Mycol Progress (2015) 14: 25
DOI 10.1007/s11557-015-1047-x

ORIGINAL ARTICLE

Molecular phylogenetics and taxonomy in Psathyrellaceae (Agaricales) with focus on psathyrelloid species: introduction of three new genera and 18 new species

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Received: 8 January 2015 / Revised: 4 March 2015 / Accepted: 6 March 2015 / Published online: 11 April 2015

Abstract Based on traditional morphology, sequence data, and phylogenetic analyses, 18 new species are here described: *Coprinellus christianopolitanus*, *Coprinopsis musae*, *C. udicola*, *Psathyrella arenosa*, *P. carminei*, *P. fennoscandica*, *P. ichnusae*, *P. lilliputana*, *P. lyckebodensis*, *P. madida*, *P. rybergii*, *P. sabuletorum*, *P. scanica*, *P. siccophila*, *P. stridvallii*, *P. sublatispora*, *P. vesterholtii*, and *Typhrasa nanispora. Psathyrella hololanigera* and *P. tenera* are reported as new to Europe and *P. parva* as new to the Nordic countries. A four-gene dataset on Psathyrellaceae were analyzed by Maximum Parsimony, Maximum Likelihood, and Bayesian methods. Constraint analyses were performed to determine limits of /Psathyrella, and to evaluate whether the /Coprinellus, /cordisporus, and /gossypina clades could be regarded with confidence as monophyletic clades outside of the clade /Psathyrella. This was not unambiguously supported. Based on the phylogenetic results, *Kauffmania* is proposed as a monotypic genus for the species *P. larga* and *Typhrasa* for *P. gossypina* and the new described species *T. nanispora*. The genus *Homophron* is formally validated and three combinations are proposed: *H. spadiceum*, *H. cernuum*, and *H. camptopodum*. The genus *Cystoagaricus* Singer is emended and the following new combinations are proposed: C. *hirtosquamulosus, C. squarrosiceps, C. olivaceogriseus*, and *C. silvestris.* Neotypes have been selected for seven species described by Fries, and ITS sequence data for these were generated. The following new combinations are proposed: *Coprinopsis canoceps*, *C. cineraria*, *C. melanthina*, *C. submicrospora*, *C. uliginicola, and Typhrasa gossypina*. Brief comments are given to other species of interest. *Psathyrella ornatispora* were found not to belong in *Psathyrellaceae*. A key to 106 psathyrelloid species in Northern Europe is provided.

Keywords *Homophron* · *Kauffmania* · *Typhrasa* · *Cystoagaricus* · Molecular phylogenetics · Systematics · Taxonomy · Species diversity · Neotype, epitype

Introduction

Psathyrella is a large genus in *Agaricales* with 1,004 records in Index Fungorum (www.indexfungorum.org) including synonyms, varieties, forms, and names currently linked to genera such as *Lacrymaria* or *Coprinopsis*. The number of recognized species in Europe is about 100 and in the Nordic countries 78 (Örstadius and Knudsen 2012). The species in *Psathyrella* are known to have a wide geographic distribution (e.g., Smith 1972; Pegler 1977, 1983; Kits van Waveren 1985; Singer 1969, 1978; Grgurinovic 1997; Bi et al. 1987; Hoashi 2008). As presently understood, the genus includes species with mostly fragile and non-deliquescent basidiomata. The cap size varies from small to large, is smooth to innately fibrillose, often hygrophanous, mostly with white to dark reddish brown colours, and a copious to scanty veil. The pileipellis is considered a hymeniderm. Clamps are present or absent. The

Electronic supplementary material The online version of this article (doi:10.1007/s11557-015-1047-x) contains supplementary material, which is available to authorized users.

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size of the spores varies and hymenial cystidia are present. The species are mostly regarded as saprotrophic and commonly growing on wood, soil, dung, plant residuals, and in swamps, but other nutritional modes has been reported such as the association with mycoheterotrophic orchids (Selosse et al. 2010) and the mycoparasitism in *P. epimyces* (Smith 1972).

The major taxonomic treatments of the genus *Psathyrella* by Smith (1972), Romagnesi (1982), Kits van Waveren (1985), and Singer (1986) were mainly based on phenotypic characters although sometimes complemented by mating tests using haploid mycelia (Galland 1972; Jurand and Kemp 1972). The infrageneric classification differs among authors. Smith, Romagnesi, and Singer include *Lacrymaria* as a subgenus while Kits van Waveren treats it as a genus of its own. According to Singer (1986) the family *Coprinaceae* comprises subfamily *Coprinoideae,* with the single genus *Coprinus*, subfamily *Psathyrelloideae* with the genera *Psathyrella* and *Macrometrula*, and subfamily *Panaeoloideae* including the genera *Panaeolina*, *Panaeolus*, *Copelandia*, and *Anellaria*.

In recent years, molecular sequence data have improved our understanding of relationships among dark spored agarics (Hopple and Vilgalys 1999; Moncalvo et al. 2002; Matheny et al. 2006). As a result, major changes to the genus classification have been suggested (Redhead et al. 2001a, b; Gams 2002). Extended specimen sampling of the major lineages within Psathyrellaceae and analyses based on sequence data of the LSU region (Vašutová et al. 2008; Padamsee et al. 2008) or a combination of the ITS and LSU regions (Larsson and Örstadius 2008) showed that the limits of *Psathyrella* are unclear. These studies suffered from poor resolution of deeper nodes but they all recovered *Coprinellus* and *Coprinus cordisporus* nested with *Psathyrella* in a large supported clade.

Recently, several studies using newly developed comparative phylogenetic methods based on alignments of multi-gene datasets have been published, aiming to explore evolutionary aspects of the development of characters within Psathyrellaceae. These studies have shed light upon the evolution of autodigestion, species evolution, and divergence times, but also on the delimitation of taxa (Nagy et al. 2009, 2010, 2011). Several new species have been described, both within *Coprinellus* and *Coprinopsis* (Nagy et al. 2012, 2013a).

Nagy et al. (2013b) presented phylogenetic analyses of a four-gene dataset sampled with the intention to cover all major clades within Psathyrellaceae. In the paper, 14 clades are recognized, not all of them well supported, and the authors suggest that these clades form the basis for a splitting and reclassification of *Psathyrella*.

Because of the phylogenetic results, several species originally described in *Psathyrella* have been transferred to other genera such as *Parasola* and *Coprinopsis* (e.g. Larsson and Örstadius 2008; this paper). Despite their phylogenetic placement they still have the apperance and habit of a *Psathyrella* species, and we will refer to such species collectively as psathyrelloid.

The study by Larsson and Örstadius (2008) had a focus on the coprophilous species in *Psathyrella*. In this study, we have expanded the specimen sampling of *Psathyrella* further, to include the majority of species that occur in Europe in an effort to identify and characterize the species that occur in Northern Europe. To identify and get support for the description of new species, a combination of classical morphology and ITS sequence data were used. To confirm or discriminate between closely related and morphologically similar species described from Europe and other parts of the world, a large number of type specimens were studied and sequenced. For some species described by Fries, neotypes are selected.

A four-gene dataset was generated in order to inferring the phylogenetic relationships among species and genera within Psathyrellaceae. In addition to the ITS and LSU regions, sequence data of two protein-coding genes (β-tubulin and Tef-1α) were selected. These are the same regions as used by Nagy et al. (2013b). Based on the phylogenetic results, we propose several taxonomical novelties and nomenclatural changes.

Materials and methods

Morphology

Many species of *Psathyrella* are fragile and important characters are easily destroyed during handling. Therefore, all basidiomata were photographed before being collected. The aim was to describe the collection complete with notes on ecology already in the field. The presence of a pseudorhiza was checked. As most species are hygrophanous, it is necessary to note the colours of moist and striate caps before they are dried. Colour names follow the Munsell soil colour charts (Munsell 1975), cited as Mu. in the text. If present, the evanescent veil on both cap and stem was described. Sometimes the veil is present only in young basidiomata and seen as fibrils close to the cap margin or as dispersed fibrils on the stem surface. When well-developed, the veil can be observed as flocci, scales, or patches on the cap surface. In most species, the stem is pulverulent or pruinose at the apex with more or less evident veil remnants below. The upper part of the veil sometimes leaves an annulus or fugacious ring-zone that must be noted. This zone is rarely present at the lower part of the stem. If possible, all stages of basidiomata development were collected in order to cover changes in cap colours and veil features. Moreover, the cap and stem surface was examined for projecting hairs that

are present in a few species (e.g., *P. tenuicula*). Before drying the material spore prints were taken and any green reaction of the gill edge in 10 % NH_4OH was observed in a microscope.

Micromorphological characters were observed using a Nikon Eclipse E200 light microscope equipped with phase contrast. Digital images were recorded with a Nikon Infinity 2 camera. For each collection, 10 to 20 mature spores were measured in water at ×1,000 magnification. Abnormally large or small spores were not considered. Other microscopic characters were studied in a 10 % NH_4OH solution and measured to nearest micron. To observe the hymenial cystidia, a complete lamella was cut off with a razor blade and soaked for a while. The gill edge was removed in order to check the cheilocystidia. The middle portion of the gill was cut out, crushmounted, and pleurocystidia, basidia, subhymenium, and hymenophoral trama studied. The layers of the pileus were observed halfway from the margin by cutting tangential to the pileus, called a 'scalp'. The cells of the pileipellis and the hyphae of the pileitrama can then be observed. If the material admitted, a radial cut to the pileus was done instead, resulting in a better picture of the different layers. In addition, if a veil was present above the pileipellis it could be more satisfactory located. Finally, the veil tissue from cap margin and the presence of clamps were checked. As for the shape of spores and cystidia the terminology of Vellinga (1988) was followed. Spores were mounted in a solution of ammonia while cystidia and other cells were mounted in a solution of ammonia stained with Congo Red before capturing digital images. To get a better resolution, most microscopical features except spores were then uniformly coloured with the program Adobe Photoshop CS2. All scale bars in the figures represent 10 μm. Line drawings of the micro-morphology are presented in association with the species descriptions.

Collections are deposited in Herbarium GB, University of Gothenburg, if not otherwise indicated. Types and other collections were studied as loans from AH, AMNH, B, BAFC, BR, C, CBM, CUP, E, F, G, GB, GDGM, GH, H, K, L, LD, MICH, NY, NYS, O, PC, S, SGO, SZE, TAA, TROM, TURA, UPS, WAG-W, WBS, WU, XAL, and ZT. Material was also received as gifts or loans from several private herbaria. Data on type specimens and other specimens morphologically studied, but not sequenced are provided as Supplementary data S1.

Specimen sampling Our sampling emphasized *Psathyrella* in Europe and its northern part, aiming to find and include representatives from all known or putative taxa of *Psathyrella*. To be more representative, the specimen sampling was extended to outside Europe, including also tropical regions and the Southern Hemisphere. Also, other genera of the *Psathyrellaceae* were to some extent taken into account.

The ITS and LSU sequence dataset from our study on coprophilous *Psathyrella* species (Larsson and Örstadius 2008) was extended and complemented. Sequences in this study were generated from 182 specimens, representing 132 species of *Psathyrella* sensu lato and, in total, 148 species in Psathyrellaceae, and includes 55 type specimens (Table 1). In addition, sequence data (ITS, LSU, β-tub, and Tef-1α) representing six *Psathyrella*, 11 *Coprinellus*, two *Coprinus cordisporus,* one *Cystoagaricus*, seven *Coprinopsis,* and four *Parasola* species were retrieved from GenBank and added to the dataset. The selection was based on previous molecular studies of Agaricales and *Psathyrellaceae* (Vellinga 2004; Padamsee et al. 2008; Vašutová et al. 2008; Nagy et al. 2011, 2012, 2013b). Based on results from earlier molecular phylogenetic studies of Agaricales (Moncalvo et al. 2002; Matheny et al. 2006), representatives of *Bolbitius*, *Mythicomyces*, *Stagnicola*, *Agrocybe*, and *Conocybe* were selected as the outgroup in the analyses.

For the neotypification of species originally described by Fries from Sweden, representative collections were selected and the ITS generated, if not already included in the large dataset.

Molecular work Sequences from four regions were generated for the study: the complete ITS region and about 1,000 base pairs (bp) of the 5′ end of the LSU nuclear ribosomal DNA, about 1,000 bp of translation elongation factor subunit 1 alpha (Tef-1α), and about 500 bp of the β-tubulin gene. DNA extractions, PCR reactions, and sequencing were performed as described in Larsson and Örstadius (2008). Primers used to amplify the complete ITS region and the 5′ end of the LSU region were ITS1F (Gardes and Bruns 1993) and LR21, LR0R, and LR7 (Hopple and Vilgalys 1999); for Tef-1α we used EF983F and EF2218R (www.aftol.org/pdfs/EF1primer); for β-tub B36f and B12r (Nagy et al. 2011). Primers used for sequencing were ITS1, ITS4 (White et al. 1990), Ctb6 (http://plantbio.berkeley.edu/~bruns/) and Lr5 (Hopple and Vilgalys 1999), EF983F, EF2218R, and 1567Ra (www.aftol.org/pdfs/EF1primers), B36f and B12r. DNA extraction, PCR, and sequencing of old type specimens follow Larsson and Jacobsson (2004).

Phylogenetic analyses Sequences were edited and assembled using Sequencher 4.1 (Gene Codes, Ann Arbor, MI, USA). Alignment of individual genes was performed using the L-INS-i strategy as implemented in MAFFT v. 7.017 (Katoh and Standley 2013). The alignment was adjusted manually using the data editor in PAUP* 4.0b12 (Swofford 2003). Sequences have been

Table 1 Data of specimens used in the phylogenetic analysis

Species	Coll. ID./Origin	Ecology/substrate	GenBank Accession Numbers		
			ITS/LSU	β-Tub	Tef 1-α
Coprinellus christianopolitanus Örstadius & E. Larss.	LÖ141-08 type/Sweden	On a lawn in a park	KC992944		KJ732823
C. silvaticus (Peck) Gminder	LÖ172-08/Sweden	On *Fagus* wood	KC992943	KJ664911	KJ732822
C. sclerocystidiosus (M. Lange & A. H. Sm.) Vilgalys, Hopple & Jacq. Johnson	LÖ407-05/Sweden	In a pasture	KC992942		
Coprinopsis canoceps (Kauffman) Örstadius & E. Larss.	LÖ148-95/Sweden	On nitrophilous soil	KC992964		
C. cineraria (Har. Takah.) Örstadius & E. Larss.	CBM-FB-24142 type/Japan	On decayed wood	KC992962		
C. cineraria	CBM-FB-32880/Japan	Unknown	KC992963		
C. marcescibilis (Britzelm.) Örstadius & E. Larss.	LÖ31-03/Sweden	In a park with *Urtica dioica*	DQ389728	KJ664919	KJ732829
C. melanthina (Fr.) Örstadius & E. Larss.	WU19918/Portugal	By *Carpobrotus edulis*	KC992961		
C. pannucioides (J. E. Lange) Örstadius & E. Larss.	LÖ143-03/Sweden	On clayey soil, *Fagus* forest	DQ389727	KJ664917	
C. submicrospora (Heykoop & G. Moreno) Örstadius & E. Larss.	AH27055 type/Spain	Among moss in woodland	KC992959	KJ664918	
C. udicola Örstadius, A. Melzer & E. Larss.	AM1240 type/Germany	On moist soil	KC992967	KJ664922	KJ732831
C. uliginicola (McKnight & A. H. Sm.) Örstadius & E. Larss.	Smith34903 (MICH) type/USA	Moist habitat	KC992960		
C. musae Örstadius & E. Larss.	JV06-179 type/Denmark	On *Musa* in a greenhouse	KC992965	KJ664920	
C. musae	JV06-180/Denmark	On *Musa* in a greenhouse	KC992966	KJ664921	KJ732830
Coprinus cordisporus T. Gibbs	LÖ41-01/Sweden	Cow dung	DQ389723	KJ664910	
Homophron cernuum (Vahl: Fr.) Örstadius & E. Larss.	LÖ134-98/Sweden	Caespitose on a stump	DQ389726	KJ664915	KJ732828
H. spadiceum (P. Kumm.) Örstadius & E. Larss.	Enderle epitype/Germany	Caespitose on a tree base	DQ389729		
H. camptopodum (Sacc.) Örstadius & E. Larss.	1997/956 (IB)/Russia	On very rotten *Betula*	KC992956		
Kauffmania larga (Kauffman) Örstadius & E. Larss.	LÖ223-90/Sweden	In a rich deciduous forest	DQ389694	KJ664912	KJ732824
K. larga	LAS97-054/Sweden	Well-decayed stump	DQ389695		
Lacrymaria glareosa (J. Favre) Watling	Heinemann8158 (BR)/Italy	Moist, *Equisetum palustre*	KC992955		
L. glareosa (J. Favre) Watling	LAS06-019/Sweden	On moist soil	KC992954	KJ664914	KJ732827
L. hypertropicalis (Guzmán, Bandala & Montoya) Cortez	Guzmán29585 (XAL)/Mexico	On soil	KC992958	KJ664916	
L. lacrymabunda (Bull.) Pat.	EL70-03/Sweden	In a pasture	DQ389724		
L. pyrotricha (Holmsk.) Konrad & Maubl.	RGC KAJ19950919/Sweden	On soil along roadside	KC992952		
L. rigidipes (Peck) Watling	LAS00-081/Sweden	Along roadside	KC992953	KJ664913	KJ732826
L. subcinnamomea (A. H. Sm.) Watling	Smith16957 (MICH) type/USA	On soil along a road	KC992951		
Parasola conopilus (Fr.: Fr.) Örstadius & E. Larss.	LÖ186-02/Sweden	On buried wood	DQ389725		KJ732832
Psathyrella abieticola A. H. Sm.	Smith58673 (MICH) type/USA	Under spruce and fir	KC992891		
P. albofloccosa Arenal, M. Villarreal & Esteve-Rav.	Sivertsen 65–89 (TROM)/ Norway	On grass remnants	DQ389708		
P. amarescens Arnolds	Arnolds02-78 (L) type/Netherlands	On wood-chips and soil	KC992852	KJ664842	
P. ammophila (Lév. & Durieu) P. D. Orton	LÖ169-01/Sweden	On sand dune	KC992871	KJ664852	KJ732766
P. ammophila	LÖ359-11/Sweden	On moist soil	KC992872	KJ664853	KJ732767
P. arenosa Örstadius & E. Larss.	LÖ220-96 type/Sweden	Dry, sandy, calcareous soil	KC992895	KJ664875	KJ732784
P. arenosa	LÖ330-01/Sweden	Dry, sandy, calcareous soil	KC992896	KJ664876	KJ732785
P. atomatoides (Peck) A. H. Sm.	LÖ249-82/Sweden	Moist on wood in a forest	KC992930		

Table 1 (continued)

Species	Coll. ID./Origin	Ecology/substrate	GenBank Accession Numbers		
			ITS/LSU	β-Tub	Tef 1-α
P. badhyzensis Kalamees	79478 (TAA) type/Turkmenistan	On soil in frondose forest	KC992883		
P. bipellis (Quél.) A.H. Sm.	LÖ207-96/Sweden	On soil in a pasture	DQ389679		
P. bipellis	LÖ50-04/Sweden	In a rich deciduous forest	DQ389680	KJ664847	KJ732761
P. bipellis	LÖ426-05/Sweden	On soil in *Fagus* forest	KC992865	KJ664848	KJ732762
P. calcarea (Romagn.) M. M. Moser	LÖ211-03/Sweden	On dry, calcareous soil	DQ389671	KJ664839	KJ732754
P. candolleana (Fr.: Fr.) Maire	LÖ38-00/Sweden	In a rich deciduous forest	DQ389720	KJ664864	
P. caput-medusae (Fr.) Konrad & Maubl.	LÖ36-94/Sweden	On a stump in a rich forest	KC992927	KJ664904	KJ732814
P. carminei Örstadius & E. Larss.	LÖ5-09 type/Italy	On soil in *Pinus* forest	KC992880	KJ664861	KJ732773
P. clivensis (Berk. & Broome) P. D. Orton	LÖ182-03/Sweden	On the great alvar	DQ389683	KJ664862	KJ732774
P. conferta Eyssart. & Chiaffi	GE02.007 (PC) type/France	On woody debris in a forest	KC992890		
P. corrugis (Pers.: Fr.) Konrad & Maubl.	LÖ171-01/Sweden	Attached to buried wood	DQ389674		KJ732757
P. cortinarioides P. D. Orton	LÖ77-00/Sweden	Moist, rich with *Alnus*	KC992936	KJ664908	
P. cotonea (Quél.) Konrad & Maubl.	LÖ136-00/Sweden	Around stump of *Fagus*	KC992870		
P. crenulata A. H. Sm.	W-K 8/10/64-5 (MICH) type/USA	In moss around tree bases	KC992957		
P. dicrani (A. E. Jansen) Kits van Wav.	LÖ270-04/Sweden	On dry, sandy soil	DQ389698	KJ664885	KJ732797
P. duchesnayensis A. H. Sm.	Smith61737 (MICH) type/USA	Under spruce and balsam	KC992869		
P. dunensis Kits van Wav.	LÖ-318-92/Sweden	On soil in a rich forest	KC992857		
P. echinata (Cleland) Grgur.	ZT12073/New Zealand	On rotten wood and bark	KC992925	KJ664900	
P. effibulata Örstadius & E. Ludw.	LÖ37-96 type/Sweden	In a field margin	DQ389672		
P. efflorescens (Berk. & Broome) Pegler	Pegler2133 (K)/Sri Lanka	On bark and coconut husks?	KC992941		
P. epimyces (Peck) A. H. Sm.	WU19965/Portugal	Parasitic on a coprinoid sp.	KC992928	KJ664905	KJ732815
P. fagetophila Örstadius & Enderle	LÖ210-85 (M) type/Sweden	Woodland among leaves	KC992902	KJ664879	
P. fatua (Fr.) Konrad & Maubl.	LÖ132-97/Sweden	On nitrophilous soil	DQ389681	KJ664859	KJ732776
P. fatua	LÖ231-08/Sweden	On dry sandy soil	KC992879	KJ664860	KJ732772
P. fennoscandica Örstadius & E. Larss.	LÖ484-05 type/Sweden	In a moist pasture with trees	KC992903	KJ664881	KJ732790
P. fennoscandica	LÖ95-96/Sweden	Moist with conifers	KC992904	KJ664882	KJ732791
P. fibrillosa (Pers.: Fr.) Maire	LÖ138-00/Sweden	Among leaves of *Fagus*	DQ389686		
P. fimiseda Örstadius & E. Larss.	LÖ56-96 type/Sweden	Cow dung	DQ389690		
P. flexispora T. J. Wallace & P. D. Orton	LÖ228-00/Sweden	On sandy soil in a pasture	KC992929		
P. fusca (J.E. Lange) A. Pearson	LÖ287-04/Sweden	On calcareous soil	KC992892		KJ732779
P. globosivelata Gröger	Schumacher035/Germany	On moist, sandy soil	KC992922	KJ664895	KJ732805
P. gordonii (Berk. & Broome) A. Pearson & Dennis	LÖ220-95/Sweden	On debris of wood	KC992924	KJ664898	KJ732807
P. hirta Peck	Ö142-00/Sweden	Cow dung	DQ389702		KJ732800
P. hirtosquamulosa (Peck) A. H. Sm.	Ramsholm800927 (H)/Finland	On decayed log	KC992945		
P. hololanigera (G. F. Atk.) A. H. Sm.	Hausknecht 071109/Italy	On sandy soil with *Pinus*	KC992908		KJ732794
P. ichnusae Örstadius, Contu, E. Larss.,& Vizzini	Contu 080106 type/Italy	On burnt soil in grassland	KC992911		KJ732795
P. impexa (Romagn.) Bon	LÖ78-93/Sweden	On a gravelly path	KC992900		
P. impexa	LÖ162-03/Sweden	In moos attached to wood	KC992901	KJ664878	KJ732789
P. jacobssonii Örstadius	LÖ256-92 type/Sweden	Moist herb-rich forest	KC992855		
P. kellermanii (Peck) Singer	de Meulder11242 (BR)/Belgium	Not given	KC992920		
P. kitsiana Örstadius	Ö217-85 type/Sweden	On or near a stump	DQ389689		
P. lacuum Huijsman	Jóhansen (C)/the Faroes	In flowerpots of *Yucca* sp.	KC992887		
P. laricina A. H. Sm.	Smith64604 (MICH) type/USA	Under larch in a plantation	KC992914		

Table 1 (continued)

Species	Coll. ID./Origin	Ecology/substrate	GenBank Accession Numbers		
			ITS/LSU	β-Tub	Tef 1-α
P. leucotephra (Berk. & Broome) P.D. Orton	LÖ138-01 (UPS)/Sweden	Caespitose on wood	KC992885	KJ664865	KJ732775
P. lilliputana Örstadius & E. Larss.	LÖ130-09 type/Sweden	On wood remnants	KC992850	KJ664840	KJ732756
P. longicauda P. Karst.	LÖ201-02/Sweden	In a copse	DQ389676	KJ664868	KJ732778
P. longicauda	LÖ254-91/Sweden	On soil in *Fagus* forest	KC992889		
P. lutensis (Romagn.) Bon	LÖ98-03/Sweden	On soil attached to sticks	DQ389685	KJ664869	
P. luteopallida A. H. Sm.	Sharp20863 (MICH) type/USA	On soil and humus	KC992884		
P. lutulenta Esteve-Rav. & M. Villarreal	21379 (AH) type/Spain	On muddy soil	KC992875	KJ664855	KJ732769
P. lyckebodensis Örstadius & E. Larss.	LÖ301-11 type/Sweden	On dry, sandy soil	KC992921	KJ664894	KJ732804
P. macrocystidiata Arnolds	Arnolds00-176 (L) type/Italy	Among litter with *Fagus*	KC992866		
P. maculata (C. S. Parker) A. H. Sm.	LÖ240-84/Sweden	On a stump in *Fagus* forest	KC992935		KJ732820
P. madida Örstadius & E. Larss.	LÖ377-06 type/Sweden	Moist, sandy soil	KC992932		KJ732818
P. madida	LÖ369-06/Sweden	Moist, sandy soil	KC992933	KJ664907	KJ732819
P. magnispora Heykoop & G. Moreno	24929 (AH) type/Spain	In chalk grassland	KC992863	KJ664846	
P. magnispora	Barta, Spittelberg/Austria	In poor, dry meadow	KC992864		
P. merdicola Örstadius & E. Larss.	LÖ45-02 type/Sweden	Cow dung	DQ389688		KJ732798
P. mesobromionis Arnolds	Arnolds01-174 (L) type/Netherlands	In poor hay field	KC992862		
P. microrhiza (Lasch: Fr.) Konrad & Maubl.	LÖ185-02/Sweden	In a rich deciduous forest	DQ389684	KJ664851	KJ732765
P. microrhiza	LÖ136-08 type/Sweden	On fire place with wood	KC992868	KJ664850	KJ732764
P. mucrocystis A. H. Sm.	LÖ103-98/Sweden	On a stump	DQ389700	KJ664901	KJ732810
P. multipedata (Peck) A. H. Sm.	LÖ237-04/Sweden	In a rich deciduous forest	KC992888	KJ664867	KJ732777
P. noli-tangere (Fr.) A. Pearson & Dennis	LÖ83-03/Sweden	Among leaves in a forest	DQ389713	KJ664890	
P. obscurotristis Enderle & M. Wilh.	Wilhelm489 (ULM) type/France	On a stump of *Quercus*?	KC992931		KJ732816
P. obtusata (Pers.: Fr.) A. H. Sm.	LÖ88-01/Sweden	In moist soil in forest	DQ389711	KJ664844	
P. olivaceogrisea A. H. Sm.	WK 8/15/63-5 (MICH) type/USA	Decaying cottonwood logs	KC992948		
P. olympiana A. H. Sm.	LÖ32-02/Sweden	On soil attached to wood	DQ389722	KJ664906	KJ732817
P. orbicularis (Romagn.) Kits van Wav.	LÖ211-04/Sweden	On dry, sandy soil	DQ389692		KJ732788
P. orbicularis	LÖ149-11/Sweden	On open dry grassland	KC992897		KJ732786
P. orbicularis	LÖ210-04/Sweden	On dry sandy soil	KC992898		KJ732787
P. orbitarum (Romagn.) M. M. Moser	LÖ257-90/Sweden	In a rich deciduous forest	DQ389673		
P. ornatispora M. Villarreal & Esteve-Rav.	AH26978 type/Spain	On soil in a greenhouse	KC992968		KJ732833
P. panaeoloides (Maire) Arnolds	LÖ44-03/Sweden	In mud of a fen	DQ389719	KJ664873	KJ732782
P. panaeoloides	LÖ293-04/Sweden	On soil in a dry pasture	KC992894	KJ664874	KJ732783
P. parva A. H. Sm.	LÖ23-08/Italy	On acid sandy soil	KC992912	KJ664884	KJ732796
P. parva	LÖ81-95/Sweden	In grassland	KC992913		
P. pennata (Fr.) A. Pearson & Dennis	LÖ206-03/Sweden	On burnt soil	DQ389710	KJ664903	KJ732813
P. pertinax (Fr.) Örstadius	LÖ259-91/Sweden	On mossy twigs of *Picea*	DQ389701		KJ732809
P. piluliformis (Bull.: Fr.) P. D. Orton	LÖ162-02/Germany	On stump of *Fagus*	DQ389699	KJ664899	KJ732808
P. potteri A. H. Sm.	LÖ271-01/Sweden	On nitrophilous soil	DQ389665		KJ732755
P. prona (Fr.) Gillet	LÖ91-99/Sweden	In a rich deciduous forest	DQ389666		
P. psammophila A. H. Sm.	Smith67836 (MICH) type/USA	In sandy soil	KC992856		
P. pseudocasca (Romagn.) Kits van Wav.	LÖ17-04/Sweden	In a rich deciduous forest	DQ389691		KJ732799
P. pseudocorrugis (Romagn.) Bon	LÖ226-06/Sweden	On soil with frondose trees	KC992917	KJ664888	KJ732801
P. pseudogracilis (Romagn.) M. M. Moser	LÖ172-02/Sweden	In a shrubbery	DQ389675	KJ664843	KJ732758
P. pseudogracilis	LÖ287-06/Sweden	On woody remnants	KC992853	KJ664870	KJ732759
P. purpureobadia Arnolds	LÖ23-94/Sweden	Gregarious on cow dung	DQ389678		
P. purpureobadia	9956 (L) type/Netherlands	In a grazed grassland	EU126026		

Table 1 (continued)

Species	Coll. ID./Origin	Ecology/substrate	GenBank Accession Numbers		
			ITS/LSU	β-Tub	Tef 1-α
P. pygmaea (Bull.: Fr.) Singer	LÖ97-04/Sweden	On wood of *Salix*	DQ389718	KJ664902	KJ732811
P. riparia A. H. Sm.	Brooks1600 (MICH) type/USA	In sandy soil along a stream	KC992860		
P. romagnesii Kits van Wav.	LÖ85-98/Sweden	Horse dung	DQ389716		
P. romagnesii	LÖ267-04/Sweden	Horse dung	DQ389715	KJ664889	KJ732802
P. romellii Örstadius	LÖ240-01 (UPS) type/Sweden	On rotten stump of *Fagus*	KC992859	KJ664845	
P. rostellata Örstadius	LÖ 228–85 type/Sweden	Deciduous wood	DQ389693		
P. rubiginosa A. H. Sm.	LÖ107-98/Sweden	Moist among plants	KC992905		
P. rufescens (Petch) Pegler	14790 (WU)/Mauritius	On soil	KC992881		
P. rybergii Örstadius & E. Larss.	LÖ373-06 type/Sweden	Among gravel on a path	KC992893	KJ664872	KJ732781
P. sabuletorum Örstadius & E. Larss.	LÖ196-98 type/Sweden	On steppe-like sandy soil	KC992919	KJ664892	
P. sabuletorum	JV90-770 (C)/Denmark	In sand dune	KC992918		
P. saponacea F. H. Møller	LÖ204-96/Sweden	Horse dung	DQ389717	KJ664871	KJ732780
P. scanica Örstadius & E. Larss.	LÖ183-09 type/Sweden	On sandy, calcareous soil.	KC992910		KJ732793
P. scatophila Örstadius & E. Larss.	LÖ64-95 type/Sweden	Horse dung	DQ389703	KJ664896	
P. seminuda A. H. Sm.	Smith34091 (MICH) type/USA	On soil	KC992907		
P. senex (Peck) A. H. Sm.	LÖ115-02/Germany	In a park, among leaves	DQ389712	KJ664880	
P. seymourensis A. H. Sm.	LÖ42-87/Sweden	On sand in an open pasture	KC992915		
P. siccophila Örstadius & E. Larss.	LÖ417-06 type/Sweden	Dry, sandy grassland	KC992916	KJ664887	
P. sp.	LÖ312-92/Sweden	On moist soil by *Alnus*	KC992851		
P. sp.	Contu 071230/Italy	In coastral grassland	KC992909	KJ664883	KJ732792
P. sp.	NL-2349/Hungary	In mown lawn	KC992858		KJ732760
P. sp.	NL-0631/Hungary	On clayey, mossy soil	KC992877	KJ664856	KJ732770
P. sp.	LÖ96-11/Sweden	On soil in a pasture	KC992923	KJ664897	KJ732806
P. spadiceogrisea (Schaeff.) Maire	LÖ92-01/Sweden	In a deciduous forest	DQ389682	KJ664858	
P. spadiceogrisea	LÖ102-98/Sweden	Among leaves in a pasture	KC992878	KJ664857	KJ732771
P. sphaerocystis P. D. Orton	LÖ126-99/Sweden	Horse dung	DQ389709	KJ664893	KJ732803
P. sphagnicola (Maire) J. Favre	LÖ233-99/Sweden	On *Sphagnum* with *Picea*	KC992937		
P. spintrigeroides P. D. Orton	LÖ122-86/Sweden	On a stump	DQ389696	KJ664891	
P. squamosa (P. Karst.) A. H. Sm.	LÖ104-95/Sweden	In a gravel at a roadside	DQ389687		
P. squamosa	LÖ164-96/Sweden	In a pasture grazed by sheep	KC992939		
P. squamosa	LÖ194-96/Sweden	On a sandy roadside	KC992940		
P. squarrosiceps Singer	Laessoe44835 (C)/Ecuador	On rotten wood	KC992950		
P. stercoraria Örstadius & E. Larss.	Kytövuori Virrat 1991 (H)/Finland	In a pasture	DQ389670		
P. stercoraria	LÖ460-05 type/Sweden	Cow dung	DQ389669	KJ664841	
P. stridvallii Örstadius & E. Larss.	LÖ104-98 type/Sweden	On a manured lawn	KC992926		KJ732812
P. suavissima Ayer	LÖ4-87/Sweden	On rotten chips	KC992899	KJ664877	
P. sublatispora Örstadius & E. Larss.	LÖ190-97 type/Sweden	In a field on sandy soil	KC992854		
P. supernula (Britzelm.) Örstadius & Enderle	LÖ250-04/Sweden	On sandy soil in a pasture	KC992867	KJ664849	KJ732763
P. silvestris (Gillet) Konrad & Maubl.	LÖ191-92/Sweden	On soil in a rich forest	KC992949		
P. tenera Peck	LÖ81-83/Sweden	In a moist *Alnus* forest	KC992849		
P. tenera	LÖ382-89/Sweden	In a moist, rich forest	DQ389667		
P. tenuicula (P. Karst.) Örstadius & Huhtinen	LÖ37-04/Sweden	Wild boar dung	DQ389704		
P. tenuicula	LÖ58-03/Sweden	On soil rich in humus	DQ389706		
P. thujina A. H. Sm.	Smith66720 (MICH) type/USA	On black muck	KC992876		
P. thujina	LÖ379-06/Sweden	On remnants of *Phragmites*	KC992873	KJ664854	KJ732768

Table 1 (continued)

Species	Coll. ID./Origin	Ecology/substrate	GenBank Accession Numbers		
			ITS/LSU	β-Tub	Tef 1-α
P. thujina	Ö31-04/Sweden	On moist soil	KC992874		
P. trinitatensis R.E.D. Baker & W.T. Dale	TL9035 (C)/Ecuador	On litter and rotten wood	KC992882	KJ664863	
P. tuberculata (Pat.) A. H. Sm.	ADK4162 (BR)/Togo	On decayed wood	KC992886		
P. tuberculata	ADK3564 (BR)/Benin	Unknown	KC992934		
P. typhae (Kalchbr.) A. Pearson & Dennis	LÖ21-04/Sweden	On remnants of *Typha*	DQ389721	KJ664866	
P. umbrina Kits van Wav.	LÖ235-04/Sweden	In a rich deciduous forest	DQ389697	KJ664886	
P. vesterholtii Örstadius & E. Larss.	JHP10.086 (C) type/Denmark	Among mosses	KC992938	KJ664909	KJ732821
P. vinosofulva P. D. Orton	LÖ2-88/Spain	In grass attached to wood	KC992861		
P. warrenensis A. H. Sm.	Smith70162 (MICH) type/USA	On grassy soil	KC992906		
Typhrasa gossypina (Bull.: Fr.) Örstadius & E. Larss.	Schumacher024/Germany	On litter of *Fagus*	KC992946		KJ732825
T. nanispora Örstadius, Hauskn. & E. Larss.	Barta980706 type/Austria	On soil in a forest	KC992947		
Agrocybe pusiola (Fr.) R. Heim	LÖ 304–05/Sweden	On calcareous soil	DQ389732		
Bolbitius excoriatus Dähnke, Hauskn., Krisai., Contu & Vizzini	LÖ23-10/Sweden	On cow dung	KC456419		KJ732834
Conocybe siliginea (Fr.) Kühner	LÖ93-04/Sweden	In a pasture	DQ389731		
Galerina marginata (Batsch) Kühner	RM3225/Sweden	On wood	AF195590		
Psilocybe semilanceata (Fr.) P. Kumm.	Holst84/Sweden	In grass	EU029945		

Sequenced specimens have been deposited in Herbarium GB if not otherwise stated

deposited in GenBank and accession numbers are listed in Table 1.

Maximum likelihood (ML) analysis was performed using RAxML 7.0.4 (Stamatakis 2006). It was tested for conflict between the genes by comparing supported clades. Support values for each gene were estimated by 1,000 rapid bootstraps and conflicts in clades with higher support than 70 was considered significant. Four different partitioning schemes were compared: all genes in one partition, each gene in separate partitions (three partitions), each gene in separate partitions and third position partitioned separately in the protein coding genes (five partitions), and each gene partitioned separately and each codon position partitioned separately (seven partitions). It was also compared if GTR plus gamma or GTR plus gamma and invariable sites was the best fit. All model comparisons were done with AIC. Support values for the catenated genes under the best fitting model were calculated from 10,000 rapid bootstraps. Seven specific constraints were implemented to test if the following could be rejected: 1) Psathyrella s.s. is monophyletic excluding /cordisporus, 2) Psathyrella s.s., /Coprinellus, and /candolleana are monophyletic excluding /cordisporus, 3) Psathyrella s.l. is monophyletic excluding /cordisporus, 4) Psathyrella s.s. including /gossypina is monophyletic, 5) Psathyrella s.s. including the /candolleana clade is monophyletic, 6) Psathyrella s.l. is monophyletic excluding /Coprinellus, 7) /Parasola is nested in Psathyrella s.l. with at least the /gossypina clade more basal (i.e., Psathyrella s.l. is not monophyletic). The constraint topologies were compared to the ML tree using the SH-test as implemented in RAxML.

Bayesian analysis was done in MrBayes 3.1.2 using the partitioning scheme and model selected in the ML analysis. Four parallel runs with four chains each (three heated) were executed. Each run had 200 million generations, sampling every 10,000th generation. Burn-in was determined using TRACER (Rambaut and Drummond 2007) and AWTY (Nylander et al. 2008). Constraints one to six above were compared using posterior odds calculated from the Bayesian MCMC run. Instead of constraint seven it was tested directly if Psathyrella sensu lato is monophyletic. Posterior odds are conservative compared to Bayes factors when assuming equal prior on all topologies (Bergsten et al. 2013).

Phylogenetic analyses were based on the concatenated gene alignments. Heuristic searches for the most parsimonious trees were performed using PAUP* (Swofford 2003). All transformations were considered unordered and equally weighted. Variable regions with ambiguous alignment were excluded and gaps were treated as missing data. Heuristic searches with 1,000 random-addition sequence replicates and TBR branch swapping were performed, saving at most 25 trees in each replicate. Relative robustness of clades was assessed by the bootstrap method using 1,000 heuristic search replicates with 100 random taxon addition sequence replicates

and TBR branch swapping, the latter saving at most 25 trees in each replicate.

Results

Phylogenetic results

The aligned complete dataset, including 31 sequences downloaded from GenBank, consisted of 218 taxa and 3,604 characters. After exclusion of ambiguous regions from the ITS region, and from intron regions of the Tef-1α and β-tub genes, 2,566 characters remained for the analysis. Of these, 1,381 were constant, 263 were variable but parsimony uninformative, and 922 (36 %) were parsimony informative.

The maximum parsimony analysis yielded 300 equally parsimonious trees (length = 8,158 steps, CI = 0.2392, and RI = 0.6112). One of the trees is presented as a phylogram in Fig. 1a and b. The bootstrap analysis recovered *Psathyrellaceae* as monophyletic including six major supported clades, /Psathyrella s. l. (including /Coprinellus and /cordisporus, 89 %), /gossypina (90 %), /Lacrymaria (100 %), /Homophron (100 %), /Coprinopsis (82 %), and /Parasola (100 %). Within /Psathyrella s.l., /Psathyrella s.s. received no support, but 19 major and minor clades within /Psathyrella s.l. were weakly to strongly supported; these are marked as subclades in the phylogram in Fig. 1a and b. Some of the subclades more or less correspond to morphological species groups and taxa, and these are further described and discussed below.

No conflict was found between genes. The model with seven partitions and GTR plus gamma and invariable sites was supported as the best by AIC. None of the constraints were significantly worse using the SH-test so in the ML framework we cannot reject that the /cordisporus and /Coprinellus clades, respectively, are outside Psathyrella s.s. or that the /gossypina and /candolleana clades, respectively, are part of /Psathyrella s.s. Neither can we reject that /Psathyrella s.l. is paraphyletic with respect to /Parasola. The ML bootstrap support values are shown in Fig. 1a and b.

The burn-in for the Bayesian analysis was set to 100 million generations. The monophyly of /Psathyrella s.l. is supported (posterior odds 32.3), but none of the other constraints received support (posterior probability to low to be measured). In a Bayesian context it was thus rejected that the /cordisporus and /Coprinellus clades are outside Psathyrella s.l., and that the /candolleana or /gossypina clades are within /Psathyrella s.s. In the Bayesian analysis, Psathyrella s.s. received a BPP value of 0.98. Bayesian supports are shown in Fig. 1a and b.

From our sampling and phylogenetic analysis we recognize 116 species as belonging to *Psathyrella,* and of these, 15 are new and described below. In addition, we also identified and described one species of *Coprinellus* and two of *Coprinopsis* as new to science.

Psathyrella ornatispora does not belong to *Psathyrellaceae* and should be moved to another genus in Agaricales. Best match in GenBank when blasting the ITS region is with *Melanophyllum haematospermum*, but with 93 % identity only. Ninety-two species were identified to occur in Northern Europe.

Discussion

In this study we find support for recognizing the clades, /Parasola, /Coprinopsis, /Homophron, /Lacrymaria, and /gossypina, as distinct lineages within Psathyrellaceae. /Coprinellus and /cordisporus fall within the larger supported clade we here named /Psathyrella s.l. The molecular support for the clade /Psathyrella s.s., that includes the majority of species described in *Psathyrella*, is low but with support from the morphology we suggest recognizing the clade as distinct.

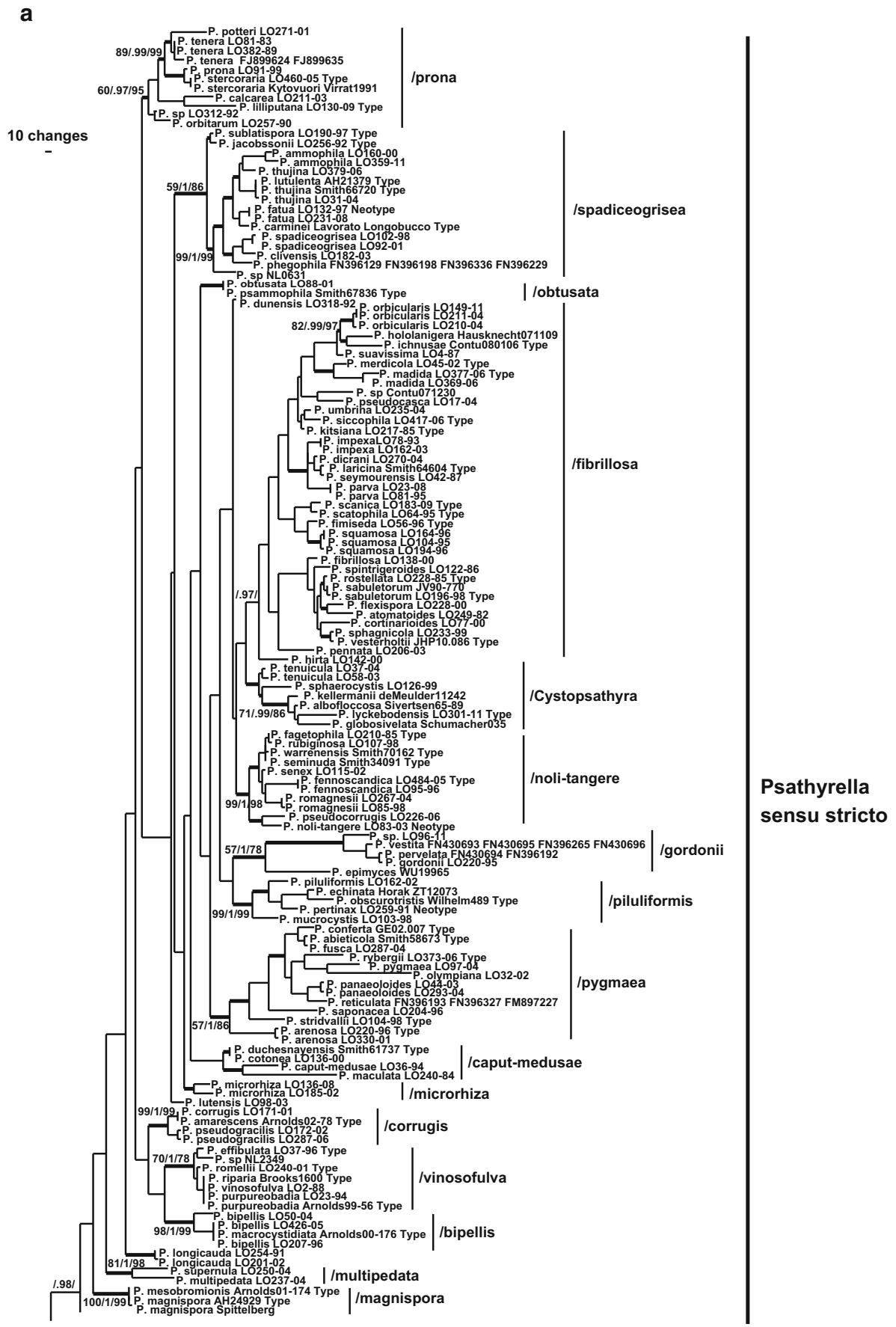
The results are very much in congruence with our previous study (Larsson and Örstadius 2008) based on ITS and LSU sequence data alone, but with the major difference that the support values for the majority of clades are higher.

Several new species, with a focus on psathyrelloid taxa, were added to the data set and particular efforts were made to find representatives for the minor, less species rich clades. We believe that it has strengthened the results and our aim to evaluate morphological characters.

The phylogeny is based on the same regions of sequence data as used in Nagy et al. (2013b), but analysed in a more traditional way. To split *Psathyrella* into several smaller genera as proposed by Nagy et al. (2013b) was not supported by our analyses, and can neither be supported nor legitimized by finding distinct and segregating morphological characters that unambiguously circumscribe the supported clades. The situation with the paraphyletic *Psathyrella* is not solved, but we believe that a more conservative approach is to prefer until stronger evidence for an alternative solution is available.

Morphological characters

A morphological characterization of the clades is difficult. For several of the already formally described and circumscribed genera within Psathyrellaceae, the phylogenetic analyses now suggest many of the corresponding clades to include a morphologically heterogeneous assemblage of species. In Table 2 a summary of discriminating characters for each major clade recognized in this study is presented with some further remarks here. Terminology of the pileipellis follows Clémençon et al. (2004). Basidia: psathyrelloid species are ususally circumscribed as having monomorphic basidia, and such species are now also shown to occur in *Coprinopsis.*


a
10 changes
P. potteri LO271-01
P. tenera LO81-83
P. tenera LO382-89
P. tenera FJ899624 FJ899635
P. prona LO91-99
P. stercoraria LO460-05 Type
P. stercoraria Kytovuori Virrat1991
P. calcarea LO211-03
P. lilliputana LO130-09 Type
P. sp LO312-92
P. orbitarum LO257-90
89/.99/99
60/.97/95
/prona
P. sublatispora LO190-97 Type
P. jacobssonii LO256-92 Type
P. ammophila LO160-00
P. ammophila LO359-11
P. thujina LO379-06
P. lutulenta AH21379 Type
P. thujina Smith66720 Type
P. thujina LO31-04
P. fatua LO132-97 Neotype
P. fatua LO231-08
P. carminei Lavorato Longobucco Type
P. spadiceogrisea LO102-98
P. spadiceogrisea LO92-01
P. clivensis LO182-03
P. phegophila FN396129 FN396198 FN396336 FN396229
P. sp NL0631
59/1/86
99/1/99
/spadiceogrisea
P. obtusata LO88-01
P. psammophila Smith67836 Type
P. dunensis LO318-92
/obtusata
P. orbicularis LO149-11
P. orbicularis LO211-04
P. orbicularis LO210-04
P. hololanigera Hausknecht071109
P. ichnusae Contu080106 Type
P. suavissima LO4-87
P. merdicola LO45-02 Type
P. madida LO377-06 Type
P. madida LO369-06
P. sp Contu071230
P. pseudocasca LO17-04
P. umbriha LO235-04
P. siccophila LO417-06 Type
P. kitsiana LO217-85 Type
P. impexaI LO78-93
P. impexa LO162-03
P. dicrani LO270-04
P. laricina Smith64604 Type
P. seymourensis LO42-87
P. parva LO23-08
P. parva LO81-95
P. scanica LO183-09 Type
P. scatophila LO64-95 Type
P. fimiseda LO56-96 Type
P. squamosa LO164-96
P. squamosa LO104-95
P. squamosa LO194-96
P. fibrillosa LO138-00
P. spintrigeroides LO122-86
P. rostellata LO228-85 Type
P. sabuletorum JV90-770
P. sabuletorum LO196-98 Type
P. flexispora LO228-00
P. atomatoides LO249-82
P. cortinarioides LO77-00
P. sphagnicola LO233-99
P. vesterholtii JHP10.086 Type
P. pennata LO206-03
82/.99/97
/.97/
/fibrillosa
P. hirta LO142-00
P. tenuicula LO37-04
P. tenuicula LO58-03
P. sphaerocystis LO126-99
P. kellermanii deMeulder11242
P. alboffoccosa Sivertsen65-89
P. lyckebodensis LO301-11 Type
P. globosivelata Schumacher035
71/.99/86
/Cystopsathyra
P. fagetophila LO210-85 Type
P. rubiginosa LO107-98
P. warrenensis Smith70162 Type
P. seminuda Smith34091 Type
P. senex LO115-02
P. fennoscandica LO484-05 Type
P. fennoscandica LO95-96
P. romagnesii LO267-04
P. romagnesii LO85-98
P. pseudocorrugis LO226-06
P. noli-tangere LO83-03 Neotype
99/1/98
/noli-tangere
P. sp. LO96-11
P. vestita FN430693 FN430695 FN396265 FN430696
P. pervelata FN430694 FN396192
P. gordonii LO220-95
P. epimyces WU19965
57/1/78
/gordonii
P. piluliformis LO162-02
P. echinata Horak ZT12073
P. obscurotristis Wilhelm489 Type
P. pertinax LO259-91 Neotype
P. mucrocystis LO103-98
99/1/99
/piluliformis
P. conferta GE02.007 Type
P. abieticola Smith58673 Type
P. fusca LO287-04
P. rybergii LO373-06 Type
P. pygmaea LO97-04
P. olympiana LO32-02
P. panaeoloides LO44-03
P. panaeoloides LO293-04
P. reticulata FN396193 FN396327 FM897227
P. saponacea LO204-96
P. stridvallii LO104-98 Type
P. arenosa LO220-96 Type
P. arenosa LO330-01
57/1/86
/pygmaea
P. duchesnayensis Smith61737 Type
P. cotonea LO136-00
P. caput-medusae LO36-94
P. maculata LO240-84
/caput-medusae
P. microrhiza LO136-08
P. microrhiza LO185-02
/microrhiza
P. lutensis LO98-03
P. corrugis LO171-01
P. amarescens Arnolds02-78 Type
P. pseudogracilis LO172-02
P. pseudogracilis LO287-06
99/1/99
/corrugis
P. effibulata LO37-96 Type
P. sp NL2349
P. romellii LO240-01 Type
P. riparia Brooks1600 Type
P. vinosofulva LO2-88
P. purpureobadia LO23-94
P. purpureobadia Arnolds99-56 Type
70/1/78
/vinosofulva
P. bipellis LO50-04
P. bipellis LO426-05
P. macrocystidiata Arnolds00-176 Type
P. bipellis LO207-96
98/1/99
/bipellis
P. longicauda LO254-91
P. longicauda LO201-02
P. supernula LO250-04
P. multipedata LO237-04
81/1/98
/multipedata
P. mesobromionis Arnolds01-174 Type
P. magnispora AH24929 Type
P. magnispora Spittelberg
/.98/
100/1/99
/magnispora
Psathyrella sensu stricto

◀ **Fig. 1** **a** and **b** One of the most parsimonius trees from the phylogenetic analysis based on sequences of a concatenated data set from four nuclear genes (ITS, LSU, β-tubulin and Tef-1α). Bootstrap, Bayes, and ML values are indicated for the major clades, thick lines indicate support of at least 50 %, 0.95, 50 %, respectively. Major and minor clades discussed in the text are indicated with scale bars and named

However, these species should be examined closer to see if some of the specimens may have both mono- and dimorphic basidia. Pseudoparaphyses: in coprinoid species basidia are surrounded by pseudoparaphyses (brachybasidioles) in a typical pattern (Uljé 2005, 59). Only rarely we find this pattern in psathyrelloid species. The psathyrelloid species *Coprinopsis marcescibilis* and *C. pannucioides* have been shown to belong in the genus *Coprinopsis* (Larsson and Örstadius 2008). In the present study, additional psathyrelloid species are combined or described as new in *Coprinopsis*. *Coprinopsis canoceps, C. melanthina, C. submicrospora*, and *C. udicola* that lack the mentioned pattern of pseudoparaphyses, while in *C. musae* and *C. uliginicola* it is present, however, somewhat diffuse in the latter. Pileipellis: the psathyrelloid species *Coprinopsis cineraria, C. marcescibilis, C. melanthina, C. pannucioides, C. submicrospora,* and *C. udicola* all have a cutis, hyphae of often inflated cells, that also occur in other *Coprinopsis* species. *Coprinopsis canoceps* has a cutis with transition to a paraderm, while the pileipellis of *C. musae* and *C. uliginicola* is difficult to assess. *Psathyrella* species have a hymeniderm, about 30 of them with a transition to a paraderm. By *Psathyrella gordonii* and *P. epimyces* the pileipellis is similar to a cutis.

Psathyrella

In this study we focus on the genus *Psathyrella* and species with psathyrelloid characteristics. We describe 15 new species known from Europe, but many of them may have a wider distribution range. Most of the species are placed within *Psathyrella* s.s., but *Typhrasa nanispora* occurs as a sister species to *P. gossypina,* in the /gossypina clade, and the two

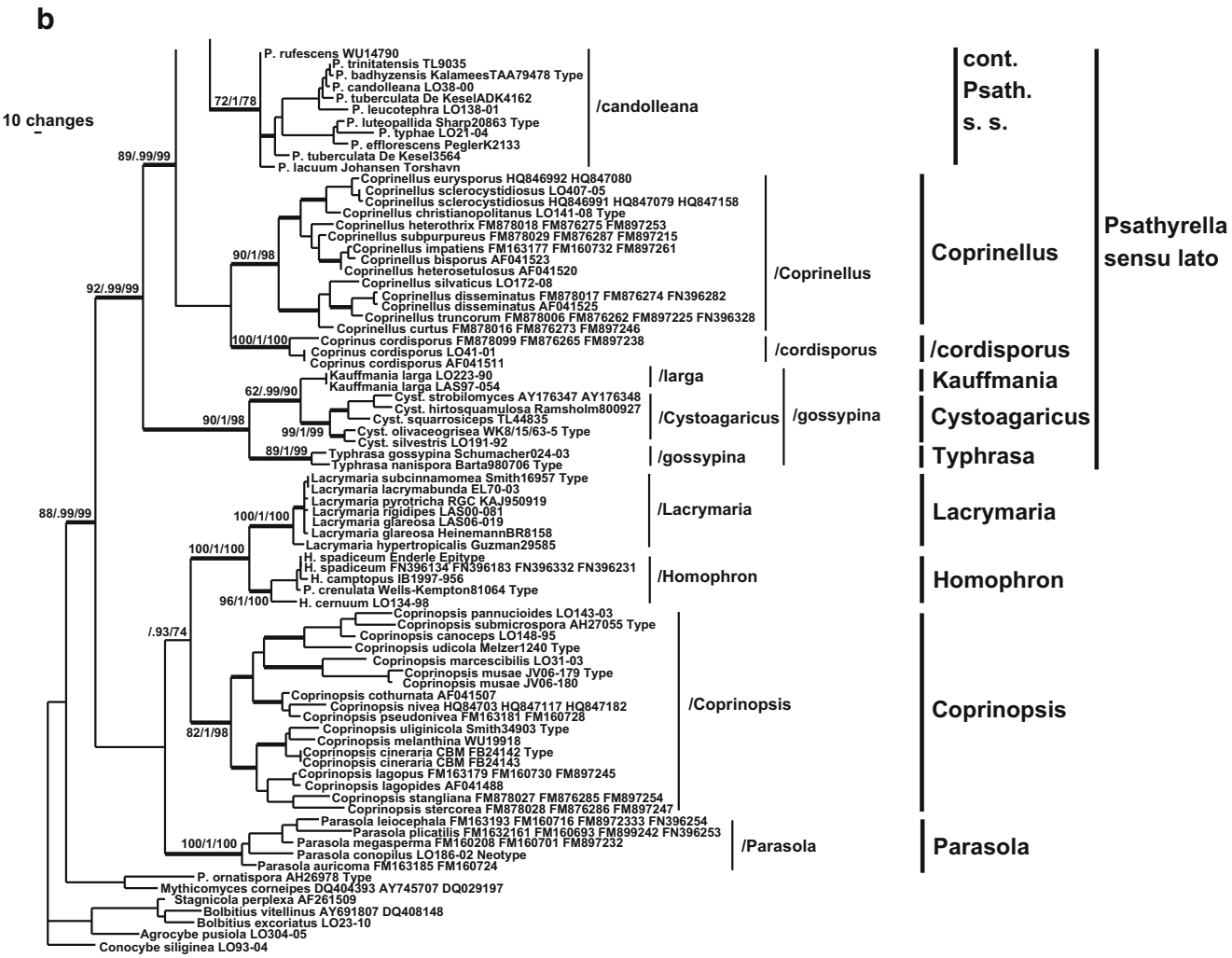


Fig. 1 (continued)

Table 2 A summary of morphological characters used to circumscribe and discriminate the nine genera and *C. cordisporus* within Psathyrellaceae, recognized in this study

	Parasola	*Coprinopsis*	*Homophron*	*Lacrymaria*	*Typhrasa*	*Cystoagaricus*	*Kauffmania*	/cordisporus	*Coprinellus*	*Psathyrella*
Veil	absent	hyphae, subglobose cells, or mixtures	absent	hyphae	hyphae	hyphae	hyphae	subglobose cells, hyphae	subglobose cells, hyphae, or absent	hyphae, rarely subglobose cells
Lamellae and cap	non-deliquescent, or collapsing	deliquescent, rarely non-deliquescent	non-deliquescent	non-deliquescent	nondeliquescent	non-deliquescent	non-deliquescent	not noticeably deliquescent	fully, partilly, or non-deliquescent	non-deliquescent
Spore surface	smooth	smooth, rarely warty or with myxosporium	smooth	often warty	smooth	smooth	smooth	smooth	smooth, rarely warty	smooth, rarely granulose or with myxosporium
Basidia	di- to trimorphic	dimorphic	monomorphic	mono- to dimorphic	monomorphic	monomorphic	monomorphic	dimorphic	mono-, di-, tri-, or tetramorphic	monomorphic
Pseudoparaphyses	present	present, rarely absent	absent	absent	absent	absent	absent	present	present	rarely present
Pileocystidia	absent	absent	simple hairs sometimes present	absent	absent	absent	absent	absent	often present	very rarely present
Sclerocystidia	absent	absent	absent	absent	absent	absent	absent	absent	sometimes present	absent
Setae (pigmented hairs on cap)	sometimes present	absent	absent	absent	absent	absent	absent	absent	absent	absent
Pileipellis	hymeniderm	cutis	hymeniderm to paraderm	hymeniderm	hymeniderm to paraderm	paraderm (C. hirtosquamulosus and C. silvestris examined)	hymeniderm to paraderm	cutis	hymeniderm to paraderm	hymeniderm, paraderm, rarely cutis
Clamps	present	present or absent	present	present	present	present	present	absent	present or absent	present, rarely absent
Cheilocystidia lageniform	absent	very rarely present	absent	absent	absent	absent	absent	often present	often present	often present

species is suggested to be placed in the new describe genus *Typhrasa*, see taxonomy section.

In total, our dataset has ITS sequence data of 49 type specimens of species described in *Psathyrella*, including the newly described species. Four of the sequences were recovered in other clades, and these species are here transferred to corresponding genera within Psathyrellaceae; see taxonomy section. The sequence of the type of *P. ornatispora* fell outside of Psathyrellaceae and the species should be transferred to another family and genus in Agaricales. The species has a deviating morphology with a granular mealy-scaly or furfuraceous cap surface, crowded free gills, very small spores, and lacks hymenial cystidia.

On a proposal from Redhead et al. (2001b) the Committee for Fungi (Gams 2002) recommended conserving the name *Psathyrella* (Fr.) Quél. with *Agaricus gracilis* Fr. as type. However, *P. gracilis* is a younger synonym of *P. corrugis* [*Agaricus corrugis* Pers., Neues Mag Bot 1:104, 1794; *Agaricus corrugis* Pers.: Fr., Syst Mycol 1:298, 1821; *Psathyrella corrugis* Pers. Konrad and Maubl., Encyclop Mycol 14:123, 1949; = *Agaricus gracilis* Fr., Syst mycol 1:299, 1821 (non-*Agaricus gracilis* Pers., Syn meth Fung:425, 1801); *Psathyrella gracilis* (Fr.) Quél., Mém Soc Émul Montbéliard, Sér. II, 5:152, 1872.]. In this study, the name *P. corrugis* is, therefore, used and is also the traditional way of naming the species in Europe.

The ITS sequence data of some type specimens indicate the occurrence of synonyms. The ITS of *P. corrugis* and the type specimen of *P. amarescens* are identical. According to Arnolds (2003) *P. amarescens* should differ from *P. corrugis* in having a red-brown to purple-brown cap, a bitter to acrid taste, and a gill edge with dark dots. We found that the species is very variable in morphology, e.g., in cap size and colour, and in the shape of the cystidia.

Psathyrella vinosofulva and *P. riparia* also have identical ITS sequences. Apart from slightly larger spores by the former they also agree morphologically. In comparison with *P. purpureobadia*, the two differ in two base pairs and one deletion event in the ITS1 region. We examined 25 collections of *P. purpureobadia*, all growing on dung. The type collection grew "in extensively grazed grassland" (Arnolds 2003). Orton (1960) reported *P. vinosofulva* to grow on soil in ash wood while Smith (1972) stated "in sandy soil along a stream" for his *P. riparia*. We consider *P. purpureobadia* to be an independent species, and *P. riparia* a later synonym of *P. vinosofulva*.

ITS sequence data of the type specimens of *P. lutulenta* and *P. thujina* and two additional specimens determined as *P. thujina* (LÖ379-06 and LÖ31-04) were included. The four collections are similar in morphology except that clamps were not found in *P. thujina* LÖ31-04. A few nucleotide differences were found in the ITS region between *P. thujina* LÖ379-06

and the other three. All together, 20 collections of *P. thujina* and the type specimen of *P. almerensis* (L) were examined by morphology alone. They were all morphologically similar except for that some of them lacked clamps. Leiden (L) generally do not allow sequencing of type collections. However, we consider both *P. almerensis* and *P. lutulenta* to be later synonyms of *P. thujina*.

The ITS sequences of the type of *P. magnispora* and the Austrian collection named *P. magnispora* differ in two base pairs in the ITS1 region. We only succeeded in generating the ITS2 region for the type specimen of *P. mesobromionis,* but the region is identical for all three sequences. Morphologically, the Austrian collection deviates by the dominance of 2-spored basidia. We only recognize one species and the oldest name is *P. magnispora.*

A key to the 106 psathyrelloid species that we recognize in Northern Europe, amended from the key in Funga Nordica (Örstadius and Knudsen 2012), including most of the herein newly described species was constructed and is provided as supplementary data S2. Besides the presence of hymenial cystidia, the size, shape, and pigmentation of the spores are important characters for species identification. Data on the spore morphology is provided with the Supplementary data S2.

Coprinellus

In most phylogenetic studies of Psathyrellaceae, the species referred to *Coprinellus* form a strongly supported clade (Larsson and Örstadius 2008; Padamsee et al. 2008; Nagy et al. 2010, 2013b). However, often, as in this study, / Coprinellus is recovered within a larger paraphyletic clade / Psathyrella s.l., Fig. 1b. We recognize *Coprinellus* as a distinct genus and we here describe the new species *C. christianopolitanus*.

/cordisporus

Coprinus cordisporus, a species with a coprinoid aspect, has taken various positions in the phylogenetic trees presented through the years (Hopple and Vilgalys 1999; Moncalvo et al. 2002; Larsson and Örstadius 2008; Vašutová et al. 2008; Padamsee et al. 2008; Nagy et al. 2010). Its rectangular to pentagonal spores can be compared to the rectangular to triangular spores in some species from the /gossypina clade. The powdery veil found in *C. cordisporus* is made up of subglobose to ellipsoid cells that also are found in species in sect. Cystopsathyra. Most interesting are the lageniform shape of the cheilocystidia in *C. cordisporus*. Similar type of cystidia can be found in many species in both *Psathyrella* and *Coprinellus,* but they are not present in other genera of Psathyrellaceae in Europe, except for the psathyrelloid species *Coprinopsis canoceps*. Pseudoparaphyses are present in *C. cordisporus*, but rarely found in *Psathyrella*. The pileipellis is a cutis. This unique set of morphological characters may explain the uncertain position on a single branch that the species gets in the phylogenies.

Based on comprehensive phylogenetic and morphologic studies of the *C. cordisporus*/*C. cardiasporus* complex Keirle et al. (2004) demonstrated *C. cardiasporus* to be a later synonym of *C. cordisporus*. They stated that *C. cordisporus* represents a complex of closely allied taxa. Based on ITS data the *C. cordisporus* complex was placed close to *Coprinellus* as in the present study. Uljé (2005) recognized four species based on morphology. Our own observations is that *C. cordisporus* is a morphologically variable species. The pileipellis of the *C. cordisporus* taxa has a cutis (Keirle et al. 2004) while the species in *Coprinellus* has a hymeniderm.

/gossypina

The clade is divided into three supported subclades that correspond to three separate genera. The subclade including *Cystoagaricus strobilomyces*, *Psathyrella hirtosquamulosa*, *P. squarrosiceps*, *P. olivaceogrisea*, and *P. silvestris* is characterized by a unique combination of characters as a pigmented layer of scales, flocci, or bundles of fibrils on cap and stem and mitriform or angular spores. We propose the combination of the four *Psathyrella* species to *Cystoagaricus*.

Psathyrella larga is an ordinary looking *Psathyrella* lacking outstanding features and is difficult to separate from for example *P. rostellata*. The new genus *Kauffmania* is here described to reflect better the species phylogenetic position.

The subclade including *Psathyrella gossypina* and *T. nanispora* is recognized and characterized by the rostrate hymenial cystidia with oily drops. The non-European species *P. canadensis, P. delineata,* and *P. fraxinophila* are also reported to have oily drops in their cystidia (Smith 1972). The collection A.H. Smith 29994 of *P. canadensis* (MICH) and the holotype of *Hypholoma delineatum* (NYS) were examined. The two species agree satisfactory in morphology with *P. gossypina*. The genus *Typhrasa* is here described for this group of species, see taxonomy section below.

Lacrymaria

/Lacrymaria is a strongly supported clade that include species with almost identical ITS and LSU sequences. The sequence variation between the species seems to be higher in the β-tubulin gene that may be more suitable for disentangle and segregate between the species. In morphology the genus *Lacrymaria* is fairly easy to identify, with species having tomentose, brown to reddish-brown caps, mottled gills, verrucose spores and pleurocystidia in small fascicles, often capitate.

Homophron

Phylogenetic analyses based on molecular data have shown that species that share the unique combination of morphological characters, as lacking a veil and having cystidia with crystals or incrustations, form a strongly supported clade (Larsson and Örstadius 2008; Padamsee et al. 2008; Vašutová et al. 2008; Nagy et al. 2012). Britzelmayr (1883) published the new name *Homophron* as a subgenus under *Agaricus*, characterized by"Velum fehlt. Stiel straff oder steif. Sporen braun." *Homophron* contained ten species among others *Agaricus spadiceus*. Kits van Waveren (1985:155) considered the name *Homophron* illegitimate referring to that Britzelmayr (1883:174) did not indicate the rank, but on page 181 the rank subgenus is clearly given. Singer (1951) combined *Homophron* as a subgenus under *Psathyrella* and selected "*P. spadicea* (Schaeff. ex Fr.) Sing." as type. Cooke (1953) raised *Homophron* to the rank of genus and selected *Agaricus particularis* Britzelm. as type, one of ten species mentioned in the original description of *Homophron* (Britzelmayr 1883). However, as no basionym was cited the combination to genus was not validly published (Donk 1962; Horak 1968). Therefore, we here propose to raise subgenus *Homophron* to genus level to validate the name and genus *Homophron* for this group of species and propose the combination of the three species, *H. spadiceum*, *H. cernuum*, and *H. camptopodum*.

Coprinopsis

In our analyses the sequence data of the type specimens of *Psathyrella submicrospora*, *P. cineraria* and *P. uliginicola* came out in the /Coprinopsis clade together with sequences of *P. canoceps* and *P. melanthina*. The species are psathyrelloid in appearance and was therefore described in *Psathyrella*. As mentioned above some of them lack the typical pattern of pseudoparaphyses that is thought to be a morphological characteristic for the genus *Coprinopsis*.

We here propose the combination of the five species to *Coprinopsis* based on the molecular results and in addition we describe the two new species, *C. musae* and *C. udicola* (Fig. 2).

Nomenclatural Novelties

Coprinellus christianopolitanus Örstadius & E. Larss., **sp. nov.** [MB 811478] – Holotype: Sweden, Skåne, Kristianstad, Tivolipark, 10.IX.2008, L. Örstadius 141–08 (GB). Fig. 4. (S3: Fig. 3a–d.)

Etymology. The epithet refers to the Latin name of Kristianstad where the fungus was found.

Pileus primo semiglobatus, 3 mm latus, 3 mm altus, flavo-brunneus, demum expansus, 5 mm latus, ochraceus, pubescens, velum non visum. Lamellae distantes, adnexae, acie alba fimbriata. Stipes 6×0.5 mm, albus, pubescens. Odor nullus. Sporae 13–16.5×8–9 μm, ellipsoideae, oblongae, poro germinativo excentrico, inconspicuo. Basidia 4-sporigera. Cheilocystidia 32–52×9–25 μm, anguste lageniformia, subcapitata vel clavata, dispersa, cellulis clavatis immixta, in NH_4OH viridiscentia. Pleurocystidia nulla. Pileocystidia 27–62×9–14 μm. Fibulae adsunt. Ad terram in horti.

Cap when young 3 mm high and 3 mm broad, semiglobate, yellow brown, when mature expanding and 5 mm broad, ochraceous, paler towards margin, pubescent sub lente, sulcate, veil not seen. Gills adnexed, distant, L=c. 13, grey with white fimbriate edge, becoming grey black. Stem 6×0.5 mm, white, pubescent. Smell none. Taste not recorded.

Spores 13–16.5×8–9 μm, av. 14.7×8.4 μm, Qav. = 1.8, ellipsoid, oblong, sometimes slightly irregular or papillate, in water dark reddish brown (Mu. 2.5YR 2.5/4), with indistinct and eccentric germ pore. Basidia 4-spored, 22–25×11–12 μm, surrounded by pseudoparaphyses. Cheilocystidia of two types: A: 32–52×9–25 μm, narrowly lageniform, often subcapitate to clavate at apex, scattered, when fresh apex turning yellow or green in a 10 % solution of ammonia, a reaction not seen in dried material, B: 17–42 μm wide, clavate, ellipsoid to sphaeropedunculate, numerous. Pleurocystidia not seen. Pileipellis a hymeniderm. Pileocystidia 27–62×9–14 μm, similar in shape and reaction of ammonia solution to the cheilocystidia of type A, sometimes thick-walled at base. Clamps present.

Habitat and distribution: Growing in a small group in a lawn of a park. Known from the type locality in southernmost Sweden.

Notes - The species can be recognized by small basidiomata, small, lageniform cystidia with subcapitate to clavate apex turning yellow or green in a 10 % solution of ammonia, and large spores with indistinct germ pore. Van de Bogart (1975) the author of *Coprinus simulans* reported "pileocystidia and caulocystidia when fresh reacting to ammonia water by becoming a bright blue-green color". A green reaction of cystidia is known also from some species of *Psathyrella*.

Coprinopsis musae Örstadius & E. Larss., **sp. nov.** [MB 811479] – Holotype: Denmark, E-Jylland, Randers, in Randers Rainforest, a tropical greenhouse, on debris of *Musa sp.*, 11.VII.2006, J. Vesterholt 06–179 (C). Figs. 2d, 5. (S3: Fig. 4a–b, d.)

Etymology. Named after its occurrence on *Musa* (bananas).

Pileus 4–11 mm latus, ovoideus, deinde conico-parabolicus, brunneolo-aurantiacus, hygrophanus, humido striatus, laevis, siccus, glaber, in sicco pallescens, velum non visum. Lamellae confertae, subangustae, fere liberae, adscendentes, cinereo-aurantiacae, acie albae. Stipes 12–34×0.8–1.5 mm, cylindraceus, albus, sursum pruinosus,

Fig. 2 Photos of six of the new described species, **a** *Psathyrella madida*, **b** *P. stridvallii*, **c** *P. carminei*, **d** *Coprinopsis musae*, **e** *P. fennoscandica*, **f** *P. vesterholtii*. Photos of all new species are provided in Supplementary data S3

deorsum innato fibrillosus, submarmoratus, velum nullum. Odore inconspicuo vel acido. Sapore nullo. Sporae 9–10.5×5.8–6.2 µm, ellipsoideae, oblongae, ovoideae, amygdaliformes, valde pallidae; poro germinativo nullo vel inconspicuo. Basidia 4-sporigera. Pleurocystidia nulla. Cheilocystidia 25–45×8–12×6–14 µm, anguste utriformia, numerosa. Fibulae adsunt. Ad lignum in sylva tropica.

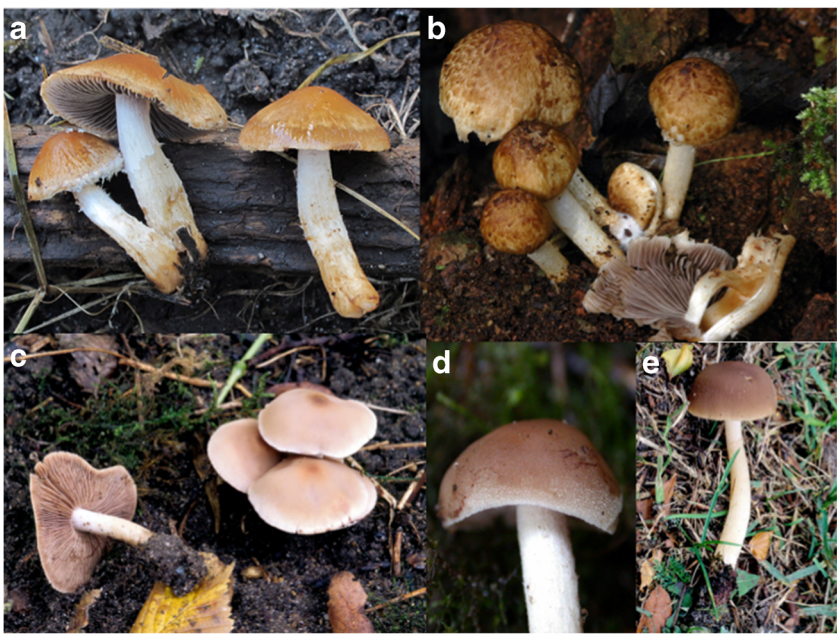


Fig. 3 Photos of species in the new described genera. **a** *Typhrasa gossypina* TL2011-389713 (C) Photo T. Laessoe. **b** *Cystoagaricus silvestris* Sweden Skåne. Benestad, Örups almskog, 18.9.2008, I. Månsson & L. Örstadius 163–08. **c** *Homophron spadiceum* Sweden, Skåne, Kristianstad, Sa Lingenäset, 11.9.2003, L. Örstadius 75–03. **d** *Homophron spadiceum* Sweden. Skåne, Kristianstad, Sa Lingenäset, 11.9.2003, L. Örstadius 75–03. **e** *Kauffmania larga* Sweden Västergötland, Habo, N. of Sjöbol, 22.10.1999, E. Grundel, LÖ197-99

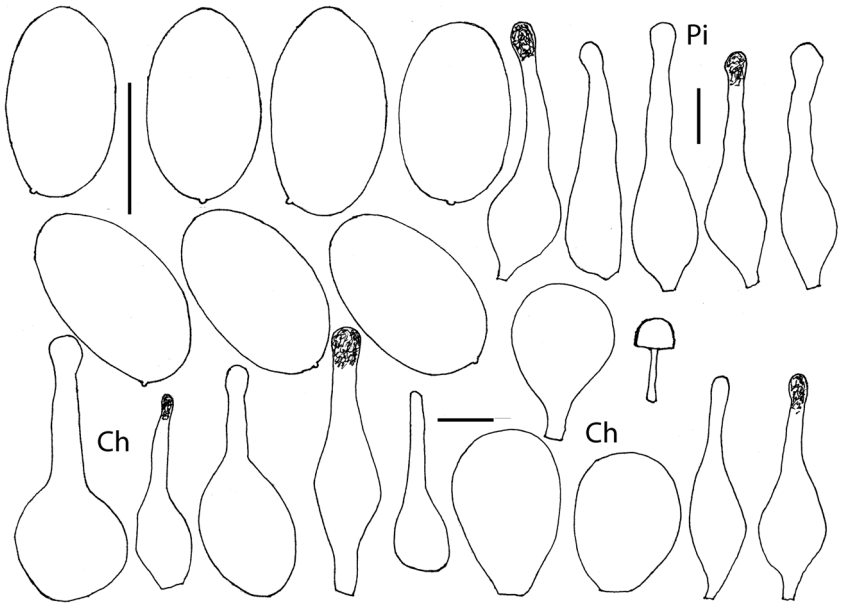


Fig. 4 *Coprinellus christianopolitanus*. L. Örstadius 141–08; Ch Cheilocystidia; Pi Pileocystidia; Basidioma ×3; Scale bars 10 μm

Cap 4–11 mm broad, ovoid, then conical, rounded conical to paraboloid, low campanulate, brownish orange (Methuen 5C4-6D4), at margin greyish orange (5B3), hygrophanous, striate almost to centre, smooth, dry, not pubescent, drying to greyish orange, orange grey, yellowish white (5B3, 6B2, 4A2), no veil seen. Gills crowded, rather narrow, almost free, adscending, greyish orange (5B3) with paler, slightly flocculose edge. Stem 12–34×0.8–1.5 mm, cylindrical or gradually widened to 2 mm at base, not bulbous, pulverulent upper part, white, downwards innately fibrillose, no veil seen, slightly marbled. Smell very faint, acidic. Taste none.

Spores 9–10.5×5.8–6.2 μm, av. 9.7–9.8×5.9–6 μm, Qav. = 1.6–1.7, ellipsoid, oblong, ovoid, in profile sometimes amygdaliform, in water hyaline to very pale brown (Mu. 10YR 8/3-8/4); germ pore absent or with a faint pore. Basidia 4-spored, 18–28×8–10 μm; pseudoparaphyses often seen. Pleurocystidia absent. Cheilocystidia numerous, 25–45×8–12 (at base) × 6–14 (at apex) μm, narrowly utriform, no clavate cells seen. Scalp cap halfway from margin: the upper layer consists of narrow hyphae indicating the presence of a suprapellis or less likely a veil, below a layer of subglobose to ellipsoid, pale yellow, 20–38 μm wide cells; pileitrama of yellow pigmented hyphae. Clamps seen on stem hyphae.

Habitat and distribution: So far only known from a tropical greenhouse where it grew on woody remnants, branches, and leaves of *Musa* (bananas).

Notes - *Coprinopsis musae* is characterized by its small size, extremely pale spores, lacking pleurocystidia, lacking veil. This psathyrelloid *Coprinopsis* comes genetically close to *C. marcescibilis* from which it differs in having smaller and significantly paler spores and smaller basidiomata. The experienced collector, Jan Vesterholt, did not notice a veil. *C. marcescibilis* has characteristic dentate flocci at cap margin. *Psathyrella typhae* belonging to another genus, is similar in morphology, but differs in having a veil and in growing on plant debris of, e.g., *Carex*, *Scirpus*, and *Typha* in wet or moist places.

Additional specimen: Denmark, E-Jylland, Randers, in Randers Rainforest, a tropical greenhouse, on remnants of *Musa*, 11.VII.2006, J. Vesterholt 06–180.

Coprinopsis udicola Örstadius, A. Melzer & E. Larss., **sp. nov.** [MB 811480] – Holotype: Germany, Sachsen, Delitzsch, 7.X.2008, A. Melzer 1240 (GB). Fig. 6. (S3: Fig. 5a–d.)

Etymology. The epithet refers to the preference of moist habitat.

Pileus 20–25 mm latus, 15–20 mm altus, conicus vel conico-convexus, saepe undulatus, humido striatus, obscure fuscus, in sicco pallescens sine roseo; velum fibrillosum. Lamellae modice confertae, sinuatae, primo albidae, dein griseo-brunneae vel atro-brunneae; acie alba fimbriata. Stipes usque ad 80×2 mm, eradicatus, albus, modice fibrillosus, apice albopulverulentus. Sporae 11.5–14×6–7 μm, anguste ovoideae, subcylindricae, oblongae, amygdaliformes, citriformes, rubidae, poro germinativo distinctae. Basidia 4-sporigera. Cheilocystidia 30–80×7–18 μm, polymorpha, lageniformia, subcylindrica, anguste utriformia, interdum flexuosa, septata, furcata vel capitata, numerosa. Pleurocystidia 30–75×10–14 μm, cheilocystidiis similia, raro vel absunt. Cellulae veli 60–125×5–17 μm. Fibulae adsunt. Caespitosus, udus.

Cap conical to conico-convex, when young about 10 mm broad and 10 mm high, mature 20–25 mm broad and 15–20 mm high, often wavy or slightly inflexed at margin, moist striate, young and mature dull

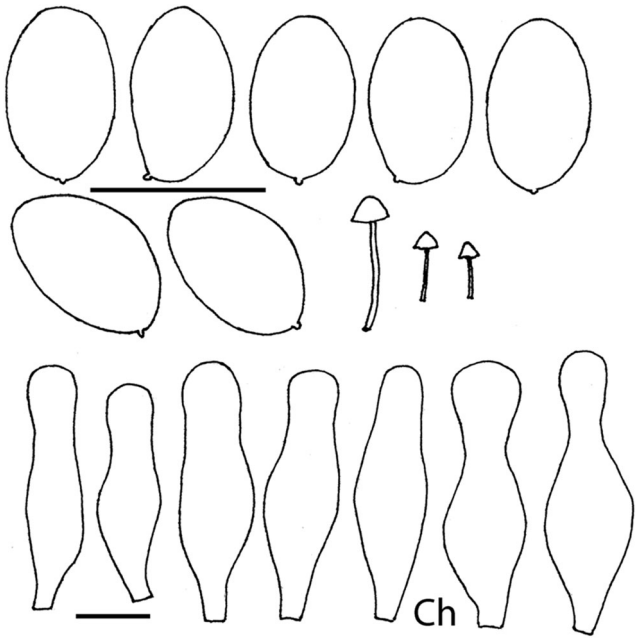


Fig. 5 *Coprinopsis musae*. J. Vesterholt 06–179; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

grey brown with a brown centre, pallescent to grey or whitish without pink; veil when young as white fibrillose remnants more than halfway from margin. Gills rather close, sinuate, unequal, at first whitish, becoming grey brown to black brown, with conspicuously micaceous, uneven, white edges similar to the ones of *Coprinellus micaceous*. Stem up to 80×2 mm, equal, often bent, no pseudorhiza, white, glossy, with sparsely fibrillose veil remnants, pulverulent at apex. Not deliquescent. Smell fungous. Taste not recorded.

Spores 11.5–14×6–7 μm, av. 12.5×6.2 μm, Qav. = 2.0, narrowly ovoid, subcylindrical, oblong, in profile amygdaloid to citriform, sometimes with a slight suprahilar depression, in water red (Mu. 2.5YR 4/8), germ pore distinct, central, rarely slightly eccentric. Basidia 4-spored, 17–25×10–11.5 μm. Cheilocystidia 30–80×7–18 μm, polymorphic, lageniform, subcylindrical, narrowly utriform, sometimes flexuous, septate, forked, or headlike at apex, abundant. Pleurocystidia 30–75×10–14 μm, similar to cheilocystidia, scattered to absent close to gill edge. Pileipellis a cutis with short, wide cells, 35–60×20–40 μm, pale brown. Pileitrama with pale pigmented hyphae. Veil cells 60–125×5–17 μm, pale. Clamps present on stem base hyphae.

Habitat and distribution: In fascicles of about twenty basidiomata, moist with *Aegopodium podagraria*, *Urtica dioica*, and *Phalaris arundinacea*. Only known from the type locality.

Notes - The species can be recognized by the shape and size of the cystidia, the pale cap, and the large, amygdaliform spores. The genetically close *Coprinopsis canoceps* has smaller spores and cystidia. *C. marcescibilis* differs in having smaller cystidia and characteristic denticulate flocci at cap margin.

Psathyrella arenosa Örstadius & E. Larss., **sp. nov.** [MB 811481] – Holotype: Sweden, Everöd, by the railway 2,3 km. N.E of the church, 19.X.1996, L. Örstadius 220–96 (GB). Fig. 7. (S3: Fig. 6a–d.)

Etymology. The epithet refers to the growing on sandy places.

Pileus 4–15 mm latus, primo convexus, tum expansoplanus, luteolo-rubidus, striatus, hygrophanus, in sicco cremeus; velum fibrillosum dispersum. Lamellae distantes, cinereae; acie concolora vel albida. Stipes 20–35×1–3 mm, pallide brunneus, apice pulverulentus, deorsum fibrillosus. Odor indistinctus; sapor mitis. Sporae 7–9×4–5 μm, oblongae, ellipsoideae, ovoideae, subphaseoliformes, subamygdaliformes, luteolo-rubrae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 25–55×7–13 μm, lageniformia, subutriformia, dispersa vel numerosa. Cheilocystidia 20–40×7–13 μm, pleurocystidiis similia, modice numerosa, cellulis clavatis immixta. Cellulae veli 15–70×2–10 μm. Fibulae adsunt. Subgregarius ad terram arenosam.

Cap 4–15 mm broad, convex, then expanded to nearly plane, yellowish red, dark reddish brown (Mu. 5YR 4/6, 3/3), faintly to distinctly striate when moist, hygrophanous, drying to cream; veil as dispersed fibres halfway from margin. Gills distant, L=11–25, adnate to adnexed, mature pinkish grey (Mu. 5YR 6/2) with white or concolorous edge. Stem 20–35×1–3 mm, slightly enlarged towards base, pale brown, pulverulent at apex, fibrillose lower part. Taste mild. Smell not distinctive.

Spores 7–9×4–5.5 μm, av. 7.3–8.5×4.4–5.2 μm, Qav. 1.6–1.8, oblong, ellipsoid, ovoid, in profile sometimes subphaseoliform or subamygdaliform, in water yellowish red (Mu. 2.5YR 5/8 – 5YR 6/8), germ pore distinct. Basidia 4-spored, 17–26×7–9 μm, sometimes partly intracellular pigmented. Pleurocystidia 25–55×7–13 μm, lageniform, subutriform, scattered to numerous, pale. Cheilocystidia of two types: A: 20–40×7–13(−20) μm, similar to the pleurocystidia, rather numerous, B: small, clavate, scattered, sometimes numerous towards cap margin. Scalp cap halfway from margin: pileipellis consists of ellipsoid, clavate to subglobose cells 10–25 μm wide, pale; pileitrama made up of strongly pigmented hyphae, sometimes incrusted. Hymenophoral trama moderately pigmented. Veil cells 15–70×2–10 μm, clamped.

Habitat and distribution: Growing solitary or in small groups among mosses in open places, on dry, sandy, or humus rich soil. Known from Denmark and the southernmost province Skåne in Sweden.

Notes - The species is recognized by its small size, scanty veil, size of spores and cystidia, and the habitat on sandy,

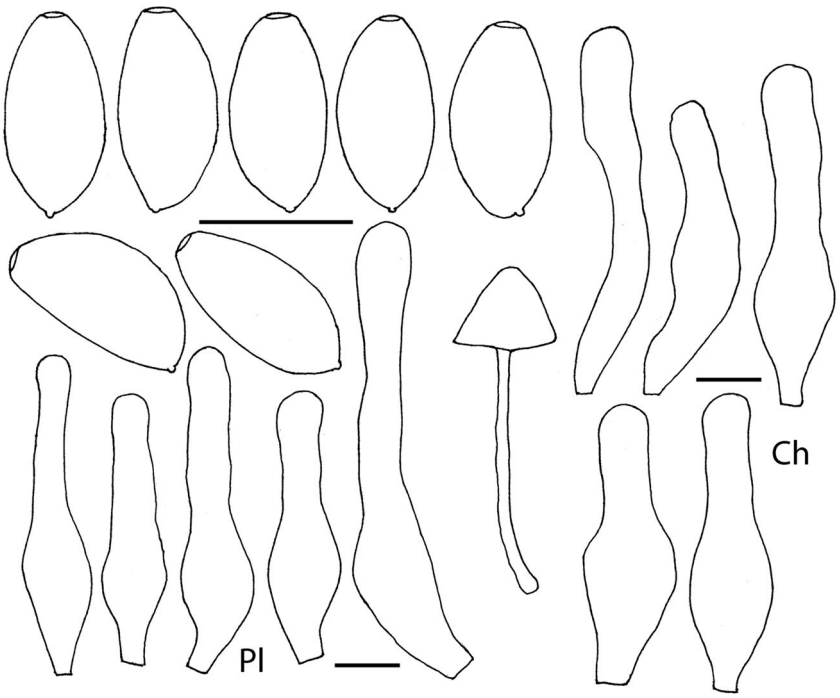


Fig. 6 *Coprinopsis udicola*. A. Melzer 1240; Pl Pleurocystidia; Ch Cheilocystidia; Basidioma ×1,5; Scale bars 10 μm

calcareous soil. *Psathyrella senex* differs in having larger basidiomata, a veil with flocci when fresh, and a habitat on debris of wood or among fallen leaves or terricolous in forests. *P. seymourensis* can be separated by a floccose veil and acute cystidia. *P. ichnusae* has broader pleurocystidia, sometimes thick-walled, paler cap, and a habitat on burnt soil.

Additional specimens: Denmark, NE. Jylland, Skagen, Grenen, 19.VIII.2000, J. Vesterholt with sons JV00-229 (C); Sjaelland, Gilleleje Feriecenter, 21.V.2012, M. Sonniks MSO2012-445438 (C); Zealand, Naestved Øvelseplads, 19.V.2010, E. Kristensen 2010–94357 (C); Sweden, Skåne, Åhus, Älleköpinge, 7.X.1999, L. Örstadius 146–99; Everöd, by the railway 2,3 km. N.E of the church, 24.IX.1987, L. Örstadius 155–87; Ivetofta, Grödby, 31.VIII.2006, L. Örstadius 250–06; Löderup, 0,5 km. N. of the seashore, 19.X.1997, L. Örstadius 184–97; N.O. of Löderup, 2.XI.2011, L. Örstadius 329–11; Lyngsjö, 0,6 km. N. of the church, 9.X.2006, L. Örstadius 360–06; Hommentorpsvägen, 28.X.2001, L. Örstadius 330–01; Ystad, Klintholmen, 2.XI.2011, L. Örstadius 328–11.

Psathyrella carminei Örstadius & E. Larss., **sp. nov.** [MB 811482] – Holotype: Italy, Calabria, Cosenza, Serra Vurga, Longobucco, 22.IX.2008, C. Lavorato (GB). Figs. 2c, 8. (S3: Fig. 7a–d.)

Etymology. In honour of Carmine Lavorato who discovered the fungus.

Pileus usque ad 35 mm latus, primo semiglobosus, tum expanso-planus, rugosus, rufo-brunneus, striatus, hygrophanus, in sicco pallescens; velum flocculosum. Lamellae adnatae, modice confertae, primo albidae, demum atro-brunneae. Stipes usque ad 55×4 mm, aequalis, ad basim incrassatus, albidus, apice pulverulentus, deorsum fibrillosus. Sapor mitis. Odor piscis similis. Sporae 9–11×5–5.5 μm, oblongae, subcylindricae, leviter irregulares, subphaseoliformes, rufo-flavae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 40–55×11–18 μm, utriformia, lageniformia, modice numerosa. Cheilocystidia 30–45×10–16 μm, pleurocystidiis similia, dispersa, cellulis clavatis immixta. Fibulae adsunt. In silva conifera (*Pinus*).

Cap up to 35 mm broad, at first semiglobate, then expanded plane, wrinkled, red brown, striate halfway when moist, hygrophanous, pallescent on drying, veil as white fugacious flocci. Gills adnate, medium spaced, when young whitish, becoming blackish brown with pale edge. Stem up to 55× 4 mm, equal, inflated towards base, whitish, pulverulent at apex, with fibrillose veil remnants downwards. Taste mild. Smell of fish.

Spores 9–11×5–5.5 μm, av. 10×5.2 μm, Qav. = 1.9, oblong, subcylindrical, slightly irregular, in profile sometimes subphaseoliform, in water reddish yellow (Mu. 5YR 6/8), with distinct germ pore. Basidia 4-spored, 22–25×8–10 μm. Pleurocystidia 40–55×11–18 μm, utriform to lageniform, rather numerous, pale. Cheilocystidia of two types: A: 30–45×10–16 μm, similar to pleurocystidia, scattered to rather numerous, B: 9–16 μm wide, clavate, numerous. Pileipellis (scalp) of 15–45 μm wide, subglobose to ellipsoid, pale cells. Pileitrama with moderately pigmented hyphae. Clamps present.

Habitat and distribution: Growing on soil in a forest with *Pinus laricio* subsp. *calabrica*. The soil is slightly acidic,

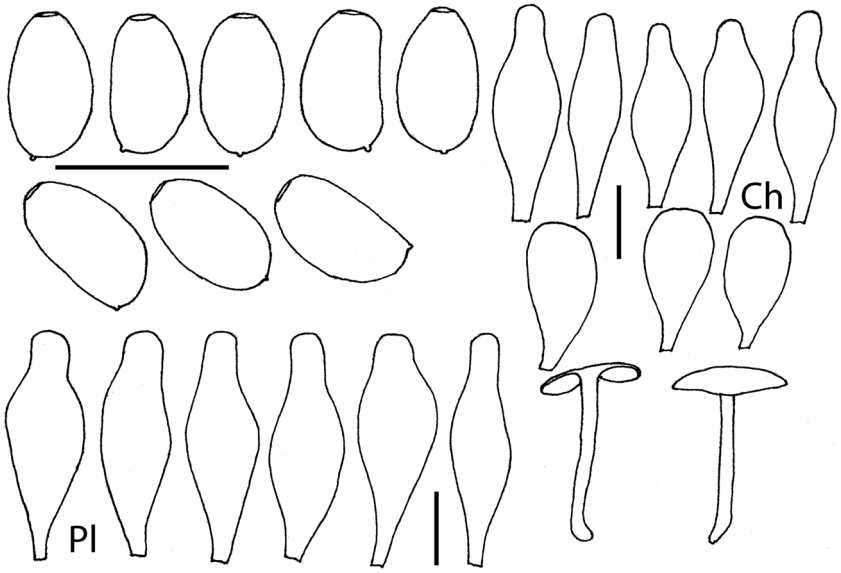


Fig. 7 *Psathyrella arenosa*. L. Örstadius 220–96; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×2; Scale bars 10 μm

pH 5,5–6. USDA-classification: Humic Psammentic, Dystrupets, mixed mesic. Location of the forest, southeast. Montane Mediterranean climate. Known only from the type locality in Italy.

Notes: The spore size, and non-forked, non-incrusted utriform cystidia are important characters for *Psathyrella carminei*. It differs from the genetically close *P. spadiceogrisea* and *P. fatua* in having larger spores and a smell of fish.

Psathyrella fennoscandica Örstadius & E. Larss., **sp. nov.** [MB 811483] – Holotype: Sweden, Träne, Stavsbacka, in a pasture grazed by cows, 12.X.2005, L. Örstadius 484–05 (GB). Figs. 2e, 9. (S3: Fig. 8a–d.)

Etymology. The epithet refers to the occurrence in Finland, Norway, and Sweden.

Pileus 15–40 mm latus, conico-convexus, raro fere planus, primo castaneus, humido striatus,

hygrophanus, in sicco pallescens; velum fibrilloso-floccosum ad dimidium ad medium, glabrescens. Lamellae subdistantes, ventricosae, adnatae, griseae, acie alba. Stipes 50–120×2–5 mm, modice rigidus, saepe ad basim bulbosus, albidus. Odor indistinctus; sapor mitis. Sporae 8–10.5×5–6×4.5–5.5 μm, ovoideae, subfusiformes, oblongae, interdum amygdaliformes, rubidae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 35–80×10–16 μm, anguste utriformia, lageniformia, conica, dispersa vel numerosa. Cheilocystidia 20–45×6–12 μm, pleurocystidiis similia, numerosa. Cellulae veli 20–100×2–8 μm. Fibulae adsunt. Solitaria vel gregaria in sylva saepe ad terram vel ad lignum.

Cap 15–40 mm broad, paraboloid, then expanded campanulate, obtusely conical, convex, rarely almost applanate, at first dark reddish brown (Mu. 5YR 3/2-3/4-4/3), when moist striate up to ¾ from margin, hygrophanous, when drying sometimes ochre-brown at centre (e.g., Mu. 5YR 6/8), then becoming pale brown or grey; veil in young stages as floccules halfway from margin and some fibres towards centre, glabrescent. Gills medium spaced, L=24–28, ventricose, adnate, at first grey, pink (Mu. 7.5YR 7/4), then reddish grey (Mu. 5YR 5/2), with minutely white floccose edge. Stem 50–120×2–5 mm, rather stiff, equal, often with distinct basal bulb, whitish, very pale brown, pulverulent striate at apex, with fugacious fibres or floccules from veil downwards. Smell not distinctive. Taste mild. Spore print black with reddish tinge (Mu. 10R 2.5/1-2.5/2).

Spores 8–10.5×5–6×4.5–5.5 μm, av. 8.7–9.7×5.2–5.7×4.9–5.3 μm, Qav. = 1.6–1.7 (in front view), 1.7–1.9 (in profile), ovoid, subfusiform, oblong, slightly angled, in profile with a slight suprahilar depression or amygdaliform, in water red (Mu. 2.5YR 4/6), almost opaque, with distinct germ pore. Basidia 4-spored, 16–26×8–9 μm. Pleurocystidia 35–80×10–16 μm, narrowly utriform, lageniform, conical, scattered to numerous, pale. Cheilocystidia of two types: A: 20–45×6–12 μm, similar to pleurocystidia, numerous, B: small, clavate, of variable frequency. Pileipellis a hymeniderm of 15–55 μm wide cells. Pileitrama made up of coarsely incrusted hyphae. Hymenophoral trama pale to moderately pigmented. Veil cells 20–100×2–8 μm, cylindrical. Clamps present on veil and stem hyphae.

Habitat and distribution: Solitary to gregarious in coniferous and deciduous forests, pastures, with *Alnus glutinosa, A. incana, Betula* sp., *Deschampsia cespitosa, Frangula alnus, Picea abies, Pinus silvestris, Populus tremula, Sphagnum* sp., *Vaccinium myrtillus*, oligotrophic, moist, on mossy, decayed branches or logs, on other debris, on soil, on grass, among leaves. So far known from Finland, Norway, and Sweden.

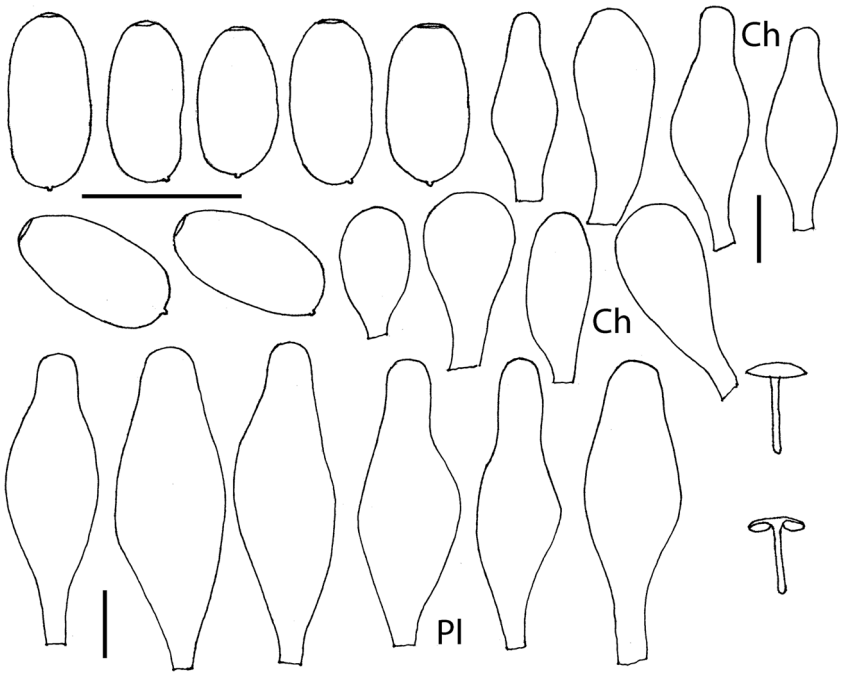


Fig. 8 *Psathyrella carminei*. C. Lavorato Longobucco; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×0,5; Scale bars 10 μm

Notes - *Psathyrella fennoscandica* is recognized by red brown cap, rather scanty veil, bulbous stem base, narrowly utriform to lageniform cystidia, dark subfusiform spores, and moist oligotrophic habitat. *Psathyrella senex* differs in having slightly smaller, paler, non-fusiform spores, and prefers richer, sometimes nitrophilous habitats.

Additional specimens: Finland, Uusimaa, Tuusula, Ruotsinkylä, 31.VIII.1993, I. Kytövuori 93-602a (H); Varsinais-Suomi, Kustavi, Rahi, Leonsaari, W. of Isoperä bay, 3.XI.1996, J. Vauras 12059 (TURA); Norway, Oppland, Søndre Land, lake Trevatna, Vassenden, 14.IX.1984, G. Gulden 336/84 (O, *Psathyrella* sp.); Sweden, Blekinge, Kyrkhult, Snövleboda, 9.IX.1993, A. Blom LÖ 189–93; Ronneby, Piskabacken, 27.IX.2001, A. Nyström LÖ 199–01; Medelpad, Borgsjö, Bergåsen, 13.IX.1995, I. Kytövouri LÖ 89–95; Höganäs, 30.VIII.1993, D. Broström LÖ 148–93; Julåsen, 3.IX.1993, J. Stålberg LÖ 171–93; 14.IX.1995, L. Örstadius 99–95; Tubbo, 28.VIII.1989, L. Örstadius 236–89; Skåne, Andrarum, Borgarehögen, 5.X.1991, L. Örstadius 245–91; Glimåkra, E. of Nygårdstorpet, 25.IX.1997, L. Örstadius 119–97; Hjärsås, N. of Immeln, 8.IX.1989, L. Örstadius 305–89; Hörröd, Rebbetuaröd, 9.IX.1989, L. Örstadius 307–89; N. Åkarp, Hillarp klint, 17.IX.1996, L. Örstadius 95–96; Näsum, Hagstad, 12.X.1995, L. Örstadius 204–95; Örkened, Örnanäs, 5.X.1996, L. Örstadius 161–96; Vinslöv, Åraslöv bog, 29.IX.2001, L. Örstadius 214–01; Småland, Femsjö, Yaberg, 17.IX.1987, L. Örstadius 115–87; Uppland, Vänge, Fiby urskog, 8.IX.1994, I. Kytövuori LÖ 46–94; Värmland, Fryksände, Gultberget, 5.X.1991, J. Stålberg 91–114; Hammarö, St. Skagene, 12.IX.1987, L. Örstadius 110–87; Högboda, 12.IX.1987, L. Örstadius 102–87; Övre Ullerud, Torsberget, 13.IX.1992, L. Örstadius 242–92, 243–92; Stora Kil, Apertin, Kil, 14.IX.1986, J. Stålberg 86:84; Västergötland, Blidsberg, Göpåsen, 19.IX.1992, H. Toresson LÖ 306–92; Fristad, Gingri, 14.IX.1990 Toresson & Örstadius 248–90; Södra Säm, Klevaberget, 16.IX.1992, L. Örstadius 261–92; Timmele, Blankered, 15.IX.1992, L. Örstadius 255–92; Tvärred, Kråkeboberget, 19.IX.1992, L. Örstadius 297–92; Västmanland, Surahammar, Kanalhagen, 25.IX.1996, L. Bsenko 96–1941; Lönnbro bog, 9.X.1997, L. Bsenko 97–5555; Väratorp West, 29.IX.1999, L. Bsenko 99–1536.

Psathyrella ichnusae Örstadius, Contu, E. Larss. & Vizzini, **sp. nov.** [MB 811484] – Holotype: Italy, Sardinia, Olbia-Tempio, Golfo Aranci, Golfo di Marinella, 6.I.2008, M. Contu (GB). Fig. 10. (S3: Fig. 9a–d.)

Etymology. The epithet refers to Ichnusa, an old name for Sardinia.

Pileus 2–18 mm latus, campanulatus vel convexus, hygrophanus sed non striatus, initio obscure ochraceo-brunneus, deinde ochraceo-argillaceus; velum album fibrillosum. Lamellae distantes vel subconfertae, sinuato-adnatae, ochraceae, dein obscure brunneae, ad aciem albo-flocculosae. Stipes 12–32×1–2 mm, valde fragilis, albus vel ochraceotinctus, sericeus. Odor atque sapor nulli. Sporae in cumulo brunneae. Sporae 7.8–9.2×4.4–5 μm, oblongae, subcylindricae, anguste ovoideae, amygdaliformes, in aqua observatae aurantiacae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 32–48×10–18 μm, utriformia vel lageniformia, dispersa. Cheilocystidia 25–35×10–16 μm,

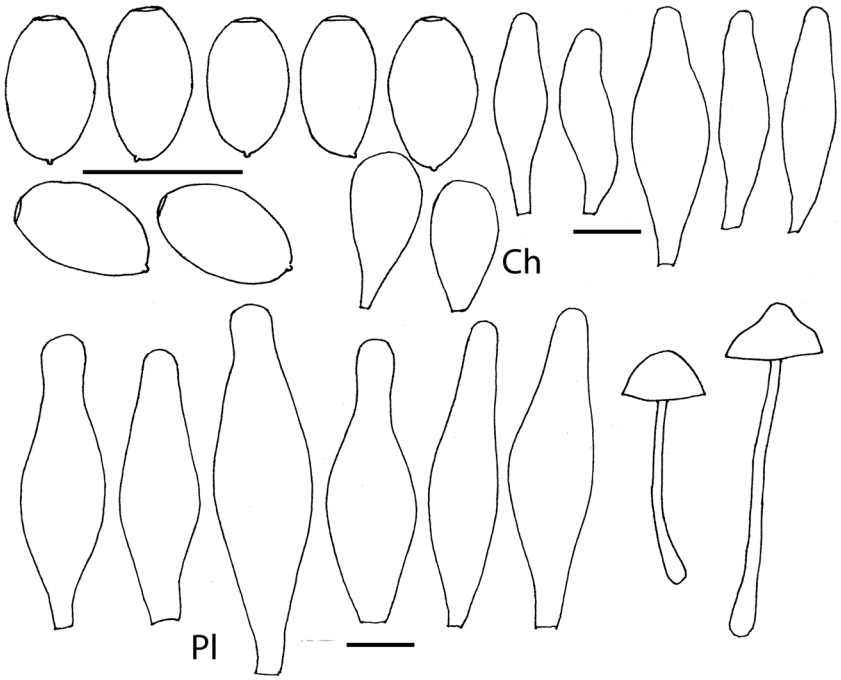


Fig. 9 *Psathyrella fennoscandica.* L. Örstadius 484–05; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

pleurocystidiis similia, dispersa vel modice numerosa, cellulis clavatis immixta. Cellulae veli 5–10 μm latae. Fibulae adsunt. Inter graminis, ad terram loco deusto, gregaria.

Cap 2–18 mm broad, at first convex, campanulate-convex to conico-paraboloid, then convex, not seen expanded plane, without a distinct umbo, not deliquescent, hygrophanous, not striate, when young and fresh dark ochre-brown, then ochre-buff; veil in young stages covered by thin fibrillose white veil remnants, still present on the margin when mature. Gills distant to medium spaced, sinuate-adnate, ochre, becoming dark bister-brown, with a paler flocculose edge. Stem 12–32×1–2 mm, very fragile, white with ochre tinge, sericeous; veil in young stages forming a dense fleece connecting stem with margin of cap. Context thin and fragile. Smell and taste none. Spore print brown.

Spores 7.8–9.2×4.4–5 μm, av. 8.3×4.6 μm, Qav. = 1.8, oblong, subcylindrical, narrowly ovoid, in profile sometimes narrowly amygdaliform, in water yellowish red (Mu. 5YR 5/8), with distinct germ pore. Basidia 4-spored, 18–20×8–9 μm. Pleurocystidia 32–48×10–18 μm, utriform to lageniform, sometimes with thickened walls, scattered, pale. Cheilocystidia of two types: A: 25–35×10–16 μm, similar to pleurocystidia, scattered to rather numerous, B: small, clavate, rather numerous. Pileipellis similar to a hymeniderm; pileitrama with rather strongly pigmented hyphae. Veil cells 5–10 μm wide. Clamps present.

Habitat and distribution: Gregarious on burnt soil in a coastal grassland near the sea. So far only known from the type locality in Italy.

Notes - The species can be recognized by the small size, rather well-developed veil, spore size, cystidia shape, and habitat. *Psathyrella ichnusae* differs from *P. arenosa* in having broader sometimes pigmented pleurocystidia, rather numerous small clavate cheilocystidia, and a habitat on burnt soil.

Psathyrella lilliputana Örstadius & E. Larss., **sp. nov.** [MB 811485] – Holotype: Sweden, Halland, Harplinge, Mannarp, 18.IX.2009, L. Örstadius 130–09 (GB). Fig. 11. (S3: Fig. 10a–d.)

Etymology. The epithet refers to the very small basidiomata that are small enough to inhabit the land of Lilliput in Swift's Gulliver's Travels.

Pileus 1–4 mm latus, semiglobosus, convexus, rufo-brunneus, leviter striatus, hygrophanus; velum disperse fibrillosum. Lamellae distantes, late adnatae, brunneae; acie alba. Stipes 6–8×0.2–0.5 mm, albidus, sparsim fibrillosus, apice pulverulentus. Odor nullus. Sporae 9.5–11×5–6 μm, oblongae, subfusiformes, citriformes, amygdaliformes, interdum subrostellatae vel irregulares, luteolo-rubrae; poro germinativo valde distinctae. Basidia 4-sporigera. Pleurocystidia 25–42×6–12 μm, anguste lageniformia, utriformia, fusiformia, subcylindrica, dispersa. Cheilocystidia 25–38×5–11 μm, pleurocystidiis similia, numerosa. Fibulae adsunt. Habitat: Ad lignum, in pascuis.

Cap 1–4 mm broad, semiglobate to convex, reddish brown, faintly striate, hygrophanous, veil as dispersed fibrils. Gills distant, L=7–8, rather broadly adnate, brown with white edge. Stem 6–8×0.2–0.5 mm, whitish, with sparsely fibrillose veil remnants, pulverulent at apex. Smell none. Taste not recorded.

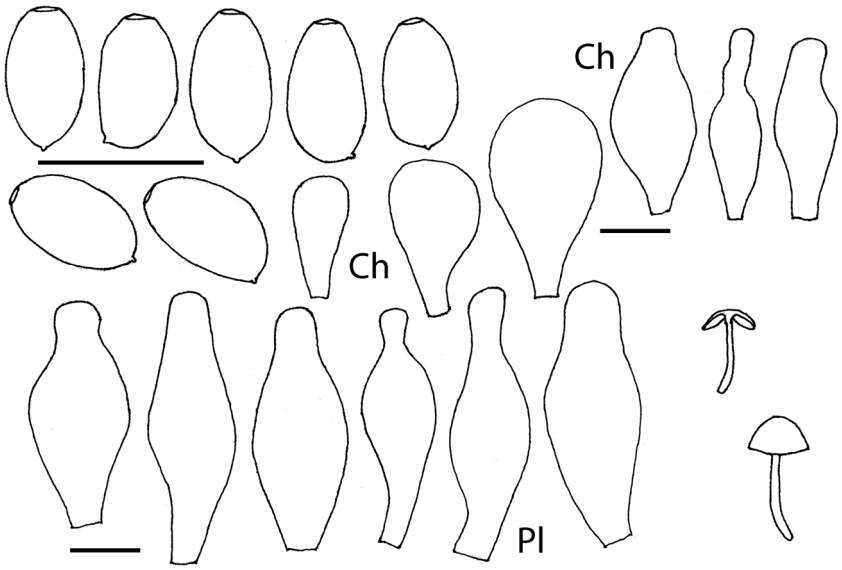


Fig. 10 *Psathyrella ichnusae*. M. Contu 080106; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

Spores 9.5–11×5–6 μm, av. 10.1×5.3 μm, Qav. = 1.9, oblong, subfusiform, sometimes snout-like projected at apex or irregular in outline, in profile citriform, amygdaliform, or with a suprahilar depression, many small oil drops, in water yellowish red (Mu. 5YR 5/6-4/6); germ pore very distinct. Basidia 4-spored, 16–19× 8–9 μm. Pleurocystidia 25–42×6–12 μm, narrowly lageniform, utriform, fusiform, subcylindrical, rarely forked, scattered, pale. Cheilocystidia 25–38×5–11 μm, similar to the pleurocystidia, numerous. Scalp cap halfway from margin: pileipellis made up of clavate to subglobose, ellipsoid to pyriform, 15–30 μm wide, pale cells; pileitrama of strong pigmented hyphae. Clamps frequently seen on septa on hyphae in the stipe.

Habitat and distribution: Growing in a small group on small remnants of deciduous wood in a pasture with *Quercus*. So far only known from the type locality.

Notes - The species can be recognized by tiny basidiomata, small cystidia, and snout-like projected spores. About 15 species in Europe are known with a cap size of 4 mm or less. Only *Psathyrella orbitarum* and *P. purpureobadia* have a mean-value of spore size matching *P. lilliputana*. The latter one can be separated by purple-tinged cap and lack of clamps. *P. orbitarum* is genetically rather closely related with

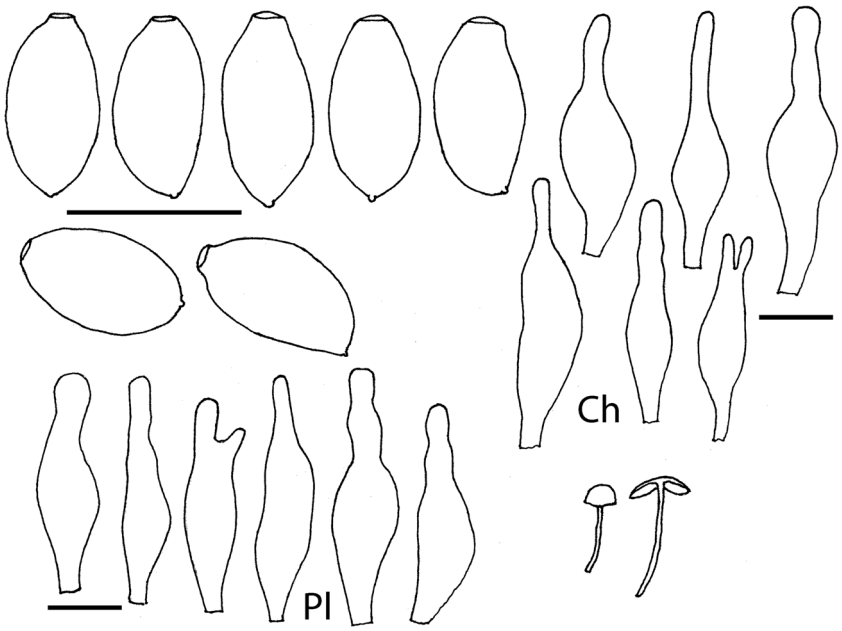


Fig. 11 *Psathyrella lilliputana*. L. Örstadius 130–09; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×4; Scale bars 10 μm

P. lilliputana but differs in having acute cystidia and regularly shaped spores.

Psathyrella lyckebodensis Örstadius & E. Larss., **sp. nov.** [MB 811486] – Holotype: Sweden, Skåne, Trolle-Ljungby, Lyckeboda, on sandy soil in a pasture, 27.X.2011, L. Örstadius 301–11 (GB). Fig. 12. (S3: Fig. 11a–d.)

Etymology. The name refers to Lyckeboda where the fungus was discovered.

Pileus 12 mm latus, conico-convexus, brunneo-fulvus, non-striatus, granulis omnino. Lamellae adnatae, distantes vel modice confertae, ventricosae, brunneo-fulvae. Stipes 40×1.8 mm, deorsum fibrillosus, apice pulverulentus. Odor nullus. Sporae 8–9.2×4–4.6 μm, oblongae, subcylindricae, brunneo-flavae; poro germinativo nullo vel inconspicuo. Basidia 4-sporigera. Pleurocystidia 55–80×12–22 μm, lageniformia, utriformia, modice numerosa. Cheilocystidia 30–75×9–22 μm, pleurocystidiis similia, numerosa, cellulis clavatis immixta. Fibulae adsunt. Habitat: Ad terram, in pascuis.

Cap 12 mm broad, conico-convex, brownish yellow (Mu. 10YR 6/8), not striate, entirely covered by grey white grains. Gills rather broadly adnate, medium spaced to distant, L=c. 14, ventricose, concolorous with cap, with a faint pruinose edge. Stem 40×1.8 mm, slightly paler than cap, white fibrillose, pulverulent at apex. Smell none. Taste not recorded.

Spores 8–9.2×4–4.6 μm, av. 8.6×4.4 μm, Qav. = 2.0, oblong, subcylindrical, sometimes with a wide upper part or a slight suprahilar depression, in water brownish yellow (Mu. 5YR 6/8); germ pore absent or rarely indistinct. Basidia 4-spored, 17–30×7.5–9 μm. Pleurocystidia 55–80×12–22 μm, lageniform to utriform, upper part rarely head-like or subacute, rather numerous. Cheilocystidia of two types: A: 30–75×9–22 μm, similar to pleurocystidia, abundant, B: small, clavate, scattered. Pileipellis an epithelium of loosely arranged often subglobose, pale cells, 15–45 μm wide; pileitrama with pale brown pigmented hyphae. True clamps and pseudoclamps seen.

Habitat and distribution: Solitary on sandy soil with some deciduous trees in a dry pasture grazed by cows. So far only known from the type locality in Sweden.

Notes - The species is distinguished by a granular cap surface, small size, and rather large hymenial cystidia. It belongs to section *Cystopsathyra* (Kits van Waveren 1985) recognized by a powdery-mealy cap surface. Less than ten species are known worldwide from the section, all of them rare. The species differs from *Psathyrella alboflocosa* in having slightly smaller, elongate spores and larger, sometimes subacute cystidia. *P. sphaerocystis* has very small cystidia, wider spores and grows on dung while *P. globosivelata* has smaller spores and often grows on remnants of Agaricales species.

Psathyrella madida Örstadius & E. Larss., **sp. nov.** [MB 811490] – Holotype: Sweden, Skåne, Åhus, Sånnarna, 12.X.2006, L. Örstadius 377–06 (GB). Figs. 2a, 13. (S3: Fig. 12a–d.)

Etymology. The epithet refers to the preferences of moist habitat.

Pileus 7–33 mm latus, conico-convexus, interdum irregularis, spadiceus, fulvus, ad marginem leviter striatus, hygrophanus, in sicco pallescens, velum fibrilloso-floccosum. Lamellae modice confertae, adnatae, ventricosae, griseo-brunneae, acie alba. Stipes 10–35×1.5–3 mm, albus, apice pruinosus, deorsum fibrillosus. Odor nullus. Sporae 7–9.5×4–5 μm, ovoideae, oblongae, subfusiformes, amygdaliformes, subcitriformes, rubidae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 35–50×12–26 μm, clavata, sphaeropedunculata, utriformia, lageniformia, numerosa vel

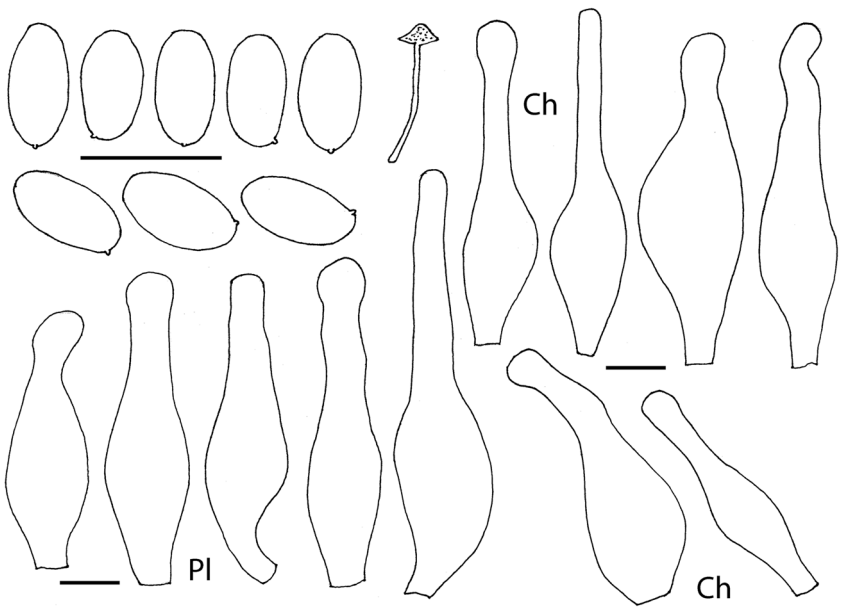


Fig. 12 *Psathyrella lyckebodensis.* L. Örstadius 301–11; Pl Pleurocystidia; Ch Cheilocystidia; Basidioma ×1; Scale bars 10 μm

dispersa. Cheilocystidia 25–55×8–35 μm, pleurocystidiis similia, numerosa. Cellulae veli 40–190×6–40 μm. Fibulae adsunt. Habitat: In solo sabuloso udo, cum *Phragmite*.

Cap 7–33 mm broad, at first semiglobate, then conico-convex, convex, expanding to plane with deflexed margin, sometimes irregular, reddish brown, reddish yellow, fulvous (Mu. 5YR 5/4, 5/6, 6/8), with the darkest colours towards centre, faintly striate at margin, hygrophanous, pallescent on drying; veil from margin to centre with a fibrillose to floccose coating, evanescent. Gills medium spaced, L=24–30, adnate, ventricose, at first white grey, becoming grey brown with white fimbriate edge. Stem 10–35×1.5–3 mm, whitish, pulverulent at apex, downwards with floccules from veil remnants. Smell none. Taste mild.

Spores 7–9.5×4–5 μm, av. 7.9–8.5×4.4 μm, Qav. = 1.8–1.9, narrowly ovoid to oblong, sometimes subfusiform, in profile narrowly amygdaliform, subcitriform or with a slight suprahilar depression, in water red to yellowish red (Mu. 2.5YR 4/6-3/6, 5YR 5/8); germ pore distinct. Basidia 4-spored, 18–26×8–9 μm. Pleurocystidia 35–50×12–26 μm, clavate, sphaeropedunculate, utriform, lageniform, numerous to scattered, pale. Cheilocystidia 25–55×8–35 μm, similar in shape to pleurocystidia, numerous. Scalp cap halfway from margin: pileipellis with subglobose, ellipsoid, 20–55 wide, pale cells, some cells also clavate reminding of a hymeniderm; pileitrama of pale pigmented hyphae. Veil cells 40–190×6–40 μm. Clamps frequent on stem base.

Habitat and distribution: Growing single or in small groups on wet to moist sandy soil close to remnants of *Phragmites communis*. The locality is often inundated during parts of the year. So far only known from the type locality.

Notes - The species is recognized by the rather pale cap, copious veil, large veil cells, cystidia shape, and the moist habitat. The two collections grew ten feet from each other. Specimen 369–06 differs from the holotype in having clavate to sphaeropedunculate pleurocystidia in addition to utriform and lageniform ones. The genetic differences, however, were small. The closely related *P. merdicola,* also with a copious veil, can be separated by smaller spores and growth on dung.

Additional specimen: Sweden, Skåne, Åhus, Sånnarna, on wet to moist sandy soil close to remnants of *Phragmites communis,*10.X.2006, L. Örstadius 369–06.

Psathyrella rybergii Örstadius & E. Larss., **sp. nov.** [MB 811491] – Holotype: Sweden, Skåne, Fjälkestad, Perstorp, 11.X.2006, Örstadius & Ryberg 373–06 (GB). Fig. 14. (S3: Fig. 13a–d.)

Etymology. In honour of the mycologist Arne Ryberg for his contributions to a better knowledge of fungi in southern Sweden.

Pileus 5–11 mm latus, campanulatus vel convexus, rufo-brunneus, striatus, hygrophanus, in sicco pallescens; velum fibrillosum. Lamellae distantes, adnatae, pallide brunneae; acie alba fimbriata. Stipes 15–22×1–1.5 mm, pulverulentus, fibrillosus. Odor nullus. Sporae 8.5–9.5×5–5.5 μm, oblongae, interdum leviter irregulares, subhexagonae, sub microscopium rufae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 35–60×10–22 μm, utriformia, numerosa. Cheilocystidia 30–45×10–16 μm, modice numerosa, pleurocystidiis similia, cellulis parvis clavatis immixta. Fibulae adsunt. Habitat: In silva frondosa.

Cap 5–11 mm broad, campanulate to convex, reddish brown (Mu. 2.5YR 5/4), striate more than halfway from margin, hygrophanous, pallescent on drying; veil present as fibres close to margin. Gills distant, L=12–14, adnate, light brown (Mu. 7.5YR 6/4), with white fimbriate edge. Stem 15–22×1–1.5 mm, pulverulent 2/3 from apex, decreasing in intensity downwards, fibrillose lower part. Smell none.

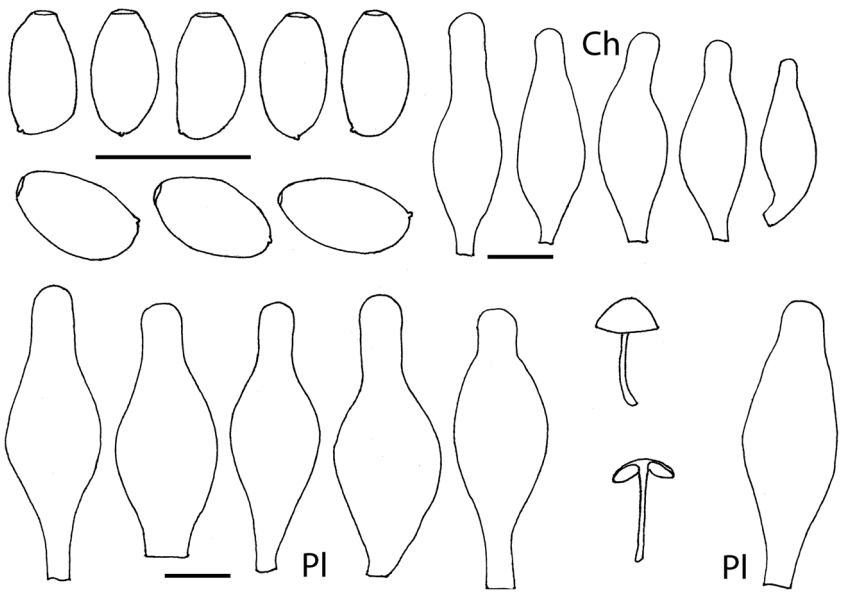


Fig. 13 *Psathyrella madida.* L. Örstadius 377–06; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

Spores 8.5–9.5×5–5.5 μm, av. 9.1×5 μm, Qav. 1.8, oblong, sometimes slightly irregular, subhexagonal, in profile sometimes subphaseoliform, in water red (Mu. 2.5YR 5/6), with distinct germ pore. Basidia 4-spored, 20–28×8–9 μm. Pleurocystidia 35–60×10–22 μm, utriform, numerous, pale yellow below apex. Cheilocystidia of two types: A: 30–45×10–16 μm, similar to pleurocystidia, rather numerous, B: small, clavate, scattered to numerous. Scalp cap halfway from margin: pileipellis with pale yellow, 20–55 μm wide, subglobose to ellipsoid cells; pileitrama and hymenophoral trama with strongly pigmented hyphae. Clamps seen at hyphae of stem base.

Habitat and distribution: On soil among gravel or sand on a path in a deciduous forest. Known from the type locality only.

Notes - The species is distinguished by its small basidiomata, rudimentary veil, utriform cystidia, habitat, and pulverulent stem. *P. panaeoloides* can be separated by often larger basidiomes, by the density of the gills (L=20–30), and by more irregular spores. Moreover, it is not known to grow among gravel in forests.

Psathyrella sabuletorum Örstadius & E. Larss., **sp. nov.** [MB 811492] – Holotype: Sweden, Skåne, N. Åsum, A3 former military camp, 29.X.1998, L. Örstadius 196–98 (GB). Fig. 15. (S3: Fig. 14a–d.)

Etymology. The name epithet refers to the habitat on sandy places.

Pileus 5–15 mm latus, conico-convexus, convexus, brunneus, striatus usque ad medium, hygrophanus, in sicco pallide brunneus; velum fibrillosum. Lamellae distantes, adnexae, pallide brunneae. Stipes 20–35×1–1.5 mm, fragilis, apice pulverulentus, deorsum fibrillosus. Odor nullus. Sporae 8–11.5×4.5–6 μm, ovoideae, oblongae, subcylindricae, interdum amygdaliformes, rufo-flavae; poro germinativo indistinctae. Basidia 4-sporigera. Pleurocystidia 35–55×8–16 μm, lageniformia, fusiformia, numerosa vel dispersa. Cheilocystidia 25–40×9–14 μm, pleurocystidiis similia, dispersa vel destituta, cellulis clavatis immixta. Fibulae adsunt. In locis siccis et apertis ad terram arenosam.

Cap 5–15 mm broad, conico-convex, convex, strong brown (Mu. 7.5YR 5/6) to reddish brown, distinctly striate to centre, hygrophanous, drying to pale brown; veil fibrillose at margin. Gills distant, L=11–16, adnexed, pale brown, with fimbriate edge. Stem 20–35×1–1.5 mm, fragile, sometimes a fibrillose zone, pulverulent at apex, fibrillose downwards. Smell none.

Spores 8–11.5×4.5–6 μm, av. 8.5–10.9×4.9–5.4 μm, Qav. = 1.7–2, ovoid, oblong, subcylindrical, sometimes slightly irregular, amygdaliform or with a suprahilar depression, occasionally subphaseoliform, in water reddish yellow (Mu. 7.5-5YR 6/8); germ pore indistinct to seemingly absent. Basidia 4-spored, 16–23×8–10 μm. Pleurocystidia 30–55×8–16 μm, lageniform to fusiform, sometimes conical or with flexuous walls, numerous to scattered. Cheilocystidia of two types: A: 25–40×8–14 μm, similar to pleurocystidia, rather numerous to absent, B: 8–18 μm wide, clavate to obpyriform, several cells deep from margin and halfway inwards, decreasing in number and then numerous to scattered. Scalp cap halfway from margin: pileipellis consists of subglobose to ellipsoid cells 15–50 μm wide and pale; pileitrama made up of faintly to moderately pigmented hyphae. Veil cells 15–60×5–10 μm. Clamps found on stem hyphae.

Habitat and distribution: Single to scattered in moss-carpets on steppe-like sandy soil in open grassland with some trees of *Pinus*, and in sand dunes. So far known from one locality in Denmark and four localities in southernmost Sweden.

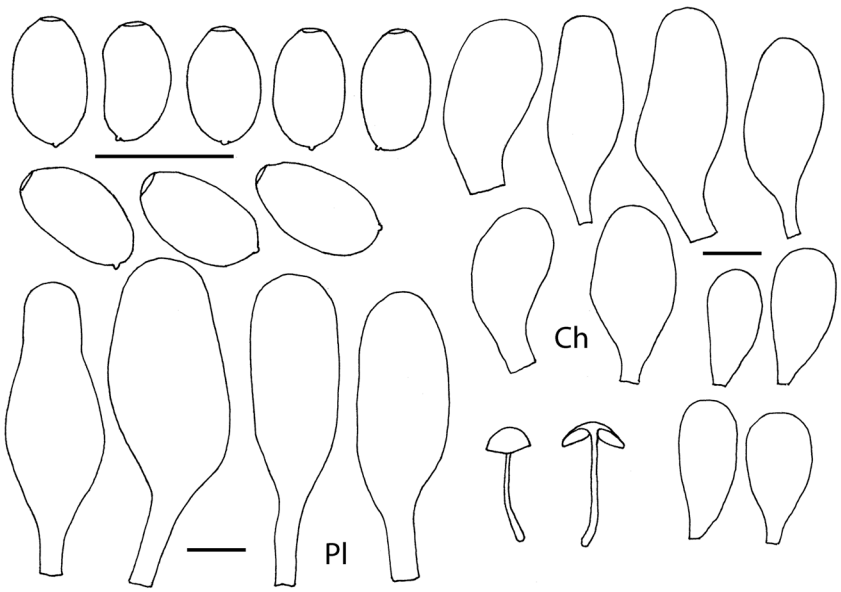


Fig. 14 *Psathyrella rybergii.* L. Örstadius 373–06; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×2; Scale bars 10 μm

Notes - *Psathyrella sabuletorum* is an ordinarily looking species characterized by small basidiomata, scanty veil, and habitat on sandy soil. The gill edge is often dominated by small clavate to obpyriform cells close to cap margin and the spore size varies significantly. It differs from *Psathyrella obtusata* in being smaller, in having amygdaliform spores, and a habitat on sandy soil. *Psathyrella flexispora* also prefers growing on sand, but has darker spores with a distinct germ pore and differently arranged gill edge where acute shaped cheilocystidia dominates. In the description we include the Danish collection with longer but not broader spores.

Additional specimens: Denmark, W. Jylland, Vejers Strand W. of Oksbøl, 3.XI.1990, M. Christensen JV 90–770, (C); Sweden, Skåne, Åhus, Älleköpinge, 31.X.2011, L. Örstadius 310–11; Horna Bränneri, 24.X.1998, L. Örstadius 187–98; 1.XI.2011, L. Örstadius 321–11; Löderup, NO Löderup, 2.XI.2011, L. Örstadius 330–11, 331–11.

Psathyrella scanica Örstadius & E. Larss., **sp. nov.** [MB 811493] – Holotype: Sweden, Skåne, Trolle-Ljungby, Lyckeboda, 29.X.2009, L. Örstadius 183–09 (GB). Fig. 16. (S3: Fig. 15a–d.)

Etymology. The name refers to the province Skåne where the fungus was discovered.

Pileus 6 mm latus, 5 mm altus, conicus, flavido-rubidus, striatus, hygrophanus, in sicco pallescens; velum non visum. Lamellae ascendentes, adnatae, distantes, ventricosae, rufo-brunneae; acie alba fimbriata. Stipes 38×0.8 mm, cylindricus, albidus, fibrillosus. Odor nullus. Sporae 8.5–9.5×4.5–5.5 μm, anguste ovoideae, oblongae, amygdaliformes, luteolo-rubrae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 30–60×10–16 μm, lageniformia, saepe subcapitata vel subclavata, numerosa. Cheilocystidia 25–50×8–16 μm, pleurocystidiis similia, numerosa, cellulis clavatis immixta. Fibulae adsunt. Habitat: Ad terram, in pascuis.

Cap 6 mm wide and 5 mm high, conical, when fresh yellowish red (Mu. 5YR 4/6), striate, hygrophanous, pallescent on drying, veil not seen. Gills ascendant, adnate, distant, L= 12, ventricose, reddish brown (Mu. 5YR 4/4), with white fimbriate edge. Stem 38×0.8 mm, cylindrical, whitish, with some scattered fibrillose veil remnants. Smell none. Taste not recorded.

Spores 8.5–9.5×4.5–5.5 μm, av. 9×5 μm, Qav. = 1.8, narrowly ovoid, oblong, in profile sometimes amygdaliform, in water yellowish red (Mu. 5YR 4/6), with distinct germ pore. Basidia 4-spored, 17–23×8–10 μm. Pleurocystidia 30–60×10–16 μm, lageniform, often with subcapitate or subclavate apex, numerous, pale. Cheilocystidia of two types: A: 25–50×8–16 μm, similar to pleurocystidia, numerous, B: small, clavate, very scattered. Scalp cap half-way from margin: pileipellis with subglobose to ellipsoid 20–32 μm wide cells, pale; pileitrama with strongly pigmented hyphae. Hymenophoral trama moderately pigmented. Clamps present on stem base mycelium.

Habitat and distribution: Solitary among moss on sandy calcareous soil in a cow-grazed pasture with *Juniperus communis*. Known from the type locality.

Notes - *Psathyrella scanica* can be recognized by small basidiomata, conical cap, scanty veil, lageniform cystidia with capitate to clavate upper part, and habitat on sandy calcareous soil. *P. perpusilla* differs in having 2-spored basidia, lageniform cystidia, often with acute to subacute apex, broad, non-amygdaliform spores, and a distinct veil.

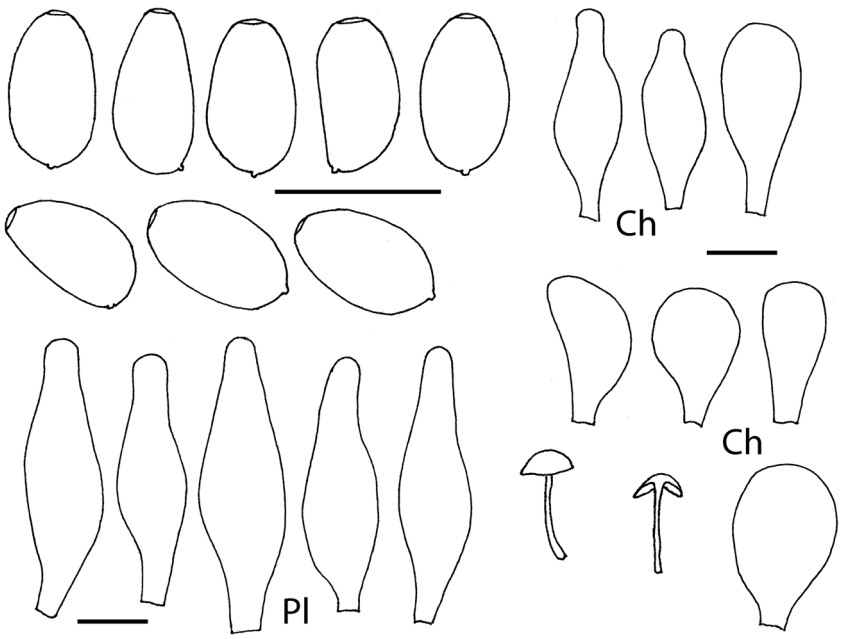


Fig. 15 *Psathyrella sabuletorum.* L. Örstadius 196–98; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

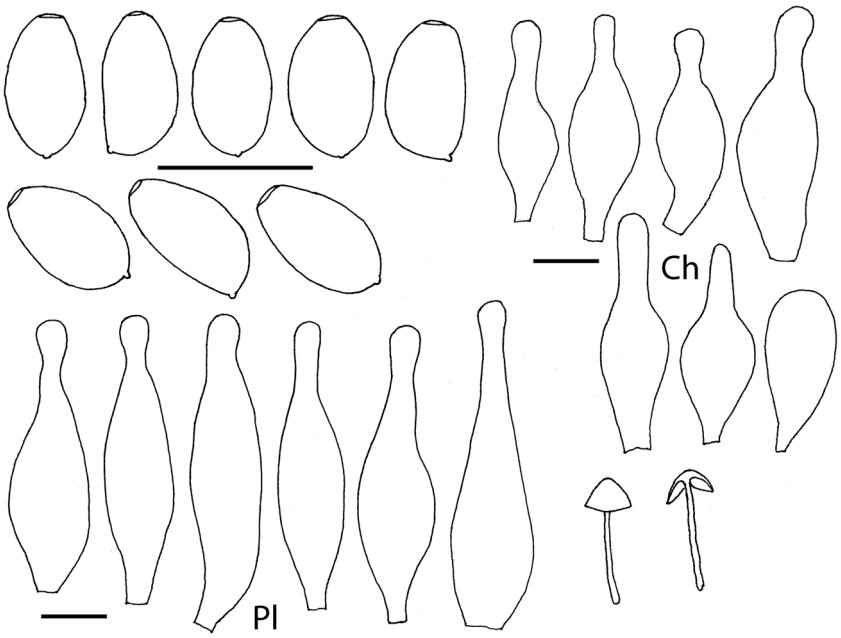


Fig. 16 *Psathyrella scanica.* L. Örstadius 183–09; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×2; Scale bars 10 μm

Psathyrella siccophila Örstadius & E. Larss., **sp. nov.** [MB 811494] – Holotype: Sweden, Skåne, Åhus, Ripa, Älleköpingegård, 24.X.2006, L. Örstadius 417–06 (GB). Fig. 17. (S3: Fig. 16a–d.)

Etymology. The epithet refers to the preference for dry places.

Pileus 8–14 mm latus, primo semiglobatus, deinde convexus, fulvo-cinnamomeus, usque ad 2/3 diametro pellucide striatus, hygrophanus, in sicco pallescens; velum fibrillosum. Lamellae distantes, adnatae, pallide rufo-brunneae. Stipes 20–30×1–2 mm, pallide brunneus, apice pulverulento, deorsum fibrillosus. Odor indistinctus; sapor mitis. Sporae 5.5–7×4.5–5 μm, ellipsoideae vel late ellipsoideae, pallidae; poro germinativo destitutae. Basidia 4-sporigera. Pleurocystidia 35–65×9–18 μm, anguste utriformia, lageniformia, numerosa. Cheilocystidia 25–40×8–14 μm, numerosa, cellulis clavatis immixta. Fibulae adsunt. Habitat in aridis, ad terram arenosam.

Cap 8–14 mm broad, at first semiglobate, then conico-convex, expanded convex with a low umbo, yellowish red (Mu. 5YR 5/6, 4/6, 6/6) with the darkest colours at centre, striate two thirds from margin, hygrophanous, pallescent on drying; veil as bundles of fibres close to margin, when young appendiculate. Gills distant, L=12–16, adnate, light reddish brown (Mu. 5YR 6/4); edge concolorous. Stem 20–30×1–2 mm, pale brown, upper part sometimes with a fibrillose annulate zone of veil remnants, downwards fibrillose, evanescent, pulverulent at apex. Smell indistinct. Taste mild.

Spores 5.5–7×4.5–5 μm, av. 6–6.4×4.7–4.9 μm, Qav. = 1.3, ellipsoid to broadly ellipsoid, in profile flattened on adaxial side, sometimes amygdaliform, in water reddish yellow (Mu. 7.5YR 7/8-6/8); germ pore absent. Basidia 4-spored, 20–32×8–9 μm. Pleurocystidia 35–65×9–18 μm, narrowly utriform to lageniform, with pale yellow walls below apex, numerous. Cheilocystidia of two types: A: 25–50×8–15 μm, similar to pleurocystidia, numerous, B: small, clavate, scattered. Scalp cap half-way from margin: pileipellis with subglobose to ellipsoid, 20–40 μm wide, pale yellow brown cells; pileitrama with strongly pigmented hyphae. Clamps seen on mycelium hyphae.

Habitat and distribution: In small groups in open, dry, calcareous grassland with patches of sand steppe, grazed by horses and cows, together with species like *Geastrum schmidelii* and *Poronia punctata*. Known from two localities in the southernmost province of Skåne, Sweden.

Notes - The species is distinguished by small basidiomata, scanty veil, broad spores, absence of a germ pore, narrowly utriform cystidia, and habitat on dry, calcareous grassland. *Psathyrella stridvallii*, also in the present paper, has narrower, darker spores, and slightly larger basidiomata.

Additional specimens: Sweden, Skåne, Everöd, 500 meters east of Nybo farm, 4.XI.2010, L. Örstadius 98–10.

Psathyrella stridvallii Örstadius & E. Larss., **sp. nov.** [MB 811495] – Holotype: Sweden, Skåne, Kristianstad, Egna hem, 22.VIII.1998, L. Örstadius 104–98 (GB). Figs. 2b, 18. (S3: Fig. 17a–d.)

Etymology. In honour of the late Leif Stridvall and his wife Anita, who sent hundreds of specimens of *Psathyrella* on loan, contributing to a better understanding of the genus.

Pileus 10–30 mm latus, conico-convexus, demum expanso-planus, initio spadiceo-brunneus, striatus, hygrophanus, in sicco pallescens; velum cito evanidum.

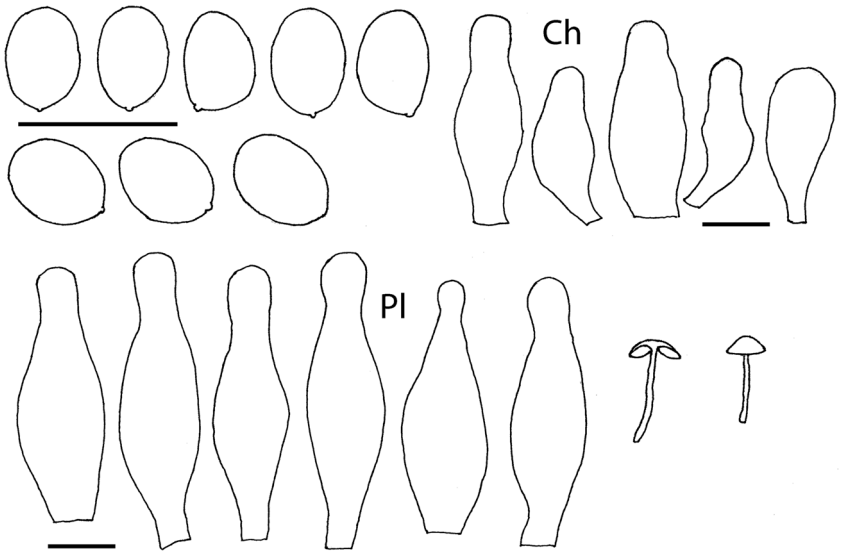


Fig. 17 *Psathyrella siccophila.* L. Örstadius 417–06; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

Lamellae modice confertae, anguste adnatae, fusco-brunneae; acie dilute alba. Stipes 30–40×2–3 mm, albidus, interdum brunnescens. Odor atque sapor indistincti. Sporae 5.5–7×3.5–4.5 μm, ovoideae, ellipsoideae, oblongae, saepe amygdaliformes, in aqua observatae aurantiacae, poro germinativo destitutae vel indistinctae. Basidia 4-sporigera. Pleurocystidia 25–50×10–16 μm, utriformia, clavata, numerosa. Cheilocystidia 25–40×8–14 μm, pleurocystidiis similia, numerosa, cellulis clavatis immixta. Cellulae veli 2–6 μm latae. Fibulae adsunt. Habitat: Ad terram in silva frondosa vel in horti.

Cap 10–30 mm broad, conico-convex, then expanded plane, often wavy, when young dark reddish brown (Mu. 5YR 3/4), striate at margin or halfway to centre, hygrophanous, drying from margin to brown grey, sometimes with ochraceous tinges, micaceous; veil rudimentary as scattered fibrils close to margin in young stages. Gills medium spaced, L=30–33, narrowly adnate, when young light brown (Mu. 7.5YR 6/4), when mature reddish brown (Mu. 5YR 5/4); edge faintly white. Stem 30–40×2–3 mm, fistulose, whitish, brown discolouring when handled, pulverulent at apex, glabrous or with some fibrils downwards. Smell faint. Taste mild. Spore print reddish black (Mu. 10R 2.5/1).

Spores 5.5–7×3.5–4.5 μm, av. 6.2–6.4×3.9–4 μm, ovoid, ellipsoid, oblong, in profile often amygdaliform, in water yellowish red (Mu. 5YR 5/8); Qav. = 1.6; germ pore absent or indistinct. Basidia 4-spored, 18–22×7–8 μm. Pleurocystidia 25–50×10–16 μm, utriform, clavate, numerous, sometimes with yellow pigmented walls below apex. Cheilocystidia of two types: A: 25–40×8–14 μm, similar to pleurocystidia, numerous, scattered towards cap margin, B: small, clavate, scattered, numerous towards cap margin, sometimes difficult to separate from the first type. Pileipellis a hymeniderm of 20–55 μm wide cells; pileitrama of coarsely to moderately incrusted hyphae. Veil cells 2–6 μm broad. Clamps present.

Habitat and distribution: Solitary to subgregarious on soil in a rich deciduous forest and on a manured lawn. Known from two localities in Sweden.

Notes - The species is recognized by small basidiomata, rudimentary veil, small spores, and utriform cystidia. *Psathyrella piluliformis* differs in being larger, having a membranaceous veil between cap margin and stem, and a lignicolous habitat. Moreover, the spores are slightly smaller, irregular in outline, sometimes phaseoliform, and paler. *P. siccophila* with about the same spore length and cystidia shape can be separated by broader and paler spores. The three species are not closely related genetically.

Additional specimens: Sweden, Skåne, Nosaby, Eknabben, 29.V.1991, L. Örstadius 130–91.

Psathyrella sublatispora Örstadius, S.-Å. Hanson & E. Larss., **sp. nov.** [MB 811496] – Holotype: Sweden, Valleberga, Löderup – Kåseberga, 19.X.1997, S.-Å. Hanson & L. Örstadius 190–97 (GB). Fig. 19. (S3: Fig. 18a–d.)

Etymology. The name refers to the relatively broad spores.

Pileus 10–25 mm latus, convexus, interdum umbonatus vel undulatus, castaneus, striatus, in sicco pallescens; velum fibrillosum. Lamellae modice confertae, adnexae, brunneae; acie alba fimbriata. Stipes 40–70×1.5–2 mm, subradicatus usque ad 15 mm, pallide brunneus, apice pulverulentus, deorsum fibrillosus. Odor atque sapor indistincti. Sporae 9.5–11×5.5–7 μm, oblongae, ellipsoideae, raro ovoideae, interdum subamygdaliformes, rubidae, poro germinativo distinctae. Basidia 4-sporigera. Pleurocystidia 40–50×10–16 μm, conica, lageniformia, dispersa. Cheilocystidia 25–40×8–13 μm, pleurocystidiis similia, numerosa, cellulis clavatis immixta. Fibulae adsunt. Habitat: In silva frondosa vel in arvo sicco.

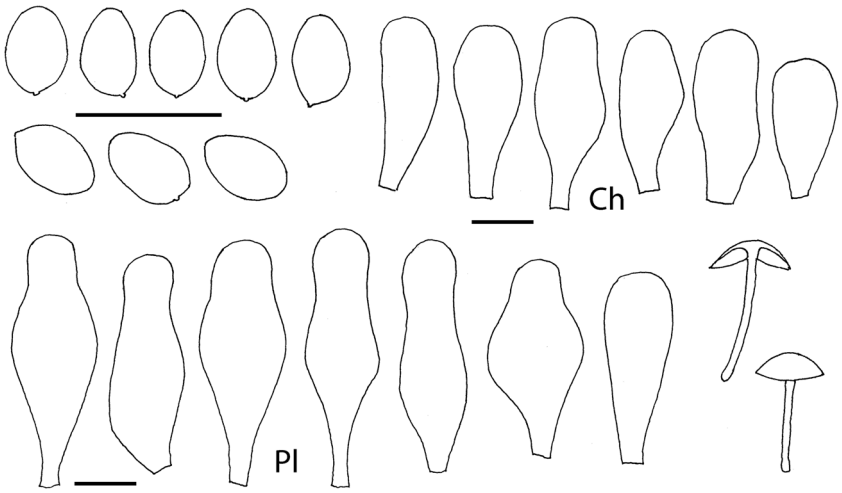


Fig. 18 *Psathyrella stridvallii.* L. Örstadius 104–98; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

Cap 10–25 mm broad, convex, sometimes with umbo or wavy, dark reddish brown (Mu. 5YR 3/4) with darker umbo, striate almost to centre, pallescent on drying; veil as dispersed fibres halfway to centre. Gills medium spaced, L=20–24, adnexed, brown, with white fimbriate edge. Stem 40–70× 1.5–2 mm, with a 8–15 mm long pseudorhiza, pale brown, fibrillose lower part, pulverulent at apex. Smell and taste not distinctive.

Spores 9.5–11×5.5–7 μm, av. 10.1–10.7×6–6.4 μm, Qav. = 1.7, oblong, ellipsoid, rarely ovoid, with obtuse base and apex, in profile sometimes subamygdaliform, in water red (Mu. 2.5YR 4/8-5/8), with distinct germ pore. Basidia 4-spored, 18–24×9–10 μm. Basidia or other cells in hymenium sometimes partly brown intracellular pigmented, sometimes surrounded by pseudoparaphyses like coprinoid species. Pleurocystidia 40–50×10–16 μm, conical to lageniform, scattered, pale. Cheilocystidia of two types: A: 25–40×8–13 μm, similar to pleurocystidia, numerous or rather numerous, B: 10–15 μm wide, clavate, scattered to numerous, increasing in frequency towards cap margin. Scalp cap half-way from margin: pileipellis with subglobose to ellipsoid 10–40 μm wide cells, pale; pileitrama with strongly pigmented hyphae. Hymenophoral trama moderately pigmented. Clamps seen on stem hyphae.

Habitat and distribution: Solitary to gregarious, on the margin of an old potato field on sandy soil with *Senecio vulgaris*, *Polygonum aviculare*, *Chenopodium album* and *Artemisia vulgaris*, also among grass on a path through a grove. Found on two localities in Sweden.

Notes - The species is recognized by the relatively broad spores Qav. = 1.7, pointed cystidia, pseudorhiza, and a preference for growing on nitrophilous soil. *Psathyrella orbitarum* and *P. orbicularis* differ in having more elongate spores, reflected in the mean-values for the two species: Qav. = 1.8–2.1. Moreover, *P. orbitarum* lacks a pseudorhiza and *P. orbicularis* has less frequent clavate cells on gill edge near cap margin. The two species are molecularly well separated from *P. sublatispora*.

Additional specimens: Sweden, Skåne, Kristianstad, Näsby park, 22.X.2000, L. Örstadius 264–00 (GB).

Psathyrella vesterholtii Örstadius & E. Larss., **sp. nov.** [MB 811497] – Holotype: Sweden, Västerbotten, Saxnäs, 26.VII.2010, Laessoe & Petersen JHP-10.086 (GB). Figs. 2f, 20. (S3: Fig. 19a–d and 20).

Etymology. In honour of the late Jan Vesterholt, who first discovered the species.

Pileus 8–25 mm latus, campanulatus, conico-convexus, deinde expanso-convexus, rufo-brunneus vel brunneus, striatus, hygrophanus, velum disperse fibrillosum. Lamellae modice confertae, angustae, adnatae, brunneae; acie alba. Stipes 30–80×1–4 mm, sursum annulato-membranaceus, deorsum fibrillosus. Sporae 9–11×5–6 μm, ovoideae, oblongae, subfusiformes, amygdaliformes, rubidae vel luteolo-rubrae, poro germinativo subdistinctae. Basidia 4-sporigera. Pleurocystidia 45–85×9–22 μm, lageniformia, obtuse fusiformia, utriformia, subcylindrica, luteola, numerosa. Cheilocystidia 30–60×10–18 μm, pleurocystidiis similia, modice numerosa, cellulis clavatis immixta. Cellulae veli 30–150×5–40 μm. Fibulae adsunt. In sylva inter muscos.

Cap 8–25 mm broad, campanulate, conico-convexus, then expanded convex, reddish brown to brown, striate, hygrophanous; veil remnants as dispersed fibrils. Gills medium spaced, L=c. 25–35, narrow, adnate, brown with white edge. Stem 30–80×1–4 mm, upper part with a membranaceous annulus, downwards fibrillose. Smell and taste unknown.

Spores 9–11×5–6 μm, av. 9.8–10.4×5.2–5.7 μm, Qav. = 1.8–1.9, ovoid, oblong, subfusiform, in profile amygdaliform or with a slight suprahilar depression, rarely subphaseoliform,

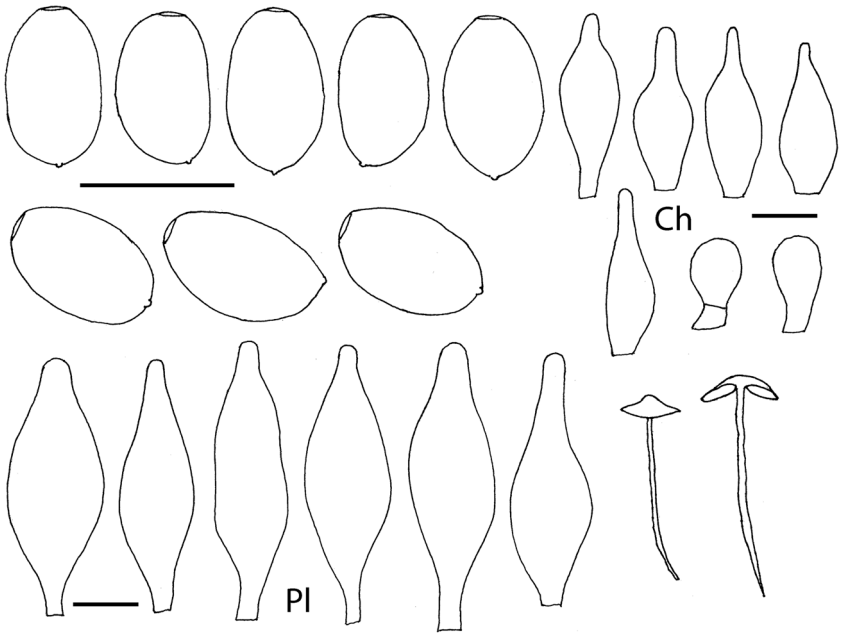


Fig. 19 *Psathyrella sublatispora.* L. Örstadius 190–97; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

in water red to yellowish red (Mu. 2.5–5YR 5/8), with rather distinct germ pore. Basidia 4-spored, 18–22×9–10 μm. Pleurocystidia 45–85×9–22 μm, lageniform, obtusely fusiform, utriform, subcylindrical, with thickened yellow walls, numerous. Cheilocystidia of two types: A: 30–60×10–18 μm, similar to pleurocystidia, rather numerous, B: small, clavate, numerous. Scalp cap halfway from margin: pileipellis of subglobose to ellipsoid 20–60 μm wide cells. Pileitrama made up of rather strongly pigmented hyphae. Veil cells 30–150×5–40 μm, ventricose, cylindrical. Clamps present.

Habitat and distribution: Solitary or in small groups in moss carpets (compare below) in coniferous forests. Known from four localities in the Faroes and Sweden, all north of latitude 62° N but south of the arctic circle.

Notes - The species is recognized by a membraneous annulus, large yellow cystidia, and habitat among mosses. T. Hallingbäck, expert on bryophytes, kindly tried to determine the mosses on a photo of the holotype collection: *Hylocomium* sp. (probably *H. splendens*), *Dicranum* (probably *D. majus*) and *Lophozia* (probably *L. ventricosa*). The

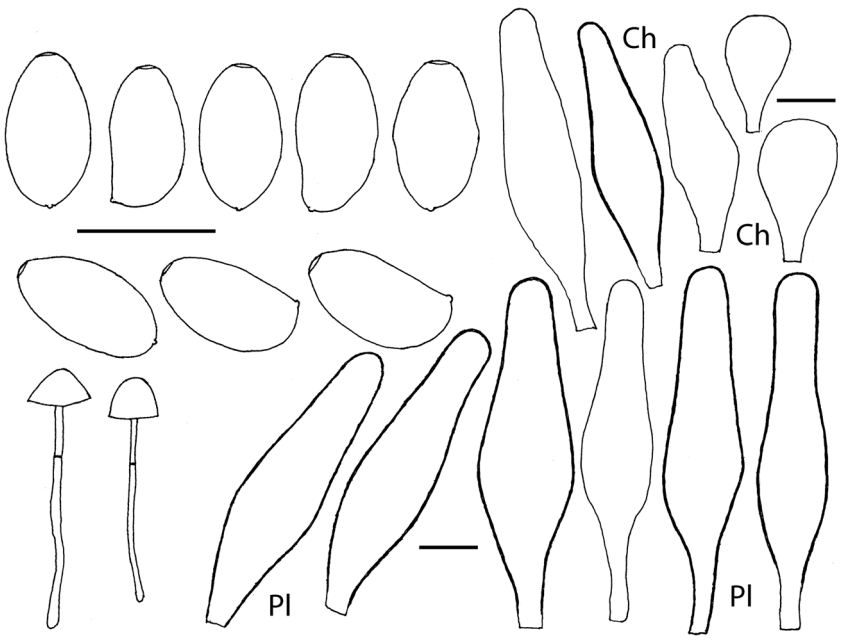


Fig. 20 *Psathyrella vesterholtii.* J.H. Petersen JHP-10.086; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

genetically closely related *Psathyrella sphagnicola* differs from all four collections of *P. vesterholtii* in having smaller spores and pleurocystidia. *P. fibrillosa* is similar by habitat and yellow-pigmented cystidia but can be separated by smaller spores, more acute cystidia, and lack of a membraneous annulus.

Additional specimens: The Faroes, Eysturoy, Selatrad, 22.VIII.1992, J. Vesterholt F3507, (C); Streymoy, Torshavn, Vidalundin, 31.VII.1988, J. Vesterholt 514, (C). Sweden, Jämtland, Kall, Lindvallen, 12.VIII.1996, S. Jacobsson 96004, (GB).

New recognized genera, species, and combinations

Kauffmania Örstadius & E. Larss., **gen. nov.** [MB811613] – Type: *Kauffmania larga* (Kauffman) Örstadius & E. Larss.

Diagnostic characters. – Basidiomata large, veil present, often connected to wood. Cap dark reddish brown, moist striate, hygrophanous, pallescent on drying. Gills crowded, adnate to adnexed, pale, becoming reddish brown, with white fimbriate edge. Stem rather firm. Spores medium-sized, pale, with indistinct to absent germ pore. Basidia or other cells in hymenium sometimes brown intracellular pigmented. Hymenial cystidia present. Pileipellis a hymeniderm sometimes with transition to a paraderm. Clamps present.

Etymology. – The genus name refers to the American mycologist Calvin Henry Kauffman who described the type species.

Note. – A monotypic genus recognized by large sized basidiomata, scanty veil, and pale spores.

Kauffmania larga (Kauffman) Örstadius & E. Larss., **comb. nov.** [MB811614]≡*Psilocybe larga* Kauffman, Publications Mich. geol. biol. Surv., Biol. Ser. 5 26: 279. 1918 – Holotype: U.S.A., Michigan, Washtenaw, Dexter Rd., 6.VI.1910, C. H. Kauffman (MICH!). Figs. 3e, 21.

Selected description: Smith, Mem. N.Y. bot. Gdn 24: 125–126, 1972.

Cap 30–140 mm, at first hemispherical, then expanded convex to plane, sometimes umbonate, when young dark reddish brown to dark brown (Mu. 7.5YR 4/4), at maturity cinnamon, dark yellow brown to yellowish red (Mu. 5YR 5/6), sometimes glossy, when moist striate up to half-way from margin, hygrophanous, drying pale buff or cream, veil as white fibrils at margin, connecting to the stem in young fruitbodies. Gills adnate to adnexed, ventricose, crowded, L=30–40, at first beige, becoming reddish brown to brown (Mu. 7.5YR 4/4), with white flocculose edge under a lens. Stem 40–110×4–15 mm, enlarged below, hollow, rather firm, whitish, pulverulent at apex, silky fibrillose below. Smell faint, sometimes like tomato leaves. Taste mild.

Spores 7.5–10×4.5–6.5 μm, av. 8–9.6×5–5.8 μm, Qav. = 1.5–1.7, ellipsoid, oblong to ovoid, sometimes slightly irregular in outline, in profile sometimes phaseoliform, reddish yellow (Mu. 5YR 6/8), germ pore indistinct to absent. Basidia 18–36×8–10 μm, 4-spored. Basidia or other cells in hymenium sometimes in part with brown intracellular pigmentation. Pleurocystidia 40–90×10–24 μm, mostly utriform, sometimes obtusely fusiform, lageniform to clavate, rarely forked or rostrate, numerous, walls yellow. Cheilocystidia of two types: A: 35–90×10–22 μm, similar to pleurocystidia, numerous to scattered, B: small, clavate, scattered to numerous. Pileipellis a hymeniderm sometimes with transition to a paraderm of 20–60 μm wide cells; pileitrama of pale to moderately pigmented hyphae. Veil cells 20–150×2–10 μm, cylindrical. Clamps present.

Habitat and distribution: Gregarious to scattered in deciduous or coniferous forests on rotten wood, wood chips, sticks or twigs, or directly on soil, in dry or moist places, on acid- or

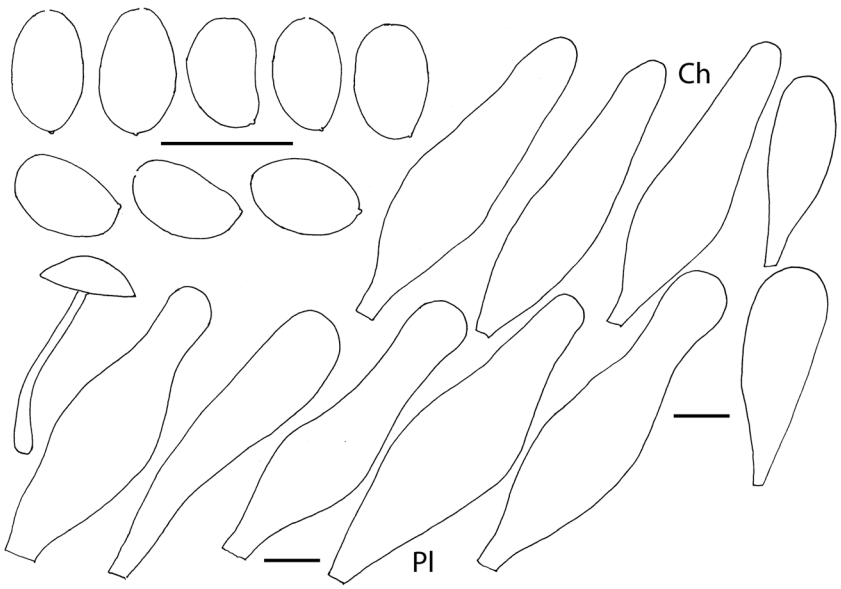


Fig. 21 *Kauffmania larga*. C. H. Kauffman holotype; Pl Pleurocystidia; Ch Cheilocystidia; Basidioma ×0,5; Scale bars 10 μm

base-rich soil; summer to autumn; so far recorded from Denmark, Finland, Germany, Iceland, Norway, Sweden, and North America, but probably overlooked.

Notes – Kauffmania larga is recognized by its large size, scanty veil, and pale spores. The cystidia are large, mostly utriform and numerous. *Psathyrella rostellata* differs in having a well-developed veil in shape of large patches at cap margin, also reflecting in 4–20 μm wide veil cells. Moreover, the cystidia are lageniform to fusiform, at apex with a rostrum which often is bent or forked.

Selected specimens examined: Denmark: NE. Jylland. Høstemark Skov, S. of Mou, 1.X.1994, J. Vesterholt & S. Hansen (C, JV94-763). Finland: Etelä-Häme. Tammela, Mustiala, 1.VIII.1881, P. A. Karsten 4996 (H). Germany: Brandenburg. Um Buchwäldchen, 28.IX.2002, L. Örstadius 16–02. Iceland: S.-Múl.: Hallormsstaður, Ljósárkinn, 20.VI.1986, H. Hallgrímsson (AMNH, FA-13976). Norway: Akershus. Ås, Nordbyveien v/Dylterud, 2.VIII.1977, K. Østmoe 96/77 (O, as *Psathyrella* sp.). Sweden: Västergötland, Habo, N. of Sjöbol, 22.10.1999, E. Grundel LÖ197-99. USA: Michigan. Washtenaw, Dexter Rd., 6.VI.1910, C. H. Kauffman (MICH, holotype of *Psilocybe larga*).

Cystoagaricus

Murrill (1945) described the new species *Nolanea strobilomyces* Murrill. According to Singer (1947) the species was not nolanoid. He found it necessary to describe a new genus and transfer the species, hence *Cystoagaricus strobilomyces* (Murrill) Singer. The shape and dark colour of the spores combined with structure of gill edge and pileipellis made it impossible for Singer to identify the species in genera like *Inocybe*, *Psathyrella* or *Agaricus*. Singer found it more proper to place *Cystoagaricus* in Leucocoprinaceae than in Coprinaceae, the latter family corresponding to our days Psathyrellaceae. Four species belong to *Cystoagaricus* according to Index Fungorum. Horak (1980), however, recognized only one species, *C. strobilomyces.* He examined ten collections, among them the type, and gave a detailed description.

The phylogenetic position of *Cystoagaricus strobilomyces* in the present paper together with *C. silvestris* and allies is not surprising as the species have in common a brown squamulose cap surface, rather small, subrectangular, mitriform, or phaseoliform shaped spores, and utriform cystidia.

Some species described by Smith (1972) should in the near future be examined closer to see if they belong to *Cystoagaricus*.

***Cystoagaricus* Singer emend. Örstadius & E. Larss.** – Type: *Cystoagaricus strobilomyces* (Murrill) Singer, Mycologia 39(1): 86, 1947. Fig. 22.

Basidiomata small to medium sized, non-deliquescent, lignicolous. Cap grey, brown, dark brown, sometimes olivaceous, fibrillose, squamulose, spiny, or squarrose, striate or not; veil present. Lamellae often crowded, adnate to adnexed, pale, becoming dark brown. Stem fibrillose, scaly, or with an annulus. Context sometimes blackening. Spores small to medium-sized, often irregular, subtriangular, subrectangular, or mitriform. Cheilo- and pleurocystidia present, often utriform or clavate.

Cystoagaricus strobilomyces (Murrill) Singer, Mycologia 39(1): 86, 1947. Holotype: USA, Florida, Murrill, F-16520 (FLAS).

Selected descriptions: Horak, Sydowia 33:64–70, 1980; Singer, Mycologia 39:85, 1947.

Collection examined: New Caledonia: Paita, Mt. Mou, 1200 m, 22.II.1977, Horak (ZT, 77/35). Fig. 22a.

Cystoagaricus squarrosiceps (Singer) Örstadius & E. Larss., **comb. nov.** [IF551032]≡*Psathyrella squarrosiceps* Singer, Nova Hedwigia 29:53. 1978 – Holotype: Ecuador, *R. Singer B7276* (F!). Fig. 22b.

Selected description: Singer (l.c.).

Additional collection examined: Ecuador, Napo, Anangu, Rio Napo, 20.6–5.7.1983, T. Laessoe 44834 (C).

Cystoagaricus olivaceogriseus (A.H. Sm.) Örstadius & E. Larss., **comb. nov.** [IF551033]≡*Psathyrella olivaceogrisea* A.H. Sm., Mem NY bot Gdn 24:47. 1972 – Holotype: USA, Alaska, *Wells-Kempton 8/15/63-5* (MICH!). Fig. 22c.

Selected description: Smith (l.c.).

Cystoagaricus silvestris (Gillet) Örstadius & E. Larss., **comb. nov.** [IF551034]≡*Hypholoma silvestre* Gillet, Hyménomycètes: 568. 1878 – Holotype (France, missing?). Fig. 3b.

Selected descriptions: Kits van Waveren, Persoonia, Suppl Vol 2:121, 1985 (as *P. populina*); Romagnesi, Bull Soc mycol Fr 98:62, 1982.

Selected collections examined: Finland: Ahvenanmaa. Jomala, Ramsholm, 27.IX.1980, M. Korhonen & R. Tuomikoski (H). Sweden: Skåne. Benestad, Örups almskog, 18.IX.2008, I. Månsson & L. Örstadius 163–08. Fig. 22d.

Cystoagaricus hirtosquamulosus (Peck) Örstadius & E. Larss., **comb. nov.** [IF551031]≡*Agaricus hirtosquamulosus* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 53. 1873 – Holotype: USA, New York, *C.H. Peck* (NYS 1479!). Fig. 22e.

Selected descriptions: Musumeci, Boll Gr Micol G Bres 49:9–57, 2006. Smith, Mem NY bot Gdn 24:44, 1972.

Additional collections examined: Estonia: Heimtali, S. of Viljandi, 26.VIII.1989, J. Vesterholt 89–459 (C). Finland, Ahvenanmaa, Jomala, Ramsholm, 27.IX.1980, M. Korhonen & R. Tuomikoski (H).

Typhrasa Örstadius & E. Larss., **gen. nov.** [MB 811499] – Type: *Typhrasa gossypina* (Bull.) Örstadius & E. Larss.

Diagnostic characters. – Basidiomata medium-sized, with well-developed veil, growing on wood or on soil. Cap brown, striate or not, hygrophanous. Gills crowded, adnate to adnexed, pale, becoming brown, with white edge. Spores

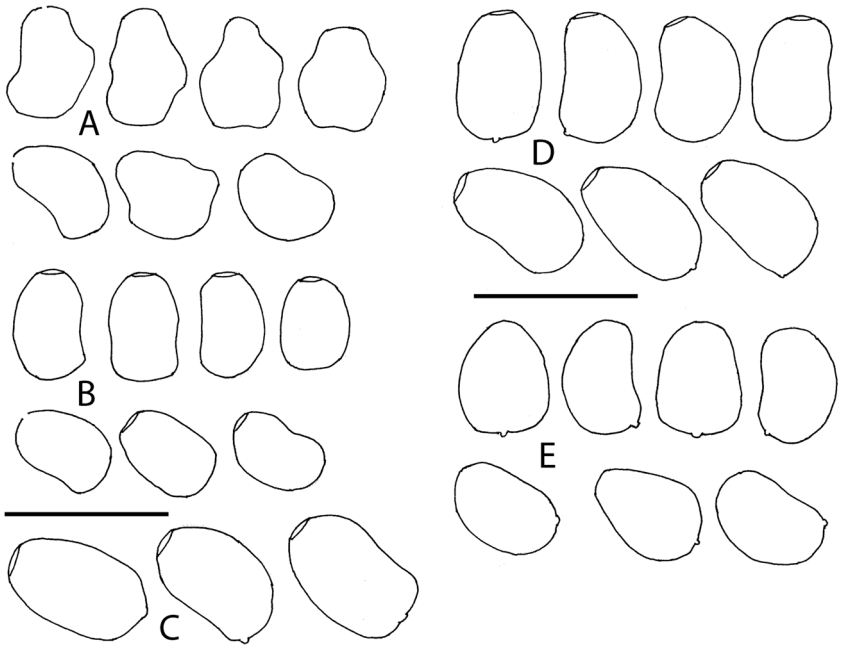


Fig. 22 *Cystoagaricus*. Spore shapes from five species; **a**. *C. strobilomyces;* **b**. *C. squarrosiceps*; **c**. *C. olivaceogriseus*; **d**. *C. silvestris*; **e**. *C. hirtosquamulosus*; Scale bars 10 μm

small to medium-sized, with colours from red to reddish yellow. Hymenial cystidia large, rostrate, and with intracellular oily drops or globules. Pileipellis with a hymeniderm or a paraderm. Clamps present.

Etymology. – The genus name is an anagram of *Psathyra* an illegitimate genus earlier containing many psathyrelloid species.

Typhrasa gossypina (Bull.: Fr.) Örstadius & E. Larss., **comb. nov.** [MB811616]≡*Agaricus gossypinus* Bull., Herb France 9:pl 425 Fig. 2, 1789 – Lectotype designated here: Bulliard, Herbier de la France 9:plate 425, Fig. 2, 1789. Figs. 3a, 23.

Selected descriptions: Arnolds, Fungi non delineati 26: 63, 2003; Kits van Waveren, Persoonia, Suppl. Vol. 2:251, 1985; Kühner & Romagnesi, Fl Analyt Champ Super:362, 1953.

Cap 10–70 mm, at first conical to campanulate, then convex, finally expanded plane with umbo, when young dark brown to dark reddish brown, striate at margin, hygrophanous,

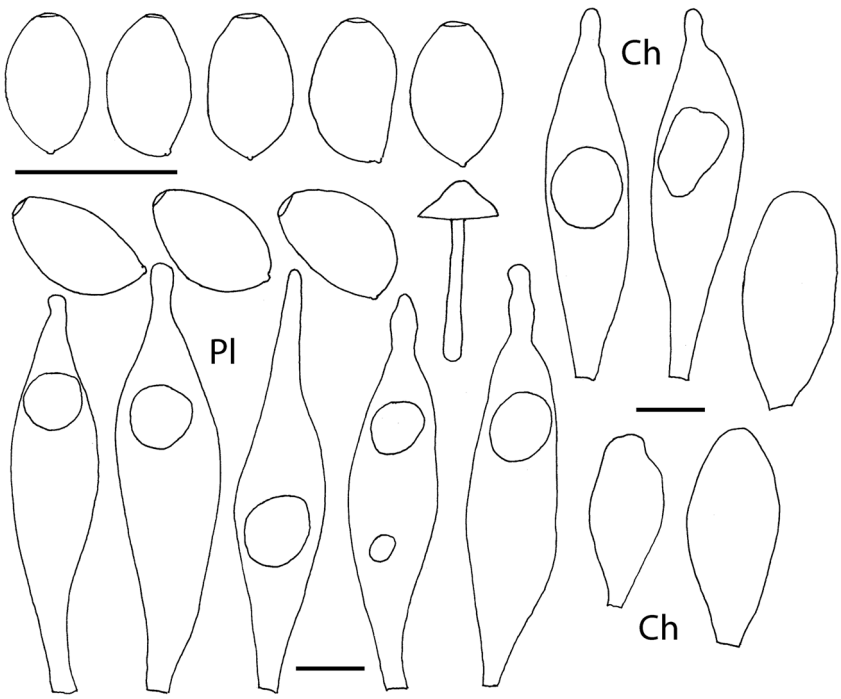


Fig. 23 *Typhrasa gossypina*. R.K. Schumacher 024; Pl Pleurocystidia; Ch Cheilocystidia; Basidioma ×1; Scale bars 10 μm

drying pale ochraceous brown, veil as fibres or flocci near the margin, appendiculate at margin. Gills broadly adnate, sometimes with tooth, medium spaced, L=30–38, when young pale brown, becoming dark brown with white fimbriate edge. Stem 25–100×3–10 mm, equal or thickened towards base, whitish, pulverulent at apex, with fibrils and flocci from veil remnants below, sometimes with a fugacious, hanging, striate ring. Smell none or "etwas säuerlich-kakaoartig" and taste "mild" (R. K. Schumacher pers. comm.).

Spores 7–9×5–6×4.5–5.5 μm, av. 7.6–8.5×5–5.8×4.7–5.3 μm, Qav. = 1.4–1.6 and 1.5–1.7, ovoid, subfusiform, ellipsoid, oblong, broadly ellipsoid, in profile often amygdaloid or with suprahilar depression, sometimes subphaseoliform, yellowish red (Mu. 5YR 5/8), with distinct germ pore. Basidia 4-spored, 18–30×9–11 μm. Pleurocystidia 35–80×10–18 μm, fusiform to conical, often with a long rostrum, rarely clavate, with one, rarely two large internal oily drops, pale or rarely yellow pigmented below apex, numerous. Cheilocystidia of two types: A: similar in size, shape, and frequency to pleurocystidia, B: small, clavate, scattered to numerous; gill edge rarely faintly pigmented. Pileipellis a hymeniderm sometimes a transition to a paraderm of 15–55 μm wide cells; pileitrama made up of pale pigmented hyphae with scattered incrustations; an intracellular pigmented layer sometimes present between pileipellis and pileitrama. Veil cells 25–120×4–10(−20) μm, cylindrical to ventricose. Clamps present.

Habitat and distribution: Solitary, gregarious or caespitose in deciduous or coniferous forests with *Betula, Fagus, Quercus*, *Picea* or *Pinus*, on logs, twigs, wood chips and fireplaces; rarely reported from many countries in Europe and North America.

Notes. – *Typhrasa gossypina* is recognized by large rostrate cystidia with intracellular oily drop and rather wide spores. It lacks outstanding macroscopical features. The cap is usually 10–30 mm broad but Orton (1960) measured it up to 70 mm for his *Psathyrella xanthocystis*. *T. gossypina* is separated from *P. fibrillosa* by the intracellular oily drop and in having pale, long rostrate cystidia. It differs from *T. nanispora* in having larger spores.

Selected collections examined: Denmark: Sjaelland. Nørreskov, 24.IX.2011, T, Laessøe (C, TL2011-389713). England: Wiltshire, VII.1941, unknown collector (L). Finland: Sompion Lappi. Sodankylä, Pullinpuoti, Ammattikoulu, 24.VIII.1992, I. Kytövuori 92–910 (H). Germany: Brandenburg. E. Fürstenwalde, "Beerenbusch", 13.IX.2003, R. K. Schumacher 024. The Netherlands: Drente. Gees, 28.I.1975, K. Booy (L). Norway: Oslo, Oslofjord, Gressholmen, 7.X.2013, A. Molia & T. Laessøe, AM241s-2013 (O). Portugal: Beira Litoral. Esmoriz, 1.I.1990, D. Olofsson LÖ 71–90. Sweden: Uppland. Värmdö, 3.XII.2000, H.-G. Toresson LÖ 3–01. Wales, Lake Vyrnwy, 10.IX.1979 (L, coll. Kits van Waveren).

Additional collections examined: USA: New York. Suffolk, Port Jefferson, Aug. 1904, G. F. Atkinson (NYS 983, holotype of *Hypholoma delineatum*); Washington. Pierce Co, Lower Tahoma, Mt. Rainer Nat'l Park, 9.VIII.1948, Smith 29994 (MICH, as *Psathyrella canadensis*).

Typhrasa nanispora Örstadius, Hauskn. & E. Larss., **sp. nov.** [MB 811500] – Holotype: Austria, Wien, Lainzer Tiergarten, Wienerblick, 6.VII.1998, T. Barta (GB!). Fig. 24. (S3: Figs. 20a–d.)

Etymology. The epithet refers to the small spores.

Pileus 35–55 mm latus, convexus, flavo-brunneus, ferrugineus, carneus tinctus, hygrophanus sed non striatus, velum gossypino-squamulosum, ad marginem appendiculatum. Lamellae anguste adnatae, confertae, griseofuscae, acie albida. Stipes 45–55×8–13 mm, ad basim paulum incrassatus, subradicatus, pallide brunneus, fibrilloso-flocculosus brunneus vel olivaceo-brunneus obtectus. Sporae 5–6×3–4 μm, ovoideae, ellipsoideae, oblongae, phaseoliformes, sub microscopium pallidae, poro germinativo instructae. Basidia 4-sporigera. Pleurocystidia 40–75×12–18 μm, copiosa, fusiformia, clavata, rostrata, globus intracellularis praesens similis *Typhrasa gossypina*. Cheilocystidia 35–70×10–17 μm, similia pleurocystidiis, numerosa. Cellulae veli 30–100×4–14 μm. Fibulae adsunt. Habitat: Ad terram vel ad lignum subterreum.

Cap 35–55 mm broad, expanded convex with broad obtuse umbo, at centre yellow brown, rust brown, tan (Kornerup & Wanscher 6E8-6E6), towards margin distinctly paler, goldblond (5-6C4), with tinge of flesh colour, hygrophanous but not striate when collected, smooth to slightly rugose; veil as large, white cottony patches scattered on entire surface (not visible on the photo), partly appendiculate at margin. Gills adnexed, crowded, narrow, grey brown with white edge. Stem 45–55×8–13 mm, thickened towards base, sometimes almost bulbous and with a pseudorhiza (attached to buried wood?), pale brown, beige white at apex, slightly darker lower part, fistulose, covered with brown to olive brown fibrils and flocci. Flesh whitish, without smell. Spores 5–6×3–4 μm, mean-value 5.4×3.4 μm, Qav. = 1.6, ovoid, ellipsoid, oblong, in profile often phaseoliform, reddish yellow (Mu. 7.5YR 7/6-7/8); germ pore rather distinct. Basidia 4-spored, 14–27×5.5–6.5 μm. Pleurocystidia 40–75×12–18 μm, fusiform, clavate, at apex often with a rostrum 2–10 μm in length, with intracellular globule like in *Typhrasa gossypina*, abundant, with slightly yellow walls. Cheilocystidia 35–70×10–17 μm, similar to pleurocystidia, numerous. Pileipellis a paraderm of subglobose, clavate, or irregular shaped 15–30 μm wide cells. Pileitrama of moderately yellow brown pigmented hyphae incrusted or not; gill trama rather pale. Veil cells 30–100×4–14 μm. Clamps seen on hyphae of stem and veil.

Habitat and distribution: On bare soil, maybe attached to buried wood, in a forest dominated by

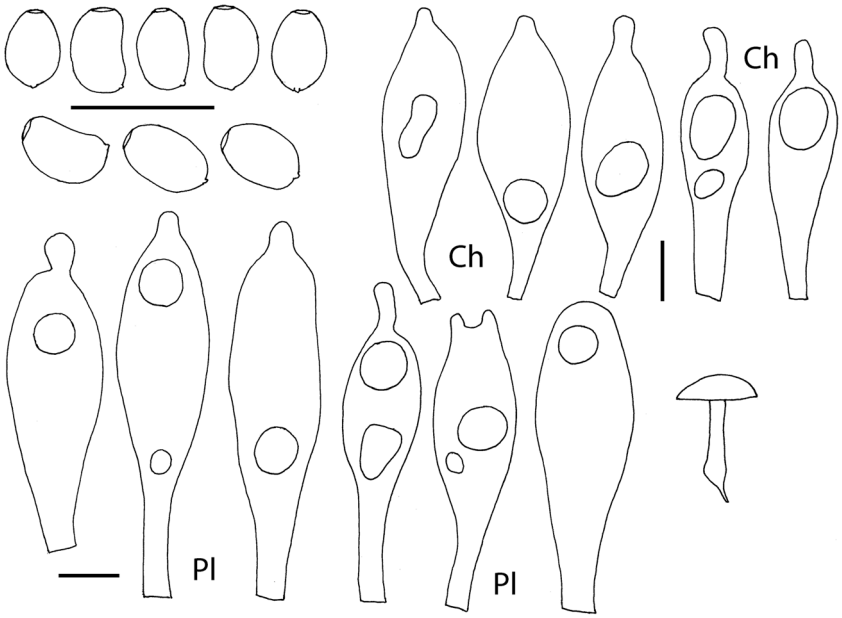


Fig. 24 *Typhrasa nanispora*. T. Barta 980706; Pl Pleurocystidia; Ch Cheilocystidia; Basidioma ×0,5; Scale bars 10 μm

deciduous trees. So far only known from the type locality in Austria.

Notes - *Typhrasa nanispora* is recognized by rather large basidiomata, well-developed veil, small and pale spores, and abundant fusiform, rostrate cystidia equipped with an intracellular globule. The closely related *Typhrasa gossypina* also has cystidia with globules but differs in having larger and darker spores. *Psathyrella laevissima, P. maculata, P. obscurotristis, P. piluliformis*, all with spores less than 6 μm in length, differ in having smaller, less frequent cystidia lacking intracellular globules. In addition, the basidiomata of *P. laevissima* and *P. obscurotristis* are smaller. *P. maculata* has a white soon black discolouring veil.

Homophron (Britzelm.) Örstadius & E. Larss., **gen. stat. nov.** [MB811630]≡*Agaricus* subgenus *Homophron* Britzelm., Ber naturhist Ver Augsburg 27:174, 1883≡ *Homophron* (Britzelm.) W. B. Cooke, Gen Homobas 45:100, 1953, (nom. inval., no basionym cited) – Type: *Agaricus spadiceus* Schaeff., Fung. Bavariae 4:27, 1774, selected by Singer, Lilloa 22:468, 1951≡*Psilocybe spadicea* P. Kumm., Führ Pilzk (Zerbst):71, 1871.

Description: Basidiomata small to large, fragile to rather rigid, non-deliquescent, lignicolous. Pileus brown, striate, hygrophanous. Lamellae close to crowded. Stem central. Veil absent. Spores small to medium sized, moderately pigmented to hyaline, with indistinct to absent germ pore. Basidia 4-spored. Pleurocystidia often thick-walled and with crystals or incrustations at apex. Pileipellis a hymeniderm or transition to a paraderm. Clamps present.

Notes – The combination of absence of veil and presence of thick-walled cystidia with crystals is unique in Psathyrellaceae.

Homophron spadiceum (P. Kumm.) Örstadius & E. Larss. **comb. nov.** [MB811631]≡*Agaricus spadiceus* Schaeff., Fung Bavariae 4:27, 1774 (nom. inval., non *Agaricus spadiceus* Scop. 1772. *Psilocybe spadicea* P. Kumm. in Führ Pilzk (Zerbst): 71,1871. – Lectotype (designated by Örstadius in Windahlia 24:21. 2001): Schaeffer, Fung Bavariae 1, pl. 60, Figs. 4 and 6, 1762 – Epitype (designated by Örstadius in Windahlia 24:21. 2001): Germany, Bavaria, M. Enderle (GB!, isoepitype M!, GenBank no. DQ389729). Figs. 3c, d, 25.

Selected descriptions: Enderle, Beitr Kenntn Pilze Mitteleur 5:58–59, 1989; Kits van Waveren, Persoonia, Suppl Vol 2:161–164, 1985; Kühner & Romagnesi, Fl Analyt Champ Super:369, 1953; Ludwig, Pilzkompendium Band 2:644, 2007; Örstadius, Windahlia 24:19–24, 2001.

Cap 25–120 mm, convex, with inflexed margin, becoming plane, sometimes wavy, at first dark reddish brown, red brown (Mu. 2.5YR 3/4-4/4, 5YR 4/4), sometimes striate at margin, faintly hygrophanous, at maturity or when drying fading to pale ochraceous brown, flesh-coloured or pink (Mu. 5YR 5/8-8/4, 7.5YR 8/4), at margin covered with minute hairs (lens); veil absent. Gills adnate, very crowded, L=60–82, when young very pale brown (Mu. 10YR 8/3), then brown with red tinges (Mu. 5YR 5/4, 7.5YR 5/4-5/6) and with a slightly flocculose edge. Stem 25–100×3–12 mm, rigid, equal or slightly thickened towards base, pale brown, flocculose at apex or half-way down, fibrillose below. Context rather firm. Taste mild and smell pleasant. Spore print dark reddish brown (Mu. 5YR 3/3).

Spores 6.5–11×4–5.5 μm, av. 7.2–10.3×4.1–5.3 μm, Qav. = 1.7–1.9, ovoid, oblong, or subcylindrical, sometimes irregular in outline, in profile sometimes phaseoliform, rarely amygdaloid, thin-walled, very pale brown (Mu. 10YR 8/4), germ pore absent or rarely indistinct. Basidia 4-spored, 16–36×6–8 μm.

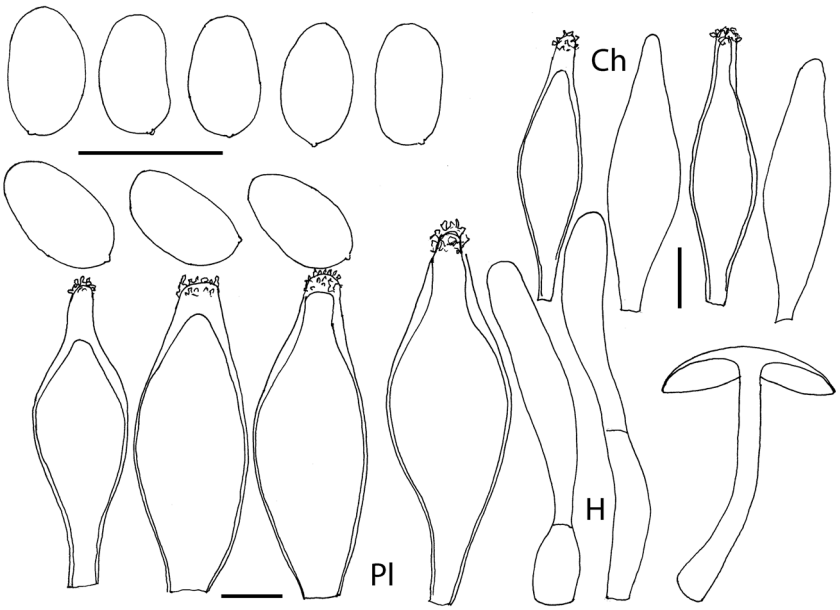


Fig. 25 *Homophron spadiceum*. M. Enderle epitype; Pl Pleurocystidia; Ch Cheilocystidia; H Hairs from cap margin; Basidioma ×1; Scale bars 10 μm

Pleurocystidia 30–80×10–24 μm, lageniform, fusiform to conical, often rostrate with apex covered with crystals, wall up to 3 μm thick near apex, yellow or not, abundant, rarely rather scattered. Cheilocystidia of two types: A: 40–85×8–22 μm, similar to pleurocystidia, scattered to abundant, B: 30–90×6–28 μm, clavate, utriform or cylindrical, scattered or rarely numerous. Caulocystidia present at apex and similar to shape of cheilocystidia. Hairs at cap margin originating from globose cells of pileipellis, septate or not; terminal cells of the hairs 40–180×6–18 μm, versiform, cylindrical, clavate, lageniform etc., rarely similar to pleurocystidia. Pileipellis a hymeniderm with transition to a paraderm of 12–40 μm wide cells; pileitrama of moderately pigmented hyphae, rarely incrusted; hymenophoral trama of membranal pigmented hyphae. Clamps present on stem hyphae.

Habitat and distribution: Usually caespitose around deciduous trees and conifers, both stumps and at the base of living trees, e.g., *Abies pinsapo, Acacia xanthophloea, Aesculus, Alnus, Bambusa, Betula, Castanea, Fagus, Morus alba, Picea, Pinus, Populus, Quercus faginea,* and *Ulmus*; known from many countries in and outside Europe.

Notes – The species is distinguished by the absence of veil, hairy cap margin, very pale spores, and caespitose growth. Moreover, the rostrate cystidia are often thick-walled and provided with crystals. *H. cernuum* differs in having paler basidiomata, smaller and darker spores, and obtuse cystidia.

Selected collections examined: Belgium: Antwerpen. Retie, Prinsenpark, 11.XI.1993, Volders 93222 (BR, holotype of *Psathyrella imleriana*). Finland: Ahvenanmaa. Jomala, Prästgården Ramsholmen, 24.IX.1994, J. Vauras 9754 F (TURA). Germany: Bayern. Leipheim-Riedheim, 11.XI.1998, M. Enderle (GB, epitype of *Psathyrella spadicea*; M, isoepitype). The Netherlands: Overijssel. Delden, 20.X.1975 (L, coll. Kits van Waveren, as *Psathyrella variata*). Sweden: Skåne. Kristianstad, S:a Lingenäset, 11.IX.2003, L. Örstadius 75–03. USA: Idaho. Bonner Co., Priest Lake, 6.X.1964, A. H. Smith 71092 (MICH, holotype of *Psathyrella variata*). New York. North Elba, Aug., C. H. Peck (NYS 2690, holotype of *Agaricus saccharinophilus*).

Homophron cernuum (Vahl: Fr.) Örstadius & E. Larss., **comb. nov.** [MB811632]≡*Agaricus cernuus* Vahl in Fl Danic 6(17):9, pl. 1008, Fig. 1, 1790. ≡ *Agaricus cernuus* Vahl: Fr., Syst mycol (Lundae) **1**:298, 1821. – Holotype missing (C). – Lectotype (designated here): *Agaricus cernuus* Vahl, Fl Danic 6(17):9, pl. 1008, Fig. 1, 1790. – Epitype (designated here): Denmark, Sjaelland, Risø, Boertmann 8.XI. 2013 (GB!, GenBank no. KJ939632)

Note: The illustration Vahl refers to when describing the species is ambiguous and therefore an epitype was selected. The ITS sequence of the type specimens of *P. crenulata* A.H. Sm (MICH!, KC992957) was shown to be identical with the ITS of *Homophron cernuum*. The two species are also congruent in morphology, so we regard *P. crenulata* as a later synonym.

Selected descriptions: Gröger, Boletus 1: 1, 1984; Kits van Waveren, Persoonia, Suppl Vol 2:76, 1985; Kühner & Romagnesi, Fl Analyt Champ Super:368, 1953; Ludwig, Pilzkompendium Band 2:642, 2007.

Selected collections examined: Denmark, Sjaelland, Risø, 8.XI.2013, D. Boertmann (GB, epitype, ATLAS DB2013-652266). Finland, Varsinais-Suomi. Dragsfjärd, Örö, Örö island, 14.X.1999, J. Vauras 15664 (TURA 8633). Germany,

Bayern. Goaslweide, 12.X.2002, P. Karasch (herb. Karasch G/109-02). Norway, Oppland. S. Land hd, Odnes hotell, 24.IX.1977, J. Stordal 18841 (O, as *Psathyrella* sp.). Sweden, Dalarna. Falun, Önsbacken, 28.X.1977, R. Morander 2843 (S).

Homophron camptopodum (Sacc.) Örstadius & E. Larss., **comb. nov.** [MB811633]≡*Agaricus camptopus* Peck, Ann Rep NY State Mus 31:35. 1879 (nom. illegit., non *Agaricus camptopus* Berk., 1850). *Psilocybe camptopoda* Sacc., Syll Fung 5:1057. 1887; *Psathyrella camptopoda* (Sacc.) A.H. Sm., Mycologia 42:127. 1950. – Holotype: USA, New York, Sept, Peck (NYS!).

Selected description: Smith, Mem. N.Y. bot. Gdn 24: 245, 1972.

Collections examined: Russia, Kamchatka, Avacha River Valley, N.E. of Razdolny, 31.VII.1997, T. Laessoe (IB 1997/956). Kamchatka, Esso, Bystraya River Valley, 8 km. N.E. of Esso, 9.VIII.1997, U. Peintner (IB 1997/957). USA, Idaho, Bonner Co, Priest Lake, 11.X.1956, A.H. Smith 54450 (MICH). New York, Catskill Mountains, Sept., C.H. Peck (NYS 617, holotype of *Agaricus camptopus*). New York, Savannah, October, C.H. Peck (NYS 3290, holotype of *Psilocybe unicolor*). Washington, Jefferson Co, 30.VI.1939, A.H. Smith 14719 (MICH).

Coprinopsis canoceps (Kauffman) Örstadius & E. Larss., **comb. nov.** [IF551035]≡*Hypholoma canoceps* Kauffman, Pap Mich Acad Sci 5:132. 1926 – Holotype: USA, Oregon, Oct 1922, *Kauffman* (MICH!).

Coprinopsis cineraria (Har. Takah.) Örstadius & E. Larss., **comb. nov.** [IF551036]≡*Psathyrella cineraria* Har. Takah., Mycoscience 41(1):18. 2000 – Holotype: Japan, *Takahashi* (CBM FB-24142!, GenBank no. KC992962).

Coprinopsis melanthina (Fr.) Örstadius & E. Larss., **comb. nov.** [IF551037]≡*Agaricus melanthinus* ("*melantinus*") Fr., Öfvers K Vetensk Akad Förh 8:49. 1852, "1851" – Holotype lacking.

Note: The species was described by Fries from a Swedish collection. Since then no further records have been reported in Sweden and therefore we await to typify the species.

Coprinopsis submicrospora (Heykoop & G. Moreno) Örstadius & E. Larss., **comb. nov.** [IF551038]≡*Psathyrella submicrospora* Heykoop & G. Moreno, Mycotaxon 83:426. 2002 – Holotype: Spain, *Heykoop & Villarreal* (AH 27055!, GenBank no. KC992959).

Coprinopsis uliginicola (McKnight & A.H. Sm.) Örstadius & E. Larss., **comb. nov.** [IF551038]≡*Psathyrella uliginicola* McKnight & A.H. Sm., Mem NY bot Gdn 24:100. 1972 – Holotype: USA, Wyoming, *Smith 34903* (MICH!, GenBank no. KC992960).

Neotypes selected for species described by Fries

Parasola conopilus (Fr.) Örstadius & E. Larss., Mycol. Res. 112(10):1180, 2008≡*Agaricus conopilus* Fr., Syst mycol (Lundae) **1**:504, 1821 – **Neotype (designated here)** [MBT200684]**:** Sweden, Skåne, Ivetofta, Krogstorp, 2002-10-22, L. Örstadius 186–02 (GB!, GenBank no. DQ389725).

Psathyrella candolleana (Fr.) Maire apud Maire, Mém. Soc. Sci. Nat. Maroc. 45:112, 1937≡*Agaricus candolleanus* Fr., Observ. mycol. (Havniae) 2:182, 1818 – **Neotype (designated here)** [MBT200683]: Sweden, Bohuslän, Lysekil, Bro, SO Kibbestens torvemyr, 1973-08-17, L. & A. Stridvall 73/030 (GB!, GenBank no. KM030175)

Psathyrella caput-medusae (Fr.) Konrad & Maubl., Encyclop. Mycol. 14: 127, 1949 [1948]≡*Agaricus caput-medusae* Fr., Epicr. syst. mycol. (Upsaliae):216, 1838 [1836–1838] – **Neotype (designated here)** [MBT200681]: Sweden, Västergötland, Trollhättan, Lextorp, 1993-08-30, L. & A. Stridvall 93/062 (GB!, GenBank no. KM030174)

Psathyrella fatua (Fr.) Konrad & Maubl., Encyclop. Mycol. 14(1):125, 1949 [1948]≡*Agaricus stipatus y. fatuus* (Fr.) Fr., Syst. mycol. (Lundae):296 (1821). – **Neotype (designated here)** [MBT 200685]: Sweden, Skåne, Österslöv, Lövhall, 1997-10-11, L. Örstadius 132–97 (GB!, GenBank no. DQ389681).

Psathyrella noli-tangere (Fr.) A. Pearson & Dennis, Trans. Br. mycol. Soc. 31(3–4): 184, 1948 [1947]. ≡ *Agaricus noli-tangere* Fr., Epicr. syst. mycol. (Upsaliae):234, 1838 [1836–1838] – **Neotype (designated here)** [MBT200686]**:** Sweden, Skåne, V. Vram, Stackedala, 2003-09-14, L. Örstadius 83–03 (GB!, GenBank no. DQ389713).

Psathyrella pennata (Fr.) A. Pearson & Dennis, Trans. Br. mycol. Soc. 31(3–4):184, 1948 [1947]. ≡ *Agaricus pennatus* Fr., Syst. mycol. (Lundae) 1:297, 1821 – **Neotype (designated here)** [MBT200687]: Sweden, Skåne, Kiaby, Kjugekull, 1984-10-01, L. Örstadius 216–84 (GB!, GenBank no. KJ939633).

Psathyrella prona (Fr.) Gillet, Hyménomycètes (Alençon): 618, 1878≡*Agaricus pronus* Fr., Epicr. syst. mycol. (Upsaliae):239, 1838 [1836–1838]. – **Neotype (designated here)** [MBT200688]: Sweden, Skåne, Trolle-Ljungby, Fårabäck, 2000-10-17, L. Örstadius 237–00 (GB!, GenBank no. KJ939634).

Species new to Europe and/or to the Nordic countries

Psathyrella hololanigera (G.F. Atk.) A.H. Sm., Mem NY bot Gdn 24:130. 1972≡*Hypholoma hololanigerum* G.F. Atk., Annls mycol 7:371. 1909. Fig. 26. (S3: Fig. 21a–d.)

Cap 18–30 mm broad, up to 10 mm high, flat convex, sometimes with low umbo, fresh brown, yellowish brown, near the margin paler, and here soon drying to ochraceous, brownish-ochre, hygrophanous, striate; veil strongly devoloped as squamules or flocci, appendiculate at margin. Gills distant, adnate, pale brown, becoming moderately dark brown, with concolorous edge. Stem up to 80×3 mm, white to whitish, with fibrillose remnants from the white veil. Context without smell.

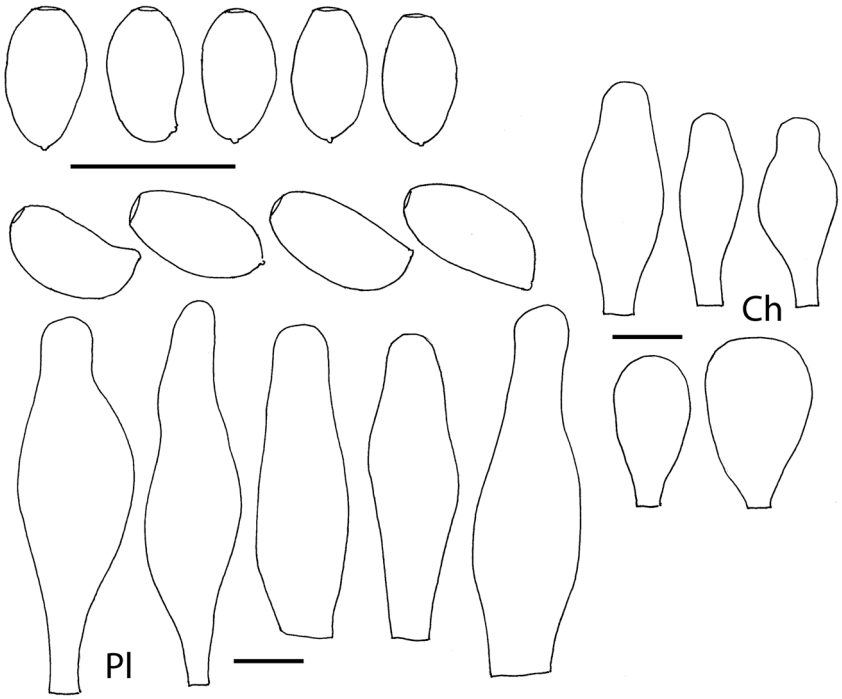


Fig. 26 *Psathyrella hololanigera*. G.F. Atkinson 15192; Pl Pleurocystidia; Ch Cheilocystidia; Scale bars 10 μm

Spores 7.5–9.5×4–5 μm, av. 8–8.7×4.3–4.5 μm, Q=1.9, oblong with acute to obtuse base, in profile flattened on adaxial side, amygdaliform or with a distinct suprahilar depression, phaseoliform, with oil drop, in water yellowish red (Mu. 5YR 5/8-6/8), with distinct germ pore. Basidia 4-spored, 17–28×8–10 μm. Pleurocystidia 35–60×11–20 μm, narrowly utriform, subcylindrical, lageniform, pale, numerous. Cheilocystidia of two types: A: 25–40×8–11 μm, similar to pleurocystidia, scattered near cap margin, then increasing and becoming numerous, B: small, clavate to sphaeropedunculate, numerous close to cap margin, then decreasing and becoming scattered. Scalp cap half-way from margin: pileipellis with 20–30 μm wide, pale, ellipsoid to subglobose cells; pileitrama with strongly pigmented hyphae. Hymenophoral trama with rather pale hyphae. Veil cells on cap 30–125×5–22 μm. Clamps seen on veil and stem hyphae.

Habitat and distribution: Solitary or in a small group on leaf litter in pine forest on sandy soil with *Quercus ilex*, *Rhuscus*, *Phillyria* etc., in the USA on strongly decayed wood in woods. Known from single collections in Italy and North America.

Specimens examined. Italy, Emilia-Romagna, Ravenna, Pineta di Classe, 9.XI.2007, A. Hausknecht (WU). USA, New York, Ithaca, 9.VII.1903, G.F. Atkinson 15192 (CUP!, holotype of *Hypholoma hololanigerum*).

Additional specimen examined. The Netherlands, Drenthe, Anloo, Plot Q65, 10.XI.1987, P.-J. Keizer 87324 (WAG-W!, holotype of *Psathyrella rhombispora* P.-J. Keizer).

Notes - The species can be recognized by the copious veil, the spores with a distinct suprahilar depression and the cystidia shape. The examined type agrees satisfactory with the European find. *Psathyrella kitsiana* differs in having smaller spores, 6.5–8×3.5–5 μm, av. 7.2–7.8×3.9–4.8 μm and moreover the germ pore is lacking or indistinct. The two species differ molecularly. *Psathyrella rhombispora* (Keizer 1993) is difficult to separate from the two mentioned species. The spores of the examined type lacked a germ pore and measured 7.8–9×4.2–5 μm, mean-value 8.3×4.6 μm. The collector observed no velar remains on the cap but some flocci on the stem. *P. rhombispora* should be sequenced to get information of its phylogenetic position.

Psathyrella parva A.H. Sm., Mem NY Bot Gdn 24:433. 1972. Fig. 27. (S3: Fig. 22b–d.)

Cap 2–15 mm broad, when young semiglobose, then expanded convex, moist chestnut-brown, date-brown, dark brown, subfulvous, dingy tan, then cinnamon-buff, hygrophanous, faintly striate, drying to buff or pinkish buff; surface covered by white flocci or fibrils from veil remants, soon disappearing. Gills adnate to adnexed, distant L=12–15, ventricose, at first ochraceous or pale brown, becoming avellaneous to greyish-brown with paler edges. Stem 10–35×0.3–1.5 mm, equal, delicate, fragile, white overall, pruinose above, fibrillose below. No smell or taste present. Spore print brown.

Spores 6–8×4–5 μm, av. 6.2–7.4×3.9–4.6 μm, Qav. = 1.4–1.7, ellipsoid, ovoid, with obtuse poles, in profile rarely subamygdaliform or subphaseoliform, in water

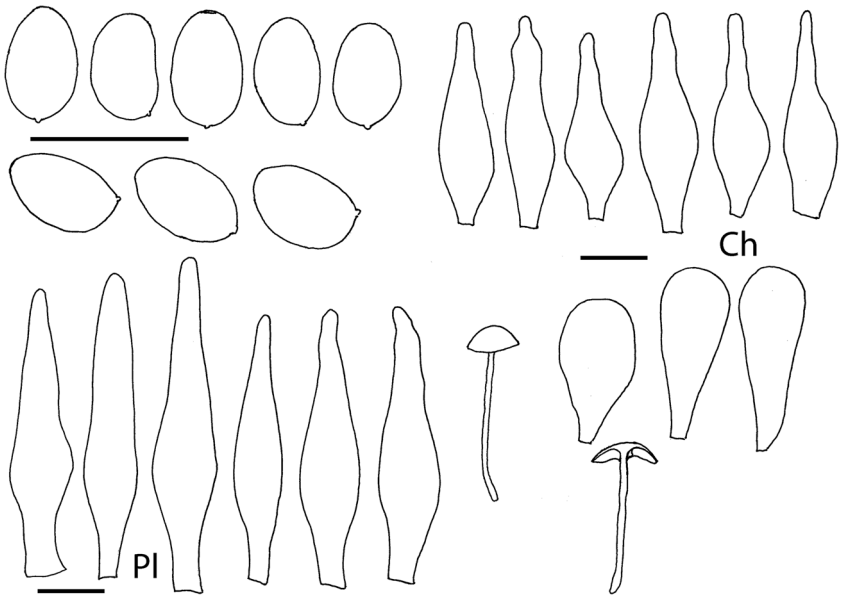


Fig. 27 *Psathyrella parva*. Contu 071227; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

yellowish red (Mu. 5YR 5/8-6/8); germ pore indistinct to absent. Basidia 4-spored, 12–23×6–9 μm. Pleurocystidia 25–60×7–13 μm, narrowly lageniform, conical, fusiform, with acute to obtuse apex, rarely bent or forked, with pale to slightly yellow walls, scattered to numerous. Cheilocystidia of two types: A: 25–55×5–14 μm, similar to pleurocystidia, numerous to scattered, B: small, clavate, scattered, absent to rather numerous. Scalp cap halfway from margin: pileipellis with subglobose to ellipsoid 15–50 μm wide cells, pale; pileitrama with incrusted hyphae. Veil cells 15–90×4–16 μm, pale, clamped.

Habitat and distribution: Solitary to gregarious on sand in wasteland near scrub oak, in open calcareous grassland or on acid sand in a coastal grassland near the sea; autumn to nearly winter; known from Denmark, Italy, Norway, Sweden, and the USA.

Notes - *Psathyrella parva* is recognized by small basidiomata, a rather scanty veil, small spores, indistinct germ pore, small often acute cystidia, and a habitat on sandy soil. Also *P. seymourensis* grows on sand but can be separated by slightly larger basidiomata, slightly larger spores, and a distinct germ pore. More material is needed to separate the two species more clearly.

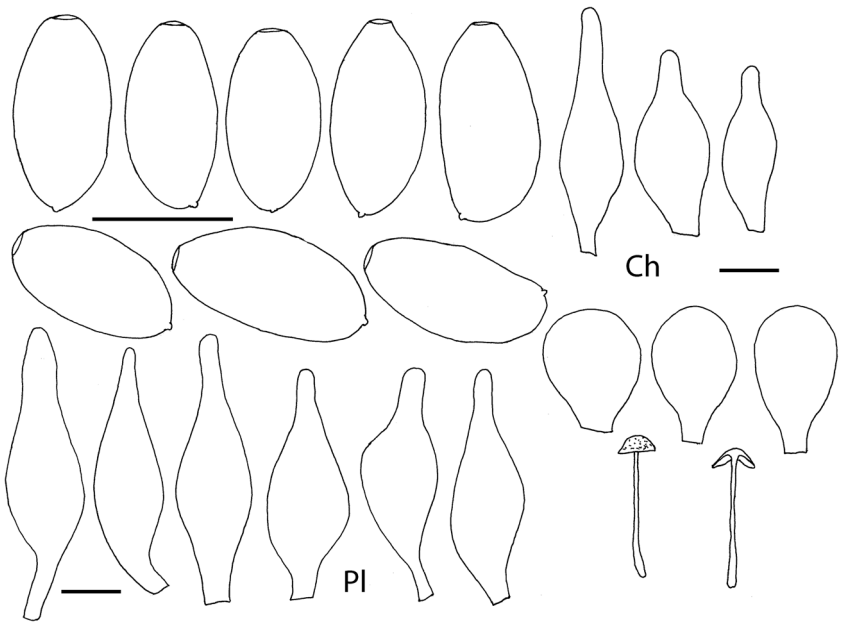


Fig. 28 *Psathyrella tenera*. L. Örstadius 81–83; Pl Pleurocystidia; Ch Cheilocystidia; Basidiomata ×1; Scale bars 10 μm

P. umbrina differs in having larger basidiomata and paler spores.

Specimens examined. Denmark, E. Jylland, Vorsø, Horsens Fjord, 1.XI.1982, T. Laessoe TL-Vorsø-854, (C); Italy, Sardinia, Olbia, Pittulongu, 27.XII. 2007, M. Contu, (GB); Norway, Telemark, Bamble, Langøya, 10.X.2012, A. Molia & T. Laessøe AM-330 g-2012, (O 245716); Bamble, Langøya, 15.X.2013, A. Molia & T. Laessøe AM-263a-2013, (O 22035); Bamble, Eikstrand, 13.X.2012, A. Molia & T. Laessøe AM-336 g-2012, (O 245581); Sweden, Medelpad, Stöde, Vigge, 12.IX.1995, E. Malm LÖ81-95, (GB); Skåne, Åhus, Älleköpingegård, 14.X.1995, L. Örstadius 211–95; USA, Michigan, Washtenaw, Crooked Lake, Waterloo State Recreation Area, 20.X.1971, A.H. Smith 81026, (MICH! holotype).

Psathyrella tenera Peck, Rep NY St Mus nat Hist 47:144. 1894. Fig. 28. (S3: Fig. 23b–d.)

Cap 5–15(−20) mm broad, at first semiglobose to paraboloid, then expanded conico-convex or convex, dark reddish brown (Mu. 2.5YR 3/4-2.5/4), dark brown, when moist striate at margin, hygrophanous, drying to reddish brown and later to ochraceous grey, cream or whitish; veil when young covering entire surface with dispersed flocci, evanescent. Gills broadly adnate to narrowly adnate with tooth, distant, L=13–14, when young pale ochraceous grey, grey brown, becoming dark brown, with white fimbriate edge, faintly to distinctly red underlined. Stem 30–70×0.7–2 mm, cylindrical, slightly thickened towards base or subbulbous, sometimes curved, pale brown to ochraceous, towards base brown, covered with white veil remnants, pulverulent at apex. Taste not recorded. Smell faint.

Spores 12–17×6–7.5 μm, av. 13–14.7×6.3–7.1 μm, Qav. 1.9–2.2, subcylindrical, oblong, narrowly limoniform, in profile with faint to distinct suprahilar depression, amygdaliform, in water red to dark red (Mu. 2.5YR 4/6-4/8-3/6), with distinct to very distinct germ pore. Basidia 4-spored, 18–34×10–14 μm. Pleurocystidia 30–65×10–16 μm, lageniform to conical with often narrow and pointed upper part, sometimes flexuous, scattered, sometimes rather numerous, pale. Cheilocystidia of two types: A: 25–50×9–17 μm, similar to pleurocystidia, numerous to scattered, B: small, clavate, numerous especially close to cap margin. Scalp cap halfway from margin: pileipellis made up of subglobose, ellipsoid to clavate cells 15–50 μm wide, pale to yellow. Pileitrama of heavily or sometimes moderately encrusted hyphae; gill trama strong to pale pigmented. Veil cells 15–60×4–14 μm. Clamps seen at stem and veil hyphae.

Habitat and distribution: *Psathyrella tenera* grows single to subcaespitose on wet or moist ground in deciduous forest or open grassland in calcareous areas, in fens or close to rivulets, directly on earth or attached to decaying leaves, woody debris and rotten straw. So far known from Austria, Norway, Sweden, and North America.

Notes - In the original description nothing is said about a veil on the cap but other characters agree satisfactory with the examined European material. In the type material the spores were seen with suprahilar depression and a small papillate apex. Other features of the species are the small basidiomata, copious veil, large spores, and a moist habitat. It comes close to *Psathyrella potteri* from which it differs in having a darker, striate cap with well-developed veil. Moreover, *P. potteri* prefers to grow in dry, nutrient rich places. *P. prona* can be separated by 2-spored basidia, a scanty veil, and dry habitat.

Specimens examined. Austria, Wien, Mauerbach, 11.IX.1990, E. Ludwig; Norway, Oppland, Lunner, Søndre Oppdalen øvre, 14.VI.1978, T. Brandrud 18–78, (O, 171816); 25.VI.1978, T. Brandrud 30–78 (O, 171815); Svalbard, Barentsburg, 15.VIII.1988, G. Gulden 100/88, (O, 74539); Sweden, Skåne, Baldringe, Lyckås, 1.X.1989, L. Örstadius 382–89, (GB); 25.V.2011, L. Örstadius 24–11; Ivetofta, Gyetorp, 12.VI.2000, A. Ryberg LÖ18-00; Kristianstad, Björket, 5.VII.1992, L. Örstadius 143–92; Maglehem, Blåherremölla, 2.VIII.1990, L. Örstadius 158–90; Ravlunda, Haväng, 10.VII.1983, L. Örstadius 81–83, (GB); USA, New York, Jefferson Co., Pierrepont Manor, June Peck, (NYS3146!, holotype).

Acknowledgments The authors want to express their gratitude to several contributors of valuable material and for assistance of various kinds: Eef Arnolds, David Boertmann, Manfred Enderle, Guillaume Eyssartier, Tomas Hallingbäck, Sven-Åke Hanson, Anton Hausknecht, Stig Jacobsson, Thomas Laessøe, Karl-Henrik Larsson, Erik Ljungstrand, Erhard Ludwig, Andreas Melzer, Jens H. Petersen, Arne Ryberg, Laszlo Nagy, Svengunnar Ryman. To the curators of the following herbaria: AH, AMNH, B, BAFC, BR, C, CBM, CUP, E, F, G, GDGM, GH, H, K, L, LD, MICH, NY, NYS, O, PC, S, SGO, SZE, TAA, TROM, TURA, UPS, WAG-W, WBS, WU, XAL, ZT. Financial support was received from The Swedish Taxonomy Initiative, ArtDatabanken, SLU, Uppsala (EL)

References

Arnolds E (2003) Rare and interesting species of *Psathyrella*. Fungi Non Delineati 26:1–76

Bergsten J, Nilsson AN, Ronquist F (2013) Bayesian tests of topology hypotheses with an example from diving beetles. Syst Biol 62:660–673

Bi Z, Li T, Zheng G (1987) A preliminary study on the genus *Psathyrella* from Guangdong province of China. Guihaia 7:23–27

Bogart van de F (1975) The Genus *Coprinus* in Washington and Adjacent Western States. Dissertation. University of Washington

Britzelmayr M (1883) Dermini und Melanospori aus Südbayern. Bericht des Naturhistorischen Vereins Augsburg 27:147–196

Clémençon H, Emmett V, Emmett EE (2004) Cytology and plectology of the hymenomycetes. Bibl Mycol 199:1–488

Cooke WB (1953) The genera of the Homobasidiomycetes. Spec Publ Div Myc Dis Surv US Department of Agriculture 3: 100pp

Donk MA (1962) The generic names proposed for Agaricaceae. Beihefte zur Nova Hedwigia 5:1–320
Galland MC (1972) Caractères mycéliens des *Psathyrella* (Fr.) Quél. (Agaricales). Rev de Mycologie 36:141–174
Gams W (2002) Report of the committee for fungi: 10. Taxon 51:791–792
Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizas and rusts. Mol Ecol 2:113–118
Grgurinovic C (1997) Larger Fungi of South Australia. Botanic Gardens of Adelaide and State Herbarium
Hoashi Y (2008) *Psathyrella turcosomarginata*, a new species with cheilocystidia possessing mucoid deposits staining bluish green in ammonia solution. Mycoscience 49:385–387
Hopple JS Jr, Vilgalys R (1999) Phylogenetic relationships in the mushroom genus *Coprinus* and dark spored allies based on sequence data from the nuclear gene coding for the large ribosomal subunit RNA: divergent domains, outgroups, and monophyly. Mol Phylogenet Evol 13:1–19
Horak E (1968) Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). Beiträge zur Kryptogamenflora der Schweiz 13:1–741
Horak E (1980) Taxonomy and distribution of two little known, monotypic genera of Agaricales: *Amparoina*, *Cystoagaricus*. Sydowia 33: 64–70
Jurand M, Kemp RFO (1972) Surface ultrastructure of Oidia in the Basidiomycete *Psathyrella coprophila*. J Gen Microbiol 72:575–579
Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol. doi:10.1093/molbev/mst010, Online January 16
Keirle MR, Hemmes DE, Desjardin DE (2004) Agaricales of the Hawaiian Islands. 8. Agaricaceae:*Coprinus* and *Podaxis*; Psathyrellaceae: *Coprinopsis*, *Coprinellus* and *Parasola*. Fungal Divers 15:33–124
Keizer PJ (1993) Ecology of Macromycetes in roadside verges planted with trees. CIP -Gegevens Koninklijke Bibliotheek, Den Haag, p 290
Kits van Waveren E (1985) The Dutch, French and British species of *Psathyrella*. Persoonia Suppl 2:1–300
Larsson E, Jacobsson S (2004) The controversy over *Hygrophorus cossus* settled using ITS sequence data from 200-year-old type material. Mycol Res 108:781–786
Larsson E, Örstadius L (2008) Fourteen coprophilous species of *Psathyrella* identified in the Nordic countries using morphology and nuclear rDNA sequence data. Mycol Res 112:1165–1185
Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo JM, Ge ZW, Yang ZL, Slot JC, Ammirati JF, Baroni TJ, Bougher NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNitis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellinga EC, Vilgalys R, Hibbett DS (2006) Major clades of Agaricales: a multilocus phylogenetic overview. Mycologia 98: 982–995
Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime CM, Hofsetter V, Verduin SJ, Larsson E, Baroni TJ, Thorn GR, Jacobsson S, Clémencon H, Miller OK (2002) One hundred and seventeen clades of euagarics. Mol Phylogenet Evol 23:357–400
Munsell (1975) Munsell soil color charts. Macbeth, Baltimore
Murrill WA (1945) New Florida fungi. Proc Florida Acad Sci 7:107–127
Nagy LG, Kocsubé S, Papp T, Vágvölgyi C (2009) Phylogeny and character evolution of the coprinoid mushroom genus *Parasola* as inferred from LSU and ITS nrDNA sequence data. Persoonia 22:28–37
Nagy LG, Urban A, Örstadius L, Papp T, Larsson E, Vágvölgyi C (2010) The evolution of autodigestion in the mushroom family Psathyrellaceae (Agaricales) inferred from Maximum Likelihood and bayesian methods. Mol Phylogenet Evol 57:1037–1048
Nagy LG, Walther G, Házi J, Vágvölgyi C, Papp T (2011) Understanding the evolutionary processes of fungal fruiting bodies: correlated evolution and divergence time in the Psathyrellaceae. Syst Biol 60:303–317
Nagy LG, Házi J, Vágvölgyi C, Papp T (2012) Phylogeny and species delimitation in the genus Coprinellus with specieal emphasis on the haired species. Mycologia 104:254–275
Nagy LG, Desjardin ED, Vágvölgyi C, Kemp R, Papp T (2013a) Phylogenetic analyses of *Coprinopsis* section *Lanatuli* and *Atramentarii* identify multiple species within morphologically defined taxa. Mycologia 105:112–114
Nagy LG, Vágvölgyi C, Papp T (2013b) Morphological characterization of clades of the Psathyrellaceae (Agaricales) inferred from a multigene phylogeny. Mycol Prog 12:505–517
Nylander JAA, Wilgenbusch JC, Warren DL, Swofford DL (2008) AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24: 581–583
Örstadius L, Knudsen H (2012) *Psathyrella* (Fr.) Quél. In: Knudsen H, Vesterholt J (eds) Funga Nordica. Agaricoid, boletoid, cyphelloid and gasteroid genera. Nordsvamp, Copenhagen, pp 692–728
Orton PD (1960) New check-list of British Agarics and Boleti. Part 3: notes on genera and species in the list. Trans British Mycol Soc Suppl 43:159–439
Padamsee M, Matheny PB, Dentinger BT, McLaughlin DJ (2008) The mushroom family Psathyrellaceae: evidence for a large-scale phylogeny of the genus *Psathyrella*. Mol Phylogenet Evol 46:415–429
Pegler DN (1977) A preliminary agaric flora of East Africa. Kew Bull Addit Ser 6:1–615
Pegler DN (1983) Agaric flora of the Lesser Antilles. Kew Bull Addit Ser 9:1–668
Rambaut A, Drummond AJ (2007) Tracer v1.4, Available from http://beast.bio.ed.ac.uk/Tracer
Redhead SA, Vilgalys R, Moncalvo JM, Johnson J, Hopple JS Jr (2001a) *Coprinus* Pers. and the disposition of *Coprinus* species sensu lato. Taxon 50:203–241
Redhead SA, Vilgalys R, Moncalvo JM, Johnson J, Hopple JS Jr (2001b) Proposals to conserve the name *Psathyrella* (Fr.) Quel. with a conserved type and to reject the name *Pselliophora* P. Karst. (Basidiomycetes: Psathyrellaceae). Taxon 50:275–278
Romagnesi H (1982) Études complémentaires de quelques espèces de Psathyrella ss. lato (*Drosophila* Quélet). Bull. Trim de la Soc Mycol de France 98:5–68
Selosse M-A, Martos F, Perry BA, Padamsee M, Roy M, Pailler T (2010) Saprotrophic fungal mycorrhizal symbionts in achlorophyllus orchids. Plant Signal Behav 5:1–5
Singer R (1947) New genera of fungi. III. Mycologia 39:77–89
Singer R (1951) The "Agaricales" (Mushrooms) in modern taxonomy. Lilloa 22:1–830
Singer R (1969) Mycoflora australis. Nova Hedwigia Beihefte 29: 1–405
Singer R (1978) Interesting and new species of basidiomycetes from Ecuador II. Nova Hedwigia 19:1–98
Singer R (1986) The Agaricales in modern taxonomy, 4th edn. Koeltz Scientific Books, Koenigstein
Smith AH (1972) The North American species of *Psathyrella*. Mem N Y Bot Gard 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. Sinauer, Sunderland
Uljé CB (2005) *Coprinus*. In: Noordeloos ME, Kuyper TW, Vellinga EC (eds) Flora Agaricina Neerlandica 6:22–109. CRC press, Boca Raton

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

Vellinga EC (1988) Glossary. Pp. 54–64. In: Bas C, Kuyper THW, Noordeloos ME, Vellinga EC. Flora Agaricina Neerlandica, vol 1. Critical monographs on families of Agarics and Boleti occurring in the Netherlands. AA Balkema, Rotterdam/Brookfield

Vellinga EC (2004) Genera in the Agaricaceae – evidence from nrITS and nrLSU sequences. Mycol Res 108:354–377

White TJ, Bruns T, Lee L, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sininski JJ, White TJ (eds) PCR protocols, a guide to methods and applications. Academic Press, New York, pp 315–322