

The genus *Pleurotus* in Argentina: mating tests

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In order to study the sexual compatibility, monosporic cultures from 32 strains belonging to four out of the six *Pleurotus* species recorded from Argentina were obtained. All tested species have a heterothallic multifactorial tetrapolar mating system. *P. pulmonarius* and *P. ostreatus* could be separated by interspecific crossings only. Our mating tests confirm the synonymy of *P. smithii* with *P. cystidiosus*. Compatibility tests confirm that in Argentina there are, so far, 5 *Pleurotus* species, namely *P. albidus*, *P. cystidiosus*, *P. djamor*, *P. ostreatus* and *P. pulmonarius*.

Keywords: Argentina, *Pleurotus*, sexual compatibility, systematics.

An exhaustive study of the genus *Pleurotus* for Argentina based on macro- and micromorphology was undertaken (Lechner et al., 2004). In order to learn about the relationships among species from the biological standpoint, we undertook mating tests among different strains, utilizing, in several cases, fruit body production to obtain a spore print and monosporic cultures.

Already Bensaude (1918), Kniep (1920) and Vandredies (1923) proposed that mating tests studies could be useful for defining species. Boidin (1986) pointed out that the study of sexual compatibility was a very useful tool for the study of the taxonomy, especially of wood decaying species, which are easy to culture. According to Petersen & Hughes (1999), there are three, most applicable, species concepts: the morphological, the phylogenetic and the biological. For the determination of the species concept, all data ought to be considered, but mating tests studies could be the most informative. Many authors have studied compatibility systems for the delimitation of species: Boidin (1980, 1986), Boidin & Lanquetin (1965, 1977, 1984) and Hallenberg (1984) worked on several genera of Corticiaceae s.l. and other basidiomycetes; Petersen (1995a, 1995b, 1994, 1992), Nicholl & Petersen (2000) and Petersen & Hughes (1998, 1993) studied

mating types in agarics of the genera *Omphalotus*, *Lentinula* and *Pleurotus*, among others. The aim of this work is i) to contribute to a better delimitation of intersterility groups of *Pleurotus* in Argentina, and to ii) ascertain the accuracy of monosporic culture crossing as a tool for the identification of *Pleurotus* species.

Materials and Methods

Specimens collected were tentatively determined based on micro- and macromorphological studies.

Strains used – The Argentinean cultures used for mating compatibility tests are listed in Tab. I, with data on their origin, collection number, substrate, date and collector.

Other strains used: *P. cystidiosus*, MALAYSIA, Selangor, 1985, coll. K.M. Graham, MUCL 28.690. *P. djamor* var. *roseus*, BRASIL, São Paulo, on leaf of Agavaceae in garden, coll. Edson De Paula, MUCL 35.018 (*P. ostreatoroseus* = *P. djamor*); *P. ostreatus*, ITALY, IX-93, commercial strain, BAFC 2067.

Test strains: The following strains from the University of Tennessee (TENN) were utilized as standard strains for interspecific crossings: *P. cornucopiae* (PCORN) TENN 8763, Austria, 16-VI-96; *P. djamor* (PDJAM) TENN 6346, Malaysia, IV-95; *P. ostreatus* (PO) TENN 6689; Austria; *P. pulmonarius* (PPULM) TENN 4203, Sweden, Västergötland, 18-IX-91, on *Fraxinus* sp.

Fruit body production – To obtain basidiomata, traditional methods for fruiting species of *Pleurotus* were used (Zadrazil, 1974; Stamets, 1993). A mixture of sawdust (70%), wheat meal (10%), oatmeal (4%) and CaCO₃ (1%) was introduced into 40 × 25 cm polypropylene bags and autoclaved at 120 °C for 2 hours. After cooling they were inoculated with spawn, and incubated in the dark at 25 °C. After 15 days, bags were kept at 18–20 °C with 9 h light/15 h darkness photoperiod to induce basidiome formation. Fruit bodies were obtained from strains BAFC 120, 695, 809, 1003, 2034, 2067, 2545 and 2787.

Mating studies – Monosporic cultures were obtained from water dilutions of fresh spore prints on sterile aluminum paper; spores were suspended in 10 ml of sterile-distilled water containing 0.01 mL of Tween 80 to avoid agglutination. This solution was diluted to 1/10, 1/100 and 1/1000. Petri dishes containing Nobles' medium (Nobles, 1948) were inoculated with 1 ml of each of these dilutions and incubated in the dark at 25 °C. Individual monosporic cultures were isolated from germinating single spores. All isolates were examined for clamp connections under the stereomicroscope. Isolates with clamp connections were discarded, only isolates without clamp connections were used for mating studies. Self-crossings for each strain were carried out in order to obtain the mating types. Haplonts were confronted in pairs in Petri dishes using 7 mm diameter blocks as inoculum. Plates were incubated in the dark at 25 °C, and after one

week. Mycelia were screened for clamp connections within the contact zone and on the obverse sides of donor inoculum blocks under the microscope (Burnett, 1968). Presence of clamp connections is considered as a positive mating result, which means that both strains are compatible (+); absence of clamp connections indicates incompatibility (-).

For interspecific crossings, mating types of monosporic cultures obtained from morphologically determined collections were confronted with test strains. The results of these crossings allowed us to confirm or reject such identifications.

To confirm identification of *Pleurotus* collections with similar micro- and macromorphology, two or three monosporic isolates were confronted. When monosporic cultures of doubtful species were lacking, di-mon crossings (the Buller phenomenon) were undertaken (Boidin, 1980).

Table I: List of *Pleurotus* isolates from Argentina used in the study.

Species	BAFC N°	Locality	Substrate	Date	Collector
<i>P. albidus</i>	2787	Buenos Aires, La Lucila	In canker of <i>Salix humbold- tiana</i>	05. 05. 1996	Unknown
	809	Buenos Aires, La Plata	On stump	March 1996	J. Deschamps
	1315	Buenos Aires, La Plata	On fallen trunk	18. 06. 1999	E. Albertó
	101	Buenos Aires, Llavallo, Sta. Catalina	On living <i>Ulmus</i> tree	08. 05. 2000	E. Albertó
	1221	Buenos Aires, Llavallo, Sta. Catalina	On fallen trunk	06. 05. 1999	E. Albertó
	1350	Buenos Aires, Llavallo, Sta. Catalina	On fallen trunk	06. 05. 1999	B. Lechner
	1399	Buenos Aires, Llavallo, Sta. Catalina	On stump	25. 08. 1999	E. Albertó
	1330	Buenos Aires, Llavallo, Sta. Catalina	On fallen trunk	15. 04. 1999	B. Lechner
	695	Buenos Aires, Pergamino	On <i>Salix</i> sp.	06. 04. 1996	E. Albertó
	1354	Buenos Aires, San Clemente	On fallen trunk	13. 06. 1999	E. Albertó
	136	Buenos Aires, Tigre	On <i>Populus</i> sp.	10. 03. 1997	Claudio Lázzari

Species	BAFC N°	Locality	Substrate	Date	Collector
	2545	Capital Federal	On <i>Cordyline</i> sp.	10. 06. 1989	A. Martinez
	1100	Capital Federal, University City	On fallen trunk	25. 08. 1999	B. Lechner
	190	Córdoba, La Punilla	On <i>Populus</i> sp.	25. 02. 2001	N. Manero & B.J. Lechner
	215	Misiones, Pto. Libertad	On dead tree of <i>Araucaria angustifolia</i>	10. 04. 1985	J. Deschamps
<i>P. cystidiosus</i>	73	Buenos Aires, La Plata	On <i>Platanus</i> sp.	March 1994	H. Spinedi
	188	Capital Federal, Barrio La Paternal	On dead zone of <i>Platanus</i> sp.	18. 04. 2000	S. Frachia
<i>P. djamor</i> var. <i>djamor</i>	821	Misiones, El Palmital del cruce	On <i>Ficus</i> sp. fallen trunks	28. 05. 2001	E. Albertó
<i>P. djamor</i> var. <i>roseus</i>	815	Misiones, El Palmital del cruce	On fallen trunk	28. 05. 2001	E. Albertó
<i>P. ostreatus</i>	2034	Capital Federal	Unknown	18. 04. 1994	Pablo Pica
	120	Neuquen, Moquehue	On trunk of <i>Araucaria araucana</i>	March 1993	J. del Vas
<i>P. pulmonarius</i>	1003	Buenos Aires, Ezeiza	On living declining tree of <i>Populus</i> sp.	25. 07. 1987	J. Deschamps
	76	Misiones, San Pedro	On branches of <i>Araucaria angustifolia</i>	27. 05. 2001	E. Albertó & O. Popoff
	263	San Pedro, S 26° 32', W 54° 04'	On branches of <i>A. angustifolia</i>	27. 05. 2001	D. Krueger

Results

Mating types were assigned after self-crossing of the 126 obtained monosporic cultures (Tab. II). Among the strains tested, seven strains had four mating types, while three others (BAFC 1003, 815 and 821) had three mating types. Self-crossings from eight monosporic cultures from BAFC 809 resulted all negative; the same occurred with ten monosporic cultures from BAFC 76. However, crossings between

monosporic cultures of these strains and monosporic cultures of *P. albidus* and *P. pulmonarius*, respectively, resulted positive.

The charts of intra- and interspecific confrontations between different cultures are illustrated in Figs. 1–5. All four species studied, *Pleurotus albidus*, *P. djamor*, *P. ostreatus* and *P. pulmonarius*, exhibited a heterothallic tetrapolar sexual compatibility system.

Table II. Mating types assigned to monosporic cultures (*P. albidus*: BAFC 1221, 1350 and 1354, 1399; *P. djamor*: BAFC 815 and 821; *P. ostreatus*: BAFC 120, 2067; *P. pulmonarius*: BAFC 263 and 1003). Monosporic cultures are denoted as numbers of each strain.

Species	BAFC	Monosporic cultures used	Mating type of monosporic cultures			
			A ₁ B ₁	A ₁ B ₂	A ₂ B ₁	A ₂ B ₂
<i>P. albidus</i>	1221	8	4, 6, 14	10, 11, 12	5	9
	1350	10	2, 4, 10	1, 5, 9, 19	13	3, 7
	1354	8	6, 8	9	2, 7	3, 10, 11
	1399	8	7	1, 5, 11	2, 6, 8, 10	–
<i>P. djamor</i>	815	9	1, 2, 3, 5	–	4, 7, 8, 9	6
	821	8	1, 3, 4	5, 8, 9, 11	–	6
<i>P. ostreatus</i>	120	10	5	2, 9	1, 3, 7, 11	4, 8, 10
	2067	9	11, 14	9, 10, 12	4	7, 8, 15
<i>P. pulmonarius</i>	263	9	6, 10	4, 5	1, 2, 9	11, 15
	1003	12	2, 3, 7, 9, 13	5, 10, 11	–	1, 4, 8, 12

Pleurotus albidus (Berk.) Pegler

Pairing among mating types obtained from self-crossing (BAFC 1221, 1350, 1354 and 1399), and monosporic cultures (BAFC 695, 809, 2545, and 2787) with test strains of *P. ostreatus*, *P. djamor*, *P. pulmonarius* and *P. cornucopiae* (Figs. 1–4) showed no compatible matings. Pairing among *Pleurotus albidus* strains BAFC 1221 with 1350, 1354, 1399, 695, 809 and 2545 resulted positive (Figs. 2–3).

Di-mon crossings between monosporic and polysporic cultures were undertaken (Fig. 5) to confirm taxonomic delimitation of several strains that had tentatively been identified as *P. albidus* based on morphological characteristics such as pileus of fragile nature, white to cream color and remarkable lacinate-crenate margin (Lechner et al, 2004). Positive results were obtained for BAFC 136, 215, 575, 607, 695, 809, 317, 1221, 1315, 1319, 1330, 1350, 2545 and 2787. These strains constitute clearly an intersterility group within *Pleurotus*. Several specimens showed great morphological variability, observed

not only in collections from nature, but also in fruit bodies obtained in culture. Due to their anastomosed lamellae on the stipe (BAFC 809) some resemble *P. cornucopiae*, whereas others (e.g. BAFC 136) form more plane and shorter basidiomes, without such characteristics. These variations might suggest the existence of two different species. However, mating tests allowed us to conclude that these morphological variations are intraspecific, and may be possibly caused by environmental constraints.

***Pleurotus cystidiosus* O. K. Miller**

It was not possible to obtain monosporic cultures of *P. cystidiosus* from Argentina since fruit bodies obtained in culture did not produce viable spores. Positive results of pairings were observed when BAFC 73, determined as *P. smithii* by Spinedi (1995), and BAFC 188 were

BAFC 120		BAFC 2067				BAFC 1354				BAFC 1350				
			4	7	10	11	3	9	8	7	10	5	13	7
		5	+				-				-			
		2		+				-				-		
		7			+				-				-	
4				+				-				-		
BAFC 120		PO TEN 6689				PPULM TEN 4203				BAFC 2034				
			4	36	15	6	10	1	14	9	10	8	4	5
		5	+				-				+			
		2		+				-				+		
		7			+				-				+	
4				+				-				+		
BAFC 2067		BAFC 1354				BAFC 1350				PPULM TEN 4203				
			3	9	8	7	10	5	13	7	10	1	14	9
		4	-				-				-			
		7		-				-				-		
		10			-				-				-	
11				-				-				-		

Fig. 1: Crossings of monosporic cultures of *Pleurotus ostreatus* with *P. pulmonarius* and *P. albidus*. First row: *P. ostreatus* (BAFC 120) crossed with *P. ostreatus* (BAFC 2067) and *P. albidus* (BAFC 1354 and BAFC 1350); Second row: *P. ostreatus* (BAFC 120) crossed with *P. ostreatus* (TEN 6689), *P. pulmonarius* (TEN 4203) and with *P. ostreatus* (BAFC 2034); Third row: *P. ostreatus* (BAFC 2067) crossed with *P. albidus* (BAFC 1354 and BAFC 1350) and *P. pulmonarius* (TEN 4203).

crossed with monosporic cultures of strain *P. cystidiosus* MUCL 28690, showing that both belong to *P. cystidiosus* intersterility group (Fig. 5). Macro- and micromorphological studies are consistent with this result. The collections of *P. smithii* showed the presence of pileo-cystidia (Lechner et al., 2004), absent in the original description of this species given by Guzman (1975).

***Pleurotus djamor* (Fr.) Boedijn**

Monosporic cultures of two collections (BAFC 815, BAFC 821) were confronted with test strains of *P. djamor*. Positive results confirmed our morphological identification (Fig. 4). Di-mon crossing between the monosporous culture of *P. djamor* from TENN and MUCL 35018, identified as *P. ostreatoroseus* Singer, resulted positive too.

		BAFC 2034				BAFC 695		BAFC 2545		BAFC 1003		
		8	10	4	5	4	5	6	7	10	1	13
BAFC 2067	4	-				-	-	-		-		
	7		+			-	-	-		-		
	10			+		-	-	-			-	
	11				+	-	-	-		-		

		PPULM TEN 4203				BAFC 1399			BAFC 809		BAFC 2787	
		10	1	14	9	5	8	7	5	6	5	7
BAFC 2067	4	-				-			-		-	
	7		-				-		-		-	
	10			-				-	-		-	
	11				-	-			-		-	

		BAFC 1221				BAFC 1350				PO TEN 6689			
		5	6	9	12	5	13	10	7	4	36	15	6
BAFC 1354	3	+				+				-			
	9		+				+				-		
	8			+				-				-	
	7				+			+					-

Fig. 2: Crossings of monosporic cultures of *Pleurotus* strains. First row: *Pleurotus ostreatus* crossed with *P. ostreatus* (BAFC 2034), *P. albidus* (BAFC 695 and BAFC 2545) and *P. pulmonarius* (BAFC 1003); Second row: *P. ostreatus* crossed with *P. pulmonarius* (TEN 4203), *P. albidus* (BAFC 1399, BAFC 809, BAFC 2787); Third row: *P. albidus* crossed with *P. albidus* (BAFC 1221, BAFC 1350), and *P. ostreatus* (TEN 6689)

Pleurotus ostreatus (Jacq.: Fr.) Kummer

Results of intraspecific crossing showed that the three collections (BAFC 120, 2034 and 2067) belong to the same species (Figs. 1–2). BAFC 1003, which initially was identified as *P. ostreatus* based exclusively on morphological studies, resulted negative in crossing with BAFC 2067 (Fig. 2).

Pleurotus pulmonarius (Fr.) Quélet

Pairing among test strains of *P. pulmonarius* with BAFC 76, 263 and 1003 resulted positive (Fig. 4). Pairing between BAFC 263 and 2067 of *P. ostreatus* resulted not compatible (Fig. 4). We selected interspecific crossing between strains of *P. ostreatus* and *P. pulmonarius*, because both species are very similar. It is very difficult, if

		PDJAM TEN 6346				PPULM TEN 4203				PCORN TEN 8763			
		11	5	13	8	1	14	10	9	1	7	5	12
BAFC 1354	3	-				-				-			
	9		-				-				-		
	8			-				-				-	
	7				-				-				-
		BAFC 1350				PCORN TEN 8763				PPULM TEN 4203			
		10	5	13	7	1	7	5	12	10	1	14	9
BAFC 1221	9	+			+	-				-			
	5		+	+			-				-		
	12		+	+				-				-	
	6	+			+				-				-
		BAFC 1399			BAFC 695		BAFC 809		BAFC 2545				
		5	8	7	4	5	5	6	6	7			
BAFC 1221	9	+			+	+	10	+	+				
	5		+		+	+	5	-	+	+			
	12			+	-	-	13	+		+			
	6	-			-	-	7	-		+			

Fig. 3: Crossings of monosporic cultures of *Pleurotus* strains. First row: *P. albidus* (BAFC 1354), crossed with *P. djamor* (TEN 6346), *P. pulmonarius* (TEN 4203) and with *P. cornucopiae* (TEN 8763); Second row: *P. albidus* crossed with *P. albidus* (BAFC 1350), *P. cornucopiae* (TEN 8763) and *P. pulmonarius* (TEN 4203); Third row: *P. albidus* (BAFC 1221) crossed with *P. albidus* (BAFC 1399, BAFC 695, BAFC 809, BAFC 2545).

not impossible to separate *P. ostreatus* from *P. pulmonarius* based exclusively on micro- and macroscopic features.

Discussion

Our mating compatibility studies allow to confirm five intersterility groups in Argentina: *Pleurotus albidus*, *P. cystidiosus*, *P. djamor*, *P. ostreatus* and *P. pulmonarius*. The *P. albidus* intersterility group is attributed to a larger sample of isolates that were available from a wide variety of locations and substrates throughout Argentina.

In previous studies on mating relationships in *Pleurotus*, extensive intracollection mon-mon pairings (e.g. Anderson et al., 1973; Hilber, 1982; Bresinsky et al., 1987, Petersen, 1995b) and di-mon pairings (e.g. Vilgalys et al., 1993) were performed to determine

		BAFC 76			
		4	7	10	11
PPULM TEN 4203	1	+			
	6		+		
	7			+	
	8				+

		BAFC 1003			
		1	5	10	3
	1	+			
	5		+		
	10			-	
	3				+

		BAFC 263			
		4	11	6	2
	4	+			
	11		+		
	6			+	
	2				+

		BAFC 1350			
		5	10	13	7
BAFC 263	9	-			
	12		-		
	13			-	
	11				-

		BAFC 263			
		4	11	6	2
	4	+			
	11		+		
	6			+	
	2				+

		BAFC 2067			
		11	10	4	7
	11	-			
	10		-		
	4			-	
	7				-

		BAFC 821			
		1	6	8	11
PDJAM TEN 6346	11	+			
	5		+		
	13			+	
	6				+

		BAFC 815			
		1	3	6	8
	1	+			
	3		+		
	6			+	
	8				+

		BAFC 1221			
		9	5	12	6
	9	+			
	5		-		
	12			-	
	6				-

Fig. 4: Crossings of monosporic cultures of *Pleurotus* strains. First row: *P. pulmonarius* (TEN 4203) crossed with *P. pulmonarius* (BAFC 76, BAFC 1003, BAFC 263); Second row: *P. pulmonarius* (BAFC 263) crossed with *P. albidus* (BAFC 1350), *P. pulmonarius* (BAFC 263) and *P. ostreatus* (BAFC 2067); Third row: *P. djamor* (TEN 6346) crossed with *P. djamor* (BAFC 821, BAFC 815) and *P. albidus* (BAFC 1221).

mating types from each individual prior to performing intercollection matings. In this study, we attempted to maximize the number of intercollection matings by using mon-mon and di-mon pairing with testers from known intersterility groups in *Pleurotus*.

The extensive collection data available for most isolates from this study support our view that the intersterility groups represent good species that differ in a number of significant morphological characteristics (Lechner et al., 2004).

P. cystidiosus is a widespread species covering large regions of the northern hemisphere (North America, Europe and Asia) as well as the southern part of Africa (Zervakis, 1998). For Central and South America there is a record of *P. smithii* in Mexico (Guzmán, 1975),

		MONOSPORIC CULTURE (n)																	
		BAFC 809		BAFC 695		BAFC 1221		BAFC 1350		BAFC 2067			PPULM TEN 4203		PDJAM TEN 6346		PCYS MUCL 28690		
		6	8	4	5	6	12	5	13	4	7	10	10	14	5	6	1	4	14
DICARIONT CULTURE (n+n)	BAFC 136	+	+					+	+			-							
	BAFC 215							+				-							
	BAFC 575							+				-							
	BAFC 607								+			-							
	BAFC 809			+	+							-							
	BAFC 317					+	+	+	+			-							
	BAFC 1315								+			-							
	BAFC 1319								+			-							
	BAFC 1330								+			-							
	BAFC 2545								+	+		-							
	BAFC 2787	+	+																
	BAFC 2034								-	-		+							
	BAFC 2067	-	-																
	BAFC 188																+	+	+
	BAFC 73																-	+	-
BAFC 1003											-	-	-	-	+				
MUCL 35018														+	+				

Fig. 5: Di-mon crossing between monosporic cultures of *P. albidus* (BAFC 809, BAFC 695, BAFC 1221, BAFC 1350), *P. ostreatus* (BAFC 2067), *P. pulmonarius* (TEN 4203), *P. djamor* (TEN 6346) and *P. cystidiosus* (MUCL 28690) with polysporic cultures of *P. albidus* (BAFC 136, BAFC 215, BAFC 575, BAFC 607, BAFC 809, BAFC 317, BAFC 1315, BAFC 1319, BAFC 1330, BAFC 2545, BAFC 2787), *P. ostreatus* (BAFC 2034, BAFC 2067), *P. cystidiosus* (BAFC 188, BAFC 73), *P. pulmonarius* (BAFC 1003) and *P. djamor* (MUCL 35018).

Peru (Guzmán et al., 1980), Cuba (Rodríguez-Hernández & Camino-Vilaró 1990), Brazil (Capelari, 1999) and Argentina (Spinedi, 1995). Capelari & Fungaro (2003) studied the growth rate in culture, dikaryon-monokaryon matings, and genetic variability. They concluded that the criteria used to separate *P. cystidiosus* from *P. smithii* are unsatisfactory and should be considered synonym. The macro- and micromorphological study of Spinedi's collections made in a previous work (Lechner, et al. 2004) and positive results of pairings between cultures of *P. smithii* and *P. cystidiosus* here obtained, permit us confirm the supposed synonymy of these two taxa, and to reaffirm that *P. cystidiosus* is the only synnematoïd (producing an anamorph with synnemata) *Pleurotus* species in South America.

Some *Pleurotus* species can be characterized by a unique range of distribution in Argentina. For example, the *P. cystidiosus* group is distributed along eastern Argentina, in a temperate zone; the *P. ostreatus* group extends from southern to central Argentina, the cold to temperate area; the *P. djamor* group occurs in the subtropical northeast Argentina;

P. pulmonarius is distributed over two broad geographic regions in both northern (subtropical) and central (temperate) Argentina. *P. albidus* was collected from central to north of Argentina, in great diversity of substrates from diverse species of living trees to stumps and fallen trunks. According to Albertó et al. (2002) *P. albidus* fruits from Central America to central Argentina.

Pleurotus cystidiosus, *P. djamor*, *P. ostreatus* and *P. pulmonarius* intersterility groups show strong preferences for hosts tree species (Tab. I): *P. albidus* (also known in Argentina as *P. laciniatocrenatus* Speg.) was collected in great diversity of substrates from diverse species of living trees to stumps and fallen trunks.

In summary, interspecific crossings permit to separate morphologically very similar species like *P. pulmonarius* and *P. ostreatus* (Lechner et al., 2002). Moreover, mating tests confirmed the synonymy of *P. smithii* with *P. cystidiosus*, and helped to unambiguously identify strains with differing micromorphology within *P. albidus*. Sexual compatibility studies confirmed the heterothallic tetrapolar mating type of all Argentinean *Pleurotus* species, with the presence of multiple alleles as previously reported by Hilber (1982) and Petersen (1995 a).

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