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Megacollybia (Agaricales)

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Abstract

The genus *Megacollybia*, originally proposed for *M. (Collybia) platyphylla*, has traditionally been treated as monotaxic. A phylogenetic reconstruction based on ITS rDNA sequences indicates that several species are involved, with strong phylogeographic signal. Although morphological characters are largely qualitative, examination of basidiomata suggests that specimens included in discrete clades can be distinguished at the species level. On these bases (phylogenetic, morphological), several new taxa are proposed: *M. clitocyboidea*, *M. texensis*, *M. fusca*, *M. subfurfuracea*, *M. rodmani* (with f. *murina*) and *M. marginata*. *Tricholomopsis fallax* is transferred to *Megacollybia*; *M. platyphylla* remains the type species of the genus but appears to be restricted to Europe, Scandinavia and western and central Russia.

Key words: Taxonomy, systematics, biogeography, phylogeny, phylogeography

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Introduction

By the time Kotlaba and Pouzar (1972) segregated *Megacollybia*, *Collybia* (*Tricholomopsis*, *Oudemansiella*, *Megacollybia*) *platyphylla* had become a popular name in use throughout Europe and eastern North America. As long as workers from these regions did not seriously collect in each others' territory this single name seemed applicable for what was considered to be a transAtlantic organism. The name was also applied to far east-Asian basidiomata which seemed to resemble those from Europe.

Comparing photos by Phillips (1981: 44, as *Tricholomopsis platyphylla*) of the mushroom from Europe, by Phillips (1991: 46 under the same name) for the mushroom in North America, and Halling and Mueller (2005: 151, as *M. platyphylla*) for the mushroom in Costa Rica, it is a wonder that the same epithet has been applied for such disparate morphological forms. The photo from Huffman et al. (1989: Fig. 93) may show yet another taxon from the midsection of North America.

Singer (1986) and Smith (1960) considered that *Tricholomopsis* sheltered a complex of about 30 species [*T. rutilans* (typus generis), *T. decora*, etc.] of brightly colored, centrally stipitate agarics fruiting on wood, but included, sometimes as a separate section *Platyphyllae* (Singer, 1986: 253), *T. platyphylla* (*typus sectionis*). Singer (1986) listed several names under sect. *Platyphyllae*, most of which he considered to belong in other genera or were unpublished. Oblique reference to South American species of *Platyphyllae*, "...confirming the position of the whole group within *Tricholomopsis*" (Singer 1986: 252, ftnt) furnished no data.

The conjecture that *Tricholomopsis* and *Megacollybia* are separate entities has been supported by molecular data, most convincingly by Moncalvo, et al. (2002), in which *Tricholomopsis rutilans* is found in a poorly supported clade (24, /tricholomopsis) with *Clavaria fusiformis*, *Marasmius rhyssophyllus* and *Collybia aurea*, of which all of the latter three can find more comfortable morphogeneric placements. *Megacollybia platyphylla*, conversely, is in a clade (27, /hydropoid) with three *Gerronema* taxa, *Clitocybula oculus*, two *Hydropus* taxa and a *Porotheleum* and these findings have recently been confirmed by the six-locus analyses of Matheny et al. (2006). *Tricholomopsis fallax* ITS sequences are most closely related to *Megacollybia platyphylla* by blast search, then to *Clitocybula* and *Gerronema* but not to *Tricholomopsis* sensu stricto.

Petersen and Gordon (1994) reported that eastern North American *Megacollybia* had not yielded to monokaryon culture, while spores from EuroScandinavian collections not only underwent in vitro spore germination, but crossed in culture and exhibited a tetrapolar mating system. Combining these data with morphology, it was suggested that a more thorough investigation of *Megacollybia* sensu lato could be profitable. Any study of *Megacollybia*, whether morphological or molecular, must start with knowledge of western European *Megacollybia platyphylla* since the epithet was adopted from Persoon. Material from west-central Germany should serve as the foundation for comparison of other collections. In the literature, good descriptions of the western European organism have been furnished by Boekhout (in Bas et al., 1999), Breitenbach and Kränzlin (1991) and Gulden (in Hansen and Knudsen, 1992).

Our project had the following objectives: 1) to investigate whether a single species epithet could accommodate many collections of *Megacollybia platyphylla* from across its purported range; 2) to determine infrageneric clades and their relationships within

Megacollybia; 3) to explore whether phylogeographic signal was present in a phylogenetic reconstruction of the genus; 4) to propose and describe whatever additional taxa might be necessary as a result of the study; and 5) to explore the relationship of *Megacollybia* with *Tricholomopsis fallax* , a closely related species reported from the North American temperate western coast (British Columbia, Washington, Idaho, Oregon) and the dry southwest (Arizona) .

Macro- and micromorphology were combined with an ITS-based phylogenetic reconstruction to investigate collections from eastern and western North America, Scandinavia, western and eastern Europe, western, central and far eastern Russia, east Asia, Central America and northern South America. Using the western European organism as prototype, results include: 1) the eastern North American organism requires a new species epithet (*M. rodmani*); 2) temperate east Asia shelters a species (*M. marginata*) closely related to but distinct from the northern and western European organism; 3) northern South America produces yet another species (*M. fusca*); and 4) there are at least three lineages represented across North America. *Tricholomopsis fallax* falls within *Megacollybia* and transfer to *Megacollybia* is proposed. Thus, reflected in the ITS-based phylogeny, *Megacollybia* must include at least seven species, with more to come as additional geographic areas are explored.

Materials and Methods

Color notations in quotation marks are from Ridgway (1912); those cited alphanumerically (i.e. 7B3) are from Kornerup and Wanscher (1967). BF = bright field microscopy; PhC = phase contrast microscopy. TENN = herbarium of the University of Tennessee, Knoxville. Other herbarium acronyms are from Index Herbariorum (http://sciweb.nybg.org/science2/IndexHerbariorum.asp). TFB = number from Tennessee fieldbooks assigned to specimens for documentation (i.e. notes, photos, etc.), supplanted by TENN numbers when accessioned into TENN herbarium. GSMNP = Great Smoky Mountains National Park, straddling the border between Tennessee and North Carolina, USA. In species descriptions, characters in Italics are considered diagnostic for the taxon.

Abbreviations of basidiospore statistics are as follows: x = number of spores measured; Q = spore length divided by spore width; Q^m = median Q value over the spore population; L^m = median spore length over the spore population.

Collections from which DNA sequences were obtained are listed in Table 1. Specimens examined morphologically are listed under each taxon in “Specimens examined.” Basidiomata used for both purposes appear in both places.

Molecular protocols

Procedures for DNA extractions were described in Mata et al. (2007). PCR amplification of the ribosomal ITS1-5.8S-ITS2 region was carried out with primers ITS1F and ITS4. DNA sequencing followed manufacturer’s directions for Big Dye Terminator mix (ABI) with forward primer ITS5 and reverse primer ITS4. Intermediate sequencing primers ITS2 and ITS3 were used as necessary. Primers ITS2, ITS3, ITS4 and ITS5 are described in White et al. (1990); primer ITS1F is described in Gardes and Bruns (1993). Cloning was accomplished with a Promega pGem-T vector and JM109 competent cells (Promega Corp., Madison, WI) following manufacturer’s instructions when direct sequencing did not resolve a sequence. Five clones per collection were sequenced. Restriction sites were determined by the GCG

Table 1 — GenBank Numbers for collections used in this study

Collection No.	Herbarium Designation	GenBank No	Name	Collection Location
Outgroups				
CIF2004-32c1	FCME 25069	EU623635	*Clitocybula sp.*	USA, Tennessee, GSMNP
CIF2004-32c3	FCME 25069	EU623636	*Clitocybula sp.*	USA, Tennessee, GSMNP
12058	TENN60306	EU623637	*Clitocybula sp.*	USA, Tennessee, GSMNP
PBM 1156 (CUW)	PBM 1156 (CUW)	DQ192178[1]	*Clitocybula oculus*	USA, New Hampshire
11833	TENN60718	EU623642	*Gerronema sp*	Russia, Primorsky Territory, Kedrovaya Pad
ASM10506	EIU ASM10506	EU623638	*Gerronema albidum*	USA, North Carolina, GSMNP
12519	TENN60718	EU623640	*Gerronema strombodes*	USA, Tennessee, GSMNP
12783c1	TENN61350	EU623641	*Gerronema stromboides*	USA, Tennessee, GSMNP
DJL05-NC72		EU623639	*Gerronema strombodes*	USA, North Carolina, GSMNP
Redhead 5175	DAOM 194858	U66434[1]	*Gerronema subclavatum*	USA, Florida, Gainesville
Megacollybia clitocyboidea				
11832	TENN60717	EU623646	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11864	TENN60748	EU623647	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11868c1	TENN60747	EU623648	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11868c2	TENN60747	EU623649	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11868c3	TENN60747 LE226526	EU623643	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11884c1	TENN60766	EU623653	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11884c2	TENN60766	EU623655	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11884c3	TENN60766	EU623654	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11884c6	TENN60766	EU623656	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11887SS1	TENN60768	EU623645	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11887SS8	TENN60768	EU623650	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11893c3	TENN60774	EU623644	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11893c6	TENN60774	EU623651	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
11893c8	TENN60774	EU623652	*M. clitocyboidea*	Russia, Primorsky Territory, Kedrovaya Pad
EN07-27		EU623657	*M. clitocyboidea*	Japan, Honshu
EN07-237c1		EU623658	*M. clitocyboidea*	Japan, Honshu
EN07-237c2		EU623661	*M. clitocyboidea*	Japan, Honshu
EN07-237c3		EU623662	*M. clitocyboidea*	Japan, Honshu
EN07-237c4		EU623663	*M. clitocyboidea*	Japan, Honshu
Bau1c1 (=Bau5343)	TENN62229	EU623665	*M. clitocyboidea*	China, Jilin Provence

Bau1c2	TENN62229	EU623666	*M. clitocyboidea*	China, Jilin Provence
Bau1c3	TENN62229	EU623667	*M. clitocyboidea*	China, Jilin Provence
Bau1c4	TENN62229	EU623668	*M. clitocyboidea*	China, Jilin Provence
Bau1c5	TENN62229	EU623669	*M. clitocyboidea*	China, Jilin Provence
Bau2c1 (=HMJAU4024)	TENN62230	EU623670	*M. clitocyboidea*	China, Jilin Provence
Bau2c2	TENN62230	EU623671	*M. clitocyboidea*	China, Jilin Provence
Bau2c4	TENN62230	EU623673	*M. clitocyboidea*	China, Jilin Provence
Tak1c1	TENN62233	EU623675	*M. clitocyboidea*	Japan, Hokkaido
Tak2c1	TENN62232	EU623676	*M. clitocyboidea*	Japan, Hokkaido
Tak2c4	TENN62232	EU623678	*M. clitocyboidea*	Japan, Hokkaido
Tak2c5	TENN62232	EU623679	*M. clitocyboidea*	Japan, Hokkaido
Tak2c3	TENN62232	EU623680	*M. clitocyboidea*	Japan, Hokkaido
Tak3	TENN62231	EU623664	*M. clitocyboidea*	Japan, Hokkaido
Megacollybia marginata				
11859c1	TENN60743	EU623681	*M. marginata*	Russia, Primorsky Territory, Kedrovaya Pad
11860c1	TENN60744	EU623682	*M. marginata*	Russia, Primorsky Territory, Kedrovaya Pad
11861	TENN60745	EU623683	*M. marginata*	Russia, Primorsky Territory, Kedrovaya Pad
11862c1	TENN60746	EU623684	*M. marginata*	Russia, Primorsky Territory, Kedrovaya Pad
11869	TENN60752	EU623685	*M. marginata*	Russia, Primorsky Territory, Kedrovaya Pad
11888h1	TENN60769	EU623686	*M. marginata*	Russia, Primorsky Territory, Kedrovaya Pad
11888h2	TENN60769	EU623687	*M. marginata*	Russia, Primorsky Territory, Kedrovaya Pad
Megacollybia platyphylla				
7206ss3	TENN58493	EU623689	*M. platyphylla*	Czech Republic
10315c1	TENN57963	EU623704	*M. platyphylla*	Germany
10512c6	TENN57742	EU623705	*M. platyphylla*	Germany
10819ss3_russia	TENN58227	EU623707	*M. platyphylla*	Russia, Leningrad Region
11447ss3	TENN59308	EU623703	*M. platyphylla*	Austria
11569	TENN59541	EU623691	*M. platyphylla*	Finland
11570	TENN59524	EU623706	*M. platyphylla*	Finland
11572	TENN59523	EU623712	*M. platyphylla*	Finland
11617	TENN59580	EU623709	*M. platyphylla*	Russia, Novgorod Region
11627	TENN59520	EU623708	*M. platyphylla*	Russia, Novgorod Region
11684	culture only LE(BIN)1112	EU623711	*M. platyphylla*	Russia, Caucasus

11685	LE226527	EU623710	*M. platyphylla*	Russia, Leningrad region, Pudost
12147	TENN60086	EU623702	*M. platyphylla*	Russia, Samara Region, Zhigulevsky Reserve
12163c1	TENN60102	EU623694	*M. platyphylla*	Russia, Samara Region, Zhigulevsky Reserve
12163c3	TENN60102	EU623695	*M. platyphylla*	Russia, Samara Region, Zhigulevsky Reserve
12163c4	TENN60102	EU623696	*M. platyphylla*	Russia, Samara Region, Zhigulevsky Reserve
12163c5	TENN60102	EU623697	*M. platyphylla*	Russia, Samara Region, Zhigulevsky Reserve
12210	TENN60147	EU623701	*M. platyphylla*	Russia, Samara Region, Zhigulevsky Reserve
AH1647	AH1647	EU623690	*M. platyphylla*	Spain
LE212075	LE212075	EU623692	*M. platyphylla*	Russia, Altai Republic
LE212073	LE212073	EU623693	*M. platyphylla*	Russia, Altai Republic
LE212076	LE212076	EU623700	*M. platyphylla*	Russia, Novosibirsk
LE202274	LE202274	EU623688	*M. platyphylla*	Russia, Northern Caucasus, Teberda Biosphere Reserve
NHP256-2004	LE226525 Culture =LE(BIN)1925	EU623713	*M. platyphylla*	Russia, Leningrad Region, Otradnoye
NHP47-06	LE212070	EU623698	*M. platyphylla*	Russia, Rostov Region, Veshenskaya
NHP49-06	LE212071	EU623699	*M. platyphylla*	Russia, Rostov Region, Veshenskaya
olrim422	none	AY805612[1]	*M. platyphylla*	Sweden
Megacollybia fallax				
AHS45002	MICH 45002	EU623714	*M. fallax*	USA, Idaho
Environmental Sample	none	EU218887[1]	*M. fallax*	Canada, Vancouver Island
11560ss1	TENN59446	EU623721	*M. fallax*	USA, Washington
AHS45432	MICH 45432	EU623722	*M. fallax*	USA, Idaho
11561	TENN59447	EU623723	*M. fallax*	USA, Washington
DAOM208710	DAOM 208710	EU623724	*M. fallax*	USA, Idaho
AN11591c1	AN11591	EU623715	*M. fallax*	USA, Arizona
AN11591c2	AN11591	EU623716	*M. fallax*	USA, Arizona
AN11591c3	AN11591	EU623717	*M. fallax*	USA, Arizona
AN11591c4	AN11591	EU623718	*M. fallax*	USA, Arizona
AN011587	AN011587	EU623719	*M. fallax*	USA, Arizona
Megacollybia texensis				
DPL7405c1	TENN62058	EU623725	*M. texensis*	USA, Texas
DPL7405c2	TENN62058	EU623726	*M. texensis*	USA, Texas
DPL7405c3	TENN62058	EU623727	*M. texensis*	USA, Texas
DPL7405c4	TENN62058	EU623728	*M. texensis*	USA, Texas
DPL7405c5	TENN62058	EU623729	*M. texensis*	USA, Texas

DPL7682c1	TENN62059	EU623730	*M. texensis*	USA, Texas
DPL7682c2	TENN62059	EU623731	*M. texensis*	USA, Texas
DPL7682c3	TENN62059	EU623732	*M. texensis*	USA, Texas
DPL7682c4	TENN62059	EU623733	*M. texensis*	USA, Texas
DPL7682c5	TENN62059	EU623734	*M. texensis*	USA, Texas
11676c13	TENN59935	EU623735	*M. texensis*	USA, Texas, Hardin Co.
11676c16	TENN59935	EU623736	*M. texensis*	USA, Texas, Hardin Co.
11676c17	TENN59935	EU623737	*M. texensis*	USA, Texas, Hardin Co.
11676c20	TENN59935	EU623738	*M. texensis*	USA, Texas, Hardin Co.
Megacollybia fusca				
AEFM1012c1	AEFM1012 (NY)	EU623741	*M. fusca*	Colombia
AEFM1012c3	AEFM1012 (NY)	EU623742	*M. fusca*	Colombia
AEFM1012c4	AEFM1012 (NY)	EU623743	*M. fusca*	Colombia
MCA1179c2	BRG, isotype LSU	EU623739	*M. fusca*	Guyana
MCA1179c3	BRG, isotype LSU	EU623740	*M. fusca*	Guyana
Megacollybia subfurfuracea				
11075c3	TENN59558	EU623744	*M. subfurfuracea*	USA, Arkansas
11075c5	TENN59558	EU623748	*M. subfurfuracea*	USA, Arkansas
11075c7	TENN59558	EU623746	*M. subfurfuracea*	USA, Arkansas
12095c1	TENN60343	EU623749	*M. subfurfuracea*	USA, Tennessee, Strawberry Plains
12095c6	TENN60343	EU623750	*M. subfurfuracea*	USA, Tennessee, Strawberry Plains
12264	TENN60861	EU623767	*M. subfurfuracea*	USA, Tennessee, GSMNP
REH8897	REH8897 (NY)	EU623751	*M. subfurfuracea*	USA, New York, New York Bot. Gard.
/costaricensis				
7903h2	TENN53803	EU623752	*/costaricensis*	Costa Rica
7903h1	TENN53803	EU623753	*/costaricensis*	Costa Rica
Megacollybia rodmani				
11083c24	TENN56566	EU623789	*M. rodmani*	USA, Arkansas, Newton Co
11083c27	TENN56566	EU623790	*M. rodmani*	USA, Arkansas, Newton Co
11083c28	TENN56566	EU623787	*M. rodmani*	USA, Arkansas, Newton Co.
11484	TENN59429	EU623765	*M. rodmani*	USA, Tennessee, GSMNP
11485	TENN59430	EU623761	*M. rodmani*	USA, Tennessee, GSMNP
11487	TENN59432	EU623788	*M. rodmani*	USA, Tennessee, GSMNP
11688ss1	culture only	EU623764	*M. rodmani*	USA, Missouri
11764	TENN59878	EU623766	*M. rodmani*	USA, Tennessee, GSMNP
11784	TENN60013	EU623792	*M. rodmani*	USA, Tennessee, GSMNP

12264	TENN60861	EU623747	*M. rodmani*	USA, Tennessee, GSMNP
13160	TENN61269	EU623759	*M. rodmani*	Canada, Quebec
13170	TENN61248	EU623760	*M. rodmani*	USA, Tennessee, GSMNP
AEFM1333b c2	AEFM1333(NY)	EU623777	*M. rodmani*	Costa Rica
AEFM1333b c3	AEFM1333(NY)	EU623778	*M. rodmani*	Costa Rica
AEFM1333b c5	AEFM1333(NY)	EU623779	*M. rodmani*	Costa Rica
AVoltic-2c1	Personal Herb.[3]	EU623780	*M. rodmani*	Canada, Nova Scotia
AVoltic-2c3	Personal Herb.	EU623769	*M. rodmani*	Canada, Nova Scotia
AVoltik-1h1	Personal Herb.	EU623776	*M. rodmani*	Canada, Nova Scotia
AVoltik-1h2	Personal Herb.	EU623791	*M. rodmani*	Canada, Nova Scotia
Cif2004-71c1	FCME 25109	EU623785	*M. rodmani*	USA, Tennessee, GSMNP
Cif2004-71c2	FCME 25109	EU623781	*M. rodmani*	USA, Tennessee, GSMNP
Cif2004-71c3	FCME 25109	EU623782	*M. rodmani*	USA, Tennessee, GSMNP
Cif2004-71c4	FCME 25109	EU623783	*M. rodmani*	USA, Tennessee, GSMNP
Cif2004-71c5	FCME 25109	EU623784	*M. rodmani*	USA, Tennessee, GSMNP
Cif2004-19h1	FCME 25056	EU623786	*M. rodmani*	USA, Tennessee, GSMNP
Cif2004-19h2	FCME 25056	EU623763	*M. rodmani*	USA, Tennessee, GSMNP
Cif2004-31	FCME 25068	EU623768	*M. rodmani*	USA, Tennessee, GSMNP
DAOM195782	DAOM195782	EU623771	*M. rodmani*	Canada, Quebec
DAOM215618	DAOM215618	EU623775	*M. rodmani*	Canada, Ontario
FCME13275	FCME13275	EU623758	*M. rodmani*	Mexico
FCME19183	FCME19183	EU623757	*M. rodmani*	Mexico, Est. Hidalgo
JLM1597	TENN61956	EU623762	*M. rodmani*	USA, Tennessee, GSMNP
PMB2431	CIU PBM2431	EU623770	*M. rodmani*	USA, Massachusetts
REH5346c3	REH5346 (NY)	EU623772	*M. rodmani*	Canada, Quebec
REH5346c4	REH5346 (NY)	EU623773	*M. rodmani*	Canada, Quebec
REH5346c5	REH5346 (NY)	EU623774	*M. rodmani*	Canada, Quebec
REH7947	REH7947(NY)	EU623755	*M. rodmani*	Costa Rica
REH8293	REH8293 (NY)	EU623754	*M. rodmani*	Costa Rica

c refers to clone number; ss refers to single spore isolate number; h refers to a haplotype number; GSMNP = Great Smoky Mountains National Park, USA; Kedrovaya Pad= Kedrovaya Pad Nature Reserve, Khasansky Dist., Primorsky Territory, Russia.

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map program (GCG 2000). Restriction digestions with Nsi I were carried out according to manufacturer's directions (Promega Corp., Madison, WI).

Molecular Data Analyses

Initial sequence alignments were carried out using the "pileup" program in GCG which performs UPGMA, followed by manual adjustments to the alignment. *Gerronema* and *Clitocybula* were selected as outgroups based on Moncalvo et al. (2002), and on blast similarity in GenBank. There was a large ca. 90bp variable insertion in the ribosomal ITS1 area that separated New World and Old World *Megacollybia* and data were analyzed with and without this area by treating gaps as missing or as a 5th base in parsimony analysis. No gap coding was attempted.

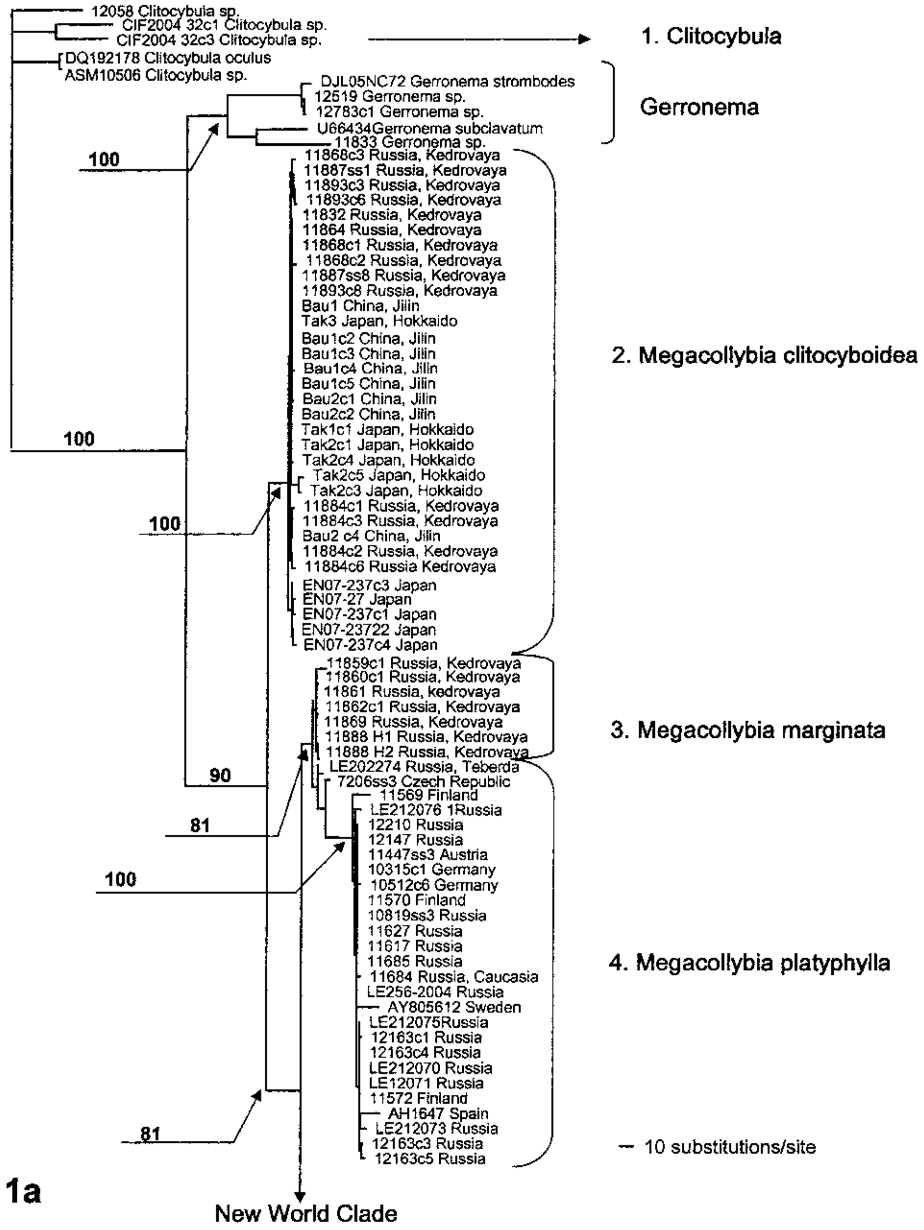
Both Parsimony and Bayesian analyses were performed. Parsimony relies on the concept that the tree needing the fewest changes in state along its branches is the best. Bayesian analysis searches for trees that are consistent with both the data and with a selected model of evolution. Maximum parsimony was performed using PAUP* (Swofford 2002). Characters were unordered and weighted equally. The number of trees retained was limited to 1000; multistate taxa were interpreted as uncertainty; starting trees were obtained via stepwise addition; addition sequence = furthest; the number of trees held at each step during stepwise addition = 1; the branch-swapping algorithm was a tree-bisection-reconnection (TBR); the steepest descent option was not in effect. One-thousand bootstrap replicates were performed. Modeltest was used to determine the appropriate model of evolution for Bayesian analysis (Posada and Crandall 1998). The model selected by Model Test was a general time reversible model with rate variation among sites (GTR+G). Bayesian analysis was performed using Mr. Bayes (Huelsenbeck and Ronquist 2000) with the following settings; nst = 6, basefreq = estimate. The MCMC search was run with 4 chains for 500,000 generations with sampling every 100 generations. The first 1,000 trees were discarded based on preliminary analyses showing that likelihood values had reached stability with the first 1000 trees. Posterior probabilities were estimated by sampling trees generated after likelihood values diverged. For Bayesian analysis, the ca. 90bp ITS1 insertion was included in the analysis.

Results

Molecular analyses

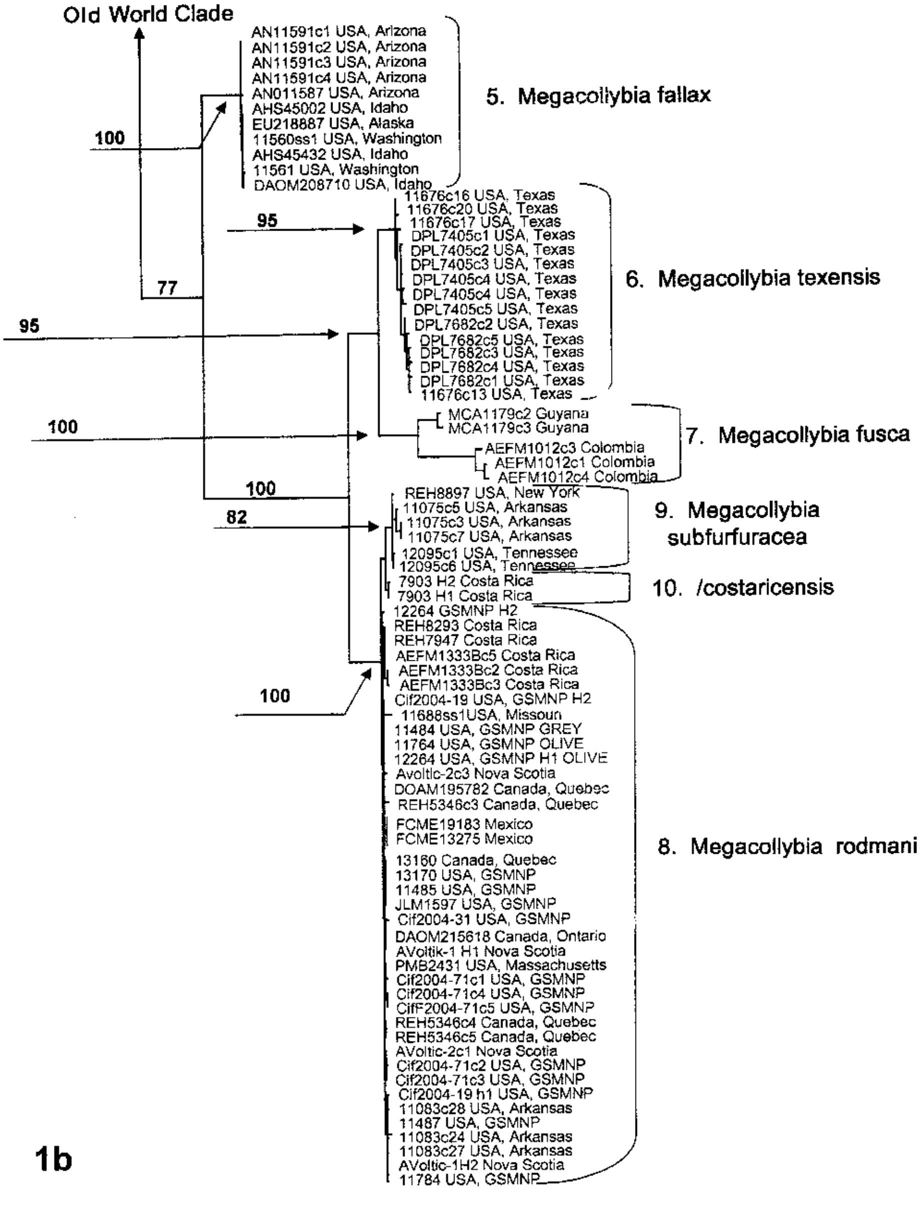
Heterozygosity for indels was common in *Megacollybia* collections and some sequences could not be resolved without cloning, especially in collections from Texas, Arkansas and Kedrovaya Pad Nature Reserve in Russia. Heterozygosity was usually due to 1-2bp indels, often an increase or decrease in the number of base pairs in runs of a single base. Apparently, there is considerable genetic diversity within this genus and hybridization of within-clade haplotypes is common. The average sequence divergence between clones of the same individual in *Megacollybia* was 0.423% (STD = 0.206). The frequency of bp cloning errors was approximately 0.15%. Haplotypes were always found in the same clade in phylogenetic analyses. Cloning was also necessary when specimens were contaminated with a second fungus such as *Candida* sp. (see under *M. texensis* below)

Parsimony and Bayesian analyses produced seven major clades (Figs. 1a, b, 2). One of these clades is morphologically and genetically subdivided into two additional clades (clades 8, 9, 10). Species comprising each clade are described and named below. Parsimony analysis with the ca. 90bp ITS1 insertion region included or excluded produced the same terminal taxa, as

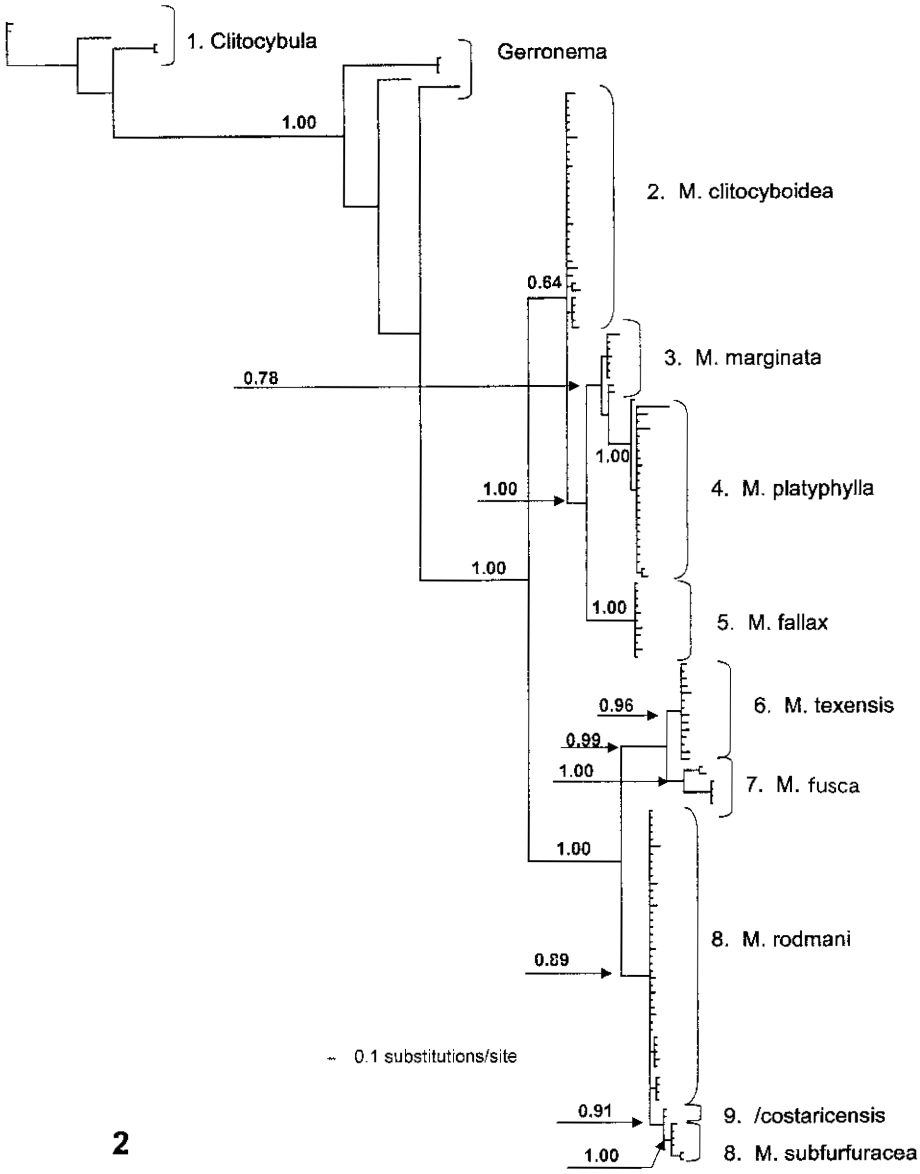


1a

FIG 1a, b. One of 1000 most parsimonious trees of length 1230 steps. Boot strap support is given to the left of the node, followed by the Bayesian posterior probability. Of 914 total characters:All characters were unordered and of equal weight; 322 characters were constant, 93 variable characters were parsimony-uninformative, 499 characters were parsimony-informative. Gaps were treated as “fifth base.” Numbers adjacent to clades refer to numbers in manuscript under “results.”



did Bayesian analysis with the insertion region included. The position of *Megacollybia fallax*, however, was unstable depending on the analysis, sometimes grouping with other New World taxa when the insertion was included in analyses (Fig. 1b) and grouping with Old World taxa when the insertion was excluded in parsimony analysis, or included in Bayesian analysis (Fig. 2). While the complex nature of gaps in this data set made gap-coding unfeasible, exemplars



2

FIG. 2. Bayesian analysis using a GST+G model. Posterior probabilities are given to the left of the node.

of *M. fallax, M. clitocyboidea* and *M. rodmani* were extensively gap-coded and compared for sequence homology. These data suggest that *M. fallax* is closer to *M. clitocyboidea* (94.7% sequence homology) than to *M. rodmani* (90.66% sequence homology). Given the sequence divergence for the ca. 90bp insertion between *M. fallax* and other New World taxa and extensive small indels, the ambiguity is understandable and sequences from other genes will ultimately be required to resolve the placement of *M. fallax* relative to other *Megacollybia* taxa.

In temperate Asia, two taxa were identified: *M. clitocyboidea* and *M. marginata*. Otherwise, Eurasia seems represented by one species (*M. platyphylla*). The New World supports at least five species (*M. fallax*, *M. texensis*, *M. fusca*, *M. subfurfuracea*, *M. rodmani*), with the likelihood of more to be revealed. There is a possibility of further cryptic species in both *M. platyphylla* and *M. rodmani* based on sequence divergence and morphology.

Taxonomic characters

Rexer and Kost (1989a, b) carefully reported and illustrated the various tissues of *M. platyphylla*. All the material studied was from Germany, and there is no reason to doubt their species identification. Their observations were made in the context of what they considered a taxonomic alliance [*M. platyphylla*, *Oudemansiella mucida*, *Xerula radicata* (as *Oudemansiella*) and *Strobilurus esculentus* based, in part, on Redhead's (1987) placement of these genera]. The present paper considers several putative taxa within *Megacollybia*, however, and because distinguishing characters among taxa are more quantitative than qualitative, we consider it important to review taxonomic characters in the genus, largely as a guide to future considerations in identifying or describing specimens.

General considerations: The accompanying phylogenetic reconstruction has been used as a guide to taxonomic delimitations. The task for morphology, therefore, has been to attempt to separate the major (and sometimes minor) clades into recognizable morphotaxa. For the most part, this is very difficult, for once geographic location has been dismissed as a character, little else is unique or startling. Some quantitative differences can be found, however, and these can be summarized as follows.

Basidiome size and stature: Generally speaking, basidiomata across the genus are collybioid (*M. platyphylla*, *M. marginata*, *M. texensis*) or clitocyboid (*M. clitocyboidea*). Three species are characterized by stouter, somewhat tricholomoid or russuloid basidiomata (*M. fusca*, *M. rodmani* f. *murina*, *M. fallax*).

Pileus surface: Pileus surface of almost all basidiomata is characterized as fibrillose, delicately radially streaked, or, in age, rimose. This texture, when seen on juvenile basidiomata or the disc of mature basidiomata, may be so congested with pileipellis terminal cells as to appear minutely scabrous (especially *M. clitocyboidea*, and in /costaricensis), or, if interrupted, as minutely squamulose. In all cases, however, the pileus surface attains its radial streaking over the limb. This streaking may become somewhat diffuse toward the pileus margin, and can be mistaken for a striate margin.

In rain, the radial streaks may be somewhat detersile, and when interrupted, can appear squamulose. Such secondary phenomena should not be mistaken for a common, truly squamulose appearance of the pileus disc.

The radial streaks are produced by pigmented, superficial, radially oriented surface hyphae. These pigmented hyphae (ranging microscopically from weakly olivaceous gray to dark olivaceous brown and macroscopically from olive-gray to olive-black) form differentiated terminal cells also oriented radially. These cells are consistently clavate, conspicuously clamped, occasionally transversely septate and can be quite thick-walled.

Intriguingly, the delicate radial streaks are often interrupted by small lenticular openings (approx. 1–2 × 0.3–0.5 mm) revealing the white tissue of the outer pileus trama. In numerous specimens from worldwide locations, these small openings were covered by small, delicate, white cocoons, sometimes still containing the larvae of an insect. The identity of the insect(s) is unknown, but the phenomenon raises the question of whether it is the insect larvae which cause the small lacunae originally, or whether they merely take advantage of the opening (with the possibility of moisture and/or nutrients) for pupation.

Pileus trama: Invariably, the pileus trama is white, remaining so on drying. Upon drying, it is friable, not tough or woody or even compact. This texture is caused by the greatly inflated tramal cells (sometimes over 50 µm diam), which can be thick-walled and appear ornamented on the inner wall surface. These hyphae are rarely branched, are long-celled (cells often over 750 µm long) and only obscurely clamped. Interwoven with these inflated cells are slender (2.5–5 µm diam), frequently branched, frequently clamped, thin- to firm-walled hyphae. This mixture of hyphal types has been judged "sarcodimitic" (Corner, 1966) a term whose meaning has been altered over the years (see Corner, 1991; Redhead, 1987; Bas et al., 1990: 65–66).

Lamellae: Basidiomata of all taxa ordinarily exhibit adnexed to adnate lamellae, usually with a significant tooth merging into the longitudinal ridges of the stipe. Lamellae are subdistant, usually broad (up to 20 mm in some cases), but not remarkably thick. Although usually described as white, lamellae are often slightly tinted yellow-olive to pallid olive-gray. Typically, lamellae are transversely streaked with paler colors, and in drying, the outer portion of lamellae turns taffy colored or light ochraceous buff, while the area closest to the pileus attachment remains off-white with delicate streaks into the more mellow color. The transverse streaking is sometimes pronounced and accompanied by some relief as delicate transverse ridges.

Interlamellar areas are usually smooth and hymenial, but occasionally can be transversely ridged or anastomosed.

Two instances of marginate lamellar edges have been encountered. In one instance (*M. marginata*), lamellae are delicately and abruptly marginate with a deep olive-brown or olive-black edge. This is caused by strongly pigmented cheilocystidia. In the other instance (*M. platyphylla* form A), the delicate lamellar edge is purple (in dried material). Cheilocystidia appear hyaline (BF), and the marginate appearance may be the result of exposure to frost or perhaps contact. This condition, while distinguishing a small clade, is probably not indicative of taxonomic rank.

Basidia: Across the genus, basidial form and dimensions are quite uniform. Basidia fit generally within 35–43 × 8–11 µm and although a few collections seemed to form long basidia, these collections invariably were included in clades of which the other members were more typical. All basidia are clavate, clamped, thin-walled, hyaline, 4-spored, with usually a few, scattered, small, refringent guttules.

Basidioles: Dominating the hymenium together with scattered mature basidia, basidioles are consistently digitate, sometimes gnarled, lobed or otherwise contorted, but never mucronate or torpedo-shaped.

Basidiospores: Basidiospores throughout the genus present little variation in size and shape, as descriptions of individual taxa will attest. All fit within a narrow range of dimensions, 6–10 × 5–7 µm with similar Q and L^m values. Spores are thin-walled, ellipsoid to somewhat ovate, always somewhat flattened adaxially, with a significant hilar appendage and consistently inamyloid. Contents of mature spores show 1-few refringent guttules which, in fresh material, can obscure accurate observation of the spore wall.

Basidiospores left overnight in KOH swell significantly over the same spores freshly mounted; they are also without guttules, and decidedly more plump (subglobose rather than ellipsoid to ovate).

Lamellar trama: In all examined basidiomata, the lamellar trama exhibits large areas of intricately interwoven hyphae, usually termed “regular” (see Bas et al., 1999: 172). Singer’s (1986: 251) report of “hymnophoral trama regular or subregular, consisting of rather long, sometimes even voluminous hyphae which are strongly interwoven to subparallel” appears as part of his description of *Tricholomopsis* and is not easily teased apart with recognition of *Megacollybia*. In at least *M. clitocyboidea*, however, a distinct central plate or strand is differentiated, with intricately interwoven tissue between the central strand and subhymenium. The central stratum is broader toward the pileus context and narrower toward the gill edge, often disappearing there.

Vascular hyphae: Also known as gloeoplerous hyphae, these hyphae are somewhat refringent under PhC, are common in pileus and lamellar tramae, and can be abundant. They are seen as meandering through otherwise differentiated tissue (i.e. through the lamellar trama), and range from almost unbranched to frequently branched, but rarely septate and apparently rarely clamped (or without clamps). These gloeoplerous hyphae are strongly cyanophilous, although cotton blue-lactic acid mounting medium is of little use for observing diagnostic microstructures of basidiomata.

Cheilocystidia: Cheilocystidia were plentiful in all basidiomata examined. Occasionally, cheilocystidia protrude beyond basidia on the lamellar edge, and while noteworthy, this feature proved unreliable as a distinguishing character. Cheilocystidia were typically broadly clavate, variable in length and width, firm- to thick-walled (wall up to 1.0 µm thick, and then usually irregular on inner surface), conspicuously clamped and hyaline (BF; pigmented in *M. marginata*). In some collections, cheilocystidia were observed as transversely septate, but, while a diminutive clamp connection was only rarely seen at this septum, it is probably present and the cheilocystidial terminal cell is sessile (not pedicellate) on the penultimate cell. Under PhC, cheilocystidial contents appear somewhat darker than basidial contents, but this may be a function of condensed protoplasm; under BF this feature is not visible, and cheilocystidia (except those of *M. marginata*) are hyaline.

Clamp connections: Previous literature (Singer, 1986) has pointed out that clamp connections in this complex (including, for example, *Clitocybula* and *Gerronema*) are conspicuous. In some traditions, they would be known as “medallion clamps,” for often a visible aperture can be seen in the crook of the “hook cell” of the clamp. This feature is especially noticeable when searching for subbasidial (or subhymenial) clamp connections, where they are easily demonstrated. They are also obvious on the slender hyphae of tramal tissue, but the inflated hyphae of these tissues exhibit smaller, more obscure clamp connections on the constricted septa. These demonstrations, fortunately, are unneeded, for all collections examined exhibited similar, conspicuous clamps.

In examining for pileipellis terminal cells or cheilocystidia, the basal clamp is often disarticulated, but the telltale angular base on these structures reflects that a clamp was present.

Stipe surface: Hyphae of the stipe surface can be seen as two types: 1) a superficial network producing differentiated terminal cells; and 2) true surface hyphae. The superficial network varies from an arachnoid reticulum to a considerable (up to 25 µm thick) layer. In all instances, the tissue comprises slender (2.5–5 µm diam), thin- to firm-walled, conspicuously clamped, rarely branched, hyaline hyphae. The stipe cortical tissue is often coherent (disar-

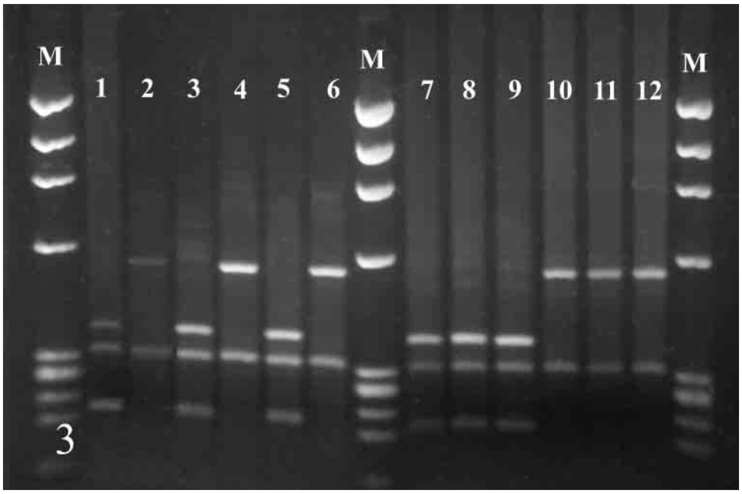


FIG. 3. Restriction digestions with *Nsi* I for collections from the Kedrovaya Pad Reserve in the Russian Primorsky district. M= Phi X Hae III digestion; *Megacollybia marginata* lanes 1 = 11859, 3 = 11860, 5 = 11861, 7 = 11862, 8 = 11869, 9 = 11888; *Megacollybia clitocyboidea* lanes 2 = 11832, 4 = 11864, 6 = 11868, 10 = 11884, 11 = 11887, 12 = 11893. Weak bands have been photographically enhanced.

ticulating as sheets of hyphal parts rather than as free hyphae), and composed of two hyphal types: 1) somewhat inflated, usually thick-walled hyphae never as inflated as those of pileus or lamella trama; and 2) slender, more frequently branched, longitudinal hyphae. Little variation was seen in this tissue.

The terminal cells produced by the superficial external layer are repent to somewhat bent outward, and range from narrowly to broadly clavate. They could be termed caulocystidia and, except for some differences in dimensions, are considered hardly worthy of taxonomic rank.

Discussion and naming of taxa

1. Outgroups [Figs. 1A, 2 – clade 1]

Species of *Clitocybula* and *Gerronema* were used as outgroups in this study. A recent paper by Barrasa et al. (2006) furnishes a key to species of *Clitocybula* in Europe and North America, and the contribution by Bigelow (1973) summarized the genus, with emphasis on North America.

2. *Megacollybia clitocyboidea* [Figs. 1A, 2 – clade 2, Figs. 4–7]

Several collections of putative *M. platyphylla* were gathered recently from Kedrovaya Pad Nature Reserve south of Vladivostok in far eastern Russia. ITS sequences showed that basidiomata belonged to two distinct clades: one related to EuroScandinavian *M. platyphylla* (viz. *M. marginata*), the other to a haplotype unique to temperate eastern Asia (viz. *M. clitocyboidea*). The latter clade is sister to all other *Megacollybia* taxa and would seem to be basal in the genus. Restriction digests of the ITS region with *Nsi* I, were carried out on all Kedrovayan collections and conclusively showed that there was no interbreeding between the two clade genotypes (Fig. 3). Thus, *M. marginata* and *M. clitocyboidea* appear to be two distinct biological species.

Because basidiomata are thought to resemble those of *Clitocybe*, one of the Asian species has been named *M. clitocyboidea*.

Megacollybia clitocyboidea R.H. Petersen, S. Takehashi & Nagas. sp. nov.

Pileus 35–108 mm latus, convexus ad planus vel depressus, brunneus ad fusco-brunneus, fibrillosus ad subrimosus. Lamellae adnatae, uncinatae ad subdecurrentes, latae, lacteae ad eburneae. Stipes 50–130 × 3–12 mm, equalus ad sursum decrescens, brunneus ad olivaceo-brunneus. Pileocystidia 33–136 × 6–22 µm, clavata, olivacea, fibulata, levis. Sporae 6–9.5 × 5–7.5 µm (*n* = 167; *Q* = (1.00–)1.07–1.60; Q^m = 1.24; L^m = 7.28 µm), lato-ellipsoideae ad lato-ovatae, levae, tenuitunicatae, hyalinae. Basidia 28–50 × 7–11 µm, clavata, tenuitunicata, fibulata, tetraspora. Pleurocystidia nulla. Cheilocystidia 20–65 × (6–)9–17 µm, angusto- ad lato-clavata, fibulata, tenuitunicata. Caulocystidia 30–158 × 10–15 µm, pedicellata ad elongate capitulata, pallidobrunnea. Asia occidentalis, temperata.

Holotype: JAPAN, Hokkaido, Sorachi Prov., Iwamizawa-shi, Tonebetu, 30.VIII.2005, coll. S & C Takehashi, ST 3 (TENN 62231).

Basidiomata (Figs. 4–5) collybioid to clitocyboid, occasionally large and tricholomatoid. **Pileus** 35–108 mm broad, convex when young, expanding to plane and shallowly to deeply depressed, at times weakly or distinctly papillate-umbonate,*"mummy brown" (6F8) to "clove brown" (6F5)* at first, later discoloring to grayish brown to yellowish brown ("buffy brown;" 6D4-5D3-4) with center often remaining dark brown to blackish; *disc surface minutely scabrous or furfuraceous* with minute olive-black, olive-brown to fuscous brown scabers almost solid in center, becoming less frequent outward and less discrete and nearly obscure over outer limb; pileus limb surface becoming smooth outward, basically ivory colored but increasingly radially streaked with olive-brown to olive-black pileipellis hyphae on the yellowish background so that at pileus margin there is no evidence of yellow pigments; margin inrolled when young, becoming extended with age, not striate, concolorous with limb (–6D4), often eroded, becoming inrolled upon drying. Pileus flesh thin, up to 4 mm thick over stipe, off-white, almost absent outward, soft, becoming friable upon drying. **Lamellae** adnexed to adnate to shallowly decurrent, subdistant to distant, thin (and parchment-like when dry), ivory colored, "pale olive buff" (3B2), by maturity "pale cinnamon pink" (5A2) to "pearl gray" (23B2), ventricose, up to 12 mm deep, on drying becoming light ochraceous buff, very brittle and delicately transversely streaked as though hygrophanous (but not so); interlamellar surface often intricate cross-ribbed outward, mostly translucent, showing color of pileus surface; *lamellar edge not marginate*. **Stipe** central, 50–130 mm long, 3–12 mm broad apically, 4–20 mm broad near base, smooth to silky-shining, or at times pruinose-scaly downward, off-white apically, *sordid pallid fuscous downward, "buffy brown" (6D4) when young, paler by maturity ["pale vinaceous fawn" (17A2), downward near "light drab" (17B2), "pale pinkish buff", "deep olive buff" (3C3)],* occasionally with reluctant reddish-brown staining; base always somewhat enlarged, sometimes geniculate, with very tight, thin whitish tomentum; **rhizomorphs** occasional, white, ropy. **Taste** and **odor** not distinctive.

Habitat: China, rotten wood, mixed forest; Japan, in hardwood forests or rarely in bamboo stands, on and around rotten stumps, or on the ground on rotten wood or roots; Russia, very rotten hardwood logs.

Pileipellis a repent layer of slender, radial hyphae; hyphae 3–4.5(–8) µm diam, smooth (no evidence of incrustation in KOH), firm-

FIGS. 4, 5. *Megacollybia clitocyboidea,* basidiomata. Fig. 4. TAK 3. Fig. 5. TAK 1. Fig. 4 = 1.8×. Fig. 5 = 1×.

walled (wall up to 0.4 µm thick), conspicuously and frequently clamped, often (but not invariably) cytoplasmically pigmented (olive, dull brown or yellowish brown; KOH, BF), often producing upturned, inflated terminal (and often subterminal) cells; **pileipellis terminal cells** (pileocystidia; Fig. 6A, B) 33–126 × 6–22(–31) µm, subflagelliform, digitate, clavate, inequilaterally clavate, vermiform to subcapitulate, often curved, conspicuously clamped, cytoplasmically pigmented (olive; usually strongly), smooth, firm-walled, occasionally hyaline and in rare instances inflated up to 38 µm broad, broadly clavate. Pileus trama constructed of

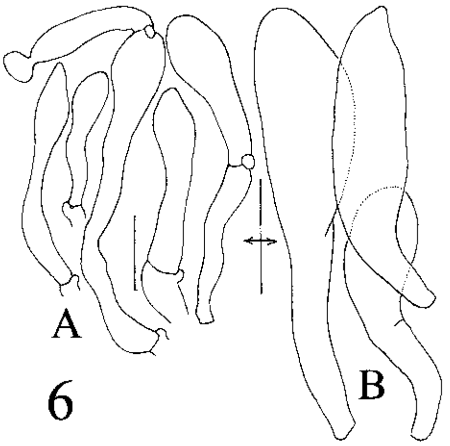


FIG. 6. *Megacollybia clitocyboidea.* Pileipellis terminal cells. A. TAK 3. B. TAK 2. Standard bar = 20 µm.

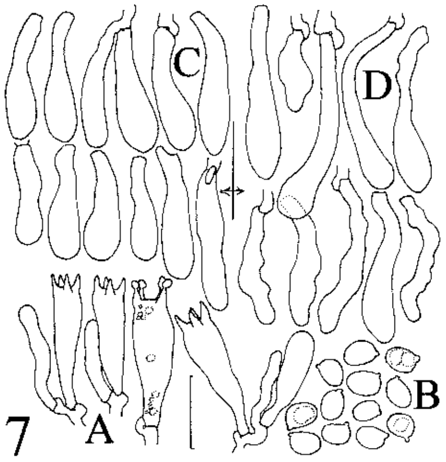


FIG. 7. *Megacollybia clitocyboidea.* A. Basidia. B. Basidiospores. C, D. Cheilocystidia. A, B, D. BAU 5343. C. Tak 3. Standard bar = 20 µm.

two hyphal types: 1) inflated up to 45 µm diam, thin- to thick-walled (wall up to 1.0 µm thick, irregularly thickened and appearing mottled or banded; PhC), long-celled, constricted at septa, inconspicuously clamped, hyaline; and 2) slender (3–8 µm diam), firm-walled, hyaline, frequently branched, frequently clamped, smooth, not mottled. **Basidia** (Fig. 7A) 28–50 × 7–11 µm, clavate, thin-walled, conspicuously clamped, 4-spored (perhaps rarely 2-spored), hyaline; contents homogeneous or 1-few-guttulate; basidioles 25–45 × 5–10 µm, clavate. **Basidiospores** (Fig. 7B) 6–9.5 × 5–7.5 µm [*n* = 167; *Q* = (1.00–)1.07–1.60; Q^m = 1.24; L^m = 7.3 µm]), broadly ellipsoid to broadly ovate, flattened adaxially, smooth, thin-walled, hyaline; contents homogeneous to 1-few-guttulate. **Cheilocystidia** (Figs. 7C, D) not or rarely protruding beyond basidia, 20–65 × (6–) 9–17 µm, digitate, narrowly or broadly clavate or sphaeropedunculate (rarely with short apical outgrowths), occasionally transversely septate, conspicuously clamped (but often disarticulated from clamp), *thin-walled*; contents homogeneous, occasionally with 1–3 amorphous (but well-defined) dark inclusions (PhC). Stipe surface near apex an arachnoid layer of slender [2.5–4(–7) µm diam] hyphae producing repent or out-turned terminal cells (**caulocystidia**) 30–more than 158 × 10–15 µm with narrowly rounded to subcapitate ends. Inner tissue (perhaps 50–100 µm deep): hyphae similar, 7–13(–24) µm diam, hyaline, coherent, clamped. Stipe flesh constructed of two hyphal types, both hyaline, both clamped, both longitudinally arranged, both free (not adherent): 1) inflated hyphae 8–more than 30 µm diam, thick-walled (wall up to 1.5 µm thick, long-celled, constricted at septa, irregular in outline and somewhat mottled, especially in wider individuals); and 2) slender, 6–13 µm diam, frequently branched and frequently clamped, firm-walled.

Commentary: Characters which separate this Asian taxon from others include: 1) grayish brown, dark olive-brown to olive-black pileus (at least pileus disc); 2) minutely scabrous or furfuraceous pileus disc; and 3) cheilocystidia with thin walls (not firm-walled). The other

Asian taxon known to us is *M. marginata*, immediately recognizable by its delicately marginate lamellae.

In *M. clitocyboidea*, cheilocystidia are often difficult to distinguish from basidia. Under PhC, basidia are usually paler and include small guttules, while cheilocystidia appear empty and are usually uniformly dark.

The aquarelle in Imazeki and Hongo (1965: Fig. 33, as *Tricholomopsis*) and the color photographs in Imazeki et al. (1988: 117, as *Oudemansiella*) seem to represent *M. clitocyboidea* both in color (dull neutral brown pileus, stipe off-white apically, sordid pallid fuscous downward), and stature (depressed pileus disc).

DNA of TENN 60766 showed it to be the product of two haplotypes, differing in a few base pairs. One of the haplotypes was identical to that of TENN 62230, while the other did not match any other haplotype of *M. clitocyboidea*. Likewise, TENN 62232 was the product of two haplotypes, one identical to several other homozygous collections, but the other unique. TENN 62232 and TENN 62229 also were heterozygous, with similar patterns. Such results strongly indicate that hybridization is occurring among populations of *M. clitocyboidea*. Conversely, there is no evidence of hybrids between *M. clitocyboidea* and *M. marginata*.

Petersen and Gordon (1994) noted that European *M. platyphylla* emitted a pleasant, floral perfume in culture. TENN 60766 (*M. clitocyboidea*, Russia) produced a pleasant, citrus-like odor in culture, absent from the few other cultures of Asian *Megacollybia* collections.

Vassilyeva (1973: 126) reported *Oudemansiella platyphylla* from the Primorsky Region of far eastern Russia, but which of the taxa in the area (or perhaps more than one) was described remains open to question. With pileus 8–14 cm broad and stipe 8–10 × 1–2 cm, perhaps larger basidiomata were intended (i.e. EN 07-27NR; TAK 1).

Specimens examined: **CHINA**, Jilin Prov., Antu Co., Beihe, forest behind fire tower, 14.VIII.1988, coll. R.H. Petersen (as *Megacollybia* sp.), TFB 1451 (TENN 48647); Jilin Prov., Fusong Co., Lushuihe, 26.VII.2006, coll. & det. T. Bau (as *Oudemansiella platyphylla*), Bau 5343 (TENN 62229); same location, 28.VI.2005, coll. & det. T. Bau, HMJAU 4024 (TENN 62230). **JAPAN**, Honshu, Tottori Pref., Tottori-shi, Koyama, 16.VI.2007, coll. M Yoshimura, det. E Nagasawa (as *M. platyphylla*), EN 07-27NR (TMI); Tottori-shi, Hamasaka (near Tanegaike Pond), 26.VI.2007, coll. M Kanbe, det. E Nagasawa (as *M. platyphylla*), EN 07-30 (TMI); Tottori-shi, Tatsurami, 9.IX.2007, coll. Yukihiro Nishio, det. E Nagasawa (as *M. platyphylla*), EN 07-27NR (TMI); Hokkaido, Ishikari Prov., Sapporo-shi, Mt. Moiwa, 31.VII.2005, coll. T. Takazawa, ST 2 (TENN 62232); Hokkaido, Sorachi Prov., Iwamizawa-shi, Tonebetu, 30.VIII.2005, coll. S & C Takehashi, ST 3 (TENN 62231, holotype); same location, 30.VIII.2005, coll. S & C Takehashi, ST 1 (TENN 62233). **RUSSIA**, Primorsky Territory, Khasansky Dist., Kedrovaya Pad Nature Preserve, N 43˚ 05.869’, E 131˚ 33.403’, 17.VIII.2005, coll. RHP, TFB 11832 (TENN 60717); same location, N 43˚ 06.074’, E 131˚ 33.125’, 20.VIII.2005, coll. R.H. Petersen (as *M. platyphylla*), TFB 11864 (TENN 60748); same location, N43˚ 07’ 01”, E 131˚ 29’ 14”, 22.VIII.2005, coll. O. Morozova, TFB 11884 (TENN 60766); same location, 22.VIII.2005, coll. A. Kovalenko (as *M. platyphylla*), TFB 11893 (TENN 60774).

3. *Megacollybia marginata* [Figs. 1A, 2 – clade 3, Figs. 8, 9]

Several collections of solitary *Megacollybia* basidiomata were gathered south of Vladivostok, Russia, in 2005. The only separating character in the field was the delicately marginate lamellae of one group of collections, versus the non-marginate lamellae of the other. Since that time, additional collections of the non-marginate taxon have been examined and sequenced (see under *M. clitocyboidea*), but the marginate-gilled taxon remains known only from the original collections. Both taxa appear to be new.

The extent of distribution of *M. marginata* is unknown but Imai (1938: 116) reported under the name *Collybia platyphylla* a fungus with “lamellae ..., edge wavy or subserrate and tinged with dark-brown color” from Hokkaido and Kuriles (Kunashiri Is.). These phylogeographical data resemble findings by Aanen et al. (2000) in European and American *Hebeloma velutipes*, Matsumoto et al (2005) with *Pleurocybella porrigens* and Terashima et al. (2006) with *Armillaria mellea* subsp. *nipponica*.

Megacollybia marginata R.H. Petersen, Morozova & J.L. Mata, sp. nov.

Pileus 35–85 mm latus, planus ad leviter depressus, atrofuscus ad atrobrunneus, radiofibrillosus, siccus. Lamellae adnatae, ventricosae, ad 13 mm latae, albo-olivaceae ad eburneae, margine delicate atrobrunneo. Stipes 50–80 × 10–12 mm, equalus ad sursum decrescens, olivaceoalbus ad pallide griseus. Pileocystidia 35–96 × 7–15(–25) µm, elongate-clavata, olivacea ad atro-olivacea, tenui- ad crassitunicatae, fibulata. Sporae 6.5–10 × 5–7 µm (Q = 1.11–1.54, Q^m = 1.30; L^m = 8.53 µm), subglobosae ad late ellipsoideae ad ovatae, laevae, tenuitunicatae, hyalinae. Basidia 30–41 × 7–10 µm, clavata, tenuitunicata, fibulata, tetraspora. Pleurocystidia nulla. Cheilocystidia 31–65 × 7–15 µm, clavata ad late clavata, fibulata, tenui- ad crassitunicata. Caulocystidia (20–)35–80 × 6–14 µm, clavata ad subventricosa, prope hyalina. Rossica orientalis.

Holotype: RUSSIA, Primorsky Reg., Khasansky Dist., Kedrovaya Pad Nature Reserve, N 43° 06’ 37”, E 131° 31’ 31”, 20.VIII.2005, coll. O Morozova (as *M. platyphylla*), TFB 11869 (TENN 60752).

Basidiomata collybioid or clitocyboid. **Pileus** 35–85 mm broad, plane to shallowly or strongly depressed, occasionally with small umbo; disc dark fuscous brown (“sepia,” 4F8, “bister,” 5F8, “clove brown,” 6F5), usually without scabers or squamules (but occasionally minutely scabrous or minutely hispid), becoming glabrous-shining and “olive brown” (5E5) upon drying, densely radially streaked; limb somewhat lighter (5D3) in color, sometimes with small lenticular scars revealing white flesh; margin thin, not striate, usually downturned to gently inrolled. **Lamellae** adnate with insignificant tooth, ventricose, close to subdistant, up to 13 mm broad, distinctly olivaceous when young (“deep olive buff”), becoming off-white by maturity (“pale pinkish cinnamon”), ochraceous buff with some delicately transverse streaking of pale ochraceous buff, mostly curled upon drying, obscuring lamellar edge; *lamellar edge delicately but distinctly marginate to dark brown*. **Stipe** 50–100 mm long, 3–6 mm broad in midsection, somewhat expanded apically and basally (up to 12 mm broad) and there off-white, terete, pallid olivaceous to drab in midsection (“deep olive buff”), significantly lined or ridged, occasionally staining rufous in the field, drying to dark neutral brown (upward “olive brown,” downward somewhat paler, “tawny olive”, 5C5). **Rhizomorphs** occasional, white, ropy. **Odor** and **taste** none.

Habitat: Apparently endemic to far eastern Russia; on or near very rotten wood of *Alnus* (?).

Pileipellis terminal cells (Fig. 8A) 35–96 × 7–15(–25) µm, mostly long-clavate, prostrate to semi-erect, single or in fascicles, thin- to firm-walled, conspicuously clamped, moderately to strongly pigmented (especially distally); contents homogeneous. Pileus outer flesh constructed of two hyphal types: 1) 13–65 µm

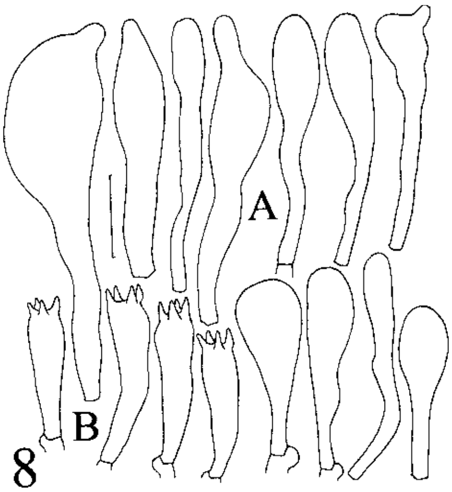


FIG. 8. *Megacollybia marginata*, TENN 60752. A. Pileipellis terminal cells. B. Basidia. Standard bar = 20 µm.

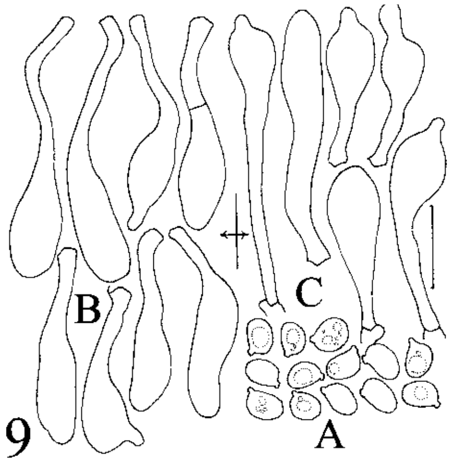


FIG. 9. *Megacollybia marginata*, TENN 60752. A. Basidiospores. B. Cheilocystidia. C. Caulocystidia. Standard bar = 20 µm.

diam, irregularly thick-walled (wall up to 1.5 µm thick), obscurely blotched or perhaps ornamented, hyaline, constricted at septa, obscurely clamped; and 2) 3.5–6 µm diam, thin-walled, frequently branched, infrequently but conspicuously clamped, interwoven among wide hyphae. **Basidia** (Fig. 8B) 30–41 × 7–10 µm, 4-spored, clamped, thin-walled; contents with a few scattered guttules; basidioles similarly shaped as basidia, not mucronate. **Basidiospores** (Fig. 9A) 6.5–10 × 5–7 µm (*n* = 65, *Q* = 1.11–1.54, Q^m = 1.30; L^m = 8.53 µm), broadly ellipsoid, rarely subglobose, flattened adaxially, thin-walled, smooth, hyaline in KOH, inamyloid; contents 1-few guttulate. **Cheilocystidia** (Fig. 9B) abundant, protruding beyond basidia singly or in 2-3s, 31–65 × 7–15 µm, nearly sessile (rarely) to long-pedicellate, clavate to broadly clavate, rarely with 1-2 apical outgrowths, subhyaline singly, pale pinkish to pale tan (100×, BF) in mass, conspicuously clamped, thin- to firm-walled. Stipe tissues composed of parallel hyphae, 4–20 µm diam, hyaline, constricted somewhat at septa in broader hyphae; wall up to 2 µm thick. **Caulocystidia** (Fig. 9C) (20–) 35– more than 80 × 6–14 µm, pedicellate, narrowly clavate to subsphaeropedunculate, uncommonly with apical mammiform or strangulate outgrowth, firm- to thick-walled (wall never more than 0.7 µm thick), conspicuously clamped, subhyaline; contents homogeneous.

Commentary: Phylogenetically, the temperate Asian marginate (*M. marginata*) and non-marginate (*M. clitocyboidea*) forms are only distantly related, with the marginate form closely related to the typical European *M. platyphylla*. Nonetheless, the two temperate Asian taxa covered here are almost indistinguishable morphologically except for the very delicate brown or black lamellar edge. Even then, basidiomata of TENN 60769, belonging in the clade of marginate collections, is not so, and is thus virtually indistinguishable from *M. clitocyboidea*. Whether this constitutes evidence of hybridization between the two forms or population variability remains unknown.

Cheilocystidia are clearly pigmented in mass, causing the marginate lamellar edge. Microscopically, however, the cytoplasmic pigment is immediately bleached by KOH (not as drastically in H_2O), and if not viewed within a few seconds, appears almost totally hyaline.

Two specimens currently listed in *M. platyphylla* form B, a collection from the Czech Republic (TFB7206/TENN58493) and one from Terebda (LE202274) have sequences related to (but not the same as) *M. marginata* but lack marginate gills. These collections may represent an intermediate taxon between *M. marginata* and *M. platyphylla*.

Specimens examined: **RUSSIA**, Primorsky Region, Khasansky Dist., Kedrovaya Pad Nature Reserve, N side of Kedrovaya River, N 43° 05.869', E 131° 33.418', 19.VIII.2005, coll. A. Kovalenko, TFB 11859 (TENN 60743); same data, coll. A. Kovalenko, TFB 11860 (TENN 60744); same location, N 43° 06.074', E 131° 33.125', 20.VIII.2005, coll. R.H. Petersen (as M. platyphylla), TFB 11861 (TENN 60745); same data, coll. R.H. Petersen, TFB 11862 (TENN 60746); same data, coll. R.H. Petersen (as M. platyphylla), TFB 11869 (TENN 60752, holotype); same location, S side of Kedrovaya River, N 43° 07.01', E 131° 29.14', 22.VIII.2005, coll. O. Morozova, TFB 11888 (TENN 60769).

4. *Megacollybia platyphylla* [Figs. 1A, 2 – clade 4, Figs. 10-14]

Collections conforming to the original concept of *M. platyphylla* seem distributed throughout Europe, Scandinavia and even to southwestern Siberia (Novosibirsk Region and Altai Republic). Of all the major infrageneric clades, /platyphylla seems the most homogeneous morphologically as well as phylogenetically.

A summary of typonyms for *Agaricus platyphyllus* reveals the historical difficulties in placing the species. Also implied in the list are differing generic concepts by various authors, often stretched to accommodate this species. Placement is especially anachronistic in *Oudemansiella* and *Hydropus*, both characterized by prominent cystidia not found in *Megacollybia*. Singer's (1939, 1986) and Smith's (1960; Smith et al., 1979) concept of *Tricholomopsis* co-opted *T. platyphylla*, but Malençon and Bertault's (1975) placement most closely approximates the phylogenetic placement of *M. platyphylla* by Moncalvo et al. (2002).

Megacollybia platyphylla (Pers.: Fr.) Kotl. & Pouzar. 1972. Ceska Mykol. **26**: 220.

Basionym: *Agaricus platyphyllus* Persoon: Fries. 1821. Systema Mycologicum **1**: 117.

[≡ *Agaricus platyphyllus* Persoon. 1796. Observ. Mycol. **1**: 47; pre-validation date]

≡ *Collybia platyphylla* (Pers.: Fr.) P. Kumm. 1871. Führ. Pilzk. 117.

≡ *Tricholomopsis platyphylla* (Pers.: Fr.) Singer. 1939. Schweiz. Zeitschr. Pilzk. **17**: 13.

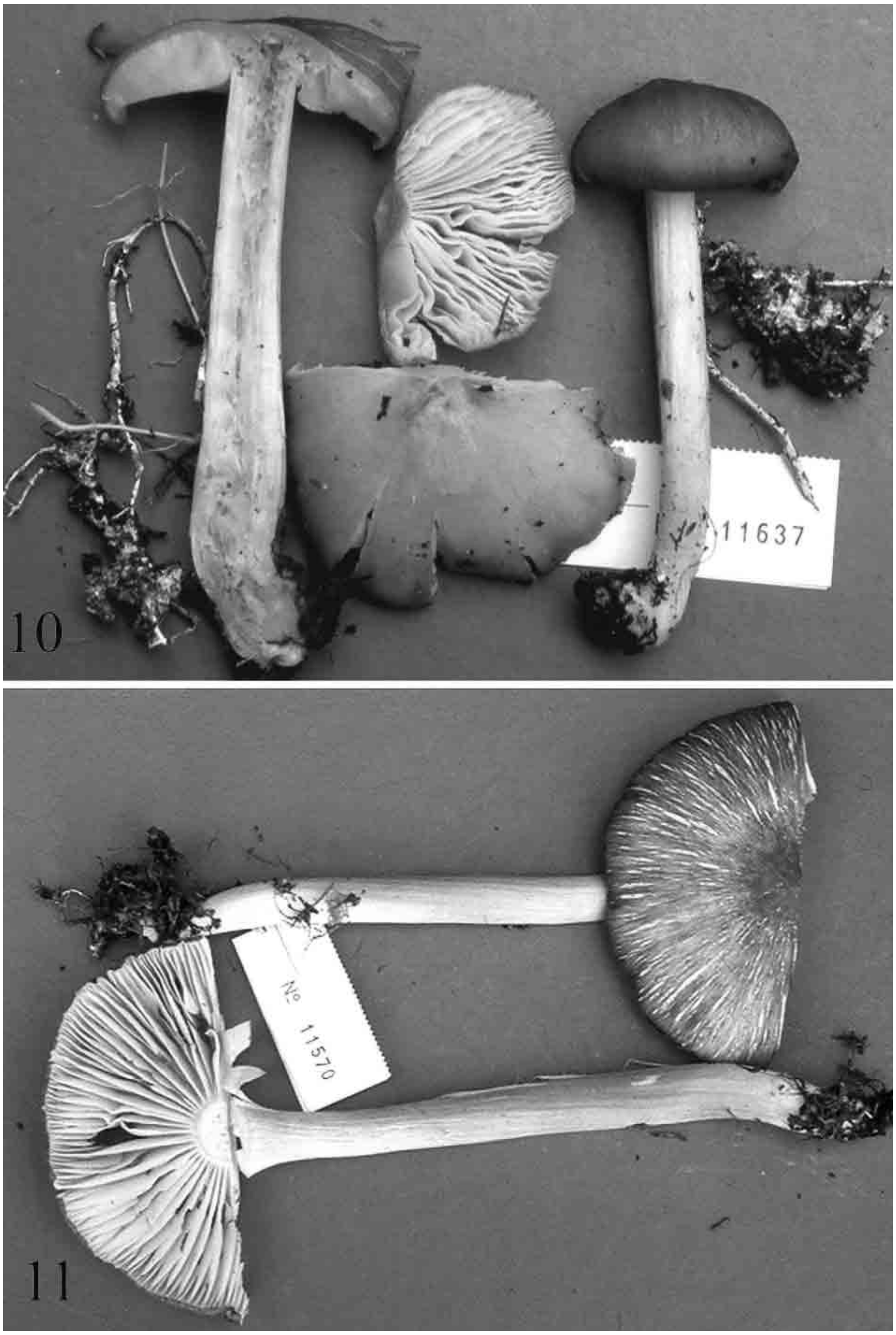
≡ *Clitocybula platyphylla* (Pers.: Fr.) Malençon & Bertault. 1975. Trav. Inst. Sci. Cherifien, ser. bot. **33**: 398 (nom. inval.); *C. platyphylla* (Pers.: Fr.) E. Ludwig. 2001. *in* Pilzkompendium. Bd. 1: 58.

≡ *Hydropus platyphyllus* (Pers.: Fr.) Kühner. 1980. Bull. mens. Soc. Linn. Lyon, num. spec. **49**: 895.

≡ *Oudemansiella platyphylla* (Pers.: Fr.) M. M. Moser. 1983. *in* Gams, Kleine Kryptogamenfl., rev. ed. 5 **IIb/2**: 156.

Exemplar: GERMANY, Mecklenberg-Vorpomme, Mecklenburg-Strelitz, Burg Stargar, N 53° 31' 7.6", E 13° 18' 56.5", 24.V.1999, coll. R. H. Petersen & K. W. Hughes, TFB 10315 (TENN 57963).

Basidiomata (Figs. 10, 11) collybioid. **Pileus** 40–85 mm broad, campanulate when young, becoming plane to slightly raised over



FIGS. 10, 11. *Megacollybia platyphylla*, basidiomata. Fig. 10. TFB 11637. Fig. 11. TFB 11570. Numerals = 4 mm.

the disc when mature, radially fibrillose to delicately radially rivulose; disc usually minutely scabrous, furfuraceous, minutely squamulose or densely radially streaked, “buffy brown” (6D4), “deep olive” (4E6), “dark olive” (4F5), “olive brown” (5E5), “hair brown” (6E3), outward radially fibrillose to radially streaked, 5B3 to 5C4 with olive tint, “deep olive buff” (3C3), “olive buff” (3B3), “tawny olive” (5C5) to “sayal brown” (6C5), occasionally significantly paler and without scabrous or furfuraceous disc (i.e. TENN 59308); flesh solid, off-white, sometimes with hints of “wood brown” (7C4) where bruised; margin not striate, thin, often eroded, becoming inrolled upon drying. **Lamellae** adnate to adnexed, thick, subdistant, ventricose (–13 mm broad), segmentiform, white when fresh, in age “tilleul buff” (7B2), “vinaceous buff” (9B2), “pale olive buff” (3B2), “pale ochraceous buff” (4A- B2), “cream color” (3A3), “pale pinkish cinnamon” (6A2), drying very brittle; lamellar edge not marginate, sometimes slightly paler than lamellar face. **Stipe** 45-80 mm long, 5-8 mm broad apically, more or less equal, terete, usually somewhat enlarged downward, lined or “muscled” (i.e. russuloid), expanded apically and expanded at base, terete, off-white to “pale olive buff” (3B2) apically, downward “deep olive buff” (3C3), “dark olive buff” (3C5), 4B2, “pale ochraceous buff” (4A2) to “light ochraceous buff” (5A4) where handled. **Odor** and **taste** not distinctive. **Rhizomorphs** white, round in cross-section, only occasionally branched, with small resupinate attachments to substrate evident.

Habitat: Europe, Scandinavia, western and central Russia; on well-rotted wood, including *Fagus*.

Pileipellis over pileus disc a superficial layer of intricately, tightly interwoven, slender (2–4 µm diam), thin-walled, conspicuously clamped, weakly to strongly pigmented hyphae producing repent to upturned terminal cells; **terminal cells** (Fig. 12A) 44–128 × 8–21 µm (at widest point), narrowly clavate, clavate to broadly clavate, occasionally sphaeropedunculate, rarely apically mucronate or apically lobed, rarely transversely septate, firm-walled, conspicuously clamped, cytoplasmically pigmented olive. **Pileipellis near margin** of mature basidiome similar to disc; terminal cells (48–) 68–151(–168) × 7–19 µm (at widest point), thickly imbricate to scattered, elongate-digitate, narrowly clavate to clavate, rarely transversely secondarily septate, firm-walled, mostly olive, but some hyaline, conspicuously clamped; contents weakly to moderately pigmented with some hyaline individuals with subtly mottled appearance (PhC). **Pileus trama** hyphae of two types: 1) inflated, long-celled hyphae 13–28 µm diam, firm- to thick-walled (wall up to 1.0 µm thick, and then irregular on

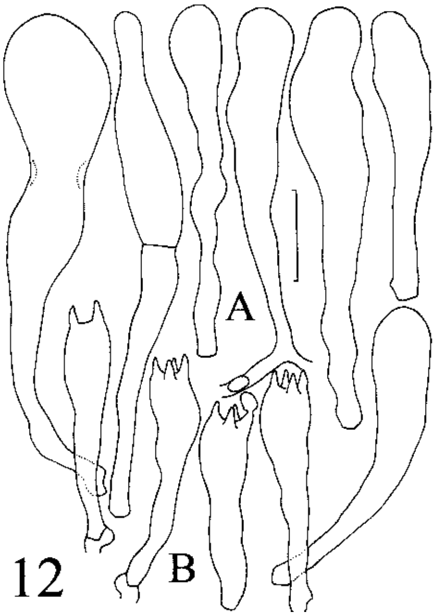


FIG. 12. *Megacollybia platyphylla*, TENN 57963. A, pileipellis terminal cells. B. basidia. Standard bar = 20 µm.

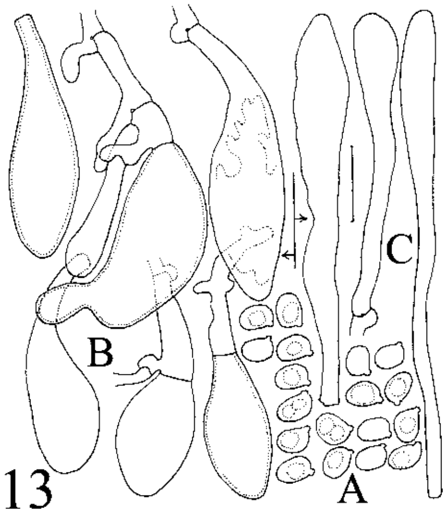


Fig. 13. *Megacollybia platyphylla,* TENN 57963. A. Basidiospores. B. Cheilocystidia. C. Caulocystidia. Standard bar = 20 µm.

inner surface), obscurely clamped, hyaline; and 2) 4–7 µm diam, frequently clamped, frequently branched, interwoven among inflated hyphae. **Lamellar trama** irregular, apparently sarcodimitic, of two hyphal types: 1) inflated up to 27 µm diam, long-celled, thin-walled, obscurely clamped, hyaline, often with inner surface of wall irregularly thickened; and 2) 3–4 µm diam, sinuate to tortuous, interweaving hyphae, conspicuously and frequently clamped, hyaline, thin-walled. Numerous subrefringent vascular hyphae apparently modified from the slender tramals, with no clamps observed. Hymenium composed of basidia and basidioles; **basidia** (Fig. 12B) (28–)32–48(–55) × (6–)8–12 µm, clavate, four-spored; contents with a few scattered, small, refringent (PhC) guttules; basidioles 32–44 × 6–8 µm, digitate to narrowly clavate, slender and often sinuate. **Basidiospores** (Fig. 13A) (6.0–)6.8–9.5(–10) × (4–)5.2–7(–9) µm [*n* = 310, *Q* = (1.00–)1.05–1.67(–1.73), Q^m = 1.26, L^m = 8.16 µm], subglobose, broadly ellipsoid to ovate, somewhat flattened adaxially, hyaline, inamyloid, acyanophilous, often in small clumps of - 6 individuals; wall thin, smooth; contents uni- or multiguttulate. **Lamellar edge** fertile, with scattered cheilocystidia often protruding beyond basidia; **cheilocystidia** (Fig. 13B) (20–)30–75(–86) × 6–22(–28) µm, pedicellate to long-pedicellate, clavate to sphaeropedunculate, rarely fusoid-ventricose or with slender, digitate apical outgrowths, conspicuously clamped, occasionally transversely septate toward base (with or without clamp connection), thin- to occasionally firm-walled; contents homogeneous, hyaline (BF); abundant gnarled, often branched cystidioles ca 3 µm diam, conspicuously clamped occasionally present. Occasional cheilocystidia produced up to 100 µm away from lamellar edge. **Stipe surface** hyphae near stipe apex superficial, slender (2.5–5 µm diam), interwoven but longitudinal, producing **caulocystidia** (Fig. 13C) (16–)32–147 × 6–12(–16) µm (at widest point), clavate to subsphaeropedunculate, slender, repent to out-turned, hyaline, firm-walled, conspicuously clamped. **Stipe trama** “sarcodimitic,” of two hyphal types: 1) up to 28 µm diam, firm- to thick-walled (wall up to 2 µm thick), obscurely clamped, long-celled; and 2) 3–5 µm diam, frequently branched, conspicuously clamped, thin-walled, hyaline, interwoven. Scattered vascular hyphae, 5–8 µm diam, thin-walled, subrefringent, aseptate, meandering (not strictly longitudinal), strongly cyanophilous. **Rhizomorphs** constructed of two types of hyphae, tightly packed, longitudinal, free (not coherent): 1) generative, 5–11 µm diam, thin-walled, hyaline, frequently septate, ?clamped, interwoven; and 2) skeletal, 1.5–3 µm diam, thick-walled (wall 1 µm thick to obscuring cell lumen), not cyanophilous, ?aseptate or arising from a clamp connection. Outer surface of rhizomorphs a tomentum of tightly interwoven, pseudoparenchymatous cells involving bits of substratum.

Commentary: Literature indicates that pleurocystidia are rare or absent, and we have observed cheilocystidia (with similar form to lamellar edge structures) formed some distance away from the lamellar edge. Boekhout (in Bas et al., 1999) reported "pleurocystidia absent;" his description and illustration of cheilocystidia match the structures we have seen. Gulden (in Hansen and Knudsen, 1992) wrote "Cheilocystidia prominent ... lageniform ... pleurocystidia few or absent." The illustration matches the structures we have seen. Rexer and Kost (1989a) did not report the presence of pleurocystidia.

It appears that fertile basidia collapse as soon as spores are discharged and so are hardly visible thereafter. Scarcity of fertile basidia may be reflected in the often rare basidiospores.

Except for the preponderance of immature hymenium, TENN 57963 can act as an exemplar for the true (European) concept of *M. platyphylla*. It comes from generally the right place, and has basidiomata of most ages plus well-developed rhizomorphs. It conforms well to the European literature. Basidiomata are usually smaller than those of eastern North America, which also have a somewhat different color scheme.

Petersen and Gordon (1994) described early attempts to culture *M. platyphylla* from single basidiospores, reporting that the European representatives cultured easily, but that the eastern North American entity, while germinating in vitro, did not progress to a mycelial state, and therefore could not be self-crossed (but see under *M. rodmani*). J. L. Mata (unpubl. data) was able to successfully show sexual intercompatibility among several Finnish collections, thus implying that not only was a tetrapolar mating system present, but that the mating genes contained multiple alleles. The collections used in those intercollection pairings included TFB 11569, which, although intercompatible with four other Finnish specimens, is somewhat different molecularly.

In a separate set of pairings, four collections from Euroscandia (TFB 4252, Sweden; TFB 1147, Austria; TFB 10813, TFB 10819, both Russia) were found to be totally or partially intercompatible.

In addition, Petersen and Gordon (1994) reported that European cultures emitted a pleasant, floral perfume, while the North American cultures were without odor, a further indication that the two taxa were distinguishable. Basidiomatal differences, while qualitative, were also noted.

Numerous additional German specimens were examined by Rexer and Kost (1989a).

Specimens examined: **AUSTRIA**. Lower Austria, Waldviertel, Forest vic. Dobrasperre, 48° 38' N, 15° 48' E, 24.IX.2001, col. R.H. Petersen & H. Vogelmayr TFB 11447 (TENN 59308); Lower Austria, Vienna, 23rd District, Mauerwald, N 48° 9.004', E 16° 15.087', 28.IX.2001, coll. E. Grand, TFB 11471 (TENN 59338). **FINLAND**, Etelä-Häme, Liesjärvi National Park, trail from Korteniemi, 6.VIII.2002, coll. S.A. Redhead, TFB 11572 (TENN 59523); same location, 6.VIII.2002, coll. E. Grand, TFB 11570 (TENN 59524 PHOTO). **GERMANY**, Mecklenburg-Vorpomme, Mecklenburg-Strelitz, Carpin, Müritz Nat. Park, N 53° 20' 35.7", E 13° 11'f 40.5", 25.V.1999, coll. K.W. Hughes, TFB 10319 (TENN 57967); same location, 25.V.1999, coll. D. Krüger, TFB 10512 (TENN 57442); Mecklenberg-Vorpomme, Mecklenburg-Strelitz, Burg Stargar, N 53° 31' 7.6", E 13° 18' 56.5", 24.V.1999, coll. R.H. Petersen & K.W. Hughes, TFB 10315 (TENN 57963; exemplar); Baden Würtenberg, Tübingen Stadt, Tübingen Hagelloch, Schönbuch Natupark, Bettelbach Valley, 48° 32' 49" N, 9° 01'59" E, 355 m, 31.V.1999, col. D. Krüger, TFB 10522 (TENN 57752). **RUSSIA**, Leningrad, Lodeynove-Pole. Dist., Kut-Lakhta, Nyzhnesvirsky Nature Reserve, road to Gumbaritsky Ornithological Station, 60˚36’ N, 33˚ 07’ E, 29.VIII.1999, col. N. Psurtseva & R.H. Petersen TFB 10819 (TENN 58227); Leningrad Region, Lodeynoye Pole Dist., Nyzhnesvirsky Nature Reserve, bank of River Pel’fchuzhnaya, N 60˚ 36.775’, E 33˚ 07.628’, 28.VIII.1999, col. N. Psurtseva, TFB 10813 (TENN 58222); Novgorod Region, Valdai Dist., Valdaisky coll. R.H. Petersen (as *M. platyphylla*), TFB 11637 (TENN 59600); Novgorod Region, Valdai District, Road to Valdaisky National Park, 57˚ 57’ N, 33˚19’E, 20.VIII.2003, col. N. Psurtseva TFB 11617 (TENN 59580 PHOTO); Novgorod Region, Valdai District, Kasnaya Gorka, 58˚ 06’ N, 33˚ 13’ E, 21.VIII.2003, col. R.H. Petersen et al. TFB 11627 (TENN 59590 PHOTO); Samara Region, vic Bakhilovo, Zhigulevsky Nature Reserve, top of Big Bakhilovo Mt., N 53˚ 26.012’, E 49˚ 41.350’, 10146 ft elev., coll. R.H. Petersen (as *M. platyphylla*), TFB 12147 (TENN 60086); Novosibirsk Region, Akademgorodok, vic. Novosibirsk State University, VIII.2006, coll. and det. A. Gorbunova, no. LE212076; Toguchinsky Dist., vic Kotorovo, 10.VIII.1973, leg & det. N.V. Perova, LE212074; same location, 6.VII.1974, leg & det. NV Perova, LE212068 ; Samara Region, Bakhilovo Co., vic. Bakhilovo, old Volga Riverbed forest, N 53˚ 23.989’, E 49˚54.958’, 86 m elev., 16.VIII.2004, coll. R.H. Petersen, TFB 12163 (TENN 60102). SWEDEN, vic Trollhättaän, village Rommele, c. 1 km S Tokebäcken, 21.IX.1991, coll. L. & A. Stridvall, TFB 4252 (TENN 50588).

Megacollybia platyphylla: infraspecific forms

Within the larger clade comprising specimens of *M. platyphylla* sensu stricto, there occur. three clusters of collections which differ somewhat morphologically and phylogenetically, although none are considered sufficiently distinguishable to warrant taxonomic rank. One group (form A) occurs across a considerable distance of southern Russia, a second group (form B) was seen from the Caucasus and Czech Republic, and the third group (form C) was gathered in Finland.

Megacollybia platyphylla form A

Basidiomata collybioid to xeruloid. **Pileus** (mature) 45–95 mm broad, plane to shallowly convex with somewhat depressed disc; disc uniformly pigmented, delicately squamulose or minutely furfuraceous, almost olive-black; limb distinctly to hardly radially streaked (but streaks may be partially detersile), almost olive-black against off-white background, becoming obscure so that margin is uniformly olive-brown; margin extended when fresh, tightly inrolled upon drying, obscurely or not striate, thin, eroded. **Lamellae** adnexed to adnate to shortly decurrent (or significant tooth), ventricose or not appearing so, –12 mm broad, thin, subdistant, white to off-white when fresh, uniformly dull ochraceous buff upon drying, with delicate transverse streaking remaining off-white; lamellar edge not marginate or *very delicately marginate to dark purple*, delicately eroded. **Stipe** 70–90 mm long, perhaps 5–8 mm broad apically, 4–6 mm broad in midsection, gradually expanded downward to 9–10(–17) mm broad at base, off-white when fresh, uniformly dull tan on drying, perhaps slightly discolored with handling, significantly lined or ridged; context stuffed, white. **Rhizomorphic strands** not included. **Odor** and **taste** not recorded.

Pileipellis terminal cells (disc) densely scattered or in small fascicles, 33–96(– more than 210) × (8–)14–37 µm, vermiform, narrowly to broadly clavate, firm- to thick-walled (wall never more than 1.5 µm thick, and then irregular over inner surface), smooth, conspicuously clamped, commonly transversely septate; contents homogeneous, strongly cytoplasmically pigmented but with common hyaline individuals. **Basidia** 30–40(–53) × 8–12 µm, clavate, clamped, thin-walled, 4-spored, conspicuously clamped; contents with only a very few scattered, small, refringent guttules. Basidioles often with gnarled apical outgrowths, but usually digitate. Basidiospores 6.5–10 × 5–7 µm [n = 39; Q = 1.08–1.64; Q^m = 1.31; L^m = 8.0 µm], ellipsoid to ovate, flattened adaxially, thin-walled, hyaline; contents aguttulate to 1–3-guttulate. Cheilocystidia arising from basidial cymes, not protruding beyond basidia or protruding up to 15 µm singly or in 2–3s, 32–94 × 13–24 µm, narrowly to broadly clavate, rarely to commonly transversely septate, firm-walled, conspicuously clamped; contents homogeneous, hyaline. Stipe outer trama coherent, strictly parallel, longitudinal, composed of two hyphal types: 1) up to 14 µm diam, thick-walled (wall up to 1.0 µm thick), hyaline, speckled (as though ornamented); and 2) 3–4 µm diam, hardly branched, very rarely septate, obscurely clamped. Stipe surface an arachnoid to relatively thick network of slender (2.5–4 µm diam) hyphae, producing relatively few to plentiful differentiated terminal cells. Terminal cells (caulocystidia) 24–74(– more than 180) × 4–15(–30) µm, digitate to clavate, firm- to thick-walled (wall up to 0.7 µm thick), conspicuously clamped, thin- to firm-walled.

Commentary: Three of four basidiomata have delicately marginate gills, but not to dark brown or black (as expected with pigmented cheilocystidia and seen in *M. marginata*), but to dark purple (25×, even after drying). Cheilocystidia are hyaline, however, which might indicate that the marginate lamellar edge is caused by weather conditions or perhaps by handling, but not by natural marginate condition.

All four collections exhibit large, strongly pigmented pileipellis terminal cells. Unlike most collections of *M. platyphylla*, these cells are commonly transversely septate, but whether this feature has taxonomic value is unknown.

Caulocystidia are sometimes poorly developed and often seem to be in small fascicles. The superficial “arachnoid network” on stipe surface is rather variable in thickness, which might indicate that it is under some edaphic control.

The delicate purple margin in LE 212073 on the only fragment of exposed lamella seems to link this collection to LE 212075, also from Altai Republic. DNA from LE 212075 matches that of two other Russian collections from Rostov Region (between and north of Black Sea and Caspian Sea, near the border with Ukraine). Thus the four collections seem to span considerable distance in the Russian south, clustered around the N 50th parallel. If true, then similar forms should be found in Kazakhstan and perhaps the Ukraine.

Specimens examined: **RUSSIA**, Altai Republic, southern shore of Teletskoye Lake, embouchure of river Chulyshman, 13.VIII.1996, leg & det. I.A. Gorbunova, LE 212075; Altai Republic, Shebalinsky Dist., vic village UstÅf-Sema (~N 50˚ 8’ E 85˚ 8’) 10.VIII.1997, leg & det. I.A. Gorbunova, LE 212073; Rostov Region, vic. Veshenskaya, village Kalininsky, gully Semenovskaya, N 49˚ 31’ 36.1”, E 41˚ 50’ 28.0”, 9.X.2006, leg & det. N.V. Psurtseva, NVP 47-06 (LE 212070); same data, NVP 49-06 (LE 212071).

Megacollybia platyphylla form B

Basidiomata collybioid. **Pileus** –100 mm broad, convex, innately radially fibrillose; disc “fuscous” (6E4; pallid sordid gray with very weak yellowish tint in TENN 58493), drying glabrous-shining (not scabrous or furfuraceous); limb weakly to strongly radially streaked, “buffy brown” (6D4), drying glabrous-shining; margin thin, lacerate, not striate, becoming tightly inrolled on drying (not so in TENN 58493). **Lamellae** thin, somewhat ventricose, adnexed to adnate-decurrent by a tooth, "marguerite yellow" (30A2), to white (in TENN 58493 taking on a ruddy orange tint on drying), easily heavily eroded, upon drying with very delicate transverse streaking of paler color, close (not at all subdistant), perhaps –8 mm broad; lamellar edge not marginate. **Stipe** –85 mm long, slender, lined, white with "buffy brown" (6D4) vesture, expanded somewhat at base. **Odor** and **taste** none.

Habitat: Caucasus area of Russia, in *Betula-Populus-Abies* forest; Czech Republic, on rotten hardwood, including *Fagus*.

Pileipellis terminal cells 26– more than 183 × 7–31 µm, digitate to clavate to broadly clavate, often with mammiform tip on larger individuals, strongly pigmented (almost hyaline in TENN 58493) but with common hyaline, thick-walled individuals (wall up to 1.0 µm thick, and then usually irregular on inner surface), firm-walled, conspicuously clamped, commonly transversely septate. **Basidia** 37–50 × 9–11 µm, clavate to pedicellate-clavate, thin-walled, clamped, 4-spored; contents with scattered refringent guttules. **Basidiospores** 7.5–10 × 5.5–7.5 µm [n = 34, Q = 1.14–1.64; Q^m = 1.34; L^m = 8.9 µm], ellipsoid to subovate, flattened somewhat adaxially, thin-walled, inamyloid, hyaline; contents uni- several-guttulate. **Cheilocystidia** protruding beyond basidia only in 1–2s, but then sometimes significantly, 26–57 × 9–22 µm, sessile to clavate or broadly clavate to nearly sphaeropedunculate, firm-walled, conspicuously clamped; contents homogeneous, hyaline.

Commentary: Within *M. platyphylla*, a small clade segregates, comprising two sequenced specimens, one from the Caucasus (LE202274), the other from Czech Republic (TFB7206). One additional specimen from the Caucasus can be added based on morphology, but this small group seems somewhat internally incongruent, and hardly separable morphologically from typical *M. platyphylla*. When single-basidiospore isolates of TFB 7206 were paired with Finnish isolates, total interINcompatibility was found (J. L. Mata, unpubl. data). As noted under *M. marginata*, these collections have ITS sequences that are close to but not the same as *M. marginata*. Thus, these collections may represent one or more transitional forms or introgressive hybridization (see also commentary under *M. marginata*).

Pileipellis terminal cells may be unusually long (often with no visible basal septum/clamp), strongly pigmented in the Russian specimens, but significantly paler in the Czech basidiome. Pileipellis terminal cells may be unusual in the high number of transversely septate individuals.

Specimens examined: **CZECH REPUBLIC**, vic. Prague, vic. Jevany and Cerné Voderady, 30 km ESE of Prague, 8.VII.1994, coll. R.H. Petersen, TFB 7206 (TENN 58493). **RUSSIA**, Republic of Karachaevo — Cherkessia, Northern Caucasus Mts., Teberda State Biosphere Reserve, Malaya Khatipara, N ~43° 40', E ~41° 40', 2.VII.1998, coll. & det. R. Botashev (as *M. platyphylla*) , no. LE 202274; Krasnodar Region, Caucasus Nature Biosphere Reserve, N 43° 50.546', E 39° 45.852', 12.IX.1996, coll. RHP (as *M. platyphylla*), TFB 8906, (TENN 55526).

Megacollybia platyphylla form C [Fig. 14]

Basidiomata (Fig. 14) collybioid. **Pileus** 50–65 mm broad, nearly hemispherical when immature, expanding to shallowly convex with shallow umbo and uplifted margin, radially fibrillose with scurfy center; disc "fuscous black" (6F4), "deep olive" (4E6) to "dark olive" (4F5), minutely broken-furfuraceous, outward "chaetura drab" (2F2) fading to "hair brown" (6E3) "citrine drab" (4D5) alternating with

FIG. 14. *Megacollybia platyphylla* form C, basidiomata. TFB 11569. Numerals = 4 mm.

"deep olive buff" (3C3) when expanded, here and there split to reveal "olive buff" (3B3) pileus trama; margin fluted, concolorous with disc, downturned to inrolled in dried condition. **Lamellae** adnate, up to 10 mm deep, ventricose, subdistant, in 3 ranks, subsinuate, "tilleul buff" (7B2) when young, mellowing toward "vinaceous buff" (9B2) toward maturity (never white); margin eroded. **Stipe** 53–65 × 3–4 mm, more or less equal, straight but curved at base, lined, hardly twisted, near "deep olive buff" (3C3), slightly expanded apically and there white; base white, with white, tight tomentum; context narrowly hollow to moderately stuffed. **Odor** and **taste** none. **Rhizomorphs** white, less than 1 mm diam, webbed, resupinate where attached to wood, flattened throughout, branched, somewhat mealy.

Habitat: Southern Finland, on very rotten hardwood.

Pileipellis terminal cells (disc) not in scabers but densely scattered over surface, 36–160 × 11–32 µm, conspicuously clamped, clavate to broadly clavate, often with an apical outgrowth or mamma, often somewhat thick-walled, and often transversely septate near base; contents densely pigmented (olive-brown); common hyaline individuals scattered among others, with thick walls (wall up to 1 µm thick, but very irregular in inner wall surface); contents (in just the right plane of view) appearing mottled or very subtly banded (PhC). Subpellis a thin, tightly interwoven tissue of slender (1.5–3 µm diam), hyaline, conspicuously clamped hyphae. Pileus flesh "sarcodimitic." **Basidia** 36–57 × 8–12 µm, narrowly clavate to clavate, (2–3-)4-spored, clamped; contents with a few scattered, small guttules; basidioles 26–34 × 4–9 µm, clavate, rarely cylindrical or lobed. **Basidiospores** 6.8–7.6(–10) × 5.5–6.4(–8) µm [n = 20, Q = 1.06–1.55, Q^m = 1.27, L^m = 7.8 µm], broadly ellipsoid to subglobose, somewhat flattened adaxially, hyaline, inamyloid, thin-walled, smooth; contents uni- to few-guttulate. **Cheilocystidia** sparse, locally common, occasionally protruding beyond basidia, 29–65(–88) × 6–20 µm, clavate, broadly clavate to pedicellate-bulbous, rarely apically diverticulate or knobbed, thin-walled, conspicuously clamped, hyaline (occasional individuals appear empty); contents homogeneous, hyaline. Stipe surface of strictly parallel, slender (3–7 µm diam), long-celled hyphae, occasionally producing clavate side branches or terminal cells (**caulocystidia**); caulocystidia narrowly clavate to clavate, 6–13 µm diam, smooth, hyaline, repent to rarely recurved. Stipe flesh of two hyphal types, both hyaline; 1) 18–more than 40 µm diam, thick-walled (wall never more than 1 µm thick, irregular in outline, arising from slender hyphae, constricted at septa, conspicuously clamped; and 2) 3–8 µm diam, thin-walled (diaphanous and often semi-collapsed), frequently branched, frequently clamped, interwoven with inflated hyphae. Slender hyphae occasionally ending blindly, elongate-clavate (“endocystidia”), 80– more than 170 × 9–24 µm, thin-walled, arising from a clamp connection, hyaline. **Rhizomorph** cortex composed of hyaline, thin-walled hyphae 2–11 µm diam, with little differentiation into diameter classes, conspicuously clamped, more frequently on slender hyphae than on wider (not strictly sarcodimitic); rhizomorph medulla of “skeletal hyphae,” 1.5–3 µm diam, apparently aseptate, thick-walled (wall up to 0.5 µm thick or occluding cell lumen), hyaline, non-cyanophilous, flexuous.

Commentary: Somewhat darker pileus colors, caused by darker and more congested pileipellis terminal cells seem to distinguish these two Finnish collections from typical European forms. Likewise, the mixture of hyaline pileipellis terminal cells as well as heavily pigmented, mottled, occasional transversely septate individuals also seems unique. Whether rhizomorph appearance and structure is distinguishable from that of the typical European taxon is questionable until more specimens are examined. The European entity seems to produce rhizomorphs that are round in cross-section, often more than a millimeter diam, while these Finnish collections exhibit more slender, flattened rhizomorphs. One of the specimens (TENN 59541) was successfully sequenced, and the ITS sequence also is somewhat unique.

Specimens examined: **FINLAND**, Etelä-Hame, Tammelo, Torronsuo Nat. Park, map grid 6740: 314, 8.VIII.2002, coll. RHP, TFB 11577 (TENN 59530); Etelä-Häme, Liesjärvi National Park, trail from Korteniemi, N 61° 00’, E 24° 30’, 6.VIII.2002, coll. E Grand, TFB 11569 (TENN 59541).

5. *Megacollybia fallax* [Figs. 1B, 2 – clade 5, Figs. 15-18]

A small but discrete clade appears basal to other North American collections and includes the type specimen of *Tricholomopsis fallax* A.H. Smith. Sequences were obtained from specimens from Arizona, Idaho and Washington, indicating an extended range for a species reported by Smith as “known only from central Idaho.” Singer (1986) accepted taxa surrounding *M. platyphylla* as *Tricholomopsis* Singer (1939. Schweiz. Zeitschr. Pilzk. **17**: 13) sect. *Platyphyllae* Singer (1943. Ann. Mycol. **41**: 68.). Smith (1960. Brittonia **12**: 45) emended the diagnosis of the section, but all these proposals preceded Kotlaba and Pouzar’s (1972) proposal of *Megacollybia*.

Mata (unpubl. data) found low-percentage intercompatibility between TFB 11560 and

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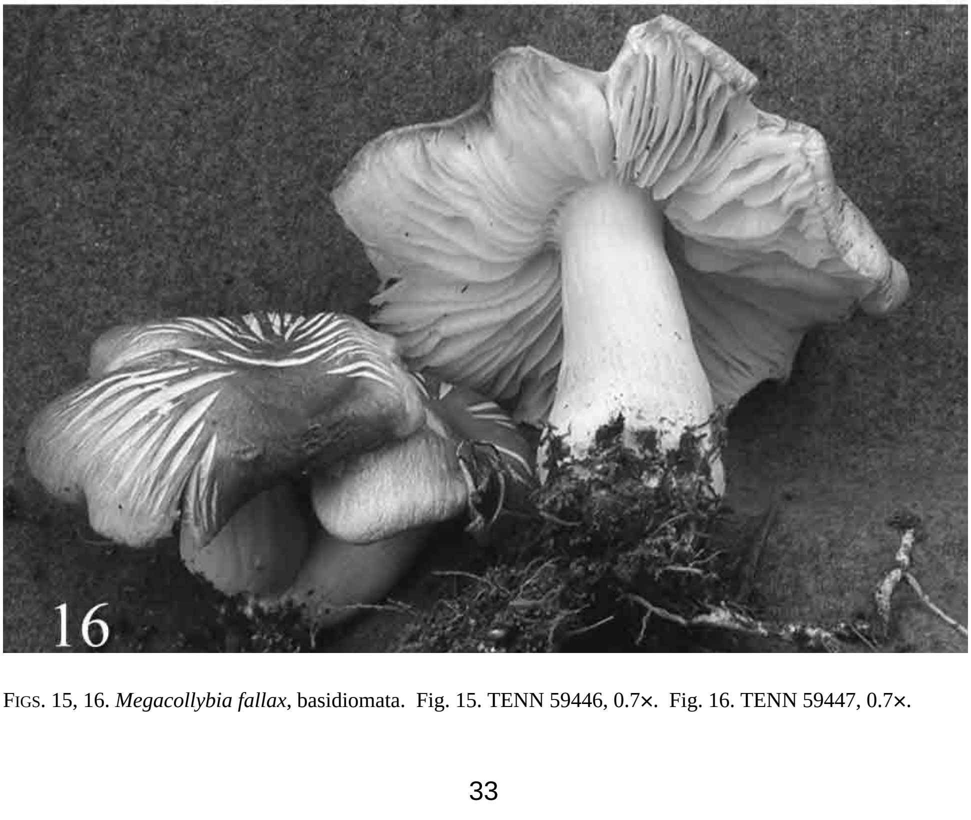

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FIGS. 15, 16. *Megacollybia fallax*, basidiomata. Fig. 15. TENN 59446, 0.7×. Fig. 16. TENN 59447, 0.7×.

TFB 11561. These collections, however, when paired with European isolates, were totally interincompatible. The western United States organism, therefore, seems sexually isolated from the European *M. platyphylla*.

Altogether, *T. fallax* surely belongs with other taxa in *Megacollybia*, as confirmed by phylogenetic placement of DNA sequences. A nomenclatural transfer is necessary, as follows:

Megacollybia fallax (A.H. Sm.) R.H. Petersen & J.L. Mata, comb. nov.

Basionym: *Tricholomopsis fallax* A.H. Smith. 1960. Brittonia **12**: 48.

Holotype: UNITED STATES. Idaho, Valley Co., near McCall, Lake Fork Creek, Payette National Forest, 44° 52.48" N, 116° 2.75" W, 28.VII.1954, on conifer log, col. AH Smith, no. 45432 (MICH).

Basidiomata tricholomoid (Figs. 15, 16). **Pileus** 40–70(–120) mm broad, 30–50 cm high, obtuse when young, the margin incurved, remaining unexpanded or becoming broadly convex to nearly plane, dry, dark gray-brown on disc, outward streaked with gray to sordid deep gray-olive fibrils, soon radially rimose with wide lenticular lacunae exposing context; margin lobed, soon lacerate in age, thin, whitish; context white, thin but fairly tough, unchanging on bruising. **Lamellae** adnate, close, ventricose (up to 20 mm broad), off-white when young, becoming pale yellow before maturation, finally creamy ochraceous, not marginate, transversely veined, occasionally intervenose; edges even to slightly eroded, not changing color when bruised. **Stipe** 40–110 mm long, 10–17(–30) mm thick, equal or tapering slightly downward, solid, yellowish in the cortex, the pith paler; surface white to whitish yellow but paler than the gills, naked except for fibrillose striations; rhizomorphs sparse, thick (up to 4 mm diam), white, round in cross-section. **Odor** and **taste** not distinctive.

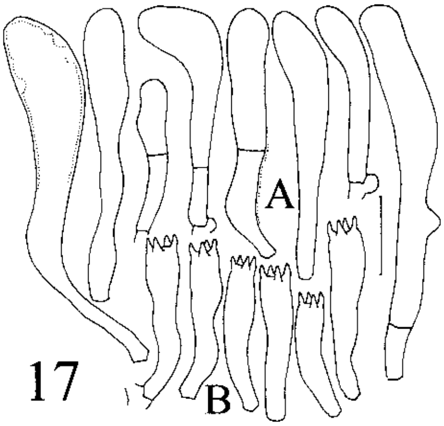


FIG. 17. *Megacollybia fallax*, TENN 59447. A. Pileipellis terminal cells. B. Basidia. Standard bar = 20 µm.

Habitat: Western North America (Arizona, Pacific Northwest); solitary to gregarious on rotten conifer logs or lignous soil.

Pileus cuticle not differentiated as such but the surface with numerous **pileipellis terminal cells** (Fig. 17A) 28–99 × 8–20 µm, narrowly clavate to clavate, firm- to thick-walled (wall never more than 1 µm thick and then irregular over inner surface), moderately cytoplasmically pigmented, occasionally transversely septate (with no clamp), conspicuously clamped, rarely with some minute residual debris or slimy sheath. Outer pileus flesh constructed of two hyaline, clamped hyphal types: 1) inflated up to 25 µm diam, thick-walled (wall up to 1.0 µm thick, irregular on inner surface), constricted at septa, obscurely clamped; and 2) slender (3–4.5 µm diam), thin-walled, frequently branched, frequently clamped, interwoven amongst inflated hyphae. **Basidia** (Fig. 17B) (30–)36–47(–52) × (6–)8–11 µm, clavate, thin-walled, (2-)4-spored; basidioles 28–48 × 4–10 µm, clavate; contents with a few, small, refringent guttules. **Basidiospores** (Fig. 18A) (5.6–)6–8.5(–10) × (4.0–)5–7(–8.0) µm [n = 83; Q = (1.00–)1.12–1.57; Q^m = 1.36; L^m = 7.6 µm], subglobose, ellipsoid to

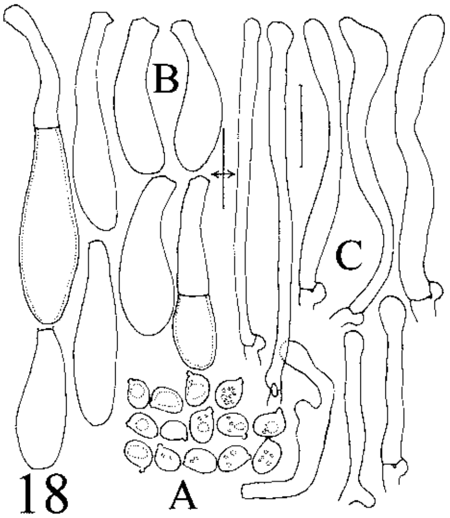


FIG. 18. *Megacollybia fallax*, TENN 59447. A. Basidiospores. B. Cheilocystidia. C. Caulocystidia. Standard bar = 20 µm.

narrowly ovate, flattened adaxially, thin-walled, inamyloid; contents aguttulate or 1-few guttulate. Central strand of lamellar trama subparallel-interwoven; hyphae 4–12 µm diam, thin- to firm-walled, flanked on either side by a narrow strip of parallel hyphae 1.5–3 µm diam. **Cheilocystidia** (Fig. 18B) occasionally protruding beyond basidia (but not generally), 25–55(–80) × (6–)9–16 µm, clavate to broadly clavate, occasionally with small apical outgrowths, firm-walled, occasionally secondarily transversely septate, conspicuously clamped, hyaline; contents homogeneous. Upper stipe delicately silky, white; surface a layer (–50 µm thick) of slender (3–4.5 µm diam), thin-walled, frequently clamped, commonly branched, hyaline hyphae, producing rounded terminal cells (**caulocystidia**) (Fig. 18C) 26–88 × 3–8 µm diam (at widest point), clavate, conspicuously clamped, hardly inflated, elongate-digitate to hardly clavate.

Commentary: Diagnostic characters (Smith, 1960) are difficult to ascertain. Smith (1960. Brittonia **12**: 48–49) wrote: "The yellow pigment in the pilocystidia, the lack of diversity in the shape of the cheilocystidia, and the yellow pigment in the gills and cortex of the stipe distinguish this species from *T. platyphylla*. The habitat on wood of conifers is also an important field character ..." Under *T. platyphylla*, Smith cited specimens from eastern North America as well as specimens from California, Montana, New Mexico, Oregon and Washington. To our knowledge, *T. fallax* is found from Arizona north to British Columbia, and *M. rodmani* (*T. platyphylla* of Smith, 1960, pro parte) only in the eastern parts of North America.

Cheilocystidia of *T. fallax* are just as variable as those of other taxa, although perhaps more commonly transversely septate, so Smith's report of "lack of diversity in the shape of the cheilocystidia" is not a distinguishing character, but merely contributes to placement of *T. fallax* within the same complex as taxa regarded here as *Megacollybia*.

Some quantitative characters can be applied to these western North American collections to help distinguish them. 1) Basidia of *T. fallax* are generally somewhat longer (35–43 × 7–10 µm) than those of other taxa (for *M. rodmani*: 25–38 × 7–10 µm), attributable to a cylindrical stalk-like base. 2) Pileus color in *T. fallax* (Smith, 1960: "more or less streaked with gray fibrils as in *T. platyphylla*") (notes with Parker specimens: "grayish brown," "medium grayish brown") somewhat paler than in *M. rodmani* and with radial streaks more widely separated, revealing white underlying pileipellis. 3) In *T. fallax,* caulocystidia from near stipe apex are hardly inflated (3–8 µm diam at widest point) while they are inflated and subbulbous (5–18 µm diam) in *M. rodmani*. 4) In our experience, *T. fallax* is limited to western North America, while *M. rodmani* seems distributed in eastern North America. 5) Reflecting its distribution, *T. fallax* is reported only from rotting conifer wood and debris, while *M. rodmani* prefers hardwood (in spite of Smith's report to the contrary).

Mata (unpubl. data) found low-percentage intercompatibility between TFB 11560 and TFB 11561. These collections, however, when paired with European isolates, were totally interINcompatible. The western United States organism, therefore, is sexually isolated from the European *M. platyphylla*.

Specimens examined: **UNITED STATES**; **Arizona**, Pima Co., Mt. Bigelow, Santa Catalina Mots., Coronado National Forest, 25.VII.1972, col. K. Muetin (as *Collybia platyphylla*), KM 214 (011591; AN); Pima Co., Mt. Lemon, 8.V.1959, col. Leathers & Keener (as *Megacollybia platyphylla*), PH 3503 (011589, AN). **Idaho** (all as *Tricholomopsis fallax*), Valley Co., Lake Fork creek, Payette lakes, on conifer log, 14.VII.1954, col. A.H. Smith, 44965 (MICH; paratype); same location, 18.VII.1954, col. AH Smith, 45133 (MICH; paratype); same location, 1954, col. A.H. Smith, 45389 (MICH; paratype); same location, 29.VI.1958, col. C.S. Lowthry & A.H. Smith, no. 58401 (MICH; paratype); same location, 15.VII.1958, col. T Westerdale no. 58870 (MICH; paratype); same location, 14.VII.1954, col. H.E. Bigelow, 44955 (MICH; paratype); same location, 16.VII.1954, col. A.H. Smith, 45002 (MICH; paratype). **Washington**, Pond Oreille Co., vic Metalline Falls, 2 mi S of Slate Creek, W of highway 31, 48° 54.226' N, 117° 19.934' W, 2500' elev, 30.V.2002, coll. D. Parker, TFB 11560 (TENN 59446); Pond Oreille Co., Lake Lucerne, highway 31, 2 mi from Canadian border, 28.VI.2002, coll. D. Parker, TFB 11561 (TENN 59447).

6. *Megacollybia texensis* [Figs. 1B, 2 – clade 6, Figs. 19-21]

A small clade of specimens, all from eastern Texas, may be found as sister to some specimens from Guyana and Colombia and is genetically distinct from *M. rodmani*. Collections were contaminated with a species of *Candida* related to a GenBank sequence deposited as *C. fungicola*. From cloned ITS sequences, the Texas collections are heterozygous for different but related haplotypes. Haplotypes of TENN 62058 (DPL7405) differed by only a few base pairs, but the two haplotypes from TENN 59935 (TFB 11676) are found in two different minor clades, one of which also includes one of the haplotypes from TENN 62059 (DPL7682). TENN 62059 produced four haplotypes, distributed over the entire /texensis clade. The maximum within-clade divergence for this clade is 0.85% considering all base pairs or 0.71% considering indels as a single event. Parental strains, therefore, remain unclear, but for its hybrid state, morphological characters of all these specimens are remarkably similar.

We conclude that the Texas material represents a separate and new species, as follows:

Megacollybia texensis R.H. Petersen & David P. Lewis, sp. nov.

Pileus 40–85 latus, planus ad parum depressus, pallide griseo-brunneus, fibrillosus ad subrimosus, radio-fibrillosus, siccus. Lamellae adnatae ad subdecurrentae, ventricosae, lactea ad eburneae, non-marginatae. Stipes 50–145 × 3–8 mm, equalus ad sursum decrescens, brunneus ad olivaceobrunneus. Pileocystidia 29–125 × 7–15 µm, clavata, olivacea, tenui- ad crassitunicatae, fibulata, levis. Sporae 6.5–10 × 5–7.5 µm (Q = 1.07-1.60; Q^m = 1.28; L^m = 7.9 µm), ellipsoideae ad ovatae, levae, tenuitunicatae, hyalinae. Basidia 26–36 × 7–10(–12) µm, clavata, tenuitunicata, fibulata, tetraspora. Pleurocystidia nulla. Cheilocystidia 25-67 × (11–)19–22 µm, lato-clavata, fibulata, tenui- ad crassitunicata. Caulocystidia (24–)47–150 ×

FIG. 19. *Megacollybia texensis*, basidiomata. DPL 7863. 0.7×.

7–20 µm, pedicellata ad elongate clavata, hyalina, tenui- ad crassitunicata, fibulata. America septentrionalis; austro-centralis.

Holotype: UNITED STATES, Texas, Hardin Co., Lance Rosier Unit, Big Thicket National Preserve, Teel Rd., N 30° 16. 629’, W 94° 31. 532’ 11.XI.2006, coll. D.P. Lewis, DPL 7682 (TENN 62059).

Basidiomata (Fig. 19) collybioid to xeruloid, gracile. **Pileus** 40–85 mm broad, plane to slightly depressed, and then occasionally with small, shallow umbo, medium gray-brown to pallid gray-tan, closely to sparsely, delicately radially streaked (sometimes almost invisibly so), smooth, not drying glabrous; margin inturned to plane or delicately uplifted at maturity, often ragged to lacerate, thin, not striate; flesh thin throughout, drying fragile and parchment-like. **Lamellae** adnate with small to considerable decurrent tooth, ventricose, up to 12 mm deep, subdistant, in 3–4 ranks, thin to somewhat thick, white to off-white when fresh, drying to light ochraceous buff, not marginate, often locally transversely striped as though hygrophanous; interlamellar areas smooth, often without hymenium; lamellar edge often deeply eroded. **Stipe** 50–145 mm long to substratum, 3–8 mm broad apically, terete, equal to gradually expanded downward to 4–9 mm broad, delicately lined, perhaps minutely silky, hardly twisted, neutral pale drab downward where handled (nearly concolorous with pileus), often abruptly expanded at base into a irregular knot or sometimes extended as a stout pseudorhiza; **rhizomorphic strand** presence or abundance unknown.

Habitat: Eastern Texas; on soil in hardwood or mixed hardwood-pine forests.

Pileipellis an arachnoid network (too thin to be a layer) of slender (3–5 µm diam), radially

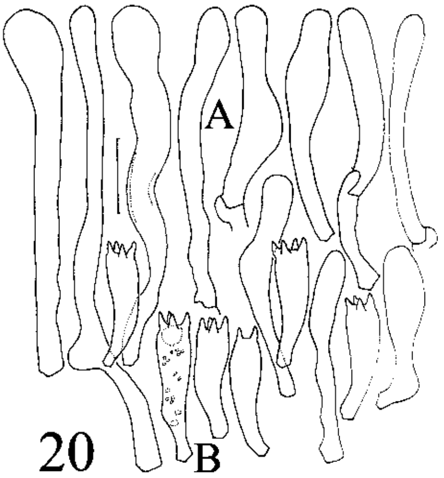


FIG. 20. *Megacollybia texensis*. TENN 62059. A. Pileipellis terminal cells. B. Basidia. Standard bar = 20 μm.

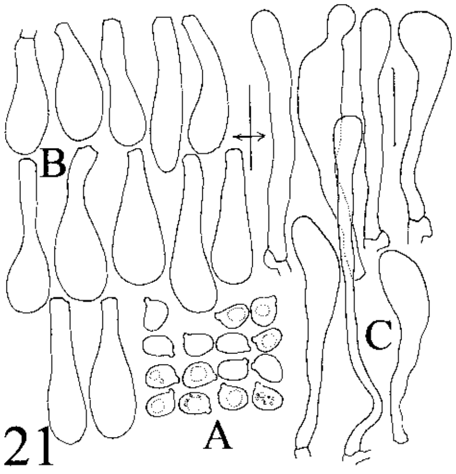


FIG. 21. *Megacollybia texensis*. TENN 62059. A. Basidiospores. B. Cheilocystidia. C. Caulocystidia. Standard bar = 20 μm.

oriented, firm-walled, hyaline, frequently conspicuously clamped, occasionally branched hyphae producing sparse terminal cells over disc; **terminal cells** (Fig. 20A) 29–125 × 7–15 μm, elongate-clavate, narrowly clavate to clavate, firm- to thick-walled (wall never more than 0.7 μm thick), conspicuously clamped, weakly pigmented when part of a pigmented radial streak, to subhyaline when between radial streaks. **Pileus outer context** constructed of two hyaline hyphal types: 1) inflated up to 35 μm diam, firm- to thick-walled (wall never more than 0.7 μm thick, irregularly thickened on inner surface), constricted somewhat at septa, occasionally adventitiously branched; and 2) slender (2.5–4.5 μm diam), frequently branched, frequently clamped hyphae similar to those of the superficial hyphae of the pileus surface, interwoven among inflated hyphae. **Pleurocystidia** absent or as cheilocystidia produced a short distance from lamellar edge. **Basidia** (Fig. 20B) 26–36 × 7–10(–2) μm, clavate, thin-walled, clamped, 4-spored, hyaline; contents with several refringent guttules scattered throughout, but often with a large apical guttule just before maturity. **Basidiospores** (Fig. 21A) 6.5–10 × 5–7.5 μm [n = 128; Q = 1.07-1.60; Q^m = 1.28; L^m = 7.9 μm], ellipsoid to ovate, flattened adaxially, thin-walled, hyaline, inamyloid; contents 1-several-guttulate. Lamellar edge sterile, usually extending in KOH up to 25 μmm beyond hymenium. **Cheilocystidia** (Fig. 21B) 25–67 × (11–)19–22 μm, broadly clavate, pedicellate to nearly sessile, firm- to thick-walled (wall never more than 0.5 μm thick, irregular over inner surface), hyaline, conspicuously clamped, rarely transversely septate in lower pedicel; contents homogeneous. Upper stipe with closely lined ridges sometimes covered with basidia and cheilocystidia. Downward, **stipe surface** with intricate layer (arachnoid to 20–25 μm thick) of slender (3–4.5 μm diam), thin-walled, frequently clamped, rarely branched hyphae, producing copious out-turned caulocystidia; **caulocystidia** (Fig. 21C) (24–)47– more than 150 × 7–20 μm, elongate-clavate, clavate to various contortions of clavate, firm- to thick-walled (wall never more than 1 µm thick, often irregular on inner surface when thickened), hyaline, conspicuously clamped; contents homogeneous, appearing “empty” in bulb but more densely cytoplasmic (dark under PhC) in pedicel. **Outer stipe flesh** constructed of somewhat inflated (up to 13 µm diam), thick-walled (wall up to 1.5 µm thick), coherent (shearing off as plates, not as liberated hyphae), long-celled, rarely clamped, hyaline hyphae strictly parallel and longitudinal.

Commentary: Diagnostic microscopic characters are difficult to ascertain unless compared to those of other taxa. Based on herbarium specimens with minimal accompanying notes, the following separating characters can be offered: 1) basidiome stature gracile, collybioid or xeruloid; 2) stipe base often (?always) abruptly expanded; 3) pileus pallid grey-tan with very delicate radial streaks (20×); 4) small basidia as compared to those of other taxa; 5) outer stipe flesh of coherent, hardly inflated hyphae; 6) upper stipe with superficial layer of tangled, slender hyphae; and 7) caulocystidia plentiful and variable.

Basidial stature is closer to that found in the rest of the genus, not that of *M. rodmani* f. *murina*, i.e. large pileus, thin flesh, thin, eroded pileus margin, ventricose lamellae and somewhat slender stipe that is longer than pileus diameter.

Lamellar edge in some specimens is unique in extending in KOH some 20–25 µm beyond hymenium (but not gelatinous as seen in *Xerula*). Cheilocystidia, therefore, are not generally mixed with basidia, but are produced by a separate hyphal system. Conversely, cheilocystidia show less variation than in other taxa of *Megacollybia*.

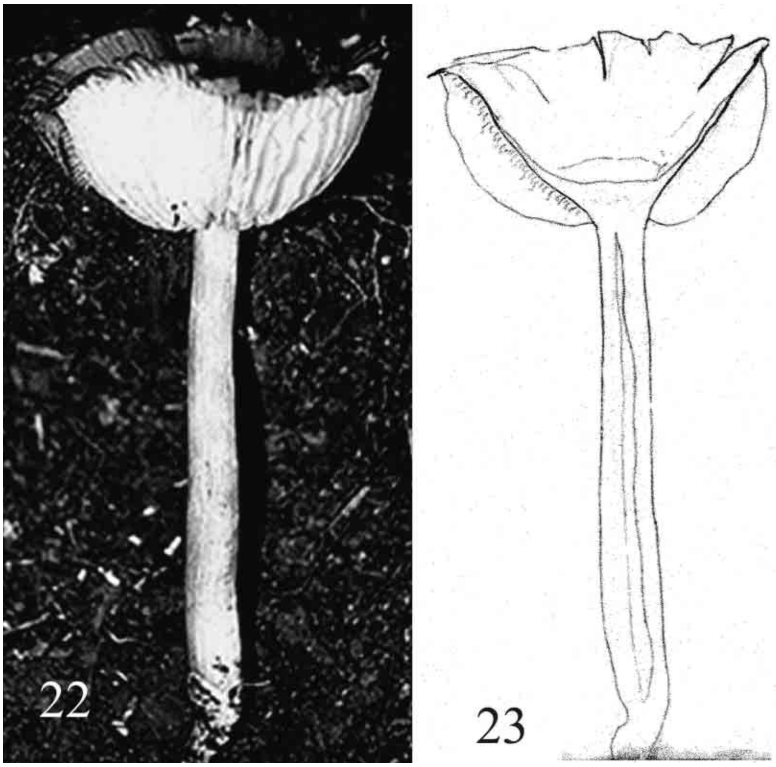
The superficial layer of intricate hyphae producing caulocystidia is somewhat more luxuriant than typical of the genus, and caulocystidia are especially abundant. Variation amongst caulocystidia is great, both in length, apical shape and wall thickness.

The similarity among pileipellis terminal cells, cheilocystidia and caulocystidia is striking throughout the genus. Shape and origin does not differ, but extent of pigmentation (especially of pileipellis terminal cells in *M. clitocyboidea* and *M. rodmani* f. *murina*), abundance (pileipellis terminal cells in scabers or patches in Asiatic species; caulocystidia in *M. texensis*), and prominence of cheilocystidia (protruding beyond basidia in *M. rodmani* f. *murina*) can be used as separating characters.

Specimens examined: **UNITED STATES** (all as *Megacollybia platyphylla*), **Texas**, Hardin Co., Lance Rosier Unit, Big Thicket National Preserve, Teel Rd., N 30˚ 16. 629’, W 94˚ 31. 532’, 11.XI.2006, coll. D.P. Lewis, DPL 7682 (TENN 62059); same location, 17.VI.2006, coll. D.P. Lewis, DPL 7405 (TENN 62058); Lumberton, Village Creek State Park, 28.VI.2003, coll. D.P. Lewis, DPL 6711, TFB 11676 (TENN 59935); Henderson Co., Athens, Athens Botanical Garden, 31.X.2004, coll. D.P. Lewis, DPL 7081 (TENN 62057)

7. *Megacollybia fusca* [Figs. 1B, 2 – clade 7; Figs. 22-25]

This clade is composed of sequences from two specimens from Colombia and Guyana in South America. ITS Sequences from Guyana and from Colombia are sufficiently different (4.05% divergence if gaps are coded as a single event) that these collections may well represent two species, but with only a single collection from each region, we are taking a conservative approach at this time and placing them under a single species epithet. Phylogenetically, collections from Guyana and Colombia are separate from their sister clade, *Megacollybia texensis*. A new species is proposed:



FIGS. 22, 23. *Megacollybia fusca*, MCA 1179. Fig. 22. Basidioma in the habitat, 0.8×. Fig. 23. Field sketch, 0.8×.

Megacollybia fusca J.L. Mata, M.C. Aime, & T. W. Henkel, sp. nov.

Pileus 110–150 mm latus, convexus juvenilus, planus ad depressus, luteobrunneus ad atroluteobrunneus, radio-fibrillosus, siccus. Lamellae adnatae ad subdecurrentae, ventricosae, lacteae, delicate marginatae. Stipes 60–170 × 10–18 mm, equalus ad sursum decrescens, brunneus ad luteobrunneus. Pileocystidia 48–112 × 10–25 µm, clavata, ventricosa ad subfusoidea, brunnea, tenuitunicata, fibulata, levis. Sporae 5.6–10 × 4.4–7.2 µm (*n*= 50, Q = 1.07–1.44, Q^m = 1.28, L^m = 7.6 µm), latae ellipsoideae ad ovatae, levae, tenuitunicatae, hyalinae. Basidia 25–30(–41) × 6–11 µm, clavata, tenuitunicata, fibulata, tetraspora. Pleurocystidia nulla. Cheilocystidia 28–60 × 11–25 µm, lato-clavata, fibulata, tenuitunicata. Caulocystidia 28–90 × 8–20 µm, elongato-pedicellata, clavata ad subventricosa, pallidobrunnea. America Australis; septentrionalis.

Holotype: GUYANA. REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River, 20 km east of Mt. Ayanganna, near confluence of Potaro River and Alukyadongbaru Creek, within 2 km of a permanent base camp at 5˚ 18’ 04.8” N; 59˚ 54’ 40.4” W; elevation 710m, Dicymbe corymbosa dominated forest, , 10.VI.2000, coll. Karol, MCA 1179 (BRG, Isotype LSU).

Basidiomata (Figs. 22, 23) collybioid to xeruloid. **Pileus** 110–150 mm in diameter, 30–50 mm deep, convex when young, later broadly plane to deeply depressed or everted, with an irregular orbicular outline; surface radially fibrillose, fibrils most concentrated over disc, becoming flat appressed squamulose in some toward margin, taupe (4E5) overall or yellow-brown (5F5), remaining darker at disk; margin uplifted, with broad tears in some, partially eroded. Context up to 10 mm thick at the center, to very thin outwards, watery white, unchanging. **Lamellae** adnate to sinuate, 7–15 mm broad, subdistant, white, appearing hygrophanous; margin smooth, finely stippled taupe to yellow brown; lamellulae in two tiers of different lengths, frequently anastomosing and with intervenose projections present. **Stipe** 60–170 × 10–14 mm , with a subbulbous base up to 18 mm diam, tip of base sometimes tapered and abruptly radicating; surface appressed fibrillose, appearing longitudinally streaked, brown (4D4) to yellow brown (5F5), paler and pruinose toward the apex; interior hollow at center, white, thick and tough; context fibrous to cottony. **Rhizomorphic strand** present, white. Colors unchanging on bruising. **Odor** faint; **taste** none.

Habitat: Colombia, in *Quercus humboldtii* forests; Guyana, in forests dominated by the leguminous, ectomycorrhizal tree *Dicymbe corymbosa*.

Pileipellis a parallelocutis; suprapellis composed of **terminal cells** (Figs. 24A, B), 48–112 × 10–25 µm, mostly long to short clavate, or ventricose to subfusoid, some mucronate, semiprostrate, ± intertwined, single or more often in fascicles, with brown-pigmented vacuolar contents, thin-walled; subpellis ± 40 µm thick, composed of filamentous hyphae, 2–8 µm diam, ± radially oriented. Pileus trama undifferentiated to loosely interwoven; hyphae narrow, less than 6 µm diam, or broad up to 30 µm diam, filamentous, hyaline singly; wall thin to slightly thickened. **Lamellar trama** irregular; hyphae 6–20(–30) µm diam, hyaline; wall thin.

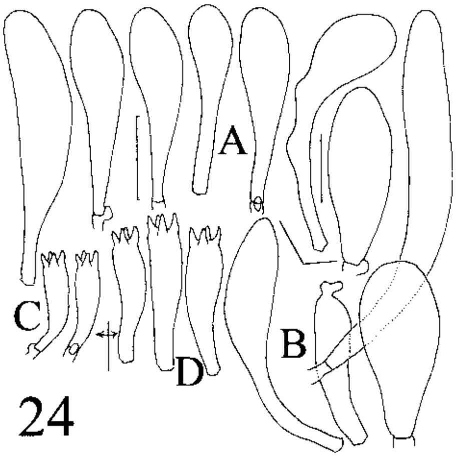


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FIG. 24. *Megacollybia fusca*. A, B. Pileipellis terminal cells. C, D. Basidia. A, C. MCA 1179. B, D. AEFM 1892. Standard bar = 20 µm.

Hymenium composed of **basidia** (Figs. 24C, D) 25–30(–41) × 6–11 µm, typically clavate, four-spored; and basidioles 20–26(–40) × 5–6(–10) µm, digitate to narrowly clavate, occasionally cylindrical; wall thin. **Basidiospores** (Figs. 25A, B) 5.6–10 × 4.4–7.2 µm ($n = 50$, $Q = 1.07–.44$, $Q^m = 1.28$, $L^m = 7.6$ µm), broadly ellipsoid to subglobose in side view and profile, adaxially flattened, hyaline, inamyloid, acyanophilous, wall thin, smooth, typically uniguttulate. Pleurocystidia none. **Cheilocystidia** (Figs. 25C, D) abundant, 28–60 × 11–25 µm, mostly clavate-inflated to broadly clavate, sometimes pedicellate, or sphaeropedunculate, rarely fusoid-ventricose or submucronate, sometimes transversely septate towards base (but not clamped), thin-walled, conspicuously clamped. **Stipe tissues** parallel, of two hyphal types: 1) up to 32 µm diam, thick-walled (wall up to 2 µm thick); and 2) 4–6 µm diam, frequently branched, frequently clamped. **Caulocystidia** (Figs. 25E, F) common on upper stipe, scattered and uncommon to rare downwards, 28–90 × 8–20 µm, typically

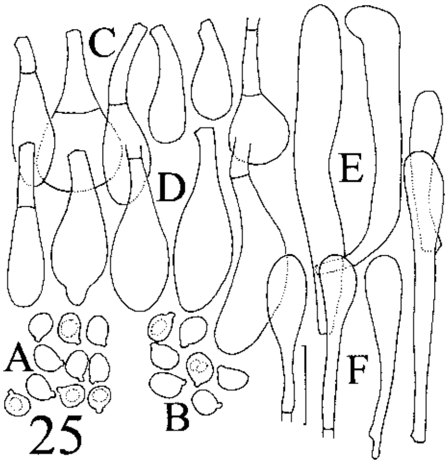


FIG. 25. *Megacollybia fusca*. A, B. Basidiospores. C, D. Cheilocystidia. E, F. Caulocystidia. A, C, F. MCA 1179. B, D, E. AEFM 1892. Standard bar = 20 µm.

long-pedicellate, clavate to short ventricose, or submucronate, with brownish vacuolar pigmentation.

Commentary: Overall macroscopic and microscopic characteristics of *M. fusca* are similar to other species in *Megacollybia*, differing only in smaller details. A brown-gray pileus coloration of *M. fusca* is similar to all other species but the shape of pileipellis terminal cells seems to be more variable. Cheilocystidia are numerous but in general they seem not to achieve long dimensions and appear more inflated when compared to other American species such in *M. rodmani* and *M. texensis*. Ecology and distribution of *M. fusca* is unique as it appears to be associated with *Dicymbe* forests from the Pakaraima Mountains of western Guyana and oak-dominated forests of southwestern Colombia.

Specimens examined: **COLOMBIA**. Departamento de Antioquia, Municipio de Támesis, vereda Rio Frío, *Quercus humboldtii*, 23.VI.1992, col A.E. Franco-Molano AEFM 1012 (NY). **GUYANA**, REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River, 20 km east of Mt. Ayanganna, near confluence of Potaro River and Alukyadongbaru Creek, within 2 km of a permanent base camp at 5° 18’ 04.8” N; 59° 54’ 40” W; elevation 710m, *Dicymbe corymbosa* dominated forest, , 10.VI.2000, coll. Karol, MCA 1179 (BRG, *Isotype* LSU).

8. *Megacollybia rodmani* [Figs. 1B, 2 – clade 8; Figs. 26-31]

Phylogenetic information, morphological observations and a few sexual compatibility pairings all suggest that the eastern North American representative of *Megacollybia* differs significantly from European *M. platyphylla*. Although two poorly differentiated forms seem to occur (here named), only a single species is accepted at this time.

The species epithet intends to recognize James Rodman, long a Program Coordinator in the Biological Sciences Program of the National Science Foundation (USA), in appreciation of his service to biological systematics.

Megacollybia rodmani R.H. Petersen, K.W. Hughes & E.B. Lickey, sp. nov.

Pileus plerumque ad 100 mm latus, convexus juvenilus, planus ad leviter convexus, olivaceo-griseus ad olivaceo-brunneus, brunnescens, radio-fibrillosus, siccus. Lamellae adnatae ad adnexae, ventricosae, lacteae ad eburneae, non-marginatae. Stipes –80 × 10–25 mm, equalus ad sursum decrescens, albus ad pallide griseus. Pileocystidia 23–74 × 6–16 µm, clavata, ventricosa ad subfusoidea, subhyalina, tenui- ad crassitunicatae, fibulata. Sporae 6–10 × 5–7.5 µm (Q = 1.07-1.67; Q^m = 1.33; L^m = 7.9 µm), subglobosae ad latae ellipsoideae ad ovatae, laevae, tenuitunicatae, hyalinae. Basidia 25–38 × 7–10 µm, clavata, tenuitunicata, fibulata, tetraspora. Pleurocystidia nulla. Cheilocystidia 28–65 × 7–18 µm, clavata ad late clavata, fibulata, tenui- ad crassitunicata. Caulocystidia 25–72 × 5–18 µm, clavata ad subventricosa, prope hyalina. America Septentrionalis; orientalis.

Holotype: UNITED STATES, Tennessee, Sevier Co., vic. Gatlinburg, GSMNP, Greenbrier, Porter's Creek Rd., 5.V.2002, coll. R.H. Petersen & K.W. Hughes, TFB 11485 (TENN 59430).

Basidiomata stout, fleshy, tricholomatoid to collybioid. **Pileus** often 100 mm broad or more, convex when young, soon shallowly depressed over disc and there darkly pigmented, smooth, outward over limb and to margin obscurely, delicately streaked in dark colors from dark brown with olive tints to almost black with olive tints, in the typical form changing to neutral brown on drying; margin inturned when immature, by maturity plane or uplifted; flesh white to off-white, soft when fresh, punky when dried. **Lamellae** adnexed to adnate, usually with small decurrent tooth, ventricose, subdistant, thick to thin, up to 15 mm deep, off-white to pallid olive or pallid yellowish shades, in f. murina changing to ochraceous buff with pale buff inner surfaces, in 3-5 ranks, delicately transversely ridged and/or streaked as though hygrophanous (but not so), often eroded to irregularly serrate, brittle when dried and then crisped; interlamellar surface rugose, ridged to buttressed. **Stipe** up to 80 mm long, 10–25 mm broad, smooth, minutely lined, usually not twisted, apically concolorous with lamellae, downward off-white to pallid olive, slowly discoloring to gray or brownish in handling; base not or gradually expanded, often attached to ropy, white rhizomorphic strands; flesh white, stuffed to hollow (especially when mature) with thick rind. Odor none; taste not distinctive.

Habitat: Eastern North America and Central America (Costa Rica to Newfoundland); on or juxtaposed to very rotten wood; when on forest debris, then probably attached to buried wood in hardwood forests.

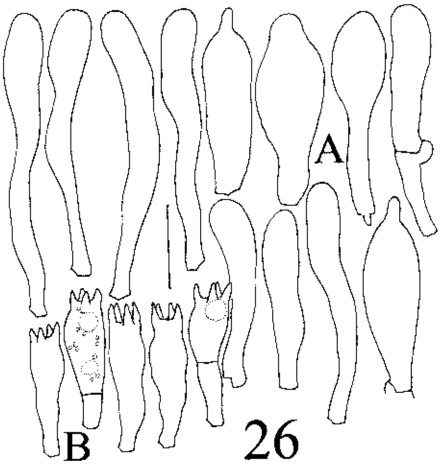


FIG. 26. *Megacollybia rodmani* f. *rodmani*. TENN 59430. A. Pileipellis terminal cells. B. Basidia. Standard bar = 20 µm.

Pileipellis a repent layer of slender (3–6 µm diam), radially oriented hyphae, either moderately cytoplasmically pigmented (composing dark radial streaks) or subhyaline (in areas between dark streaks); **pileipellis terminal cells** (Fig. 26A) *never in scabers, never in patches*, 23–74 × 6–16 µm, nearly sessile to elongate-clavate, firm-walled, weakly pigmented, conspicuously clamped, without hyaline thick-walled individuals; contents homogeneous, subhyaline. **Pileus flesh** over stipe up to 15 mm thick, constructed of two hyphal types, both hyaline, both clamped; 1) inflated, 10–50 µm diam, somewhat thick-walled (wall up to 1 µm thick, irregular on inner surface), appearing obscurely mottled, including small circular wall structures, constricted at septa, conspicuously clamped; and 2) 3–10 µm diam, thick-walled (wall up to 0.7 µm thick), frequently branched, frequently conspicuously clamped, smooth (on both wall surfaces). **Pleurocystidia** absent, or as cheilocystidia produced a few micrometers from lamellar edge. Subhymenium a tightly interwoven layer of intricately tortuous, slender (2.5–4 µm diam), frequently clamped hyphae producing basidia and often coralloid, branched or lobed hymenial elements. **Basidia** (Fig. 26B) 25–38 × 7–10 µm, clavate, thin-walled, 4-spored, clamped; contents with a few scattered, refringent (PhC) guttules; sterile hyphal tips (?young basidioles) gnarled, often branched, filamentous, 2.5–3.5 µm diam, hyaline, thin-walled, clamped. **Basidiospores** (Fig. 27A) 6–10 × 5–7.5 µm (Q = 1.33; L^m = 7.9 µm), subglobose, ovate or ellipsoid, flattened somewhat adaxially, thin-walled, inamyloid; contents 1-few guttulate, refringent (PhC). **Lamellar trama** composed of two hyaline, firm- to thick-walled, clamped, hyphal types: 1) inflated up to 35 µm diam, firm- to thick-walled (wall never more than 0.5 µm thick), constricted at septa, obscurely clamped; and 2) slender, 2.5–4 µm diam, frequently branched, frequently clamped, thin-walled, interwoven among inflated hyphae. **Lamellar edge** composed of loosely tangled slender (2.5–4.5 µm diam), tortuous, frequently septate, frequently clamped hyphae producing cheilocystidia. **Cheilocystidia** (Fig. 27B) usually plentiful, prominent or not so, clavate, broadly clavate to subsphaeropedunculate, firm- to thick-walled (wall never more than 0.7 µm thick), hyaline; contents homogeneous. Stipe surface a repent, arachnoid network or layer (–30 µm thick) of slender (3–5.5 µm diam), conspicuously clamped hyphae producing pedicellate terminal cells (**caulocystidia**) (Fig. 27C) 25–72 × 5–18 µm, firm- to thick-walled (wall never more than 0.7 µm thick), clavate to subbulbous, out-turned; outer stipe flesh a thick layer of strictly parallel, tightly packed, often coherent hyphae of two types: 1) inflated up to 25 µm diam, usually thick-walled, hyaline, long-celled, obscurely clamped; and 2) slender (3–5.5 µm diam), straight, stiff, long-celled, rarely clamped hyphae not interwoven with inflated hyphae. **Rhizomorphic strands** usually thick, terete, prominent, extensive, sometimes extending for a meter or more in rotten wood, white; cortical tomentum of tightly interwoven, irregular, thick-walled, clamped hyphae; medullary tissue of skeletal hyphae, slender (1.5–2 µm diam), thick-walled (wall up to 0.5 µm thick, often obscuring cell lumen), inamyloid, non-cyanophilous, rarely clamped.

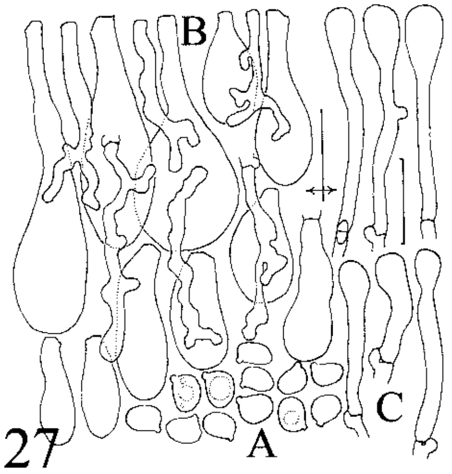


FIG. 27. *Megacollybia rodmani* f. *rodmani*. TENN 59430. A. Basidiospores. B. Cheilocystidia. C. Caulocystidia. Standard bar = 20 µm..

Commentary: In *Megacollybia*, distinguishing morphological characters are difficult to find and even more difficult to describe. It is necessary to examine numerous specimens from scattered locations to estimate characters which could be used in the field or with the aid of a microscope. In this case, a molecular phylogenetic reconstruction provides a guide, and the task is to find characters which bind collections within a clade, and diagnostic characters which separate clades. Thus, the eastern North American taxon, here proposed as *M. rodmani*, forms a distinct clade. Problems arise when two forms can be identified within the clade: they must be summarized together, and then separated. It is possible that they form two “cryptic species,” insufficiently separated by ITS sequences. Additional molecular work may solve this problem.

Two collections from Mexico [Hidalgo, Pachuca-Laredo, km 163, 31.VIII.2002, coll. J. Cifuentes (as *M. platyphylla*), TFB 10989 (FCME 19183); Guerrero, km 0–2 desv. al Cerro del Huizteco, 29.VI.1981, coll. R.M. Villegas Rios (as *Oudemansiella platyphylla*), no. 13275 (FCME)] yielded ITS sequences typical of *M. rodmani*. The basidiomata could not be accurately attributed to either infraspecific form, however. This situation extends the distribution of the species into the transvolcanic axis of central Mexico, where fresh material should be sought.

With several specimens of *M. rodmani* there are notes that spores germinated on agar starting at 18 hours, and attained maximum percentages around 24–36 hours. Our observations, however, indicate that spore germination rarely succeeds in producing viable hyphae, and it was long considered impractical to grow enough strains to perform a self-cross. Mata (unpubl. data) succeeded in performing intercollection pairings using four collections from Eastern United States, concluding that low-percentage intercompatibility was demonstrated among the four. Conversely, two collections from western United States, while partially intercompatible, were totally interINcompatible with eastern United States collections. In light of results in this paper, such interINcompatibility is to be expected.

8.1 *Megacollybia rodmani* forma *rodmani* (autonym; forma typica).

Basidiomata collybioid. **Pileus** shallowly convex, often shallowly depressed at center; disc smooth, glabrous-shining when dry, not furfuraceous or scabrous, usually shallowly depressed, “Saccardo’s umber” (5E8), “dark olive buff” (3C5), “tawny olive” (5C5) to “buffy brown” (6D4), outward minutely fibrillose, delicately shining when dried, delicately radially streaked, “tawny olive” (5C5), “deep olive buff” (3C3) and “tilleul buff” (5B2); margin thin, minutely lobed, not striate, inturned when immature, later sometimes uplifted, often lacerate in age; flesh thin except over stipe, white, changing to “light ochraceous buff”when dried. **Lamellae** adnexed to adnate with small decurrent tooth, subdistant, ventricose, -19 mm deep, thin, white, “cartridge buff,” “cream buff”(4A4), “pale olive buff” (3B2) usually eroded to sublacerate in age, in 4-5 ranks, sometimes diffuse-stained to tan (“sayal brown” 6C5) , and changing so on drying, not marginate; interlamellar surface rugulose, as though interveined. **Stipe** up to 80 mm long, 4-7 mm broad, hardly twisted, unlined to delicately lined, “cream buff” (4A4) apically, “cartridge buff” to “ivory yellow” downward, loosely stuffed to hollow; base occasionally expanded. **Rhizomorphic strands** occasional. **Taste** none; **odor** weakly musky.

Basidiospores 6–10 × 5–7 µm (n = 238; Q = 1.07–1.67; Q^m = 1.29; L^m = 7.8 µm), ellipsoid to ovate, flattened adaxially, thin-walled; contents 1-few-guttulate. ***Cheilocystidia*** 20–58(–86) × 8–25 µm, *not protruding beyond basidia*, obscure but plentiful, pedicellate to nearly sessile, clavate to subbulbous, clamped, firm- to (rarely) thick-walled (wall never more than 0.7 µm thick), hyaline, occasionally transversely septate, hyaline; contents homogeneous. **Caulocystidia** sparse, 32– more than 100 × 5–12 µm (at widest point), elongate-digitate to subbulbous or clavate, firm-walled, occasionally transversely septate, conspicuously clamped, hyaline; contents homogeneous. Stipe flesh constructed of two hyphal types: 1) inflated up to 25 µm diam, thick-walled (wall up to 1.0 µm thick), irregular in outline, obscurely sculptured on inside surface, constricted somewhat at septa, obscurely clamped; and 2) slender, 3–5 µm diam, firm-walled, rather stiff, straight, rarely branched, even more rarely clamped, hyaline. Lower stipe covered with the same arachnoid layer of slender hyphae, which seem not to produce caulocystidia but lie repent on the stipe surface. Stipe flesh of coherent, thick-walled (wall up to 1.5 µm thick), somewhat inflated (up to 24 µm diam), strictly longitudinal hyphae.

Commentary: Pileipellis terminal cells are bland — weakly pigmented, firm-walled, clamped, clavate — typical of the genus except generally shorter and less pigmented. Pileus color (with olive shades) and obscure cheilocystidia seem characteristic of f. *rodmani*. The lax pileus and thin margin also point in that direction. Moreover, not only do pilei of f. *rodmani* dry very brittle and fragile, but stipes seem not nearly as stout as when fresh, unlike f. murina, where stout stature and basidiome colors remain more or less intact upon drying.

Cheilocystidia shape and size in f. *rodmani* are not remarkable, quite like those of other species of *Megacollybia* and allies, but unlike those of f. *murina*, are not prominent (rarely protruding beyond basidia).

Specimens examined (f. *rodmani*): **CANADA, Quebec**, vic. Quebec City, 29.VII.2006, coll. J.L. Mata, TFB 13160 (TENN 61269). **UNITED STATES**, **Arkansas**, Newton Co., vic. Salus, Ozark Highlands Trail at Moonhull Rd, N 35˚44.474', W 93˚ 27.734' 29.V.2003, coll. R.H. Petersen (as *M. platyphylla*), TFB 11083 (TENN 56566); **Tennessee**, Cocke Co., GSMNP, Cosby Campground, Nature Loop Trail, 13.V.2002, coll. J.L. Mata, TFB 11492 (TENN 59436); same data, coll. E. Grand, TFB 11491 (TENN 59435); Sevier Co., vic. Gatlinburg, GSMNP, Greenbrier, Porter's Creek Rd., 5.V.2002, coll. R.H. Petersen & K.W. Hughes, TFB 11485 (TENN 59430; holotype); same data, TFB 11487 (TENN 59432).

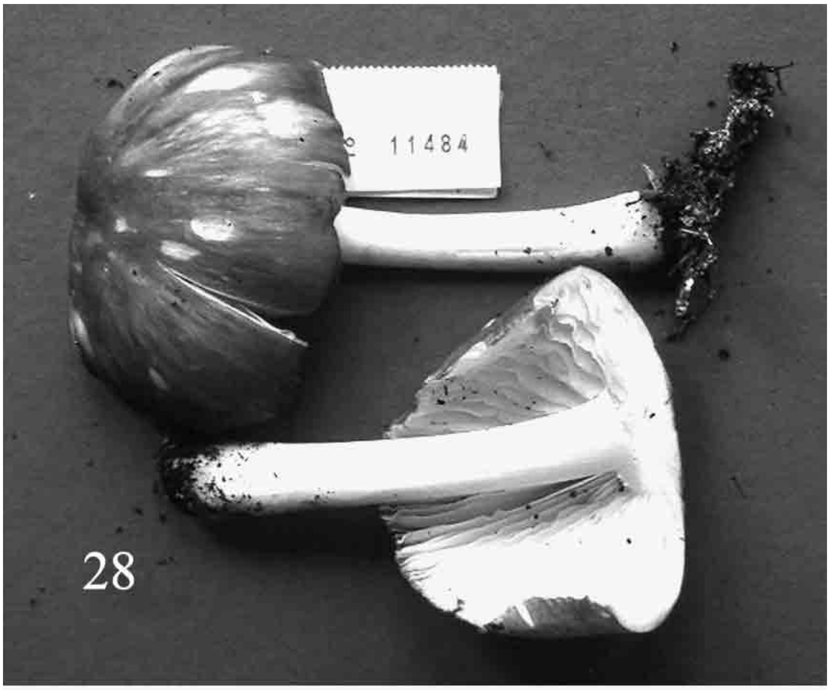
8.2 *Megacollybia rodmani* forma *murina* R.H. Petersen & K.W. Hughes, f. nov. [Figs. 28-31]

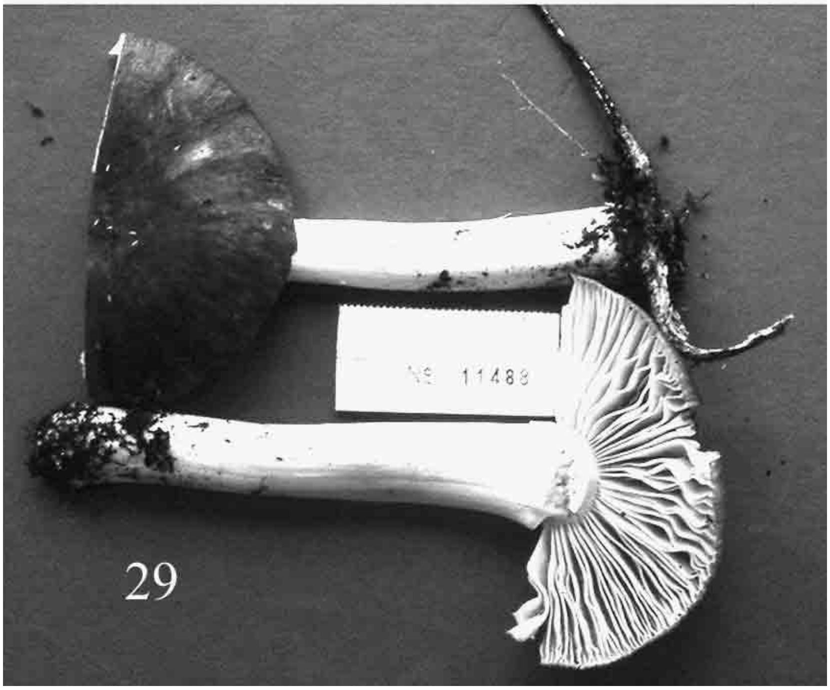
Similis forma rodmani, vel pileus atrobrunneus, atro-olivaceus ad atrofuscus; lamellae pallide eburneus ad pallide olivaceus. America Septentrionalis; occidentalis.

Holotype: UNITED STATES, Tennessee, Sevier Co., vic. Gatlinburg, GSMNP, Greenbrier, Porter's Creek Rd., 5.V.2002, coll. R.H.Petersen & K.W. Hughes, TFB 11488 (TENN 59433).

Basidiomata (Figs. 28, 29) tricholomoid or russuloid, stout, solid. **Pileus** commonly 80 mm broad or more, convex, smooth, shallowly depressed over disc, *"chaetura drab" (2F2), "chaetura black" (2F3), "dark grayish olive" (2F4) to "fuscous" (6E4)*, radially fibrillose, becoming glabrous-shining on drying; margin inturned (especially in drying). **Lamellae** adnexed to adnate with small tooth, ventricose, up to 13 mm deep, in 4 ranks, "pale olive buff" (3B2) to "cartridge buff," not marginate. **Stipe** 60–90 × 15–25 mm, fleshy, silky apically, white to "pale olive buff" (3B2), usually darkening somewhat on handling, fibrous, enlarged at base, sometimes twisted, fibrous, stuffed. **Rhizomorphic strands** common, usually extensive, white, terete; context "dimitic" with slender (1–2 µm diam), thick-walled, non-cyanophilous skeletal hyphae. **Taste** not distinctive; **odor** none.

Pileus outermost layer a tangled arachnoid layer of slender (3—5 µm diam), firm-walled, frequently clamped, moderately pigmented hyphae; **pileipellis terminal cells** (Fig. 30A) 25– more than 150 × 7–15 µm, sessile to elongate-pedicellate, clavate, often tortuous, often with small outgrowths (like false clamps), conspicuously clamped, firm-walled, *moderately to strongly pigmented*; contents homogeneous.





FIGS. 28, 29. *Megacollybia rodmani* f. *murina*. Basidiomata. Fig. 28. TFB 11484. Fig. 29. TFB 11488. Numerals = 4 mm.

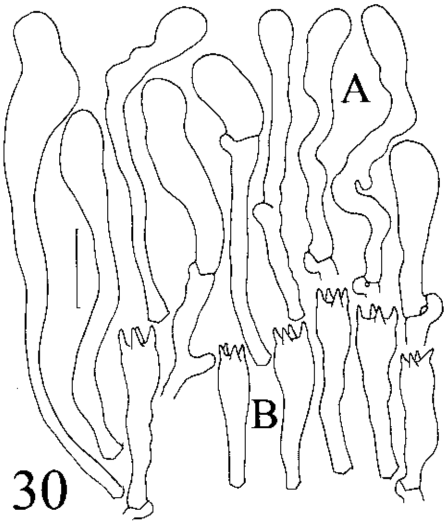


FIG. 30. *Megacollybia rodmani* f. *murina*. TENN 59433. A. Pileipellis terminal cells. B. Basidia. Standard bar = 20 µm.

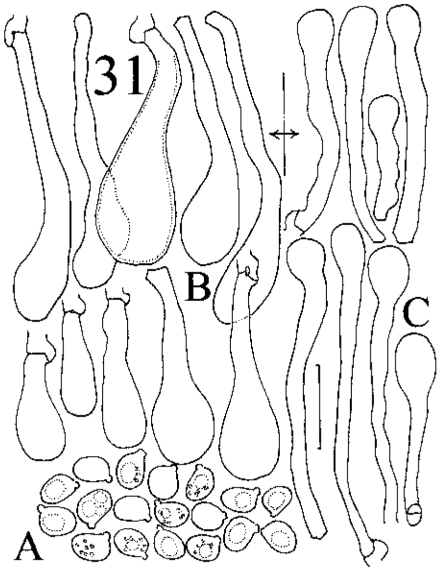


FIG. 31. *Megacollybia rodmani* f. *murina*. TENN 59433. A. Basidiospores. B. Cheilocystidia. C. Caulocystidia. Standard bar = 20 µm.

Basidia (Fig. 30B) 26–43 × 7–11 µm, clavate, thin-walled, 4-spored, clamped; contents with scattered small, refringent guttules. Gnarled basidioles absent, but subhymenium a tightly, freely (not coherent) interwoven layer of gnarled hyphae frequently branched, very frequently and prominently clamped. **Basidiospores** (Fig. 31A) 7–10 × 5.5–7.5 µm (*n* = 174; *Q* = 1.00–1.67; Q^m = 1.25; L^m = 7.7 µm), globose (rarely), ellipsoid to ovate, flattened adaxially, thin-walled, hyaline; contents obscurely uniguttulate. ***Cheilocystidia*** (Fig. 31B) 24–79 × 7–19 µm, densely scattered (lamellar edge nearly sterile), *protruding beyond basidia* up to 15 µm, short- to long-pedicellate, clavate to broadly clavate, firm- to thick-walled (wall never more than 0.5 µm thick), conspicuously clamped, hyaline; contents homogeneous. **Caulocystidia** (Fig. 31C) from near stipe apex 31–115 × 6–10 µm, clavate to subbulbous, conspicuously clamped, firm- to thick-walled (wall up to 1.0 µm thick), hyaline. Stipe apex (c 10 mm from gills attachment) delicately ridged and lined, between ridges is white, silky. Stipe surface with a tissue (perhaps 20–30 µm thick) of slender (3–5.5 µm diam), branched, conspicuously clamped, firm-walled, hyaline hyphae which produce somewhat inflated terminal cells (caulocystidia). **Midstipe caulocystidia** 25– more than 115 × 6–11 µm (at widest point), obscure, repent, as terminal cells or as side branches, usually slightly curved abaxially, usually long-pedicellate, subbulbous, firm-walled; contents homogeneous.

Commentary: In f. *murina*, pileus color remains dark upon drying and stipe remains stout. In f. *rodmani*, pileus color changes to neutral tan and stipe appears much more slender when dried.

For TENN 59429, pileus color and convexity and large, protruding cheilocystidia all denote f. *murina*, but lamellae were shallow, adnexed (not adnate), and seem to have changed on drying color to ruddy (as in f. *rodmani*). In the herbarium specimen, the stipe seems slender, not stout as in f. *murina*, all of which may indicate that the two forms interbreed.

In f. *murina*, cheilocystidia in all collections were prominent, protrude beyond basidia and are very plentiful. Moreover, in f. *murina*, cheilocystidia seem to be formed some micrometers away from the lamellar edge and therefore could be counted as pleurocystidia.

Specimens examined (f. *murina*): **CANADA, Quebec**, vic Quebec City, 29.VII.2006, coll. unknown (MSA foray participant), TFB 13159 (TENN 61268). **UNITED STATES, Tennessee**, Sevier Co., vic. Gatlinburg, GSMNP, Greenbrier, Porter's Creek Rd., 5.V.2002, coll. R.H. Petersen & K.W. Hughes, TFB 11488 (TENN 59433, holotype); same data, TFB 11586 (TENN 59431); same data, TFB 11484 (TENN 59429).

9. *Megacollybia subfurfuracea* [Figs. 1B, 2 – clade 9, Figs. 32, 33]

A small clade comprising two specimens, one from Arkansas, the other from eastern Tennessee, can be identified as sister to /rodmani, the dominant assemblage of eastern North America. The following morphological characters diagnose /subfurfuracea: 1) the texture of the pileus disc is minutely furfuraceous, with pileipellis terminal cells apparently erect and gathered into minute scabers; 2) pileipellis terminal cells unusually large and often mammiform; 3) pileus colors with distinct olivaceous tint, becoming neutral brown upon drying; and 4) friable, fragile condition of pileus and lamellar tissues upon drying. There is little genetic separation based on ITS sequences between this taxon and *M. rodmani* but because morphocharacters do not match any other taxon in *Megacollybia*, a new species is proposed.

Megacollybia subfurfuracea R.H. Petersen, sp. nov.

Pileus 70–110 mm latus, planus ad leviter convexus, pallide olivaceo-griseus ad pallide flavo-olivaceus, brunnescens, radio-fibrillosus, siccus. Lamellae adnatae ad adnexae, subventricosae, eburneae, delicati-marginatae. Stipes 45–72 × 5–17 mm, equalus ad sursum decrescens, brunneus ad luteobrunneus. Pileocystidia 40–113 × 9–47 µm, scabrosa as squamulosa, clavata, ventricosa ad subfusoidea, saepe submammiformea, brunnea, tenui- ad crassitunicatae, fibulata. Sporae 6.5–9(–12.5) × 5.5–7.5(–8) µm (Q = 1.07–1.67; Q^m = 1.26; L^m = 7.90 µm), latae ellipsoideae ad ovatae, laevae, tenuitunicatae, hyalinae. Basidia 27–43 × 8–9 µm, clavata, tenuitunicata, fibulata, tetraspora. Pleurocystidia nulla. Cheilocystidia 28–65 × 7–18 µm, clavata, fibulata, tenuitunicata. Caulocystidia 20–210 × 6–23 µm, clavata ad subventricosa, prope hyalina. America Septentrionalis; austro-centralis.

Holotype: UNITED STATES, Arkansas, Faulkner Co.,vic. Conway, Woody Hollow State Park, N 35° 17.221', W 92° 17.220', 27.V.2003, coll. K.W. Hughes (as *M. platyphylla*), TFB 11075 (TENN 59558).

Basidiome collybioid. **Pileus** (mature) 70–110 mm broad, plane to shallowly convex, shallowly depressed over disc, pallid olivaceous gray (4B-D2), greenish olive ("Isabella color," 4D6), "citrine drab" (4D5), "buffy citrine" (3D5) to dull grayish brown ("buffy brown," 6D4), becoming neutral brown ("sayal brown" 6C5) "tawny olive" (5C5) upon drying; disc minutely furfuraceous (30×), not streaked, somewhat darker than limb or margin; inner limb and limb (10–11 mm from center and outward) obscurely, densely streaked in olivaceous brown; margin downturned, thin, entire, eroded in age, not striate; pileus flesh snow white, friable. **Lamellae** adnexed to adnate, with or without tooth, subsinuate, ventricose, at least 11 mm deep “cartridge buff” to “cream buff” (deteriorated), close to subdistant, thin, in 3–4 ranks, on drying becoming “ochraceous buff” with delicate transverse streaks of “light ochraceous buff.” **Stipe** 45–72 mm long, 5–7 mm broad apically, 6–9 mm broad in midsection, expanded somewhat (6–15 mm broad) at base, off-white to “cartridge buff” (pale cream color), minutely lined to delicately ridged, not twisted, expanded slightly at base, reluctantly discolored to grayish where handled. **Rhizomorphs** absent from in-hand material. **Taste** and **odor** not recorded.

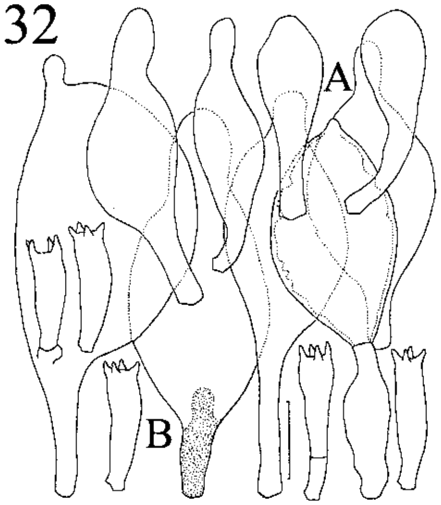


Fig. 32. *Megacollybia subfurfuracea*. TENN 59558. A. Pileipellis terminal cells. B. Basidia. Standard bar = 20 µm.

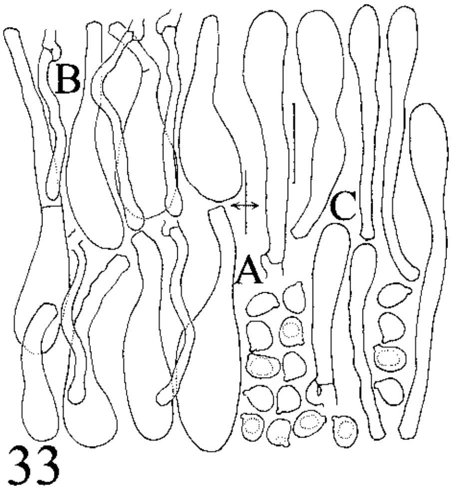


Fig. 33. *Megacollybia subfurfuracea*. TENN 59558. A. Basidiospores. B. Cheilocystidia. C. Caulocystidia. Standard bar = 20 µm.

Pileipellis terminal cells (Fig. 32A) over disc nearly erect, in rough, minute patches (scabers or furfuraceous), 40–113 × 9–47 µm, thin- firm- to thick-walled (wall never more than 1.0 µm thick, and then irregular on inner surface), with pedicel easily obscured by collapsed surrounding tissue, narrowly clavate to broadly clavate, occasionally to commonly with submammiform tip, conspicuously clamped, moderately to weakly pigmented. **Basidia** (Fig. 32B) 27–43 × 8–9 µm, clavate, clamped, thin-walled, 4-spored; contents with a few very small refringent guttules (PhC). **Basidiospores** (Fig. 33A) 6.5–9(–12.5) × 5.5–7.5(–8) µm (*n* = 38; *Q* = 1.07–1.67; Q^m = 1.26; L^m = 7.9 µm), broadly ellipsoid to broadly ovate, flattened adaxially, thin-walled; contents 1–few-guttulate, refringent (PhC). **Cheilocystidia** (Fig. 33B) protruding beyond basidia singly or in 2–3s, 28–65 × 7–18 µm, pedicellate, narrowly to broadly clavate, rarely with irregular apical outgrowths, thin- to firm-walled (wall never more than 0.5 µm thick), conspicuously clamped, hyaline: contents homogeneous; numerous filamentous (2.5–3.5 µm diam), subtly capitulate (capitulum 3.5–4 µm), conspicuously clamped, thin-walled, hyaline, hyphal tips amongst cheilocystidia. Upper stem ridged, silky between ridges. **Caulocystidial terminal cells** (Fig. 33C) 20– more than 210 × 6–23 µm, digitate, narrowly clavate to clavate, firm- to thick-walled (wall never more than 0.7 µm thick), smooth, conspicuously clamped, weakly pigmented (off-hyaline).

Commentary: Pileipellis terminal cells are the largest thus far seen in the genus, and commonly (at least half of the larger individuals) mammiform. Their position on the pileus disc (erect to semi-erect, in minute scabers or roughly furfuraceous) is unlike that of other North American taxa, but reminiscent of species of temperate Asia.

Cheilocystidia seem somewhat larger than usual in the genus, but this would not be reflected merely in measurements. The filamentous hyphal tips among cheilocystidia is novel.

Specimens examined: **UNITED STATES, Arkansas**, Faulkner Co.,vic. Conway, Woody Hollow State Park, N 35° 17.221', W 92° 17.220', 27.V.2003, coll. K.W. Hughes (as *M. platyphylla*), TFB 11075 (TENN 59558, holotype); **Tennessee**, Sevier Co., Strawberry Plains, vic Hickory Township, 19.IX.2004, coll. E.B. Lickey (as *M. platyphylla*), TFB 12095 (TENN 60343).

10. Clade costaricensis [Figs. 1B, 2 – clade 10.]

This small clade, represented by a single, immature specimen, not only segregates based on ITS sequence, but also by macromorphology. It cannot be formally proposed, since a convincing holotype specimen is not yet available. Two photographs show the organism: Halling and Mueller, 2005; Mata, 1999. Both show a tricholomoid or russuloid mushroom with **pileus** almost black, strongly convex with inturned margin, strongly radially fibrillose; **lamellae** off-white, subdistant, perhaps ventricose; stipe stout, white.

Pileipellis terminal cells semi-erect, appearing minutely (30×) scurfy, furfuraceous or roughened, almost black ("chaetura black"), 31–81 × 7–2 µm, digitate, narrowly clavate to clavate (never broadly clavate), thin- to firm-walled (wall never more than 0.3 µm thick), conspicuously clamped, occasionally transversely septate (without clamp), moderately pigmented or hyaline; contents homogeneous. **Cheilocystidia** mostly clavate-inflated, sometimes uneven in shape and lobed, frequently with a secondary septum; wall thin. **Basidiospores** not found.

Exemplar: **COSTA RICA**, Prov. San José, Bosque Experimental de Villa Mills, 22.VI.1995, coll. R.E. Halling, TFB 7903 (TENN 53803).

Commentary: Although this specimen occurs within a small clade with Arkansas and Tennessee collections, it is surely not the same organism. Key differentiating character include: 1) pileus hemispherical; 2) pileus almost black; 3) pileipellis terminal cells narrower than most others; 4) in a squash, copious oily or viscid residue leaches from the pileus flesh (apparently not from the pileipellis).

Discussion

The micromorphological characters here considered informative differ little from the morphological analysis of *M. platyphylla* offered by Rexer and Kost (1989a). They not only depicted these structures, but described how each was produced and the tissues from which they arose. Their analysis, however, was limited to a single species (*M. platyphylla*) and compared its micro-characters to those of taxa thought related through presence of "sarcodimitic" tissue construction. Redhead's (1987) elucidation of the Xerulaceae, based essentially on the same premise, included all of the genera studied by Rexer and Kost (1989a,b) (plus others), but Corner's rejoinder (1991) was not yet available. The subsequent phylogenetic reconstruction by Moncalvo et al. (2002) showed that the taxa included by Redhead (1987) and by Rexer and Kost

(1989a) were distributed over at least two clades: *Oudemansiella* (inclusive of *Xerula* for Rexer and Kost) and *Strobilurus* in the /physalachrioid clade and *Megacollybia* in /hydropoid. Similarities in microstructure represented across all of these organisms appeared to be convergent rather than synapomorphic.

Phylogenetic reconstruction, when combined with micromorphological analyses, demonstrates that the most discriminating taxonomic character in *Megacollybia* is geography. There are few discriminating morphological characters in *Megacollybia* suggesting morphological stasis during sequence divergence and establishment of reproductively isolated populations. Similar morphological stasis in the face of sequence divergence was seen in studies by Mueller et al (2001) comparing macrofungi from China and Eastern North America.

The clear separation of Old and New World *Megacollybia* into two major clades and the finding that there is considerable unique genetic variability within them suggests that the major clades are not recent. Similar New World-Old World north-temperate disjuncts within macrofungal genera have been observed in other studies (Vilgalys, 1986, 1991; Vilgalys and Miller, 1983, 1987a, 1987b, Zervakis et al., 1994, 2004; Gordon, 1994; Gordon and Petersen, 1997, 1998; Shen et al. 2002).

Surprisingly, eastern North American *Megacollybia* is divided into two distinct and apparently non-interbreeding clades, a clade from Texas (*M. texensis*) that is related to collections from South America and a much larger northeastern clade which extends from Costa Rica through Nova Scotia and includes *M. rodmani, M. subfurfuracea* and /costaricensis, the latter two differentiated from *M. rodmani* on the basis of non-overlapping haplotypes and morphology. A number of studies (Lickey et al., 2002, 2003; Mata et al., 2007) have indicated that eastern North American taxa may have arrived in their present geographic locations after migrating from separate refugia following the glacial maximum in North America. We, and others (see Halling, 2001; Redhead, 1989), have repeatedly found connections between Central America and eastern North America and we have speculated that Central America was a refugium during periods of glaciation but other refugia, notably along the Mississippi River, surely existed (Delcourt and Delcourt, 1984).

The partitioning of eastern North American *Megacollybia* taxa into small endemic clades in Texas and Arkansas could reflect speciation events that occurred in glacial refugia or during subsequent migrations, but it is possible that migration patterns of opportunistic saprophytic fungi may have differed from those of mycorrhizal fungi, which may be more dependent on co-migration with their host taxa (see Halling, 2001; Horak 1983). In Mexico, additional taxa may be found due to complex physiographic events including the east-west volcanic belt capping the tropical MesoAmerican region (Morrone, 2006; Morrone, et al., 2002) and additional sampling.

One potential biogeographic problem concerns the distribution of *M. platyphylla* in Russia. *Megacollybia clitocyboidea* appears basal to the rest of the genus, and (to this time) its collections are limited to temperate Asia. *Megacollybia marginata* and *M. platyphylla* are closely related, spanning Eurasia and there is a possible additional taxon (*M. platyphylla* form B) found in the Czech Republic and the Caucasus that appears transitional between *M. marginata* and *M. platyphylla*. Morphology and phylogeny concluded that the *Megacollybia* taxon in western Russia (i.e. west of the Ural Mountain range) was the same as that in western Europe and Scandinavia, namely typical *M. platyphylla*. Along the eastern coast of Russia, however, at least two other taxa (*M. marginata,* *M. clitocyboidea*) occurred sympatrically. Care was taken, therefore, to examine and sequence material from middle Russia. The results are not conclusive, but *M. platyphylla* extends as far east as the Altai Republic, considerably east of the Urals. Thus the Urals are not acting as a barrier to distribution of *M. platyphylla*. It seems more likely that a combination of the Siberian Boreal Forest and the Russia Steppe may present the barrier. Concomitantly, the far eastern Russian taxa may be limited to the ameliorated climate adjacent to the Sea of Japan. If this is the case, these taxa may be added to others endemic along the Pacific Rim (Hughes and Petersen, 2004; Petersen and Hughes, 2002, 2005, 2007). The intimate sympatry of two reproductively isolated species in Kedrovaya Pad (*M. marginata, M. clitocyboidea*) raises the question of whether these species evolved allopatrically and then migrated into common territory or whether this is an example of sympatric speciation. Our current studies cannot answer that question.

Megacollybia fallax is a western North American species geographically extending from Arizona to Washington and Idaho. Interestingly, an environmental sample recovered from an orchid inflorescence collected on Vancouver Island (GenBank EU218887) is *M. fallax* by ITS sequence. *Megacollybia fallax* is not known to be either mycorrhizal or endophytic and this may be accidental contamination from a spore rain. Alternately, this finding could represent a new role for *M. fallax*. The unresolved position of *M. fallax* makes biogeographical conclusions difficult but its somewhat closer sequence homology with Asian *M. clitocyboidea* raises the possibility that *M. fallax* represents an ancient migrant across the Bering Strait which has since significantly diverged. In other genera, notably *Flammulina, Panellus* and *Amanita muscaria*, there is evidence for such migrations (Geml et al. 2006; Hughes et al. 1999; Jin et al. 1998)

The finding that a presumed globally distributed species was in fact several distinct taxa, defined by morphology, sequence divergence and in some cases inferred ability to intercross, is not surprising. Increasingly, global partitioning is being revealed in fungi, even in the face of strong balancing selection for mating genes in fungi and conservation of ability to intercross (Vilgalys, 1986, 1991; Vilgalys and Miller, 1983, 1987a, 1987b, Zervakis et al., 1994, Gordon, 1994; Gordon and Petersen, 1997, 1998; James, et al. 2001).

Except for *M. fusca* (and /costaricensis), all *Megacollybia* taxa appear to be North Temperate in distribution, perhaps extending into tropical areas such as Costa Rica. This is illusory, however, for this paper covers only taxa of which we have seen material, especially if DNA sequences could be derived. There may be taxa in Southeast Asia, most of China and other areas, with which we are not familiar, and which await elucidation. For example, Pegler (1986) included two species under *Tricholomopsis*, *T. nigra* (Petch) Pegler (≡ *Clitocybe nigra* Petch) and *T. crocobapha* (Berk. & Broome) Pegler (≡ *Agaricus crocobapha* Berk. & Broome), descriptions of which could apply to *Megacollybia*. *Tricholomopsis* is diagnosed as lignicolous, but this could include buried wood or woody debris. No placement in an infrageneric group was furnished, and no taxon in this paper answers to the descriptions of these taxa.

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摘　　要

ヒロヒダタケ属（ハラタケ目）

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ヒロヒダタケ属 *Megacollybia* は，ヒロヒダタケ *M. (Collybia) platyphylla* に基づいて提案され，従来１属１種からなる属として取り扱われてきた。今回，rDNA ITS 領域の塩基配列に基づいて本属の系統学的再検討を行ったところ，広義のヒロヒダタケは地理的分布と密接な関連性を示す数種を含むとの結果が得られた。形態学的な特徴は大部分において質的なものであったが，各クレードの標本（子実体）は形態学的特徴に基づいて種レベルで識別可能であった。分子系統学的および形態学的研究結果に基づいて，*M. clitocyboidea, M. texensis, M. fusca, M. subfurfuracea, M. rodmani* （新品種 f. *murina* を含む) および *M. marginata* を新種および新品種として報告した。また，*Tricholomopsis fallax* をヒロヒダタケ属に転属した。ヒロヒダタケはヒロヒダタケ属の基準種として残るが，今のところその分布はヨーロッパ，スカンジナビア，および西および中央ロシアに限られているようである。