out similarities between the floras of eastern North America and eastern Asia. Actually, a student of Linnaeus had defended a Linnaean thesis on the subject a century earlier

(Hallenius 1750). Similar distributions were reported for mosses and ferns (Kato and Iwatsuki 1983; Iwatsuki 1994). Whether this concept extends to higher fungi is still an open question. Similarities between eastern North America and eastern Asia were reported for lichenized fungi (Culberson 1972; Dey 1976) and macrofungi (Hongo and Yokoyama 1978; Wu and Mueller 1997; Wu et al. 2000). Tulloss (2005) expanded somewhat on *Amanita* Grayan species pairs outlined by Yang (2000a), furnishing no less than ten pairs disjunctly distributed. Although higher plants exhibit almost identical disjunct clades, separation of these geographic areas is so old that invariably mutations have caused differences in the Grayan taxa.

Preliminary studies on clavarioid fungi indicated a distributional pattern of some complexes extending from southeastern United States (anchored by the Appalachian Mountains) to mountainous areas of South America, portions of New Zealand (Petersen 1988), at least southeastern Australia, and finally to Japan. Notable among these complexes were the brightly colored, fasciculate simple clubs of *Ramariopsis* Corner emend. R.H. Petersen [flame-orange of *R. laeticolor* (Berk. & M.A. Curtis) R.H. Petersen and banana yellow of *R. fusiformis* (Sowerby) R.H. Petersen in eastern North America, to blood-red of *R. miyabeana* (Ito) R.H. Petersen of Pacific landmasses; Petersen 1978b], some echinulate-spored *Ramaria* Fr. ex Bonorden taxa [especially *Ramaria (Ra.) zippellii* (Lév.) Corner from Japan, New Zealand, and other Pacific islands and its synonym *Ra. grandis* (Peck) Corner from southeastern United States; Petersen 1977]. *Gloeocantharellus* Singer and *Tetrapyrgos* E. Horak, although based on species from southeastern United States (Smith and Hesler 1943; Singer 1945; Horak 1983b, 1986), are better represented across the Pacific landmasses and Southeast Asia (Corner 1966; Honan and Desjardin 2006). This pattern seems repeated by *Scytinopogon* Singer, *Pterula* Fr., and *Tremellodendropsis* D.A. Crawford. None of these groups seems rich in Europe or temperate western North America. Hongo and Yokoyama (1978) sketched a disjunct distribution for *Lactarius indigo* (Schwein.) Fr. DNA evidence may shed further light on this distribution. It remains for molecular investigations to show more precisely to what extent taxa have diverged and to frame a time period in which the separation took place.

Although linking some mushrooms to the Grayan disjunct pattern (Wu and Mueller 1997), Mueller et al. (2001) later reevaluated their data using molecular tools. They examined three genera: *Xerula* Maire, *Armillaria* Staude, and *Suillus* Gray. Only *Xerula hispida* Halling & G.M. Mueller was supported as a disjunct species. *Xerula furfuracea* (Peck) Redhead, Ginns & Shoemaker collections did not form a monophyletic group. Disjunct populations of *Suillus spraguei* (Berk. & M.A. Curtis) Kuntze were shown to be paraphyletic. Finally, *Suillus americanus* (Peck) Snell and *S. sibiricus* (Singer) Singer, which appeared to conform to Grayan distribution, were circumboreal. Conversely, *Oudemansiella mucida* (Schrad.) Höhn. spans Eurasia (always on *Fagus*) from the United Kingdom to Japan, but it is absent from North America (although *Fagus* is present). Recognizing that morphospecies were probably not congruent,

Petersen (1988) and Petersen and Zang (1986, 1989) described several new taxa of *Ramaria* that resembled those of temperate western North America (not eastern North America, as conjectured by Gray).

Wang et al. (2004) found that within collections identified as *Sparassis crispa* (Wulfen) Fr., three clades could be distinguished: Asian, American, and European. The American (called the radicata clade) and Asian clades were sisters, while the European clade was sister to the combined Asian/American clade. Although different species epithets were assigned, the phylogeographic inference points toward a Grayan relationship. Not as convincing, a single collection of *S. spathulata* (Schwein.) Fr. from Japan was included in an otherwise American clade.

Studies with *Grifola* (Gray) using β-tubulin and ribosomal internal transcribed spacer (ITS) sequences showed strong support for separation of North American and Asian isolates of *G. frondosa* (Dicks.) Gray, despite previous studies indicating they were morphologically the same (Shen et al. 2002).

Gondwanan distribution

Australia, New Zealand, Antarctica, and South America (as well as southern Africa) were once associated in the larger Gondwanan continent that produced an angiosperm radiation, presumably together with associated fungi. Some present-day agaric distributions reflect this ancient association. Conspecific relationships between the Antipodals and South America may reflect ancient Gondwanan patterns or more recent human-mediated introduction of fungi.

The total methodology as outlined above cannot be applied to many macromycetes that seem to be Gondwanan. The pioneering work by Singer (1952b, 1953, 1954, 1969) and Horak (1971a,b, 1983a) has emphasized agarics in association with *Nothofagus*, and within that assemblage, emphasis has been on ectotrophic mycorrhizal symbionts. Saprotrophs, however, suffer from scanty collecting in temperate South America: relatively little is known of *Marasmius* Fr., *Marasmiellus* Murrill (Singer 1973), *Mycena* Roussel, *Gymnopus*, and other genera from Patagonia and Tierra del Fuego (Horak 1979; Raithelhuber 1987, 1988, 1991). Superficially, the macromycota of Australia (May and Wood 1997, and included bibliography) and New Zealand (McKenzie 2004, and included bibliography) would appear relatively well known, but extant checklists lack authenticity, being compilations of names reported from the Antipodes but not verified or redescribed stringently. The several papers by Horak, Segedin, and Stevenson (see bibliography in McKenzie 2004) have chipped away at the New Zealand macromycetes, and the book by Grgurinovic (1997) has provided an illustrated guide for Australia. A checklist is now also available for New Caledonia (Horak and Mouchacca 1998).

In a survey of *Armillaria mellea* (Vahl) P. Kumm. using DNA sequences of considerable resolution [ITS, Inter-Genic Spacer (IGS)], Coetzee et al. (2000) concluded that

Fig. 1. Distribution of *Artomyces* (*Clavicorona*) clades. A bootstrap consensus tree derived by parsimony analysis of *Artomyces* ribosomal internal transcribed spacer (ITS) sequences is given in the *insert* with clades *numbered*. Clade distributions are mapped
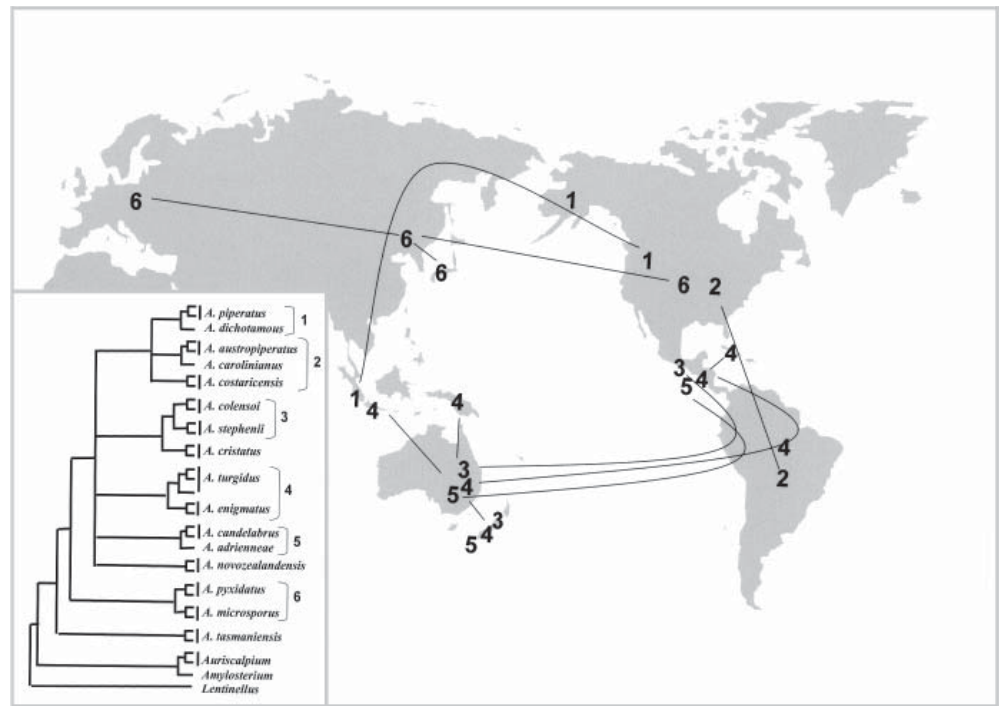
this "species" comprised at least four genetically isolated entities, which were labeled according to their origins, as "Europe," "Western North America," "Eastern North America," and "Asia." In an IGS phylogenetic reconstruction across the genus, all sequences of putative *A. mellea* segregated into a monophyletic clade, sister to the clade of all other included *Armillaria* taxa. Although the four segregants appeared to be genetically (phylogenetically) isolated, no compatibility tests were performed, and the four entities were not given taxonomic rank.

Along the same lines, Coetzee et al. (2001) surveyed numerous *Armillaria* taxa to ascertain infrageneric relationships. Although most species from Australia/New Zealand [*A. luteobubalina* Watling & Kile, *A. pallidula* Kile & Watling, *A. fumosa* Kile & Watling, *A. novae-zelandiae* (G. Stev.) Herink, *A. limonea* (G. Stev.) Boesw.] formed a well-defined, monophyletic clade together with two African taxa (*A. heimii* Pegler, *A. fuscipes* Petch), one Antipodal species, *A. hinnulea* Kile & Watling, showed clear relationships to Northern Hemisphere species, including *A. mellea* and *A. tabescens* (Scop.) Emel. The means for such migration (or origin and subsequent migrations) across the equator remain unknown, although human mediation is one candidate.

The Antipodes represent a region of high species diversity for the genus *Artomyces* (*Clavicorona*; Lickey et al. 2003). A phylogenetic analysis based on ribosomal ITS sequences showed distinct relationships between species clades in the Antipodals and *Artomyces* species found in South and Central America, suggesting an older Gondwanan relationship between South America and the Antipodes (Fig. 1).

Petersen and Hughes (2004) reported on some species of *Lentinellus* [*L. pulvinulus* (Berk.) Pegler, *L. occidentalis*

R.H. Petersen/*L. novae-zelandiae* (Berk.) R.H. Petersen] with distributions in South America and the Antipodes, but other taxa occurring in these regions are worldwide geographically, somewhat obfuscating clear Gondwanan distribution in the genus. Tulloss (2005) noted the disjunct occurrence of *Colombobalanus* and *Amanita* species associated with the Asian and South American hosts.

Transberingian distribution

The possibility of migration between Eurasia and North America via the Bering Strait during glacial maximums when a land bridge existed has been suggested (Graham 1972, 1993), and there is some evidence that the land bridge was occupied by tundra vegetation during these times. The most recent glacial maximum ended about 20 000 years ago (ya). There is limited evidence that the cold-tolerant fungi *Flammulina velutipes* (Curtis) Singer and *Panellus stypticus* (Bull.) P. Karst. were able to cross the land bridge (Hughes et al. 1999; Jin et al. 2001a). Although there is little morphological difference between most collections of *F. velutipes* from western Europe and North America, there is a well-supported clade comprising a collection from British Columbia on the Pacific North American coast and two collections from China (Fig. 2). Two collections from Argentina also appear in this clade. Two possibilities exist for the relationship between China and British Columbia. The first is human-mediated transfer, but the British Columbia collection has unique apomorphies not seen in the two collections from China, which suggests that the transfer is not recent. Alternately, *F. velutipes* may have migrated across the Bering land bridge during the last glacial maximum. The

Fig. 2. Phylogeny of *Flammulina velutipes* collections based on ribosomal ITS sequences. A parsimony bootstrap consensus tree is shown. Bootstrap values are to the *left* of the supported node, followed by Bayesian support values in *bold type*. *Arrows* mark collections from China and British Columbia
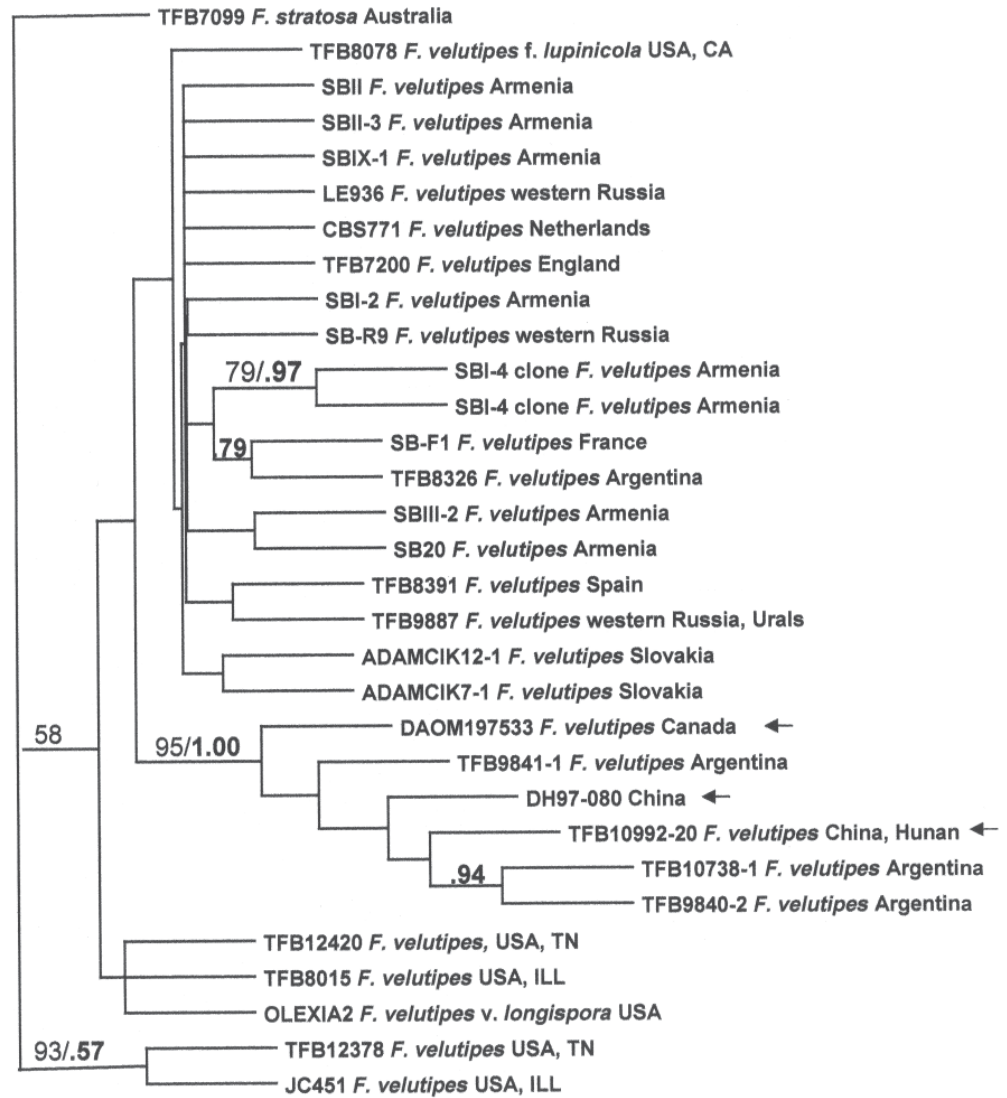
placement of Argentine specimens in this clade is not explained but may be human mediated. Wood and wood products were shipped from Pacific North American ports in great volumes early in the 20th century, and some of those wood products were destined for South American ports and, to a certain extent, vice versa.

Chapela and Garbelotto (2004) described several migrational patterns for the *Tricholoma matsutake* (S. Ito & S. Imai) Singer complex, one of which originated in northwestern North America and progressed across the Bering Strait to northeastern Asia, essentially the reverse of the Transberingian migration usually accepted and already described above. Phylogenetic reconstructions, however, are largely based on the efficacy of the outgroup employed, especially when chronology is superimposed on phylogeny. Chapela and Garbelotto (2004) used *Clitocybe lateritia* J. Favre as an outgroup organism together with *Tricholoma bakamatsutake* Hongo. Moncalvo et al. (2002) found that *C. lateritia* was in a relatively unrelated clade (unnumbered for them, but part of the "Omphalina group") from that which included members of the matsutake complex (their

clade 37, "tricholoma," within clade 36, "/tricholomatoid"). Whether the chronology and/or migration patterns outlined by Chapela and Garbelotto (2004) remain supportable will be tested in the future.

Panellus stypticus distribution also shows a relationship between collections from eastern Asia and the Pacific Coast of North America, suggesting possible migration between Asia and North America via the Bering land bridge (Jin et al. 2001a). Although *P. stypticus* is predominantly a Northern Hemisphere species, it has also been collected in Australia and New Zealand; in the Southern Hemisphere, however, the collections are morphologically and genetically aberrant and the collections show a high degree of self-sterility, characteristics suggesting a genetic bottleneck. Isozyme patterns connect northern Asian populations with collections from Australia and New Zealand, leading to the suggestion that *P. stypticus* migrated to Australia and New Zealand via Malaysia (Jin 1999). Earlier, Horak (1983a) had proposed an Indo-Malayan migration pathway from a south Pacific origin to the Northern Hemisphere, and it is likely that other examples of migration between the

Northern and Southern Hemispheres via Malaysia will be identified.

Halling and Ovrebo (1987), noting the rather distinctive lilac coloration of lamellae in *Rozites* P. Karst., drew similarities of the genus in the Colombian *Quercus* forests and the Southern Hemisphere Pacific landmasses (New Zealand, Papua New Guinea; Horak 1983a; Horak and Taylor 1981). A Malaysian-American migrational pattern was concluded and, once having surmounted the Beringian land bridge, some forms seemed to have migrated southward through the Americas to reach southernmost distribution in central Colombia (Halling and Ovrebo 1987). Although this seeming Pacific Rim distribution for the genus satisfied morphological criteria, it has been shown (Peintner et al. 2002) that *Rozites* is a polyphyletic assemblage that has arisen repeatedly in disparate clades of *Cortinarius*. Thus, to treat *Rozites* as a discrete unit with traceable distribution, in hindsight, seems inappropriate, and the question of biogeographic patterns needs to be revisited.

Widening distributions

Pleurotus abieticola

Some years ago, we (Petersen and Hughes 1997) described a new species of *Pleurotus* (*P. abieticola*) fruiting on conifer wood in the Sichote-Alin Biosphere Reserve northeast of Vladivostok, Russia. *Pleurotus* micromorphology is difficult, but the basidiomata seemed uniquely thin fleshed, with a brown pileus surface. Establishment of single-basidiospore isolates (SBIs) permitted intercompatibility tests with a battery of other species, and the Russian collections were found to be genetically isolated. Finally, ITS sequences from the two extant collections formed a monophyletic clade independent of all other clades in the genus. The data were firm that the collections represented a new species.

Later, a survey of old photographs showed similar basidiomata from northern China (Jilin and Heilongjan Provinces) collected some years previously. SBIs from these Chinese collections were found to be compatible with the Russian SBIs, and ITS sequences were identical. Distribution of the *Pleurotus* was extended to inland northern China (Albertó et al. 2002).

In 2002, while collecting fungi north of St. Petersburg in the Leningrad Region of Russia (not far from the Finnish border), a collection was made of an otherwise undistinguished *Pleurotus*, field identified as *P. pulmonarius* (Fr.) Quél. Later, ITS sequences showed that the fungus was *P. abieticola* (Hughes, unpublished data), some 11 000 km from its original descriptive location.

Most recently, in screening old collections of *Pleurotopsis longinqua* (Berk.) E. Horak from Alaska, one collection was represented by only two small, immature basidiomata thought to lack the characteristic pinkish color of the pileipellis. Sequences from cultures of this collection, however, showed it to be *P. abieticola*, now across the Bering Strait (Hughes, unpublished data). Here is a case of a fungus in which morphological characters failed for one or more reasons, but molecular evidence shows the fungus to be circumboreal, now to be expected on dead conifers in northeastern Canada. What could have been interpreted as a northern Pacific Rim fungus now must be considered much more widely distributed.

Flammulina rossica

Also from the neighborhood of Vladivostok came a collection of *Flammulina* reputed to be *F. velutipes*. Unlike that species, however, the cap was white (not russet or orange-tan) and dry (not glutinous). SBIs and molecular analyses showed the collection to be sexually (Petersen et al. 1999) and molecularly (Hughes et al. 1999) isolated. In 1996, in Alaska, similar basidiomata were collected on dead *Salix* trunks at the base of a glacier. Intercompatibility tests and molecular analysis showed that the collections were the Vladivostok organism, but the organism was named *Flammulina rossica* Redhead & R.H. Petersen (Redhead and Petersen 1999), even though it was trans-Beringian.

More recently, the organism has been detected in western Europe as part of a small complex including *F. rossica* and *F. elastica* (Lasch) Redhead & R.H. Petersen, which appear to hybridize, at least in vitro (Hughes, unpublished data). Further, *F. rossica* appeared in a small collection of *Flammulina* isolates used in a publication about variability in Japanese strains of *F. "velutipes"* (Nishizawa et al. 2003; Hughes, unpublished data), from New York state (collection by Dr. T.J. Baroni), from interior Russia (Valdai Reserve in Novgorod Region), and, surprisingly, from northern Thailand (Hughes, unpublished data). Thus, the distribution of *F. rossica* is now widespread and not Asian or trans-Beringian. Without molecular techniques, this discovery would have been postponed indefinitely.

Island biogeography

Numerous theories have been added to the basic tenets of island biogeography, but two principles seem overarching. First; the farther away from the mainland one progresses, the more depauperate the flora (mycota) becomes. Under this principle, the mycota of the Malaysian and Indonesian islands should become less species rich as they recede from the Indian subcontinent, until the outer islands (in this case perhaps still north of Wallace's Line) support a relatively poor mycota. Second, however, once a fungus has been introduced to an island, it may be relatively free both to spread over that island (and therefore produce more spores for dissemination) and to mutate into variant but survivable forms. This concept is known as the "founder effect." In short, distance reduces the mycota, but islands breed variants.

But how does this relate to the Pacific landmasses? A brief answer is – very imperfectly. At this time, knowledge of Pacific island agarics is so embryonic that little can be said. We know, for example, that *Pleurotus djamor*, originally described from Amboy in Timor (Rumphius 1750), is

now known from many locations around the worldwide tropics, and its morphological variability ranges across stature and color (Nicholl and Petersen 2000) and, therefore, names (Albertó et al. 2002). The same is true of *Lentinus sajor-caju*, another Rumph taxon (see Pegler 1983), which fruits all over Southeast Asia and the lower Indian subcontinent. To claim these agarics to be phenomena of island biogeography is negligent of their much wider distributions. Once sufficient collecting has been accomplished, some estimate of indigenous versus more widely distributed taxa can be made, such as the surveys of marasmioid fungi across Pacific landmasses by Desjardin and Horak (1997a,b).

According to Corner (1994), *Oudemansiella* (*Xerula*) *altissima* (Massee) Corner occurs in Singapore as well as some islands of Malaysia and Indonesia. According to Petersen and Nagasawa (2006), however, its range includes southern Japan and subtropical China (under the name *Xerula globospora* R.H. Petersen & Nagasawa). The origin of the taxon (which is two spored and therefore may be an asexual state), of course, has long since been obscured, so the possibility of island biogeography as its midwife cannot be stated. The same could be said of Petch's *Marasmius* species described from Ceylon (Sri Lanka; Petch 1915, 1947), of which some still appear endemic.

Desjardin and Horak (2002) and Desjardin et al. (2002) reported that "The center of diversity of *Mycena* sect. *Longisetae* appears to be southeast Asia." Of 11 total species, only a single species [*M. aciculata* (A.H. Sm.) Desjardin & E. Horak] seems to occur in the North Temperate Zone. In a survey of Hawaiian agarics, Desjardin and Hemmes (1997) considered 13 of 17 members of the Hygrophoraceae to be indigenous. Young (2005) estimated that 74% of reported Australian Hygrophoraceae were endemic. Likewise, Petersen (1988) concluded that the small species complex of spiny-spored *Clavaria* Fr. taxa was doubled worldwide by the indigenous taxa in New Zealand.

More complex, however, might be the case of *Pleurotus pulmonarius* in New Zealand. Petersen (1995a) established a "standard battery" of tester strains of *Pleurotus*, against which SBIs of unidentified collections could be paired as a reliable identifier. The battery operated without fail until a single collection from New Zealand proved to be intercompatible with several other "species," in a variety of dikaryotization patterns (Petersen and Ridley 1996). To this day, we have no evidence to suggest that this multiple sexual compatibility occurs outside New Zealand, but such an organism could act as a conduit for "pass-through" hybridization wherever it can survive. Whether this property is primitive or advanced cannot be ascertained at this time.

In a series of seminal papers, it was shown that *Lentinula edodes* (Berk.) Pegler, the shiitake of Japanese markets, was spread across Asia from the Antipodes to Japan, and as far west as Nepal and interior China. At least three morphotaxa were described from various locations, but they were shown to be sexually intercompatible (Shimomura et al. 1992). Hibbett (1992) and Hibbett et al. (1998) summarized this situation, describing five phylogenetic clades within the species-rank *L. edodes*, all of which were genetically weakly related to *Lentinula* Earle taxa from the New World (Mata et al. 2001). Not only could island biogeography and time of separation account for the variation in morphology of the geographically isolated forms of *L. edodes*, but the investigations indicated that sexual compatibility and recognition might be expected to remain in place in spite of adequate time and distance to allow for morphological variation.

Historically, regions of high species diversity for a given genus have suggested either a center of origin or an area in which there has been rapid species radiation. Several such areas exist on the Pacific Rim. For the genus *Artomyces* Jülich, New Zealand and Australia are unusually specious with 11 species. The same is true of Central America with 8 species. Contrast this with the number of species known from North America (3), South America (3), and Europe (2). Central America is also a center of diversity for *Gymnopus* (Mata et al. 2006) and *Rhodocollybia* Singer (Mata et al. 2004). The reasons for diversity in Central America probably include varied terrain ranging from coastal to mountainous within a short distance, genetic mixing as plants and associated fungi moved into the Central American refugium during the last glaciation, and the recent formation of the Panamanian Isthmus between North and South America, leading to an interchange of species from the different hemispheres.

Similarly, *Clavicorona* (*Artomyces*) *microspora* Qiu X. Wu & R.H. Petersen has been reported only from Japan (Wu and Petersen 1992) whereas *C. pyxidata* is found in "nearby" China (Jilin and Heilongjiang Provinces). Is *C. microspora* a product of island biogeography? Is it the only species of *Clavicorona* on Honshu?

"Subpruinosus" distribution

Although cursory investigations on the agarics of the Hawaiian Islands had been published previously, the systematic collecting by Hemmes and Desjardin (2002) has yielded numerous new taxa as well as some with interesting extralimital distributions. One such is *Collybia* (*Gymnopus*) *subpruinosus* (Murrill) Dennis. Originally described by Murrill from Jamaica, Desjardin et al. (1999) reported it from California and from Hawai'i. Mata et al. (2006) were able to pair SBIs from California and Hawai'i and found that these collections were partially sexually compatible, indicating that a single biological species was involved. No cultures from the Jamaican station have been available, however, so the biological species concept has remained untested over the full range of the species.

Based on morphological characters, Desjardin (1995) supplied similar distribution patterns for some members of *Mycena* sect. *Sacchariferae*: *M. spinosissima* (Singer) Desjardin from Colombia, Puerto Rico, and Hawai'i, *M. sotae* Singer from Bolivia, Puerto Rico, and Hawai'i, and *M. adscendens* (Lasch) Maas Geest. from California and Hawai'i. It is tempting to consider the migration of the islands of the Greater Antilles through the geological opening of Central America before the closing of the Panamanian Isthmus some 3.5 mya as one explanation for this Caribbean to

Hawai'i distribution (another is human mediated), but it is among the patterns that will be augmented or challenged by increased collecting and especially genetic and molecular experiments. *Mycena amazonica* Singer from Brazil and Hawai'i, *M. discogena* Singer from Chile and Hawai'i, and *Galerina velutipes* Singer from Argentina and Hawai'i may also fit this pattern. Such distributions rest on very sparse collecting in South America but relatively more common collecting in Puerto Rico and California.

A somewhat similar but wider distribution has been reported for *Entoloma stylophorum* (Berk. & Broome) Sacc. by Horak and Desjardin (1993). Stations include Madagascar, Singapore, Papua New Guinea, Solomon Islands, Hawaiian Islands, and Trinidad (southern Caribbean). Similarly, *Gloiocephala epiphylla* Massee has been reported from Argentina, Ecuador, Hawaiian Islands, New Caledonia, Puerto Rico, Jamaica, Japan, and Venezuela. A similar distribution was reported for *Ripartitella brasiliensis* (Speg.) Singer by Ovrebo (1988). At what point distribution patterns are no longer of the "*subpruinosus* type" and become pantropical may be dictated by time and increased collecting in Africa and subtropical North and Central America.

Even more disjunct distributions were reported for *Galerina atkinsoniana* A.H. Sm. and *G. decipiens* A.H. Sm. & Singer (north-central United States and Hawai'i) by Horak et al. (1996). Similarly, *Camarophyllopsis hymenocephala* (A.H. Sm. & Hesler) Arnolds seems disjunct from eastern United States (North Carolina to Hawai'i).

Probable human mediation

When human migrants from Europe spread across the world in the age of empires or later, they carried their favorite companions with them, including birds (English sparrow), mammals (mice, rats, cats), and trees (maples, oaks, pines). Hundreds of species were introduced to new habitats either purposefully or accidentally. We have investigated three such introductions, although in no case did we realize the situation until well into the study.

Flammulina velutipes

Monokaryon isolates from worldwide collections are sexually compatible, so a single "biological species" comprises the very variable "morphospecies." Restriction fragment length polymorphisms (RFLPs), however, allow separation of numerous strains that are often geographically distinguishable. Thus, a European strain, an eastern American strain, and a northwest America strain could be identified through a combination of RFLPs. This in itself was surprising, for it indicated that current transoceanic interbreeding was extremely low or absent, just as we had found with other, less-popular mushrooms. However, some geographic distributions could not be accounted for by continental drift or other natural phenomena. For example, a strain with a *Bst*UI site was found in far eastern Russia, Japan, temperate western North America (that is, Transberingian), and

New Zealand. A second example: a strain with loss of a *Bgl*I site was found in Europe, South America (temperate Argentina), eastern Australia, and New Zealand. Temperate Argentina has been popular with German and Italian immigrants, and Australia and New Zealand are full of imported English host trees. Moreover, ITS sequences showed little difference among these strains, indicating that they have not been separated long enough to undergo significant mutations. Human transportation seems the only logical explanation.

In temperate Argentina, dikaryon cultures of *F. velutipes* were shown to be heterozygous, and when monokaryons were tested for RFLPs, these basidiomata were found to be hybrids between a strain of *F. rossica* found in temperate western North America and *F. velutipes* of European origin (Hughes and Petersen 2001). Such hybridization in nature had not been previously reported, and this finding showed that when brought together (not necessarily in the same place at which the collections were made), interspecific hybridization was possible in *Flammulina*. Since then, at least in vitro interspecific hybridization has also been seen in *Omphalotus* Fayod (Petersen and Hughes 1998) and *Gymnopus* (Vilgalys 1991).

Parenthetically, *F. velutipes* var. *lupinicola* Redhead & R.H. Petersen fruits on the dead root stocks of *Lupinus arboreus* in the salt-spray zone of the California coast. This halophilic strain may be sought along the eastern Pacific Rim wherever its host occurs.

Pleurotopsis longinqua

A small, unassuming pleurotoid mushroom we first collected in New Zealand was identified for us by Dr. Egon Horak, who knew it, he reported, from temperate South America. Basidiospores germinated easily, and a tetrapolar mating system was reported (Petersen 1992b). Later, the same fungus, although larger and more colorful and luxuriant, was collected in Tasmania, and Antipodal populations were found to be sexually intercompatible: a single biological species was involved, although with considerable morphological variation (Petersen and McCleneghan 1995). Still later, *P. longinqua* was found along the coast of Chile, and finally collections were made on the Olympic Peninsula of western North America. All collections were sexually compatible, and this single species exemplified a Pacific Rim distribution (Petersen and McCleneghan 1996).

Selected collections were subjected to molecular methods, and ITS sequences were found to differ remarkably little over the entire geographic range (Hughes et al. 1998). Although enormous distances separated these populations, they had not been apart long enough to support significant mutations. We are convinced that this fungus, too, has been transported around the Pacific Ocean, surviving only in temperate climates with abundant rainfall, but fruiting on several host trees, a requirement for survival of widespread infections.

A similar wide distribution has been reported for *Galerina nana* (Petri) Kühner (Horak et al. 1996), reported

from southern South America (Argentina, Chile), south Pacific landmasses (New Zealand, Australia), Japan, Canada, and California. Such a distribution must require accommodation to several woody host trees.

Some interesting cases

Xerula

Recent investigation into the genus *Xerula* in temperate east Asia has revealed distributional data. While the floristic works on Chinese fungi by Tai (1979) and Teng (1939, 1996) are outdated nomenclaturally and taxonomically, recent publications on the genus by Yang (2000b), Yang and Zang (1993), and Yang and Zhang (2003) helped to bring data on *Xerula* in the Far East up to date. Petersen and Nagasawa (2006) confirmed the occurrence of *Xerula* (*Oudemansiella*) *amygdaliformis* (Zhu L. Yang & Zang) R.H. Petersen & Nagasawa, originally described from southwestern China, in Japan, while Yang (2000b) reported *X*. (*O*.) *hongoi* Dörfelt from China.

Yang (2000b) described *Oudemansiella orientalis* Zhu L. Yang, the only species of the genus with pileal hairs in the pileipellis. In fieldwork in the Kedrovaya Reserve south of Vladivostok, Russia, a collection of this species (or very similar) was made, extending the range of this unique complex from Yunnan, China, to temperate far eastern Russia. Such a distribution may conform to the physiographic schema by Wu (1979), in which a floristic element was traced from interior southwest China along the Chinese coast, through the Korean Peninsula into southeastern Russia (see Vassilieva 1973) and southern Japan (termed "Sino-Japan forest subkingdom" by Wu 1979).

Southern Japan supports the northernmost distribution from the tropical and subtropical western Pacific landmasses. Corner (1934, 1994) described specimens (*Oudemansiella* Speg. for him) from Indonesia (Sumatra), Singapore, and Malaysia, and although the descriptions are not easily deciphered, examination of his specimens (at E) make identification clear. Two species described by Petersen and Nagasawa (2006) as *Xerula sinopudens* R.H. Petersen & Nagasawa [Corner's *O. longipes* (Bull.) Maire] and *Xerula globospora* R.H. Petersen & Nagasawa (Corner's *O*. aff. *radicata* in 1934; *O. altissima* in 1994) appear to be widespread in these tropical areas and are found in (at least) southern Japan.

Megacollybia "platyphylla"

By the time Kotlaba and Pouzar (1972) segregated *Megacollybia* Kotl. & Pouz., *Collybia* (*Tricholomopsis*, *Megacollybia*) *platyphylla* (Pers.) P. Kumm. had become a popular name in use throughout Europe and eastern North America. So long as workers from these regions did not seriously collect in each others' territory, this single name seemed comfortable for what was considered to be a trans-Atlantic organism. The name was also applied to far eastern basidiomata that resembled those from western Europe.

Recently, among the collections from Kedrovaya Biosphere Reserve south of Vladivostok, several collections of putative *M. platyphylla* were gathered. ITS sequences showed that basidiomata were of two haplotypes, one related to a western European/Scandinavian organism, the other a haplotype unique to temperate eastern Asia. The actual distribution of the second haplotype is unknown, but Japan and Kamchatka are logical candidates for its distribution. These data resemble findings by Aanen et al. (2001) in European and American *Hebeloma velutipes* Bruchet, Matsumoto et al. (2005) with *Pleurocybella porrigens*, and Terashima et al. (2006) with *Armillaria mellea* subsp. *nipponica* Y.C. Cho & Igarashi.

The eastern North American *Megacollybia* taxon has not yielded to monokaryon culture, while the Euro-Scandinavian organism not only undergoes in vitro spore germination but exhibits a tetrapolar mating system (Petersen, unpublished data). Combining these data with morphology and phylogenetics, it is obvious that the eastern North American organism requires a new species epithet. Another closely related species fruits from the western North American temperate coast (Washington, Idaho, Oregon) through the dry southwest (Arizona) and was named *Tricholomopsis fallax* A.H. Sm. by Smith. Pertinent adjustments have been reported elsewhere (Hughes et al. 2006).

Mycena viscidocruenta

An odd Pacific distribution appears to include an organism described from South Australia as *Mycena viscidocruenta* Cleland (small, bright red basidiomata on small sticks in South Australia). Although we have not studied type or authentic material, an ITS sequence has been deposited in Genbank under this name.

In Kedrovaya, a small, bright red agaric fruits on the dead catkins of *Alnus*, and ITS sequences from those collections closely match the sequence deposited for *M. viscidocruenta*. If these bright red fungi are contaxic, they are certainly not *Mycenas* [but perhaps *Resinomycena* Redhead & Singer, as suggested by Moncalvo et al. (2002)]. Whatever they are, a distribution pattern extending from South Australia to temperate Primorsky is certainly new.

Conclusion

Early understanding of Pacific and Pacific Rim macrofungi was centered in the research institutions of Europe and North America. Encouraged and supported by extranational empires, early contributions came from collections by colonial, military, religious, and mercantile personnel. More recently, contributions from Asian mycologists have expanded our understanding of distributions. Yet we are still presented with very imperfect ideas about the mycota itself, its distribution patterns, and its ecological restrictions. Forest decimation, rapid and affordable international transpor-

tation, and enormous intercontinental commerce (especially in natural products) are all introducing fungi to locations and ecosystems heretofore strange to them, but their survival will further obfuscate clear understanding of the macrofungi of the Pacific and its Rim. For these reasons, there is considerable urgency to expand collections from remaining natural areas while the possibility still exists.

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