

Intercontinental interbreeding collections of *Pleurotus pulmonarius*, with notes on *P. ostreatus* and other species

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Morphological taxonomic characters have been found insufficient to separate *Pleurotus ostreatus* from *P. pulmonarius*. Utilizing cultures and preserved specimens from many locations in the North Temperate Zone, the following conclusions were drawn: 1) these two species comprise separate sterility groups (= biological species); 2) the range of *P. pulmonarius* extends throughout the North Temperate Zone; 3) no infraspecific barriers to sexual compatibility exist between within-continent and between intercontinental populations. A representative collection of *P. pulmonarius* is designated in the absence of an appropriate type specimen.

Keywords: Mating systems, syngameons, allopatry, sympatry, biological species, *Pleurotus*.

Although the literature dealing with taxonomy and compatibility systems in *Pleurotus* is already voluminous (see bibliographies by Hilber, 1982; Bresinsky & al., 1977; 1987), members of the *P. ostreatus* complex [variously considered to include two to several species, but centered on *P. ostreatus* (Jacq.: Fr.) Kummer and *P. pulmonarius* Fr.] are still separated with difficulty. Morphological characters, such as pileus color, spore size and shape, cystidial characters, all fail to distinguish *P. ostreatus* from *P. pulmonarius* (Bresinsky & al., 1987), with some characters being modified by climatic or substrate differences.

A second source of confusion is literature in which names were not secured to herbarium specimens and concepts to which names were not given. Anderson & al. (1973) and Anderson & Wang (1972) cultured two taxa of *Pleurotus* in Minnesota. One was identified as *P. sapidus* Kalch., the other remained unnamed, but only a single dikaryon culture of “*P. sapidus*” attributed to Anderson can be found (in ATCC). Likewise, Ohira (1977) reported on *P. ostreatus* from Japan, including several incompatible isolates for which no name was supplied. The identity of such unnamed collections may be revealed through incompatibility tests and enzyme profiles.

All workers agree that discrete intersterility groups, or biological species, occur within the *P. ostreatus* complex, and that incompatibility of collections, as represented by monokaryotic, or single-spore isolates, is convincing evidence that different species are involved (Hilber, 1982; Bresinsky & al., 1987). Most recently, however, collections of *Pleurotus* taxa traditionally treated as separate species have proven intercompatible, giving new impetus to studies on intercollection and "interspecific" compatibility as a method of species diagnosis. Isolates of *P. citrinopileatus* Singer were compatible with those of *P. cornucopiae* (Pers.) Rolland (Ohira, 1990). Likewise, isolates of *P. salmoneostramineus* Vas., basidiomata of which are pink, were compatible with those of *P. djamor* (Fr.) Boedijn, basidiomata of which range from white to tan to pinkish tan (Neda & al., 1988). In subg. *Coremiopleurotus*, single-spore isolates of *P. cystidiosus* Miller and *P. abalonus* Han & al. are partially compatible (Kettner, 1980).

The abbreviated key presented by Bresinsky & al. (1987) attempted to separate *P. ostreatus* from *P. pulmonarius*, but some characters useful in central Europe (i.e. pileus color, fruiting seasonality) were not applicable in eastern North America. There, pileus color in *P. ostreatus* and *P. pulmonarius* overlaps significantly, and thus not even this character can be used to separate the taxa.

Finally, the literature indicates that at least *P. pulmonarius* (and quite probably *P. ostreatus*) is not represented by a type specimen, making even morphological taxonomy unstable.

After several seasons of worldwide collecting and culturing, a sizeable library of cultures of *Pleurotus* taxa has been established, vouchered by documented herbarium specimens. When morphological examination failed to conclusively separate taxa of the *P. ostreatus* complex among these collections, a study was undertaken to identify intersterility groups within those cultures, based on sexual compatibility with certain authoritative collections from Europe, and to ascertain relationships of the complex to other members of the genus.

Materials and methods

Abbreviations and definitions

ATCC = American Type Culture Collection; OKM = Dr. Orson K. Miller, Jr.; RHP = R.H. Petersen; RV = Dr. Rytas Vilgalys; TENN = herbarium, University of Tennessee; VT = Virginia Polytechnic Institute and University. Self-cross = pairings of single-spore isolates from a single basidiome. Intercollection mating = pairings of single-spore isolates from single basidiomata of geographically separate collections. Compatibility/incompatibility = ability/inability of paired monokaryon isolates to form dikaryotic mycelium as implied by presence

of clamp connections (when used for intercollection matings, usually referred to as "intercompatibility/interincompatibility)." Contact zone = the area between inoculum blocks of paired isolates.

Specimens used

In the following enumeration, asterisks denote collections used as representative of geographic regions (so-called "primary" collections); TENN numbers refer to herbarium voucher specimens; collection numbers refer to field numbers assigned to specimens and cultures. All collections have been confirmed as belonging to their intersterility group (see Materials and methods below).

Pleurotus cornucopiae. – CZECHOSLOVAKIA: ATCC dikaryon culture [no. 42045*]: "O. Hilber (strain) 4R. *Ulmus* sp. Taxonomy (Z. Mykol. 44: 31–50. 1978)". and monokaryon cultures produced by basidiomata from this culture. As *Pleurotus citrinopileatus*: – CHINA: Jilin Prov., Baihe local market, 7. 8. 88, coll. RHP, no. 1420 (TENN no. 48569); Jilin Prov., Baihe, Chang Bai Shan Nature Preserve, 10. 8. 88, coll. RHP, no. 1440* (TENN no. 48297).

Pleurotus "djamor". – MEXICO: Tabasco, vic. Teapa, Estacion Agronomica UNAM, 20.10.91, coll. RHP, on hardwood, no. 4326* (TENN no. 50405); Veracruz, vic. Catemaco, UNAM Biological Field Station Tuxcla, 24. 10. 91, coll. RHP, no. 4375 (TENN no. 50449); same location, same date, no. 4381 (TENN no. 50455). – UNITED STATES: Puerto Rico, Forest Preserve Rio Abajo, 5. 12. 90, coll. RHP & S. Gordon, on hardwood log, no. 3467* (TENN no. 49017).

Pleurotus ostreatus. – CZECHOSLOVAKIA: location unknown, Ginterova dikaryon strain no. 31, monokaryon isolate D330.1 donated by Dr. R. Vilgalys. – SWEDEN: Vastergotland, vic. Gothenburg, Bokedalen Forest, 17. 11. 91, coll. Robert Daun, on *Fagus* log, designated BOK* (TENN no. 50820); Vastergotland, Gothenburg, Slottsskogen, 28. 11. 91, coll. Stig Jacobsson, on *Salix* sp., Jacobsson no. 91070 (TENN no. 50821). – UNITED STATES: Tennessee, Cocke Co., date unknown, on hardwood log, dikaryon tissue culture D261 (= VT 1463; ATCC 66376), monokaryon isolate D261.50 donated by Dr. R. Vilgalys (VT no. RV83/233); Knox Co., Lyndhurst Cemetery, 23. 12. 90, coll. RHP & KWH, on hardwood stump, no. 3505 (TENN no. 50910); Knox Co., Bearden, 28. 11. 88, coll. RHP & KWH, on *Quercus*, no. 56637* (TENN no. 50912); Knox Co., Knoxville, 27. 12. 90, coll. RHP & KWH, on *Acer*, no. 3507 (TENN no. 50911).

P. pulmonarius. – CANADA: British Columbia, vic. Whisler, 6. 10. 90, coll. North American Mycological Association, substrate unknown, no. 3400/17* (TENN no. 49656). – CHINA: Guizhou, Fanjing Shan Nature Preserve, 31. 7. 91, coll. RHP, hardwood log, no. 4121* (TENN no. 58066); Jilin Prov., Baihe, Chang Bai Shan Nature Preserve, fire tower behind hotel, 14. 8. 88, coll. RHP, on conifer stump, no. 1455* (TENN no. 48286); same location, same date, conifer log, no. 1456 (TENN no. 49298); same location, 7. 8. 88, coll. RHP, no. 1413 (TENN no. 48282); Jilin Prov., Songjianghe, CBSNP, 9. 8. 88, coll. RHP, on *Picea* log, no. 1423 (TENN no. 48301); same location, same date, no. 1425 (TENN no. 48295); same location, 10. 8. 88, coll. RHP, on *Abies* log, no. 1426 (TENN no. 48262); same location, same date, on *Abies* log, no. 1427 (TENN no. 48304); Yunnan Prov., Simao Pref., 6 km west of Simao, 5. 8. 90, coll. Q. Wu & Y. Li, on hardwood log, no. 3127* (TENN no. 49374). – JAPAN: Tottori Pref., Tottori City, Tottori Mycological Institute grounds, 2. 10. 89, coll. E. Nagasawa and RHP, on *Quercus* logs; no. 2360* (TENN no. 48337); Tochigi Pref., vic. Lake Chuzenjiko, 27. 9. 89, coll. RHP, on hardwood log, no. 2318 (TENN no. 48222). – RUSSIA: Terr. Primorsk, Dist. Ternei, Sikhote Alin Biosphere Preserve, Vasnaya, south side of river, 14. 9. 90, coll. RHP, on *Betula* log, no. 3277* (TENN

no. 49526); same location, Vasnaya, 10. 9. 90, coll. RHP, on hardwood log, no. 3192 (TENN no. 49615); same location, Blagadotnoya, 26. 9. 90, coll. RHP, on hardwood log, no. 3378 (TENN no. 49422). – SWEDEN, Vastergotland, Gothenburg, Botanical Garden forest, 17. 9. 91, coll. RHP and Robert Daun, on ?*Ulmus* log, no. 4192 (TENN no. 50gl3); Vastergotland, Kinnekulle Nature Reserve, 18. 9. 91, coll. RHP, on *Fraxinus* trunk, no. 4203* (TENN no. 50539). – SWITZERLAND: Valle Maggia, 29. 9. 91, coll. Frank Graf, on ?*Fagus* branch, no. 4267* (TENN no. 50603). – UNITED STATES: New York, Tompkins Co., Ringwood Forest, 30. 8. 88, coll. RHP, on *Fagus* trunk, no. 1711* (TENN no. 50914); North Carolina, Buncombe Co., date unknown, on hardwood log, dikaryon tissue culture D352, monokaryon isolate D352.2 donated by Dr. R. Vilgalys (Duke Univ. no. RV 88/45); Macon Co., Highlands, Clear Creek Rd., 26. 9. 88, coll. J. Parkinson, no. 1777* (TENN no. 48076); Macon Co., Slick Rock Picnic Area, 22. 5. 89, coll. RHP, no. 56656 (TENN no. 48675); Swain Co., Great Smoky Mountains National Park, Indian Creek, 27. 9. 88, coll. RHP, on hardwood, no. 1785 (TENN no. 50915); same location, same date, no. 1786 (TENN no. 48029); same location, same date, no. 56602 (TENN no. 48164).

Pleurotus salmoneostramineus. – JAPAN: original location unknown, collection date unknown, s.n.*, basidiomata from Edible Mushroom Institute, Hokken Sangyo Company Ltd.

As *Pleurotus ostreatoroseus*. – MEXICO: Jalisco, Guadalajara, 9.86, coll. L. Guzman-Davalos, on dead *Yucca*, Guzman-Davalos no. 3766* (IBUG 75).

Pleurotus sp. – UNITED STATES: Idaho, date unknown, on *Populus*, monokaryon isolate D260 donated by Dr. R. Vilgalys (VT no. OKM 18812).

Media and growth conditions

All inoculum and crossing experiments were grown and performed on malt extract (Difco: 1.5%) agar (Difco Bacto: 2.0%), at room temperature (21–24° C). All cultures were stored at 4–5° C. All cultures are maintained in the fungus culture collection at TENN, and dikaryon cultures of collections marked with asterisk (*) above have been deposited at ATCC.

Self-cross experiments

For primary collections, self-crosses among 12 single-spore isolates were performed, and four tester strains representative of four mating types (when possible) selected for each collection. For auxiliary collections, self-crosses were not performed.

Intercollection pairings

For primary collections, tester strains from all collections were paired in all combinations (Fig. 1). For auxiliary collections, four random single-spore isolates were mated to a single tester strain of a primary collection from the same geographical area to ascertain the intersterility group to which the collection belonged. In all cases, random isolates of auxiliary collections were mated to *P. "djamor"* (3467), *P. ostreatus* (BOK) and *P. pulmonarius* (4203), the three taxa

whose basidiomata were most similar, and often to more than one collection of these species.

In order to secure this study to another ongoing investigation of *Pleurotus* the following single monokaryon isolates donated by Dr. Rytas Vilgalys were paired with tester strains of all primary collections named above to confirm the taxonomic congruence of the two studies: 261.58 (eastern North American *P. ostreatus*), 352.2 (*P. pulmonarius*), 330.1 (European *P. ostreatus*), and 260 (unnamed *Pleurotus* species). Tester strains of Ohira (199Q), collection 1440 (*P. citrinopileatus*) and ATCC 42045 (*P. cornucopiae*) were paired to confirm results reported by Ohira (1990). Likewise, tester strains of *P. ostreatoroseus* (from spore print donated by Dr. Laura Guzman Davalos) were crossed with tester strains of *P. salmoneostramineus*.

Results

Self-cross experiments

As expected, based on the literature (see summary by Hilber, 1982; Nagai and Nukumizu, 1952), all primary collections were bifactorial (= tetrapolar). In almost all cases, four mating types were recovered. In one case (*P. pulmonarius*, 4267, Switzerland) only three mating types were recovered.

Intercollection matings

Isolates of all primary collections sorted into discrete intersterility groups (Fig 1). In some cases, these intersterility groups were congruent to easily separated morphotaxa (i.e. *P. "djamor"*) or complexes which previous studies had shown to belong to a single biological species (i.e. *P. cornucopiae* + *P. citrinopileatus*). In the *P. ostreatus*-*P. pulmonarius* complex, two discrete intersterility groups were identified. One, taxonomically anchored by collection BOK from Sweden, was identified as *P. ostreatus*, but basidiomata of intercompatible North American collections were found to differ significantly in morphology from "stereotype" European specimens. The other, taxonomically anchored in collection 4203 from Sweden, was identified as *P. pulmonarius*. Examination of literature and documented herbarium material from these collections failed to separate this species from *P. ostreatus*, especially as the two species occur in eastern North America.

Although insufficient material was available for accurate assessment of the geographic range of compatible populations in *P. ostreatus*, ample collections of *P. pulmonarius* existed for such an assessment. As shown above, intercompatible collections of *P. pulmonarius*

	PULMONARIUS										OSTREATUS				SP	CORNUCOPIAE		DJAMOUR		SALMONO-STRAMINEUS			
	E-NA		BC	NE-ASIA		C-ASIA		EUR		EUR	E-NA		EUR	ASIA		MEX	PR	JAP	MEX				
	1777	1711	3823	3460 17	3277	1486	2380	3127	4121	4287	4208	BOK	3301	06687	381 53	280	42046	1440	4336	3467	S.M.	IBUG 75	
1777(4)	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
1711(4)		+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
382.2(1)			+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
3400/17(4)				+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
3277(4)					+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
1486(4)						+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
2380(4)							+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
3127(4)								+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
4121(4)									+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
4287(3)										+	+	-	-	-	-	-	-	-	-	-	-	-	-
4208(4)											+	-	-	-	-	-	-	-	-	-	-	-	-
BOK(4)												+	+	+	-	-	-	-	-	-	-	-	-
330.Y(1)													+	+	-	-	-	-	-	-	-	-	-
56837(4)														+	-	-	-	-	-	-	-	-	-
28158(1)															+	-	-	-	-	-	-	-	-
260(1)																+	-	-	-	-	-	-	-
42046(4)																	+	-	-	-	-	-	-
1440(4)																		+	-	-	-	-	-
4326(4)																			+	-	-	-	-
3467(4)																				+	-	-	-
S.M.(4)																						+	-

Fig. 1. – Results of intercollection matings of *Pleurotus* species. (Above): Species epithets, geographic regions (E-NA = eastern North America; BC = British Columbia; NE-Asia = northeastern Asia; C-Asia = central Asia; EUR = Europe; MEX = Mexico; PR = Puerto Rico; JAP = Japan. Collections numbers (for more data, see Materials and methods). (Left): Collection numbers (number of single-spore tester strains). + = universal production of clamp connections on mated dikaryons; - = clamp connections not formed.

were found throughout the North Temperate Zone; in Europe, North America and Asia.

Our study also confirmed results on other putative taxa (cf Fig. 1): 1) *P. cornucopiae* and *P. citrinopileatus* belong to a single biological species (Ohira, 1990); and 2) an intercollection pairing between tester strains of *P. "ostreatoroseus"* (Mexico, IBUG 75) and *P. salmonostramineus* (Japan, see list of cultures above) was universally intercompatible. The latter result is taxonomically unsecured because the Japanese collection came from commercial sources, but serves as a

further indication of *Pleurotus* species with widespread geographic ranges.

Identification and typification of *Pleurotus pulmonarius*

Basic to any systematic considerations must be typification. To our knowledge, *P. pulmonarius* has not been typified, even though the name is in common usage in Europe thanks to recent attention to species separation by intersterility groups (Hilber, 1982; Bresinsky & al., 1987). Typification of *P. ostreatus* cannot be accomplished in this paper, for type material (by this time requiring dikaryon and single-spore cultures of the type collection) should come from the environs of Austria, whence we have no specimens or cultures.

In order to make a case for typification of *P. pulmonarius*, care must be taken to associate the selected specimen with the original description, locality and substrate. Fries (Systema Mycologicum, 1821: 186) placed his new species in *Agaricus* tribus *Pleurotus*, subtribus *Aegeritaria*, rather than in subtribus *Concharia* with *P. ostreatus*. Subtribus *Aegeritaria* was diagnosed as follows: "Velum nullum. Stipes excentricus l. lateralis, raro obsoletus. Pileus carnosus, tenax, irregularis, junior etiam horizontalis. Lamellae non decurrentes, etiam quando ob stipitis pileive formam fornicatae, determinato-desinentes." To this, the following observation was added: "Fungi serotini, lignatiles, inodori, una species sapore stiptico notabilis. Plures esculenti videntur; larvis valde infesti." The species with styptic taste was *Pleurotus* [*Panellus*] *stypticus*. Other species in the subtribe were *P. ulmarius* and *P. tessulatus*, now considered to belong in *Hypsizygos*, *P. palmatus*, now placed in *Rhodotus*, and *P. serotinus*, *P. stypticus*, and *P. mitis*, all now in *Panellus*. Most of these familiar taxa are characterized by basidiomata with discrete stipes (at least usually; except for *P. serotinus*) which varied from central through eccentric to nearly lateral. Whether the lamellae of all these species can be considered as NOT decurrent is doubtful.

Within this subtribe, *P. pulmonarius* was diagnosed as follows: "...pileo obovato molli glabro cinereo-alutaceo, lamellis adnatis lividis, stipite laterali brevissimo villosa." The following observations were added: "Substantia mollis, sed tenax alba. Pileus siccus fere alutaceus, 2-3 unc. latus, etiam subreniformis. Lamellae simplices, latae, distinctae, ob situm cum stipite rectilineum! decurrentes apparent; sed aequaliter et determinato-desinentes. Ad *Betulae truncos prostratos*. Oct. (v.v.)".

In all collections on which our study was based, basidiome stipes were never lateral, but nearly always strongly eccentric, with pileus tissue extending 1-5 mm behind the attachment of stipe with pileus.

Whether Fries could have considered this stature as laterally stipitate cannot be judged. Under *P. ostreatus*, however, Fries described stipe placement as "...stipite sublaterali." This is exactly the situation found in the collections cited below under *P. pulmonarius*.

Under *P. ostreatus*, Fries described the pileus as "... carnosus glabro e nigricante-cinereo expallente...", [fleshy, glabrous, from blackish-cinereous to paler] differing from the pileus of *P. pulmonarius*, which was "...obovato molli glabro cinereo-alutaceo,..." [obovate, soft, smooth, grayish alutaceous]. Lamellae of *P. ostreatus* were "...postice anastomosantibus eglandulosis albis,..." [anastomosing behind, without spots, white], while those of *P. pulmonarius* were "...adnatis lividis,..." [adnate, livid].

Fries gave no clue as to the origin of the species epithet, especially in light of the words "obovato" and "subreniformis" to describe the pileus. Indeed, young basidiomata of the collections cited below were uniformly spoon-shaped, which, if the stipe attachment is taken as the base, must be considered obovate. Subreniform could refer to some perceived unequal development of the pileus, but our experience indicates that by maturity, pilei may be circular, very broadly obovate, lobed, or somewhat distorted in various configurations. We suspect, however, that the epithet referred to the young basidiomata which, in outline, were lung-shaped.

Considering the present taxonomic state in this complex, in which morphology seems inadequate to separate *P. ostreatus* from *P. pulmonarius* (at least in North America), but in which sexual incompatibility is generally accepted as a fundamental separating character, it is important to select a neotype specimen for which cultures, especially single-spore tester strains, are available. This is so for TENN 50539 (culture collection no. 4203), collected some 50 kms north of Gothenburg, in a deciduous forest preserve (and thus likely not to be disturbed in the future). While this location is not ideal (it is generally accepted that prior to 1821, Fries collected most of his specimens from the vicinity of Femsjo, southeast of Gothenburg, with *Betula* as one of the dominant tree genera), and the specific substrate incorrect, the specimen is typical of the "common usage" name (the collection was readily identified by two Swedish amateur mycologists at the time of collection), and matches the illustration and description under this name by Ryman (1984), and the illustration in the Swedish edition of the book by Phillips and Jacobsson (1982).

In some cases, specimens included in the distribution of the exsiccata by Lundell and Nannfeldt ("Fungi Exsiccati Suecici Praesertim Upsaliensis") have been used to neotypify Fries's species, and that exsiccatum was consulted. To our knowledge, no specimen appears under the name *P. pulmonarius*. Instead, number 710 (Lundell and Nannfeldt, 1939) was distributed as *P. ostreatus*. In contradistinction,

however, the notes which accompanied the specimen read as follows: "...on ...stump of a frondose tree. ...The gathering distributed here represents a medium sized, pale form in the fresh state exactly agreeing with the illustration in Konrad & Maublanc, Icon. Sel. Fung. pl. 305 (as *P. spodoleucus*)." The illustration and the exsiccata notes both point toward *P. pulmonarius*. Thus, it is probable that *P. pulmonarius* was taken as a pale form of *P. ostreatus*, even in Sweden, where the former name originated.

In summary, the specimen listed below satisfies all morphological parameters of the species, but was collected from *Fraxinus* wood, not from *Betula*. For this reason, the specimen cannot serve as a neotype, but is designated as a "representative specimen," to be supplanted with a more appropriate specimen from *Betula* proven to belong to the same intersterility group. This proposal is intended to provide a starting place for delimitation of morphospecies and biological species in *Pleurotus*.

Pleurotus pulmonarius Fries. 1821. *Systema Mycologicum* 1: 187.

Proposed representative collection: Sweden, Vastergotland, Kinnekulle Nature Reserve, 18.9.91, coll. RHP, on *Fraxinus* trunk, TENN no. 50539 (field book and culture number 4203; tester strains and polypore dikaryon culture deposited at ATCC and the laboratory of Dr. Nils Hallenberg, Botanical Institute, University of Gothenburg, Gothenburg, Sweden).

The following macroscopic description of basidiomata of *P. pulmonarius* is provided to show the range of variation of characters, especially pileus color. Admittedly, the description will not distinguish *P. pulmonarius* from *P. ostreatus* over much of their ranges, but, together with designation of a representative collection proposed above, will serve as a basis for morphotaxonomic delineation of this species.

Pileus up to 15 cm broad, spoon-shaped when young, obovate to rounded-cuneiform in outline when young, expanding to broadly obovate (lung-shaped), broadly spathulate to nearly circular by maturity, tough and leathery when young, becoming less so by maturity, and often flaccid in age; surface smooth, with texture of wet leather when young, remaining so if not water-soaked, occasionally hoary with fine pruina near attachment in late maturity, sometimes hygrophanous at least in patches or streaks, usually finely striatulate at margin; color of disc from deep brown [interior Asia: "Natal brown," Verona brown"(Ridgway, 1912)] to neutral brown (Asia: "sayal brown") to gray-brown (Europe: "drab," "hair brown") to dull violaceous gray-tan (throughout the range: "wood brown," "tilleul buff," "vinaceous buff," "avellaneous,") or paler, especially outward (eastern North America, Scandinavia: off-white, "pale ochraceous

salmon," "pale ochraceous buff," "pale cinnamon pink," "pale pinkish cinnamon," "pale vinaceous fawn," "pale pinkish buff") often with a pinkish tint ("pinkish buff") or yellowish tint (ivory, "chamois," "light ochraceous buff," "cream buff"), especially in hygrophanous streaks. – *Lamellae* always deeply decurrent, often almost to the stipe base as shallow lines, up to 11 mm deep, entire or sometimes cracking but not serrulate, somewhat thick, white, off-white, to pale cream shades (throughout the range) "pale pinkish buff," "cartridge buff," "pale cinnamon pink," "pale ochraceous buff," "pale pinkish cinnamon," "cream buff") occasionally with pallid violaceous tint ("tilleul buff"). – *Stipe* very variable, from almost absent (and then a tough knot) to obvious and discrete (up to 45 x 15 mm), never lateral but always with at least a narrow pileus overhang and occasionally subcentral (especially when fruiting from the upper surface of the substrate), usually strigose-tomentose downward, usually concolorous with lamellae (white, off-white, "tilleul buff," "cartridge buff") sometimes discoloring at base to dull violaceous gray ("avellaneous"), and apparently rarely staining brown (Sweden: "sayal brown"). – *Spore print* usually white, but occasionally recorded as pale violet (Asia, eastern North America). – *Odor* of basidiomata sometimes fishy, never strong; taste mildly to strongly agaricoid; consistency tough, chewy. – *Cultures* (mono- and dikaryon) consistently with sweet perfumed odor.

Concomitantly, the following description of pileus colors in *P. ostreatus* will serve to show the similarity of that species to *P. pulmonarius*, especially in eastern North America: European pilei violaceous brown (Bresinsky & al., 1987), steel gray, gray, grey-lilac, blue-blackish (Moser, 1983), grayish brown, blackish brown (both authors). Eastern North American basidiomata: pileus colors "wood brown" inward, outward "vinaceous buff," "cinnamon buff," "pinkish buff," light brown (6E5; Kornerup & Wanscher, 1967); lamellae off-white ("pale pinkish buff," 4B3) to very pallid violet-gray ("tilleul buff").

From notes accompanying herbarium specimens, it seems clear that *P. pulmonarius* usually fruits on angiosperm wood, at least through Europe, eastern North America and most of Asia. Collections from northern China, however, were consistently on gymnosperm wood, indicating either flexibility within the fungus genome to adapt in this way or some physiological evolutionary event.

Examination of the list of specimens utilized (above), supplemented by other literature, clearly indicates little overlap in the seasonality of fruiting of *P. ostreatus* and *P. pulmonarius*. Throughout its range, *P. pulmonarius* fruits from late summer (August) to early autumn (mid September), while *P. ostreatus* fruits from late autumn (October) through mid-winter (January in temperate climates), to early spring

(early April). Both taxa often fruit in early to mid-spring, however, and at that time they will be difficult to separate in eastern North America.

Discussion

Syngameons in *Pleurotus*

There appear to be at least three examples of rather distinct morphotaxa exhibiting intercompatibility, and therefore considered as single biological species. The report by Ohira (1990) of intercompatibility between *P. citrinopileatus* and *P. cornucopiae* has been confirmed during this study using collections previously unreported. The expected ranges of the two species are widely separated; eastern Europe and northeastern Asia, respectively. Both species produce several centrally stipitate pilei with deeply decurrent lamellae on a common, usually branched stipe, but the former produces bright lemon-yellow pilei, while the latter is characterized by cream-colored pilei.

A second example has been reported by Neda & al. (1988) and Murakami & Takemaru (1990) for *P. salmoneostramineus* and *P. djamor*, where the former normally produces pink basidiomata, but with occasional albino individuals, and the latter ranges from white to tan to pinkish tan. The core of geographic distribution for this complex is eastern Asia, with *P. djamor* from warmer climates and *P. salmoneostramineus* from more temperate areas. Thus far, our tropical American collections labelled as *P. "djamor"* have been incompatible with our isolates of *P. salmoneostramineus*. If these neotropical collections were truly *P. djamor*, they should be intercompatible with *P. salmoneostramineus* as reported by Neda & al. (1988). Moreover, our study has shown that *P. ostreatoroseus* (from spore prints only) is intercompatible with *P. salmoneostramineus* (obtained from commercial Japanese sources). Neotropical collections labelled *P. "djamor"* are also incompatible with *P. ostreatoroseus*, further implying that the name *P. djamor* is probably misapplied to the neotropical taxon.

The third example involves the European form of *P. ostreatus*, with gray, deep gray, blue-gray to brown-gray pileus, and the North American form with tan to pallid tan pileus, the latter morphologically virtually inseparable from *P. pulmonarius*. Again, the two forms of *P. ostreatus* seem separated by great distance, in this case the Atlantic Ocean. It would seem safe to conjecture, at least for the first and third examples, that reproductive barriers exist in the form of geographic separation, but that *in vitro* interbreedability demonstrates an absence of genetic barriers.

Species concepts and *P. pulmonarius*

In the formulation of any modern species concept, interbreeding, either real or potential, plays a dominant role (Templeton, 1989; Bock, 1986). In our study, dikaryons resulting from compatible crosses did not fruit, so no conclusion as to the fertility of these crosses can be made, but numerous papers have reported fruiting of such dikaryons, and it would seem safe to conjecture that such dikaryons are fertile (see Bresinsky et al., 1977, 1987). To imply that universally interbreeding collections of *P. pulmonarius* are to be found over the entire North Temperate Zone, and to know that these are incompatible with collections of *P. ostreatus*, is fundamental to the circumscription of both species. It is also valuable to know that partial incompatibility did not occur among collections of *P. pulmonarius* included in this study, and that no common mating type genes have been found within this relatively large sampling. The numbers of mating type alleles must be quite large at both the A and B locus.

With such data, it seems apparent that no genetic barriers exist within the biological species *P. pulmonarius*, whether within a somewhat restricted area (100 km² in eastern Siberia, 400 km² in the southern Appalachian Mountains) or between intercontinental populations. In fact, universal nuclear migration in compatible matings was inferred both in self-crosses and intercollection matings.

Likewise, whether reproductive barriers exist in nature cannot be determined from this study. A different resolutional level, perhaps analysis of isoenzyme profiles (Prillinger & Molitoris, 1979), might determine whether *in vivo* intercontinental interbreeding takes place. Unlike other basidiomycete interbreeding systems which show cohesive morphological characters within intersterility groups (*Collybia*: Vilgalys & Miller, 1983; *Armillaria*: see Anderson, 1986; Anderson & Ullrich, 1982; Berubé & Dessureault, 1987), or linked to continental populations within a single intersterility group (*Panellus stypticus*: Petersen & Bermudes, 1992a, b; *Collybia*: Vilgalys, 1992), several biological species of *Pleurotus* include significantly variable morphotaxa. These morphotaxa also appear to range from allopatric (European and American forms of *P. ostreatus*; *P. cornucopiae* and *P. citrinopileatus*) to sympatric (in the broadest sense of that term; *P. salmoneostramineus* and *P. djamor*). The allopatric model could also be applied to the situation in *Omphalotus*, where four geographically widely separated morphotaxa were reported to be sexually intercompatible (Petersen, 1977).

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