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ORIGINAL ARTICLE

Coprinellus radicellus, a new species with northern distribution

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Abstract A new coprophilous species, *Coprinellus radicellus*, is presented and described on the basis of morphological characters and a species phylogeny inferred from ITS1–5.8S–ITS2 and beta-tubulin gene sequences. The species is characterized by lageniform pileo- and caulocystidia, 8- to 11-μm long ellipsoid basidiospores with a central germ-pore, globose cheilocystidia, an often rooting stipe, the lack of pleurocystidia and velar elements. These characters distinguish *C. radicellus* from all other described species in subsection *Setulosi*. It comes closest to *C. brevisetulosus* (Arnolds) Redhead, Vilgalys & Moncalvo and *C. pellucidus* (P. Karst.) Redhead, Vilgalys & Moncalvo both morphologically and phylogenetically, but is distinct from both. Another five representatives of morphologically recognizable groups of subsection Setulosi were included in the phylogenetic analyses and found were distinct from *C. radicellus*, both morphologically and phylogenetically. To date, this new species is known only from Scandinavia, which is surprising in view of the uniform geographical distributions of most setulose *Coprinellus* species. A key to coprophilous taxa of *Coprinellus* with pileo- and caulocystidia is presented. Three new combinations are proposed.

Keywords *Coprinus* sensu lato · Phylogeny · Systematics · Internal transscribed spacer · Beta-tubulin

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Introduction

Species of subsection *Setulosi* of the genus *Coprinellus* are widely considered to be a problematic group of fungi, due to difficulties in identification and unsettled species concepts (Lange 1952; Lange and Smith 1953; Orton and Watling 1979; Uljé and Bas 1991; Uljé 2005). In addition, this group includes some of the smallest known species of agarics, their pileus not exceeding 1 mm in diameter in some cases (e.g., *C. heptemerus*). These factors have led to an underestimation of actual species numbers and distributions in certain groups (Nagy 2006).

Species of subsection *Setulosi* are characterized by very small to medium-sized fruiting bodies, lageniform pileo- and caulocystidia on the cap and stipe, mostly globose or ellipsoid cheilocystidia and often by ellipsoid basidiospores. Globose or cylindrical veil elements may be present on the pileus surface. A significant portion of the species colonizes excrements of various herbivorous animals, more rarely vegetable refuse or soil (Uljé and Bas 1991; Uljé 2005). In spite of the apparent morphological synapomorphies, subsection *Setulosi* appears polyphyletic in recent phylogenetic studies (Hopple and Vilgalys 1999; Padamsee et al. 2008; Nagy et al. 2010) with *C. disseminatus, C. verrucispermus, C. curtus, C. heptemerus* and *C. silvaticus* nested within the clade of *C. micaceus* and *C. domesticus*.

Early studies using mating experiments have pointed out that species delimitation of setulose *Coprinellus* taxa requires a narrow concept from the morphological point of view (Lange 1952). Since then, several new taxa have been described (Uljé 1988; Uljé and Bas 1991; Uljé and Noordeloos 2003; Nagy 2006), and several authors have reported potentially undescribed species, but deliquescence and the small size of the fruiting bodies have hampered formal description in many cases by eliminating important

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microscopic characters (Enderle and Bender 1990; Uljé and Bas 1991; Nagy 2008). Within Europe, there are 36 taxa currently recognized in subsection Setulosi (Uljé 2005; Nagy 2006).

In this paper, we address the autonomy of a morphologically peculiar group of collections against other setulose *Coprinellus* taxa based on morphology and phylogenetic analyses. We use sequence data of two genes, ITS1–5.8S–ITS2 and beta-tubulin, and test the monophyly of the putative new species against several morphologically similar, coprophilous species of *Coprinellus*.

Materials and methods

Morphological examinations

Field-collected fruiting bodies were dried in silica-gel in order to stall deliquescence. Dried material was mounted in 10% NH_4OH. Microanatomical examinations, measurements and microphotographs were made on a Zeiss Axiolab light microscope. For measurements of basidiospores and other microcharacters, a sample of at least 20 measurements was made from each specimen. Numbers in parentheses after 'Basidiospores' refer to the number of basidiospores measured and the number of specimens and collections they originate from, respectively. To test the significance of differences in spore sizes of *C. brevisetulosus* and *C. radicellus*, we performed a two-tailed *t* test with unequal variances. Type materials have been deposited in the Hungarian National History Museum (Bp), isotype and other accompanying specimens are in the Szeged Microbiological Collections (SZMC). Herbarium abbreviations are given according to Thiers (2010).

Taxon sampling, molecular techniques and phylogenetic analyses

The monophyly of *C. radicellus* specimens was tested against several taxa selected on the basis of morphological similarity. To this end, we included specimens of the morphologically very similar *C. brevisetulosus, C. pellucidus*, as well as representatives of the larger morphologically recognizable groups of the subsection *Setulosi*, i.e. *C. congregatus, C. heterosetulosus*, *C. marculentus, C. bisporus* and *C. hiascens* in the phylogenetic analyses (Table 1). *Coprinellus micaceus* was used as an outgroup, based on former phylogenetic studies utilizing broader samplings of the coprinoid taxa (Walther et al. 2005; Larsson and Orstadius 2008; Nagy et al. 2009).

Table 1 Origin, herbarium number of specimens and the GenBank accession numbers of the corresponding ITS and beta-tubulin sequences

Taxon	Voucher	Source	Accession numbers	
			ITS	Beta-tubulin
Coprinellus bisporus (J.E. Lange) Vilgalys, Hopple & Jacq. Johnson	NL-0158	Sweden, Öland	GU227705	-
	NL-0152	Sweden, Öland	GU227704	GU227722
C. brevisetulosus (Arnolds) Redhead, Vilgalys and Moncalvo	NL-1956	Hungary, Alföld	GU227709	GU227724
	NL-1445	Hungary, Alföld	GU227710	GU227726
	NL-2908	Hungary, Alföld	GU227711	GU227725
C. congregatus (Bull.) P. Karst.	NL-2138	Hungary, Alföld	GU227702	GU227723
	NL-0588	Hungary, Alföld	GU227703	GU227727
C. heterosetulosus (Locq. ex Watling) Vilgalys, Hopple & Jacq. Johnson	NL-1233	Hungary, Alföld	GU227707	GU227728
	NL-1059	Hungary, Alföld	GU227708	-
C. hiascens (Fr.) Redhead, Vilgalys & Moncalvo	NL-1350	Hungary, Alföld	GU227720	GU227729
C. marculentus (Britzelm.) Redhead, Vilgalys & Moncalvo	NL-1167	Hungary, Alföld	GU227706	GU227730
C. micaceus (Bull.) Vilgalys, Hopple & Jacq. Johnson	NL-3888	Hungary, Alföld	GU227721	-
C. pellucidus (P. Karst.) Redhead, Vilgalys and Moncalvo	NL-1076	Hungary, Alföld	GU227713	GU227731
	NL-1446	Hungary, Alföld	GU227712	GU227732
	NL-2928	Slovakia, Brzno	GU227714	GU227733
	NL-2344	Hungary, Alföld	GU227715	GU227734
C. radicellus sp nov.	NL-0594	Sweden, Öland,	GU227716	GU227735
	NL-2121	Sweden, Öland	GU227717	-
	NL-0957	Norway, Steinkjer	GU227718	GU227736
	NL-3168	Sweden, Halland	GU227719	GU227737

Genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen), following the manufacturer's instructions. The ITS1–5.8S–ITS2 region and a portion of the gene coding for beta-tubulin were amplified by PCR using the primer pairs ITS1–ITS4 (White et al 1990) and B36f–B12r (Thon and Royse 1999), respectively. PCR fragments were sequenced using the same primers on ABI automated sequencers (LGC Genomics, Germany). The Pregap and Gap4 programs of the Staten package (Staden et al. 2000) have been used for contig assembly. GenBank accession numbers are listed in Table 1.

Alignments were computed by means of the Probalign algorithm (Roshan and Livesay 2006), using default settings. Intron regions in the beta-tubulin gene were excluded from the phylogenetic analyses, because their excessive divergence hampered the unambiguous alignment. Best-fit substitution models were selected for each alignment in Modeltest 3.7 (Posada and Crandall 1998), with preference for the results of the sample size-corrected version of the Akaike Information Criterion (AICc). To check for congruence of the two gene regions, we used the approximately unbiased test as implemented in CONSEL v. 0.1 (Shimodaira and Hasegawa 2001). Indels in the ITS alignment were coded as a binary partition by means of the simple indel coding algorithm (Simmons and Ochoterena 2000) using the program FastGap (Borchsenius 2007). Phylogenetic reconstruction was performed on the concatenated nucleotide matrix, including gap data, by Bayesian MCMC and Maximum Likelihood. In addition, clade support was estimated by ML bootstrapping.

Maximum likelihood estimation was performed in PhyML 3.0 (Guindon and Gascuel 2003). The model selected by ModelTest was invoked, leaving the substitution rates, equilibrium frequencies of nucleotides and the values of the gamma shape parameter to be estimated by PhyML. The branch-swapping algorithm was set to Nearest Neighbor Interchanges. Non-parametric bootstrap analysis was performed using 1,000 replicates. The Maximum Likelihood analyses were performed by deleting the binary partition of coded indel regions.

Bayesian MCMC was run using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Four independent chains were run in two replicates using default priors and proposal mechanism. The model suggested by ModelTest as best fitting the data was invoked. The concatenated matrix was divided in two partitions, corresponding to the ITS and beta-tubulin genes. Indel gain-loss events were modeled by a 2-state Markov model implemented for restriction sites in MrBayes, with correction for invariant sites not included in the matrix. Four million generations were run, sampling every 100th set of parameters. The quality of posterior distributions and convergence to stationarity were inspected using Tracer 1.4 (Rambaut and Drummond 2008) and the convergence diagnostics implemented in MrBayes. Trees sampled before stationarity were discarded as burn-in. Post burn-in trees were used to compute a 50% Majority Rule phylogram in MrBayes.

Results

ITS and beta-tubulin sequences were generated for 19 ingroup specimens plus *C. micaceus* as outgroup (Table 1). After removal of missing data at the 5' and 3' end for each gene in the concatenated alignment, as well as intron regions, the aligned dataset consisted of 1,162 sites of nucleic acid alignment (ITS1–5.8S–ITS2: 755 sites, beta-tubulin: 407) and 105 characters representing indels of the ITS region. Of these, 195 (ITS1–5.8S–ITS2), 161 (beta-tubulin) and 61 (indels) characters were parsimony-informative. On the basis of the AICc criterion in ModelTest, the General Time Reversible model (GTR) with a gamma-distributed rate heterogeneity was found to fit best both alignments (ITS and beta-tubulin).

Tree topologies inferred under Maximum Likelihood and Bayesian MCMC (Fig. 1) were largely congruent and recovered the same clades on the species level. On the other hand, ML and Bayesian inference disagreed about the topology at the deeper nodes of the tree. The Bayesian analysis converged to the stationary distribution within one million generations (based on likelihood plots and the average standard deviation of split frequencies), so we established the burn-in to the conservative value of 2 million generations. The consensus tree computed from 40,002 trees after excluding the burn-in is depicted in Fig. 1. All morphologically recognized species formed monophyletic clades strongly supported by both Bayesian posterior probabilities and ML bootstrap values. Specimens of *C. radicellus* formed one strongly supported clade (BPP: 1.00, MLBS: 100%).

In the Bayesian analysis, *C. brevisetulosus, C. pellucidus* and *C. radicellus* formed one clade, although support for this relationship is weak (BPP: 0.82). On the ML tree, these species were placed in basal positions to the rest of the setulose *Coprinellus* species. It is noteworthy that the monophyly of the clade of *C. brevisetulosus, C. pellucidus* and *C. radicellus* was supported by several indel characters in the ITS region (Fig. 2), which may be an explanation for the topology inferred under Bayesian estimation (ML analyses did not include indel data). For instance, positions 136–141, 457, 469, 542, and 629–630 support the monophyly of this clade. The monophyly of *C. radicellus* specimens was also indicated by gaps (positions 136–141, 455–462). On the basis of molecular and morphological differences, we propose the description of a new species.

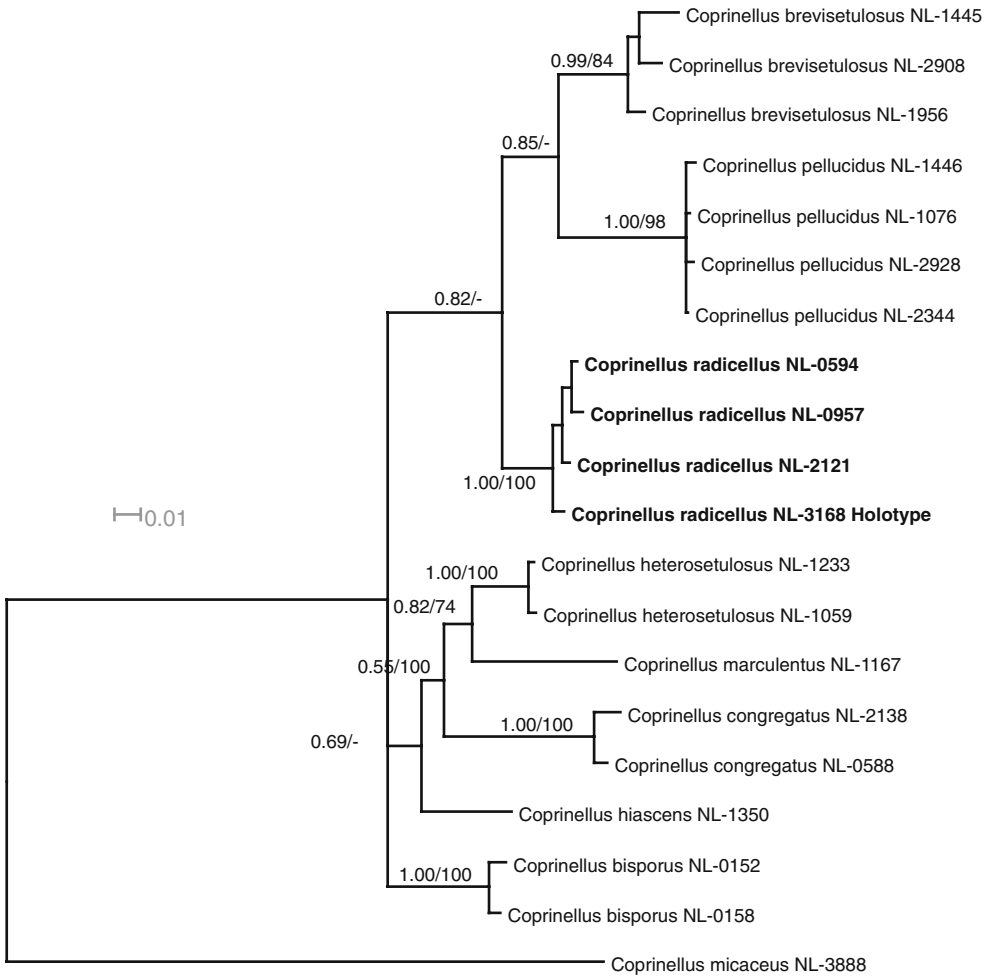

Fig. 1 Bayesian 50% Majority Rule phylogram, inferred from the combined ITS + beta-tubulin + gap dataset. Support values represent Bayesian posterior probabilities/Maximum Likelihood bootstrap percentages

Taxonomy

Coprinellus radicellus Házi, L. Nagy, Papp & Vágvölgyi, sp. nov. Mycobank MB 515524; Fig. 3

Pileus 1–5×1–4 mm, late ellipsoideus vel subglobosus atque perluciditate striatus in inexpanso tempore, usque ad 10 mm latus, convexo-applanatus atque reflexus, anguste sulcatus in expanso tempore, leviter pruinosus, aliquandum florem lactis tinctus, plerumque ochraceofuscus sed etiam melleofuscus, austerior in centro, in vetustate cinerascens. Lamellae remotae, ventricosae, usque ad 0,8 mm latae, ex albo cinerascentes vel nigricantes, ad marginem fimbriatae. Stipes 10–40×0,3–0,8 mm, filiformis, aequalis vel ad basim contractus, plerumque radicans, sclerotio carens, dense pubescens, in iuvenili tempore albus vel pallide florem lactis tinctus, deinde aereolutescens vel fuscidulus. Sporae 8–11×4.6–5.5 μm, fere 9.48×4.91 μm, ellipsoideae vel subcylindratae, ad apicem obtusae, parvo hilo atque centrali, 1.4–1.7 μm lato, germinabili poro praeditae, haud vel vix lentiformes, purpureofuscae. Basidia clavata, biformia, tetraspora, 18–25×8–9 μm. Cheilocystidia globosa, subglobosa vel clavata, brevistipitata, quibus cum lageniformibus ad marginem pilei intermixta. Pleurocystidia absentia. Pileocystidia lageniformia, ad acutum apicem contracta, leptoparietata, haud crustata, 32–70×9–14 μm. Sclerocystidia atque velum absentia. Caulocystidia lageniformia vel cylindrata, ad longum et acutum apicem contracta, 25–73×6–12 μm. Fibulae absentes.

Type material: SWEDEN, Halland, Mannarp, on cow dung on wooded pasture, 18 Sept. 2009, *L. Nagy & L. Örstadius, SZMC-NL-3168* (Holotype, Bp) Isotype in Szeged Microbiological Collections, SZMC. Sequences of the type specimen have been submitted to GenBank under the accession numbers GU227719 (ITS1–5.8 S–ITS2) and GU227737 (beta-tubulin).

Etymology: 'Radix' = root, referring to the tendency of the stipe to root in the substrate.

Description: *Pileus* 1–5×1–4 mm when closed and young, broadly ellipsoid to subglobose, expanding to convex-applanate with uprolled margin up to 10 mm broad; when young translucently striate in moist state; surface radially striate, finely sulcate when expanding, with fine pruinosity observable under hand-lens; ochre-brown sometimes cream-colored but also quite dark melleous-brown in some cases, darker and more cinnamon colored in the center, on ageing

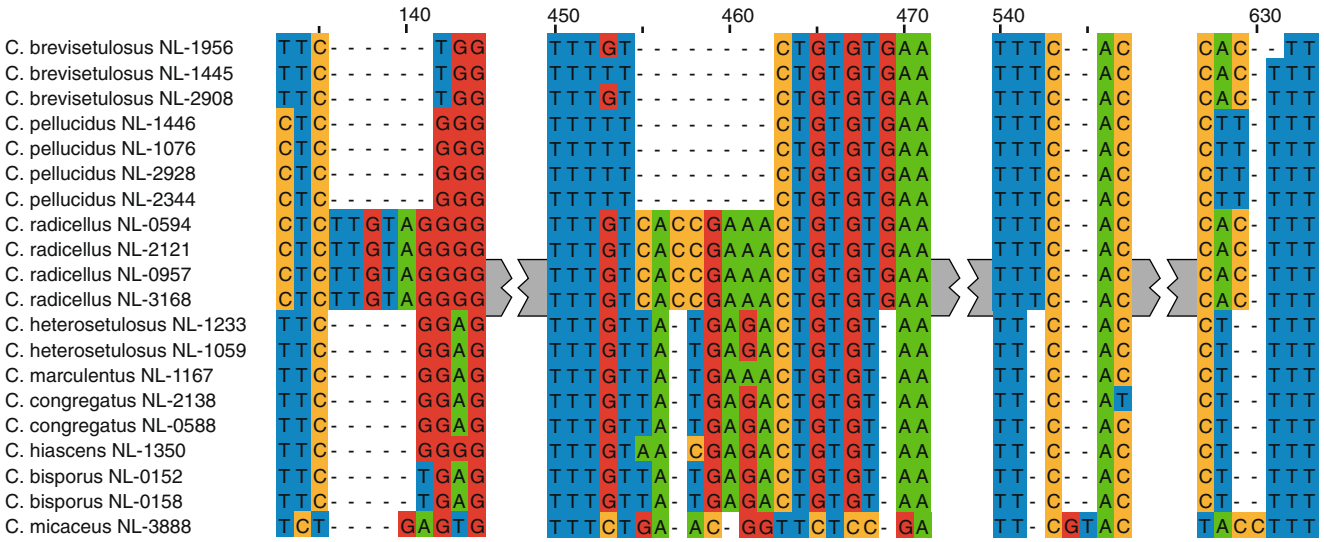

Fig. 2 Phylogenetically informative indel characters of the ITS alignment

becomes more greyish from the margin on, deliquescent. *Lamellae* free, crowded, ventricose, up to 0.8 mm broad, white when young, later grayish to blackish, with a very finely fimbriate edge. *Stipe* 10–40×0.3–0.8 mm, slender, fistulose, equal, or tapering towards the base, generally rooting in the substrate, sometimes just growing on the surface; sclerotium absent; surface densely pubescent all over; color white to pale cream when young, on ageing a warm bronze-yellow to brownish color develops.*Basidiospores* (57,2,1) 8–11×4.6–5.5 µm, on average 9.48×4.91 µm, ellipsoid to subcylindrical, with an obtuse apex and a small hilum, not or very slightly lentiform, reddish brown in 10% NH_4OH, germ-pore central, 1.4–1.7 µm wide; *basidia* clavate, bimorphic, 18–25×8–9 µm, four-spored; *pleurocystidia* absent; *cheilocystidia* abundant, globose, subglobose or clavate with a short pedicel, mixed with some lageniform ones towards margin of the pileus, 9–20×8–14 µm; *pileocystidia* abundant, lageniform with tapering neck ending in a more or less acute apex, thin-walled, not incrusted 32–70×9–14 µm; *sclerocystidia* absent; veil not seen; *caulocystidia* dense on the stipe surface, lageniform or cylindrical with a long, tapering neck and a rather acute apex, often without basal swelling 25–73×6–12 µm; clamp connections absent.

Substrate and habitat: Growing on old cow dung, in the company of other coprinoid species: *Coprinus poliomallus* Romagn., *Coprinopsis luteocephala* (Watling) Redhead, Vilgalys & Moncalvo, *Coprinellus congregatus*. Found in open grazed areas, such as woody meadows or grazed mosaic forests.

Distribution: Known from several spots in Sweden and Norway (Scandinavia). Within Sweden, the species is known from Öland (Nagy 2006), Halland (present paper) and Skåne (Leif Örstadius, personal communication).

Other collections examined: SWEDEN, Halland, Mannarp, on cow dung, 18 Sept. 2009, *L. Nagy & L. Örstadius* (*SZMC-NL-3156*), ibid. 18 Sept. 2009, *L. Nagy & L. Örstadius* (*SZMC-NL-2759*), ibid., 18 Sept. 2009, *L. Nagy & L. Örstadius* (*SZMC-NL-3157*), Öland, Torslunda parish, Ugglemosse backarna, *Juniperus–Corylus* mosaic forest, on cow dung, 24 Sept. 2006, *L. Nagy & T. Knutsson* (*SZMC-NL-0594*), Öland, Torslunda parish, Hönstorps utmarker, *Juniperus–Corylus–Quercus–Betula* mosaic forest, on old cow dung, 25 Sept. 2007, *L. Nagy & T. Knutsson* (*SZMC-NL-2121*), NORWAY, Steinkjer, Skrattasen, on cow dung, in a grazed *Picea* forest, 5 Sept. 2009, *L. Nagy & M. Jeppson* (*SZMC-NL-0957*).

New combinations

Based on morphological and molecular evidence (Uljé 2005; Nagy 2006; Nagy et al. 2010), three additional coprophilous species should be recombined in *Coprinellus*. These taxa have hymenidermal pileipellis, globose velar cells as well as pileo- and caulocystidia, which place them in the genus *Coprinellus* as circumscribed by Redhead et al. (2001). Based on preliminary phylogenetic work (results not shown), *C. doverii* and *C. parvulus* belong to the core Setulosi clade, whereas *C. pusillulus* belongs to the *C. micaceus* clade, close to *C. heptemerus*.

Coprinellus doverii (L. Nagy) Házi, L. Nagy, Papp & Vágvölgyi, comb nov. (MB 518759)

Basionym: *Coprinus doverii* L. Nagy in *Mycotaxon* 98: 148. (2006)

Coprinellus parvulus (P.-J. Keizer & Uljé) Házi, L. Nagy, Papp & Vágvölgyi, comb nov. (MB 518760)

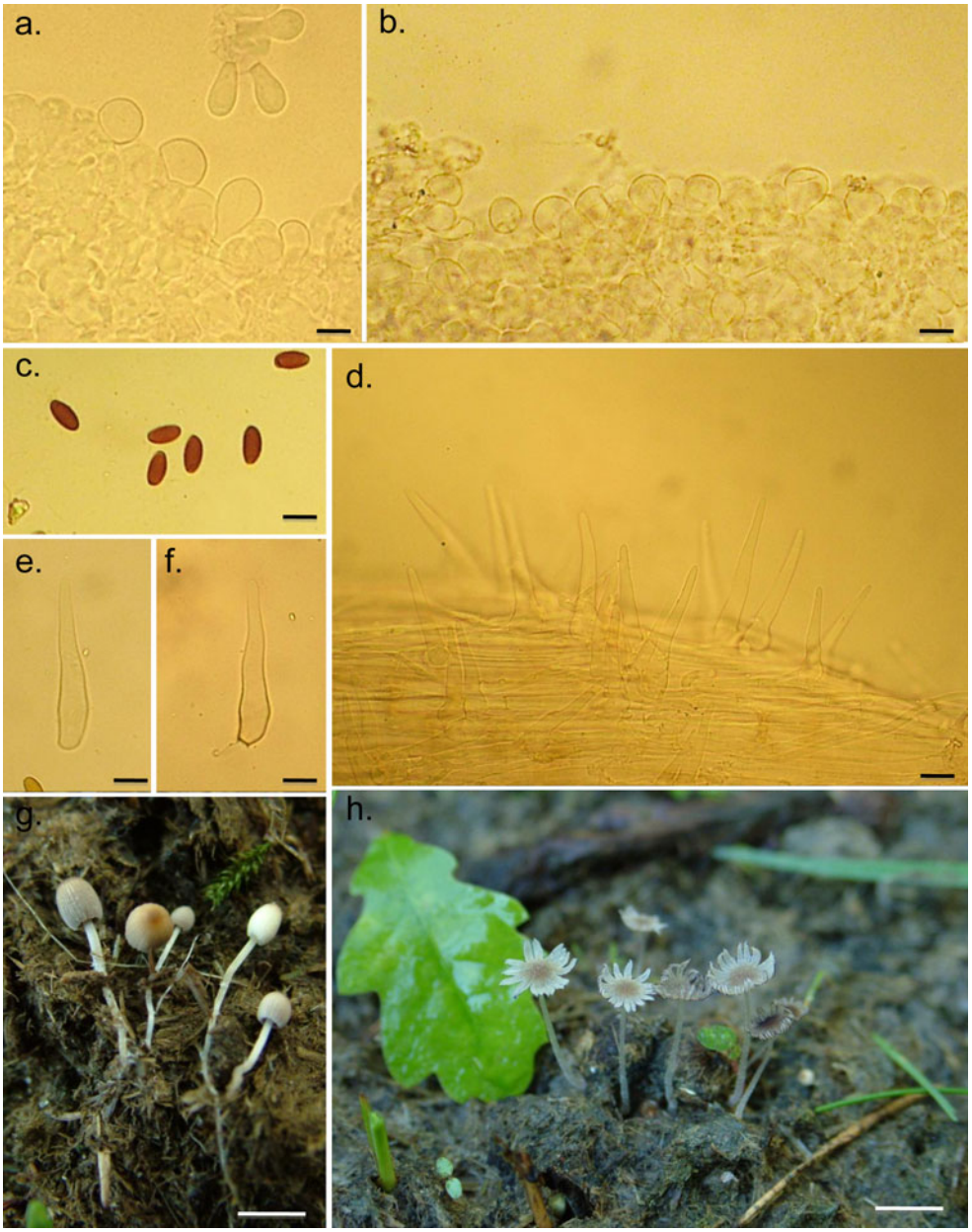

Fig. 3 *Coprinellus radicellus*. **a**,**b** Cheilocystidia, **c** spores, **d** caulocystidia, **e**,**f** pileocystidia, **g** young fruiting bodies showing radicant stipes, **h** mature fruiting bodies in situ. *Scale bar* (**a**–**f**) 10 μm, (**g**,**h**) 10 mm

Basionym: *Coprinus parvulus* P-J. Keizer & Uljé in *Persoonia* 18: 281. (2003)

Coprinellus pusillulus (Svrček) Házi, L. Nagy, Papp & Vágvölgyi, comb nov. (MB 518761) (=*C. heptemerus* f. *parvisporus*)

Basionym: *Coprinus pusillulus* Svrček in *Česká Mykol.* 37(4): 233 (1983)

Discussion

In this paper, we have shown that *Coprinellus radicellus* represents a monophyletic lineage in *Coprinellus* with affinities to species having ellipsoid basidiospores, central germ-pore and no veil on the pileus (*C. brevisetulosus, C. pellucidus*). We included six representative morphologically recognizable groups of setulose *Coprinellus* species in the analyses to test the autonomy of our new species against these species groups. All taxa formed clades distinct from that of *C. radicellus*.

Of the *Coprinellus* species with pileo- and caulocystidia (i.e. the subsection *Setulosi*), *C. radicellus* is most similar to *C. brevisetulosus* and *C. pellucidus* and also shows higher phylogenetic affinity to these species (Fig. 1). *C. brevisetulosus* differs in having pleurocystidia, ellipsoid cheilocystidia, a non-radicate stipe, and the basidiospores are significantly broader when measured in frontal view (5–6.5 μm; Table 2; Uljé and Bas 1991; Uljé 2005; Nagy

Table 2 Spore size differences between *C. brevisetulosus* and *C. radicellus*. *P* values of significance were estimated by a two-tailed *t* test. All spores were measured in frontal view. Values are given in μm

	C. brevisetulosus (*n*=60)	*C. radicellus* (*n*=120)	*P* value
Length	(8.5–) 10.2 (–9.5)	(8–) 9.8 (–12)	0.0008
Width	(4.8–) 5.43 (–6.2)	(4–) 4.9 (–6.5)	2.7449×10^{-13}

2008). *Coprinellus pellucidus* has much smaller spores measuring 7–9×3–4 μm, and generally smaller, non-radicant fruiting bodies. The shape of the pileus of *C. radicellus* is broadly ellipsoid or subglobose, which is very similar to that of *C. pellucidus*. On a morphological basis, one additional species can be recognized in this group differing from *C. radicellus, C. pellucidus* as well as *C. brevisetulosus*. This undescribed species is known from one locality in Germany (Enderle and Bender 1990) and one in Switzerland (SZMC-NL-1752). It is morphologically closest to *C. brevisetulosus*, but it differs in having strongly branched caulocystidia, similar to that of *C. ramosocystidiatus* Bender (Enderle and Bender 1990).

Coprinellus congregatus and *C. ephemerus* (Bull.) Redhead, Vilgalys & Moncalvo might also come close in general appearance, but they are different in having ellipsoid pleurocystidia and larger, 12- to 14-μm long, basidiospores with an eccentric germ-pore. In addition, these species have larger fruiting bodies with non-radicant stipe. There are several other species macroscopically resembling *C. congregatus*, like *C. sclerocystidiosus* (M. Lange & A.H. Sm.) Vilgalys, Hopple & Jacq. Johnson, *C. subimpatiens* (M. Lange & A.H. Sm.) Redhead, Vilgalys & Moncalvo, *C. callinus* (M. Lange & A.H. Sm.) Vilgalys, Hopple & Jacq. Johnson, and *C. eurysporus* (M. Lange & A.H. Sm.) Redhead, Vilgalys & Moncalvo, which differ from *C. radicellus* in having larger spores, non-coprophilous habitat and larger fruiting bodies. *C. heterosetulosus* has a similar habitat and habit, but it differs from the new species in having sclerocystidia on the pileus, and lentiform spores with a strongly eccentric germ-pore. The two collections included in the phylogenetic analyses are placed in a different position from *C. radicellus* with strong support (BPP: 1.00, MLBS: 100%).

Taxa related to *Coprinellus hiascens*, such as *C. heterothrix* (Kühner) Redhead, Vilgalys & Moncalvo, *C. velatopruinatus* (Bender) Redhead, Vilgalys & Moncalvo, *Coprinus minutisporus* Uljé or *Coprinellus* sp. (NL-0177) differ in having cylindrical to diverticulate veil elements on the pileus surface. In addition, most of these species are terrestrial, except for *Coprinellus* sp. (NL-0177), which grows on cow dung. However, this species has smaller, 6- to 9-μm-long, subglobose spores, a non-radicate stipe and cylindrical veil on the pileus.

C. marculentus, C. plagioporus (Romagn.) Redhead, Vilgalys & Moncalvo and *C. subpurpureus* (A.H. Sm.) Redhead, Vilgalys & Moncalvo form a rather uniform group in the subsection *Setulosi*, characterized by dark brownish colors, cylindrical or clavate pileocystidia and generally a non-coprophilous habitat. These characters readily separate them from *C. radicellus*. *C. marculentus* is often growing on dung, but that species has larger, hexagonal spores with eccentric germ-pore.

Several other setulose species have globose veil elements on the pileus unambiguously distinguishing them from *C. radicellus*. These species include *C. curtus* (Kalchbr.) Vilgalys, Hopple & Jacq. Johnson, *C. heptemerus* (M. Lange & A.H. Sm.) Vilgalys, Hopple & Jacq. Johnson, *C. disseminatus* (Pers.) J.E. Lange, *C. verrucispermus* (Joss. & Enderle) Redhead, Vilgalys & Moncalvo, *Coprinus silvaticus* Peck and *C. doverii* (L. Nagy) Házi, L. Nagy, Papp, Vágvölgyi.

It is noteworthy that *C. radicellus* is known only from the Nordic countries where it seems to be widespread, albeit not common. Although *Coprinus* sensu lato taxa have been subject to numerous taxonomic studies (Josserand 1950; Lange 1952; Lange and Smith 1953; Enderle and Bender 1990; Redhead et al. 2001; Uljé and Bas 1991), geographic patterns of their distribution are largely unknown. Keirle et al. (2004) reported several *Coprinus* sensu lato species from the Hawaiian Islands which are primarily known from the temperate regions of the northern hemisphere. Other groups of Agaricomycetes are well known for their species exhibiting differential preference for geographic regions. This is most pronounced in mycorrhizal fungi, such as boletes, *Cortinarius* or *Russula*, to mention just a few, where altitude and latitude strongly influences the species distributions, in addition to the distribution of their host plants, and are considered useful taxonomic characters (Kauserud et al. 2007; Larsson and Orstadius 2008; Wollan et al. 2008). For instance, *Amanita muscaria* has been reported to involve three cryptic species each with disparate geographic distribution, but more or less the same host plants (Geml et al. 2006). Although limited evidence exists for the differential distribution of certain species of *Coprinellus* (Nagy 2006; present study) and the divergence between collections of *Coprinopsis phlyctidospora* originating from various geographic areas (Suzuki et al. 2002),

this source of information has not been exploited in taxonomic studies of *Coprinus* sensu lato taxa. Based on the distribution of *C. radicellus*, we raise the possibility that the distribution of the saprotrophic *Coprinus* sensu lato species can also show geographic patterns, and this may be more common among these fungi than assumed formerly. Patterns of geographic distribution and any accompanying morphological differences should therefore be studied more carefully in coprinoid and saprotrophic fungi also.

Key to coprophilous *Coprinellus* species with pileo- and caulocystidia

1a Pileus with globose, thick-walled or cylindrical veil elements 2
1b Pileus devoid of veil 8
2a Spores nodulose or hexagonal 3
2b Spores smooth 4
3a Spores nodulose, 7–10 μm long ***C. doverii*** (L. Nagy) Házi, L. Nagy, Papp & Vágvölgyi
3b Spores hexagonal, 10–12 μm long ***C. marculentus*** (Britzelm.) Redhead, Vilgalys and Hopple
4a Veil on pileus diverticulate (like *C. hiascens*) ***Coprinellus*** sp. SZMC-NL-0177
4b Veil made up of globose elements 5
5a Spores on average less than 7.5 μm long ***C. parvulus*** (Keizer & Uljé) Házi, L. Nagy, Papp & Vágvölgyi
5b Spores >7.5 μm 6
6a Globose velar elements on pileus strongly thick-walled and often brownish colored ***C. curtus*** (Kalchbr.) Vilgalys & al.
6b Velar elements thin-walled 7
7a Spores 12–17×7–9 μm ***C. heptemerus*** (M. Lange & A. H. Sm.) Vilgalys & al.
7b Spores 7–11×4–5.5 μm ***C. pusillulus*** (Svrček) Házi, L. Nagy, Papp & Vágvölgyi
8a Basidia two-spored 9
8b Basidia four-spored 11
9a Sclerocystidia present on pileus ***C. sassii*** (M. Lange & A.H. Sm.) Redhead & al.
9b Sclerocystidia absent 10
10a Pleurocystidia absent; strictly coprophilous species ***C. bisporus*** (J.E. Lange) Vilgalys & al.
10b Pleurocystidia present or absent, usually growing on vegetable debris, or wood-chips, sometimes on dung ***C. bisporiger*** (P.D. Orton) Redhead & al.
11a Sclerocystidia present; germ-pore eccentric ***C. heterosetulosus*** (Locq. ex Watling) Vilgalys & al.
11b Sclerocystidia absent 12
12a Pleurocystidia present; cheilocystidia globose–ellipsoid 13
12b Pleurocystidia absent; cheilocystidia globose 16
13a Spores 8–11.5 μm long; pileocystidia up to 70 μm long 14
13b Spores larger (>12 μm) ; pileocystidia longer 15
14a Caulocystidia unbranched ***C. brevisetulosus*** (Arnolds) Redhead & al.
14b Caulocystidia branched ***Coprinellus*** sp. (SZMC-NL-1752)
15a Clamp connections present ***C. ephemerus*** (Bull.) Redhead & al.
15b Clamp connections absent ***C. congregatus*** (Bull.) P. Karst
16a Spores 7–9 μm long and 3–4 μm broad, pileus 2-4 mm high when young, stipe non-radicate ***C. pellucidus*** (P. Karst.) Redhead & al.
16b Spores 8–11 μm long and 4–6.5 μm broad, pileus somewhat larger, 1-5 mm high when young, stipe often radicate ***C. radicellus*** sp. nov.

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