An investigation of /omphalotaceae (Fungi: Euagarics) with emphasis on the genus *Gymnopus*

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Clade /omphalotaceae (Moncalvo *et al.* 2002) comprises several genera of the traditional family Tricholomataceae (a group of white-spored mushrooms). Using ITS 1-5.8S-ITS 2 sequences of nuclear ribosomal DNA, we present a phylogenetic reconstruction of /omphalotaceae. In order to use taxo-nomenclatural names as accurately as possible, we have compared voucher basidiomata to type specimens and have employed sexual compatibility experiments to probe the genetic cohesion of putatively related collections. Numerous generic type species are placed within the phylogeny and taxonomic implications are discussed. An area of tandem repeats was discovered in numerous species, with implications for their phylogenetic placement. In some widely distributed species phylogeographic signals were inferred. A few new taxa and a few new nomenclatural combinations are proposed.

Key words: Basidiomycota, molecular phylogeny, ribosomal RNA, tandem repeat.

In two recent papers (Moncalvo *et al.* 2000, 2002), cladistic analyses of the "eu-agarics" (mushrooms and close relatives) were presented based on ribosomal nuclear large subunit DNA sequences (nLSU). In the later paper (Moncalvo *et al.* 2002), 117 fungal clades were distinguished and discussed. Those seminal papers furnished a relatively comprehensive "backbone" phylogenetic reconstruction showing phylogenetic relationships across this large group of fungi for the first time and provided an initial overview of a clade described as /omphalotaceae containing the morphologically dissimilar fungal genera *Anthracophyllum, Omphalotus* (Jack 'O Lantern fungus), *Rhodocollybia, Lentinula* (Shiitake mushrooms) and assorted members of *Gymnopus, Marasmiellus* and *Marasmius* (Fig. 1). The latter three genera in /lentinuloid (Fig. 1) are a highly speciose and understudied group of litter binding/decay fungi.

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Hibbett *et al.* (1995) employed sequences from some collybioid fungi as an outgroup for a phylogeny of *Lentinula* intended to estimate a molecular timetable for evolutionary and biogeographic events.

Toward the understanding of fungi in /omphalotaceae, some taxa of *Gymnopus* from Indonesia were described and placed in an nLSU-based phylogeny inclusive of only those species (Wilson *et al.* 2004). Wilson and Desjardin (2003, 2005), in nLSU-based phylogenies, included numerous taxa theretofore phylogenetically unplaced but considered "gymnopoid" and/or "marasmioid". In the latter paper (Wilson & Desjardin 2005), considerable discussion centered around phylogenetic placement and taxonomic/nomenclatural equivalents to clades.

Considerable morphotaxonomic foundation was laid for these phylogenetic inquiries by European authors before mid-twentieth century, and thereafter by papers by Halling (1979, 1981, 1983, 1990, 1994, 1997) and Antonín & Noordeloos (1993, 1997). These and others (Vilgalys 1986, 1991; Vilgalys & Miller 1983) provided morphospecies delineations and accurate descriptions which hopefully, could identify the taxa whose sequences appeared in subsequent phylogenetic reconstructions.

DNA-based phylogenetic reconstructions have presented opportunities to examine various clades at higher resolutions and with more robust data sets. This paper intends to present such an examination of one clade, /omphalotaceae (Moncalvo *et al.* 2002; Fig. 1). A number of intersecting factors influenced our choice to examine /omphalotaceae. First, JLM was completing a dissertation on *Gymnopus*, *Rhodocollybia* and *Lentinula* in Costa Rica, and had acquired the expertise to critically examine field-collected specimens morphologically. Second, as part of that dissertation and for more general reasons, JLM and KWH had generated numerous nrITS sequences for taxa in these clades. Third, RHP had already reported on mating systems in several members of the clades (Petersen 1995; Petersen & Gordon 1994), and had unpublished data on additional taxa. Fourth, we had already published on *Omphalotus* (Petersen & Hughes 1998; Hughes & Petersen 1998) and *Neonothopanus* (Petersen & Krisai-Greilhuber 1999). Fifth, our herbarium specimens vouchered many cultures of members of these clades, so ample material was at hand. Sixth, L.R. Hesler examined several type specimens of *Collybia* (Hesler 1957, 1959), publication on which was supported by his notes and photos, to which we had access.

By using multiple methods, we intend to: 1) place numerous taxa on an ITS-based phylogenetic reconstruction; 2) examine and clarify previous infrageneric and generic alliances; 3) place type species of several genera in order to examine the phylogenetic validity of some

genus names; 4) place members of suspected heterogeneous genera (i.e. *Marasmiellus*) as a means of elucidating the alliances to which they belong; 5) report mating systems for hitherto unreported taxa and to deposit tester strains in a public culture collection; and 6) furnish a more refined scaffold on which to place future identified and unidentified collections.

As the number of workers with access to molecular techniques and instrumentation has increased, numbers of sequences deposited in publicly accessible databases (i.e. Genbank, etc.) have increased dramatically. Ancillary to this increase, however, has been an increase of improbable identifications of organisms putatively represented by these sequences, leading to confusion and misinformation when sequences and/or names are anomalous in phylogenies and require some explanation. In this paper, we have attempted to correctly identify/name the organisms represented using multiple techniques: 1) comparison of basidiomata of field-collected specimens (from which DNA was extracted either directly or indirectly; see Materials and Methods) to type specimens or other authoritative material when possible; 2) preservation of voucher specimens so subsequent workers can examine the same material; and 3) through intercollection pairing experiments, to test the limits of phyletic and biological species (i.e. intersterility groups versus clades).

Ancillary to the phylogeny presented here, some taxa are proposed as new to science (*Gymnopus mesoamericanus; G. junquilleus; G. parvulus; G. luxurians var. copeyi;* see Appendix 1), and new combinations are proposed (*Gymnopus exculptus, G. readii, G. pseudo-omphalodes;* see Appendix 2).

While the intent of the phylogeny is to outline relationships among taxa in /omphalotaceae (Moncalvo *et al.* 2002), a number of taxa which serve as types of various taxonomic groups are placed. These include *G. alkalivirens* (type of *Gymnopus* sect. *Alkalivirentes*), *G. dryophilus* (type of *Gymnopus* sect. *Levipedes*), *G. androsaceus* (type of *Setulipes* and of *Marasmius sensu* Earle), *G. fusipes* (type of *Gymnopus*), *G. alliaceus* (type of *Mycetinis* and *Marasmius* sect. *Alliacei*), *G. peronatus* (type of *Marasmius* sect. *Peronatae*), *G. confluens* (type of *Gymnopus* sect. *Vestipedes*), *G. juniperinus* (type of *Marasmiellus*) and *G. ramealis* (type of *Collybiopsis* and *Marasmiellus* sect. *Rameales*). Conversely, *Micromphale sensu* Earle (type = "*Pleurotus fimbriatus* (Bolt.)" now known as *Hypsizygus*), *Collybidium* Earle (type = "*Agaricus velutipes* (Curt.) Fries, Syst. Myc. 1: 119. 1821" now known as *Flammulina*) and *Gymnopus* "Roussel" *sensu* Earle (type = "*Collybia longipes* (Bull.)" now included in *Xerula*) are not taken up in this phylogeny.

Materials and Methods

DNA extraction and purification

Monokaryon and dikaryon cultures were obtained as described by Gordon and Petersen (1997) and maintained on malt extract agar (MEA) slants (MEA: 15 g/L Difco Malt Extract, 20 g/L Difco Agar) at 10 °C. For DNA extractions, cultures were grown in PD broth (24 g/L Difco Potato Dextrose Broth) until colonies were 2 – 3 cm in diameter, then sacrificed. Tissue was also obtained from dried herbarium specimens. Tissues were ground in 750 µL Carlson lysis buffer (Carlson *et al.* 1991) and incubated at 75 °C for 30 min. Tissue debris was removed by centrifugation and the supernatant extracted with 750 µL chloroform: iaoamyl alcohol (24: 1). The top layer was removed and measured, and an equal volume of isopropanol was added to precipitate DNA. DNA was washed with 200 µL 70 % cold ethanol, air dried and suspended in 100 µL TE buffer. PCR amplification of the ribosomal ITS 1-5.8S-ITS 2 region was carried out with primers ITS 1F and ITS 4b (Gardes & Bruns 1993) or ITS 4 (White *et al.* 1990). DNA sequencing followed manufacturer's directions for Big Dye Terminator mix (ABI) with forward primer ITS 5 and reverse primer ITS 4. Sequences were aligned and compared using the GCG suite of programs (GCG 2000).

Data Analyses

Initial sequence alignments were carried out by using the "pileup" program in GCG which performs UPGMA followed by manual adjustments to the alignment. Related clusters of sequences were grouped together and aligned to form subclades. Finally, subclades were grouped into a final data set and were re-aligned against each other. *Anthracophyllum* ssp., *Nothopanus eugrammus* and *Omphalotus* ssp. were selected as the outgroup based on data from Moncalvo *et al.* (2002; Fig. 1). *Anthracophyllum* was the most basal group of /omphalotaceae in the Moncalvo *et al.* (2002) analysis and in these analyses. For the sake of consistency, and because of uncertainties concerning correct placement of putative sister taxa, the same outgroup was used for all analyses.

The ITS sequence data set used in this study was large and contained highly variable regions that could not be aligned across the entire data set with confidence. These areas were excluded from analyses based on the entire data set, including a variable ca. 34 bp tandem repeat in the ITS 2 region which was present in some clades but not others. Removal of areas of poor alignment is a conservative way to solve alignment issues but can lead to a loss of resolution (Sanderson & Shaffer 2002).

Maximum parsimony using PAUP* (Swofford 2002) was performed with and without gaps treated as a fifth base One-hundred bootstrap replicates were performed. Gaps were complex and no gap coding was attempted. Model test (Posada & Crandall 1998) was used to evaluate the data set and to select the best model for Bayesian analysis. The model selected by Model Test was a general time reversible model with rate variation (gamma) and both variable and invariable sites (GTR + G + I). Bayesian analysis was performed using MrBayes (Huelsenbeck & Ronquist 2001) with the following settings consistent with the GTR + G + I model. The maximum likelihood model employed 6 substitution types ("nst = 6"), with base frequencies estimated from the data ("basefreq = estimate"). Rate variation across sites was modeled using a gamma distribution, with a proportion of sites being invariant (rates = "invgamma"). The Markov chain Monte Carlo search was run with 4 chains for 500,000 generations, with trees sampled every 100 generations (the first 1000 trees were discarded as "burnin" based on preliminary analyses showing that likelihood values had reached stability with the first 1000 trees). The posterior probabilities were estimated by sampling trees generated after likelihood values converged.

In citing support for clades, Bayesian posterior probabilities and parsimony bootstrap values are cited numerically (ex. 74 posterior probability and 83 % bootstrap value = .74 / 83 %). Bootstrap support values greater than 70 % and Bayesian posterior probabilities greater than 0.80 were considered good support for a clade. Bootstrap support less than 50 % is not shown on figures.

The two major sub-clades in *Gymnopus* were re-analyzed separately, as were smaller clades, using the maximum alignable ITS sequence data in each case (see figure legends for individual analyses) and with *Anthracophyllum* + *Neonothopanus* + *Omphalotus* as the outgroup.

Within *G. biformis* and related species, there were variable numbers of a ca. 34 bp repeat in the ITS 2 region. A copy of each repeat element was isolated and aligned with repeat elements from all collections within this complex. Alignment was performed using the GCG program pileup, followed by manual alignment. Results of the phylogenetic analysis were used to make decisions about homology of the various repeat elements and to assign the repeats numbers based on the hypothesized order of evolution (1 through 5). Assumptions in these analyses were that repeats arose by tandem duplication and no translocation was involved. Repeat elements within the ITS 2 region were aligned by homology group for analyses (data not shown). Data were subdivided further by species to examine within-species repeat relationships.

Sexual compatibility experiments

Basidiospores were obtained from spore drop on agar medium (see Gordon & Petersen 1992) or by dilution of a spore print on aluminum foil. Spores were spread on MEA and germination was observed frequently until discrete mycelial units were formed. Single-basidiospore isolates (SBIs) were excised using a modified dentist's explorer. SBIs were examined for presence/absence of clamp connections, and only clampless isolates were employed in pairing experiments.

Pairing experiments were of two types: 1) self-cross experiments in which 12 SBIs were paired in all combinations. After colony maturation, contact zones were examined for presence/absence of clamp connections. Once all pairings had been inspected, data were adjusted to produce a mating pattern (i.e. bipolar vs. tetrapolar, etc.); 2) SBIs from different infra- or interspecific collections were paired (intercollection pairings). Total pairings were usually either four or eight, noted below under each appropriate taxon (i.e. n = 4; n = 8). Dikaryon cultures were obtained by overgrowth of SBIs. Such cultures were often used as a source of DNA. All cultures were stored as described by Petersen & Hughes (1998) in the culture collection of the University of Tennessee (CulTENN).

Morphological observations

Portions of dried specimens were rehydrated in an aqueous solution of 95% ethanol, then sectioned and placed in 3% KOH. Sections were examined under phase contrast microscopy, or with Congo Red and/or phloxine under bright field microscopy. Melzer's reagent was used to test for detrinoidity and cotton blue for cyanophilous reaction of basidiospores (Largent *et al.* 1977). Colors in alphanumeric codes in parentheses are from Kornerup & Wanscher (1976). Basidiospore measurements and statistics are as in Mata *et al.* (2004a).

Abbreviations and editorial marks

Noting that some genera starting with the same first letter (i.e. *Micromphale, Marasmius, Marasmiellus*) could be confusing when abbreviated, such genera are cited using two letters, as follows: *Ca = Caripia; Co = Collybia; Cp = Campanella; Ma = Marasmius; Me = Marasmiellus; Mi = Micromphale.* In other instances, the first letter is unique (i.e. *Anthracophyllum; Neonothopanus; Gymnopus; Rhodocollybia, Setulipes* etc.) and the second letter was not needed.

Herbarium acronyms are used in agreement with Index Herbariorum (New York Botanical Garden web page; http://sciweb.nybg.org/science2/IndexHerbariorum.asp). SBI = single-basidiospore isolate; putative haploid, monokaryon cultures used in pairing experiments. TFB = Tennessee field book (used as the number of a collection or culture). TENN = Fungus Herbarium of the University of Tennessee. GSMNP = Great Smoky Mountains National Park. JLM, KWH, RHP refer to authors of the paper. Taxon names enclosed in quotation marks (genus name, species epithet, fieldbook nickname) signify less than authoritative use (i.e. type specimen not compared; some doubt as to true identity, etc.). Exclamation point (!) indicates that a cited type specimen (holo-, lecto-, neo-, or epitype) was examined as part of this study.

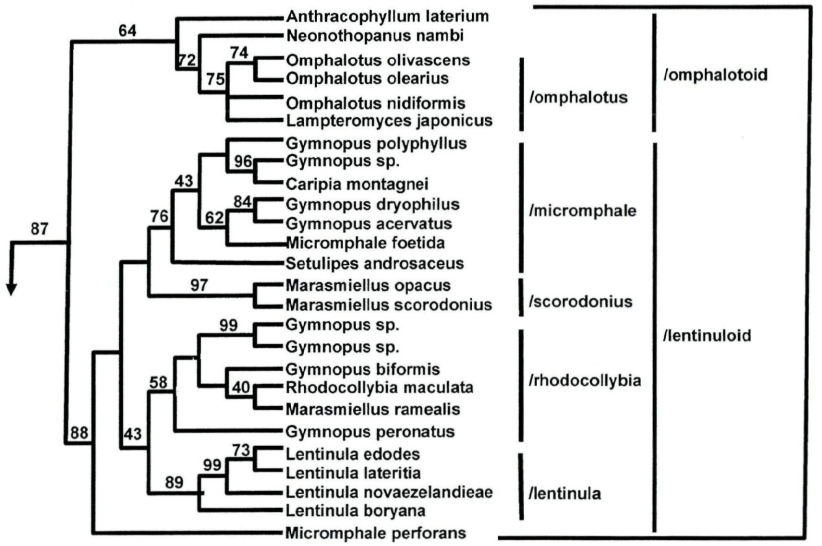


Fig. 1. Phylogeny of /omphalotaceae based on nLSU sequence data from Moncalvo *et al.* (2002).

Results

Omphalotus, Lentinula, Rhodocollybia

Results of Bayesian and parsimony analyses for all ITS sequence data in /omphalotaceae are given in Fig. 2, but in order to align sequences in clades A-N using the entire /omphalotaceae data set, 313 bp within areas of poor alignment were removed (Fig. 2). *Omphalotus, Lentinula* and *Rhodocollybia* appear as monophyletic clades, but with moderate support for *Rhodocollybia*. Four additional

clades were present in analyses but with low support, clades A, B, C and D.

The position of *Neonothopanus* as basal to *Omphalotus* is well-supported in Bayesian analysis, but not strongly in parsimony analysis (.92 / 58 %; Fig. 2). In some parsimony analyses, *Omphalotus* and *Neonothopanus* are sister clades.

Within *Omphalotus,* two subclades occur. *Omphalotus olivascens, O. olearius, O. japonicus* and *O. subilludens* are in a well-supported clade (*Omphalotus* clade 1; Figs. 2, 3). The widespread Euro-American species, *O. illudens,* is found in a second clade together with *O. mexicanus* (*Omphalotus* clade 2; Figs. 2, 3). The position of *O. nidiformis* is variable, depending on the analysis.

The single clade comprising *Lentinula* and *Rhodocollybia* is supported in Bayesian analysis but not in parsimony analysis (.88 / < 50 %; Fig. 2) and in parsimony analyses, *Lentinula* is basal to *Rhodocollybia.* Examination of sequences for the two genera shows considerable sequence divergence between *Lentinula* and *Rhodocollybia.* Support for *Lentinula per se* is strong (.93 / 100 %) but integrity of *Rhodocollybia* as a monophyletic unit is only moderately supported in Bayesian analysis (0.68 / 79 %; Fig. 2). Infragenerically, *Rhodocollybia* is characterized by high sequence divergence (Figs. 2, 3). Sequences of some subtropical American taxa (*R. turpis, R. amica, R. lignitilis, R. unakensis, R. tablensis*) are highly divergent from each other and from those in the sister infrageneric clade. Their position within a phylogeny varies with gap treatment and type of phylogenetic analysis performed. They appear in a clade together with *R. maculata* in most analyses and share a G → A transition in the 5.8S gene with *R. maculata. Rhodocollybia sp.* from Greenland is basal to a clade consisting of *R. pandipes* (Central America) and *R. butyracea,* the latter broadly distributed in the Northern Hemisphere (Fig. 3). *Rhodocollybia butyracea* collections TFB 8250 (Alaska), OKM27562 (Colorado) and TFB 7452 (Sweden) appear together in a well-supported *R. butyracea* subclade (Fig. 3) and share two unique deletions (14 bp and 11 bp) in the ITS 1 region. The remaining *R. butyracea* collections form a well-supported (.98 / 93 %) distinct clade and may represent a separate species or infraspecific entity.

Gymnopus "acervatus"

The sole sequence representing this name was derived from a North American collection, and in Bayesian analysis appears on a long, unsupported branch (Fig. 2). Because this is the only collection of this morphotaxon, the sequence was included in the overall

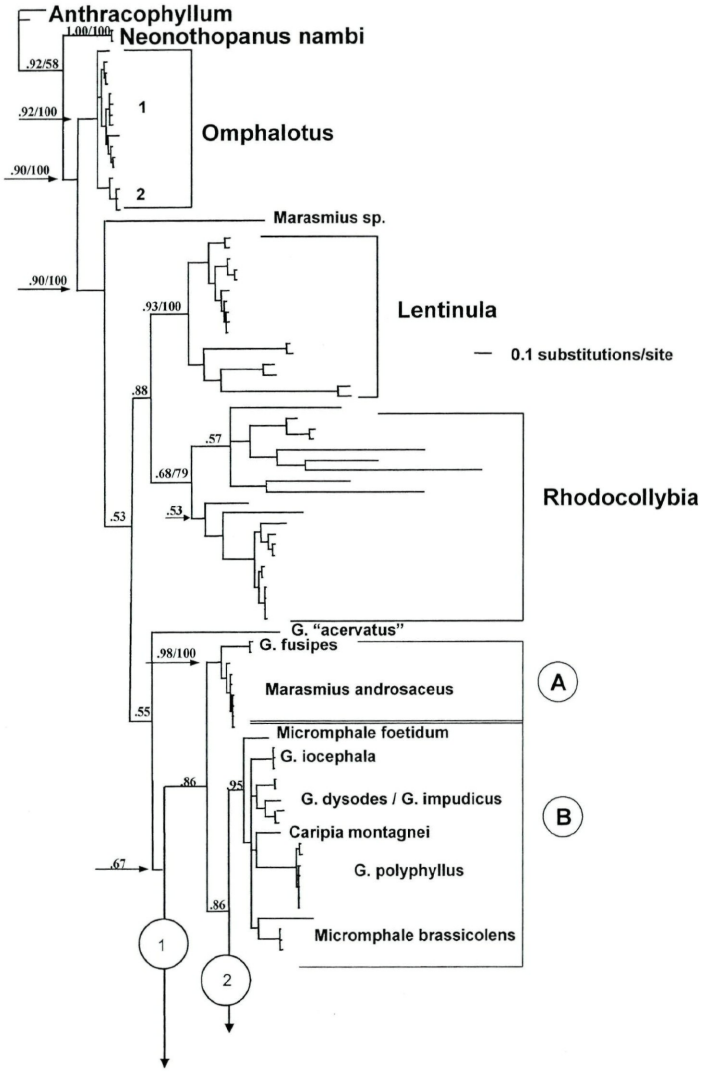


Fig. 2. Bayesian strict consensus tree of entire sequence data set based on 500,000 generations with trees sampled every 100 generations. Areas of uncertain alignment and long insertions present in only a few taxa were eliminated (313 characters). Burnin was set at 1000. Posterior probabilities are given for basal clades. *Anthracophyllum, Neonothopanus* and *Omphalotus* comprised the outgroup. Parsimony bootstrap support values are given to the right of the posterior probability where the same node is supported in both analyses. For parsimony analysis: Characters were unordered and equally weighted. Starting tree was obtained by stepwise addition. Addition sequence was furthest. The branch-swapping algorithm was tree-bisection-reconnection. Gaps were treated as a fifth base. Tree length = 8401. Consistency index (CI) = 0.28. Homoplasy index (HI) = 0.71.

Fig. 2 continued.

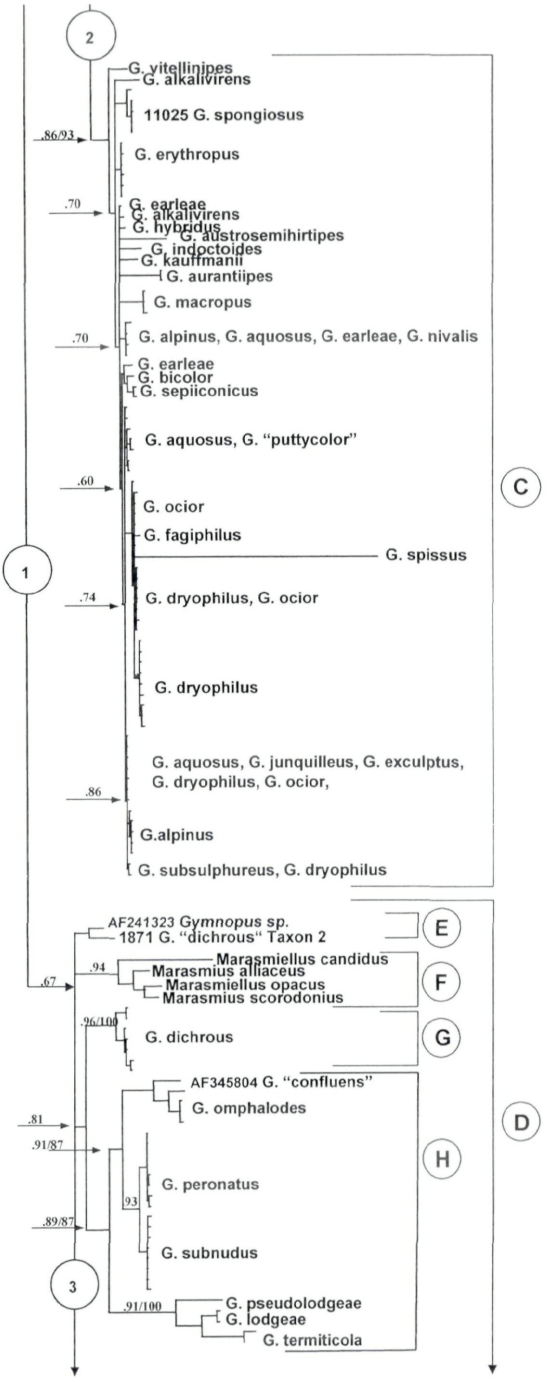
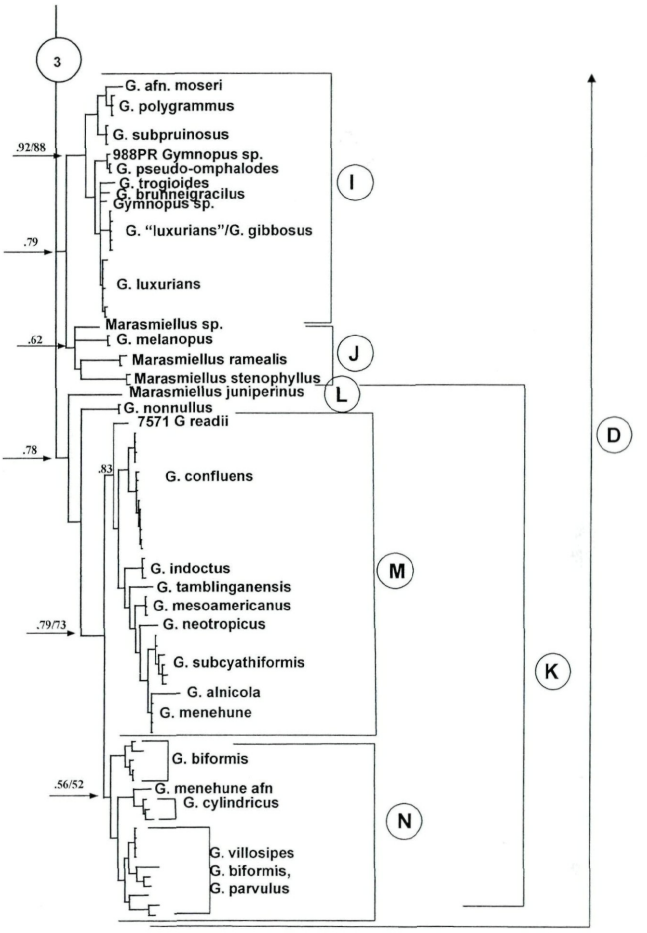


Fig. 2 continued.



analysis; however, alignment difficulties were so great that the sequence was deleted from further analyses. Because the species epithet was coined for a European organism, European collections are required for more accurate placement of this species.

Gymnopus (Clades A – N)

In order to refer to clades objectively, clades within *Gymnopus* have been assigned letters (Figs. 2 – 14). So far as possible, lettered clades are equated with taxo-nomenclatural names in Discussion.

Gymnopus (clades A – N) is a sister clade to *Lentinula/Rhodocollybia* but with poor support (.55 / <50 %; Fig. 2). This clade is

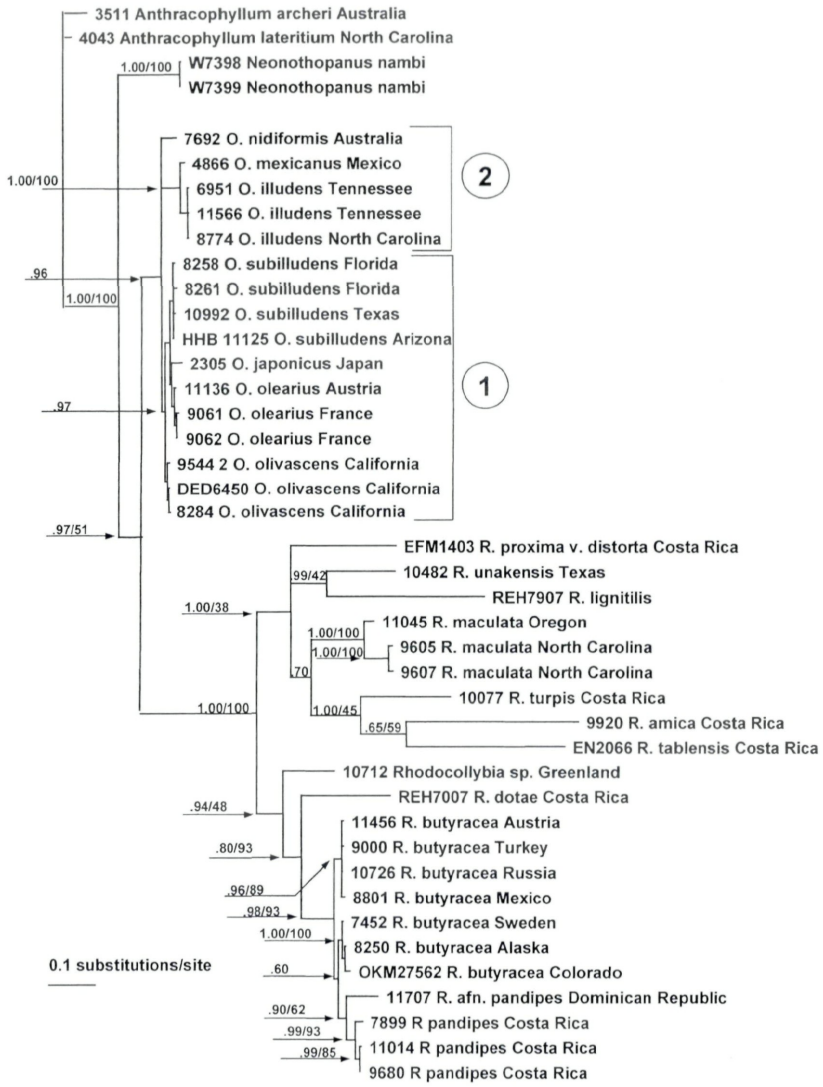


Fig. 3. Bayesian strict consensus tree of *Rhodocollybia* based on 500,000 generations with trees sampled every 100 generations. Burnin was set at 1000. Posterior probabilities are given for basal clades. *Anthracophyllum, Neonothopanus* and *Omphalotus* comprised the outgroup. Parsimony bootstrap support values are given to the right of the posterior probability where the same node is supported in both analyses. Characters were unordered and equally weighted. Starting tree was obtained by stepwise addition, the addition sequence was furthest. The branch-swapping algorithm was tree-bisection-reconnection, parsimony informative sites = 357, tree length = 1312, gaps treated as missing, CI = 0.57, HI = 0.42.

dominated by *Gymnopus* morphotaxa (as well as many others). While support for individual clades is often strong, the relative relationships among clades varies with the type of analysis and with the proportion of the ITS sequence used in an analysis.

Clades A/B/C (Figs. 2, 4)

The association of clades A, B, and C is poorly supported (.86 / < 50 %). Data for this grouping were re-analyzed with a more complete data set (21 bp removed for uncertain alignment; Fig. 4).

Clade A

Clade A encompasses the *typi generum* of *Gymnopus (G. fusipes)* and *Setulipes (S. androsaceus)* and is well-supported (1.00 / 100 %). A self-cross using *G. fusipes* TFB 11333 (France) revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 4$; $A_2B_2 = 1$; $A_1B_2 = 7$; $A_2B_1 = 12$. A self-cross using TFB 11439 (Austria) also revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 3$; $A_2B_2 = 2$; $A_1B_2 = 6$; A_2B_1 = not represented in the sample. When tester strains of TFB 11439 were paired with those of TFB 11333 (n = 8), pairings were universally intercompatible, indicating that a single intersterility group representing *G. fusipes* extends from at least central France to eastern Austria.

Self-crosses and intercollections pairings of *S. (Marasmius) androsaceus* were reported in Gordon (1994) and Gordon & Petersen (1997). Two populations were identified: 1) northern North America and Europe, fruiting on conifer needles; and 2) southeastern North America, fruiting on dead deciduous leaves. Sequences were limited to the Euro-American population (Fig. 4).

Clade B

Additional *typi generum, Micromphale (Mi. foetidum)* and *Caripia (Ca. montagnei)* are present in clade B. In our phylogenetic reconstruction, *Mi. foetida* appears basal to clade B, basidiomata of which share disagreeable odor. A self-cross of *Mi. foetida* using TFB 11434 (Austria) showed a tetrapolar mating system. Tester strains: $A_1B_1 = 3$; $A_2B_2 = 9$; $A_1B_2 = 10$; $A_2B_1 = 7$. TFB 11434 was paired with TFB 11431 (*M. brassicolens;* n = 8), but all pairings were incompatible. *G. salakensis,* an Indonesian taxon (Wilson *et al.* 2004), is found in a small clade within clade B).

Two collections of *Gymnopus dysodes* from North America in clade B (TFB 11040, TFB 11474) differ from material from Dominican

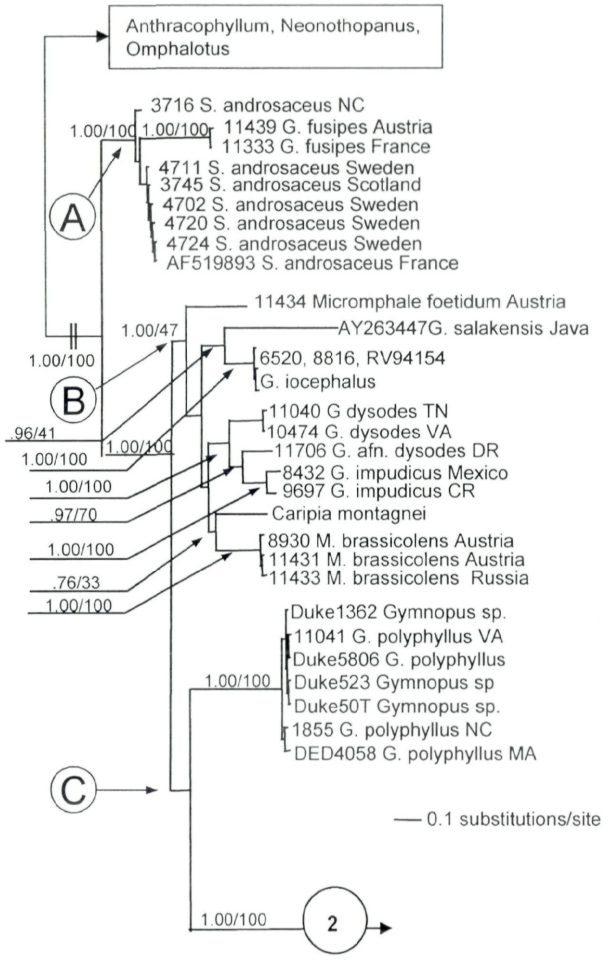
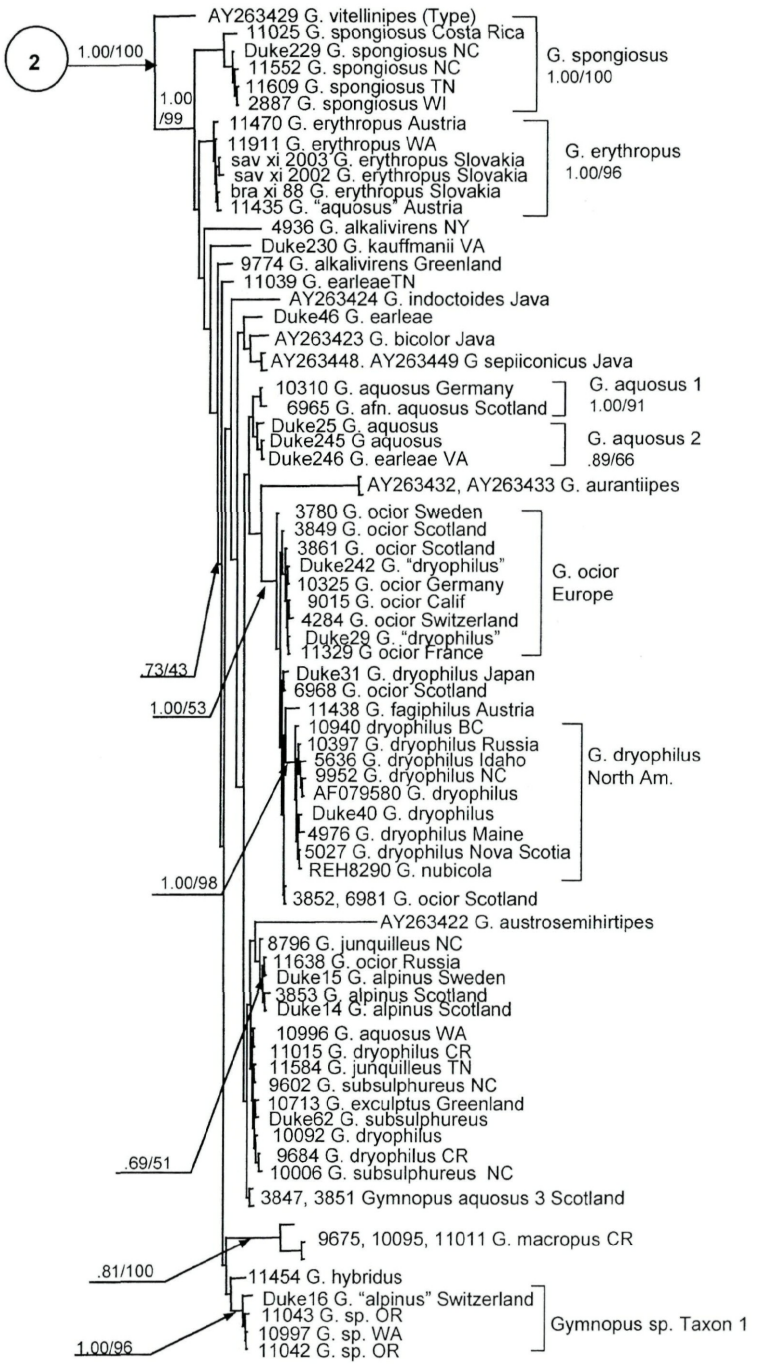


Fig. 4. Bayesian strict consensus tree of *Marasmius androsaceus*, *Micromphale foetidum*, *Gymnopus polyphyllus* and the *Gymnopus "dryophilus"* complex based on 500,000 generations with trees sampled every 100 generations. Burnin was set at 1000. Posterior probabilities are given for basal clades. *Anthracophyllum*, *Neonothopanus* and *Omphalotus* comprised the outgroup. Twenty-one of 1038 bases were eliminated as unalignable. Parsimony bootstrap support values are given to the right of the posterior probability where the same node is supported in both analyses. For parsimony analysis: Characters were unordered and equally weighted. Starting tree was obtained by stepwise addition. Addition sequence was furthest. The branch-swapping algorithm was tree-bisection-reconnection, parsimony informative sites = 406, tree length = 1237, gaps treated as missing, CI = 0.59, HI = 0.41.

Fig. 4 continued.



Republic (TFB 11706; Fig. 4). A self-cross using TFB 11040 revealed a superficially bipolar mating system. Tester strains: $A_1 = 3, 5$; $A_2 = 1, 2$. An alternative interpretation of the grid was possible (viz. Ginns 1974), however, in which dual mating types were assigned to some isolates, with the resulting conclusion of tetrapolarity. Conversely, a self-cross using TFB 10474 revealed a clearly tetrapolar mating system. Tester strains: $A_1B_1 = 3$; $A_2B_2 + A_1B_2 = 8$; $A_1B_2 = 6$; $A_2B_1 = 1$. Again, dual mating types were indicated, the result of either amphithallism or double spore harvest.

An intercollection pairing experiment using TFB 11040 (TN) × TFB 10474 (VA; n = 8) showed universal intercompatibility. Likewise, TFB 11190 (Dominican Republic-not sequenced) was universally intercompatible with TFB 11706 (Dominican Republic). Conversely, a similar experiment using TFB 11190 (DR) × TFB 10474 (VA, n = 8) was universally interINcompatible, indicating that the taxon from Dominican Republic belonged to a different intersterility group from the southeastern North American population. Although basidiomata are superficially similar, collections of *G. dysodes* (TFB 10474, TFB 11190) were universally interINcompatible with collections of *G. luxurians* (TFB 10350, TFB 10355).

Gymnopus impudicus appears in the same clade with *G. dysodes*, an association that is strongly supported (1.00/100). Collection TFB 9694 *(G. impudicus)* was compatible with TFB 9687, TFB 9697, TFB 9700 and TFB10013 also from the same location but collected during a different year (Mata 2002).

Collections of *Mi. brassicolens* used for sequencing originated in Austria and the Caucasus (Russia), and formed a well-supported clade. Two self-crosses were performed with *Mi. brassicolens*, both revealing tetrapolar mating systems. Tester strains of TFB 11433 (Austria): $A_1B_1 = 6$; $A_2B_2 = 3$; $A_1B_2 = 8$; $A_2B_1 = 7$. Tester strains of TFB 11431 (Austria): $A_1B_1 = 6$; $A_2B_2 = 7$; $A_1B_2 = 13$; $A_2B_1 = 14$. When tester strains of the two collections were paired (n = 8), all pairings were compatible, although the specimens were collected within a few hundred meters of each other and could feasibly share mating types. Intercollection pairings of TFB 11431 × TFB 11434 *(Mi. foetida)* and TFB 11433 × TFB 11434 were universally interINcompatible.

Clade C

The association of *G. polyphyllus* with the *G. dryophilus* complex (Clade C; Fig. 4) is not well-supported in Bayesian analysis nor in maximum parsimony (.59 / 50 %) where *G. polyphyllus* is part of clade B. Such lack of support is common to many of the deeper nodes within the entire phylogenetic reconstruction. *Gymnopus polyphyllus per se,* however, is a well-supported monophyletic clade.

Clade C; ("Levipedes," Fig. 4) includes numerous poorly separated groups based on ITS sequence data. Sequence differences in this group are few, often uninformative and complicated by a prevalence of dubious morphological identifications of phenotypically plastic species complexes. Several poorly supported clades appear dominated by collections bearing a single name (i.e. *G. dryophilus, G. ocior, G. aquosus,* etc.) but careful examination usually reveals disparate names as well. Included in these "adventitious" names are *G. alpinus, G. macropus, G. fagiphilus, G. junquilleus, G. hybridus, G. nubicola, G. earleae, G. sepiiconicus* and *G. aurantiipes*).

Subclades within the *dryophilus* complex are genetically heterogeneous and differ from each other by only 5 – 10 bp. Synapomorphies suggest variable affiliations. For example, the last clade in Fig. 4 ("*Gymnopus.* sp.") has 9 synapomorphies. Synapomorphy 1 ties this clade to *G. erythropus* and *G. spongiosa;* 2 ties this clade to *G. sepiiconicus* from Java; 3 ties this clade to *G. erythropus, G. sepiiconicus* and *G. macropus;* 4 ties this clade to everything except *G. macropus;* 5 ties this clade to the *G. dryophilus-G. ocior* group; 6 ties this clade to everything but the *G. dryophilus-G. ocior* group; 7 ties this group to *G. ocior* but not to *G. dryophila* and/or *G. erythropus, G. sepiiconicus* and *G. macropus;* 8 ties this clade to *G. spongiosus* and *G. alkalivirens;* and 9 ties this clade to *G. erythropus- G. alkalivirens.*

Although clearly a member of clade C, *G. vitellinipes* is basal to the *dryophilus* complex. The species is based on a collection from the Old World tropics (Java, Bali) and the sequence was derived from the type specimen

Gymnopus spongiosus and *G. erythropus* appear in well-supported clades. The appearance of TFB 11435, morphological *G. aquosus,* in this clade is aberrant.

Gymnopus earleae appears in two places within clade C but we have not examined Duke46, putative *G. earleae.* A self-cross of *G. earleae* (TFB 11039) revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 5$; $A_2B_2 = 10$; $A_1B_2 = 4$; $A_2B_1 = 8$.

Morphological *G. aquosus* is polyphyletic. Collections under this name are composed of two small but well-supported clades. TFB 6965 and TFB 10310 represent *G. aquosus* 1; Three Duke specimens, two of unknown origin, represent *G. aquosus* 2. Although these clades appear well-supported separately, support for association between them is low (.48 / 41 %). Another *G. aquosus* clade representing Scottish material (TFB 3847 and TFB 3851) is found near the bottom of clade C (Fig. 4; *G. aquosus* 3) and putative *G. aquosus* appears in one additional place in the phylogeny.

Mating experiments using Scottish collections identified as *G. aquosus* (*G. aquosus* 1 and 3) proved these collections intercompatible (Fig. 5). Examination of sequences for *G. aquosus*, clades 1, 2 and 3 showed 18 variable base positions of 737 total bases in the ITS area (2.4 %), sufficient to place these in separate clades within the *G. dryophilus* complex.

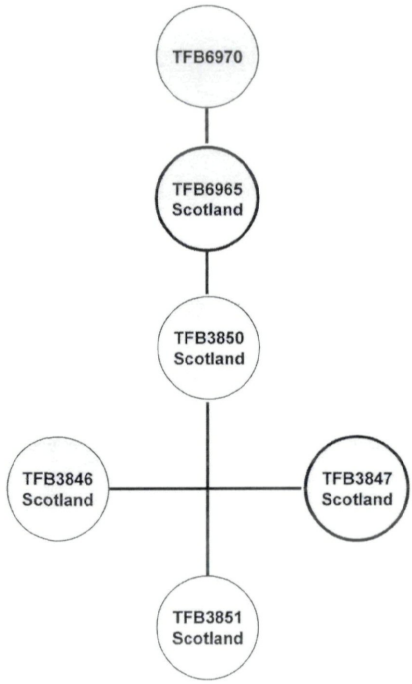


Fig. 5. Crosses among putative collections of *G. aquosus*. All collections are from Scotland. Bold lines around circles indicate collections in the phylogenetic analysis.

Gymnopus ocior and *G. dryophilus* are composed of a moderately supported clade (1.00 / 53 %) but do not assort well into monophyletic species groupings and two other morphological names, *G. nubicola* (Costa Rica) and *G. fagiphilus* (Austria), are found within this clade.

A self-cross using TFB 3849 (*G. ocior*, Scotland) revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 1$; $A_2B_2 = 2$; $A_1B_2 = 5$; $A_2B_1 = 18$. Figure 6 shows intercollection pairings among putative *G. ocior* collections, but includes two collections (TFB 3854, TFB 3857) field-identified as *G. aquosus* by British mycologists, again attesting to unreliability of morphological (at least color) characters in the classification of basidiomata of such taxa. Collections TFB 6968,

TFB 3849 and TFB 6981 have only a single variable base among them. A self-cross of *G. dryophilus* using TFB 11455 (Austria) revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 7$; $A_2B_2 = 1$; $A_1B_2 = 14$; $A_2B_1 = 6$.

A self-cross using TFB 8796 (as *G. junquilleus* in Fig. 4; USA, NC) revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 1$; $A_2B_2 = 2$; $A_1B_2 = 6$; $A_2B_1 = 3$. An intercollection pairing of TFB 8796 × TFB 11584 (USA, TN) was intercompatible. Collection TFB 8796 was paired with TFB 11455 (*G. dryophilus;* n = 8) and was interINcompatible; TFB 8796 was paired with TFB 9602 and TFB 10006 (*G. subsulphureus;* n = 8) and was interINcompatible with both. Collections TFB 8796 and TFB 11584 represent an intersterility group that is distinct from *G. dryophilus* or *G. subsulphureus*.

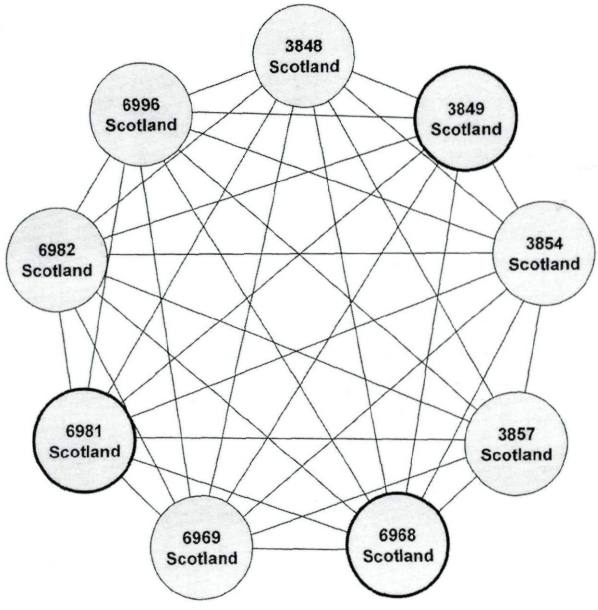


Fig. 6. Crosses among collections of *G. ocior*. All collections are from Scotland. Bold lines around circles indicate collections in the phylogenetic analysis.

Gymnopus alpinus appears in a clade with moderate support (.69 / 51). A self-cross of TFB 3858 (*G. alpinus*-not sequenced) revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 3$; $A_2B_2 = 2$; $A_1B_2 = 6$; $A_2B_1 = 9$. Intercollection pairings showed TFB 3858 to be intercompatible with TFB 3853 (Scotland) and these two collections to form a separate intersterility group within the *G. dryophilus* complex. Morphology of collection TFB 3853 indicates it is *G. alpinus:*

deep brown pileus colors, large spores and clavate-nodulose cheilocystidia.

Gymnopus exculptus (distinguished by yellowish lamella) appears with low support in a mixed clade. When TFB 10713 (*G. exculptus;* Greenland) was paired with *G. ocior* TFB 9898 (Russia), TFB 11329 (France) and TFB 3849 (UK, n = 8), all pairings were interINcompatible. Further, phylogenetic analyses place *G. ocior* and *G. exculptus* in different clades.

Three collections were made in the US Pacific Northwest (TFB 11043, TFB 11044) but, while intercompatible, these collections were universally interINcompatible with TFB 11039, *G. earleae,* which they resemble and sequences differ from those of eastern US *G. earleae.* The western collections differ among themselves in stature but not in micromorphology. This taxon remains unnamed (Taxon 1).

Superclade D

Superclade D consists of nine clades (Fig. 2): 1) "Taxon 2" (clade E); 2) *Ma. alliaceus, Me. opacus* and *Ma. scorodonius* (clade F); 3) *G. dichrous* (clade G); 4) *G. omphalodes, G. peronatus, G. subnudus* (clade H); 5) *G. gibbosus, G. luxurians, G. subpruinosus, G. polygrammus* (clade I); 6) *Me. stenophyllus, G. melanopus, Me. rameales* (clade J); 7) *Me. juniperinus* (clade L); 8) *G. nonnullus, G. confluens* complex (clade M); and 9) *G. biformis* complex (clade N). Clades L – N make up superclade K.

Clades E, F, G/H, I/J and K (= L/M/N) are all sister clades with moderate Bayesian support but not high support in parsimony analysis [posterior probabilities: F = .94; G/H = .81; I/J = .79; K = .78 (Fig. 2)]. These clades appear in both Bayesian and parsimony analyses of the entire data set (Fig. 2) and in data sets consisting only of taxa within subclades of sect. *Vestipedes,* but relationships among these clades are unclear and vary with the type of analysis and amount of sequence data excluded from the analysis.

Sequences of some taxa within clade D contain between two and five copies of a variable ca. 34 bp repeat (Table 2). There is a region roughly homologous to repeat 4 in clade C. This is discussed further under clade N *(Gymnopus biformis).* The presence of a variable duplicated region in clade N, particularly in *G. biformis* (Table 3), complicated phylogenetic analyses. Analyses were performed with and without parts or all of the repeat area with varying results (data not shown). For this reason, each of the major clades within clade D was analyzed separately, using the maximum alignable sequence data available for that clade.

Clade E (Fig. 2)

True *G. dichrous* appears in clade G (Figs. 2, 7). While TFB 1871 is morphologically indistinguishable from *G. dichrous,* it appears in clade E. Clade E consists of TFB 1871 together with a sequence from an environmental sample, AF241323, but the two sequences are distinct from each other and probably represent different taxa.

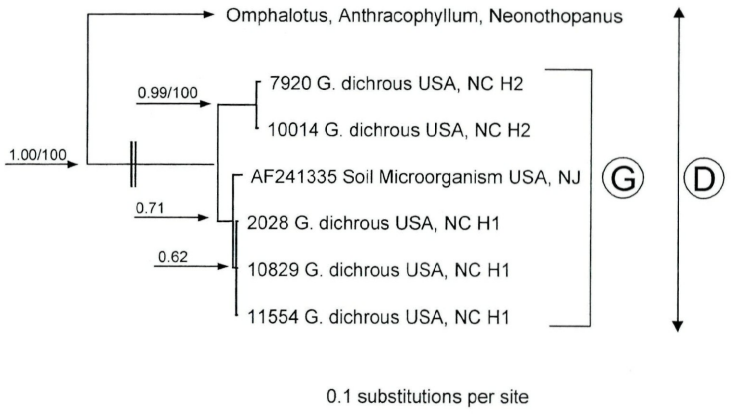


Fig. 7. Bayesian strict consensus tree of *Gymnopus dichrous* based on 500,000 generations with trees sampled every 100 generations. Burnin was set at 1000. Posterior probabilities are given for basal clades. *Anthracophyllum, Neonothopanus* and *Omphalotus* comprised the outgroup. Parsimony bootstrap support values are given to the right of the posterior probability where the same node is supported in both analyses. For parsimony analysis: Characters were unordered and equally weighted. Starting tree was obtained by stepwise addition. Addition sequence was furthest. The branch-swapping algorithm was tree-bisection-reconnection, parsimony informative sites = 364, tree length = 670, gaps treated as fifth base, CI = 0.84, HI = 0.16.

Clade F (Fig. 2)

Marasmiellus opacus, Ma. alliaceus, Ma. scorodonius and *Me. candidus* group together in a moderately supported clade (.94 pp; Fig. 2). In our study, *Me. candidus* is basal to this clade but this position is only supported in Bayesian analysis.

We performed a self-cross of *Marasmius alliaceus,* the type species of *Marasmius* sect. *Alliacei* Kühner (Antonín & Noordeloos, 1993), using TFB 11352 (France), which revealed a tetrapolar system. Tester strains: A_1B_1 = 2; A_2B_2 = 3; A_1B_2 = not represented in the sample; A_2B_1 = 8.

Clade G (Figs. 2, 7, 8)

Gymnopus dichrous forms a well-supported clade (0.96 / 100; Fig. 2). Two haplotypes were identified within *G. dichrous* (Fig. 7). These haplotypes were sexually intercompatible (Fig. 8) and represent a single biological species. An unidentified environmental sample also falls within this clade.

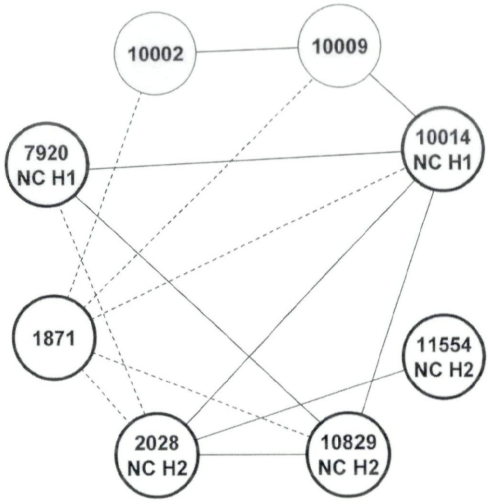


Fig. 8. Crosses among collections of Gymnopus dichrous. Dashed lines indicate crosses were attempted but failed. Solid lines indicate crosses succeeded. No lines indicate that a cross was not made. H1 and H2 represent haplotypes of *G. dichrous*. Circles with bold lines represent collections with ITS sequences in this study.

Clade H (Figs. 2, 9)

A Bayesian consensus tree for clade H is given in Fig. 9. The major clades, *G. lodgae* and associated taxa, *G. omphalodes, G. peronatus* and *G. subnudus,* are well-supported in both Bayesian and parsimony analyses (.89 / 87, Fig. 2)

Parsimony and Bayesian analyses differed with respect to the position of *G. pseudolodgeae.* In parsimony analysis, *G. pseudolodgeae* was basal to the clade, while in Bayesian the positions were reversed. *Gymnopus pseudolodgeae* is morphologically similar to *G. lodgae* but ITS sequences of the two taxa are quite divergent (Fig. 9). The sequence for *G. pseudolodgeae* is *ex typus* (see Mata 2002; Mata *et al.* 2004 a).

A self-cross using *G. pseudolodgeae* TFB 10493 revealed a bipolar mating system, with little mitigating evidence. An inter-

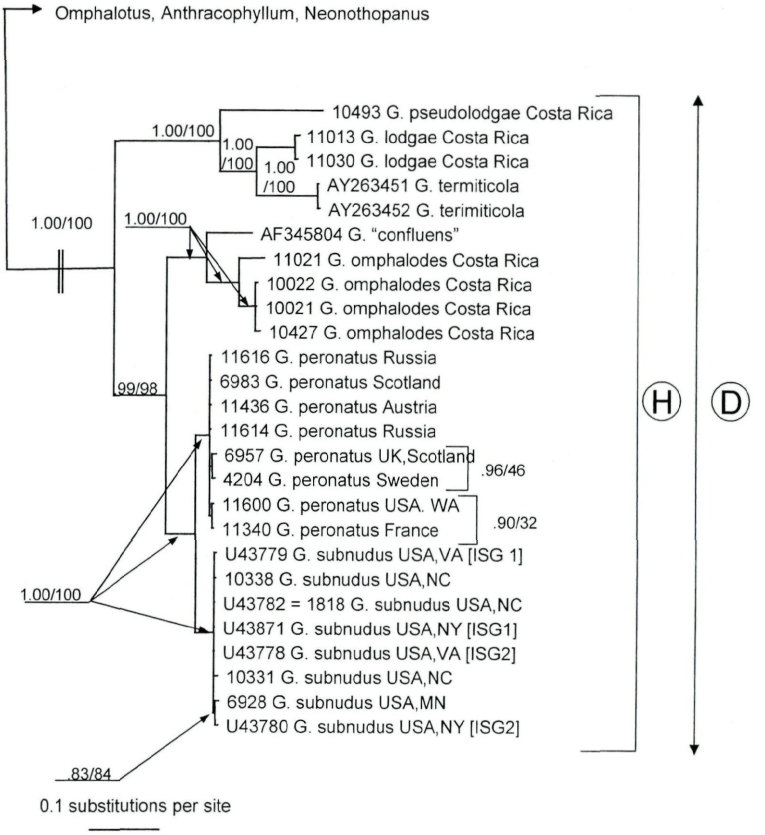


Fig. 9. Bayesian strict consensus tree of/peronati based on 500,000 generations with trees sampled every 100 generations. Burnin was set at 1000. Posterior probabilities are given for basal clades. *Anthracophyllum, Neonothopanus* and *Omphalotus* comprised the outgroup. Parsimony bootstrap support values are given to the right of the posterior probability where the same node is supported in both analyses. For parsimony analysis: Characters were unordered and equally weighted. Starting tree was obtained by stepwise addition. Addition sequence was furthest. The branch-swapping algorithm was tree-bisection-reconnection, parsimony informative sites = 513, tree length = 1227, gaps treated as fifth base, CI = 0.74, HI = 0.26. ISG = intersterility groups (Murphey 1995; Murphey & Miller 1997).

collection pairing between TFB 10493 and TFB 11013 (*G. lodgeae;* n = 8) was universally interINcompatible.

Gymnopus omphalodes, G. peronatus and *G. subnudus* formed well-supported monophyletic clades (Fig. 9). A collection deposited as *G. "confluens"* was basal *to G. omphalodes.* In three series of pairing experiments, collections of *G. peronatus* from western North America were found to belong to the same biological species as collections from Europe (Fig. 10).

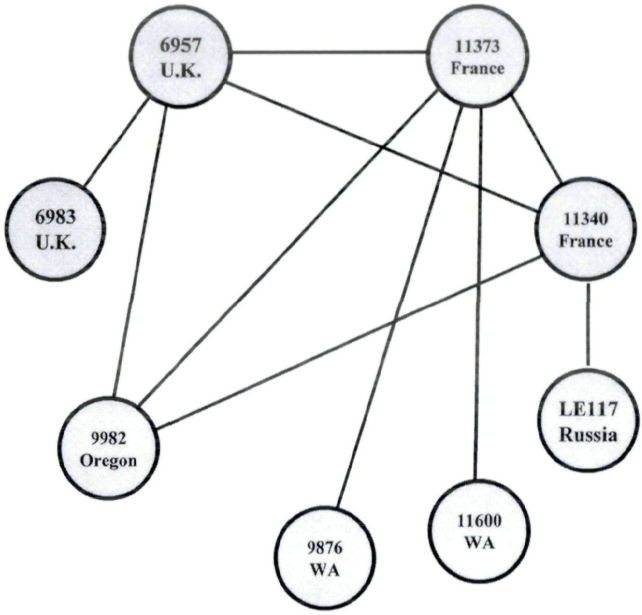


Fig. 10. Crosses among collections of *Gymnopus peronatus*. Bold lines indicate successful crosses. No lines indicate that a cross was not attempted.

Clade I (Figs. 2, 11)

Clade I is moderately supported in Bayesian and parsimony analyses (.92 / 88 %). The clade comprises a number of tropical *Gymnopus* taxa and the Euro-American *G. luxurians*, and is sister to a seemingly anomalous clade of traditionally *Marasmiellus* taxa (clade J). Most subclades within clade I are well-supported and appear to segregate single species or small groups (Fig. 11).

Collections of *G. subpruinosus* and *G. polygrammus* form a well-supported (.96 / 70 %) monophyletic clade in both Bayesian and parsimony analyses. *Gymnopus subpruinosus* collections from California and Hawaii are identical in sequence and form a monophyletic clade (1.00 / 99 %). Results of a self cross of TFB 9529 (*G. subpruinosus;* USA, California) showed *G. subpruinosus* to be tetrapolar. Tester strains: $A_1B_1 = 1$; $A_2B_2 = 3$; $A_1B_2 = 2$; $A_2B_1 = 7$.

All three sequences of *G. polygrammus* were derived from Puerto Rican collections. A self-cross using TFB 9628 revealed a tetrapolar mating system. Tester strains: $A_1B_1 = 2$; $A_2B_2 = 14$; A_1B_2 = not represented in the sample; $A_2B_1 = 11$. An intercollection pairing of TFB 9628 × TFB 9631 (n = 4) was universally intercompatible.

Sequence AY263431, *Gymnopus afn. moseri* from Indonesia, is basal to three collections of *G. polygrammus* and is morpho-

logically more similar to them than with authentic *G. moseri* (Wilson & Desjardin 2003, 2005).

Three collections, from Costa Rica and Puerto Rico form a small but well-supported clade (1.00 / 100 %) designated as *Gymnopus afn. pseudo-omphalodes*.

The *trogioides/gibbosus/luxurians* clade is moderately supported (.85 / 43 %, Fig. 11). *Gymnopus trogioides* is sister to the *G. gibbosus* and *G. luxurians* subclades, which are well-supported.

The *G. gibbosus* clade is a small, well-supported group (1.00 / 98 %, Fig. 11) that includes *G. gibbosus* and two collections of uncertain identity from the Hawaiian Islands. Sequences of putative *G. gibbosus* were derived from Indonesian collections by Wilson *et al.* (2004). Sequences of *G. gibbosus* differ from *G. "luxurians"* (Hawaii) by 1 bp. The organism reported as *G. luxurians* from the Hawaiian Islands (Desjardin *et al.* 1999) differs from Euro-American *G. luxurians* by 23 bp or 3.39 %. Collections TFB 11585 and TFB 11586 (both *G. "luxurians"*, Hawaii), were paired with TFB 4283 (*G. luxurians*, Switzerland), TFB 10350 (USA, NC), TFB 10476 (USA, TN) and TFB 10447 (USA, TN) (n = 8) and showed universal interINcompatibility. Sexual interINcompatibility and sequence differences may indicate that Hawaiian collections represent a separate taxon, affiliated with or the same as *G. gibbosus*.

The *G. brunneigracilis* sequence is found together with that of a New World tropical collection (TFB 11026, *G. luxurians* var. *copeyi*, (see Appendix 1). The two sequences are 97 % homologous. Support for this clade is poor (Fig. 11).

A single collection of *G. luxurians var. copeyi* (TFB 11026) was collected in Costa Rica as *G. dichrous*. A self-cross revealed a tetrapolar mating system (Mata 2002). Intercollection pairing experiments using TFB 11026 × North American collections of *G. dichrous* (TFB 10009, TFB 10014; n = 4) were universally interINcompatible, although inter-North American collections were intercompatible. The ITS sequence placed this collection in a sister clade to Euro-American *G. luxurians* (Fig. 12), and the Costa Rican specimen shared several characters with *G. luxurians*, especially basidioma morphology, habit on wood, and diagnostic inflated, conspicuous cheilocystidia. Basidiospores as described by Halling (1983; for North Temperate *G. luxurians*) were somewhat narrower (9.8 – 11.8 × 3.2 – 4.4 µm), and basidia somewhat shorter (20.5 – 27 × 4.2 – 6.6 µm) than those of TFB 11026 (basidiospores 8.8 – 12.8 × 4.0 – 5.6 µm; basidia 29 – 40 × 6 – 8 µm).

Gymnopus luxurians collections from Europe, North America and the Dominican Republic are monophyletic, differing from each other by only 1 – 2 bp.

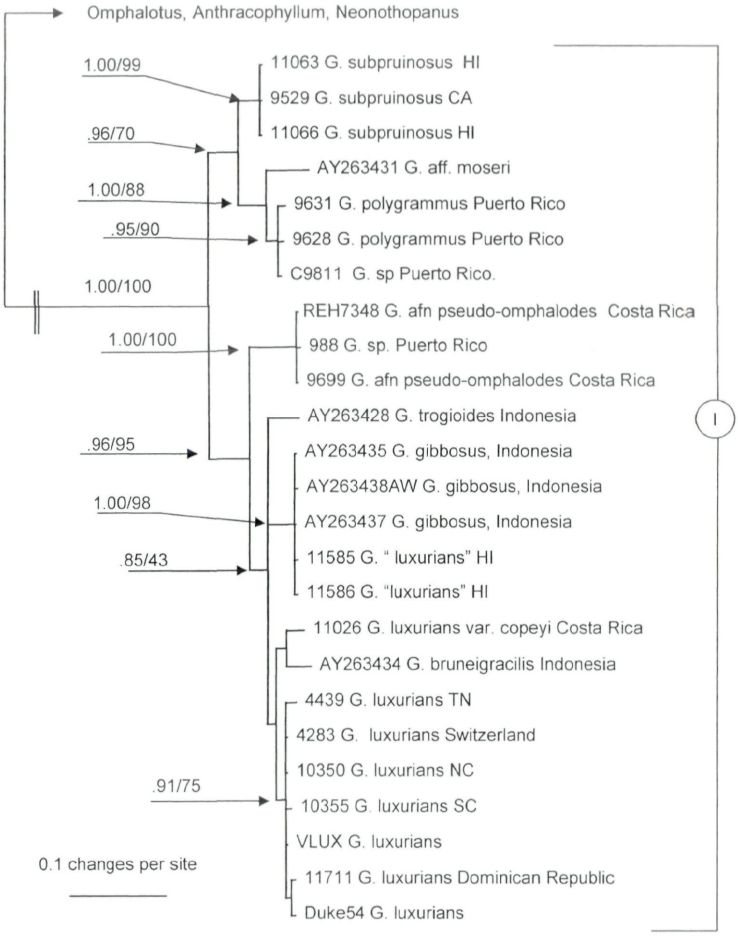


Fig. 11. Bayesian strict consensus tree of *G. luxurians* and related taxa based on 500,000 generations with trees sampled every 100 generations. Burnin was set at 1000. Posterior probabilities are given for basal clades. *Anthracophyllum, Neonothopanus* and *Omphalotus* comprised the outgroup. Parsimony bootstrap support values are given to the right of the posterior probability where the same node is supported in both analyses. For parsimony analysis: Characters were unordered and equally weighted. Starting tree was obtained by stepwise addition. Addition sequence was furthest. The branch-swapping algorithm was tree-bisection-reconnection, parsimony informative sites = 251, tree length = 502, gaps treated as missing, CI = 0.74, HI = 0.26.

A self-cross was performed using TFB 10355 and showed a tetrapolar mating system. Tester strains: A_1B_1 = not represented in the sample; $A_2B_2 = 1$; $A_1B_2 = 12$; $A_2B_1 = 7$; $A_1B_1 + A_1B_2 = 9$. Several series of intercollection pairing experiments were performed (Fig. 13): 1) TFB 4283 (Switzerland) × TFB 10355 (South Carolina; n = 8),

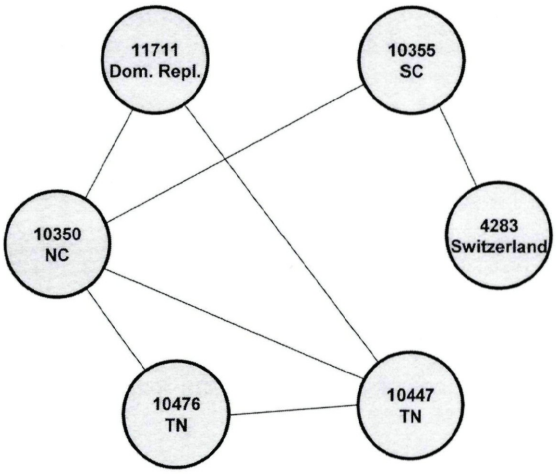


Fig. 12. Crosses among collections of *Gymnopus luxurians*. Bold lines indicate successful crosses. No lines indicate that a cross was not attempted.

universally intercompatible; 2) TFB 10355 × TFB 10350 (North Carolina; n = 4), universally intercompatible; 3) round-robin of TFB 10350, TFB 10447 (Tennessee), TFB 10476 (Tennessee), all intercompatible; 4) TFB 11711 (Dominican Republic) × TFB 10350 (North Carolina) and TFB 11711 × TFB 10447 (Tennessee; n = 8), overwhelmingly intercompatible.

Clade J (Fig. 2)

Clade J (Fig. 2) comprises three small sister clades: 1) one sequence from an unidentified *Marasmiellus* collection from North Carolina; 2) two sequences of *G. melanopus* from Indonesia; and 3) two sequences of *Me. ramealis* from Sweden plus two sequences of North American *Me. stenophyllus*. *Marasmiellus ramealis* was always found within superclade D usually associated with *G. melanopus* (Indonesia) plus *Me. stenophyllus* but sometimes as a separate clade, dictated by the analysis. The clade is poorly supported in Bayesian analysis (.62) and even more poorly supported in parsimony analysis.

Superclade K (Fig. 2, 13)

A large and seemingly heterogeneous assemblage, clade K is poorly supported (.78 / < 50 %; Fig. 2). It is sister to clades E, F, G/H and I/J, all of which have similar poor support. In Bayesian analysis of the complete *Gymnopus* data set (Fig. 2), *Me. juniperinus*

is basal to clades M and N containing *G. biformis, G. confluens* and *G. cylindricus*. In a parsimony semi-strict consensus tree (data not shown), *Me. juniperinus* is associated with *G. fusipes* and *Ma. androsaceus,* again with poor bootstrap support. When data were reanalyzed, deleting the clades A-C and using more base pairs of the ITS sequence data, *Me. juniperinus* was basal to clade K in all analyses (including and excluding tandem repeat regions) but additional taxa were sometimes included within the *biformis* clade (Fig. 13). In the re-analysis, *G. nonnullus* remains basal to clade K and is strongly supported (1.00 / 100 %). Clade M/N is well-supported (.97 / 62 %; Fig. 13) but clade M is only moderately supported (.97 / 36 %) and clade N is poorly supported. Support for subclades varies, apparently influenced by inclusion/exclusion of *G. readii,* a divergent species from New Zealand, and by the inclusion or exclusions of a tandem repeat present in much of clade D.

Three strongly supported sequences of *G. indoctus* appear basal to a primarily tropical clade (Fig. 13). A sequence from Indonesia, *G. tamblinganensis,* is in this clade (Fig. 13), as are *G. alnicolus* and *G. neotropicus,* both from Costa Rica.

Gymnopus mesoamericanus is phenotypically similar to *G. biformis* but clearly separated on the basis of DNA sequence. It is proposed as a new taxon (see Appendix 1).

Gymnopus subcyathiformis, also phenotypically similar to *G. biformis,* is represented by collections from Mexico, Costa Rica, Puerto Rico and the Dominican Republic. A self-cross of nine SBIs from collection *G. subcyathiformis* TFB 10436 (as *G. impudicus* in Mata 2002) revealed a tetrapolar mating system. Mating types: $A_1B_1 = 8$; $A_2B_2 = 2$; $A_1B_2 = 7$; $A_2B_1 = 3$. A second self-cross used TFB 11035 [as *G. biformis*]. A small sample of SBIs (5) showed a tetrapolar mating system. Tester strains: $A_1B_1 = 1$; $A_1B_2 = 2$; $A_2B_1 = 7$; A_2B_2 not represented in the sample. Intercollection pairings among TFB 10433, TFB 10435, TFB 10436 and TFB 10437 demonstrated that these specimens from tropical Costa Rica were intercompatible.

An intercollection pairing experiment using TFB 11714 [Dominican Republic] × TFB 7230 [USA, South Carolina; *G. biformis;* n = 4] was uniformly interINcompatible. Of 20 putative SBIs harvested of TFB 11714, 19 bore clamp connections, indicating either extremely poor germling harvesting or strongly amphithallic behavior.

G. menehune appears in a single well-supported clade (.95 / 93 %) that includes sequences from Hawaii and Indonesia. The species may be considered to extend to other Pacific Ocean landmasses. A self-cross was accomplished with SBIs harvested from collection TFB11587 (USA, Hawaii). The mating system was tetrapolar. Tester strains: $A_1B_1 = 3$; $A_2B_2 = 4$; $A_1B_2 = 6$; $A_2B_1 = 2$.

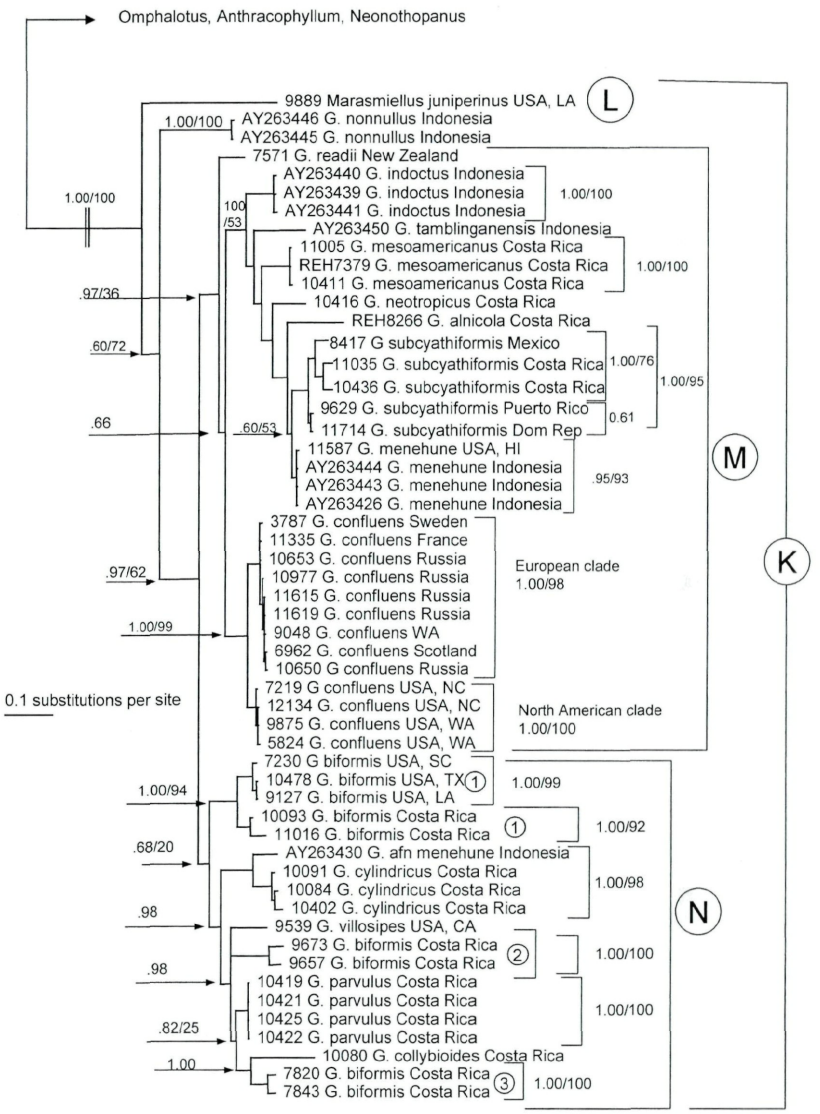


Fig. 13. Bayesian strict consensus tree of Clade K in Figure 2 based on 500,000 generations with trees sampled every 100 generations. Burnin was set at 1000. Posterior probabilities are given for basal clades. *Anthracophyllum, Neonothopanus* and *Omphalotus* comprised the outgroup. A total of 101 characters (tandem repeat area) were removed from the analysis. Parsimony bootstrap support values are given to the right of the posterior probability where the same node is supported in both analyses. For parsimony analysis: Characters were unordered and equally weighted. Starting tree was obtained by stepwise addition. Addition sequence was furthest. The branch-swapping algorithm was tree-bisection-reconnection, gaps were treated as missing data. Parsimony informative sites = 355, tree length = 1128, CI = 0.56, HI = 0.43.

The *G. confluens* complex as represented in Fig. 13 is limited to European and American collections, but subclades can be identified, including a strongly supported (1.00 / 100 %) North American clade (TFB 9875, TFB 5824, TFB 7219, TFB 12134). European collections (including southern Ural Mountains of Russia) segregate into a strongly supported (1.00 / 98 %) sister clade, but include a California collection. That a Washington collection (TFB 9875) and the California collection (TFB 9048) should be found in two sister clades may indicate that *G. confluens* along the coast of western North America comprises at least two strains, one of Eurasian origin, the other American, all in the face of complete intercollection intercompatibility (Fig. 14).

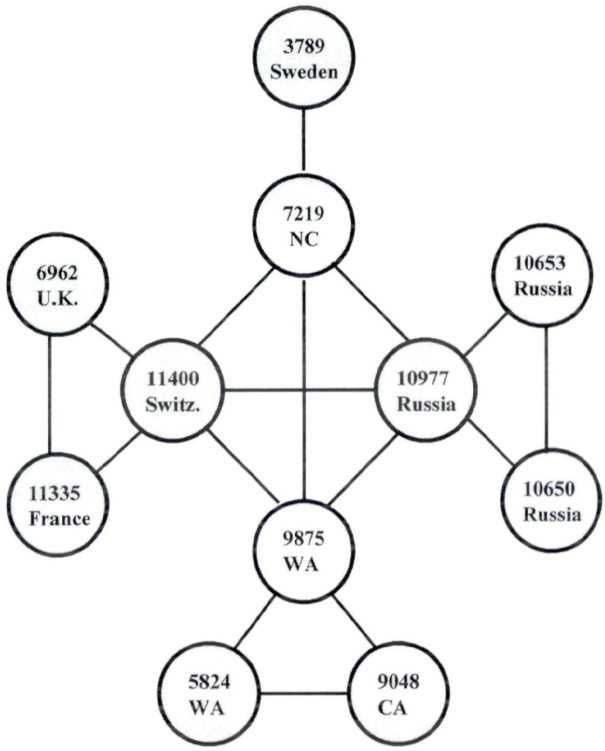


Fig. 14. Crosses among collections of *Gymnopus confluens*. Bold lines indicate successful crosses. No lines indicate that a cross was not attempted.

In *G. confluens*, basidiospores shed directly on agar germinate slowly (starting at one week, for at least seven weeks) and very sparsely (perhaps 1/10 000). Often not enough SBIs can be harvested for an ample self-cross. Moreover, because spores often germinate in

the heaviest area of the spore print, it is difficult to isolate a single germinating spore without other ungerminated (but perhaps soon to germinate) spores.

We performed three self-crosses using TFB 7219 (USA, North Carolina: tester strains: A_1B_1 = 6; $A_2 2B_2$ = 8; A_1B_2 = 5; A_2B_1 = 4.); TFB 9048 (USA, California: tester strains A_1B_1 = 16; $A_2B_2 + A_2B_1$ = 3; $A_2B_2 + A_1B_2$ = 11; A_2B_1 = 15) and TFB 11400 (Switzerland; tester strains A_1B_1 = 1; A_2B_2 = 2; A_1B_2 = 4; A_2B_1 = 7). In all cases, tetrapolarity was clear or easily inferred.

A complex series of intercollection pairings was accomplished, using collections in the phylogenetic reconstruction plus three additional collections (Fig. 14). All intercollection pairings (n = 8) exhibited partial to universal intercompatibility, indicating that a single biological species occurred through temperate North America and Europe. Sexual intercompatibility is supported by placement in a single strongly supported (1.00 / 99 %) clade (Fig. 13).

Clade N (Figs. 2, 13)

Clade N is poorly supported (.68 / 20 %, Fig. 2). Although treated here as a single clade, at least three subclades are easily identified, equating to single species or small species complexes.

Morphological *G. biformis* is polyphyletic in analyses based on parsimony with gaps treated as a fifth base and in Bayesian analyses (Fig. 13). In both parsimony and Bayesian analyses, sequence data were analyzed with the entire repeat area eliminated and with only repeats 1, 2 and 5 eliminated (see Table 3). Phylogenies differed with respect to relationships between and within clades with different treatments of repeat data.

Gymnopus biformis clade is well-supported (1.00 / 94 %). The clade clearly segregates two subclades, one of southeastern North American collections (1.00 / 99 %), the other of Costa Rican material (1.00 / 92 %). A self-cross was performed using TFB 7230 (USA, South Carolina) and revealed a tetrapolar mating system. Tester strains: A_1B_2 = 1; A_2B_2 = 11; A_1B_2 = 18; A_2B_1 = 2. An intercollection pairing experiment used TFB 9111 (USA, Louisiana), TFB 9516 (USA, Louisiana), TFB 7230 (USA, South Carolina) and TFB 9127 (USA, Louisiana). All pairings were compatible indicating a single biological species. When SBIs of TFB 11035 *(G. subcyathiformis)* were paired with those of TFB 7230 (*G. biformis;* USA, SC), TFB 9657 (*G. biformis,* Costa Rica) and TFB 10425 (*G. parvulus;* Costa Rica), all pairings were interINcompatible (Mata, 2002). In a separate pairing experiment, collections TFB 9657 and TFB 9673 (*G. biformis* 2, Costa Rica) were paired against each other (n = 4). No clamp connections were observed in any of these pairings (data not shown) in spite of the

fact that collections TFB 9673 and TFB 9657 appear in the same clade. Collections TFB 9673 and TFB 9657 however, differ in sequence (97 % similarity) and may represent cryptic species. In pairings of TFB 9657 and TFB 11016 (both *G. biformis* from Costa Rica but found in separate clades) with TFB 7230 and TFB 9111 (*G. biformis;* USA, Louisiana; not included in phylogeny; n = 4) no clamp connections were observed (data not shown).

The positions of tandem repeat elements within morphological *G. biformis* are given in Table 3. Repeats in positions three and four were present in all collections of *G. biformis*. The repeat in position two in collection TFB 7230 from South Carolina was an exact tandem duplication of position three within the same collection. Repeat in position two is present in only this collection and may therefore be a relatively recent event. In collections TFB 7820 and TFB 7843, the region between the repeat in position one and position three is occupied by a sequence that does not have homology to a repeat region. A search for a matching pattern using "BestFit" in GCG identified a homologous region immediately 5' to the repeat area.

Gymnopus afn. *menehune* from Indonesia appears as basal to *G. cylindricus* with strong clade support (1.00 / 99 %). The sequence similarity suggests that this clade may represent a wide-spread species or species complex.

A clade containing *G. villosipes* and *G. parvulus* (Fig. 13) is well-supported in Bayesian analysis but not in parsimony analysis (.98 / <50 %). A self-cross using *G. villosipes* TFB 9539 revealed a tetrapolar mating system. Tester strains: A_1B_1 = 7; A_2B_2 = 1; A_1B_2 = 13; A_2B_1 = 9. No additional material was available for intercollection pairings.

Micromorphological characteristics of *G. parvulus* are similar to those in *G. biformis* but spore dimensions and quotient appear to be different [i.e. *G. parvulus:* x = 7.2 × 3.5 µm, Qx = 2.08; *G. biformis:* x = 8.1 × 3.7 µm, Qx = 2.21; *G. biformis var. lobatus:* x = 7.3 × 3.4 µm, Qx = 2.10]. It was not possible to recover enough SBIs of *G. parvulus* to perform a self-cross. Three SBIs from collection TFB 10422 were paired with six of TFB 10425 resulting in 33 % compatibility. When SBIs (n = 4) of TFB 10422 and TFB 10425 were paired with TFB 9657 and TFB 11016 *(G. biformis)* no clamp connections were observed.

A small clade, which includes an authenticated name (TFB 10080, *G. collybioides*) and two unsecured collections (TFB 7820 and TFB 7843, originally collected as *G. biformis*), is well-supported in Bayesian analysis (1.00 pp), but not so in maximum parsimony. Sequences for the two *G. biformis* collections, however, are divergent from *G. collybioides* and probably do not represent the same taxon.

Discussion

1. Relative support weakness/strength for deep nodes

Repeatedly, deep nodes in our phylogeny are supported in Bayesian analysis but not in maximum parsimony. This may support the hypothesis that Bayesian analysis tends to over-estimate relationships, while parsimony may underestimate (Simmons *et al.* 2004). Bayesian analysis produced a better resolved phylogeny than parsimony analysis but a number of well-supported clades are evident in both types of analyses.

Within outgroups (*Anthracophyllum, Neonothopanus, Omphalotus*) nodes are strongly supported using both analytical methods (Fig. 2), but next higher orders of nodes are supported only in Bayesian analysis [i.e. segregation of *Lentinula/Rhodocollybia* from *Gymnopus* (.55 pp); segregation of clades A, B/C from the rest of *Gymnopus* (.86 pp); most nodes within clade D, etc.). This is a problem common to many comprehensive ITS phylogenetic reconstructions, largely because divergent sequences are difficult to align accurately and parts of the sequence may be saturated with mutations.

2. Unidentified sequences

Two "unnamed" sequences derived from soil and/or litter samples are found within this phylogeny. They are GenBank No. AF241335 within the *G. dichrous* clade (Fig. 7), and GenBank No. AF241323 in clade E (Fig. 2: Polishook *et al.* unpubl.). Because these sequences were obtained directly from environmental sampling with no associated basidiomata, the "morpho-identity" of the "unidentified sequences" cannot be ascertained. It might be assumed that somatic mycelial cells of *Gymnopus* were harvested in soil or litter, but in only rare instances (i.e. a clade homogeneous for an organism indigenous to the geographic location of the soil/litter sample) can an identity warrant a guess. It is obvious that sequences of many "soil" fungi will be placed in phylogenies of sexually reproductive groups once such phylogenies represent many known fungal taxa (i.e. sequences of mitosporic soil fungi in phylogenies of Ascomycota, etc.). Placement within a phylogeny, however, does not dictate an identity, and whether these soil/litter organisms exist *only* as mycelium, or whether they are associated with an organism known to fruit but perhaps not previously reported or not fruiting simultaneous to the soil/litter sampling cannot be accurately assessed. Occurrence of "chimeric sequences" as artifacts of laboratory processing may "create" sequences which remain unidentified for the foreseeable future (Wang & Wang 1997,

Thompson *et al.* 2002). Such situations raise questions concerning the relationships of "unidentified" sequences to putative biodiversity (Vandenkoornhuyse *et al.* 2002; O'Brien *et al.* 2005). Figures reporting large numbers of hitherto undiscovered soil/litter organisms remain unreliable as long as the data bases for known, sexually reproducing taxa are still rudimentary.

3. Role of mating systems in species concepts

Frequently, data on sexual compatibility pairing experiments are reported above. These experiments were performed in order to test the internal cohesion of species and to evaluate sexual barriers between putative species. Sexual compatibility experiments were previously used in *Gymnopus* (as *Collybia*) by Vilgalys (1991), Vilgalys & Miller (1983, 1987b) and Vilgalys & Johnson (1987) and in other groups as well (*Flammulina;* Petersen *et al.* 1999), *Pleurotus* (Vilgalys *et al.* 1993; Petersen 1995b), *Lentinellus* (Petersen & Hughes 2004) and *Omphalotus* (Petersen & Hughes 1998) to define intersterility groups.

For example, *G. luxurians* collections from Europe and eastern North America were sexually intercompatible, but collections from the Hawaiian Islands (Hemmes & Desjardin 2002), while intercompatible with one another, were interINcompatible with Euro-American collections. While it might be tempting to invoke long-term geographic separation as the cause of such interINcompatibility, experience with other taxa (see *G. subpruinosus*) indicates some suppression of compatibility, but not total inhibition. Moreover, this result is supported phylogenetically (Fig. 11), and raises doubts concerning the identification of the Hawaiian basidiomata.

Gymnopus peronatus collections from Europe and western North America were universally sexually intercompatible (Fig. 10). Although segregation of subclades within *G. peronatus* in clade H is moderately supported (Fig. 9; 0.96 / 46 %; 0.90 / 32 %), all these collections appear within a single well-supported clade (1.00 / 100 %). This coincides with the report of recent introduction of the species to western North America, with little time for species level mutations to have occurred.

In *G. confluens* (clade M; Fig. 13), Euro-American collections were universally intercompatible with North American material. By and large, the two disjunct populations segregated into two well-supported clades (1.00 / 98 %; 1.00 / 100 %; Fig. 13), suggesting that they have been geographically separated for a considerable time period.

In the numerous collections placed in the *biformis* complex (see Fig. 13), haploid cultures were not available, so pairing data could not

be applied to this taxonomically difficult complex. It was necessary, therefore, to balance morphological and phylogenetic analyses without the aid of pairing results.

4. Phylogeographic signal

In phylogenetic reconstructions intended to probe relationships among taxa or collections, phylogeographic signal can sometimes be inferred. Such is the case for *G. peronatus* and *G. confluens* (see above). In a larger context, some clades appear unique for geographic distributions. For example, clade N and much of clade M (Fig. 13) currently appear to include exclusively tropical taxa often spread over large distances (i.e. Central America, Caribbean, Hawaiian Islands, Indonesia). Superficially, a putative pan-tropical belt is obvious, but veracity of phylogeographic signal is only as strong as the next taxonomic and geographic sample to be added to the clade and may be affected by added sequence data. One clade of *G. biformis* comprises both Costa Rican collections and collections from the southeastern United States. A similar pattern was observed with *Artomyces pyxidatus* (Lickey *et al.* 2002) and with *Flammulina populicola* and *F. mexicana* (Hughes *et al.* 1999). Central America may represent a glacial refugium from which plants and their associated fungi migrated northward or upward as the northern climate warmed following the end of the last glacial period, 20,000 years before present.

5. Equating clades with taxo-nomenclatural groups

All phylogenetic reconstructions for the foreseeable future must be judged as temporary, awaiting more robust data sets and revised methods of analysis. While it is tempting to use taxo-nomenclatural names within phylogenies (we have done this above at species and infraspecific ranks), the concordance of clades to genera and infrageneric designations may also be transitory. In an attempt to avoid this problem, therefore, we have used a minimum of taxo-nomenclatural names under Results, but take them up here.

6. /omphalotoid (Figs. 1, 2, 3)

Moncalvo *et al.* (2002) showed two major clades within /omphalotaceae (Fig. 1): 1) /omphalotoid, including *Anthracophyllum, Neonothopanus, Omphalotus* and *Lampteromyces,* and 2) /lentinuloid for all other taxa.

Three generic and suprageneric taxa were taken up by Moncalvo *et al.* (2002) as basal to the /omphalotaceae (Fig. 1). Thorn *et al.* (2000) included taxa from these genera in a phylogeny using partial sequences of 25S rDNA to segregate the Pleurotaceae, but coincidentally revealed a clade (called by them Marasmiaceae) including several organisms in our phylogenetic reconstruction [i.e. *Omphalotus nidiformis, O. japonicus, Neonothopanus nambi* (as *Nothopanus eugrammus*), *Gymnopus dryophilus* and *Lentinula edodes*] as well as *Crinipellis campanella* and *Marasmius delectans*. The integrity of this clade (without *Crinipellis* and *M. delectans*) has been maintained through additional analyses by Moncalvo *et al.* (2000, 2002).

In our analyses, *Neonothopanus* and *Omphalotus* appear basal to *Lentinula* and *Rhodocollybia*. This is consistent with Moncalvo *et al.* (2002) where, based on ribosomal LSU sequences, these genera were sister to a large mixed clade comprising (their use of generic names) *Gymnopus, Lentinula* and *Rhodocollybia* as well as taxa from other genera (Fig. 1). Wilson & Desjardin (2005; LSU-based) included *Rhodocollybia* taxa, which segregated in a discrete clade nested within numerous *Gymnopus* taxa rendering *Gymnopus* polyphyletic. In our analyses, however, *Lentinula* and *Rhodocollybia* appear as outgroups to *Gymnopus* (Fig. 2). Regions of *Lentinula* and *Rhodocollybia* ITS 1 and ITS 2 sequences aligned poorly with *Gymnopus* and these regions were eliminated from the analyses in Fig. 2. The remaining data were insufficient to clearly place *Lentinula* and *Rhodocollybia* with respect to *Gymnopus*.

6.1. *Anthracophyllum*

The phylogeny by Moncalvo *et al.* (2002) included *Anthracophyllum lateritium*, characterized by small, pleurotoid basidiomata with blackish hymenophore and sooty red pileus surface, in clade /omphalotaceae and smaller clade /omphalotoid, but outside /omphalotus. It appeared basal to /omphalotoid, with next closest relative *Neonothopanus nambi*.

Anthracophyllum lateritium has had a checkered taxonomic history. Originally described in *Xerotus*, it was later transferred as *Plicatura lateritia* by Murrill, and eventually to *Anthracophyllum* (Singer & Digilio 1951: 206). Singer alluded to green staining of the hymenophore in alkaline solutions, quite like the tissue of *Gymnopus alkalivirens*, but we cannot find a combination for *lateritia* in *Collybia*. Pegler (1987) redescribed type material of *A. lateritium* and Pegler & Young (1989) summarized the genus worldwide. Petersen (1995b) reported on "facultative" amphithallism in *A. lateritium*, but tetrapolarity in *A. archeri*.

6.2. *Neonothopanus*

Petersen & Krisai-Greilhuber (1999) presented the taxonomic and nomenclatural background of *Pleurotus eugrammus* (Mont. *apud* Fr.) Dennis, the use of this epithet as type of *Nothopanus* Singer (1944), and the necessary correction to these opinions. Because Singer's *Nothopanus* was placed in synonymy under *Pleurotus* as a result, the new genus *Neonothopanus* was described, typified by *Ne. nambi*. It is this combination which is found in the phylogenies by Moncalvo *et al.* (2000, 2002: Fig. 1) and that presented here (Fig. 2).

Moncalvo *et al.* (2002) placed *Ne. nambi* in clade /omphalotaceae, and in the nested clade /omphalotoid, but outside /omphalotus, together with *Anthracophyllum lateritium*. In our study, the position of *Neonothopanus* is well-supported in Bayesian analysis, but not in maximum parsimony (Fig. 2). As noted above, in some parsimony analyses, *Omphalotus* appears as a sister clade to *Neonothopanus*.

6.3. *Omphalotus*

Species of *Omphalotus* and *Lampteromyces* produce secondary metabolites also found in members of the Paxillaceae (see bibliographies in Hughes & Petersen 1998; Petersen and Hughes 1998) and in hydnoid Thelephoraceae (atromentin; Gill & Steglich 1987). On this basis, placement of the genus remained in some doubt. Singer (1986) maintained placement of *Omphalotus* in the Paxillaceae (and therefore in the Boletales for some authors; see Kämmerer *et al.* 1985) but Binder *et al.* (1997) sequenced part of the 28S rRNA gene, and placed *Omphalotus olearius* and *O. japonicus* within the Agaricales and Moncalvo *et al.* (2000) reported that *Omphalotus* was found in a clade within what was accepted as the Tricholomataceae. Its placement remained constant in the most recent comprehensive phylogeny (Moncalvo *et al.* 2002).

In Moncalvo *et al.* (2002), based on LSU sequences, *O. olivascens* and *O. olearius* appeared in the same clade. In our study, *O. olivascens, O. olearius, O. japonicus* and *O. subilludens* are in a well-supported clade (*Omphalotus* clade 1; Figs. 2, 3), consistent with earlier studies based on mating experiments and restriction fragment patterns of the ribosomal ITS region. The widespread Euro-American species, *O. illudens,* is found in a second clade together with *O. mexicanus* (*Omphalotus* clade 2; Figs. 2, 3), also consistent with earlier analyses (Hughes & Petersen 1998; Petersen & Hughes 1998; Kirchmair *et al.* 2004). Recently, Kirchmair *et al.* (2004) presented an expanded *Omphalotus* phylogeny based largely on a non-overlapping data set. Therefore, we make no attempt to further resolve phylogenetic relationships among *Omphalotus* collections used in this

paper. *Lampteromyces japonicus* has also been transferred to *Omphalotus* (Kirchmair *et al.* 2002), but Neda (2004) suggested that *O. guepiniformis* is a prior name for this taxon.

Kirchmair *et al.* (2004), using three methods of data analysis, were unable to resolve the position of *O. nidiformis* (transferred from *Pleurotus* by Miller 1994), which never appeared basal to all other members of the genus. In Bayesian analysis of ITS sequences (Fig. 3), this species is a sister clade to the two major *Omphalotus* clades but in parsimony analysis it is basal to the two remaining *Omphalotus clades* (data not shown).

Recently, new interest has been shown in illudanes, secondary products produced by mycelium of *Omphalotus* spp. and *O. japonicus*. Illudin S and illudin M have been shown to cause death of several tumor and cancer cells through inhibition of DNA synthesis, and a considerable literature has been amassed (see bibliographies in Amato *et al.* 2002; McMorriss *et al.* 1999; Tanaka *et al.* 1996). Kirchmair *et al.* (1999) identified illudins from *O. nidiformis* and *O. olivaceus* var. *indigo*, Kirchmair *et al.* (2002) from *O. mexicanus* and Burgess *et al.* (1999) characterized illudins F, G and H from *O. nidiformis*. Omphalotin A, yet another secondary metabolite produced by *O. olearius*, was found to be significantly nematocidal (Mayer *et al.* 1999; Buchel *et al.* 1998). None of these illudane compounds has been reported from *Anthracophyllum* or *Neonothopanus*, which (to our knowledge) remain untested. While similar compounds are produced by *Pteridium aquilinum* (bracken fern), their presence in /omphalotaceae appears to be an isolated synapomorphy.

Basidiomata and *in vitro* mycelium of *Omphalotus* species are well-known for bioluminescence, and *Neonothopanus* has been reported so also (as *Nothopanus eugrammus*, Corner 1981). This property can be altered by edaphic growth conditions (Weitz *et al.* 2001). We can find no such report for the basidiomata or mycelium of *A. lateritium*.

7. Separation of /omphalotoid from /lentinuloid

Within /omphalotaceae, Moncalvo *et al.* (2002) showed two major clades: /omphalotoid (see above) & /lentinuloid (all other taxa in this study; Fig. 1). This dichotomy is reflected in both Bayesian and parsimony analyses (Fig. 2) and is strongly supported (.90 / 100 %). *Lentinula* and *Rhodocollybia* were placed in separate clades (/lentinula and /rhodocollybia, respectively; Fig. 1), both included in /lentinuloid. These findings are consistent with our studies but the relative positions of *Rhodocollybia* and *Lentinula* with respect to *Gymnopus* differ.

7.1. *Lentinula*

Pegler (1975) placed *Lentinus edodes* and *L. boryanus* in *Lentinula* by virtue of the non-decurrent lamellae (soon becoming free) and presence of inflated, sclerified (generative) hyphae. Other distinguishing characteristics of the genus are: 1) pileipellis fibrillose to squamose; 2) stipe central to excentric, firm; and 3) veil evanescent. Morphological characteristics shared with other genera in /lentinoid (Moncalvo *et al.* 2002; i.e. *Gymnopus, Rhodocollybia*) include: 1) lamellae white to off-white to cream, crowded; 2) cheilocystidia present (mostly sphaeropedunculate, clavate to broadly clavate, or flexuous and narrowly clavate); 3) pileipellis a parallelocutis, sometimes gelatinized; 4) hyphal system monomitic; 5) basidiospores white in mass, hyaline, inamyloid; and 6) hyphae broad and thick-walled (as in *Neonothopanus*).

Pegler (1983a) produced a monograph for *Lentinula* which included five morphological species *(L. edodes, L. lateritia, L. novaezelandiae, L. boryana, L. guarapiensis).* The morphospecies *L. lateritia* and *L. novaezelandiae* form a biological species with *L. edodes* in Asia-Australia-Oceania. *Lentinula cubensis* (Cuba, coll. C. Wright, no. 115, K [!]), a synonym of *L. boryana,* is the type species of the genus. While *L. guarapiensis* is known only from the type specimen, *L. boryana* and *L. raphanica* are distributed sympatrically from Brazil north to the Gulf of Mexico region in the United States (Mata *et al.* 2001) and Caribbean landmasses. A third species, *L. aciculospora,* has been collected only in southern Central America at high elevations (Mata & Petersen, 2000).

Two types of phylogenies have included *Lentinula* taxa: 1) phylogenies intended to emphasize the genus for one reason or another (Hibbett 1992; Hibbett & Donoghue 1996; Hibbett *et al.* 1995, 1998; Mata *et al.* 2001); and 2) phylogenies intended for another reason but including *Lentinula* taxa as well (Hibbett & Donoghue 1995; Thorn *et al.* 2000; Binder *et al.* 2006). In a phylogeny aimed at an arrangement of taxa of the Polyporaceae based on SSU mitochondrial DNA sequences, Hibbett & Donoghue (1995) placed *L. boryana* and *L. edodes* in a clade with *Pleurotus ostreatus* and *P. tuberregium.*

Hibbett (1992) furnished a thorough taxonomic/nomenclatural history for *L. edodes,* and presented a phylogeny based on "ribosomal RNA gene sequences" in which *L. edodes* appeared closely related to *Collybia earleae,* with the sister clade composed of *Ossicaulis lignatilis* and *Mycena galericulata.* Hibbett *et al.* (1995), using ITS sequences, showed numerous clades of Old World *Lentinula* consistently separated from two collections from Mexico. These segregants were further examined by Hibbett & Donoghue (1995).

Using an expanded data set, ITS sequences later confirmed that numerous populational strains of *L. edodes* segregated into at least three morphological taxa (Hibbett *et al.* 1998). Mata *et al.* (2001) added New World collections under the names *L. boryana, L. raphanica* and *L. aciculospora,* and showed that the genus included two major clades which matched New and Old World distributions. This clade structure is confirmed in our phylogenetic reconstruction (implied in Fig. 2; data not shown).

7.2. *Rhodocollybia*

Singer (1986) included what is accepted today as *Rhodocollybia* in *Collybia* sect. *Striipedes* (typified by *Co. fusipes*). Within sect. *Striipedes* were three stirpes: st. *Maculata* (including *Co. maculata*), st. *Butyracea* (including *Co. butyracea*) and st. *Fusipes* (including *Co. fusipes*). The former two stirpes conform to the two large subclades within *Rhodocollybia* in our analysis (Fig. 3) and are clearly discerned in the phylogeny by Mata *et al.* (2004 c) but cannot be distinguished in an LSU-based phylogeny (Wilson & Desardin 2005). This distinct separation in Bayesian analysis could serve as the basis for a generic unit for the *butyracea* complex. Addition of sequences from African and Asian taxa may help to resolve this situation.

For Moncalvo *et al.* (2002), *Rhodocollybia maculata (typus generis)* grouped with at least three species of *Gymnopus* and *Marasmiellus ramealis* in /rhodocollybia, sister clade to /lentinula (Fig. 1). These two clades, together with a small clade, /scorodonius, and a larger clade, /micromphale, comprised /lentinuloid, sister clade to /omphalotoid (see above). As could be expected, resolution at the level of LSU sequences grouped organisms considered less related at the ITS sequence resolution. In Mata *et al.* (2004 b), *Omphalotus, Gymnopus* and *Lentinula* all appeared basal to *Rhodocollybia,* but the limited number of taxa of these genera (three, four and three, respectively) used in that analysis may have influenced the resulting phylogeny.

As shown by Mata (2002) and Mata *et al.* (2004 c), *R. dotae* (presently known only from Costa Rica) is phylogenetically enigmatic, sometimes basal to the entire genus, but usually nested with the genus but basal to an infrageneric clade (Fig. 3). Mata *et al.* (2004 c) noted macromorphological similarities among basidiomata of *R. dotae, R. turpis* and *R. maculata.*

Compared to the Northern Hemisphere, Central America seems to harbor significant genetic diversity within *Rhodocollybia.* This finding is consistent with other studies which identify this as a region

rich in species diversity and with a high proportion of endemic species (see Lickey *et al.* 2003; Halling 1997).

Collections used in our study were geographically limited and may represent only a small proportion of the total genetic diversity present in the genus.

8. *Gymnopus* (Clades A – N; Fig. 2)

Moncalvo *et al.* (2002) reported that *Gymnopus* taxa were included in two clades, /rhodocollybia (see above) and /micromphale (Fig. 1). While both clades were included in the larger clade /lentinuloid, they were not sister clades. In /rhodocollybia, at least three *Gymnopus* taxa were found [*G. peronatus, G. biformis,* and *Gymnopus* sp. (2); Fig. 1]. The two named taxa have generally been accepted as belonging in *Gymnopus* sect. *Vestipedes* (Halling 1983; Antonín & Noordeloos 1997). In /micromphale, four *Gymnopus* taxa appeared (*G. acervatus, G. dryophilus, G. polyphyllus* and *Gymnopus* sp.; Fig. 1). Of these, *G., dryophilus* has been placed in sect. *Levipedes, G. acervatus* in sect. *Vestipedes* subsect *Vestipedes* and *G. polyphyllus* in subsect. *Impudicae* (Halling 1983; Antonín & Noordeloos 1997). Together with these *Gymnopus* taxa were species of *Rhodocollybia, Setulipes, Caripia* and *Micromphale.*

Likewise, Wilson & Desjardin (2003, 2005) used Bayesian analysis of nLSU sequences and concluded that *Gymnopus* taxa were found in two clades which they labeled as /marasmiellus (their clade B; including *Ma. juniperinus, typus generis*) and /gymnopus (including *G. fusipes, typus generis*). /marasmiellus is the least supported clade of three sister clades (including their clade C, labeled *Rhodocollybia*), roughly equivalent to our use of this name plus what might be construed as our use of *Collybiopsis* (*q.v.*), and an unnamed clade which might equate to *Gymnopus* sect. *Peronati* (*q.v.*, but see caveats by Wilson & Desjardin, 2005). None of these clades appear to be supported in maximum parsimony analysis. Better supported (.68 / <50 %) is /gymnopus (their clade D), which appears to be equivalent to the taxa shown in our Fig. 3 (*Micromphale,* the *G. polyphyllus* complex, *Gymnopus s.s., Micromphale* and *Gymnopus* sect. *Levipedes*). Sister to /gymnopus was their clade E (*Lentinula:* 1.00 / 92 %). Combined /gymnopus and clade E was sister to a well-supported (1.00 / 95 %) clade F *(Mycetinis).* In this study using ITS sequences, *Lentinula* appears as a separate genus and *Mycetinis* (our clade F) is nested well within *Gymnopus* sect. *Vestipedes* (Fig. 2). The seeming discrepancy in these relationships may be caused by the resolution of LSU sequences versus ITS sequences and/or the robustness of the data set, but probably not due to differences in data analysis.

8.1. Clade A (Figs. 2, 4)

In both parsimony and Bayesian analyses, *G. fusipes, typus generis* of *Gymnopus,* groups with *S. androsaceus* (*typus generis* of *Setulipes;* Figs. 2, 4). In Bayesian analysis, clade A is basal to a clade consisting of *Micromphale* and related *Gymnopus* taxa (Figs. 2, 4) and clade C, containing *G. dryophilus* and related species. In parsimony analysis, clade A is a sister clade to the remaining *Gymnopus, Marasmius* and *Marasmiellus* species. Clade A represents the irreducible *Gymnopus* (which name is priorable to *Setulipes*), and could be referred to as *Gymnopus sensu stricto.*

Halling (1983) furnished an abbreviated history of Fries's (1821, 1838) treatment of *Agaricus* tribus *Collybia.* In *Epicrisis,* Fries (1838) introduced four sections of tribus *Collybia,* namely *Striipedes, Levipedes, Vestipedes* and *Tephrophanae.* Much later, after *Collybia* was *de facto* proposed at genus rank (Kummer 1871) and after typification of all taxa became mandatory, the name *Collybia* was conserved with *C. tuberosa* as type, which effectively removed *Collybia* from the taxa treated here (Hughes *et al.* 2001). For the residue of taxa included in the traditional, wide sense of *Collybia,* S.F. Gray's (1821) genus name, *Gymnopus,* claimed priority and was adopted (see Antonín & Noordleoos 1997).

Modern nomenclatural rules include the concepts of autonyms and retroactivity. In this case, when Gray (1821) proposed the genus name *Gymnopus,* subgenus and section names were automatically also proposed, although not explicitly. Thus, the core section of *Gymnopus* must be sect. *Gymnopus,* and if *G. fusipes* typifies the genus name, then it also typifies the section. Although *G. fusipes* is phylogenetically almost isolated in its own clade (Figs. 2, 4), that clade must equate to *Gymnopus* (not *Striipedes,* in which *G. fusipes* was usually included). Antonín & Noordleoos (1997) reached the same conclusion based on morphological characters.

8.1.1. *Gymnopus fusipes*

General placement of *G. fusipes* was shown by Mata *et al.* (2004 b), but the two taxa placed in clade A to this time would seem to differ markedly in basidiomatal characters of stature, stipe insertion and pileipellis structure. Basidiomata of *G. fusipes* are well-marked by brown colors, fleshy, relatively stout stature, and fasciculate, rooting stipes. Antonín & Noordeloos (1997) designated an iconotype [Bulliard, Herb. France pl. 516(!)] and an epitype (France,. Dept. Loir et Cher, Montrichard, 19.IX.1955, coll. Uffelie, s.n., L!) for the species. The pileus epicutis of *G. fusipes* (epitype) bears a strong resemblance to that observed in sect. *Levipedes.* Terminal

epicuticular cells are not radially oriented, but branched/lobed/coralloid, whereas hyphae of the subpellis may be more radially oriented. This results in a pileipellis which appears as a trichoderm (cf. Antonín & Noordeloos 1997).

Because *G. fusipes* is involved in root rot, recent work has been done on the physiology of the species (Camy, *et al.* 2003). A series of papers has explored the ecology, forest pathology and somatic incompatibility in *Gymnopus fusipes* (Marçais *et al.* 1998a, b; Marçais & C. Delatour 1996; Marçais *et al.* 2000).

8.1.2. *Setulipes androsaceus (Ma. androsaceus)*

Earle (1909) adopted the genus name *Marasmius* typified by *M. androsaceus*. By a process of conservation, *Marasmius* has since been legislated as typified by *M. rotula,* so *Marasmius sensu* Earle is to be rejected. In an attempt to accurately circumscribe *Marasmius, Marasmiellus* and *Collybia,* Antonín (1987) segregated *Setulipes,* typified by *S. androsaceus,* thought to be anomalous in any of the three genera in which it had been placed. Leading characters were: "structure of the epicutis with single irregular broom cells, setose, fully insititious stipe of horny consistency, the distinct dextrinoid hyphae (at least in the stipe) and well developed cheilocystidia." In radial section view, pileipellis cells appear stoutly but irregularly branched, resembling the *rameales* structure of *Marasmiellus* and some *Mycena* species. In paradermal scalp, however, these cells can be seen as a loose "dryophila-type," more or less interlocking to form a jig-saw puzzle appearance. The most striking difference between these pileipellis structures ("*dryophila*-type" and *S. androsaceus*) is the presence of many small protuberances besetting the pileipellis cells in *S. androsaceus,* which, especially on the cheilocystidia, are very similar to those of "broom cells" in *Marasmius,* doubtlessly a leading reason for this traditional placement of *S. androsaceus* in *Marasmius*. Pileipellis structure in *S. androsaceus* was illustrated by Antonín (1987) and Antonín & Noordeloos (1993).

Gordon *et al.* (1994) reported a tetrapolar mating system for *S. androsaceus* (as *Ma. androsaceus*), using a North American specimen (TFB 2705). Lamoure (1989), based on previous literature (Piroard 1956; Terra 1953; Yen 1950a, b), also reported tetrapolarity for this species.

Gordon (1994) and Gordon & Petersen (1997) reported on an extensive study of *Ma. androsaceus* from North America and Europe. Although morphologically undistinguishable, two exclusive populations were delineated based on sexual compatibility data, one from northern North America and Europe, fruiting on conifer duff,

the other from the southern Appalachian Mountains, fruiting on *Quercus* litter. These populations were also segregated by laccase electrophoretic patterns. In the phylogeny presented here, care was taken to select strains from both intersterility groups, and the resulting sequences form a well supported clade in parsimony analysis (97%) but in Bayesian analysis, *Ma. androsaceus* is polyphyletic, separating on the basis of geography with *G. fusipes* as a long branch within this clade (Fig. 4). With the type species of *Gymnopus* and *Setulipes* placed in the same clade, *Gymnopus* must claim priority. *Marasmiellus androsaceus (Setulipes androsaceus)* was transferred to *Gymnopus* by Mata *et al.* (2004b).

8.2. Clade B (Figs. 2, 4)

Moncalvo *et al.* (2002) identified a clade (LSU) which they named "/micromphale" because it included *Mi. foetida (typus generis;* Fig. 1). Smaller clades subsumed in /micromphale were as follows: 1) poorly supported: *Gymnopus polyphyllus,* "*Gymnopus* sp." and *Caripia montagnei (typus generis);* 2) moderately supported: *G. dryophila, G. acervatus* and *Mi. foetida;* and 3) poorly supported: *Setulipes androsaceus (typus generis).* Thus /micromphale sheltered species of four morphogenera. Clade /micromphale was sister clade to /scorodonius (*Me. opacus, Ma. scorodonius;* see Discussion under *Mycetinis*). In our phylogenetic reconstruction (ITS), Moncalvo *et al.*'s (2002) /micromphale accounts for a significant portion of *Gymnopus* and related taxa.

The relative position of *Mi. brassicolens* and *G. polyphyllus* varies between Figs. 2 and 4. Analyses in these two figures are based on different proportions of the ITS sequence with Fig. 4 representing analyses based on better alignment and fewer bases removed for alignment difficulties (see figure legends and Methods).

Micromphale dates from Nees von Esenbeck (1801. Syst. Fung. p 466), adopted by S.F. Gray (1821). For some authors, *Micromphale* taxa were placed in *Marasmius s.l.,* and Kühner (1933, 1936) described *Marasmius* sect. *Gloeonemae* to house *Ma. foetidus* and perhaps *Ma. perforans.* Antonín & Noordeloos (1997) placed *Micromphale* in synonymy under *Marasmiellus.*

When *Micromphale* is accepted at genus rank, the autonymic sect. *Micromphale* is dictated, and must include *Mi. foetida (typus generis).* Because both species of *Micromphale (Mi. foetida, Mi. brassicolens)* included in our phylogenetic reconstruction nest within *Gymnopus s.l.* (and sister to *Gymnopus s.s.*), nomenclatural transfer of these species epithets into *Gymnopus* is warranted. Assuming that *Marasmiellus* would be conserved over *Micromphale,* some transfers were proposed in that direction (Antonín *et al.* 1997).

Mata *et al.* (2004b), in a phylogenetic reconstruction based on LSU sequences designed to place *Me. juniperinus (typus generis),* also placed *Mi. foetida (typus generis)* and *G. fusipes (typus generis).* While *G. dryophilus, G. polyphyllus* and *G. acervatus* appeared in the same clade as *Mi. foetida, S. androsaceus* appeared in a sister clade together with *G. fusipes. Micromphale foetida* was transferred to *Gymnopus* by Mata *et al.* (2004b) as was *Marasmiellus juniperinus.*

Basidiomata of several, if not all, members of the *Micromphale* clade emit a fetid or disagreeable odor. Glutamyl-peptides, precursors of compounds with polysulphide odor (Moncalvo *et al.* 2002; Gmelin *et al.* 1976) appear common to the group.

Although including the type species of *Caripia* and the type of *Collybia* sect. *Impudicae, Micromphale* predates both other names. Although this would seem to dictate use of *Micromphale* for this clade, clade B is clearly within *Gymnopus sensu lato,* and not of genus rank. We are not proposing this transfer for *Ca. montagnei,* a clearly reduced form.

8.2.1. *Gymnopus iocephalus*

Gymnopus iocephalus from the southeastern US forms a monophyletic group. Halling (1983) resurrected and validated *Collybia* subg. *Collybia* sect. *Iocephalae* Singer (*nom. nud.*), later transferred as *Gymnopus* sect. *Iocephalae* (Singer ex Halling) Halling (Antonín *et al.* 1997). Basidiomata exhibit purple or violaceous coloration, pigments which turn blue in KOH. The section is monotypic, with *G. iocephalus,* basidiomata of which emit a foetid odor, as monotype. Lamoure (1989) reported heterothallic behavior for *Mi. foetida,* but did not specify bi- or tetrapolarity. Petersen & Gordon (1994) reported a tetrapolar mating system for *Collybia iocephala,* using TFB 6520. This is consistent with our findings.

8.2.2. *Gymnopus impudicus*

Antonín & Noordeloos (1997) proposed *Gymnopus* sect. *Vestipedes* subsect. *Impudicae,* based on inclusion of *G. impudicus,* together with *G. (Micromphale) brassicolens, G. hariolorum* (here considered a synonym under *G. polyphyllus*), *G. graveolens* and *G. herinkii,* the latter two not included in our phylogenetic reconstruction.

They took care to separate *G. hariolorum* from *G. confluens* as known in Europe, and these two species appear in separate, only distantly related clades in our phylogenetic reconstruction.

8.2.3. *Caripia montagnei*

Corner (1950: 196 – 197), while including these reduced basidiomata with the clavarioid fungi, noted that they might better be placed among cantharelloid taxa. Later (Corner 1996: 82 – 83), he was able to trace basidiomatal ontogeny, and in some individuals, was able to observe rudimentary gill-like folds in the hymenium. Moreover, Corner (1950) observed some obscure, submerged, relatively undifferentiated hymenial cystidia, perhaps reflective of the cheilocystidia found in members of clade D (Fig. 2).

The sequence in our phylogeny was furnished by Dr. Jean-Marc Moncalvo from DNA of JMCR143 (Genbank AF261327), the same source as that in Moncalvo *et al.* (2002). We have not examined the voucher specimen for this sequence.

8.3. Clade C (Figs. 2, 4)

Although presently typified by *Co. tuberosa*, *Collybia* was previously typified by *Co. dryophila* (Quelet 1872; Singer 1949). Although modern nomenclature dictates that the type of a genus must be the type of autonymic infrageneric taxa (i.e. sect. *Collybia*), Singer (1949) placed *Co. dryophila* in *Collybia* sect. *Levipedes*. Once the type species of *Collybia* was recognized as *Co. tuberosa*, sect. *Levipedes* became a non-autonymic infrageneric taxon (in *Gymnopus*), with *Co. dryophila* remaining as type. Halling (1994) proposed the generic segregation of *Collybia* from *Gymnopus* (type = *G. fusipes*), and later (Halling, 1997) recombined sect. *Levipedes* (type = *G. dryophilus*) into *Gymnopus*. This segregation was confirmed in phylogenetic reconstructions (Hughes *et al.* 2001; Moncalvo *et al.* 2002). Thus, *G. dryophilus* has been the constant type of sect. *Levipedes*, regardless of the placement of the section.

As its name implies, sect. *Levipedes* ("smooth feet") was apposed to sect. *Vestipedes* ("vestured feet") of *Collybia*, although several other sections were accepted. This character, however, was gradually displaced by the structure of the pileipellis. Instead of radially oriented branched or unbranched hyphae, the pileipellis seen in members of sect. *Levipedes* is a *textura* of loosely, intricately placed, irregularly inflated hyphae more or less resembling a jig-saw puzzle, best seen in paradermal "scalps." This hyphal arrangement has become known as the "dryophila-type" and now constitutes the dominant morphological character defining the group.

Gymnopus dryophilus is the type species of *Gymnopus* sect. (or subg.) *Levipedes* (see Singer 1986) and clade C is equated with this infrageneric name. Sect. *Levipedes* has been investigated more than any other comparable group in *Gymnopus*. While not all the

European or American taxa were included in previous studies (much less those of Asia, South America and Africa), morphology, pairings experiments and DNA-DNA hybridization studies have shown that some taxa, while morphologically variable, remain intercontinentally sexually intercompatible.

8.3.1. *Gymnopus polyphyllus* (Fig. 4)

Gymnopus polyphyllus forms a strongly supported monophyletic clade (Fig. 4) but its position with respect to clades B and C remains uncertain. Halling (1983) distinguished basidiomata of *Co. polyphylla* by unpleasant odor, crowded lamellae and presence of cheilocystidia. *Collybia hariolorum* was considered a European species, separable from *Co. polyphylla* by lack of cheilocystidia. Conversely, Antonín & Noordeloos (1997) observed irregularly branched cheilocystidia ("always present"), but did not mention *G. polyphyllus*. Petersen & Gordon (1994) reported a tetrapolar mating system for G. *polyphyllus* (as *Collybia*), using TFB 1855. Lamoure (1954, 1989) and Piroard (1956) reported heterothallism in *G. hariolorum* (as *Collybia,* here considered to be a synonymous name to *G. polyphylla*), but were unable to further define the extent of polarity. Until material of both species can be compared side by side, synonymy remains in question.

8.3.2. *Gymnopus dryophilus* complex (Fig. 4)

As shown by several workers, *G. dryophilus* could be conceived as a species complex. Vilgalys & Miller (1983) reported on four "biological species" in the complex from North America, identifying them as Group I (*Co. dryophila* (Bull.: Fr.) Kummer), Group II (*Co. subsulphurea* Peck), Group III [*Co. earleae* (Murr.) Murr.] and Group IV (*Co. brunneola* Vilgalys & Miller). This group remained coherent in phenetic analyses (Vilgalys 1986). Later, these biological species were noted as N-I, N-II, N-III and N-IV, respectively.

Vilgalys & Miller (1987a) reported four morphotaxa within the complex in Europe [*Co. ocior* (Pers.) Vilgalys. & Miller, *Co. alpina* Vilgalys & Miller, *Co. dryophila, Co. aquosa* (Bull.: Fr.) Kummer], equating these to intersterility groups (E-1, E-II, E-III, E-IV, respectively; Vilgalys & Miller, 1987b).

Vilgalys & Johnson (1987) reported some intercontinental sexual intercompatibility between North American and European "biological species," leading to proposals of infraspecific taxa (Vilgalys 1991): *Co. ocior* ssp. *brunneola* (Vilgalys & Miller) Vilgalys, *Co. alpina* ssp. *subsulphurea* (Peck) Vilgalys. Supporting DNA-DNA hybridization experiments were included. *Collybia dryophila,* by then

known to be intercompatible from Europe, North America and Asia, while suspected of sheltering infraspecific taxa, was not subdivided, and *Co. aquosa* and *Co. earleae* remained without infraspecific differentiation, each limited to a single continent. Furthermore, these species (and their infraspecific taxa) could be distinguished based on a combination of cheilocystidial size and shape together with rhizomorph and lamellar color. Although subjected to various modes of analysis, these taxa remained stable.

Halling (1997) examined the complex chiefly using tropical American specimens. Included in sect. *levipedes* were *G. mucubajiensis* (Dennis) Halling and *G. spongiosus* (Berk. & Curt.) Halling. Basidiomatal tissues of these species were green-staining in alkaline solutions (see under *G. alkalivirens*). Proposed as new was *G. macropus* Halling (*q.v.*) and *G. nubicola* Halling (*q.v.*). Páramo habitat, small differences in cheilocystidial shape and prominence, and waxy taste and odor separated *G. nubicola* from *G. dryophilus*. Halling (1997) noted that true *G. dryophilus* and other expected taxa of sect. *Levipedes* were not yet documented from low-elevation tropical locales, but only from high-altitude areas as far south as northern Ecuador.

In some taxa of subclades of Clade C, micromorphological characters of our collections (in dried condition) were compared to those of neotype or holotype specimens in order to arrive at the names used here. This clade remains a difficult group, whether treated morphologically, genetically or molecularly.

Our phylogeny represents the first attempt to place these taxa of the *G. dryophilus* complex using ITS sequences. The exercise has not been totally successful. In both Bayesian and parsimony analyses, Clade C is poorly differentiated and contains numerous, rarely monophyletic morphospecies. Sequences within the section vary little, and show reticulating patterns of relationships. These reticulating relationships are true for all of the *dryophilus* complex, explain the lack of resolution in this group and suggest that this clade represents a wide-spread interbreeding complex that has only recently undergone fragmentation and morphological speciation. This reticulation plus morphological plasticity also make members of this group exceptionally difficult to assign to morphotaxa. Addition of additional gene sequences might help to resolve the clade.

In this study, the clade would appear to be EuroAmerican in distribution, but this is an artifact of source material. Surely, other worldwide representatives will be added.

8.3.3. Green-staining basidiomata

Basidiomatal tissues of a small number of *Gymnopus* species stain green, olive green or dull green (the *"alkalivirentes"* of sect.

Levipedes) or blue (*G. iocephala* and allies) in the presence of alkaline solution (typically 3 – 15 % aqueous KOH). Some morphotaxonomic literature has featured such agarics (Halling 1979, 1981, 1990). This feature, however, has not been considered cohesive, and the taxa have been distributed over at least two infrageneric groups (i.e. *Gymnopus* sect. *Iocephali; Gymnopus* sect. *Levipedes*). In the phylogeny presented here, this distribution is supported, with most taxa found in clade C (*Gymnopus* sect. *Levipedes*).

Other species with similar green reaction to alkali are *G. semihirtipes, G. fuscopurpureus* and *G. fagiphilus*. Segregation of *G. akalivirens* and related species is based on presence of brown incrusting pigment in various parts of the basidiomata, its ability to turn green in KOH, and some other microscopic elements (Halling 1979, 1981, 1990).

8.3.4. *Gymnopus spongiosus-Gymnopus erythropus* (Fig. 4)

Morphological distinction between *G. erythropus* and *G. spongiosus* is made with some difficulty, but the collections under these names sort into separate and well-supported clades. The holotype specimen of *G. spongiosus* is from South Carolina (Curtis 1257, K!), and our material has been compared to it. We are informed that the type specimen of *G. erythropus* is preserved in wine and therefore unavailable for examination (M. Noordeloos, pers. comm.)

A similar morphospecies species to *G. spongiosus* is *G. semihirtipes*. The latter exhibits brown granules in the hyphae of the stipe that can be seen in water mounts, but which dissolve in KOH and turn green.

The ITS sequence of collection TFB 11435 falls within a *G. erythropus* clade. Notes taken on TFB 11435 (as *G. aquosus*) indicated a brown pileus ["sayal brown" to "snuff brown," outward "pinkish buff" (Ridgeway 1912)], adnexed, uncrowded, slightly pinkish lamellae ("pinkish buff"), terete, brown stipe ("sayal brown") expanded at base, and "pinkish buff" rhizomorphs. These colors are too dark for *G. aquosus*, and the ITS sequence of this specimen did not show a characteristic *G. aquosus* sequence apomorphy. The collection is presumably misidentified.

8.3.5. *Gymnopus alkalivirens* (Fig. 4)

Although we have not examined the type specimen, Halling (1979) gave an account which included the type, and later (Halling 1981, 1990) contrasted *G. alkalivirens* to *G. fuscopurpureus*.

8.3.6. *Gymnopus earleae* (Fig. 4)

Hesler (1959) reported on the type specimen of *G. earleae* (as *Collybia*) and we also consulted his personal notes (unpubl. data) on that specimen to confirm our identification. Both Hesler (1959) and Vilgalys & Miller (1983) drew attention to a dull greenish color change of stipe tissue in alkaline solution (KOH, 2 – 15 %). Such a color change may be used as a common character with *G. erythropus*, *G. spongiosus* and *G. alkalivirens* also in this clade.

Gymnopus earleae (TFB 11039, USA Tennessee) is tetrapolar. Vilgalys & Miller (1983) also reported a tetrapolar system for this species (coll. RV 150/153) using a Virginia specimen.

Two collections of putative *G. earleae* from Oregon (TFB 11043, TFB 11044) were interINcompatible with TFB 11039, suggesting that western and eastern collections represented two distinct intersterility groups. The Oregon collections appear as *G. sp* at the base of clade C (Fig. 4). In contrast, Vilgalys & Miller (1983) reported intercompatibility between one California collection and several Virginia specimens of *C. earleae*. Collection 11043 falls within a well-supported subclade together with Duke 16 *(G. "alpinus")*, TFB 10997 and TFB 11042 with varying morphology. This clade may represent an unusually plastic species of *Gymnopus*.

8.3.7. Old World tropical taxa (Fig. 4)

Three species included by Wilson *et al.* (2004) and Wilson & Desjardin (2005) in the Indonesian *Gymnopus* mycota (*G. indoctoides*, *G. bicolor*, *G. sepiiconicus*) are found within a somewhat disparate group, with the latter two closely related. *Gymnopus aurantiipes*, an Indonesian species (Wilson *et al.* 2004), appears basal to a large clade including North Temperate taxa on a poorly supported branch. Such a basal position is also seen in *G. vitellinipes* and *G. austrosemihirtipes* and raises the question of a possible Old World tropical origin of *Levipedes*.

8.3.8. *Gymnopus ocior-Gymnopus dryophilus* (Fig. 4)

Gymnopus ocior and *G. dryophilus* appear in the same clade and may represent sister taxa, one European, one North American. Basidiomata of *G. ocior* share similar prostrate, diverticulate-lobed, clavate to subsphaeropedunculate cheilocystidia and spore dimensions, resembling those of the neotype [France, Paris, Noordeloos 77.310; L!]. All were identified in the field as *G. aquosus*, but cheilocystidia in the type specimen of *G. aquosus* [!]

were more obtuse (and similar to those of collections in the *G. aquosus* clade; *q. v.*).

Vilgalys & Johnson (1987) showed some intercompatibility between collections of European *G. ocior* and North American *C. brunneola,* leading to the proposal of *Collybia ocior* ssp. *brunneola.* We were unable to sample material of *C. brunneola* and thereore could not confirm this taxonomy.

The clade dominated by collections under *G. dryophilus* is well-supported (1.00 / 98 %). Concomitantly, other collections bearing this name are found in at least two other clades, attesting to plasticity of characters and therefore questionable identifications.

Cheilocystidia in *G. dryophilus* are typically narrowly clavate to cylindrical, frequently nodulose-diverticulate-flexuous, and usually prostrate and collapsed. Vilgalys & Johnson (1987) showed that collections of *G. dryophilus* from Europe, North America and Asia were sexually intercompatible, and members of this clade reflect this cosmopolitan distribution. Lamoure (1989) reported a tetrapolar mating system for *C. dryophila,* citing several sources as the basis for her report (Kühner 1946a, b; Piroard 1956; Yen 1950a).

MesoAmerican specimens under *G. dryophilus* (TFB 10092, TFB 9684, TFB 11015) were identified as such (Mata 2002), but field notes on specimens indicate that the cream to cream-yellow colors of the lamellae were very similar to those of basidiomata from USA labeled as *G. subsulphureus* and *G. junquilleus.* Spore dimensions were variable, and cheilocystidia were very much branched and diverticulate apically, more distinctly so than observed in the larger *G. dryophilus* clade. These three collections are found in a nearby, but less related clade.

8.3.9. *Gymnopus fagiphilus* (Fig. 4)

Austrian (TFB 11438) and Scottish (TFB 6995-not sequenced) specimens identified as *G. fagiphilus* exhibited somewhat darker colors, especially of the pileus. These collections were paired (n = 8) and found to be interINcompatible.

8.3.10. *Gymnopus nubicola* (Fig. 4)

REH 8290 (Costa Rica) was identified as *G. nubicola,* distinguished from *G. dryophilus* (Halling 1997) by more reddish pileus colors and pinkish rhizomorphs, the latter similar to those of *G. subsulphureus.* Placement of the collection, however, indicates that it is merely a color form of *G. dryophilus.*

8.3.11. *Gymnopus austrosemihirtipes* (Fig. 4)

This Indonesian species (Wilson *et al.* 2004) appears basal to a small, poorly supported clade which includes disparate names. Such a basal position may also be seen in *G. vitellinipes* and *G. aurantiipes*.

8.3.12. *Gymnopus junquilleus* (Fig. 4)

Although appearing in a clade of otherwise disparate names, two intercompatible collections were deemed worthy of proposal as a new species (see Appendix 1). Although Vilgalys & Miller (1983) drew attention to the yellow coloration of basidiomata (especially lamellae) of *Co. subsulphurea,* yellow colors of basidiomata of *G. junquilleus* are even brighter than those of *G. subsulphureus*. The two collections of *G. junquilleus* differ by 2 of 738 base pairs.

8.3.13. *Gymnopus exculptus* (Fig. 4)

Our collections of *G. exculptus* were furnished by other collectors during fieldwork in Greenland. Basidiomata were distinguished by yellowish lamellae. Antonín & Noordeloos (1997) listed *C. exculptus* as a synonym under *G. ocior* but Greenland collections were not compatible with either *G. ocior* or *G. aquosus,* also distinguished by yellowish lamella. We conclude, therefore, that our material of *C. exculptus* represents a taxon separate from these others, although clearly in the *G. dryophilus* complex. A new combination is necessary based on these data (see Appendix 2).

8.3.14. *Gymnopus macropus* (Fig. 4)

Three collections of this Meso-/South American species are found on a well-supported (.81 / 100 %), independent clade. Although based on a type specimen from Colombia (Antioquia, Guaren, Halling 5263, NY!; Halling 1997), all sequences were derived from Costa Rican material. Spores of *G. macropus* are longer than those of *G. dryophilus* and cheilocystidia are broadly clavate and often apically blunt in contrast to diverticulate and lobed in *G. dryophilus*. Phylogenetic position supports taxonomic species-rank status.

8.3.15. *Gymnopus hybridus* (Fig. 4)

Although no SBIs of *G. hybridus* were established, DNA was extracted from dried herbarium basidiomata. Romagnesi (1952) did not explicitly designate a type specimen, and a type could

not be located in herb. Kühner at G (P. Clerc, pers. comm.). Kühner & Romagnesi (1954) indicated specific locations and dates of collections. Romagnesi (1952) considered basidiomata of *G. hybridus* (as *Marasmius*) to be foetid, and together with the dark, strongly striate pileus, the species could be taken as a member of *Micromphale;* however, its sequence places it within the *G. dryophilus* complex.

8.3.16. *Gymnopus sp.* (Taxon 1; Fig. 4)

There is good support (1.00 / 96 %) for a clade (Fig. 4; bottom) predominantly from western North America together with a collection from Switzerland. The Swiss collection differs by 3 bp from the North American collections. This clade comprises several morphotaxonomic epithets found in other clades (*G. alpinus, G. earleae, G. aquosus, G. "nivalis"*), but without DNA from appropriate type collections for comparison with sequences from this group, it will be difficult to determine correct identifications.

9. Superclade D (Figs. 2, 7, 9, 11, 13)

Superclade D is at least as species-rich as clade C. Singer (1986) did not adopt subgenera in *Collybia,* but sect. *Vestipedes* was typified by *Co. confluens* (here in clade M). Although inclusive of several subclades equated with morphotaxonomic names, superclade D generally equates to *Gymnopus* sect. (or subg.) *Vestipedes.*

In the phylogeny presented here, clade D represents basidiomata which exhibit prominent cheilocystidia. Antonín & Noordeloos (1997) placed *G. confluens, G. luxurians* and *G. peronatus* in sect. *Vestipedes* based on this character. The section was typified by *G. confluens* (following Singer 1986). It would appear that sect. *Vestipedes sensu* Antonín & Noordeloos (1997) and *sensu* Halling (1983) is monophyletic, although not strongly supported (.67 pp). Here, sect. *Vestipedes* (cladeD) comprises taxa placed in five clades: 1) *G. pseudo-omphalodes, G. luxurians,* etc. (clade I; Fig. 11), 2) *G. dichrous* (clade G; Fig. 7); 3) *G. peronatus,* etc. (clade H; Fig. 9); 4) *G. confluens,* etc. (clade M; Fig. 13); and 5) *G. biformis, G. collybioides, G. cylindricus* (clade N; Fig. 13).

In all ITS sequences in clade D, an area of divergent tandem repeats, approximately 34 bp each, was found. Section *Levipedes* has an area that is roughly equivalent to one of the repeats. The number of repeats was between 2 and 5 (Tables 2, 3). Once all repeats were accounted for, the irreducible region was found to occupy position four relative to all repeats (see Table 2). Because of its ubiquitous occurrence, position four appears to be the oldest sequence repeat

element. It is present as a second copy (in position 3) in "Taxon 2" (clade E; Fig. 2) which has sequence homology to clade J and to *Me. ramealis* which is in clade J. This second copy (position 3) is also present in *G. dichrous* (clade G; Fig. 7). Based on sequence homology, it would appear that the element has duplicated at least three times. Within *G. biformis* (see clade N), the element is again duplicated (Table 2). Collections of *G. biformis* with three and four copies of the region are found, thus far, in the southeastern United States only. We speculate that the duplication may have occurred in allopatric populations isolated in glacial refugia. The repeat in position five in *G. indoctus* (clade M) has homology to the *G. indoctus* repeat in position four.

9.1. Clade F (Fig. 2)

The relative position of clade F varies with analysis and with the number of repeat elements excluded from analyses, but the clade is found at both LSU (Wilson & Desjardin 2003, 2005) and ITS resolutions. Inclusion in this study was based on Moncalvo *et al.* (2002) which showed *Me. opacus* and *Ma. scorodonius* (= *Gymnopus scorodonius;* Mata *et al.* 2004b) within /omphalotaceae (Fig. 1). At genus rank, the name *Mycetinis* Earle [1909 (Bull. New York Bot. Gard. 5: 414 1909); Horak 1968] is available, with *My. alliaceus* as its type. Earle indicated that his genus name was intended to accommodate *Marasmius* & *Mycinopsis* Schroeter (1889), and that it included *Marasmius* & *Mycena* subsect. *Chordales* "of the Sylloge" (i.e. Saccardo). Earle stated the type species as "*Marasmius alliaceus* (Jacq.) Fries, Epicr. 383. 1838" although the correct statement should have been *Agaricus alliaceus* (Jacq.) Fries 1821 Syst. Mycol. 1: 140. Earle's usage can be considered a correctable error. Donk (1962: 193) considered *Mycetinis* (or *Mycetinus*) as a probable *lapsus calami* for "Mycenitis."

Wilson & Desjardin (2005) also found support for this clade which they designated *Mycetinis* Earle. In the study by Wilson & Desjardin (2005; based on nLSU sequences), *Me. candidus* belongs to /tetrapyrgos, a clade which appeared basal to all included *Gymnopus* species. In Moncalvo *et al.* (2002), in which *Tetrapyrgos* was not included, *Me. opacus* and *Ma. scorodonius* appear together (/scorodonius; Fig. 1), basal to what we identify as clades A – C (Fig. 2). Wilson & Desjardin (2003, 2005) recognized *Mycetinis* (*My. ramealis, typus generis*) as an independent genus and proposed transfer into *Mycetinis* of four additional epithets traditionally accepted to represent *Marasmius* taxa. Our data place *Mycetinis* as nested within *Gymnopus* sect. *Vestipedes* (clade D), and deeply nested within *Gymnopus*. Based on ITS sequences, *Mycetinis* does not appear

to represent an independent genus. At best, we could identify *Gymnopus* sect. *Vestipedes* subsect. *Mycetinis* (this combination not proposed here), were any supraspecific status to be proposed at all. As such, it would be at equal rank with *Gymnopus* sect. *Vestipedes* subsect *Peronati,* and others.

9.1.1. *Marasmiellus candidus*

Wilson & Desjardin (2005) found *Me. candidus* in clade /tetrapyrgos, although micromorphologically it is also discordant in that taxonomic complex. As the type species of *Marasmiellus* sect. *Candidi,* this sectional epithet will be subsumed under either *Tetrapyrgos* (viz. Wilson & Desjardin 2005) or *Gymnopus* (this study; clade F). Whether other taxa placed in sect. *Candidi* will also find affinities in *Gymnopus* remains to be seen.

9.1.2. *Marasmiellus scorodonius*

Our use of this binomial is based on Desjardin (1989), who compared American collections to representative material [Sweden, Uppsala, Kungparken, 1853, coll. EP Fries (FH)]. Antonín & Noordeloos (1993: 111) established a neotype for *Ma. scorodonius* (Sweden, Stockholm, 1889, Romell, Fungi exs. Scand. No. 1; BR and other distributions). Moncalvo *et al.* (2002) showed that *Ma. scorodonius* was closely related to *Me. opacus* at the LSU resolution. Here, this association is confirmed at ITS resolution.

Marasmiellus scorodonius is usually accepted as belonging to *Marasmius* sect. *Alliacei* (Kühner 1933; Desjardin 1989). Gilliam (1975) preferred the name *Chordales* for this section, based on priority, and this choice was perpetuated by Antonín & Noordeloos (1993). Sect. *Chordales,* however, is typified by *Ma. chordalis,* a later synonym of *Ma. undatus,* which was shown by Petersen (2000) to be placed in the Physalacriacae (as Xerulaceae), together with *Ma. pyrrocephalus*. The latter was proposed as the type of *Rhizomarasmius* (Petersen 2000). Thus, sect. *Chordales* does not belong in clade /lentinuloid, as also shown by Moncalvo *et al.* (2002).

Lamoure (1989) reported a tetrapolar mating system for *Ma. scorodonius,* citing previous reports as her sources (Kühner 1945; Piroard 1956; Terra 1953; Yen 1950b). Gordon (1994) and Gordon & Petersen (1998) reported that North American and European collections of *Ma. scorodonius* were sexually intercompatible and morphologically intermixed. Laccase electrophoretic profiles, however, completely segregated these two populations, suggesting that modern genetic interbreeding across the Atlantic Ocean was not

occurring. Placement in a clade nested within *Gymnopus* necessitates a new combination (see Appendix 2).

9.1.3. *Marasmiellus opacus*

Desjardin *et al.* (1993) reported a tetrapolar mating system for *Me. opacus,* based on collections from the southern Appalachian Mountains. The species was also reported from Japan. Further study is warranted to determine if these disjunct taxa are conspecific.

10. Clade G (Figs. 2, 7)

Gymnopus dichrous forms a well-supported monophyletic clade. Pileipellis structure in *G. dichrous* is very similar to that of *G. confluens,* the type species of sect. *Vestipedes* (clade D), but also similar to that which characterizes Singer's (1986) and Halling's (1983) concept of *Collybia* sect. *Subfumosae.* Also placed in sect. *Subfumosae* was *Co. biformis,* here placed in clade N.

Although our material of *G. dichrous* was not compared with a type, Desjardin (1989) provided a detailed study of the type specimen. Morphology of specimens included in this clade and representing *G. dichrous* agrees with that reported for the type specimen.

11. Clade H (Figs. 2, 9)

Clade H (Fig. 9) comprises *G. lodgae* and associated taxa, *G. omphalodes, G. peronatus* and *G. subnudus.*

Kühner (1933, 1936) conceived of *Marasmius* sect. *Peronatae* to include *Ma. peronatus* (Bolton), *Ma. confluens* (Persoon), *Ma. impudicus* Fries and *Ma. cauveti* Kühner. Some attempt was made to separate the group from other sections of the genus based on pileipellis construction, but Kühner admitted that he had not studied this structure in detail for sect. *Peronatae.* Nonetheless, although Kühner was not bound by the later nomenclatural stricture on autonyms, the generally accepted type species of *Marasmius (Ma. rotula)* was included in its epinymic section *Rotulae,* so *Peronatae* was available as a non-autonymic section name.

From 1949 (Singer 1949) forward, Singer (1962, 1975, 1986) maintained *Collybia* sect. *Vestipedes* as inclusive of Kühner's (1936) *Marasmius* sect. *Peronatae.* For Singer, the type species of sect. *Vestipedes* was *Co. confluens.* Here, we consider *G. confluens* to be placed in a different clade (M) from *G. peronatus* (and allies; clade H), so we choose to use *peronati* for a somewhat more restrictive group. Antonín & Noordeloos (1997) also considered *G. peronatus* as a

member of sect. *Vestipedes,* and Antonín *et al.* (1997) transferred sect. *Vestipedes* to *Gymnopus.*

Mata (2002) identified a clade for which he resurrected Kühner's *Marasmius* sect. *Peronati* (as *Gymnopus* sect. *Peronati, comb. prov.*), in which basidiomata exhibited prominent pleurocystidia (as well as cheilocystidia) and offered a bitter or acrid taste. Included were *G. lodgeae, G. pseudolodgeae, G. omphalodes, G. subnudus,* and *G. peronatus,* here all found in clade H. „Sect. *Peronati*" was separated from sect. *Vestipedes* in Mata's (2002) phylogeny, which was based on subtropical taxa, but here it is placed within sect. *Vestipedes.* As a consequence, it can be assigned subsection rank (see Appendix 2).

Like pileipellis construction in sect. *Vestipedes,* hyphae of the pileipellis in subsect. *Peronati* are generally cylindrical, repent, radially oriented, sometimes diverticulate and sometimes present erect terminal cells. Such pileipellis construction differs from that found in sect. *Levipedes* (*dryophila*-type; see there). Subsect. *Peronati,* however, differs from both sects. *Levipedes* and remaining *Vestipedes* in production of pleurocystidia. Moreover, members of subsect. *Peronati* appear to be litter decomposers, as opposed to the wood-decomposers found in clade I (*G. luxurians,* etc.; Figs. 2, 11).

In our observations, pleurocystidia in specimens of subsect. *Peronati* appear to arise from the lamellar trama, just below the subhymenium. According to Largent *et al.* (1977) cystidia originating from the lamellar trama are termed pseudocystidia (or macrocystidia). Pseudocystidia usually have cellular contents that react in different chemical stains (i.e. gloeocystidia). Pseudocystidia observed in members of subsect. *Peronati* appear hyaline and homogeneous in content and do not react in KOH, Melzer's reagent, cresyl blue, or sulfobenzaldehyde. Although technically such cystidioid elements may be pseudocystidia, we are reluctant to apply terminology unfamiliar to workers in this taxonomic group.

Presence of pleurocystidia in *G. peronatus* escaped the attention of European mycologists until Antonín & Noordeloos (1997) referred to it. In *G. peronatus* they are typically fusoid-lanceolate and may pass unnoticed in thick cross-sections. Presence of pleurocystidia in *G. subnudus* was first reported by Murphy & Miller (1997). We have not examined the type of *G. subnudus* and Desjardin (1989) did not report presence of pleurocystidia. Pleurocystidia of tropical members of subsect. *Peronati (G. omphalodes, G. lodgeae, G. pseudolodgeae)* are typically conspicuous, fusoid-ventricose and protrude well beyond the hymenium.

Petersen & Gordon (1994) reported a tetrapolar mating system for *G. "dichrous",* using TFB 1871 (USA, North Carolina). Subsequently, this collection was found to be interINcompatible with

all other tested collections under this name (Fig. 3). In fact, this morphologically indistinguishable collection appears in poorly supported clade E (Fig. 2) together with a sequence derived from sampling of leaf litter (GenBank AF241323: Polishook, J.D. *et al.* unpublished). AF241323 and TFB 1871 do not represent the same taxon.

11.1. *Gymnopus lodgeae*

Our collections of *G. lodgeae* were compared to the holotype of the species (Costa Rica. Prov. Heredia, Sarapiquí, La Selva OTS Biol. Stat. 23.XII.1979, Lodge 294, F!). Based on ITS data, Costa Rican specimens of *G. lodgeae* and *G. pseudolodgeae* are only distantly related to other members in clade H, but seem more similar in ITS signal to *G. termiticolus* (Wilson *et al.* 2004), an Old World tropical taxon.

A self-cross using TFB 9678 (Costa Rica) revealed a tetrapolar mating system (Mata 2002). An intercollection pairing between TFB 11013 and TFB 10030 (n = 4) showed 50 % intercompatibility.

11.2. *Gymnopus pseudolodgeae*

Mata (in Mata *et al.* 2004a) described *G. pseudolodgeae* from Costa Rican material. Basidiomata of *G. pseudolodgeae* strongly resemble those of *G. lodgeae*, but basidiospores (for *G. pseudolodgeae*, 4.8 – 6.4 × 2.4 – 3.6 µm; for *G. lodgeae* 5.6 – 8.8 × 2.4 – 4.0 µm) and pleurocystidia (for *G. pseudolodgeae* 40 – 80 × 8 – 12 µm; for *G. lodgeae* 60 – 190 × 8 – 20 µm) differ.

11.3. *Gymnopus omphalodes*

Our collections of *G. omphalodes* are only from Costa Rica where this species may represent an endemic. A somewhat divergent sequence (AF345804) deposited in GenBank as *G. confluens* appears in this well-supported (1.00 / 100 %) clade. This collection was deposited by Korean workers and, while certainly not correctly identified, highlights the problem of incorrectly applied epithets in phylogenetic reconstructions.

Mata & Petersen (1999) reported a tetrapolar mating system for *G. omphalodes,* using TFB 10023. Intercollection crosses using 11 Costa Rican collections in all combinations showed that all of them belonged to a single biological species (Mata 2002).

Pileipellis structure in *G. omphalodes,* with common erect side branches of suprapellis hyphae, resembles that found in *Marasmiellus,*

and this species was considered such by Singer (1973. Nova Hedwigia, Beih. 44: 118). Our use of the binomial *G. omphalodes* is based on descriptions by Dennis (1951) and Singer (1973), and on identifications by Dr. R.E. Halling (pers. comm.). Although we have not examined type material, Halling (pers. comm.) furnished descriptive notes on it, and the species has been taken up elsewhere (Mata 2002; Mata & Petersen 1999).

11.4. *Gymnopus peronatus*

Our collections of *G. peronatus* were compared with the neotype [United Kingdom, Yorkshire, Halifax, Elland Park Wood, 7. IX.1 996, A Leonard (neotype of *Agaricus peronatus* Bolt. E!)]

Several morphological characters separate basidiomata of *G. peronatus* from others: 1) lamellae yellowish to ochraceous when mature (usually paler when very young, and mellowing to tan shades in age); 2) distinctly vestured stipe; 3) weakly acrid taste; and 4) usual association with extensive mycelial sheets in the litter.

Lamoure (1989) summarized several references (Kniep 1928; Kühner 1945, 1947; Yen 1950a) and reported *Co. peronata* as tetrapolar. For our study, using TFB 9982 (Oregon), a self-cross revealed an apparently bipolar mating system. Tester strains: A_1 = 8, 11; A_2 = 1, 3. Although blocks of compatible pairings were clear, „barrage" contact zone morphology and re-arrangement of the initial pairing grid (see Ginns 1974) indicated that unbalanced tetrapolarity (in which two mating types were absent from the sample) could also be concluded.

In three series of pairing experiments, collections of *G. peronatus* from western North America were found to belong to the same biological species as collections from Europe (Fig. 10). In fact, ITS sequences of all collections appearing in the phylogeny differ little, supporting the case that *G. peronatus* has not been geographically fragmented long enough for substantial molecular deviation. This may support the hypothesis that *G. peronatus* has been introduced in western North America only recently. Thus far, it is unknown from eastern North America.

11.5. *Gymnopus subnudus*

G. subnudus has been the object of detailed research (Murphy 1992, 1995; Murphy & Miller 1993, 1997). Murphy & Miller (1997) identified two intersterility groups within *G. subnudus* with virtually identical ITS sequences. While a northern clade is evident within *G. subnudus,* it does not uniquely represent an intersterility group.

The other intersterility group is also found within a complex consisting of identical sequences. These data suggest that the two morphologically indistinguishable intersterility groups are relatively widespread and at least parapatric.

Murphy (1992) reported the first bipolar mating system in *Collybia*, using *Co. subnuda*. Petersen (1995 a), using some of the same SBIs as Murphy, interpreted self-cross grids (collections TFB 1818, TFB 3833) as arguably tetrapolar (data not shown). Equally ambiguous data have been generated from *G. peronatus* (see above).

The causes of such sexual ambiguity can be several: in addition to apparent bipolarity, an unusually high percentage of "single-spore isolates" are found to be dikaryotic, either through amphithallic sorting of post-meiotic basidial nuclei or through harvest of double spores caused by basidiospore clumping, to which Vilgalys & Miller (1983) drew attention. In a different paradigm, some mating types might be associated with slow spore germination and result in overwhelming selection of two mating types. Finally, other groups of *Gymnopus* (*viz.* sect *Levipedes*) exhibit reluctance to mingle haploid mycelia, and in sect. *Peronatae* such a trait may inhibit anastomosis and therefore dikaryotization. Whatever the cause, members of clade H are either bipolar in an otherwise tetrapolar genus, or, if scattered "barrage" and "flat" contact zones are considered, an extremely unbalanced tetrapolar mating system.

12. Clade I (Figs. 2, 11)

Basidiomata of sect. *Vestipedes* which exhibit prominent cheilocystidia but no pleurocystidia, can be further subdivided into two clades, one including taxa with lignicolous basidiomata [*G. pseudo-omphalodes, G. luxurians* (clade I)], the other apparently with litter-decomposing fruiting habit [*G. biformis, G. collybioides, G. cylindricus, G. confluens, G. neotropicus* (clade K; Fig. 13)]. Whether this distinction will remain valid as additional taxa are added remains to be seen.

Wilson & Desjardin (2003, 2005; LSU sequences) identified a poorly supported clade which they called /marasmiellus, since it included *Me. juniperinus (typus generis)*. In our analysis (ITS sequences), *Me. juniperinus* is basal to clade K (Fig. 13). In their clade /marasmiellus and in our clade I, however, a number of common taxa are found, including *G. luxurians, G. subpruinosus, G. gibbosus* and others. These two clades, therefore, can be judged roughly equivalent. While we cannot adopt "/marasmiellus," we can find no previously used name for clade I. We have given it an informal clade name, "/luxuriantes."

12.1. *Gymnopus subpruinosis*

Gymnopus subpruinosus was originally described based on Jamaican specimens collected by Murrill (Pennington 1915: 266), Desjardin *et al.* (1999) reported and illustrated *G. subpruinosus* from the Hawaiian Islands, and commented that it had also been found in California. Desjardin *et al.* (1999) examined the type specimen of *Ma. subpruinosus* Murrill in order to compare Hawaiian specimens to it. Hemmes & Desjardin (2002) included the species in the Hawaiian mycota. Our material was compared to the descriptions and illustrations above. It is likely, given the sequence homology, that Hawaiian collections have been recently established from North American mainland populations or vice-versa.

One collection (TFB 9529, California) in our study was marginally intercompatible (1:8 pairings) with TFB 11063 (Kauai). Whether this small sample indicates that the time period of separation of the two populations is sufficient to establish partial reproductive isolation cannot be conjectured. With identical ITS sequences and inseparable basidiomatal morphology, the two collections probably belong to the same species. Collection TFB 11066 (Hawaii) agrees morphologically. Biological conspecificity of Caribbean collections remains an open question.

12.2. *Gymnopus pseudo-omphalodes*

These Mesoamerican specimens conform to the key by Dennis (1961) for a fungus from Venezuela and form a small but well-supported clade. We have not examined the type specimen of *Co. pseudo-omphalodes* [Venezuela, Est. Miranda, Guatopo, 25.VI.58, Dennis no. 1108, K; *teste* Pegler 1983b], so our use of this name is not totally secure.

Likewise, the binomial *Co. fibrosipes* was applied to TFB 9699 by Mata (2002), who examined the type specimen (Wright, Cuba, K!), so this name was investigated as well. Dennis examined the type specimen, did not report presence of cheilocystidia, but described pileus colors close to those from TFB 9699. The type specimen, however, was (and is) in dubious condition. It was decided that TFB 9699 agreed in more characters with *G. pseudo-omphalodes* than with *Co. fibrosipes,* necessitating one new combination (see Appendix 2).

12.3. *Gymnopus "luxurians"* (Hawaiian Islands)

The organism reported as *G. luxurians* from the Hawaiian Islands (Desjardin *et al.* 1999) differs from Euro-American *G. luxurians* by

3.39 % and is reproductively isolated from European and North American *G. luxurians*, suggesting that the Hawaiian *G. luxurians* is a separate taxon. We are reluctant to describe it, however, without being familiar with fresh material from the Hawaiian Islands (our material was furnished as dried basidiomata and spore prints by D. Hemmes).

Wilson & Desjardin (2003) deposited two nLSU sequences of *G. luxurians*, one from North Carolina (TENN 57910) and one from Hawaiian Islands (DEH 1304). At LSU resolution, the two sequences were apparently not identical. The sequence of North American *G. luxurians* was deleted by Wilson & Desjardin (2005), but the Hawaiian sequence would seem to represent the discordant element discussed here.

12.4. *Gymnopus luxurians*

The epithet, *G. luxurians*, is based on Alabama material [Alabama, Auburn, VII.1896, Underwood and Earle, NYS; isotype NY!]. Throughout its range, basidiomata are most commonly found on sawdust, mulch or very rotten wood. It is becoming increasingly commonly collected as use of fermented mulch for landscaping grows in popularity. It is apparently a relatively recent introduction to Europe. Its presence in southern North America may indicate a subtropical distribution, reflected in material from Dominican Republic. Hemmes & Desjardin (2002) described *G. luxurians* from the Hawaiian Islands, assuming it to be introduced, probably by human mediation (but see above). Our crossing studies demonstrate that a single biological species extends from central Europe to eastern North America and south into the Caribbean.

12.5. *Gymnopus luxurians var. copeyi*

Small microscopic differences, phylogenetic placement and sexual interINcompatibility with North American *G. luxurians* indicate that this Costa Rican specimen represents a separate infraspecific taxon (see Appendix 1).

13. Clade J (Fig. 2)

Clade J (Fig. 2) comprises three small sister clades: *Marasmiellus* sp. (North Carolina), *G. melanopus* (Indonesia); and *Me. ramealis* (Sweden) and North American *Me. stenophyllus*. The clade is not well supported and individual taxa are often found in other associations, depending on the analysis.

13.1. *Marasmiellus ramealis*

Marasmiellus ramealis was included by Moncalvo *et al.* (2002) in this general clade (/lentinuloid; Fig. 1), and our data further place it in a clade comprising collections of a wood-rotting *Gymnopus* species. As with other *Gymnopus* clades, *Marasmiellus* taxa appear basal to this monophyletic lineage.

Marasmiellus ramealis (Bulliard) Fries was designated as *typus generis* of *Collybiopsis* Earle (1909). Earle did not designate a type specimen, however, but his elevation of Schroeter's *Marasmius § Collybiopsis* required a European type specimen. Antonín & Noordeloos (1993) designated a neotype [FRANCE, Dpr. Pas de Calais, Boulogne sur Mer, 14. X. 73, leg. ME Noordeloos, no. 7310, L; *non vide*]. Our concept of this species was taken from Antonín & Noordeloos (1997), and care was taken to select a European collection for our study. The pileipellis structure of *Me. ramealis* is that of a parallelocutis, composed of cylindrical hyphae that are mostly radially oriented, repent, and rarely branched (i.e. never a "*dryophila*-type" structure). Antonín & Noordeloos (1997) explained that for *Me. ramealis* the cutis forms a transition into a trichoderm. Largent *et al.* (1977) defined a trichoderm as pileipellis composed of ± filiform elements of unequal lengths arranged anticlinally (i.e. erect terminal cells); these terminal cells in *Me. ramealis* typically are highly diverticulate or knobbed, i.e. presenting a "rameales-structure" as defined in Largent *et al.* (1977). Placement of *Me. ramealis* within gymnopoid taxa led to a new combination (Mata *et al.* 2004b) and our current data using an expanded data set are consistent with that study.

At the same time, *Ma. ramealis* is the type of *Marasmiellus* sect. *Rameales* (J. Lange) Singer (viz. Antonín & Noordeloos, 1997), so other members of this section may be expected to be sheltered in this clade as additional data are uncovered. *Marasmiellus stenophyllus* is also found in clade J, anticipated because Desjardin (1997) placed the two species in sect. *Rameales* subsect. *Ramealini*.

Wilson & Desjardin (2005) placed *Me. ramealis* together with *Campanella eberhardii* in a small, unannotated clade. Support for segregation of *Me. ramealis* was strong (1.00 / 100 %) but *Cp. eberhardii* was relatively distant and without support. Placement of a *Campanella* species, however, opens the possibility of further inclusion of members of this genus in clade J.

Placement of the type species of *Marasmiellus (Me. juniperinus)* and of *Collybiopsis (Co. ramealis)* in different clades (J and L, respectively) resurrects questions about the synonymy of the two genus names (Antonín *et al.* 1997; Antonín & Noordeloos 1997: 158). Although a proposal to conserve *Marasmiellus* over *Collybiopsis* was

planned (Antonín *et al.* 1997), it has not been formalized (V. Antonín, pers. comm.), and, according to our analysis, is unwarranted. If clade J is assumed to belong to *Gymnopus,* appropriate epithet transfers must be proposed. Nonetheless, clade J can be equated with *Collybiopsis*.

13.2. *Marasmiellus stenophyllus*

Marasmius stenophyllus Montagne (1854. Ann. Sc. Nat. IV 1: 116.) was based on a Leprieur specimen from French Guiana [Leprieur 1027, PC], so the species must include stations in the New World tropics.

Singer (1973) proposed numerous infrageneric taxa to be included in *Marasmiellus,* including sect. *Dealbati* subsect. *Dealbatini. Marasmiellus stenophyllus* was placed in this subsection, with material examined from Florida to northern Argentina. The section was characterized by stipitate (usually eccentrically so) basidiomata, pileipellis hyphae with a minimum of side branches (i.e. a very reduced rameales structure) and small spores. The subsection represented basidiomata with little pigmentation on the pileus or stipe. Desjardin (1997) included some species as fruiting in the southern Appalachian Mountains, some distance and ecotype from Singer's northernmost report from central Florida. Singer (1986: 324) eventually included several species in this subsection.

Our use of the binomial *Me. stenophyllus* is based on Desjardin's (1997) summary of southern Appalachian *Marasmiellus* species. Mata *et al.* (2004b) placed *Ma. stenophyllus* within *Gymnopus* and made the transfer to *Gymnopus* as *G. stenophyllus.*

Whether additional species from this subsection will also be placed in this clade remains for future research.

Presence of *M. stenophyllus* in clade J further supports the polyphyletic distribution of *Marasmiellus. Marasmiellus opacus* (sect. *Rameales* subsect. *Opacini* for Singer, 1986) is found in clade F. *Me. juniperinus* (sect. *Marasmiellus* for Singer) is found alone in clade L. Thus, *Marasmiellus,* if accepted in the present wide sense (cast as a synonym under *Micromphale* by Antonín & Noordeloos, 1997), is a candidate for fractionation.

13.3. *Gymnopus melanopus*

Known molecularly from two collections from Indonesia, *G. melanopus* shares with other members of clade J a habit on wood, relatively small size, and micromorphological resemblance to other members of clade D.

14. Superclade K (Figs. 2, 13)

A large and seemingly heterogeneous assemblage, clade K is poorly supported. Morphological characteristics common in clade K are as follow: 1) pileipellis a parallelocutis, composed of cylindrical, radially oriented, repent hyphae, which sometimes are diverticulate (occasionally, terminal cells are sub-erect to erect, or coralloid); 2) stipe covered by a pruina; and 3) cheilocystidia generally clavate, but often lobed and flexuous. These characters are also expressed by surrounding clades. Clade H shares the same characteristics but is distinguished from clade K by the presence of pleurocystidia and perhaps bipolar mating system.

Clade K, which is dominated by tropical taxa, is as unresolved as superclade C. Names have been difficult to assign in both clades due to phenotypic plasticity, especially exacerbated in clade C by geographical distance (North Temperate distribution). In clade K, tropical distributions pervade, but even though phenotypic plasticity seems relatively small, genotypic variation is evident through segregation of numerous small clades.

Collybia subg. *Collybia* sect. *Subfumosae* Singer (1962, *nom. nud.*, val. Halling 1983) was proposed to accommodate *Co. subfumosa* (Spegazzini) Singer. Singer, using his own collections identified as *Co. subfumosa,* saw a complex pileipellis reminiscent of a "ramealis" structure and fixed this to his (Singer's) concept of *Co. subfumosa.* Because this pileipellis structure was thought to be unique in the genus, Singer proposed sect. *Subfumosae* for species exhibiting such a pileipellis constuction. Halling (pers. comm.) examined Spegazzini's type specimen and was unable to detect any specific pileipellis structure on the poorly preserved basidiomata. Nonetheless, the concept on which the section was based has persisted, with *Co. biformis* as one of the taxa (among others) placed therein. Acknowledging the weak association of *G. biformis* to the original intent of sect. *Subfumosae,* clade K can be equated with the commonly understood circumscription of the section.

14.1. *Marasmiellus juniperinus* (Figs. 2, 13)

Marasmiellus juniperinus, the type species of *Marasmiellus,* is found basal to superclade K [inclusive of clades L-N in Bayesian analysis (0.78 / < 50 %)]. Its position is uncertain in parsimony analysis where it appears as sister to a number of clades including those sheltering *G. confluens* and *G. biformis.* Mata *et al.* (2004b) previously demonstrated, based on a phylogeny of ribosomal ITS sequences of gymnopoid taxa, that *Me. juniperinus* was part of the *Gymnopus* clade although its precise placement was consistently

poorly supported. Wilson & Desjardin (2005), using nLSU, found *Me. juniperinus* and closely associated nodes to be basal to a clade dominated by *Gymnopus* taxa. Sister clades included *Rhodocollybia, Marasmiellus* and *Gymnopus* species. They used placement of *Me. juniperinus* as the basis for their clade /marasmiellus, but that clade included taxa placed in our clades J and L. We prefer to allow clade K to remain unequated with a taxo-nomenclatural name. Instead, we have used informal names for the two major constituent subclades M and N.

Although it would appear obvious that *Me. juniperinus* must be placed within *Gymnopus,* placement of the numerous other species assigned to *Marasmiellus* remains largely unknown. Transfer of the binomial as *Gymnopus juniperinus* was proposed by Mata *et al.* (2004b).

14.2. *Gymnopus nonnullus*

Wilson & Desjardin (2005) found the Indonesian *G. nonnullus* (listed as var. *attenuatus* in their Table 1) basal to a well-supported clade generally equating to our clade K. Our study includes many additional sequences, but *G. nonnullus* remains basal and strongly supported. This placement contributes to a hypothesis of Old World origins for several groups of gymnopoid fungi.

14.3. Superclade M/N (Figs. 2, 13)

Basidiomata of taxa in this superclade show a parallelocutis structure in the pileipellis, frequently with erect terminal cells, and clavate to sphaeropedunculate, lobed cheilocystidia. In our study, the association of clades M and N is well-supported (Fig. 13)

14.3.1. Clade M (Figs. 2, 13)

All species in clade M degrade leaf-litter and most participants (except *G. confluens*) are from tropical climates. Although not all members of clade M were explored sexually, investigated examples exhibited tetrapolar mating systems (see results).

When Kühner (1933, 1936) proposed sections in *Marasmius ss.* Kühner, *M. confluens* was placed in sect. *Peronati,* along with *Ma. peronatus*. Later, Singer (1949, 1986) and Antonín & Noordeloos (1997) included Kühner's sect. *Peronati* as a subset of *Collybia* (later *Gymnopus*) sect. *Vestipedes*. In our study, despite placement of *G. peronatus* and *G. confluens* in different clades (H and M, respectively), both clades are sheltered under clade D, equating

to *Gymnopus* sect. *Vestipedes*. Support for clade M is minimal (.83 / <50 %).

Gymnopus confluens, under various genus names, has consistently remained the type species for sect. *Vestipedes*. In our analysis, sect. *Vestipedes* is a comprehensive group represented by clade D. Antonín & Noordeloos (1997) placed *G. confluens* in sect. *Vestipedes* subsect. *Vestipedes*, but to equate clade M to subsect. *Vestipedes* (correctly) would be linguistically confusing. We have given clade M the informal name "/confluentes."

14.3.2. *Gymnopus readii*

Stevenson's (1964) watercolor drawing and field notes of *G. readii* agree with the photo and field notes for TFB 7571. Horak's (1971) drawings and notes of microscopic characteristics on the type specimen match very well with the characters of this specimen. When Horak examined the type specimen of *Crinipellis readii* he realized that a transfer to *Collybia* would create a later homonym to *Co. readii* Stevenson. Placement of *G. readii* is poorly supported. No prior combination of the basionym in *Gymnopus* exists (see Appendix 2).

In New Zealand, a similar species to *G. readii* is *Co. kidsonii*, which can be distinguished by an umbonate pileus, distant lamellae, and overall paler colors of basidiomata. *Collybia vinacea* has similar microscopic characteristics to *G. readii* but overall colors of basidiomata of *Co. vinacea* are vinaceous pink. Presumably, transfers of these epithets to *Gymnopus* will be necessary.

14.3.3. *Gymnopus mesoamericanus*

Mata (2002) furnished an ITS maximum parsimony phylogenetic reconstruction using Costa Rican specimens of *Gymnopus* and related taxa. That phylogeny showed a single Costa Rican collection of putative *G. confluens* (REH7379) in a clade with *G. neotropicus* (TFB 10416) and separated from North Temperate *G. confluens* (TFB 7219). This separation is strongly confirmed (1.00 / 100 %) in our study, using several collections of Costa Rican and North Temperate basidiomata and as a result, a new species is proposed for the Costa Rican collections (see Appendix 1). No sexual compatibility pairings between Costa Rican and North Temperate *G. confluens* collections were accomplished.

Basidiomata of *G. mesoamericanus* resemble those of the neotype specimen of *G. confluens* [Belgium, Prov. Namur,Grande Tinémont near Han-sur-Lesse, 26. IX. 74, leg. M Noordeloos, no. 7479, L!] and in the field, Mesoamerican basidiomata may be misidentified. Only

telltale morphological characters separate the Costa Rican specimens: 1) gregarious habit, not caespitose to densely gregarious; 2) reddish brown to purple-brown stipe colors instead of orange-brown to gray-brown. Basidiospores and cheilocystidia are indistinguishable.

14.3.4. *Gymnopus neotropicus*

Our Costa Rican specimen under *G. neotropicus* was compared favorably to the holotype [Bolivia, La Paz, Nor Yungas, Coroico, 15. II. 1956, col. R Singer *B 1173*, LIL!].

14.3.5. *Gymnopus alnicola*

Now known from Costa Rica and Ecuador (Mata *et al.* 2004a), collections were compared to type material of *G. biformis* (holotype; USA,. New York, Rennselaer Co., VIII.1902, CH Peck, NYS!), *G. confluens* (see above) and *G. luxurians* (see above). The sequence in our study is *ex typus*.

14.3.6. *Gymnopus subcyathiformis*

We compared our collections to Murrill's type (Mexico, Colima, 3 – 4.I.1910, Murrill 615, NY!). Desjardin *et al.* (1999) also examined this type, proposed transfer of the epithet to *Gymnopus* and distinguished it from *G. menehune* from the Hawaiian Islands. Murrill (in Pennington 1915) described *Ma. subcyathiformis* as having a depressed pileus with brown-violet colors, in combination with pallid lamellae and pruinose stipe. *Gymnopus biformis* has much more umbilicate and convex shaped pilei and is collected on a pine-oak substrate preference. Basidiomata of *G. johnstonii* are much smaller and have a garlic-like odor.

Initially, TFB 10436 was thought to represent a morph of *G. impudicus*. Spore dimensions and colors of basidiomata of *G. impudicus* and varieties of *G. biformis* are very similar, but cheilocystidial shape and dimensions are somewhat different, i.e. appearing concatenate in *G. impudicus*, in contrast to more clavate to sub-sphaeropedunculate and lobed in *G. biformis*.

14.3.7. *Gymnopus menehune*

TFB 11587 was furnished by Dr. D.E. Hemmes as a spore print, with the dried specimen as a loan. It was compared with the isotype [USA, Hawaiian Islands, Hawai'i, 3. VIII. 1993, DED 5866, NY!]. Wilson & Desjardin (2005; LSU) showed one sequence labeled

as *Gymnopus* aff. *menehune* from Indonesia which differed substantially from others under this binomial. In our analysis, this sequence also diverged, being placed in clade N.

14.3.8. *Gymnopus confluens*

Our collections of *G. confluens* were compared to the neotype specimen [Belgium. Namur Prov., vic. Han-sur-Lesse, 26. IX. 1974, Noordeloos no. 79, L (L0053911)!].

Lamoure (1989) cited two references (Lamoure 1954; Oddoux 1957) as reports of heterothallism in *Co. confluens,* but neither report could specify tetrapolarity, assumed by Lamoure.

15. Clade N (Figs. 2, 13)

Basidiomata of all members of clade N share the following characteristics: 1) small stature of basidiomata (pileus < 4 cm diam); 2) humicolous habit; 3) stipe with a pruinose vesture; and 4) pileipellis a parallelocutis, composed of cylindrical, radially oriented hyphae, typically diverticulate hyphae and with frequent erect terminal cells. Species are separated by basidiospore dimensions and shapes and size of cheilocystidia/caulocystidia, but differences are very small.

The presence of *G. cylindricus, G.* aff, *menehune, G. villosipes, G. collybioides* within clade N creates significant taxo-nomenclatural problems. *Gymnopus cylindricus* is morphologically distinct and should remain as a separate morphospecies. *Gymnopus* afn. *menehune* is phylogenetically related to *G. cylindricus* but is a Malaysian species while *G. cylindricus* is Central American. Further collecting on a larger geographic scale may enlarge the geographical distribution of taxa within clade N and clarify affinities.

American tropical to subtropical species morphologically similar to *G. biformis* are *G. menehune* described from Hawaii (clade M), *G. subcyathiformis* (clade M), *G. johnstonii* from Puerto Rico (not in our study), *G. cylindricus* from Costa Rica, and *G. collybioides* from Brazil (both clade N). Lamellae of basidiomata of *G. menehune* are more crowded and do not form a pseudocollarium as in *G. biformis;* cheilocystidia are abundant, clavate to lobed (Desjardin *et al.* 1999). Basidiomata of *G. collybioides* are much smaller and lamellae are much more crowded than those of *G. biformis,* but microscopic elements are similar (Mata 2002). *Gymnopus cylindricus* is characterized by the cylindrical shape of the cheilocystidia in combination with narrowly ellipsoid to cylindrical spores (Mata *et al.* 2004 a). The type specimen of *G. subcyathiformis* (see above) is very similar to our collections of *G. biformis* in lamellar distance, stipe

vesture, and spore dimensions, although presence of cheilocystidia in *G. subcyathiformis* could not be ascertained positively. All of the above-mentioned species have diverticulate projections on the hyphae of the pileus epicutis. *Gymnopus johnstonii* is similar in stature and habit to *G. biformis,* with pileus more grayish, stipe less pubescent, and cheilocystidia more nodulose (Dennis 1951; Pegler 1983 b). *Gymnopus villosipes* is also morphologically similar to *G. biformis* but it fruits on pine litter (Desjardin *et al.* 1997). Sequences of numerous specimens collected in neotropical America appear to fit in the overall morphological concept of *G. biformis*. All told, clade N seems uniquely New World tropical/subtropical, with *G. biformis* extending into eastern North America.

15.1. *Gymnopus biformis*

While well-supported (1.00 / 94 %), the clade clearly segregates two subclades, one of southeastern North American collections (1.00 / 99 %), the other of Costa Rican material (1.00 / 92 %).

According to Halling (1983), descriptive characteristics for basidiomata of *G. biformis* include: pileus convex to plane, often depressed to umbilicate, with rugulose sulcate margin, reddish brown to cinnamon brown to flesh in color; lamellae usually forming a pseudocollarium; and stipe slender, covered with a pubescence, tawny to vinaceous brown toward the base. In North America, basidiomata representing *G. biformis* could be confused with those of *G. subnudus* but can be separated by comparing relative lamellar crowding and color, color of the stipe vesture, anatomy of the pileipellis, subtrate and, to a lesser extent, taste. Beside these reported distinctions, it can be added that cheilocystidia in basidiomata of *G. biformis* tend to have considerable variation in shape (i.e. typically contorted, frequently lobed, knobbed or diverticulate), and the range of basidiospore length is lower, by 1 – 2 µm, than that reported for the type specimen (USA, New York, Renssalaer Co., no date, C.H. Peck, NYS!) and natural populations of *G. subnudus,* i.e. 8.6 – 10.4(– 12) µm (Desjardin 1989; Halling 1983). The southernmost report for *G. subnudus* is Mexico (Villaruel-Ordaz *et al.* 1993).

15.2. *Gymnopus* aff. *menehune*

Wilson & Desjardin (2003, 2005) recognized that this collection, while resembling *G. menehune,* was relatively distantly related (based on LSU sequences). In our study (ITS sequences), the sequence is quite separated from those of true *G. menehune* (clade M), although sympatric with them.

15.3. *Gymnopus cylindricus*

The *"cylindricus/parvulus"* clade is well-supported in Bayesian analysis (.98), but not so in maximum parsimony. The small *"cylindricus"* clade, conversely, is well-supported (1.00 / 98 %) and includes Old World and New World taxa. Mata (in Mata *et al.* 2004a) described *G. cylindricus* from Costa Rica. Basidiomata were similar to those of *G. confluens* (clade M) and *G. polyphyllus* (clade B; Figs. 2, 4), but basidiospores were acicular (8.8 – 13.16 × 3.2 – 4.8 µm) and cheilocystidia were cylindrical and obvious (24 – 65 × 6 – 9 µm). Its mating system remains undescribed.

15.4. *Gymnopus villosipes/parvulus* clade (Fig. 13)

15.4.1. *Gymnopus villosipes*

Desjardin *et al.* (1997) compared California material to the type of *Marasmius villosipes* Cleland from Australia, and concluded that the species was probably introduced into Australia. Our specimen was field-identified by Desjardin (pers. comm.) and conformed to the description furnished by Desjardin *et al.* (1997). Desjardin *et al.* (1997) correctly surmised its relationship with *G. biformis,* confirmed here.

15.4.2. *Gymnopus biformis* 2

Mata (2002) provisionally described *G. biformis* var. *lobatus (nom. prov.)* based on the lobed configuration of cheilocystidia. Macro- and microscopic characteristics are similar to those found in the typical variety of *G. biformis*. Basidiomata of var. *"lobatus"* appear to lack the densely strigose-pubescent vesture of the stipe seen in those of var. *biformis*. Also, pilei seem to be more depressed-umbilicate, with more orange-brown to tan colors, lamellae less distantly spaced, and stipes that turn black with age. Microscopically, spores seem to be similar, but cheilocystidia appear to be consistently more lobate and furcate than those observed in specimens of var. *biformis*. *Gymnopus biformis var. "lobatus,"* a morphovariety, appears polyphyletic and may represent an environmentally influenced morphology rather than a genetic variant. For this reason, we have chosen not to describe this as a new variety as originally proposed based on morphology (Mata 2002).

15.4.3. *Gymnopus parvulus*

Gymnopus biformis var. parvulus (nom. prov.) was provisionally proposed as new by Mata (2002). Basidiomata of *G. parvulus* appear

to be much smaller in stature than those of *G. biformis,* and pileus colors in *G. parvulus* are more orange-brown to tan. Additionally, the base of the stipe does not blacken as in *G. biformis var. "lobatus". Gymnopus parvulus* is described as new (see Appendix 1).

15.4.4. *Gymnopus collybioides*

Basidiomata of *G. collybioides* have a very slender stipe that is proportionally long in relation to the pileus diameter, and white lamellae that are very crowded and do not form a pseudocollarium (Mata 2002). Costa Rican specimens were compared with the type specimen of *Clitocybe collybioides* Speg. [Brazil, Apiahy, IV.1888, coll. J Puiggari, no. 2893, LPS!] and considered conspecific. The species, therefore, seems to be a South American entity reaching its northernmost limit in Central America. Desjardin *et al.* (1999) reported the species from the Hawaiian Islands, but we have not examined that material.

A self-cross of *G. collybioides* using TFB 9690 (Costa Rica, not in phylogeny) revealed a tetrapolar mating system (Mata 2002).

Voucher specimens for TFB 7820 (as *G. biformis* var. *biformis*) and TFB 7843 (as *G. ?subnudus*) cannot be located in TENN. Because of this, morphological identity cannot be confirmed and we are forced to designate the name for the closest identified sequence backed by a voucher specimen – in this case, *G. collybioides*. Nonetheless, segregation of these two collections is well-supported (1.00 / 100 %) and so is difficult to overlook.

15.4.5. *Gymnopus biformis* 3 (Fig. 13)

Gymnopus collybioides is basal to a third morphological *Gymnopus biformis* clade but the sequences of *G. biformis* and *G. collybioides* are too divergent to represent the same species. *Gymnopus biformis* 3 may represent a yet-unnamed taxon or true *G. biformis* in which the repeat element has perturbed the phylogenetic placement.

16. Evolutionary Patterns within *Gymnopus*

At least three different evolutionary processes can be identified within *Gymnopus*. Within clade C (*G. dryophilus* and related taxa), there is considerable morphological differentiation but little ITS sequence divergence and some sequence evidence that this clade represents fragmentation of a once interbreeding population. This clade may represent relatively recent speciation events coupled

with some morphological divergence. Clade K, on the other hand, represents a group in which there is little morphological differentiation but significant ITS sequence differentiation. In this group, sequence data must be used to define species boundaries and cryptic species will be found with the addition of more collections. This group is largely tropical. Finally, within clade D, evolution has occurred with respect to a tandem repeat found in the ITS 2 region. Once an initial duplication occurred, the area seems to have become destabilized and duplications have been gained and lost in different evolutionary lineages within this group, even within populations of the same putative species. The evolutionary history of the repeat itself may differ from the evolutionary history of the rest of the sequence such that inclusion of the repeats may bias the actual phylogeny.

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Tab. 1. – Collections used in this study.

Field No	Herbarium No	Name	Location	GenBank No.
TFB 3511	TENN50049	*Anthracophyllum archeri*	Australia	DQ444308
TFB 4043	TENN50256	*Anthracophyllum lateritium*	USA, North Carolina	DQ444309
JMCR 143	JMCR 143	*Caripia montagnei*		DQ449988
	KACC 500037	*Gymnopus "confluens"*	Korea	AF345804
D29	Duke29	*Gymnopus "dryophilus"*		DQ480098
TFB 11042ss1	TENN 59456	*Gymnopus "nivalis"*	USA, OR	DQ449982
TFB 11585	DEH 2318	*Gymnopus "luxurians"*	USA, Hawaii	DQ450019
TFB 11586	DEH 2319	*Gymnopus "luxurians"*	USA Hawaii	DQ450020
AY263431	SFSU-AWW10	*Gymnopus aff moseri*	Indonesia, Java	AY263431
TFB 11706	TENN 59545	*Gymnopus afn. dysodes*	Dominican Rep.	DQ480110
AWW113	SFSU AWW113	*Gymnopus afn. menehune*	Indonesia, Bali	AY263430
TFB 4936	TENN 51249	*Gymnopus alkalivirens*	USA, NY	DQ450000
TFB 9774	TENN 58672	*Gymnopus alkilivirens*	Greenland	DQ480112
REH8266	TENN 54324	*Gymnopus alnicola*	Costa Rica	AF505770

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
D15	Duke15	*Gymnopus alpinus*	Sweden	DQ480101
TFB 3853	TENN 55834	*Gymnopus alpinus*	U.K., Scotland	DQ480114
D14	Duke14	*Gymnopus alpinus*	U.K., Scotland	DQ480102
TFB 3853	TENN 55831	*Gymnopus alpinus*	UK, Scotland	no sequence
D16	Duke16	*Gymnopus alpinus* RV	Switzerland	DQ480104
TFB 11435	TENN 59296	*Gymnopus aquosus*	Austria	DQ449999
TFB 10310	TENN 57958	*Gymnopus aquosus*	Germany	AY256691
TFB 6965	TENN 55883	*Gymnopus aquosus*	U.K., Scotland	DQ450003
D25	Duke25	*Gymnopus aquosus*		DQ450002
D245	Duke245	*Gymnopus aquosus*		DQ480096
TFB 10996	TENN 59738	*Gymnopus aquosus*	USA, WA (JFA)	DQ449971
TFB 3847	TENN 55826	*Gymnopus aquosus*	U.K., Scotland	DQ449976
TFB 3851	TENN 55934	*Gymnopus aquosus*	U.K., Scotland	DQ449977
TFB 10997	Held by L. Norvell	*Gymnopus aquosus*	USA, WA	DQ449981
D246t	Duke246t	*Gymnopus aquosus*	USA, VA	DQ480095
AWW118	SFSU-AWW118	*Gymnopus aurantiipes*	Java	AY263432
AWW131	SFSU-AWW131	*Gymnopus aurantiipes*	Java	AY263433
AWW65	SFSU AWW65	*Gymnopus austrosemihirtipes*	Java	AY263422
AY263423	SFSU-AWW116	*Gymnopus bicolor*	Java	AY263423
TFB 10478	TENN 58541	*Gymnopus biformis*	USA, Texas	DQ450054
TFB 9127	TENN 55753	*Gymnopus biformis*	USA, Louisiana	AY256699
TFB 10093	TENN 58088	*Gymnopus biformis*	Costa Rica	DQ450055
TFB 11016	TENN 58624	*Gymnopus biformis*	Costa Rica	DQ450056
TFB 7820	culture only	*Gymnopus biformis*	Costa Rica	DQ450063
TFB 9111	TENN 55740	*Gymnopus biformis*	USA, Louisiana	no sequence
TFB 9516	TENN 56273	*Gymnopus biformis*	USA, Louisiana	no sequence
TFB 10034	TENN 56746	*Gymnopus biformis*	Costa Rica	no sequence
TFB 11034	TENN 58641	*Gymnopus biformis*	USA, Tennessee	no sequence
TFB 9673ss2	TENN 56634	*Gymnopus biformis* (2)	Costa Rica	DQ450059
TFB 9657	TENN 56618	*Gymnopus biformis* (2)	Costa Rica	AF505775
TFB 7230	TENN 53558	*Gymnopus biformis* (3)	USA, South Carolina	AF505771
TFB 7843ss4	culture only	*Gymnopus biformis* (3)	Costa Rica	DQ450064
AWW01	SFSU AWW01	*Gymnopus brunneigracilis*	Indonesia, Java	AY263434
TFB 10080	TENN 58020	*Gymnopus collybioides*	Costa Rica	AF505772
TFB 3787	TENN 50524	*Gymnopus confluens*	Sweden	DQ450044
TFB 11335ss2	TENN 59219	*Gymnopus confluens*	France	DQ450045
TFB 10650ss4	TENN 58231	*Gymnopus confluens*	Russia	DQ450046

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
TFB 10653	TENN 58242	*Gymnopus confluens*	Russia	AY256697
TFB 10977	LE(BIN)183	*Gymnopus confluens*	Russia	DQ450047
TFB 11615	TENN 59578	*Gymnopus confluens*	Russia	DQ450048
TFB 11619	TENN 59582	*Gymnopus confluens*	Russia	DQ450049
TFB 9048	TENN 55695	*Gymnopus confluens*	USA, CA	DQ450050
TFB 6962ss8	TENN 55880	*Gymnopus confluens*	U.K., Scotland	DQ450051
TFB 7219	TENN 53522	*Gymnopus confluens*	USA, NC	AF505773
TFB 12134	TENN 60062	*Gymnopus confluens*	USA, NC	DQ450052
TFB 5824	TENN 52248	*Gymnopus confluens*	USA, Washington	DQ450053
TFB 9875	TENN 59500	*Gymnopus confluens*	USA, Washington	AY256698
TFB 10084	TENN 58024	*Gymnopus cylindricus*	Costa Rica	AY256696
TFB 10091	TENN 58086	*Gymnopus cylindricus*	Costa Rica	DQ450057
TFB 10402	TENN 58097	*Gymnopus cylindricus*	Costa Rica	AF505776
TFB 1871	TENN 48443	*Gymnopus dichrous*	USA, NC	AF505766
TFB 7920	TENN 53792	*Gymnopus dichrous*	USA, NC	DQ450007
TFB 10014	TENN 56726	*Gymnopus dichrous*	USA NC	AY256702
TFB 2028	TENN 48637	*Gymnopus dichrous*	USA, NC	DQ450008
TFB 10829	culture only	*Gymnopus dichrous*	USA, NC	DQ480115
TFB 11554	TENN 60161	*Gymnopus dichrous*	USA, NC	DQ450009
D242	Duke242	*Gymnopus dryophilus*		DQ480097
D31	Duke31	*Gymnopus dryophilus*	Japan	DQ480099
TFB 10940	TENN 58535	*Gymnopus dryophilus*	Canada, BC	DQ449962
TFB 10397	TENN 58257	*Gymnopus dryophilus*	Russia, Leningrad	DQ449963
TFB 5636	TENN 52412	*Gymnopus dryophilus*	USA, ID	DQ449964
TFB 9952	TENN 57012	*Gymnopus dryophilus*	USA, NC	AY256690
WC228	Culture only	*Gymnopus dryophilus*		AF079580
D40	Duke40	*Gymnopus dryophilus*		DQ480100
TFB 4976	TENN 51289	*Gymnopus dryophilus*	USA, ME	DQ449965
TFB 5027	TENN 51438	*Gymnopus dryophilus*	Canada, NS	DQ449966
TFB 11015	TENN 58623	*Gymnopus dryophilus*	Costa Rica	AF505787
TFB 10092	TENN 58087	*Gymnopus dryophilus*	Costa Rica	DQ449974
TFB 9684	TENN 56645	*Gymnopus dryophilus*	Costa Rica	DQ449975
TFB 11455	TENN 59316	*Gymnopus dryophilus*	Austria	no sequence
TFB 11400	TENN 59285	*Gymnopus dyrophilus*	Switzerland	no sequence
TFB 11040	TENN 59141	*Gymnopus dysodes*	USA, TN	AF505778
TFB 10474	TENN 58367	*Gymnopus dysodes*	USA, VA	DQ449987
TFB 11190	TENN 59805	*Gymnopus dysodes*	Dominican Republic	no sequence

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
TFB 11039ss5	TENN 59140	*Gymnopus earleae*	USA, TN	DQ449994
Duke46	D46	*Gymnopus earleae*		DQ480094
TFB 11043	TENN 59457	*Gymnopus earleae*	USA, OR	AY256694
TFB 11044	TENN 59458	*Gymnopus earliae*	USA, Oregon	no sequence
TFB 11470ss3	TENN 59331	*Gymnopus erythropus*	Austria, Vienna	AF505786
TFB 11911	JFA12910	*Gymnopus erythropus*	USA, WA	DQ449998
	SAV XI 2003	*Gymnopus erythropus*	Slovakia	DQ449995
	SAV XI 2002	*Gymnopus erythropus*	Slovakia	DQ449996
	BRA XI 88	*Gymnopus erythropus*	Slovakia	DQ449997
TFB 9898	LE-41	*Gymnopus exculptus*	Russia, Chelybinsk	no sequence
TFB 10713	TENN 58799	*Gymnopus exculptus*	Greenland	no sequence
TFB 10718	at Oslo	*Gymnopus exsculpta*	Greenland, Sisimuit	DQ449973
TFB 6995	TENN 55914	*Gymnopus fagiphilus*	UK, Scotland	no sequence
TFB 11438	TENN 59299	*Gymnopus fagiphilus*	Austria	AF505783
TFB 7239	TENN 53531	*Gymnopus fasciatus*	USA, North Carolina	no sequence
TFB 9699	TENN56660	*Gymnopus afn pseudo-omphalodes*	Costa Rica	AF505763
TFB 11439	TENN 59300	*Gymnopus fusipes*	Austria	AF505777
TFB 11333	TENN 59217	*Gymnopus fusipes*	France	AY256710
AWW112	SFSU AWW112	*Gymnopus gibbosus*	Indonesia, Java	AY263435
AWW66	SFSU AWW66	*Gymnopus gibbosus*	Indonesia, Java	AY263438
AWW95	SFSU AWW95	*Gymnopus gibbosus*	Indonesia, Java	AY263437
TFB 11454	TENN 59315	*Gymnopus hybridus*	Austria	DQ449980
TFB 8432	TENN 55261	*Gymnopus impudicus*	Mexico	DQ480109
TFB 9697	TENN 56658	*Gymnopus impudicus*	Costa Rica	AF505779
AWW125	SFSU-AWW125	*Gymnopus indoctoides*	Java	AY263424
AWW17	SFSU AWW17	*Gymnopus indoctus*	Indonesia	AY263440
AWW04	SFSU AWW04	*Gymnopus indoctus*	Indonesia	AY263439
AWW32	SFSU AWW32	*Gymnopus indoctus*	Indonesia	AY263441
TFB 6520	TENN 52970	*Gymnopus iocephalus*	USA, NC	DQ449984
TFB 8816	TENN 55437	*Gymnopus iocephalus*	USA, GA	DQ449985
RV 94154	DUKE RV 94154	*Gymnopus iocephalus*		DQ449986
TFB 8796	TENN 55224	*Gymnopus junquilleus*	USA, NC	DQ449969
TFB 11584	TENN 59532	*Gymnopus junquilleus*	USA, TN	AY256693
D230	Duke230	*Gymnopus kauffmanii*	USA, VA	DQ450001
TFB 11013ss2	TENN 58621	*Gymnopus lodgeae*	Costa Rica	AF505757

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
TFB 11030ss10	TENN 58638	*Gymnopus lodgeae*	Costa Rica	AY256705
TFB 9678	TENN 56639	*Gymnopus lodgeae*	Costa Rica	no sequence
TFB 4439	TENN50937	*Gymnopus luxurians*	USA, TN	DQ450021
TFB 4283	TENN50619	*Gymnopus luxurians*	Switzerland	DQ450022
TFB 10350	TENN57910	*Gymnopus luxurians*	USA, NC	AF505765
TFB 10355	TENN57914	*Gymnopus luxurians*	USA, SC	DQ450023
TFB 11711	TENN59547	*Gymnopus luxurians*	Dominican Republic	DQ450024
d54	DUKE54	*Gymnopus luxurians*	Unknown, not in GB	DQ480105
VLUX	DUKE-VLUX	*Gymnopus luxurians*	Unknown, not in GB	DQ480106
TFB 10009	TENN 56721	*Gymnopus luxurians*	USA, North Carolina	no sequence
TFB 10447	TENN 58141	*Gymnopus luxurians*	USA, Tennessee	no sequence
TFB 10476	TENN 58839	*Gymnopus luxurians*	USA, Tennessee	no sequence
TFB 9675	TENN 56636	*Gymnopus macropus*	Costa Rica	DQ449978
TFB 10095	TENN 58090	*Gymnopus macropus*	Costa Rica	AF505788
TFB 11011	TENN 58619	*Gymnopus macropus*	Costa Rica	DQ449979
AWW50	AWW50	*Gymnopus melanopus*	Indonesia, Java	AY263442
AWW54	SFSU AWW54	*Gymnopus melanopus*	Indonesia, Java	AY263425
TFB 11587	DEH 2320	*Gymnopus menehune*	USA, HI	DQ450043
AWW87	SFSU AWW87	*Gymnopus menehune*	Indonesia, Java	AY263444
AWW15	SFSU AWW15	*Gymnopus menehune*	Indonesia, Java	AY263443
DED5866	SFSU DED5866	*Gymnopus menehune*		AY263426
REH7379	TENN 54460	*Gymnopus mesoamericanus*	Chile	AF505768
TFB 11005	TENN 58613	*Gymnopus mesoamericanus*	Costa Rica	DQ450035
TFB 10411	TENN 58106	*Gymnopus mesoamericanus*	Costa Rica	DQ450036
TFB 10416	TENN 58110	*Gymnopus neotropicus*	Costa Rica	AF505769
AWW55	SFSU AWW55	*Gymnopus nonnullus*	Indonesia	AY263446
AWW05	SFSU AWW05	*Gymnopus nonnullus*	Indonesia, Java	AY263445
REH8290	NY REH8290	*Gymnopus nubicola*	Costa Rica	AF505781
TFB 3780ss7	TENN 50517	*Gymnopus ocior*	Sweden	DQ449955
TFB 3849	TENN 55828	*Gymnopus ocior*	U.K., Scotland	DQ449956
TFB 3861	TENN 55866	*Gymnopus ocior*	U.K., Scotland	DQ449957
TFB 10325	TENN 57973	*Gymnopus ocior*	Germany	DQ449958
TFB 9015	TENN 55665	*Gymnopus ocior*	USA, CA	DQ449959

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
TFB 4284	TENN 50620	*Gymnopus ocior*	Switzerland	DQ449960
TFB 11329ss2	TENN 59213	*Gymnopus ocior*	France	AF505782
TFB 6968	TENN 55886	*Gymnopus ocior*	U.K., Scotland	DQ449961
TFB 3852	TENN 55830	*Gymnopus ocior*	U.K., Scotland	DQ449967
TFB 6981	TENN 55899	*Gymnopus ocior*	U.K., Scotland	DQ449968
TFB 11638	TENN 59601	*Gymnopus ocior*	Russia	DQ449970
TFB 3854	TENN 44832	*Gymnopus ocior*	UK, Scotland	no sequence
TFB 3857	TENN 56235	*Gymnopus ocior*	UK, Scotland	no sequence
TFB 10021	TENN 56733	*Gymnopus omphalodes*	Costa Rica	DQ450010
TFB 10022	TENN 56734	*Gymnopus omphalodes*	Costa Rica	AY256700
TFB 11021ss2	TENN 58629	*Gymnopus omphalodes*	Costa Rica	AF505761
TFB 10427ss1	TENN 58121	*Gymnopus omphalodes*	Costa Rica	DQ450011
TFB 10023	TENN 56735	*Gymnopus omphalodes*	Costa Rica	no sequence
TFB 10419	TENN 58113	*Gymnopus parvulus*	Costa Rica	DQ450060
TFB 10421	TENN 58115	*Gymnopus parvulus*	Costa Rica	DQ450061
TFB 10425ss1	TENN 58119	*Gymnopus parvulus*	Costa Rica	DQ450062
TFB 10422ss1	TENN 58116	*Gymnopus parvulus*	Costa Rica	AF505774
TFB 11600	TENN 59492	*Gymnopus peronatus*	USA, WI	DQ450012
TFB 6983	TENN 55902	*Gymnopus peronatus*	U.K., Scotland	AY256706
TFB 11614	TENN 59577	*Gymnopus peronatus*	Russia, Novgorad	DQ450013
TFB 11616	TENN 59579	*Gymnopus peronatus*	Russia, Novgorad	DQ450014
TFB 11436	TENN 59297	*Gymnopus peronatus*	Austria	DQ450015
TFB 6957	TENN 55876	*Gymnopus peronatus*	U.K., Scotland	DQ450016
TFB 4204	TENN 50540	*Gymnopus peronatus*	Sweden	DQ450017
TFB 11340ss2	TENN 59224	*Gymnopus peronatus*	France	AF505760
TFB 9982	Held by L. Norvell	*Gymnopus peronatus*	USA, Oregon	no sequence
TFB 9631	TENN56592	*Gymnopus polygrammus*	Puerto Rico	AY256701
TFB 9628	TENN56589	*Gymnopus polygrammus*	Puerto Rico	DQ450028
TFB 1855	TENN 48507	*Gymnopus polyphyllus*	USA, NC	DQ449992
TFB 11041	TENN 59455	*Gymnopus polyphyllus*	USA, VA	AY256695
D5806	Duke5806	*Gymnopus polyphyllus*		DQ480089

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
DED4058	SFSU-DED4058	*Gymnopus polyphyllus*	USA, Massachusetts	DQ480111
TFB 10493ss1	TENN 58598	*Gymnopus pseudolodgeae*	Costa Rica	AF505747
REH7348		*Gymnopus pseudo-omphalodes*		AF505762
TFB 7571	TENN 53687	*Gymnopus readii*	New Zealand	DQ450034
AWW29	SFSU-AWW29	*Gymnopus salakensis*	Java	AY263447
AWW117	AWW117	*Gymnopus sepiiconicus*	Java	AY263448
AWW127	AWW126	*Gymnopus sepiiconicus*	Java	AY263449
c9811	DUKE c9811	*Gymnopus sp.*	Puerto Rico	DQ480107
988pr	DUKE988pr	*Gymnopus sp.*	Puerto Rico	DQ480108
	GB12227	*Gymnopus sp.* (Soil sample)	USA, NJ	AF241323
D1362	Duke1362	*Gymnopus sp.*		DQ480090
D50t	Duke50t	*Gymnopus sp.*		DQ480091
D523	Duke523	*Gymnopus sp.* (polyphyllus clade)		DQ480092
GB11239	GB11239	*Gymnopus sp.* (Soil sample)	USA, NJ	AF241335
TFB 11026	TENN58634	*Gymnopus luxurians var. copeyi*	Costa Rica	AF505764
TFB 11025-4	TENN 58633	*Gymnopus spongiosus*	Costa Rica	AF505785
TFB 2887	TENN 49077	*Gymnopus spongiosus*	USA, Wisconsin	AF505784
TFB 11552	TENN 59739	*Gymnopus spongiosus*	USA, North Carolina	DQ449993
TFB 11609	TENN 59640	*Gymnopus spongiosus*	USA, Tennessee	DQ480113
229	Duke229	*Gymnopus spongiosus*		DQ480093
TFB 8417	TENN 55243	*Gymnopus subcyathiformis*	Mexico	DQ450037
TFB 11035	TENN 58642	*Gymnopus subcyathiformis*	Costa Rica	AF505767
TFB 9694	TENN 56655	*Gymnopus subcyathiformis*	Costa Rica	DQ4500039
TFB 10436	TENN 58130	*Gymnopus subcyathiformis*	Costa Rica	DQ450040
TFB 9629	TENN 56590	*Gymnopus subcyathiformis*	Puerto Rico	DQ450041
TFB 11714ss1	TENN 59550	*Gymnopus subcyathiformis*	Dominican Repl	DQ450042
TFB 10433	TENN 58122	*Gymnopus subcyathiformis*	Costa Rica	no sequence

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
TFB 10435	TENN 58129	*Gymnopus subcyathiformis*	Costa Rica	no sequence
TFB 10436	TENN 58130	*Gymnopus subcyathiformis*	Costa Rica	no sequence
TFB 10437	TENN 58130	*Gymnopus subcyathiformis*	Costa Rica	no sequence
TFB 6928	culture only	*Gymnopus subnudus*	USA, MN	AY256707
TFB 10338	TENN 57895	*Gymnopus subnudus*	USA, NC	AF505759
TFB 10331	TENN 57892	*Gymnopus subnudus*	USA, NC	DQ450018
U43780	JFM 1480	*Gymnopus subnudus*	USA, NY	U43780
U43779	JFM 1302	*Gymnopus subnudus*	USA, VA	U43779
U43782	RHP 1818	*Gymnopus subnudus*	USA, NC	U43782
U43781	JFM 1482	*Gymnopus subnudus*	USA, NY	U43781
U43778	JFM 898	*Gymnopus subnudus*	USA, VA	U43778
TFB 11063	TENN59474	*Gymnopus subpruinosus*	USA, Hawaii	DQ450025
TFB 9529	TENN56242	*Gymnopus subpruinosus*	USA, California	DQ450026
TFB 11066	TENN59477	*Gymnopus subpruinosus*	USA, Hawaii	DQ450027
TFB 9602	TENN 56321	*Gymnopus subsulphureus*	USA, NC	DQ449972
D62	Duke62	*Gymnopus subsulphureus*		DQ480103
TFB 10006	TENN 56718	*Gymnopus subsulphureus*	USA, NC	AY256692
AWW39	SFSU AWW39	*Gymnopus tamblinganensis*	Indonesia	AY263450
AWW106	SFSU AWW106	*Gymnopus termiticola*	Indonesia, Java	AY263451
DED7264	SFSU DED7264	*Gymnopus termiticola*	Indonesia, Java	AY263452
AWW51	SFSU AWW51	*Gymnopus trogioides*	Indonesia, Java	AY263428
TFB 9539	TENN 56252	*Gymnopus villosipes*	USA, California	DQ450058
AWW127	SFSU-AWW127	*Gymnopus vitellinipes* (Type)	Indonesia – Java	AY263429
TFB 9447	TENN 37996	*Lentinula aciculospora*	Costa Rica	AY016443
TFB 10418	TENN 58112	*Lentinula asiculospora*	Costa Rica	AY016444
CRA1	RGT960624/09	*Lentinula boryana*	Costa Rica	AF031175
TFB 10827	TENN 58368	*Lentinula boryana*	Brazil	AY016440
THL1		*Lentinula edodes*	Thailand	U33087
CHN1	STCL124	*Lentinula edodes*	China	AF031183

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
AUS 1	RV 95 – 376	*Lentinula edodes*	Australia, Queensland	AF031179
NEP1	TMI1546	*Lentinula edodes*	Nepal	AF031191
JPN3		*Lentinula edodes*	Japan	U33091
PNG2		*Lentinula lateritia*	Papua New Guinea	U33084
PNG4		*Lentinula lateritia*	Papua New Guinea	U33086
PNG7		*Lentinula lateritia*	Papua New Guinea	U33072
TAS 1		*Lentinula lateritia*	Australia, Tasmania	U33076
NZL4		*Lentinula novaezelandieae*	New Zealand	U33075
TFB 9156	TENN 54887	*Lentinula raphanica*	Florida	AY016441
TFB 9564	TENN 56477	*Lentinula raphanica*	Puerto Rico	AY016442
TFB 3775	TENN 50512	*Marasmius alliaceus*	Sweden, Gothenburg	no sequence
TFB 9168	TENN 55766	*Marasmiellus aff pluvius*	USA, TN	DQ450029
D83	Duke83	*Marasmiellus candidus*		DQ480088
TFB 9889	TENN 59540	*Marasmiellus juniperinus*	USA, LA	AY256708
TFB 11499ss2	Culture only	*Marasmiellus opacus*	USA, TN	DQ450005
TFB 4727	TENN 50324	*Marasmiellus rameales*	Sweden	DQ450030
DED4425	SFSU DED4425	*Marasmiellus rameales*	USA, NC	DQ450031
TFB 11558	TENN 59444	*Marasmiellus stenophyllus*	USA, NC	DQ450032
TFB 11559	TENN 59449	*Marasmiellus stenophyllus*	USA, NC	DQ450033
TFB 8935	TENN 55555	*Marasmius alliaceus*	Russia, Caucasia	DQ450004
TFB 11352	TENN 59237	*Marasmius alliaceus*	France	no sequence
TFB 4749	TENN 50346	*Marasmius scorodonius*	Switzerland	DQ450006
TFB 4754	TENN 50351	*Marasmius sp.*	Switzerland	DQ449983
TFB 11431	TENN 59293	*Micromphale brassicolens*	Austria, Vienna	DQ449990
TFB 11433	TENN 59294	*Micromphale brassicolens*	Austria, Vienna	DQ449991
TFB 8930	TENN 55550	*Micromphale brassicolens*	Russia, Caucasia	DQ449989
TFB 11434	TENN 59295	*Micromphale foetidum*	Austria	AF505780
W7398	Watling 127/95	*Neonothopanus nambi*	Malaysia	DQ444306

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
W7399	Watling 193/95	*Neonothopanus nambi*	Malaysia	DQ444307
TFB 6951	TENN 54507	*Omphalotus illudens*	USA, Tennessee	AY313271
TFB 11566	TENN 59448	*Omphalotus illudens*	USA, Tennessee	AY313272
TFB 8774	TENN 55202	*Omphalotus illudens*	USA, North Carolina	AY313273
TFB 2305	Culture only	*Omphalotus japonicus*	Japan	AY313286
TFB 4866	TENN 51283	*Omphalotus mexicanus*	Mexico	AY313274
TFB 7692	Vilgalys E5332	*Omphalotus nidiformis*	Australia	AY313275
TFB 11136	TENN 59677	*Omphalotus olearius*	Austria	AY313276
TFB 9061 b	Culture only	*Omphalotus olearius*	France	AY313277
TFB 9062 b	Culture only	*Omphalotus olearius*	France	AY313278
TFB 9544	TENN 56257	*Omphalotus olivascens*	USA, California	AY313279
DED6450	DED6450	*Omphalotus olivascens*	USA, California	AY313280
TFB 8284	TENN 55337	*Omphalotus olivascens*	USA, California	AY313281
TFB 8258	TENN 54323	*Omphalotus subilludens*	USA, Florida	AY313282
TFB 8261	TENN 54320	*Omphalotus subilludens*	USA, Florida	AY313283.
TFB 10992	TENN 59518	*Omphalotus subilludens*	USA, Texas	AY313284.
HBB11125	Culture only	*Omphalotus subilludens*	USA, Arizona	AY313285.
TFB 9920	TENN 56602	*Rhodocollybia amica*	Costa Rica	AF505754
TFB 11456	TENN 59317	*Rhodocollybia butyracea*	Austria	AF505751
TFB 9000	TENN 55660	*Rhodocollybia butyracea*	Turkey	AY313289
TFB 10726	LE(BIN)1232	*Rhodocollybia butyracea*	Russia	AF505750
TFB 8801	TENN 56303	*Rhodocollybia butyracea*	Mexico	AY313290
TFB 7452	TENN 53580	*Rhodocollybia butyracea*	Sweden	AY313293
TFB 8250	Culture only	*Rhodocollybia butyracea*	Alaska	AY313292
OKM27562	OKM27562	*Rhodocollybia butyracea*	USA, Colorado	DQ444317
REH7007	REH7007	*Rhodocollybia dotae*	Costa Rica	AF505758
REH7907	REH7907	*Rhodocollybia lignitilis*	Costa Rica	AF505753
TFB 11045	TENN 59459	*Rhodocollybia maculata*	USA, Oregon	AY313296
TFB 9605	Culture only	*Rhodocollybia maculata*	USA, North Carolina	AF505756

Tab. 1 continued.

Field No	Herbarium No	Name	Location	GenBank No.
TFB 9607	Culture only	*Rhodocollybia maculata*	USA, North Carolina	AY313297
TFB 7899	TENN 53838	*Rhodocollybia pandipes*	Costa Rica	AY313294
TFB 11014	TENN 58622	*Rhodocollybia pandipes*	Costa Rica	AT505752
TFB 9680	TENN 56641	*Rhodocollybia pandipes*	Costa Rica	AY313295
TFB 11707	TENN 59546	*Rhodocollybia pandipes afn.*	Dominican Republic	AY313288
EFM1403	EFM1403	*Rhodocollybia proxima var. distorta*	Costa Rica	AF505748
TFB 10712	TENN 58798	*Rhodocollybia sp.*	Greenland	DQ444318
EN2066	EN2066	*Rhodocollybia tablensis*	Costa Rica	AF505755
TFB 10077	TENN 58017	*Rhodocollybia turpis*	Costa Rica	AF505749
TFB 10482	TENN 58545	*Rhodocollybia unakensis*	USA, Texas	AY313298
TFB 3716	TENN 50704	*Setulipes androsaceus*	USA, NC	DQ444311
TFB 4711	TENN 50308	*Setulipes androsaceus*	Sweden	DQ444314
TFB 3745	TENN 50482	*Setulipes androsaceus*	Scotland	DQ444312
TFB 4702	TENN 50299	*Setulipes androsaceus*	Sweden	DQ444313
TFB 4720	TENN 50317	*Setulipes androsaceus*	Sweden	DQ444315
TFB 4724	TENN 50321	*Setulipes androsaceus*	Sweden	DQ444316
MUCL35155	Culture only	*Setulipes androsaceus*	France	AF519893

AWW = Andrew Wilson, DED = Dennis Desjardin, DEH = Don Hemmes, REH = Roy E. Halling, Duke = Rytas Vilgalys, WC = Pennsylvania State Culture Collection, ss = single spore isolate.

Tab. 2. – Number of tandem repeats of a ca. 34 bp sequence in the ribosomal ITS 2 region.

Species	Repeat 1	Repeat 2	Repeat 3	Repeat 4	Repeat 5
Gymnopus "dichrous"			yes[1]	yes	
Gymnopus alnicola			yes	yes	
Gymnopus biformis	variable	variable	yes	yes	
Gymnopus brunneigracilis				yes	
Gymnopus confluens			yes	yes	
Gymnopus collybioides			yes	yes	
Gymnopus cylindricus			yes	yes	
Gymnopus dichrous			yes[1]	yes	
Gymnopus gibbosus				yes	
Gymnopus indoctus			yes	yes	yes

Tab. 2 continued.

Species	Repeat 1	Repeat 2	Repeat 3	Repeat 4	Repeat 5
Gymnopus lodgeae				yes	
Gymnopus luxurians				yes	
Gymnopus melanopus				yes	
Gymnopus menehune			yes	yes	
Gymnopus afn. menehune			yes	yes	
Gymnopus mesoamericanus			yes	yes	
Gymnopus afn. moseri				yes	
Gymnopus nonnullus			yes[1]	yes	
Gymnopus neotropicus			yes	yes	
Gymnopus omphalodes				yes	
Gymnopus parvulus			yes	yes	
Gymnopus peronatus				yes	
Gymnopus polygrammus				yes	
Gymnopus pseudolodgeae				yes	
Gymnopus pseudo-omphalodes				yes	
Gymnopus readii			yes	yes	
Gymnopus subcyathiformis			yes	yes	
Gymnopus subnudus				yes	
Gymnopus subpruinosus				yes	
Gymnopus tamblinganensis			yes	yes	
Gymnopus termiticola				yes	
Gymnopus trogioides				yes	
Gymnopus villosipes			yes	yes	
Marasmiellus candidus				yes	
Marasmiellus alliaceus				yes	
Marasmiellus juniperinus			yes	yes	
Marasmiellus opacus				yes	
Marasmiellus sp.				yes	
Marasmiellus ramealis			yes[1]	yes	
Marasmiellus stenophyllus				yes	
Marasmius scorodonius				yes	

[1] These collections contain repeat 3 plus some additional sequence material at the end of repeat 3 which is not present in other collections.

Tab. 3. – Presence of repeat elements within the *G. biformis* complex

Field No.	Species	Collection location	Repeat 1	Repeat 2	Repeat 3	Repeat 4
TFB 7230	*G. biformis* 3	USA, SC	yes	other	yes	yes
TFB 7820	*G. biformis* 1	Costa Rica	yes	yes	yes	yes
TFB 7843	G. *biformis* 3	Costa Rica	yes	yes	yes	yes
TFB 9127	*G. biformis* 1	USA, LA	yes		yes	yes
TFB 9657	*G. biformis* 2	Costa Rica			yes	yes
TFB 9673	*G. biformis* 2	Costa Rica			yes	yes
TFB 10093	*G. biformis* 1	Costa Rica			yes	yes
TFB 10478	*G. biformis* 1	USA, TX	yes		yes	yes
TFB 11016	*G. biformis* 1	Costa Rica			yes	yes

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Appendix 1. *Gymnopus* taxa proposed as new

Gymnopus junquilleus R. H. Petersen and J. L. Mata, *sp. nov.* – Fig. 15.

Basidiomata in statura Gymnopus dryophilus *similares. Pileo 25 – 65 mm diam, valido-convexo juvenilis, plano-umbonato maturo, hygrophano, ubique intenso flavido, luteo ad stramineo, glabro. Lamellae liberae, congestae, angustae,*

flavo-alba. Stipes flava, glabra, ad basim expanda, fistulosa et subgeniculata. Sporae (4.8 –)5.2 – 6.4 × (2.8 –)3.2 – 3.6 µm (Qx = 1.76), lacrymoideae ad ellipsoideae, tenuitunicatae, albae, hyalinae, inamyloideae. Epicutis structuram "dryophila" similem habentibus. Cheilocystidia vulga, prostrata, 19 – 40(– 72) × 4 – 12 µm, clavata vel subsphaeropedunculata, saepe diverticulata, rara ramosa. Pleurocystidia destitute.

Holotypus *(hic designatus).* – UNITED STATES, North Carolina, Macon Co., Bull Pen Rd., Ellicott Rock trailhead, 35° 01.01' N, 83° 08.19' W, 10. VIII. 96, coll. T Thompson, TFB 8796 (TENN 55224).

Description. – Pileus (Fig. 15A) 20 – 65 mm broad, strongly convex when young, shallowly convex to plane-subumbonate when mature, hygrophanous, "maize yellow" (3A4), "buff yellow" (4A5) to "light buff" (3A2) where dry; disc or hygrophanous areas "ochraceous buff" (5A5) or with tint of "cinnamon buff" (6B4), flesh, yellow, reluctantly bruising brownish around larval tunnels. – Lamellae close to crowded, free, shallow, "baryta yellow" (3A5), "straw yellow" (2A4), "maize yellow," sometimes with fleshy tints. – Stipe smooth, usually compressed, gradually tapering upward, fistulose and subgeniculate at base, "pale yellow orange" (4A3), "capucine orange" to "pinard yellow" (2A5) upward, downward "straw yellow," "xanthine orange" (6C8) to "zinc orange" (6B7), reluctantly bruising to "Mikado brown" (7C6). – Rhizomorphs off-white to "pinkish buff" (6A3). Odor and taste none. – Pileus epicutis (Fig. 15B) composed of non-radially arranged elements, i.e. a "*dryophila* type" epicutis. – Basidia (Fig. 15C) 20 – 26 × 6 – 7 µm, clavate to broadly

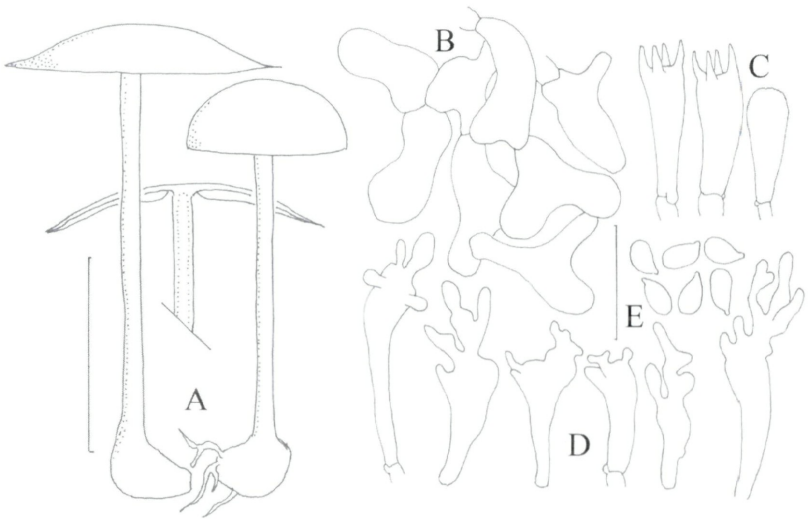

Fig. 15. *Gymnopus junquilleus.* A. Basidiomata. B. Pileipellis; paradermal scalp. C. Basidia. D. Cheilocystidia. E. Basidiospores. Standard bar = 40 mm for basidiomata, 20 µm for microstructures.

clavate, four-sterigmate, clamped. – Basidioles 12 – 22 × 4 – 6 µm, mostly clavate, some submucronate. – Pleurocystidia absent. – Cheilocystidia (Fig. 15D) abundant, prostrate, arising from horizontal hyphae, 19 – 40(– 72) × 4 – 12 µm, irregularly clavate or subsphaeropedunculate, and then sometimes apically diverticulate, or long pedicellate and lobed, diverticulate and/or furcated, rarely ramose; wall thin. – Clamps common in all tissues. – Basidiospores (Fig. 15E) (4.8 –)5.2 – 6.4 × (2.8 –)3.2 – 3.6 µm (n = 40, x = 5.8 × 3.3 µm, Q = 1.50 – 2.00, Qx = 1.76), lacrymoid to ellipsoid in side view, ellipsoid to broadly ellipsoid in profile, hyaline, inamyloid; wall thin.

Additional material examined. – USA, Tennessee, Sevier Co., Great Smoky Mountains Nat. Park, Greenbrier, 31.VIII.2002, coll. RH Petersen & KW Hughes, TFB 11584 (TENN 59532).

Gymnopus mesoamericanus JL Mata, *sp. nov.* – Fig. 16.

Basidiomata similares Gymnopus confluens, *sed: 1) habitus gregarious; 2) stipite brunneus vel brunneo-incarnatus vel griseo-brunneus. Pileus 15 – 60 mm diam, obtuso-conicus juvenilis, aplanus ad subumbonatus maturus, humidus, hygrophanus, ad centro brunneus, ad margine bubalinus. Lamellae adnexae, aggregatae, angustae, albo juvenilae, cremeus maturus. Stipes 50 – 140 × 1 – 3 mm, equalae, sicca, pubescentibus, rubro- ad purpureo-brunnea. Sporae 7.2 – 8.4 × 3.2 – 4.8 µm (Qx = 2.19), angusto-ellipsoideae ad lacrymoideae, tenuitunicatae, hyalinae, inamyloideae. Cheilocystidia 14 – 53 × 5 – 11 µm, conspicua, clavata, lobata ad ramosa. Pleurocystidia destituta.*

Holotypus *(hic designatus).* – COSTA RICA, Provincia de San José, Cantón de Pérez Zeledón, Villa Mills, Estación Experimental CATIE, 9° 33' 03" N, 83° 40' 56" W, 2880 m, 23. VI. 2000, col. JL Mata & RH Petersen, *TFB 11005* (TENN 58613).

Description. – Pileus (Fig. 16A) 15 – 60 mm diam, at first obtusely conic to broadly campanulate, with age applanate or shallowly umbonate; surface moist, hygrophanous even when moist, finely rugulose-subsulcate when dry, translucent, at disc brown (6E6 – 8), cinnamon brown (6D – E6 – 5), when moist, fading to light brown (6D5, 6C4 – 6) or grayish orange (5B3), near margin sometimes almost white; margin curved to uplifted, crenate, sometimes irregular, translucent; context extremely thin, white and unchanging, or pale tan, cream (2 – 3A2) with age. – Lamellae adnexed, extremely crowded, narrow and thin, at first white, with age pale tan or grayish orange (5B3); margin fimbriate; lamellulae in several tiers of different lengths. – Stipe 50 – 140 × 1 – 3(– 6) mm, strict, ± equal to slightly broader at apex and base, or compressed and cleft; surface dry, pubescent overall with white hairs, ground color reddish brown (8E8 – 8E6), purple brown (8F8 – 9F8), dark brown or gray brown, near apex orange brown (6C8); interior hollow; consistency fibrous and tough. Basal mycelium binding substrate white to pale

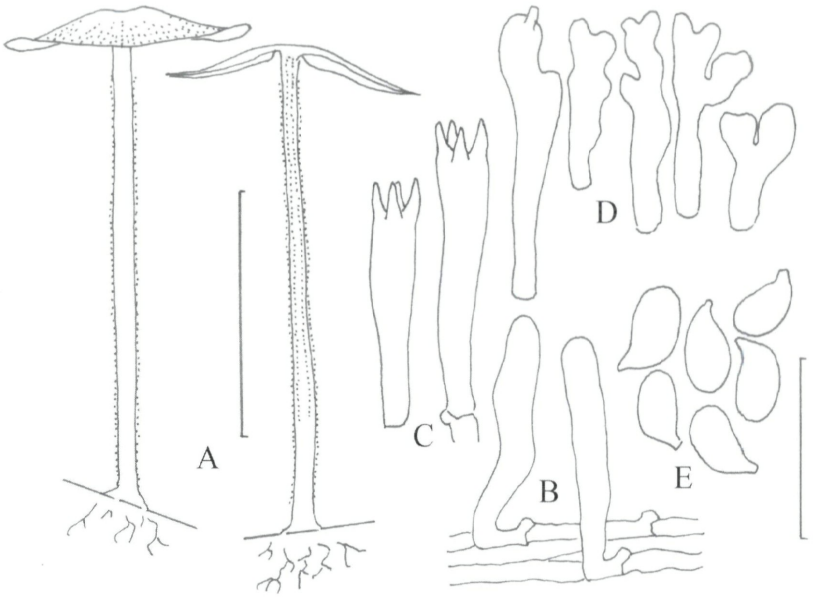

Fig. 16. *Gymnopus mesoamericanus*. A. Basidiomata. B. Pileipellis. C. Basidia. D. Cheilocystidia. E. Basidiospores. Standard bar = 40 mm for basidiomata, 20 µm for microstructures.

ochraceous. Odor slightly farinaceous or mild; taste mild. Habitat in vegetation of *Quercus* spp; gregarious, on humus. – Pileus epicutis (Fig. 16B) a cutis; hyphae 2 – 6 µm diam, cylindrical, rarely diverticulate, not branched, not gelatinized, radially oriented, ± interwoven, pale yellow in mass, hyaline singly; wall thin; terminal cells common, prostrate to erect, in fascicles. – Pileus trama ± loosely interwoven; hyphae 3 – 14 µm diam, hyaline; wall up to 0.8 µm thick. Gloeoplerous hyphae rare, up to 4 µm diam. – Lamellar trama regular to subregular; hyphae 2 – 10 µm diam, hyaline; wall thin. Pleurocystidia absent. Lamellar margin sterile. – Basidia (Fig. 16C) 21 – 28 × 5 – 6 µm, clavate; sterigmata four; basidioles 14 – 23 × 3 – 4 µm, clavate or cylindrical. – Cheilocystidia (Fig. 16D) conspicuous, 14 – 53 × 5 – 11 µm, short or long clavate, submucronate, ± flexed, with clamp connections; apex frequently knobbed or lobed, occasionally furcate or ramose. Stipe tissues forming a cutis; hyphae 4 – 14(– 20) µm, cylindrical, parallel, frequently septate, pale yellowish in mass, hyaline singly; wall up to 1.6 µm thick. Gloeoplerous hyphae rare, up to 8 µm diam. – Caulocystidia up to 200 × 6 µm, cylindrical, flexed, forming an entangled and interwoven mat of hyphae; apex often furcate. All tissues inamyloid; clamp connections present in all tissues. – Basidiospores (Fig. 16E) white yellowish (2A2) in spore deposit,

(6.4 –)7.2 – 8.4(– 9.6) × 3.2 – 4.8 µm (n = 85/4, x = 8.3 × 3.8 µm, Q = 1.80 – 2.63, Qx = 2.19), narrowly ellipsoid or lacrymoid in side view, subfusoid or subcilindrical in face view, hyaline, inamyloid; wall smooth, thin.

Additional material examined. – COSTA RICA. Provincia de San José, Cantón de Dota, San Gerardo de Dota, ±500 m along road from Interamerican Highway toward San Gerardo, 9° 42' 52" N, 83° 58' 28" W, 3000 m, 17. X. 1994, col. RE Halling, *REH 7379* (NY). Cantón de Pérez Zeledón, Villa Mills, Finca Alejandrina, along Interamerican Hwy at km 95 near Hotel La Georgina, 9° 33' 43" N, 83° 44' 22" W, 3000 m, 23. VI. 1994, col. RE Halling, E. Franco, M Mata, L Umaña, *REH 7341* (NY); Estación Experimental CATIE, 9° 33' 03" N, 83° 40' 56" W, 2880 m, 20.VI.1999, col. JL Mata, *TFB 10411* (TENN 58106); Provincia Puntarenas, Canton Coto Brus, Sabalito, Estación Biológica Las Alturas, 8° 56' 59" N, 82° 50' 02" W, 1420 m, 26. V. 1994, col. E Franco-Molano, M Mata, J Johnson, L Umaña, *EFM 1191* (NY).

Gymnopus parvulus J. L. Mata R. H. Petersen & K. W. Hughes ***sp. nov.*** – Fig. 17.

Basidiomata similaris ad Gymnopus biformis *sed distinctas per staturas parvulus. Pileus 10 – 22 mm diam, membranaceus, convexus juvenilis, planus ad depressus maturus, fibrillosus, sulcato-crenatus, aurantio-brunneus juvenilis, bubalinus maturus. Lamellae adnatae ad liberis cum pseudocollariae, congestae, angustae, albae. Stipes 30 – 50 × 1 – 2 mm, tenuis, terete ad semi-compressis, pruinosis, brunneis ad aurantio-brunneis. Sporae 5.6 – 8.0 × 2.8 – 3.6 µm (Qx = 2.08), lacrymoideae ad angusto-ellipsoideae, albae, tenuitunicatae, hyalinae, inamyloideae. Cheilocystidia 13 – 36 × 4 – 12 µm, clavata, cylindrical vel fusoidea, lobata. Pleurocystidia destituta.*

Holotypus *(hic designatus).* – COSTA RICA. Provincia de Cartago, Cantón Pérez Zeledón, vic. Villa Mills, Km 95 on Inter American Highway past CATIE Experimental Station, Estación Biológica Cuericí, 9° 33' 17" N, 83° 40' 04" W, 2560 m, 21. VI. 1999, col. JL Mata, TFB 10419 (TENN 58113).

Description. – Pileus (Fig. 17 A) 10 – 22(– 35) mm diam, at first convex to applanate, then somewhat centrally depressed and more aplanate with age; surface radially fibrillose, opaque, entirely sulcate-crenate, translucent, when young uniform orange brownish (6D7 – 6C5), brown to light brown (5/6D8 – 5C6/8), at center light orange brown (6C5/6) with age, near margin beige, pinkish buff (6B4/5), tawny buff (5B4/5) to buff (5C4 – 5B3); margin curved to plane, crenate-sulcate; context very thin. – Lamellae adnate to free, forming a pseudocollarium, narrow, close, white to off-white (2A2); margin even, fimbriate to eroded; lamellulae in three tiers of different lengths, some anastomosing or with intervenose projections. – Stipe 30 – 50(– 70) × 1 – 2(– 4) mm, equal, terete to

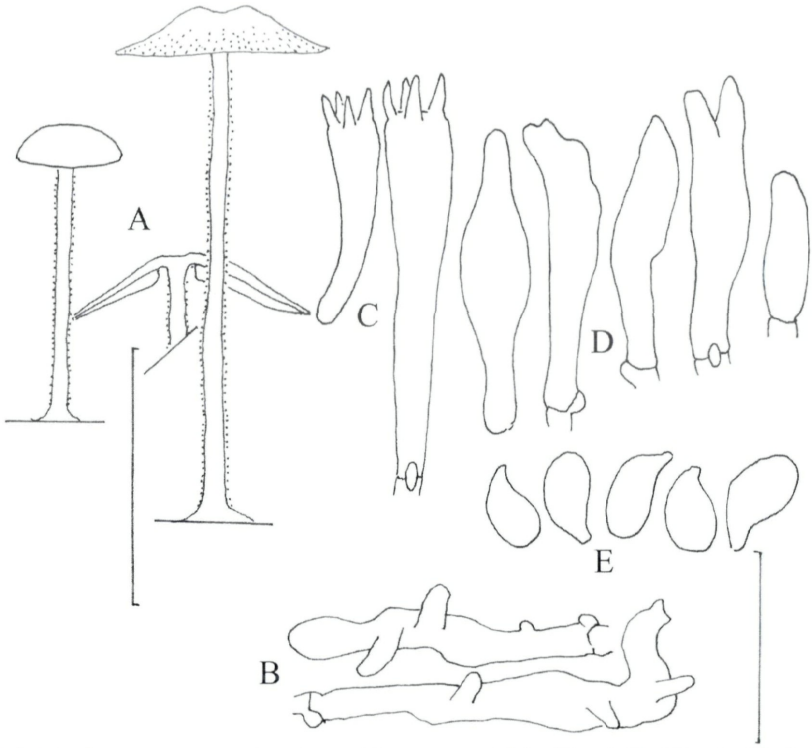

Fig 17. *Gymnopus parvulus*. A. Basidiomata. B. Pileipellis. C. Basidia. D. Cheilocystidia. E. Basidiospores. Standard bar = 40 mm for basidiomata, 20 µm for microstructures.

± compressed, occasionally flaring at apex with age; surface covered entirely with a fine white vesture, towards base brown to reddish brown (7D/E8), dark brown (7F8) to light brown (7E6/7), fading in color apically; interior hollow; consistency tough, cartilaginous. Basal mycelium a disc, white to creamy. Odor not distinctive or pleasant; taste mild or mealy. Habitat directly on leaves in leaf litter; scattered. – Pileus epicutis (Fig. 17B) a cutis; hyphae 2 – 8 µm diam, cylindrical, not branched, occasionally diverticulate, radially oriented, ± interwoven, pale brown to pale olive brown in mass, hyaline singly, pale orange in Melzer's; wall thin; terminal cells, cylindrical to clavate, occasionally strangulate, erect, frequently with diverticula. – Pileus trama interwoven to loosely interwoven, rarely ± radially oriented; hyphae 2 – 10(– 16) µm diam, hyaline, inamyloid; wall thin to 0.8 µm thick. – Lamellar trama subregular to irregular, rarely interwoven; hyphae 2 – 8(– 12) µm diam, hyaline, inamyloid; wall thin. – Basidia (Fig. 17C) 20 – 38 × 4 – 10 µm, clavate; sterigmata four; basidioles 17 – 28 × 4 – 7 µm, clavate to

cylindrical. Pleurocystidia absent. Lamellae edge sterile or fertile. – Cheilocystidia (Fig. 17D) 13 – 36 × 4 – 12 µm, typically broadly clavate, sometimes subfusoid, cylindrical or flexuous; apex frequently lobed, knobbed or with irregular appendages, rarely furcate. – Stipe epicutis parallel; hyphae 2 – 10 µm diam, pale brownish in mass, hyaline singly, inamyloid; wall up to 1.6 µm thick. – Caulocystidia up to 160(– 260) × 10(– 15) µm, cylindrical, strangulate, occasionally septate, with clamp connections; single or forming fascicles; apex obtuse. Clamp connections present in all tissues. – Basidiospores (Fig. 17E) 5.6 – 8.0(– 8.8) × 2.8 – 3.6(– 4.8) µm (n = 180/8, x = 7.2 × 3.5 µm, Q = 1.60 – 2.75, Qx = 2.08) lacrymoid to narrowly ellipsoid in side view, narrowly ellipsoid to subcylindrical in face view, hyaline, inamyloid; wall smooth, thin.

Additional material examined. – COSTA RICA. Provincia Cartago, vic. Estrella, Palo Verde, 9° 46' 59" N, 83° 56' 71" W, 1700 m, 28. VI. 1998, col. JL Mata & RH Petersen, TFB 9663 (TENN 56624). Provincia San José, Cantón Dota, Finca El Jaular, 9° 39' 39" N, 83° 52' 01" W, 2300 m, 17. VI. 1999, col. JL Mata, TFB 10082 (TENN 58022); same location, 29. VI. 2000, col. JL Mata & RH Petersen, TFB 11028 (TENN 58636); Cantón Pérez Zeledón, vic. Villa Mills, Km 95 on Inter American Highway past CATIE Experimental Station, Estación Biológica Cuericí, 9° 33' 17" N, 83° 40' 04" W, 2560 m, 24. VIII. 1995, col. E Franco & M Mata, EFM 1446 (NY); same location, 21. VI. 1999, col. JL Mata, TFB 10421 (TENN 58115), TFB 10422 (TENN 58116), TFB 10424 (TENN 58118), TFB 10425 (TENN 58119).

Gymnopus luxurians* var. *copeyi J.L. Mata & R.H. Petersen, ***var. nov.*** – Fig. 18

Pileus ad 30 mm diam, convexus ad applanus ad subumbonatus, fibrillosus, siccus, sulcatus, ad centro bubalino-brunneus, ad margine pallido-brunneus. Lamellae adnexae juvenilis, pseudocollariis maturae, subdistantibus, fusco-cremeae; margin sulcatae. Stipes ad 50 mm × 3 mm, tereto, curvo, pruinoso, hygrophano, brunneo. Basidiosporae 8.8 – 12.8 × 4.0 – 5.6 µm (Qx = 2.13), lacrymoideae ad subovoideae, hyalinae, inamyloideae. Cheilocystidia 32 – 60 × 10 – 18 µm, inflata, clavata vel subsphaeropedunculata, obtusa ad diverticulata. Pleurocystidia destituta. Basidiomata in lignum Quercus silvorum habitatis

Holotypus *(hic designatus).* – COSTA RICA, Prov. San José, Cantón de Dota, vic. Copey, road to Providencia, 28. VI. 2000, coll. JL Mata *et al.* TFB 11026 (TENN 58634).

Description. – Pileus (Fig. 18A) up to 30 mm diam, broadly convex to aplanate, shallowly umbonate; surface radially fibrillose, appearing silky, dry, opaque, sulcate halfway towards margin, at center buff brown (6D6), towards margin pale brown (6C4 – 5C4); margin curved, sulcate. Context thin, off white. Odor and taste mild. – Lamellae adnexed at first, seceding into a pseudocollarium, 2 mm broad (± narrow), subdistant, cream grayish (3/4A2 – 3/4B2); margin

serrulate; lamellulae in three tiers of different lengths. – Stipe up to 50 × 3 mm, equal, terete, curved; surface finely velvety, hygrophanous, near apex cream colored, towards base brown (6D7); hollow, ± cartilaginous. Habitat on wood; solitary. – Pileus epicutis (Fig. 18B) a cutis; hyphae 2 – 16 µm diam, filamentous, repent, radially oriented, ± interwoven, occasionally diverticulate, pigment-incrusted, banded, light brown in mass, orange in IKI, hyaline singly, with clamp connections; wall thin. Pileus trama interwoven; hyphae 4 – 18 µm diam, hyaline, inamyloid, with clamp connections; wall thin. – Lamellar trama regular; hyphae 2 – 8 µm diam, hyaline, inamyloid, with clamp connections; wall thin. – Basidia 29 – 40 × 6 – 8 µm, clavate; four-sterigmate. Basidioles 29 – 38 × 6 – 8 µm, clavate. – Cheilocystidia (Fig. 18C) 32 – 60 × 10 – 18 µm, inflated, clavate to broadly clavate, sphaeropedunculate; apex obtuse or diverticulate. – Pleurocystidia absent. – Stipe epicutis parallel; hyphae 4 – 12 µm diam, straw colored in mass, hyaline singly, inamyloid, with clamp connections; wall up to 1 µm thick. – Caulocystidia (Fig. 18D) up to 60 × 17 µm diam, inflated, broadly clavate; apex often with long diverticulae projections; arising from a dense mat of hyphae, 2 – 6 µm diam. – Basidiospores (Fig. 18E) 8.8 – 12.8 × 4.0 – 5.6 µm (n = 20, x = 9.9 × 4.7 µm, Q = 1.71 – 2.45, Qx = 2.13) pip-shaped to lacrymoid, or obovoid in side view, ellipsoid in profile, often gutulate, hyaline, inamyloid; wall thin, smooth.

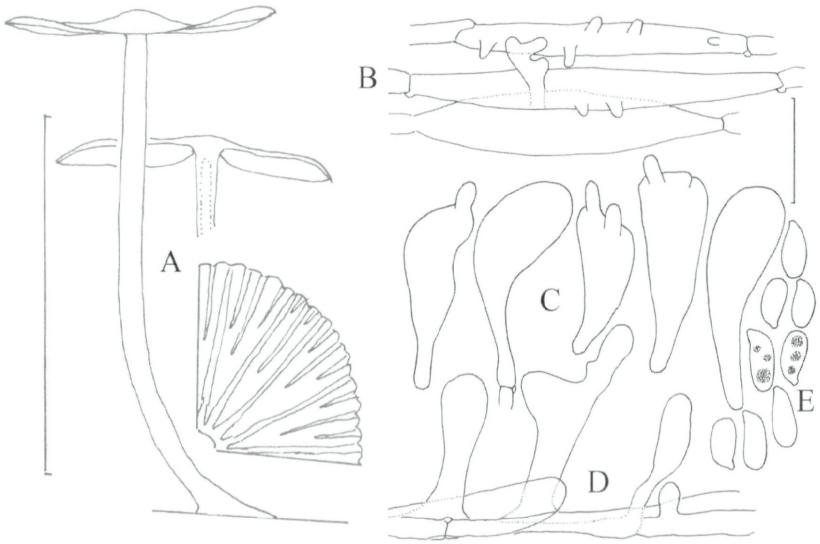

Fig. 18. *Gymnopus luxurians* var. *copeyi*. A. Basidiomata. B. Pileipellis. C. Cheilocystidia. D. Caulocystidia. E. Basidiospores. Standard bar = 40 mm for basidiomata, 20 µm for microstructures.

Appendix 2. Proposed new nomenclatural combinations

Gymnopus* sect. *Vestipedes* subsect. *Peronati (Kühner) Mata and Petersen, comb. et stat. nov.

Basionym. – *Marasmius* sect. *Peronati* Kühner. 1933. Botaniste 25: 85.

Gymnopus exculptus (Fries) J.L. Mata, *comb. nov.*

Basionym. – *Agaricus exculptus* Fries. 1838. Epicrisis. 93.

Gymnopus pseudo-omphalodes (Dennis) Mata, *comb. nov.*

Basionym. – *Collybia pseudo-omphalodes* R.W.G. Dennis. 1961. Kew Bull. 15: 74.

Gymnopus readii (Stevenson) J.L Mata, comb. nov.

Basionym. – *Crinipellis readii* Stevenson, Kew Bull. 19: 43, 1964.
[≡ *Collybia stevensonii* Horak, New Zeal. J. Bot. 9: 450. 1971 (*nom. nov.*)]