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Amanita—distribution in the Americas with comparison to eastern and southern Asia and notes on spore character variation with latitude and ecology

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This paper is dedicated to my generous mentor, Dr. Cornelis Bas of Leiden.
He transformed *Amanita* taxonomy.

Abstract—Similarity of lists of taxa for *Amanita* sections *Amanita*, *Validae*, and *Lepidella* is computed for lists from six Western Hemisphere regions within the natural ranges of *Quercus* and the *Pinaceae*—Prov. Québec, Canada; New Jersey and Long Island, USA; central Mexico; Costa Rica; the Chiricahua Mountains, USA; and Andean Colombia. For the first two sections, the pattern of distribution reflected in similarity measures is compared to similarity measures for areas of southern and eastern Asia in which *Quercus* and the *Pinaceae* are also major symbionts of *Amanita*. Data suggest higher endemism in the American regions than in the Asian ones. Factors that may influence this difference are discussed. Biogeographic affinity was computed for the Western Hemisphere nations with regard to Mexico and for the east Asian regions with regard to southwestern China. Variation of three spore characters (amyloidity, shape, and size) with latitude and habitat is examined and apparent trends reported. Hypotheses are offered for environmental pressures contributing to evolution of spore size and shape and for biogeography of taxa. Data supporting rejection or acceptance of hypotheses are reviewed. The combination *Amanita floridana* is validated.

Key words—*Amarrendia*, central Africa, South America, *Torrendia*, tropical habitat

It is now conjectured that there are 900 to 1,000 species of *Amanita* Pers. worldwide (Bas 2000; Tulloss 2000*a*). Of these, half or slightly more have been described. Half or more of the conjectured species are believed to occur in the Western Hemisphere. Data and specimens from 150 years of mycological collecting (beginning with the holotype of *A. flavorubens*) were examined to elucidate patterns of distribution of *Amanita* taxa in the Americas. Nevertheless, so many undescribed taxa are known or expected to be found that this paper must be considered provisional and the subject requires revisiting in the future.

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Materials and methods

1. Regions of study

Six Western Hemisphere regions within the combined natural ranges of *Quercus* and the *Pinaceae* were selected for comparison of their suites of species in *Amanita* sections *Amanita*, *Validae* (Fr.) Quél., and *Lepidella* (E. J. Gilbert) Corner & Bas: (1) Prov. Québec, Canada; (2) New Jersey and Long Island, New York, USA (NJ/LI); (3) Chiricahua Mountains, Cochise Co., Arizona, USA (AZ); (4) central Mexico (CTR. MEX.—states of Hidalgo, Mexico, Michoacan, Puebla, Tlaxcala, and Veracruz); (5) the Cordillera Talamanca, Costa Rica (CR); and (6) Andean Colombia (COL). The regions of interest span approximately 50 degrees of latitude (5°N to 55°N) and approximately 40 degrees of longitude (60°W to 100°W).

Past work concerning distribution on a north-south cline in the Americas north of and including Andean Colombia is summarized by Halling (2001).

2. Selection of taxonomic groups for comparison

Sections of the genus were selected for apparent relative stability of the lists of taxa known from the regions of interest—for the current relatively slow rate of growth in the size of most of those lists (Tulloss unpub. data). Unfortunately, while known to some considerable extent, central Mexico has probably not been as thoroughly explored as the other regions of study; collections from the region have not been as thoroughly revised as in the other regions; and its counts of taxa are probably underestimated—perhaps significantly so.

Sections *Amanita* and *Lepidella* have had monographic treatment in the last 35 years—North American taxa of the former by Jenkins (1977) and worldwide taxa of the latter by Bas (1969). The remaining three sections of the genus are either in great flux taxonomically with many undescribed species (section *Vaginatae* (Fr.) Quél. and to a lesser degree section *Amidella* (E. J. Gilbert) Konrad & Maubl.) or are confusing at present due to inadequate understanding of a significant number of the species (*Phalloideae* (Fr.) Quél.). Moreover, some apparently useful macrochemical characters cannot be checked on dried material.

3. Compilation of lists of taxa from the study regions

Lists of taxa for the study were based on review of exsiccata to the degree possible—with limited dependence on the literature. Then-current keys to taxa in several of the regions of interest appear as appendices in (Tulloss 1998*a*).

Resources upon which I relied in part for the data concerning Québec were due to J. Deprés et al. (2002), Y. Lamoureux (1999; pers. corresp.), and R. Pomerleau (1980).

Material examined from Arizona comprises, for the most part, collections made as part of the Chiricahua Mycoflora Project, organized and directed by J. A. Menge and F. H. Nishida. I have access to the *Amanita* collections from the five+ year project. Many of these collections were annotated by me when fresh.

Material examined from Mexico primarily comes from ENCB, FCME, LBUG, MEXU, NY, RET, TLXM, and XAL and represents the work of a large number of collectors. Among the many recent collections examined most were made by or with A. Estrada-Torres, A. Kong-Luz, and A. Montoya-Esquivel and other faculty and students at Universidad de Tlaxcala. To date, my own field work has been carried out in the states of Hidalgo, México, and Tlaxcala. I'm also grateful to have received as a gift the poster presented by Herrera Fonseca and Guzmán-Dávalos (2002).

Material examined from Costa Rica is largely from the Cordillera Talamanca and was collected by A. E. Franco-Molano, L. D. Gómez, R. E. Halling, J. L. Mata, G. M. Mueller, R. Singer, R. E. Tulloss, and others. I have also received a collection of duplicates from InBio courtesy of M. Mata and a number of *Amanita* collections from the Área de Concervacion Guanacaste (on loan from F and NY). Further, I had full access to Singer's notes on *Amanita* in the region (F).

Material examined from Colombia includes collections revised for the study of *Amanita* in the Colombian Andes by Tulloss et al. (1992*b*). Material of a few taxa not treated in that work, largely collected by A. E. Franco-Molano (COL), has also been revised.

To provide a second model of geographically connected regions with a high degree of similarity in suites of species in the selected sections, similarity was computed for lists of taxa from (1) Japan, (2) southwestern China, (3) the states of Himachal Pradesh and Uttaranchal, India; and (4) the Northwest Frontier Province, Pakistan. The Asian regions selected span approximately 25 degrees of latitude (20°N to 45°N) and approximately 75 degrees of longitude (70°E to 145°E).

The lists for Japan and China are based on some personal review of material and, largely, on the following works: Bas (1969), Bas and Hatanaka (1984); Chen et al. (2001); Hongo (1953, 1957, 1959, 1961, 1967, 1969, 1970, 1971, 1974*a*, 1974*b*, 1975, 1977, 1978, 1982, 1983); Hongo and Yokoyama (1978); Imai (1933, 1938, 1939); Imazeki and Hongo (1957, 1965, 1987); Imazeki, Otani and Hongo (1988); Imazeki and Toki (1965); Nagasawa and Hongo (1985); Nagasawa and Mitani (2000); Oda et al. (2000, 2001); Tulloss and Bhandary (1992), Tulloss et al. (1992*a*), Yang (1994, 1997, 2000*a*, 2000*b*, 2001, 2002*a*, 2002*b*); Yang and Chen (2003); Yang and Doi (1999); Yang, Zang and Yuan (2000); and Yang and Zhang (2002).

The lists for India are based on examination of exsiccata and a conservative reading of Indian literature as recorded in (R. P. Bhatt et al. 2003). Material examined from India, besides collections cited by Kumar et al. (1990) and Tulloss et al. (2001), were collected by the authors of those works or were cited by V. K. Bhatt et al. (1999), were cited in the doctoral thesis of V. K. Bhatt, were collected by S. L. Stephenson (deposited in BPI), or are under examination as part of current research of K. C. Semwal with Tulloss and others.

The lists for Pakistan come from recent work of Tulloss et al. (2001) and material sent to Tulloss by R. Boehne and K. Nazir.

Data for central Africa was largely obtained from Bas (1969; 1982), Beeli (1935), Buyck (1994), Gilbert (1940-41; 1941), Härkönen et al. (1994), Heim (1936; 1940), Pegler (1978), Pegler and Shah-Smith (1997), Walleyn (1996), Walleyn and Verbeken (1998*a*; 1998*b*), and my own research. Many collections from the region were provided to me by D. Arora.

Collections were examined from many herbaria including the following: ALA, BAFC, BPI, C, COL, CSU, CUP, CUVC, DAOM, F, FH, ENCB, FCME, GUH, HKAS, HMAS, HONGO, HPUB, HUA, K, L, LAH, LBUG, MEXU, MICH, NY, NYS, O, PC, PM, PSO, RET, SFSU, TLXM, TNS, UBC, UCB, USJ, WTU, and XAL.

In the tables of raw data (Appendix), "+" indicates that a species is present in a given region of interest; and "i" indicates that a species may be present, but is known to be (or possibly is) introduced.

4. Methods for computing list similarity and biogeographic affinity

The similarity metric applied is the tripartite similarity index of Tulloss (1997) in the version now available on the internet (Tulloss and Tulloss 2004*a*; 2004*b*). The value of the metric ranges from 0 through 1 inclusive. The value 0 indicates no elements in common between two compared sets, and the value 1 indicates complete identity between two compared sets. This metric and the supporting worldwide web pages are implemented in HTML, PHP, and a PostgreSQL database hosted in the XAPServer environment.

Biogeographic affinity is often measured using the Simpson coefficient. The purpose of the computation is to compare a list from a region under study with a "canonical" list for another region. Biogeographic affinity is not a measure of similarity (Tulloss 1997) because the Simpson coefficient is nonlinear (Hayek 1994) and ambiguous. The Simpson coefficient has the potential for reversing the comparison depending on the relative size of the lists being compared. I prefer simply to treat biogeographic affinity as the percentage of list items in the study region that are list items in the canonical list. This produces the result desired from the Simpson coefficient without the ambiguous possibilities ever arising. The size of the canonical list plays no direct role in the computation (another reason why, in my opinion, biogeographic affinity is not a workable similarity metric).

5. Matters of presentation

Herbaria name abbreviations are conformant with Holmgren, Holmgren and Barnett (1990), with the exception of HKAS (herbarium of the Kunming Institute of Botany, Academia Sinica, PRC), HONGO (personal herbarium of T. Hongo), HPUB (herbarium of the Department of Biosciences, Himachal Pradesh University, Simla, India), RET (the author's herbarium) and TLXM (herbario del Laboratorio de Micología, Universidad de Tlaxcala, Tlaxcala, México).

Spore shape naming conventions follow Bas (1969: 311). **Q'** stands for the average ratio of length/width for all spores measured for all specimens examined of a given taxon. In *Amanita*, the values of this variable range from about 1.03 to about 3.50. Q stands for the length/width ratio of a single spore.

Author citations for all *Amanita* taxa from the regions of study, except supraspecific taxa, are listed in appendix tables of this paper. Author citations for species not from the regions of study will be found in the body of the paper. Abbreviations in author citations follow Kirk and Ansell (1992).

Road map to this paper

There are four components to this paper. They are dealt with at different lengths as appropriate according to available data.

The first deals with similarity and biogeographic affinity based on the lists of taxa of the selected subsections in the regions of study. This component of the paper is concerned with distribution, relations of sets of taxa from different regions (biogeography), vicariance, and endemism.

The second topic of the paper is dealt with in brief and concerns the distribution of the two subgenera of the genus—*Amanita* (defined by the taxa's having inamyloid spores) and *Lepidella* (E. J. Gilbert) Veselý *emend.* Corner & Bas (defined by the taxa's having amyloid spores).

The third topic of the paper concerns the apparent relationship of spore shape to latitude within the genus *Amanita*.

The fourth topic of the paper concerns the apparent reduction in spore size in the genus *Amanita* in lowland, primary tropical forest with leguminous ectomycorrhizal trees that dominate in scattered groves or occur singly in an otherwise arbuscular-mycorrhizal matrix—as described by Henkel et al. (2002) and Henkel (2003).

Some hypotheses of evolutionary advantages that might be granted by the trends reported are discussed in the third and fourth parts of the paper. These topics are presented as possible areas for further study.

Similarity & biogeographic affinity—Americas and Asia

Appendix Table 1 lists 26 taxa (including unpublished taxa) of *Amanita* section *Amanita* known from the combined regions of interest. A significant number of the taxa are believed to be good species, but have not been formally described. These entities are simply given alphanumeric codes consistent with my earlier publications, such as the keys in (Tulloss 1998*a*).

Table 1 provides a summary of the similarity relationships embedded in the data of Appendix Table 1 by displaying a matrix of the similarity metrics for all pairs of the six regions under consideration. Each cell of the matrix that represents a distinct comparison contains a triple of numbers and, below them, a similarity measure. The numbers represent (from left to right) the number of taxa occurring in both regions, the number of taxa occurring in the first region and not the second, and the number of taxa occurring in the second region and not the first. The order of the last two values is not material because of symmetry in the similarity metric used. The reader can check on list sizes in the appendix tables.

Appendix Table 2 presents the raw presence/absence data for the 33 taxa of *Amanita* section *Validae* known from the regions of interest and has the same format as Appendix Table 1. Table 2 provides the similarity measures for pairs of regions based on the presence/absence data of Appendix Table 2 and has the same format as Table 1.

Table 3 and Appendix Table 3 are similarly related and similarly formatted and present data for 47 species of *Amanita* section *Lepidella*.

The total number of taxa for which data are presented is 106.

Table 1. Regional similarity—*Amanita* sect. *Amanita* in Americas

	NJ/LI	AZ	QUÉBEC	CTR. MEX.	CR	COL
NJ/LI	-	0	[10,0,5] 0.74	[2,13,7] 0.11	[1,4,14] 0.12	0
AZ		-	0	[2,2,7] 0.27	[2,2,3] 0.45	[2,2,0] 0.58
QUÉBEC			-	[1,8,9] 0.11	[1,4,9] 0.12	0
CTR. MEX.				-	[3,6,2] 0.39	[2,0,7] 0.29
CR					-	[2,3,0] 0.49
COL						-

1. *Amanita* section *Amanita* in the Americas

With regard to *Amanita* section *Amanita*, Appendix Table 1 and Table 1 indicate that while the Québec and NJ/LI regions are the most species-rich regions and share a relatively large number of taxa, in the current state of knowledge, they share no taxa with the Arizona and Colombian regions. While the Arizona region has only four known taxa in section *Amanita*, it shares two of these with all three regions to its south; and, since these regions also have relatively few known taxa in the section, the similarity metric generates relatively high values in the three cases.

The facts that the Québec and NJ/LI regions have the largest lists and that the measure of similarity between their lists is so high (0.74)—the highest measure of similarity for any of the pairs of lists reviewed for this paper—may be related to a number of factors including the geographical proximity of the two regions, extended history of mycological study in those regions, and the partial overlap of forest habitat types. In particular, the Northern Hardwood-*Tsuga* forest type is present in northwestern New Jersey as well as being common in southern Québec.

Only the section *Amanita* lists for the Mexican and Costa Rican regions share at least one taxon with lists of taxa of every other region. This is reflected in Table 1 by the following: Cells in rows and columns labeled with the two regions' names contain no entries with a similarity measure of zero. It appears that Mexico and Costa Rica may represent an intersection of distributions of sets of taxa in section *Amanita*—one associated with eastern North America and another with western North America.

Examining biogeographic affinity to Mexico, the computed values are as follows: Prov. Québec, 10%; NJ/LI 13%; Chiricahua Mountains, 50%; Costa Rica, 60%; Andean Colombia, 100% (1 of 2 taxa is possibly introduced). Note that the number of known taxa in the last three regions is quite small. It appears that areas of relative low diversity (Chiricahua Mountains and Andean Colombia) show less endemism in section *Amanita*. To highlight another set of biogeographic relations, the computations can be repeated to show affinity to the NJ/LI region of study (the most heavily studied by the author): Prov. Québec, 100%; Chiricahua Mountains, 0%; central Mexico, 22%; Costa Rica, 20%; Andean Colombia, 0%.

Table 2. Regional similarity—*Amanita* sect. *Validae* in Americas

	NJ/LI	AZ	QUÉBEC	CTR. MEX.	CR	COL
NJ/LI	-	[1,2,18] 0.07	[7,1,12] 0.45	[2,7,17] 0.13	0	0
AZ		-	[1,7,2] 0.16	[3,0,6] 0.42	0	0
QUÉBEC			-	[2,6,7] 0.25	0	0
CTR. MEX.				-	[1,8,4] 0.13	[1,8,3] 0.14
CR					-	[2,3,2] 0.45
COL						-

2. *Amanita* section *Validae* in the Americas

In *Amanita* section *Validae* (Appendix Table 2 and Table 2), the Québec, NJ/LI, and Mexican regions are most species-rich. As in section *Amanita*, there is a relatively high degree of similarity between the section *Validae* lists of taxa for the first two areas.

Amanita flavorubens is a curious species from the point of view of this study in that it is the only one in the sections of *Amanita* examined that is present in both the northeastern North American and southwestern USA study areas.

Table 2 reveals less similarity among regions of study than in the case of section *Amanita*. In other words, there appears to be a higher degree of endemism in section *Validae* than in section *Amanita*. The zeros in the “CR” and “COL” columns reflect the lack of known taxa shared between the lists of taxa for the two most southerly regions examined and the three most northerly. Once more, Mexico appears to represent a “cross roads” for distributions of taxa of northeastern North America and taxa of the southwestern USA.

With regard to biogeographic affinity to the Mexican region of study, the computations yield the following: Prov. Québec, 33% (note: *one of three* species); NJ/LI, 11%, Chiricahua Mountains, 100%; Costa Rica, 20%; Andean Colombia, 25%. Biogeographic affinity to the NJ/LI region of study is computed for purposes of comparison: Prov. Québec, 88%; Chiricahua Mountains, 33% (note: *one of three* species); Mexico, 22%; Costa Rica, 0%; Andean Colombia, 0%. The known number of species of section *Validae* is low for most of the regions of study (3 to 9 species in all regions except NJ/LI where, after 25 years’ collecting by the author, 19 named or undescribed taxa have been recorded).

Table 3. Regional similarity—*Amanita* sect. *Lepidella* in Americas

	NJ/LI	AZ	QUÉBEC	CTR. MEX.	CR	COL
NJ/LI	-	0	[3,0,23] 0.16	[4,22,12] 0.18	[1,25,4] 0.05	0
AZ		-	0	[2,4,14] 0.16	0	0
QUÉBEC			-	[1,2,15] 0.08	0	0
CTR. MEX.				-	[1,15,4] 0.08	0
CR					-	[1,4,1] 0.25
COL						-

Readers familiar with the study of *Amanita* in Andean Colombia by Tulloss et al. (1992*b*) may remark the absence of *Amanita flavoconia* var. *sinapicolor* Tulloss, Ovrebo & Halling from Appendix Table 2. Additional field observations in Costa Rica have convinced Tulloss, Halling and G. M. Mueller (unpub. data) that the supposed variety *sinapicolor* simply comprises collections of var. *inquinata* that have been exposed to direct sunlight in montane habitat resulting in loss or alteration of the reddish pigment component in the pileus and some desiccation, with the latter, in turn, causing incompletely inflated (hence, more nearly globose) spores. Thus the two characters thought to distinguish the varieties are now interpreted to be based on meteorological, not genetic, factors. The cited authors will propose reduction of *A. flavoconia* var. *sinapicolor* to taxonomic synonymy with *A. flavoconia* var. *inquinata*.

3. *Amanita* section *Lepidella* in the Americas

In examining distribution of taxa in *Amanita* section *Lepidella*, we have a larger number of taxa (47) with which to deal than in the previous cases. They appear to be concentrated, for the most part, between and including the NJ/LI and central Mexican regions of study—temperate to subtropical areas. The work of Bas (1969) provided a foundation for the systematics of section *Lepidella* that is superior to that available for any other section of the genus. Since 1969, the naming of new species has often made good use of Bas' information and his methodology; hence, the section still remains in relatively good order taxonomically. From Table 3 and Appendix Table 3, it is immediately clear that the small sets of species in Colombia and Costa Rica share few members (to date, only one—*Amanita polypyramis*, known from Costa Rica) with the sets from the other regions.

With regard to biogeographic affinity to Mexico, the following values are computed: Prov. Québec, 33% (note: one of three species); NJ/LI, 15%; Chiricahua Mountains, 33%; Costa Rica, 20%; Andean Colombia, 0%. Again, the extensive study of the NJ/LI region by a taxonomist focused on *Amanita* probably has an unbalancing effect on this data. It should be expected that the percentages for the study regions (possibly, least likely for Prov. Québec and Andean Colombia) will increase as more is learned of the undoubtedly large Mexican mycota.

Biogeographic affinity to the NJ/LI region of study is computed for purposes of comparison: Prov. Québec, 100%; Chiricahua Mountains, 0%; central Mexico, 25%; Costa Rica, 20%; Andean Colombia, 0%.

No region has at least one species in common with every other as in the previous cases, but Mexico still maintains its condition of sharing at least one taxon with the three regions to its north and with Costa Rica to the south.

Because there is considerable reliable information about species in section *Lepidella*, it is possible to project what further distribution overlaps between the study regions may be demonstrated in the future. I suspect that all currently known Costa Rican taxa may eventually be demonstrated to occur in Mexico. As to a greater degree of similarity between the Mexican region and regions of study to the north, it is very likely that the set of taxa common to the lists for the NJ/LI and Mexican regions will be expanded after further study. For example:

- Visits to sites in central Mexico have sometimes quickly yielded several species of section *Lepidella* that are familiar from collecting areas in New Jersey—e.g., *A. atkinsoniana*, *A. daucipes*, and *A. polypyramis*. I also have found a number of collections (given alphanumeric codes) that appear to be possible vicariants of taxa known from the New Jersey region (see Appendix Table 3). These observations incline me to believe that my experiences will be repeated on future collecting trips.
- *Amanita nauseosa*, apparently a taxon of Caribbean origin (Tulloss unpub. data) has been found as far north as Baltimore, Maryland, USA (Tulloss unpub. data), but not yet in New Jersey.
- Specimens strongly suggesting "*A. talamancae*" have been collected in northern New York State (Tulloss unpub. data).

There are several taxa in the present list for section *Lepidella* that appear to occur without any woody ectomycorrhizal symbiont: "*A. eremites*," "*A. macerisolum*," *A.*

nauseosa, *A. prairiicola*, “*A. savannae*,” and *A. thiersii*. These belong to *Amanita* subsection *Vittadiniae* Bas. Such taxa occur in a diversity of habitats available in regions of study beyond those for which they are listed: high altitude desert, wet savanna, subtropical and tropical lowlands, high elevation prairies, gardens, and lawns. In the Western Hemisphere, species in the subsection occur from western Canada (Tulloss unpub. data) to Patagonia (Bas 1969; Tulloss unpub. data). *Amanita thiersii* demonstrates a connection to Puebla edo., México from an area stretching at least from Illinois (W. Sundberg pers. corresp.) to eastern Texas (Bas 1969). A number of taxa in subsection *Vittadiniae* occurring in the USA overlap the range of *A. thiersii* in Texas and, hence, might well be found further south. Among these are *A. silvifuga* Bas (1969) and *A. subcaligata* (A. H. Sm. & P. M. Rea) A. H. Sm. *ex* Tulloss *in* Volk & Burds. (=*A. salmonea* Thiers) (Bas 1969; Tulloss unpub. data).

4. Comparison to studies of other groups of basidiomycetes in central Mexico and the U.S.

Dr. J. Cifuentes (pers. corresp.) called to my attention other studies that report taxa shared by regions of central Mexico with the eastern and western mycota of the U.S.

In a section of his doctoral thesis, A. Estrada-Torres (1994) discusses biogeographical issues concerning the *Gomphaceae.* He notes that taxa studied in the state of Tlaxcala, Mexico, include several groupings associated with regions to the north. He expresses the relations in terms of biogeographical affinity: 21.6% of the taxa studied are classed as widely distributed in the Northern Hemisphere; 13.5%, as being shared only with the western U.S.; 8.1%, as being shared only with the eastern U.S.; and the remainder, as elements known, at that time, only from his region of study.

In the doctoral thesis of Cifuentes (1996), biogeographical affinities of stipitate hydnums of the eastern (7.5%) and western (also, 7.5%) regions of the U.S. were calculated with regard to study areas in central and southern Mexico. Affinities were also recognized with Europe and tropical America. In addition endemic and widespread Northern Hemisphere groupings were recognized. Recent studies have indicated that at least some of the taxa formerly treated under European names have proved to be endemic (Cifuentes, pers. corresp.)

Both studies addressed regions of central Mexico (exclusively in the first case). Both studies demonstrated biogeographical affinities to central Mexico of the eastern and western U.S. Both studies demonstrated a group of apparent Mexican endemics, and continuing studies have increased the number of endemics. Hence, the pattern present in the *Amanita* data of this paper echoes previous results in very distinct groups of mycorrhizal basidiomycetes.

5. Additional comments regarding the American regions of study

In the three sections examined, the lists of taxa of the two northernmost regions are most similar to each other; and the same is true for lists of taxa of the two southernmost regions.

The greatest diversity of symbionts for *Amanita* apparently occurs between the NJ/LI region and central Mexico.

Of the regions studied, the Chiricahua Mountains show the strongest biogeographical relationship to central Mexico. The Chiricahua Mountains are well known for their floristic link to Mexico. Many of the species of pine and oak present in the Chiricahuas are Madrean species at the northern limit of their mainly Mexican distribution (Elmore 1976; Miller and Lamb 1985; Perry 1991). This is especially true in the Pinyon-Juniper and Pine-Oak belts as identified by Elmore (1976)—4,500 to 8,000 feet elev. The mountains are well known among ornithologists for their providing an opportunity to view bird species such as the Elegant Trogon (*Trogon elegans*, the most northerly occurring taxon of the Trogonidae) at the extreme northern limit of their ranges (e.g., Farrand 1983). The Sierra Madre Occidentale apparently serves as a biogeographical link between the Chiricahua Mountains and the central Mexican regions of study. The upper elevations in the Chiricahuas are largely linked to the north and west biogeographically. It is worth noting that at least three taxa present in the Chiricahuas (one per section treated in this paper) have northern limits in the West far to the north of Cochise Co.—*A. muscaria* subsp. *flavivolvata*, *A. novinupta*, and *A. smithiana* (see following bullet list). The latter two appear to be rare in the Chiricahua Mountains—even during recent years of record rainfall.

Based on current knowledge, a relatively small number of studied *Amanita* taxa in the three sections examined (10 taxa (9 species) of 106 taxa considered) are known to be rather widely distributed naturally within the combined natural ranges of *Quercus* and the *Pinaceae* in the Americas:

- *atkinsoniana* (amyloid spores) Québec at least to central Mexico (Michoacan edo.)
- *citrina sensu auct. amer.*, (amyloid spores) Québec at least to central Mexico (Hidalgo edo.)
- *farinosa* (inamyloid spores) Québec at least to Costa Rica
- two varieties (taken together) of *A. flavoconia* (amyloid spores) Québec to Andean Colombia
- *muscaria* subsp. *flavivolvata* (inamyloid spores) ranging from southern Alaska (Tulloss unpub. data) and the USA coast of the Gulf of Mexico at least to Costa Rica in the wild, with other occurrences (possible or certain introductions) southward (e.g., Tulloss et al. 1992b; Tulloss unpub. data on Argentine collections) and at least one site (possible introduction) in Massachusetts (Tulloss unpub. data)
- *novinupta* (amyloid spores) southwestern Canada to central Mexico (Tulloss and Lindgren 1994; Tulloss unpub. data)
- *polypyramis* (amyloid spores) New Jersey to Costa Rica (Morales-Torres et al. 1999; Tulloss, Halling and G. M. Mueller unpub. data)
- *smithiana* (amyloid spores) southwestern Canada to central Mexico (Tulloss and Lindgren 1992; Tulloss unpub. data)

- *xylinivolva* (inamyloid spores) Arizona to Andean Colombia (Tulloss et al. 1992b; Tulloss 1998; Tulloss unpub. data).

6. Southern and eastern Asian similarity and biodiversity

For purposes of comparison and contrast, lists of taxa were examined for a group of relatively well-known regions of study in southern and eastern Asia distributed within a narrower range of latitude and a significantly greater range of longitude as noted in the “Methods” section, above: Japan, southwestern China (SWC), Himachal Pradesh and Uttaranchal states in India (HP/UT), and the Northwestern Frontier Province of Pakistan (NWFP).

Table 4. Regional similarity—*Amanita* sect. *Amanita* in Asian regions

	Japan	SWC	HP/UT	NWFP
Japan	-	[6,5,7] 0.50	[4,7,6] 0.40	0
SW China		-	[2,8,11] 0.17	0
India (HP/UT)			-	[1,9,1] 0.14
Pakistan (NWFP)				-

The raw data tables for this set of regions are Appendix Table 4 (24 taxa of *Amanita* section *Amanita*) and Appendix Table 5 (10 taxa of *Amanita* section *Validae*). Their format is the same as that of Appendix Table 1. Table 4 and Table 5 provide the corresponding matrices of similarity measures and follow the format of Table 1.

Biogeographic affinity to southwestern China in the case of *Amanita* section *Amanita* is as follows: Japan, 55%; Indian region of study, 20%; NWFP, Pakistan, 0%. Biogeographic affinity to southwestern China in the case of *Amanita* section *Validae* is as follows: Japan, 100%; Indian region of study, 67%; NWFP, Pakistan, 100%. Yang, Zang, and Yuan (2000) briefly treat the biogeographic affinity of the amanitas of southwestern China to those of Japan.

In *Amanita* section *Validae*, we have the interesting situation of two species—*A. flavipes* and *A. orsonii* distributed over nearly 75 degrees of longitude in the North Temperate Zone—a range extending over more than 7,200 km. (For comparison, a species with circumarctic distribution would extend 15,800 km around the 65th parallel if the distance between the coasts of Greenland and Norway is omitted.)

> Note: Prior to going to press, I received a copy of an interesting article by Zhang et al. (2004) that provides molecular and morphological evidence that there may be more than one taxon now classified under the name *A. flavipes*.

The collecting regions all fall within a belt of forest (now extensively fragmented locally) including *Quercus* and several genera of the *Pinaceae* as major components. The *Times Atlas* (1985) characterizes these forests as Subtropical Forest, Monsoon

Forest, Tropical Rain Forest, and Dry Tropical Forest. The relative continuity of available symbionts in a few genera and the restriction to latitudes north of the Tropic of Cancer both may be factors that permit the two species of section *Validae* cited above to have such an extended range.

Table 5. Regional similarity—*Amanita* sect. *Validae* in Asian regions

	Japan	SWC	HP/UT	NWFP
Japan	-	[5,3,0] 0.70	[3,2,3] 0.55	[2,0,3] 0.49
SW China		-	[4,2,4] 0.56	[2,0,6] 0.32
India (HP/UT)			-	[2,4,0] 0.42
Pakistan (NWFP)				-

The relatively high values for measures of similarity in Table 5 reflect a lower degree of endemism (based on current knowledge) for species of section *Validae* in the Asian regions of study than is observed in the Western Hemisphere regions. This is strongly supported by the high values for biogeographic affinity to southwestern China computed for section *Validae*. On the other hand, my lack of familiarity with the undescribed taxa of the Asian study regions also may have an effect on the species counts and, hence, the computations. (Compare the low number of provisional names and species “codes” in the east Asian appendix tables with the greater frequency of such names in the appendix tables including Western Hemisphere taxa.)

7. The Central American biological “bottle-neck”

Among factors which may be at play in the more limited similarity of lists of taxa in the Western Hemisphere group of study regions, are the absence of naturally occurring *Pinus* in Costa Rica and Colombia, the geologically recent appearance of the isthmus including Costa Rica, the *more* recent migration of *Quercus* into Colombia, and the fact that the selected regions of study extend from well north of the Tropic of Cancer to well south of it. It has been repeatedly observed that both *Quercus* and *Amanita* species numbers are markedly reduced—by about an order of magnitude—between Mexico and Costa Rica. Mexico has between 112 species of *Quercus* according to Schandly as cited by Miller and Lamb (1985) and 150 species according to the work of Rzedowski as cited by Kappelle (1995). Costa Rica has less than 12 or up to 17 species of *Quercus* according to several authorities cited by Kappelle (1995).

The absence of naturally occurring pine south of Nicaragua and El Salvador (Perry 1991) undoubtedly also has a severe effect on the species richness of *Amanita* in Costa Rica and Colombia. Human predation and severe bark beetle epidemic attacks brought pine in El Salvador to the point where it “practically disappeared” toward the end of the last century (Perry 1991: 211).

The *Amanita* taxa with long north-south ranges are clearly capable of forming mycorrhizae with both *Quercus* and members of the *Pinaceae* (and sometimes with taxa in other families of plants as well). *Amanita muscaria* subsp. *flavivolvata*, with its very extended natural range is one such taxon and *A. flavoconia* is another.

The nineteenth century naturalist, Thomas Belt, recorded that about 80% of the birds he collected in Nicaragua were species known at that time from the region to his south, but not from the Atlantic forest to his north (Belt, 1874: 377-378); and he reflects on this interruption in distribution. He describes the end of the "great Atlantic forest" as being to the north and west of an intrusion of the Gulf of Honduras into the mainland of the isthmus along with the presence of the valleys of Humuya and Goascoran in Honduras, "which, along with the central plain of Comayagua, constitute a great transverse valley running north and south from sea to sea, and cutting completely through the chain of the Cordilleras. The highest point of this pass is 2850 feet above the sea, and the country around is composed of undulating savannahs and plains covered with grass." Such a region, along with the termination of a major forest habitat, might well serve to complicate and strengthen a partial blockade to the spread southward of the forest's trees and any *Amanita* symbionts.

8. Possible examples of Graysian distribution

This subject has been repeatedly treated in the past (e.g., Hongo and Yokoyama 1978; Yang 2000*a*). Yang, in particular, has listed pairs of related *Amanita* taxa with Graysian distribution, and the list that follows is a variation of his. One notable example includes the species of stirps *Hemibapha* that has a major center of distribution ranging from Pakistan and India to Siberia in the north and insular southeast Asia in the south and a lesser center of distribution in eastern North America and Central America. Some other pairs of closely phenetically related taxa with an apparent Graysian distribution are *A. abrupta* and *A. sphaerobulbosa* Hongo, *A. bisporigera* G. F. Atk. and *A. subjunquillea* var. *alba* Zhu L. Yang, *A. cokeri* and *A. eijii* Zhu L. Yang, and *A. farinosa* and *A. farinosa sensu auct. Asia orient.* Additional such pairings are *A. flavoconia* vars. and *A. flavipes*, *A. frostiana* and *A. subfrostiana*, *A. magnivolvata* Peck and *A. oberwinklerana* Zhu L. Yang and Yoshim. Doi, *A. rubescens sensu auct. USA orient.* and *A. orsonii*, and *A. westii* (Murrill) Murrill and *A. sculpta* Corner & Bas. Moreover, the following two sets of taxa could be so paired: all known (described and undescribed) species of sect. *Amidella* in the Americas (a major center of distribution for the small section) and *A. avellaneosquamosa* (S. Imai) S. Imai and *A. clarisquamosa* (S. Imai) S. Imai *in* E. J. Gilbert. See, also, the discussion of "*A. conara*" in the following section.

9. Possible Malayo-American and Andean Australo-antarctic elements

Only two potential ectomycorrhizal symbionts are recorded with *Amanita* in Andean Colombia—*Quercus humboldtii* and *Colombobalanus* (=*Trigonobalanus*) *excelsa* (Tulloss et al. 1992*b*).

The latter tree is representative of a group of Malayo-American taxa thought to have migrated from the Northern Hemisphere where they are now extinct (Van der Hammen 1989). The single species of *Amanita* occurring with *Colombobalanus* in Colombia [*A. aureomonile* Tulloss & Franco-Mol. in sect. *Phalloideae*] is possibly also classifiable as Malayo-American. *Amanita* "*conara*," as a member of *Amanita* subsection *Gymnopodae* Bas [otherwise known from Australia, Malaya, and Japan (Corner and Bas 1962; Bas 1969; Reid 1980; Hongo 1982; Wood 1997)] and *Amanita humboldtii* Singer [with its phenetically closest related species native to New Zealand (*A. pekeoides* G. S. Ridl.) and Pakistan and northern India (*A. umbrinolutea* (Secr. *ex* Gillet) Bataille)] (Tulloss unpub. data) might be associated with the historically Andean Australo-antarctic element recognized in Colombian montane vegetation by Van der Hammen (1989). At this time, *A. humboldtii* and *A. aureomonile* are known only from Andean Colombia.

The range of "*A. conara*" beyond Costa Rica is uncertain; however, it should be noted that a species of subsection *Gymnopodae*—*A. ochrophylla* (Cooke & Massee) Cleland—was reported from *Quercus* forest in Guerrero edo., México by Guzmán (1975). Guzmán's macroscopic description fits "*A. conara*" rather well; and his measurements for spores are similar to those of "*A. conara*" (Tulloss, Halling and Mueller unpub. data). The material Guzmán cited has not yet been revised by me, but it appears that "*A. conara*" may occur in Mexico. Just as this paper was in final draft, an apparent second undescribed species of subsection *Gymnopodae* (species CR18) was confirmed in Prov. Puntarenas, Costa Rica—further increasing the evidence for a Malayo-American component in the amanitas of that study region.

10. "Southern end of the line" in the Western Hemisphere

The observation made in this section is based on recent studies in Guyana (Simmons et al. 2002) as well as earlier studies in Amazonia (Bas 1978) and southeastern Brazil (Bas and de Meijer 1993), a summary of data on species of Chile and much of South America (Garrido and Bresinsky 1985; Garrido 1987), an extensive revision of collections from Argentina (Tulloss unpub. data), and Bas' 1969 monograph. The data derived from these sources indicate that, with the exception of apparently imported taxa in gardens, parks, and tree plantations, the ectotrophs of South America outside Andean Colombia have a set of symbionts in *Amanita* disjunct from any of the lists of taxa in this paper's appendices.

Many amanitas in South America from southern Brazil northward and east of the Andes are symbionts of leguminous or polygonaceous plants (Bas 1978; T. W. Henkel pers. corresp.; D. J. Lodge pers. corresp.); and a few amanitas of the region (as well as many in the continent's southern "cone") may not require a mycorrhizal partner. The border of the Andean Colombian region appears to be the "end of the line" for amanitas associated with *Quercus* and members of the *Pinaceae*. Taking the view from the south, although much work remains to be done, it seems few *if any Amanita* taxa of tropical South America have become symbionts of *Quercus*, of members of the *Pinaceae*, or, for that matter, of other families including species known to form mycorrhizae with the "northern" *Amanita* species such as the *Betulaceae*, *Ericaceae*, *Juglandaceae*, *Salicaceae*, etc. For example, Lodge et al. (*in press*) report that *Amanita* taxa mycorrhizal with *Coccoloba* in the Greater Antilles have not formed effective mycorrhiza with *Pinus*.

> Note: I am pleased to be able to include the following information and hypotheses concerning *Dicymbe* groves and their symbionts offered by T. W. Henkel, a prepublication reader of this paper: "Mounting evidence suggest that the ectomycorrhizal genus *Dicymbe*, endemic to the greater Guiana Shield, is most closely related to the *Caesalpinaceae* of West Africa (e.g., *Gilbertiodendron* et al.) and not the other numerous arbuscular mycorrhizal caesalps that characterize the Neotropics. [A probable] part of the reason that the Amazonian/Guiana Shield amanitas appear totally endemic so far is that they may have speciated *in situ* and in isolation with specific caesalps of Gondwanan origin. If this is the case, they have been geographically isolated due the relictual distribution of their hosts upon which they are apparently strongly dependant. Given the affinities of *Dicymbe* at least, one might expect to find similar African amanitas associated with caesalps. However, this hasn't proven true to date with *Boletaceae, Russulaceae, Cortinarius,* and *Inocybe* from the Guyana site—phylogenetic studies indicate long isolation of the site's taxa from African relatives (Herendeen et al. 2003; Henkel et al. 2005). This hypothesis would help explain the across-the-board novelty of Singer's Amazonian and our Guyanan collections.
>
> "We need better information on the legume genus *Aldina* because it is confirmed ectomycorrhizal at Singer's site, our site, and Moyersoen's site in southern Venezuela, but is not closely related to *Dicymbe.* Almost all other reports of ectomycorrhizal legumes in the Neotropics (including *Swartzia, Hymenaea,* et al. in Central America and the Caribbean) are pure conjecture and not based on root excavations. What I think has gone on is that investigators have found ectomycorrhizal basidiomes in a forest, likely associated with nondescript nyctaginaceous or polygonaceous understory trees (e.g., *Neea, Pisonia, Coccoloba*) and have assumed that one of the invariably common legume canopy trees was the host, or, possibly have simply found saprotrophic members of otherwise ectomycorrhizal fungal groups. As a member of a group often collected without apparent ectomycorrhizal hosts, *A. grallipes* [see Table 7] is a candidate for the latter explanation."

In comparison, members of the *Pinaceae* (*Abies*, *Cedrus*, *Keteleeria*, and *Pinus* (D. Arora pers. corresp.; Kumar et al. 1990; Tulloss et al. 2001; Tulloss unpub. data; Yang 1997; Yang, Zang and Yuan 2000) are available symbionts for *Amanita* in all of the collecting areas selected for the comparative study of Asian regions. Moreover, members of the *Fagaceae* (*Castanopsis*, *Lithocarpus*, or *Quercus*) are known to be available symbionts for *Amanita* in the Asian study regions everywhere except in Pakistan.

There is no marked "end of the line" phenomenon associated with the limits of the combined Asian regions of study. Looking westward, in *Amanita* section *Vaginatae*, at least one species known from the Pakistani and Indian regions of study is also well-known from much of Europe and western Asia—*A. umbrinolutea* (R. P. Bhatt et al. 2003; Tulloss et al. 2001; Tulloss unpub. data). Taking the view southward, many *Amanita* taxa appearing in the Asian region of study or their phenetically close relatives are mycorrhizal with members of the *Dipterocarpaceae* (e.g., *Dipterocarpus* and *Shorea*) and other subtropical and tropical trees with ranges extending well southward of the areas of study—through both peninsular and insular southeast Asia and at least into northeastern Australia. In the latter region, at least a few taxa closely related to some from the Asian region of study are mycorrhizal with eucalypts (Arora pers. corresp.; Boedijn 1951; Corner and Bas 1962; Halling unpub. data; Smits 1994; Tulloss unpub. data; Wood 1997).

11. Possible role of deserts of northern Mexico—vicariant taxa

The northern Mexican deserts may play a role similar to that of the Atlantic Ocean in terms of evolution of new taxa. There are pairs of amanitas on the opposite sides of the Atlantic Ocean that are candidates for treatment as vicariant pairs—*A. cylindrispora* Beardslee of eastern North America and *A. gilbertii* Beauseign. of southern Europe and the Mediterranean region (H. E. Hallen unpub. data; Tulloss unpub. data); *A. basii* Guzmán & Ramírez-Guillén of central Mexico and *A. caesarea* (Scop.:Fr.) Pers. of southern Europe and the Mediterranean region (Guzmán and Ramírez-Guillén 2001; Tulloss unpub. data); and others.

> Note: In my opinion, the last pair of taxa mentioned here are inadequately distinguished to justify the proposal of a new species from the information in the protologue. (Based on the protologue, Neville and Poumarat (2004) consider *A. basii* a synonym of *A. caesarea*.) The confusion is magnified by distinguishing the species with so few characters that both species are reported from both sides of the Atlantic. From my examination of material from both Mexico and Europe, I'm inclined to believe that there are indeed two taxa, that *A. basii* is a good species, and that the two species' ranges are completely separated by the intervening ocean.

There are also a striking number of pairs of extremely phenetically similar sister taxa within the Americas themselves. A notable set of such pairs are separated at present by the deserts of Northern Mexico and the absence of suitable ectomycorrhizal symbionts in wet Caribbean coastal regions of Texas and eastern Mexico—two blockades that have disappeared or been reduced during past ice ages. Some taxa that currently exist both in Mexico and in the USA do not show any noticeable morphological differences between populations north of the deserts and those south of the desert region. However, there are some very closely related pairs of taxa that may have diverged in only a few morphological characters from common ancestors

Pairs of taxa that illustrate this "limited divergence" (often in spore shape and in one obvious macroscopic character such as pigment of the basidiocarp or robustness of the stipe) are *A. flavoconia* var. *flavoconia* (north) and *A. flavoconia* var. *inquinata* (south) (Tulloss et al. 1992*b*); *A. pelioma* Bas (north) and *A. sp. M34* (south) (Tulloss unpub. data); and *A. arkansana* Rosen (north) and "*A. garabitoana*" Tulloss, Halling & G. M. Muell. nom. prov. (south) (Tulloss, Halling and Mueller unpub. data).

Notes on distribution of subgenera

The distributions of the two subgenera of *Amanita* are quite different. The species with amyloid spores (subgenus *Lepidella*) and the species with inamyloid spores (subgenus *Amanita*) both occur commonly in warmer climes, but the northern extremes of *Amanita* distribution belong to *Amanita* subgenus *Amanita* and, particularly, to its subordinate section *Vaginatae*. As in the case of plants, taxa of alpine regions are similar to those of the subarctic; for example, *A. nivalis* Grev. (section *Vaginatae*) is well-known to be found in both subarctic and alpine habitats in Europe with dwarf *Salix*.

Table 6. Species per section studied for three studied regions in the Americas

	inamyloid spores	*amyloid spores*	
	Amanita	*Lepidella*	*Validae*
QUÉBEC	10	3	8
NJ/LI	15	27	19
CTR. MEX.	9	16	9

Partially illustrating the distribution of taxa with amyloid spores vs. those with inamyloid spores, Table 6 provides the number of known taxa for each of the sections of interest for the most species-rich study regions. Note the differences between Québec and NJ/LI in the amyloid-spored sections. As mentioned previously, taxa in central Mexico are probably undercounted.

Here are three additional examples of northern regions and their amanitas:

- Alaska, USA - Dr. G. A. Laursen (ALA) has kindly sent me all collections of *Amanita* made during his collecting with Dr. S. L. Stephenson and others in Alaskan tundra in the years 1990-1992. All 58 collections belong in subgenus *Amanita*. While final determinations of most of the material have not been made, 86% of the collections are assignable to section *Vaginatae*.
- Greenland - None of the 10 amanitas known from Greenland have amyloid spores (Knudsen and Borgen 1984; Tulloss 1994; Tulloss and Borgen 1996; Borgen and Tulloss unpub. data). Three of these species (including the two not in section *Vaginatae*) are very rare; and one (*A. muscaria* var. *muscaria*) has not been reported from Greenland since 1888 (Knudsen and Borgen 1984).
- Norway - Species with amyloid spores are concentrated in the south of the country and, somewhat farther northward, along the west-facing coast; but still make up only 7 species (9 taxa) of the up to 25 species (28 taxa) reported recently by Tulloss and Gulden (1999). Moreover, sections *Amidella* and *Lepidella* appear to be absent from the Norwegian mycota.

All six sections are known from all continents with one exception—*Amanita* section *Amidella* is still not known to be represented in South America.

Notes on spore shape variation in relation to latitude

1. Topic road map

Because of the exceptionally wide distribution of taxa of section *Vaginatae* (previous topic), the present topic begins by examining spore shape in relation to latitude in this large section. After establishing the pattern of more numerous taxa with narrow spores in temperate and subtropic regions compared to taxa occurring at lower latitudes, the five other sections of the genus are examined revealing a similar trend in each. Comparison with a report on polypore spores, indicates that the mycorrhizal amanitas reverse the trend noted for the nonmycorrhizal group.

Fall rate of spores as reported by Ingold (1965) is reviewed in the hopes of generating some hypotheses that could lead to an explanation of the trends observed.

Several questions are then posed. Some are partially explored and hypotheses evaluated to the degree permitted by existing data. If an individual taxon has a very extended range including boreal forest, temperate regions, and subtropic latitudes, do its spores show variation in shape over this range? Given an apparent relation of the narrowest spored taxa to fire-prone, "leaky" ecosystems, is there a supportable explanation based on spore fall rate or other shape-related factor? Are there environmental pressures on boreal, alpine, and subarctic taxa that could help to explain a trend toward subglobose spores?

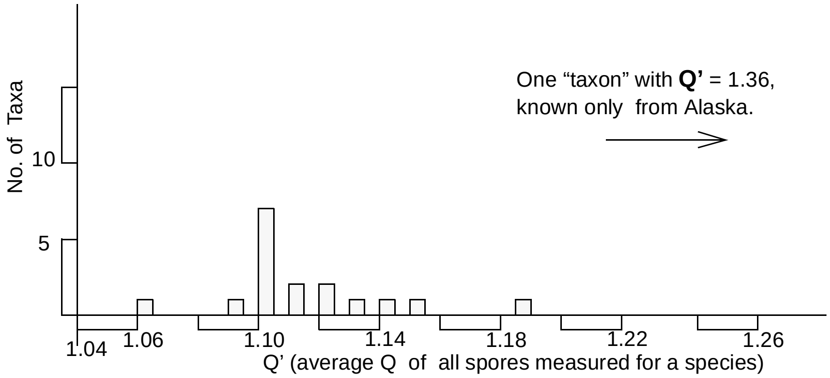

Fig. 1. Number of taxa of subarctic, alpine and boreal habitat with various values of average length/width ratio (average for all spores measured in a species) for 18 species of section *Vaginatae* for which data were available.

2. Spore shape variation in section Vaginatae

The range of spore shape [terminology defined by Bas (1969: 321)] is very limited in the species of the most northern latitudes. While temperate and tropical regions of the world have their species of *Amanita* with elongate (**Q’** between 1.60 and 2.0), cylindric (**Q’** between 2.0 and 3.0), or even bacilliform (**Q’** > 3.0) spores, the spores of those taxa of *Vaginatae* in the far north are dominantly (94%) subglobose (Fig. 1).

Reviewing data on section *Vaginatae* from Greenland (six taxa) and Norway (14 taxa), no entities of section *Vaginatae* were found among these with **Q’** > 1.25. In contrast, the percentage of species of *Vaginatae* with **Q’** > 1.25 is 31% in NJ/LI, 37% in Arizona and New Mexico, 38% in the Mexican region of study, and 27% in Costa Rica.

Comparing a *relatively* well-known tropical region, the number for central Africa is 65%.

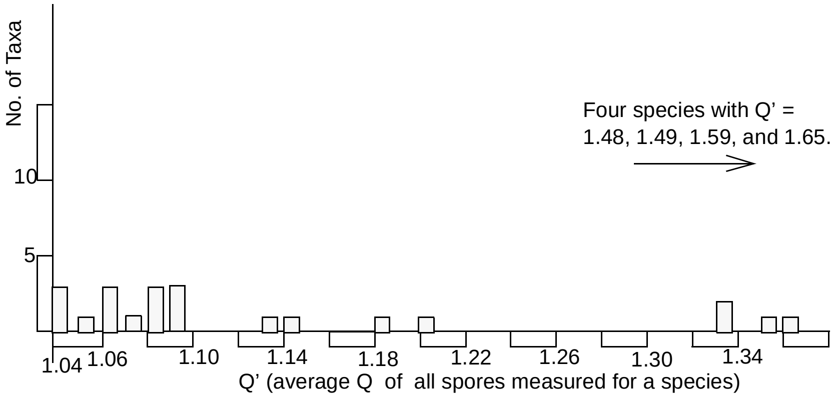

Fig. 2. Number of taxa of NJ/LI with various values of **Q'** for 26 species of section *Vaginatae* for which data were available.

The taxa of section *Vaginatae* known from New Jersey and Long Island and for which sufficient data is available (many are undescribed) presently number 26. The distribution of spore shape for these taxa is presented in Fig. 2. It is apparent that the shape is much more variable than in the case of the northern regions discussed above. Although there is a concentration of taxa with globose to subglobose average spores, 38% of the taxa (10) have broadly ellipsoid to ellipsoid or elongate average spores.

In comparison to the data of Fig. 2, central Africa has a minimum of 17 known taxa in section *Vaginatae*. There is evidence that this represents a significant undercounting of such taxa (Tulloss and F. V. Alofe unpub. data). Of the known taxa 35% have **Q'** below 1.3; 47% have ellipsoid average spores; 12%, elongate average spores; and 6%, cylindric average spores. The corresponding numbers for the NJ/LI region are 69%, 27%, 4%, and 0%.

In the case of the NJ/LI region, many of the taxa with higher **Q'** are annulate species; however, there are exannulate taxa in the northern temperate and subtropical zone with broadly ellipsoid to ellipsoid to elongate spores. One group of such taxa are those phenetically related to *A. mairei* Foley in the Mediterranean region (Tulloss 1994; unpub. data); another includes several taxa associated with *Coccoloba* along Caribbean coasts (e.g., *A. dunicola* Guzmán and *A. yucatanensis* Guzmán).

At least eleven probably good new species with **Q'** between 1.16 and 1.60 have been counted by the author in Canada, Mexico, and the USA. Worldwide, published and unpublished, at least 145 taxa fall in the same category (Tulloss unpub. data). Referring to Fig. 1, we note that *only one* of these 145 is known to occur in subarctic, alpine, or boreal environments.

There are nine taxa known from section *Vaginatae* having **Q'** exceeding 1.60. All but two of these are known from the eastern USA. The most elongate spores known from section *Vaginatae* belong to

- the poorly known, annulate species *A. cokeriana* Murrill (Florida, USA), with **Q'** = 1.90 (Tulloss unpub. data)
- the weakly annulate species "*A. nigeriana*" Tulloss & F. V. Alofe *nom. prov.* (Osun State, Nigeria), with **Q'** = 2.09 and a high percentage of spores falling in Bas' "cylindric" category (Tulloss & F. V. Alofe unpub. data).
- the exannulate species ***A. floridana*** (Murrill) Dav. T. Jenkins *ex* Tulloss comb. nov. (Florida, USA, see note immediately below), with **Q'** = 1.86 (Tulloss unpub. data) and *A. pallidochracea* A. E. Wood (New South Wales, Australia), with **Q'** = 1.81 (Wood 1997)

Note: Basionym: *Amanitopsis floridana* Murrill. 1949. *Mycologia* 41: 490.
≡*Vaginata floridana* (Murrill) Murrill. 1949. *Mycologia* 41: 490.
≡*Amanita floridana* (Murrill) Dav. T. Jenkins *comb. inval*. 1986. *Amanita N. Amer.*: 66. [Lacking full and direct reference to basionym. ICBN §33.2]
Type study: Jenkins. 1979. *Mycotaxon* 10: 179. Type study: Tulloss (in prep.).
HOLOTYPE: FLAS

3. Distribution of elongate- to bacilliform-spored taxa by section

In other sections of *Amanita* that include elongate-, cylindric-, or bacilliform-spored taxa, those taxa also occur almost entirely in temperate, subtropical, or tropical regions. There are 25 taxa world-wide with elongate spores in section *Amanita*; ten of these occur in Mexico, the USA, or Canada (including one species, *A. wellsii*, with a range extending from the central Appalachians of the USA through the boreal forest to northern limits of *Alnus*). All but the single exception cited occur only in temperate or subtropical regions.

In the small section *Amidella*, nearly two-thirds of the known taxa have **Q'** > 1.60; and 90% of these taxa have their entire ranges within the temperate, subtropical, or tropical regions.

Two examples have been given above of countries with subarctic to boreal environments in which *Amanita* section *Lepidella* is apparently absent. In the northern part of the northern temperate zone, few taxa of this section occur around the world (see the taxa of the Québec region of study in this paper or the few species of section *Lepidella* among the 27 amanitas listed for Switzerland by Breitenbach and Kränzlin (1995)). Worldwide, section *Lepidella* is assigned 81 taxa with average spores elongate, cylindric, or bacilliform—about 35% of the section's total taxa worldwide (Tulloss unpub. data). The narrowest spores in the section occur in taxa from the Americas; the only five taxa in the section known to have bacilliform average spores all occur in the SE USA. Species with dominantly cylindric spores number 25 worldwide, of which six are known only from Australia; one is known only from the Mediterranean region and southern Europe; and the remainder (18) are known only from the USA (mostly from the southeastern states).

Amanita section *Phalloideae* is thought to contain less than 70 taxa worldwide at present. Of these, seven to eight have spores with **Q'** greater than 1.60; one is known only from Australia; and the remainder are known only from Mexico and the eastern USA (largely from southeastern states). Five to six taxa are known to have cylindric average spores, and they all fall in the group from the Americas. None have bacilliform average spores.

Amanita section *Validae* includes 124 taxa for which spore shape and size information is available. Of these, up to 13 have elongate (up to 11 taxa) or cylindric (2 taxa) average spores. None have bacilliform average spores. Both the cylindric-spored taxa are from the USA (one reported from California; one, from Alabama). The elongate-spored taxa are reported from central Africa (*A. rubescens* var. *congolensis* Beeli), Australia (two taxa described from New South Wales), and the eastern and southeastern USA (up to 8 taxa).

Apparently, there are, at the very least, fewer restraining factors for elongate to bacilliform spore shape in temperate, subtropical, and tropical regions than there are in alpine, subarctic, and boreal regions. It is important to note that the number of taxa of *Amanita* known from the New World tropics is very limited at present and, while several monographic studies exist at this writing, the only large scale, modern monographs treating amanitas are the study of section *Lepidella* by Bas (1969) and the study of *Amanita* in southwestern China by Yang (1997). Many type studies remain to be done, and, as noted above, only about half of the species of *Amanita* that may exist have been described.

4. Contrast with the situation reported for polypores

Among central African amanitas (Fig. 5, below), 17 of 44 (39%) of known taxa have elongate or cylindric average spores (Tulloss unpub. data). In the NJ/LI region of study 28 of 105 taxa (27%) have elongate, cylindric, or bacilliform average spores (Tulloss unpub. data). It is worth noting that 17 of these 28 are species of section *Lepidella* at or near the northern limit of their ranges (Tulloss unpub. data)—none of these occur in Prov. Québec and the great majority are members of the group discussed below in section 7.

The trend reported here for *Amanita* spores appears to be the reverse of the case for polypores reported by Ryvarden (1993), in which the most northern taxa studied (European and North American) had a slightly greater tendency to be cylindric to allantoid than did the tropical (East African) taxa.

5. Fall rate of spherical vs. elongated spores

In his work on spore liberation, Ingold (1965:14-15) reported studies on fall rate of ellipsoid particles carried out by a certain A. Fonda "under the aegis of the National Coal Board." Essentially, the more elongated the form of an ellipsoid particle of a given mass, the slower it falls. When random positioning of the particle is taken into account, the fall rate is slower than if it falls with the major diameter vertically oriented (i.e., any tumbling tends to slow the fall further—a phenomenon that has no effect on a spherical particle). In *Amanita* elongate spores tend to develop with the major diameter roughly parallel to the ground and ejection occurs approximately in this position—the position that (*without* tumbling) is associated with the slowest rate of fall.

Given the above and the fact that, because of their stipe length, almost all amanitas eject their spores into turbulent air, I have assumed that *Amanita* spores tumble as they fall and almost never fall in a position with the major axis perpendicular to the ground. I have supposed that Fonda's curve of the mean terminal velocity of randomly oriented ellipsoids is most representative of the relative terminal velocity of variously shaped *Amanita* spores. The relative terminal rate of fall of spherical spores is defined as 1.0. The approximate range of relative terminal rate of fall of ellipsoid spores is 0.945 - 0.96; that of elongate spores, 0.91 - 0.945; that of cylindric spores, 0.83 - 0.91; and that of bacilliform spores has a maximum at 0.83. A few species of *Amanita* produce some spores with Q of 4.0 or even 5.0; such spores would have approximate relative terminal rates of fall of 0.775 and 0.72, respectively.

6. Do individual taxa with broad distribution show spore shape variation related to latitude?

Lodge (pers. corresp.) suggested exploration of spore shape related to theoretical rate of fall; also, she put forward the following question: In cases of possible vicariant taxa or of species with extended north-south ranges, is there evidence of pressure for elongation of spores in more tropical (parts of) ranges?

The answer to the latter question appears to be that there is no such evidence available from the regions of study in the Americas. Either spore shape and size do not show very much change in the cases examined (*muscaria* subsp. *flavivolvata*, *wellsii*, *xylinivolva*, *polypyramis*, *daucipes*, *flavorubens*, *pelioma*/*species M34*, etc.); or there is evidence of a reverse tendency (*flavoconia* vars.).

Recent ice ages repeatedly compressed ranges of the Northern Hemisphere symbionts of *Amanita* contributing to remixing of the gene pool of the species of interest or regeneration of the northern distributional areas of these species from southern US and Mexican stocks. One might suppose that these forces served to modify any pressures for change that may have been (or are) present. The relative uniformity of symbionts over the ranges of the above species has been noted. In addition, the fact that the taxa we have listed are montane in the southern parts of their ranges while occurring at or near sea level in the northern parts suggests some requirement for stability in their environments. Hence, whatever the latitude-related effect may be, it would probably have less impact in the group of taxa with extended ranges than is observed in a diverse set of taxa with restricted ranges.

7. Relation of narrow spores to dry, fire-prone, or "leaky" ecosystems

Many species of section *Lepidella* with markedly narrow spores occur in the southeastern USA at low elevations in the coastal plains of the Atlantic Ocean and Gulf of Mexico, from Cape Cod, Massachusetts (*A. subsolitaria*) to the pine plains of eastern Texas where there occur at least a dozen species in the group (Tulloss unpub. data). Currently existing conditions may have contributed to the development of narrow spores—for example, pressure due to frequent fire or low nutrient content of deep sandy soils in the "leaky ecosystem" (Woodwell 1979) of dry coastal plain regions. It is tempting to believe that the deeply inserted stipes and/or significantly elongated bulbs of many of the very narrow-spored species in section *Lepidella* are adaptations to the dry, low-nutrient, fire-prone environment. The common symbionts (e.g., *Pinus rigida*) of these amanitas are believed adapted to these conditions. Among the plant adaptations are dormant basal buds that are activated by loss of the major stem, subsurface table-like structures from which new sprouting can occur in similar circumstances, regeneration of leaves directly from a burned trunk, cones that open at elevated temperature during cooling immediately following a fire, staggered delay in germination of seeds, formation of mycorrhizae deep in the soil rather than near the surface, etc. (Good et al. 1979; Ledig and Little 1979; Whittaker 1979). The very narrow-spored Australian taxa cited above are species of dry eucalypt forest.

The known taxa of *Torrendia* Bres. (sequestrate amanitas) could be viewed as supporting the idea that environmental stress (in this case, again, dry and "leaky" ecosystems) can lead to spore elongation. Bas (1975) provides morphological evidence and argument supporting evolution of *T. pulchella* Bres. from a clamp-bearing ancestor in *Amanita* section *Vaginatae*. Reportedly, spores of this Mediterranean area species (known at least from Algeria, France, Morocco, Portugal, and Spain) have upper limit of length (excluding upper extreme) of 18 µm and **Q'** of about 2.8. A similar origin is arguably the case for the recently described *T. grandis* Bougher (1999) and *T. inculta* Bougher (1999)—with the same pair of values being (14.5 µm, 1.48) and (14 µm, 1.84), respectively (unusually, for *Amanita* studies, including the apiculus in the measurement). *Torrendia arenaria* f. *arenaria* O. K. Mill. & Horak (1992) was described from West Australia and has a reported nonextreme upper limit of spore length and **Q'** of 13.5 µm (including the apiculus in the measurement) and 1.51, respectively. The spores are inamyloid; the stipe is totally elongating; the basidia are reported to lack clamp connections; hence, descent from a clampless ancestor in section *Vaginatae* seems arguable for *T. arenaria*.

> Note: During the final preparation of this paper, I received a copy of a poster presented by H. E. Hallen et al. (2004). The poster reports on molecular work concerning *Amanita, Amarrendia,* and *Torrendia*. Trees based on sequencing of ribosomal ITS and 28S rDNA are computed based on a large number of taxa in the *Amanitaceae*. There are significant differences in the placement of *Torrendia* within the two trees. The morphological arguments above are supported by the 28S tree which places *T. grandis, T. inculta*, and *T. pulchella* in a clade comprising taxa within the morphologically defined stirps *Hemibapha* (Tulloss 1998*b*) within section *Vaginatae sensu* Corner & Bas (1962). *Torrendia arenaria* is placed closest to a species of section *Lepidella* that is placed within a clade otherwise comprising taxa of section *Validae*. In the ITS tree, only *T. grandis* and *T. inculta* appear and both are placed in the clade otherwise representing section *Amanita*. This conflicts with morphological evidence: *Amanita* section *Amanita* is defined by inamyloid spores and the placement of the developing stipe tissue eccentrically (off-cen-

ter upward) in the developing "button." All known taxa of *Torrendia* have totally elongating stipes that are centrally positioned in the "button" stage.

Note: Only four taxa in *Amanita* are known to consistently have at least 30 percent of basidia bisterigmate—these are all rather small species from eastern North America with combined ranges from the Atlantic coastal plain (discussion of ecosystem above, three of the four species present) inland to the Appalachian Mountains (Tulloss 1989; 1993) and at least as far west as the limit of distribution of eastern North American *Quercus* species.

Note: In characters of present interest, *T. arenaria* f. *lutescens* O. K. Mill. & Horak (1992) differs by having **Q'** = 1.29. The differentiating macroscopic character of the forma is yellowing of cut or abraded tissue. This latter character was discussed by Tulloss (1998, 2000*b*) based on North American collections of *Amanita* and considered a probable effect of an unknown "infecting" agent. Such "infected" specimens (e.g., such collections of *A. subsolitaria*) may have stunted or deformed spores.

The very narrow-spored species are the species that would have spores with the slowest fall rate according to Ingold (above). In a dry, more or less open forest, these spores would have the ability to travel farthest. In the case of the U.S. species, storms often track from the Gulf of Mexico roughly northward—relatively parallel to the similarly forested Atlantic coastal plain extending from Florida to Massachusetts. So both long distance (during storms with minimal UV from sunlight) and short distance dispersal is possible even for the relatively fragile *Amanita* spore. This could be an advantage because very hot and rapidly spreading fires are common in the habitat. An experiment examining the relative frequency of reintroduction of the narrow-spored species in their ranges along the Atlantic coast in the US (e.g., since the end of the last glaciation) could be enlightening on this point.

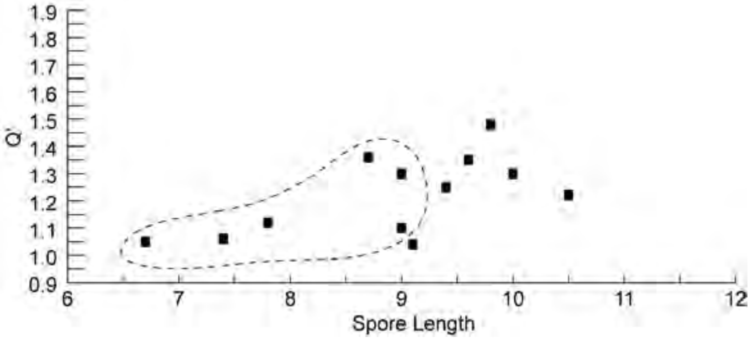

Fig. 3. A scatter plot of spore length versus **Q'** for the spores of species known from Brazil and Guyana. Points representing species with spore length less than or equal to 9.0 and **Q'** less than 1.4 have been encircled.

Another possibility is that the probable relative antiquity of section *Lepidella* has provided time for diversification in response to a complex sequence of pressures that no longer all exist, such as the stresses of major extinction events. Research since the 1960's, both morphological and molecular, has consistently indicated a basal position for section *Lepidella* in subgenus *Lepidella* or (especially when species of subsection *Vittadiniae* are taken into account) in *Amanita* as a whole (Bas 1969; Weiss et al. 1998: Fig. 3; Drehmel et al. 1999; Hallen pers. corresp.). The geographical clustering of very narrow-spored taxa might be interpreted as indicating their ranges are relictual.

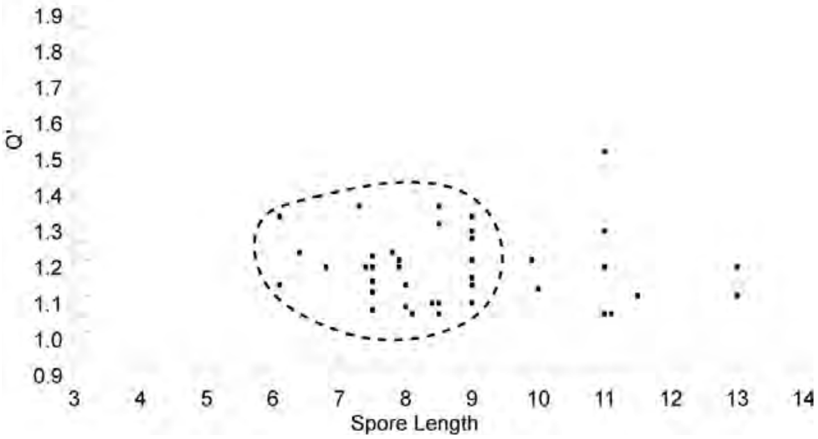

Fig. 4. A scatter plot of spore length versus **Q'** for the spores of species known from Singapore and Malaya. Points representing species with spore length less than or equal to 9.0 and **Q'** less than 1.4 have been encircled.

8. Environmental pressures on circumarctic taxa

One might also consider whether the dominance of subglobose spores in the circumarctic taxa is the result of evolutionary pressures contrasting with those of the “leaky” ecosystems discussed above.

The growing season is short in subarctic and alpine regions and the soils adaptable to plant growth may be very uniform in large areas (bogs and heaths for example). Hence, there is advantage to a short-lived spore (thin-walled, unpigmented, and thus liable to UV damage) reaching the substrate quickly. Imperfectly globose spores have somewhat greater dispersibility and, hence, add ability for a species to survive local extinction. This spore form (relative terminal rate of fall of about 0.94 to 1.0) is indicated in the data of Fig. 1.

NOTES ON SPORE SIZE REDUCTION IN THE TROPICS

1. *Amanita* spore size in lowland tropical forest

Lodge (pers. corresp.) made the suggestion that I expand this paper to include more information concerning *Amanita* spore size in lowland tropical forest.

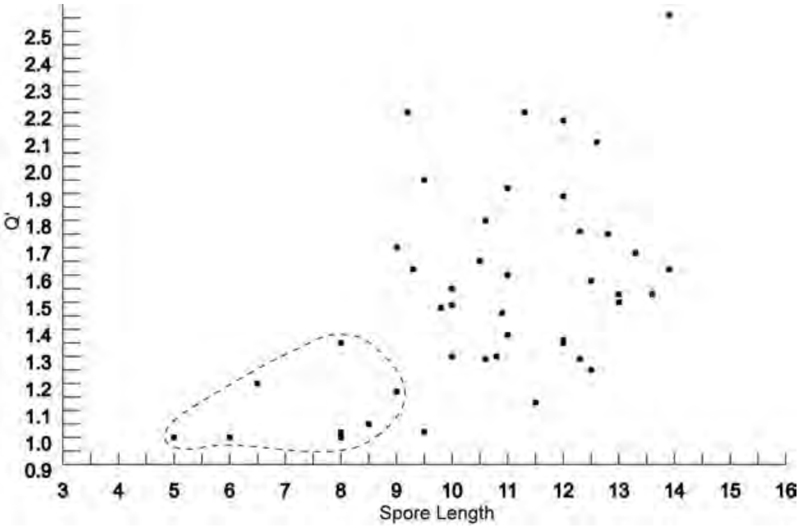

Fig. 5. A scatter plot of spore length versus **Q'** for the spores of species known from Central Africa. Points representing species with spore length less than or equal to 9.0 and **Q'** less than 1.4 have been encircled.

In the cases of some of the Asian and many of the South American tropical taxa of *Amanita*, the forest habitat is highly diverse and available symbionts are likely to be widely and irregularly separated (in contrast to the more northern forests) or, as in the case of *Dicymbe* symbionts in Guyana, forms a matrix lacking in ectotrophs in which isolated dense groups of ectotrophs occur (e.g., Henkel et al. 2002). Widely scattered dispersal of potential symbionts is true in some African forests, but this is *not* true of some of the habitats in which numerous African amanitas have been collected—such as the extensively human-modified *Uapaca* or *Brachystegia* miombo woodland over 300 m elev. that is cool in the rainy season and has plentiful available symbionts (B. Buyck pers. corresp.; Buyck 1994; Härkönen et al. 1994; Wilson 2001; Henkel et al. 2002; Alofe unpub. data). Hence, although probably far from complete, the data sets from Brazil and Guyana and Malaya and Singapore (Figs. 3 and 4) could be assumed to be more representative of highly diverse tropical forests than the African forests (Fig. 5) for which data is available.

2. The polypore case—a contrast

Besides spore shape, Ryvarden (1993) also examined polypore spore size change with relation to latitude. The ten largest-spored African polypore taxa had spores 7% to 75% larger than their correspondingly ranked species in the list of ten largest-spored European taxa.

Table 7. Taxa of tropical forest in Brazil and Guyana

Species	95th percentile spore length	High diversity forests w/ very few or isolated ectotrophs	Forests w/ low species diversity or abundant ectotrophs	Secondary forest w/ moderate no. of ectotrophs
aurantiobrunnea Simmons et al. (sect. *Phalloideae*)	9.4	+		
calochroa Simmons et al. (sect. *Amanita*)	7.8	+		
campinaranae Bas (sect. *Validae*)	6.7	+		
coacta Bas (sect. *Vaginatae*)	10.0			+
craseoderma Bas (sect. *Vaginatae*)	9.0	+		
crebresulcata Bas (sect. *Vaginatae*)	10.5			+
cyanopus Simmons et al.(sect. *Validae*)	8.7	+		
grallipes Bas & de Meijer (sect. *Lepidella,* possibly *not* ectomycorrhizal with native trees)	9.6	+		
lanivolva Bas (sect. *Amanita,* but having a very unusual membranous volval sac)	9.8	+		+
perphaea Simmons et al.(sect. *Validae*)	7.4	+		
sulcatissima Bas (sect. *Amanita*)	9.0		+	
xerocybe Bas (sect. *Amanita*)	9.0	+	+	

In *Amanita*, tropical taxa are known to include the species with the smallest recorded spore sizes (Gilbert 1940-41; Corner and Bas 1962; Bas 1978; Simmons et al. 2002). For example, 9 of 44 (20%) central African amanitas (Fig. 5) have 95% of spores 8 µm or less long; 3 of 12 (25%) of the sufficiently known amanitas of Brazil and Guyana share the same characteristic (Fig. 3), while an additional 3 (25%) have 95% of spores with length 9 µm or less. Of the taxa described by Corner and Bas (1962) from Singapore and Malaya (Fig. 4), 15 of 39 (38%) have 95% of spores 8 µm or less long, when spores are measured from fresh material; and 14 (36%) additional taxa have 95% of spores 9 µm or less long when measured from exsiccata.

3. Small spores not characteristic of northern temperate region *Amanita* species

On the other hand, *none* of 105 amanitas from the NJ/LI region of study have 95% of spores 8 µm or less long and only three (3%) have 95% of spores 9 µm or less long. Among Swiss amanitas, Breitenbach and Kränzlin (1995) list no taxa having spores with an upper length limit (exclusive of the upper extreme value presented) less than 10 µm long. Ninety European specific and infraspecific taxa are treated by Neville and Poumarat (2004). They exclude sect. *Vaginatae* and exannulate taxa in sect. *Amanita*. Among those taxa for which spore data is provided (often with small sample size), 10% have 95% of spores 9 µm long or less, but only one has 95% of spores measured falling under 9 µm—*A. erythrocephala* Neville, Poumarat & Aste (95th percentile of spore length = 8.0 µm), which the authors now consider a probable recent introduction to Europe. For spore size and shape, the trends reported for polypores appear reversed in *Amanita.*

4. Small spores not typical of Southern Hemisphere *Amanita* species

One could hypothesize that small spores are a characteristic of amanitas of the Southern Hemisphere; however, an examination of the *Amanita* lists for Australia and New Zealand casts considerable doubt on that supposition (Bas 1969; Gilbert 1940-41; Grgurinovic 1997; Miller 1992*a* and 1992*b*; Reid 1978 and 1980; Ridley 1991; Tulloss unpub. data; Tulloss et al. 1995). In Australia there are no *Amanita* taxa with the reported upper limit of spore length (excluding upper extreme) below 8.5 µm. There are eight of 86 known indigenous taxa with adequate available information (9%) that have such a limit of spore length less than or equal to 9 µm; six of these eight values are exactly 9 µm. In New Zealand, there are *no* taxa with such a spore length limit less than 9 µm and three of 15 indigenous taxa (20%) with such a value equal to 9 µm. To go a little further afield and cast further doubt on the hypothesis, there are 18 indigenous taxa with adequate information reported from Argentina and Chile (Garrido 1987; Garrido and Bresinsky 1985; Tulloss and Horak unpub. data). Of these, there are none with reported non-extreme upper limit of spore length less than 8.3 µm; and there are four (22%) with such upper limit less than or equal to 9 µm of which two taxa have such limit equal to 9 µm. Evidence indicates that nearly all taxa with maximum reported spore length (excluding upper extreme) under 8.3 µm occur in diverse tropical forest.

5. Hypotheses based on Ingold's report on spore liberation

Ryvarden put forward the hypothesis that the larger spores of some tropical polypores might provide a larger "reserve for germination, thus ensuring an accrued life potential in less favourable environments." Based on Ingold (1965), such spores are also more likely to strike immobile, vertically aligned cylindric objects—such as tree trunks—a valuable trait for parasitic or saprophytic fungi (see data on polypores, above).

What hypothesis could be put forward for the situation we observe in terrestrial and dominantly mycorrhizal *Amanita* taxa? It appears that small generally more globose spores may provide an advantage for species dispersal and survival. Small spore size may result in more time spent aloft due to turbulence, and small spores with low **Q'** have the best chance of being blown around obstacles such as tree trunks (Ingold 1965: 9-11). This would be an advantage in diverse tropical forests where appropriate symbionts may be scattered (Lodge pers. corresp.).

More habitat details are available for the South American taxa than for the Asian taxa (Bas 1978; Bas and de Meijer 1993; Simmons et al. 2002; Singer and da Silva Araujo 1979). This allows us to examine the relationship between spore length and diversity of known habitat (Table 7). In Guyana, the habitats with the highest and lowest diversity of ectomycorrhizal symbionts may occur adjacently or nearly so; and some taxa are known to occur in both habitats. First we notice that the species of sections *Vaginatae* and *Lepidella* are, as in Asia, adapted without reduction of spore length to the degree seen in taxa of other sections—especially those of sections *Amanita* and *Validae*. Of the three taxa with the relevant spore measurement less than 8.3 µm, two occur only in high diversity tropical forest with symbionts collected in segregated groves. Of the four species only known from forests with plentiful ectotrophs (excluding species of section *Vaginatae*), three have spores with the relevant measurement greater than or equal to 8.7 µm. As more is learned of the species in the table and more species are found, it will be interesting to see if these or other trends are observable in the data. There are more *Amanita* taxa to be described from Henkel's Guyana collections. While many of them are from section *Vaginatae* (Bas pers. corresp.; Henkel et al. 2002), there are still a significant number from other sections (Henkel, pers. corresp.).

The species bearing small spores tend to have spores limited in shape—**Q'** < 1.3 - 1.4 (Figs. 3-5). This could be related to the amount of material that must be packaged within the spore. To sustain this subtopic's hypothesis, we must assume that the small spore's limitation to being ellipsoid on average does not override the hypothetical advantage of small size. Why the supposed advantage of small spores is not seen more frequently in sections other than the widely morphologically and phylogenetically separated sections *Amanita* and *Validae*, also remains an open question.

6. Summary of discussion of spore size

In summary, the spore size data offers support to the hypothesis that "small-spored" species in *Amanita* (especially those with spores having the 95th percentile of length reported less than 8.3 µm) have a very high likelihood of being species of diverse tropical forest dominated at least locally by nonectomycorrhizal trees to which forests the spores may be adapted for aerial "roaming" around tree trunks. This character could increase the potential for germination near widely scattered individual symbionts or tightly grouped groves of symbionts—only available at some distance from a spore's source.

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APPENDICES

Appendix Table 1. *Amanita* section *Amanita*—American regions of interest

Species	Québec	NJ/LI	AZ	Ctr. Méx.	CR	Col.
1. *albocreata* G. F. Atk.	**1. +**	**1. +**				
2. *crenulata* Peck	**2. +**	**2. +**				
3. *farinosa* Schwein.	**3. +**	**3. +**		**1. +**	**1. +**	
4. *frostiana* (Peck) Sacc.	**4. +**	**4. +**				
5. *guzmanii* Cifuentes, Villegas & Santiago				**2. +**		
6. *multisquamosa* Peck	**5. +**	**5. +**				
7. *muscaria* subsp. *flavivolvata* Singer			**1. +**	**3. +**	**2. +**	**1. +i**
8. *muscaria* var. *guessowii* Veselý	**6. +**	**6. +**				
9. *muscaria* var. *persicina* Dav. T. Jenkins		**7. +**				
10. *parcivolvata* (Peck) E. J. Gilbert		**8. +**				
11. *roseitincta* (Murrill) Murrill		**9. +**		**4. +**		
12. *russuloides* (Peck) Sacc.	**7. +**	**10. +**				
13. *velatipes* G. F. Atk.	**8. +**	**11. +**				
14. *wellsii* (Murrill) Sacc.	**9. +**	**12. +**				
15. *xylinivolva* Tulloss, Ovrebo & Halling			**2. +**	**5. +**	**3. +**	**2. +**
16. sp. 32	**10. +**	**13. +**				
17. sp. 34		**14. +**				
18. sp. AZ7			**3. +**			
19. sp. AZ16			**4. +**			
20. sp. HON2					**4. +**	
21. sp. HON9					**5. +**	
22. sp. M17				**6. +**		
23. sp. M20				**7. +**		
24. sp. M21				**8. +**		
25. sp. M22				**9. +**		
26. sp. S1		**15. +**				

Appendix Table 2. *Amanita* section *Validae*—American regions of interest

Species	Québec	NJ/LI	AZ	Ctr. Méx.	CR	Col.
1. "*antioquiana*" Tulloss & Franco-Molano nom. prov.						**1. +**
2. *brunneolocularis* Tulloss, Ovrebo & Halling					**1.+**	**2. +**
3. *brunnescens* G. F. Atk.	**1. +**	**1. +**				
4. *citrina sensu auct. amer.*	**2. +**	**2. +**		**1. +**		
5. *citrina* f. *lavendula* (Coker) Veselý		**3. +**				
6. *elongata* Peck	**3. +?**	**4. +**				
7. *flavoconia* G. F. Atk. var. *flavoconia*	**4. +**	**5. +**				
8. *flavoconia* var. *inquinata* Tulloss, Ovrebo & Halling				**2. +**	**2.+**	**3. +**
9. *flavorubens* (Berk. & Mont.) Sacc.	**5. +**	**6. +**	**1.+**	**3. +**		
10. *morrisii* Peck		**7. +**				
11. *novinupta* Tulloss & J. Lindgr.			**2.+**	**4. +**		
12. *picea* Tulloss, Ovrebo & Halling						**4. +**
13. *porphyria* Alb. & Schwein.:Fr.	**6. +**					
14. *rubescens sensu auct.* E. USA	**7. +**	**8. +**				
15. *rubescens* var. *alba* Coker	**8. +**	**9. +**				
16. *salmonescens* Tulloss		**10. +**				
17. *spissa* var. *alba* Coker *non* Rick		**11. +**				
18. sp. 6		**12. +**				
19. sp. 10		**13. +**				
20. sp. 18		**14. +**				
21. sp. 19		**15. +**				
22. sp. 23		**16. +**				
23. sp. 36		**17. +**				
24. sp. 43		**18. +**				
25. sp. AZ10			**3.+**	**5. +**		
26. sp. CR7					**3.+**	
27. sp. CR14					**4.+**	
28. sp. CR15					**5.+**	
29. sp. M11				**6. +**		

Appendix Table 2*.* *Amanita* section *Validae*—American regions of interest

Species	Québec	NJ/LI	AZ	Ctr. Méx.	CR	Col.
30. sp. M18				**7. +**		
31. sp. M28				**8. +**		
32. sp. M30				**9. +**		
33. sp. N20		**19. +**				

Appendix Table 3*.* *Amanita* section *Lepidella*—American regions of interest

Species	Québec	NJ/LI	AZ	Ctr. Méx.	CR	Col.
1. *abrupta* Peck	**1. +**	**1. +**				
2. *advena* Tulloss, Ovrebo & Halling					**1. +**	**1. +**
3. *atkinsoniana* Coker	**2. +**	**2. +**		**1. +**		
4. *canescens* Dav. T. Jenkins		**3. +**				
5. *chlorinosma* (Peck) Lloyd		**4. +**		**2. +?**		
6. *cinereopannosa* Bas		**5. +**				
7. *cokeri* (E. J. Gilbert & Kühner) E. J. Gilbert		**6. +**				
8. *“conara”* Tulloss, Halling & G. M. Muell. nom. prov.					**2. +**	
9. *“costaricensis”* Tulloss, Halling & G. M. Muell. nom. prov.					**3. +**	
10. *“crassifolia”* Bas nom. prov.		**7. +**				
11. *daucipes* (Mont.) Lloyd		**8. +**		**3. +**		
12. *“eremites”* Tulloss nom. prov.			**1. +**			
13. *limbatula* Bas		**9. +**				
14. *longipes* Bas *ex* Tulloss & Jenkins		**10. +**				
15. *“macerisolum”* Tulloss nom. prov.			**2. +**			
16. *microlepis* Bas		**11. +**				
17. *mutabilis* Beardslee		**12. +**				
18. *nauseosa* (Wakef.) D. A. Reid				**4. +**		
19. *onusta* (Howe) Sacc.	**3. +**	**13. +**				
20. *parva* (Murrill) Murrill		**14. +**				
21. *polypyramis* (Berk. & Curt.) Sacc.		**15. +**		**5. +**	**4. +**	
22. *prairiicola* Peck			**3. +**			

Appendix Table 3. *Amanita* section *Lepidella*—American regions of interest

Species	Québec	NJ/LI	AZ	Ctr. Méx.	CR	Col.
23. *ravenelii* (Berk. & Curt.) Sacc.		**16. +**				
24. *rhopalopus* Bas		**17. +**				
25. *salmonea sensu* Guzmán				**6. +**		
26. *"savannae"* Tulloss & Franco-Molano nom. prov.						**2. +**
27. *smithiana* Bas			**4. +**	**7. +**		
28. *subsolitaria* (Murrill) Murrill		**18. +**				
29. *"talamancae"* Tulloss, Halling & G. M. Muell. nom. prov.					**5. +**	
30. "*tephrea*" Bas nom. prov.		**19. +**				
31. *tephrea sensu* Cifuentes et al.				**8. +**		
32. *thiersii* Bas				**9. +**		
33. sp. 4		**20. +**				
34. sp. 5		**21. +**				
35. sp. 9		**22. +**				
36. sp. 11		**23. +**				
37. sp. 30		**24. +**				
38. sp. 38		**25. +**				
39. sp. 39		**26. +**				
40. sp. 40		**27. +**				
41. sp. AZ12			**5. +**			
42. sp. AZ26			**6. +**	**10. +**		
43. sp. CR18					**6. +**	
44. sp. M5				**11. +**		
45. sp. M23				**12. +**		
46. sp. M31 (*cf. griseofarinosa*?)				**13. +**		
47. sp. M32 (*cf. rhopalopus*)				**14. +**		
48. sp. M33 (*cf. subsolitaria*)				**15. +**		
49. *sp. M34* (*cf. pelioma*)				**16. +**		

Appendix Table 4*. Amanita* section *Amanita*—Asian regions of interest

Species	Japan	SWC	HP/UT	NWFP
1. *altipes* Zhu L. Yang et al.		**1. +**		
2. *concentrica* T. Oda et al.	**1. +**		**1. +**	
3. *emilii* Riel *sensu auct. ind.*			**2. +**	
4. "*emodipanthera*" Tulloss & Bhandary nom. prov.			**3. +**	
5. *farinosa sensu auct. asia.*	**2. +**	**2. +**		
6. *kwangsiensis* Y. C. Wang (=*sychnopyramis* f. *subannulata* Hongo)	**3. +**	**3. +**		
7. *melleiceps* Hongo	**4. +**			
8. *mira* Corner & Bas		**4. +**		
9. *muscaria* (L.:Fr.) Lam. var. *muscaria*	**5. +**		**4. +**	
10. *orientigemmata* Zhu L. Yang & Yoshim. Doi	**6. +**		**5. +**	
11. *pantherina sensu* S. P. Abraham & J. L. Kachroo			**6. ?**	**1. +**
12. *pantherina sensu* A. Kumar et al.			**7. +**	
13. *pantherina* var. *lutea* W. F. Chiu		**5. +**	**8. +**	
14. *parvipantherina* Zhu L. Yang et al.		**6. +**		
15. *pseudogemmata* Hongo	**7. +**	**7. +**		
16. *pseudopantherina* Zhu L. Yang nom. prov.		**8. +**		
17. *pulchella* S. Imai	**8. +**			
18. *rubrovolvata* S. Imai	**9. +**	**9. +**	**9. +**	
19. *rufoferruginea* Hongo	**10. +**	**10. +**		
20. *sinensis* Zhu L. Yang var. *sinensis*	**11. +**	**11. +**		
21. *subfrostiana* Zhu L. Yang		**12. +**		
22. *subglobosa* Zhu L. Yang		**13. +**		
23. V. K. Bhatt sp. 6			**10. +**	
24. Tulloss et al. sp. PAK5				**2. +**

Appendix Table 5*. Amanita* section *Validae*—Asian regions of interest

Species	Japan	SWC	HP/UT	NWFP
1. *citrina* var. *grisea* (Hongo) Hongo	**1. +**	**1. +**		
2. *flavipes* S. Imai	**2. +**	**2. +**	**1. +**	**1. +**
3. *fritillaria* (Berk.) Sacc. f. *fritillaria* (=*spissacea* S. Imai)	**3. +**	**3. +**	**2. +**	

Appendix Table 5. *Amanita* section *Validae*—Asian regions of interest

Species	Japan	SWC	HP/UT	NWFP
4. *fritillaria* f. *malayensis* Corner & Bas		**4. +**		
5. *fritillaria sensu* A. Kumar et al.			**3. +**	
6. *fulvaurantia* Locq. & T. N. Lakh.			**4. +**	
7. *innatifibrilla* Zhu L. Yang nom. prov.		**5. +**		
8. *orsonii A.* Kumar & T. N. Lakh.	**4. +**	**6. +**	**5. +**	**2. +**
9. *pilosella* Corner & Bas f. *pilosella*		**7. +**	**6. +**	
10. *sepiacea* S. Imai	**5. +**	**8. +**		