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THE CREPIDOTACEAE (BASIDIOMYCOTA, AGARICALES): PHYLOGENY AND TAXONOMY OF THE GENERA AND REVISION OF THE FAMILY BASED ON MOLECULAR EVIDENCE[1]

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Advances in phylogenetic systematics have clarified the position of most major homobasidiomycete lineages. In contrast, the status of the Crepidotaceae, a historically controversial family of dark-spored agarics, remains unaddressed. In this paper, current morphology-based classifications of the agaric genera of the Crepidotaceae were evaluated by parsimony and constraint analyses of sequence data from the nuclear large subunit rDNA. Taxa analyzed included the type species for each agaric genus allied in the family by Singer: *Crepidotus*, *Simocybe*, *Pleurotellus*, *Tubaria*, and *Melanomphalia*. Contrary to traditional classifications, results suggest that the crepidotoid fungi have three separate origins within the euagarics. The Crepidotaceae sensu stricto (s.s.) includes *Crepidotus* and *Simocybe* and represents a separate lineage of dark-spored euagarics. *Pleurotellus* is congeneric with *Crepidotus*. Results indicate the exclusion of both *Tubaria* and *Melanomphalia* from the Crepidotaceae s.s. *Tubaria* is allied with the strophariaceous taxa *Phaeomarasmius* and *Flammulaster*, while *Melanomphalia* has arisen from within a lineage of light-spored omphalinoid euagarics representing an independent acquisition of basidiospore pigmentation. Other pleisiomorphic and newly uncovered synapomorphic characters are discussed in detail along with the taxonomic status of each genus, and a revised family description is provided.

Key words: Agaricales; *Crepidotus*; *Melanomphalia*; molecular phylogeny; mushroom systematics; *Pleurotellus*; *Simocybe*; *Tubaria*.

Recent advances in phylogenetic systematics of the homobasidiomycetes have both reinforced and encouraged reassessment of traditional classification systems for these fungi. Large-scale molecular analyses have uncovered an evolutionary lineage of homobasidiomycetes that is roughly equivalent to the Agaricales sensu (s.) Singer (1986) with several notable exceptions, now known as the euagarics (Hibbett et al., 1997; Moncalvo et al., 2000; Moncalvo et al., 2002).

Phylogenetic systematics of select euagaric lineages has been the subject of many recent studies (e.g., Liu et al., 1997; Johnson and Vilgalys, 1998; Drehmel et al., 1999; Hopple and Vilgalys, 1999). Comprehensive molecular analyses of the euagarics as a whole was first undertaken by Moncalvo et al. (2000), providing a phylogenetic framework for examining evolutionary lineages in the agaric fungi. Their analysis included representative taxa from all of Singer's (1986) families with the exception of the Gomphidiaceae Maire ex Jülich and the Crepidotaceae (Imai) Singer. Phylogenetic study of the Gomphidiaceae has since been undertaken (Miller and Aime, 2001; Miller et al., 2002) although these fungi are now considered to be gilled members of the suilloid (Boletales) lineage and not true agarics. The present study provides the first such analysis to focus on the agaricoid genera of the Crepidotaceae.

The earliest classification for the crepidoti was by Imai (1938), who erected the monogeneric tribe Crepidoteae to accommodate those species of agarics with eccentric, lateral, or absent stipes, subdecurrent lamellae, and ocherous or ferruginous spores. In the ensuing years, nine genera gradually came to be included in the Crepidotaceae (Singer, 1951a, 1962, 1971, 1973). The last edition of *The Agaricales in Modern Taxonomy* (Singer, 1986) lists the agaricoid (mushroom-forming) genera *Tubaria* (W.G. Sm.) Gillet, *Melanomphalia* M.P. Christ., *Simocybe* Karst., *Crepidotus* (Fr.) Staude, and *Pleurotellus* Fayod, as well as four cyphelloid (without gills) genera, *Episphaeria* Donk apud Sing. ex Donk, *Phaeosolenia* Speg., *Pellidiscus* Donk, and *Chromocyphella* de Toni and Levi, as the members of this family. No modern systematic treatments of the family have been published as a whole since the works of Singer.

Members of the family as circumscribed by Singer have little or no known economic importance, occur worldwide in a variety of habitats, and are phenotypically diverse. Singer's (1986) definition of the Crepidotaceae includes a heterogeneous group of genera with pip-shaped, ellipsoid, or globose basidiospores usually without a germ pore, and with pale yellow to dark-brown spore prints. The inamyloid spores may be either smooth walled or ornamented. Hyphae may or may not form clamp connections; cheilocystidia are nearly always present, but pleurocystidia are rare. Species may be pleurotoid, collybioid, omphalinoid, or cyphelloid in habit and are secondary decomposers found on various types of organic debris

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and wood. Development is not known for all species but is believed to be gymnocarpic or hemiangiocarpic. As a family, these fungi were believed by Singer (1986) to be related to the Cortinariaceae R. Heim ex Pouzar, Entolomataceae Kotl. and Pouzar, and Paxillaceae R. Maire apud Maire, Dumée and Lutz.

The treatments by many modern authors followed Singer's with minor modifications, while others proposed major revisions to Singer's system, including the abolition of the Crepidotaceae. Most of these treatments include placing some or all of the Crepidotaceae genera within other families, especially the Cortinariaceae and/or the Strophariaceae Singer and A.H. Smith (e.g., Moser, 1978; Kühner, 1980; Jülich, 1981; Bas, 1988; Breitenbach and Kränzlin, 1995; Hawksworth et al., 1995; Kirk et al., 2001).

Morphological and biological studies of the crepidoti have provided further evidence that makes obvious the need for a critical reassessment of the current classification systems for these fungi. For example, morphological studies, especially of the pileipellis, have suggested that *Simocybe* might be more closely related to *Agrocybe* Fayod (Bolbitiaceae Singer) (Romagnesi, 1962; Watling and Largent, 1976). Basidiospore germination in members of *Crepidotus* is markedly different from that in species of *Tubaria*, suggesting a more distant common ancestry for them than proposed by Singer (Aime and Miller, 2002). Singer based his transfer of both *Tubaria* and, later, *Melanomphalia* into the Crepidotaceae on a single species, *M. thermophila* (Sing.) Sing. (Singer, 1951a, 1962, 1971); recent study of type and newly collected material has shown this species to be, in fact, a *Crepidotus* (Aime et al., 2002). In addition, numerous studies have questioned the validity of delimiting genera based on single morphological characters (e.g., Smith, 1968; Watling and Largent, 1976), such as has been done in circumscribing *Pleurotellus* from *Crepidotus*, which are delimited solely on the basis of spore pigmentation.

Given the diverse phenotypes, contradictory proposed classifications, biological differences, and the fact that generic and higher level systematics in the Crepidotaceae have been largely neglected, this study was undertaken to assess phylogenetic relationships for these fungi by analyzing molecular sequence data. Nuclear DNA sequences encoding a portion of the large ribosomal subunit (nLSU) have been shown to be effective at resolving phylogenetic relationships for agarics and related fungi at the generic (e.g., Johnson and Vilgalys, 1998; Drehmel et al., 1999; Hopple and Vilgalys, 1999; Dahlman et al., 2000) and family or ordinal levels (e.g., Miller et al., 2000; Moncalvo et al., 2000, 2002; Thorn et al., 2000). Sequences from the type species from each of the five proposed agaric members of the Crepidotaceae were assembled, as were other specific exemplars from each genus selected to cover a broad range of the phenotypic and geographic diversity found within these fungi. The Crepidotaceae sequences were analyzed within a data set chosen to include representatives from all major lineages of dark-spored euagarics including sequences from other families to which various components of the Crepidotaceae have been hypothesized to belong in alternative classifications. Our primary goals were to (1) test the monophyly of the Crepidotaceae s. Singer and evaluate alternative classifications of the family, (2) elucidate phylogenetic relationships and provide a detailed discussion of the taxonomic status for each agaric genus allied in the family by Singer, (3) re-evaluate morphological characters previously used to delimit these genera and identify features that characterize various clades that were detected in this study, and (4) redefine the Crepidotaceae within a phylogenetic framework.

MATERIALS AND METHODS

Taxonomic sampling—A total of 44 taxa were selected for analysis. Taxa analyzed, along with classification according to Singer (1986), phylogenetic lineage according to Moncalvo et al. (2000) where applicable, and GenBank accession numbers are in Appendix 1 (see Supplemental Data accompanying online version of this article). Sixteen taxa of Crepidotaceae s. Singer, including the type species for each genus, were sampled (GenBank accession numbers AF205669, AF205677, AF205679, AF205685 to AF205686, AF205695, AF205606 to AF205608, AF205610 to AF205612, AF367931 to AF367934); exsiccata used as sources for DNA are also listed in Appendix 1. To assess the relationships of the Crepidotaceae s. Singer within the euagarics, a collection of nLSU sequences were selected from previous studies (Chapela et al., 1994; Lutzoni, 1997; Johnson and Vilgalys, 1998; Hopple and Vilgalys, 1999; Moncalvo et al., 2000; Moncalvo et al., 2002) to include three representatives from each major lineage of dark-spored euagarics (designated Q through W) as identified in Moncalvo et al. (2000). Dark-spored euagarics were sampled extensively because all treatments of the Crepidotaceae ally them within this group, and additional sampling of omphalinoid fungi (Moncalvo et al., 2000, lineage K) was included because preliminary analyses (not shown) suggested an affinity of *Melanomphalia* with this group. For rooting purposes, outgroup taxa were chosen from within the Boletales (Moncalvo et al., 2000, lineage AA) because prior phylogenetic analysis of both the nLSU (Moncalvo et al., 2000) and mitochondrial and nuclear ribosomal subunit DNA sequences (Hibbett et al., 1997) suggest that the boletes and euagarics are sister lineages, and it has been shown that outgroup choice should, ideally, be confined to taxa sharing a sister group relationship to the ingroup under study (Hopple and Vilgalys, 1999).

DNA extraction, amplification, and sequencing—Standard DNA isolation methods were used with hexadecyltrimethylammonium bromide extraction buffer (Zolan and Pukkila, 1986). The 5′-end of the nLSU gene was targeted for sequencing and phylogenetic analysis as this region carries nearly 50% of the phylogenetic signal present within the nLSU molecule (Hopple and Vilgalys, 1999). Standard amplification and sequencing parameters follow Vilgalys and Hester (1990) and Moncalvo et al. (2000). Amplification was achieved with primer pair 5.8SR/LR7 (Vilgalys and Hester, 1990) or LR5/LR0R (Moncalvo et al., 2000). Primers LR0R, LR3R, LR5, and LR16 (Moncalvo et al., 2000) were used in sequencing reactions. The four sequence chromatograms generated per sample were compiled using SeqMan II v. 4.03 (DNAStar Inc., 1997) to produce a single contiguous sequence for each sample.

Phylogenetic analysis—Sequences were manually aligned in PAUP* 4.0b8 (Swofford, 2001). Gaps were introduced to maintain alignment through regions where indels occurred in one or more sequences. Regions with ambiguous alignment were removed from analysis. Alignments are available from the lead author by request. Analysis was performed on a Power Macintosh OS workstation. Methods for unweighted maximum parsimony analysis (UMP) follow Aime et al. (2002). Methods for weighted maximum parsimony analysis (WMP) follow Moncalvo et al. (2000) and apply a stepmatrix based on dinucleotide frequencies and substitution rate estimates as observed in that work. Support for clades was assessed by calculating bootstrap (Hillis and Bull, 1993) and jackknife frequencies (Lanyon, 1985) by performing 1000 replicates of random addition sequence replicates with TBR (tree-bisection-reconnection) branch swapping.

Additionally, constraint analyses were performed to test the probability that different groupings of Crepidotaceae taxa were monophyletic. Topological constraint trees were generated in the following manner. All members of *Crepidotus* and *Pleurotellus* were assigned to a single taxset; *Simocybe* taxa were assigned to a second taxset, and *Tubaria* taxa was assigned to a third taxset; all other ingroup taxa, with the exception of *M. nigrescens*, and the two outgroup taxa were assigned to a fourth taxset. No topological constraints

were enforced within any taxset. Separate analyses were then run with the following monophyletic constraints between taxsets: (1) no constraints; (2) taxset 1, 2, 3, and *M. nigrescens*; (3) taxset 1 and 2; (4) taxset 1, 2, and 3; (5) taxset 1, 2, and *M. nigrescens*; (6) taxset 1 and 3; (7) taxset 1 and *M. nigrescens*. For each of these analyses, WMP, with weightings based on nucleotide frequencies as already described and using 20 random addition sequence replicates with TBR branch swapping, was conducted in PAUP*. Scores for each of the 20 most parsimonious trees uncovered were recorded for each constraint set. Tree scores were analyzed statistically in JMP v.3.2.1 (SAS Institute Inc., 1997).

RESULTS

In all, the data matrix assembled consisted of 44 taxa aligned across 1200 positions; 188 positions were excluded from analysis due to ambiguities in alignment, and by trimming the extreme 5′ and 3′ ends; 231 of the remaining characters were parsimony-informative. A single shortest UMP tree was found of length 1193, CI = 0.450, RI = 0.527. A single shortest WMP tree of length 5057.4, CI = 0.456, RI = 0.535 was also found. Trees generated by both weighted and unweighted parsimony analyses were not different in topology. Bootstrap and jackknife support of terminal clades is stronger than for internal nodes. Figure 1 depicts the bootstrap 50% majority-rule consensus tree generated with these data, which is topologically congruent with both UMP and WMP trees.

Tree scores generated by 20 WMP random addition replicates enforcing six different topological constraints and without constraints are supplied and statistically compared in Appendix 2 (see Supplemental Data accompanying online version of this article). Imposing monophyly in all combinations among the different genera of the Crepidotaceae resulted in trees that were significantly longer (Appendix 2) than the trees produced without constraint (Fig. 1) except when only *Crepidotus* and *Simocybe* are constrained together. Figure 2 depicts the shortest tree obtained for each constraint set.

Ten lineages of brown-spored agarics were revealed, corresponding to previously reported lineages with two additions: The crepidotoid lineage of *Crepidotus* [type *C. mollis* (Fr.) Staude], *Pleurotellus* [type *P. hypnophilus* (Pers.:Berk.) Fayod], and *Simocybe* [type *S. centuncula* (Fr.:Fr.) Karst.] (Fig. 1, clade I); and a lineage consisting of *Tubaria* [type *T. furfuracea* (Fr.) Gillet], *Phaeomarasmius* Scherff., and *Flammulaster* Earle (Fig. 1, clade II). Deeper relationships between these lineages could not be ascertained in this study. The genus *Melanomphalia* (type *M. nigrescens* M.P. Christ.) is strongly supported within a clade of white-spored omphalinoid fungi, in exclusion from the dark-spored euagarics (Fig. 1, clade III). The position of *M. nigrescens* was confirmed by nLSU sequencing of an additional collection of this taxon (data not shown).

DISCUSSION

In contrast to Singer's (1986) classification, sequence data from the first 1200-base region of the nLSU molecule indicate that the Crepidotaceae sensu lato (s.l.) is polyphyletic, nor do these data reflect any of the alternative classifications proposed for the genera examined. Both *Tubaria* (Fig. 1, clade II) and *Melanomphalia* (Fig. 1, clade III) have originated independently from the core members of the Crepidotaceae s.s. (Fig. 1, clade I). Although strong statistical support via bootstrapping and jackknifing for some of these lineages is low, the conclusions reached by WMP are fully supported by analysis

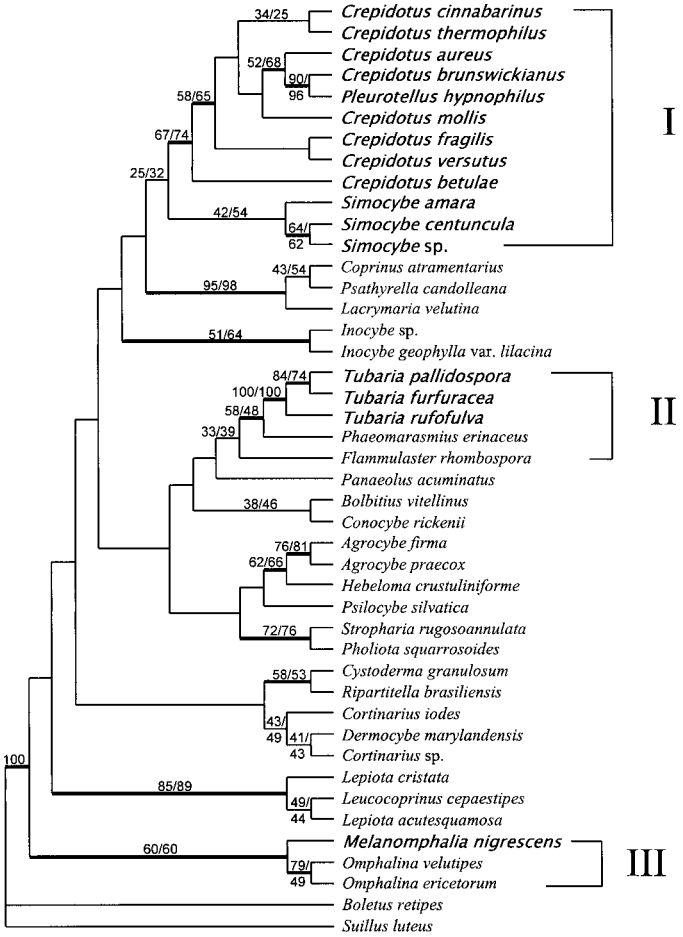

Fig. 1. Phylogenetic assignment of the genera of the Crepidotaceae sensu lato based on a portion from the 5′ end of the nLSU. Bootstrapping 50% majority-rule consensus tree depicted. Bootstrap and jackknife values (1000 replicates of full maximum parsimony analysis each) are indicated above branches supported by more than 25% of replicates. Bold lines indicate branches with bootstrap support of >50%. Bold type indicates taxa allied within the Crepidotaceae by Singer. Roman numerals designate clades referred to in the text.

of trees produced by enforcing monophyletic constraints on the genera of the Crepidotaceae s.l. (Appendix 2). A detailed discussion follows.

Phylogenetic inference—Several methods for evaluating support for phylogenetic clades have been debated and utilized. Decay indices (Bremer, 1988) are a valuable method of detecting support for branches, but are impractical for large data sets (Moncalvo et al., 2000). Bootstrap (Hillis and Bull, 1993) and jackknife (Lanyon, 1985) values have gained wide acceptance in systematic literature, but in actuality provide an indication only of the degree of support for a particular clade or node given the specific technique and data matrix analyzed (Hillis and Bull, 1993). In many instances, however, such as when rates of character change are high enough to randomize some characters (i.e., saturation or high homoplasy), bootstrap values can not be used as measures of accuracy or the probability that a given tree or clade represents the true phylogeny (Hillis and Bull, 1993).

In the present data matrix, >20% of the characters were parsimony-informative. This is well beyond the optimal range

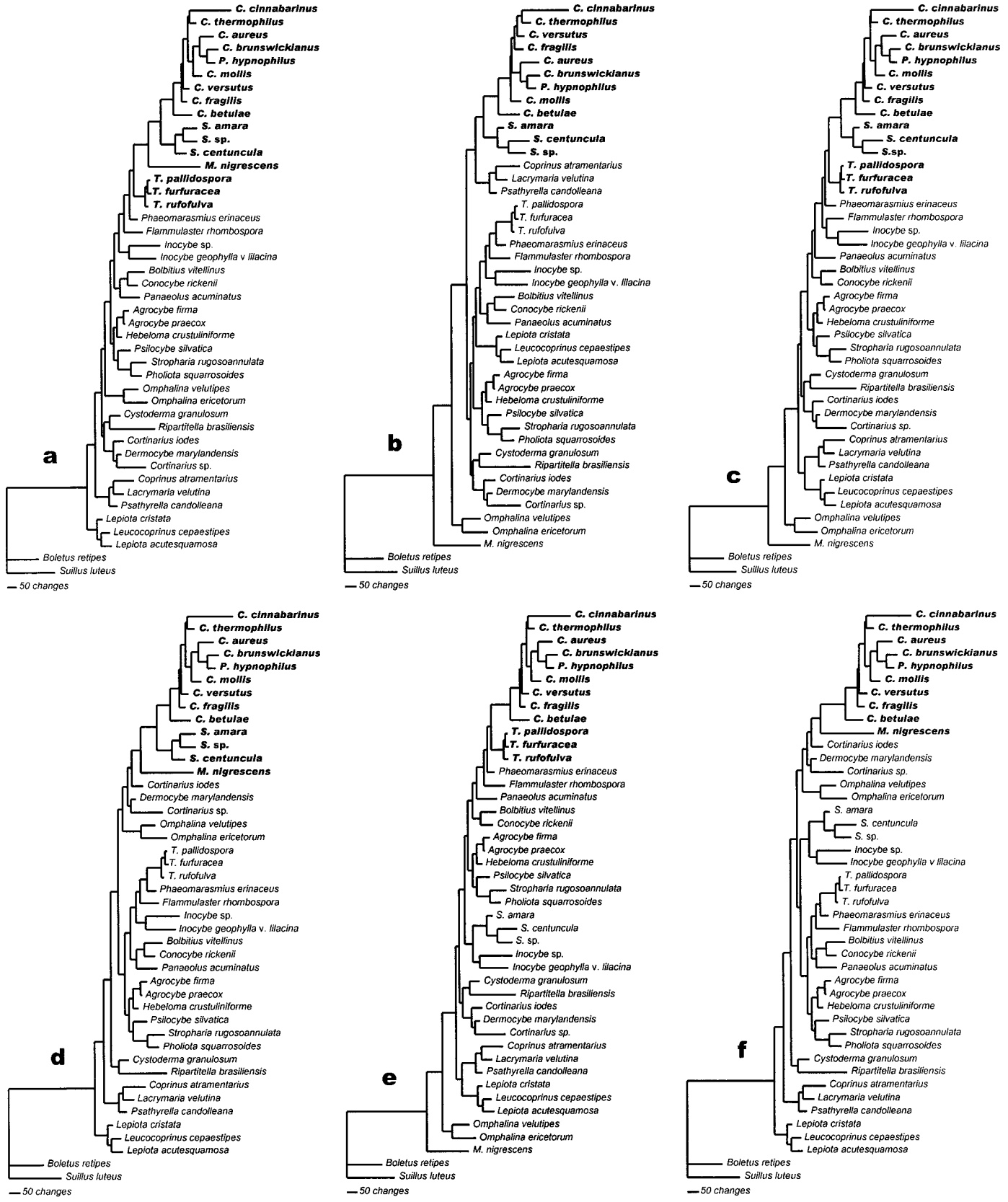

Fig. 2a–f. Topological constraint trees generated with weighted parsimony analysis (WMP). The shortest tree of 20 WMP trees generated for each constraint set is presented. Taxa constrained to monophyly are indicated in bold type; topological constraints of terminal taxa were not enforced within each monophyletically constrained set. Tree values = (a) 5144.9 (*Simocybe*, *Crepidotus* [includes *Pleurotellus*), *Tubaria*, and *Melanomphalia*]; (b) 5057.6 (*Crepidotus* and *Simocybe*); (c) 5070.9 (*Crepidotus*, *Simocybe*, and *Tubaria*); (d) 5109.5 (*Crepidotus*, *Simocybe*, and *Melanomphalia*); (e) 5063.7 (*Crepidotus* and *Tubaria*); (f) 5105.8 (*Crepidotus* and *Melanomphalia*).

of 5–15% (Olmstead and Palmer, 1994) and, given the broad phylogenetic range sampled and low consistency index, indicates that the variable positions within the matrix are probably saturated by change (Hillis and Huelsenbeck, 1992). Phylogenetic resolution in parsimony analyses in such instances can be improved by increasing taxon sampling, as the probability increases that more homoplasic characters will be correctly interpreted as such (Olmstead and Palmer, 1994), although the debate between whether increasing sample size (Graybeal, 1998; Hillis, 1998) or increasing character numbers (Kim, 1998) in phylogenetic analyses is still unresolved. However, further confirmation of the clade I association of *Crepidotus* and *Simocybe* and the exclusion of *Tubaria* from this clade was independently achieved when the number of euagaric taxa in the data set was dramatically increased (see Moncalvo et al., 2002) and also by increased sampling of nucleotide characters from additional molecules (specifically, the entire nLSU region and SSU regions for a cross-section of exemplar taxa from across the euagarics) (J. M. Moncalvo and M. C. Aime, unpublished data).

An additional method for evaluating the probability that the three crepidotoid lineages uncovered by the parsimony analyses were accurate depictions of phylogeny was devised by comparing tree lengths derived from WMP analysis of the data matrix to tree lengths derived from the same method but with monophyletic constraints imposed on various combinations of crepidotoid genera (Appendix 2, Fig. 2). In all cases, trees derived when *Tubaria* and or *Melanomphalia* are constrained within the Crepidotaceae (as defined by the type genus *Crepidotus*) were significantly (in most cases, $P < 0.001$) worse phylogenetic hypotheses than that of *Crepidotus* (including *Pleurotellus*) and *Simocybe* as the true familial components (Appendix 2). When *Melanomphalia* is constrained within the Crepidotaceae, *Omphalina* becomes part of the dark-spored euagarics, which is in contradiction to all previous classifications and nucleotide-based phylogenetic analyses (Fig. 2a, d, and f). Likewise, when *Tubaria* is constrained within the Crepidotaceae, *Phaeomarasmius* and *Flammulaster* become basal to the family, contrary to previous phylogenetic hypotheses and analyses (Fig. 2a, c, and e).

A detailed taxonomic evaluation of each genus is beyond the scope of this paper; such work has been extensively addressed by other authors. Systematics of *Crepidotus* will be discussed in a separate paper. A discussion of the other genera of the Crepidotaceae s.l. within a phylogenetic context is herein provided.

Clade I: the Crepidotaceae s.s.—*Crepidotus* and *Simocybe* are sister taxa representing the Crepidotaceae based on allegiance to the type *C. mollis* (Fig. 1). The sister lineage to the Crepidotaceae cannot be resolved with these data, nor was it recovered within the expanded analyses of Moncalvo et al. (2002), although any sister relationship between the Crepidotaceae s.s. and either the Entolomataceae or the Paxillaceae, as suggested by Singer (1986) is contraindicated by all analyses. Nor is it likely from these and other analyses (Moncalvo et al., 2002, and M. C. Aime, unpublished data) that any member of the Strophariaceae s.l. shares a sister relationship with the Crepidotaceae s.s. The most likely candidates in all phylogenetic analyses thus far are that either a component of the Coprinaceae s.l. (Fig. 1) or the genus *Inocybe* (Fr.) (Moncalvo et al., 2002) shares a sister relationship with the Crepidotaceae s.s., although neither of these relationships would reflect any previously proposed classification for the Agaricales.

Simocybe—The nomenclatural debate surrounding the group of agarics now conserved and typified under *S. centuncula* (Greuter et al., 1994) has been treated previously [Singer, 1973; Redhead, 1984 as *Naucoria* (Fr.) Kumm.; Reid, 1984 as *Naucoria*; Horak and Miller, 1997]. Approximately 25 species are now allied in *Simocybe* (Hawksworth et al., 1995). All known members are saprotrophic. *Simocybe* is geographically distributed worldwide (Redhead and Cauchon, 1989) and has been monographed from the Neotropics (Singer, 1973), lower Pacific (Horak, 1979a, b, 1980b), and the United Kingdom (Reid, 1984; Watling and Gregory, 1989 as *Ramicola* Velenovsky).

Singer's (1973) transfer of *Simocybe* to the Crepidotaceae is by no means universally accepted. Most early classifications placed *S. centuncula* and its allies within the Cortinariaceae, and this system is still followed in most modern treatments (e.g., Jülich, 1981; Bas, 1988; Hawksworth et al., 1995; Grgurinovic, 1997). Such positions can usually be traced to early nomenclaturial difficulties in delimiting *Naucoria* (mycorrhizal, Cortinariaceae) from segregate genera including *Simocybe*.

Alternatively, *Simocybe* has been placed within the Strophariaceae (Kühner, 1980) or Bolbitiaceae and synonymized with *Agrocybe* based on striking similarities in pileipellis construction between *Simocybe* and *A. firma* (Pk.) Sing. (Romagnesi, 1962). The present study shows that *A. firma* and *Agrocybe* in general have no close affinities to the members of *Simocybe* (Fig. 1), which is in support of Watling and Largent's (1976) observation that given the fact that differences in construction also occur in the cuticle of the two taxa, the similarities that exist may be due to convergence and not phylogeny.

Similarities in pileus structure between *Tubaria* and *Simocybe* have also been noted (Watling and Largent, 1976; Vellinga, 1986). True members of *Simocybe* all possess numerous pileocystidia terminal cells in the epicutis, which can resemble the velum-producing cells found in the pileipellis of tubarii. The *Simocybe* pileipellis is of simple construction, however, as in *Crepidotus* (Watling and Largent, 1976), and the pileocystidia originate from the pileipellis as differentiated termini whose function is not analogous to that of the similar-appearing cells in *Tubaria*. Species of *Simocybe* are gymnocarpic (Horak, 1979a, 1980b), and reports of hemiangiocarpy are most likely based on nongeneric elements no longer considered to be allies of *S. centuncula* as now circumscribed.

Pleurotellus—*Pleurotellus* was originally typified by Fayod (1889) based on Berkeley's interpretation of Persoon's description of *Agaricus hypnophilus*. Later, Fayod became doubtful as to whether he had correctly determined Persoon's taxon and renamed his type collection *Pleurotellus graminicola* (Donk, 1962; Nordstein, 1990). Only two species are commonly accepted in the genus (Hawksworth et al., 1995), the identity of which are discussed in Nordstein (1990), yet the generic concept contains heterogeneous elements (Singer, 1962; Watling, 1988). While Orton (1960) interprets *Pleurotellus* as white-spored relatives of *Pleurotus* (Fr.) Kumm., of no affinity to *Crepidotus*, most consider the two closely related (e.g., Singer, 1961; Hesler and Smith, 1965; Watling and Gregory, 1989; Nordstein, 1990; Senn-Irlet, 1995), although opinions vary as

to whether *Pleurotellus* differs from other crepidoti on the generic level.

Proponents of segregating *Pleurotellus* and *Crepidotus* do so because of two morphological distinctions: the absence of clamp connections and the very pale-yellow to subhyaline spore print color in *Pleurotellus* (e.g., Pilát, 1948; Watling and Gregory, 1989; Singer, 1951a, 1962, 1986; Pegler and Young, 1972). Clamp connections, while useful taxonomically for the circumscription of species, are not reliable indicators of phylogeny in many groups (Watling and Largent, 1976), and *Crepidotus* contains several lineages that have clamps and others that do not (Aime, 2001 and unpublished data), so the character alone is not unique to *Pleurotellus*. Therefore, only the single character state of loss of spore pigmentation distinguishes the former from the latter. *Pleurotellus*, as represented here by the type, *P. hypnophilus*, is a component of *Crepidotus* (Fig. 1). Because the use of single characters for circumscribing genera can introduce artificiality into classifications (Smith, 1968), and *P. hypnophilus* is in all other characters consistent with *Crepidotus*, *Pleurotellus* should be considered congeneric with *Crepidotus*.

The taxon represented by *P. hypnophilus* (Pers.:Berk.) Fayod has been reported from all over the world under a large number of synonyms, and the correct specific epithet for it has been the subject of much discussion (Hesler and Smith, 1965; Nordstein, 1990; Senn-Irlet, 1995; Bandala et al., 1999). The first description that can be unambiguously applied to this taxon is that of Peck (1886) for *Crepidotus herbarum* (Pk.) Sacc. However, the older name of *Agaricus hypnophilus* Pers. ex Berk. takes precedent, if, as has been noted by Singer (1961), Berkeley correctly interpreted Persoon's taxon, for which a type no longer exists. Berkeley's type does exist and was the basis for Fayod's establishment of *Pleurotellus*. Several studies show it to be conspecific with the taxon analyzed in this paper (Singer, 1961; Donk, 1962; Horak, 1968); therefore, the name *C. hypnophilus* (Pers.:Fr.) Nordstein takes precedent over *C. herbarum*, as has already been recognized by Nordstein (1990).

However, Senn-Irlet (1995) has investigated the possibility that an older Friesian name, *Agaricus epibryus* Fr., exists for this taxon. Because no type for *A. epibryus* apparently exists and the original description (Fries, 1821) could be applied to many species of *Crepidotus* or even *Pleurotus* and allied genera, several differing concepts have been applied to this name in the past (Pilát, 1950; Singer, 1951b; Senn-Irlet, 1995). Senn-Irlet's interpretation was based on that of Quélet (1888), and she considers *C. herbarum* and *C. hypnophilus* to be synonyms for *C. epibryus* (Fr.) Quél. (Senn-Irlet, 1995). Although the argument is convincing, a few problems exist with this interpretation: (1) Quélet's (1888) description of *C. epibryus* is as vague as Fries' and could equally fit other taxa within and even outside the confines of *Crepidotus*, (2) Quélet actually considers *A. epibryus* as a *Crepidotus* in works as early as 1872, wherein the spores are described in more detail as being ''pruniform,'' or plum-shaped, which is not the case with the taxon under question here (Quélet, 1872), and (3) the only substrate given for both Fries' (1821, 1836–1838) and Quélet's (1872, 1888) taxon is moss, whereas the taxon under question is almost exclusively confined to herbaceous and grassy substrates, and hardwoods, not moss (Peck, 1885; Watling and Gregory, 1989; Nordstein, 1990; Bandala et al., 1999), hence the name *C. herbarum* and Fayod's later change to *P. graminicola*.

Nonetheless, a neotype has been established for *C. epibryus* (Senn-Irlet, 1995), and this name is now accepted (Bandala et al., 1999), for the taxon that was previously more commonly known as *C. herbarum* or *P. hypnophilus*; the name *C. epibryus* (Fr.) Quél. s. Senn-Irlet should be applied to it. This species has been previously described and illustrated by Senn-Irlet (1995), Bandala et al. (1999), Horak (1968, as *P. graminicola*), Nordstein (1990, as *C. hypnophilus*), and Hesler and Smith (1965, as *C. herbarum*).

Clade II: Tubaria and allies—The data presented in this and in Moncalvo et al. (2002) show this genus to be most closely allied with *Phaeomarasmius* and *Flammulaster*, and only distantly related to the members of the Crepidotaceae s.s. (Fig. 1). Basidiospore germination and vegetative morphology of *T. furfuraceae* were studied by Ingold (1983) and shown to be considerably different from that of *Crepidotus* species (Aime and Miller, 2002), lending additional support to a proposed phylogenetic hiatus between the two genera. *Tubaria* contains approximately 15 saprotrophic species occurring worldwide in temperate climes (Hawksworth et al., 1995), and only a few European species have been monographed (Lange, 1938; Romagnesi, 1940, 1943).

Singer (1951a) transferred *Tubaria* from the Cortinariaceae to the Crepidotaceae and the rationale behind this decision was discussed in Aime et al. (2002). Other authors still ally this genus with the Cortinariaceae s.l. (Romagnesi, 1940; Vellinga, 1986; Grgurinovic, 1997) or place it within the Strophariaceae s.l. (Moser, 1978). *Tubaria* has the distinction of being the only genus within Singer's Crepidotaceae in which some members undergo hemiangiocarpic development and have spore prints that may display orange tones. Morphological delimitation and generic concepts between and within *Flammulaster*, *Phaeomarasmius*, and *Tubaria* have been repeatedly evaluated (Romagnesi, 1940; Watling, 1967; Kühner, 1969; Harmaja, 1978; Moser, 1978; Horak, 1980a; Vellinga, 1986). The present study is in support of the classification of Moser (1978) which proposes a relationship between the three genera *Phaeomarasmius*, *Flammulaster*, and *Tubaria*.

Numerous characters and character suites have been hypothetical indicators of phylogeny in agarics. The alliance of *Tubaria*, *Flammulaster*, and *Phaeomarasmius* is best understood through the work of Watling and Largent (1976), which emphasizes pileipellis anatomy in drawing conclusions about higher-level relationships in the agarics. The members of all three genera possess an unusual pileipellis that contains inflated hyphae occurring in chains, usually encrusted with brown pigment (Watling and Largent, 1976; Harmaja, 1978; Vellinga, 1986). These chains of hyphae appear to be the same elements that give rise to the partial veil present in these species, yet appear to originate from, and be an integral part of, the cutis rather than the stipe. The resulting partial veil is usually fugacious, and persistent in one species (Watling, 1967). All taxa tested so far are KOH+ on the pileus (Watling, 1967; Vellinga, 1986), which appears to be a secondary unifying character.

Clade III: Melanomphalia and its allies—Perhaps the most interesting result of this study is the alliance of *Melanomphalia* with a subset of the genus *Omphalina* Quél. Generic affinities for *Melanomphalia* have never been certain (Lange, 1940; Montag, 1996), with the type itself seemingly holding a rather isolated position even within the genus as expanded by Singer

(Watling, 1988). The genus was hypothetically allied with the Gomphidiaceae by Christiansen (1936) and early authors (Lange, 1940) and with the Cortinariaceae (Singer, 1955) until its transfer to the Crepidotaceae (Singer, 1971) based on similarities between *Crepidotus thermophilus* (Sing.) Aime, Baroni, and O.K. Miller and some *Crepidotus* species as previously discussed elsewhere (Aime et al., 2002).

Similarities between the type, *M. nigrescens* and some *Omphalina* have previously been noted (Montag, 1996). Christiansen (1936) also recognized similarities between *Omphalina* and his genus, although the differences in spore pigmentation and ornamentation had always been viewed as too striking to consider other similarities as anything other than evidence of parallel evolution between these genera.

Taxonomically, the omphalinoid fungi have also been a difficult and heterogeneous group to delimit (Bigelow, 1970; Redhead and Weresub, 1978; Norvell et al., 1994), and recent phylogenetic analyses have uncovered three distinct lineages of polyphyletic origin (Lutzoni, 1997; Moncalvo et al., 2000). What is extremely interesting is that *M. nigrescens*, within the confines of this study shows a sister relationship with a clade previously identified as the true *Omphalina* (Lutzoni, 1997), which includes lichenized fungi (Fig. 1). This merits closer scrutiny of the phylogeny and ecology of *M. nigrescens*, which has only been reported on soil (Christiansen, 1936; Montag, 1996) or adventitiously on limestone or in association with herbaceous VAM plants (Watling, 1988), and as such was one of the only non-lignicolous members of the Crepidotaceae s. Singer.

This association is also extraordinary in that it suggests an independent origin of dark spore pigmentation in the euagarics. Historically, much weight has been attached to certain aspects of basidiospore morphology, especially pigmentation, in deriving hypotheses regarding agaric phylogeny. Interestingly, loss of spore wall pigmentation has now been shown through molecular studies to have occurred in several agaric cohorts, such as has occurred in the Agaricaceae (Johnson and Vilgalys, 1998), and the Crepidotaceae with *C. epibryus* s. Senn-Irlet, but the acquisition of pigmented spores from an unpigmented ancestor appears to be a rarer phenomenon.

Prior work has shown that at least one species previously placed within *Melanomphalia* is, in fact, a *Crepidotus* (Aime et al., 2002), and preliminary study of other taxa currently placed in the genus also suggests that most are more naturally allied within *Crepidotus* or other genera (M. C. Aime, unpublished data). At present, *Melanomphalia* appears to be a monotypic genus. The taxonomic disposition of other species currently allied in *Melanomphalia* and detailed phylogeny are under further investigation.

Redefining the Crepidotaceae—Initially, the macroscopic character of habit delineated *Simocybe* from *Crepidotus*. Transfers of some pleurotoid taxa from *Crepidotus* to *Simocybe* based on microscopy (Singer, 1973; Watling, 1988; Horak and Miller, 1997), and of some stipitate taxa to *Crepidotus* (Aime et al., 2002) have blurred the macroscopic distinctions between the two, but result in a more natural classification based on microscopic characters. Chiefly, *Simocybe* can be diagnosed from *Crepidotus* by (1) basidiospores which are always smooth and differ from smooth-spored *Crepidotus* species in that the adaxial side is typically applanate to depressed; and (2) abundant pileo-, caulo-, and cheilocystidia (the latter two most typically subcapitate), lending a pruinose appearance to these structures macroscopically. Additionally, many *Simocybe* members have an olivaceous tint to the pileus, lacking in *Crepidotus*.

The Crepidotaceae s.s. are differentiated from all other euagaric lineages by the following suite of characters: saprotrophic on woody or herbaceous matter; gymnocarpic; spore prints within the pale yellow to brown range, not pink, purple-brown, orange, or black; simple cuticle, although differentiated termini in the form of pileocystidia may be present; cheilocystidia always present; pleurocystidia absent in most taxa and never thick-walled or originating from the lamellar trama; basidiospores entire, with neither a true germ pore nor plage, smooth or ornamented but never angular or reticulate.

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