FUSE
Fungal Systematics and Evolution
VOLUME 4
DECEMBER 2019
PAGES 97–170

doi.org/10.3114/fuse.2019.04.08

A revision of the genus *Psathyrella,* with a focus on subsection *Spadiceogriseae*

P. Voto[1], F. Dovana[2], M. Garbelotto[3]

[1]Via Garibaldi 173, 45010 Villadose, Italy
[2]Department of Life Sciences and Systems Biology, University of Torino, Viale P.A. Mattioli 25, I-10125, Torino, Italy
[3]Department of Environmental Science, Policy, and Management; University of California, Berkeley, CA 94720, USA

*Corresponding author: matteog@berkeley.edu

Key words:
key
molecular phylogenetics
new taxa
systematics
taxonomy

Abstract: Specimens belonging to taxa traditionally assigned to the subsection *Spadiceogriseae* of the genus *Psathyrella* were analyzed both morphologically and molecularly. Samples included mainly European collections, selected GenBank accessions, and specimens of various North American taxa described by Smith (1972) and deposited at the Herbarium of the University of Michigan (MICH). Three additional taxa from Africa and Central America were also included. Bayesian and Maximum Likelihood analyses of two loci (ITS and *Tef-1α*) independently and together supported the monophyletic nature of the subsection *Spadiceogriseae*, and identified nine statistically supported clades within the subsection. North American and European species often fell within the same clade, suggesting a relatively recent origin of the subsection or human induced intercontinental movement. While this study determines for the first time that the presence of a white veil is diagnostic for the entire subsection, very few morphological traits were associated with individual clades, but clades were often distinctively different in terms of habitat association, suggesting that trophic interactions may have driven the evolution of this group of fungi.

Combined, morphological and DNA analyses revealed both expected and unexpected synonymies. The new combinations *P. vesiculosa, P. ochrofulva* and *P. sanjuanensis* are proposed, and the new species *P. rogersiae* is described. New information is provided on the taxonomic status and distribution of several species including *P. agrariella*, *P. albescens*, *P. atrifolia*, *P. bivelata*, *P. fatua*, *P. kauffmanii*, *P. aff. kauffmanii*, *P. incondita*, *P. infida*, *P. nitens*, *P. niveobadia*, *P. phegophila*, *P. pseudocorrugis sensu* Kits van Waveren, *P. subnuda*. In total, 13 synonymies were proposed. Based on DNA data, five species of uncertain validity were confirmed as valid, while six species may be ambiguous and may require an in-depth re-analysis. The information gathered in this study was used to generate a key to the species of the subsection *Spadiceogriseae*.

INTRODUCTION

In the morphology-based infrageneric classification of the genus *Psathyrella* by Kits van Waveren (1985), the section *Spadiceogriseae* (subgenus *Psathyra*), type species *P. spadiceogrisea*, includes taxa with spores of medium dimension, pleurocystidia not muricate and mainly utriform with rounded to obtuse apex, and a veil neither granulose nor strongly fibrillose-squamulose. In the same 1985 study, Kits van Waveren further split the section in the two subsections *Spadiceogriseae* and *Lutenses*. Species with gill edges predominantly lined by large numbers of conspicuous sphaeropedunculate to clavate cells, here called paracystidia, amidst a minority of pleurocystidioid cells were placed in the first subsection. Based on this study (see discussion), we include a white veil as an additional morphological trait relevant for species within the subsection.

As we demonstrate in this paper, Kits van Waveren's subsection *Spadiceogriseae* is a well constructed taxonomic unit which has the important advantage to receive full recognition by the molecular evidence, even when applied on a worldwide scale. This subsection only needs to be integrated with *P. ammophila* which, evidently because of its large and dark spores, the Dutch author placed in the subgenus *Psathyrella*, keeping and emending Morgan's (1907) taxon *Deconica Ammophilae* [section *Ammophilae* (Morgan) Kits van Wav. emend., monospecific].

In the earlier work by Romagnesi (1944) the species of this homogenous group are placed in section *Fatuae* (characterized by colorless gill trama) subsection *Spadiceogriseae* Romagn. (type species *Drosophila spadiceogrisea*), but not all of them as *Drosophila frustulenta sensu* Romagnesi which, fide Kits van Waveren (1985), corresponds to *P. clivensis*, is the type species assigned to section *Hydrophilae* (defined on pigmented gill trama) subsection *Frustulentae*. Therefore, Romagnesi (1944) only partially realized the importance of the parameter of dominating paracystidia (which he used for the delimitation of subsection *Spadiceogriseae* inside section *Fatuae*) placing it at a lower level than that of the gill trama pigmentation.

Recently, Örstadius & Knudsen (2012) and Örstadius *et al.* (2015) have published important studies on the genus *Psathyrella* including a modern revision of some species belonging to subsection *Spadiceogriseae*. However, they have not treated this subsection directly; in their keys formal supraspecific taxa are ignored and dichotomic steps are primarily based on partitions of spore length.

When we started this study, a number of ambiguities about European species morphologically belonging to subsection *Spadiceogriseae*, many of which present in Kits van Waveren's monograph (1985), and not resolved by the two modern works aforementioned, were still awaiting a definitive formal recognition by the scientific community (*e.g. P. agraria*, *P. casca*, *P. niveobadia*, *P. phaseolispora*, *P. phegophila*, and *P. pseudocorrugis sensu* Kits van Waveren).

More complex and unresolved is the taxonomy of North American species within the subsection *Spadiceogriseae*, mostly because the taxonomic work by Smith (1972) on North American specimens predated that of Kits van Waveren (1985) by over a decade. Predominance of paracystidia had no recognition at any supraspecific level in his systematic plan. He used the taxon subgenus *Psathyrella* section *Fatuae* for species with spores of medium length and pleurocystidia utriform to broadly rounded at apex, and used the subsection *Fatuae* only to delimit the terrestrial species. *Psathyrella kauffmanii*, for instance, is in subgenus *Pseudostropharia* because of being annulate. The formal species descriptions themselves show that Smith was not aware of the taxonomical importance of the morphological feature of the dominance of paracystidia later used by his European colleague to define the subsection *Spadiceogriseae*. Hence, while he noted the presence of both types of cystidia on gill edges, he did not define their exact frequency ratio, save for those cases when clavate cystidia were exceedingly prevalent. The first aim of this work, therefore, was to search through Smith's monograph for those descriptions revealing a possible inclusion of North American taxa in the subsection *Spadiceogriseae*.

As should be expected, the differences in taxonomic approach by the two systematists resulted in the definition of species that may be difficult to compare based on their original description. Thus, the second aim of this study was to provide a unified classification of a good selection of North American and European taxa.

Finally, our study attempts to clarify the taxonomic position of some of the species described by Smith, either characterized by ambiguously shaped pleurocystidial apices, a trait that makes uncertain their assignment within sections *Spadiceogriseae* or *Pennatae*, or characterized by unclear gills edge patterns, a trait that makes uncertain their assignment to subsections *Spadiceogriseae* or *Lutenses*.

MATERIALS AND METHODS

Samples analyzed

Table 1 lists all of the specimens described included in the study. In brief, morphological and molecular analyses were attempted on a total of 98 samples, including 60 North American, one Central American, 35 European and two African specimens. A total of 47 holotypes and five paratypes were included in this study.

We note that due to limited sample size, types vouchers of the following taxa could not be obtained from the Herbarium at the University of Michigan (MICH): *P. ambusta*, *P. flexuosipes*, *P. incondita*, *P. carolinensis*, *P. lactobrunnescens*, *P. latispora*, *P. praecox* and *P. subcinerascens*. Paratypes of *P. flexuosipes*, *P. incondita* and *P. praecox* were loaned to us. Unfortunately, the type vouchers of some European species, *e.g. P. niveobadia*, *P. phaseolispora*, *P. phegophila*, and of the South American species *P. macquariensis* could not be obtained. Finally, although we obtained a type for the following species, they failed to produce a DNA sequence: *P. affinis*, *P. almerensis*, *P. ovaticystis*, *P. psammophila*, *P. rugulosa*, *P. solheimii*, *P. solheimii var. sanjuanensis, P. tenacipes*, *P. velibrunnescens*, *P. yaoundeana*. Table 2 lists all additional sequences used in the ITS phylogenetic analysis and retrieved both from GenBank or UNITE.

Morphology

Spore color was assessed in water suspensions. Dried material was first imbibed with either 5 % KOH or 10 % NH_4OH. A 5 % KOH stain was used to determine pigmentation of the marginal cystidia and of the underlying cells. A 10 % NH_4OH dilution was used to determine traits of pleurocystidia including wall thickness, presence of incrustation, and pigmentation. Congo red was used for staining and picture-documentation of microscopical features of interest.

A number of words in Smith's monograph that are not used in the European terminology were interpreted as follows. Inequilateral (spore shape in profile) = amygdaliform. Terete (spore shape) = bidimensional, in contrast to flattened tridimensional spores which need to be described in length, width in side view, and width in profile. Acute, obtuse, rounded and truncate (spore pole and cystidial apex): we maintain Smith's description of four levels of rotundity, from sharp (acute) through midway (obtuse) to broadly curved (rounded) or flat (truncate). Distant, close and crowded (frequency of gills): we substitute the term 'close' with the expression 'moderately crowded'.

When observed in 10 % NH_4OH, pleurocystidia may show an irrelevant greenish tint, only yellowish to brownish pigments are considered relevant. The cystidial cells on the gill edge in *Psathyrella* are often of two types; cheilocystidia and paracystidia. We call cheilocystidia those resembling pleurocystidia, while we call paracystidia, *sensu* Huijsman (1955), those having an apically undifferentiated shape (that is clavate, spheropedunculate, obpyriform, sometimes slender and more or less cylindrical); the term "dominating" in the text is used to indicate the predominance on gills edges of either one of the two types of cells described above. However, two ambiguous cases can sometimes occur, i.e. either some marginal cells may have an intermediate shape with a subtle differentiation at the apex, or the pleurocystidia themselves may also be undifferentiated in shape, *e.g.* ellipsoid to clavate. In both cases, a clear-cut distinction between the two types of marginal cells is not possible. The shape of cheilocystidia is usually omitted in our descriptions because it generally mirrors that of the pleurocystidia, except for a tendency to bear somewhat smaller dimensions. Sometimes, they may be partially described if they conspicuously deviate from the main pleurocystidial pattern; however, cheilocystidia may be characterized by a narrower apex or a slenderer neck than pleurocystidia.

Presence of a germ pore is assessed in KOH, while its shape is assessed in water, as it may tend to swell when observed in alkali. The letter Q indicates the quotient of bidimensional spores, that is the ratio length/breadth, but when the spores are tridimensional, the symbols fQ and pQ are used instead to indicate the quotient in front and, respectively, in profile view

The term avQ stands for the average value of Q.

Table 1. Data of specimens used in this study. Names previously proposed by other authors are identified by an asterisk.

Species	Coll. ID/Origin	Revised proposed name (*)	Ecology	GenBank Accession Numbers	
				ITS/LSU	*Tef 1-α*
Drosophila pallidispora Murrill → *P. neotropica* A.H. Sm.	Earle572 (NY00649148) type/CU		In soil in a garden	–	–
Psathyrella abieticola A. H. Sm.	Smith58673 (MICH5337) type/US		Under spruce and fir	KC992891	–
P. aff. *kauffmanii*	PRM897750/CZ	? *P. velibrunnescens*	On very rotten trunk of *Fagus*	AM712260	–
P. affinis A.H. Sm.	MICH11857 type/US		On wet leaves in swamp	–	–
P. agraria Endere ad int.	KR0030008 type/DE		In a mossy cornfied	KU307507	–
P. agrariella (G.F. Atk.) A.H. Sm.	MICH47933/US	*P. albescens*	On sandy humus	MF326008	MF521824
P. agrariella	MICH65241/US	? *P. albescens*	In moist soil and moss under *Salix*	MF325951	–
P. agrariella	MICH47939/US	=?	On sawdust pile	MF325950	–
P. agrariella var. *ochrofulva* A.H. Sm.	MICH11858 type/US	*P. ochrofulva* comb. nov.	On sandy humus in cut-over hardwoods	MF325987	–
P. albanyensis A.H. Sm.	MICH11862 type/US		On soil under aspen and conifers	MF325952	MF521823
P. albescens Hesler & A.H. Sm.	MICH11863 type/US		On decaying chip	–	MF521817
P. albescens	MCVE29106/IT		In a park	MF325953	MF521822
P. albescens	MCVE29107/IT		Among brambles and *Robinia*	MF326009	MF521821
P. albescens	MCVE29111/IT		On humus of *Quercus ilex*	–	MF521820
P. albescens	MCVE29113/IT		On humus at margin of wood	MF325954	MF521819
P. albescens	MCVE29116/IT		Among hardwood trees	MF325955	MF521818
P. almerensis Kits van Wav.	J. Daams (L) type/NL	*P. thujina**	On remnants of culms of *Typha*, *Phragmittes* and *Cirsium*	–	–
P. almerensis	LÖ31-04/SE	*P. thujina**	On moist soil	KC992874	–
P. almerensis	LÖ379-06/SE	*P. hellebosensis**	On remnants of *Phragmites*	KC992873	KJ732768
P. alnicola A.H. Sm.	MICH11868 type/US		Under alder	MF325957	MF521815
P. amarella A.H. Sm.	MICH11869 type/US	*P. spadiceogrisea*	On leaf mold in hardwood forest	MF325958	–
P. ammophila (Durieu & Lév.) P.D. Orton	LÖ169-01/SE		On sand dune	KC992871	–
P. ammophila	LÖ359-11/SE		On moist soil	–	KJ732767
P. angusticystis A.H. Sm.	MICH11873 type/US	*P. psammophila*	On debris in a clearing	MF325959	–
P. argillacea A.H. Sm.	MICH65256 paratype/US		Habitat unknown	–	MF521814
P. atomatoides (Peck) A. H. Sm.	LÖ249-82/SE		Moist on wood in a forest	KC992930	–
P. atrifolia (Peck) A.H. Sm.	MICH32732/US	*P. praetenuis*	Among cottonwood tree	MF325960	MF521813
P. atrifolia (Peck) A.H. Sm.	MICH65288/US	*P. praetenuis*	Habitat unknown	–	–
P. atrifolia (Peck) A.H. Sm.	MICH65287/US	=?	Habitat unknown	–	–
P. bivelata Contu	MCVE29104/IT		On grassy soil	MF325961	MF521812
P. bivelata	MCVE29117/IT		On soil in urban flowerbed	MF325962	MF521811
P. candolleana (Fr.: Fr.) Maire	LÖ38-00/SE		In a rich deciduous forest	DQ389720	–

Table 1. (Continued).

Species	**Coll. ID/Origin**	**Revised proposed name (*)**	**Ecology**	**GenBank Accession Numbers**	
				ITS/LSU	***Tef 1-α***
P. candolleana	EB990221/IT		Among debris in clearing of pinewood	KF281384	–
P. carinthiaca Voto	MCVE25611 type/AT		On humus in spruce forest	MF325963	–
P. carminei Örstadius & E. Larss.	LÖ5-09 type/IT	*P. owyheensis*	On soil in *Pinus* forest	KC992880	KJ732773
P. clivensis (Berk. & Broome) P. D. Orton	LÖ182-03/SE		On the great alvar	DQ389683	KJ732774
P. corrugis(Pers.: Fr.) Konrad & Maubl.	LÖ171-01/SE		Attached to buried wood	–	KJ732757
P. corrugis	MCVE29121/IT		On litter of pine-needles	MF325964	–
P. cortinarioides P.D. Orton	MCVE28713/IT		On soil in chestnut and birch wood	MF326010	MF521810
P. cortinarioides	LÖ77-00/SE		Moist, rich with Alnus	KC992936	–
P. ellenae var. *yubaensis* Thiers & A.H. Sm.	MICH11919 type/US		On humus in conifer woods	MF326011	–
P. ephemera A.H. Sm.	MICH11921 type/US		On black muck in a swamp	MF325965	–
P. fagetophila Örstadius & Enderle	LÖ210-85 (M) type/SE		Woodland among leaves	KC992902	–
P. fatua (Fr.) Konrad & Maubl.	LÖ231-08/SE		On dry sandy soil	–	KJ732772
P. fatua	LÖ132-97 neotype/SE		On nitrophilous soil	DQ389681	–
P. fatua	MCVE29105/IT		On litter of *Quercus ilex*	MF325966	MF521809
P. fatua	MCVE29108/IT		On buried roots	MF325967	MF521808
P. fatua	MCVE29109/IT		On soil at the top of a ditch bank	–	MF521807
P. fatua	MCVE29110/IT		On litter of *Quercus ilex*	–	MF521806
P. fatua	MCVE29115/IT		In grass	–	MF521805
P. fatua	MCVE29122/IT		On soil in a park	MF325968	MF521804
P. fatua	MCVE29123/IT		On humus at margin of wood	–	MF521803
P. fatua	MCVE29124/IT		On grassy ground at the top of a river bank	–	MF521802
P. flexuosipes A.H. Sm.	MICH32961 paratype/US		On debris	MF325969	–
P. fragrans A.H. Sm.	MICH5347 type/US		On conifer debris	MF325970	MF521801
P. fulvoumbrina A.H. Sm.	MICH5833 type/US	*P. umbrosa*	Under aspen and fir	MF417625	MF521800
P. fusca (J.E. Lange) A. Pearson	LÖ287-04/SE		On calcareous soil	KC992892	KJ732779
P. fusca	Smith75099 (MICH48491)/US	*P. kauffmanii*	In wet soil	MF325971	MF521799
P. gordonii (Berk. & Broome) A. Pearson & Dennis	MCVE28708/IT		On grassy soil	MF325972	MF521798
P. gordonii	MCVE28710/IT		On horse-manured soil	MF325973	MF521797
P. griseopallida Thiers & A.H. Sm.	MICH11939 type/US		On sandy soil near an oak log	MF325974	MF521796
P. hellebosensis Deschuyteneer & Melzer	MCVE29114/IT		On soil by a river	MF325956	MF521816
P. hirta Peck	LÖ142-00/SE		Cow dung	–	KJ732800
P. incondita A.H. Sm.	MICH36450 paratype/US		On elm wood	MF325975	–
P. incondita	MICH36451 paratype/US	=?	Under pines	MF325976	MF521795
P. infida Quél.	MCVE29119/IT		On moist soil with deciduous trees	MF325977	MF521794

Table 1. (Continued).

Species	Coll. ID/Origin	Revised proposed name (*)	Ecology	GenBank Accession Numbers	
				ITS/LSU	*Tef 1-α*
P. kauffmanii A.H. Sm.	MICH11962 type/US		On hardwood debris	–	MF521792
P. kauffmanii	MCVE29101/ES		In beech leaf litter	MF325978	MF521793
P. leucotephra (Berk. & Broome) P.D. Orton	MCVE28705/ES		On soil under *Populus* and *Platanus*	MF325979	MF521791
P. limicola var. *subpectinata* A.H. Sm.	MICH11965 type/US		On wet soil along stream	MF325980	–
P. longicauda P. Karst.	LÖ201-02/SE		In a copse	–	KJ732778
P. lubrica A.H. Sm.	MICH11957 type/US	*P. spadiceogrisea*	On muck	–	MF521771
P. lutulenta Esteve-Rav. & M. Villarreal	AH21379 type/ES	*P. thujina**	On muddy soil	KC992875	KJ732769
P. magnispora Heykoop & G. Moreno	24929 (AH) type/ES		In chalk grassland	KC992863	–
P. mazzeri A.H. Sm.	MICH11963 type/US	*P. albescens*	In a pasture	MF325981	MF521790
P. microrhiza (Lasch: Fr.) Konrad & Maubl.	LÖ185-02/SE		In a rich deciduous forest	–	KJ732765
P. nitens A.H. Sm.	MICH11983 type/US		On debris	MF325982	MF521789
P. nitens	MICH33251/US		On debris	MF325985	MF521787
P. nitens	MICH33252/US		On alder debris	MF325986	MF521786
P. nitens	MICH33249/US	=?	On humus	MF325983	MF521788
P. nitens	MICH33250/US	=?	On humus	MF325984	–
P. niveobadia (Romagn.) M.M. Moser	MCVE30076/IT		On humus around a stump of *Fagus*	MK400421	MK408675
P. niveobadia	MCVE29102/IT		Around a stump of *Fagus*	MF325996	MF521780
P. obtusata (Pers.: Fr.) A. H. Sm.	LÖ88-01/SE		In moist soil in forest	DQ389711	–
P. obtusata	MICH49136/US		On hardwood logs	–	–
P. obtusata	MICH65721/US	*P. atomatoides*	Habitat unknown	MF326013	–
P. obtusata	MICH33261/US	=?	On debris of cedar slash	MF326012	–
P. olivaceopallida A.H. Sm.	MICH11990 type/US	*P. kauffmanii*	On humus in hardwoods	MF325988	–
P. oregonensis A.H. Sm.	MICH5840 type/US		On conifer wood	MF325989	–
P. ovaticystis Pegler	Pegler1433 (K(M)196311) type/UG		Among leaf litter	–	–
P. owyheensis A.H. Sm.	MICH5357 type/US		In grass near cow dung	MF325990	MF521785
P. pennata (Fr.) A. Pearson & Dennis	LÖ206-03/SE		On burnt soil	–	KJ732813
P. phegophila Romagn.	Tassi97076/FR	*P. kauffmanii*	On leaves and debris in calcareous *Fagus* wood	–	–
P. piluliformis (Bull.: Fr.) P. D. Orton	MCVE29118/IT		On stump of frondose tree	MF325991	MF521784
P. piluliformis	LÖ162-02/DE		On stump of *Fagus*	DQ389699	KJ732808
P. praecox A.H. Sm.	MICH49251 paratype/US	*P. spadiceogrisea*	On soggy leaf mold near edge of pond	MF325992	MF521783
P. praetenuis A.H. Sm.	MICH5361 type/US		On debris of cottonwood tree	MF325993	MF521782
P. pratensis A. H. Sm.	MICH12009 type/US		In pasture on sod near cow manure	MF325994	–
P. psammophila A. H. Sm.	Smith67836 (MICH12012) type/US		In sandy soil	KC992856	–
P. pseudogordonii Kits van Wav.	P.D. Orton (K) type/GB	*P. gordonii**	On stumps of *Fagus*	–	–

Table 1. (Continued).

Species	Coll. ID/Origin	Revised proposed name (*)	Ecology	GenBank Accession Numbers	
				ITS/LSU	*Tef 1-α*
P. pseudogordonii	Pérez-De-GregorioPG121105 (MCVE28705)/ES	*P. leucotephra*	On soil under *Populus* and *Platanus*	MF325979	MF521791
P. pseudolimicola A.H. Sm.	MICH5366 type/US		On mud in a cow pasture	–	MF521781
P. rogersiae Voto, Garbelotto & Chiarello	MCVE29120 type/IT		In moist plain with hygrophilous plants	MF325995	–
P. rostellata Örstadius	LÖ 228–85 type/SE		Deciduous wood	DQ389693	–
P. rugulosa A.H. Sm.	MICH12040 type/US		On a spruce log	–	–
P. seminuda A. H. Sm.	Smith34091 (MICH12043) type/US		On soil	KC992907	–
P. septentrionalis A.H. Sm.	MICH12045 type/US		On hardwood	MF326014	–
P. septentrionalis var. *vesiculosa* A.H. Sm.	MICH12044 type/US	*P. vesiculosa* comb. nov.	On hardwood logs	MF326015	–
P. solheimii McKnight & A.H. Sm. Mem.	MICH12054 type/US		On moist soil under aspen	–	–
P. solheimii var. *sanjuanensis* A.H. Sm.	MICH12055 type/US	*P. sanjuanensis* comb. nov.	Under aspen	–	–
P. sp	NL-0631/HU		On clayey, mossy soil	KC992877	KJ732770
P. spadiceogrisea (Schaeff.) Maire	LÖ102-98/SE		Among leaves in a pasture	–	KJ732771
P. spadiceogrisea	LÖ92-01/SE		In a deciduous forest	DQ389682	–
P. spadiceogrisea	Tassi04005 (MCVE29103)/FR		In a park	MF325997	MF521779
P. spadiceogrisea	Smith74295 (MICH49606)/US	*P. kauffmanii*	Debris	MF325998	–
P. sphaerocystis P. D. Orton	LÖ126-99/SE		Horse dung	–	KJ732803
P. sphagnicola (Maire) J. Favre	LÖ233-99/SE		On *Sphagnum* with *Picea*	KC992937	–
P. squamosa (P. Karst.) A. H. Sm.	LÖ194-96/SE		On a sandy roadside	KC992940	–
P. subargillacea A.H. Sm.	MICH12058 type/US	*P. psammophila*	On rotten wood	MF325999	–
P. subnuda (Karsten) A.H. Sm.	MICH33421/US	*P. abieticola*	On burned soil	MF326000	MF521778
P. subvinacea A.H. Sm.	MICH12085 Type/US	*P. kauffmanii*	On underside of logs	MF326001	MF521777
P. sulcatotuberculosa (J. Favre) Einhell.	MCVE29112/IT		On moist soil by a rice field	MF326002	–
P. tenacipes A.H. Sm.	MICH12091 type/US		On drying muck and small sticks in ash swamp	–	–
P. tenera Peck	LÖ81-83/SE		In a moist *Alnus* forest	KC992849	–
P. thujina A.H. Sm.	Smith66720 (MICH12097) type/US		On black muck	KC992876	MF521776
P. umbrosa A.H. Sm.	MICH12102 type/US		On soil among rotten wood	MF326003	MF521775
P. velatipes A.H. Sm.	MICH12106 type/US	*P. ammophila*	In a parking strip	MF326004	MF521774
P. velibrunnescens A.H. Sm.	MICH12107 type/US		On *Alnus* debris	–	–
P. subnuda var. *velosa* A.H. Sm.	MICH5376 type/US	*P. abieticola*	On debris of cottonwood tree	MF326005	MF521773
P. velosa	MICH33441/US		Habitat unknown	MF326006	–
P. vesiculocystis A.H. Sm.	MICH5380 type/US	*P. abieticola*	On conifer duff	MF326007	MF521772
P. warrenensis A. H. Sm.	Smith70162 (MICH5382) type/US		On grassy soil	KC992906	–
P. yaoundeana Mossebo & Pegler	Mossebo42B (K(M)55648) type/CM		Among grass	–	–

Table 2. List of sequences used in the ITS analysis without matching morphological analysis, including original Collection ID, origin when available, and GenBank or UNITE accession number.

Species	Coll. ID/Origin	GenBank/UNITE Accession Numbers
Psathyrella ammophila	O-F-253115/NO	UDB037642
Psathyrella ammophila	LO99/NO	UDB017672
Psathyrella ammophila	AH:947/ES	KY350223
Psathyrella ammophila	SZMCNL 3398	FN396112
Psathyrella ammophila	AH24456	KY350224
Psathyrella ammophila	LO169-01/SE	KC992871
Psathyrella ammophila	AH947	MF966506
Psathyrella ammophila	AH24456	MF966486
Psathyrella casca	AM1814/DE	MF668177
Psathyrella cascoides	AV080419/DE	MK045734
Psathyrella cascoides	DW170430/DE	MK026744
Psathyrella cf. gracilis	SOC997/US	FJ235146
Psathyrella clivensis	AM1913/FR	MK129249
Psathyrella fatua	DD8849/BE	MK182811
Psathyrella fatua	DW160426/DE	MH997496
Psathyrella fatua	SZMC-NL-0603	FN396142
Psathyrella fatua	AM1726/DE	MK072832
Psathyrella fatua	DD0223/BE	MK182825
Psathyrella fatua	AH33718	MF966492
Psathyrella fatua	AH:33718/ES	KY350222
Psathyrella fatua	DD2601/BE	MK182826
Psathyrella fatua	DD2602/BE	MK182822
Psathyrella fatua	DD0222/BE	MK182821
Psathyrella fatua	AH22059	MF966485
Psathyrella fatua	LO231-08	KC992879
Psathyrella fatua	AM445/DE	MK045704
Psathyrella jacobssonii	LO256-92/SE	KC992855
Psathyrella mammifera	HMJAU21908/CN	MG734734
Psathyrella mammifera	HMJAU 37882/CN	MG734740
Psathyrella marquana	AM1693/DE	MF668178
Psathyrella microrhiza	TU106657/EE	UDB011850
Psathyrella microrhiza	TU106614/EE	UDB011827
Psathyrella phegophila	AH45940/ES	KY350219
Psathyrella phegophila	HMJAU 28267/CN	MG734728
Psathyrella phegophila	BRNM705637	AM712277
Psathyrella phegophila	HMJAU 37848/CN	MG734738
Psathyrella prona	303322/US	MK607583
Psathyrella pseudogracilis	TU106565/EE	UDB011802
Psathyrella spadiceogrisea	TU118645/EE	UDB018041
Psathyrella spadiceogrisea	TU106529/EE	UDB011718
Psathyrella spadiceogrisea	TU106528/EE	UDB011717
Psathyrella spadiceogrisea	TU106574/EE	UDB011808
Psathyrella spadiceogrisea	TENN:068273/US	KY744152
Psathyrella spadiceogrisea	AM1244/DE	MK045702
Psathyrella spadiceogrisea	BRNM705637/CZ	AM712276
Psathyrella spadiceogrisea	GENT JR3565/BE	MK045679
Psathyrella spadiceogrisea	AM1242/DE	MK045696

Table 2. (Continued).

Species	Coll. ID/Origin	GenBank/UNITE Accession Numbers
Psathyrella spadiceogrisea	LO102-98/SE	KC992878
Psathyrella spadiceogrisea	AM1671/DE	MK045698
Psathyrella spadiceogrisea	HIAS120608/DE	MK045697
Psathyrella spadiceogrisea	SZMC-NL-0440	FM878024
Psathyrella spadiceogrisea	AM1581/ES	MK045703
Psathyrella spadiceogrisea	CBS 171.47/PT	MH856203
Psathyrella striatoannulata	INB3978642/CR	KY350221
Psathyrella striatoannulata	INB4162132	KY350220
Psathyrella sublatispora	AH40381/ES	MF966502
Psathyrella sublatispora	LO190-97/SE	KC992854
Psathyrella subspadiceogrisea	HMJAU 35992 type/CN	KY678465
Psathyrella subspadiceogrisea	HMJAU 35996/CN	KY678466
Psathyrella thujina	AM1656	KY680791
Psathyrella thujina	AM1849	KY680792

Pictures of pleurocystidia and marginal cells are used to show their shape and sometimes their color or incrustations in ammonia or KOH; otherwise, they are shown in Congo red. The most relevant spore shapes are illustrated in the Figures, while spore color is better described in writing, due to possible distortions of the digital imagery or to the small number of fully ripe spores.

All species studied and described have clamps and 4-spored basidia, therefore these two features are generally omitted.

Material studied

Personal collections and duplicates of some of the material received as a gift are deposited in the fungarium of Museo di Storia Naturale di Venezia (The Venice Museum of Natural History, MCVE). All of Smith's types, paratypes and other collections used in this study were on loan from the University of Michigan Fungarium (MICH). When the small size of a type specimen prevented a loan, the collection manager selected for us an available paratype from other collections cited by Smith (1972). Other collections were received on loan from the Royal Botanic Garden at Kew (K), the Naturalis Biodiversity Center (former National Herbarium of Leiden, L), the Fungarium of the New York Botanical Garden (NY), and from private fungaria. Unfortunately, we were not able to obtain the types of *P. niveobadia*, *P. phegophila, P. phaseolispora* and *P. macquariensis*. Table 1 reports all samples studied, including the specimens sequenced, the GenBank accession numbers of the sequences generated, host and state of collection, and, when appropriate, the name assigned to them following our revision.

DNA extraction, PCR and sequencing

DNA was extracted from all dried sporocarps as described by Swo *et al.* (2004). Briefly, samples were ground to a fine dust using a bead mill, suspended in a CTAB extraction buffer before being frozen using dry ice and then thawed using a heating block set at 70 °C, for three freeze-thaw cycles. Samples were then incubated at 70 °C for 30 min before being fully submerged in phenol : chloroform : isoamyl alcohol (25:24:1) and centrifuged for 15 min at 13 000 g. Finally, DNA was purified from the supernatant using the GeneClean Turbo kit (QBiogene, Inc). Samples that failed to amplify using this extraction procedure were extracted using the NaOH protocol described by Osmundson *et al.* (2013). Briefly, 200 µL of 0.5 N NaOH were added to the ground lyophilized tissue. Samples were briefly vortexed, then 5 µL were transferred to a new tube containing 495 µL of 100 mM Tris, pH 8.0; 1 µL of this mixture was used as template DNA in a 25 µL PCR reaction.

Two genomic loci were selected to conduct the phylogenetic analyses. The markers were the nuclear ribosomal Internal Transcribed Spacer (ITS) and the translation elongation factor 1-alpha (*Tef-1α*). Primers used for the amplification and sequencing of ITS were 5'-CTTGGTCATTTAGAGGAAGTAA-3' (ITS1f; forward) and 5'-TCCTCCGCTTATTGATATGC-3' (ITS4; reverse) (Gardes & Bruns 1993), while those used for *Tef-1α* were 5'-GCYCCYGGHCAYCGTGAYTTYAT-3' (983 forward) and 5'-ACHGTRCCRATACCACCRATCTT-3' (1567 reverse) (http://www2.clarku.edu/faculty/dhibbett/Protocols_Folder/Primers/Primers.pdf). Amplification reactions were performed in the following 25 µL reaction mixture: 5× buffer, 0.2 mM dNTPs, 1.25 U/ µL of GoTaq polymerase (Promega Corp. Madison, WI), 2.0 mM $MgCl_2$ (Invitrogen Corp. Carlsbad, CA, USA), 0.50 uM each non-degenerate primer or 0.64 uM each degenerate primer, and approximately 20 ng of DNA. The PCR program was: 95 °C for 3 min, followed by 35 cycles of 95 °C for 40 s, different annealing temperature (53 °C for ITS, and a touchdown between 66 °C and 56 °C with a 1 °C decrease at each cycle for *Tef-1α*) for 55 s, 72 °C for 55 s, and an extension step at 72 °C for 7 min. The purified PCR amplicons of ITS and *Tef-1α* were Sanger-sequenced in-house at the Forest Pathology and Mycology Laboratory (Berkeley, USA). All amplicons were forward and reverse sequenced with the related primers, and consensus sequences were generated by using the Geneious software, v. 9.0.5 (Biomatters, Ltd). Chromatograms of each sequence were analyzed by using both Geneious and SnapGene® Viewer. The minimum acceptable phred score considered per base was 20.

Molecular analyses

Analyses were performed on the four following datasets: 1)- the first included 160 ITS sequences, 68 generated by this study, 83 obtained from GenBank and nine from UNITE; 2)- the second included 72 *Tef-1α* sequences, 56 generated by this study and 16 selected from GenBank; 3)- the third included both ITS and *Tef-1α* sequences for 52 taxa, 43 generated by this study, and nine selected from GenBank; 4)- the fourth included ITS and *Tef-1α* sequences for 224 taxa, both sequenced in this study and previously analyzed by Örstadius *et al*. (2015). The sequences of *Bolbitius vitellinus* (AFTOL730) and *Mythicomyces corneipes* (AFTOL972) were selected as outgroups in all of the analyses.

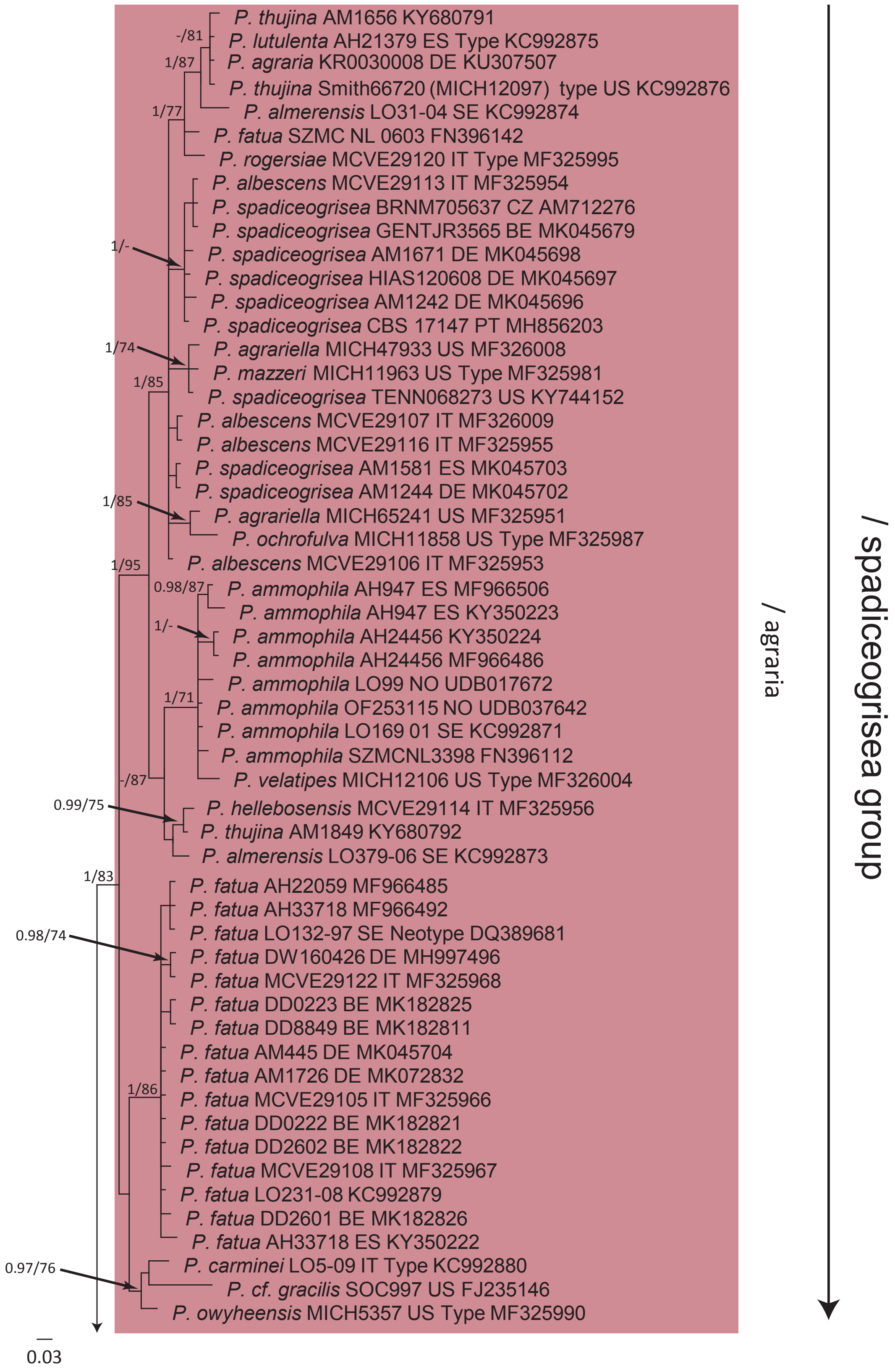


Fig. 1. Bayesian phylogram obtained from the general nrITS sequence alignment of *Psathyrella* spp. *Bolbitius vitellinus* was used as outgroup taxon. Only BPP values ≥ 0.95 and MLB values ≥ 70 % are given above clade branches.

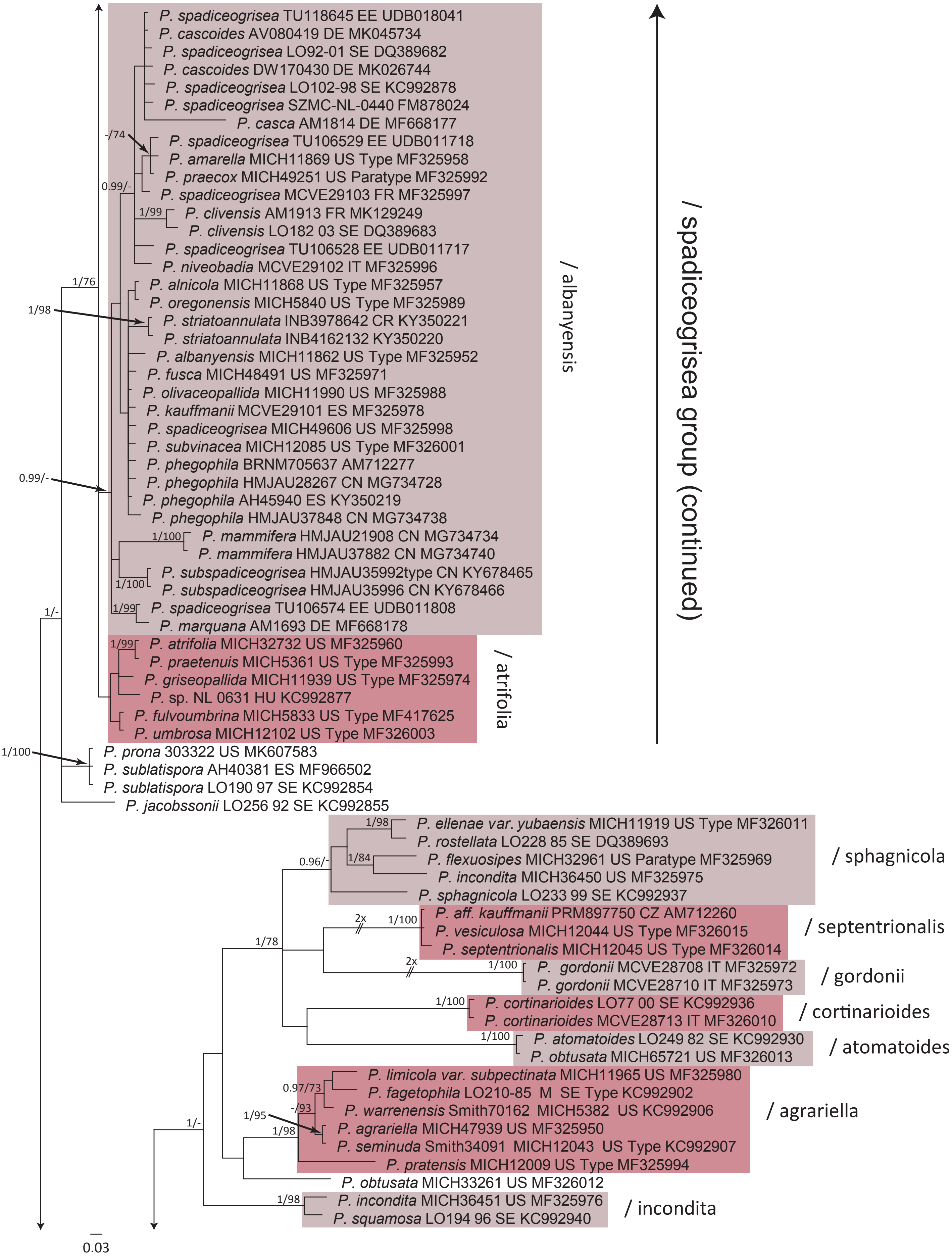


Fig. 1. (Continued).

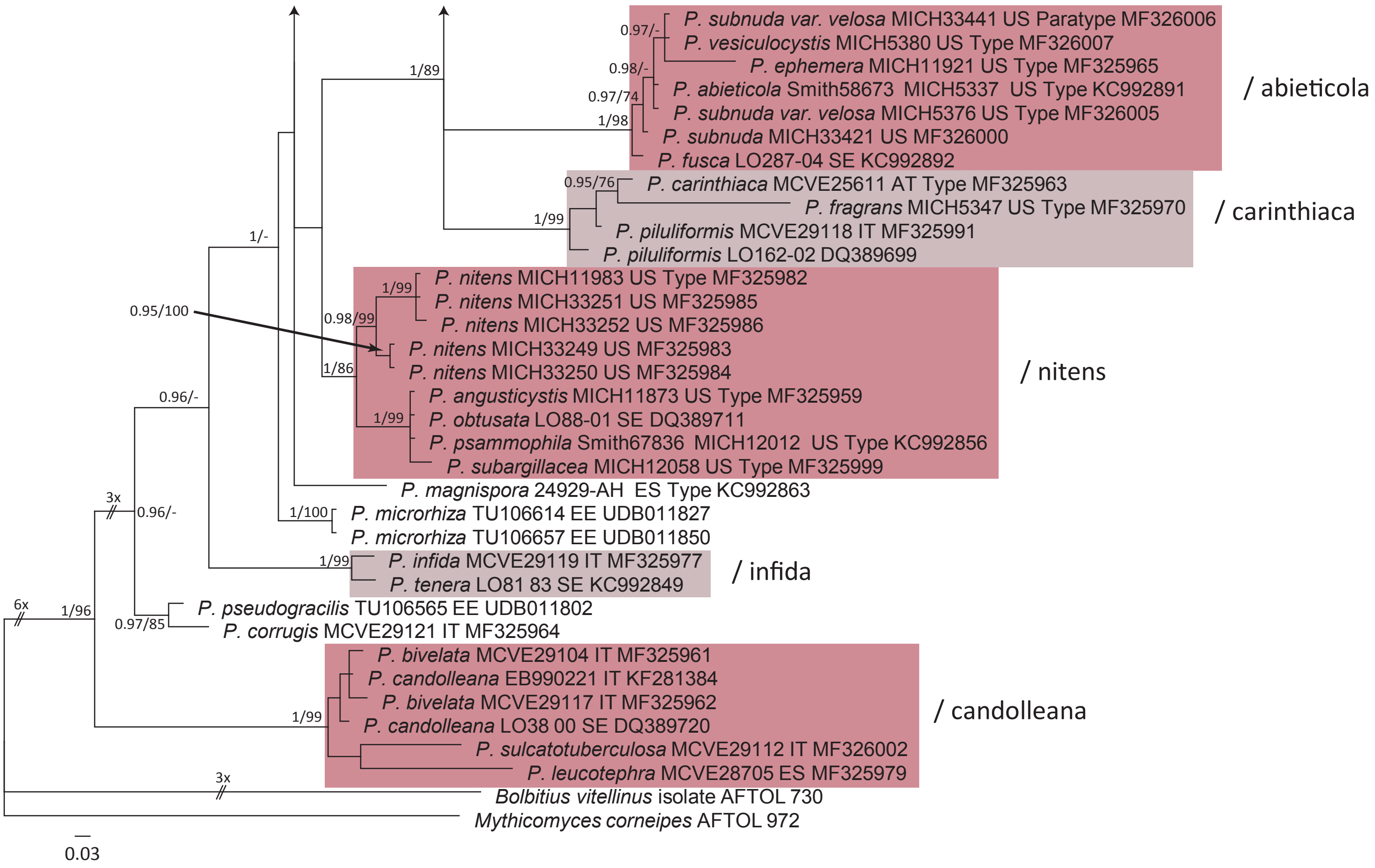


Fig. 1. (Continued).

Sequences of each dataset were first aligned using MAFFT v. 7.017 (Katoh *et al.* 2002) using default conditions for gap openings and gap extension penalties. Finally, alignments were manually adjusted using Geneious v. R 11.1.4 (https://www.geneious.com, Kearse *et al.* 2012). The model of sequence evolution GTR +GAMMA+I was selected with the program Modeltest v. 3.7 (Posada & Crandall 1998). A partition homogeneity test was performed with PAUP v. 4.0a (build 159) (Swofford 2003) to assess character congruence between ITS and *Tef-1α* data sets. All datasets were analyzed using Bayesian inference (BI) and maximum likelihood (ML) criteria. The ITS and *Tef-1α* data sets were partitioned. BI analysis was performed using MrBayes v. 3.2 (Ronquist *et al.* 2012) with four incrementally heated simultaneous Monte Carlo Markov Chains (MCMC) run for 10 M generations in datasets 1,2,3 and for 20 M generations in dataset 4. Trees were sampled every 1 000 generations and the first 25 % trees were discarded as “burn-in” . ML was performed with RAxML v. 7.2.8. (Stamatakis 2006) in Geneious v. R 11.1.4 (Kearse *et al.* 2012), using a total of 1 000 bootstrap replicates (Felsenstein 1985) to assess the relative robustness of the branches of maximum likelihood in RAxML. Only BPP values ≥ 0.95 and MLB values ≥ 70 % were reported in phylogenetic trees (Figs 1, 2). Pairwise % identity values of ITS and *Tef-1α* sequences were calculated using MEGA v. 10.0.4 (Kumar *et al.* 2018). BI analyses of the fourth dataset were run on the CIPRES Science Gateway (Miller *et al.* 2010).

Molecular data were used to contrast or support the extensive morphology-based taxonomy, and to resolve uncertainties that could not be resolved solely based on morphology. Nucleotide homology calculated using BLAST (Altschul *et al.* 1990) and positioning of sequences on phylogenetic trees were both used to infer presence or absence of molecular conspecificity. When both ITS and *Tef-1α* were >98 % homologous, and the taxa from which both sequences were derived fell as immediate neighbors on a BI tree, this evidence was regarded as strong support of conspecificity. ITS and/or *Tef-1α* homology < 97 % was used to support lack of conspecificity, while > 98 % homology of the ITS only was regarded as inconclusive. If homology levels between two taxa were 97–98 %, the phylogenetic positioning of the taxa bearing the sequences was analyzed. Additionally, in these cases, it was analyzed whether heterozygosities or indels were located in introns or exons, and whether they were synonymous or not. Non-synonymous exonic heterozygosities and indels in exons were taken as indication of higher divergence between taxa.

Taxonomy

1. *Psathyrella kauffmanii* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 69. 1972. Figs 4, 5.

Molecular heterotypical synonyms and misapplied names proposed here: *Psathyrella olivaceopallida* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 138. 1972; *Psathyrella subvinacea* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 124. 1972; *Psathyrella fusca sensu* A.H. Smith, *Mem. N. Y. Bot. Gard.* **24**: 355. 1972, p.p.; *Psathyrella spadiceogrisea sensu* A.H. Smith, *Mem. N. Y. Bot. Gard.* **24**: 354. 1972, p.p.

Morphological heterotypical synonyms proposed here: *Psathyrella carolinensis* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 142. 1972;

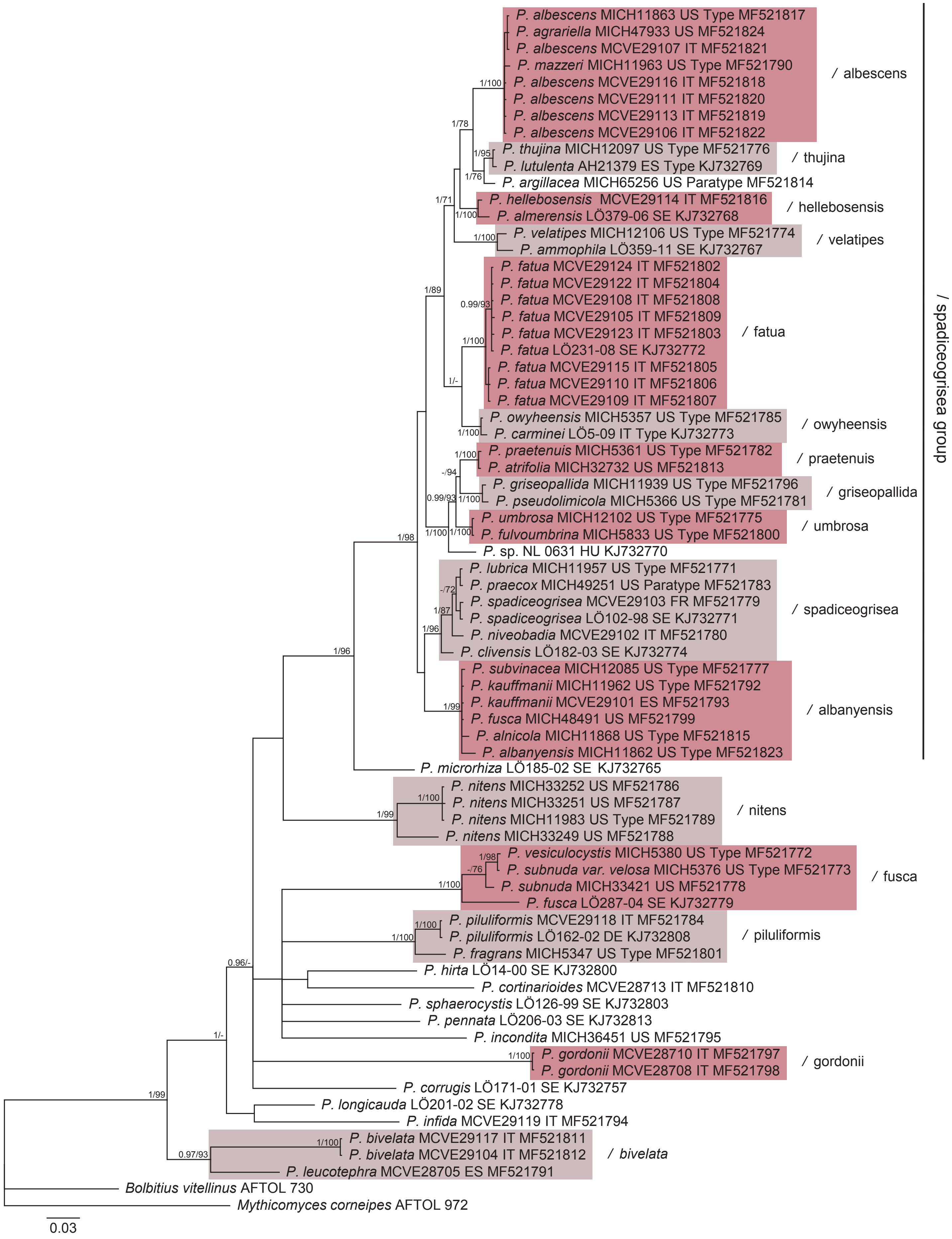


Fig. 2. Bayesian phylogram obtained from the general *Tef-1α* sequence alignment of *Psathyrella* spp. *Bolbitius vitellinus* was used as outgroup taxon. Only BPP values ≥ 0.95 and MLB values ≥ 70 % are given above clade branches.

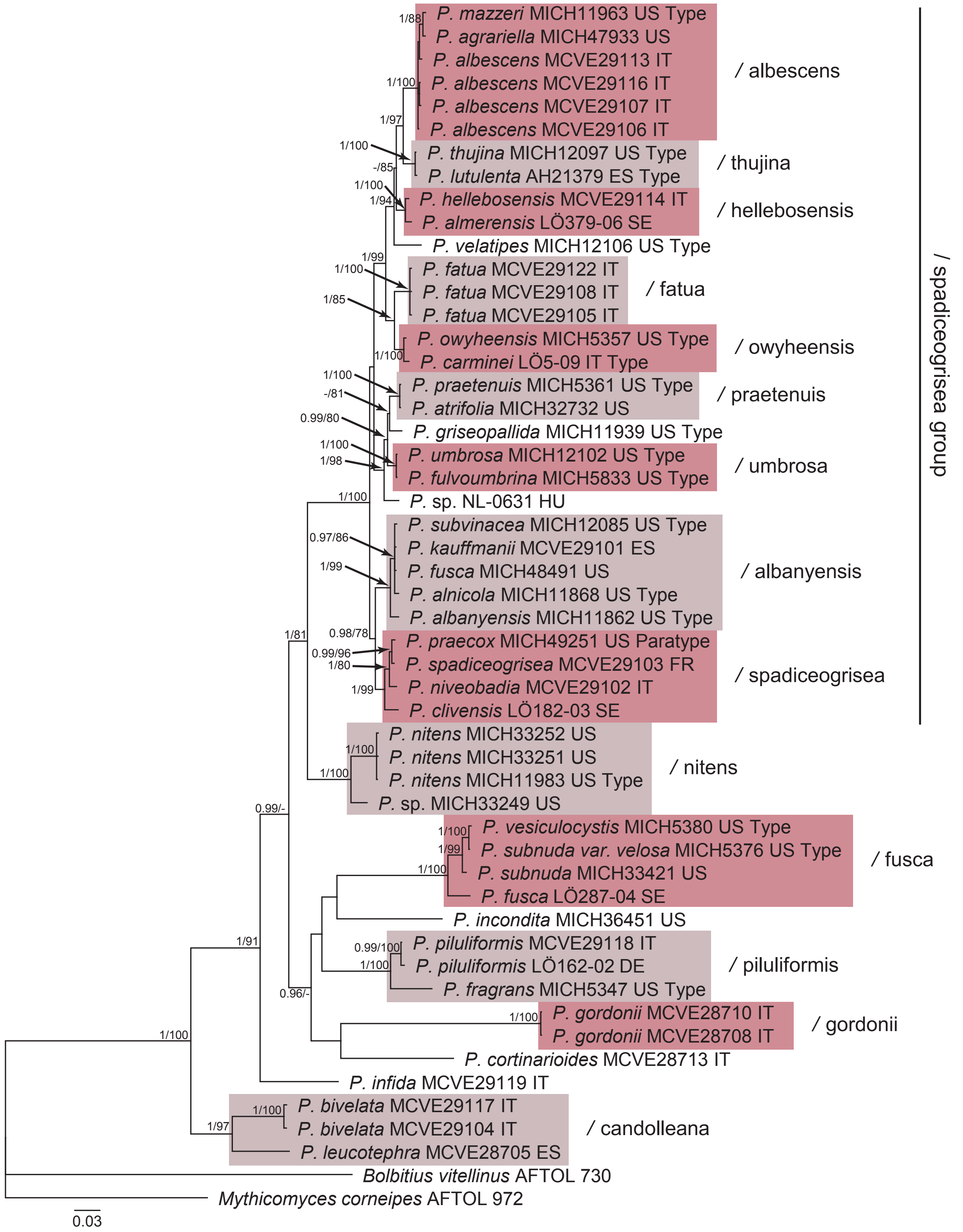


Fig. 3. Bayesian phylogram obtained from combined nrITS and *Tef-1α* sequence alignment of *Psathyrella* spp. *Bolbitius vitellinus* was used as outgroup taxon. Only BPP values ≥ 0.95 and MLB values ≥ 70 % are given above clade branches.

Psathyrella kauffmanii var. exannulata A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 71. 1972; *Psathyrella phegophila* Romagn., *Persoonia* Suppl. vol. **2**: 282. 1985.

Pileus 20–80(–90) mm broad, in early stages ovate to obtusely conical, more or less umbonate campanulate, finally expanding through convex to plane and more or less wavy to lobed and rugulose, margin at first inflexed; when young dark, chestnut-brown to cinnamon-brown or honey-brown, possibly with violaceous shades, when mature dark greyish brown to tobacco-brown, hygrophanous, discoloring through warm ochraceous, olivaceous ochraceous, ochraceous brown, ochraceous grey-brown, greyish ochre, cinnamon-buff, finally fading to greyish, buff, greyish ochraceous, pale olivaceous ochraceous, sometimes with pinkish to pale violaceous grey tints; faintly translucently striate when moist. *Veil* white to whitish, when young strongly connecting margin of pileus and stipe, when mature leaving usually fugacious fibrils around the margin of pileus and appressed fibrils to floccules on lower half of stipe, also appendiculate at margin, sometimes as a more or less membranous, more or less incomplete annulus with striate upper surface on stipe. *Lamellae* adnate, sometimes with a decurrent tooth; narrow to moderately broad in age; crowded or moderately crowded; when young whitish to greyish or brownish greyish, finally brownish grey, dark brownish grey to purple-brown or dark reddish brown; edge white fimbriate or not. Stipe 40–120 × (2.5–)3–10(–13) mm, sometimes gradually broadened towards base, extreme base sometimes laterally narrowed to a short pseudorhiza; white, not or little discoloring brownish in age over the basal area; apex pruinose to sometimes striate-sulcate, sometimes fibrillose to flocculose on lower portion. *Context* fragile, thin at margin to moderately thick at centre in pileus, fragile to firm in stipe, pale to concolorous with surface. *Odor* indistinctive to mild. *Taste* mild to slightly bitter. Spore deposit dark purple-brown. *Spores* (6.2–)6.8–10.3(–11) × (3.8–)4–5.7(–6) µm, on average 7.5–8.9 × 4.5–5.3 µm, Q (1.4–) 1.5–2(–2.3), avQ 1.6–1.82; in front view elliptic, oval, oblong, sometimes irregularly angular-oval, irregularly angular-oboval, angular-oblong, base truncate to subtriangular, sometimes rounded, in profile adaxially flattened to subamygdaliform or subphaseoliform, sometimes elliptic; dark reddish brown to dark red; germ pore little to moderately distinct, mainly more or less truncate to depressed, 1.4–1.8 µm broad. *Basidia* 4(2)-spored, 15–34 × 7–11 µm. *Pleurocystidia* (22–)26–56(–70) × 9–24 µm; (broadly) utriform to (broadly) ellipsoid or clavate, sometimes lageniform; apex rounded to obtuse, sometimes subobtuse, often capitate to subcapitate, forked or not, incrusted or not; walls sometimes or rarely weakly yellowish; numerous to scattered. *Cheilocystidia* 19.5–55(–70) × 7.5–20(–25) µm, rarely attenuate to subacute, pigment like pleurocystidia, scattered, sometimes moderately numerous or locally numerous. *Paracystidia* 9–40 × 4–20 µm, sometimes cylindrical-elongate, walls sometimes inconspicuously yellowish pigmented, rarely incrusted, numerous, dominating. Cells below marginal cystidia rarely weakly yellowish pigmented and incrusted. *Clamps* present.

Habitat: Caespitose to gregarious or scattered, on or connected to wood or woody debris. The host tree of MCVE29101 and the types of *P. kauffmanii var. exannulata* and *P. phegophila* is European beech (*Fagus sylvatica*). The substrates of the types of *P. kauffmanii, P. olivaceopallida* and *P. subvinacea* are indicated only in general terms, as hardwoods and logs; however, habitat where types of these species were collected has a dominance of sugar maples (*Acer saccharum*), American beeches (*Fagus grandifolia*), and northern red oaks (*Quercus rubra*) or other oaks (*Quercus* spp.). The holotype of *P. carolinensis* was from forest humus at 1 220 m. a.s.l. Kits van Waveren (1985) considers *Drosophila fusca sensu* Malençon & Bertault 1970 a misinterpretation of *P. phegophila,* and in this case the host tree is a *Quercus ilex* in Morocco at an elevation of almost 2 000 m. a.s.l.

Collections examined from MICH: *Psathyrella kauffmanii* A.H. Sm., **holotype**, Smith 66602; *Psathyrella kauffmanii var. exannulata* A.H. Sm., **holotype**, Smith 6285; *Psathyrella olivaceopallida* A.H. Sm., **holotype**, Smith 66685; *Psathyrella subvinacea* A.H. Sm., **holotype**, Hoseney

Fig. 4. *Psathyrella kauffmanii*. MCVE2910. Photo M.À. Pérez-De-Gregorio.

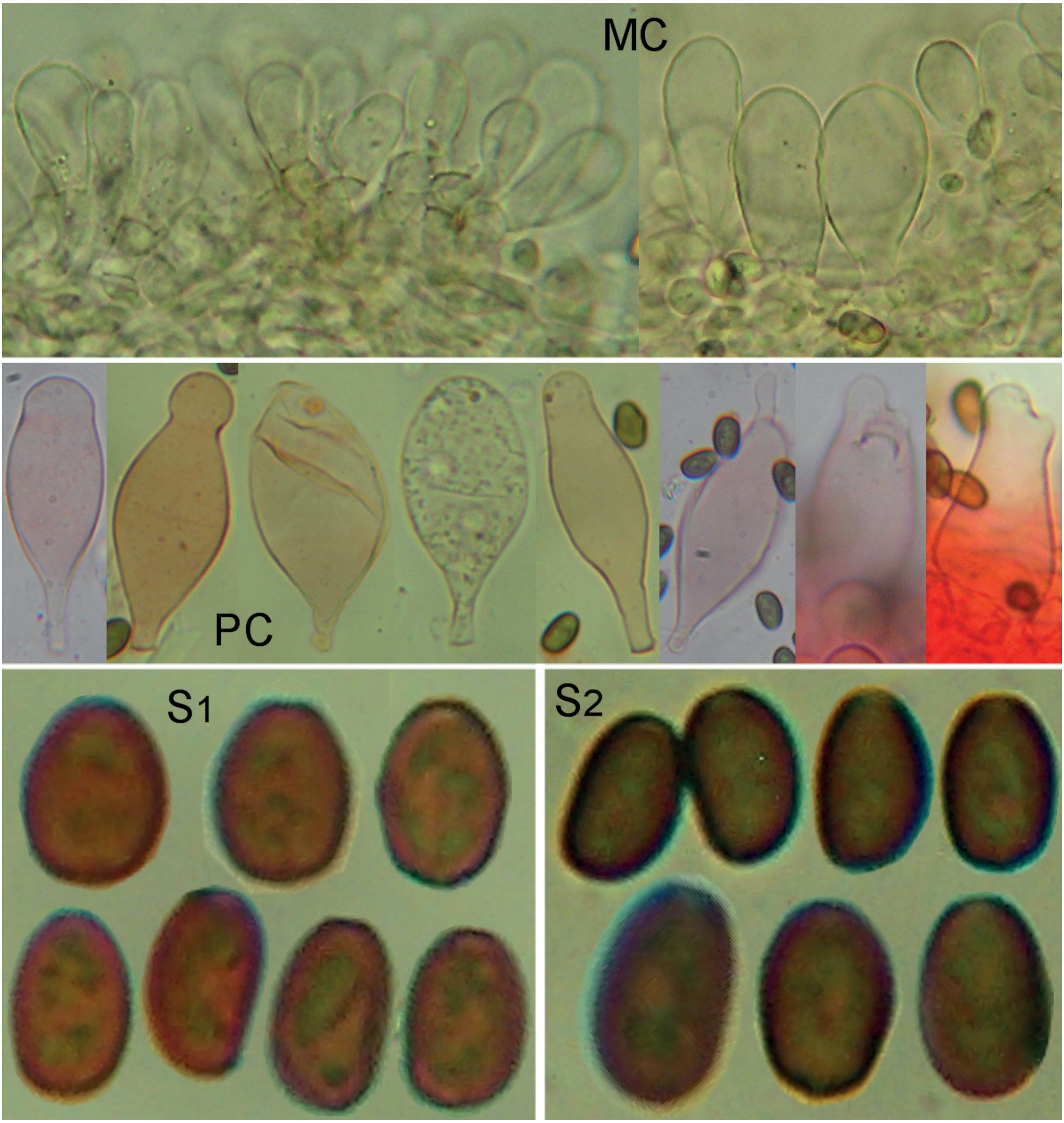


Fig. 5. *Psathyrella kauffmanii*. A.H. Smith 66602, MICH11962; MC Marginal Cystidia in KOH; PC Pleurocystidia; S1 Spores in water; S2 Spores in KOH.

641; *Psathyrella fusca sensu* A.H. Smith, Smith 75099; *Psathyrella spadiceogrisea sensu* A.H. Smith, Smith 74295.

Other material examined: **France**, Île-de-France, Yvelines, forêt de Saint-Germain, gregarious on woody debris in calcareous beechwood, 16. Nov. 1997, *G. Tassi* 9776, printed description in Tassi (2010). **Spain**, Girona, Santa Pau, la Fageda d'en Jordà, 560 m. a.s.l., gregarious in beech leaf litter, 7 Oct. 2000, *J. Carbó & M.À. Pérez-De-Gregorio* JC-20001007.11 (duplicate MCVE29101), Fig. 4, *Tef-1α* MF521793, ITS MF325978, printed description in Pérez de Gregorio *et al.* (2010).

Notes: In old exsiccata it often happens that only a limited number of dark spores may be found; however, the dark color and not very distinct germ pore of the spores, together with pleurocystidia shape, are diagnostic when comparing this species with the other lignicolous species of the subsection. The sometimes annular veil and the habitat usually represented by *Fagus* can also be diagnostic. However, the use of host or habitat to corroborate the diagnosis should be done with caution, because *Fagus* is a known host also for the closely related species *P. niveobadia*.

Because we could not examine the original material of *P. phegophila*, we have selected a Spanish collection (MCVE29101) that matches it satisfactorily, and that is fully described by both text and pictures of the sporocarps in their natural habitat (Pérez de Gregorio *et al.* 2010). DNA sequences of the two loci studied and the morphology are a perfect match with sequences and morphology of the holotype of *P. kauffmanii*. Another collection we consider a good European representative of this taxon comes from France and was described and illustrated by Tassi (2000), as voucher 97076. Thanks to Tassi's courtesy, this sample was loaned to us, but, unfortunately, DNA extraction from this specimen failed. It is to be noted that until now, European reports always lack the annulus, like *P. kauffmanii var. exannulata*, one of the synonyms ascertained in this study.

We could not obtain the holotype of *P. carolinensis*, however, judging from its original description, and considering all the variability observed within *P. kauffmanii* during the course of this study, we consider it to be another synonym of *P. kauffmanii*.

Together with all the taxa regarded as conspecific, *P. kauffmanii* also creates a compact cluster with three other species described below: *P. albanyensis, P. alnicola*, *P. oregonensis*.

Psathyrella albanyensis has tridimensional and peculiarly cordiform to pentagonal spores. *Psathyrella alnicola* is typically associated with alders. *Psathyrella oregonensis* is characterized by high ITS molecular homology with both *P. kauffmanii* and *P. alnicola* (ITS homology was 100 % with *P. alnicola* and 99 % with all other comparable material of *P. kauffmanii*), however, based on one collection available to us, it can be stated that this species differs from them because it is found in coniferous habitats and because it has broader tridimensional spores. Thus, based on available evidence, we conclude that *P. oregonensis* is an autonomous taxon, maybe to be regarded as an intermediate species between *P. kauffmanii* and *P. albanyensis*. It has been often stated that high homology of ITS sequence among closely related, albeit distinct, taxa is not necessarily indicative of conspecificity, and may be due to interspecific horizontal gene transfer followed by allelic sweeps that effectively eliminate those ITS alleles that were originally present in the "receiver" fungal species (discussed in Bergemann *et al.* 2009). In order to determine the exact phylogenetic relationships among the above taxa, sequence information from additional loci will be needed.

Psathyrella striatoannulata, recently described from central America, is also strikingly near *P. kauffmanii*, based both on molecular (approximately 99 % ITS homology) and morphological data. Both taxa share the following: a striate membranous annulus, pleurocystidia often undifferentiated and possibly pigmented and incrusted, the general habit and colors of the basidiomes. However, its authors report that incrustations at the apices of the pleurocystidia distinctively stain reddish brown in NH_4, although this feature tends to gradually disappear in old specimens. A further molecular comparison is needed to resolve the relationship between these two species. We believe the descriptions of *Psathyrella* spec. 3 by Ludwig (2007a) and of *P. obtusata var. aberrans sensu* Breitenbach & Kränzlin (1995) may represent *P. kauffmanii*.

1a. ***Psathyrella kauffmanii*** A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 69. 1972. Fig. 5.

Typus: *Psathyrella kauffmanii* A.H. Sm. **USA**, Michigan, Huron Mts. Marquette Co., Big Bay, 16 Jun. 1963, *A.H. Smith* 66602 (MICH11962), on hardwood debris. *Tef-1α* MF521792.

Loan of four sporocarps in good condition and a slice of pileus for micro-morphology investigation.

Spores (6.2–)6.8–8.5(–9.3) × (3.8–)4.3–5.2(–5.7) µm, Q 1.5–1.7; in front view elliptic to suboval, sometimes (narrowly) oval to angular-oval, base often truncate to subtriangular, in profile adaxially flattened to subphaseoliform; few dark red; germ pore subdistinct, more or less truncate, ± 1.5 µm broad. *Pleurocystidia* (22–)33–55 × 13–23 µm, utriform to ellipsoid or clavate; apex obtuse, sometimes subobtuse, often capitate, sometimes forked, rarely rostrate, often incrusted; walls sometimes weakly pigmented; moderately numerous. *Cheilocystidia* 19.5–49 × 9.5–18 µm, scattered. *Paracystidia* 10–35 × 5–19(–24) µm, often cylindrical-elongate, numerous, dominating.

1b. ***Psathyrella kauffmanii var. exannulata*** A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 71. 1972.

Typus: *Psathyrella kauffmanii var. exannulata* A.H. Sm. **USA**, Michigan, Oakland Co., Highland Recreation Area, Haven Hill, 11 Jun. 1937, *A.H. Smith* 6285 (MICH11961), in a beech wood.

Loan of one sporocarp in good condition and a half pileus for micro-morphology investigation.

Spores 6.9–9.1 × 4.3–5.6(–6), Q 1.4–1.9; in front view elliptic to oval, sometimes oblong, (narrowly) angular-oval, base often truncate to subtriangular, in profile adaxially flattened, sometimes subphaseoliform; mostly orangish to reddish brown, very few dark reddish brown to dark red; germ pore subdistinct, mainly truncate, 1.5–1.8 µm broad, *Pleurocystidia* 35–47 × 12–19 µm; utriform, sometimes clavate, often or sometimes irregular in ventral part; apex rounded, subcapitate or not, often or sometimes incrusted; walls sometimes weakly yellowish, numerous. *Cheilocystidia* 28–42 × 10–18 µm, scattered. *Paracystidia* 9–35 × 5–18 µm, walls sometimes yellowish pigmented, numerous, dominating.

Notes: Our attempts to extract and amplify DNA failed, however by morphological comparison we think this material can be viewed as conspecific with *P. kauffmanii*. We note that Smith (1972) reports spores color in KOH as *'cocoa color and remaining so a long time'*, therefore not dark; however, we had difficulty in finding dark spores in many old exsiccata of *P. kauffmanii* and conspecific materials.

1c. ***Psathyrella olivaceopallida*** A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 138. 1972.

Typus: *Psathyrella olivaceopallida* A.H. Sm. **USA**, Michigan, Cheboygan Co., Burt Lake, Colonial Point, 20 Jun. 1963, *A.H. Smith* 66685 (erroneously reported as 4991) (MICH11990), scattered to gregarious on humus in hardwoods. ITS MF325988.

Loan of one sporocarp lacking a slice of pileus for micro-morphology investigation.

Spores (7–)7.3–9.2(–10) × 4.1–5(–5.1), Q 1.55–1.9(–2) µm; in front view elliptic, oblong to narrowly oval, sometimes oblong- to angular-oval, base often truncate to subtriangular, in profile adaxially flattened, sometimes subphaseoliform; few dark reddish brown; germ pore moderately distinct, often more or less truncate, 1.4–1.5 µm broad. *Pleurocystidia* 29–43 × 10–22 µm; broadly utriform, utriform, ellipsoid, sometimes lageniform, clavate; apex rounded to obtuse, subcapitate or not, often forked, sometimes incrusted; walls sometimes weakly yellowish, numerous. *Cheilocystidia* 28–43 × 10–20 µm, in part (broadly) lageniform with short to elongate neck and subobtuse to subacute apex, pigmented like pleurocystidia, scattered. *Paracystidia* –28 × –15 µm, often weakly yellowish, numerous, dominating. Cells below marginal cystidia hyaline.

Notes: Although the molecular evidence provided by the ITS sequence alone is inconclusive as stated above, we retain this species a synonym of *P. kauffmanii*. Smith may have found its only collection when the sporocarps were already discolored: the pale olive tint implied by the name and the greyish and pinkish tones on fading reported in Smith's (1972) description belong to the chromatic set of the pileus of *P. kauffmanii*.

1d. *Psathyrella subvinacea* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 124. 1972.

Typus: *Psathyrella subvinacea* A.H. Sm. **USA**, Michigan, Washtenaw Co., Waterloo State Recreation Area, 31 Aug. 1967, *F. Hoseney* 641 (MICH12085), on underside of logs on wooded side of sand hill. *Tef-1α* MF521777, ITS MF326001.

Loan of three sporocarps in good condition for micro-morphology investigation.

Spores 6.8–9.2(–10.5) × 4.2–5.2(–5.7), Q 1.4–1.8(–2.2); in front view elliptic, oval to oblong-oval, sometimes (narrowly) angular-oval, base rounded, truncate to subtriangular, in profile elliptic to subamygdaliform, sometimes subphaseoliform; almost all spores pale to very pale, mostly hyaline to very pale purplish brown, some violaceous orange, very few dark violaceous brown; germ pore indistinct. *Pleurocystidia* 32–50 × 10–24 µm; (broadly) utriform; apex often subcapitate, sometimes forked, sometimes incrusted; walls often weakly yellowish below apex. *Cheilocystidia* 26–42 × 12–19 µm, pigmented like the pleurocystidia, scattered. *Paracystidia* 9–40 × 6–18 µm, walls often weakly yellowish pigmented, numerous, dominating. Cells below marginal cystidia weakly yellowish pigmented, sometimes incrusted.

Notes: Apart from the very pale pigmentation of the spores, which was likely due to delayed maturation, both molecular and morphological characters identify this taxon as conspecific with *P. kauffmanii*.

1e. *Psathyrella spadiceogrisea* *sensu* A.H. Smith p.p.

Material examined: **USA**, Michigan, Jackson Co., Munith woods, 13 May 1967, *A.H. Smith* 74295 (MICH49606), debris. ITS MF325998.

Loan of three full sporocarps and a pileus, in good condition for micro-morphology investigation.

Spores 7.5–10.3(–11) × 4.2–5.3(–5.6) µm, on average 8.9 × 4.7 µm, Q (1.4–)1.6–2(–2.3), avQ 1.73–1.83; in front view oblong, elliptic, narrowly oval, rarely oblong-oval or angular-oval, base rounded, rarely truncate to subtriangular, in profile adaxially flattened to subamygdaliform, sometimes subphaseoliform; reddish brown to dark red; germ pore moderately distinct, mostly more or less truncate to subdepressed, ± 1.5 µm broad. *Pleurocystidia* 28–51 × 13–22 µm; (broadly) utriform, sometimes ellipsoid; apex rounded, often subcapitate, often forked, sometimes incrusted; walls hyaline; scattered. *Cheilocystidia* 30–41 × –15(–18) µm, scattered. *Paracystidia* 10–30 × 5–14 µm, often yellowish, numerous, dominating. Cells below marginal cystidia scarcely yellowish pigmented or incrusted.

Notes: We have attempted to understand Smith's concept of *P. spadiceogrisea* by examining a Smith's collection selected for this purpose by MICH staff. For this material, we have obtained a molecular sequence only for the ITS, which places it in the same subclade as *P. kauffmanii*. Its terete spores exclude conspecificity with *P. albanyensis* and *P. oregonensis*. Nonetheless, we have compared it with *P. kauffmanii* and found a good correspondence between the two. Because the only relevant difference between the two is the slightly greater spore length and, consequently, the slightly greater spore quotient, we retain this collection as a synonym of *P. kauffmanii*. Unfortunately, we could not discover any significant details about the habitat in which these samples were collected. This suggested synonymy does not necessarily apply to the other vouchers Smith deposited in MICH under this name, which should be considered and evaluated separately.

1f. *Psathyrella fusca* *sensu* A.H. Smith p.p.

Material examined: **USA**, Michigan, Oakland Co., Proud Lake, 3 Sep. 1967, *A.H. Smith* 75099 (MICH48491), in wet soil. *Tef-1α* MF521799, ITS MF325971.

Loan of three sporocarps in good condition and a fragment of pileus for micro-morphology investigation.

Spores 6.9–8.1 × 4.3–5.4 µm, in front view oval to elliptic, often angular-oval, base often truncate to subtriangular, in profile adaxially flattened, sometimes subphaseoliform; dark reddish brown to dark red; germ pore moderately distinct, often more or less truncate, 1.4–1.7 µm broad. *Pleurocystidia* 36–56 × 14–19 µm; utriform; apex rounded, often subcapitate, sometimes forked, no incrustation seen; walls hyaline; moderately numerous. *Cheilocystidia* 30–55 × 11–20 µm, scattered, sometimes locally numerous. *Paracystidia* 12–31 × 6–20 µm, often weakly yellowish, sometimes incrusted, numerous, dominating.

Notes: We have attempted to understand Smith's concept of *P. fusca* by examining a Smith's collection selected for this purpose by MICH staff. It has turned out to correspond, both morphologically and molecularly, to *P. kauffmanii*. This result does not necessarily apply to the other vouchers Smith deposited in MICH under this name.

2. *Psathyrella alnicola* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 176. 1972. Fig. 6.

Typus: *Psathyrella alnicola* A.H. Sm. **USA**, Idaho, Idaho Co., French Creek Grade, Salmon River, 6 Sep. 1964, *A.H. Smith* 70222 (coll. *K.A. Harrison*) (MICH11868), under alder. *Tef-1α* MF521815, ITS MF325957.

Loan of one sporocarp in good condition and a half pileus for micro-morphology investigation.

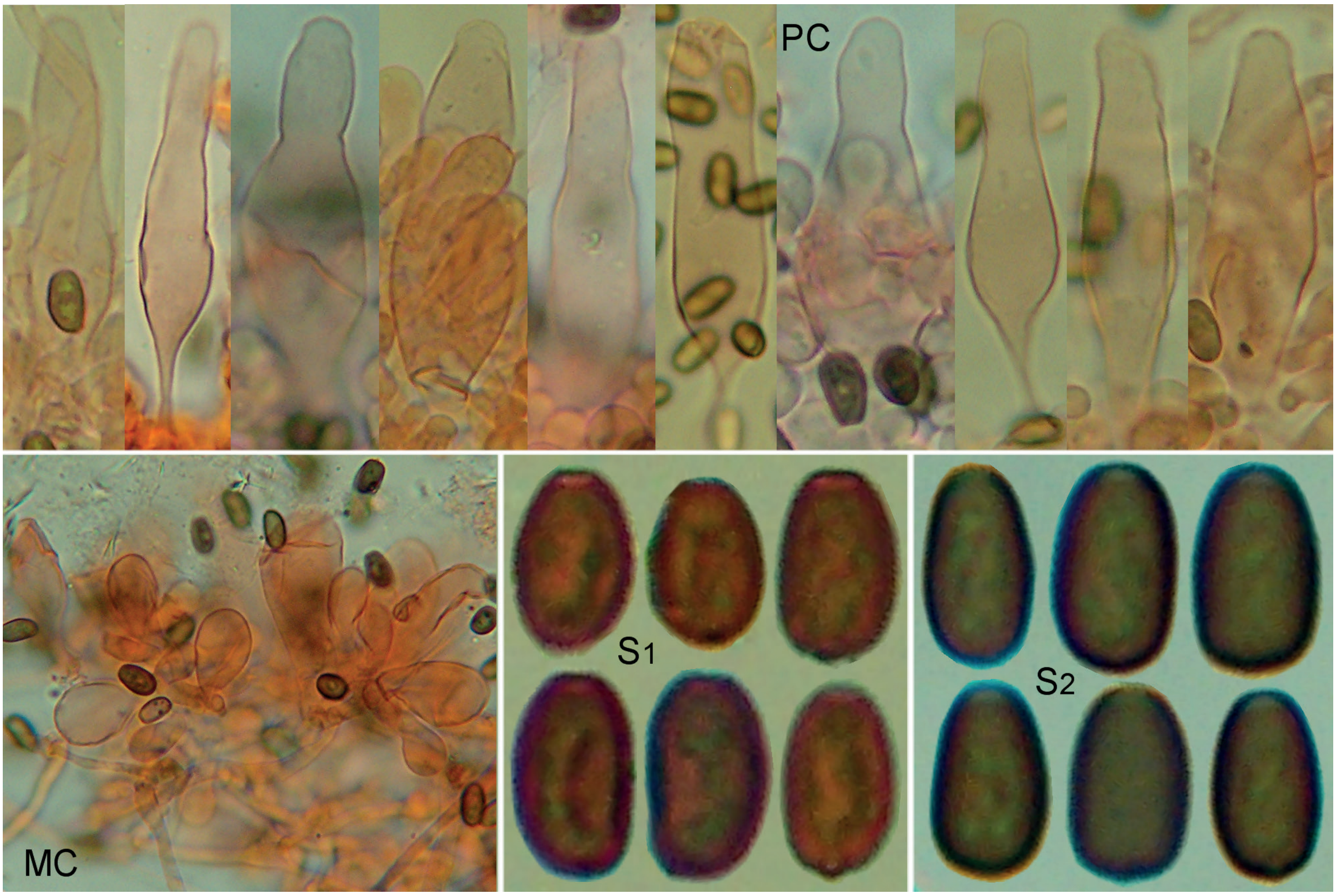


Fig. 6. *Psathyrella alnicola*. A.H. Smith 70222, MICH11868; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

Spores 7.9–10 × 4.6–5.7(–6.2) µm (8–11 × 5–6 µm in Smith 1972), Q 1.45–2; in front view elliptic, oval to oblong, sometimes (narrowly) angular-oval, base rounded to truncate, sometimes subtriangular, in profile adaxially flattened, elliptic to subamygdaliform, sometimes subphaseoliform; dark reddish brown to dark red; germ pore subdistinct, more or less truncate, 1.5–1.7 µm broad. *Pleurocystidia* (37–)45–67(–83) × (10–)13–20(–32) µm; utriform to conical-lageniform, rarely subcylindrical; apex obtuse to rounded, obscurely subcapitate or not, sometimes forked, sometimes incrusted; walls sometimes weakly pigmented, moderately numerous. *Cheilocystidia* 35–62 × 15–17 µm, scattered. *Paracystidia* 8–48 × 4–25 µm, sometimes cylindrical-elongate, sometimes weakly pigmented, rarely incrusted, numerous, dominating.

Notes: The holotype and other five collections determined by Smith are undoubtedly associated with alder (*Alnus*). Collection of the holotype was made from under a single alder, even if many Ponderosa pines (*Pinus ponderosa*) and Douglas-firs (*Pseudotsuga menziesii*) coexisted in the same site. The 99 % identity of both ITS and *Tef-1α* sequences with all other *P. kauffmanii* studied here clearly identifies a very close relationship between the two taxa, however, the hygrophilous *Alnus* habitat is clearly distinct from the mesophilous habitat characteristic of *P. kauffmanii*.

3. ***Psathyrella solheimii*** McKnight & A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 67. 1972. Fig. 7.

Typus: *Psathyrella solheimii* McKnight & A.H. Sm. **USA**, Wyoming, Albany Co., Laramie Mts., Pole Mountain, Happy Jack Winter Sports Area, 27 Jun. 1944, *W.G. Solheim* 2178 (MICH12054), on moist soil under aspen, especially around beaver dams.

Loan of two portions of pilei for micro-morphology investigation.

Spores (7.4–)7.5–9.6(–10) × 4.9–5.6 µm (broader, 8–10 × 5–6.2 µm, in Smith 1972), Q (1.4–)1.5–1.9, av Q 1.66; in front view oblong, elliptic, narrowly to cylindrical- oval, sometimes subangular-oval, base broadly rounded, truncate to subtriangular, in profile adaxially flattened to subelliptic, sometimes subamygdaliform, rarely subphaseoliform; dark red-brown; germ pore moderately distinct, truncate to subrounded, 1.1–1.7 µm. *Pleurocystidia* (24–)30–45(–52) × (10–)11.5–21 µm, ellipsoid-utriform, fusiform-utriform, utriform, (broadly) clavate, sublageniform, ellipsoid, sometimes ellipsoid mucronate, obconical; apex broadly rounded to obtuse, rarely subacute, sometimes forked, rarely subcapitate, not incrusted; scattered. *Cheilocystidia* 17–33(–38) × 7–18 µm, sometimes lageniform-mucronate, hyaline, scattered to moderately numerous. *Paracystidia* 10–22(–25) × 5.5–16(–18) µm, numerous, dominating; intermediate cells with slightly bulging to submucronate apex, 17–32 × 11.2–17.5 µm, scattered to moderately numerous towards the stipe. Marginal cystidia and cells below them hyaline or very pale, not incrusted.

Notes: Unfortunately, DNA extraction of this material failed, but based on the morphological evidence, we consider it to belong to the subsection *Spadiceogriseae*. Smith (1972) keys it

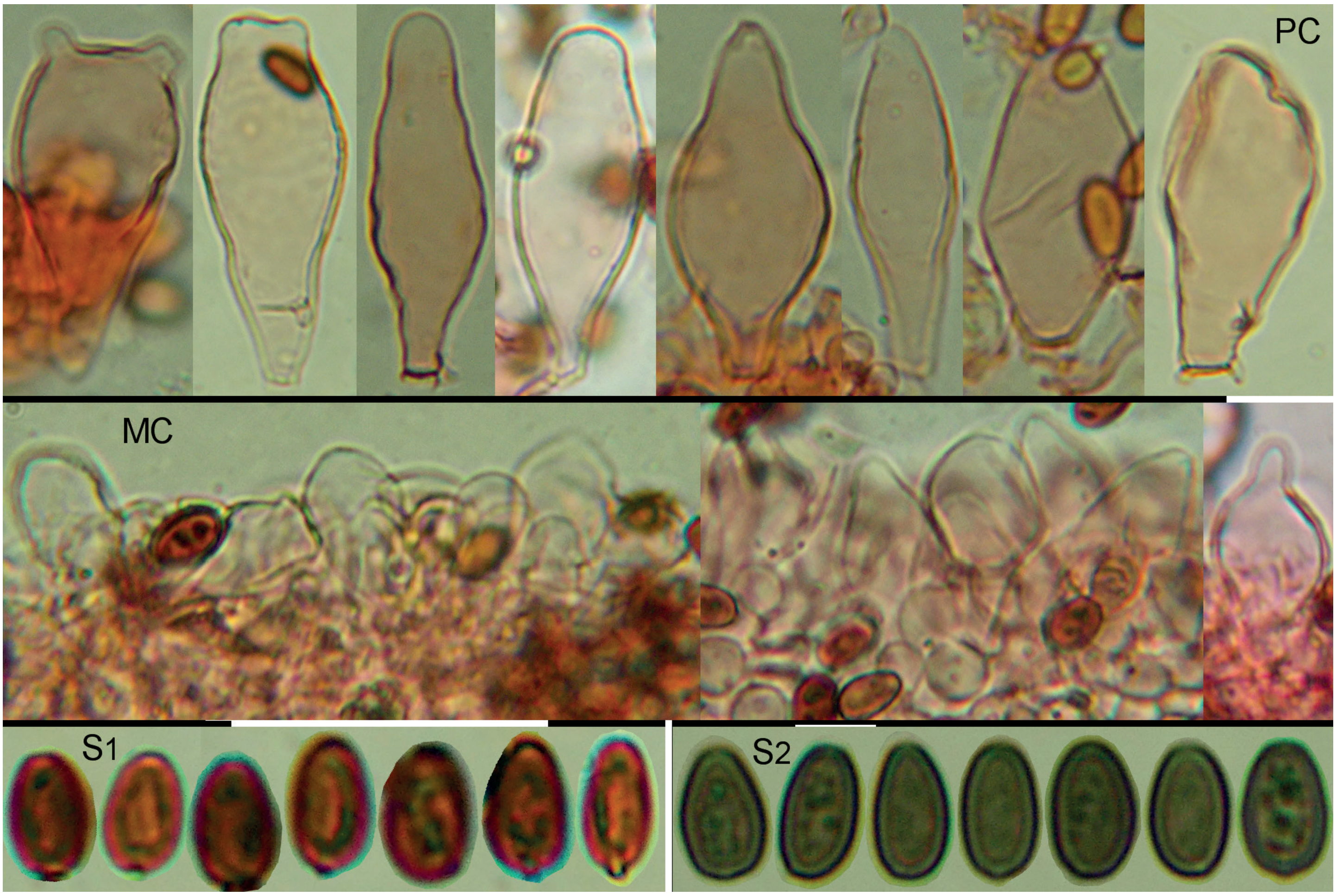


Fig. 7. *Psathyrella solheimii*. W.G. Solheim 2178, MICH12054; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

just beside *P. kauffmanii*, stating that the latter differs in longer and often forked pleurocystidia, and in slightly larger spores. This was possibly true when comparing *P. solheimii* to Smith's description of *P. kauffmanii* only, but when we take into account all of the materials we have studied identified as *P. kauffmanii*, we see those divergences disappear. A difference we can suggest is that the pleurocystidia apices often tend to have a tapering shape in *P. solheimii*, while in *P. kauffmanii* they tend to have a more rounded, often capitate, shape. Moreover, the habitat under aspen on moist soil, especially around beaver dams, is in contrast with the mainly dry and beech dominated habitat associated with *P. kauffmanii*. We have also checked *P. solheimii* against *P. alnicola*, given they both share alder as habitat, but their respective pleurocystidia show a marked disparity: on average they are shorter and thicker in *P. solheimii*, while they are longer and slenderer, and often with an elongate apex, in *P. alnicola*. Moreover, gill edge cells are often mucronate in *P. solheimii* and never so in *P. alnicola*. Until new molecular data are made available, we opted to retain *P. solheimii* as a separate species.

4. *Psathyrella sanjuanensis* (A.H. Sm.) Voto, Dovana & Garbel, ***comb. nov.*** MycoBank MB831131. Fig. 8.
Basionym: *Psathyrella solheimii var. sanjuanensis* A.H. Sm., *Mem. N. Y. Bot. Gard*. 24: **68**. 1972. *A.H. Smith* 51837, MICH12055.

Typus: *Psathyrella solheimii var. sanjuanensis* A.H. Sm. **USA**, Colorado, San Miguel Co., Ophir, 4 Aug. 1956, *C. Barrows & A.H. Smith* (*A.H. Smith* 51837) (MICH12055), under aspen.

Loan of two small fragments of pilei for micro-morphology investigation.

Spores (8–)8.2–9.8(–10.7) × (5–)5.2–5.8(–6) µm, on average 9.3 × 5.5 µm, Q (1.4) 1.5–1.9(–2.15), avQ 1.7; in front view elliptic, sometimes cylindrical, narrowly oval, oblong, base broadly rounded to subtruncate, sometimes obtuse, in profile subamygdaliform to adaxially flattened, rarely subphaseoliform; dark red-brown; germ pore distinct, rounded to subtruncate, sometimes slightly eccentric in profile, 1.3–1.7 µm. *Pleurocystidia* 33–50 × 10–16 µm, utriform to lageniform, often elongate in upper part; apex rounded, often subcapitate, rarely capitate, sometimes forked with up to 20 µm long protrusions; scattered. *Cheilocystidia* 24–40(–45) × 7.5–13(–15) µm, in part fusiform-lageniform with obtuse apex, apex rarely subcapitate or forked, numerous to abundant and dominating from mid gill towards the stipe, scattered to absent towards the pileus margin. *Paracystidia 12*–25(–30) × 7–13(–16,5) µm, absent or inconspicuous towards the stipe, numerous and dominating towards the pileus margin. Marginal cystidia and cells below them not pigmented, not incrusted.

Notes: The longest strip of gill edge we could examine was 4.5 mm long. Starting from the pileus margin towards the stipe end, we found that paracystidia went from being numerous and dominating (in 2 mm long gill segment) to being absent or inconspicuous. Conversely, cheilocystidia showed an inverse trend and went from being absent or rare to being numerous, even abundant, and dominating (in 2.3 mm long

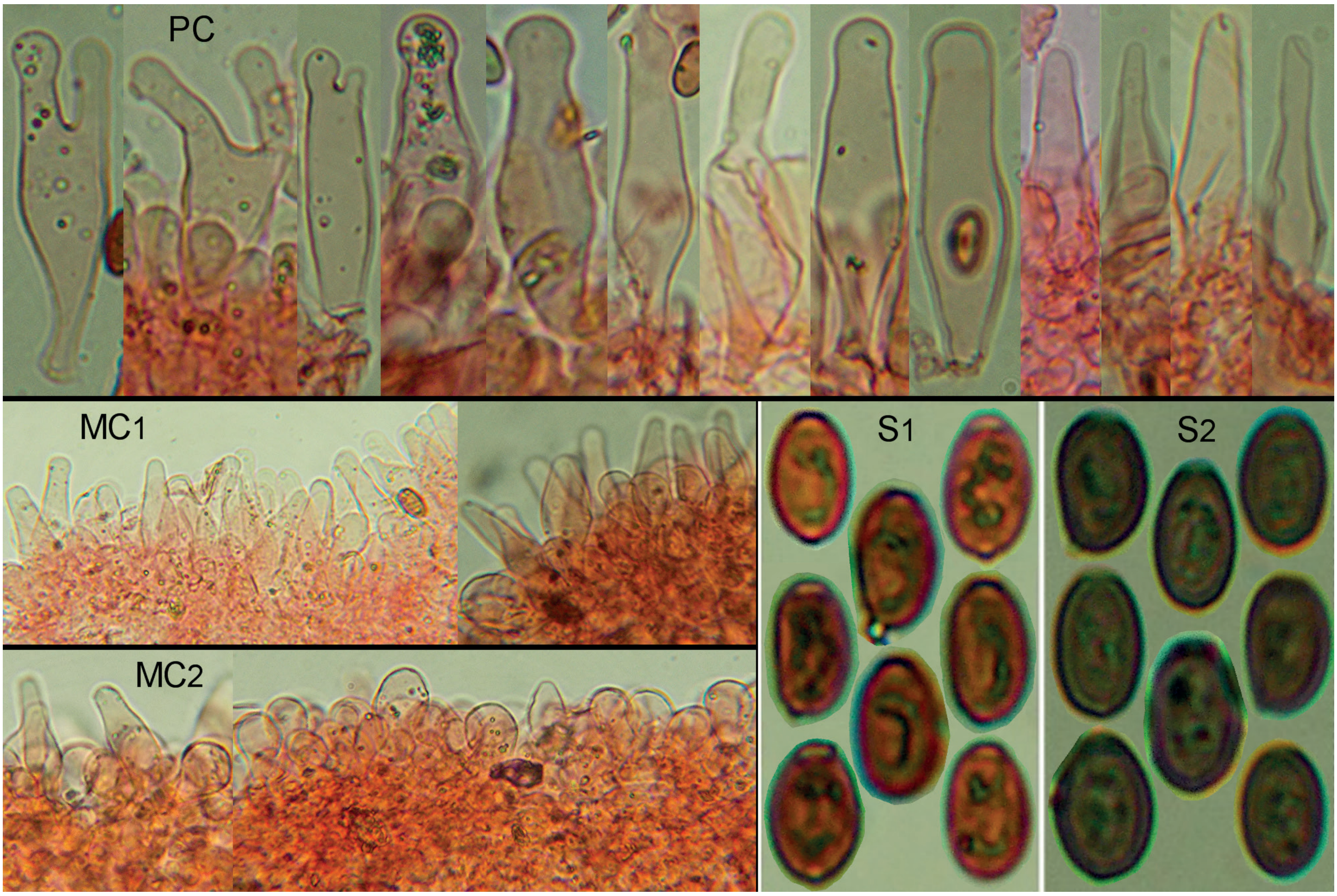


Fig. 8. *Psathyrella solheimii var. sanjuanensis*. A.H. Smith 51837, MICH12055; PC Pleurocystidia; MC1 Marginal Cystidia towards the pileus margin; MC2 Marginal Cystidia towards the stipe; S1 Spores in water; S2 Spores in KOH.

gill segment). Paracystidia were small and had approximately the same dimensions as basidia [20–31 × 8–12(–15) µm], even where they were dominating. Although we lack the support of molecular evidence, we assume this collection does not belong to the subsection *Spadiceogriseae*, rather it better fits into the sister subsection *Lutenses*. Based on such cumulative evidence, we see no reason to maintain its affiliation with *P. solheimii*, and propose to elevate it to the species rank. Interestingly, Smith (1972) too had suggested this taxon could '*eventually deserve recognition as an autonomous species*', a statement he made based mainly on the shape of pleurocystidia and on the consistency and colour of the annulus.

5. *Psathyrella oregonensis* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 157. 1972. Fig. 9.

Typus: *Psathyrella oregonensis* A.H. Sm. **USA**, Oregon, Clackamas, Beaver Creek, Mt Hood National Forest, 24 Oct. 1947, *A.H. Smith* 28182 (MICH5840), on conifer wood. ITS MF325989.

Loan of one sporocarp with incomplete pileus for micromorphology investigation.

Spores 7–10(–10.7) × 5–6.7 × 4.4–5.5 µm, fQ 1.3–1.7, avQ 1.5, pQ 1.4–1.9, avQ 1.7; in front view oval, elliptic, angular- to triangular-oval, base mainly truncate, in profile elliptic, subamygdaliform, subphaseoliform; reddish brown to dark red; germ pore little distinct, 1.4–1.7 µm broad. *Pleurocystidia* (31–)37–66(–76) × 11.5–17 µm; slenderly utriform, sometimes thickly utriform, sublageniform, subcylindrical, subconical; apex rounded to obtuse, often subcapitate, sometimes forked in Smith's description, sometimes elongate, sometimes incrusted; walls hyaline; numerous. *Cheilocystidia* 30–43 × 15–20 µm, scattered. *Paracystidia* –39 × –21 µm, sometimes rhomboid, almost hyaline, numerous, dominating.

Notes: *Psathyrella latispora* is one of the holotypes MICH could not loan, however, based on its description, it belongs to subsection *Spadiceogriseae*. Its type was collected cespitose from unspecified coarse wood debris, and shares a number of similarities with *P. oregonensis* from which it is mainly differentiated for having terete spores.

6. *Psathyrella rugulosa* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 158. 1972. Fig. 10.

Typus: *Psathyrella rugulosa* A.H. Sm. **USA**, Tennessee, Sevier Co., Great Smoky Mts. National Park, near Clingman's Dome, 24 Jun. 1945, *L.R. Hesler* 17027 (MICH12040), on a spruce log.

Loan of one sporocarp in good condition for micro-morphology investigation.

Spores (6.2–)7.5–8.8(–9.8) × (4–)4.3–5.2(–5.3) µm, Q (1.4–) 1.5–1.8(–2.3), avQ 1.7; in front view elliptic to suboval, base mainly obtuse to rounded, in profile adaxially flattened to

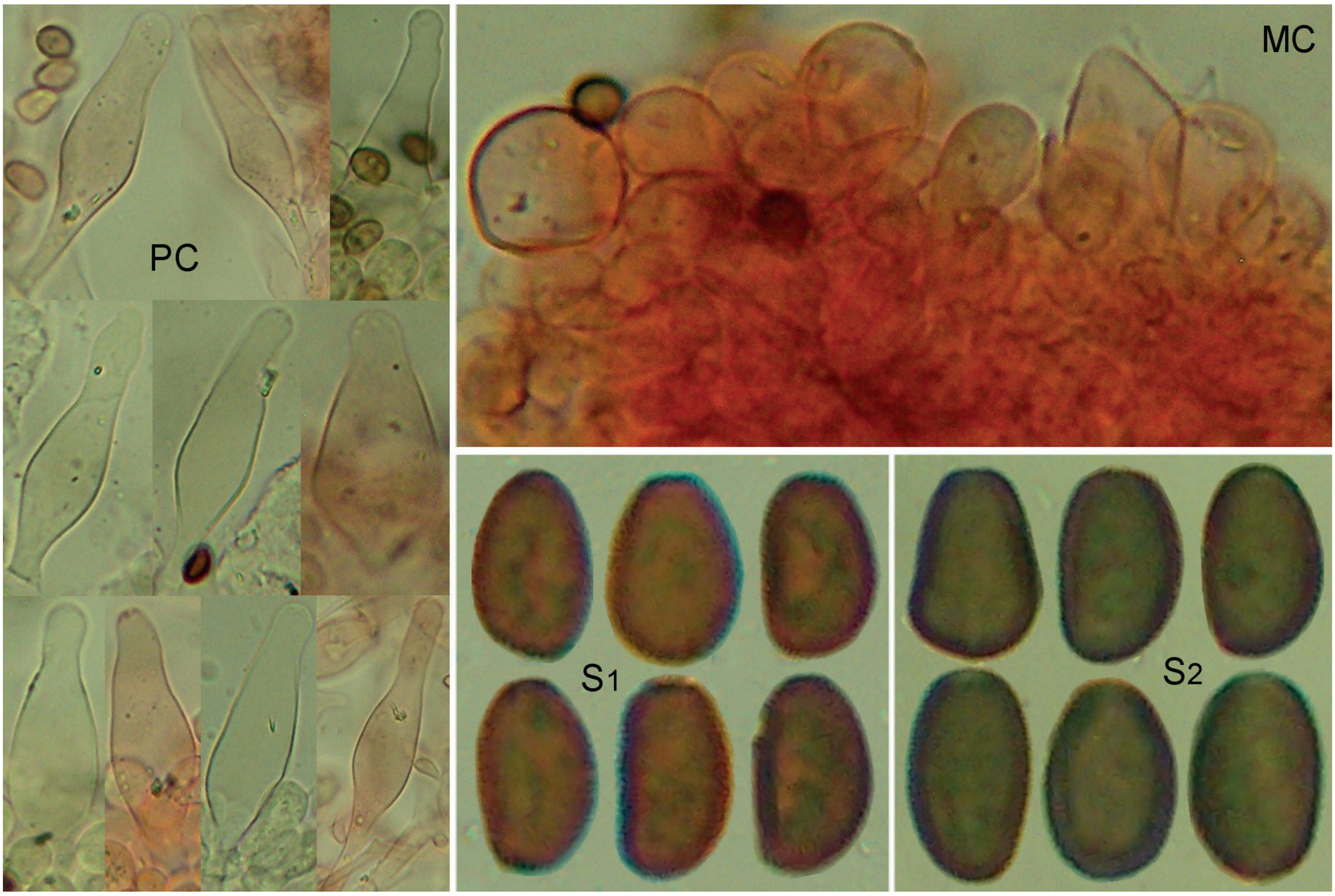


Fig. 9. *Psathyrella oregonensis*. A.H. Smith 28182, MICH5840; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

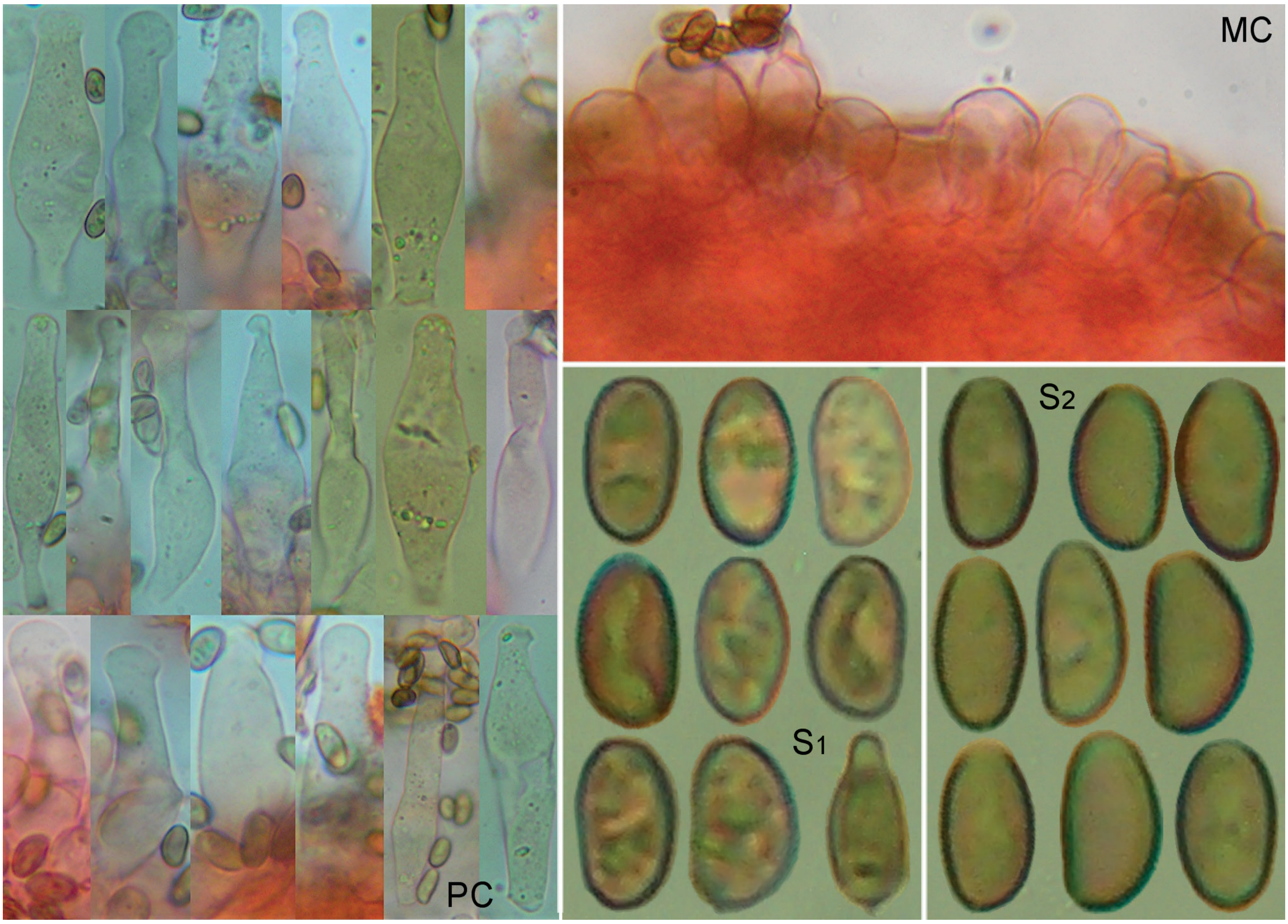


Fig. 10. *Psathyrella rugulosa*. L. R. Hesler 17027, MICH12040; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

subphaseoliform, sometimes narrowly subamygdaliform or with a faint suprahilar depression, rarely phaseoliform; pale, few at most dull orangish; germ pore little distinct (callus), mainly subtruncate. *Pleurocystidia* 38–65 × 9–17 µm, utriform to subcylindrical, often with elongate-cylindrical neck, rarely subellipsoid or ventricose-conical; apex (4–)6–10 µm broad, rounded, sometimes obtuse to subacute, often (laterally) subcapitate, rarely forked, sometimes incrusted; numerous. *Cheilocystidia* up to 60 × 15 µm, scattered. *Paracystidia* –30 × –20 µm, numerous, dominating.

Notes: Smith (1972) reported spores with distinct and narrowly truncate germ pore. Unfortunately, DNA extraction failed on this material; however, general morphological evidence places it into subsection *Spadiceogriseae*. Due to its pale spores and indistinct germ pore it resembles *P. clivensis*, however, because of its appendiculate veil and conifer habitat, Smith (1972) placed it near *P. oregonensis,* from which it differs because of its pale and terete spores.

7. *Psathyrella albanyensis* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 140. 1972. Fig. 11.

Morphological heterotypical synonyms proposed here: *Psathyrella subcinerascens* A.H. Sm., Mem. *N. Y. Bot. Gard*. **24**: 172. 1972.

Typus: *Psathyrella albanyensis* A.H. Sm. **USA**, Wyoming, Albany Co., Laramie Mts., drainage at the northeast base of Pole Mt., 27.V.1956, *W.G. & R. Solheim* 4438 (MICH11862), on soil under aspen and conifers at 2 438 m a.s.l. (8 000 feet). *Tef-1α* MF521823, ITS MF325952.

Loan of three sporocarps in good condition and a pileus for micro-morphology investigation.

Spores (6.2–)6.7–8.3 × 4.5–6.3 × 4.2–5.2 µm, (7–9 × 5–6 × 4–5 µm in Smith's description), fQ (1.2–)1.3–1.5(–1.6), pQ 1.45–1.7(–2.2); in front view oval, elliptic to subcylindrical, often subtriangular or cordiform to subpentagonal, sometimes subglobose, base often truncate, apex sometimes attenuate and snout-like projected, in profile elliptic, sometimes subamygdaliform; reddish brown to dark red; germ pore indistinct, sometimes distinct but very small, at most 1 µm. *Pleurocystidia* 31–45 × 12–17(–19) µm; utriform, ellipsoid-rhomboid, sometimes fusiform, subcylindrical, apical part often attenuate to conical or submucronate, apex obtuse to sometimes subobtuse or subrounded, not incrusted, walls hyaline; moderately numerous. *Cheilocystidia* 19–40 × 14–15(–21) µm, scattered. *Paracystidia* 10–33(–36) × 6–16(–23) µm, with walls weakly yellowish pigmented and sometimes incrusted, numerous, dominating. Cells below marginal cystidia weakly yellowish pigmented and with incrustations.

Notes: The molecular analysis nests this taxon within the *P. kauffmanii* complex; morphologically it is characterized by often tridimensional, often pentagonal-like spores, both pleuro- and cheilocystidia showing a tendency to an attenuate and conical

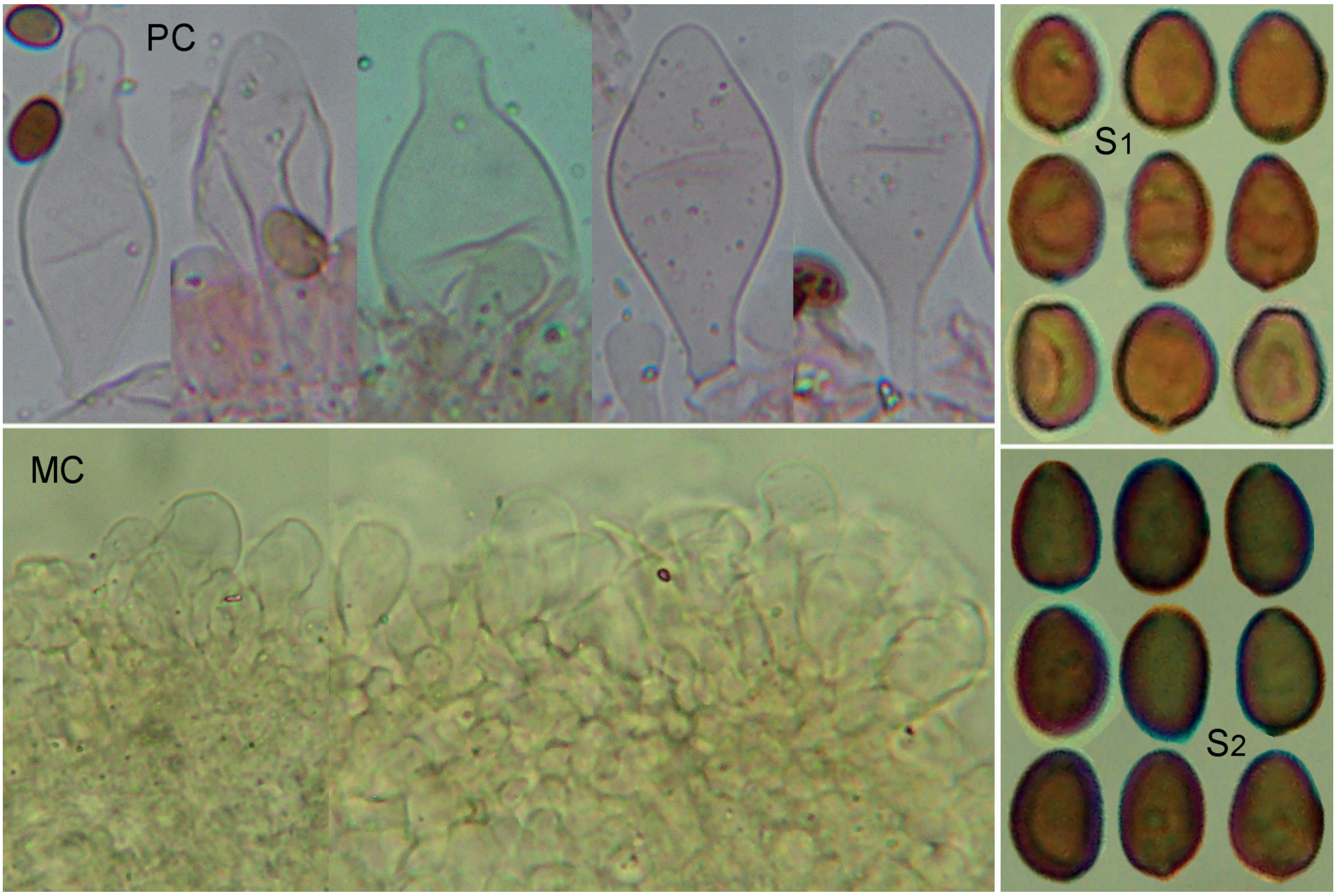


Fig. 11. *Psathyrella albanyensis*. W.G. & R. Solheim 4438, MICH11862; PC Pleurocystidia; MC Marginal Cystidia in KOH; S1 Spores in water; S2 Spores in KOH.

apex, small and slender sporocarps with reddish rusty tints on the pileus. Its habitat occurs at very high elevations (> 1 500 m a.s.l.), in association with conifers and occasionally with aspen (*Populus tremuloides*). *Psathyrella oregonensis* appears to be its closest relative, based on its tridimensional spores and habitat represented by conifers.

Psathyrella subcinerascens is represented only by the holotype, and was one of the Smith's species MICH could not loan because of limited sample size. It was collected on muck near beaver ponds in a mountain setting, thus suggesting that arboreal debris may be a common habitat for this species. We have noticed many morphological similarities with *P. albanyensis* and propose the conspecificity of these two species.

8. *Psathyrella ovaticystis* Pegler, *Kew Bulletin Additional Series* **VI**: 428. 1977. Fig. 12

Typus: *Psathyrella ovaticystis* Pegler. **Uganda**, Buganda Province, Mengo Distr., Zika Forest, 12 Jun. 1968, *D.N. Pegler* 1433 (K(M) 196311), among leaf litter.

Loan of one sporocarp lacking a slice of pileus for micro-morphology investigation and molecular analysis.

Spores 6.2–8.8(–9.1) × 4.2–5.1 µm, on average 7.8 × 4.9 µm, Q 1.5–1.8, avQ 1.6; in front view oval to cylindrical oval, irregularly to angularly cylindrical-elliptical, irregularly to angularly oboval, base broadly rounded to sometimes truncate, in profile adaxially flattened to subphaseoliform; few spores darkish reddish brown and with little to moderately distinct, mostly truncate, 1.4–1.7 µm broad germ pore. *Pleurocystidia* 20–32 × (9–)11–16 [apex 8–12.5(–15) µm broad when differentiated], cylindrical-utriform, clavate-utriform, ellipsoid, clavate, ovoid, sometimes utriform; apex rounded to almost truncate, sometimes subcapitate, not forked, not incrusted, often collapsed in exsiccate material; walls not pigmented; moderately numerous to scattered. *Cheilocystidia* 18–28 × 9–16 µm, scattered to locally moderately numerous. *Paracystidia* 11–25(–30) × 7.5–15(–19) µm, dominating.

Notes: Pegler (1977) reports the dimension of the pileus to be 10 mm and the stipe' s dimension to be 40 × 1.5 mm, therefore it can be deduced that his collection consists in one only specimen. Some characters of this taxon recall *P. kauffmanii*: color (Pegler 1977: '*fuscobrunneae … dark fuscous brown*' without indication of the liquid of observation) and shape of spores, and shape of cystidia. However, it has distinctly shorter (20–26 × 9–12 µm in Pegler 1977), bulkier on average, oftener undifferentiated pleurocystidia. The carpophore has a reduced, slender habitus and is devoid of veil. Although the DNA analysis failed, the general micro morphological features seem to place it into the subsection *Spadiceogriseae*, possibly close to the *P. kauffmanii* complex.

9. *Psathyrella spadiceogrisea* (Schaeff.) Maire, *Mém. Soc. Sci. Nat. Maroc*. **45**: 113. 1937. Figs 13 (as *P. spadiceogrisea*), 14 (as *P. lubrica*), 15 (as *P. praecox*), 16 (as *P. amarella*).

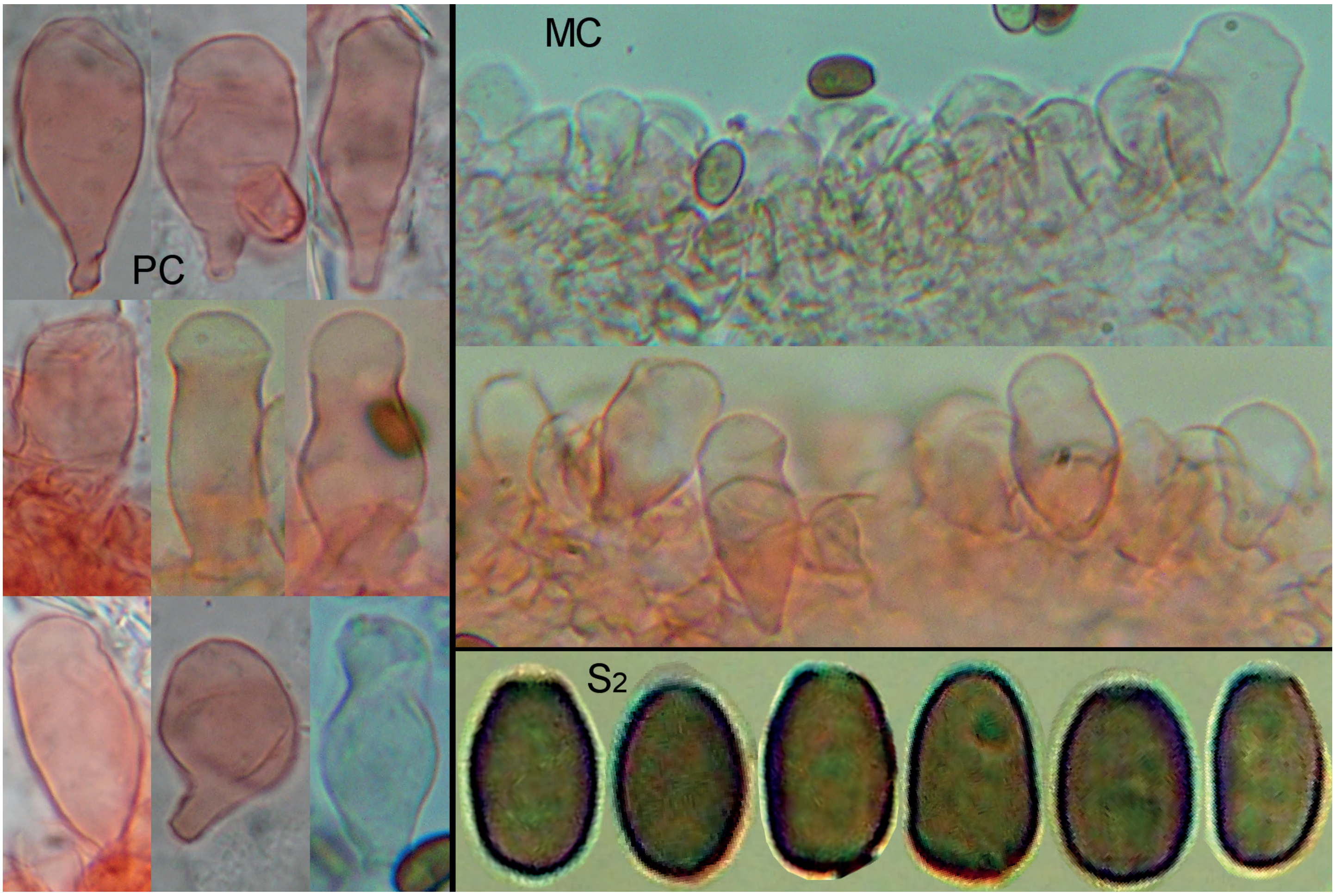


Fig. 12. *Psathyrella ovaticystis*. D.N. Pegler 1433, K(M) 196311; PC Pleurocystidia; MC Marginal Cystidia; S2 Spores in KOH.

Fig. 13. *Psathyrella spadiceogrisea*. MCVE29103. Photo G. Tassi.

Molecular heterotypical synonyms proposed here: *Psathyrella amarella* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 353. 1972; *Psathyrella lubrica* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 144. 1972; *Psathyrella praecox* A.H. Sm*., Mem. N. Y. Bot. Gard*. **24**: 352. 1972.

Pileus 15–55 mm broad, in early stages obtusely conical with inflexed margin, finally conical-convex to plane, obtusely umbonate or not, sometimes radially rugulose in old sporocarps; when young dark reddish brown sometimes with a violaceous tinge, discoloring to brown, dark brown, cinnamon brown, rust brown, ochraceous brown, brownish orange, yellow brown, dark yellow brown, grey brown, yellow red, sometimes shiny, hygrophanous, fading cream to alutaceous or whitish, often with greyish tint; translucently striate when moist. *Veil* white, fugacious, when young on pileus with flocci or fibrils around margin, sometimes fringed at margin, on stipe with appressed fibrils. Lamellae adnate, moderately broad in age, crowded to moderately crowded; when young pale alutaceous to hazel-brown, finally purplish brown; edge white. *Stipe* 40–80×1.5–8 mm, generally equal; white to whitish; apex pruinose, base sometimes fugaciously felted. *Context* thick in the centre of pileus and thin towards the margin, fragile to moderately fragile in stipe, pale. *Odor* indistinctive. Taste mild to bitterish. Spore deposit dark purple-brown. *Spores* (6–)7–10.1(–10.7) × (3.5–)3.8–5.5(–5.8) µm, on average 7.7–9 × 4.3–5.2 µm, Q (1.4–) 1.6–2.2, avQ 1.75–2; in front view elliptic, narrowly oval, oblong, subcylindrical, sometimes narrowly angular-oval, base often more or less truncate, in profile subphaseoliform to adaxially flattened, rarely amygdaliform; reddish brown; germ pore distinct, more or less truncate, 1.3–1.7 µm broad. *Basidia* 4-spored, 18–24(–30) × 7–9(–10) µm. *Pleurocystidia* 30–64 × 9–20 µm, mainly utriform, also fusiform to lageniform, sometimes broadly utriform, subcylindrical, obtusely subconical; apex rounded to subobtuse, rarely acute, rarely subcapitate, sometimes forked, sometimes incrusted; walls sometimes thickened, sometimes yellow brown pigmented; numerous, rarely scattered. *Cheilocystidia* 25–45 (–50) × 10–18 µm, rare to scattered, rarely absent or rather numerous. *Paracystidia* 8–33(–42) × 5–17(–20) µm, sometimes rhomboid, rarely incrusted; walls sometimes thickened and lightly pigmented (overall towards base); numerous, dominating. Cells below marginal cystidia rarely incrusted, rarely slightly pigmented. Clamps present.

Habitat: gregarious or cespitose; on woody debris, in leaves, on muck; in deciduous woods, in parks, on paths.

Collections examined from MICH: *Psathyrella amarella* A.H. Sm., Ammirati 2925; *Psathyrella lubrica* A.H. Sm., **holotype**, Smith 15019; *Psathyrella praecox* A.H. Sm., **paratype**, Potter 4490.

Other material examined: **France**, Essonne, Mennecy, Parc de Villeroy, ? Apr. 2004, gregarious, on humus, *G. Tassi* 04005 (duplicate MCVE29103, *Tef-1α* MF521779, ITS MF325997), Fig. 13.

Notes: As the holotype material of *P. spadiceogrisea* seems not to be existing anymore we refer, for its molecular concept, to Örstadius *et al.* (2015) and, for its morphological concept, to the German description of the basionym *Agaricus spadiceogriseus* by Schäffer (1771) (later followed by a latin description in Schäffer 1774) which includes a color drawing in table 237 (iconotypus). Our morphological concept also matches that by Örstadius *et al.* (2008) but for some little differences as they, probably, included also *P. niveobadia* in their description.

Schäffer (1800) later authored a reprinted version of its original table displaying a different pileus coloration including distinct violaceous tints, and dirty pinkish for the smallest sporocarps. The first color can also be found in *P. fatua* (see Figs 36, 38, 40) and *P. albescens* (see Fig. 27) when undergoing the drying process; the distinct pink color, instead, is only known for *P. fatua* (see Figs 37, 39). More comments on Schäffer's table and description are included in the notes about *P. albescens*, but -based on the points above- it is likely that Schäffer's reprinted drawings may also include *P. fatua* collections.

The features of *P. spadiceogrisea* show a range of variability. The initial strong tints of the pileus can linger into the mature stage, until the pileus remains fresh, and may discolor into greyish tints. The pleurocystidia are with or without the following: incrustations, pigmentation or forked apex. Morphological variability and the unrecognized presence in Europe of the American taxon *P. albescens* (see below), at least until now, have led to misinterpretations, superfluous synonyms, and contradicting interpretations. Many subspecific taxa have been reduced to synonymy: *P. spadiceogrisea* f. *mammifera*, *P. spadiceogrisea* f. *phaeophylla* and *Drosophila spadiceogrisea* f. *russifolia* by Ludwig (2007); *P. spadiceogrisea* f. *vernalis* both by Ludwig (2007) and by Örstadius (2007). Also Ludwig (2007) synonymized *P. spadiceogrisea* f. *exalbicans* to *P. fatua*. Some of these synonymies, particularly the last two, may be incorrect as their propounder did not know about the presence of *P. albescens* in Europe; this however would not change the main point that none of them are to be regarded as good species.

The four vouchers we have analyzed in this study display some degree of slight intraspecific variability in their molecular identity too. However ITS sequence homology values were always higher than 98.0 % among the type of *P. amarella*, the paratype of *P. praecox,* and samples LÖ92-01 and MCVE29103 of *P. spadiceogrisea*. Similarly, *Tef-1α* sequence homology values were always higher than 99.0 % among the type of *P. lubrica*, the paratype of *P. praecox*, and samples LÖ102-98 and MCVE29103 of *P. spadiceogrisea*.

In MCVE29103 (G. Tassi's voucher 04005), composed of both young and mature specimens, the pilei are date brown, ochraceous in the center, and encircled in the primordial and young stages by a conspicuous band of white veil (see Fig. 13).

These macro morphological traits are similar to those described for *P. niveobadia*; however the micro-morphological features of this material overlap with those of *P. spadiceogrisea*.

The holotype of *P. amarella* shows some pleurocystidial apex with a thickened and pigmented wall. All of the material examined has shown a sparse presence of little incrustations on pleurocystidia apex, but never a nucous covering.

The lack of strong morphological differences and the similarity of DNA sequences all suggest these collections represent the same species.

Psathyrella marquana and *P. cascoides* are two very recently described species. The former has characters that, although close to those of *P. spadiceogrisea*, are different enough to represent its own species, and it is included in our key. The latter instead, has characters fully consistent with those of *P. spadiceogrisea*, and therefore it has to be regarded as a synonym.

Descriptions of *P. casca* in the literature are mostly misidentifications of *P. spadiceogrisea* or *P. niveobadia*. Kits van Waveren's (1985) interpretation was reported by Örstadius *et al.* (2008) as synonym to *P. spadiceogrisea*. Actually, we suspect it, and also *P. casca sensu* Tassi (2000), to represent *P. niveobadia* instead. We consider *P. casca* a dubious name.

For comparison with *P. niveobadia* see below.

9a. *Psathyrella lubrica* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 144. 1972. Fig. 14.

Typus: *Psathyrella lubrica* A.H. Sm. **USA**, Michigan, Oakland Co, Kent Lake, near New Hudson, 28 May 1940, *A.H. Smith* 15019 (MICH11957), on muck. *Tef-1α* MF521771.

Loan of two sporocarps in good condition and a portion of pileus for gross morphology investigation.

Spores 7.5–9 × 3.8–5.5 µm, Q (1.46–)1.61–1.9(–1.93), avQ 1.75; in front view elliptic, narrowly oval, subcylindrical, sometimes narrowly angular-oval, base rounded to more or less truncate, in profile adaxially flattened to subphaseoliform; reddish brown; germ pore moderately distinct to distinct, more or less truncate,1.3–1.7 µm broad. *Pleurocystidia* 45–62 × 10–18 µm; utriform to fusiform-utriform or lageniform, sometimes subcylindrical; apex obtuse to subobtuse, sometimes rounded to subacute, rarely subcapitate, sometimes forked, sometimes incrusted; walls hyaline; numerous. *Cheilocystidia* 25–40 × 10–15 µm, scattered. *Paracystidia* –33 × –13 µm, sometimes rhomboid, numerous, dominating. Cells below marginal cystidia hyaline, not incrusted.

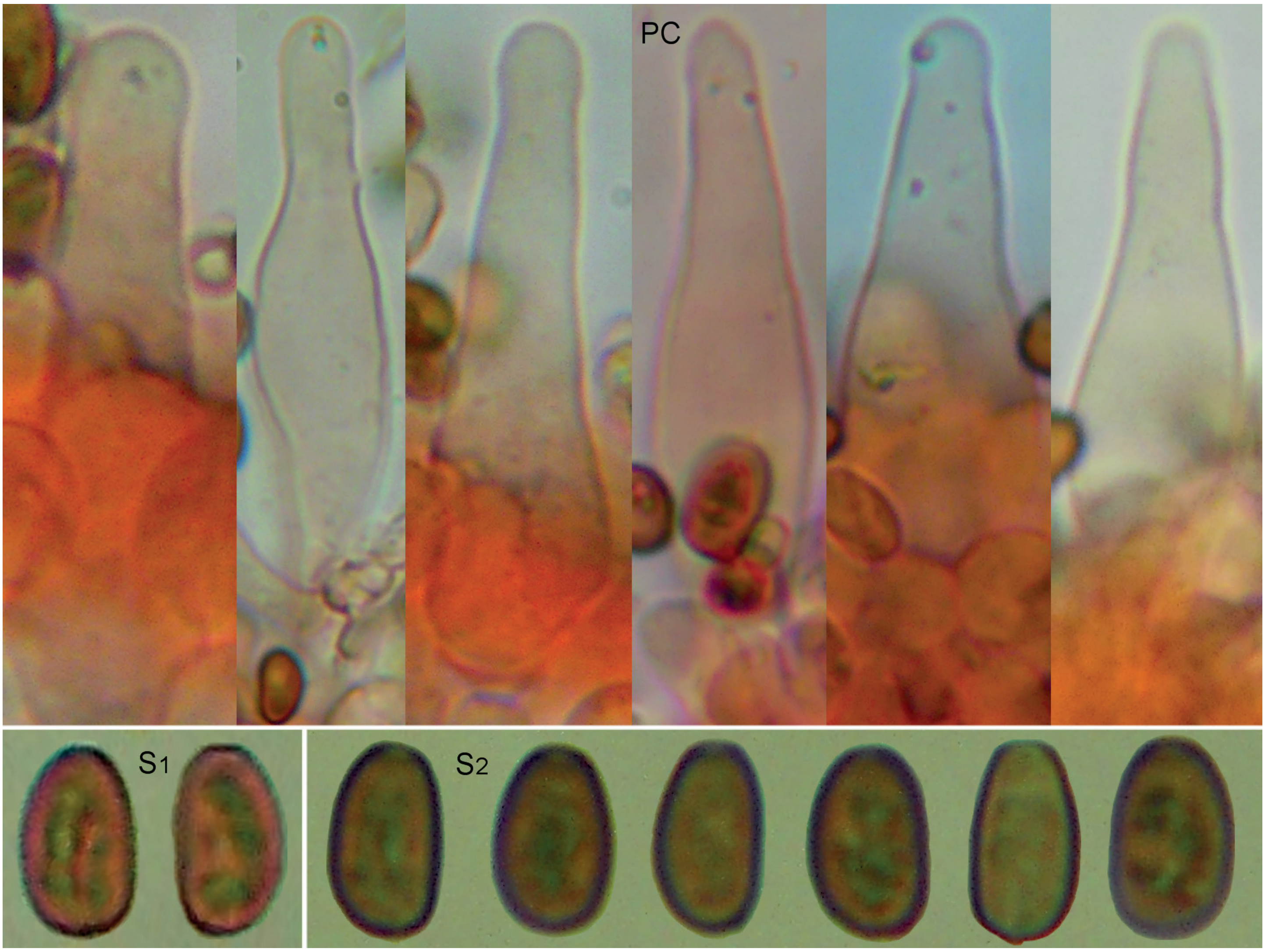


Fig. 14. *Psathyrella lubrica*. A.H. Smith 15019, MICH11957; PC pleurocystidia; S1 Spores in water; S2 Spores in KOH.

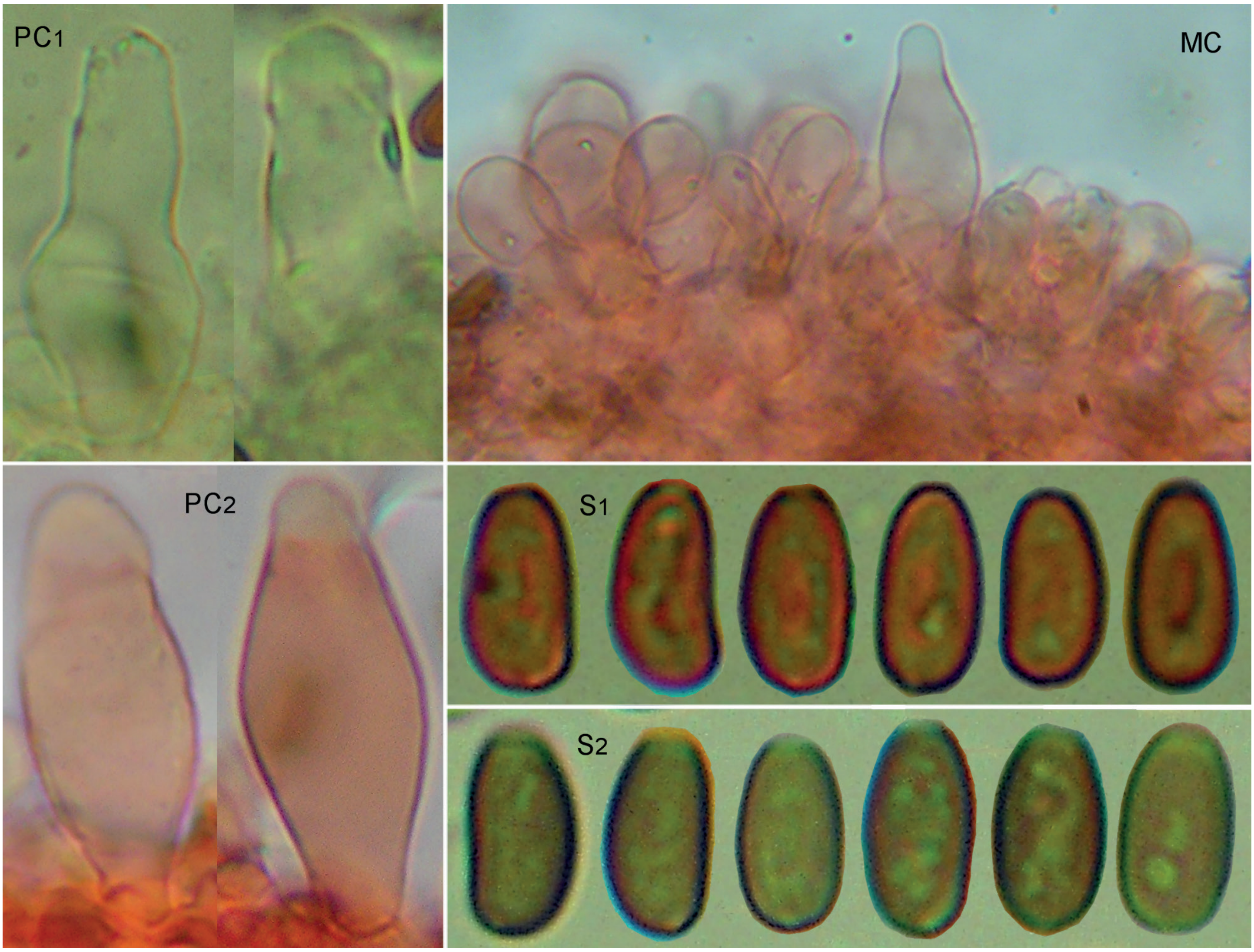


Fig. 15. *Psathyrella praecox*. V. Potter 4490, MICH49251; PC1 Pleurocystidia in NH_4OH; PC2 Pleurocystidia in Congo red; MC Marginal Cystidia in Congo red; S1 Spores in water; S2 Spores in KOH.

9b. *Psathyrella praecox* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 352. 1972. Fig. 15.

Paratype: *Psathyrella praecox* A.H. Sm. **USA**, Michigan, Gratiot Co., Ithaca, Schovence's woods, 18 May 1948, *V. Potter* 4490 (MICH49251), on soggy leaf mold near edge of a pond. *Tef-1α* MF521783, ITS MF325992.

Loan of various sporocarps in good condition for gross morphology investigation.

Spores 7.5–10.1 × 3.8–5.1 µm, Q 1.7–2.2, avQ 2; in front view elliptic, cylindrical to oval, sometimes narrowly angular-oval, base often more or less truncate, in profile adaxially flattened to subphaseoliform, sometimes phaseoliform or subamygdaliform; reddish brown; germ pore distinct, often truncate, ± 1.6 µm broad. *Pleurocystidia* 32–43 × 10–17 µm; utriform, sometimes fusiform-utriform, subcylindrical; apex rounded to obtuse, not subcapitate, sometimes forked, sometimes incrusted; walls sometimes pigmented; numerous. *Cheilocystidia* 31–36 × 11–12 µm, rare. *Paracystidia* 8–31 × 5–17 µm, rarely incrusted, walls sometimes thickened and weakly pigmented, numerous, dominating.

Notes: Smith (1972) reports narrower spores, (6–)7–9 × 3.3–3.8 µm. Both morphology and DNA reveal that this paratype is a later synonym of *P. spadiceogrisea*. This result does not necessarily apply to the holotype, which could not be obtained due to scarcity of material; however, from the general description of the species we conclude that *P. praecox* is to be considered a synonym of *P. spadiceogrisea*.

9c. *Psathyrella amarella* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 353. 1972. Fig. 16.

Typus: *Psathyrella amarella* A.H. Sm. **USA**, Michigan, Baraga Co., Silver River Area, Dynamite Hill Road, 7 Feb. 1969, *J.F. Ammirati* 2925 (MICH11869), gregarious on leaf mold in a hardwood forest. ITS MF325958.

Loan of one pileus in good condition for gross morphology investigation.

Spores 7–9.4 × 4–5 µm, Q 1.6–2.1; in front view elliptic, subcylindrical, (narrowly) oval, base often more or less truncate, in profile subphaseoliform to adaxially flattened; reddish brown; germ pore distinct, subtruncate to rounded, ± 1.2–1.6 µm broad. *Pleurocystidia* 30–48 × 10–15(–20) µm; utriform,

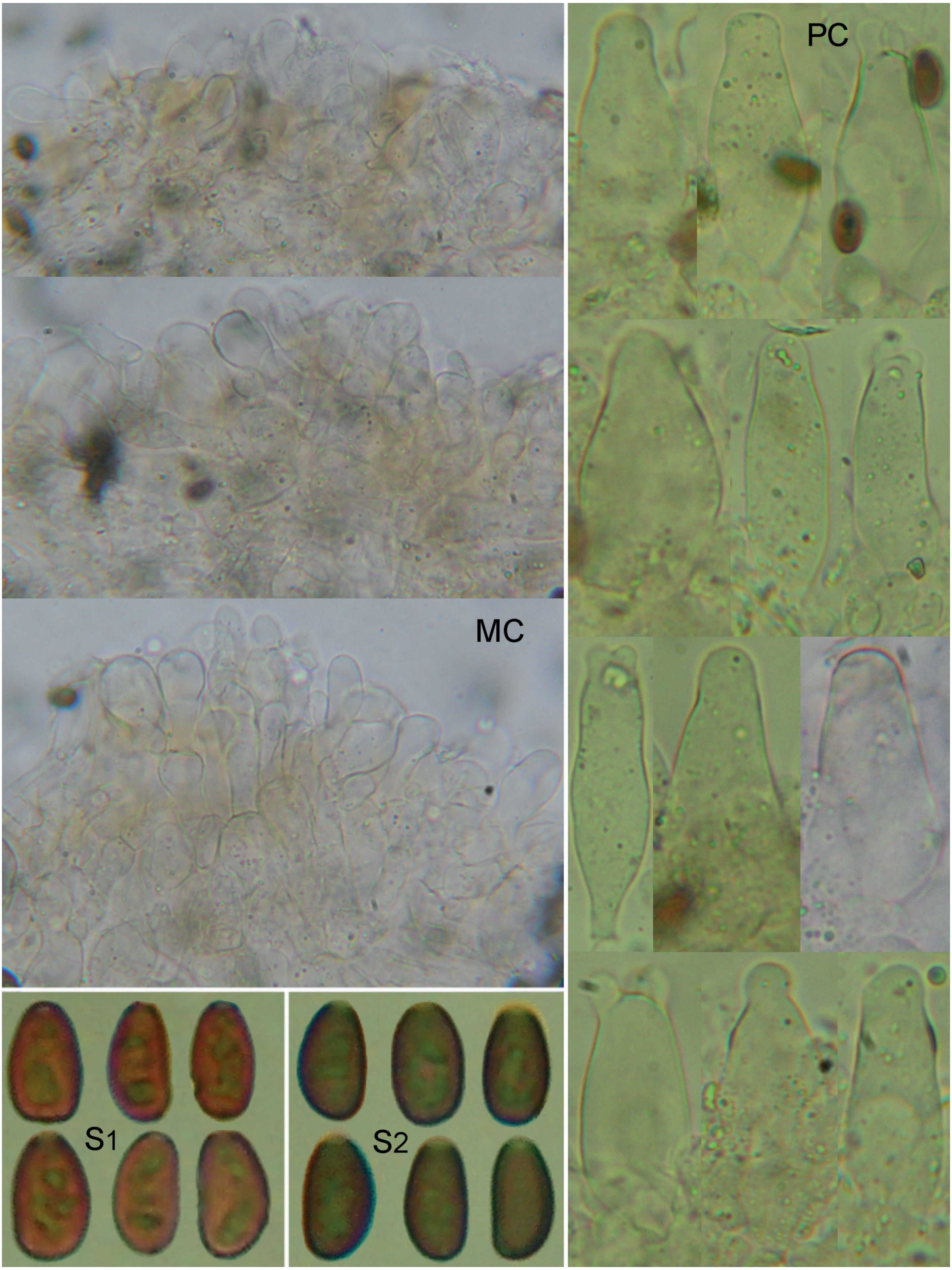


Fig. 16. *Psathyrella amarella*. J.F. Ammirati 2925, MICH11869; MC Marginal Cystidia in KOH; PC Pleurocystidia in NH_4OH; S1 Spores in water; S2 Spores in KOH.

ellipsoid-utriform, sometimes clavate-utriform to obtusely fusiform; apex rounded, sometimes subacute, not subcapitate, often forked to irregular, sometimes incrusted; walls sometimes thickened, sometimes reddish brown pigmented; moderately numerous. *Cheilocystidia* 20–33(–42) × 8–13 µm, scattered and visible in mass. *Paracystidia* 11–31(–40) × 5–17(–25) µm, often cylindrical, walls sometimes thickened and pigmented with a very slightly ochraceous hue (detectable in mass); numerous, dominating. Cells below marginal cystidia slightly pigmented, sometimes incrusted.

Notes: The molecular comparison of this species with the other examined material of *P. spadiceogrisea* shows that the ITS nucleotide homology ranges between 98 % and 99 % identity with 1 to 14 mismatches. Unfortunately, we could not add the evidence of a second locus; however, apart from the bitter taste, we think its morphological traits fit well into the concept of *P. spadiceogrisea*.

10. *Psathyrella niveobadia* (Romagn.) M.M. Moser, *Kleine Kryptogamenflora die Röhrlinge und Blätterpilze (Agaricales)* **2b/2**: 276. 1978. Figs 17–22.

Pileus 15–72 mm broad, in early stages obtusely conical to paraboloid with inflexed margin, then hemispherical, finally through convex to plane, obtusely umbonate or not, often radially rugulose in old sporocarps; when young dark, violaceous brown to reddish brown or date-brown, possibly still dark when mature, discoloring to ochraceous brown at centre, more brown to greyish brown in periphery, hygrophanous, fading cream to grey-cream or grey-beige, sometimes with olivaceous tints; not translucently striate or only at extreme margin. *Veil* white, fugacious, when young of fibrils on margin and connecting margin to stipe. *Lamellae* 3–6 mm broad, adnate to broadly adnate, crowded to moderately crowded; when young grey brown, finally more or less dark brown; edge white. *Stipe* 30–130(–200) × 3.5–10 mm, cylindrical, sometimes very broad at apex (up to 17 mm) and then tapering downwards, sometimes a little broadening towards the base, often with a short to 10 cm long rooting base; hollow since when young; white, discoloring pale brownish with age; apex pruinose. *Context* fairly thick and tenacious in the pileus, distinctly thick and rigid in the stipe cortex, only fragile in the rooting stipe base portion. *Odor* weak to indistinctive. Spore deposit purplish brown. *Spores* 6.9–9.5(–10) × (3.9–)4.2–5 µm, on average 7.4–8.3 × 4.5–4.7 µm, Q (1.5–) 1.55–2(–2.25), avQ 1.7–1.8; in front view elliptic to cylindrical or narrowly oval-cylindrical, base truncate to broadly rounded, in profile phaseoliform, subphaseoliform or adaxially flattened, rarely indented above the apiculus; orange-brown to reddish orange brown (darkish reddish brown in NH_4); germ pore distinct, rounded, 1.0–1.5 µm broad. *Pleurocystidia* (26–)35–60(–70) × (10–)14–18(–22) µm, utriform, lageniform, clavate, clavate-mucronate, fusiform or irregularly tapering towards the apex, sometimes cylindrical-utriform, ellipsoid-utriform; apex broadly rounded to narrowly obtuse, sometimes truncate or subacute, subcapitate or not, sometimes distinctly capitate, sometimes forked, sometimes incrusted, often with grossly mucous masses which gradually disappear in exsiccata and, perhaps, also with age of sporocarps; walls often or sometimes slightly thickened especially at apex and yellow brown pigmented; base sometimes with one or two septa; scatter to numerous. *Cheilocystidia* 21–35(–45) × 12–22 µm, scattered. *Paracystidia* 11–30(–40) × 7–18 µm; walls sometimes slightly thickened and pale brown; numerous, dominating. Cells below marginal cystidia generally not incrusted and not pigmented.

Fig. 17. *Psathyrella niveobadia*. MCVE29102 Photo B. De Ruvo.

Fig. 18. *Psathyrella niveobadia*. MCVE29102. Photo B. De Ruvo.

Habitat: gregarious to caespitose; often growing in spring, lowlands to mountains; on broadleaves woody debris or around stumps, dry to moist.

Material examined: **France**, Aisne, près de Russy-Bémont, vallée de Russy, forêt de Retz, at the margin of the wood, gregarious on soil and on debris, 14 Feb. 1993, *G. Tassi* 93014 (9314). **Italy**, Teramo, Rocca Santa Maria, loc. Ceppo, 1 350 m a.s.l., caespitose around stump of *Fagus*, 4 May 2003, *B. de Ruvo*, Figs 17, 18, (duplicate MCVE29102, *Tef-1α* MF521780, ITS MF325996, more pictures of this collection in http://www.ambmuggia.it/forum/topic/478-psathyrella-fatua/); Pescara, Lettomanoppello, Parco nazionale della Majella, 1 300 m a.s.l., gregarious to fasciculate among debris of leaves and needles or around a *Fagus* stump in a calcareous mixed wood of *Fagus*, *Picea*, *Abies* and *Pinus*), 13 May 2018, 18 May 2018 and 20 May 2018, *A. Micucci*, Figs 19–22, (MCVE30076, *Tef-1α* MK408675, ITS MK400421).

Fig. 19. *Psathyrella niveobadia*. MCVE30076. Photo A. Micucci.

Fig. 20. *Psathyrella niveobadia*. MCVE3007. Photo A. Micucci.

Fig. 21. *Psathyrella niveobadia*. MCVE30076. Photo A. Micucci.

Notes: The case of *P. niveobadia* remains a little ambiguous. We could not examine the French holotype of its basionym, *Drosophila niveobadia*, therefore, we have studied two French collections kindly provided to us by G. Tassi. The gross morphology of voucher 04005 (duplicate MCVE29103) recalls that of *P. niveobadia,* but decidedly belongs to *P. spadiceogrisea* (see discussion above). The other voucher, 93014, has microscopical characters in line with those of *P. niveobadia* (shape of pleurocystidia, some pleurocystidia apex thick-walled, dimension and orange-brown color of spores, small germ pore) but, regretfully, DNA extraction failed.

Two other specimens from central Italy (collectors *Micucci*, MCVE30076, and *De Ruvo*, MCVE29102), show morphological characters that match perfectly those of *P. niveobadia* described by Kits van Waveren (1985). They possess, and this is particularly true for Micucci's specimen, all the main expected diagnostic features for this species, including: the thickness and rigidity of the stipe cortex and, to a lesser extent, of the pileus, which is scarcely, if at all, striate; the possibly rooting stipe base; the orange-brown spores which are on average 7.4–8.3 × 4.5–4.7 µm large; the distinctly thickwalled pleurocystidia apex which can be subcapitate or particularly narrow to tapered. From our own observations we can add grossly mucous coverings (in sufficiently fresh specimens at least) of the pleurocystidia apex which is not reported in Kits van Waveren's (1985) description. We regard other characters in Kits van Waveren's (1985) description as less relevant, not exclusive or unstable; thus, for instance, identifications based mainly on pileus color and veil development, as emphasized in Kits van Waveren's (1985) notes, could actually confuse this species with *P. spadiceogrisea*, while based mainly on rhomboid shape of paracystidia the species in question could actually be *P. fatua*.

Molecular comparisons between the two Italian specimens and the *P. spadiceogrisea* samples included in this paper have produced somewhat ambiguous results, though. *Tef-1α* nucleotide homology levels ranged between 98.14 % and 98.67 %, suggesting a possible conspecificity, but ITS nucleotide homology values ranged between 96.77 % and 99.02 %, only partially corroborating conspecificity. Because Micucci's sequences were obtained in late 2018, they were not used when constructing the phylogenetic trees, thus their exact placement in the phylogeny of the subsection is unknown. However, taking into consideration the morphological differences listed above and the presence of some, albeit limited, genetic divergence between *P. spadiceogrisea* and *P. niveobadia* in the combined phylogenetic tree (Fig. 3), we have decided to keep the species *P. niveobadia* separate from *P. spadiceogrisea*. Of course, we also acknowledge the specimens belonging to these two species may instead represent extremes of a rather variable single species.

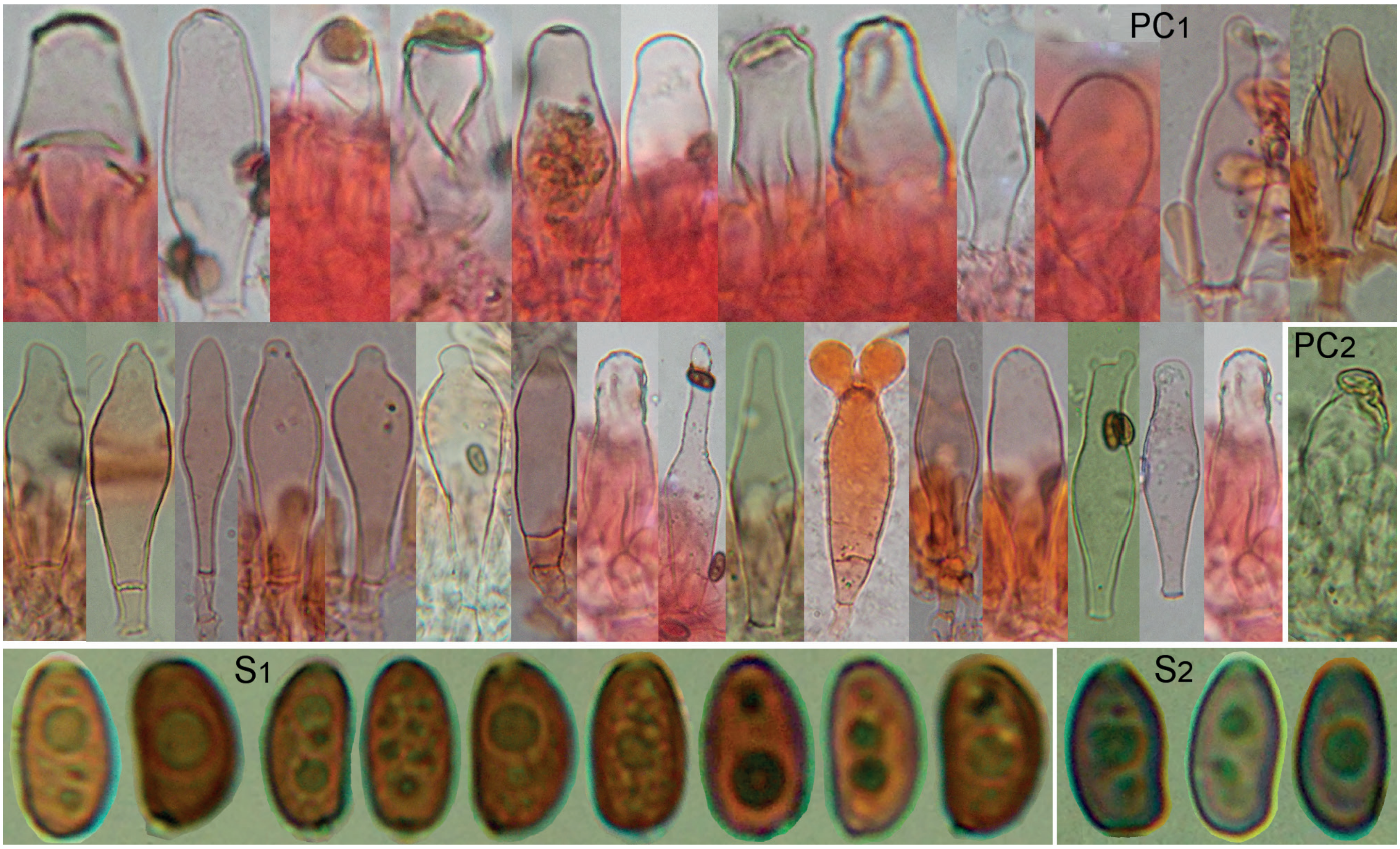


Fig. 22. *Psathyrella niveobadia*. A. Micucci, MCVE30076; PC1 Pleurocystidia in Congo red; PC2 Pleurocystidium in NH_4OH; S1 Spores in water; S2 Spores in KOH.

Other images in color drawings are in Tassi (2000: 368, pl. 7) and Ludwig (2007b, pl. 378, figs 98.38A–98.38B).

11. *Psathyrella albescens* Hesler & A.H. Sm., Mem. N. Y. Bot. Gard. 24: 133. 1972. Figs 23–32 (as *P. albescens*), 33 (as *P. mazzeri*).

Molecular heterotypical synonyms proposed here: *Psathyrella agrariella sensu* A.H. Smith, *Mem. N. Y. Bot. Gard*. **24**: 411. 1972, p.p.; *Psathyrella mazzeri* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 356. 1972.

Pileus 10–70 mm broad, in early stages hemispheric to convex, then campanulate to convex, finally convex to plane and rarely slightly depressed at centre, umbonate or not, sometimes radially rugulose, sometimes wavy, margin for some time more or less inflexed, finally straight to sometimes reflexed; when young, dark yellowish brown to cinnamon-brown; when mature, cinnamon-brown, yellowish brown, brownish orange, light to medium Dresden brown, rarely pinkish buff, often moist or shiny, hygrophanous, discoloring to white with ochraceous centre for a time, finally drying from margin to greyish or greyish violaceous; translucently striate when moist. Veil white, when young with fibrils or flocci around the margin of pileus and connecting it to stipe, when mature as fugacious fibrils around the margin of pileus or appendiculate or folded back on the gills, on stipe usually with few appressed fibrils, once as a fragile submembranous annulus. *Lamellae* (broadly) adnate to slightly decurrent, moderately broad, not or slightly ventricose, crowded; when young whitish to pale pinkish buff or dull brown, finally purplish brown to blackish brown; edge white, fimbriate. *Stipe* 20–100(–140) × 1.5–6(–12) mm, often broadening towards base or towards both apex and base, extreme base sometimes bent, subrooting or characterized by a short to 50 mm long pseudorhiza; watery white to whitish, often discoloring brownish; apex pruinose, sometimes subsquamulose or striate, base often felted to subtomentose. *Context* pale, fragile to rather rigid, in pileus thin. *Odor* and taste indistinctive to mild. Spore deposit purplish black to blackish brown. *Spores* (6.3–) 6.7–10.2(–11.7)×(3.5–)3.7–5.4(–5.5) µm, on average 7.4–9 × (4.1–)4.5–4.9 µm, Q (1.5–)1.6–2.4(–2.6), avQ (1.70–)1.80–1.90(–2.16); in front view oblong to elliptic or oval to narrowly oval, sometimes (sub) angular-oval to cylindrical or irregular, rarely obscurely narrowly oboval or with a median constriction, base broadly rounded to truncate, sometimes triangular, in profile adaxially flattened to subphaseoliform, phaseoliform or indented above the apiculus, sometimes subamygdaliform; orange-brown to orangish reddish brown; germ pore distinct, more or less truncate, 1.3–1.8 µm broad. *Basidia* 4-spored, 16–24(–29) × 6–9(–10) µm. *Pleurocystidia* (28–)32–68(–70) × (8–)10–23(–28) µm, utriform to broadly utriform, subcylindrical, fusiform to ellipsoid-rhomboid, rarely lageniform or clavate; apex rounded to obtuse, sometimes subtruncate, rarely subobtuse, subcapitate or not, forked or not, incrusted or not; walls sometimes or often thickened, sometimes brownish pigmented; numerous, sometimes moderately numerous. *Cheilocystidia* 21–50 (–58) × (7–)10–18(–25) µm, similar in incrustations and pigment to the paracystidia, rare to scattered or sometimes locally numerous. *Paracystidia* 8–48(–56) × 4–28(–30) µm, sometimes incrusted, walls sometimes or often thickened and

Fig. 23. *Psathyrella albescens*. MCVE29113. Photo P. Voto.

Fig. 24. *Psathyrella albescens*. MCVE29113. Photo P. Voto.

Fig. 25. *Psathyrella albescens*. MCVE29107. Photo P. Voto.

Fig. 26. *Psathyrella albescens*. MCVE29107. Photo P. Voto.

Fig. 27. *Psathyrella albescens*. MCVE29107. Photo P. Voto.

Fig. 28. *Psathyrella albescens*. Voto 20160313. Photo P. Voto.

Fig. 29. *Psathyrella albescens*. MCVE29116. Photo M. Maletti.

Fig. 30. *Psathyrella albescens*. MCVE29111. Photo P. Voto.

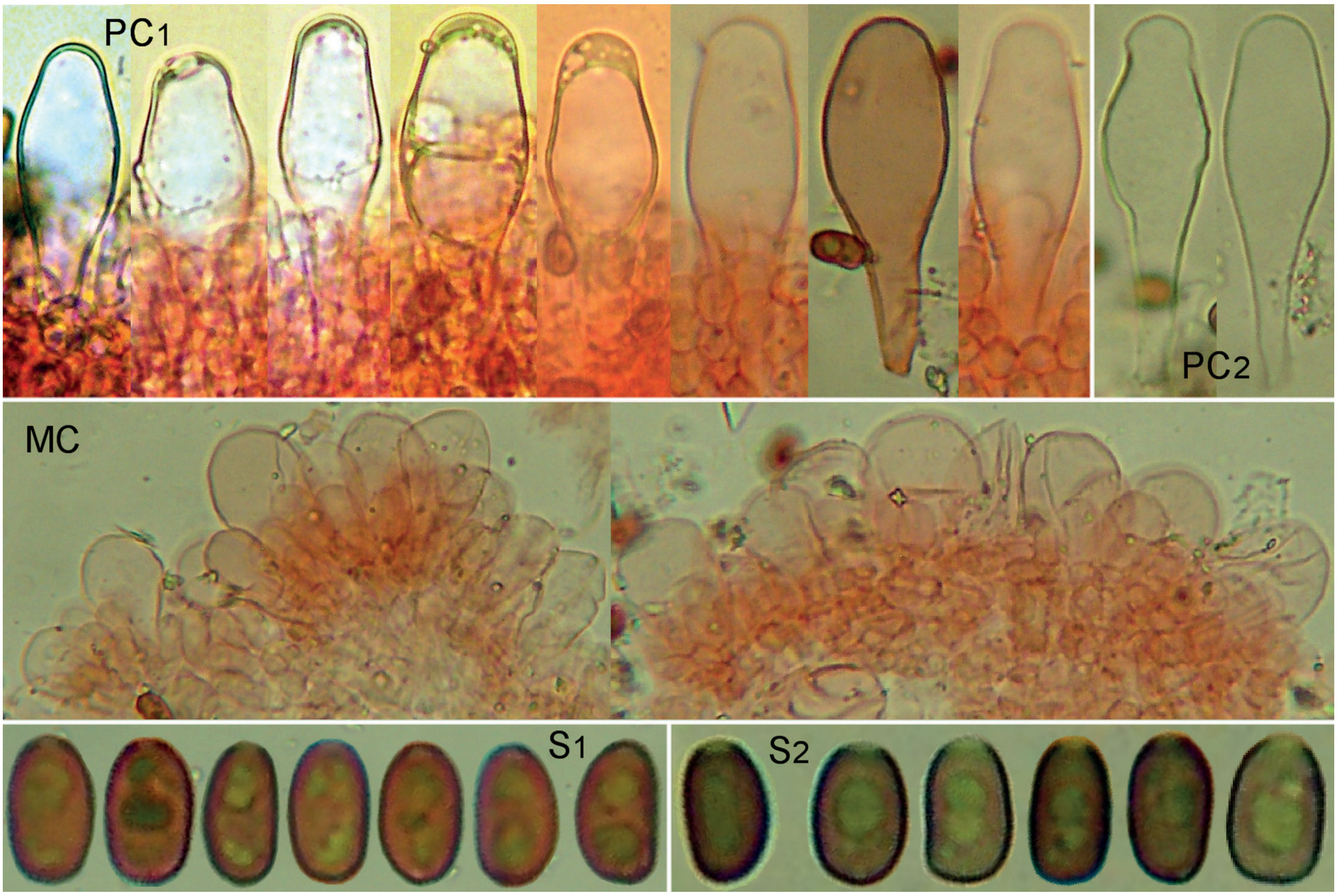


Fig. 31. *Psathyrella albescens*. P. Voto, MCVE29113; PC1 Pleurocystidia in Congo red; PC2 Pleurocystidia in NH_4OH; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

yellowish to brownish pigmented; very numerous, dominating. Cells below marginal cystidia sometimes incrusted, sometimes locally yellowish pigmented. Clamps present.

Habitat: Solitary to gregarious or subcespitose; on woody debris, in leaves, in grass, on sandy humus; in parks, at margin of woods or in wood clearings or in wood paths, in pastures, at roadsides.

Collections examined from MICH: *Psathyrella agrariella sensu* Smith, *Smith* 25099 and *McKnight* F949; *Psathyrella albescens* Hesler & A.H. Sm., **holotype**, *Hesler* 18895; *Psathyrella mazzeri* A.H. Sm., **holotype**, *Mazzer* 6023.

Other material examined: **Italy**, Belluno, Nevegal, about 1 000 m a.s.l., gregarious on debris at margin of forest, 24 Sep. 2010, *P. Voto*, Figs 23, 24, 31 (MCVE29113, *Tef-1α* MF521819, ITS MF325954); Rovigo, Sant'Apollinare, 6 m a.s.l., 18 Nov. 2006, gregarious by a roadside among litter of brambles and *Robinia pseudoacacia*, *P. Voto*, Figs 25–27 (MCVE29107, *Tef-1α* MF521821, ITS MF326009); Rovigo, Crespino, 3 m a.s.l., solitary in a park, 31 Oct. 2006, *P. Voto* (MCVE29106, *Tef-1α* MF521822, ITS MF325953); Rovigo, Villadose, 3 m a.s.l., gregarious in a park under *Tilia platyphyllos*, 13 Mar. 2016, *P. Voto* 20160313, Fig. 28; (Pesaro Urbino, Monti delle Cesane, botanical garden, gregarious among hardwood trees, 29 Apr. 2012, *M. Maletti*, Fig. 29 (MCVE29116, *Tef-1α* MF521818, ITS MF325955); Venezia, Chioggia, S. Anna, Nordio forest, 2 m a.s.l., 12 Dec. 2007, solitary on humus of *Quercus ilex*, *P. Voto*, Fig. 30 (MCVE29111, *Tef-1α* MF521820); at same location, 31 Oct. 2011, gregarious on woody debris, *P. Voto* 20111031.1; at same location, 5 Nov. 2015, gregarious on woody debris, *P. Voto* (MCVE29332).

Notes: *Psathyrella albescens* is difficult to distinguish from *P. spadiceogrisea* based on micro morphological characters. We cite the occurrence of two traits: possibly capitate pleurocystidia that are absent or seldom found in *P. spadiceogrisea*, and spores with a greater tendency to be phaseoliform or indented above the apiculus. More consistent differences can be found in the gross morphology and are listed below. The young pilei of *P. spadiceogrisea* have a reddish brown (in agreement with Schäffer's, 1771 table nr. 237) to dark reddish brown or violaceous brown color, often retained until maturity, while *P. albescens* pilei are at most dark yellowish brown at first, and quickly become discolored to brownish orange, never attaining a dark brown or reddish tint. Furthermore, the discoloring pilei of *P. spadiceogrisea* usually fade to cream or alutaceous tints, while those of *P. albescens* usually fade to white. The veil of *P. spadiceogrisea* is fugacious and conspicuously located on the margin of the pileus where it is usually no longer present in mature sporocarps (in agreement with Schäffer's, 1774 description of 'velo et annulo destitutus'), rarely and exclusively in early stages of development it is in form of appendiculate flocci. Conversely, in favorable climatic conditions, the veil of *P. albescens* can be still appendiculate from the margin of the pileus or folded back on the gills or, rarely, annulate on the stipe in mature sporocarps. Often, *P. albescens* has a stipe base that is more or less swollen and can be subrooting or characterized by a pseudorhiza up to 50 mm long. Conversely, this trait is not reported by Schäffer (1774) for *P. spadiceogrisea*, which has a stipe base at most slightly attenuated. Finally, *P. spadiceogrisea* is only found on woody material, while *P. albescens* can also be found in grasslands.

The features that can differentiate *P. albescens* from *P. fatua* are slight and often they can do so only partially. The first has a veil at times still appendiculate or folded back on the gills, rarely annular, in mature specimens, while the second has a quickly evanescent veil on the margin. The first species has a discoloring pileus without distinct pinkish shades, at most and rarely pinkish buff, and with a disk never attaining vivid colors: at most it may only have a dull ochraceous tint. The second species has discoloring pilei that may attain pinkish shades on the margin, and vivid yellow tints on the disk. The gill edge is not pigmented in the first species, but it can be red in the second. Pleurocystidia can be brownish, forked, or incrusted in the first, while in the second they are never brownish, and rarely forked or weakly incrusted. Spores of *P. albescens* are orange-brown to orangish reddish brown and often phaseoliform to indented above the apiculus, while those of *P. fatua* are brown to dark red, rarely phaseoliform or indented above the apiculus, sometimes subphaseoliform.

We expect this species to be present in herbaria of European mycologists under the different names *P. fatua*, *P. pseudocorrugis sensu* Kits van Wav., *P. niveobadia*, and *P. spadiceogrisea*.

Based on our evaluation, at least one voucher determined as *P. agrariella* by Smith is actually *P. albescens*, thus rendering Smith's concept of *P. agrariella* dubious (see descriptions of Smith 25099 and Mc Knight F949 below).

11a. *Psathyrella albescens* Hesler & A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 133. 1972. Fig. 32.

Typus: *Psathyrella albescens* Hesler & A.H. Sm. **USA**, Tennessee, Knox, Farragut, 20.II.1949, L. R. Hesler 18895 (MICH11863), on decaying chip pile. *Tef-1α* MF521817.

Loan of a portion of pileus in good condition for micromorphology investigation.

Spores 6.7–8.5(–10) × 3.7–4.4(–4.9) µm, Q (1.4–)1.6–2(–2.3), avQ 1.88; in front view oblong to elliptic, sometimes irregular, sometimes obscurely narrowly oboval or with median constriction, rarely angular-oval, base rounded, sometimes more or less truncate, in profile adaxially flattened to subphaseoliform, sometimes indented above the apiculus; orange-brown to orangish reddish brown; germ pore distinct, mostly more or less truncate, about 1.6–1.7 µm broad. *Pleurocystidia* 35–52 × 13–17 µm, utriform, sometimes subcylindrical, ellipsoid-rhomboid; apex rounded to obtuse, sometimes subcapitate, forked or incrusted; walls sometimes thickened and pigmented; numerous. *Cheilocystidia* small, scattered. *Paracystidia* 8–48 × 6.5–28 µm, often with yellowish incrustations, walls often thickened, numerous, dominating. Cells below marginal cystidia conspicuously incrusted.

11b. *Psathyrella mazzeri* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 356. 1972. Fig. 33.

Typus: *Psathyrella mazzeri* A.H. Sm. **USA**, Michigan, Allegan Co., Vivian Baker Farm near Otsego, 16 May 1970, *S.J. Mazzer* 6023 (MICH11963), scattered to gregarious in open pasture with *Phleum pratense* and *Dactylis glomerata*. *Tef-1α* MF521790, ITS MF325981.

Loan of two sporocarps in good condition for micro-morphology investigation.

Spores 6.8–9.3(–10) × 3.8–5.2(–5.5) µm, Q (1.45–)1.65–1.9(–2.1), avQ 1.79; in front view elliptic, oblong to narrowly oval, rarely oval to subangular-oval, base rounded, rarely truncate, in profile subphaseoliform to adaxially flattened, sometimes phaseoliform to indented above the apiculus; orange-brown; germ pore distinct, mostly more or less truncate, more or less 1.7–1.8 µm broad. *Pleurocystidia* 32–51 × 10–16 µm; utriform, rarely lageniform; apex rounded, often subcapitate; incrustations and pigment not seen; more or less numerous. *Cheilocystidia* 21–35 × 10–14 µm, scattered. *Paracystidia* 10–35 × 4–10 µm, moderately incrusted, walls hyaline, numerous, dominating. Cells below marginal cystidia hyaline, moderately incrusted.

12. *Psathyrella agrariella* (G.F. Atk.) A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 411. 1972.

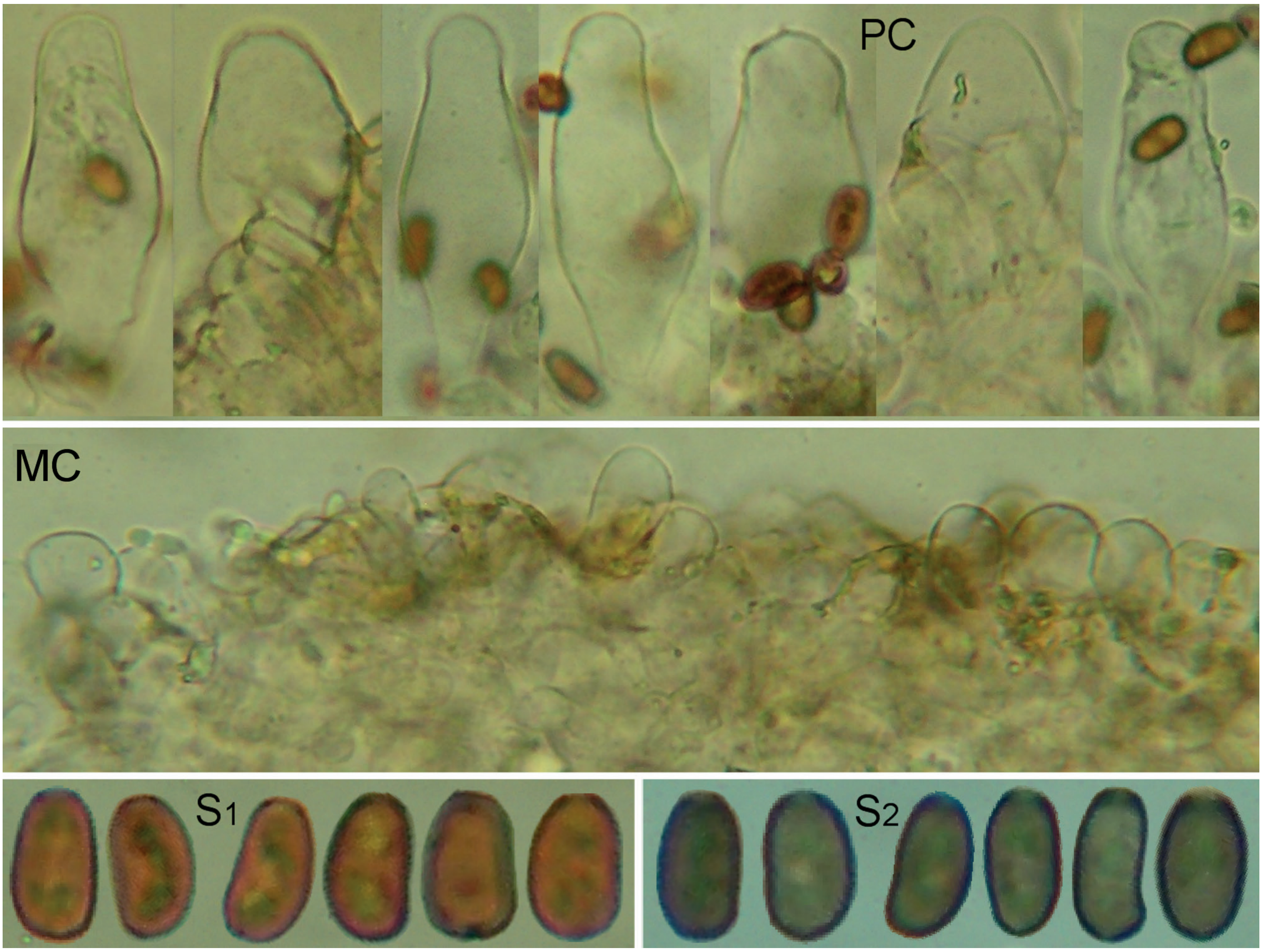


Fig. 32. *Psathyrella albescens*. L.R. Hesler 18895, MICH11863; MC Marginal Cystidia in KOH; PC Pleurocystidia in NH$_4$OH; S1 Spores in water; S2 Spores in KOH.

Smith (1972) transferred *Psilocybe agrariella* to *Psathyrella* but, apparently, without personally revising the original material; in fact among the material examined he indicated only a number of other collections that he deemed to represent that species. MICH staff has provided us with three of those vouchers and they have come out to represent at least two different taxa. Smith 28713 has dominating cheilocystidia, and molecularly is close to *P. seminuda* and clearly out of subsection *Spadiceogriseae*. Smith 25099 has dominating paracystidia and matches *P. albescens* both in morphology and DNA sequence. McKnight F949 also resembles *P. albescens* based on macro and micro-morphology, but the molecular evidence based only on the ITS sequence is inconclusive.

In Atkinson's basionym description of *Psilocybe agrariella,* the pileus is pale reddish brown to pale rufous, the stipe is concolorous to the pileus at the base, the carpophores dimension is small, and the pleurocystidia are defined lanceolate to subventricose. These parameters above are shared with *P. agrariella var. ochrofulva*. The cheilocystidia are described as broadly ventricose and shorter than the pleurocystidia, sometimes very broad and bluntly mucronate: therefore it is unclear whether true paracystidia are present or not, although clavate to pyriform cells are reported at stipe apex intermixed with pleurocystidioid cells. We conclude that the true identity of *Psilocybe agrariella* remains dubious until the holotype is morphologically revised and sequenced. We also suggest that Smith's concept of *Psathyrella agrariella* should be rejected both because of Smith's vague description of the gill edge cystidia, which are reported as broadly ventricose, mucronate or saccate, without an indication of the ratio between them, and because of the lack of homogeneity in his vouchers.

12a. Smith 25099, MICH47933.

= ***Psathyrella albescens*** Hesler & A.H. Sm.

USA, Michigan, Oakland Co., Proud Lake, 26 May 1947, coll. *Lange & Smith*, on sandy humus. *Tef-1α* MF521824. ITS MF326008.

Loan of a dozen and more sporocarps in good condition for micro-morphology investigation.

Spores 6.3–9.1 × 4–5.2 µm, Q 1.5–1.8, avQ 1.7; in front view elliptic to oval or angular-oval, sometimes subtriangular, irregular, base generally truncate, in profile subphaseoliform to adaxially flattened; orange-brown, rarely orangish reddish brown; germ pore distinct, ± 1.5 µm broad. *Pleurocystidia* 28–50 × 10.5–16.5 µm; utriform; apex obtuse to rounded, sometimes

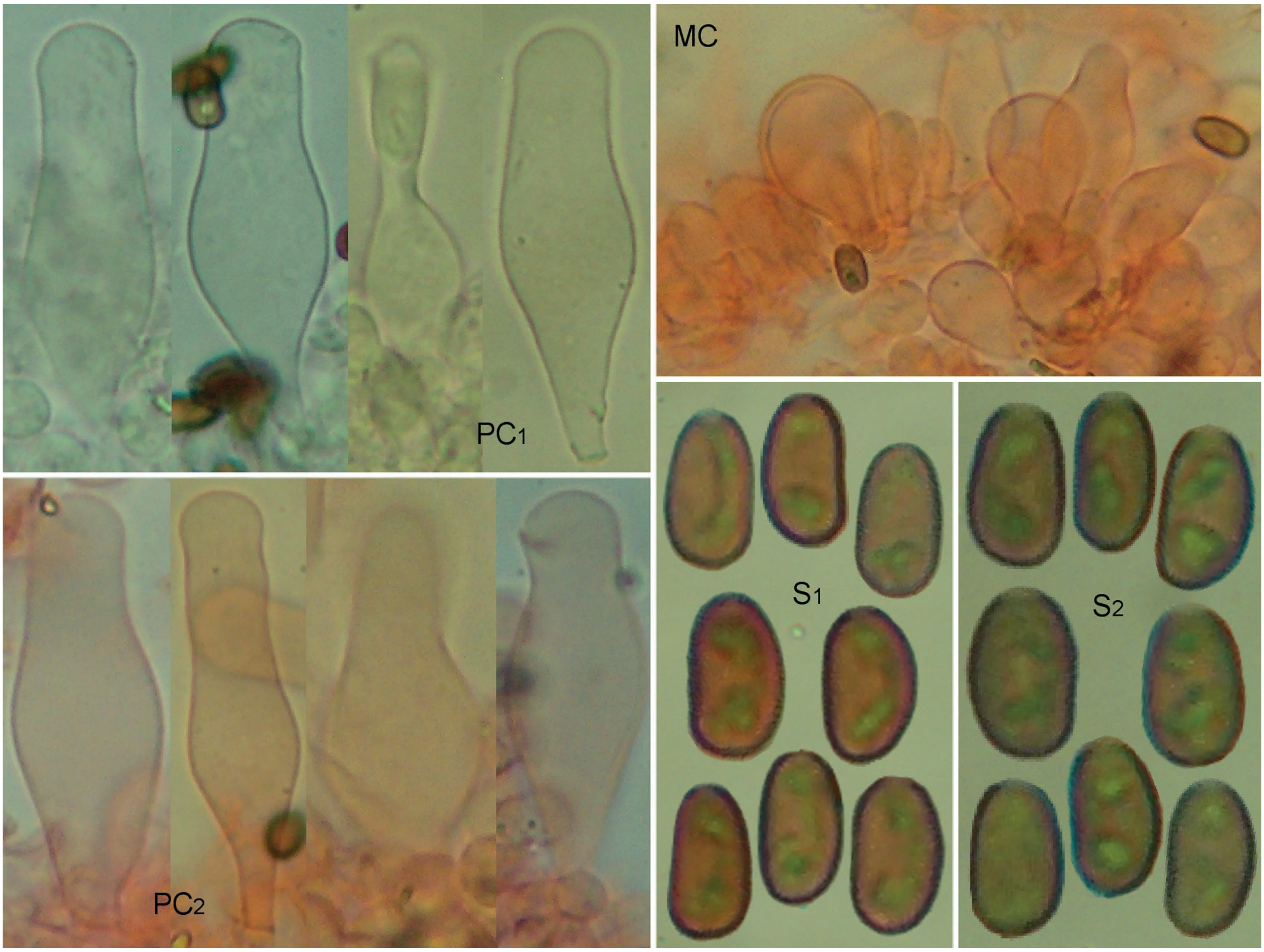


Fig. 33. *Psathyrella mazzeri*. S.J. Mazzer 6023, MICH11963; PC1 Pleurocystidia in NH_4OH; PC2 Pleurocystidia in Congo red; MC Marginal Cystidia in Congo red; S1 Spores in water; S2 Spores in KOH.

or often subcapitate, sometimes forked, sometimes incrusted, walls hyaline or almost so; moderately numerous. *Cheilocystidia* 27–37 × 11.5–18 µm, moderately numerous. *Paracystidia* –30 × –22 µm, often incrusted, numerous, dominating. Cells below marginal cystidia hyaline or almost so.

Notes: The material received was composed of solitary to clustered sporocarps with stipes progressively slightly broadened towards the base and at that point bent and attached to woody debris; in many pilei the margin had a greyish tint. ITS and *Tef-1α* sequences put it in synonymy with *P. albescens*, the morphology is coherent with this result.

12b. Mc Knight F949, MICH65241

?= ***Psathyrella albescens*** Hesler & A.H. Sm.

USA, Utah, Duchesne Co., two miles south of Moon Lake, 9 Jul. 1955, coll. *K.H. Mc Knight & R. Duke*, in moist soil and moss under *Salix*. ITS MF325951.

Loan of numerous sporocarps in good condition for micro-morphology investigation.

The notes from the collector report the following: pileus 1.5–5.5 cm across, buffy brown to bistre when moist and a fibrillose annulus; in the exsiccata, we saw long stipes, up to 90 × 3 mm, and distinct fibrillose veil remains at the stipe apex.

Spores 7–10.1(–12) × 4.4–5.4(–5.7) µm, Q 1.5–2.1(–2.3), avQ 1.76–1.86; in front view elliptic to oval, sometimes irregular, base rounded to truncate, in profile subphaseoliform to adaxially flattened, sometimes subamygdaliform; orange-brown to orangish reddish brown; germ pore distinct, round to rarely truncate, 1.5–1.8 µm broad. *Pleurocystidia* 34–53 × 7.7–11.5 µm; utriform, subcylindrical, sometimes cylindrical, flexuous; apex 6–12 µm broad, rounded to more or less truncate, sometimes or often subcapitate, often forked, often incrusted, walls often slightly thickened, sometimes pigmented; numerous. *Cheilocystidia* 30–45 × 9.5–11 µm, scattered to sometimes somewhat clustered. *Paracystidia* –32 × –17 µm, often pigmented, hardly incrusted, numerous, dominating. Cells below marginal cystidia locally slightly pigmented.

Notes: The ITS sequence of this voucher has a high homology with sequences of the various *P. albescens* collections, but its homology is even higher with the sequence of *P. agrariella var.*

ochrofulva. Although we lack here the corroborating evidence of a second locus, the micro morphological traits are very similar to those of *P. albescens,* and the possible presence of an annulus is already demonstrated for that species by our Italian material MCVE29113. Moreover, the bistre color of the fresh pileus corresponds to the dark yellow brown color described for *P. albescens* by Smith.

12c. A.H. Smith 28713, MICH47939.

=?

USA, Michigan, Washtenaw Co., Dexter, 18.V.1948, on sawdust pile. ITS MF325950.

Loan for micro-morphology investigation of numerous sporocarps in good condition.

Spores (7.2–)7.5–8.7(–9) × 4.2–5 µm, Q 1.6–2, avQ 1.7–1.8; in front view elliptic, sometimes oval, base obtuse, in profile adaxially flattened to subamygdaloid, sometimes subphaseoliform; reddish to brownish red; germ pore generally distinct, generally truncate, sometimes eccentric in profile, ±1.5 µm broad. *Pleurocystidia* 27–52 × 9–15 µm; utriform, sublageniform, sometimes subcylindrical; apex obtuse to rarely rounded, (4–)5–7(–10) µm broad, rarely subcapitate, rarely forked, often incrusted; numerous. *Cheilocystidia* (20–)23–34(–45) × 7–11(–13) µm, numerous, inconspicuously (because small and often recurved to repent) dominating. *Paracystidia* 11–25(–30) × 6–11(–15) µm, often incrusted, walls yellowish pigmented, numerous. Cells below marginal cystidia forming a yellowish discontinuous band approximately 25 µm broad towards the stipe, becoming pale fulvous and up to approximately 100 µm in width towards the pileus margin, generally not incrusted.

Notes: The material received was composed of solitary to clustered sporocarps with most stipes progressively slightly broadened towards base and there attached to woody debris; the pilei had a greyish to greyish violaceous margin; most gills had a purplish edge partly visible by a lens. The phylogenetic evidence places this material very close to *P. seminuda* (DNA nucleotide homology: ITS= 99 % with a single mismatch) but we have found some morphological divergences, such as narrower, terete spores, distinctly smaller pleuro- and cheilocystidia and the presence of numerous, though small, paracystidia not cited for *P. seminuda*. As for the slightly pigmented gill edge it is to be noticed that *P. seminuda* is described with cheilocystidia often rusty brownish colored.

13. ***Psathyrella ochrofulva*** (A.H. Sm.) Voto, Dovana & Garbel, ***comb. nov.*** MycoBank MB831128.
Basionym: *Psathyrella agrariella var. ochrofulva* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 411. 1972. *A.H. Smith* 33628, MICH11858. Fig. 34.

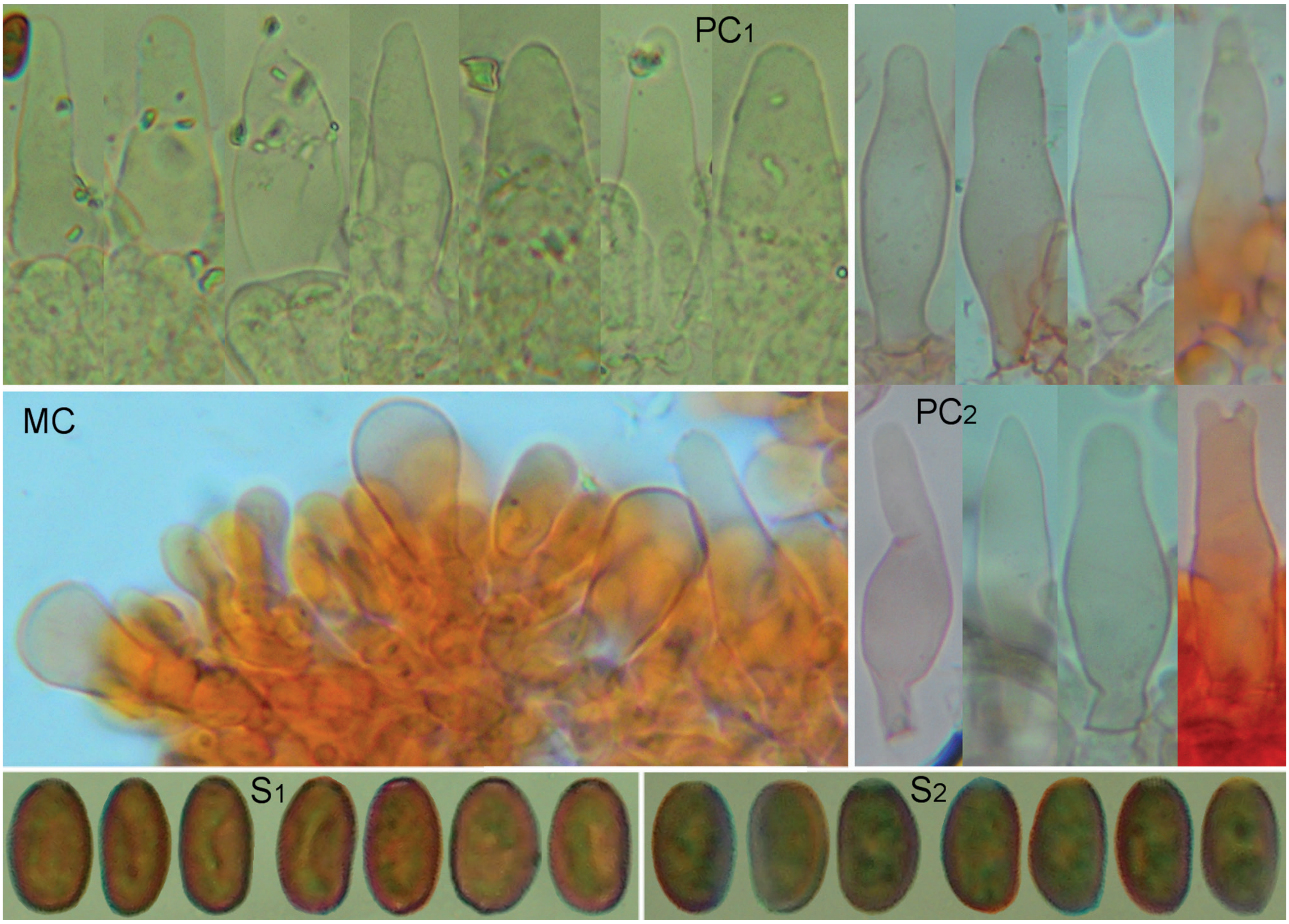


Fig. 34. *Psathyrella ochrofulva*. A.H. Smith 33628, MICH11858; PC1 Pleurocystidia in NH_4OH; PC2 Pleurocystidia in Congo red; MC Marginal Cystidia in Congo red; S1 Spores in water; S2 Spores in KOH.

Typus: *Psathyrella agrariella var. ochrofulva* A.H. Sm. **USA**, Michigan, Cheboygan Co., Colonial Point Hardwoods near Burt Lake, 13 Sep. 1949, *A.H. Smith* 33628 (MICH11858), gregarious on sandy humus in cut-over hardwoods. ITS MF325987.

Loan of one pileus in good condition for micro-morphology investigation.

Spores (7.5–)8–10.1 × 4.5–5.6(–6) µm [7–9(–10) × 3.8–4.5(–5) µm in Smith, 1972], on average 9 × 5–5.3 µm, Q 1.4–2.2, avQ 1.7–1.8; in front view elliptic to oval, sometimes cylindrical, base rounded to truncate, in profile adaxially flattened to subelliptic, sometimes subphaseoliform; reddish brownish; germ pore distinct, rounded to subtruncate, about 1.4–1.8(–2) µm broad. *Pleurocystidia* 30–50(–53) × 11–17 µm, the smaller ones towards gill edge; utriform, conical, fusiform, lageniform, sometimes ellipsoid, subcylindrical, submucronate; apex obtuse, sometimes rounded or subacute, sometimes forked or truncate, sometimes incrusted, walls sometimes slightly pigmented; moderately numerous. *Cheilocystidia* 23–36 × 11–13 µm, inconspicuous, scattered. *Paracystidia* 9–30 × 4.5–16 µm, sometimes incrusted, walls sometimes or often slightly thickened and yellowish pigmented, numerous, dominating. Cells below marginal cystidia with pale pigment, incrusted.

Notes: The ITS sequence places this taxon as an immediate relative of *P. albescens,* but this sample has very variable pleurocystidia, and, in accordance with Smith's description, a relevant number of them are subfusiform, progressively attenuate towards the apex, resulting in an undifferentiated transition between the ventricose and the apical part. This is a pattern not usually found in *P. albescens*. Moreover, differently from *P. albescens*, we have only found some subphaseoliform spores, none distinctly phaseoliform or indented above the apiculus. The pileus is yellowish fulvous when young, and dull reddish cinnamon when mature, but red pigmentation in the pileus of *P. albescens* is currently unknown. Given that we have demonstrated how Smith's concept of *P. agrariella var. agrariella* is not univocal, we believe *P. ochrofulva* stands alone as an autonomous species.

Psathyrella lactobrunnescens, described only from the type collection on hardwood debris, is a species that could not be loaned for scarcity of material. Judging from its description, it belongs to subsection *Spadiceogriseae*, and, based on a provisional morphological analysis, it resembles *P. ochrofulva,* with whom it shares some peculiar characters such as little differentiated, apically attenuate and never capitate pleurocystidia; small and fragile sporocarps; and pigmented paracystidia. On the contrary, its pilei are described as conical and hardly expanding, while they are obtuse to convex or plane in *P. ochrofulva*. The chromatic evolution of the pileus, initially white and striate, then greyish brown, and finally faded white again, is unusual and may suggest an albino form.

14. *Psathyrella fatua* (Fr.) Konrad & Maubl., *Encycl. mycol.* **14** (Agaricales 1): 125. 1948. Figs 35–43.

Pileus 8–52(–62) mm broad, in early stages broadly conical to paraboloid, then expanding to convex, finally plane, with straight to reflexed margin, subumbonate or not, sometimes rugulose to wavy in old sporocarps; when young reddish brown, when mature already discolored through brown to ochraceous brown, yellowish brown, brownish orange, pale to medium Dresden brown, pale pinkish chestnut brown, yellow red, sometimes shiny, hygrophanous, quickly fading to whitish, cream, alutaceous, pale to rich pink, pale greyish to pinkish violaceous, with centre pale greyish ochraceous, pale ochraceous, yellowish to vivid yellow, whitish, pale pinkish ochre, finally drying from margin to greyish violaceous; translucently striate when moist. *Veil* white, quickly evanescent, when young of flocci or fibrils on stipe (mainly on lower half) and on the margin of the pileus or appendiculate from it. *Lamellae* broadly adnate and usually with a subdecurrent tooth, moderately broad, not or slightly ventricose, crowded to moderately crowded; when young clay to pale brownish grey, then through pinkish clay, lilaceous grey-brown or purplish grey to finally dark purplish brown; edge white, sometimes reddish brownish pigmented. *Stipe* (10–)20–110(–125) × (1–)2–5.5(–7) mm, straight to flexuous, equal to slightly progressively broadened towards base, sometimes bent towards base, extreme base sometimes attenuate or characterized by a pseudorhiza; white, sometimes discoloring pale brownish; apex pruinose and sometimes striate, base sometimes felted to substrigose. *Context* rather rigid in the stipe that usually snaps when bent, whitish to pale, sometimes more

Fig. 35. *Psathyrella fatua*. MCVE29105. Photo P. Voto.

Fig. 36. *Psathyrella fatua*. MCVE29109. Photo P. Voto.

Fig. 37. *Psathyrella fatua*. MCVE29122. Photo P. Voto.

Fig. 38. *Psathyrella fatua*. MCVE29124. Photo P. Voto.

Fig. 39. *Psathyrella fatua*. MCVE29124. Photo P. Voto.

Fig. 40. *Psathyrella fatua*. MCVE29124. Photo P. Voto.

Fig. 41. *Psathyrella fatua*. Voto 20181105.2. Photo P. Voto.

Fig. 42. *Psathyrella fatua*. MCVE29115. Photo M. Maletti.

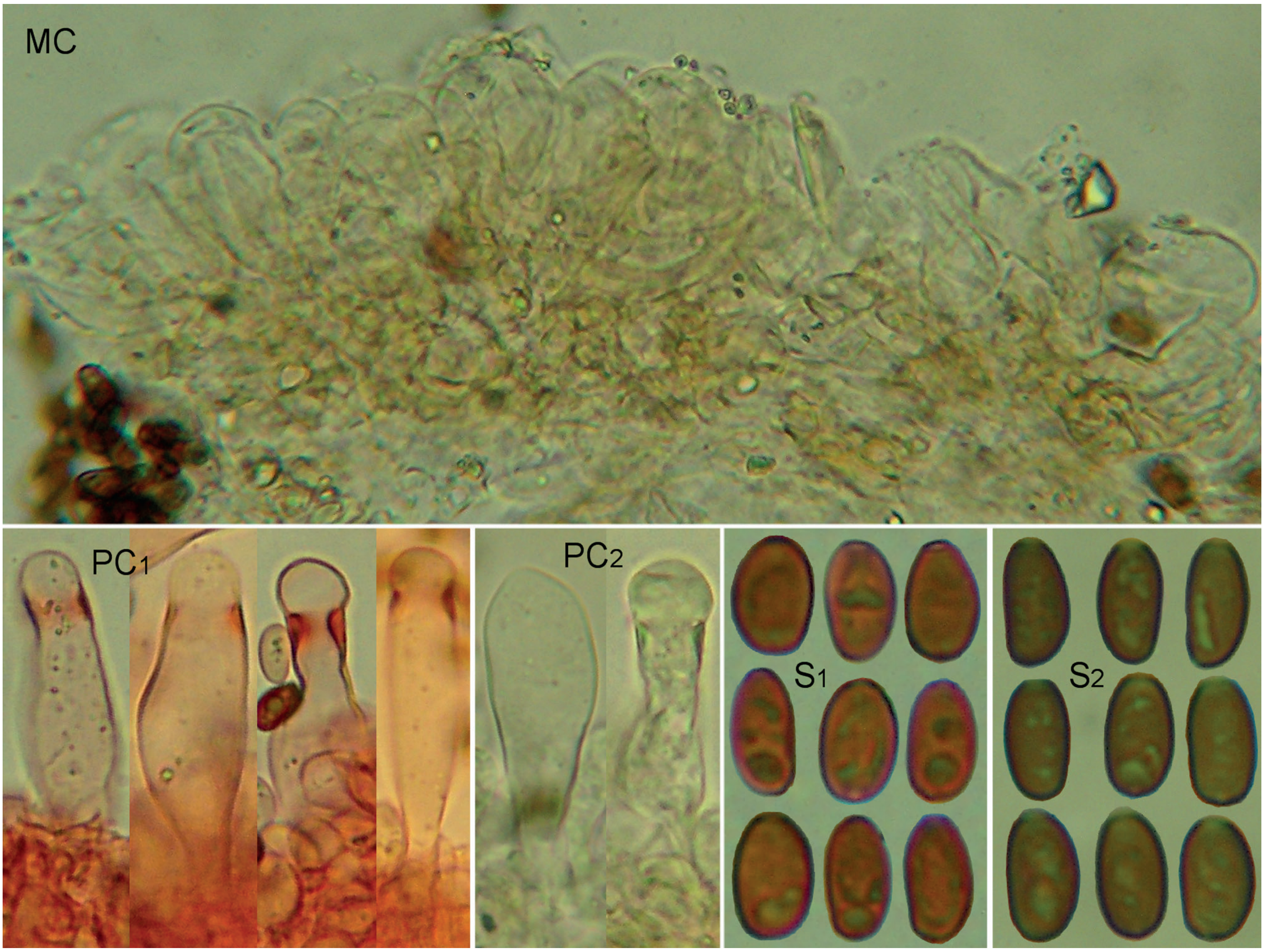


Fig. 43. *Psathyrella fatua*. Voto, MCVE29109; MC Marginal Cystidia in KOH; PC1 Pleurocystidia in Congo red; PC2 Pleurocystidia in NH_4OH; S1 Spores in water; S2 Spores in KOH.

pigmented in stipe base. *Odor* and taste indistinctive. Spore deposit purplish black. *Spores* (6.3–)6.8–10.5(–11.7) × 4–5.6 µm, on average 7.7–9 × 4.5–5.2 µm, Q (1.4–)1.5–2.2(–2.3), avQ 1.6–2; in front view elliptic, oval, oblong, subcylindrical, sometimes irregular, rarely angular-oval to cylindrical-oboval, base truncate, rounded to obtuse, in profile adaxially flattened to subamygdaliform, rarely or sometimes subphaseoliform, rarely phaseoliform or indented above the apiculus; brown to dark red; germ pore distinct, rounded to truncate, 1.2–2(–2.4) µm broad. *Basidia* 4-spored, 15–25 × 7.5–10 µm. *Pleurocystidia* (21–)30–60(–65) × 9–19(–21) µm, broadly to narrowly utriform, fusiform, conical, lageniform, sometimes submucronate, rarely clavate, ellipsoid, subcylindrical to rhomboid; apex rounded to obtuse, rarely subobtuse, sometimes or often subcapitate, rarely forked or incrusted; walls hyaline or very slightly yellowish but never brownish, sometimes thickened below apex; numerous to scattered. *Cheilocystidia* 20–45(–60) × 8–18 µm, rare to scattered, sometimes (locally) moderately numerous. *Paracystidia* 8–40(–45) × 5–23(–35) µm, sometimes incrusted; walls often thickened and yellowish to reddish brown pigmented (overall towards base); numerous, dominating. Cells below marginal cystidia often incrusted, pale yellow to yellowish brown with pigment often more concentrated at septa and in discontinuous wall traits. Clamps present.

Habitat: Solitary, gregarious to cespitose; in foliar and on woody debris in broadleaf wood stands, in parks, on paths, in grass; dry; on calcareous and nitrophilous soil.

Material examined: **Italy**, Venezia, Chioggia, S. Anna, Nordio forest, 2 m a.s.l., 29 Oct. 2006, gregarious on litter of *Quercus ilex*, *P. Voto*, Fig. 35 (MCVE29105, *Tef-1α* MF521809, ITS MF325966); at same location, 31 Oct. 2007, gregarious on litter of *Quercus ilex*, *P. Voto* (MCVE29110, *Tef-1α* MF521806); Rovigo, Crespino, 1 m a.s.l., 28 Nov. 2006, gregarious on soil at the top of a ditch bank, *P. Voto*, Figs 36, 43 (MCVE29109, *Tef-1α* MF521807); Rovigo, Villadose, 3 m a.s.l., 19 Nov. 2013, gregarious on dry grassy soil in a wooded park, *P. Voto*, Fig. 37 (MCVE29122, *Tef-1α* MF521804, ITS MF325968); at same location, river Adigetto, 16 Nov. 2014, gregarious on often moist grassy ground at the top of the river bank, *P. Voto*, Figs 38–40 (MCVE29124, *Tef-1α* MF521802); at same location on a different spot, 5 Nov. 2018, gregarious, *P. Voto* 20181105.2, Fig. 41; at same location on a different spot, 16 Nov. 2015, gregarious and subcespitose, *P. Voto* (MCVE29333); Pesaro Urbino, Fano, loc. Roncosambaccio, gregarious on buried roots, 24 Nov. 2006, *M. Maletti* 1867 (duplicate MCVE29108, *Tef-1α* MF521808, ITS MF325967); Pesaro Urbino, Monte Giano, loc. Rio Secco, 14 Oct. 2011, gregarious among grass on disturbed soil, *M. Maletti* 3035, Fig. 42 (duplicate MCVE29115, *Tef-1α* MF521805).

Notes: One of our aims was to provide molecular evidence supporting the presence of pilei with pinkish tints and of reddish gills' edges within this species. Ludwig (2007b) was, to our knowledge, the first to report a possible red underlining of the gill edge. A number of collections we have examined show these two parameters can be variously combined, even in materials collected in the same place. Cross comparisons of the sequences originated from various samples show that all of our materials share a minimum homology value of 99.7 % at the ITS locus and an average 99 % *Tef-1α* identity, with the only exception of MCVE29124 which shares a 97 % to 98 % identity with all others. However molecular evidence does not provide substantial support to split this single voucher from the others. In conclusion, our molecular identification of *P. fatua* includes material with (see Figs 35, 37, 39) or without a more or less evident pinkish peripheral half of the discoloring pileus, and with (see Fig. 37) or without a pigmented gill edge.

Elements differentiating *P. fatua* from *P. spadiceogrisea* are listed below. Spores are less frequently phaseoliform and rarely indented above the apiculus. Pleurocystidia are never brown, are more varied in shape (utriform, lageniform, fusiform, conical), and sometimes are more or less capitate, rarely forked or incrusted. Gill edges are possibly pigmented. Sporocarps are smaller and with a rapidly discoloring pileus that is never dark colored when mature, while it may be pinkish. For differences between *P. fatua* and *P. albescens,* see notes provided for the latter.

15. *Psathyrella tenacipes* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 440. 1972. Fig. 44.

Typus: *Psathyrella tenacipes* A.H. Sm. **USA**, Michigan, Cheboygan Co., Wolf Bog, 13 Jun. 1948, *A.H. Smith* 28718 (incorrectly 28717 in original description) (coll. *Singer, DiGilio & Smith*) (MICH12091), described as gregarious on muck and small sticks partly burned in protologue, described as gregarious on drying muck in ash swamp in Smith's handwritten field notes.

Loan of various sporocarps in good condition for micromorphology investigation.

Spores 7–9.5(–10.1) × 4.6–5.7 µm (7–9 × 4.5–5.5 in Smith 1972), Q (1.45) 1.6–1.85(–1.9), avQ 1.7; in front view suboval to elliptic, sometimes subangular to suboblong, base rounded to subtruncate, in profile adaxially flattened, sometimes subamygdaliform to subphaseoliform, orangish reddish brown; germ pore distinct, truncate, 1.2–1.7 µm broad. *Pleurocystidia* 28–50 × 9–14(–16) µm, (narrowly) utriform, sometimes lageniform to subcylindrical; apex 4.5–8(–10) µm broad, rounded to obtuse, often or sometimes subcapitate, not incrusted; walls thin, hyaline; moderately numerous. *Cheilocystidia* 24–30 × 10–15 µm, scattered. *Paracystidia* –30 × –17(–20) µm; walls thickened and yellowish pigmented in larger ones, numerous, dominating. Cells below marginal cystidia yellowish pigmented.

Unfortunately, DNA extraction failed for this species, which otherwise is remarkable for the presence of some peculiar

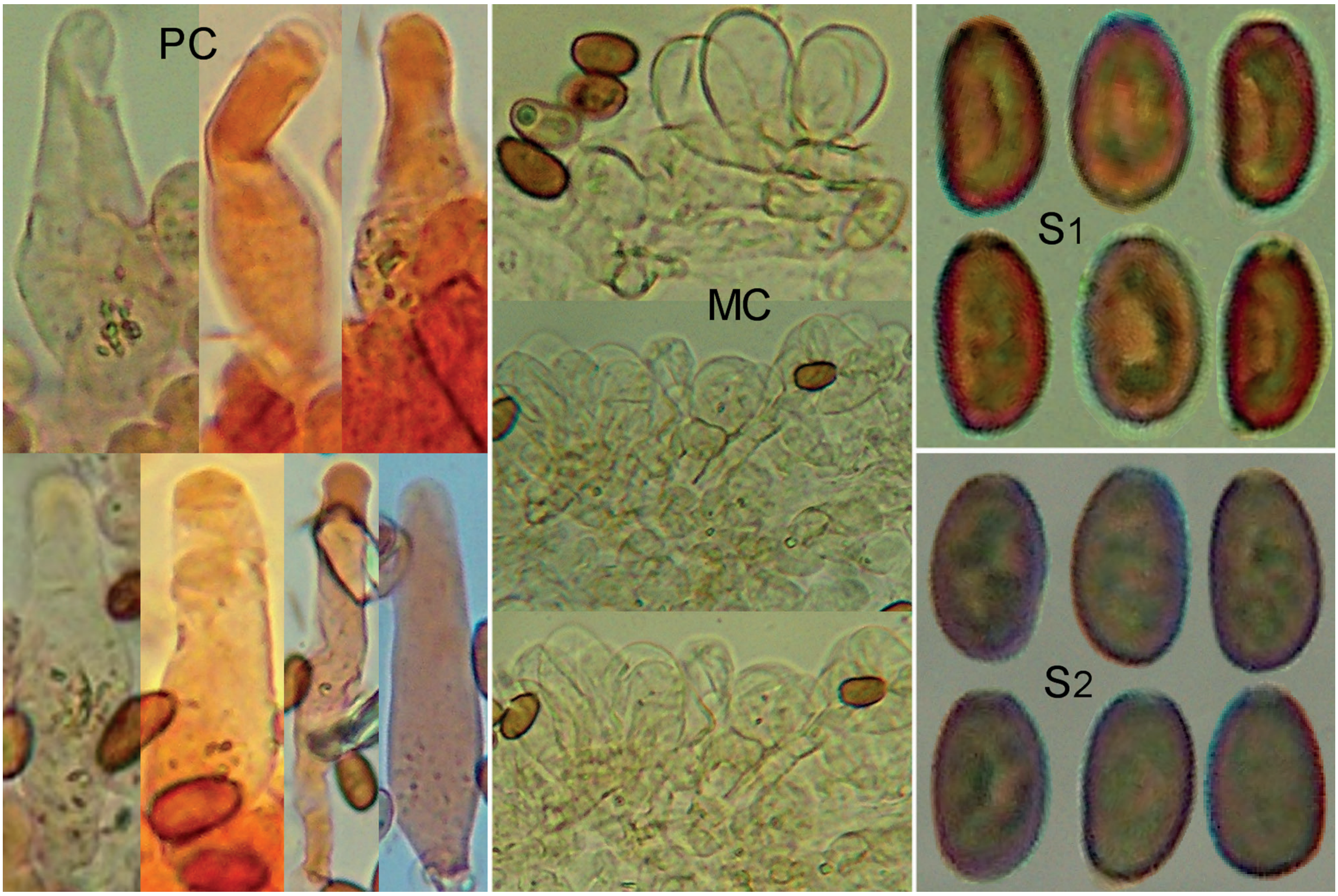


Fig. 44. *Psathyrella tenacipes*. A.H. Smith 28718, MCVE12091; PC Pleurocystidia; MC Marginal Cystidia in KOH; S1 Spores in water; S2 Spores in KOH.

characters, such as a scarce and very fugacious veil; a tubular, pliant, fairly tough stipe; pallid brownish gill edges and bistre but soon discoloring pileus color. Based on micro- and gross morphology, we see some similarity between *P. tenacipes* and *P. fatua*, possibly suggesting conspecificity. However, because of the lack of molecular evidence of *P. fatua* from any American collections included in this study, we are not yet ready to recognize this common European species as being present in North America.

16. *Psathyrella owyheensis* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 174. 1972. Fig. 45.

Molecular heterotypical synonyms proposed here: *Psathyrella carminei* Örstadius & E. Larss., *Mycol. Prog*. **14**: 18. 2015.

Typus: *Psathyrella owyheensis* A.H. Sm. **USA**, Idaho, Owyhee Co., Sands Basin, 27 Apr. 1969, *E. Trueblood* 3135 (MICH5357), gregarious in native grass near cow dung. *Tef-1α* MF521785, ITS MF325990.

Loan of two sporocarps in good condition for micro-morphology investigation.

Spores (7.5–)8.8–11.1(–12.5) × (3.8–)4.5–5.7(–6.5) µm, on average 9.4 × 5.2 µm, Q (1.4–)1.6–2(–2.5), avQ 1.8–1.9; in front view oval, elliptic, oblong, sometimes subcylindrical, sometimes or often slightly irregular between median portion and base, base obtuse to broadly rounded, in profile subelliptic to subamygdaliform, sometimes subphaseoliform; dull orange; germ pore distinct, often truncate, 1.5–2 µm broad. *Pleurocystidia* 37–59 × 12–16 µm, utriform to lageniform, sometimes subcylindrical; apex obtuse, sometimes subcapitate, rarely forked or incrusted; walls sometimes weakly yellowish pigmented; more or less scattered. *Cheilocystidia* 22–35 × 9–12 µm, scattered. *Paracystidia* –23 × –15 µm, walls hyaline or almost so, numerous, sometimes incrusted, dominating.

Notes: The molecular sequences of the holotype of *P. carminei* deviates by a few bases from the holotype of *P. owyheensis* (DNA nucleotide homology: ITS = 99 % identity, *Tef-1α* = 98 % identity), we consider this to be a good double locus evidence of conspecificity; micro-morphology matches well too. We could not ascertain the exact trophism of the holotype (and only collection) of *P. owyheensis*: it could be the nitrogen-rich soil, due to the nearby dung, or grassy material, we cannot even exclude sagebrush (*Artemisia tridentata*) debris as this plant is widely distributed in the Sands Basin. *Psathyrella carminei* is reported on soil in a forest with pines but there are a number of species in subsection *Spadiceogriseae* growing both with and without association to woody material, *e.g. P. fatua*, *P. clivensis* and *P. albescens*. *Psathyrella carminei* is said to smell of fish while *P. owyheensis* has indistinct odor, but we know of other *Psathyrella*

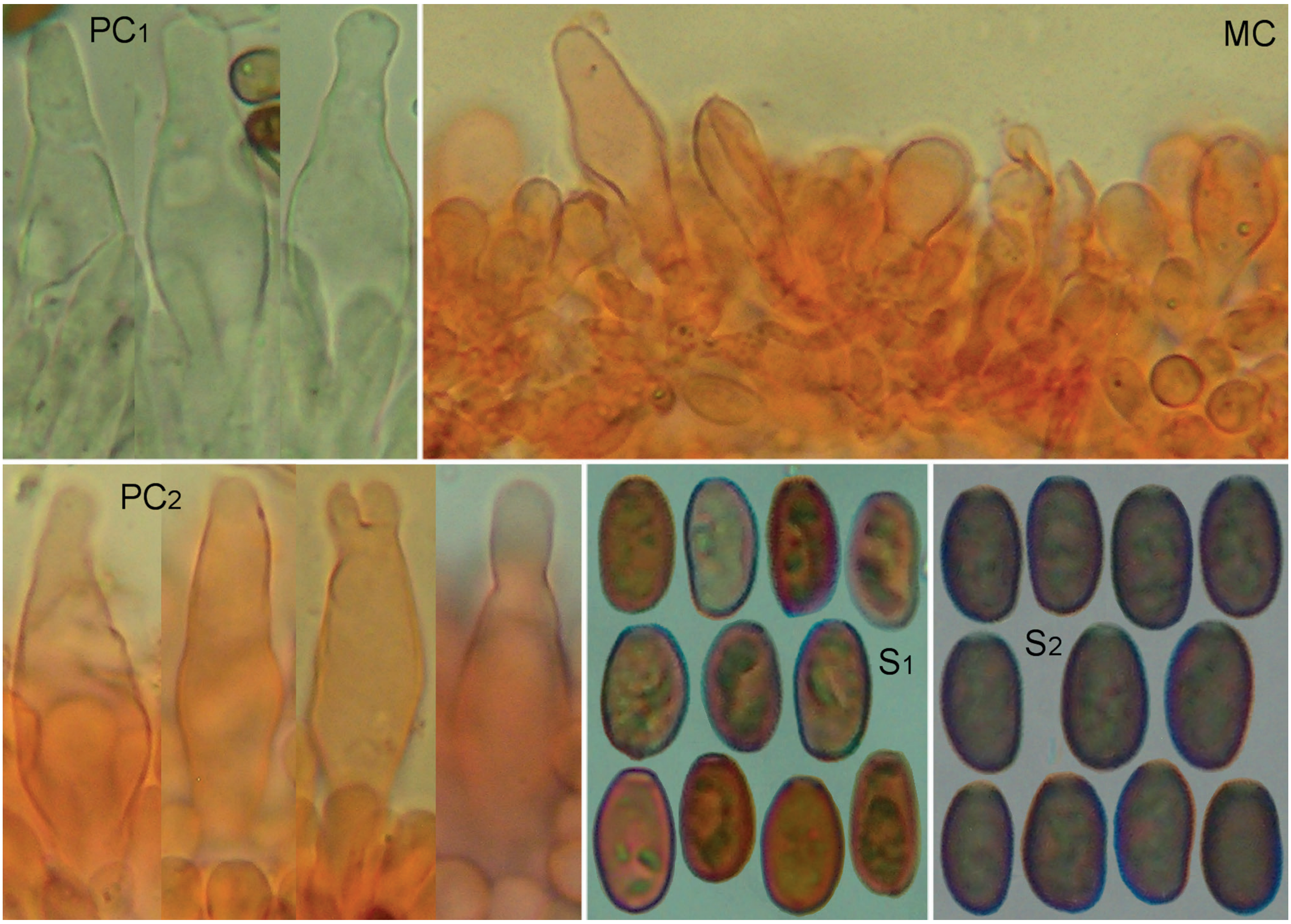


Fig. 45. *Psathyrella owyheensis*. E. Trueblood 3135, MICH5357; PC1 Pleurocystidia in NH_4OH; PC2 Pleurocystidia in Congo red; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

species, *e.g. P. bipellis* and *P. saponacea*, which may or may not possess a peculiar odor.

17. *Psathyrella hellebosensis* Deschuyteneer & Melzer, Bull AMFB **10**: 5. 2017. Figs 46, 47.

Spores (6.5–)7–8.5(–11) × 4.7–5.3(–5.6) µm, Q (1.4–)1.5–1.8, in front view oval to angular-oval, with a base often subtruncate, in profile rarely subphaseoliform, reddish brown, with distinct germ pore. *Pleurocystidia*, 43–58(–64) × 11–15(–17) µm, utriform, often forked to three-lobed. *Paracystidia* sometimes incrusted and locally weakly yellowish pigmented, dominating.

Material examined: **Italy**, Pesaro, loc. Villa Ceccolini, near river Foglia, 26 Mar. 2011, *M. Maletti* 2768 (MCVE29114), gregarious on soil in an unkempt open riparian site. *Tef-1α* MF521816, ITS MF325956.

Notes: The colors and habitus of this Italian collection are in perfect agreement with the description of this species. The molecular evidence of the *Tef-1α* DNA region clearly isolates this species from neighboring allied taxa, and places it confidently among species of the subsection *Spadiceogriseae* that are not found in association with woody material.

Two other species should be mentioned here because of their non-lignicolous habitat. *Psathyrella agraria* (Enderle 1996), reported from mossy soil in a cornfield (*Zea mays*, *Poaceae*), shares a 99 % ITS identity with the types of *P. lutulenta* and *P. thujina*, however it has spores mainly and distinctly phaseoliform, and its habitat is not specifically defined wet or moist soil. It remains a dubious European taxon. *Psathyrella phaseolispora*, whose type could not be studied, is a species described based on a single dilapidated old specimen found in a manured *Poa-Lolietum* grassland, and resembles *P. clivensis* but with distinctly phaseoliform and somewhat more pigmented spores, and a somewhat more defined germ pore; it too remains dubious. However, pending more morphological descriptions or convincing molecular evidences, we decided to insert these two species in our key to facilitate their identification from more collections.

Fig. 46. *Psathyrella hellebosensis*. MCVE29114. Photo M. Maletti.

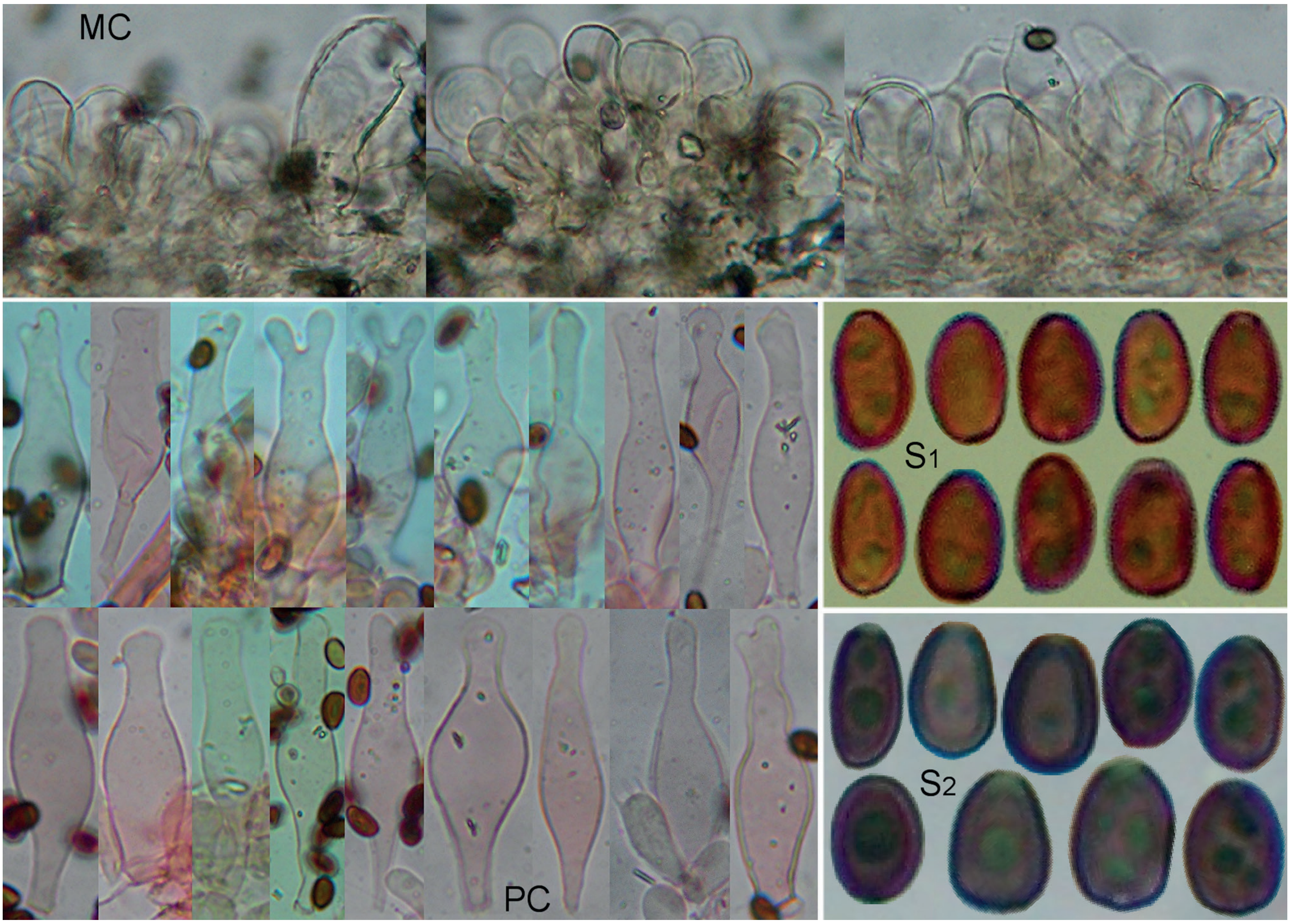


Fig. 47. *Psathyrella hellebosensis*. P. Voto, MCVE29114; MC Marginal Cystidia in KOH; PC Pleurocystidia; S1 Spores in water; S2 Spores in KOH.

18. *Psathyrella rogersiae* Voto, Garbelotto & Chiarello, ***sp. nov.*** MycoBank MB831126. Figs 48, 49.

Etymology. The epithet is a dedication to Patricia Rogers, a collection manager in the University of Michigan Herbarium who helped us navigate the collections at the MICH herbarium.

Typus: **Italy**, Veneto, Vicenza, Trissino, river Guà, about 100 m a.s.l., 28 Mar. 2013, *O. Chiarello* (MCVE29120). ITS MF325995.

Pileus 30–40 mm latus, mox convexus sed margine inflexa, per mature leviter undulatus et interdum leviter umbonatus; primo umbrinus vel murinus, per mature brunneus, deinde spadiceus, hygrophanus, in sicco cinereus; humido leviter striatus. Velum album, fibrillosum, pauper, fugax. Lamellae adnatae, modice ventricosae, subdistantes; initio griseae, deinde purpureae, acie alba. Stipes 35–50 × 3.5–6 mm, cylindraceus, albus. Odor ut sapor indistincti. Sporae (6.8–)7.5–10 × 4.6–5.2(–5.5) µm, oblongae, ellipsoideae, subovoideae, nonnullae subphaseoliformes, in aqua observatae aurantiacae-brunneae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 34–54(–59) × 13.3–16.5 µm, utriformia vel sublageniformia, apice obtusa, interdum vel saepe subcapitata, raro furcata, numerosa. Cheilocystidia 28–45 × 7.5–15 µm, pleurocystidiis similia vel fusoidea, dispersa sed modice numerosa ad stipitem. Paracystidia 15–35 × 7.5–21 µm, interdum leviter flavida ut crassitunicata, numerosa. Fibulae adsunt. Gregaria in udo prati.

Pileus 30–40 mm broad, soon convex with inflexed margin, when mature slightly wavy and sometimes slightly umbonate; when young dark brown to dark grey-brown, when mature brown to dark yellowish brown, hygrophanous, fading through various tints of yellowish brown (greyish, dull, medium, bright), finally pale grey; faintly translucently striate when moist. *Veil* white, as a scarce and fugacious fringe on margin of pileus. *Lamellae* adnate or with a decurrent tooth; moderately narrow to somewhat ventricose in age; about

Fig. 48. *Psathyrella rogersiae.* MCVE29120. Photo O. Chiarello.

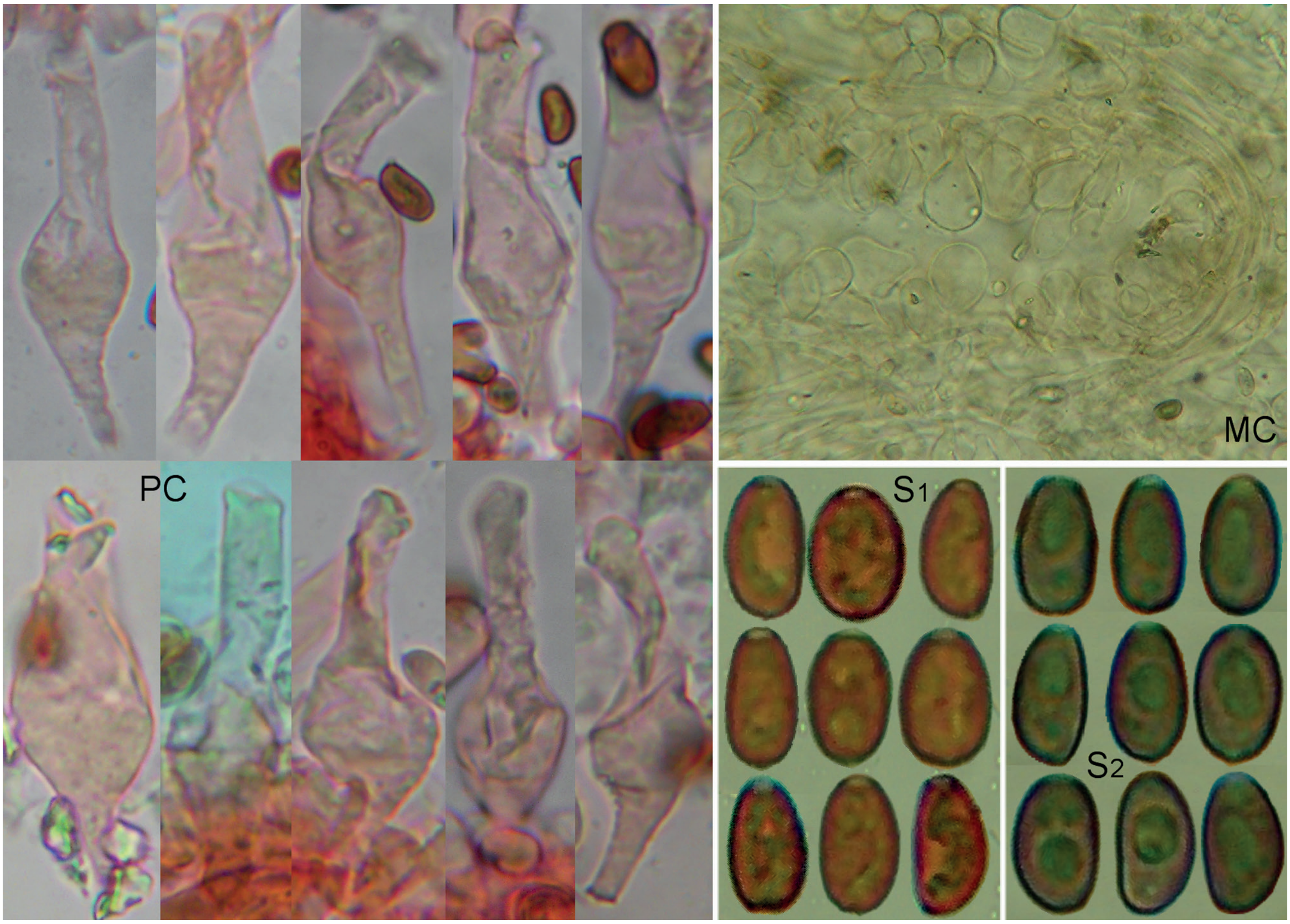


Fig. 49. *Psathyrella rogersiae.* O. Chiarello, MCVE29120; PC Pleurocystidia; MC Marginal Cystidia in KOH; S1 Spores in water; S2 Spores in KOH.

28 when mature; when young greyish, finally purplish; edge white. *Stipe* 35–50 × 3.5–6 mm, cylindrical, occasionally bent towards apex or base; white, a little discoloring brownish over the basal area; apex pruinose, naked or with very scarce velar fibrils. *Odor* and taste indistinctive. *Spores* (6.8–)7.5–10 × 4.6–5.2(–5.5) µm, on average 8.2–9.2 × 4.8–5 µm, Q (1.5–)1.53–1.88 (–1.96), avQ 1.68–1.75; smooth; in front view elliptic to suboval, sometimes sub angular-oval, oblong, base rounded to subtruncate, in profile adaxially flattened, sometimes subphaseoliform, rarely distinctly phaseoliform; dull orange to brownish orangish; germ pore distinct, rounded, 1.3–1.7 µm broad. *Basidia* 4-spored, 17–28 × 8–11 µm. *Pleurocystidia* 34–54(–59) × 13.3–16.5 µm, with quotient 2.7–3.8(–4.2), on average 3.42; utriform to sublageniform, with often elongate and sometimes eccentric neck, apex rounded to obtuse, often or sometimes subcapitate, rarely forked; numerous. *Cheilocystidia* 28–45 × 7.5–15 µm, sometimes varying to obtusely subfusiform, scattered at margin of pileus to moderately numerous towards stipe. *Paracystidia* 15–35 × 7.5–21 µm, sometimes elongate-ellipsoid, walls sometimes thickened and yellowish pigmented, numerous, dominating. Cells below marginal cystidia incrusted and weakly yellowish pigmented. Pileipellis of clavate to subglobose, 13–30(–40) µm broad cells; underlying hyphae with incrusted pigment. Clamps present.

Habitat: Gregarious; in sandy grassland near a river bank, the area is a moist, often flooded, permeable alluvial plain with *Salix alba* trees and various hygrophilous plants, such as *Carex* spp., *Phragmites australis*, *Typha latifolia*, *Scirpus* spp., *Ranunculus aquatilis*.

Notes: The ITS sequence places this fungus in the subclade *P. albescens*. The differences against *P. albescens* are many and evident, ranging from not thickset utriform pleurocystidia and somewhat less phaseoliform spores to distinctly dark grey brown colors of pileus, scarce veil and hygrophilous habitat; *P. ochrofulva* is a tiny, differently colored species with different pleurocystidia and habitat. Because of its hygrophilous habitat it can be compared to the American taxon *P. thujina*, which Örstadius *et al.* (2015) proposed as a prior name for the European *P. almerensis* and *P. lutulenta*, but its smaller spores and slenderer pleurocystidia represent a distinctive combination of characters. It is also comparable to *P. hellebosensis* which differs mainly because of its more pigmented, largely ovoid to angular-ovoid spores.

19. *Psathyrella argillacea* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 367. 1972. Fig. 50.

Paratype: *Psathyrella argillacea* A.H. Sm. **USA**, Wyoming, Albany Co., Laramie River, North Fork River, 27 Jul. 1950, *A.H. Smith* 35220 (MICH65256). *Tef-1α* MF521814.

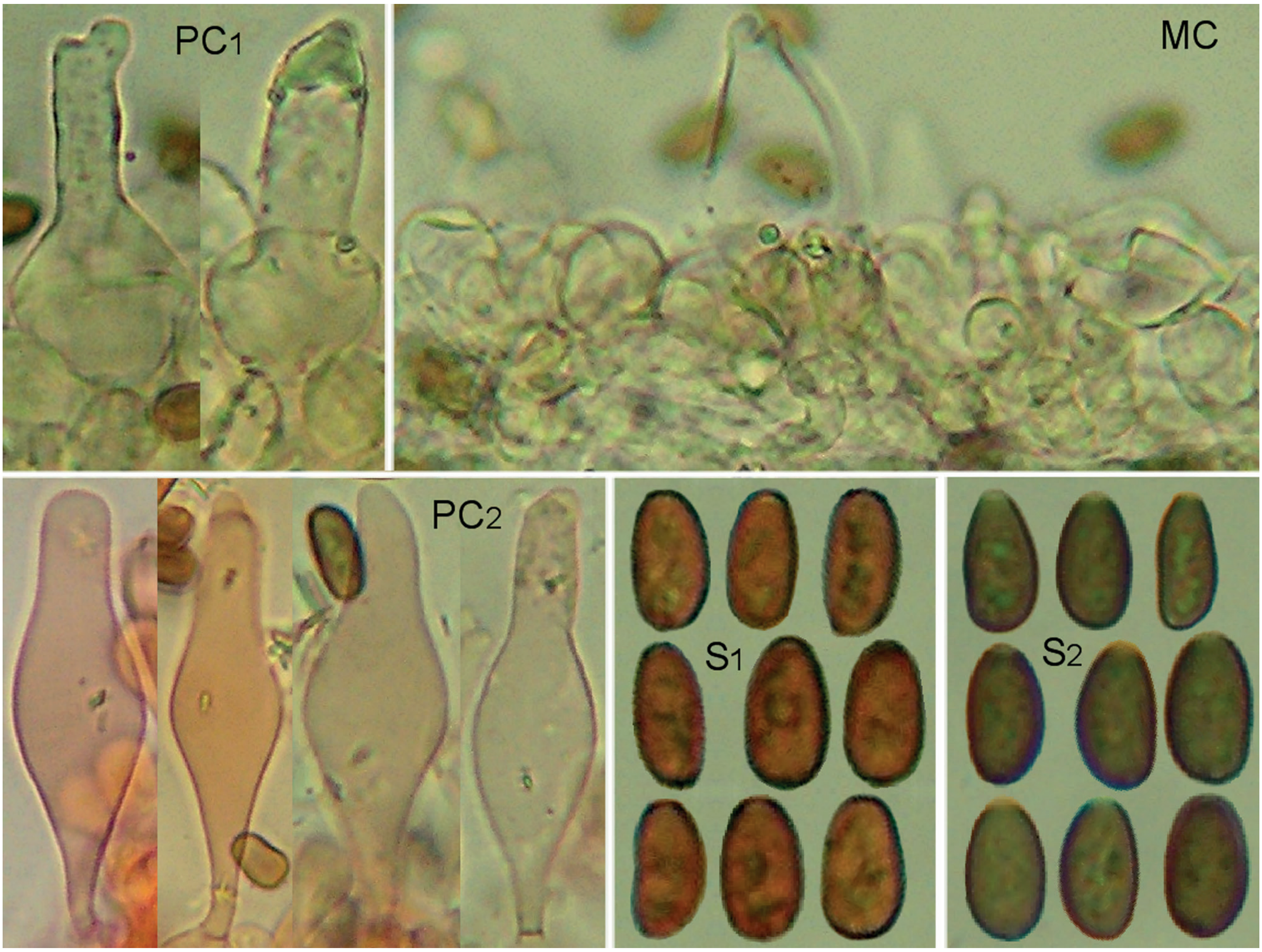


Fig. 50. *Psathyrella argillacea*. A.H. Smith 35220, MICH65256; PC1 Pleurocystidia in NH_4OH; PC2 Pleurocystidia in Congo red; MC Marginal Cystidia in KOH; S1 Spores in water; S2 Spores in KOH.

Loan of three pilei and some entire or broken stipes for gross morphology investigation.

Spores 7.3–11 × 4.4–5.6(–6.2) µm, Q 1.5–2.5, avQ 1.8–2; in front view elliptic to (narrowly) oval, base rounded to subtruncate, in profile adaxially flattened, subcylindrical to subamygdaliform, rarely subphaseoliform; dull orangish brown to brown; germ pore distinct, rounded to subtruncate, about 1.8 µm broad. *Pleurocystidia* 38–55 × 12–15 µm; utriform, fusiform-utriform; apex obtuse to rounded, rarely subacute, often forked, often incrusted, walls sometimes brownish pigmented; moderately numerous. *Cheilocystidia* 25–45 × 12–15 µm, scattered. *Paracystidia* 12–30 × 5–19.5 µm, sometimes ellipsoid, often incrusted, walls often thickened and yellowish pigmented, numerous, dominating. Cells below marginal cystidia slightly incrusted and pigmented.

Notes: Best match when blasting the sequence of this material is with the holotype of *P. lutulenta* but with a weak identity that undoubtedly excludes conspecificity. No field notes are attached to this paratype and on careful examination of the whole exsiccata no fragments of non-fungus material could be found for a clue to the habitat; however the holotype, which we could not study for scarcity of material, and all other collections examined by Smith (1972) are reported on hardwood debris and litter, moreover Smith (1972) placed the species in subsection *Lauricolae* expressly characterized by lignicolous habitat. The lack of macro characters in the description of this paratype prevents a thorough comparison with *P. owyheensis*, a very similar species based on micro-morphology (see key). Yet, the two are surely different based on DNA evidence.

20. *Psathyrella umbrosa* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 391. 1972. Fig. 51.

Molecular heterotypical synonyms proposed here: *Psathyrella fulvoumbrina* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 413. 1972.

Typus: *Psathyrella umbrosa* A.H. Sm. **USA**, New Mexico, Rio Arriba Co, Sangre de Cristo Mountains, Aug. 1963, *C.A. Barrows*, 1416 (MICH12102), densely gregarious on soil filled with rotten wood. *Tef-1α* MF521775, ITS MF326003.

Loan of three sporocarps in good condition for micro-morphology investigation.

Spores (6.7–)7.1–9.3 × 4.3–5.7 µm, Q 1.4–2.1; in front view suboblong to broadly oval, rarely subangular-oval, base mainly broadly rounded, rarely subtruncate, in profile subelliptic to adaxially flattened or subphaseoliform, sometimes subamygdaliform, apex truncate in front view and in profile; orangish to vaguely reddish brown; germ pore distinct, truncate,

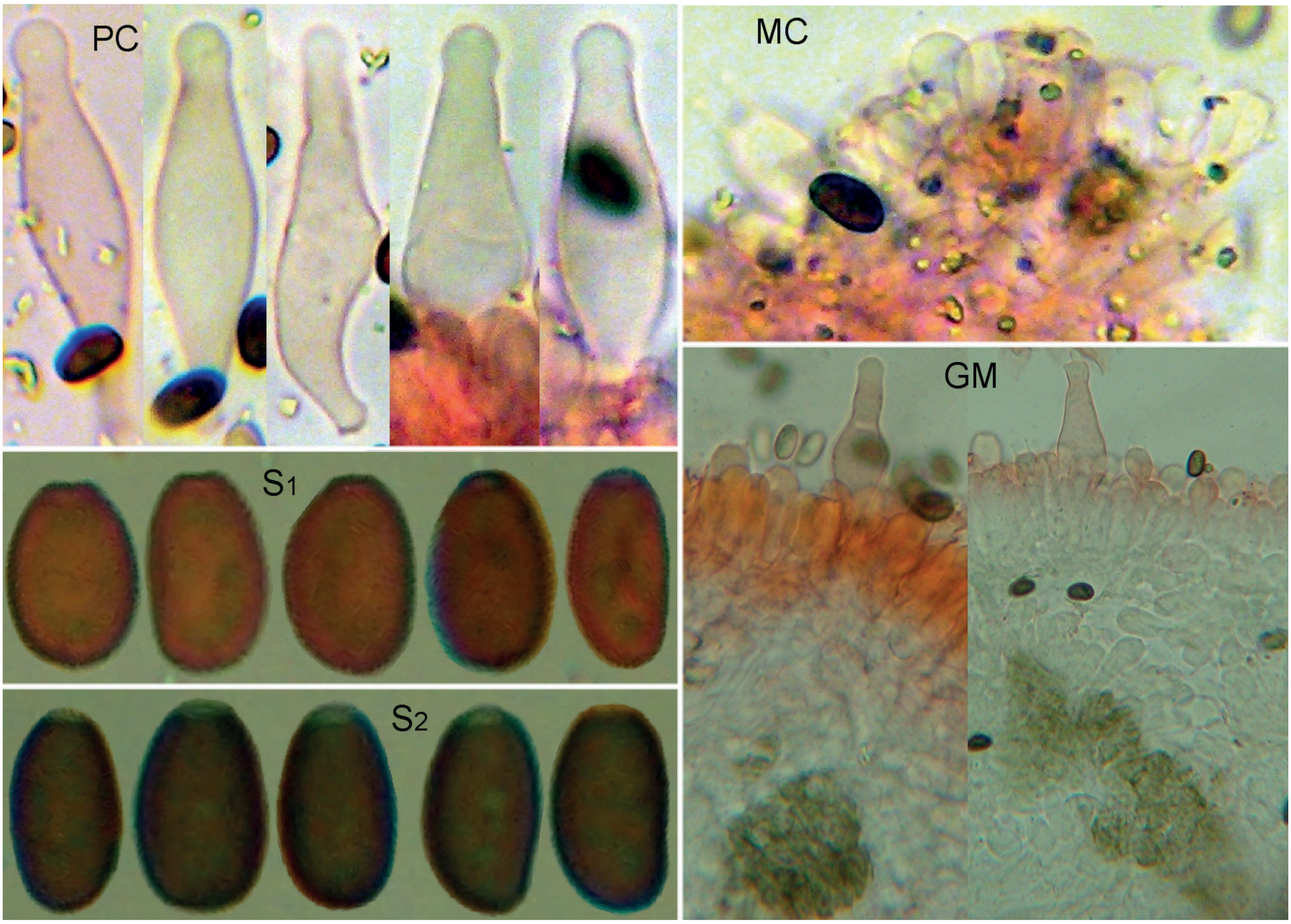


Fig. 51. *Psathyrella umbrosa*. C.A. Barrows 1416, MICH12102; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH; GM Greenish masses/incrustations in hymenium.

1.5–1.8 µm broad. *Pleurocystidia* 31–51 × 10.5–16 µm, utriform to sublageniform or subfusiform, sometimes ventricose-conical; apex obtuse to subcapitate; walls hyaline; moderately numerous. *Cheilocystidia* 23–40 × 8–14 µm, scattered. *Paracystidia* mainly 9–12 × 5–7 µm, some 22–32 × 9–13 µm, dominating among numerous basidia and basidiola.

20a. *Psathyrella fulvoumbrina* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 413. 1972.

Typus: *Psathyrella fulvoumbrina* A.H. Sm. **USA**, Idaho, Owyhee Co, Boulder Creek, South Fork, 4 Jun. 1969, *E. Trueblood* 3167 (MICH5833), gregarious under aspen and fir. *Tef-1α* MF521800, ITS MF417625.

Loan for micro-morphology investigation of four sporocarps in good condition.

Spores 7–8.7(–9.5) × 4.4–5.7 µm, Q 1.3–1.9; in front view elliptic to oval, base broadly rounded, in profile subelliptic to adaxially flattened or subamygdaliform, rarely subphaseoliform; red-brown; germ pore distinct, mostly truncate, 1.5–1.8 µm broad. *Pleurocystidia* 33–55 × 10–22 µm, narrowly utriform, narrowly sublageniform, narrowly fusiform-utriform, broadly ventricose-conical; apex subcapitate or not, sometimes (irregularly) capitate, sometimes subacute, sometimes forked; walls hyaline; moderately numerous. *Cheilocystidia* 22–27 × 9–12 µm, scattered. *Paracystidia* mainly small, some 20–30 × 10–13 µm, dominating among numerous, up to 10 µm broad basidia and basidiola.

Note: There is full correspondence, both molecular and morphological, between *P. fulvoumbrina* and *P. umbrosa* therefore they are synonyms.

21. *Psathyrella praetenuis* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 110. 1972. Fig. 52.

Molecular heterotypical synonyms proposed here: *Psathyrella atrifolia sensu* A.H. Smith, *Mem. N. Y. Bot. Gard.* **24**: 146. 1972, p.p.

Typus: *Psathyrella praetenuis* A.H. Sm. **USA**, Idaho, Bonner Co., Upper Priest River, 1 Oct. 1968, *A.H. Smith* 76781 (MICH5361), gregarious on debris under cottonwood trees. *Tef-1α* MF521782, ITS MF325993.

Loan of three sporocarps in good condition for micro-morphology investigation.

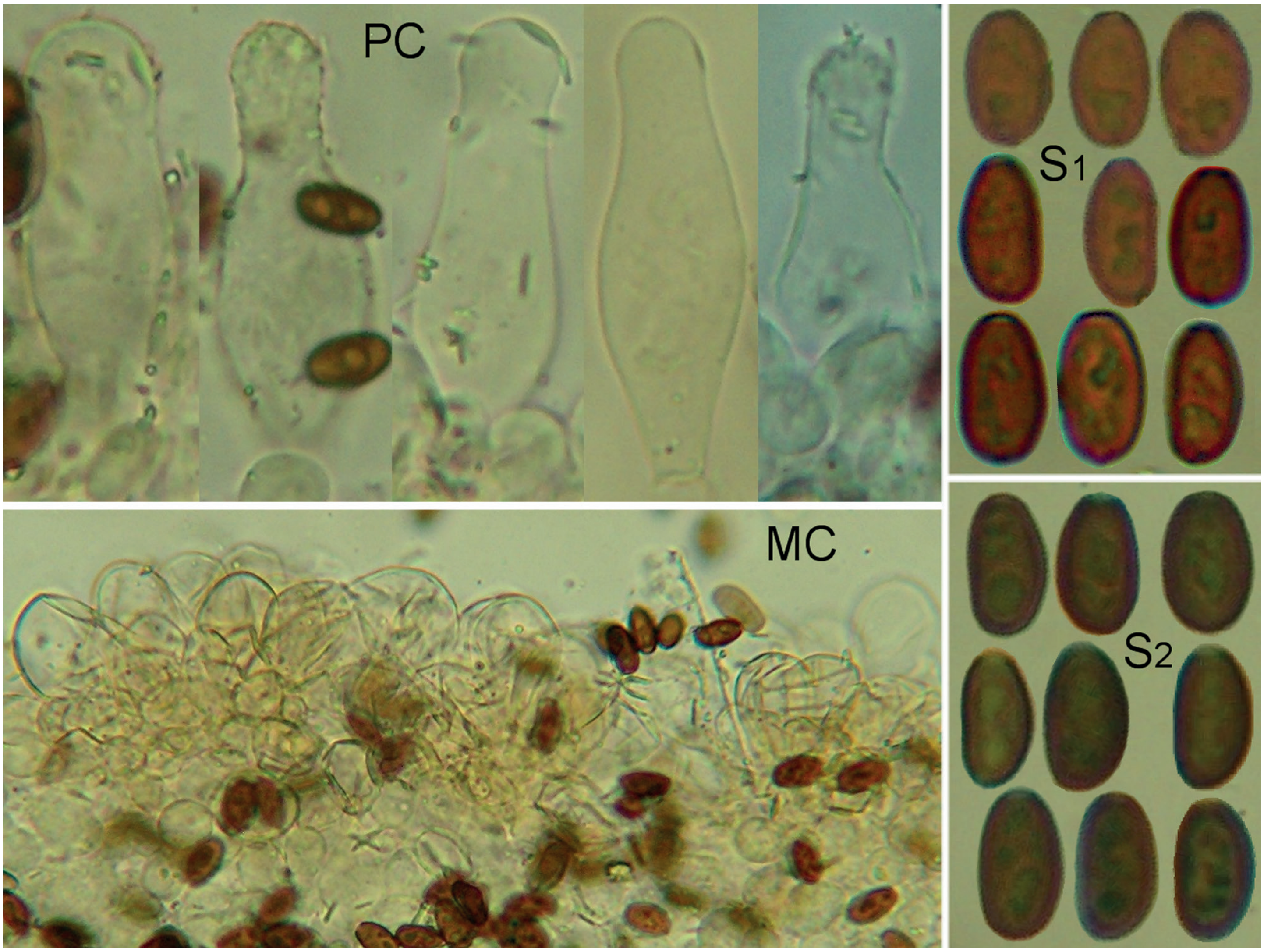


Fig. 52. *Psathyrella praetenuis*. A.H. Smith 76781, MICH5361; PC Pleurocystidia in NH_4OH; MC Marginal Cystidia in KOH; S1 Spores in water; S2 Spores in KOH.

Spores (7.5–)8–11(–11.8) × 4.5–6 µm, Q (1.5–)1.7–2.1(–2.2), avQ 1.9; in front view elliptic to oblong, sometimes suboval, base rounded, in profile subelliptic to subamygdaliform, sometimes subphaseoliform; sordid brown with a reddish orangish tinge; germ pore distinct, mostly truncate, 1.6–1.7 µm broad. *Pleurocystidia* 33–55 × 11.5–17 µm, utriform, sometimes subcylindrical; apex obtuse, sometimes forked, sometimes (irregularly) subcapitate, often incrusted; walls sometimes brownish pigmented; more or less moderately numerous. *Cheilocystidia* 22–50 × 11–22 µm, scattered. *Paracystidia* 9–39(–49) × 7–22 µm, sometimes submucronate, walls often thickened and pale yellowish pigmented; numerous, dominating. Cells below marginal cystidia faintly yellowish pigmented and incrusted.

Notes: Smith (1972) defines this species as devoid of any trace of veil but places it in subgen. *Pannucia*, section and subsection *Appendiculatae* on the assumption that sporocarps may start with an appendiculate veil. For further comments see next species.

Psathyrella atrifolia* (Peck) A.H. Sm., *Contr. Univ. Mich. Herb*. **5**: 38. 1941.

*The original name '*atrofolia*' should be correctly spelled '*atrifolia*'.

Notes: Smith (1972) has proposed a description of this taxon based on numerous collections but he did not report having revised the holotype of the basionym, *Hypholoma atrofolium* Peck. We have attempted to understand Smith's concept of *P. atrifolia* by examining three of his collections selected for this purpose by MICH staff. There is a conspicuous correspondence, both molecular (DNA nucleotide homology: ITS= 100 %) and morphological, between *P. praetenuis* and Smith 73945 (MICH32732) therefore they are conspecific; it is to be noticed that both materials were found among cottonwood tree (*Populus deltoides*) debris. Smith 87038 (MICH65288), found under aspen (*Populus* spp.), is likewise morphologically identical but failed to produce a sequence; however, we consider it conspecific too. DNA extraction failed also with Smith 86968 (MICH65287), habitat unknown, but in this case we have found some differences in the spore parameters and it may not be identical to the other vouchers, indeed it recalls *P. argillacea*. Of course these results do not necessarily apply to the other vouchers Smith deposited in MICH under this name, nor can we be assured of the correct identity between Smith's concept and Peck's basionym as Peck described only, and partially too, the spores among the microscopical characters. Here follows our revision of Smith 73945.

21a. A.H. Smith 73945, MICH32732.

= ***Psathyrella praetenuis*** A.H. Sm.

Material examined: **USA**, Idaho, Bonner Co., Priest Lake, Tule Bay, 10 Oct. 1966, in a cottonwood flat. *Tef-1α* MF521813, ITS MF325960.

Loan of many sporocarps in good condition for micro-morphology investigation.

Spores (7.4–)8.3–9.7(–11.1) × (3.9–)4.5–5.7(–6.3) µm, on average 9 × 5.1 µm, Q (1.5–)1.7–1.9(–2.2), avQ 1.85; in front view elliptic, suboval to oblong sometimes angular-oval, base rounded to subtruncate, in profile adaxially flattened to subellipsoid, rarely or sometimes subphaseoliform, sordid brown with a reddish orangish tinge; germ pore distinct, mostly truncate, 1.6–1.8 µm broad. *Pleurocystidia* 30–54 × 10–20(–21.5) µm, utriform; apex obtuse to rounded, rarely subacute, sometimes forked, rarely incrusted; walls hyaline; moderately numerous. *Cheilocystidia* 26–44 × 10–15 µm, rare. *Paracystidia* 9–38 × 6–19.5 µm, sometimes submucronate, walls often thickened and pale yellowish brownish pigmented, scarcely incrusted; numerous, dominating. Cells below marginal cystidia often pale yellowish brownish pigmented, scarcely incrusted.

22. ***Psathyrella griseopallida*** Thiers & A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 417. 1972. Fig. 53.

Typus: *Psathyrella griseopallida* Thiers & A.H. Sm. **USA**, California, San Diego Co, Lake Henshaw, San Luis Rey Campground, 10 Mar. 1970, *H.D. Thiers* 25079 (MICH11939), Smith's protolog: gregarious on sandy soil near an oak log, Thiers's field note: gregarious in vicinity of dead oak logs. *Tef-1α* MF521796, ITS MF325974.

Loan of one entire pileus and a narrow slice of pileus for micro-morphology investigation.

Spores (7.3–)8.85–11.9(–13.4) × (4.3–)4.8–5.7(–6.2) µm (8–10 × 4–5 µm in Smith, 1972), on average 10.2 × 5.29 µm, Q (1.6–)1.7–2(–2.2); in front view oblong, oval, subtriangular, base rounded to sometimes truncate, in profile adaxially flattened to faintly subphaseoliform, sometimes subamygdaliform, rarely phaseoliform; red-brown; germ pore distinct, truncate to broadly rounded, 1.7–2 µm broad. *Pleurocystidia* (28–)32–60 × 10–19 µm, utriform, subcylindrical, conical, ventricose-conical, sometimes subellipsoid to sublageniform; apex obtuse to rounded, sometimes or often subcapitate, sometimes incrusted; walls hyaline; (moderately) numerous. *Cheilocystidia* 22–50 × 10–17 µm, mainly lageniform to attenuate, apex mainly obtuse to sometimes subacute, scattered to locally moderately numerous. *Paracystidia* 8–28(–30) × 5–17 µm, apex often incrusted, walls thickened and at most very faintly pigmented in larger ones, otherwise thin and hyaline, numerous, dominating.

Note: Fragments of leaves are clearly recognizable scattered among the exsiccata and connected to some stipe bases, confirming the association with arboreal material.

23. ***Psathyrella pseudolimicola*** A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 262. 1972. Fig. 54.

Typus: *Psathyrella pseudolimicola* A.H. Sm. **USA**, Idaho, Idaho Co, Seven Devil's Mountains, Nezperce National Forest, Papoose Creek, 10 Aug. 1962, *A.H. Smith* 65850 (MICH5366), gregarious on mud in a cow pasture (mud and manure present). *Tef-1α* MF521781.

Loan of three sporocarps in good conditions for micro-morphology investigation.

Spores 8.5–10.7(–11.8) × 4.9–5.9(–6.7) µm, on average 9–10.5 × 5–5.5 µm, Q (1.6–)1.7–1.9(–2); in front view (narrowly) oval to elliptic-oval, base obtuse to rounded, sometimes

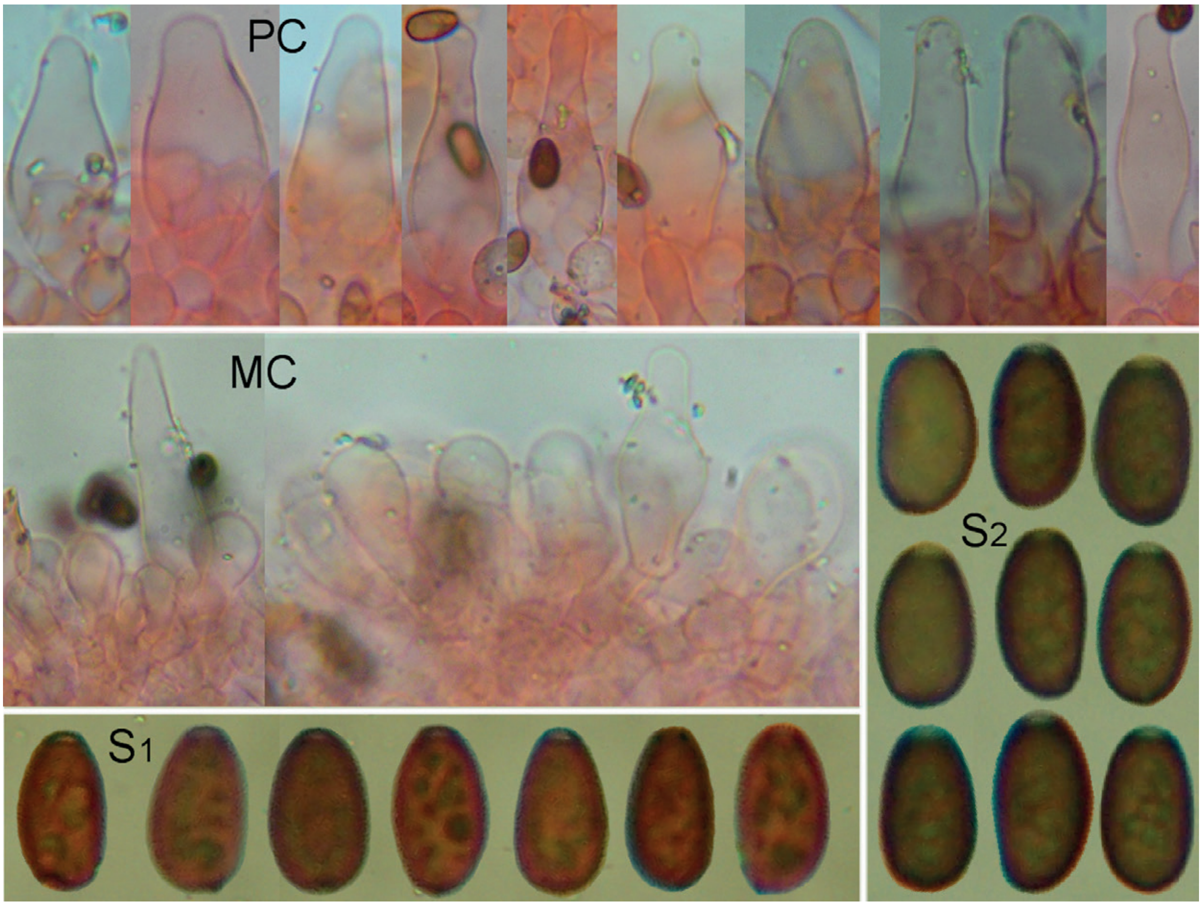


Fig. 53. *Psathyrella griseopallida*. H. D. Thiers 25079, MICH11939; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

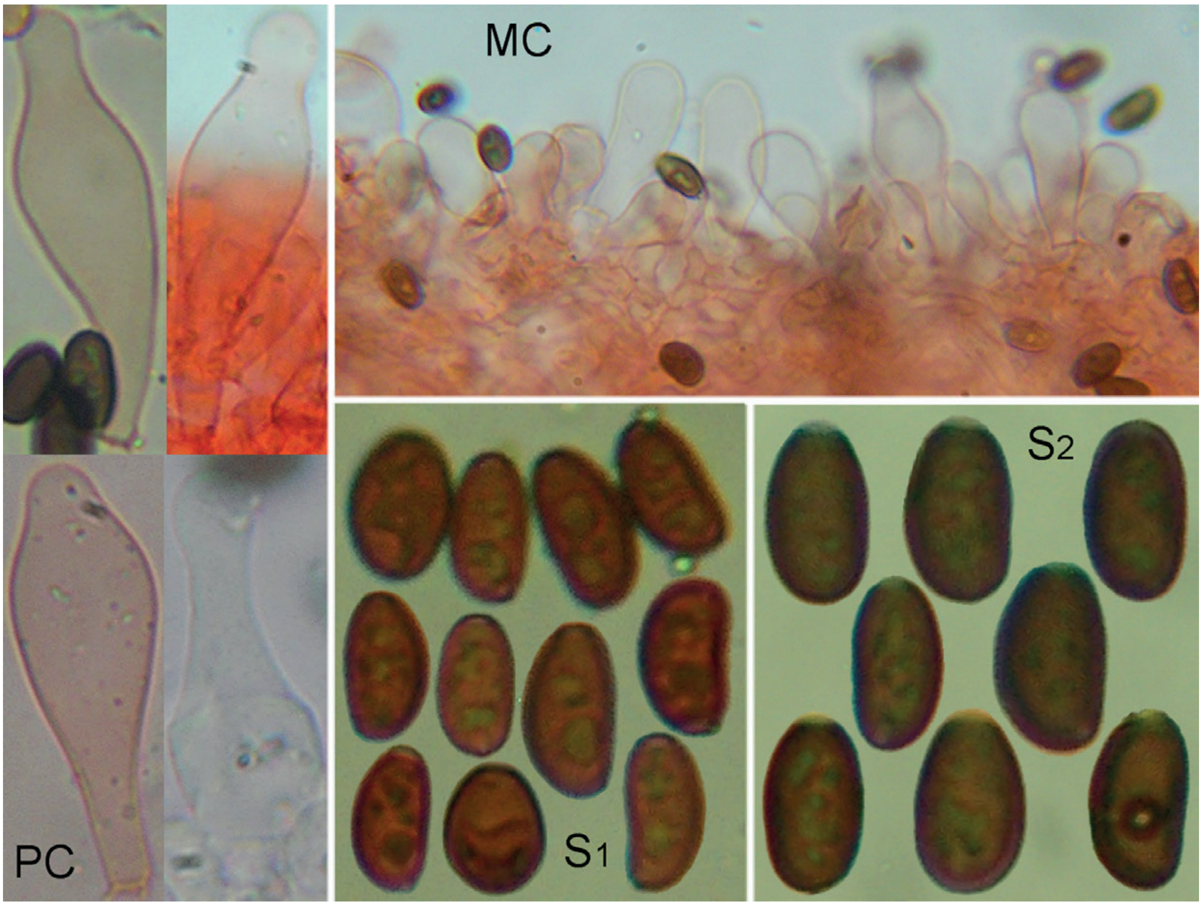


Fig. 54. *Psathyrella pseudolimicola*. A.H. Smith 65850, MICH5366; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

truncate, in profile (narrowly) adaxially flattened-ellipsoid to subphaseoliform, sometimes phaseoliform; reddish brown; germ pore distinct, rounded to subtruncate, 1.5–1.9 µm broad. *Pleurocystidia* 33–53 × 10–16(–19) µm, utriform, sometimes ellipsoid-utriform, lageniform; apex rounded to obtuse, subcapitate or not; walls sometimes faintly pigmented; scattered to moderately numerous. *Cheilocystidia* 25–43 × 12–13 µm, often (broadly) lageniform, sometimes cylindrical-utriform (recalling the broadly cylindrical-utriform pleurocystidium sketched by Smith 1972), scattered. *Paracystidia* up to 35 × 15 µm, hyaline, numerous, dominating. Cells below gill edge hyaline.

Notes: Smith (1972) reports the spores 8.5–11 × 4.5–5 (up to 12 × 6) µm as if he had found only a few broader spores. The molecular evidence places it beside the previous species, *P. griseopallida*, but at a consistent distance (DNA nucleotide homology: *Tef-1α* = 95 %). Smith (1972) commented having a doubt as to whether this species is coprophilous or not as '*it was not found on cow dung though ample opportunity was at hand*'; on examination of the exsiccata multiple loosen dried leaves and a small amount of crumbled unidentifiable plant material were found in the box with the dried fungi but none attached at stipe bases. We presume the habitat to be either herbicolous or on nitrogen-rich soil.

24. ***Psathyrella velatipes*** A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 442. 1972. Fig. 55.
= ***Psathyrella ammophila*** (Durieu & Lév.) P.D. Orton

Typus: *Psathyrella velatipes* A.H. Sm. **USA**, Michigan, Washtenaw Co., Ann Arbor, Liberty St., 30 Sep. 1971, *A.H. Smith* 80623 (MICH12106), gregarious-cespitose in a parking strip. *Tef-1α* MF521774, ITS MF326004.

Loan for gross morphology investigation of four sporocarps, some of which broken.

Spores (8.2–)8.7–10.5(–12) × 5–5.8 µm, on average 9.9 × 5.5 µm, Q (1.5–)1.7–2.1(–2.2), avQ 1.8; in front view cylindrical-oblong to elliptic, base obtuse, in profile subamygdaliform, sometimes subphaseoliform, base often with a suprahilar depression; reddish brown; germ pore distinct, sometimes eccentric in profile, 1.8–2(–2.5) µm broad. *Pleurocystidia* 28–40 × 11–15 µm; narrowly utriform, lageniform, sometimes fusiform-conical to flexuous, rarely ovoid-utriform to thickly utriform, often emerging for only 10 µm length or less, neck often elongate; apex obtuse to rounded, sometimes subcapitate, rarely forked; scattered. *Cheilocystidia* 28–55 × 10–15 µm, sometimes submucronate, pigment as in the paracystidia, rare to scattered towards margin of pileus, moderately numerous towards stipe. *Paracystidia* –37 × –21 µm, often incrusted, walls often thickened and yellowish pigmented moreover towards base, numerous, dominating. Cells below marginal cystidia often incrusted and yellowish pigmented.

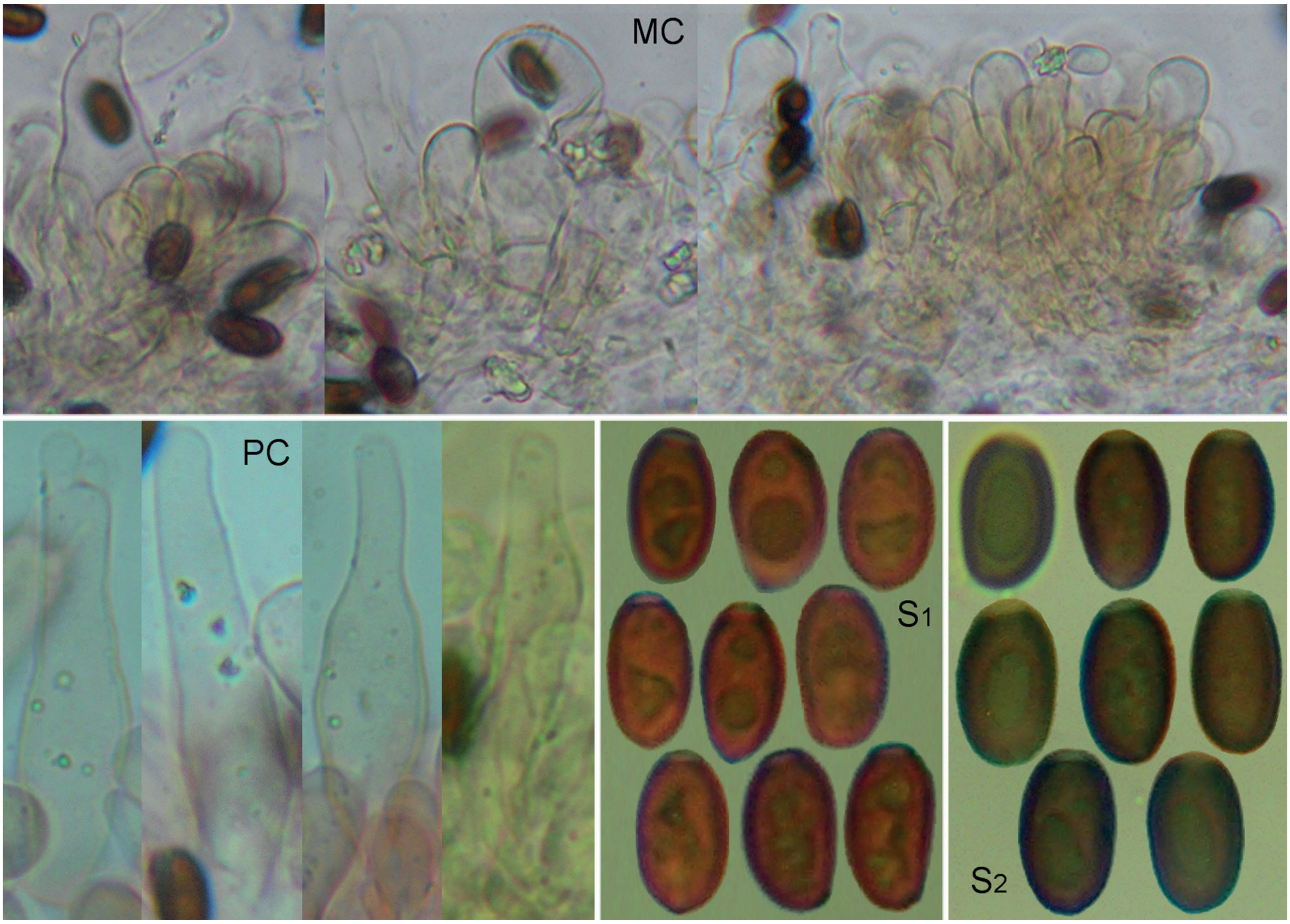


Fig. 55. *Psathyrella velatipes*. A.H. Smith 80623, MICH12106; MC Marginal Cystidia in KOH; PC Pleurocystidia; S1 Spores in water; S2 Spores in KOH.

Notes: There is morphological and molecular evidence that this species corresponds to *P. ammophila*. The distinctly pigmented marginal cells recall the description of *P. ammophila* f. *marginata* by Bon (1988). Smith (1972) was particularly impressed by the '*distinct fibrillose scurfy*' covering of the stipe, but we know that *P. ammophila* has initially a dense velar coating possibly leaving wooly layers on the stipe too. The habitat in Ann Arbor town, far away from the sea shore and sand dunes, is not an obstacle for recognition of this species as sand from river or lakeshore caves is often used in making the foundation of urban green areas; moreover coarse soil, probably including grains of sand, was found attached to the stipe base. The spores of *P. ammophila* are usually described as larger by European mycologists, but Heykoop *et al.* (2017) report collections with smaller spores, similar in size to those of *P. velatipes*. Actually this species spores have a very wide range, both in dimension and in quotient: (7.5–)8.5–14 × (4.7–)5–8.5 µm, avQ 1.5–1.9.

Smith (1972) considered *P. arenulina* the American counterpart of *P. ammophila* and Kits van Waveren (1985) treated it as a synonym. We have not studied this material but, basing on Smith's (1972) description, it shares almost all characters, including scarcity of pleurocystidia, indeed none reported ('*normally very scarce and easily overlooked*' in Kits van Waveren, 1972 for *P. ammophila*). Only the pileus is unusually '*widely and irregularly striate*' while the spores in KOH are '*cocoa-color slowly becoming darker*' which, as we explain further, generally corresponds to a medium, not dark, color in water. Overall we accept this synonymy.

Psathyrella dunarum, created on the base of a solitary sporocarp found on a mossy coastal sand dune, has a strongly striate pileus, scarce subobtusely lageniform pleurocystidia and orange-brown, 8–9 × 4.5–5.5 µm, on average 8.7 × 5.4 µm, spores. We see a strong correspondence between *P. dunarum* and *P. ammophila* therefore, unless molecular evidence should demonstrate convincingly the existence of an autonomous species, we consider them synonyms.

25. *Psathyrella neotropica* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 108. 1972. Fig. 56.
Basionym: *Drosophila pallidispora* Murrill, *Mycologia* **10**(2): 64 (1918). Typus: Cuba, Herradura, 17 Aug. 1907, *F.S. Earle* 572 (NY 00649148), in soil in a garden.

Loan for gross morphology investigation of fragments of pilei and stipes.

Spores (7–)8–12.2(–13.8) × 5–7.5(–8.5) µm [9–12(–13)×5–6.5 µm in revision of Smith, 1972], on average 10.25 × 6.4 µm, Q 1.3–1.9(–2.05), avQ 1.6; wall often irregular in shape or with protrusions, swellings or discontinuities, in front view suboval to elliptic, sometimes cylindrical, base rounded to truncate, in profile adaxially flattened, amygdaliform, subamygdaliform, elliptical, phaseoliform to subphaseoliform; yellowish; germ

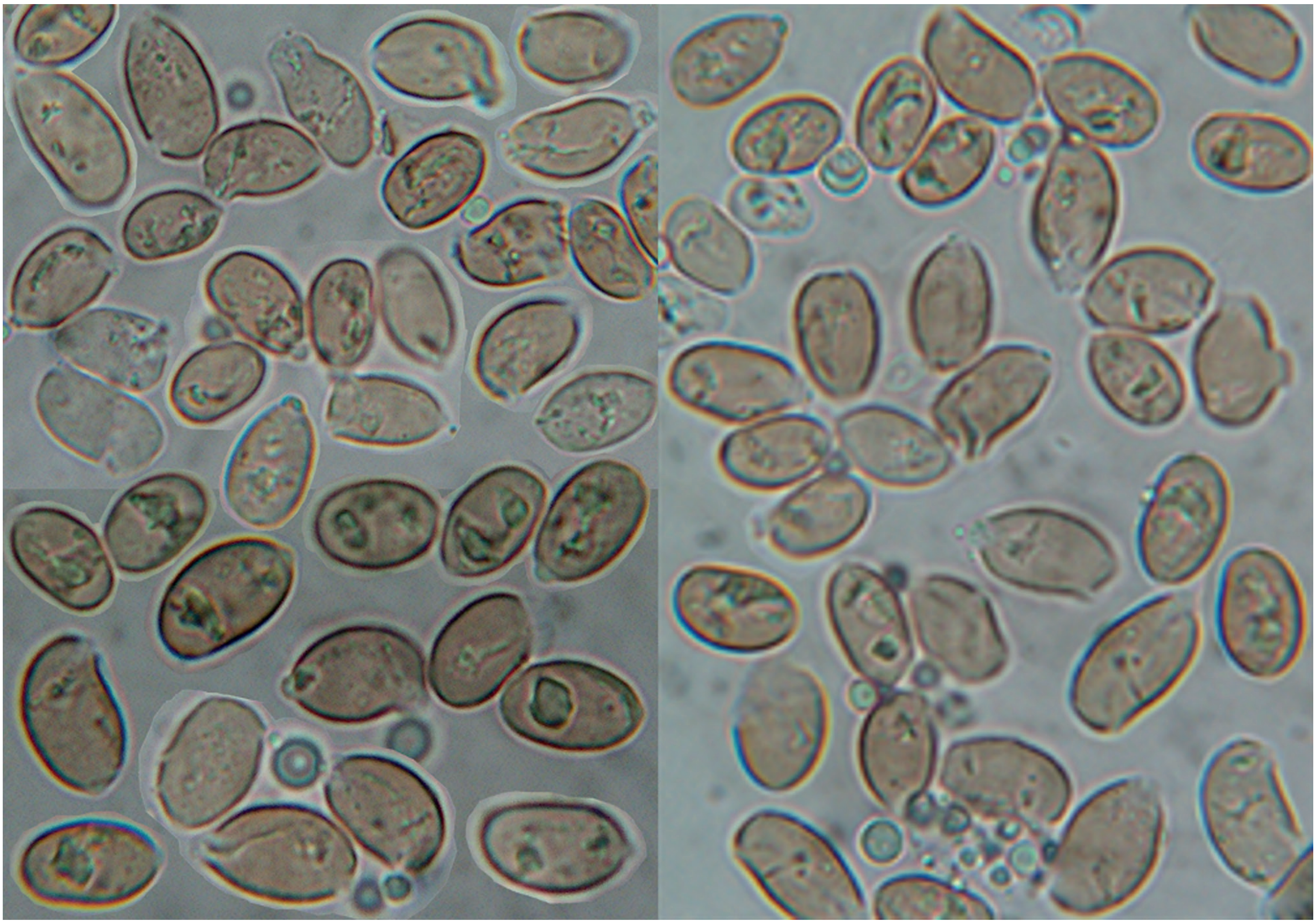


Fig. 56. *Psathyrella neotropica*. F. S. Earle 572, NY 00649148; Spores in NH_4OH.

pore generally absent to indistinct (callus), sometimes as a protruding bubble in alkali, rounded, 1.5–1.8 µm broad when discernible. Hymenial cystidia, basidia and clamps could not be observed because the material revived very badly.

Notes: Unfortunately, DNA sequencing failed because of contamination and likewise our morphological revision too was strongly hampered by poor rehydration of the sample. However we are able to report an unpublished private revision, included in the holotype box, Pegler made in 1986 in which he reported spores 8.5–12×5.5–7 µm, on average 9.5–10.5 × 5.7–6.3 µm, Q 1.4, very pale, pleurocystidia ventricose-fusoid, cheilocystidia spheropedunculate. Pegler's notes seem to clearly implicate that paracystidia are dominating on the gill edge; this and the description by Smith (1972) of broadly rounded apex of pleurocystidia confidently places this taxon into subsection *Spadiceogriseae*. Beyond the anomalous characteristics of the spore outline, which we tend to view as a casual sufferance and not as a taxonomical attribute, we can remark on the short pleurocystidia, 28–37 × 10–14 µm, as reported by Smith (1972). Although we cannot know its phylogenetic position, for some traits this material is reminiscent of the European *P. clivensis* which we have not found in any of the American materials studied.

26. *Psathyrella septentrionalis* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 134. 1972. Fig. 57.

Typus: *Psathyrella septentrionalis* A.H. Sm. **USA**, Michigan, Chippewa Co., Tahquamenon Falls State Park, near Paradise, 2 Jul. 1951, *D. Palmer* 36553 (MICH12045), on hardwood. ITS MF326014.

Loan of two sporocarps and a pileus in good condition for micromorphology investigation.

Spores (7–)7.3–8.7(–9) × 4.1–5(–5.2) µm, Q 1.6–2(–2.1); in front view elliptic to narrowly oval, base obtuse, sometimes rounded, in profile adaxially flattened to subphaseoliform, sometimes distinctly phaseoliform; orangish to reddish brown; germ pore distinct, 1–1.5(–1.7) µm broad. *Pleurocystidia* 35–53 × (7–)9.5–20(–22) µm, utriform to obtusely ventricose-conical, sometimes cylindrical-ellipsoid, conical to sublageniform; apex obtuse to rounded, rarely subacute, sometimes subcapitate or somewhat irregular, rarely capitate, rarely incrusted; moderately numerous to numerous. *Cheilocystidia* 24–50 × 13–22(–25) µm, numerous to abundant, dominating. *Paracystidia* 8–15 × 6–10 µm and numerous, 15–20 × 10–15 and moderately numerous.

Notes: This is one of those species where we could not know, by means of Smith's (1972) vague description only, whether or not it had the attributes of subsection *Spadiceogriseae*; molecular evidence and abundant, dominating cheilocystidia clearly exclude it.

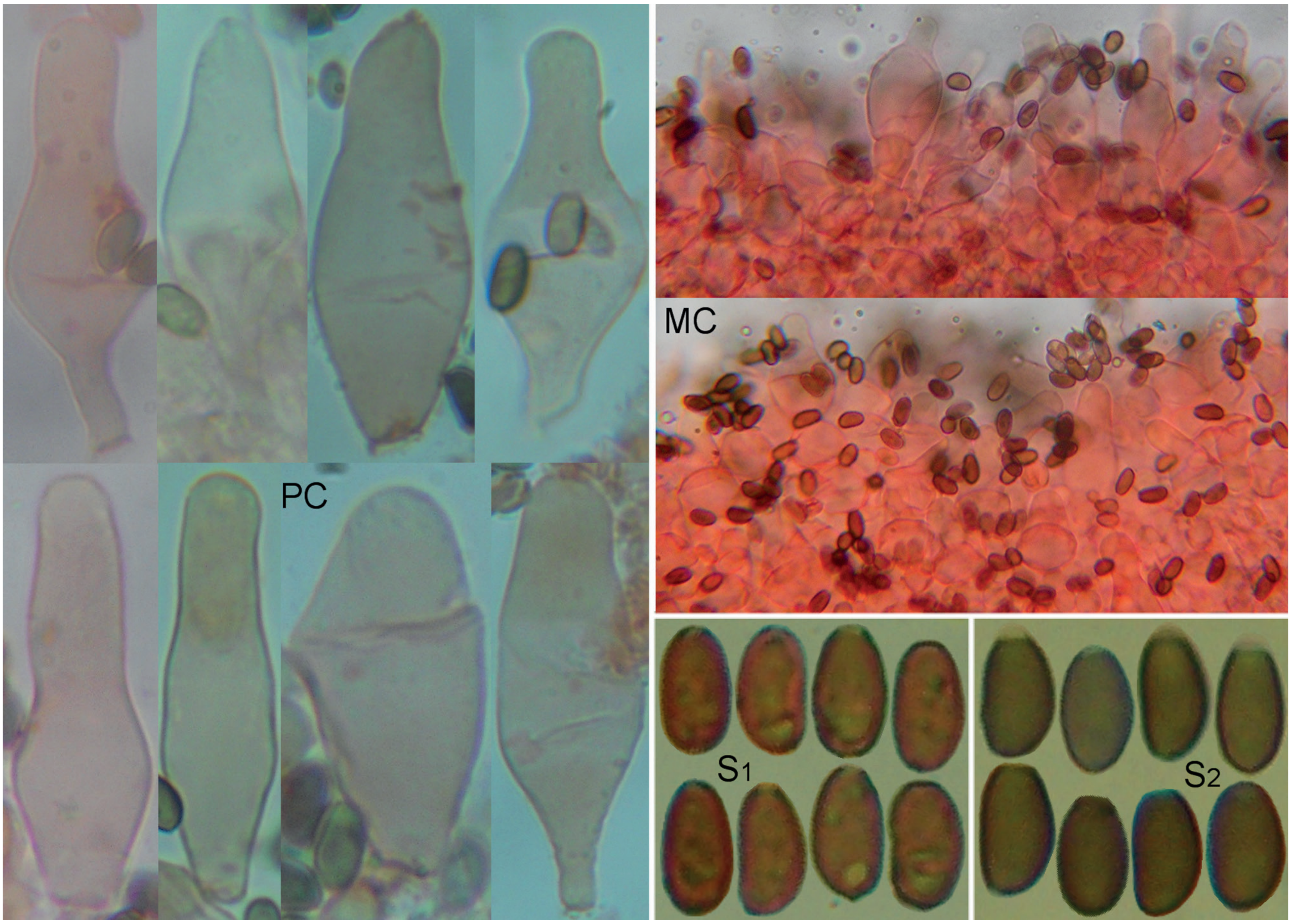


Fig. 57. *Psathyrella septentrionalis*. D. Palmer 36553, MICH12045; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

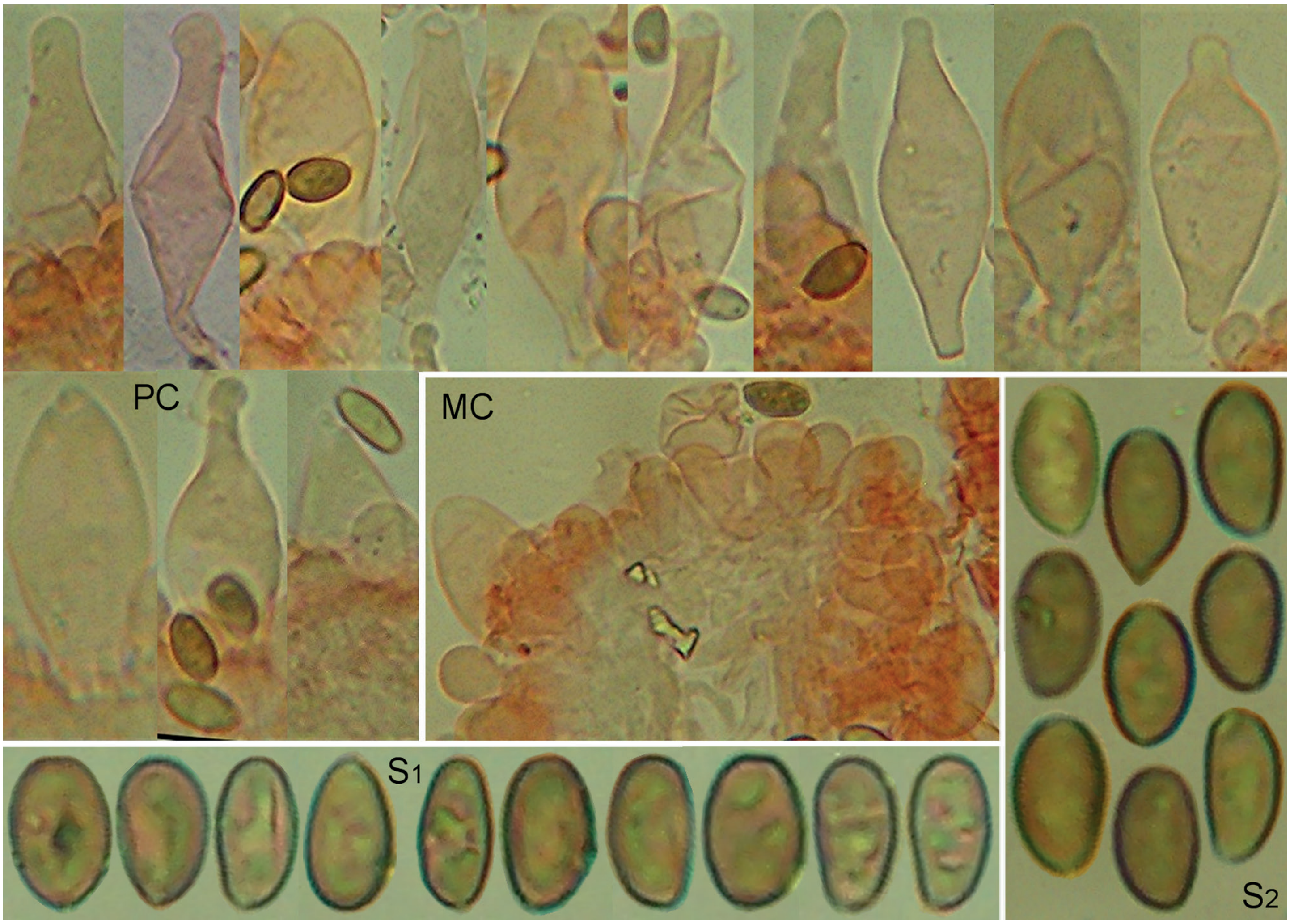


Fig. 58. *Psathyrella vesiculosa*. A.H. Smith 63485, MICH12044; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

27. ***Psathyrella vesiculosa*** (A.H. Sm.) Voto, Dovana & Garbel, ***comb. nov.*** MycoBank MB831130. Fig. 58.
Basionym: *Psathyrella septentrionalis var. vesiculosa* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 136. 1972. *A.H. Smith* 63485, MICH12044.

Typus: *Psathyrella septentrionalis var. vesiculosa* A.H. Sm., **USA**, Michigan, Chippewa Co, Tahquamenon River, White House Landing, 30 Jun. 1961, *A.H. Smith* 63485 (MICH12044), cespitose on hardwood logs. ITS MF326015.

Loan of two sporocarps and a pileus in good condition for micro-morphology investigation.

Spores 6.9–9.9(–10.6) × 3.5–5.5 µm, Q 1.4–2.1(–2.6), avQ 1.8–1.9; in front view oblong to elliptic, base obtuse to attenuate, in profile adaxially flattened or with a faint suprahilar depression, sometimes amygdaliform, subamygdaliform to subphaseoliform; pale orange-brown, pale dull orange; germ pore indistinct (callus), ± 1,5–1,7 µm broad. *Pleurocystidia* 29–50 × (10–)13–17 µm, utriform, fusiform, conical, clavate-mucronate to lageniform, sometimes ellipsoid; apex obtuse to subacute, sometimes subcapitate; very numerous. *Cheilocystidia* 30–45 × 9–15 µm, apex often subacute, scattered. *Paracystidia* 7–37 × 4–20 µm, apex sometimes obscurely mucronate to obscurely acutely papillate, hyaline, numerous, dominating.

Notes: Smith (1972) described the spores of *P. septentrionalis var. vesiculosa* as '*in KOH chocolate color, gradually fading and with an ochraceous tinge (in about three hours)*' and with a distinct germ pore, but we found them distinctly pale immediately and the germ pore indistinct; he also detected longer pleurocystidia, up to 60 µm. *Psathyrella septentrionalis* and *P. vesiculosa* show a molecular proximity (DNA nucleotide homology: ITS = 99 % with five mismatches) but there are a number of micro morphological elements that distinguish *P. vesiculosa*, such as the spores (distinctly paler, somewhat slenderer, often attenuate at base, scarcely subphaseoliform), the gill edge dominated by the paracystidia, and partly the pleurocystidia which are somewhat slenderer and less rounded at apex. In macro morphology, we also notice that the pileus of *P. septentrionalis* is described as obtuse to convex, expanding from broadly convex to plane (Smith's plates 43b, 46a and 46b clearly confirm this), while the pileus of *P. vesiculosa* is described as obtusely conical becoming campanulate. Predominance of paracystidia and, partly, shape of pleurocystidia may induce to consider *P. vesiculosa* a possible member of subsection *Spadiceogriseae*, but it has a colored veil and, as we anticipated in the introduction, this parameter has to be given a relevant discriminating importance. This is one of those species evidencing that dominating paracystidia alone are not exclusive of subsection *Spadiceogriseae*.

28. *Psathyrella velibrunnescens* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 128. 1972. Fig. 59.

Typus: *Psathyrella velibrunnescens* A.H. Sm. **USA**, Washington, Jefferson Co., Bottom, Clearwater River, 9 May 1939, *A.H. Smith* 13240 (MICH12107), on *Alnus* debris.

Loan of a slice of a pileus for micro-morphology investigation.

Spores 7.7–9.5(–10) × 4.5–5.1(–5.4) µm, Q 1.6–2.1(–2.2), avQ 1.8; in front view oblong to elliptic, sometimes oval, base mainly obtuse, in profile adaxially flattened to subphaseoliform; dull orangish or paler; germ pore indistinct (callus). *Pleurocystidia* 40–79 × 9–17 µm, utriform to subcylindrical, often elongate-cylindrical in upper part; apex mainly rounded, sometimes or often (irregularly) subcapitate; very numerous. *Cheilocystidia* 27–51 × 9–12(–19) µm, scattered. *Paracystidia* 9–41×5–23 µm, numerous, dominating. No pigment or incrustation seen on any type of cystidia.

Notes: Unfortunately DNA extraction failed on this material, but, based on morphological evidence, we consider *P. velibrunnescens* to pertain to the *P. septentrionalis* complex. We note that Kits van Waveren (1985), on the contrary, regards it as an American subspecies of *P. chondroderma* (= *P. pertinax*). For further comment see notes to the following species.

29. *Psathyrella aff. kauffmanii*, Czech Republic, Bohemia, Volary, Černý Kříž, Mount Šumava, Jelení vrch area, 870 m. a.s.l., 13 Jul. 2000, *J. Holec* 61/2000 (PRM897750, erroneously registered in GenBank as BRNM:705626), gregarious on very rotten trunk of *Fagus sylvatica* in a mixed forest with also *Picea abies* and *Abies alba*. ITS AM712260.

?= ***Psathyrella velibrunnescens*** A.H. Sm.
(Description produced from data and images received from Vašutová).

Pileus 15–40 mm, campanulate, red-brown, hygrophanous, distinctly radially rugulose. Veil yellowish whitish at margin of pileus. *Lamellae* pale violet-brown. Stipe 40–70 × 7–9 mm, cylindrical, whitish, brownish towards the base, innately white marbled. Smell rubber-like. *Spores* 7.5–9 × 4–5 µm, Q±1.7–2.1, avQ±1.8, in front view elliptic, in profile subphaseoliform, rarely subamygdaliform to adaxially flattened, light to medium brown, germ pore little distinct (callus). *Pleurocystidia* (40–) 46–60(–72) × 12–14 µm, utriform to sublageniform, with apex obtuse to rounded, rarely subacute. *Cheilocystidia* 30–40 × 11–15 µm, scattered. *Paracystidia* 20–34 × 9–13 µm, numerous, dominating.

Notes: When blasting the ITS sequences of *P. septentrionalis* and *P. vesiculosa* in GenBank we have discovered that they allied with *P. aff. kauffmanii* from Europe synthetically

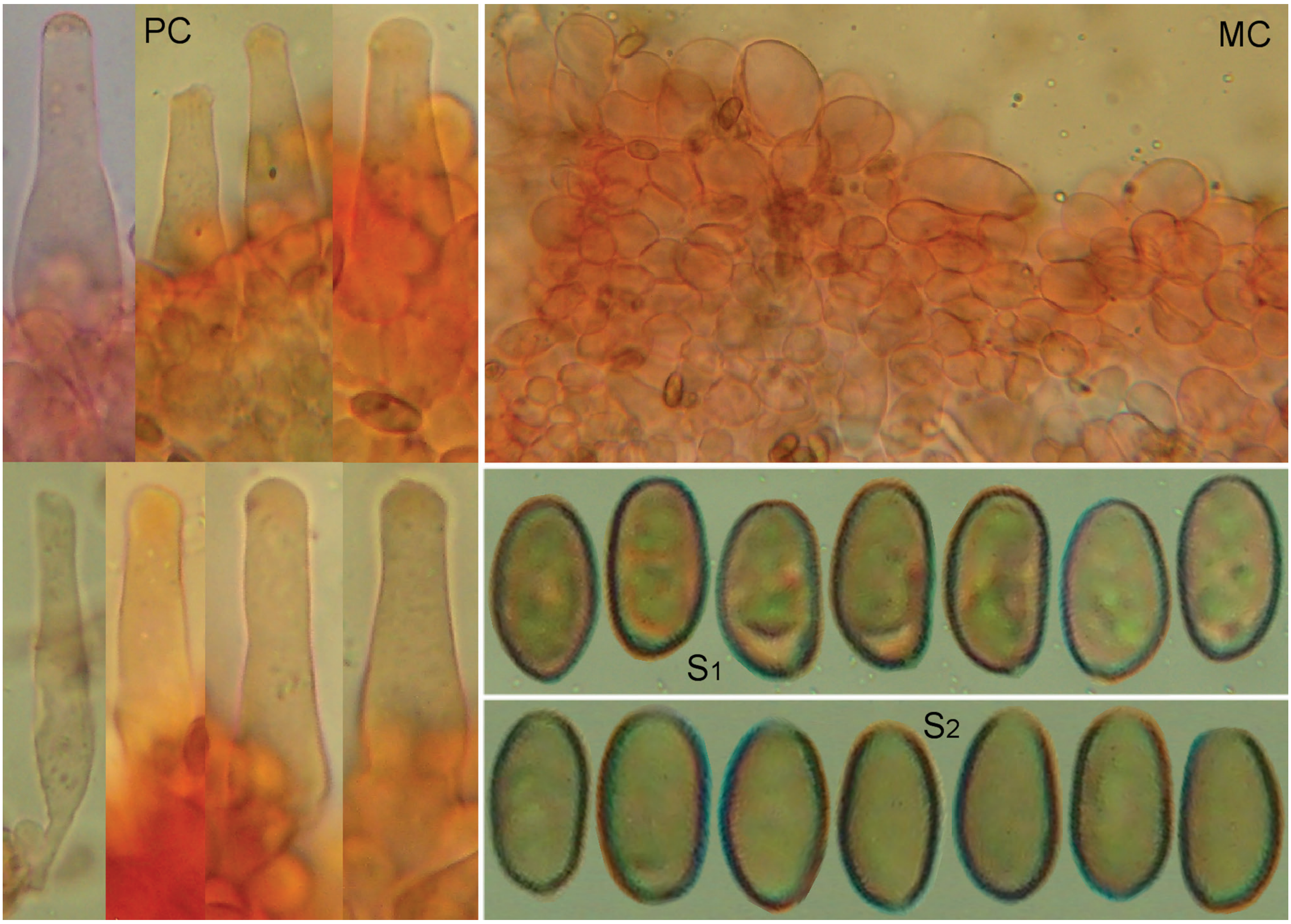


Fig. 59. *Psathyrella velibrunnescens*. A.H. Smith 13240, MICH12107; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

described in Vašutová *et al.* (2008). Upon our request, Vašutová has provided us with a more detailed description, has shown us some images of microscopical characters, and has discussed with us the molecular outcome. Various characters link *P. aff. kauffmanii* to *P. vesiculosa*: the gill edge dominated by paracystidia, the pale spores, the little distinct germ pore, the slender pleurocystidia, the yellowish veil at the margin of a campanulate pileus; on the contrary the often phaseoliform spores with rounded, not attenuate base seem to differentiate them; moreover *P. aff. kauffmanii* has very thickset, 7–9 mm broad, stipes, while *P. vesiculosa* has slender, 1.5–5 mm broad stipes. A more interesting comparison, though not based on phylogenetic data, can be made with the unsequenced *P. velibrunnescens*. A very strong correspondence can be noticed between the two, both in gross and micro characters as well as in the lignicolous habitat and, but for the lack of molecular support, we would suggest their conspecificity. However, while we wish Vašutová to find and describe it again in more detail, surely *P. aff. kauffmanii* has been shown to be a European species on its own right. It only remains to understand whether it may be autonomous from or conspecific with any of the American species of the phylogenetic cluster to which it belongs.

Psathyrella conica, recently described from China, shares many morphological characters with the last three species here described, namely *P. vesiculosa*, *P. velibrunnescens* and *P. aff. kauffmanii*. Like them, it has paracystidia dominating, utriform pleurocystidia, pale spores with an indistinct or absent germ pore, campanulate to conical pilei and a lignicolous habitat. Moreover, like them it is molecularly outside of *spadiceogrisea* clade and has a veil which its authors have noticed not to be merely white ('*white to dirty white*'). We strongly suspect that, just as *P. aff. kauffmanii* is a European representative of *P. vesiculosa* group, *P. conica* could be instead an Asian member of the same group.

30. *Psathyrella obtusata* (Fr.) A.H. Sm., *Contr. Univ. Mich. Herb*. **5**: 55. 1941, *sensu* Smith, *Mem. N. Y. Bot. Gard*. **24**: 385. 1972.

We have attempted to understand Smith's (1972) concept of *P. obtusata* by examining three Smith vouchers, Ammirati 2811, Harrison 8023 and Smith 73998, selected for this purpose by MICH staff. Our revision of these materials has revealed that they represent three different species: Harrison 8023 has the gill edge dominated by the cheilocystidia, Ammirati 2811 and Smith 73998 have the gill edge lined with numerous paracystidia often mucronate to attenuate at the apex.

30a. *J.F. Ammirati* 2811, MICH49136.

= ***Psathyrella obtusata*** (Fr.) A.H. Sm.

Material examined: **USA**, Michigan, Baraga Co., Huron River, Skanee Road, 25 Jun. 1969, on hardwood log.

Loan of two sporocarps in good condition for micro-morphology investigation.

The original gross description by the collector reports pilei color ranging from watery sayal brown to dark brown, fading to clay color at centre and tan at margin; stipe more or less up to 6 mm broad at apex, white fibrillose, sordid brownish in age; odor slight, taste slightly raphanoid. *Spores* (5.5–)6.7–8.3(–9.1) × 4.3–5.6(–6) µm, Q 1.4–1.7; in front view elliptic to oval, sometimes somewhat irregular, base generally rounded, in profile adaxially flattened to subphaseoliform; dull orangish to reddish orangish; germ pore little distinct, small. *Pleurocystidia* (35–)40–63 × (7.5–)8–16(–17.5) µm; narrowly utriform, narrowly fusiform, (flexuously) conical, sometimes sublageniform; apex obtuse, sometimes subacute, rarely subcapitate to submucronate, often incrusted; walls sometimes slightly thickened and pale yellowish below apex; numerous. *Cheilocystidia* 28–43 × 8.5–15.5 µm, locally scattered to numerous, locally dominating. *Paracystidia* 13–40 × 9.5–20(–27) µm, often mucronate to attenuate, yellowish, often incrusted towards base, numerous, locally dominating. Cells below marginal cystidia yellowish pigmented and incrusted.

Note: We failed to sequence this material but it has the typical characters of *P. obtusata*.

30b. *K.A. Harrison* 8023, MICH65721. Fig. 60.

= ***Psathyrella atomatoides*** (Peck) A.H. Sm.

Material examined: **Canada**, Nova Scotia, Victoria Co., Forks Baddeck, 22 Sep. 1968, densely cespitose on sawdust pile. *K.A. Harrison* 8023, MICH65721. ITS MF326013.

Loan of numerous sporocarps in good condition for micro-morphology investigation.

The original gross description by the collector reports pilei up to 3.6 cm broad, slightly conic to subumbonate, sometimes expanding to nearly convex, hygrophanous, when young dark brown, when dried tan, radially striate, veil connecting pileus and stipe when young then fibrillose on margin; gills up to 2 mm broad, close, dark smoky brown; stipe 30–35 × 3–4 mm, covered by fibrils. *Spores* 6.8–8.5(–9.1) × 3.8–4.8 µm, Q 1.5–1.9(–2.1); in front view oblong, elliptic to oval, base generally obtuse, in profile amygdaliform, subamygdaliform to adaxially flattened, sometimes subphaseoliform to narrowly elliptic or subfusiform; strong orange-brown to red-orange; germ pore indistinct to little distinct, small. *Pleurocystidia* 45–65 × 10–15(–17) µm; lageniform to conical, sometimes subutriform, fusiform, irregularly cylindrical-mucronate; apex subobtuse to subacute, rarely subcapitate, often incrusted; walls often thickened and yellowish to yellowish brownish below apex; numerous to moderately numerous. *Cheilocystidia* 32–60 × 10–12 µm, more often fusiform-conical, scattered near pileus margin, numerous elsewhere, dominating. *Paracystidia* 22–28 × 9–10 µm, often incrusted, more or less scattered, numerous near pileus margin. Cells below marginal cystidia pigmented near pileus margin, hyaline elsewhere.

Notes: This material is in good molecular concordance, though with evidence provided by only one locus (DNA nucleotide homology: ITS= 99 % with 1 mismatch), with *P. atomatoides*; morphology too is very similar except for the distinct reddish pigmentation of the gill edge in a short, 3 mm long, segment near the pileus margin, in correspondence with the dominance zone of the paracystidia.

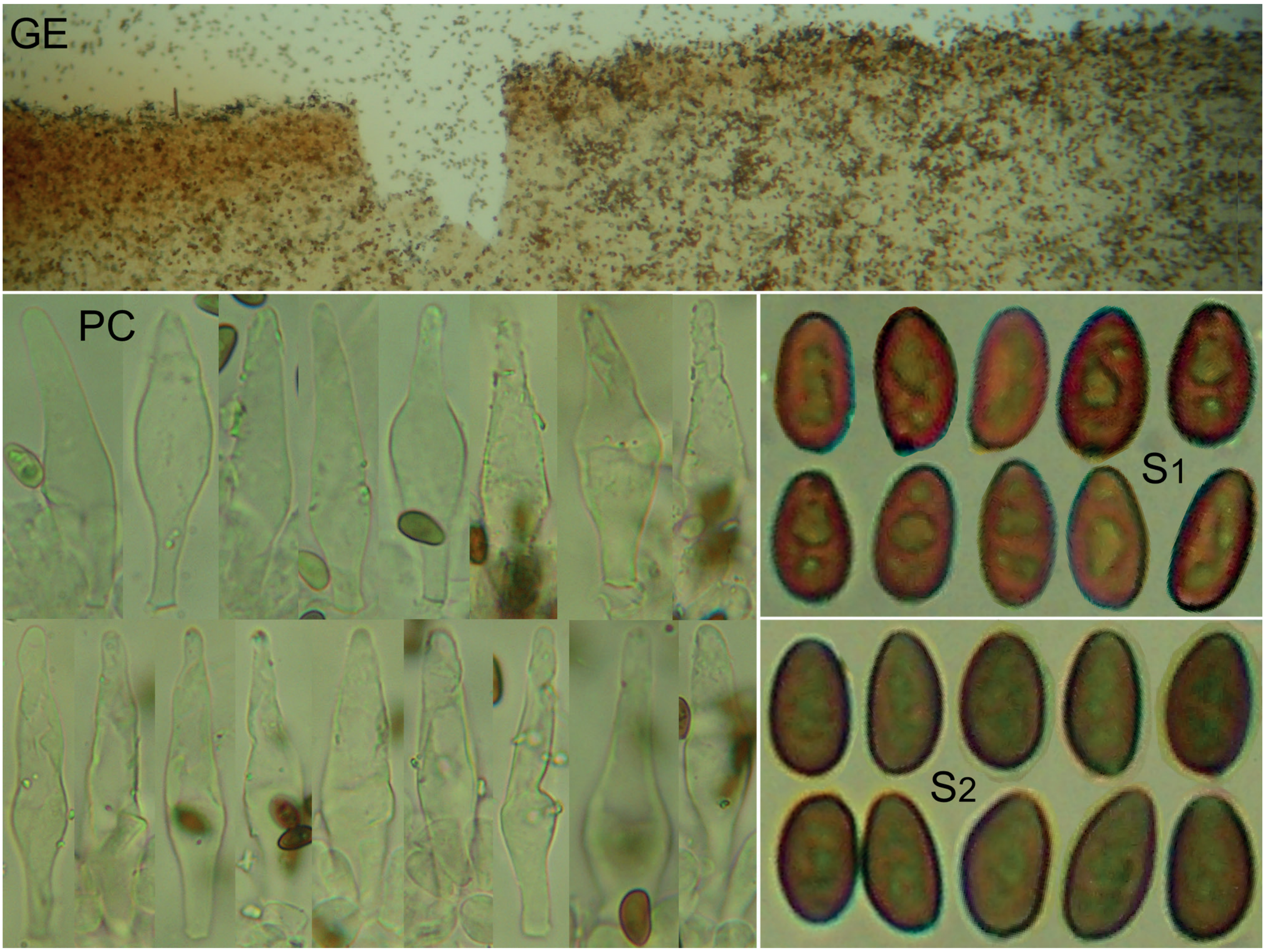


Fig. 60. *Psathyrella obtusata*. K. A. Harrison 8023, MICH65721; GE Gill edge at pileus margin; PC Pleurocystidia in NH_4OH; S1 Spores in water; S2 Spores in KOH.

30c. *A.H. Smith* 73998, MICH33261. Fig. 61.

=?

Material examined: **USA**, Idaho, Bonner co., Priest River, Priest River Experimental Forest, 6 Oct. 1966, on debris of cedar slash, *A.H. Smith* 73998, MICH33261. ITS MF326012.

Loan of five, entire or broken, sporocarps in good condition for micro-morphology investigation.

The original gross description by the collector reports pilei watery tawny when moist, striate half way; veil of white particles at margin; gills broad, adnate, when young brownish, when mature near hair brown; stipe pallid, soon honey below, thinly fibrillose. *Spores* 7–8.5(–9.2) × 4.2–5 µm, on average 7.9 × 4.55 µm, Q 1.5–2, avQ 1.7; in front view elliptic to oval, base rounded to obtuse, in profile amygdaliform, subamygdaliform to somewhat adaxially flattened, sometimes subphaseoliform; reddish brown; germ pore distinct, rounded to truncate, 1.4–1.7 µm broad. *Pleurocystidia* 29–45(–52) × 10–16 µm; variable, ellipsoid, fusiform, conical, lageniform, sometimes narrowly utriform, sublageniform, flexuous; apex subacute to obtuse, sometimes acute, rarely minutely rounded subcapitate, sometimes incrusted; numerous to moderately numerous. *Cheilocystidia* 21–33 × 8.5–12(–14) µm, moderately numerous to locally rare. *Paracystidia* 14–23(–26) × 8–12.5 µm, often mucronate to subpapillate, hyaline, numerous. Cells below marginal cystidia hyaline.

Notes: This voucher corresponds neither to any European species, nor to any American material sequenced in this work; however phylogenetic analysis, though based on one locus only, clearly places it outside subsection *Spadiceogriseae*. Smith (1972) has described some species with *Pennatae*-type pleurocystidia and a conspicuous presence of paracystidia on the gill edge so it should be placed among, and compared with, them, which is outside this paper's purpose.

31. *Psathyrella limicola var. subpectinata* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 416. 1972.

Typus: *Psathyrella limicola var. subpectinata* A.H. Sm. **USA**, Wyoming, Carbon Co., Lower French Creek, Medicine Bow Mountains, 30 Jun. 1950, *A.H. Smith* 34407 (MICH11965), gregarious on wet soil along stream. ITS MF325980.

Loan for gross morphology investigation of three sporocarps in good condition.

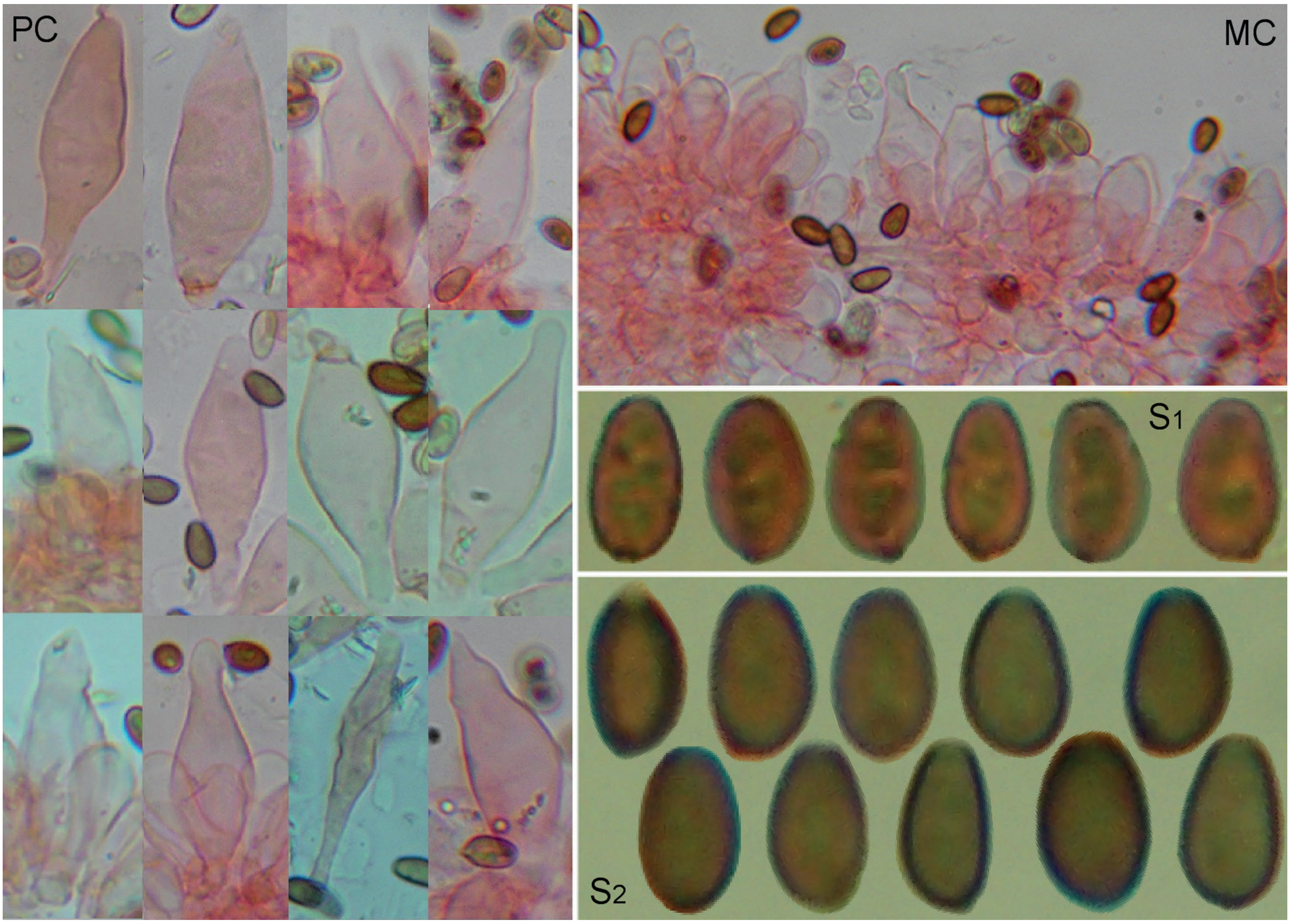


Fig. 61. *Psathyrella obtusata*. A.H. Smith 73998, MICH33261; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

Spores 6.8–9.3 × 3.8–5 µm, Q (1.6–)1.8–2.1(–2.3), avQ 1.9; in front view (narrowly) oval to elliptic, base rounded, in profile subamygdaliform to subphaseoliform, sometimes adaxially flattened; reddish brown; germ pore indistinct to moderately distinct, sometimes distinct, rounded to truncate, 1.2–1.6 µm broad. *Pleurocystidia* 29–41 × 10–13 µm; utriform to fusiform-utriform; apex subrounded, sometimes subcapitate, sometimes weakly incrusted, walls slightly pigmented; moderately numerous. *Cheilocystidia* 20–30(–37) × 8–10 µm, walls sometimes thickened and weakly pigmented in lower half, generally numerous, generally dominating. *Paracystidia* 8–20(–28) × 6–13 µm, sometimes irregular, walls in larger ones sometimes thickened and weakly pigmented, numerous, locally dominating where larger ones are crowded. Cells below marginal cystidia sometimes with thickened and weakly pigmented walls.

Notes: This material has a 99 % ITS nucleotide homology with a number of species outside of subsection *Spadiceogriseae*: *P. warrenensis*, *P. seminuda*, *P. fagetophila*, and Smith 28713, one of the Smith vouchers under the name of *P. agrariella*.

32. *Psathyrella affinis* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 232. 1972. Fig. 62.

Paratype: *Psathyrella affinis* A.H. Sm. **USA**, Michigan, Oakland Co., Highland Lake, 14 Jun. 1945, *A.H. Smith* 20414 (MICH11857), gregarious to scattered on wet leaves in swamp.

Loan for gross morphology investigation of two pilei.

Spores (6.8–)8–10.4(–12.5) × (4.6–)5.4–6.2(–6.8) µm, Q (1.4–)1.5–1.6(–2.1); in front view (broadly) oval, sometimes subtriangular to elliptic, base often subtruncate, in profile adaxially flattened, elliptic, subphaseoliform; orange-brown; germ pore distinct to indistinct, sometimes eccentric in profile, rounded, 1.3–1.6 µm broad. *Basidia* 8–13 µm broad, some 2-spored. *Pleurocystidia* 25–40 × 10–17(–20) µm; ventricose-lageniform, sometimes utriform to lageniform; apex 4.5–6(–7.5) µm broad, obtuse, sometimes subobtuse to subrounded, sometimes subforked; more or less moderately numerous. *Cheilocystidia* 27–38 × 11–15 µm, more or less scattered to locally absent. *Paracystidia* 7.5–31(–36) × 7–17(–22.5) µm, often incrusted towards base, walls sometimes faintly pigmented, numerous, dominating.

Notes: Unfortunately we failed to sequence this material, so we have no molecular information about its phylogenetic position. The pleurocystidial shape is particular: the obtuse, never rounded nor acute to subacute, apex is somewhat ambiguous but the neck is much slenderer than the ventricose portion, looking on the whole unfit for section *Spadiceogriseae*.

33. *Psathyrella nitens* A.H. Sm.

Because of scarcity of material, the holotype could be obtained for DNA sequence only. The MICH staff has selected four other

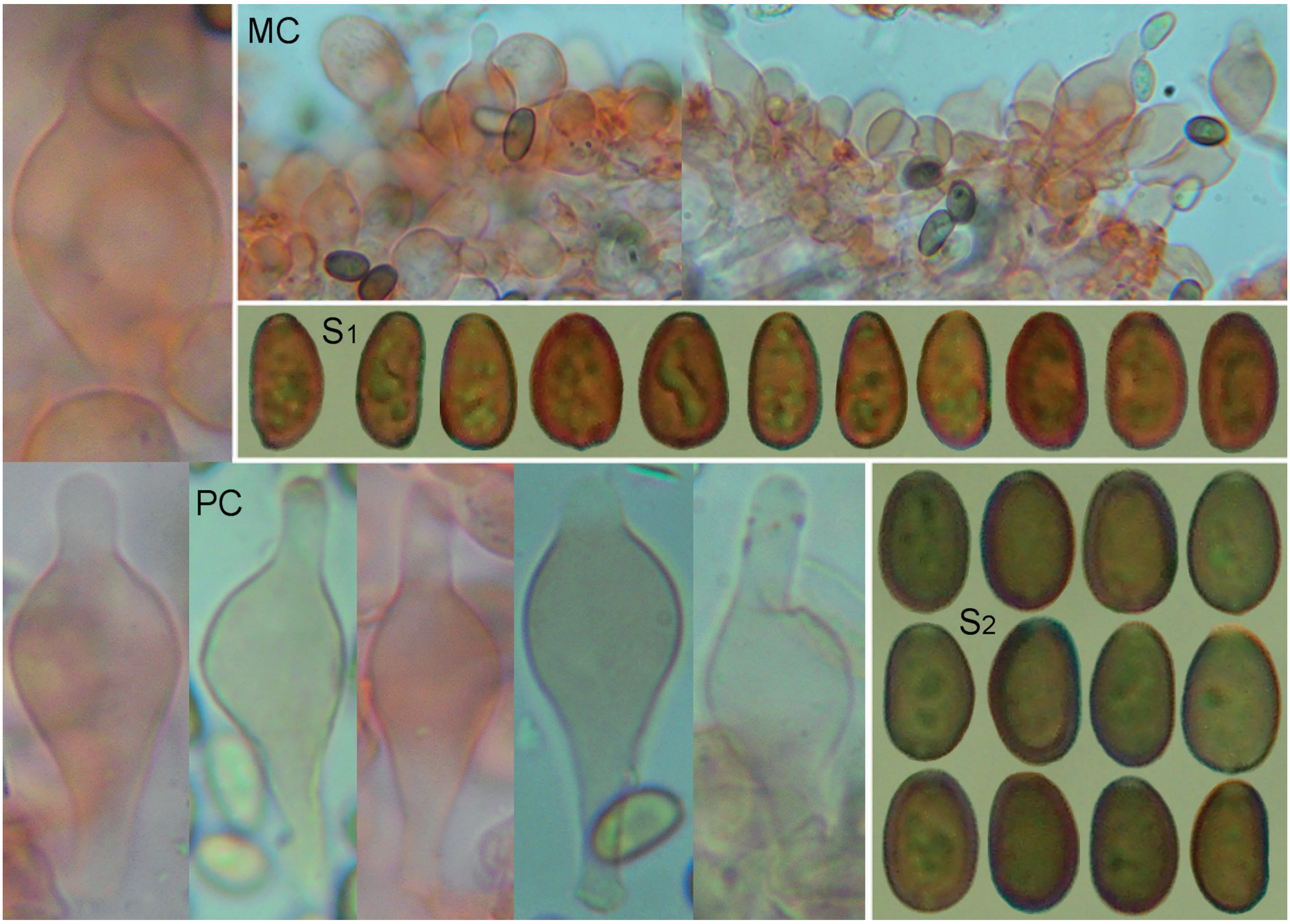


Fig. 62. *Psathyrella affinis*. A.H. Smith 20414, MICH11857; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

collections from the same site by Smith and deposited under the same name for micro-morphology investigation. Two of them, Smith 30241 and Smith 30239, correspond molecularly to the holotype and morphologically to the description given by Smith (1972) therefore they are confidently assigned to the typical *P. nitens*. Smith 29642 deviates significantly from the holotype (DNA nucleotide homology: ITS= 99 %, *Tef-1α* = 94 %) and we have found that the spores are appreciably smaller, the pleurocystidia and paracystidia are somewhat smaller and the apex of the pleurocystidia are more obtuse. Smith 30175 is distinctly closer to Smith 29642 (DNA nucleotide homology: ITS= 99 % with 1 mismatch) than to the other three vouchers (DNA nucleotide homology: ITS= 99 % with 8 to 9 mismatches) and it too displays the same differences exactly as found in Smith 29642 therefore they are conspecific; we consider them a separate taxon from *P. nitens* and report their morphological revision in a unified description. All these vouchers fall outside of subsection *Spadiceogriseae* and nest beside *P. obtusata*; their pleurocystidia are never thickly utriform and the apex is sometimes more or less acute but never rounded, the gill edge has often intermediate, mucronate to rhomboid, cells.

33a. *Psathyrella nitens* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 320. 1972.

Typus: *Psathyrella nitens* A.H. Sm. **USA**, Washington, Pierce Co., Mt. Rainier National Park, Lower Tahoma Creek, 21 Aug. 1948, *A.H. Smith*, 30388 (coll. *D.E. Stuntz*) (MICH11983), on debris; only for molecular sequence. *Tef-1α* MF521789, ITS MF325982.

Loans for micro-morphology investigation: **USA**, Washington, Pierce Co., Mt. Rainier National Park, Lower Nisqually, 18 Aug. 1948, *A.H. Smith* 30239 (MICH33251), on debris, *Tef-1α* MF521787, ITS MF325985; **USA**, Washington, Pierce Co., Mt. Rainier National Park, Lower Tahoma, 18 Aug. 1948, *A.H. Smith* 30241 (MICH33252), on alder debris, *Tef-1α* MF521786, ITS MF325986.

Spores 8.3–11.2(–12) × 5–6.5(–6.8) µm, Q 1.4–1.7(–1.9); in front view oval to elliptic, base obtuse to broadly rounded, in profile suboval, amygdaliform to subamygdaliform, sometimes subphaseoliform; reddish brownish; germ pore distinct, mainly truncate to subtruncate, 1–1.7 µm broad. *Pleurocystidia* 42–75(–87) × 11–17.5 µm; lageniform, conical, subutriform, usually with elongate neck; apex acute to subobtuse, sometimes subcapitate or forked, incrusted or not; moderately numerous. *Cheilocystidia* 25–45(–49) × 11–12.5(–16) µm, mainly with neck very short, looking mucronate, to medium long (2–10 µm), locally numerous and in tufts. *Paracystidia* 16–36 × 8–14 µm, walls sometimes or often thickened, yellowish pigmented, numerous, dominating. Cells below marginal cystidia with yellowish pigment.

33b. *A.H. Smith* 29642, MICH33249; *A.H. Smith* 30175; MICH33250. Fig. 63.

=?

Loans for micro-morphology investigation: **USA**, Washington, Pierce Co., Mt. Rainier National Park, Lower Tahoma, 30 Jul. 1948 (*Smith* 29642), *Tef-1α* MF521788, ITS MF325983; at same location, 16 Aug. 1948, coll. *D.E. Stuntz & B. Knowles*, on humus (*Smith* 30175), ITS MF325984.

No description was attached to either voucher by the collectors.

Spores (7.5–)8.1–9.6(–10.5) × (4.5–)5–5.6(–5.8) µm, on average 8.9 × 5.2 µm, Q (1.44) 1.52–1.88(–2), avQ 1.70; in front view elliptic, sometimes suboval, base rounded, in profile adaxially flattened, sometimes amygdaliform to subamygdaliform; reddish brownish; germ pore distinct, mainly truncate, 1.1–1.5 µm broad. *Pleurocystidia* 40–60 × 8.8–16 µm; narrowly utriform to lageniform, sometimes fusiform to conical, sometimes flexuous, neck variably long; apex obtuse, rarely subacute, sometimes incrusted; moderately numerous to numerous. *Cheilocystidia* (18–)31–45 × 7–15 µm, apex sometimes incrusted, scattered to numerous. *Paracystidia* 11–24(–38) × 6–12(–17) µm, walls sometimes or often thickened and slightly yellowish pigmented towards base, moderately numerous to numerous and intermixed with many basidia and basidiola. Cells below marginal cystidia mostly or only locally with yellowish pigment, sometimes incrusted.

34. *Psathyrella psammophila* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 357. 1972.

Molecular heterotypical synonyms proposed here: *Psathyrella angusticystis* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 383. 1972; *Psathyrella subargillacea* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 386. 1972.

Typus: *Psathyrella psammophila* A.H. Sm. **USA**, Michigan, Washtenaw Co., Pinckney Recreation Area, 7 May 1964, *A.H. Smith*, 67836 (MICH12012), on sandy soil. ITS KC992856.

Loan for micro-morphology investigation of a slice of a pileus in good condition.

Spores 7.5–9.3(–11) × (4.4–)4.7–5.5(–5.7) µm, on average 8.2 × 5 µm, Q 1.5–1.7(–2), avQ 1.6; in front view broadly oval to elliptic, base rounded, in profile subphaseoliform to adaxially flattened, sometimes distinctly phaseoliform; brownish orange, sometimes with a vague reddish shade; germ pore mainly indistinct and small. *Pleurocystidia* 40–60 × 10–16(–18) µm; utriform, rarely cylindrical-ellipsoid to clavate; apex obtuse, sometimes rounded, sometimes mucronate to subcapitate,

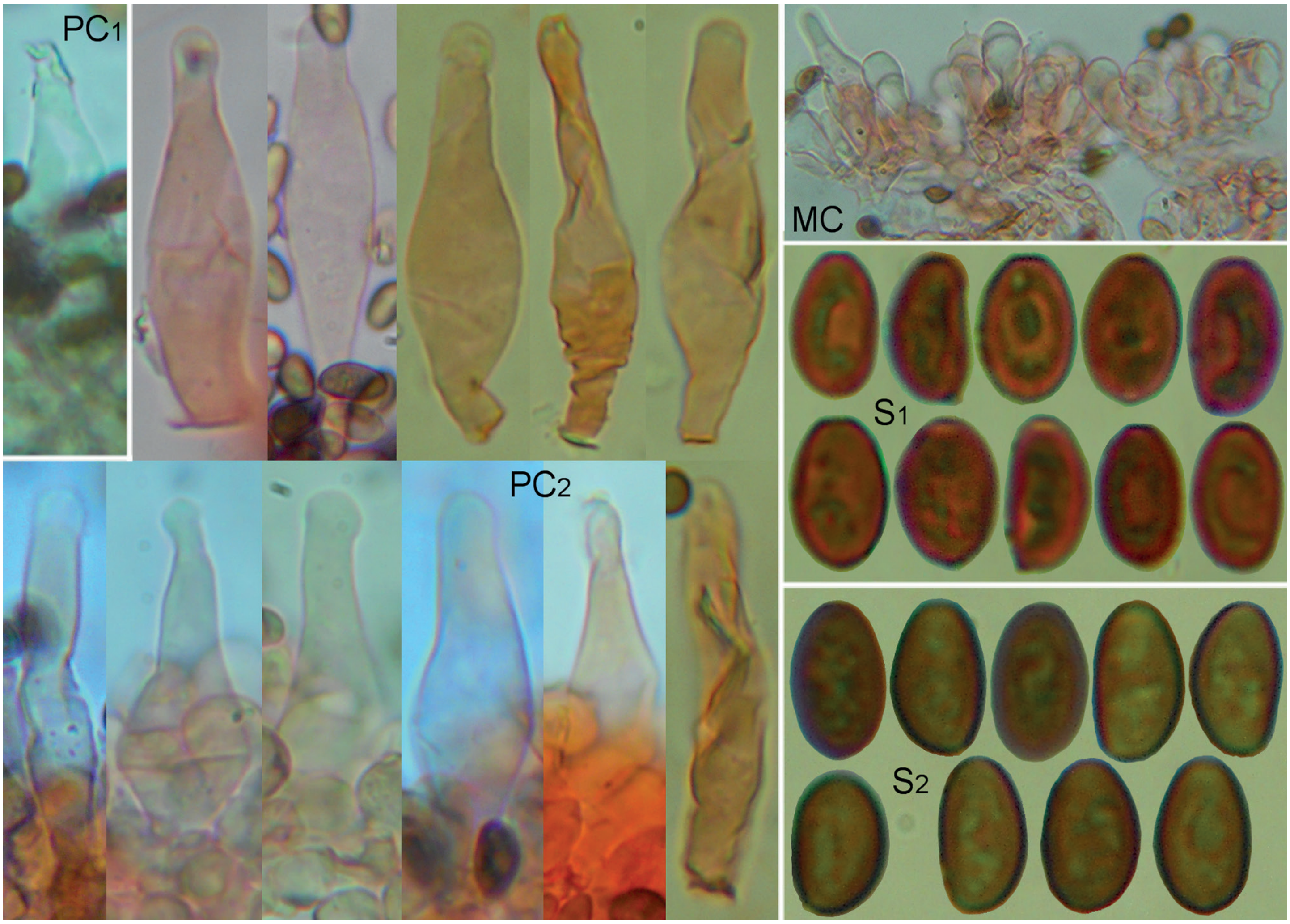


Fig. 63. *Psathyrella nitens*. A.H. Smith 29642, MICH33249; PC1 Pleurocystidium in NH_4OH; PC2 Pleurocystidia in Congo red; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

rarely forked, often incrusted; walls often weakly thickened and yellowish pigmented; numerous. *Cheilocystidia* 25–40(–50) × 8–15 µm, sometimes subacute, moderately numerous to scattered. *Paracystidia* –20 × –15 µm, sometimes mucronate, often incrusted, numerous.

Notes: On accurate observation of the holotype material it can be noticed that some debris of little twigs or grass stems are attached at the stipe base. We have found the ITS sequence in GenBank, unfortunately we have failed to add the *Tef-1α* region sequence.

Psathyrella psammophila is very close to the two following species, *P. subargillacea* and *P. angusticystis* (DNA nucleotide homology: ITS = 99 % with 4 and 1 mismatches respectively). A number of characters join these three taxa together such as small sporocarps, rudimentary veil, fragile context, pale colored and campanulate to broadly conical, never expanded, mature pileus, moderately crowded to distant (not distinctly crowded) gills, spore parameters in general including the little distinct germ pore, cheilocystidia generally sparse, paracystidia numerous but generally small, general feature of pleurocystidia. In all three cases we lack a second locus evidence; however, as we have found no relevant morphological difference, we consider both taxa conspecific with *P. psammophila*, the slightly paler spores of *P. angusticystis* being the only different element we could possibly point out in objection.

34a. *Psathyrella subargillacea* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 386. 1972.

Typus: *Psathyrella subargillacea* A.H. Sm. **USA**, Michigan, Luce Co., Tahquamenon Falls State Park, near Paradise, 23 Jun. 1963, *A.H. Smith*, 66717 (coll. *A.H. Smith & S. Brough*) (MICH12058), on rotten wood. ITS MF325999.

Loan for micro-morphology investigation of one almost entire pileus in good condition.

Spores (7.2–)7.5–9.5(–11.2) × 4.3–5.3(–6.2) µm, on average 8.5 × 4.9 µm, Q (1.55–)1.65–1.95(–2.15), avQ 1.75; in front view oval to elliptic, base subtruncate, rounded to obtuse (tapered in Smith's sketches), in profile adaxially flattened to subphaseoliform, sometimes subamygdaliform to phaseoliform; brownish to reddish orange; germ pore small and indistinct (callus). *Pleurocystidia* (30–)46–68 × (8–)10–17 µm; conical, subcylindrical, fusiform, sometimes ellipsoid, ellipsoid-mucronate, narrowly utriform, lageniform; apex 4–8 µm broad, obtuse, sometimes rounded, rarely subacute, sometimes subcapitate, rarely forked, sometimes weakly incrusted; walls sometimes weakly thickened below apex; moderately numerous. *Cheilocystidia* 25–48 × 7.5–17 µm, scattered to moderately numerous. *Paracystidia* –23 × –20 µm, sometimes rhomboid to mucronate, walls often pigmented and thickened, numerous. Cells below marginal cystidia weakly pigmented.

34b. *Psathyrella angusticystis* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 383. 1972.

Typus: *Psathyrella angusticystis* A.H. Sm. **USA**, Michigan, Emmet Co., Wilderness Point, Wilderness State Park, 24 Sep. 1953, *A.H. Smith*, 43146 (MICH11873), gregarious on debris in a clearing. ITS MF325959.

Loan for micro-morphology investigation of one sporocarp and a half cut lengthwise, both in good condition.

Spores (7.3–)7.7–9.3(–10) × 4.4–5.5(–6.2) µm, Q (1.45–)1.6–1.9(–2.05), avQ 1,74; in front view oval to elliptic, sometimes irregular, base rounded, in profile subphaseoliform to subamygdaliform; pale dull orangish; germ pore indistinct (callus). *Pleurocystidia* (30–)38–63 × 7–17 µm; narrowly utriform, fusiform, conical, sometimes cylindrical to ellipsoid, rarely thickly utriform; apex obtuse to subacute, rounded, rarely acute, often subcapitate, sometimes forked, rarely rostrate; often incrusted; walls sometimes weakly pigmented; numerous. *Cheilocystidia* 25–55 × 8–17 µm, often with subacute apex, incrustations not seen, scattered, towards margin of pileus numerous. *Paracystidia* 10–28 × 6–20 µm, incrusted, numerous, often dominating.

35. *Psathyrella incondita* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 405. 1972.

Since the holotype could not be obtained because of its scarcity, the MICH staff has selected two other collections Smith determined and deposited under this name. Our revision has evidenced they are unequivocally two different taxa: Harrison 10471 comes molecularly near *P. flexuosipes* and could represent the true *P. incondita*, Hoseney 1728 is distant from it. Both materials fall outside of section *Spadiceogriseae*.

35a. *K.A. Harrison* 10471, MICH36450.

?= ***Psathyrella incondita*** A.H. Sm.

Material examined: **USA**, Michigan, Marquette Co., Ives Lake, Loop Rd., 21 Jul. 1971, det. *Smith*, gregarious on elm wood, *K.A. Harrison* 10471, MICH36450. ITS MF325975.

Loan for micro-morphology investigation of two sporocarps and some fragments of pileus.

Spores (6.2–)7–8.7 × 3.3–4.4 µm, Q 1.8–2.45(–2.6), avQ 2–2.1; in front view cylindrical to oblong, sometimes irregular, base obtuse, in profile mainly subamygdaliform to subphaseoliform; pale reddish brown to brownish orangish; germ pore distinct, mainly truncate, ±1.5 µm broad. *Pleurocystidia* 33–64 × 10–16.5 µm; lageniform, ventricose-fusiform, conical, utriform, ellipsoid; apex 3.5–6.5 µm broad, subacute to obtuse, sometimes irregular to bent, often incrusted; numerous. *Cheilocystidia* (25–)35–50(–52) × 9–15 µm, often incrusted, moderately numerous, dominating. *Paracystidia* –25(–31) × –11 µm, more or less numerous. Cells below marginal cystidia hyaline.

35b. *F.V. Hoseney* 1728, MICH36451. Fig. 64.

=?

Material examined: **USA**, Michigan, Livingston Co., Hell, Fralick's Tree Farm, 28 Oct. 1970, det. Smith, under pines, *F.V. Hoseney* 1728, MICH36451. *Tef-1α* MF521795, ITS MF325976.

Loan of various sporocarps entire and in fragments for micro-morphology investigation.

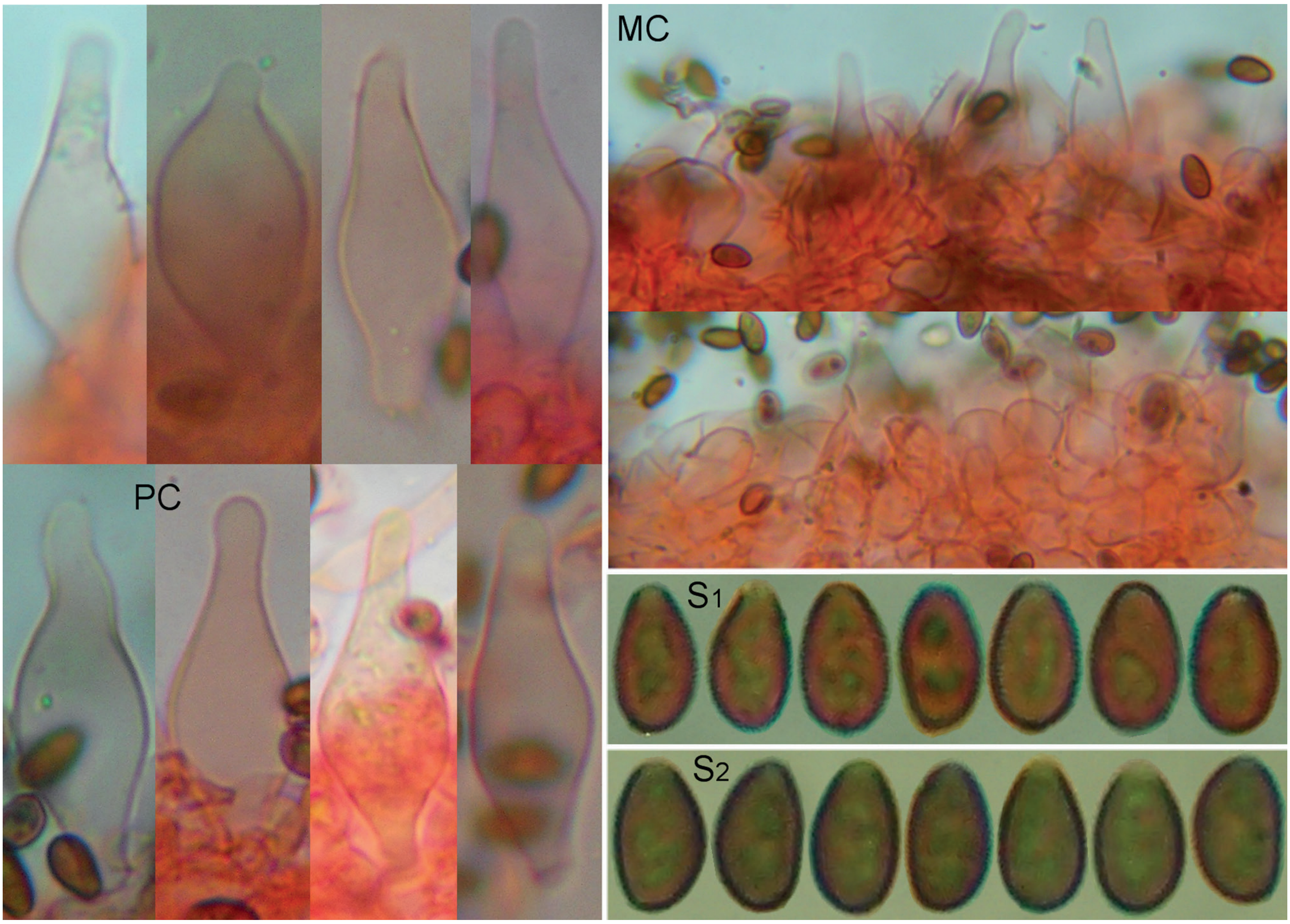


Fig. 64. *Psathyrella incondita.* F. V. Hoseney 1728, MICH36451; PC Pleurocystidia; MC Marginal Cystidia at centre of gill; S1 Spores in water; S2 Spores in KOH.

The notes of gross morphology by the collector report pileus 4.7 cm broad and stipe up to 5 mm thick at apex.

Spores (6.1–)6.8–8.1(–9.5) × (3.7–)4–4.8(–5.7) µm, on average 7.7 × 4.4 µm, Q 1.5–1.9(–2.05), avQ 1.7; in front view oval, sometimes oval-sublimoniform to triangular, base rounded, in profile subelliptic to adaxially flattened, amygdaliform to sublimoniform, sometimes oval; orange-brown; germ pore moderately distinct to indistinct, 1–1.2 µm broad. *Pleurocystidia* (23–)25–40 × (8–)10–15 µm; lageniform to broadly ventricose-lageniform, sometimes subutriform, sometimes flexuous towards apex; apex obtuse, sometimes subacute, submucronate, subcapitate, often incrusted; walls sometimes sub hyaline; scattered. *Cheilocystidia* 22–39 × (7.5–)9–15 µm, moderately numerous at centre of gill edge, more scattered elsewhere. *Paracystidia* –27 × –16 µm, sometimes rhomboid, hyaline, moderately numerous at centre of gill edge, inconspicuous elsewhere. Gill edge at centre with equal dominance of both types of cells or with locally alternate predominance. Cells below marginal cystidia hyaline.

Notes: The best reliable match when blasting the ITS region is with LO194-96 and LO164-96, two vouchers representing *P. squamosa*, with 99 % identity; when blasting the *Tef-1α* region none is above 90 % identity but it must be noticed that *Tef-1α* regions of the two aforesaid vouchers are not sequenced. However micro morphological characters do not fully correspond to those of *P. squamosa*.

36. *Psathyrella flexuosipes* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 145. 1972.

Paratype: *Psathyrella flexuosipes* A.H. Sm. **USA**, Oregon, Douglas Co., Lake Tahkenitch, 21 Nov. 1935, *A.H. Smith* 3578 (MICH32961), on debris. ITS MF325969.

Loan for gross morphology investigation of one sporocarp with a broken pileus.

Spores 7–9(–10) × 4.1–5.3 µm, Q (1.3–)1.5–2.1, avQ 1.7; in front view oval to elliptic, base rounded, in profile adaxially flattened, subamygdaliform, subphaseoliform; bright reddish; germ pore distinct, truncate to subrounded, 1.5–1.8 µm broad. *Pleurocystidia* 38–60 × 9–17 µm; fusiform-utriform, fusiform, ventricose-fusiform to ventricose-conical, sometimes (slenderly) utriform; apex obtuse, never acute or broadly rounded, often (grossly) incrusted; numerous to moderately numerous. *Cheilocystidia* 30–60 × 7.5–16 µm, sometimes minutely incrusted, numerous and generally dominating. *Paracystidia* 9–35 × 7–18 µm, sometimes submucronate, sometimes incrusted, walls sometimes or often thickened and yellowish pigmented, numerous and locally dominating.

Notes: We wanted to study this species because Smith (1972) did not specify the ratio between cheilocystidia and paracystidia but, unfortunately, MICH could not loan the holotype for scarcity of material. However, this paratype does not belong to subsection *Spadiceogriseae* and has no closely resembling counterpart in Europe.

37. *Psathyrella abieticola* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 348. 1972. Figs 65–66A (as *P. subnuda var. velosa*), 66B (as *P. vesiculocystis*).

Molecular heterotypical synonyms and misapplied names proposed here: *Psathyrella subnuda sensu* A.H. Smith, *Mem. N. Y. Bot. Gard*. **24**: 138. 1972, p.p.; *Psathyrella subnuda var. velosa* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 139. 1972; *Psathyrella vesiculocystis* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 349. 1972.

Pileus 15–40 mm broad, in early stages obtusely conical to convex with straight margin, expanding broadly conic to broadly convex or sub plane, moist or not; dark cinnamon-brown, rusty cinnamon, Mars brown, buckthorn brown, hygrophanous, fading to dull clay color, dingy tan, cinnamon buff, somewhat pale cinnamon-drab, brownish grey; translucently striate when moist. Veil white, quickly evanescent, when young with few thin patches of fibrils along the margin appendiculate fragments, thin and fibrillose on stipe. *Lamellae* adnate to ascending-adnate; narrow to moderately broad; moderately crowded; when young brownish to dingy cocoa-color, finally violaceous fuscous to dark vinaceous brown; edge white. *Stipe* 30–110 × 1–6 mm, equal or nearly so; white, watery white to pallid, not discoloring; apex pruinose. *Context* (very) fragile, thin in pileus, concolorous to surface. *Odor* and taste indistinctive. Spore deposit fuscous black. *Spores* (7–)7.7–10(–11.2) × (5–)5.5–7.2 × (4–)4.4–5.5 µm, fQ 1.3–1.6, pQ 1.5–2; in front view broadly oval, often or sometimes (irregularly) angular-oval, sometimes broadly elliptic, rarely subglobose, triangular, oboval or mitriform, base obtuse to broadly rounded, sometimes truncate, apex often attenuate to sometimes snout-like projected, in profile subelliptic to adaxially flattened, rarely subamygdaliform, oval or subphaseoliform; dusky brown with a reddish to orange-red shade; germ pore distinct, mainly truncate, sometimes somewhat oblique in profile, 1.6–2(–2.5) µm broad. *Basidia* 4-spored, 17–25 × 6–11(–11.8) µm. *Pleurocystidia* 33–60(–65) × 9–20 µm, broadly utriform to subcylindrical, often or sometimes ellipsoid-saccate to subclavate, sometimes sublageniform; apex broadly rounded to obtuse, rarely subcapitate, rarely incrusted; walls hyaline, sometimes thickened below apex; moderately numerous, rarely numerous. *Gill edge cystidia* 8–33(–48) × 4.5–19(–25) µm, a mixture of three types of cystidia: distinctly utriform to sometimes sublageniform, 25–33 × 12–13 µm, usually scattered; ellipsoid to rhomboid, 21–29 × 10–17 µm, numerous; saccate to clavate, 9.5–30 × 6–17 µm, numerous. *Caulocystidia* up to 140 × 20 µm, utriform to clavate. Clamps present.

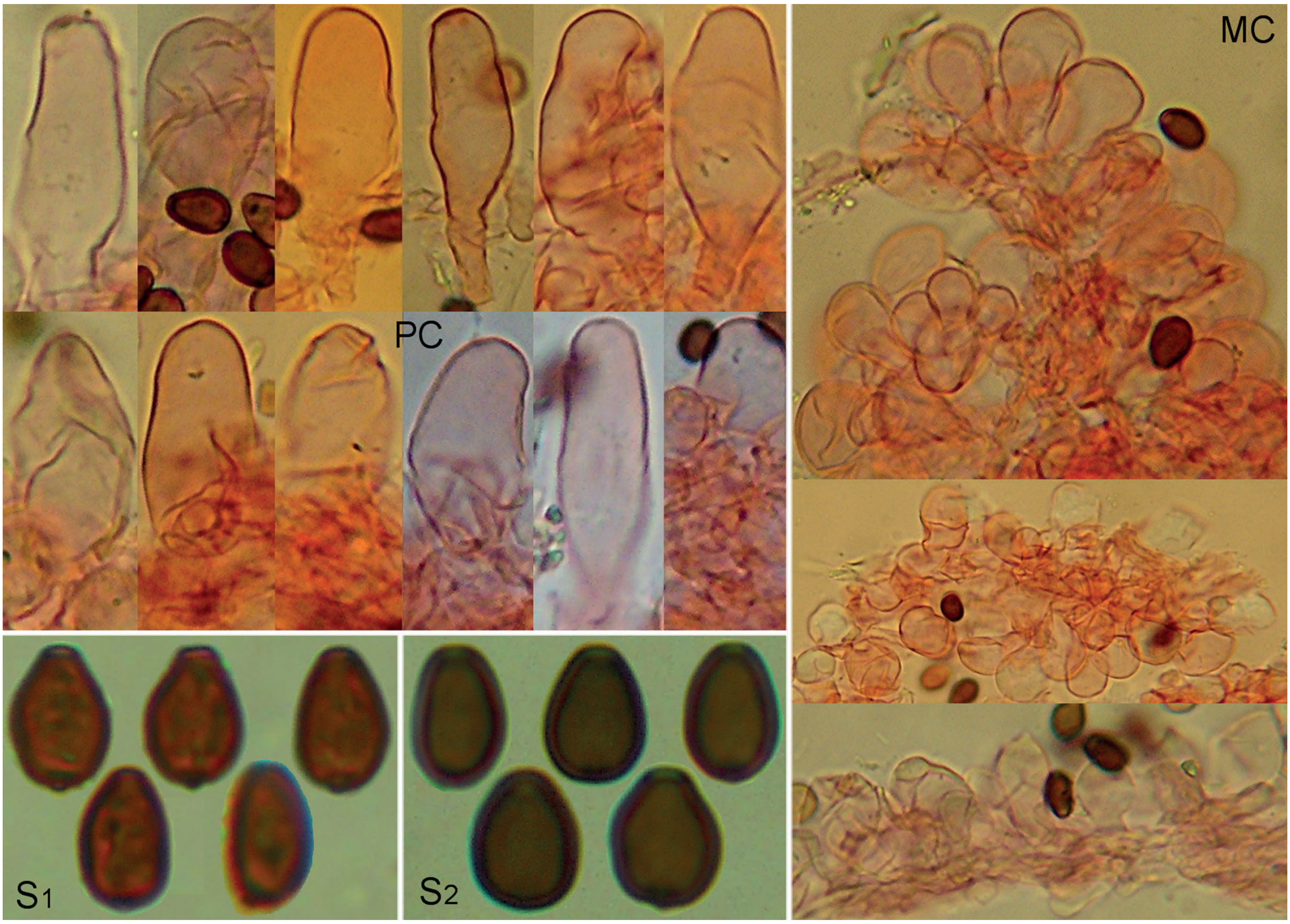


Fig. 65. *Psathyrella subnuda var. velosa.* F. P. Sipe, 1100, MICH33441; PC Pleurocystidia; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

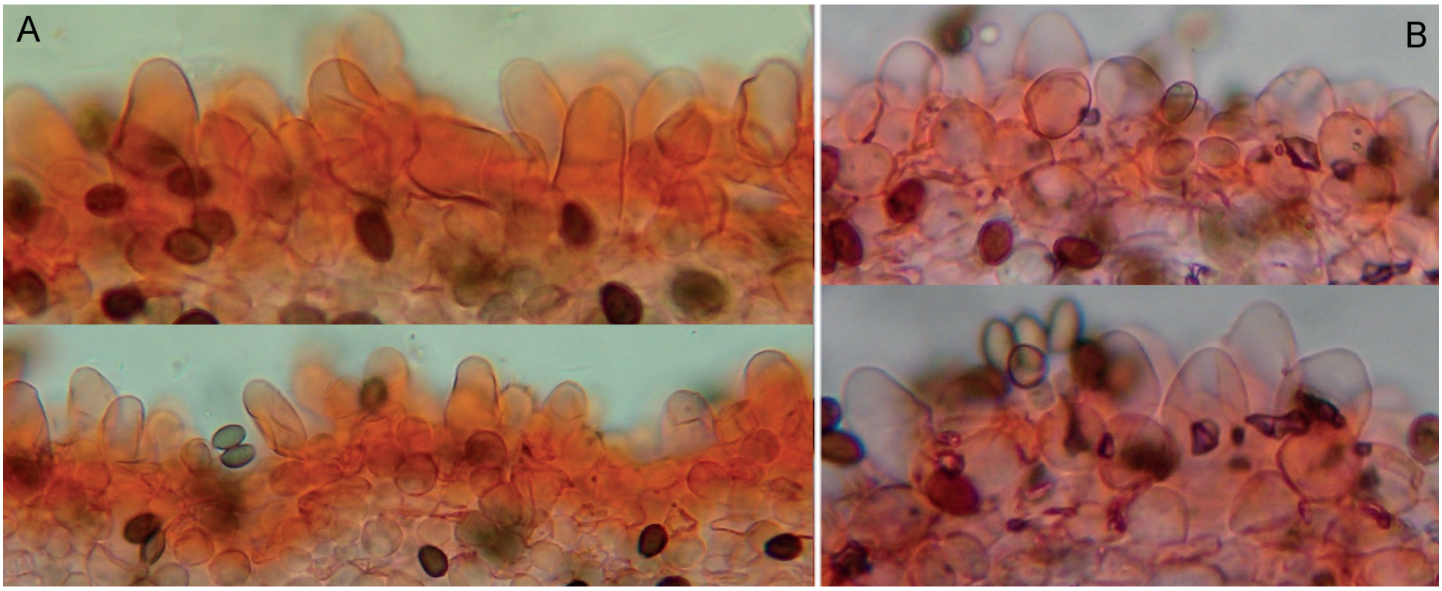


Fig. 66. A. *Psathyrella vesiculocystis*. A.H. Smith & H. D. Thiers 70089, MICH5380; Marginal Cystidia. **B.** *Psathyrella subnuda*. A.H. Smith 56936, MICH33421; Marginal Cystidia.

Habitat: Gregarious or scattered; on humus of cottonwood or conifer, once on burned soil.

Collections examined from MICH: *Psathyrella subnuda sensu* A.H. Smith, *Smith* 56936; *Psathyrella subnuda var. velosa* A.H. Sm., **holotype**, *Smith* 73947; *Psathyrella vesiculocystis* A.H. Sm., *Smith & Thiers* 70089.

Notes: The full description above comprises our revision and Smith's (1972) description of all taxa we acknowledge as conspecific, with exclusion of Smith's (1972) description of *P. subnuda*. The presence of many pleurocystidia not distinctly utriform but subcylindrical, ellipsoid-saccate to subclavate makes the gill edge cystidial pattern highly composite and a neat distinction between cheilocystidia and paracystidia hardly applicable. Sometimes the intermediate marginal cells are very small and can be ambiguously confused with the surrounding paracystidia, making these latter seem dominating.

We have not examined material of *P. abieticola,* but we have found strong molecular correspondence between *P. vesiculocystis*, *P. subnuda var. velosa*, and the holotype of *P. abieticola* present in GenBank (accession nr. KC992891). According to Smith's (1972) description, we see a good overlap of the morphological data, including the tridimensional, strongly oval to angular-oval spores with truncate base and attenuate to snout-like projected apex. For comments on *P. subnuda sensu* Smith see below.

Psathyrella fusca is a common, relatively similar European species but it is clearly not conspecific based on strong molecular evidence and very different spores.

37a. *Psathyrella subnuda var. velosa* A.H. Sm., *Mem. N. Y. Bot. Gard.* **24**: 139. 1972. Fig. 65.

Typus: *Psathyrella subnuda var. velosa* A.H. Sm. **USA**, Idaho, Bonner Co, Tule Bay, Priest Lake, 5 May 1966, *A.H. Smith* 73947 (MICH5376), on debris in cottonwood flat; only for molecular sequence. *Tef-1α* MF521773, ITS MF326005.

Paratype studied: *Psathyrella subnuda var. velosa* A.H. Sm. **USA**, Oregon, Pruetts place, 20 Nov. 1949, *F.P. Sipe*, 1100 (det. *Smith*) (MICH33441), habitat not reported. ITS MF326006.

Loan for micro-morphology investigation of very tiny fragments, the largest measuring 2 mm.

The notes from the collector report a pileus 3–4 cm broad, conical, smooth, light cinnamon drab, expanded when older, without surface structures; stipe white, fragile gills drab with white edge; spores up to 10 × 7 µm, reddish, dark with violet tints in deposit. *Spores* 8.2–10(–10.7) × 6–7.1 × 4.8–5.5 µm, fQ 1.3–1.5, pQ 1.6–2; in front view oval, triangular, angular-oval to mitriform, base truncate to broadly rounded, apex often attenuate to sometimes snout-like projected, in profile subelliptic to adaxially flattened, dusky brown with an orange-red shade; germ pore distinct, mostly truncate, sometimes somewhat oblique in profile, 1.6–2 µm broad. *Pleurocystidia* 33–55 × 12–20 µm, broadly to cylindrical utriform or ellipsoid-saccate, apex broadly rounded, sometimes obtuse; walls hyaline, sometimes thickened; moderately numerous. *Gill edge cystidia* 10–33 × 7–16(–19) µm, a mixture of scattered distinctly utriform cells, scattered obtusely fusoid cells and numerous, small to large, saccate to clavate cells.

Notes: We could only observe scattered little traits of gill edge and we believe that most utriform and, overall, fusoid marginal cells must have collapsed, at least in their apical part, given the badly fragmented state of the material received.

37b. *Psathyrella vesiculocystis* A.H. Sm., *Mem. N. Y. Bot. Gard*. **24**: 349. 1972. Fig. 66A.

Typus: *Psathyrella vesiculocystis* A.H. Sm. **USA**, Idaho, Idaho co, French Creek Grade, Salmon river near Burgdorf, 4 Sep. 1964, *A.H. Smith & H.D. Thiers* 70089 (MICH5380), gregarious on conifer duff. *Tef-1α* MF521772, ITS MF326007.

Loan of one sporocarp and one pileus in good condition for micro-morphology investigation.

Spores 7.8–9.8 × (5–)5.5–6.5(–7) × (4–)4.5–5.5 µm, fQ 1.3–1.55, pQ 1.6–2; in front view oval to subangular-oval, base obtuse to broadly rounded, sometimes truncate, apex often attenuate to snout-like projected, in profile adaxially flattened; dusky brown with an orange-red shade; germ pore distinct, mainly truncate, sometimes somewhat oblique in profile, 1.6–1.8 µm broad. *Pleurocystidia* 37–60 × 12–20 µm, broadly utriform, subcylindrical to subclavate, apex broadly rounded; walls hyaline; moderately numerous. *Gill edge cystidia* 8–48 × 4.5–18 µm, a mixture of some distinctly utriform cells and numerous, dominating, small to large, saccate, clavate and subellipsoid cells in variable number.

Notes: Smith (1972) detected some broader cheilocystidia, up to 25 µm broad, and reported occasional subechinulate protrusions near the apex of pleurocystidia. These last however are only the deceptive optical result of inwardly collapsed thin-walled apices sometimes leaving a rugged or spiked crater; this occurrence has been observed also in the following collection, Smith 56936 (*P. subnuda sensu* A.H. Smith).

37c. *Psathyrella subnuda* (P. Karst.) A.H. Sm., *Contr. Univ. Mich. Herb*. **5**: 61. 1941.

We have attempted to understand Smith's (1972) concept of *P. subnuda* by examining the voucher Smith 56936 selected for this purpose by MICH staff. We have found a sufficiently good correspondence, both morphological and molecular, with *P. abieticola*. This result does not necessarily apply to the other vouchers Smith deposited in MICH under this name. The basionymous name *Psathyra subnuda* P. Karst. *sensu* auct. Eur. is generally associated to *P. spadiceogrisea*. Kits van Waveren (1985), and Romagnesi, in personal communication to him, considered it extremely dubious.

Smith 56936, MICH33421. Fig. 66(b).

= ***Psathyrella abieticola***

Material examined: **USA**, California, Humboldt Co., Trinidad, 22 Dec. 1956, on burned soil, *Smith* 56936, MICH33421. *Tef-1α* MF521778, ITS MF326000.

Loan of one sporocarp in good condition with pileus and stipe separated for micro-morphology investigation.

The notes of gross morphology by the collector report pileus mars brown, veil absent, stipe dull white and not darkening. *Spores* (7.2–)7.7–10(–11.2) × 5.2–7.2 × 4.4–5.5 µm, fQ 1.3–1.6, av. fQ 1.45, pQ 1.5–1.8 (1.9), av. pQ 1.6; in front view oval, broadly elliptic, sometimes (irregularly) angular-oval, rarely oboval, base obtuse to rounded, rarely subtruncate, apex attenuate or not, rarely snout-like projected, in profile adaxially flattened, rarely subphaseoliform; dusky reddish brown; germ pore distinct, mainly truncate, sometimes somewhat oblique in profile, 1.6–2(–2.5) µm broad. *Pleurocystidia* 33–55 × 11–17 µm; utriform to subcylindrical, sometimes sublageniform; apex rounded, sometimes subcapitate; walls hyaline, sometimes thickened; moderately numerous. *Gill edge cystidia* 9.5–33 × 6–17 µm, a mixture of three types of cells: distinctly utriform to sublageniform, 25–33 × 12–13 µm, scattered; ellipsoid to rhomboid and 21–29 × 10–17 µm, numerous; saccate to clavate and 9.5–30 × 6–17 µm, numerous.

38. *Psathyrella infida* Quél., *Bull. Soc. bot. Fr*. **23**: 329. 1877. Figs 67–69.

Pileus 10–20 mm broad, in early stages conical-campanulate and umbonate with inflexed margin, finally convex and subumbonate or not, radially rugulose in old sporocarps; when young dark to blackish brown, hygrophanous, discoloring reddish to ochraceous brown, at centre remaining for a time so then fading to ochre, in periphery fading to white, at margin keeping for a time an ochre-brown color often with a pinkish tint; translucently striate when moist. *Veil* white, already reduced to scarce or absent on most pilei but still present as small to large flocks on some young pilei (see Fig. 62, at the centre) and as small tufts on lower half stipe. *Lamellae* adnate, broad, not or little ventricose, distant (about 16–18); greyish then purplish grey or with brownish tinge; edge pale, reddish towards margin of pileus. *Stipe* 18–40(–55) × 1.8–2.5 mm, cylindrical, often flexuous; concolorous with pileus, hygrophanous, discoloring white to translucent-hyaline in upper half, pale to subconcolorous with pileus in lower half; apex apparently not pruinose, base sometimes with appressed mycelium. *Spores* (10.5–)11–13.7(–15) × (5.2–)6.2–7(–8) µm, on average 12–12.5 × 6.4–6.6 µm, Q (1.7–)1.75–2(–2.2), avQ 1.85–1.9; in front view elliptic, base obtuse, in profile elliptic to subamygdaliform, sometimes adaxially flattened to narrowly limoniform, apex sometimes snout-like projected; dark brown; germ pore distinct, truncate, 1.5–2 µm broad. *Basidia* 4-spored, 11.5–12.5 µm broad. *Pleurocystidia* 23–63 × 11.5–16(–22) µm, fusiform to lageniform, rarely utriform or conical; neck short and more or less rostrate to long, sometimes flexuous; apex subacute, rarely obtuse; moderately numerous. *Cheilocystidia* –50 × 11–15 µm, scattered to locally moderately numerous. *Paracystidia* 15–40 × 9–20(–29) µm; walls often thickened, hyaline to slightly pigmented towards base; numerous and dominating. Cells below marginal cystidia yellow-brown to pale yellow-brown pigmented. Clamps present.

Habitat: Gregarious to cespitose; among moist grass of alluvial plain near river bank with *Salix alba* trees and various hygrophilous plants.

Collection examined: **Italy**, Vicenza, Trissino, near the river Guà, on moist soil with deciduous trees, 28 Mar. 2013, *O. Chiarello* (det. *P. Voto*), MCVE29119. *Tef-1α* MF521794, ITS MF325977.

Notes: We base our concept of *P. infida* on Romagnesi as he studied French material and is presumably the most reliable in understanding Quélet's short diagnosis. Therefore we refer to Kits van Waveren's (1985) description as he reports a full description received from Romagnesi and adds one's own microscopical observations of an exsiccatum received by the same French mycologist.

Kits van Waveren (1985) cites a description by Einhellinger (1973) but that German material is reported as having larger spores and 2(1)-spored basidia thus suggesting it may represent *P. prona*.

The above description of our collection fits well with that by Kits van Waveren (1985). The main features of this species are large dark spores, fusiform to lageniform pleurocystidia, small sporocarps, distant and broadly adnate to triangular gills, strongly developed but evanescent flocculose veil, pileus possibly drying with pinkish shades at margin, gill edge possibly

Fig. 67. *Psathyrella infida*. MCVE29119. Photo O. Chiarello.

Fig. 68. *Psathyrella infida*. MCVE29119. Photo O. Chiarello.

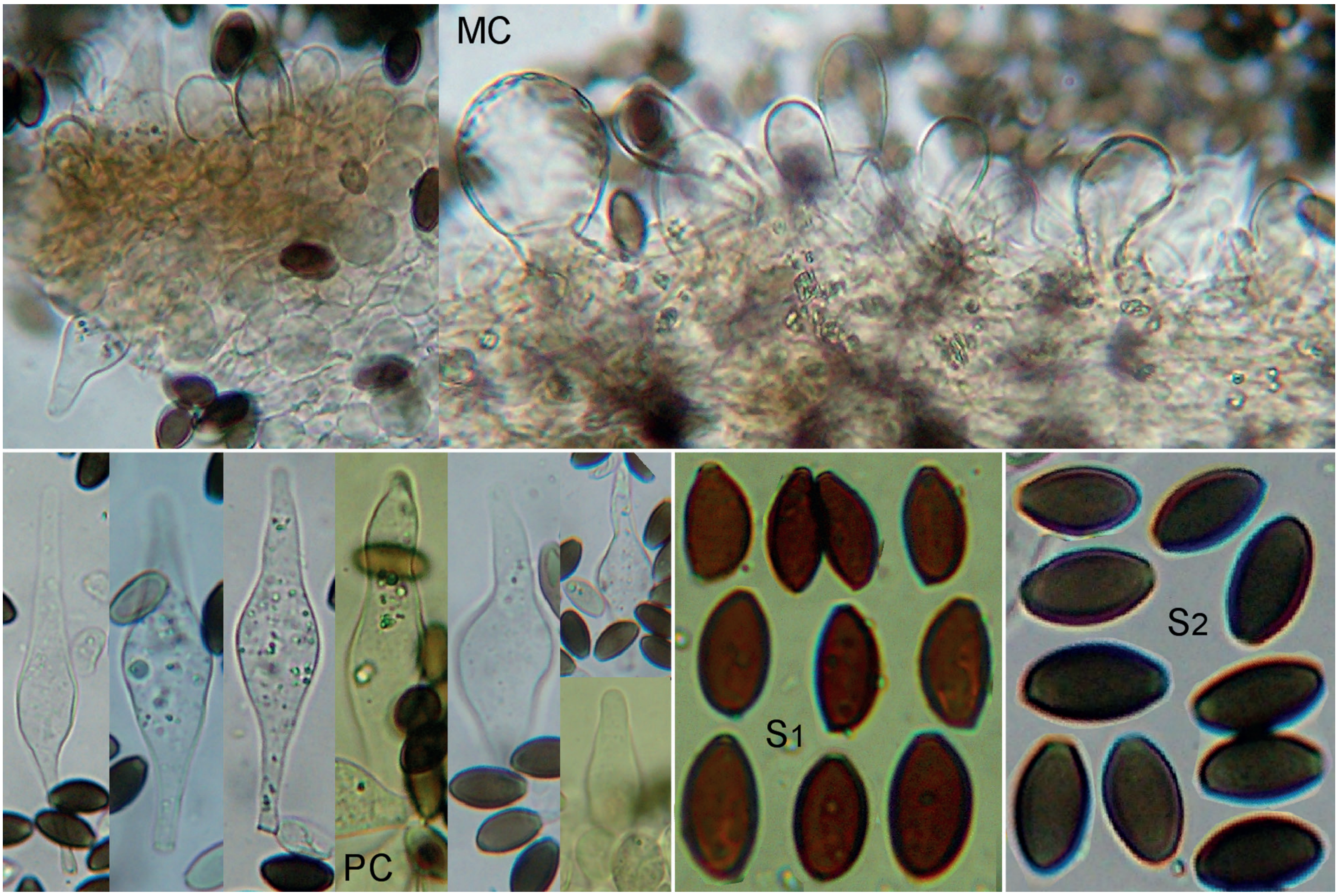


Fig. 69. *Psathyrella infida*. O. Chiarello, MCVE29119; MC Marginal Cystidia in KOH; PC Pleurocystidia; S1 Spores in water; S2 Spores in KOH.

reddish pigmented, habitat associated to deciduous trees in moist to dry soil.

From a morphological perspective, various species are very similar, the closer allies among them are *P. romagnesii*, which has more distant gills and smaller sporocarps, *P. orbicularis*, which has the gill edge dominated by cheilocystidia, *P. orbitarum*, which has smaller spores on average.

The ITS sequence of our sample is very similar to that of *P. tenera* found in GenBank (DNA nucleotide homology: ITS = 99 % with 7 mismatches). It shares the moist habitat and many morphological characters (for micro-characters of *P. tenera* we refer to Smith 1972, and to Örstadius *et al.* 2015 who both have revised Peck's type). However, there are two relevant elements of differentiation given by the spores which are distinctly shorter and have consequently a lower quotient and by the gill edge which is markedly dominated by small to large paracystidia intermixed with generally scattered cheilocystidia. Unfortunately only the ITS region sequence is available in GenBank for *P. tenera*; however, until a second locus contradicting evidence should emerge, we consider this collection a consistent representative of *P. infida* and a good species in its own right.

39. ***Psathyrella bivelata*** Contu., *Bull. Soc. Mycol. Fr.* **107**: 86. 1991. Figs 70–73.

This species is very close to *P. candolleana* from which it differs for having larger spores, (6.5–)7.5–12.5(–15) × (4.2–) 4.5–6.7(–7.5) µm, on average 9–9.5 × 5–5.5 µm, of a medium to somewhat pale reddish brown color and with presence of some 2-spored basidia. The habitat of *P. bivelata* is, at least as up to now ascertained, herbicolous and possibly associated to nitrogen-rich soil but we cannot exclude it could also be detriticolous on woody humus outside of woods. However, two peculiar characters bond both species together: the presence of a strong stripped incrustation on the pileal general veil cells and the broadly ellipsoid to globose shape of a number of the same cells, this last character possibly more emphasized in *P. bivelata*. In gross morphology these two characters produce a tendency of the general veil to turn brownish, or even to be so already in young specimens, and to reduce itself to little flocks.

After its original collection in Sardinia, Italy, in 1989 a long period of oblivion followed, until it was found for a second time in 2006, again in Italy, precisely in Veneto. Since then, we have identified this species in other collections from the same region. The first Veneto collection including images was fully described by Voto (2007), although images of the type were not included in the protologue. Due to the fact that CAG, where the type is hosted, does not loan any material, we have now provided a reference sequence for that collection and we have re-deposited it as MCVE29104. More illustrations are in Voto (2013) (under the name of *P. candolleana*, voucher D030208, now MCVE29117) and Voto (2011). More images from the Veneto collections are in this paper, including two additional illustrations of MCVE29104.

Materials examined: **Italy**, Veneto, Rovigo, Villadose, 3 m a.s.l., gregarious in grass in garden, 10 Nov. 2005, *P. Voto*, Fig. 70, 71 (MCVE29104, *Tef-1α* MF521812, ITS MF325961); at same location, 6 May 2006; at same location, 28 May 2006, at same location, 6 Jun. 2006; Rosolina Mare, 0–1 m a.s.l., gregarious in grass in garden, 10 Nov. 2007, *P. Voto*, Figs 72, 73 (MCVE29330); Vicenza, 39 m a.s.l., caespitose in grass in urban flower bed near a *Platanus*, 27 May 2012, *E. Zanella* (MCVE29117, former Voto D030208, *Tef-1α* MF521811, ITS MF325962).

40. ***Psathyrella yaoundeana*** Mossebo & Pegler, *Kew Bulletin* **53**: 1001. 1998. Fig. 74.

Typus: *Psathyrella yaoundeana* Mossebo & Pegler. **Cameroon**, Yaoundé, Cité-Verte, 30 Oct. 1996, *D.C. Mossebo* 42B (K(M)55648), among grass.

Loan of two entire sporocarps somewhat mouldy for micromorphology investigation.

The authors described this taxon as provided with frequent, obtusely ventricose-lageniform to broadly fusoid pleurocystidia (utriform with rounded to obtuse apex by their sketched illustration and following our terminology) and with a mixture, without frequency ratio, of obtusely clavate, utriform to sublageniform cells on the gill edge. These data made it an eligible species of subsection *Spadiceogriseae* and the authors themselves commented that it most closely approached *P. spadiceogrisea*. In our revision we could find no pleurocystidia but we noticed that various cheilocystidia, dislodged by pressure on the coverslip, floated and casually anchored themselves on the gill sides. Cheilocystidia are about 21–37 × 12–17(–22) µm large, the gill edge has the typical pattern of that of *P. candolleana* with absent to very inconspicuous paracystidia. Spores (6.2–) 6.5–8.5(–9.8) × (3.7–)4.2–5(–5.5) µm, Q (1.4–)1.6–2, avQ 1.7

Fig. 70. *Psathyrella bivelata*. MCVE29104. Photo P. Voto.

Fig. 71. *Psathyrella bivelata*. MCVE29104. Photo P. Voto.

Fig. 72. *Psathyrella bivelata*. Voto20071109.2. Photo P. Voto.

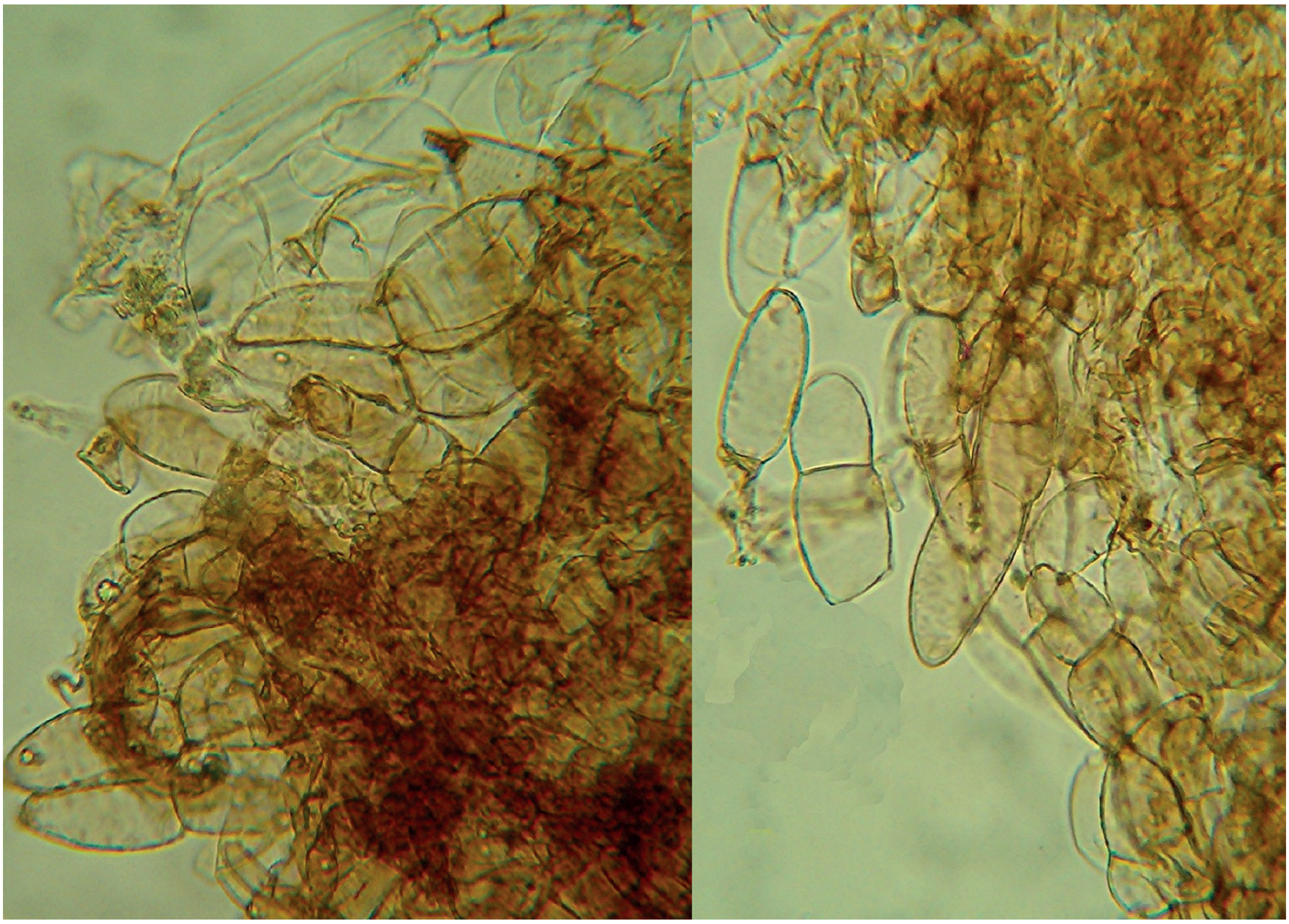


Fig. 73. *Psathyrella bivelata*. Voto20071109.2; Cells of general veil on pileus in Congo red.

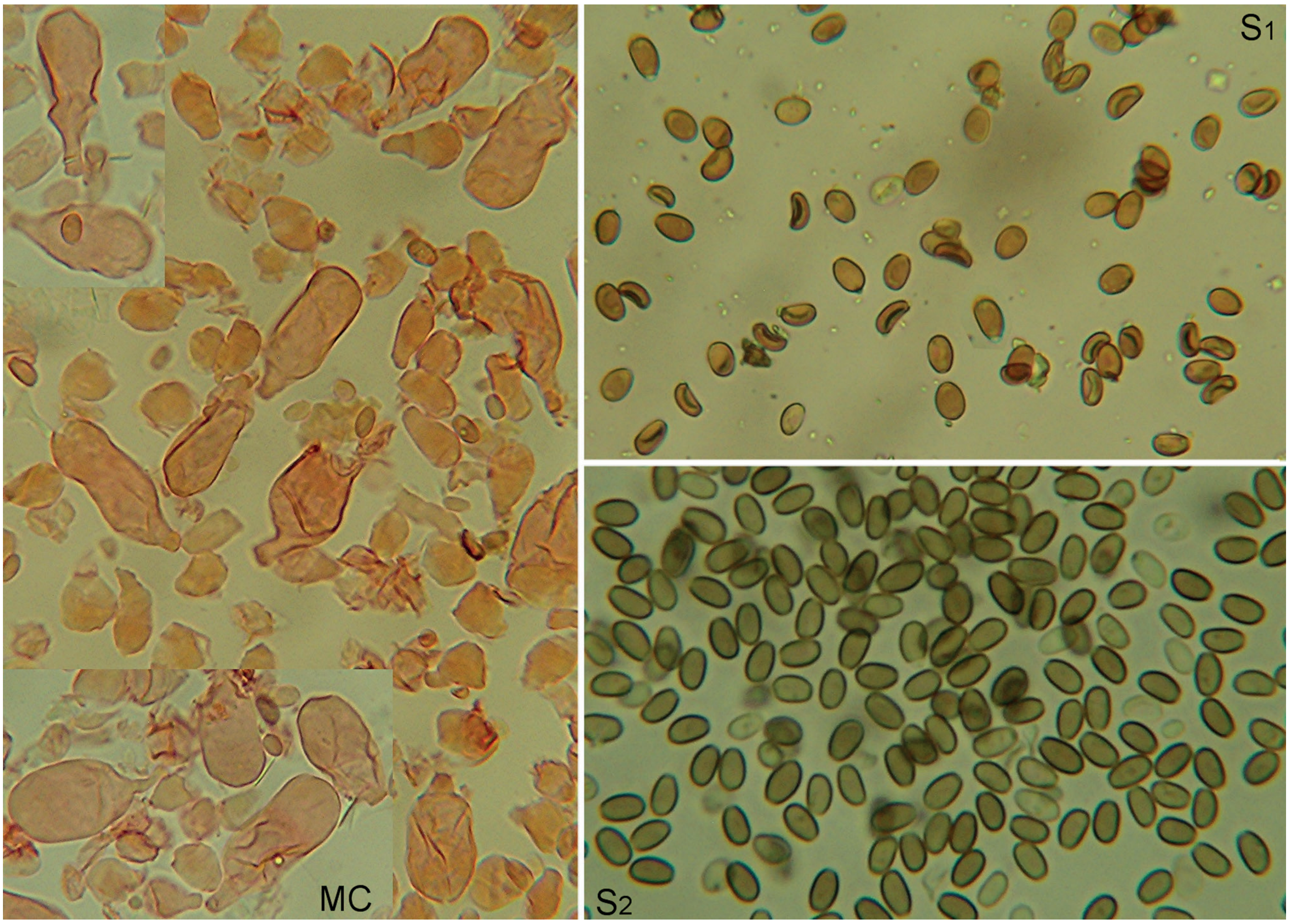


Fig. 74. *Psathyrella yaoundeana*. Mossebo 42B, K(M)55648; MC Marginal Cystidia; S1 Spores in water; S2 Spores in KOH.

[we have also found a number of broader spores, up to 5.7(–6.3) µm with Q 1.3–1.5], in front view elliptic to oval, base rounded, in profile mainly adaxially flattened to subphaseoliform, sometimes phaseoliform to elliptic; pale brown with a vague reddish shade; germ pore distinct, rounded, 1–1.7 µm broad.

We failed to obtain the ITS sequence and only obtained a dirty unusable sequence of the *Tef-1α* region from this sample; however, on the whole, we are convinced this material belongs to section *Spintrigerae*.

Phylogeny

The ITS alignment included 673 characters, and contained 380 (56.5 %) variable sites; the *Tef-1α* alignment included 607 characters, and contained 335 (55.2 %) variable sites; the concatenated ITS and *Tef-1α* alignment included 1 281 characters, and contained 679 (52.0 %) variable sites. The partition of homogeneity tests found no conflicts between the ITS and the *Tef-1α* alignments. Both Maximum Likelihood and Bayesian analyses produced the same tree topologies. Only the Bayesian trees with posterior probability and bootstrap values are shown. The most significant differences between the ITS (Fig. 1) and the *Tef-1α* (Fig. 2) trees were mostly due to variation in the list of taxa covered by each, due to failed sequencing of one of the loci for some samples. The concatenated ITS-*Tef-1α* tree was characterized by higher statistical support of its branches, and can be used to infer the overall phylogenetic relationships among the *Psathyrella* samples analyzed. In the concatenated tree, *Psathyrella* samples were all placed in a monophyletic group containing several statistically supported clades, including a clade representative of the subsection *Spadiceogriseae*. The *nitens* clade is placed as the closest relative to the *spadiceogrisea* clade, while the *candeollana* clade appears as the most distantly related to the *spadiceogrisea* group, at least among the taxa include in this analysis. Refer to the tree in the Supplementary Fig. 1 for a better coverage of species to identify the closest relatives to the *spadiceogrisea* group. In an intermediate position between the *nitens* and the *candeollana* clade, the analysis identified a clade including the three subclades *fusca*, *piluliformis*, and *gordonii* and the two taxa *P. incondita* and *P. cortinarioides*. *Psathyrella infida* was a solitary taxon outside all of the clades and subclades identified by this analysis.

The *spadiceogrisea* group was further subdivided in nine strongly supported groups, identified in Fig. 3 by the following subclades: *albescens, thuijna, hellebosensis, fatua, owyheensis, praetenuis, umbrosa, albanyensis, spadiceogrisea*. These nine subclades provide a strong and exhaustive framework to understand the evolution of species within the section *Spadiceogriseae*, and to differentiate between potential gross misidentifications (taxa falling in different subclades), and nomenclature issues caused by the close relatedness of sister taxa (taxa falling within the same subclade) possibly due to the lack of distinctive morphological traits. Besides the limited morphological variation when comparing closely related taxa, the composition of taxa within each subclade may be associated with geographic range and/or with habitat.

Pairwise genetic distances within clades were in general low [ITS (0.000)<u>0.006</u>(0.020), *Tef-1α* (0.000)<u>0.007</u>(0.020); (min)<u>average</u>(max)], even for morphologically distinct species, and five clades included both North American and European species suggesting either a recent evolutionary divergence, or a dynamic phylogeographic history resulting in the intercontinental movement of species. No distinctive morphological trait was associated with clades, except for the *albanyensis* clade characterized by dark, often tridimensional spores, and with a little to moderately distinct germ pore. Clades though did differ in habitat association as follows. Clades *spadiceogrisea* and *albanyensis* were found in association with woody substrates, even in the case of *P. clivensis*, which apparently grows in grasslands but is also associated with woody debris. Clades *umbrosa* and *praetenuis* appeared to be intermediate and include both lignicolous and non-lignicolous species. All remaining clades seemed to be distinctively more detached from woody substrates and included species growing in grasslands or in “specialized” habitats such as wetlands populated by hygrophilous plants (*e.g. P. thuijna*), and sandy substrates (*P. ammophila*).

In spite of the fact that the bulk of the sequences of the largest dataset came from the published study by Örstadius *et al.* (2015), the concatenation of *Tef-1α* and ITS failed to meet the requirements of the partition of homogeneity tests. Nonetheless, we opted to provide the phylogenetic tree resulting from this larger dataset in the supplementary materials (Supplementary Fig. 1). The resulting tree has in fact the convenience of being directly comparable with that of Örstadius *et al.* (2015), of including a larger number of taxa within and outside the section *Spadiceogriseae*, and of allowing for a relative placement of the group within the genus. Once again, the *spadiceogrisea* group results as monophyletic and includes nine well supported clades. Three species, namely *P. sublatispora*, *P. prona* and *P. jacobssonii*, made up an additional clade that - based on ITS analysis - could be regarded either as part of the same group, or as a sister clade to the subsection (Fig. 1).

Based on morphology and molecular analyses combined, this study describes a new species (*P. rogersiae*), renames three species (*P. vesiculosa*, *P. ochrofulva*, *P. sanjuanensis*), identifies as present in Europe two taxa previously described only in North America (*P. albescens*, *P. kauffmanii*), resolving the related nomenclature issues, and suggests the possible presence in Europe of a third American species (see notes about *P. velibrunnescens* and *P. aff. kauffmanii*). Five species of uncertain status were fully validated (*P. bivelata*, *P. carinthiaca*, *P. fragrans*, *P. infida*, *P. aff. kauffmanii*).

The analysis of the holotypes of *P. fusca*, *P. spadiceogrisea*, *P. agrariella*, *P. atrifolia* and *P. subnuda* is still missing, however the combined DNA and morphological analysis of non-typical vouchers (Smith 1972) reveals that Smith may have had an ambiguous concept of these species. In particular, the last three species remain dubious. Likewise, the analysis of the holotypes is still missing for *P. niveobadia*, *P. phaseolispora* and *P. agraria ad int.*, three European taxa Smith never studied; the latter two species remain dubious while we propose a provisional solution for the first.

Finally, in this study we have identified 13 heterotypical synonyms (see Table 1). All of the specific taxonomic contributions of this paper are listed in Table 1. We have previously discussed our approach with regards to how DNA sequence information was used to confirm or contest species boundaries, especially when morphology was insufficient to make that call. In brief, while DNA homology < 97 % was used with confidence to identify distinct taxa, highly homologous sequences (> 98 %) cannot be used by themselves to exhaustively determine conspecificity, because of possible transfer of alleles between species, especially if closely related. High DNA homology at one locus can though be used to support conspecificity if such conspecificity is further suggested by homology at another locus, morphology, habitat, and geographic range. We have regarded homology levels of 97 % and 98 % as border-line, and looked for non-synonymous polymorphisms in exonic regions (DNA variation resulting in a variation in aminoacids transcribed) or for indels (insertion or deletions) in intronic regions to suggest the evolutionary significance of this relatively small variation in DNA sequences. Individual species description drew on such DNA-based comparisons when needed.

DISCUSSION

A first clue of monophyly of the subsection *Spadiceogriseae* supported by molecular evidence was provided in Vašutová *et al.* (2008), though based only on three vouchers. The parsimonious tree in Örstadius *et al.* (2015) show that such monophyly is confirmed when applied to a wider European range of species. The results obtained through the present work confirm the monophyly of a joint clade *spadiceogrisea* in Europe and America, with four cases that need be discussed in detail.

a) *P. umbrosa* has paracystidia which, although dominating the gill edge, are mainly unusually small and intermixed with numerous basidia and basidiola;
b) *Psathyrella* sp. (NL-0631) is described as having scattered cheilocystidia and very scattered paracystidia;
c) *P. ochrofulva* (and *P. lactobrunnescens*, if indeed it belongs to the clade *spadiceogrisea*) has often fusiform to conical pleurocystidia equipped with highly variable, mainly obtuse, apex, which is unusual in comparison to usually utriform to lageniform cystidia with mainly rounded apex;
d) *P. aff. kauffmanii* and *P. vesiculosa* are outside of the clade *spadiceogrisea* but are morphologically associated to the subsection *Spadiceogriseae*. However, it can be noted that they, together with the unsequenced *P. velibrunnescens*, are characterized by a distinctly pigmented veil, which is otherwise unknown in this group. From this last cited case we infer that a white veil must be included among the morphological parameters defining the subsection *Spadiceogriseae*.

Based on morphological analysis and on sequence data from both ITS and *Tef-1α,* nine statistically well-supported clades comprise the subsection *Spadiceogriseae*. ITS data alone identified an additional clade including *P. prona*, *P. sublatispora*, and *P. jacobssoni* that, although rather distantly related to the other clades, could be regarded as being included in the subsection. However, these three taxa were not included in this study, and therefore no direct comparative morphological data or *Tef-1α* sequence information is available to confirm their taxonomic placement. Due to the distinct positioning of this clade within an expanded - yet still monophyletic - *P. spadiceogriseae* subsection, morphology-based taxonomic positioning may also be more ambiguous than for the other taxa beloging to a more narrowly defined subsection.

The paramount character of the subsection *Spadiceogriseae*, i.e. the dominance of paracystidia on the gill edge, can be present also in other subdivisions of the genus and, therefore, this character must have originated independently multiple times in the evolution of *Psathyrella*. Yet, the set of characters that together define the subsection *Spadiceogriseae* is morphologically unambiguous.

The revision, based on both morphological and molecular data, of a number of samples and holotypes, has resolved some problematic taxonomic situations, the more relevant of which are listed immediately below.

The European *P. phegophila* has been shown to be a solid species with a transcontinental range, though its correct and prior name has to be the Smith epithet *P. kauffmanii*; this result is only morphology-based as we lack the type sequence and morphological revision of *P. phegophila*, however the European collection we selected as a reference point is perfectly adherent to its concept.

Previously unknown in Europe, the American species *P. albescens* is discovered and documented in the old continent; this taxon was until now repeatedly misidentified in Europe.

Although our conclusions were not based on the sequencing of the type, nor on its morphological examination, we propose to accept the autonomy of the European species *P. niveobadia,* after analyses of some collections fully matched its morphological concept. We were also able to describe the differences with its closest relative, *i.e. P. spadiceogrisea*. Our molecular comparisons revealed there is some evolutionary divergence between the two species, however, because this divergence is modest and ambiguous when comparing results from the two loci, we expect future analyses based on multiple loci will be necessary to definitely confirm or discard our decision.

Based on the examination of some samples with pigmented gill edge and pinkish pileus margin, we propose, with molecular corroboration, that the taxon described with the informal name of *P. pseudocorrugis sensu* Kits van Waveren (1985) should be considered an intraspecific variation of *P. fatua*. The correct, original interpretation, *P. pseudocorrugis sensu* Romagnesi, on the contrary, is a species outside subsection *Spadiceogriseae* because of its gill edge dominated by cheilocystidia (Örstadius & Knudsen 2008).

The little-known Czech material present in GenBank under the provisional name of *P. aff. kauffmanii* is more completely described here, and we show that it nests within a small complex of American species.

A critical examination of the clade *spadiceogrisea* in the *Tef-1α* tree indicates that species within this clade may not be distributed randomly within subclades, but there may be trophism-based grouping. In subclades *spadiceogrisea* and *albanyensis*, all species grow strictly associated with arboreal material and humus, with the only partial exception of *P. clivensis* growing usually in grassland but also found directly attached to (buried) sticks (Tassi 2000). A second group, containing *Psathyrella* sp. NL-0631 and subclades *umbrosa* and *praetenuis*, has an intermediate situation with three lignicolous species and two others not associated with arboreal material. The subclades *albescens*, *thujina*, *hellebosensis*, *fatua*, *owyheensis* and the species *P. ammophila*, on the contrary, only include one species, *P. argillacea*, collected consistently in association with arboreal material. All other fungi of this last grouping are generally found in open fields, grasslands, pastures, etc. with the partial exceptions of *P. fatua*, *P. albescens* and *P. owyheensis* which extend their trophism to both kinds of habitat. Some species in this complex have developed strict associations with specialized habitats, such as the association with hygrophilous plants in moist to wet soil reported for *P. thujina* and allied taxa, or the association with sandy habitats reported for *P. ammophila*.

Spore color in the subsection *Spadiceogriseae* is broadly assignable to two categories: (a) brown, pale reddish, orange or paler, and, (b) red-brown or darker. Generally, and using Smith's terminology, spores of the first group in KOH have a cocoa color or paler tones possibly turning slowly to chocolate color. Those in the second group are from the beginning, or rapidly turn into, a chocolate or a darker color when in KOH. Of course, intermediate situations can occur. Because Smith (1972) described spore color only in KOH, this observation can offer a possible clue for deducing spore color in water of *Psathyrella* species described by Smith and not yet revised.

Some species outside of subsection *Spadiceogriseae* have been studied here as well. The holotypes of *P. fragrans* and *P. carinthiaca* were sequenced and, based on their molecular and morphological characters, they can be confirmed as close to, but autonomous from, *P. piluliformis*. Collections of the little-known European species *P. infida* and *P. bivelata* are respectively described and commented upon and their phylogenetic sequences have been generated to offer a molecular reference point. Finally, MCVE28713 represents an interesting rare albinistic occurrence of *P. cortinarioides*, and was also sequenced.

Key to subsection *Spadiceogriseae*

At the conclusion of this study, we provide an intercontinental key of the subsection *Spadiceogriseae*. Note that besides all the species previously discussed in this paper, the key also includes an additional taxon, identified in GenBank as *Psathyrella* sp., voucher NL-0631, and belonging to the *P. umbrosa* complex.

Psathyrella affinis, *P. basii*, *P. cortinarioides*, *P. dunensis*, *Kauffmania larga* (formerly *P. larga*), *P. obtusata*, *P. pertinax*, *P. psammophila* and *P. sanjuanensis* though not belonging to the clade *spadiceogrisea*, are included in the key because they have, or occasionally may have, the gill edge lined by numerous paracystidia and/or they may have utriform pleurocystidia. The users of this key should take into consideration the limited knowledge of variability in morphology and habitat for the species described with few or only one collection. After each species name, the continent where its occurrence is ascertained is reported in brackets; in the most recurrent cases of America and Europe the initial letters A and E respectively are affixed instead.

A document by Voto, containing a key to all European species of *Psathyrella* and a list of the principal synonyms with reference to their first propounders, is also published online in the website of The Associazione Micologica ed Ecologica Romana - A.M.E.R. (www.ameronlus.it/chiavi_micologia.php).

1. Germ pore absent to indistinct; spores pale to orangish (light to medium brown in *P. aff. kauffmanii*, (pale) yellow-brown in *P. subspadiceogrisea*) **2**
1. Germ pore distinct and/or spores distinctly pigmented **10**

2. Spores 4.5–6.5 µm broad or more **3**
2. Spores 6.5–10 × 3.5–5.5 µm **5**

3. Pileus 30–140 mm; pleurocystidia 40–90 × 10–24; associated to woody debris .... see *Kauffmania larga* (A, E)
3. Pileus within 40 mm broad **4**

4. Pleurocystidia 28–37 × 10–14 µm; found on soil in garden .... ***P. neotropica*** (A)
4. Pleurocystidia 35–60 × 10–18 µm; associated or not to woody debris .... ***P. clivensis*** (E)

5. Veil yellow to brown colored; pileus conical to campanulate; lignicolous .... see *P. vesiculosa* (A), *P. velibrunnescens* (A), *P. aff. kauffmanii* (E), *P. conica* (Asia)
5. Veil white **6**

6. Spores on average 7–8 µm long **7**
6. Spores on average longer **9**

7. Pleurocystidia often yellow below the apex; spores not triangular, often phaseoliform; veil flocculose, extending to halfway or centre of the pileus; smell indistinct .... see *P. cortinarioides* (E)
7. Pleurocystidia not pigmented; spores partly subtriangular, not or sometimes phaseoliform; veil scanty **8**

8. Pileus –75 mm broad; stipe 30–90 × 5–12 mm; smell sometimes sweetish .... see *P. pertinax* (E)
8. Pileus –23 mm broad, at start brown with darker centre; stipe 30–50 × 2.5–3 mm; smell indistinct; spores (pale) yellow-brown .... ***P. subspadiceogrisea*** (Asia)

9. Pleurocystidia utriform to subcylindrical, often with elongate-cylindrical neck, rarely subellipsoid or ventricose-conical; apex (4–)6–10 µm broad, mainly rounded, sometimes obtuse to subacute; paracystidia never mucronate .... ***P. rugulosa*** (A)
9. Pleurocystidia more varied, with apex mainly obtuse; paracystidia sometimes mucronate .... see *P. obtusata* (A, E), *P. psammophila* (A)

10. Growing on wood, in woody debris, leaf litter, humus, in parks or forests **22**
10. Growing in open fields, grasslands, pastures, on herbaceous debris, among hygrophilous plants, in nitrogen rich soil, arenicolous, on dry to wet soil **11**

11. Spores on average less than 9.3 µm long and 5.1 µm broad **12**
11. Spores longer and/or broader **16**

12. Spores often distinctly ovoid to angular-ovoid, reddish brown; pleurocystidia often capitate to forked; on moist soil .... ***P. hellebosensis*** (E)
12. Spores different **13**

13. Pileus usually still distinctly greyish brown when mature, not pink at margin; gill edge not pigmented; spores rarely or sometimes phaseoliform; pleurocystidia not or rarely incrusted, forked or brownish **14**
13. Pileus quickly discoloring, usually to brownish orange shades, sometimes with pinkish tints, fading to white, drying greyish violaceous; gill edge sometimes pigmented; stipe at the base sometimes bent, swollen, or equipped with a pseudorhiza [If pleurocystidia fusiform with apex in part mucous or subcapitate, see *P. dunensis* (E)] **15**

14. Spores reddish brown; in moist, often flooded, permeable alluvial plain with *Salix* and hygrophilous plants .... ***P. rogersiae*** (E)
14. Spores orangish; in open pastured ground or in forest soil .... ***P. owyheensis*** (A, E)

15. Pleurocystidia (narrowly) utriform, sometimes fusiform, rarely lageniform or clavate, capitate or not, forked or not, incrusted or not, sometimes brownish; spores often ± phaseoliform, to ± indented above the apiculus, orangish brown to orangish reddish brown; veil mature sometimes still appendiculate at the margin of the pileus, folded back on the gills or, rarely, annular on the stipe; gill edge rarely weakly pigmented; pileus at most and rarely pinkish buff .... ***P. albescens*** (A, E)
15. Pleurocystidia utriform, lageniform, fusiform, conical, rarely clavate, capitate or not, rarely incrusted or forked, never brownish; spores rarely phaseoliform or indented above the apiculus, sometimes subphaseoliform, brown to dark red; veil fugacious; gill edge sometimes red; pileus sometimes discoloring with distinct to weak pinkish tints .... ***P. fatua*** (E)

16. Spores mainly and distinctly phaseoliform **17**
16. Spores at most sometimes subphaseoliform, not or rarely distinctly phaseoliform **18**

17. Spores 9.7–11.6(–12.5) × (5.2–)5.5–6(–6.5), on average about 10.7 × 5.8 µm .... ***P. agraria** ad int*. (E)
17. Spores 8–10 × 5–6 µm, on average 9 × 5.5 µm .... ***P. phaseolispora*** (E)

18. Spores pale, orangish to reddish yellow **19**
18. Spores more pigmented, generally distinctly reddish brown **20**

19. Stipe with a conspicuous white, woolly ring; on soil in a flood-plain, Hungary .... ***Psathyrella* sp.** NL-0631 (E)
19. Stipe without a ring; in open pastured ground or in forest soil .... ***P. owyheensis*** (A, E)

20. Habitat arenicolous on coastal dunes or inland, not associated to moist soil or hygrophilous plants; spores (7.5–)8.5–14 × (4.7–)5–8.5 µm, avQ 1.5–1.9 .... ***P. ammophila*** (A, E)
20. Habitat different, associated to hygrophilous plants in moist soil or on mud in cow pastures **21**

21. Growing in wet to moist soil among hygrophilous plants (*e.g. Typha*, *Phragmites*, *Cirsium*, *Epilobium*); sometimes clampless .... ***P. thujina*** (A, E)
[If pleurocystidia (ventricose-) lageniform to obconical, see *P. basii* (E)]
21. Habitat different, on mud in a cow pasture (it is dubious whether this species is coprophilous/nitrophilous or not) .... ***P. pseudolimicola*** (A)

22. Spores tridimensional or broader than 5.5 µm in front view, strongly pigmented; germ pore little distinct; stipe without a ring [if pleurocystidia mainly ventricose-lageniform with obtuse apex, see *P. affinis* (A)] **23**
22. Spores on average < 5.5 µm broad, not or inconspicuously tridimensional; some species with a moderately distinct germ pore [If spores (8–)8.2–9.8(–10.7) × (5–)5.2–5.8(–6) µm, dark, germ pore distinct, on moist soil under aspen, see *P. sanjuanensis* (A)] **25**

23. Spores often cordiform to pentagonal, 7–9 × 4.5–6.3 × 4–5 µm, fQ 1.3–1.5; on soil in a mixture of aspen and conifers at about 2 438 m a.s.l. (8 000 feet) .... ***P. albanyensis*** (A)
23. Spores not cordiform, on average > 5.5 µm broad at least in front view **24**

24. Spores 9–12 × 5.5–7 µm; on unspecified sticks .... ***P. latispora*** (A)
24. Spores 7–10(–10.7) × 5–6.7 × 4.4–5.5 µm; on conifer wood .... ***P. oregonensis*** (A)

25. Pleurocystidia 20–32 × (9–)11–16 µm long, with mainly undifferentiated apex; veil absent or scarce; pileus 10 mm; stipe 40 × 1.5 mm; spores dark, oval, cylindrical oval, oboval, sometimes irregular or angular, with broadly rounded to subtruncate base; germ pore little to moderately distinct .... ***P. ovaticystis*** (Africa)
25. Pleurocystidia larger and/or more differentiated; different combination of characters **26**

26. Pleurocystidia in NH$_4$ often with reddish brown mucoid to granular coverings and granular contents, utriform to clavate or cylindrical, sometimes slightly thick-walled and pigmented, 45–52 × 14–21 µm; stipe with a striate, membranous ring; spores 7.5–9.5(–10) × 4–5.5 µm .... ***P. striatoannulata*** (A)
26. Pleurocystidia apex generally not equipped with coverings and contents staining reddish brown in NH$_4$ **27**

27. Spores dark, often with a truncate to subtriangular base, sometimes (irregularly) angular-oval or angular-oblong; germ pore moderately to little distinct; veil when mature often still distinct with floccules at the margin or appendiculate or as a membranous ring; pleurocystidia forked or not, incrusted or not, sometimes or rarely weakly pigmented **28**
27. Different combination of characters; without a ring (occasionally in *P. albescens*); if spores dark then germ pore distinct (see *P. fatua*) **30**

28. Pleurocystidia mainly slender, (37–)45–67(–83) × (10–)13–20(–32) µm, never clavate, often with a tapering and elongate upper portion, scarcely subcapitate; gill edge cystidia never mucronate; in association with *Alnus* .... ***P. alnicola*** (A)
28. Pleurocystidia shorter, (22–)26–56(–70) × 9–24 µm, sometimes clavate, with an apex often broad, tapering or not in the upper portion; gill edge cystidia sometimes or often mucronate; mainly in association with *Alnus* or *Fagus* **29**

29. In mesophilous habitat, mostly with *Fagus*; cheilocystidia rarely attenuate to subacute at the apex; pleurocystidia utriform to ellipsoid or clavate, sometimes lageniform, with an often capitate to subcapitate apex, (22–)26–56(–70) × 9–24 µm .... ***P. kauffmanii*** (A, E)
29. In moist habitat under *Alnus*; cheilocystidia often mucronate; pleurocystidia more varying: utriform, clavate, sublageniform, mucronate, obconical, with a rarely subcapitate apex, (24–)30–45(–52) × (10–)11.5–21; spores (7.4–)7.5–9.6(–10) × 4.9–5.6 µm .... ***P. solheimii*** (A)

30. Spores on average < 9.2 µm long and < 5.1 µm broad **34**
30. Spores on average longer and/or broader **31**

31. Spores reddish orangish to dull orange; pileus sometimes fading to pinkish buff **32**
31. Spores reddish brown **33**

32. Pleurocystidia utriform to lageniform, sometimes subcylindrical, apex rarely forked or incrusted; paracystidia (sub) hyaline; spores in front view sometimes oblong to subcylindrical or slightly irregular; context rigid; odor sometimes of fish .... ***P. owyheensis*** (A, E)
32. Pleurocystidia utriform, apex often forked or incrusted; paracystidia often yellowish; spores not so; context fragile .... ***P. argillacea*** (A)

33. Pileus clay color turning to greyish tints, 1–3 cm; stipe 20–30 × 2–4 mm, equal; spores medium reddish brown; on oak debris .... ***P. griseopallida*** (A)
33. Pileus discoloring to cinnamon buff with a slightly redder centre, fading pale date brown, 3–5 cm; stipe 60–120 × 3–6 mm, subclavate; spores sordid reddish brown; often on *Populus* debris .... ***P. praetenuis*** (A)

34. Paracystidia mainly 9–12 × 5–7 µm, some –32 × –13 µm, hyaline, among numerous basidia and basidiola; pleurocystidia rarely to sometimes forked, hyaline, never incrusted or pigmented; pileus pale dingy cinnamon brown turning dark brown when mature, fading to pallid, 1–3 cm broad; stipe 20–50 × 1–3 mm; spores sometimes or rarely subphaseoliform, (6.7–)7–9.3(–9.5) × 4.3–5.7 µm .... ***P. umbrosa*** (A)
34. Paracystidia generally more conspicuous; different combination of characters **35**

35. Pleurocystidia sometimes brownish, forked or capitate, apex often with pigmented thickwalled traits or covered with grossly mucous masses disappearing in old exsiccata; pileus not or scarcely striate, when young with dark tones of violaceous brown to reddish brown, possibly still dark when mature, 15–72 mm; stipe 30–130(–200) × 3.5–10 mm, base often attenuate to strongly rooting; spores on average 7.4–8.3 × 4.5–4.9 µm, orange-brown to reddish orange brown (darkish reddish brown in NH$_4$), often phaseoliform; context of pileus and especially of stipe cortex thick, rigid, tenacious .... ***P. niveobadia*** (E)

35. Pleurocystidia apex not mucous; stipe base at most subrooting or equipped with a pseudorhiza; spores brown, reddish brown, dark red (see *P. albescens* and *P. tenacipes* with orangish reddish brown spores); context not distinctly thick and rigid (but species with somewhat rigid stipe cortex can occur, *e.g. P. fatua*, *P. albescens*, *P. tenacipes*) **36**

36. Pleurocystidia often little differentiated between ventricose and apical part, sometimes or often subcapitate, not forked, not incrusted, not pigmented; paracystidia yellow and gill edge pallid brownish; pileus becoming distinctly rugulose, not discoloring pinkish, 10–40 mm; spores orangish reddish brown, 7–9.5(–10.1) × 4.6–5.7 µm, sometimes subphaseoliform; stipe rather stringy, fibrous, cartilaginous-pliant, 30–60 × 2–3.5 mm; in moist to wet habitat (on muck and small sticks partly burned in the protologue, on drying muck in ash swamp in the field notes) .... ***P. tenacipes*** (A)

36. Different combination of characters; in dry habitat **37**

37. Pileus –20 mm broad, striate; pleurocystidia often little differentiated, apex mainly obtuse or subacute, rarely rounded, never capitate; stipe –30 × –2.5 mm; paracystidia sometimes or often with a pale pigment (gill edge possibly pigmented?) [If pileus usually drying with pinkish tints, pleurocystidia apex in part mucous or subcapitate, see *P. dunensis* (E)] **38**

37. Larger sporocarps or else different combination of characters **39**

38. Pileus yellowish fulvous to reddish cinnamon, mature broadly convex to plane; pleurocystidia conical, utriform-conical, fusiform, ellipsoid, also utriform, subcylindrical, lageniform, slightly pigmented, apex sometimes mucronate, forked, truncate, incrusted; spores orange-brown (in KOH bright cocoa slowly turning chocolate in Smith 1972) .... ***P. ochrofulva*** (A)

38. Pileus white turning greyish brown when mature and fading white, obtusely conical and hardly expanding; veil apparently absent; pleurocystidia mainly subfusoid to subutriform, not pigmented, not mucronate, not forked, not incrusted; spores in KOH dark cocoa brown slowly turning darker in Smith (1972) .... ***P. lactobrunnescens*** (A)

39. Pileus not striate, hardly expanding, 25–30 mm broad, bronze brown, then gray- to clay-brown or pale ochre to cream; stipe 50–70 × 3–4 mm; spores rarely subphaseoliform, reddish brown, 8–10.5 × 4.5–5 µm; germ pore small; pleurocystidia utriform to subutriform, scarcely subcapitate, rarely yellowish brown incrusted .... ***P. marquana*** (E)

39. Pileus striate when fresh, usually expanding; sporocarps of the same dimension or larger; different combination of characters **40**

40. Pleurocystidia sometimes capitate, rarely incrusted or forked, never brownish; spores brown to dark red, rarely phaseoliform, sometimes subphaseoliform; pileus reddish brown, quickly discolouring through brown to brownish orange or paler, sometimes with distinct to weak pink tints, 8–50 (60) mm broad; gill edge sometimes red; stipe (10–)20–110 × 1–5.5(–7) mm, base sometimes attenuate or with a pseudorhiza .... ***P. fatua*** (E)

40. Pleurocystidia sometimes brownish, incrusted, forked; spores not dark red; gill edge generally not pigmented; spores on average 7.4–9 µm long, usually often ± phaseoliform to ± indented above the base; pileus rarely with vague pinkish shades (*P. albescens*) **41**

41. Pileus when young dark yellowish brown to cinnamon-brown, discolouring through shades of brownish orange (rarely pinkish buff) to finally white, 10–70 mm; stipe 20–100(–140) × 1.5–6(–12) mm, base often attenuate, subrooting or equipped with a pseudorhiza; veil mature sometimes still appendiculate or folded back on the gills, rarely annulate; spores orangish brown to orangish reddish brown; pleurocystidia subcapitate or not .... ***P. albescens*** (A, E)

41. Pileus dark (violaceous) reddish brown, when mature sometimes often still strongly pigmented, usually not fading completely white, 15–55 mm; stipe 40–80 × 1.5–8 mm, base at most sub attenuate; veil mature fugacious; spores reddish brown; pleurocystidia rarely capitate .... ***P. spadiceogrisea*** (A, E)

ACKNOWLEDGEMENTS

We are grateful to the curators of the following herbaria: K, MICH, NY, and particularly wish to express our gratitude to the MICH's Collection Manager and correspondent, Patricia Rogers, for her collaboration in answering our many questions about the MICH specimens studied. We wish to thank Kathy Richmond, of the Southern Idaho Mycological Association (SIMA), who verified a collection site in Idaho, Joaquim Carbó, Ottorino Chiarello, Alessio Micucci, Miquel À. Pérez-De-Gregorio, Bruno de Ruvo, Marco Maletti, Gerard Tassi, Renato Tizzoni, Evelina Zanella and Marino Zugna who supplied us with gifts of collections and pictures; thanks are also due to Giovanni Robich of the herbarium MCVE who for a time assisted us in communicating with the herbaria. Also, we are grateful to L. Örstadius and L. Nagy for providing to us details about their *Psathyrella* sp. NL-0631, and to M. Vašutová for the collaboration on *P. aff. kauffmanii.* The key also includes an additional

taxon, identified in GenBank as *Psathyrella* sp., voucher NL-0631, which belongs to the *P. umbrosa* complex. This was possible thanks to courtesy of L. Nagy, who collected it together with Z.S. Gorliczai, and to L. Örstadius, who examined it microscopically.

REFERENCES

Altschul SF, Gish W, Miller W, *et al.* (1990). Basic local alignment search tool. *Journal of Molecular Biology* **215**: 403–410.

Bergemann S, Smith A, Parrent J, *et al.* (2009). Genetic population structure and distribution of a fungal polypore, *Datronia caperata* in mangrove forests of Central America. *Journal of Biogeography* **36**: 266–279.

Bon M (1988). Flore Mycologique du Littoral. *Documents Mycologiques* **19**: 62–64.

Breitenbach J, Kränzlin F (1995). Champignons de Suisse. Contribution à la connaissance de la flore fongique de Suisse. Tome IV. *Champignons à lames 2ème partie*. Mykologia, Luzern.

Einhellinger A (1973). Die Pilze der Pflanzengesellschaften des Auwaldgebiets der Isarzwischen München und Grüneck. *Berichte der Bayerischen Botanischen Gesellschaft zur Erforschung der heimischen Flora* **44**: 5–100.

Enderle M (1996). Studien in der Gattung *Psathyrella*. IV. *Beitrage zur Kenntnis der Pilze Mitteleuropas* **10**: 35–58.

Felsenstein J (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783–791.

Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for Basidiomycetes application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Heykoop M, Moreno G, Alvarado P, *et al.* (2017). El género *Psathyrella* (Fr.) Quél. s.l. en España. VI. Especies nuevas o raras y reevaluación de otras. *Boletín de la Sociedad Micológica de Madrid* **41**: 71–98.

Huijsman HSC (1955). Observations on Agarics. *Fungus* **25**: 18–43.

Ivors KL, Hayden KJ, Bonants PJM, *et al.* (2004). AFLP and phylogenetic analyses of North America and European populations of *Phytophthora ramorum. Mycological Research* **108**: 378–392.

Katoh K, Misawa K, Kuma K, *et al.* (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30**: 3059–3066.

Kearse M, Moir R, Wilson A, *et al*. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**: 1647–1649.

Kits van Waveren E (1985). The Dutch, French and British species of *Psathyrella*. *Persoonia Supplement* **2**: 1–300.

Kumar S, Stecher G, Li M, Knyaz C, *et al.* (2018). MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* **35**: 1547–1549.

Ludwig E (2007a). Pilzkompendium Band 2, Beschreibungen. *Die größeren Gattungen der Agaricales mit farbigem Sporenpulver (ausgenommen Cortinariaceae)*. Fungicon-Verlag, Berlin.

Ludwig E (2007b). Pilzkompendium Band 2, Abbildungen. *Die größeren Gattungen der Agaricales mit farbigem Sporenpulver (ausgenomme Cortinariaceae)*. Fungicon-Verlag, Berlin.

Miller MA, Pfeiffer W, Schwartz T (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, New Orleans, LA: 1–8.

Morgan AP (1907). North American species of *Agaricaceae*. *Journal of Mycology* **13**(91): 143–153.

Örstadius L, Knudsen H (2008). *Psathyrella* (Fr.) Quél. In: *Funga Nordica –Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera. Vol. 1* (Knudsen H, Vesterholt J, eds). Nordsvamp, Copenhagen: 587–623.

Örstadius L, Knudsen H (2012). *Psathyrella* (Fr.) Quél. In: *Funga Nordica –Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera (2nd ed.). Vol. 1* (Knudsen H, Vesterholt J, eds). Nordsvamp, Copenhagen: 692–728.

Örstadius L, Ryberg M, Larsson E (2015). Molecular phylogenetics and taxonomy in *Psathyrellaceae* (*Agaricales*) with focus on psathyrelloid species: introduction of three new genera and 18 new species. *Mycological Progress* **14**: 25.

Osmundson T, Eyre C, Hayden K, *et al.* (2013). Back to basics: an evaluation of NaOH and alternative rapid DNA extraction protocols for DNA barcoding, genotyping, and disease diagnostics from fungal and oomycete samples. *Molecular Ecology Resources* **13**: 66–74.

Pegler DN (1977). A preliminary agaric flora of East Africa. Kew bullettin additional series, 6. Her Majesty's Stationery Office.

Pérez-De-Gregorio MÀ, Roqué C, Carbó J (2010). Dos *Psathyrella* interesantes halladas en Girona. *Micologia e Vegetazione Mediterranea* **25**: 23–32.

Posada D, Crandall KA (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817–818.

Romagnesi H (1944). Classification du genre *Drosophila* Quélet. *Bulletin Mensuel De La Societe Linneenne De Lyon* **13**: 51–54.

Ronquist F, Teslenko M, van der Mark P, *et al.* (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.

Schäffer JC (1771). *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur Icones 3*. Regensburg.

Schäffer JC (1774). *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur Icones 4*. Regensburg.

Schäffer JC (1800). *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur Icones nativis coloribus expressae*. Editio nova. Vol. 3–4. Erlangae, Apud J.J. Palmium.

Smith AH (1972). The North American species of *Psathyrella*. *Memoirs of the New York Botanical Garden* **24**: 1–633.

Stamatakis A (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Swofford DL (2003). *PAUP*: phylogenetic analysis using parsimony. *and other methods). Version 4.0b10*. Sinauer Associates, Sunderland.

Tassi G (2000). Le genre *Psathyrella*. Espèces rares ou intéressantes. II. *Bulletin de la Société mycologique de France.* **116**: 343–384.

Vašutová M, Antonin V, Urban A (2008). Phylogenetic studies in *Psathyrella* focusing on sections *Pennatae* and *Spadiceae* - new evidence for the paraphyly of the genus. *Mycological Research* **112**: 1153–1164.

Voto P (2007). *Psathyrella bivelata*, seconda stazione italiana e *Psilocybe flocculosa*, nuova per l'Italia. *Rivista di Micologia* **2**: 145–157.

Voto P (2011). *Psathyrella carinthiaca sp. nov.* e nuove segnalazioni di *P. bivelata*. *Rivista di Micologia* **2**: 121–133.

Voto P (2013). Note su *Psathyrella candolleana* e *P. pseudogordonii*. *Rivista di Micologia* **3**: 247–261.

Supplementary Material: http://fuse-journal.org/

Fig. S1. Bayesian phylogram obtained from combined nrITS and *Tef-1α* sequence alignment of *Psathyrella* spp. *Bolbitius vitellinus* was used as outgroup taxon. Only BPP values ≥ 0.95 and MLB values ≥ 70 % are given above clade branches. In addition to sequences generated by this study and to select GenBank accessions, most sequences published by Örstadius *et al*. (2015) are included in this tree.

Fig. S1, part 1

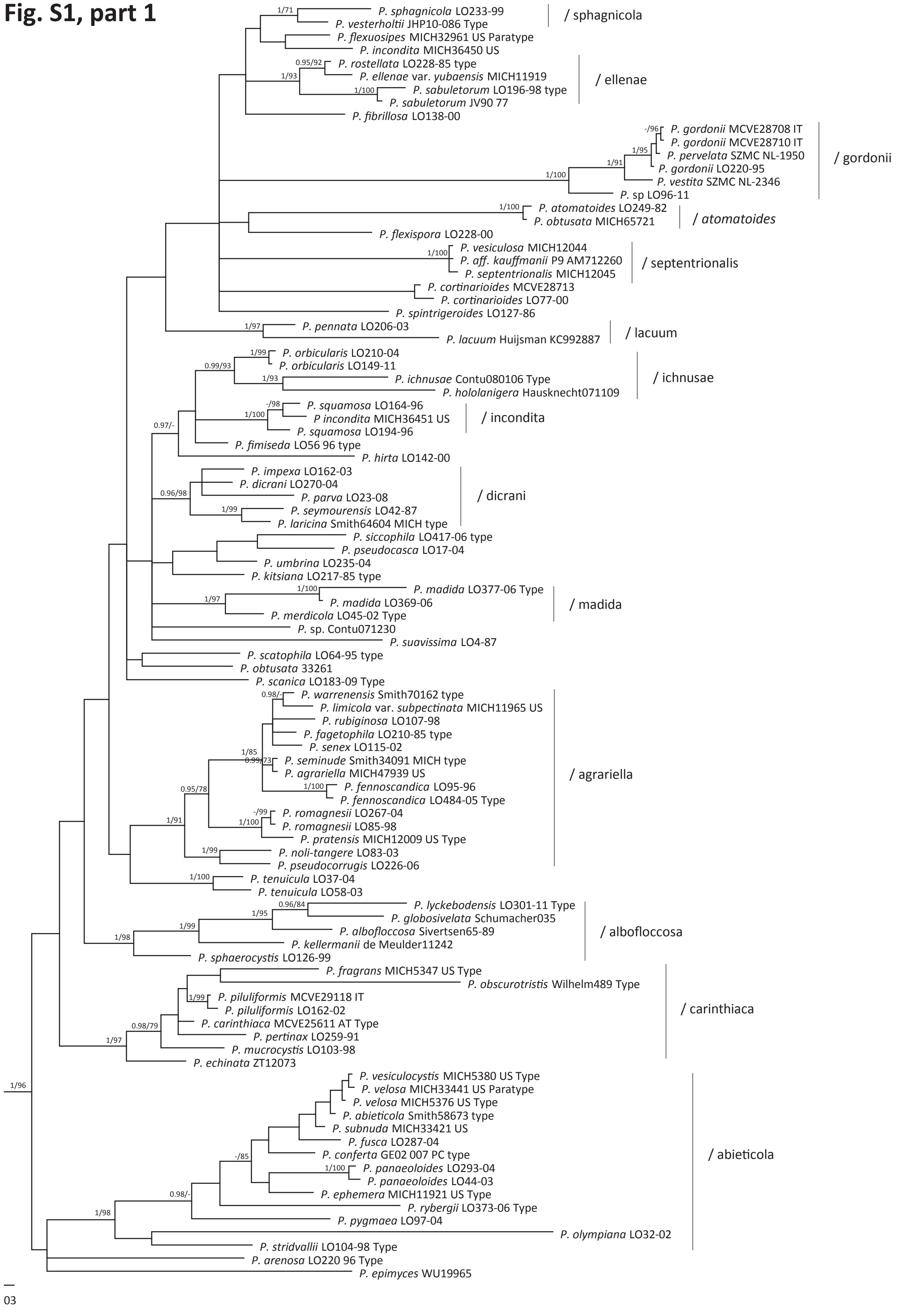
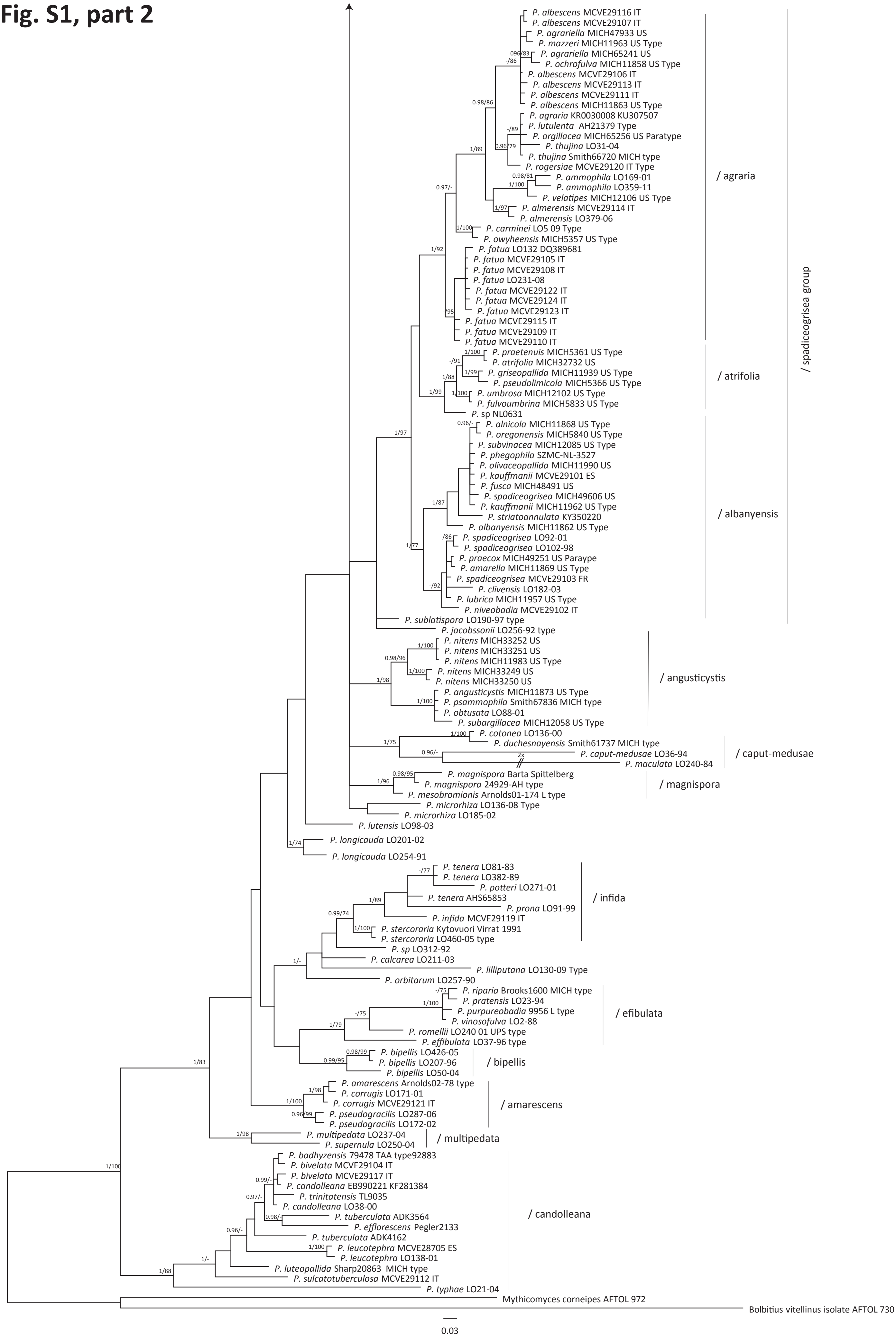

1/71
P. sphagnicola LO233-99
P. vesterholtii JHP10-086 Type
P. flexuosipes MICH32961 US Paratype
P. incondita MICH36450 US
/ sphagnicola
0.95/92
P. rostellata LO228-85 type
1/93
P. ellenae var. yubaensis MICH11919
1/100
P. sabuletorum LO196-98 type
P. sabuletorum JV90 77
/ ellenae
P. fibrillosa LO138-00
-/96
P. gordonii MCVE28708 IT
P. gordonii MCVE28710 IT
1/95
P. pervelata SZMC NL-1950
1/91
P. gordonii LO220-95
1/100
P. vestita SZMC NL-2346
P. sp LO96-11
/ gordonii
1/100
P. atomatoides LO249-82
P. obtusata MICH65721
/ atomatoides
P. flexispora LO228-00
1/100
P. vesiculosa MICH12044
P. aff. kauffmanii P9 AM712260
P. septentrionalis MICH12045
/ septentrionalis
P. cortinarioides MCVE28713
P. cortinarioides LO77-00
P. spintrigeroides LO127-86
1/97
P. pennata LO206-03
P. lacuum Huijsman KC992887
/ lacuum
1/99
P. orbicularis LO210-04
0.99/93
P. orbicularis LO149-11
1/93
P. ichnusae Contu080106 Type
P. hololanigera Hausknecht071109
/ ichnusae
-/98
P. squamosa LO164-96
1/100
P incondita MICH36451 US
P. squamosa LO194-96
/ incondita
0.97/-
P. fimiseda LO56 96 type
P. hirta LO142-00
P. impexa LO162-03
P. dicrani LO270-04
0.96/98
P. parva LO23-08
1/99
P. seymourensis LO42-87
P. laricina Smith64604 MICH type
/ dicrani
P. siccophila LO417-06 type
P. pseudocasca LO17-04
P. umbrina LO235-04
P. kitsiana LO217-85 type
1/100
P. madida LO377-06 Type
1/97
P. madida LO369-06
P. merdicola LO45-02 Type
/ madida
P. sp. Contu071230
P. suavissima LO4-87
P. scatophila LO64-95 type
P. obtusata 33261
P. scanica LO183-09 Type
0.98/-
P. warrenensis Smith70162 type
P. limicola var. subpectinata MICH11965 US
P. rubiginosa LO107-98
P. fagetophila LO210-85 type
P. senex LO115-02
1/85
0.99/73
P. seminude Smith34091 MICH type
P. agrariella MICH47939 US
0.95/78
1/100
P. fennoscandica LO95-96
P. fennoscandica LO484-05 Type
/ agrariella
-/99
P. romagnesii LO267-04
1/91
1/100
P. romagnesii LO85-98
P. pratensis MICH12009 US Type
1/99
P. noli-tangere LO83-03
P. pseudocorrugis LO226-06
1/100
P. tenuicula LO37-04
P. tenuicula LO58-03
0.96/84
P. lyckebodensis LO301-11 Type
1/95
P. globosivelata Schumacher035
1/99
P. albofloccosa Sivertsen65-89
1/98
P. kellermanii de Meulder11242
/ albofloccosa
P. sphaerocystis LO126-99
P. fragrans MICH5347 US Type
P. obscurotristis Wilhelm489 Type
1/99
P. piluliformis MCVE29118 IT
P. piluliformis LO162-02
/ carinthiaca
0.98/79
P. carinthiaca MCVE25611 AT Type
1/97
P. pertinax LO259-91
P. mucrocystis LO103-98
P. echinata ZT12073
1/96
P. vesiculocystis MICH5380 US Type
P. velosa MICH33441 US Paratype
P. velosa MICH5376 US Type
P. abieticola Smith58673 type
P. subnuda MICH33421 US
P. fusca LO287-04
-/85
P. conferta GE02 007 PC type
/ abieticola
1/100
P. panaeoloides LO293-04
P. panaeoloides LO44-03
0.98/-
P. ephemera MICH11921 US Type
P. rybergii LO373-06 Type
1/98
P. pygmaea LO97-04
P. olympiana LO32-02
P. stridvallii LO104-98 Type
P. arenosa LO220 96 Type
P. epimyces WU19965
03

Fig. S1, part 2


P. albescens MCVE29116 IT
P. albescens MCVE29107 IT
P. agrariella MICH47933 US
P. mazzeri MICH11963 US Type
096/83
-/86
P. agrariella MICH65241 US
P. ochrofulva MICH11858 US Type
P. albescens MCVE29106 IT
P. albescens MCVE29113 IT
P. albescens MCVE29111 IT
P. albescens MICH11863 US Type
0.98/86
P. agraria KR0030008 KU307507
P. lutulenta AH21379 Type
-/89
P. argillacea MICH65256 US Paratype
0.96/79
P. thujina LO31-04
1/89
P. thujina Smith66720 MICH type
P. rogersiae MCVE29120 IT Type
0.98/81
P. ammophila LO169-01
1/100
P. ammophila LO359-11
0.97/-
P. velatipes MICH12106 US Type
1/97
P. almerensis MCVE29114 IT
P. almerensis LO379-06
1/100
P. carminei LO5 09 Type
P. owyheensis MICH5357 US Type
1/92
P. fatua LO132 DQ389681
P. fatua MCVE29105 IT
P. fatua MCVE29108 IT
P. fatua LO231-08
P. fatua MCVE29122 IT
P. fatua MCVE29124 IT
-/95
P. fatua MCVE29123 IT
P. fatua MCVE29115 IT
P. fatua MCVE29109 IT
P. fatua MCVE29110 IT
1/100
P. praetenuis MICH5361 US Type
-/91
P. atrifolia MICH32732 US
1/99
P. griseopallida MICH11939 US Type
1/88
P. pseudolimicola MICH5366 US Type
1/99
1/100
P. umbrosa MICH12102 US Type
P. fulvoumbrina MICH5833 US Type
P. sp NL0631
0.96/-
P. alnicola MICH11868 US Type
P. oregonensis MICH5840 US Type
1/97
P. subvinacea MICH12085 US Type
P. phegophila SZMC-NL-3527
P. olivaceopallida MICH11990 US
P. kauffmanii MCVE29101 ES
P. fusca MICH48491 US
P. spadiceogrisea MICH49606 US
1/87
P. kauffmanii MICH11962 US Type
P. striatoannulata KY350220
P. albanyensis MICH11862 US Type
-/86
P. spadiceogrisea LO92-01
1/77
P. spadiceogrisea LO102-98
P. praecox MICH49251 US Paraype
P. amarella MICH11869 US Type
P. spadiceogrisea MCVE29103 FR
-/92
P. clivensis LO182-03
P. lubrica MICH11957 US Type
P. niveobadia MCVE29102 IT
P. sublatispora LO190-97 type
P. jacobssonii LO256-92 type
1/100
P. nitens MICH33252 US
P. nitens MICH33251 US
0.98/96
P. nitens MICH11983 US Type
1/100
P. nitens MICH33249 US
1/98
P. nitens MICH33250 US
P. angusticystis MICH11873 US Type
1/100
P. psammophila Smith67836 MICH type
P. obtusata LO88-01
P. subargillacea MICH12058 US Type
1/100
P. cotonea LO136-00
1/75
P. duchesnayensis Smith61737 MICH type
0.96/-
P. caput-medusae LO36-94
2x
P. maculata LO240-84
0.98/95
P. magnispora Barta Spittelberg
1/96
P. magnispora 24929-AH type
P. mesobromionis Arnolds01-174 L type
P. microrhiza LO136-08 Type
P. microrhiza LO185-02
P. lutensis LO98-03
1/74
P. longicauda LO201-02
P. longicauda LO254-91
-/77
P. tenera LO81-83
P. tenera LO382-89
P. potteri LO271-01
1/89
P. tenera AHS65853
P. prona LO91-99
0.99/74
P. infida MCVE29119 IT
1/100
P. stercoraria Kytovuori Virrat 1991
P. stercoraria LO460-05 type
P. sp LO312-92
1/-
P. calcarea LO211-03
P. lilliputana LO130-09 Type
P. orbitarum LO257-90
-/75
P. riparia Brooks1600 MICH type
P. pratensis LO23-94
1/100
P. purpureobadia 9956 L type
-/75
P. vinosofulva LO2-88
1/79
P. romellii LO240 01 UPS type
P. effibulata LO37-96 type
0.98/99
P. bipellis LO426-05
0.99/95
P. bipellis LO207-96
P. bipellis LO50-04
1/83
P. amarescens Arnolds02-78 type
1/98
P. corrugis LO171-01
1/100
P. corrugis MCVE29121 IT
0.96/99
P. pseudogracilis LO287-06
P. pseudogracilis LO172-02
1/98
P. multipedata LO237-04
P. supernula LO250-04
1/100
P. badhyzensis 79478 TAA type92883
P. bivelata MCVE29104 IT
P. bivelata MCVE29117 IT
0.99/-
P. candolleana EB990221 KF281384
P. trinitatensis TL9035
0.97/-
P. candolleana LO38-00
0.98/-
P. tuberculata ADK3564
P. efflorescens Pegler2133
0.96/-
P. tuberculata ADK4162
1/100
P. leucotephra MCVE28705 ES
1/-
P. leucotephra LO138-01
1/88
P. luteopallida Sharp20863 MICH type
P. sulcatotuberculosa MCVE29112 IT
P. typhae LO21-04
Mythicomyces corneipes AFTOL 972
Bolbitius vitellinus isolate AFTOL 730
/ agraria
/ atrifolia
/ albanyensis
/ spadiceogrisea group
/ angusticystis
/ caput-medusae
/ magnispora
/ infida
/ efibulata
/ bipellis
/ amarescens
/ multipedata
/ candolleana
0.03