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Morphological and molecular studies on *Auriculariopsis albomellea* and *Phlebia albida* and a reassessment of *A. ampla*

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Abstract: *Auriculariopsis* (Corticiaceae, Aphyllophorales) consists of two species: *A. albomellea* and *A. ampla,* the generic type. *Auriculariopsis albomellea (= Cytidiella melzeri)* is an uncommon wood decay fungus known from Europe and the United States. Studies of morphological features and analyses of sequence from the internal transcribed spacer region and a portion of the small subunit ribosomal RNA gene indicate that *A. albomellea* is closely related to *Phlebia albida.* Thus, the new combination *P. albomellea* is proposed. Basidioma descriptions and illustrations of *P. albida* and *P. albomellea* are included. In addition, morphological studies and sequence analyses of the internal transcribed spacer region and a part of the 18S rRNA gene suggest that *A. ampla* is *closely* related to *Schizophyllum commune. Auriculariopsis* is placed in synonymy under *Schizophyllum,* and the new combination *S. amplum* is proposed.

Key Words: *Cytidiella,* internal transcribed spacer, *Schizophyllum,* 18S ribosomal gene

INTRODUCTION

Pouzar (1954) created a new, monotypic genus for *Cytidiella melzeri* Pouzar, an unusual and distinctive taxon. Although closely allied to *Auriculariopsis* Maire, another monotypic genus, *Cytidiella* lacks gelatinous hyphal walls that are characteristic of *Auriculariopsis* (Pouzar, 1954). Eriksson and Ryvarden (1975), however, reported that the hyphal walls were somewhat gelatinous in *Cytidiella.* Nevertheless, they maintained *Auriculariopsis* and *Cytidiella* as separate genera, based on differences in context structure and context hyphae. Stalpers (1988) did not consider these differences significant and transferred *C. melzeri* to *Auriculariopsis.* Since *C. melzeri* is a synonym of *Cytidia albomellea* Bondartsev (Parmasto, 1968), the correct name for this taxon is *A. albomellea* (Bondartsev) Kotl. (Kotlaba, 1988).

The placement of *Auriculariopsis* and *Cytidiella* is generally thought to be in the Corticiaceae near *Merulius* and *Phlebia* (Donk, 1959; Parmasto, 1968, 1986; Eriksson and Ryvarden, 1975; Jülich, 1981). Based on cultural features and developmental studies of the hymenophore, Stalpers (1988) concluded that *Auriculariopsis* is closely allied to *Schizophyllum.* In addition, preliminary analysis of sequence data of the internal transcribed spacer (ITS) region of the ribosomal DNA repeat indicates that *A. albomellea* belongs in *Phlebia sensu stricto* and is the sister species to *P. albida* H. Post in Fr. (Nakasone, 1991). Finally, Ginns and Lefebvre (1993), in a synopsis of the corticioid basidiomycetes of North America, included *Auriculariopsis* and *Schizophyllum* in the Schizophyllaceae.

This study was undertaken to resolve the placement of *A. albomellea,* employing morphological and molecular data. *Phlebia albida* and *A. albomellea* were examined morphologically, and the ITS region and a portion of the small subunit ribosomal RNA (18S rRNA) gene were sequenced and analyzed. In addition, the affinity of *A. ampla* (Maire) Lév. to *Schizophyllum commune* Fr.: Fr. was examined using sequence data.

MATERIALS AND METHODS

Morphological studies. — Microscopic examination of basidiomata was made from freehand sections mounted in 2% (w/v) KOH and 1 % (w/v) aqueous phloxine or Melzer's reagent (Hawksworth et al., 1983). Basidiospores were mounted in Melzer's reagent and measured with a 100× objective under oil immersion. Color designations are from Kornerup and Wanscher (1978), and herbarium abbreviations are from Holmgren et al. (1990).

Fungal cultures and outgroup taxa. — Cultures from which DNA was extracted are listed in TABLE I. All cultures are on deposit at the Center for Forest Mycology Research, USDA Forest Service, Forest Products Laboratory.

Ustilago maydis was chosen as the outgroup taxon for the 18S ribosomal region because it is a member

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TABLE I. Fungal strains used in molecular studies

Number	Species Accession number	Host/substrate	Location
1	*Auriculariopsis albomellea* FP 101843	fallen branch of *Pinus resinosa* Laws.	Adams County, Wisconsin, U.S.A
2	*A. albomellea* FP 102339	fallen branch of *Pinus resinosa*	Adams County, Wisconsin, U.S.A.
3	*A. ampla* CBS 182.83	branch of *Populus*	Zeeland, Netherlands
4	*A. ampla* CBS 285.88	*Populus*	Utrecht, Netherlands
5	*Phlebia albida* GB 1833	branch of *Populus*	Lerida, Spain
6	*Phlebia centrifuga* JLL 13795	conifer	Hurkett, Ontario, Canada
7	*P. centrifuga* RLG 7588	*Pinus ponderosa*	Cochise County, Arizona, U.S.A.
8	*P. radiata* JLL 15608	*Acer* sp.	Fayetteville, Arkansas, U.S.A.
9	*Schizophyllum commune* FP 56473	stump of *Carya* sp.	State College, Pennsylvania, U.S.A
10	*S. commune* FP 101971	branches of *Paulownia* sp.	Davis, California, U.S.A.
11	*S. fasciatum* CBS 267.60		Nuevo Leon Prov., Mexico
12	*Panellus pusillus* HHB 9759	*Fagus* sp.	Leon County, Florida U.S.A.
13	*P. pusillus* FP 102581	*Liquidambar* sp.	Jefferson Parish, Louisiana, U.S.A.
14	*P. stypticus* HHB 9493	*Quercus* sp.	Leon County, Florida U.S.A.
15	*P. stypticus* OKM 3787	*Quercus rubra* L.	Laurel, Maryland U.S.A.

of the Ustomycetes, whereas the other taxa are classified in the Basidiomycetes. For the ITS analysis of the *Phlebia* taxa, *P. radiata* was designated the outgroup because it is the type species of the genus. Choosing an outgroup for the ITS analysis of *Schizophyllum* and *Auriculariopsis* was difficult because *Schizaphyllum* appears to have an isolated position in the Basidiomycetes. However, the gill edges of *Panellus stypticus* and *P. pusillus,* characterized by protruding cheilocystidia, were reminiscent of the split gill development in *Schizophyllum,* so *P. stypticus* and *P. pusillus* were chosen as outgroup taxa.

Fungal growth and DNA extraction. — Protocols for growing *Phlebia* mycelia and DNA extraction are described in Nakasone and Sytsma (1993). For the other genera, the protocols were simplified. Macerated cultures were added to 50 mL of sterile 2% malt extract broth and shaken at room temperature for 1 wk. DNA was extracted from lyophilized mycelia but not purified in a cesium chloride gradient.

Amplification and sequencing of DNA segrrwnts. — To amplify the ITS region, which includes the internal transcribed spacers, 5.8S rRNA gene and the flanking 18S and 26S rRNA genes, GeneAmp PCR reagent kit (Perkin-Elmer Cetus, Norwalk, CT) was used, and primers ITS 5 and ITS 4 were used (White et al., 1990). The samples were subjected to 30 cycles of 30 sec at 93 C, 2 min at 53 C, and 2 min at 72 C in a Perkin-Elmer Cetus DNA Thermal Cycler. The NS5-NS6 region of the 18S rRNA gene, bounded by nucleotide positions 1128 to 1435 based on *Saccharomyces cerevisiae,* was amplified by primers NS5 and NS6 or NS8 and SR9R (5'-AGAGGTGAATTCT-3') and NS6 (Elwood et al., 1985; R. Vilgalys, pers. comm.; White et al., 1990). The cycling parameters were similar to those previously described, except that the annealing temperature was set at 43 C. The amplified products were examined on a 2% agarose gel, cleaned with GeneClean (Bio 101, La Jolla, CA), and sequenced directly using a Sequenase 2.0 kit (US Biochemicals, Cleveland, OH), with modifications

described by Baum et al. (1994) and Conti et al. (1993). Double-stranded DNA products were sequenced in both directions using four primers for the ITS regions, ITS 1, ITS 2, ITS 3, and ITS 4, and three primers from the NS5-NS6 region, NS5, NS6, NS5.5R (5'-ATCAATCTGTCAATCCT-3'). Sequencing reactions were separated in acrylamide gels (6% acrylamide; 8 M urea) in Tris-borate-EDTA and 3 M sodium acetate (Sheen and Seed, 1988). Gels were run for 1.5–3 h at 50 W, constant power, dried on a vacuum dryer at 80 C, and exposed to Kodak X-OMAT AR film at room temperature for 1–5 da.

Sequence analysis. — Sequences were entered on MacClade, version 3.1 (Maddison and Maddison, 1992), and manually aligned. ITS sequences of all taxa, except *P. stypticus,* are available from GenBank (L43375–L43385). Sequence alignments are available from the author on request. When there was ambiguity in alignment, the alignment that produced the fewest number of informative characters was preferred. Insertion/deletions (indels) were treated as missing data or as a separate character set (Swofford and Begle, 1993; Baum et al., 1994). PAUP, version 3.1.1 (Swofford, 1993), was employed to obtain baseline maximum parsimony trees with unordered nucleotide data (Fitch, 1971). For tree searches, BANDB (branch and bound) and TBR (tree bisection and reconnection) branch swapping options were selected with ACCTRAN (accelerated transformation) optimization. The consistency index (CI) (Kluge and Farris, 1969) and retention index (RI) (Farris, 1989), excluding uninformative characters, are reported for base-line trees. Branch lengths include autapomorphic characters. The effect of weighting transversions 1.1, 2, and 3 more than transitions were evaluated. Different alignments were analyzed to accommodate ambiguous areas and indels. Support for monophyletic clades were estimated with decay analysis (Bremer, 1988; Donoghue et al., 1992) and bootstrap (Felsenstein, 1985). Although bootstrap (Sanderson, 1989) and decay analysis have limitations, they do give an indication of the relative support for the clades. Bootstrap analyses were implemented using 1000 replicates of heuristic searches.

RESULTS

Sequence analyses of the 18S rRNA gene. — The NS5-NS6 region of the 18S rRNA gene is about 300 base pairs (bp) in *Phlebia* and *A. albomellea* and about 700 bp in *A. ampla, S. commune,* and *Panellus* because of a ~ 400 bp insert (FIG. 1). *Ustilago maydis* was included as the outgroup taxon, and the sequence was obtained from De Wachter et al. (1992). The ~ 400 bp insert in *S. commune* and *A. ampla* was located in the same position as inserts described from *Ustilago maydis* (De Wachter et al., 1992), *Protomyces* (Nishida et al., 1993; Nishida and Sugiyama, 1994), *Sclerotinia sclerotiorum* (Wilmotte et al., 1993), and other fungi (Gargas et al., 1995). The exact location of the insert in *Panellus* was not determined. Although several attempts were made to sequence the entire insert of *A. ampla* and *S. commune,* only about 100 bp from each end of the insert were determined. The sequences of the insert were similar between the two taxa (data not shown).

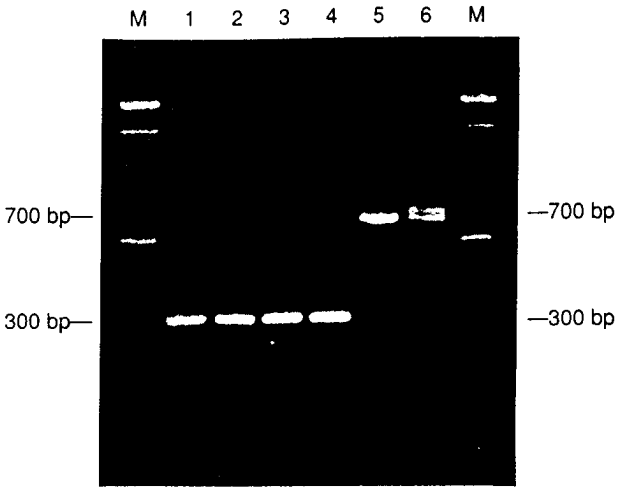


FIG. 1. Amplified products from the NS5-NS6 region of the 18S ribosomal RNA gene. Lanes 1–6 contain DNA products amplified using primers NS5 and NS6: 1, *Phlebia centrifuga* (RLG 7588); 2, *P. radiata* (JLL 15608); 3, *P. albida* (GB 1833); 4, *Auriculariopsis albomellea* (FP 101843); 5, *A. ampla* (CBS 285.88); 6, *Schizophyllum commune* (FP 56473). Lanes labelled M contain a 100 bp ladder. The 2% agarose gel was run for 1 h at 96 V in 45 mM TBE buffer and stained in dilute ethidium bromide for 10 min and destained in distilled water for 10 min.

Sequences 40 bp from the end of the NS5 primer, just after the site of the 400 bp insertion, through the NS6 primer were included in the alignment and analyses. Four gaps of 1–3 bp were required for alignment of the sequences. No intraspecific sequence divergence was observed. In addition, sequences of *Phlebia centrifuga* and *P. radiata* and of *S. commune* and *A. ampla* were identical. Sequence divergence, ignoring gaps, among the ingroup taxa ranged from 0.8% between *P. albida* and *A. albomellea* to 4.6% between *P. albida* and *S. commune/A. ampla.* Sequence divergence between *Ustilago* and the ingroup taxa ranged from 11.5–13.1 %. From the 265 nucleotide positions, there were 39 variable sites of which 12 were potentially informative. Two indels, however, were informative.

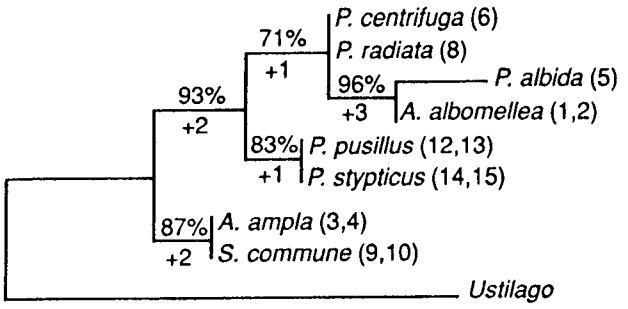


FIG. 2. Phylogram of one of the parsimonious trees based on sequences of the NS5-NS6 region of the 18S rRNA gene. Bootstrap confidence levels (%) are shown above and decay indices below the branches. Numbers in parentheses correspond to numbered taxa in TABLE I.

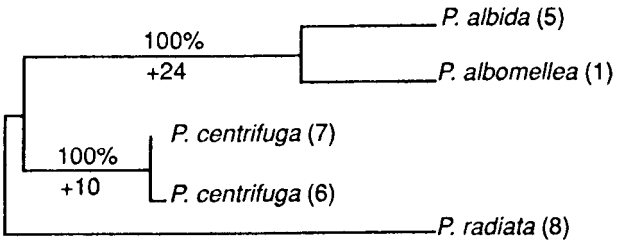


FIG. 3. Phylogram of the base-line parsimony tree based on sequences of the ITS region of *Phlebia* and *Auriculariopsis albomellea*. See FIG. 3 legend for additional information.

In the first analysis, gaps were treated as missing data, and two baseline parsimony trees of 43 steps, CI = 0.867, and RI = 0.895, excluding uninformative characters, were recovered. In the strict consensus tree (FIG. 2), taxa were grouped into three clades: all the *Phlebia* species and *A. albomellea, P. pusillus* and *P. stypticus,* and *S. commune* and *A. ampla.* Bootstrap and decay analyses indicated strong support for the *P. albida/A. albomellea, Phlebia,* and *Panellus* clades (FIG. 2). Weighting of transversions more than transitions did not change the topology of the tree. The same analyses were repeated in which gaps were treated as separate indel characters. Results were similar to that previously described, except that the trees were 3 steps longer and slightly higher CI, RI, and bootstrap values were obtained.

Sequence analysis of the ITS region. — The primers ITS5 and ITS4 amplified a region about 650 bp in length and included the ITS 1, ITS 2, 5.8S rRNA gene and flanking 18S and 26S rRNA genes (ITS region). Within the ITS region, *Phlebia* and *A. albomellea* displayed significant differences in length and sequence from *Schizophyllum* and *A. ampla.* For example, the ITS 1 region is 193-197 bp in *Phlebia* and *A. albomellea* but only 138 and 136 bp in *Schizophyllum* and *A. ampla,* respectively. Furthermore, the ITS 2 region in *A. ampla,* 183 bp long, is significantly shorter than *Schizophyllum,* 238 bp, because of a deletion adjacent to the 5.8S rRNA gene. In contrast, the 5.8S rRNA gene was nearly identical in length, 155 bp except for *S. commune* which is one base pair longer, and sequence among the taxa. Because of significant differences in length and sequence of the ITS 1 and ITS 2 regions between *Phlebia* and *A. albomellea* on one hand and *Schizophyllum* and *A. ampla* on the other hand, the two groups were analyzed separately.

Sequences of the ITS region of three species of *Phlebia* and *A. albomellea* were easily aligned with the addition of 35 gaps of 1–4 spaces. Sequence divergence was 4.0% between *P. albida* and *A. albomellea,* 9.8-10.6% between *P. albida/A. albomellea* and *P. centrifuga,* and 11.5–16.2% between the in group taxa and the outgroup taxon, *Phlebia radiata.* There are 56 nucleotide positions and 27 indels that are potentially informative. In the first analysis, gaps were treated as missing data, and a single base-line parsimony tree of 140 steps, CI = 0.967 and RI = 0.960, was recovered (FIG. 3). In this tree, *P. albida* and *A. albomellea* form one clade and the two strains of *P. centrifuga* form the other clade. This tree is well supported by decay and bootstrap analyses, as shown in FIG. 3. Weighting of transversions over transitions did not affect the tree topology. The result of treating gaps as separate indel characters was to lengthen the base-line parsimony tree (to 187 steps) but had no effect on the tree topology and did not significantly change the CI and RI values. Similarly, analyses of five alternate alignments to accommodate different gap arrangements did not affect the tree topology, but minor differences in the CI, RI, and bootstrap values were obtained from those just noted.

Sequences of the ITS region of *Schizophyllum, A. ampla,* and *Panellus* were aligned with the addition of 38 gaps of 1–59 bp. *Panellus stypticus* was designated the outgroup taxon. Sequences of the *A. ampla* strains were identical, whereas the *P. pusillus* strains differed at one nucleotide position (0.2% sequence divergence). Intraspecific sequence divergence of the *S. commune* strains was 0.7%. Complete sequences of the *P. stypticus* strains were not obtained, but the strains displayed about 0.2% sequence divergence. Interspecific sequence divergence between *Schizophyllum* and *A. ampla* was 3.6-6.0% and ranged from 17.2-20.4% between *Schizophyllum/A. ampla* and *Panellus.* In the first analysis, gaps were treated as missing data, and a single base-line parsimony tree of 158 steps, CI = 0.925 and RI = 0.957, was obtained (FIG. 4). In this tree, *Schizophyllum* and *A. ampla* formed a clade that is well supported by bootstrap (100%) and decay (+47 steps) analyses. Weighting of trans-

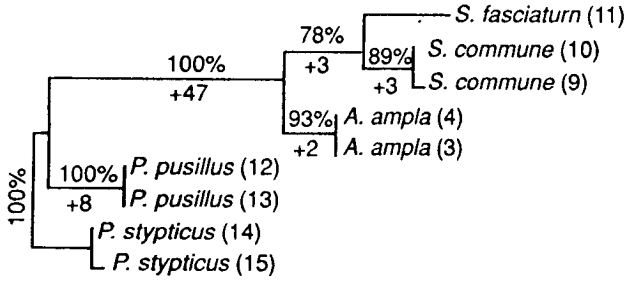


FIG. 4. Phylogram of the base-line parsimony tree based on sequences of the ITS region of *Schizophyllum, Auriculariopsis ampla,* and *Panellus.* See FIG. 3 legend for additional information.

versions over transitions did not affect die tree topology. Treating gaps as separate indel characters lengthened the base-line parsimony tree by 53 steps, but otherwise the topology was unchanged and no significant effect on the CI, RI, or bootstrap values were observed. The 59 bp gap in *A. ampla* was treated as one character in order not to weight this region too heavily. Analyses of alternate alignments to accommodate different gap arrangements did not result in changes in topology or significant differences from numerical values previously reported.

DESCRIPTION OF TAXA

Phlebia albomellea (Bondartsev) Nakasone, *comb. nov.* FIGS. 5, 9d-e

≡ *Cytidia albomellea* Bondartsev, *Bolezni Rast.* 16: 96. 1927.
≡ *Cytidiella albomellea* (Bondartsev) Parmasto, Conspect. syst. cort., p. 101. 1968.
≡ *Auriculariopsis albomellea* (Bondartsev) Kotl., *Česká Mykol.* 42: 239. 1988.
= *Cytidiella melzeri* Pouzar, *Česká Mykol.* 8: 129. 1954.
≡ *Auriculariopsis melzeri* (Pouzar) Stalpers, *Persoonia* 13: 504. 1988.

Basidiomata annual, resupinate, rarely effused-reflexed, irregularly circular or orbicular, with loosely attached or incurved margins, up to 12 mm diam, often coalescing, up to 25 × 15 mm, 400–600 µm thick, ceraceous to membranous, distinctly bilayered with a narrow, ceraceous upper layer concolorous with hymenium and a wider, membranous lower layer of white mycelium; *hymenial surface* smooth or with scattered or radially arranged, low, irregular folds or tubercles, often central mature area developing scattered to numerous warts, warts and folds brown [(6-7) E6], dark brown (7F6) to black, then greyish orange (6B4) between warts and folds, occasionally greyish orange (5B4), brownish orange (5C4, 6C7), or brown [6D (6-7), 7E8, 7F4] throughout, cracks occasionally developed in mature specimens; *margins* white to orange white (5A2), rarely appressed and fimbriate, frequently detached from substrate and curved inward, surface of incurved margins hirsute to woolly or felty, white to yellowish white.

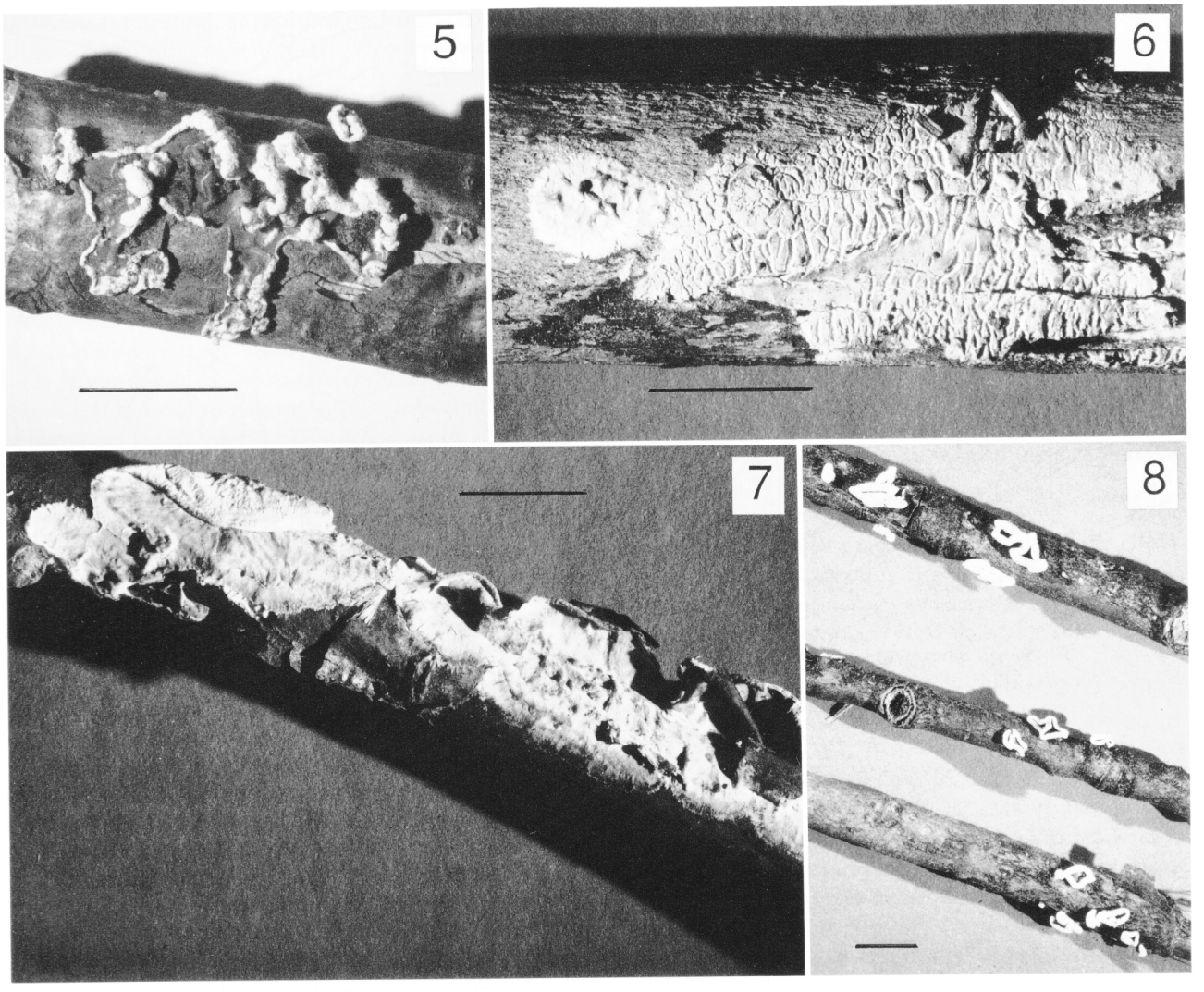
Hyphal system monomitic. *Subiculum* 200–500 µm thick, hyphae oriented parallel to substrate, loosely to densely intertwined but usually not agglutinated, however, occasionally adherent; *subicular hyphae* 2-6 µm diam, nodose septate, sparsely to moderately branched, often forming H-connections; walls hyaline, slightly thickened or up to 1.5 µm thick, typically coated with particulate, dark yellow, resinous substances. *Subhymenium* thickening, 50–70 µm thick, hyphae oriented perpendicular to substrate, tightly agglutinated; *subhymenial hyphae* 2.0–3.5 µm diam, nodose septate, short-celled, frequently branched; walls hyaline, thin to slightly thick, usually coated with particulate, dark yellow, resinous substances. *Hymenium* consisting of agglutinated basidia coated with particulate, dark yellow, resinous substances, sometimes hymenial layer overlaid with resinous substances. *Basidia* narrowly clavate, 34-45 (–50) × 5–7 µm, clamped at base, 4-sterigmate, sterigmata up to 5 µm long; walls hyaline, thin, smooth. *Basidiospores* broadly ellipsoid to ellipsoid, (6.0–)6.5-7.2(-8.5) × 3.0–4.0 µm; walls hyaline, thin, smooth, negative in Melzer's reagent.

Habitat. Fallen or attached dead corticate branches of *Pinus, Abies,* and *Alnus* in North America and *(Quercus, Corylus,* and *Pinus* in Europe; associated with a white rot.

Distribution. Canada (Yukon Territory), United States (Maine, Wisconsin, Mississippi, New Mexico, and Arizona), Spain (Canary Islands, Rodríguez-Armas et al., 1992), Czechoslovakia, France (Boidin and Gilles, 1990), Ukraine, Sweden, Iran (Hallenberg, 1981b).

Type specimen examined. UKRAINE. PROV. KIEV Tchercassy, Darnitza, in silva, in ramis emort. *Pini silvestris* L., 5 Sep. 1925 (HOLOTYPE of *Cytidia albomellea:* LE-22408).

Specimens examined (as *Cytidiella melzeri* unless otherwise indicated). CANADA. Yukon Territory: Dempster Hwy, km 244, on bark of fallen *Alnus crispa* (Ait.) Pursh., 23 Jul 1982, *J. H. Ginns 7042,* ut *A. albomellea* (DAOM 214952; CFMR). CZECHOSLOVAKIA. Bohemica, Montes " Brdské Hřebeny" in valle rivuli "Hařský potok" prope Halouny, ad ramulos *Quercus* sp. in corona arboris, 24 May 1953, *M. Svrček* (PRM-195339, PARATYPE). Turovec spud Planá nad Lužnicé, ad ramos *Quercus* sp. in corona, 29 Aug. 1949, *M. Svrček* (PRM-195340, PARATYPE). Jiřiovo Údolí spud Nové Hrady, ad truncum *Pini uncinatae* Wilk., 18 Aug. 1952, *Z. Pouzar* (PRM-195343,



FIGS. 5–8. Basidiomata of *Phlebia* and *Schizophyllum*. 5. *Phlebia albomellea* (PRM 195342); 6. *Phlebia albida* (PRM 663291); 7. *P. albida* (PRM 833950); 8. *Schizophyllum ampla* (PRM 667121). Bar = 10 mm.

PARATYPE). Vráboko pr. Cĭmelice, silva "Kovárka", ad ramos *Quercus* in corona arboris, 23 July 1964, *M. Svrček 147/64,* ut *Stereum gausapatum* (Fr.) Fr. (PRM-613727). Sobi5slavak5 blata, loco "Na Hranicích", ad truncum *Pini uliginosae* Neum. emortuum in aere, 22 Dec. 1954, *F. Kotlaba* (PRM-798324). *So*bi%lav, in turfosis SobEslavask5 blata pr. oppidum, ad corticem et lignam *P. silvestris,* 9 May 1957, *F. Kotlaba* (PRM-195341). Montes Brdy, in valle rivuli "Halounský potok", ad ramulum iacentem *Quercus* sp., 29 Aug. 1954, *F. Kuneš* and *K. Ponner* (PRM-195342). Suchdol nad Lužnicí, ad ramum emortum in acre *Pini silvaticae,* 6 Aug. 1955, *F. Kotlaba* (PRM-628148). SWEDEN. UPPLAND: Svartsjölandet, Hillersjö, on *P. silvestris,* 30 Apr. 1905, *L. Romell 2872 1/2* (GB). SÖDERMANLAND: Södertälje, Näsets udde, on dry branch of *Q. robur* L., 1 June 1949, *P. Johansson 8720* (GB). UNITED STATES. ARIZONA Pima County, Coronado Nat. Forest, Santa Catalina Mts., Palisades, on *P. ponderosa* Douglas ex C. Laws., 2 Aug. 1974, *R. L. Gilbertson 11199* (ARIZ-AN011865), and General Hitchcock Picnic Area, on *P. ponderosa,* 30 Aug. 1969, *A. B. Budington 1314* (ARIZ-AN011866). MAINE: York, on *Alnus,* 22 Sep. 1923, *R. Thaxter,* ut *Cytidia flocculenta* (Fr.) Höhn. & Litsch. (FH). MISSISSIPPI: Harrison County, Harrison Expt. Forest, on *P. palustris* Mill., 4 Dec. 1982, *M. Blackwell 1155* (ARIZ). NEW MEXICO: Cibola Nat. Forest, Tree Spring Trail near Albuquerque, on *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr., 13 Aug. 1968, *H. H. Burdsall, Jr. 990,* ut *P. albomellea* (CFMR, ARIZ-AN011862). WISCONSIN: Adams County, Wisconsin Dells, along River Road, Crandall Plantation, on fallen corticate branches of *P. resinosa*

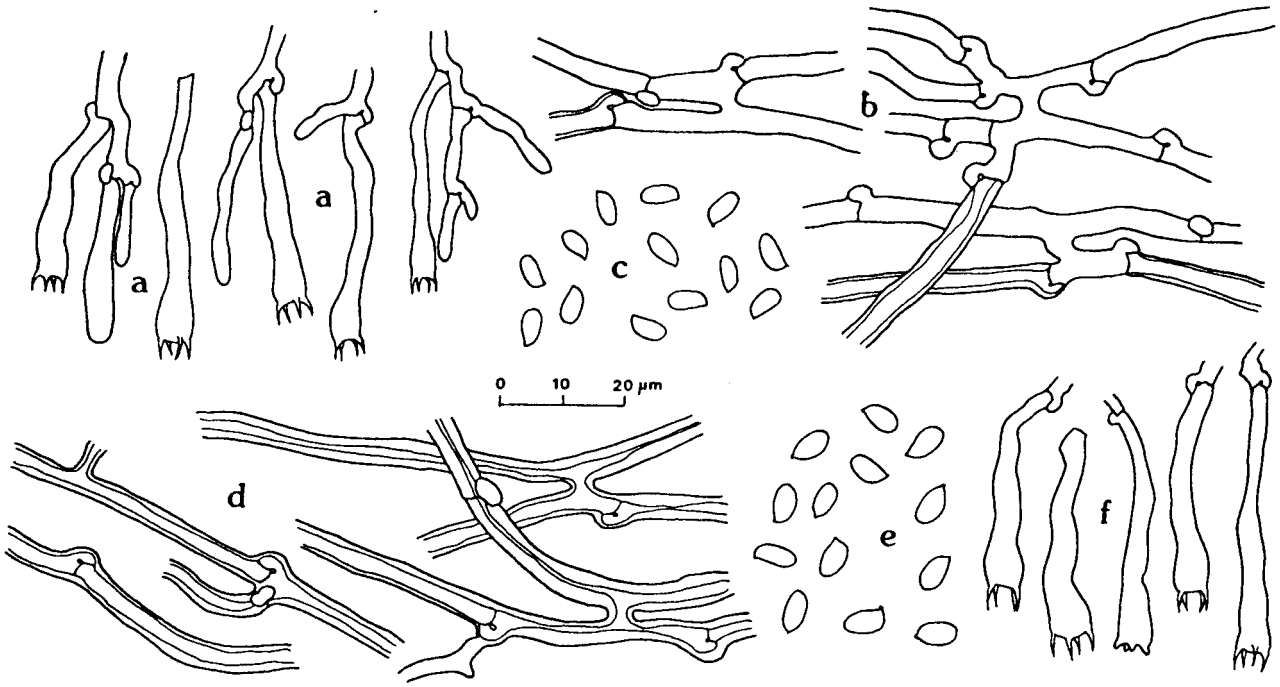


FIG. 9. Microscopic characters of *Phlebia* species. *Phlebia albida* (a–c): a, basidia; b, subicular hyphae; c, basidiospores. *Phlebia albomellea* (d–f): d, subicular hyphae; e, basidiospores; f, basidia.

Ait., 30 Oct. 1991, *K. K. Nakasone, FP 102339,* ut *P. albomellea* (CFMR).

Descriptions and illustrations. Gilbertson (1974, as *Byssomerulius incarnatus* (Schwein.) Gilb.); Eriksson and Ryvarden (1975, as *Cytidiella melzeri*).

Cultural description. Nakasone (1990, as *Cytidiella melzeri*).

Remarks.—Phlebia albomellea, also known as *Cytidiella melzeri,* is well-characterized by circular to orbicular, smooth to warted, brown basidiomata with white, woolly, incurved margins, narrowly clavate basidia and smooth, non-amyloid basidiospores. A rarely reported species in North America, *P. albomellea* appears to be more prevalent in Europe, especially in the former Czechoslovakia. Examination of the holotype specimen of *Cytidia albomellea* confirms that it is conspecific with *Cytidiella melzeri* as Parmasto (1968) determined previously.

Superficially, *P. albomellea* resembles *Cytidia salicina* (Fr.) Burt, *Auriculariopsis ampla,* and some species of *Stereum* and *Aleurodiscus* because of its discoid fruitbody and incurved margins. The ceraceous texture, thickening subhymenium, narrowly clavate basidia of *P. albomellea,* however, are features typical of many species of *Phlebia.* In particular, *P. albida* is closely related to *P. albomellea* as inferred from analysis of sequence data. Both taxa have many traits in common such as a soft, membranous subiculum, ceraceous subhymenium, H-connections between subicular hyphae, large, narrowly clavate basidia, ellipsoid basidiospores, and no cystidia.

Phlebia albida H. Post in Fr., *Monogr. hymen. sueciae* vol. II, p. 280. 1863. FIGS. 6, 7, 9a–c

= *Radulum pendulum* Fr., *Elench. fung.* I, p. 149. 1828. (*teste* Bourdot & Galzin, 1928; Donk in Boidin, 1958; *nomen dubium*).

≡ *Corticium pendulum* (Fr.) Donk in Boidin, *Rev. Mycol. (Paris), Mém. hors-série* 6: 64. 1958 (*nov. comb. in litt.*).

= *Grandinia tuberculata* Berk. & M. A. Curtis in Berk., *Hooker's J. Bot. Kew Gard. Misc.* 1: 237. 1849.

≡ *Basidioradulum tuberculatum* (Berk. & M. A. Curtis) Hjortstam, *Mycotaxon* 54: 183. 1995.

= *Radulum pallidum* Berk. & M. A. Curtis in Berk., *Grevillea* 1: 145. 1873.

≡ *Basidioradulum pallidum* (Berk. & M. A. Curtis) H. Furuk., *Bull. Gov. Forest Exp. Sta.* 261: 56. 1974.

≡ *Phlebia pallida* (Berk. & M. A. Curtis) Ginns, *Mycotaxon* 46: 322. 1993.

= *Stereum subcostatum* P. Karst., *Hedwigia* 20: 178. 1881.

≡ *Corticium subcostatum* (P. Karst.) Bourdot & Galzin, *Bull. Trimestriel Soc. Mycol. France* 24: 235. 1911.

= *Stereum album* Quél., *Compt. Rend. Assoc. Franç. Avancem. Sci., (La Rochelle)* 11: 400. 1882 [1883] (*teste* Bresadola, 1903; Pilát, 1931; *nomen dubium*).

= *Tylodon friesii* Banker, *Bull. Torrey Bot. Club* 29: 440. 1902.

Basidiomata annual, resupinate, effused-reflexed, or pileate, beginning as irregularly circular or orbicular patches, often coalescing, up to 50 × 25 mm, up to 1 mm thick, subceraceous to membranous, cracks occasional or extensive, distinctly bilayered with the upper layer narrow, subceraceous, concolorous with hymenium and lower layer wider, white, soft, tomentose, sometimes homogeneous, white, softer, tomentose throughout; *pileus* up to 10-mm radius, matted felty to fibrillose, upper surface dull yellowish white (4A2) to greyish orange (5B6), margins concolorous or somewhat darker than pileus, typically strigose with ragged edges; *hymenial surface* continuous, smooth, odontoid to rugose with scattered tubercules or papillae, tubercules more numerous in older mature areas, sometimes developing brittle, blunt, cylindrical teeth that taper slightly towards the apex, up to 3 mm long and 600 µm diam; color variable, pale yellow (4A3), brownish orange (6D7), light brown [6D(4-6)], or brown (6D7, 7D8), sometimes older areas darkening to a mottled brown (7E7) or nearly black, occasionally light orange (5A4) to greyish orange (5B4, 6B6) with a slight pinkish cast; *margins* abrupt or thinning out, fimbriate, loosely attached or detached, smooth or occasionally with small warts or coarsely radiate veins, pale yellow (4A3), light orange (5A4) to greyish orange (5B4), occasionally brown (6D7), often with a very narrow, white, fibrillose, adnate, even to slightly bayed edge.

Hyphal system, monomitic. *Subiculum* 250-800 µm thick, hyphae oriented more or less parallel to substrate, somewhat loosely or densely intertwined, not agglutinated, occasionally with abundant cubical or octagonal hyaline crystals, rarely strands of 2–5 encrusted hyphae present, sometimes in upper subiculum hyphae becoming compressed and densely compacted; *subicular hyphae* 2.5–5.0 µm diam, nodose septate, moderately branched and often forming H-connections; walls haline, thin to slightly thick, smooth. *Subhymenium* thickening, 35-145 µm thick, hyphae oriented perpendicular to substrate, dense and tightly agglutinated, often appearing degraded and indistinct; *subhymenial hyphae* 2.5-3.5 µm diam, nodose septate, short-celled and contorted, frequently branched; walls hyaline, thin, usually coated with particulate, yellow, resinous substances. *Hymenium* a dense, but not agglutinated, palisade of basidia. *Basidia* narrowly clavate, (29–) 32-45 (–54) × 5–6(–7) µm, tapering to 2.0–2.5 µm diam at base, with a basal clamp, 4-sterigmate; walls hyaline, thin, smooth. *Basidiospores* cylindrical to narrowly ellipsoid, (5.5-) 6.0–7.5(–10.0) × (2.5-)3,0-3.5(-4.0) µm; walls hyaline, thin, smooth, negative in Melzer's reagent.

Habitat. Bark covered branches of angiosperms, especially *Quercus*, and occasionally on gymnosperms; associated with a white-rot decay.

Distribution. United States (NewJersey to Iowa and Michigan to Alabama, and Colorado), Greenland (Knudsen et al. 1993), Spain, Czechoslovakia, Norway, Sweden, Finland, and Iran.

Type specimens examined. FINLAND. Mustiala, in ramos dejectos arbor. frond., 10 Oct. 1881, *P. A. Karsten* (HOLOTYPE of *Stereum subcostatun* H; ISOTYPE: GB) . SWEDEN. ÖSTERGÖTLAND: Skedevi s : n, Rejmyra, 5 Nov. 1862, H. von Post (LECTOTYPE of *Phlebia albida: S)*. UNITED STATES. SOUTH CAROLINA Society Hill, on *Carya* sp., Mar. 1849, *M. A. Curtis 2599* (HOLOTYPE of *Radulum pallidum: K;* ISOTYPE: FH); on *Carya, M. A. Curtis 1111, Herb. Berk. 179* (HOLOTYPE of *Grandinia tuberculata:* K, lSOTYPE: FH).

Specimens examined. CZECHOSLOVAKIA. Bohemica, Jiříkovo Údolí prope Nové Hrady, locus "Borkovišté" dictus, ad ramum iacetem loco sicco extra silvam Betulae pendulae, 19 Aug. 1952, *Z. Pouzar*, ut *Corticium subcostatum* (PRM-663091). Boubinsky prales, (Pašení), ad ramos sicc. Fagi, 18 Sep. 1948, *M. Svrček 1656/48* (PRM-833951). FINLAND. Mustiala, on bark of *Betula*, 24 *Nov.* 1878, *P. A. Karsten*, ut *R. Pendulum* Fr. (GB). IRAN. Gorgan, Golestan forest, fallen twig of deciduous tree, 26 Apr. to 8 May 1978, *L. & N. Hallenberg and B. Danesh-Pashuuh, NH 2231 and 2351* (GB). NORWAY HEDMARK: Kongsvinger, Overud, tynn løvtrestamme, 5 Sep. 1985, *GMJ* 36/85 (O). Ringsaker, ved Bjorge, pd løvved, 8 July 1978, E. *Høgholen 245/78* (O). Sør-Trøndelag, Dovre National Park, 900–1200 m, along side Blesebekken, on *Betula*, 15 Aug. 1983, *K. Hjortstam 13587* (GB). SPAIN. Andalucia, SE of Ronda, alt. 1100 m, on *Abies pinsapo* Boiss., 9 Apr. 1973, *N. Hallenberg 22724* (GB). Sierra Guadarrama, Madrid, on bark of deciduous wood, 15 Jan. 1975, *L. Ryvarden* (O). *CANARY* ISLANDS: Gran Canaria, Monte Cueva Corcho, on corticate twig of *Castanea*, 31 Dec. 1975, *A.-E. Torkelsen 112/76* (O). SWEDEN. VÄTERGÖTLAND: Göteborg, Kärralund, på lövträdsgren, 4 Nov. 1943, *T. Nathorst-Windahl 17691*, ut *Phlebia subcostatum* (GB). Norrbotten: Nědertorneå par., at Kurkisviken, on decayed wood of *Alnus incana* Moench, 26 Aug. 1960, *J. Eriksson 9330 (GB-4384)*. TORNE LAPPMARK: Abisko, between Abisko E and Paddos, on decayed wood of *Betula tortuosa* Ledeb., 13 Aug. 1960, *J. Eriksson 8757* (GB-4406). UNITED STATES. ALABAMA: Montgomery, *R. P. Burke 97*, ut *R. pallidum* (BPI-US0263454). COLORADO: La Plata County, San Juan Nat. Forest, Missionary Ridge, on corticate twigs of *Quercus gambelii* Nutt., 2 July 1983, *J. P. Lindsey 1068* (ARIZ-AN005944); Junction Creek Campground, on corticate twigs of *Q. gambelii*, 18

Sep. 1982, *J. P. Lindsey 1037* (ARIZ-AN005943). ILLINOIS: St. Clair County, Vulcan, on dead, decorticate hardwood, 31 Jan. 1941, *G. D. Darker 6839,* ut *R. pallidum* (BPI-US0263450). Riverside, on oak sticks, July 1902, *E. T. and S. A. Harper* 693, ut *R. pallidum* (FH). IOWA: Iowa City, on corticate *Quercus,* 6 Aug. 1936, *G. W. Martin,* ut *R. pallidum* (FH). MARYLAND: Takoma Park, on *Quercus?,* 1 Mar. 1903, *C.L. Shear,* ut *R. pallidum* (BPI-US0263046). MICHIGAN: Whitmore Lake, 17 Oct. 1914, *A. H. W. Povah 9,* ut *R. pallidum* (BPI-US0263449). NEW JERSEY: Newfield, on bark of decaying oak, 24 June 1896, *J. B. Ellis,* ut *R. pallidum* (BPI-US0263459). NEW YORK: Long Island, Jamaica, on *Quercus,* 2 NOV. 1909, *F. H. Ames,* ut *R. pallidum* (BPI-US0263453). OHIO: Cincinnati, G. C. *Lloyd 4396,* ut R. *pallidum* (BPI-US0263456). PENNSYLVANLA: Trexlertown, on corticate hardwood branches, received Dec. 1897, *W. Herbst,* ut *R. pallidum* (FH), SOUTH CAROLINA: Society Hill, on bark of dead *Quercus* branch, Mar. 1848, *M. A. Curtis 2175,* ut *Radulum molare* (FH).

Descriptions and illustrations. Eriksson et al. (1981); Furukawa (1974, as *Basidioradulum pallidum);* Ginns (1993, as *Phlebia pallida);* Lindsey (1985); Lloyd (1917, as *R. pallidum);* Miller and Boyle (1943, as *R. pallidum);* Nikolajeva (1961, as *R. pallidum).*

Cultural descriptions. Boidin (1958, as *Corticium pendulum);* Hallenberg (1981a).

Remarks.—Phlebia aibida is an uncommon species in North America and is characterized by a soft, membranous subiculum composed of nonagglutinated, thin-walled subicular hyphae and ellipsoid basidiospores. The species is quite variable in form and color, but effused-relaxed and pileate forms are typically easily identified, while resupinate forms can be problematical. In particular, thin appressed forms may develop atypical subicula composed of densely compact, agglutinated hyphae. Eriksson et al. (1981) often found a species of *Nectria* associated with specimens of *P. albida;* however, I did not notice this species in any North American collection. A closely related species, *P. canadensis* W. B. Cooke, has a similar subicular structure as *P. albida* but has spores that are significantly shorter (4.5-5.0 × 2.5–3.0 μm). Eriksson et al. (1981) consider *P. canadensis* to be nonspecific with *P. albida.*

At the macroscopic level, there is little similarity between *P. albomellea* and *P. albida. Phlebia albomellea* has a discoid habit with unattached, incurved margins, and *P. albida is* effused to effused reflexed with appressed margins. However, microscopically, the taxa are nearly identical. Context construction, subicular hyphae, basidia, and basidiospores of both taxa are similiar. Furthermore, molecular evidence clearly shows that they are closely related (FIGS. 2, 3).

In North America, the name *Phlebia albida* has been misapplied to specimens of *P. centrifuga* (Ginns and Lefebvre, 1993; Hallenberg, 1981a; Nakasone, 1990). For example, basidiocarp descriptions of *P. albida* in Cooke (1956), Gilbertson (1974), and Lindsey and Gilbertson (1978) should be referred to *P. centrifuga.* Similarly, culture descriptions of *P. albida* by Nakasone (1990) and Thind and Rattan (1977) are attributable to *P. centrifuga.* Despite this confusion, the two species are quite distinct morphologically. *Phlebia albida* is quite rare, typically is found on corticate branches of angiosperms, and develops small, soft basidiocarps with smooth or warted hymenia. In contrast, *Phlebia centrifuga,* is common on gymnosperms and develops widely effused, ceraceous to gelatinous basidiocarps with plicate to papillose hymenia. Hallenberg (1981a) demonstrated with dikaryotic-monokaryotic pairings that *P. abida* and *P. centrifuga* are incompatible. Furthermore, sequence analyses of the ITS region and the NS5-NS6 region of the 18S rRNA gene also support the distinct nature of these two taxa (FIGS. 2, 3).

In 1863 when Fries described *P. albida,* he cited an illustration. This illustration was based on a specimen that was probably collected in 1861. The plate is still extant in Sweden, although it was never published (Strid, 1994); the specimen, however, apparently does not exist. There is a specimen of *P. albida* at S from Östergötland that was collected by von Post in 1862. This specimen agrees with the protologue and may have been used by Fries when he wrote the protologue. Since no holotype was designated, the 1862 specimen at S is here designated the lectotype following the precedent established by Eriksson et al. (1981).

Examinations of the type specimens of *G. tuberculata, R. pallidum,* and *S. subcostatum* confirms that they are nonspecific with *P. abida.* Although the type specimen of *Grandinia tuberculata* is developed over sand granules (Gilbertson, 1965), which makes it difficult to examine the subicular structure, I concur with Hjortstam (1995) that *G. tuberculata* is conspecific with *P. albida.* Type materials of *Radulum pendulum* and *Stereum album* are not extant; therefore, these taxa are considered *nomina dubia.* However, it is likely that these taxa are synonyms of *P. albida* as documented in the literature. The brief description and illustration of *S. album* (Qué1et, 1883) are consistent with *P. albida.* Both Bresadola (1903) and Pilát (1931) placed *S. album* in synonymy under *S. subcostatum,* which is a synonym of *P. albida.* Similarly, I believe that it is likely from Fries' (1828) description of *R. pendulum* that the specimen he had in hand is

nonspecific with *P. albida.* This conclusion is supported by Bresadola (1903) and Donk (Boidin, 1958), who indicated that *R pendulum* is nonspecific with *S. subcostatum.* Furthermore, Bourdot and Galzin (1928) reported that *R pendulum* is a tuberculate form of *S. subcostatum.* If the type specimen of *R. pendulum is* discovered or a neotype designated, then *R. pendulum* would be the earliest name for this taxon. Presently, *Grandinia tuberculata* is the earliest confirmed name for *P. albida.* In the interest of name stability, however, the name *P. albida* should be maintained, because it has been used since 1863 and is well documented with a lectotype specimen.

Schizophyllum amplum (Lév.) Nakasone, *comb. nov.* FIG. 8

≡ *Cyphella ampla* Lév., *Ann. Sci. Nat., Bot.* 9: 126. 1848.

≡ *Auriculariopsis ampla* (Lév.) Maire, *Rech. cytol. taxon. basidiomyc.*, p. 102. 1902.

= *Stereum pubescens* Burt, *Ann. Missouri Bot. Gard.* 7: 178. 1920.

See Eriksson and Ryvarden (1975) for a description and excellent drawings and illustrations of *S. amplum.* Other descriptions are available in Burt (1920, as *S. pubescens),* Cooke (1951, as *Cytidia flocculenta* (Fr.) Höhn. & Litsch.), Cunningham (1956, as *C. flocculenta),* and Stalpers (1988).

Habitat. On dead corticate branches and twigs of *Populus, Salix,* and other woody angiosperms.

Distribution. United States (Montana, Wyoming), Netherlands, France, Spain, Romania, New Zealand, also reported from Canada, Austria, Germany, Hungary, Yugoslavia, Russia, Australia (Cooke, 1951), Iran (Hallenberg, 1981 b), and Denmark (Møller, 1942).

Type specimen examined. UNITED STATES. MONTANA: Sheridan, on frondose wood, Apr. 1892, *Mrs. L. A. Fitch, Ellis no. 7014* (HOLOTYPE of *S. pubescens:* BPI-US0285307).

Specimens examined. CZECHOSLOVAKIA. Carpatorossia, Německá Mokrá-Bradula, distr. Tiačevo, alt. 700–1200 m, on *Populus tremula* L., July 1932, *A. Pilát,* Fungi Carpatica Lignicola 54, ut *C. flocculenta* (BPI-US0285306). Slovaca, sylva "Galantská Sihoť" ap. Šhrkovec pr. Šala, ad ramum iacentem Populi albae (on bark), 24 Oct. 1972, *Z. Pouzar* (PRM-756714). Slovenica, Slovakia merid.-occident., Vinohrádky ditto apund Kúty prope Bréclav, ad ramos emortuos Populi nigrae, 13 July 1956, *F. Kotlaba,* ut *C. flocculenta* (PRM-667121). FRANCE. AVEYRON: De Caroline, sur Peuplier, Nov. 1917, *A. Galzin 23021, Bourdot 22632,* ut *C. flocculenta* (FH). ALLIER: Moulins, sur *Salix alba* L., 5 Mar. 1894, *H. Bourdot 4726,* ut *C. flocculenta* (FH), IRAN. Gorgan, Golestan forest, on fallen twig, 26 Apr. to 8 May 1978, *L. & N. Hallenberg and B. Danesh-Pashuuh, NH 2025* (GB). NETHERLANDS. Zuid-Holland, Meyendel., Bierlap, on (fallen twigs of) *Populus,* 23 Oct. 1952, *M. A. Donk 9246* (L); Wassenaar, on dead branch of *P. tremulae* in the dunes, 30 Oct. 1955, *C. Bas* 959 (GB). NEW ZEALAND. Otago, Earnscleugh Res., Ouhard, 200 m, on *Salix babylonica* L., 27 Dec. 1951, *J. D. Atkinson 10995* (BPI-US0285962). ROMANIA IASI: Botanical Garden, on deciduous wood (branch), 14 Oct. 1985, *N. Hallenberg 9092 (GB-*1478). SPAIN. LERIDA: near Bellver, Creek Valley, on branch, 17 Nov. 1986, *N. Hallenberg 10061 (GB-1803).* UNITED STATES. WYOMING: Boulder, on *Salix,* 24 May 1917, *P. S. Wolpert, J. R. Weir 9742,* ut *C. flocculenta* (BPI-US0285309).

Remarks.—Schizophyllum amplum is a rare species in North America but is more abundant in Europe. Although known as *Cytidia flocculenta,* Donk (1959, 1963) and Eriksson and Ryvarden (1975) determined that the type of *C. flocculenta* is nonspecific with *Corticium evolvens* (Fr. : Fr.) Fr. See Donk (1959) for a detailed treatment on the synonymy of *S. amplum.*

Schizophyllum amplum and *S. commune* have many traits in common. For example, basidiomata in both taxa are small, pileate to cupulate structures with free, unattached margins. The pileus or abhymenial surface is white and felty to villous and is composed of skeletal hyphae. When dried, the basidiomata are shrunken and folded with the margins curling inward but are easily revived with water and return to a flexible and pliable state. Microscopically, the basidia are narrowly clavate with a basal clamp and 4 sterigmata, the basidiospores are cylindrical to allantoid, hyaline, and smooth, and the hyphal system is dimitic. The generative hyphae are regularly nodose septate and give rise to the thick-walled, unbranched skeletal hyphae. In culture, *S. commune* is characterized by clamped hyphae with spines (Nobles, 1948; Watling and Sweeney, 1971). *Schizophyllum amplum* also produces similar spinose hyphae (Stalpers, 1988). In addition, *S. amplum* (as *C. flocculenta,* Terra, 1953) and *S. commune* (Kneip, 1920) have bifactorial incompatibility systems. Furthermore, Stalpers (1988) has shown that hymenial development in *S. amplum* and *S. commune* are similar up until the formation of split gills in *S. commune.* Split gills are formed by hyphae of the pileus trama that penetrate and develop through the hymenium to divide the hymenial surface. The subhymenium and hymenium continue to develop as the tramal hyphae grow (Essig, 1922; Watling and Sweeney, 1971; Stalpers 1988).

In addition to morphology, molecular data overwhelmingly support a close relationship between *S.*

amplum and *S. commune.* Both taxa have identical sequences in the NS5-NS6 region and only 3.6-6.0% sequence divergence in the ITS region. Parsimony analyses of the ITS and the NS5-NS6 regions indicate a close relationship among *S. commune, S. fasciatum,* and *S. amplum* (FIGS. 2, 4). In addition, *S. amplum* and *S. commune* have a ~ 400 bp insert in the same location in the NS5-NS6 region of the 18S rRNA gene. However, many unrelated fungal taxa also have introns located at this same site, which suggests horizontal transmission of this itron. Thus, it is possible that *S. amplum* and S. *commune* acquired this intron independently.

DISCUSSION

Phlebia albomellea is an unusual species. For many years it was placed in the monotypic genus *Cytidiella* and known as *C. melzeri. Cytidiella* was postulated to be closely related to or congeneric with *Auriculariopsis,* another monotypic genus, because of morphological similarities (Eriksson and Ryvarden, 1975; Hjortstam, 1987; Kotlaba, 1988; Pouzar, 1954; Stalpers, 1988). In fact, Jülich (1981) established the family Auriculariopsidaceae for *Cytidiella* and *Auriculariopsis.* However, morphological and molecular studies presented here clearly demonstrate that *P. albomellea* is congeneric with *Phlebia* and is closely related to P. *albida.* The striking habitat and microscopic similarities of *P. albomellea* and *P. albida* were generally overlooked by taxonomists, who stressed the distinctive discoid basidiocarps of *P. albomellea.* However, the discoid fruitbody type is found in many unrelated taxa and probably developed independently many times in the basidiomycetes. Cladistic analysis of the molecular data strongly supported the close relationship of *P. albomellea* to *Phlebia,* especially *P. albida.* The 4.0% sequence divergence observed between *A. albomellea* and *P. albida* in the ITS region is comparable to that observed among the closely related taxa *P. radiata, P. rufa,* and *P. acerina,* 4.1-5.6%, in the ITS 2 region alone (Nakasone, 1991).

Phlebia centrifuga was included in this study because specimens of *P. centrifuga* have often been misidentified as *P. albida* (Ginns and Lefebvre, 1993; Nakasone, 1990). The two taxa were shown to be distinct based on analyes of sequences of the NS5-NS6 and ITS regions (FIGS. 2, 3), confirming morphological and genetic studies (Hallenberg, 1981a).

Phlebia represents a classic example of a polythetic genus in that taxa within the genus share many characters, but no phenotypic trait is common to all. *Phlebia albomellea* demonstrates that the generic limits of *Phlebia* are still being determined, Besides its discoid habit, *P. albomellea* has other unusual features that are not shared by other *Phlebia* species. For instance, it has a bifactorial mating type system (Nakasone, 1990), whereas most species of *Phlehia, sensus stricto,* have a unifactorial mating type system (Boidin, 1964, 1990), In pure culture, *P. albomellea,* like *P. hydnoidea* Schwein., is slow growing and develops regularly clamped hyphae in the margin (Nakasone, 1990). This contrasts with many species of *Phlebia* that grow rapidly and develop simple septate hyphae in the margin (Boidin, 1964; Hallenberg, 1987; Nakasone, 1990; Nobles, 1958).

Although *P. albomellea* and *S. amplum* share a number of features such as a ceraceous texture, brown-colored hymenium, narrowly clavate basidia, and no cystidia, significant differences in the context structure and context hyphae exist. In *P. albomellea,* the context is homogeneous and the hyphal system is monomitic. The context and abhymenial surface are composed of nonagglutinated, regularly nodose septate, subicular hyphae with thin or thickened walls. In contrast, *S. amplum* has a duplex structure and a dimitic hyphal system. The context is composed of nodose septate, frequently branched subicular hyphae with thin to thick, gelatinized walls. The subicular hyphae give rise to hairlike hyphae that form the abhymenial tomentum. These hairlike hyphae are simple septate with rare clamps, occasionally branched, and have thick, nongelatinized walls. Although acknowledging these differences in context structure and context hyphae, Eriksson and Ryvarden (1975) chose to maintain the two taxa in different genera, *Cytidiella* and *Auriculariopsis,* whereas Stalpers (1988) decided they were congeneric and transferred *Cytidiella melzeri* (≡ *P. albomellea)* to *Auriculariopsis.*

Auriculariopsis was erected in 1902 to accommodate the species *Cyphella ampla,* an unusual species with gelatinous hyphae (Maire, 1902). *Auriculariopsis ampla* was postulated to be related to *Cytidiella* and *Merulius* (Eriksson and Ryvarden, 1975). However, Stalpers (1988) demonstrated similarities in the development of the hymenophore and cultural morphology between *Auriculariopsis* and *Schizophyllum.* In this study, molecular data also supported a close relationship between *A. ampla* and *Schizophyllum.* Both *A. ampla* and *S. commune* shared the same sequence and had a ~ 400 bp insertion at the same location in the NS5-NS6 region of the 18S rRNA gene. Moreover, the ITS region of *S. commune,* S. *fasciatum,* and *A. ampla* are similar, displaying only 3.6-6.0% sequence divergence. Similar values of sequence divergence were observed between sister species *P. albida* and *P. albomellea.*

Auriculariopsis and *Schizophyllum* are similar in habit and habitat preferences. Both taxa are gregar-

ious and typically found on dead, still attached branches of woody angiosperms. The basidiocarps, with woolly or villose pileal surfaces, are adapted to withstand dry periods and revive easily with water. Both taxa have a dimitic hyphal system, basidia of similar shape and size, and hyaline, ellipsoid basidiospores. *Schizophyllum* and *Auriculariopsis* develop spinose hyphae in culture and have a tetrapolar incompatibility system. Thus, morphological and molecular evidence overwhelmingly indicate that *Auriculariopsis* and *Schizophyllum* are congeneric. Nevertheless, some taxonomists may still be reluctant to synonymize *Auriculariopsis* under *Schizophyllum*, because the former only develops ridges while the latter has split gills.

Phlebia albomellea and *Schizophyllum amplum* clearly demonstrate how too much emphasis on a single or a few macroscopic features can be misleading in the taxonomy of corticoid fungi and the value of independent molecular data in resolving complex taxonomic problems, especially involving convergent development in gross morphology. The discoid basidiocarps of *P. albomellea* are so unusual in *Phlebia* that without molecular data, the close relationship between *P. albomellea* and *P. albida* probably would never have been discovered. Similarly, molecular data were invaluable for demonstrating the close relationship of *Auriculariopsis* and *Schizophyllum* and for supporting the synonymy of *Auriculariopsis* under *Schizophyllum*.

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