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Taxonomy of displaced species of *Tubaria*

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Abstract: A taxonomic treatment of vinaceous and reddish species of *Tubaria* (Agaricales) is presented based on morphology and nucleotide sequences. Accessions from western North America, Europe, Central America, the Caribbean and Australia are compared. Phylogenetic analysis of the 25S rRNA gene and internal transcribed spacer (ITS) regions demonstrates that *Tubaria* is not monophyletic. However the autonomy of six brown-spored, saprotrophic species—*Naucoria vinicolor, Pholiota serrulata, Phaeomarasmius confragosus, Pholiota punicea, Tubaria rufofulva* and *T. bispora* sp. nov.—is affirmed. All six species form a strongly supported monophyletic group that we label section *Confragosae* in the genus *Tubaria.* This section is related to *T. dispersa, T. albostipitata* and numerous representatives of the *T. furfuracea* complex. *Tubaria minima* is related to other lineages of dark-spored Agaricales. Taxonomic descriptions, illustrations and a key to confirmed species of section *Confragosae* are provided. Four new combinations are proposed, and one new species, *T. bispora*, is described as new from Costa Rica and Martinique. A lectotype is designated for *Pholiota serrulata.*

Key words: Agaricales, Basidiomycota, new combinations, species, systematics

INTRODUCTION

Vinaceous or red species of dark-spored Agaricales are relatively uncommon but striking in appearance when encountered in the field. Some reddish species are well known in *Cortinarius* (Ammirati and Smith 1984, Ammirati 1989, Liu et al 1995) and others documented in *Crepidotus* (Luther and Redhead 1981, Pöder and Ferrari 1984, Bandala, Montoya, Horak 2006) and *Stropharia* (Shaw and Kibby 2001, Shaw, Butlin, Kibby 2004). Descriptions of several lesser-known but conspicuously colored agarics are scattered in North American, South American and Australian literature in the genera *Tubaria* (Murrill 1917, Bougher and Syme 1998), *Phaeomarasmius* (Singer 1953), *Pholiota* (Smith and Hesler 1968) and *Naucoria* (Peck 1909, Arora 1986). We became interested in the identification of several vinaceous pigmented species of brown-spored Agaricales that inhabit wood in natural habitats or mulched landscapes in suburban areas because these species are encountered so rarely and their taxonomic affiliations poorly understood. Co-authors have studied such material from Australia, Costa Rica, Europe and the west coasts of Canada and the United States and determined these accessions to represent unclarified species of the genus *Tubaria* (W.G. Sm.) Gillet (Moser 1983, Horak 2005).

Tubaria encompasses 8–16 species in Europe (Bon 1992, Volders 2002, Horak 2005), but the total number of names of taxa admitted into the genus is 114 (http://www.indexfungorum.org). Some combinations (e.g. *T. decurrens* [Peck] Murrill) have not been catalogued by Index Fungorum. Nevertheless Moreau (2005) suggests there are more than 60 taxa worldwide. Family placement has been controversial with some authors treating *Tubaria* in the Crepidotaceae (Singer 1986), Cortinariaceae (Romagnesi 1940) or Strophariaceae (Kühner 1980, Horak 2005) based on morphological data. Recent molecular phylogenetic evidence supports the exclusion of *Tubaria* from Crepidotaceae *s. str.* (Aime, Vilgalys, Miller 2005). A multigene study by Matheny et al

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(2006) affirms this but also provides evidence that *Tubaria* is not closely related to Cortinariaceae *s. str.* or to Strophariaceae *s. str.* Rather *Tubaria* and exemplars of *Flammulaster* Earle and *Phaeomarasmius* Scherffel are nested with significant Bayesian support in a clade joining the Inocybaceae, Crepidotaceae, Panaeoleae and *Agrocybe erebia*.

Most species of *Tubaria* are characterized by small basidiomes (pileus diameter often less than 5 cm), brownish coloration, presence of a central stipe, subdecurrent to adnate lamellae, ochraceous or brown spore deposits, presence of cheilocystidia, often smooth basidiospores that lack a germ pore, a filamentous pileipellis and saprotrophic habit. At least three species from the subtropics or Asia have been described in the genus with verrucose spores—*T. thermophila* Singer, *T. verruculospora* Pegler and *T. lithocarpicola* M. Zang (Singer 1948, Pegler 1977, Zang 2001)—and two others with rugose to punctate spores from Europe or North America—*T. dispersa* (L. : Fr.) Singer and *T. decurrens* (Peck) Murrill (Kühner and Romagnesi 1953, Moreau unpublished data). These five and other species described from non-European regions (e.g. Peck 1895, Murrill 1917, Singer and Digilio 1952, Singer 1957, 1969, Grgurinivoc 1997) have not been synthesized into any coherent systematic treatment of the genus (Singer 1986), although *T. thermophila* recently was transferred to *Crepidotus* based on molecular and morphological findings (Aime, Baroni, Miller 2002). Bon (1992) established an infrageneric classification for European species of *Tubaria*, but species such as *T. confragosa* were left unclassified. Here we apply morphological and molecular methods to identify our materials to species, confirm their generic status and produce a taxonomic treatment for annulate or vinaceous-colored species of *Tubaria*. In so doing we obtained type materials of species of *Tubaria, Pholiota* and *Naucoria* to assist in identification and clarify several taxonomic and nomenclatural issues.

MATERIALS AND METHODS

Field descriptions and microscopy.—Basidiomes were documented in fresh condition. Color notations of tissues, spore deposits and anatomical characters are from Ridgway (1912), Kornerup and Wanscher (1967) and Munsell (1954). References to Ridgway (1912) are capitalized (e.g. Tawny). References to Munsell Soil Color (1976) and the Munsell Soil Color Charts (1954) are by chroma and hue (e.g. 10YR 7/6) and from Kornerup and Wanscher (1967) by plate and row number (e.g. 6D5). All other color notations are approximations. ''L'' refers to the number of lamellae that reach the stipe. Microscopic descriptions of spores and basidiome tissues were made from fresh or dried material mounted in 3% KOH or 10% NH_4OH. Extreme spore measurements are placed in parentheses. Typically 20–30 basidiospores were measured per collection. Line drawings were made with a drawing tube at 1000× for spores and 400× for other features. All materials are deposited in herbaria at AD, CUW, LIP, NY, PERTH, UC, WTU and ZT and the personal herbarium of O. Ceska (Vancouver Island, British Columbia, Canada). Herbarium acronyms follow Holmgren, Holmgren, Barnett (1990).

DNA extraction, PCR, and sequencing.—Dried material was ground in a 1.5 mL Eppendorf tube with a micropestle after freezing in liquid nitrogen. DNA extractions relied on an E.Z.N.A Fungal Miniprep Kit (Omega Bio-tek, Doraville, Georgia) following the protocol of the manufacturer. In the final step DNA was eluted with 70 µL of elution buffer. PCR amplification, purification and sequencing of the 25S ribosomal RNA gene (25S rRNA) and the 5.8S ribosomal RNA plus internal transcribed spacers (hereafter referred to as ITS) follows protocols outlined in Yang et al (2005).

DNA alignments and phylogenetic analyses.—Sequence chromatograms were edited in Sequencher 4.1 (Gene-Codes, Ann Arbor, Michigan). Sequences were aligned with Clustal X 1.83 (Thompson et al 1997) and adjusted manually in MacClade 4.0 (Maddison and Maddison 2000). We performed an initial screening of 25S sequences to determine clade affinities of our tubarioid sequences in a dataset of 105 dark-spored Agaricales. Taxon selection was based on family/clade designations in the Agaricoid clade of Matheny et al (2006), Strophariaceae *sensu* Kühner (Gulden et al 2005), Crepidotaceae *sensu* Singer (Aime, Vilgalys, Miller 2005) and the/tubaria clade in Bodensteiner et al (2004). Previously published sequences from these studies were used in addition to others drawn from Binder and Bresinsky (2002); Matheny et al (2002); Moncalvo et al (2002); Frøslev, Matheny, Hibbett (2005); Matheny (2005); Walter, Garnica, Weiß (2005); Yang et al (2005); and Matheny and Bougher (2006). Results from this phylogenetic screening determined taxon selection for a combined 25S and ITS analysis. In the combined analysis, 39 25S and 34 ITS sequences of *Tubaria* and outgroups were assembled in interleaved format in PAUP* 4.0 (Swofford 2003). The final number of taxa analyzed was 49. Ten taxa lacked 25S sequences, and 15 others lacked ITS sequences. Twenty-one new 25S sequences have been deposited at GenBank (DQ986293-DQ986303, DQ987902-DQ987906, EF051051-EF051055) along with 30 new ITS sequences (DQ987907-13, DQ989327-34, DQ991348-56, EF051056-EF051060). GenBank accessions DQ494697/AF041544 for *Stropharia rugosoannulata* and AY8183450/AY646102 *Stropharia ambigua* were used as outgroups in the combined analysis. Outgroup choice is based on Matheny et al (2006).

All datasets were analyzed with Bayesian inference using the parallel version of MrBayes 3.1.2 with default priors (Ronquist and Huelsenbeck 2003, Altekar et al 2004) and maximum parsimony (MP) in PAUP*. These alignments are available at TreeBASE (S1750). Gaps were scored as missing data. PAUP* analyses were done on a Macintosh 1.33 GHz PowerPC G4. Bayesian analyses were implemented on a Linux cluster with AMD Opteron 246 processors. Separate partitions were modeled with a general-time-reversible

(GTR) model (nst = 6) and rate heterogeneity parameters (gamma-distributed substitution rate and a proportion of invariable sites) following the AIC criterion in Modeltest 3.06 (Posada and Crandall 1998). Bayesian analyses entailed two independent runs each using four chains for 5 000 000 generations and sampling trees every 500 generations. Likelihood scores were inspected to determine stationary phases in a spreadsheet application, and multiple runs were subject to convergence diagnostics (examination of average standard deviation of split frequencies) to assess convergence of tree samples. With this information in hand we determined the number of initial trees to discard to construct 50% majority-rule consensus trees and calculate posterior probabilities (PP). PP values greater than or equal to 0.95 are considered significant. One thousand bootstrap replicates were done in PAUP* to determine parsimony support values or bootstrap proportions (BP). For bootstrapped tree searches 10 random stepwise additions with TBR were used but with MULTREES turned off. Values above 70% are considered significant.

RESULTS

25S rRNA screening of tubarioid isolates.—We initially screened clade affiliation of our 25S tubarioid sequences in a dataset of 105 25S sequences, which included representatives of 43 genera of primarily dark-spored Agaricales (the Agaricoid clade). The dataset was composed of 1463 sites (256 parsimony informative). Ten thousand trees were combined from two independent Bayesian runs after a burn-in of 5001 trees per run. Convergence diagnostics suggested that this analysis continue longer than 5 000 000 generations, however all results, including MP analyses and multiple Bayesian runs, consistently recovered similar gross topologies pertaining to *Tubaria* isolates (data not shown). Likewise all analyses of the 25S screening procedure demonstrated *Tubaria* is not a monophyletic group. One isolate, *Tubaria minima*, clusters with *Pachylepyrium carbonicola* with high bootstrap support (70%). A second *Tubaria* isolate, *T. albostipitata*, groups with a previously published sequence of *Flammulaster carpophilus* (1.0 PP/73% BP). We suspect this accession (AJ871499) is mislabeled because it is closely related to *T. albostipitata* and fails to cluster with other accessions of the *F. carpophilus* complex (Vellinga 1986). Two independent lineages of *Naucoria vinicolor*, one lineage of *Pholiota serrulata* and an unidentified *Phaeomarasmius* sequence were placed within a significantly supported clade (0.96 PP/73% BP) of 14 *Tubaria* sequences, including the type *T. furfuracea*.

The tribe Tubarieae (*Tubaria* and *Flammulaster/Phaeomarasmius* allies in Matheny et al 2006) is not closely allied with Crepidotaceae (including *Pleuroflammula*), Cortinariaceae or Strophariaceae *sensu* Gulden et al (2005). 25S rRNA sequences of *Phaeosolenia densa*, a reduced or cyphelloid brown-spored species regarded as a member of the/tubaria clade in Bodensteiner et al (2004) clustered with the outgroup Agaricaceae sequence in both MP and Bayesian analyses of 25S sequences (data not shown).

Combined 25S rRNA and ITS sequences support recognition of six species in Tubaria, *section* Confragosae.—The combined 25S rRNA and ITS supermatrix is composed of 1735 included characters (268 parsimony informative) and 49 taxa and was used to investigate species level relationships within *Tubaria*. Posterior probabilities were drawn from the last 8000 trees (burn-in of 2001 trees) sampled from two independent runs for a total of 16 000 trees. A 50% majority-rule consensus tree is shown, including branch lengths (FIG. 1).

The most inclusive clade containing *Tubaria* isolates includes 15 species of *Tubaria* and two potentially mislabeled species of *Phaeomarasmius* and *Flammulaster*. This grouping receives significant Bayesian support (0.98 PP) but weak bootstrap support (50% BP). Early isolated lineages include *T. dispersa* (with faintly roughened spores) and a clade of *T. albostipitata* (with weakly pigmented spores) and ''*F. carpophilus*''. MP and Bayesian analyses provide robust support (1.0 PP/84% BP) for a subclade including members of the *T. furfuracea* complex—*T. furfuracea* (type of *Tubaria*), *T. hiemalis* and varieties, *T. praestans, T. segestria, T. pallidospora*, and one unclarified isolate, *Tubaria* sp. PAM 184 (see Bon 1992, Volders 2002), and six species of section *Confragosae*. Isolates of the *T. furfuracea* complex form an unresolved polytomy, whereas *Confragosae* is strongly supported as monophyletic (0.98 PP/87% BP). The section includes the wine-red *Naucoria vinicolor*, maroon *T. rufofulva* and a second clade of vinaceous specimens, to which we apply the name *Pholiota punicea* A.H. Sm. & Hesler (see taxonomy below). Also included are the annulate species *Pholiota serrulata* from Australia, *T. confragosa* from north temperate regions, and the newly described species *T. bispora* from Costa Rica and Martinique. Below we present a key to aid identification of these six species.

KEY TO VINACEOUS OR ANNULATE SPECIES OF *TUBARIA*, SECT. *CONFRAGOSAE*

1. Basidiomes not vinaceous throughout and annulus absent; spore deposit ochraceous-buff or lighter than brown; some spores remaining collapsed when revived in 3% KOH . . . . *Tubaria furfuracea* (Pers. : Fr.) Gillet complex and others (see Horak 2005

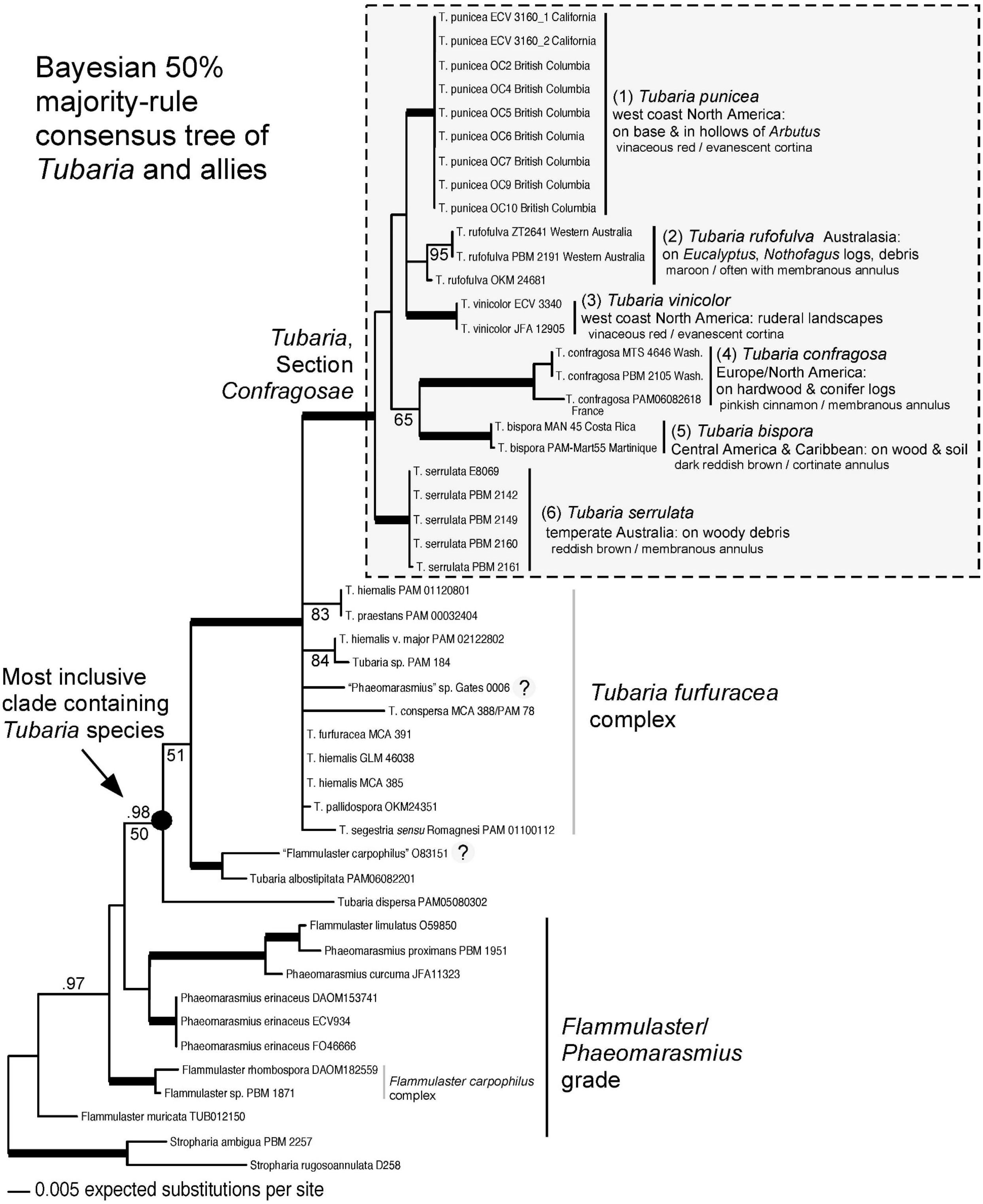

FIG. 1. A 50% majority-rule Bayesian phylogram of a supermatrix of combined 25S and ITS sequence data for the genus *Tubaria* and allies in *Flammulaster* and *Phaeomarasmius*. Thickened branches represent robust support (PP > 0.95; BP > 70%). BP values greater than 50% are shown for branches that receive less than 0.95 PP; PP values greater than 0.95 are shown for branches that receive less than 50% BP. Herbarium accession numbers are listed after taxon names. Geographic origins are provided. A question mark indicates doubtful taxonomic identity. The most inclusive clade including all *Tubaria* species (excluding *T. minima*) is indicated with an arrow and black filled circle. Six numbered lineages are resolved in *Tubaria*, section *Confragosae*. For each of these species, substrate, basidiome color and partial veil characters are summarized.

for European treatment; see Smith, Smith, Weber 1979 for a brief North American treatment)

1. Basidiomes vinaceous throughout or membranous annulus or cortinate ring present; spore deposit brown; spores not collapsed when revived in 3% KOH. 2
  2. Basidiomes vinaceous, red, or maroon 3
  2. Basidiomes reddish brown or cinnamon brown . . . 5
3. Partial veil typically forming an annulus; basidiomes maroon; known from Australasia . . . . *Tubaria rufofulva* (Cleland) D.A. Reid & E. Horak
3. Partial veil cortinate and not forming an annulus; basidiomes vinaceous or wine red; from western North America 4
  4. Occurring in ruderal landscapes with introduced vegetation in disturbed habitats . . . . *Tubaria vinicolor* (Peck) Ammirati, Matheny, et Vellinga comb. nov.
  4. Occurring in hollowed bases of *Arbutus* in natural habitats . . . . *Tubaria punicea* (A.H. Sm. & Hesler) Ammirati, Matheny, et P.-A. Moreau comb. nov.
5. Basidia 2-spored; from Costa Rica and Martinique (Lesser Antilles) . . . . *Tubaria bispora* Matheny, P.-A. Moreau, Neves, et Vellinga, sp. nov.
5. Basidia 4-spored; from Australia or North America and Europe. 6
  6. Pileus flocculose; occurring in North America and Europe . . . *Tubaria confragosa* (Fr.) Harmaja
  6. Pileus smooth; known only in Australia . . . . *Tubaria serrulata* (Cleland) Bougher et Matheny, comb. nov.

TAXONOMY

Tubaria, section **Confragosae** (Singer) Matheny, comb. nov. FIG. 1

Basionym. *Phaeomarasmius*, section *Confragosi* Singer, Sydowia 15:75. 1962.

≡ *Pholiota*, section *Confragosae* (Singer) A.H. Sm. & Hesler, North Am. Species of *Pholiota*: 39. 1968.

Comments. Six species are confirmed by molecular analyses to belong to this strongly supported monophyletic group in *Tubaria*: *T. bispora, T. confragosa, T. punicea, T. rufofulva, T. serrulata* and *T. vinicolor* (FIG. 1). The group is distinguished morphologically from other species of *Tubaria* by darker yellowish brown spore deposits and resistance of spore walls to collapse in microscopic mounts. The development of the partial veil is variable among the species in this section ranging from an evanescent cortina (*T. punicea* and *T. vinicolor*), a cortinate ring (*T. bispora*) or typically a membranous annulus (*T. confragosa*, *T. rufofulva*, and *T. serrulata*).

Both 25S rRNA and ITS sequences distinguish the *Confragosae* from the *T. furfuracea* complex, *T. dispersa* and *T. albostipitata* with significant measures of branch support. The *T. furfuracea* complex is distinguished by the lighter pigmented spore deposits (ochraceous) and spore walls that fail to revive (appearing collapsed) for some spores in microscopic mounts. Species in this group generally do not produce an annulus. The only brick-red species of *Tubaria* we suspect to belong outside the *Confragosae* is *T. pallescens* Peck, originally described from southern California (Peck 1895) (see comments under *T. punicea* and *T. vinicolor* below).

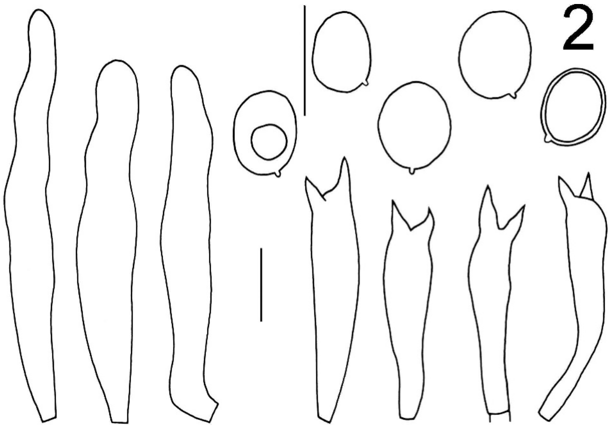

FIG. 2. *Tubaria bispora*, spores, basidia and cheilocystidia from MAN 45 (isotype). Bar = 10 µm.

Smith and Hesler (1968) considered two additional species, *Pholiota anomala* Peck and *P. canescens* A.H. Sm. & Hesler, as members of section *Confragosae* and reported each having spores with a minute germ pore. This character is reported for a few species of *Flammulaster* (Vellinga 1986), but none of the species of the *Confragosae* and other typical species of *Tubaria* we examined possess a germ pore. Nevertheless if *P. canescens* A.H. Sm. & Hesler (non-Peck) proves to be an autonomous species of *Tubaria* a new name will be required because *Tubaria canescens* Peck (see Murrill 1917) has nomenclatural priority. *Tubaria strophosa* Singer (Singer 1969) is a temperate southern hemisphere species from *Nothofagus* forests that might belong to the *Confragosae* by virtue of the presence of an annulus and brown spores. In total Singer (1986) admitted 14 species in sect. *Confragosi* (in his concept of the genus *Phaeomarasmius*). Thus sect. *Confragosae* (*Tubaria*) might contain up to as many as 20 species worldwide.

Tubaria bispora Matheny, P.-A. Moreau, Neves, et Vellinga, sp. nov. FIGS. 2, 9, 10

Pileus 0.5–1.5 cm latus, convexus, glaber, ad marginem striatus, rubrobrunneus, hygrophanus, odor mitis. Lamellae adnatae vel uncinatae, subdistantes, cinnamomeae vel rubrobrunneae. Stipes 1.0–2.0 cm longus, 1 mm crassus, aequalis, ad basim albo-tomentosus, fistulosus; velum partiale infra-apicale, ad stipitem in annulum cortinaforme. Sporae 7.0–9.0 × 5.5–6.0 µm, ellipticae, laeves. Basidia bisporigera. Cheilocystidia praesentia. Hyphae fibulatae. In ligno carioso vel ad terram in sylvis humidis. Holotypus hic designatus *MAN 45* USJ, isotypus NY.

Pileus 0.5–1.5 cm diam, hemispherical to convex, margin recurved to slightly so in age, disk flattened or sometimes depressed, smooth or minutely furfurafceous under a hand lens, (faintly) striate one-third to one-half to center; dark rusty brown with slight purplish tone when moist becoming reddish brown (8D6), hygrophanous, first fading at the center (8A3), elsewhere fading to pale cinnamon buff when dry (7A3-8A3); marginal veil fibrillose, discontinuous, light ochraceous; odor mild, taste fungoid; tissues exuding no pigments in 3% KOH solution. *Lamellae* adnate-subdecurrent to uncinate, subdistant to distant (12 L with several tiers of lamellulae), cinnamon to reddish brown (7D6); edges fimbriate under a lens. *Stipe* 1.0–2.0 cm × 1 mm, equal; surface longitudinally silky-striate, dark rusty brown when moist to shiny reddish brown (8D6) but concolorous with the pileus, with a delicate ochraceous cortinate ring on all basidiomes observed, densely pruinose at extreme apex, base with white mycelium at attachment with substrate, elsewhere somewhat fibrillose becoming smooth below; hollow. *Basidiospores* in side view 7.0–9.0 × 5.5–6.0 µm, a few 10.0 × 7.5 µm from hymenium, on average 7.6 × 5.9 µm, Q = 1.2–1.4, on average 1.3, slightly wider in frontal view smooth, elliptic to broadly elliptic or occasionally subphaseoliform, smooth, apices rounded, apiculus indistinct, wall slightly thickened, generally not collapsing in alkali mounts, brownish yellow to yellowish, germ pore absent, often with one or two guttules. *Basidia* 25–30 × 5–7 µm, 2-sterigmate, occasionally 1-sterigmate, with long straight sterigmata 5–9 µm long, subclavate, hyaline. *Pleurocystidia* none. *Cheilocystidia* in clusters on lamella edge, many 25–45 × 7–9 µm, but some up to 85 µm long, narrowly fusiform to cylindric with obtuse to swollen apices, at times subclavate, thin-walled or slightly thickened, hyaline. *Lamellar trama* regular, hyphae cylindric, generally 5–12 µm diam, weakly incrusted, yellowish brown in mass. *Pileipellis* a discontinuous trichoderm of numerous upright terminal elements, these composed of chains of cells 30–60 × 15–25 µm, elsewhere a cutis of prostrate cylindric hyphae mostly 7–15 µm diam, incrusted to coarsely so, walls slightly thickened, ‘‘Ochraceous-Tawny’’ in mass. *Stipitipellis* with few terminal cells similar to cheilocystidia at the extreme apex. *Clamps* present.

Habitat and distribution. Growing on wood in montane neotropical forest of *Quercus insignis* Martens & Galeotti, Costa Rica, also on soil along path rich in dead and decaying roots in mesophilic tropical forest, Martinique.

Specimens examined. COSTA RICA. Puntarenas Coto Brus, Zona Protectoroa Las Tablas. Sitio Tinieblas. 1450 m elev, N8°54′, W82°46′, 11 Jun 2004, leg. *M.A Neves, MAN 45* (HOLOTYPE, USJ; ISOTYPE, NY). MARTINIQUE. Case Pilote, arête Jean-Louis, 21 Aug 2005, leg. C. Lécuru and P.A. Moreau, *PAM-Mart55* (LIP; CUW).

Commentary. The combination of bisporic basidia, small basidiomes, dark reddish brown (when moist), presence of a cortinate annular zone and tropical distribution support the autonomy of *T. bispora.* Two isolates, one from montane *Quercus* forests in Costa Rica and a second from mesophilic tropical forest in the Lesser Antilles, share almost identical 25S and ITS sequences. No species of *Tubaria* were recorded previously in floristic treatments of Agaricales and other fungi in the Lesser Antilles (Pegler 1983, Courtecuisse 2006), and no descriptive information is provided for unclarified *Tubaria* spp. in a checklist of Caribbean fungi by Minter et al (2001).

Phylogenetic analyses suggest *T. bispora* is most closely related to the north temperate *T. confragosa* (FIG. 1), which has a well developed annulus, flocculose pileal surface and tetrasporic basidia. *Tubaria confragosula* (Singer) Contu, described from subtropical Argentina, appears similar to *T. bispora.* It is reported to bear both tetra- and bisporic basidia, with the larger spores produced by bisporic basidia, and a pileipellis as ‘‘ex hyphis trichodermii palisadici’’ becoming a cutis with age. Contu’s interpretation of this species (Contu 2000) collected on introduced *Eucalyptus* from Sardinia is not entirely consistent with Singer’s protolog (Singer 1953). A comparison between *T. confragosula sensu* Contu and the type of *Phaeomarasmius confragosulus* Singer requires attention.

Tubaria confragosa (Fr.) Harmaja, Karstenia 18:55. 1978. FIG. 3

≡ *Agaricus confragosus* Fr., Epicr. Syst. Myc.: 169. 1838.

≡ *Pholiota confragosa* (Fr.) P. Karst., Hattsvampar Bidr. Finlands Natur och Folk: 304. 1879.

≡ *Fulvidula confragosa* (Fr.) Singer, Rev. Mycol. 2:239. 1937.

≡ *Naucoria confragosa* (Fr.) Singer, Not. Syst. Sect. crypt. Inst. bot. Acad. Sci. U.S.S.R. 5 (‘1941’):94. 1945.

≡ *Phaeomarasmius confragosus* (Fr.) Singer, Lilloa 22:577. (‘1949’) 1951.

≡ *Tubaria confragosa* (Fr.) Kühner, Trav. Labor. La Jaysinia Samoëns 3:67. 1969 (Inval. Art. 33.3).

Pileus 3.0–6.0 cm, broadly convex to plano-convex with flattened disk, margin decurved; surface dry, not striate, flocculose or furfuraceous, margin with sparse

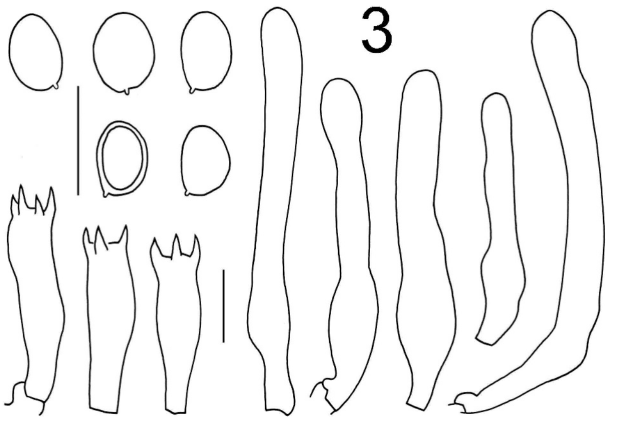

FIG. 3. *Tubaria confragosa*, spores, basidia, and cheilocystidia from PBM 2105. Bar = 10 μm.

remnants of membranous veil; reddish brown (5YR 4/3 or Rood's Brown) when moist, hygrophanous, fading at the center first, becoming pale brown (10YR 7/4 or Cinnamon-Buff), disk fading to pinkish-cinnamon, the tiny scales not white but pale brown or pinkish-cinnamon to cinnamon-buff; odor strong, like *Suillus*, flavor similar to odor, context pinkish cinnamon or pallid with pinkish tinges when faded, firm, not changing where cut or bruised; flesh negative with PDAB, slowly green in tincture of guaiac. *Lamellae* adnate, close, 35–44 L with numerous lamellulae, Hazel (5YR 4/6 or 7E8) or rusty cinnamon; edges faintly pallid and obscurely fimbriate, concolorous with faces in age; even, medium breadth to somewhat narrow, 3–4 mm broad. *Stipe* 4.0–7.5 cm × 4–6 mm, even, straight or flexuous, tough, fibrous like *Laccaria*, not fragile; veil forming a superior membranous annulus that is easily removed, in age remnants of veil may be sparse; surface fibrillose to coarsely fibrillose, with a thin pallid fibrillose superficial layer; light reddish brown (5YR 6/3-6/4-5/3 or Light Vinaceous-Cinnamon to Mikado Brown) throughout except for the white base, not at all pruinose; hollow. *Basidiospores* in side view 6.0–7.5 × 4.5–5.0 μm, on average 6.6–6.7 × 4.5 μm, Q = 1.3–1.7, on average 1.45–1.5, slightly wider in frontal view smooth, elliptic to oblong, smooth, thick-walled, Ochraceous-Tawny or rusty to cinnamon-brown (darker than *T. furfuracea* complex), unreactive in Melzer's; germ pore absent; spore deposit brown (Buckthorn Brown to Cinnamon-Brown or 10YR 5/8). *Basidia* 24–30 × 5–6 μm, 4-spored, cylindric, hyaline. *Pleurocystidia* none. *Cheilocystidia* in clusters on lamella edge, 38–70 × 4–8 μm, cylindric with swollen, obtuse, or less often indistinctly subcapitate apices, thin-walled or at times slightly thickened, hyaline. *Lamellar trama* regular, tawny cinnamon in mass, hyphae mostly 5–13 μm diam, cylindric to inflated. *Pileipellis* composed of trichodermial tufts of thin- to thick-walled hyphae, these incrusted with pigment, 8–25 μm diam, end cells undifferentiated. *Stipitipellis* composed of cylindric hyphae, mostly 5–10 μm diam, yellowish brown in mass, extreme apex with (sub)cylindric terminal cystidioid cells, at times flexuous, these slightly thick-walled or thin-walled. *Clamps* present.

Habitat. In northern Europe reported on dead deciduous wood, primarily of *Betula* and *Populus* and less frequently on *Alnus* and *Fagus* (Moser 1983). In North America on hardwood and conifer logs (Smith and Hesler 1968) ranging from east coast to west coast and as far south as North Carolina.

Specimens examined. USA. WASHINGTON: Kitsap County, Seabeck, along Hood Canal, on moss covered rotten hardwood (probably *Alnus*), 10 Jun 2001, leg. *S. Clark, PBM 2105* (WTU). Olympic National Park, Whiskey Bend Trail, on wood and needles of *Pseudotsuga*, 17 Jun 1999, leg. *C. Ammirati, MTS 4646* (WTU).

Comments. Sequence analysis supports the morphological findings of Kühner (1969) and Harmaja (1978), who placed *Phaeomarasmius confragosus* in *Tubaria*. *Tubaria confragosa* appears most closely related to *T. bispora* from Central America and the Caribbean. In our judgment the description of *Pholiota canescens* (Smith and Hesler 1968) is similar to *T. confragosa* except for the spores with a small germ pore. Excellent photos of North American *T. confragosa* can be found in Bessette, Bessette, Fischer (1997) and Lincoff (1981). The combination of the overall pinkish cinnamon coloration, well developed membranous annulus, and typically flocculose pileal surface easily distinguish the species morphologically. One European isolate differs from two western North American isolates by five 25S nucleotide positions and 12 ITS nucleotide positions.

Tubaria punicea (A.H. Sm. & Hesler) Ammirati, Matheny, et P.-A. Moreau, comb. nov. FIGS. 4, 11, 12
Basionym: *Pholiota punicea* A.H. Sm. & Hesler, North Am. Species of *Pholiota*: 40. 1968.

Pileus 1.0–5.0 cm diam, hemispheric-convex when young to convex, expanding with age to plano-convex, disk at times with a low, obtuse umbo, margin decurved, occasionally irregular or wavy when in small clusters, surface dry but shiny, translucent-striate at the margin, when young covered by a silky white veil, later finely fibrillose to smooth, wine-red (vinaceous) to blood-red but shading a lighter tone toward the margin; context reddish brown, odor not remarkable. *Lamellae* adnate to slightly decurrent, moderately close, deep vinaceous when young, brown with vinaceous tinge in age, broad. *Stipe* 2.0–9.0 cm × 2.5–6.0 mm, central, terete to compressed, at times

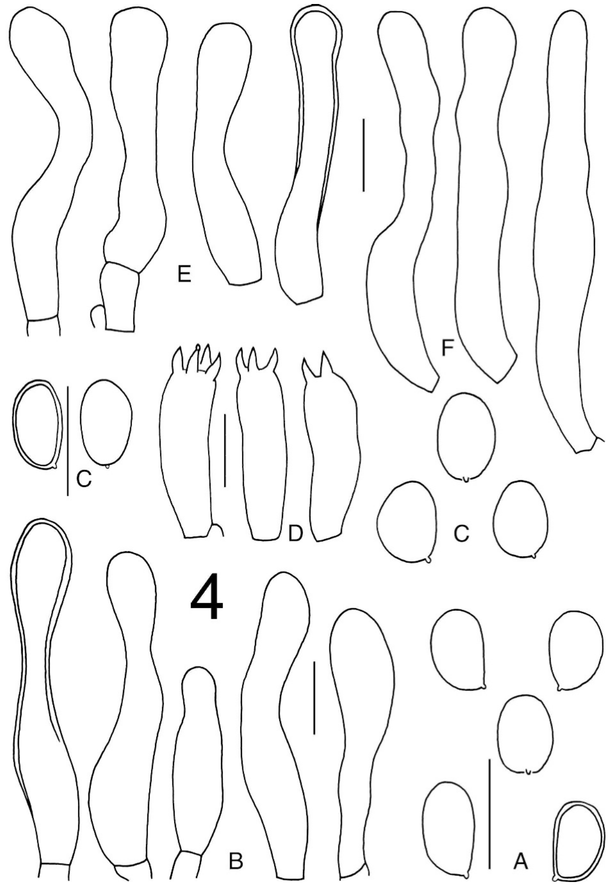

FIG. 4. *Tubaria punicea*, spores, basidia and cheilocystidia. (A) and (B) from Smith 8507 (holotype); (C), (D) and (E) from ECV 3160; (F) from OC2. Bar = 10 μm.

slightly enlarged toward the base, covered with silky white veil when young, fibrillose to coarsely fibrillose or twisted-fibrillose with striate appearance by maturity, wine-red, base white. *Spore print* cinnamon brown. *Basidiospores* in side view (6.5)7.0–9.0(9.5) × 4.0–5.5 μm, at times 9.0–10.0 × 5.0–6.0 μm, on average 7.2–7.8 × 4.6–5.1 μm, Q = 1.26–1.84, on average 1.45–1.6, slightly wider in frontal view, somewhat phaseoliform to elliptic or even oblong in side view, elliptic to ovate in face view, smooth; wall thick-walled, no apical pore visible; rusty cinnamon in KOH, dingy ochraceous in Melzer's reagent (paler), apiculus indistinct. *Basidia* 26–30 × 5–9 μm (2-) and 4-spored, narrowly clavate to subcylindric, the hymenium pale dull cinnamon as revived in KOH, many basidia with hyaline refractive content of amorphous material variously disposed, in Melzer's reagent yellowish. *Pleurocystidia* present only as scattered pseudocystidia in the hymenium, 20–33 × 3–5 μm, crooked, contents dark cinnamon in KOH. *Cheilocystidia* in clusters on lamella edge, (25)30–65(80) × 4–12(16) μm, versiform, short clavate to ovate, 15–30 × 7–10 μm, with the wall slightly to distinctly thickened and pale cinnamon in KOH, ventricose at the base (6–8 μm) with a long, narrow flexuous neck and subacute apex, utriform to dumbbell shaped with the enlarged apex as broad as the ventricose portion and rarely with a secondary septum in the constriction. *Lamellar trama* of parallel to somewhat interwoven, nongelatinous hyphae with dull cinnamon to ochraceous often asperulate walls (as revived in KOH), cells inflating to 12–15 μm in the central portion and short; subhymenium of small somewhat thick-walled cells rusty brown in KOH, not gelatinous. *Pileipellis* a cutis of appressed nongelatinous hyphae 4–10 μm diam, walls dull rusty cinnamon in KOH and often roughened with incrusting material, tramal hyphae pale cinnamon in KOH, walls slightly incrusted to smooth, cells inflated to 15 μm more or less, interwoven; all hyphae inamyloid or weakly dextrinoid. *Stipitipellis* with caulocystidia clavate to irregularly ventricose, 40–80 × 5–11 μm, walls thickened (at times irregularly) and hyaline to yellowish in KOH. *Clamps* present.

Habitat and distribution. on rotten wood or base of *Arbutus* (Pacific Madrone, Ericaceae) typically in hollowed bases of large trees, sometimes damaged by fire, in mixed forest of *Pseudotsuga*, *Arbutus* or *Quercus*; distributed along coastal areas of British Columbia south to Marin County, California, possibly more widespread. The type was collected from a burned stump at the California-Oregon state line.

Specimens examined. CANADA. BRITISH COLUMBIA: (All Canadian materials are split between the personal herbarium of O. Ceska and CUW). Vancouver Island, Miniskirt Mountain, near Victoria, N48°27.794′, W123°31.211′, 18 Dec 2005, leg. *O.* and *A. Ceska*, *OC1*, *OC2*. Vancouver Island, Mary Hill, DND property off Williams Head Road, Metchosin, N48°20.931′, W123°32.650′ and N48°28.894′, W123°32.771′, 21 Dec 2005, leg. *O.* and *A. Ceska*, *OC3*, *OC4*. Vancouver Island, Albert Head, DND property, Metchosin, N48°23.341′, W123°28.735′, 23 Dec 2005, leg. *O.* and *A. Ceska*, *OC5*. Vancouver Island, Heals Rifle Range, DND property, Saanich, Victoria, N48°32.938′, W123°28.109′, 24 Dec 2005, leg. *O.* and *A. Ceska*, *OC6*, N48°32.979′, W123°28.135′, *OC7*. Vancouver Island, Cobble Hill near Shawnigan Lake, N48°40.897′, W123°37.918′, 25 Dec 2005, leg. *O.* and *A. Ceska*, *OC8* and *OC9*. Vancouver Island, Observatory Hill, Saanich, Victoria, N48°31.280′, W123°25.228′, 26 Dec 2005, leg. *O.* and *A. Ceska*, *OC10* & *OC11*. Vancouver Island, Yew Point, Esquimalt Lagoon, Victoria, DND property, N48°26.292′, W123°27.062′, 27 Dec 2005, leg. *O.* and *A. Ceska*, *OC12*. UNITED STATES. CALIFORNIA: Marin County, Mount Tamalpais, along Trucker Trail and on the shady side of Bon Tempe Lake, 3 Mar 2003, leg. *E.C. Vellinga*, *ECV 3160* (UC). San Mateo County, Hubbard Park, 1 Dec 2006, collected for MSSF Fungus Fair, *ECV 3522* (UC). San Francisco Watershed, 1 Dec 2006, collected for MSSF Fungus Fair, *ECV 3523* (UC).

OREGON. California-Oregon state line, 6 Nov 1937, *Smith 8507* (HOLOTYPE, MICH).

Comments. The gross morphological description is based on material from British Columbia and merged with minor details from Smith and Hesler (1968). The microscopic description of Smith and Hesler (1968) is consistent with our examination of the type and reproduced here after some reformatting. It is apparent however that Smith did not fully document the type collection. Only brief notes occur on the label, which indicate blood red in all parts with a white fibrillose zone on the stipe. Our study of the holotype does not disagree much with the original description. Basidia are 1-, 2- and 4-sterigmate, which probably accounts for a larger range in spore size. Whether *P. punicea* is the same as *N. vinicolor* is unclear based on the types.

We initially designated vinaceous tubarioid collections from British Columbia, Washington and California as *Naucoria vinciolor* Peck (see below). However analysis of sequence data (FIG. 1) confirms two separate clades, one of which is ruderal in its distribution (occurring in landscaped areas with introduced vegetation) the other specific to mature (sometimes burned) bases of *Arbutus* in natural habitats. To distinguish the two clades we apply the name *Tubaria punicea* to the species that occurs on *Arbutus*. The original habitat description of *P. punicea* is more consistent with our application of the name than to the ruderal clade.

In his *Tubaria* monograph Murrill (1917) makes reference to the brick-red *T. pallescens* Peck (Peck 1895). We examined the type of *T. pallescens* (NYS) but conclude it may be more closely related to the *T. furfuracea* complex given the pale brown spores, many of which are collapsed. The stipe of *T. pallescens* is also described as yellowish, not red.

It might appear that the citation of 12 collections from British Columbia would indicate *T. punicea* is common, but this is not the case. For example, at the Cobble Hill site, more than 100 mature trees were examined before two trees were found with the fungus. Other localities were comparable to Cobble Hill. No materials of *T. punicea* and *Naucoria vinicolor* have been deposited at SFSU or WTU before this study, which further supports their rare status.

Collections OC6 and OC4 demonstrate length heterogeneity in the second spacer (ITS2). Both sequences share the same nucleotide polymorphic insertion/deletion (indel) event (James et al 2001).

Tubaria rufofulva (Cleland) D.A. Reid & E. Horak, Austral. J. Bot., Supp. Ser. 10:29. 1983. FIGS. 5, 14
Basionym: *Pholiota rufofulva* Cleland, Trans. Proc. R. Soc. S. Austr. 51:303. 1927.

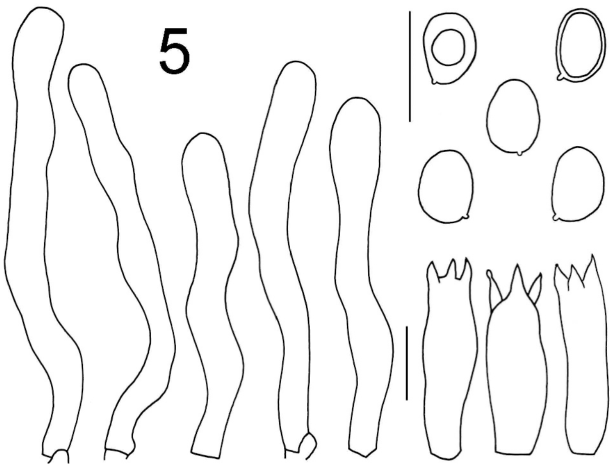

FIG. 5. *Tubaria rufofulva*, spores, basidia and cheilocystidia from PBM 2191. Bar = 10 μm.

Pileus 1.0–3.0 cm diam, convex expanding to plane, margin incurved in youth, decurved and arched in age, center depressed when mature, without umbo; surface dry, at center minutely scaly and with a hoary pubescence toward the margin, later glabrescent; margin entire but may be faintly translucent-striate in age; color maroon or Hessian Brown, Claret Brown or near Liver Brown, hygrophanous and fading to Pecan Brown or Vinaceous-Tawny; context pallid with faint rose tint, up to 2 mm thick under the disk; odor not remarkable; brown on surface with 3% KOH. *Lamellae* adnate to short decurrent, moderately close to subdistant, up to 24 L, with several tiers of lamellulae, weak red (10R 4/3-4/4) when young, dusky red (10R 3/4) in age or Hay's Russett to Chestnut or Mahogany Red, edges faintly pallid-fimbriate, up to 4 mm broad. *Stipe* 1.5–3.5 cm × 2–3 mm at apex, gradually enlarged at base up to 5 mm, cylindric, with a weakly membranous partial veil tinged rose, surface silky-fibrillose, veil rupturing to leave a cortinate ring-zone near apex; color Onion-Skin Pink to Testaceous above, deep reddish brown or Liver Brown or Hessian Brown in age, with a distinct vinaceous brown tone; context stuffed, becoming hollow, colored similarly as the surface. *Spore deposit* yellowish brown (10YR 4/4-5/4, like *Inocybe* and *T. confragosa*). *Basidiospores* in side view 5.5–7.5(8.0) × 4.0–5.0(5.5) μm or 7.0–9.5 × 4.5–6.0 μm (depending on collection), on average 6.7–7.3 × 4.3–5.0 μm or 8.0–8.0 × 4.9–5.5 μm, elliptic, less often subphaseoliform, in frontal view slightly wider and elliptic to obovoid, smooth, wall slightly thickened, apiculus indistinct, germ pore absent, yellowish brown. *Basidia* 24–26 × 6–7 μm, 4-sterigmate, subclavate. *Pleurocystidia* none. *Cheilocystidia* in clusters on lamella edge, 38–57 × 5–10 μm, cylindric or irregularly so with obtuse to swollen apices, hyaline, thin-walled. *Lamellar trama* regular, brownish yellow in mass, hyphae cylindric, about 5–10 μm diam. *Pileipellis* composed of trichodermially arranged hyphae, cylindric to inflated, up to 20 μm diam, mostly thin-walled but some with walls up to 1.0 μm thick, hyphae incrusted and containing pigment, apricot brown in mass, end cells not differentiated, tramal hyphae hyaline. *Stipitipellis* composed of cylindric brownish yellow hyphae in mass in KOH, caulocystidia not observed. *Clamps* present.

Habitat and distribution. On woody debris and logs in Karri (*Eucalyptus diversicolor*) forest in Western Australia; on sandy soil and at the base of *Eucalyptus* in South Australia (Cleland 1934). Also reported on *Nothofagus* from New Zealand and Papua New Guinea (Horak 1983).

Specimens examined. AUSTRALIA. SOUTH AUSTRALIA. Burnside, AD 9930, 25 Jul 1925 (HOLOTYPE, AD). Kinchina, 8 Jun 1925, AD 9928. Para Wirra Cons. Park, 25 Jul 1999, *AD-C 52053/PSC 319.* Flinders Case National Park, 28 Jun 2004, *AD-C 49169/PSC 1924.* Murray Danggali Cons. Park, *AD-C 52052/PSC 890.* WESTERN AUSTRALIA. Near Manjimup, Pine Creek Road, 13 Jun 1985, *ZT 2641* (ZT). Kellerberrin in dry open woodland, 20 Jul 1995, *E5557* (PERTH). Denmark, in wet tall, forest, illustrated in Bougher and Syme (1998), 22 May 1995, *E5662* (PERTH). Pemberton, in wet tall forest, 19 Aug 2001, E7038/PBM 2191 (PERTH, WTU).

Comments. The maroon color of *T. rufofulva*, also illustrated in Bougher & Syme (1998), distinguishes it from the more common *T. serrulata* (described below), at least in Western Australia (see FIGS. 13, 14). This difference also is supported by rRNA sequences (FIG. 1). Pinkish tinges characteristic of the annulus and stipe in *T. rufofulva* are not evident in *T. serrulata.* Cleland (1933) cited colors such as brown, tawny and buff in his original description of *Pholiota serrulata.* For *T. rufofulva* (as *P. rufo-fulva*) Cleland (1927) described the colors as Pecan Brown, Russet, Tawny when old, and dark maroon-brown when moist. For these reasons *T. rufofulva* and *T. serrulata* should not be considered synonyms of each other as done by Grgurinovic (1997).

Pholiota imperfecta Cleland also was listed as a synonym of *T. rufofulva* in Grgurinovic (1997). It originally was described by Cleland (1933) with smaller basidiomes and differently shaped spores (oblique vs. elliptic) compared to *P. serrulata.* However Cleland's protocol describes the pileus of *P. imperfecta* as ''ceraceo-flavo-brunneus'', the stipe as ''pallidus vel rufo-brunneus'', and the annulus as ''albidus''. Because no vinaceous or maroon colors are mentioned in the protolog, it is doubtful *P. imperfecta* represents *T. rufofulva.* However none of the collections of *P. imperfecta* at AD provide a clear picture of what species this name represents. All collections are in poor condition and of variable identity. For example AD-C 22420, which is labeled on the voucher packet as ''Type of *P. imperfecta*'', consists mainly of an *Inocybe* species with metuloid cystidia. AD-C 22421 is labeled on the voucher packet as ''Co-type (of *P. imperfecta*)'' and contains probably a *Galerina* species (spores with a distinct plage). AD 9920, AD 9921, AD 9922 and AD 9923, listed as syntypes of *P. imperfecta* by Grgurinovic (1997), are determined as matching *T. rufofulva,* except for AD 9923, which matches *T. serrulata.* Because of these ambiguities we consider *P. imperfecta* a taxon of doubtful interpretation.

Accessions of *T. rufofulva* fall into two spore-group categories. One group (including the type) has larger spores on average (8.0–8.9 × 4.9–5.5 μm) than a second group (including *PBM 2191*), which on average has smaller spores (6.7–7.3 × 4.3–5.0 μm). We have not studied material for *OKM 24681*, for which an autonomous 25S rRNA branch is shown (FIG. 1). The two spore groups of *T. rufofulva* do not appear to have any other consistent morphological differences, and there is no apparent geographical pattern distinguishing the groups. The significance of the two spore groups is unknown at this time.

Notes of material collected in Papua New Guinea cited in Horak (1983) indicate basidiomes of a smaller stature with a veil that is fragmentary or lacking and occurrence on decaying wood of *Nothofagus.* The spore size for this group is consistent with the smaller spore size of the second group referred to above.

Tubaria serrulata (Cleland) Bougher et Matheny, comb. nov. FIGS. 6, 7, 13

Basionym: *Pholiota serrulata* Cleland, Trans. Roy. Soc. South Australia 57:190. 1933.

Pileus 10–45 mm diam, hemispherical in button stage, becoming convex or plano-covex or shallowly depressed in age, disk at times umbilicate; margin incurved when young, decurved in later stages or finally uplifted and undulating, translucent-striate one-quarter to one-third to center when fresh; surface glabrous (glistening under lens), waxy-looking when fresh, not viscid, at times minutely furfuraceous when specimens have faded in color; dark reddish brown (like young *Laccaria lateritia*) (5YR 3/4, 6E7-8E8, Auburn to Argus Brown), a lighter shade toward the margin that is strong brown or yellowish brown (7.5YR 5/6) between striations, strongly hygrophanous from center outward and eventually entirely yellowish brown to pale brown (10YR 7/4 or 5A4); context watery brown to pallid, hygrophanous, 1–2 mm thick, odor not remarkable. *Lamellae* adnate to

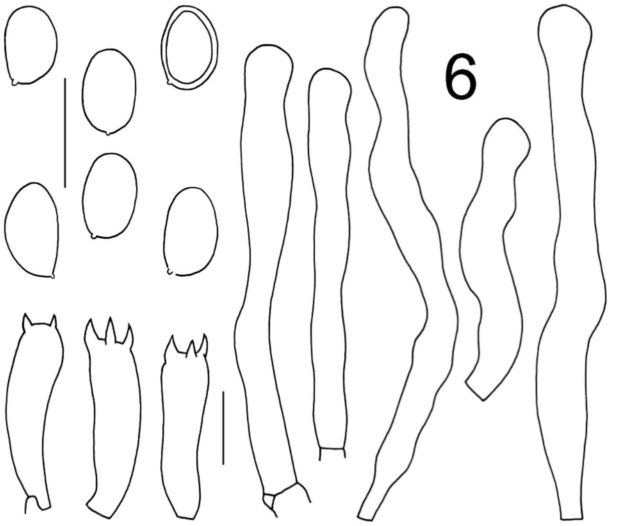

FIG. 6. *Tubaria serrulata*, spores, basidia and cheilocystidia from PBM 2161. Bar = 10 µm.

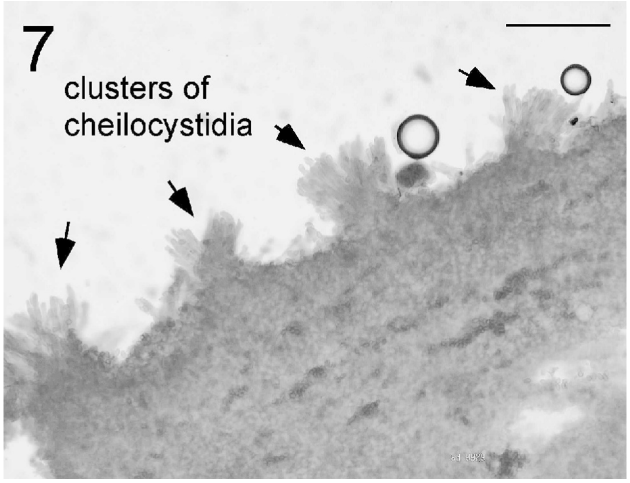

FIG. 7. Lamella edge of *Tubaria serrulata*, AD 9929 (lectotype), showing clustered cheilocystidia. Bar = 50 µm.

uncinate, moderately close, 22–30 L, with lamellulae of varying lengths, pale brown when young to strong brown in age (7.5YR 5/6, Sudan Brown to Antique Brown, 6D8-7D8), ventricose, up to 5 mm broad; edges pallid-fimbriate or crenulate to serrulate under hand lens, hygrophanous. *Stipe* 3.0–5.0 cm × 2–5 mm, cylindrical or slightly tapered toward apex, at times compressed, with a distinct superior pallid peronate-type annulus or ring-zone (fibrils of stipe funnel upward and outward to form annulus); surface dry, with a longitudinally silky-fibrillose superficial layer above and below annulus, fibrils easily removed; pallid above due to densely aggregated superficial layer, otherwise colored like the pileus throughout, occasionally dark brown (7.5YR 4/4) below the annulus; basal mycelium white but not conspicuous; context stuffed becoming hollow, concolorous with surface. *Spore deposit* yellowish brown (7.5YR 5/4, 5C6, or Tawny-Olive). *Basidiospores* in side view (6.3)6.6–8.5(8.9) × (3.6)4.0–5.0(5.5) µm, on average 7.1–8.0 × 4.2–4.8 µm, elliptic and oblong, with flattened adaxial side, in frontal view elliptic to obovoid, smooth, brownish in KOH, wall slightly thickened, apiculus not distinct. *Basidia* 27–30 × 6–7 µm, 4-sterigmate, rarely 2-sterigmate, (sub)clavate, hyaline. *Pleurocystidia* none. *Cheilocystidia* in clusters on lamella edge, 36–66 × 6–11 µm, cylindric and elongated, usually flexuous, apices obtuse to swollen but not capitate, thin-walled, hyaline. *Lamellar trama* regular, hyphae pale brownish yellow in mass, cylindric, 5–13 µm diam. *Pileipellis* an interwoven cutis of cylindric hyphae, these 5–13 µm diam, distinctly incrusted with pigment, ochraceous brown in mass, thin-walled. *Stipitipellis* composed of cylindric hyphae, no caulocystididia observed above insertion of the annulus. *Clamps* present.

Habitat and distribution. On ground on woody debris including buried remnants of *Banksia* cones in urban bushland. The type is recorded on ground from Mount Lofty, South Australia. Known from temperate Western Australia, South Australia and Victoria.

Specimens examined. AUSTRALIA. SOUTH AUSTRALIA: Belair National Park, 12 Apr 1917, *AD 9917* (AD); Belair National Park, 19 May 1925, *AD 9918* (AD); Belair National Park, 16 May 1931, *AD 9919* (AD); Mount Lofty, 29 Apr 1921, *AD 9924* (AD); Mount Lofty, 25 Apr 1924, *AD 9925* (AD); Mylor, 16 May 1925, *AD 9929* (LECTOTYPE here designated, AD); Encounter Bay, 9 May 1926, labeled ''co-type'', *AD 9931* (AD). WESTERN AUSTRALIA: Walpole, in wet tall forest, *E4637* (PERTH); Kellerberrin, dry open woodland, *E5382* (PERTH); Plavins Forest Block, east of Dwellingup, in Jarraah (*Eucalyptus marginata*) forest, 9 Jul 1996, *E5631* (PERTH); Kings Park, Perth, under *Allocasuarina* sp., 2 Jun 1997, *E5837* (PERTH); Dwellingup, in Jarrah forest, 28 Jul 1997, *E5928* (PERTH); Valema Farm, Corrigin, in *Eucalyptus loxophleba* woodland, 19 Jul 2000, *E6633* (PERTH); Corner of Ludlow and Hithergreen Road, 15 km northeast of Busselton, under *Eucalyptus gomphocephala*, *E. marginata* and *Agonis flexuosa*, 26 Jun 2001,*E6798* (PERTH); Perth, Warwick Open Space, 1 Jul 2001, *PBM 2142* (*E6899*) (WTU, PERTH); Brookton Highway, south of Perth, near Epacridaceae on granite outcrop, 3 Jul 2001, *PBM 2149* (*E6931*); Perth, Shenton Bushland, 22 Jul 2001, *PBM 2160* (*E7008*) (WTU, PERTH); same locality as above, *PBM 2161* (*E7009*) (WTU, PERTH); Kensington, Perth, urban bushland, under mixed planted eucalypts and other Myrtaceae, 13 Jul 2004, *E8069* (PERTH); Bold Park, Perth, in Jarrah woodland, 14 Jul 2004, *E8071* (PERTH); Bold Park, Perth, under Marri (*Eucalyptus calophylla*), 14 Jul 2005, *E8209* (PERTH). VICTORIA: Snowy River National Park, 29 Apr 1995, *E5270* (PERTH).

Comments. We apply the name *Pholiota serrulata* to material collected in Western Australia and Victoria after comparison with type materials of this species at AD. Grgurinovic (1997) treated *P. serrulata* as a synonym of *Tubaria rufofulva*, a disposition we do not accept mainly due to the differences in pileal color—reddish brown for *P. serrulata* and maroon for *T. rufofulva*. In the field (FIGS. 13, 14) the colors clearly distinguish the two species, which is also confirmed by rRNA sequences (FIG. 1). Lectotypification of the collection AD 9929 from Mylor, a place name mentioned by Cleland (1933) in his protolog, justifies its selection as lectotype. Other collections cited as syntypes in Grgurinovic (1997) are inappropriate selections because they are from locations other than Mylor, including AD 9919 (from Belair National Park), despite annotations on the voucher packet to the contrary written 27 May 1999.

Tubaria serrulata appears close to *T. confragosa* of the northern hemisphere given the annulus but lacks the flocculose pileus and thick-walled hyphae of the pileipellis of that species and has a differently colored pileus. A striate reddish brown and annulate species, *T. strophosa* Singer (Singer 1969), is recorded from the *Nothofagus* zone in Argentina. Based on the protolog it would appear similar to *T. serrulata*.

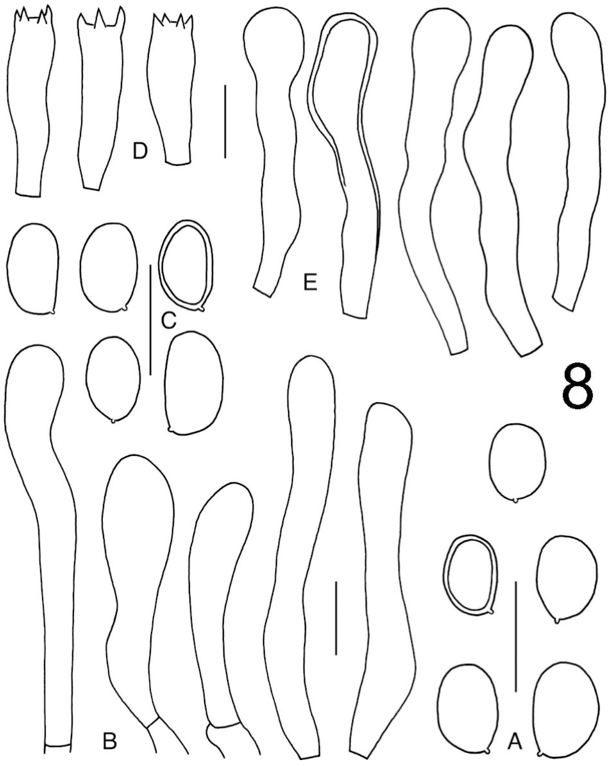

FIG. 8. *Tubaria vinicolor*, spores, basidia and cheilocystidia. (A) and (B) from (holotype, NYS); (C), (D), and (E) from ECV 3340. Bar = 10 µm.

Tubaria vinicolor (Peck) Ammirati, Matheny, et Vellinga, comb. nov. FIGS. 8, 15

Basionym: *Naucoria vinicolor* Peck, Bull. Torrey Bot. Club 36:334. 1909.

Pileus 1.0–5.0 cm expanded, conic-umbonate with incurved edge, then convex umbonate to plano-convex to plano-umbonate or applanate, at times plano-convex wavy with a shallow central depression, margin remaining more or less incurved; moist at first, more or less hygrophanous, margin opaque then somewhat striate, with some velar fibrils near margin; surface at first almost velvety tomentose to matted fibrillose or with small tomentose patches, glabrous and smoother in age, occasionally slightly greasy in appearance, edge sometimes slightly pinkish vinaceous from veil fibrils; color at first evenly rich dark red, almost blackish red to maroon red, dusky red, dark red or brighter red in places (Diamine Red, Hay's Maroon or deeper shades of these colors; 10R3/4-3/6, with some 4/6 mixed in, 2.5YR 5/4 to 2.5YR 3/6), the edge sometimes more Pompeian Red, becoming redder with age, slowly fading on disk to Hay's Russet to reddish Vinaceous Rufous or with orange-brown colors (2.5YR 5/6 to 5YR 6/8) developing in a concentric band 5 mm from margin; context more or less 3 mm thick under the disk, gradually thinner to pileus edge, subfragile, somewhat watery fresh, concolorous with surface, often duller in color; odor and flavor fungoid, mild or astringent. *Lamellae* adnate to subdecurrent or slightly decurrent, segmentiform, close, moderately crowded to subdistant or moderately spaced, up to 6 mm broad, lamellulae in three tiers, (L = 20, l = 3–9) moderately thick, edges white and finely fimbriate, sometimes eroded, faces pink (10 R 6/8) when young, Hay's Russet to light Hay's Russet or darker red and browner (10 R 4/8, 2.5 YR 4/6–8), more or less terracotta or pink orange-brown with brown spores (2.5 YR 4/6) mature. *Stipe* 2.8–7.0 cm × 2.5–5.0 mm at apex, base 5.5–7.0 mm diam, cylindrical to narrowly clavate, straight or flexuous, with a cortinate partial veil; pale pinkish vinaceous to Pale Rhodonite Pink, without annulus, few veil fibrils remaining on mature stipe where veil detaches; surface longitudinally innately fibrillose to slightly striate with vinaceous red and whitish areas, at apex silky white to pale pinkish (2.5YR 5/4), pale pinkish vinaceous to vinaceous pink or dark purple (2.5YR 3/4) below, some areas more reddish from handling, at base sometimes more pallid to watery pinkish, with white mycelium at the base; context more or less hollow, watery testaceous (dull reddish vinaceous), in places concolorous with pileus flesh. *Spore deposit* Saccardo's

FIGS. 9–15. Basidiomes of *Tubaria* species. 9. *Tubaria bispora* (MAN 45, holotype, Costa Rica, photo by M.A. Neves). 10. *Tubaria bispora* (PAM-Mart55, Martinique, photo by P.A. Moreau). 11. *Tubaria punicea* (OC 1, British Columbia, photo by A. Ceska). 12. *Tubaria punicea* (OC 2, British Columbia, photo by A. Ceska). 13. *Tubaria serrulata* (E8069, Western Australia, photo by N.L. Bougher). 14. *Tubaria rufofulva* (PBM 2191, Western Australia, photo by P.B. Matheny). 15. *Tubaria vinicolor* (ECV 3340, California, photo by J. Lennie).

Umber (heavy deposits on white paper) to orange-brown (5YR 6/8 to 7.5YR 5/8). *Basidiospores* in side view 7.0–9.0 × 4.0–5.5(6.0) μm, on average 7.6–8.0 × 4.8–5.0 μm, Q = 1.45–1.9, on average 1.6, slightly wider in frontal view, smooth, without apical germ pore, elliptic, some reniform or narrowly elliptic in side view, thick-walled, rarely if ever collapsed, brown to pale yellowish brown (in 3% KOH); apiculus small, usually distinct. *Basidia* 24–30 × 6.5–7.5 μm, 4-spored (rarely 2-spored). *Pleurocystidia* none. *Cheilocystidia* in clusters on lamella edge, 33–52 × 5.5–9.5 μm, irregularly cylindrical, widest at apex, with clamp connection, some with brownish contents. *Lamellar trama* regular, hyphae parallel to interwoven, cylindrical to broadly cylindrical, some more inflated, mostly 3–22 μm diam, thin-walled, or with thickened yellowish, refractive wall, possibly some encrusting material present, colorless, pale yellowish or pale yellowish brown, with scattered oleiferous hyphae filled with yellow-brown pigment (also seen in pileus tissue). *Pileipellis* composed of a well developed, pigmented (light rust brown) surface layer of cylindrical to enlarged more or less radially arranged, interwoven hyphae, hyphae sometimes in small mounds, terminal elements at times somewhat cystidioid, 12–16(–20) μm diam, more or less thick-walled, and/or incrusted; hyphae in subsurface layer and trama, cylindrical to enlarged, more or less radially arranged and interwoven. *Stipitipellis* composed of cylindric hyphae, mostly 5–8 μm diam, brownish yellow to yellowish brown in mass, caulocystidia not observed. *Clamps* present.

Habitat and distribution. Solitary, gregarious or caespitose, in grass covering soil and rotting wood, around stump of *Eriobotrya japonica* (Japanese plum, Rosaceae), producing basidiomes in October in Washington and during December, January and March in California.

Specimens examined. UNITED STATES. CALIFORNIA: Claremont, on open ground, Jan 1909, leg. *C.F. Baker* (HOLOTYPE of *Naucoria vinicolor*, NYS). Alameda County, Berkeley, 861 Keeler Ave, in front garden, growing in several clusters around stump of *Eriobotrya japonica*, 3 Mar 2005, leg. *E.C. Vellinga, ECV 3340* (UC). Berkeley, same locality as previous, 23 Dec 2005, leg. *E.C. Vellinga, ECV 3449* (UC). Berkeley, same locality as previous, 23 Nov 2006, leg. *E.C. Vellinga, ECV 3501* (UC). WASHINGTON. King County, Redmond, Rose Hill, 80th St. and 139th NE, leg. *D. Winkler*, 17 Oct 2003, *JFA 12905* (WTU). Redmond, same collector and locality as previous, 9 Oct 2005, *JFA 13103* (WTU).

Comments. Tubaria vinicolor is a North American vinaceous or wine red species found in ruderal landscapes with introduced vegetation. To date it is known only from the west coast. It appears closely related to two other vinaceous species, *T. punicea*, also from the west coast of North America, and *T. rufofulva*, from temperate Australia (FIG. 1). Arora (1986) reports *Naucoria vinicolor* on *Quercus* in California, as far south as Los Angeles County where it is encountered rarely. However he was not aware of *T. punicea* at the time, with which *T. vinicolor* could be confused. We were unable to study any material produced on *Quercus*. Nevertheless ecology and sequence data appear to readily distinguish *T. vinicolor* from *T. punicea*.

The type (NYS, Peck 1909) contains what appear to be two specimens, the stipes of which are in one piece, but the pilei have been broken into several pieces. One stipe base is attached directly to a piece of wood. The pileipellis structure is difficult to interpret, although it is clearly a cutis. *Naucoria* in its modern sense as *Alnicola* (see Moreau 2005) is not an appropriate generic designation for *N. vinicolor*. Species of *Alnicola* possess verrucose spores and are ectomycorrhizal.

DISCUSSION

This study contributes significantly to the systematics of the genus *Tubaria*. Both Singer (1986) and Kirk et al (2001) recognized about 15 species in the genus, to which we add *T. bispora*, *T. confragosa*, *T. punicea*, *T. rufofulva*, *T. serrulata* and *T. vinicolor*. Of these six species, four have conspicuous vinaceous or maroon basidiomes and three have a membranous annulus or distinct annular cortinate ring-zone. All have spores that are more strongly pigmented and resist collapsing when revived in microscopic mounts compared to members of the *T. furfuracea* complex.

One hundred fourteen records of epithets and infraspecific taxa have been used in *Tubaria*. A small percentage of these records are invariably synonyms (e.g. *T. autochthona* [Berk. & Broome] Sacc. and *T. dispersa* [L. : Fr.] Singer) or represent species now classified in other genera such as *Psilocybe*, *Galerina*, *Phaeogalera*, *Crepidotus* and *Flammulaster*; and many taxa probably fall in the *T. furfuracea* complex. However some species such as *Tubaria ferruginea* Maire ex E. Horak & P.-A. Moreau and *Flammulaster siparia* (Fr. : Fr.) Watling have an ambiguous position by sharing morphological characters of both genera (Vellinga 1986, Horak and Moreau 2005). Yet as we have shown arguably just as many species, if not more, remain poorly known and displaced in other Friesian genera, e.g. *Pholiota s. lat.* (Smith and Hesler 1968), *Naucoria s. lat.* (Moreau 2005), and in a broadly circumscribed but nonmonophyletic *Phaeomarasmius* (Singer 1986). Others have been subsumed under broad morphological species (Grgurinovic 1997) or remain undescribed in areas poorly studied by systematic mycologists (e.g. Australia and the neotropics).

Our results suggest that *Tubaria* is a paraphyletic group (excluding *T. minima*, not shown) in which at least one questionable isolate of *Flammulaster* is derived. However we were able to recover a strongly supported subclade of at least 14 *Tubaria* species, including one possibly mislabeled *Phaeomarasmius* isolate. At this time the most inclusive clade of *Tubaria* is composed of taxa with pileate-stipitate basidiomes, central stipe, a filamentous pileipellis incrusted with pigment, smooth or faintly roughened pale brown, ochraceous or yellowish-brown spores with a thin or thick wall, no germ pore, distinctive cheilocystidia, subdecurrent to adnate lamellae, a partial veil (cortinate or annulate), clamp connections and saprotrophic habit. No cyphelloid taxa have been established unequivocally as related to *Tubaria* based on our phylogenetic analyses. However Bodensteiner et al (2004) recovered *Phaeosolenia* as a sister taxon of one *Tubaria* sequence but with poor support. Several non-European species have been described with verrucose or ornamented spores, but sequence data for most of these are not available (see Aime, Baroni, Miller 2002, who transferred *T. thermophila* to *Crepidotus*).

Several authors have accepted a generic distinction between *Tubaria* and *Flammulaster* Earle and *Phaeomarasmius* Scherffel (Orton 1960, Watling 1967, Horak 1980, Moser 1983, Vellinga 1986, Horak 2005). Phylogenetic analyses of 25S rRNA (Aime, Vilgalys, Miller 2005) and multigene studies (Matheny et al 2006) indicate that exemplars of these genera indeed are closely related. However neither *Flammulaster* nor *Phaeomarasmius* is currently monophyletic (FIG. 1) and Singer (1986) treated them as a single genus under the name *Phaeomarasmius*. A new genus, *Phaeomyces* Horak (Horak 2005), has been described that might be affiliated with these groups as well. *Tubaria* and allies clearly merit more attention to address their generic boundaries and putative relationship to cyphelloid taxa.

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