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Taxonomy and evolutionary relationships within species of section *Rimosae* (*Inocybe*) based on ITS, LSU and mtSSU sequence data

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Key words

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phylogeny
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Abstract The present study aimed at elucidating the structure of *Inocybe* subg. *Inosperma* sect. *Rimosae* but included also representatives from subg. *Mallocybe* and the genus *Auritella*. Phylogenetic relationships were inferred using ITS, LSU and mtSSU sequence data. The analyses recovered the ingroup as a monophyletic, strongly supported clade. The results indicate that recognizing *Auritella* on the genus level renders *Inocybe* paraphyletic. The species traditionally placed in sect. *Rimosae* were found to be distributed over two strongly supported clades, Maculata and *Rimosae* s.s. The Maculata clade clusters with sect. *Cervicolores* and the two represent subg. *Inosperma* in a strict sense. *Rimosae* s.s. emerges as an independent, supported clade well separated from *Inosperma* s.s. Twenty-one terminal groups were correlated with morphologically distinct species. In addition several taxa on single branches and minor less supported clades were recovered. A key to the identified species of the Maculata and *Rimosae* s.s. clades which occur in Northwest Europe is provided.

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INTRODUCTION

Inocybe is a large genus of agaric fungi with an estimated 500 species world wide (Kirk et al. 2008), a number that is likely to increase considerably when tropical and southern temperate areas are more intensively explored. Intrageneric classifications have been based mainly on spore morphology, the form and distribution of cystidia, and stipe morphology. The spores may be ellipsoid, amygdaliform or nodulose/angular. Many species have incrusted thick-walled pleuro- and cheilocystidia (metuloids). Some large groups completely lack the metuloids but then have numerous thin-walled cheilocystidia. The stipe may be of uniform thickness or have a distinctly bulbous base. A number of classifications combining these and other characters in various ways have been proposed (Heim 1931, Kühner & Romagnesi 1953, Kühner 1980, Kuyper 1986, Singer 1986, Stangl 1989, Kobayashi 2002).

Several phylogenetic analyses of *Inocybe* using both ribosomal and protein coding genes have been published (Matheny et al. 2002, Matheny 2005, Matheny & Bougher 2006a, Matheny et al. 2009). These studies confirm that *Inocybe* is monophyletic. In a multi-gene phylogeny of Agaricomycotina Matheny et al. (2006) showed that *Inocybe* does not belong in *Cortinariaceae*, where it has traditionally been placed, but has affinities to *Crepidotaceae*. Matheny (2005) suggested that *Inocybe* should be recognized at the family level as *Inocybeaceae*, a family already proposed and described by Jülich (1982).

Matheny (2005) identified five clades within *Inocybaceae*, which he called *Inocybe*, *Inosperma*, Pseudosperma, *Mallocybe* and *Auritella*. The *Inocybe* clade holds the generic type species and includes all species with incrusted cystidia (metuloids) irrespective of spore shape. *Mallocybe*, recognized as a separate subgenus (Kuyper 1986), includes species with necropigmented basidia and thin-walled cheilocystidia originating from the subhymenium. *Auritella* was recently separated from *Inocybe* as an independent genus (Matheny & Bougher 2006a, b) and seems to represent a unique Paleotropical and Southern hemisphere lineage with species from Australia and Africa. The two clades *Inosperma* and Pseudosperma basically include the species in sections *Rimosae* and *Cervicolores* in the classification by Kuyper (1986). Pseudosperma was introduced as a clade name only and not formally assigned any classification status according to ICBN (McNeill et al. 2006).

Section *Rimosae* is in traditional classifications placed in subg. *Inosperma* (Kühner 1980, Kuyper 1986, Stangl 1989). The section includes species characterized by radially fibrillose to rimose (squamulose) caps, ellipsoid to phaseoliform spores, and absence of metuloid pleurocystidia but with densely packed, simple, cylindrical, clavate to pyriform hymenial cheilocystidia that make the gill edge look distinctly white in mature specimens. Other characters that may occur are a distinctly bulbous stem base, reddening flesh, yellow to olivaceous tinges on lamellae, and specific odours. Phylogenetic analyses in a recent publication on the biogeography of *Inocybaceae* (Matheny et al. 2009) included a broader sampling of sect. *Rimosae* than any previous study, although representatives from Europe were still few. The results indicated that the section is non-monophyletic.

Many species in *Rimosae* are known to occur on more nutrient rich soils, often on calcareous ground, others prefer more nutrient poor acid soils. Several species are found in disturbed places such as along forest paths and roadsides. They form ectomycorrhizal associations with a broad range of host trees of both gymnosperms and angiosperms (Kuyper 1986, Stangl 1989, Jacobsson 2008). Several species occur in arctic and alpine regions and are then associated with shrubs and herbs such as *Salix*, *Dryas*, and *Polygonum* (Favre 1955, Horak

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1987, Kühner 1988, Bon 1997, Ferrari 2006). A few are found on coastal sand dunes associated with *Pinus* and *Salix* (Orton 1960, Bon 1984).

The taxonomy in *Rimosae* has for a long time been confused since many species are described on small differences in macro- and micro-morphology. Authors with a conservative approach recognise 10–20 species (Kuyper 1986, Stangl 1989), others include more than 40 (Bon 1997). In the Nordic countries 8–13 species are usually recognized (Stridvall et al. 1989, Jacobsson 2008). Some European species are likely to show a northern circumpolar distribution (Ryberg et al. 2008). However, since a modern comprehensive treatment of *Inocybe* in North America is lacking the biogeographic knowledge is incomplete (Kauffman 1924, Stuntz 1947, 1954).

Inocybe rimosa, taken in a wide sense, shows a considerable morphological variation and also a broad ecological range covering all biomes from nemoral deciduous forests to the arctic-alpine zone. Some authors have advocated a narrow species concept and described a number of species and varieties (Heim 1931, Kühner 1988, Bon 1997). Kuyper (1986) choose the opposite strategy and recognized only one species, listing more than 30 species and varieties as synonyms.

The present study had three aims: to examine the phylogenetic structure and position of sect. *Rimosae*, to identify the number of North European species within *Rimosae*, and to elucidate the phylogenetic relationship among them.

MATERIALS AND METHODS

Morphological studies

Micro-morphological characters were observed using a Zeiss Axioscope 2, equipped with phase contrast. Spores and cystidia were measured in a 3 % KOH solution at × 400 and 1 000 magnification using microscope photos taken with a Canon G9 digital camera and using software AxioVision (Carl Zeiss AB). Unusually large or small spores were not considered. Collections are deposited in the herbarium of the Department of Plant and Environmental Sciences, University of Gothenburg (GB) if not otherwise indicated. Data on sequenced specimens is provided in Table 1.

Taxon sampling

Ninety-nine ingroup specimens were sequenced. They represent the majority of species within section *Rimosae* that occur in North Europe (Jacobsson 2008). In addition specimens from Estonia, France, Great Britain, Slovakia, USA, and Australia were included. Specimens were selected to represent a broad spectrum of morphological characters and ecology. Eight species of sect. *Cervicolores* and subg. *Mallocybe* were also sequenced and included in the analyses. Based on results from earlier molecular phylogenetic studies of *Agaricales* and *Inocybe* (Matheny 2005, Matheny & Bougher 2006a, Matheny et al. 2006) species of *Conocybe*, *Crepidotus*, *Naucoria*, *Pleuroflammula*, and *Simocybe*, were selected as out-group. ITS and LSU sequences for included species of *Auritella*, *Simocybe*, and *Pleuroflammula*, were taken from GenBank (AY380371, AY380395, AY635766, DQ494696, AY745706, AF205707, DQ494685, AF745706). Two GenBank sequences (DQ917657 ITS, EU600863 LSU) representing specimens identified as *Inocybe sororia* were included in the separately aligned and analysed dataset for the *Rimosae* s.s. subclade A (see below).

DNA extraction, PCR and sequencing

Sequences from three regions were generated for the study, the complete ITS region, 1200 base pairs of the 5' end of the nuclear LSU ribosomal DNA, and the mitochondrial SSU ribosomal DNA. DNA extractions, PCR reactions and sequencing were performed as described in Larsson & Örstadius 2008. Primers used to amplify the complete ITS region and the 5' end of the LSU region were ITS1F (Gardes & Bruns 1993) and LR21, LR0R and LR7 (Hopple & Vilgalys 1999), the mtSSU MS1 and MS2 (White et al. 1990). Primers used for sequencing were ITS1, ITS3, ITS4, MS1, MS2 (White et al. 1990), Ctb6 (http://plantbio.berkeley.edu/~bruns/), Lr5 and LR3R (Hopple & Vilgalys 1999).

Phylogenetic analyses

Sequences were edited and assembled using Sequencher 3.1 (Gene Codes, Ann Arbor). Sequences were aligned automatically using the software MAFFT (Katoh et al. 2002) and adjusted manually using the data editor in PAUP* (Swofford 2003). Sequences have been deposited in GenBank and accession numbers are listed in Table 1.

Heuristic searches for most parsimonious trees were performed using PAUP*. 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. Relative robustness of clades was assessed by the bootstrap method using 1 000 heuristic search replicates with 100 random taxon addition sequence replicate, TBR swapping, saving 100 trees in each replicate.

Bayesian analysis of the datasets was performed using MrBayes 3.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). MrModelTest 2.2 (Nylander 2004) was used to estimate separate best-fit models of evolution for ITS (1 and 2 combined), 5.8S, LSU, and mtSSU. The Bayesian inference was set up with model parameters estimated separately for each of the four partitions. Four parallel runs using Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) were implemented instead of the default of two to improve the inference of convergence statistics. To decrease the computational burden two chains, one hot and one cold (temperature difference set to 0.1 to increase the efficiency of metropolis coupling), were used instead of the default of four. Each chain was run for 10 million generations with tree and parameter sampling every 1 000 generations (10 000 trees). Tracer (Drummond & Rambaut 2007) and AWTY (Wilgenbusch et al. 2004) were used to examine when the chains had reached a stationary state and how many generations were appropriate to discard as burn-in. A 50 % majority-rule consensus phylogram was computed from the remaining trees; the proportions of this tree correspond to Bayesian posterior probabilities (BPP). To investigate if there were any conflict between the nuclear and mitochondrial regions, analyses were also made for these partitions separately. It was then checked if there were any conflict between the regions in nodes separating species and with more than 0.7 BPP support (cf. Lutzoni et al. 2004).

To improve the resolution and be able to use the complete ITS region in the phylogenetic analysis realignment of sequence data in the *Rimosae* s.s. subclade A and *Rimosae* s.s. subclade D were performed as described above. Heuristic searches for most parsimonious trees and bootstrap analysis were performed as above except that no restriction on saving of trees in the replicates was applied.

RESULTS

For all 99 ingroup specimens the ITS/LSU region was generated. For 54 of these also mtSSU sequences were generated

Table 1 Data of specimens sequenced in this study.

Species	Original specimen identification	Coll. ID. / Origin	Ecology, substrate	GenBank	
				ITS/LSU	mtSSU
Conocybe siliginea		*LÖ93-04* / Swe	In a pasture	DQ389731	
Crepidotus mollis		*EL45-04* / Swe	deciduous wood	AM882996	
C. mollis var. *calolepis*		*EL14-08* / Swe	deciduous wood	FJ904178	FJ904242
Inocybe cervicolor		*SJ04024* / Swe	*Picea* forest, calcareous	AM882939,	FJ904185
I. bongardii		*EL123-04* / Swe	*Quercus*, calcareous	AM882941	FJ904186
I. subhirsuta		*EL45-05* / Nor	*Dryas*, *Salix*, alpine	AM88294	FJ904187
I. cfr *calamistrata*		*KHL13071* / Costa Rica	*Quercus*	AM882948	
I. dulcamara		*EL89-06* / Swe	*Salix glauca*	FJ904122	FJ904181
I. terrigena		*EL117-04* / Swe	*Picea*, calcareous	AM882864	FJ904183
I. fulvipes		*EL37-05* / Nor	*Dryas*, *Salix*, alpine	AM882858	FJ904184
I. agardhii		*EL88-04* / Swe	*Salix*, calcareous	FJ904123	FJ904182
Naucoria salicis		*EL71a-03* / Swe	*Alnus*, *Betula*	FJ904180	
N. bohemica		*EL71b-03* / Swe	*Alnus*, *Betula*	FJ904179	FJ904243
N. submelinoides		*TAA185174* / Est	*Alnus*	AM882885	
Inocybe adaequata	*I.* cfr *rimosa*	*PC2008-0014* / GB	*Fagus* forest	FJ904177	FJ904240
	I. adaequata	*MR00022* / Swe	*Tilia*, *Corylus*	AM882706	FJ904241
I. arenicola	*I. arenicola*	*RC GB99-014* / Fra	*Pinus*, *Salix*, sand dune	FJ904134	FJ904189
	I. arenicola	*EL238-06* / Fra	*Pinus*, sand dune	FJ904133	FJ904188
I. bulbosissima	*I. fastigiata* var. *alpina*	*EL51-05* / Nor	*Dryas*, *Salix*, alpine	AM882764	
	I. fastigiata var. *alpina*	*EL66-05* / Nor	*Salix reticulata*, alpine	AM882765	FJ904224
	I. fastigiata var. *alpina*	*EL37-06* / Swe	*Salix polaris*, alpine	FJ904161	FJ904223
	I. bulbosissima	*EL75-07* / Swe	*Salix reticulata*, alpine	FJ904160	FJ904222
	I. rimosa	*EL88-06* / Swe	*Salix lapponum*, subalpine	FJ904159	FJ904221
	I. fastigiata var. *alpina*	*EL30-06* / Swe	*Salix polaris*, alpine	FJ904158	FJ904220
I. cfr *cookei*	*I. cookei*	*EL104-04* / Swe	*Corylus*	AM882952	
I. cfr *flavella*	*I. rimosa*	*GK080924* / GB	*Quercus*, *Betula*, wet	FJ904129	FJ904196
	I. majalis	*PAM05062502* / Fra	*Salix*, calcareous soil	FJ904128	FJ904195
	I. flavella	*EL118-05* / Fin	*Salix*, *Betula*, ravine	AM882782	
	I. flavella	*BJ920829* / Swe	*Salix*, *Betula*, hyperit	AM882774	
	I. flavella	*EL90-04* / Swe	*Salix*, *Betula*, calcareous	AM882773	
I. cfr *rimosa*	*I. rimosa*	*EL71-04* / Swe	*Fagus*, calcareous soil	AM882786	FJ904193
	I. perlata	*JD2008-0241* / GB	*Fagus*, *Corylus*	FJ904125	FJ904192
	I. cfr *rimosa*	*I116-06* / Australia	deciduous forest	FJ904142	
	I. fastigiata	*PAM05061101* / Fra	*Tilia*, calcareous	FJ904155	FJ904216
	I. arenicola	*JV26578* / Est	*Pinus*, calcareous	FJ904154	FJ904215
	I. rimosa	*EL127-04* / Swe	*Fagus*, *Quercus*, calcareous	AM882768	FJ904219
	I. rimosa	*TAA185135* / Est	*Pinus*, *Betula*, calcareous	AM882766	
	I. rimosa	*JV22619* / Est	*Quercus*, *Corylus*, calcareous	FJ904157	FJ904218
	I. umbrinella	*PC080925* / GB	*Pinus*, *Quercus*	FJ904153	
	I. rimosa var. *umbrinella*	*JV8125* / Fin	*Picea*, *Tilia*, *Populus*, rich	FJ904152	FJ904214
	I. cft obsoleta	*EL81-06* / Swe	*Salix glauca*, subalpine, wet	FJ904135	FJ904190
I. cfr *squamata*	*I. cft squamata*	*I93-04* / Australia	deciduous forest	FJ904141	
	I. cft squamata	*I113-05* / Australia	deciduous forest	FJ904140	
	I. squamata	*SJ92-010* / Swe	*Picea*, calcareous	AM882785	
	I. squamata	*SM92-013* / Swe	*Picea*, *Populus*, *Betula*	AM882783	
	I. squamata	*SJ92-017* / Swe	*Pinus*, *Populus*, park	AM882784	
	I. squamata	*Stordal18318* / Nor	*Picea* mixed forest	FJ904139	
	I. squamata	*JV2609* / Fin	*Picea*, *Populus*, *Pinus*	FJ904138	FJ904203
I. cookei	*I. cookei*	*MR00035* / Swe	*Corylus*, *Quercus*	AM882954	
	I. cookei	*EL191-06* / GB	*Corylus*, *Quercus*	FJ904173	FJ904234
	I. cookei	*EL70a-03* / Swe	*Fagus*, *Quercus*	AM882953	
	I. cookei	*EL73-05* / Swe	*Betula*, *Quercus*	AM882955	
	I. cookei	*EL109-04* / Swe	*Corylus*, *Quercus*	AM882956	FJ904233
I. dulcamaroides	*I. dulcamaroides*	*EL29-08* / USA	*Salix reticulata*, alpine	FJ904127	
	I. dulcamaroides	*EL112-06* / Swe	*Dryas*, alpine	FJ904126	FJ904194
I. erubescens	*I. erubescens*	*TAA185164* / Est	*Quercus*, *Tilia*, calcareous	AM882950	
	I. erubescens	*KGN980714* / Swe	*Fagus*, *Tilia*, rich soil	AM882951	FJ904239
	I. erubescens	*BH910707* / Swe	*Fagus*, park	AM882949	
I. flavella	*I. flavella*	*EL56-08* / Swe	*Corylus*, *Salix*, *Alnus*, wet	FJ904131	FJ904198
	I. flavella	*EL137-05* / Swe	*Corylus*, *Alnus*, *Quercus* wet	AM882776	FJ904199
	I. flavella	*LAS89-030* / Swe	*Alnus*, wet	AM882775	
I. xanthocephala	*I. xanthocephala*	*PAM00100606* / Fra	*Salix*	FJ904130	FJ904197
I. hygrophorus	*I. hygrophorus*	*EL97-06* / Swe	*Betula*, *Salix*, subalpine meadow	FJ904137	FJ904202
I. maculata	*I. maculata*	*EL74-05* / Swe	*Fagus*, *Quercus*	AM882959	
	I. maculata	*MR00020* / Swe	*Tilia*, *Corylus*, calcareous	AM882958	
	I. maculata	*EL121-04* / Swe	*Fagus*, *Quercus*, calcareous	AM882957	FJ904232
	I. maculata	*EL58-03* / Swe	*Fagus*, rich soil	AM882963	
	I. maculata	*EL126-04* / Swe	*Fagus*, *Quercus*, calcareous	AM882964	
	I. maculata	*EL182-08* / Slov	*Fagus*, rich soil	FJ904172	
I. maculata forma *fulva*	*I. maculata*	*EL78-03* / Swe	Mixed trees, pasture	AM882962	
	I. maculata	*EL166-08* / Swe	*Picea*, *Corylus*, calcareous	FJ904171	FJ904231
	I. cfr *maculata*	*EL114-06* / Swe	*Dryas*, *Polygonum*, alpine	FJ904170	
	I. cfr *rimosa*	*SJ05029* / Swe	*Pinus*, *Alnus*	AM882994	FJ904230
	I. maculata forma *fulva*	*EL247-06* / Fra	*Pinus*, *Populus*	FJ904169	
	I. maculata forma *fulva*	*PAM01100120* / Fra	*Betula*	FJ904168	
	I. maculata	*SJ06007* / Swe	*Betula*	FJ904167	

Table 1 (cont.)

Species	Original specimen identification	Coll. ID. / Origin	Ecology, substrate	GenBank	
				ITS/LSU	mtSSU
I. melliolens	*I. umbrinella*	*PAM05052303* / Fra	*Tilia*, calcareous	FJ904148	FJ904211
	I. melliolens	*EL224-06* / Fra	*Salix*, *Quercus*, wet	FJ904149	
I. cfr *microfastigiata*	*I. microfastigiata*	*EL113-06* / Swe	*Dryas*, alpine	FJ904156	FJ904217
I. mimica	*I. mimica*	*EBJ961997* / Swe	*Pinus*, *Picea*, calcareous	FJ904124	FJ904191
	I. mimica	*TK2004-114* / Swe	*Pinus*, *Betula*, calcareous	AM882781	
I. obsoleta	*I. obsoleta*	*EL17-04* / Swe	*Picea*, *Corylus*	AM882769	FJ904204
	I. obsoleta	*BJ890915* / Swe	*Picea* mixed forest	AM882770	
I. perlata	*I. perlata*	*BJ940922* / Swe	*Fagus*, *Betula*, meadow	AM882772	
	I. perlata	*EL74-04* / Swe	*Corylus*, *Betula*, calcareous	AM882771	FJ904205
I. quietiodor	*I. quietiodor*	*RP980718* / Swe	*Fagus*, *Quercus*, park	FJ936169	FJ904238
	I. quietiodor	*LAS97-067* / Swe	*Fagus*, *Quercus*, calcareous	AM882974	
	I. quietiodor	*LAS94-023* / Swe	*Fagus*, *Quercus*, calcareous	AM882961	
	I. quietiodor	*PAM01091310* / Fra	*Betula*, *Salix*	FJ936168	FJ904237
	I. quietiodor	*EL115-04* / Swe	*Quercus*, *Tilia*, park	AM882960	FJ904236
	I. quietiodor	*JV20202* / Nor	*Betula*, *Alnus*, calcareous	FJ904174	FJ904235
I. rhodiola	*I. rhodiola*	*PAM00090117* / Fra	*Salix*	FJ904176	
	I. rhodiola	*EL223-06* / Fra	*Salix*, wet forest	FJ904175	
I. rimosa	*I. rimosa*	*AO2008-0250* / GB	*Salix*	FJ904147	FJ904210
	I. rimosa	*EL118-08* / Swe	*Picea*, *Betula*, calcareous	FJ904146	FJ904209
	I. rimosa	*EL102-04* / Swe	*Betula*, garden	AM882761	
	I. rimosa var. *umbrinella*	*EL211-06* / Fra	*Quercus*, *Carpinus*	FJ904145	
	I. rimosa	*TK97-156* / Swe	*Corylus*, calcareous	AM882844	
	I. fastigiata var. *argentata*	*PAM03110904* / Fra	*Quercus*	FJ904144	FJ904208
	I. rimosa	*EL75-05* / Swe	*Fagus*, *Quercus*, park	AM882762	FJ904207
	I. rimosa	*SJ04007* / Swe	*Tilia*	AM882763	
	I. fastigiata var. *argentata*	*PAM06112703* / *Corsica*	*Fagus*	FJ904143	FJ904206
I. sororia	*I.* cfr *fasigiata*	*Kuoljok0512* / Swe	*Salix*, alpine meadow	FJ904150	FJ904212
	I. rimosa coll.	*JV15200* / Swe	*Salix herbacea*, alpine	FJ904151	FJ904213
I. squamata	*I. squamata*	*SJ08003* / Swe	*Betula*, *Pinus*	FJ904136	FJ904201
	I. cfr *squamata*	*TK96-109* / Swe	*Populus*, calcareous	AM882780	
	I. cfr *squamata*	*SJ85048* / Nor	*Populus*, calcareous	AM882778	
	I. curreyi	*PAM05052301* / Fra	*Populus*, *Picea*, park	FJ904132	FJ904200
I. umbrinella	*I. rimosa* var. *brunnea*	*JV13699* / Fin	*Pinus*, *Populus*, *Salix*	FJ904165	FJ904228
	I. rimosa coll.	*JV17954* / Est	*Pinus*, calcareous	FJ904166	FJ904229
	I. cfr *rimosa*	*PC081010* / GB	*Helianthemum*, calcareous	FJ904164	FJ904227
	I. cfr *rimosa*	*PC080816* / GB	*Fagus*, *Quercus*, calcareous	FJ904163	FJ904226
	I. perlata	*PAM01102912* / Fra	*Quercus ilex*	FJ904162	FJ904225

(Table 1). The aligned complete dataset, including sequences downloaded from GenBank, consisted of 119 sequences and 3 461 characters. The majority of the ITS1 and ITS2 regions was found to be too variable to be included in the analyses. After exclusion of ambiguous regions 1 985 characters remained for the analysis. Of these 1 409 were constant, 174 were variable and parsimony uninformative, and 402 were parsimony informative.

The maximum parsimony analysis yielded 63 900 equally most parsimonious trees (length = 1 812, CI = 0.4354, RI = 0.8490). Bootstrap analysis recovered *Inocybe* s.l. (including *Auritella*) as monophyletic with 91 % support. It forms together with *Crepidotus*, *Simocybe*, and *Pleuroflammula* a clade with 92 % bootstrap support.

Four major clades within the ingroup received strong support. They are here called *Auritella* (100 %), *Rimosae* s.s. (98 %), *Mallocybe* (100 %), and *Inosperma* (98 %). The *Inosperma* clade was further divided in the *Cervicolores* clade (98 %) and a moderately supported group here called the Maculata clade (72 %).

The *Rimosae* s.s. clade includes 68 sequences dispersed over 6 strongly supported subclades (Fig. 1A–F) and a number of groups that in most cases seem to correspond to species. Eight of these terminal groups have been identified as *Inocybe arenicola*, *I. mimica*, *I. dulcamaroides*, *I. flavella*, *I. squamata*, *I. hygrophorus*, *I. obsoleta*, and *I. perlata*, respectively. One distinct but non-identified clade is reported as *Inocybe* sp. Specimens identified as *I. flavella* seem to cover several taxa differing in the shape and size of spores. Small-spored specimens are together lumped as *I.* cfr *flavella* but this label seems to cover at least two taxa. Thirty-three sequences cluster to a strongly supported clade that corresponds to *I. rimosa* s.l. Within such a broadly defined *I. rimosa* five subclades corresponding to species were recovered. One is the alpine species *I. bulbosissima*, a second is *I. rimosa* s.s., a third is *I. umbrinella*, and the remaining two are tentatively identified as *I.* cfr *sororia* and *I. melliolens*. The specimens originating from deciduous forests in Australia form a strongly supported clade within *Rimosae* and represent two unidentified species. In addition several taxa on single branches and minor less supported clades were recovered (Fig. 1). These terminals may represent new species, either undescribed or described from other regions but not yet identified.

In the Maculata clade six terminal taxa were recovered as strongly supported (Fig. 1). They are identified as *Inocybe adaequata*, *I. rhodiola*, *I. erubescens*, *I. quietiodor*, *I. cookei*, and *I. maculata*, including *I. maculata* forma *fulva*.

For the separate regions, MrModelTest suggested GTR+I+G (ITS), K80+I (5.8S), GTR+I+G (LSU), and GTR+I+G (mtSSU) as optimal models; this information was employed in MrBayes. The Tracer and AWTY analysis indicated that 5 million generations would be an appropriate burn in time as a stationary state was reached for all chains well before that. This was also supported by the fact that the standard deviation of split frequencies calculated in MrBayes was below 0.01 well before this point. The last 5 000 trees of each run (20 000 trees in total) were therefore summarized into a 50 % majority-rule consensus phylogram (Fig. 1).

No conflict was found between the nuclear and mitochondrial regions according to the criteria defined in Materials and Methods.

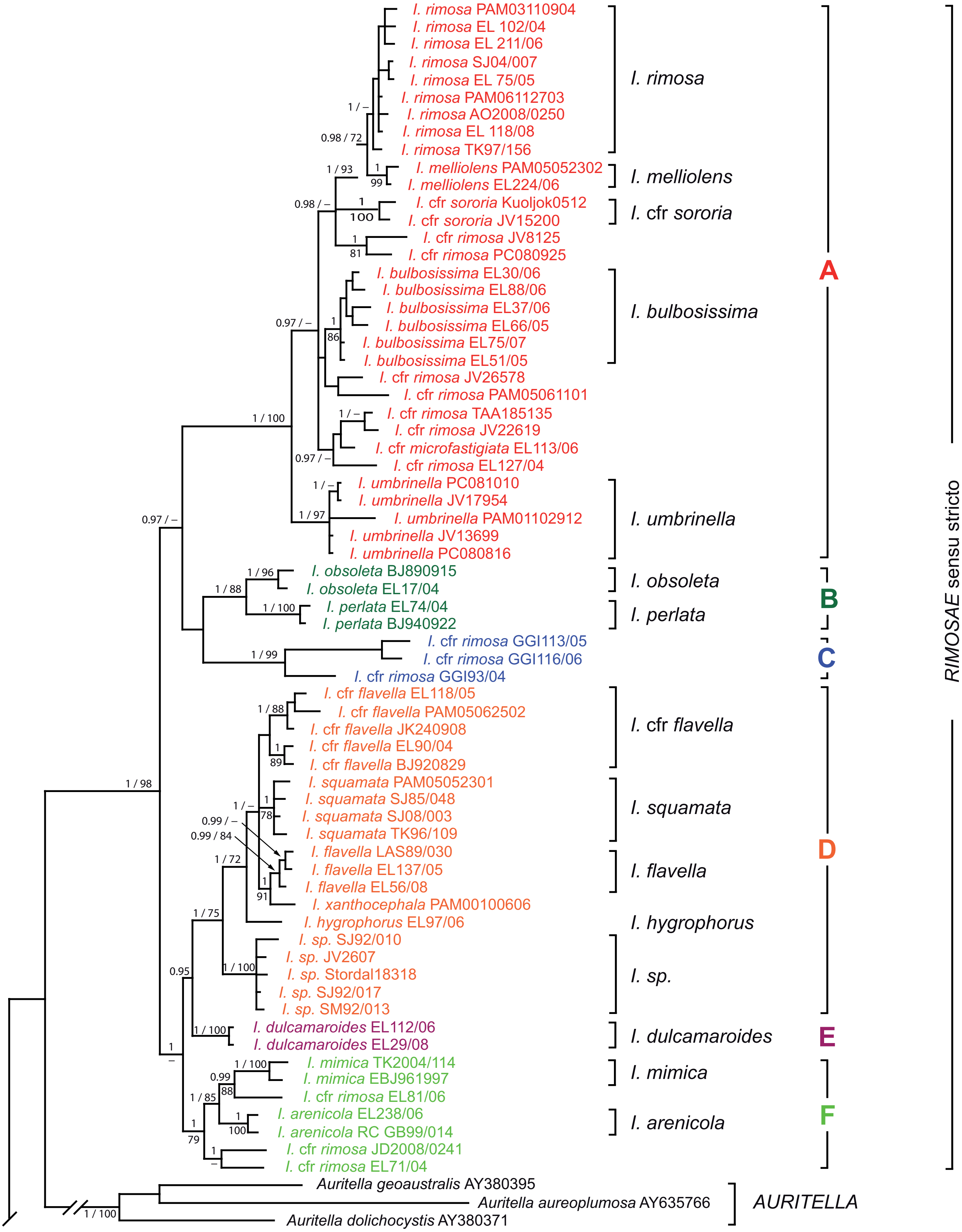
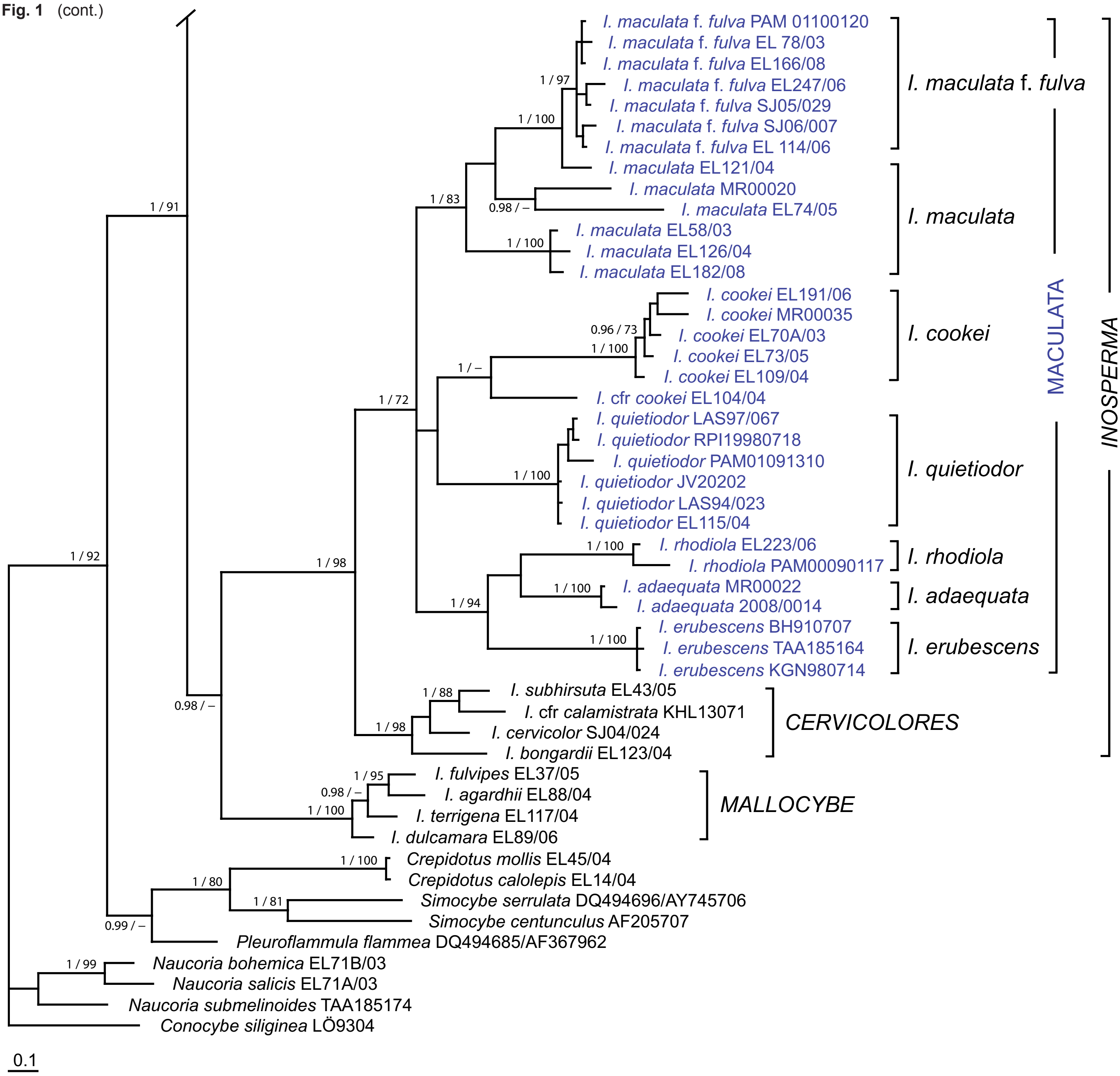


Fig. 1 Bayesian 50 % majority-rule consensus phylogram. Bayesian posterior probabilities and bootstrap values above 70 % from the maximum parsimony analysis are indicated on branches. Recovered major clades are named and marked with a scale bar and minor supported clades discussed in the text have been numbered A–F. *Conocybe siliginea* was used to root the tree.

Fig. 1 (cont.)



Also in this analysis *Inocybe*, including *Auritella*, is recovered as monophyletic with a BPP value of 1.00. The four major clades recovered in the maximum parsimony analysis, are present also in the Bayesian tree, all of them with BPP values 1.00. The *Cervicolores* (BPP 1.00) and Maculata clades (BPP 1.00) are also strongly supported. All 21 species clades from the maximum parsimony analysis of sect. *Rimosae* are also supported in the Bayesian analysis (Fig. 1). The Bayesian tree topology is more or less identical to the MP bootstrap tree. However, some additional clades were recovered with strong support, e.g. *Crepidotaceae* (BPP 0.99).

The realigned dataset of 33 taxa in the *Rimosae* s.s. subclade A included 2 819 characters. After exclusion of regions with incomplete data, mainly from the mtSSU, 2 362 characters remained for the analysis. Of these 2 126 were constant, 83 were variable and parsimony uninformative, and 153 were parsimony informative. The heuristic searches recovered 4 290 equally most parsimonious trees (length = 340, CI = 0.7853, RI = 0.8933). Fig. 2 illustrates one of these as a mid-point rooted phylogram. The bootstrap analysis recovered the same strongly supported terminal clades as in the complete parsimony analysis but also generated moderate support (78 %) for *I. rimosa* s.s. Support for the remaining species level clades were: *I. melliolens* (99 %), *I.* cfr *sororia* (98 %), *I. bulbosissima* (98 %), and *I. umbrinella* (100 %). The North American sequences representing *I. sororia* clustered with North European sequences with 100 % support.

The realigned dataset of 18 taxa in the *Rimosae* s.s. subclade D included 2 812 characters. After exclusion of regions with incomplete data, mainly from the mtSSU, 2 421 characters remained for the analysis. Of these 2 266 were constant, 57 were variable and parsimony uninformative, and 98 were parsimony informative. The heuristic search recovered 675 most parsimonious trees (length = 190, CI = 0.8526, RI = 0.9111). Fig. 3 illustrates one of these as a mid-point rooted phylogram. The bootstrap analysis recovered five strongly supported (above 90 %) clades of which four have the same topology as in the complete analyses, viz. *I. squamata* (100 %), *Inocybe* sp. (100 %), *I. flavella* (100 %), and *I.* cfr *flavella A* (99 %) while *I.* cfr *flavella B* is supported only together with *I. hygrophorus* (100 %). *Inocybe flavella* + *I. xanthocephala* (91 % in the large parsimony analysis) is not supported.

DISCUSSION

The present study aimed at elucidating the phylogenetic structure of *Inocybe* subg. *Inosperma* sect. *Rimosae* as defined by Kuyper (1986) but included also representatives from the subg. *Mallocybe* and the recently erected genus *Auritella* (Matheny & Bougher 2006a, b). The ingroup was recovered as monophyletic and strongly supported. However, our results indicate that recognizing *Auritella* on the genus level renders *Inocybe* paraphyletic. The solution is either to sink *Auritella* as a subgenus within *Inocybe*, or to split *Inocybe* into a number of smaller genera. However, our study was not designed to take a decision on that matter.

We found that the species traditionally placed in sect. *Rimosae* did not form a monophyletic clade. Instead they are distributed over two strongly supported clades: Maculata and *Rimosae* s.s. (Fig 1). The Maculata group clusters with sect. *Cervicolores* and the two combined represent subg. *Inosperma* in a new stricter sense. A more narrowly defined sect. *Rimosae* emerges as an independent supported clade well separated from *Inosperma* s.s.

In the study by Matheny (2006) a division of sect. *Rimosae* was indicated although only one representative of the *Rimosae* s.s. clade was included. In a recent biogeographic study of *Inocybaceae* more representatives of the *Rimosae* s.s. clade were included and the split topology again supported (Matheny et al. 2009). Matheny uses Pseudosperma as the clade name for what is here called *Rimosae* s.s.

Through our morphological investigations we were able to correlate 21 terminal groups within clades Maculata and *Rimosae* s.s. with morphologically distinct species (Fig. 1). The molecular support is based on data from nLSU, mtSSU, 5.8S and a few conservative regions of ITS, leaving out the variable regions of ITS because of aligning problems. The ITS region is the locus that has been most commonly used for species delimitation of fungi (Kõljalg et al. 2005, Kõljalg & Larsson 1998, Larsson & Örstadius 2008, Nilsson et al. 2008). In general *Inocybe* species show a high sequence divergence in the ITS region. Closely related species often deviate in several substitutions and insertion/deletion events and are therefore easy to identify using simple sequence comparison (Altschul et al. 1997). We also found that the terminal clades we have been able to correlate to morphological species, in general show a low within clade sequence divergence. Notable exceptions to this observation are *I. rimosa* and related species (Fig. 2 subclade A), and *I. flavella* and related species (Fig. 3 subclade D).

The Maculata clade is here represented by seven species with thin-walled, often clavate to pyriform cheilocystidia and phaseoliform spores. They usually have specific odours that differ from the spermatic smell typical of most species in the *Rimosae* s.s. clade. *Inocybe maculata* smells like raw potatoes or *Tuber*, *I. cookei* like honey, *I. erubescens* like perfumed soap, *I adaequata* and *I. rhodiola* like beetroot, and *I. quietiodor* like *Lactarius quietus*, that is, both sourish and sweetish. Having specific odours is a character they share with the species in sect. *Cervicolores*. However, odour is a very difficult and subjective character to use and although a spermatic smell characterizes most species in the *Rimosae* s.s. clade some species have other characteristics, e.g. *I. melliolens* Kühner (1988), which smells of honey when drying.

There is a trend in the Maculata clade for the stipe base to be distinctly bulbous. This characteristic is present in *I. cookie*, *I. maculata*, *I. maculata* forma *fulva*, and *I. quietiodor*, while in *I. adaequata*, *I. erubescens*, and *I. rhodiola* the bulbous base is not as pronounced. Several species are characterized by a reddening of the flesh (*I. adaequata*, *I. erubescens*, *I. rhodiola*) and this trait occurs also among species in *Cervicolores*.

Inocybe maculata is known as a variable species with considerable differences in cap colour and presence of velar remnants. These observations correspond to a high divergence among the sequences generated from specimens initially identified as *I. maculata* in a wide sense. The specimens we have sequenced can be divided in two morphotypes which also seem to correlate with ecological preferences. One type has a chocolate brown cap, often covered with conspicuous, white velar remnants. It grows associated with *Carpinus*, *Corylus*, *Fagus*, *Quercus*, and *Tilia* on rich soils, usually on calcareous ground. This type fits with the original description of *I. maculata* but unfortunately the specimens representing this morphotype do not form a monophyletic clade and the sequence divergence indicates that more than one species are involved (Fig.1, 4a). The other morphotype is more yellow to reddish brown and has less or no

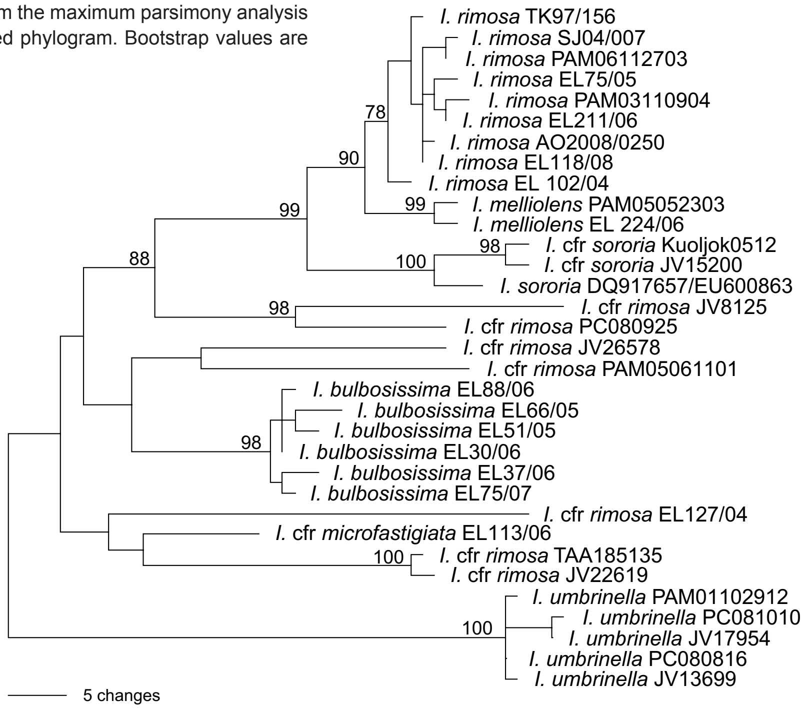


Fig. 2 One of the equally most parsimonious trees obtained from the maximum parsimony analysis of the *Rimosae* s.s. subclade A, presented as a mid-point rooted phylogram. Bootstrap values are indicated on branches.

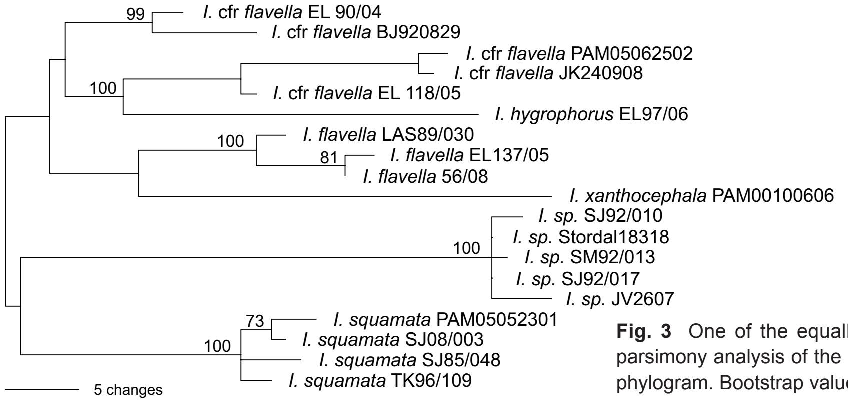


Fig. 3 One of the equally most parsimonious trees obtained from the maximum parsimony analysis of the *Rimosae* s.s. subclade D, presented as a mid-point rooted phylogram. Bootstrap values are indicated on branches.

velar remnants on the cap. This type seems to be associated with *Betula*, *Picea*, *Pinus*, *Populus*, and *Salix*, but also with *Dryas* and *Polygonum* in alpine environments. It fits the concept of *I. maculata* forma *fulva* Bon (1991, Fig. 4b) described from a coastal dune area with *Populus* in northern France. Of the seven specimens sequenced two originate from France, one of them from the same region and ecological setting as the type of forma *fulva*. Sequence data are uniform for this taxon and clade support is strong (97 %, BPP 1.0).

The *Rimosae* s.s. clade includes six strongly supported subclades (Fig. 1A–F) and altogether 15 terminal clades that we could correlate to morphologically distinguishable species. In addition *Rimosae* s.s. also includes several unidentified minor terminal clades and sequences that occur on single branches (Fig. 1). In general the species in this clade have ellipsoid to indistinctly phaseoliform spores and the cheilocystidia tend to be more cylindrical to clavate than in the Maculata clade. However, the shape of the cheilocystidia is very variable even within the same species. In this clade we also more often find that the apex of the stipe is distinctly white pruinose to flocculose. The spermatic odour and the presence of yellow to olive-yellow pigments in the lamellae are characteristic for many species in *Rimosae* s.s. The occurrence of oily refracting contents in hyphae is notable and may be connected to the spermatic odour. Kuyper (1986) found a correlation between the intensity of the olive-yellow tone of the lamellae and the strength of the spermatic odour.

***Rimosae* subclade A**. This clade corresponds to *I. rimosa* in a wide sense and includes 33 specimens (Fig. 2) originating from England, Estonia, France, and Scandinavia. They represent most of the large variation in macro-morphological characters and ecology demonstrated by the many varieties described (Heim 1931, Favre 1955, Kühner 1988, Bon 1997). Five terminal clades with moderately strong to strong support were recovered and are further discussed below. Still other sequences form unsupported groups or occur on single branches (Fig. 1, 2).

Inocybe rimosa s.s. includes nine specimens that show a great variation in cap colours from pale to ochraceous yellow brown to dark brown. In micro-morphology they are all very similar. The specimens originate from different habitats ranging from nemoral deciduous forests to boreal *Picea* forest. There is a nine base pair insertion in the beginning of the ITS region in five of the specimens but this difference could not be correlated to differences in morphology or ecology.

The specimens named *I. melliolens* originate from France. In morphology this species looks like a typical *I. rimosa* s.s. but has a strong smell of honey. We have not seen any specimens with this character from Northern Europe and the species may have a more southern distribution, even if it is described from *Dryas* vegetation in the French Alps (Bon 1997).

The LSU sequences deposited in GenBank as *I. sororia* originate from a Northwest American conifer stand (Matheny et al. 2009). They are almost identical to our sequences from two specimens from herb-rich locations and dwarf *Salix* in the alpine zone of Sweden (Fig. 2). *Inocybe sororia* is described by Kauffman (1924) from North American frondose forests. Since we have only studied the Swedish material and they deviate from the descriptions given by Kauffman (1924) and Stuntz (1947) we feel uncertain about the identity of our collections.

Inocybe bulbosissima includes specimens associated with dwarf *Salix* and *Dryas* in the alpine zone. The species is usually regarded as a variety of *I. rimosa* and then named *I. fastigiata* var. *alpina*. Another alpine species with similar characteristics is *I. microfastigiata* which is said to differ by smaller spores and a darker brown cap (Kühner 1988). A specimen with such morphology was included in this study and did not cluster with *I. bulbosissima* (Fig. 2, 4d). More specimens and sequences are required before the circumscription of *I. microfastigiata* can be clarified.

Inocybe umbrinella includes specimens with warm yellowish to reddish brown caps with a dark centre and contrasting strongly rimose and lighter periphery. The micro-morphology is almost identical to *I. rimosa*. In Bresadola´s description (Bresadola 1905) it is said to grow in gravely places with *Populus nigra*. Three of our specimens were collected in rather dry, sandy environments with *Helianthemum*, *Pinus*, and *Quercus ilex*. In our opinion these specimens fit the descriptions by Bresadola (1905) and Enderle & Stangl (1981).

Some other specimens with a dark brown cap clustering with or close to *I. rimosa* were first determined as *I. umbrinella* (Table 1). These specimens have fruit-bodies that in general are somewhat smaller than typical *I. umbrinella*. *Inocybe umbrinella* may also be confused with *I. perlata* but *I. perlata* usually has a dull dark brown cap and a flattened, less pronounced umbo.

***Rimosae* subclade B**. *Inocybe obsoleta* and *I. perlata* were recovered as independent species. Both have rather large and robust fruit-bodies and occur in mixed deciduous forests and parks, often on somewhat calcareous and nutrient rich soils. In micro-morphology they are hard to separate from *I. rimosa*. The best characters for identification are the robust fruit-bodies and the dark greyish brown colour without any yellow flush on the cap in *I. perlata* and the pale clay yellowish brown cap with distinct, white velum remnants in young specimens of *I. obsoleta*. Our interpretation of the name *I. obsoleta* is here based on specimens from North Europe only.

***Rimosae* subclade C** includes three specimens that originate from Australia. We were not able to correlate them to known species and they are provisionally named *I.* cfr *squamata* and *I.* cfr *rimosa*. They represent two species closely related to *I. rimosa* but may not occur in North Europe.

***Rimosae* subclade D** includes species that are often encountered in mixed forests with *Salix* and *Populus*. We identified *I. flavella* s.l., *I. hygrophorus*, *I. squamata*, and one undescribed species (*Inocybe* sp.). *Inocybe hygrophorus* is represented by only one specimen. It was collected in a subalpine meadow in forest with *Salix* and *Betula* and fits the original morphological description. Sequence data confirm that it is distinct from *I. flavella*. It seems to be rare or maybe overlooked as it may be mistaken for *I. flavella* or *I. rimosa*.

The two species *I. squamata* and *Inocybe* sp. are very similar in macro-morphology, with scattered appressed scales on the cap. The spores are distinctly phaseoliform and narrow in *Inocybe* sp. while in typical *I. squamata* they are broadly ellipsoid and only occasionally slightly phaseoliform. We observed that the lamellae were more yellow and the fruit-bodies on average larger in *Inocybe* sp. This possibly undescribed species also seems to have a boreal distribution judging from the known records from Sweden, Finland, and Norway. *Inocybe squamata* is, in the Nordic countries, only known from nemoral and hemiboreal regions.

The specimens determined as *I. flavella* split into three supported subclades. We have included specimens that originate from Sweden, Finland, England, and France. We identified two morpho-types, here named *I. flavella* and *I.* cfr *flavella*. The specimens are all rather similar in macro-morphology, but show a variation in the presence of yellow pigments on lamellae and stipe and in the colour and structure of the cap. No special odour was detected. In micro-morphology a variation in the length and shape of the spores can be observed. In *I. flavella* s.s. the spores are 10–12 × 5–6 µm and usually not phaseoliform. In the clade named *I.* cfr *flavella* the spores are shorter 9–10.5 × 5–6 µm and often more or less phaseoliform. The analysis including the ITS region confirm the high sequence divergence within *I. flavella* s.l. (Fig. 3). There are several species and forms described as close to *I. flavella* (Heim 1931, Orton 1960, Kuyper 1986, Kühner 1988, Bon 1997) and additional sequence data is needed to disentangle the entities involved within this clade.

***Rimosae* subclade E**. *Inocybe dulcamaroides* is an arctic-alpine species associated with *Dryas* and *Salix reticulata*. The two sequences representing this species are 100 % identical throughout the ITS region despite originating from Sweden and USA (Montana), respectively. It is reminiscent of *I. dulcamara* in that it has a short stipe in comparison to its cap diameter. This makes it a morphologically characteristic species but it is little collected and seemingly rare or overlooked (Fig. 4c).

***Rimosae* subclade F** includes the two species, *I. arenicola* and *I. mimica*, which are characterized by rather large spores. They cluster together with sequences of three specimens which could not be matched with any species descriptions. The only uniting factor we found in this clade was a preference for calcareous soil conditions. Other morphological and ecological traits show a large variation.

Most of the species discussed in this paper are typified with material that turned out to be less suitable for DNA extraction. Some collections are simply old, others, e.g. those of Marcel Bon, are apparently dried under conditions that did not preserve DNA well. Still others are very scanty, e.g. most of Kühner's type specimens. This situation is not at all unusual within fungal taxonomy. If we shall be able to take full advantage of the higher precision of species definitions made possible by molecular data, we must make extensive use of the epitypification tool offered by ICBN. Like all typification measures, also the selection of an epitype must be done with utmost care in order to preserve the intentions of the original author. Our preferred method is to first seek a profound understanding of the regional species diversity through intense field work, then match our collections with existing names, compare them to authoritative material, and finally, if necessary, select epitypes from rich, molecularly characterized collections.

This study had a focus on the species that occur in European arctic and alpine environments and in temperate regions of North Europe. Many of the species belonging in sect. *Rimosae* which are described from North America and from the Mediterranean have yet to be sampled before a more complete understanding of the phylogenetic diversity of the Maculata and *Rimosae* s.s. clades can be achieved. Only then will it be appropriate to fix names through epitypification.

TAXONOMY

Species of the Maculata clade identified in Northwest Europe

Inocybe adaequata (Britzelm.) Sacc., Syll. Fung. (Abellini) 5: 767. 1887

Specimens examined. Great Britain, England, Bucks, Kings Wood Tylers Green, 19 Aug. 2008, *P. Cullington 2008/0014*. – Sweden, Bohuslän, Valla, Sundsby, 1 Sept. 1979, *SJ79154*; Bohuslän, Tanum, Lammö, 29 Sept. 2004, *MR00022*; Västergötland, Kinnekulle, Medelplana, Råbäcks munkängar, 6 Aug. 1977, *SJ77120*:

Inocybe cookei Bres., Fungi Trident. 2, 8–10: 17. 1892

Specimens examined. Great Britain, Scotland, Ledmore oakwood, 14 Sept. 2006, *EL191-06*. – Norway, Buskerud, Hönefoss, Grunntjern, 28 Aug. 2003, *J. Vauras 20202* (TUR-A). – Sweden, Västergötland, Alingsås, Nolhagaparken, 30 Aug. 2003, *EL70A-03*; Alingsås, Nolhagaparken, 21 Aug. 2005, *EL73-05*; Alingsås, Nolhagaparken, 2 Sept. 2006, *EL150-06*; Östad, Österäng, 26 Sept. 2004, *EL109-04*; Östad, Ekedalen, 26 Sept. 2004, *EL104-04*; Östad, Östad säteri, Djurgården, 4 Sept. 2008, *EL67-08*; Göteborg, Botaniska Trädgården, 19 Sept. 1975, *SJ386*; V. Tunhem, Hunneberg, 4 Oct. 2004, *MR00035*; Töreboda, Älgarås, Velen, 6 Sept. 2003, *EL50-03*; Grimmered, Björräsakulle, 17 Aug. 1989, *SJ89002*.

Inocybe erubescens A. Blytt, Videnskabs-Selskabets Skrifter. I Math.-Naturv. Kl., 6: 54. 1905 ('1904')

Specimens examined. Estonia, Saaremaa, Tagamösa, 29 July 2004, *TAA185164*. – Sweden, Närke, Askersund, Stjärnsund, 14 July 1998, *K-G Nilsson*; Skåne, Genarp, Häckeberga, 7 July 1991, *Bernt Hägg*.

Inocybe maculata Boud., Bull. Soc. Bot. France 32: 283. 1885

Specimens examined. Denmark, Falster, Nykøbing, Fuglsang Storskov, 3 Oct. 2007, *EL136-07*. – Slovakia, Rimavská Sobota, Drňa, 3 Oct. 2008, *EL182-08*. – Sweden, Bohuslän, Tanum, Lammö, 29 Sept. 2004, *MR00020*; Halland, Fjärås, Tjolöholm, 20 Sept. 1975, *SJ389*; Västergötland, Karlsborg, Undenäs, Bölet, 5 Sept. 2003, *EL45-03*; Västergötland, Berg, Högsböla ängar, Melldalaskogen, 7 Sept. 2003, *EL58-03*; Västergötland, Medelplana, Råbäcks Munkängar, 5 Sept. 2003, *EL41-03*; Västergötland, Kinnekulle, Medelplana, Råbäcks Munkängar, 27 Sept. 2004, *EL121-04*; Västergötland, Kinnekulle, Medelplana, Råbäcks Munkängar, 27 Sept. 2004, *EL126-04*; Västergötland, Alingsås, Nolhagaparken, 30 Aug. 2003, *EL68-03*; Västergötland, Alingsås, Nolhagaparken, 21 Aug. 2005, *EL74-05.*

Inocybe maculata forma ***fulva*** Bon, Doc, Mycol. 21 (no. 81): 47. 1991

Specimens examined. France, Merlimont, Pas de Calais, 3 Nov. 2006, *EL247-06*; Isére, Chireas, 1 Oct. 2001, *PAM01100120* (LIP). – Sweden, Härjedalen, Hamra, Hamrafjället, 18 Aug. 2006, *EL114-08*; Dalarna, Rättvik, Ö. om Gärdsjöns sydände, 23 Aug. 1982, *R. Morander 4320*; Dalarna, Rättvik, Rättviksheden, 29 Aug. 2005, *SJ05-029*; Närke, Lerbäck, Udden, 13 Aug. 1997, *K-G Nilsson*; Närke, Lekhyttan, Lunnasjön, 13 Sept. 2008, *EL166-08*; Närke, Lerbäck, Runsala ravin, 11 Sept. 2008, *EL134-08*; Närke, Kvistbro, Sixtorp, Gammelhyttan, 9 Sept. 2008, *EL82-08*; Skåne, Hässleholm, Igna-

Fig. 4 a. *Inocybe maculata* (*EL182/08*); b. *Inocybe maculata* forma *fulva* (*EL82/08*); c. *Inocybe dulcamaroides* (*EL112/06*); d. *Inocybe bulbosissima* (*EL75/07*).

berga, 15 Sept. 2003, *EL78-03*; Värmland, Övre Ullerud, Torsberget SSO, 17 Aug. 1991, *Bo Jansson*; Lule Lappmark, Jokkmokk, SSO Messaure, 23 Aug. 2003, *S. Kuoljok 0337*.

Inocybe quietiodor Bon, Doc. Mycol. 6 (no. 24): 46. 1976

Specimens examined. Denmark, Lolland, Flintinge byskov, 4 Oct. 2007, *EL142-07*. – France, Isére, Claix, Le Penil, 13 Sept. 2001, *PAM01091310* (LIP); Namps-au-Val, Fremoutiers, 14 Sept. 1994, *RC/F94064* (LIP). – Sweden, Västergötland, Alingsås, 18 July 1998, *RP98/048*; Västergötland, Götene, Medelplana, 28 Sept. 1997, *LAS97/067*; Västergötland, Kinnekulle, Medelplana, Råbäck, 10 Sept. 1994, *LAS 94/023*; Västergötland, Kinnekulle, Österplana, 27 Sept. 2004, *EL115-04*; Västergötland, Kinnekulle, Medelplana, Råbäcks Munkängar, 8 Sept. 2008, *EL73-08*.

Inocybe rhodiola Bres., Fungi Trident. 1: 80. 1884

Specimens examined. France, Saint-Amand, Dréve des Prés Charniers, 31 Oct. 2006, *EL223-06*; Isére, Saint Laurent du Pont, 1 Sept. 2000, *PAM00090117* (LIP). – Italy, Cuneo, Ceva, Alessio, 12 Sept. 1980, *Bon80091207* (LIP).

Species of the Rimosae s.s. clade identified in Northwest Europe

Inocybe arenicola (R. Heim) Bon, Doc. Mycol. 12 (no. 48): 44. 1983 ('1982')

Specimens examined. Estonia, *Saaremaa*: Kaarma, Mändjala, 19 Sept. 2008, *J. Vauras 26578* (TUR-A). – France, Merlimont, Pas de Calais, 2 Nov. 2006, *EL238-06*; Quend-les-Pines, 18 May 1983, *Bon83047* (LIP). – Great Britain, Sandscale, Haws-Nears, Barrow on Furness, 31 Aug. 1999, *RC/GB99.014*.

Inocybe bulbosissima (Kühner) Bon, Bull. Mycol. Bot. Dauphiné-Savoie 32 (no. 126): 19. 1992

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KEY TO THE SPECIES OF THE *MACULATA* AND *RIMOSAE* S.S. CLADES OCCURRING IN NORTHWEST EUROPE

1. Basidiocarp ± reddening with age or handling 2
1. Basidiocarp not reddening 4

2. Pileus robust, whitish, slowly turning brick red with age or from damage . . . . *I. erubescens*
2. Frb red brown with a ± vinaceous tinge 3

3. Pileus robust, fibrillose, sometimes breaking up into scales, stipe slowly staining somewhat vinaceous. Smell rather strong, reminding of beetroot . . . . *I. adaequata*
3. Pileus more slender, fibrillose–squamose. Stipe becoming distinctly vinaceous red towards the base. Smell weak . . . . *I. rhodiola*

4. With evident, distinct smell of various compounds but not spermatic. Spores generally phaseoliform. Cheilocystidia broadly clavate to pyriform 5
4. Smell, if present, spermatic. Spores variable, mostly ellipsoid. Cheilocystidia generally slenderly clavate or cylindrical 8

5. Pileus predominantly yellow. Stipe with a distinct bulb . 6
5. Pileus brown or brownish. Stipe equal or subbulbous . 7

6. Smell of honey. Spores 7–9 × 4–5 µm, distinctly phaseoliform. Cheilocystidia pyriform . . . . *I. cookei*
6. Smell recalling *Lactarius quietus*, spores 8–11 × 5.5–6.5 µm, less distinctly phaseoliform . . . . *I. quietiodor*

7. Pileus hazel brown to dark brown, often with white, conspicuous velar patches at centre. Growing in nutrient-rich *Fagus* or *Quercus* forests . . . . *I. maculata*
7. Pileus brownish, generally with a ± fulvous tinge, white velar patches often less evident. Growing with various broad-leaved or coniferous trees *I. maculata* forma *fulva*

8. Pileus with scales (may sometimes disappear) 9
8. Pileus fibrillose-rimose, without scales 11

9. Spores 12–15 × 6–8 µm, ellipsoid. Pileus > 65 mm, reminding of *I. rimosa*, gills with a faint olivaceous tinge. Stipe initially whitish, then reddish brown. Under deciduous trees on calcareous soils. Very rare and poorly known . . . . *I. mimica*
9. Spores smaller 10

10. Spores 8–10 × 5.5–6.5 µm, broadly ellipsoid (Q = 1.4–1.6). Pileus 20–50 mm, yellowish brown; lamellae initially without or with only weak yellow tinge. With deciduous trees on calcareous soils. In temperate or hemiboreal areas . . . . *I. squamata*
10. Spores 8.5–11 × 4.5–6 µm, often somewhat phaseoliform (Q = 1.6–2.0). Pileus 30–90 mm, yellowish to reddish brown, outwards more yellow. Lamellae initially pale yellow. With deciduous and coniferous trees, boreal *Inocybe* sp.

11. Growing with *Salix repens* or *Pinus* in dune sand along coasts in western Europe. Pileus 25–70 mm, initially whitish due to thick velipellis, beneath this straw yellow or ochraceous; gills initially white. Stipe solid, often deeply buried in sand. Spores 12–16 × 6–8.5 µm . . *I. arenicola*
11. In other habitats. Pileus generally yellow to brown . . . 12

12. Pileus flocculose from a thick universal veil, ochraceous brown, 10–25 mm (reminding of *I. dulcamara*). Cheilocystidia with internal drops of brown pigments, broadly

clavate to utriform. Spores 11–14 × 7–8.5 µm. With dwarf *Salix* in arctic/alpine zones . . . . *I. dulcamaroides*

12. Pileus fibrillose-rimose. Cheilocystidia without drops . 13
13. Arctic/alpine species with a distinct, white bulb at the base and large spores, 12–15 × 6–8 µm. Pileus 10–35 mm, pale yellow, then ochraceous to reddish brown. Smell spermatic . . . . *I. bulbosissima*
13. Not so 14
14. Pileus only finely fibrillose (almost smooth in centre), pale brownish with a yellow tinge, lamellae with a yellowish olive tinge. Stipe almost equal, 50–80 × 8–12 mm. Spores 9–11 × 4.5–5.5 µm, phaseoliform. In mountainous areas, mixed forest with *Salix* . . . . *I. hygrophorus*
14. Pileus distinctly fibrillose/rimose 15
15. Pileus brown without yellow tinges 16
15. Pileus not brown, with ± yellow pigments 17
16. Large species with acute umbo, reminding of *I. rimosa*. Pileus 35–100 mm. Stipe 80–120 × 8–13 mm, becoming brownish with age. Spores 10–13 × 6–8 µm. Under deciduous trees in forests and parks . . . . *I. perlata*
16. Smaller species. Pileus 20–45 mm, hazel to cinnamon brown, usually with blunt umbo. Spores 10–13 × 5.5–6.5 µm . . . . *I. umbrinella*
17. Pileus with a distinct white velipellis. Lamellae without olivaceous tinge. Odour absent. Microscopically as *I. rimosa*. Under deciduous trees on calcareous ground *I. obsoleta*
17. Pileus without distinct white velipellis 18
18. Pileus typically distinctly umbonate and strongly rimose. Lamellae with an olivaceous yellow tinge. Smell spermatic. Spores 9.5–12.5 × 6–7 µm, generally ellipsoid and only exceptionally somewhat phaseoliform . . . . *I. rimosa*
18. Pileus fibrillose-rimulose, not strongly rimose. Lamellae initially clay-coloured lacking or with only a weak yellow tinge. Smell absent. Spores 9–12 × 5–6 µm, often phaseoliform. Cheilocystidia narrow. Pileus more yellow and less rimose 19
19. Spores 10–12 × 5–6.5 µm, not phaseoliform. Pileus 20–60 mm, fibrillose, yellowish brown, predominantly yellow towards the margin . . . . *I. flavella*
19. Spores 9–10.5 × 5–6 µm, ± phaseoliform . *I.* cfr *flavella*

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