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Agarics of alders 2 – Three new species of *Alnicola* (Agaricales, Hymenogastraceae) with a key to species associated with *Alnus alnobetula* in Europe

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Abstract. — The genus *Alnicola* (*Hymenogastraceae*) contains a majority of host-specific ectomycorrhizal species, associated with various species of alders (*Alnus* spp.). Three species associated specifically with *Alnus alnobetula* are described as new and illustrated: *Alnicola badiofusca* P.-A. Moreau *sp. nov.*, *A. pallidifolia* P.-A. Moreau & Peintner *sp. nov.*, and *A. spectabilis* P.-A. Moreau & Peintner *sp. nov.*, and a key is provided for *Alnicola* species associated with *A. alnobetula* in the Alps and Corsica.

Basidiomycota / Betulaceae / ectomycorrhizae / *Naucoria* / phylogeny / taxonomy

INTRODUCTION

The interest of mycologists for the specific ectomycorrhizal (ECM) associations of higher fungi with alder trees (*Alnus* spp., Betulaceae) has recently increased with the rise of new scientific problematics: description of underground communities by DNA extraction from mycorrhizae (Tedersoo *et al.*, 2009; Kennedy & Hill, 2010; Kennedy *et al.*, 2011) and evolutionary processes in mutualistic associations (Rochet *et al.*, 2011). The Basidiomycete genus *Alnicola* Kühner (*Naucoria sensu auct.*) represents an important part of ectomycorrhizal fungal communities associated with *Alnus* spp. worldwide (Molina, 1981; Becerra *et al.*, 2005; Tedersoo *et al.*, 2009; Kennedy *et al.*, 2011; etc.). *Alnicola* is also the most diversified genus in these communities, with at least 16 strictly alnicolous species from Europe distinguished by Rochet *et al.* (2011).

The genus *Alnicola* in its restricted sense encompasses species with spindle-shaped cheilocystidia (Moreau *et al.,* 2006a, 2006b). Three monophyletic

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sections are recognized at this time: *Amarescens* Kühner (Kühner, 1981, not validated), *Cholea* P.-A. Moreau (Moreau *et al.*, 2006a), and *Alnicola* (lectotype selected: *A. luteolofibrillosa* Kühner; Moreau, 2005). Section *Alnicola* encompasses *Alnus*-specific species whereas sect. *Amarescens* and sect. *Cholea* contain species associated with *Salix* and ECM plants other than alders. The preliminary phylogenetic analysis published by Moreau *et al.* (2006b), based on a reduced number of sporocarps and on ITS and LSU ribosomal DNA sequences, did not reach the required precision for species delimitation. New analyses, based on ITS and three other genes (RPB2, GPD, and the mitochondrial gene V9), and on a much larger number of sporocarps collected in various ecological situations in Europe, and focused on sect. *Alnicola*, gave an adequate resolution at species level (Rochet *et al.*, 2011). Some three hundred ITS sequences obtained from alder mycorrhizae were added to this analysis, which could be all equated to sequences of already sampled and identified basidiomata. This suggests that our taxonomic sampling covers at least the most frequent and representative elements of the *Alnicola* communities in Western Europe.

Morphological identification of *Alnicola* species is notoriously difficult (Orton, 1960; Kühner, 1981; Reid, 1984), which is explained by the limits in the interpretation of morphological variability: characters usually significant in other groups of brown-spored agarics, such as spore size and shape, pileipellis structure, development of veil, insertion of lamellae, and even more colours and aspect of pileus, seem to be highly variable in most species, and therefore not so significant in this genus. Moreover other potentially significant characters, such as presence of chrysobasidia, pleurocystidia, pigmentation in pileipellis and hymenophoral trama, thickness and colour of walls of cheilo- and pleurocystidia, and shape of caulocystidia, are only exceptionally mentioned in literature and never used as differential characters. For instance, such a conspicuous feature as the characteristic polymorphism of cheilocystidia in *A. luteolofibrillosa* had never been mentioned except by Jamoni (2001), while the species is one of the less ambiguously interpreted in current literature. Therefore most descriptions in literature, usually based on single collections, are difficult to interpret regarding the species variability. Finally, host specificity had never been considered as a valuable character in species definitions. Rochet *et al.* (2011) appear to have been pioneers in suggesting that most *Alnicola* species have a high specificity for each section of the subgenera of *Alnus* in Europe.

Our molecular results based on four genes (Rochet *et al.*, 2011) helped us to define the intraspecific variability of each phylogenetic species as well as their ecological distribution. As shown in a previous work (Moreau *et al.*, 2012) on *Alnicola badia* Kühner and related species, morphological distinctions, intuitive in the field and from descriptions, were well-supported by these results, especially concerning colours of lamellae, aspect of pileus – especially surface under lens and striation, veil development, smell and taste. Presence of pleurocystidia and caulocystidia are of special interest for species delimitation. Characters usually used in species definition such as spore dimensions or shape were found to be of lower importance, as well as the presence of striking purplish colours, variable within some species (see observations under *A. badiofusca*).

Following the revision of *Alnicola badia* and related species (Moreau *et al.*, 2012) as a first step towards a general revision of *Alnicola* species in Europe, we propose the description and an identification key for the species strictly associated – as far as we could establish – with *Alnus alnobetula* in Corsica and the Alps.

MATERIAL AND METHODS

Taxonomy and nomenclature – Generic and infrageneric nomenclature follows Moreau (2005). All new names proposed are deposited in Mycobank; holotypes are deposited in herb. LIP (Lille, France), isotypes in herb. IB (Innsbruck, Austria) and ZT (Zürich, Switzerland).

Basidiomata sampling – Sporocarps were collected by the authors in Austria (Tirol), France (Alps) and Switzerland (Graubünden) under *Alnus alnobetula* subsp. *alnobetula*, and in Corsica (France) under *A. alnobetula* subsp. *suaveolens*. As far as possible photographs and morphological descriptions were made the same day; all specimens were cut and air-dried. Additional collections (exsiccata, notes and pictures) were provided by collaborators from France; a revision of herbarium material (M. Bon, LIP; J. Favre, G; E. Horak, ZT; R. Kühner, G; D. Dailly-Lamoure, personal herbarium; M. Moser, IB) is also included in this work. A wider sampling of *Alnicola* species has been driven in the same conditions under *Alnus cordata*, *A. glutinosa* and *A. incana* in various parts of France (especially Corsica, Northern Alps, Nord Pas-de-Calais, Pyrenees, Île-de-France, and Southern Massif Central), Austria, Belgium, Spain, and Switzerland. Because intraspecific variability is often significant, the following descriptions are based on the holotype collection, selected amongst the most representative and abundant collections at our disposal; species variability is discussed after each description on the basis of all collections studied.

Mycorrhizae sampling – Mycorrhizae were collected in several sites in France, on roots of *Alnus alnobetula* subsp. *alnobetula* (French Alps, 5 localities) and subsp. *suaveolens* (Corsica, 2 localities), selected under binocular and preserved in 2x CTAB buffer before extraction. ITS sequences were identified at generic level by BLAST (Tatusova & Madden, 1999), sequences identified as *Alnicola* species were compared to sequences obtained from basidiomata. Detailed data will be published in a specific work (Roy *et al.*, submitted).

Descriptions – Morphological descriptions are adapted from notes taken on fresh specimens; colour coding (when quoted on fresh material) refer to Munsell (M) (1975) or Cailleux & Taylor (C) (1963). Microscopical descriptions are based on observations made at the Laboratory of Botany (Lille), with a light microscope Nachet Andromede 018 at × 100, × 400 and × 1000 magnifications on hand-sectioned mounts in Melzer's reagent, 10% KOH, and Congo red 1% in 10% NH_4OH after rehydrating in 10% KOH for a few minutes. For all described species here are presented: spore variability (measurements from spore prints), distribution map according to sporocarps and mycorrhizal samplings and herbaria revision, and an ITS map of significant nucleotide positions. Microscopic characters were observed with an optic microscope Nachet, at × 100, × 400 and × 1000 magnifications, on hand-sectioned mounts in Melzer's reagent, 5% KOH, and Congo red (1 mg in 10 ml NH_4OH) after reviving in 10% KOH during a few minutes. For all collections at least 30 spores have been measured on spore print when possible, most often from natural deposits on stipe or pileus surface, statistical treatments and notations follow Fannechère (2005); measurements were made on the software Mycomètre 2.02 (Fannechère, 2011). Estimates of spore dimensions for each collection are detailed separately in Table 1, in the corresponding description they are re-calculated on all measurements made on collections attributed to the species. In the following descriptions spore dimensions are given as follows: (minimum value) 1st decile – *average value* – 9th decile (maximum value), calculated on all spores measured for each species

Table 1. Spore measurements of representative collections of *Alnicola badiofusca*, *A. pallidifolia* and *A. spectabilis*.

	No. of measured spores	*Length (µm)*	*Width (µm)*	*Q (L/W)*
Alnicola badiofusca				
08090308	25	(7.1)7.7-*8.21*-8.9(9.3)	(4.6)4.8-*5.1*-5.5(5.9)	(1.33)1.46-*1.62*-1.82(1.89)
05090918	45	(6.8)7.6-*8.2*-8.9(9.8)	(4.3)4.6-5.0-5.4(5.7)	(1.38)1.52-*1.65*-1.76(2.00)
05091002	40	(7.2)7.8-*8.5*-9.1(9.4)	(4.3)4.6-*4.9*-5.3(5.3)	(1.48)1.54-*1.71*-1.85(2.05)
05090917	34	(7.6)8.2-*8.9*-9.1(9.6)	(4.7)4.8-*5.1*-5.5(5.6)	(1.53)1.55-*1.67*-1.82(1.89)
05091004	46	(8.1)8.3-*9.4*-9.9(10.8)	(4.7)4.9-*5.2*-5.5(5.7)	(1.56)1.63-*1.77*-1.90(2.00)
040813210	60	(8.1)8.7-*9.3*-9.7(10.5)	(3.9)4.4-*4.7*-5.1-5.2)	(1.65)1.81-*1.95*-2.08(2.31)
05091023	38	(8.9)9.8-*10.8*-11.7(12.8)	(5.5)5.7-*6.0*-6.5(6.6)	(1.55)1.64-*1.79*-1.97(2.12)
05082715	70	(9.5)10.0-*10.9*-12.0(13.8)	(5.2)5.6-*6.1*-6.5(7.0)	(1.53)1.61-*1.78*-1.93(2.15)
06080202	27	(9.0)9.9-*10.9*-11.9(12.6)	(5.5)5.8-*6.4*-7.1(7.6)	(1.58)1.61-*1.71*-1.85(1.95)
07082624	45	(9.6)10.6-*11.2*-12.0(12.6)	(5.6)5.9-*6.4*-6.8(7.2)	(1.60)1.64-*1.77*-1.94(2.02)
07082631	40	(8.6)8.9-*9.8*-10.5(11.4)	(5.3)5.9-*6.3*-6.8(7.0)	(1.444)1.48-*1.57*-1.66(1.81)
03.03	40	(6.1)6.9-*7.6*-8.1(8.6)	(3.1)3.3-*3.7*-4.0(4.1)	(1.80)1.88-*2.05*-2.27(1.94)
03.04	30	(7.8)8.2-*8.7*-9.4(9.7)	(4.6)4.8-*5.0*-5.3(5.7)	(1.62)1.64-*1.74*-1.91(1.94)
03.05	28	(7.7)8.0-8.9-10.0(10.1)	(3.8)4.2-*4.7*-5.3(5.4)	(1.53)1.69-*1.90*-2.18(2.22)
Alnicola pallidifolia				
05082715	84	(8.6)9.0-*9.8*-10.7(11.5)	(4.9)5.5-*6.0*-6.5(7.1)	(1.37)1.48-*4.66*-1.84(2.10)
05082809	36	(9.2)9.9-*10.6*-11.4(13.1)	(5.4)5.9-*6.3*-6.8(7.1)	(1.46)1.54-*1.69*-1.85(1.86)
Merc21_10	25	(8.7)8.9-*10.4*-11.4(12.1)	(4.2)5.2-*5.7*-6.1(6.4)	(1.39)1.60-*1.84*-2.07(2.12)
10082615	54	(8.3)8.7-*9.5*-10.2(10.7)	(5.0)5.6-*5.9*-6.3(6.4)	(1.39)1.48-*1.61*-1.73(1.81)
Alnicola spectabilis				
05082811	40	(9.3)9.4-*10.0*-10.9(11.3)	(4.3)4.7-*5.0*-5.4(5.7)	(1.81)1.86-*2.00*-2.19(2.34)
09082701	34	(7.9)8.2-*8.8*-9.6(10.6)	(4.1)4.4-*4.7*-5.3(5.6)	(1.67)1.69-*1.86*-1.99(2.08)

(for details see Table 1). Pileipellis structures are described and illustrated on radial sections, additional observations on suprapellis structure are made on tangential sections (scalps). Descriptive terminology for pileus structures is adapted from Heilmann-Clausen *et al.* (1997) for pileus structures (see Moreau *et al.*, 2012). Unless otherwise specified stipitipellis structures are described from upper part of stipe, 1-3 mm under lamellae.

DNA extraction, PCR amplification and sequencing – Sporocarps were collected from multiple stands of *Alnus alnobetula* at various locations in Austria, France and Switzerland; attempts were also made to obtain sequences from herbarium material of various origins. Extraction, amplification and sequencing were processed as detailed in Rochet *et al.* (2011). Unsuccessfully amplified samples were subjected to multiple amplifications at various DNA concentrations. Sequencing was done by MilleGen (Labège, France).

Alignment and phylogenetic analysis – Sequence alignments of *Alnicola* samples, including sporocarps, mycorrhizae and sequences available on GenBank and UNITE databases were aligned using MAFFT version 6 using the LINS-i method with standard settings (Katoh & Toh, 2008) and subsequently carefully refined by eye. Tree in Fig. 1 shows was constructed from a selection of ITS and RPB2 sequences (Rochet *et al.* 2011) concatenated Tree was constructed by Bayesian inference of phylogeny using Mr Bayes v3.1 (Ronquist & Huelsenbeck, 2003) as implemented in TOPALi v2.5 (Milne *et al.*, 2009). This software chose SYM + G as the optimal substitution model. Running of Four Markov chains (one cold and three hot chains: temperature = 0.2) of 1.000.000 generations with one tree sampled per 100th has resulted in the potential scale reduction factor (PSRF) reasonably close to 1.0 for all parameters. The first 5000 trees were excluded of our analyses and Posterior probabilities of each node were obtained with 50% majority rules options. All sequences used for analyses and figures in the present article are deposited in Genbank (Table 2).

TAXONOMY

– Descriptions:

1. *Alnicola badiofusca* P.-A. Moreau, *sp. nov.* **Figs 2, 3, 6b-d**

Mycobank: MB 561708

Etymology: dark bay-brown, because of general colours and darker than *A. badia* with which it has often been confused.

Illustrated references: Moreau *in* Lamoure (1997: 138), as *Alnicola cedriolens*; Breitenbach & Kränzlin (2000: 132-133), as *A. sphagneti* and as *A. subconspersa*; Borgarino in Moreau *et al.* (2011: 35).

Ab Alnicola badia Kühner differt frequentibus purpureis coloribus, supra pileum, lamellas vel summo stipite, praesentia pleurocystidiorum a sparsis ad frequentia usque in sinus, caulocystidiis omnibus lanceolatis summo stipite, pileipellique sicut trichoderma spissum articulis omnibus incrustatis cum passim incrustationibus brunneo-flavis spisso cumulo. Pileus omnino furfuraceus, brunneohepaticus, brunneo-ruber, a brunneo-rufo ad brunneo-purpureum, hygrophanus, numquam striatus. Lamellae confertae, ab argillaceis ad brunneo-purpureas. Stipes pruinatus summo, fibrillosus plus minusve torquatus infra, tenuibus caducisque vestigiis cortinae. Caro brunneo-rubra, desiccatione subflava. Odor gravis raphanoideus. Sporae 7.8-11.1 × 4.5-6.4 µm, amygdaliformes cum summo ab acuto ad productum, irregularibus echinulatis verrucis ornatae Cheilocystidia a fusiformibus ad lageniformia basi singulariter inflata vel etiam vesiculata. Species tantum sub Alno alnobetula reperta, potius acidophila, frequens in Alpis et Corsica.

Holotypus: Gallia, Corsica meridionalis, Bastelica, Val d'Ese, sub Alno alnobetula subsp. suaveolente, 10.IX.2005, in herb. P.-A. Moreau n° 05091023 (LIP) depositus.

Portrait: the most common *Alnicola* species on acidic ground, usually abundant, easily recognized by its dense tomentum on pileus and complete absence of striation, strong raphanoid smell, and stipe coarsely pruinose-floccose at upper part when untouched. Colour variations may surprise the collector but are often observable even within a single collection.

Description: **Pileus** 0.8-2.5 (3) cm, at first rounded to obtuse with incurved margin, remaining convex a long time, only flattened to slightly

Table 2. List of sequenced collections used for molecular analysis. All sequences are deposed in Genbank. [1]: erroneously labelled "*Alnicola badia*"; [2]: as "*A.* aff. *luteolofibrillosa*"; [3]: as "MG2011-a"; [4]: as "MG2011-b"; [5]: as "MG2011-c"; [6]: as "MG2011-d"; [7]: as "MG2011-e"; [8]: as "MG2011-f".

Taxon	*Voucher n°*	*Locality*	*Host-tree*	*GenBank accession number*	
				ITS	*RPB2*
Alnicola badia Kühner	PAM03082102	F, Savoie	A.alnobet	HQ714656	HQ714797
	PAM0410120	F, Corse du Sud	A.suav	HQ714657	HQ714799
	PAM05082707	F, Corse du Sud	A.suav	HQ714664	HQ714805
	PAM05082717	A, Südtirol	A.alnobet	HQ714670	HQ714811
	PAM07082637	F, Savoie	A.alnobet	HQ714676	HQ714818
Alnicola badiofusca P.-A. Moreau[3]	PAM07082624	F, Savoie	A.alnobet	HQ714677[3]	HQ714819[3]
	PAM07082631	F, Savoie	A.alnobet	HQ714675[3]	HQ714817[3]
	PAM08082710	F, Savoie	A.alnobet	HQ714710[3]	HQ714845[3]
Alnicola aff. ***badiofusca***	PAM04101206	F, Corse du Sud	A.suav	HQ714658[1]	HQ714599[1]
	PAM08090308	F, Corse du Sud	A.suav	HQ714725[3]	HQ714857[3]
Alnicola citrinella P.-A. Moreau & A. de Haan[4]	PAM08100405	F, Orne	A.glut	HQ714733	HQ714864
Alnicola dubis P.-A. Moreau & Vidonne	PAM07.01	F, Gironde	A.glut	HQ714707	HQ714841
Alnicola escharioides (Fr. : Fr.) Romagn. [2]	PAM06102208	F, Aisne	A.glut	HQ714674[2]	HQ714815[2]
Alnicola aff. ***escharioides***[2]	PAM07080901	F, Corse	A.suav	HQ714700[2]	HQ714835[2]
	PAM08090307	F, Corse	A.suav	HQ714724[2]	HQ714856[2]
Alnicola geraniolens Courtec.	PAM07111501	F, Nord	Salix sp.	HQ714774	HQ714897
Alnicola longicystis P.-A. Moreau et al. [5]	PAM04092401	F, Haute-Savoie	A.inc	HQ714667[5]	HQ714808[5]
Alnicola luteolofibrillosa Kühner	MD09100113	F, Savoie	A.alnobet	HQ714754	HQ714884
Alnicola pallidifolia P.-A. Moreau & Peintner[6]	PAM05082715	A, Südtirol	A.alnobet	HQ714669[6]	HQ714810[6]
	PAM05082716	A, Südtirol	A.alnobet	HQ714666[6]	HQ714807[6]
	PAM05082809	A, Südtirol	A.alnobet	HQ714661[6]	HQ714803[6]
	PAM05082810	A, Südtirol	A.alnobet	HQ714665[6]	HQ714806[6]
	PAM05082810b	A, Südtirol	A.alnobet	HQ714662[6]	HQ714804[6]
Alnicola silvae-novae (D.A. Reid) Courtec.	PAM08082908	F, Savoie	A.glut	HQ714715	HQ714849
Alnicola spectabilis P.-A. Moreau & Peintner[7]	PAM06102603	A, Südtirol	A.alnobet	HQ714660[7]	HQ714802[7]
Alnicola striatula (P.D. Orton) Romagn.	PAM06102102	F, Pas-de-Calais	A.glut	HQ714672	HQ714813
Alnicola umbrina (Maire) Kühner	PAM06082704	F, Isère	A.glut	HQ714671	HQ714812
	PAM06102205	F, Aisne	A.glut	HQ714673	HQ714814
	PAM06111008	F, Nord	A.glut	HQ714704	HQ714838
Alnicola xanthophylla P.-A. Moreau *et al.* [8]	PAM07103002	F, Pas-de-Calais	A.inc	HQ714705[8]	HQ714839[8]
	PAM08082805	F, Savoie	A.inc	HQ714709[8]	HQ714844[8]

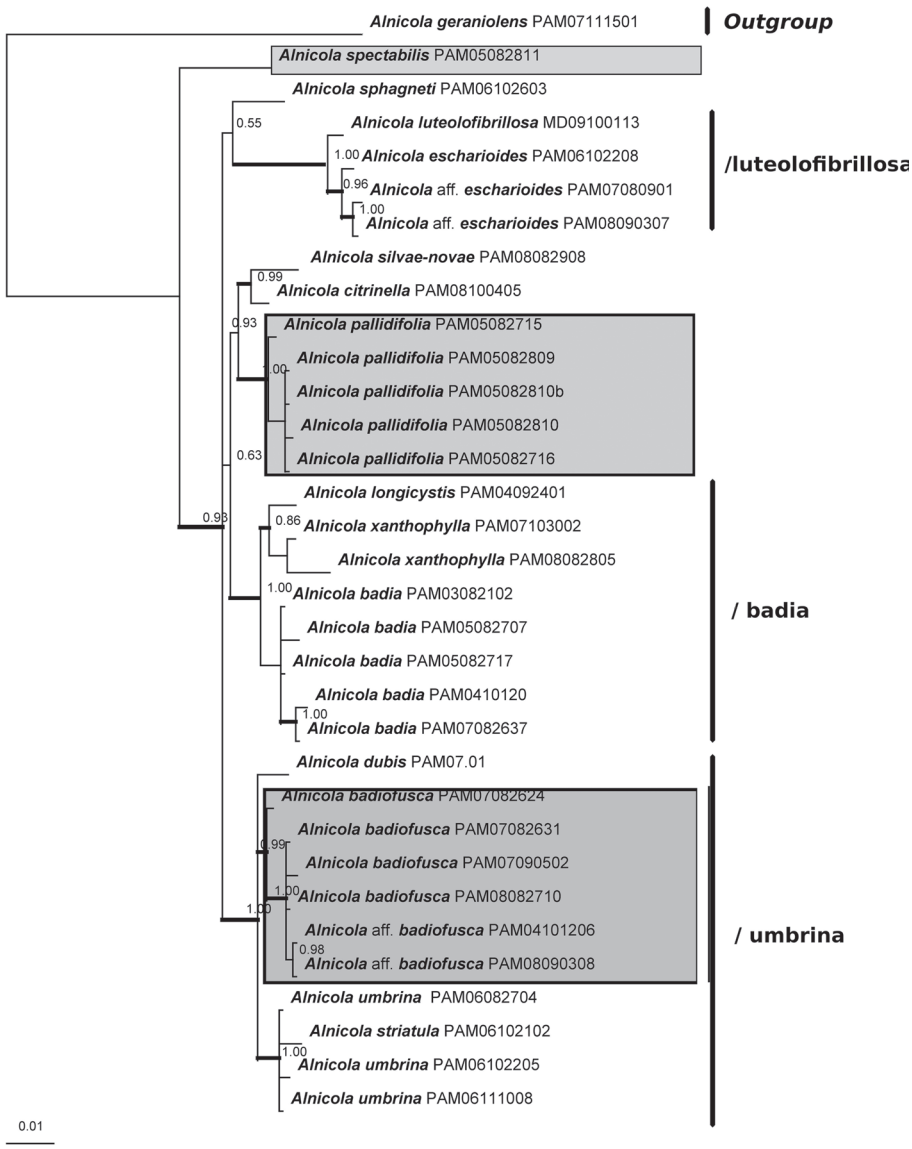

Fig. 1. Phylogenetic reconstruction of *Alnus alnobetula*-associated species of *Alnicola* in Europe. For a complete phylogeny of the subgenus see Rochet *et al.* (2011).

depressed with age, never striate (at most striolate when old and washed), at first liver-brown, reddish brown in typical forms, also dark ochre brown, foxy brown, purplish brown (around C J12), at first densely covered by pale ochre furfuraceous-squamulose tomentum making the surface apparently paler (C D54), with age glabrescent except margin remaining paler a long time; hygrophanous, slowly fading to foxy-orange, fulvous, especially at disc (C D48, M 5YR4/8, 5/8),

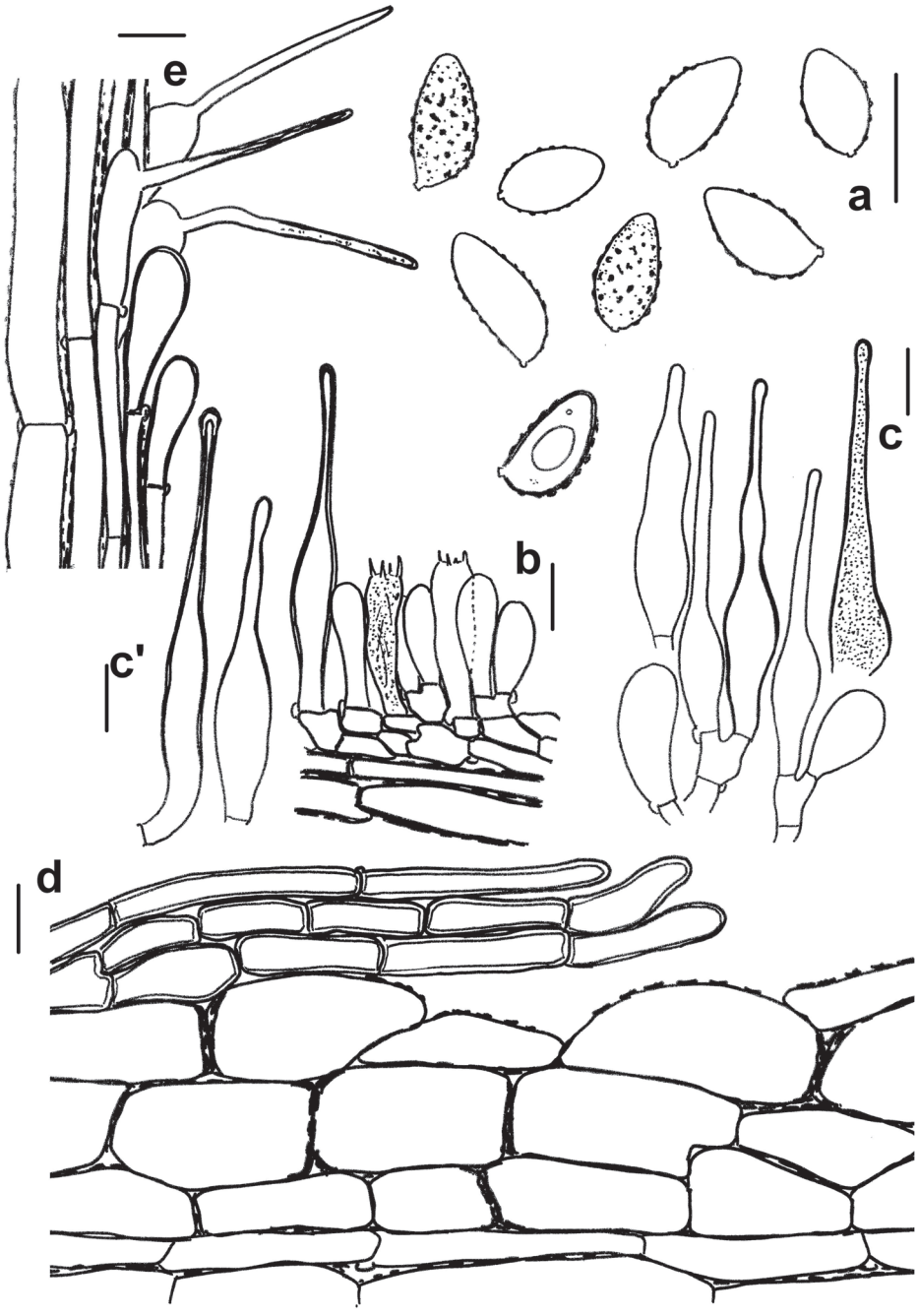

Fig. 2. *Alnicola badiofusca* P.-A. Moreau (from holotype PAM 05091023, LIP). **a**: spores; **b**: hymenium and subhymenium; **c**: cheilocystidia; **c'**: pleurocystidia; **d**: pileipellis, radial cut; **e**: stipitipellis, radial cut. Scale: bar = 10 µm.

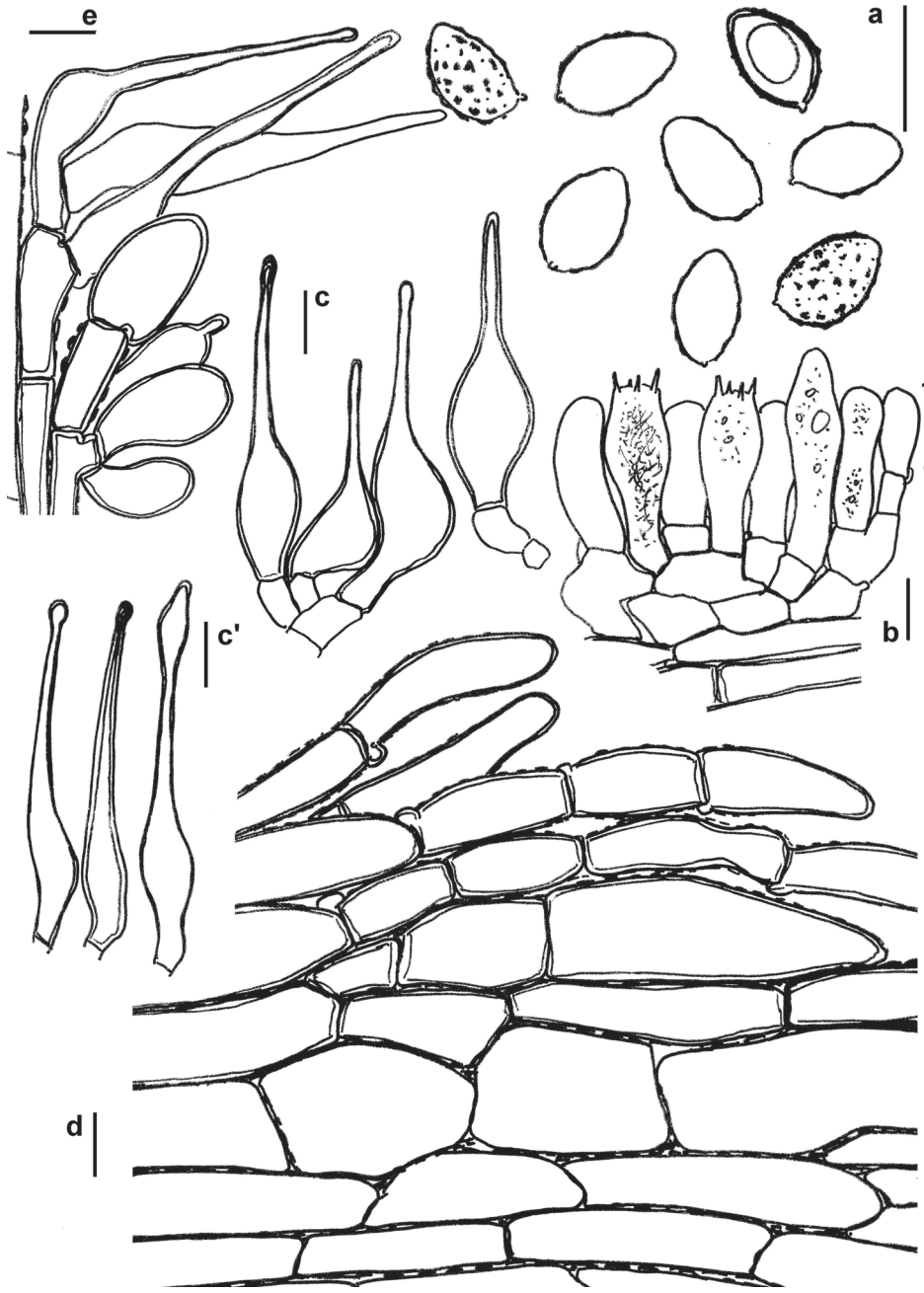

Fig. 3. *Alnicola badiofusca* P.-A. Moreau (PAM 07082631, LIP). **a**: spores; **b**: hymenium and subhymenium; **c**: cheilocystidia; **c'**: pleurocystidia; **d**: pileipellis, radial cut; **e**: stipitipellis, radial cut. Scale: bar = 10 µm.

when dry pale ochre-brown sometimes with darker disc ; when drying tomentum often erects and makes pileus uniformly paler, possibly hiding hygrophanity. **Lamellae** usually crowded, 30-36 reaching the stipe, (1) 2 series of lamellules, at first adnexed to slightly arcuate, then narrowly emarginate, at first pale argillaceous to pale ochre brown in most cases, sometimes with purplish tinges of variable intensity, when mature ochre brown, light cinnamon brown (M 5YR5/8); edge often truncate, serrulate when mature, minutely pruinose under lens. **Stipe** 2.5-4.5 (6) × 0.15-0.35 cm, cylindrical to slightly enlarged at base, when young usually entirely but sparsely floccose, distinctly pruinose-floccose 1-2 mm at apex, easily eroded and then more or less densely fibrillose-twisted, pale brown (M 2,5YR5/2) covered by white fibrils when young, rarely with slightly purplish apex, when eroded ochre-brown turning reddish brown to almost blackish from base; mycelium usually abundant at base, white, adpressed; traces of cortina only perceptible on primordia, disappearing early. **Context** reddish brown in pileus and stipe when wet, pale ochre-yellow when dry, darker in lower part of stipe to almost blackish when old; smell distinctly raphanoid; taste always mild, raphanoid.

Pileipellis a thick trichoderm, 40-120 (180) µm thick, reddish ochre-coloured, made of fascicles of chains of 4-7 hyphae, 14-42 (50) × 8-22 (30) µm, wall regularly thickened up to 0.5 µm thick, light ochre yellow, entirely minutely incrusted-punctate, some articles strongly yellow-brown incrusted; terminal articles 28-40 × 8-14 µm, very abundant, not differentiated, cylindrical, clavate to attenuate at apex. Subpellis 25-45 µm thick, hardly differentiated, made of 3-4 layers of slender parallel hyphae 7-14 µm wide, narrower towards context, not stained by KOH. Pileus context greyish ochre, made of slender hyphae 3-9 µm wide, with rough to slightly incrusted walls. **Stipitipellis** under hymenium continuously covered by dense clusters of fasciculate caulocystidia 45-80 × 6-14 µm (base) × 2-2.5 µm (apex) lanceolate with very long yellowish neck and continuously enlarged to abruptly vesiculose base, dissociated in patches 500 µm under apex, lower mixed with widely clavate erected terminations, caulocystidia very rare under the upper third of stipe length; superficial hyphae 3-6,5 µm wide, incrusted by patches. Stipe context made of slender and inflate to ampullaceous articles 3-25 µm wide, mixed with rather frequent gloeoplerous hyphae 3-7 µm wide with light yellow content in KOH. **Basidiospores** (17 coll., 743 measurements): (6.1) 7.8-*9.22*-11.1 (13.8) × (3.1) 4.5-*5.31*-6.4 (7.6) µm, Q = 1.55-*1.75*-1.99, amygdaliform with conical to somewhat elongate-subpapillate apex, rather bright yellow in KOH, not dextrinoid, uniguttulate in KOH; ornamentation as echinulate warts, sparse, 0.5-0.8 µm high, irregularly punctiform to slightly cristate, pale, almost invisible on immature spores. **Basidia** 27-35 × 9-11.5 µm, broadly clavate, hyaline when young, guttulate when mature, with many necrobasidia homogenously ochre-yellow in KOH, only lately collapsed; on PAM07082631 numerous 2- and 1-spored basidia, some even protruding with attenuate apex and guttulate content (“cystidioid!”). Subhymenium 12-15 µm thick, shortly ramose with cylindrical to ± trapezoidal articles 4-5.5 µm wide. Mediostratum 40-70 µm wide, regular, greyish-coloured, made of parallel hyphae 3-8 µm wide, rather short, cylindrical, with smooth yellowish wall. **Lamellae edge** sterile to substerile; **cheilocystidia** 32-42 (50) × 6.5-9.5 µm (base) × 2-3 µm (apex), polymorphic, mostly fusi-lageniform with usually distinct, inflate to even vesiculose base, more sparsely elongate with slender base, with variously elongate neck 8-24 (38) µm long, rarely without neck, yellowish, sometimes inflate at apex; wall yellowish, up to 0.5 µm thick. **Pleurocystidia** abundant on 200-300 µm around edge, much rarer but present up to the sinus, lanceolate, 45-75 × 5-6.5 µm (base) × 2-3.5 µm (apex), with yellow thickened wall,

neck yellowish 28-50 µm long, strongly protruding, usually with rounded to snakehead-shaped apex. **Clamps** present at all septa.

Specimens examined. FRANCE, Corse du Sud, Bocca Palmente, under *Alnus alnobetula* subsp. *suaveolens* along a stream, 12 Oct. 2004, P.-A. Moreau 04101208 (LIP); Bastelica, val d'Ese, under *Alnus alnobetula* subsp. *suaveolens*, F. Richard & P.-A. Moreau, 10 Sept. 2005, P.-A. Moreau 05091004 (LIP) and 05091023 (LIP, holotype; ZT, isotype); J. Rochet & P.-A. Moreau, 3 Sept. 2008, P.-A. Moreau 08090308 (LIP); Haute-Corse, Vizzavona, Monte d'Oro, F. Richard & P.-A. Moreau, 9 Sept. 2005, P.-A. Moreau 050907 (LIP); Casamacchioli, above the Lac de Nino, *Alnus alnobetula* subsp. *suaveolens*, 6 Sept. 2007, herb. P.-A. Moreau 07090502[1] (LIP); Savoie, Bozel, above La Rosière, under *Alnus alnobetula*, 16 Sept. 1961, R. Kühner (G, "*A. phaea* de 61"); Champagny, aulnaies des Caves de la Plagne, 17 Sept. 1961, R. Kühner (G, "*A.* de 61", 7 packs numerated from A to G, all conspecific); Pralognan-la-Vanoise, Aug. 1969, R. Kühner PR69.210 (G); Bourg-Saint-Maurice, Arc 1800, above the golf area, dense thickets of *Alnus alnobetula* along a stream, 7 Sept. 1993, P.-A. Moreau 93090701[2] and 93090703 (LIP); 23 Aug. 2003, P.-A. Moreau 03082303 (LIP); under dense thickets of *Alnus alnobetula* on rich soil, B. Buyck, 23 Aug. 2003, P.-A. Moreau 03082301 (LIP); 23 Aug. 2003, P.-A. Moreau 03082307 (LIP); ruisseau du Villard, basic watercourse under *Alnus alnobetula*, 26 Aug. 2006, P.-A. Moreau 06082608 (LIP); 26 Aug. 2007, P.-A. Moreau 07082624 and 07082631 (LIP); Landry, Barmont, under *Alnus alnobetula* subsp. *alnobetula* on rich mineral soil, 26 Aug. 2007, P.-A. Moreau 07082631 (LIP); Peisey-Nancroix, tourbière des Lanches, under a single *Alnus alnobetula* along a mesotrophic peat bog, J.-C. Déiana & P.-A. Moreau, 13 Aug. 2004, J.-C. Déiana n° 040813-2140 (LIP). SWITZERLAND, Gräubunden, Bergün, Palpuogna lake, under *Alnus alnobetula* on wet siliceous soil along a stream, 16 Aug. 2003, P.-A. Moreau 03081603 and 03081605 (LIP); 2 Sept. 2006, P.-A. Moreau 06090201 (LIP); 28 Aug. 2005, P.-A. Moreau 05082808b (LIP).

Ecology and distribution: *Alnicola badiofusca* is the most frequently observed species under *Alnus alnobetula*, especially in humus-rich sites on acidic substrate and wet conditions, usually together with *Lactarius alpinus* Peck and *Alpova alpestris* P.-A. Moreau & F. Richard; apparently absent on schist and mineral-rich places where it is replaced by *A. badia*, more tolerant to basic conditions. Alps, Corsica; probably common throughout the distribution area of its host.

Observations: *Alnicola badiofusca* is characterized by distinctly and uniformly squamulose pileus, usually dark-coloured, and the conspicuous amber-yellow pigment forming zebras and thick patches on broad hyphae of subpellis. On scalp the very large articles of subpellis are dominant, often limoniform-mucronate, only very partially covered by suprapellis in mature specimens. Otherwise high variability regarding morphological characters and spores can make its identification difficult.

Variability of the species – Spores usually show a distinct and sometimes thick ornamentation. Their dimensions and shape are surprisingly variable amongst specimens (on spore prints), but we were unable to find any morphological variation in correlation with spore variability: some collections

1 Collection illustrated in Moreau *et al.*, 2011: 35.

2 Collection illustrated in Lamoure, 1997: 28 (as "*Alnicola cedriolens*").

have predominantly narrow to almost fusiform spores (Fig. 2), other broadly amygdaliform with attenuate apex (*Inocybe*-like; Fig. 3). On hymenium spore polymorphism is often spectacular, with many macrospores and elongate teratological spores. Cheilocystidia are remarkably polymorphic, most with abruptly inflated base, but a part fusiform without neck, or cylindrical with or without appendage (somewhat reminiscent of those of *A. luteolofibrillosa*, even more polymorphic); pleurocystidia are sometimes rare but usually easily detected by their bright yellow neck protruding from hymenium, frequently with inflated to rounded apex (Fig. 2c').

Lilaceous tinges can be remarkable in some specimens (Fig. 6b), and also exist in the very close species *Alnicola umbrina* (Moreau, 2004) and *A. scolecina sensu* Romagnesi (1942), associated with *Alnus glutinosa* and *A. incana*. The presence of such tones makes the identification of these taxa easy, but it must be kept in mind that they are inconstant. Usually lilac-tinged basidiomata are found apart from non-lilac specimens of the same species, which suggests that this variation might be supported genetically at a population level.

Another common feature of *A. umbrina* and *A. badiofusca* is their abundance in their environment (especially on acidic substrate), which suggests a high competitiveness of this modern lineage (see Rochet *et al.*, 2011). ITS sequences of *A. badiofusca* are strictly identical to those of *Alnicola umbrina*, and it is impossible to separate both species with this single allel (if host identity is unknown). However (Rochet *et al.*, 2011) other genes studied (GPD, RPB2 and V9) confirm a genetic difference between populations from *Alnus alnobetula* (*A. badiofusca*) and those from *Alnus glutinosa*, *A. incana* and *A. cordata* (*A. umbrina*), in accordance with macro- and microscopical characteristic (especially absence of veil traces, pileus not striate and completely scurfy, smaller and non-fusiform spores less than 11.5 µm long in *A. badiofusca*). It is a surprise that so morphologically and ecologically differentiated species are genetically so weakly distinct; more populations should be sequenced for RPB2 outside our collecting areas in order to confirm the strict host-specificity hypothesized here.

Extralimital collections – Three collections from Corsica, of atypical ecology (peebles along streams) and devoid of reddish or purplish tones (and therefore reminiscent of *A. badia*; see Fig. 6d), are doubtfully referred to *A. badiofusca*; ITS and RPB2 sequences (PAM04101206, PAM05091004 and PAM08090308) differ from typical sequences of *A. badiofusca* by 1 and 4 substitutions on ITS and RPB2 respectively. More observations are needed on such collections which might represent a different, sister species.

2. *Alnicola pallidifolia* P.-A. Moreau & Peintner, *sp. nov.* **Figs 4, 6e-f**

Mycobank: MB 561709

= *Alnicola subescharoides* Kühner *in sched*., *pro parte*.

= *Alnicola melinoides sensu* Kühner (1926), *sensu* Jamoni (2008: 160-162).

Etymology: with pale lamellae (a distinctive character in young specimens).

Species notata pileo bicolori: ocraceo-flavo in centro, pallide luteo ad marginem, haud striato, haud hygrophano, squamuloso deinde glabro, in vetustate tessulato; lamellis albidis initio; stipite haud pruinato; sapore dulci; absentia pleurocystidiorum caulocystidiorumque. Sporae 8.9-11 × 5.5-6.4 µm, amygdaliformes apice acuto sed numquam umbonato, verrucis punctiformibus irregularibusque. Cheilocystidia lanceolata basi lageniformi. Pileipellis sicut epithelium spissum articulis globosis incrustatis, superatum

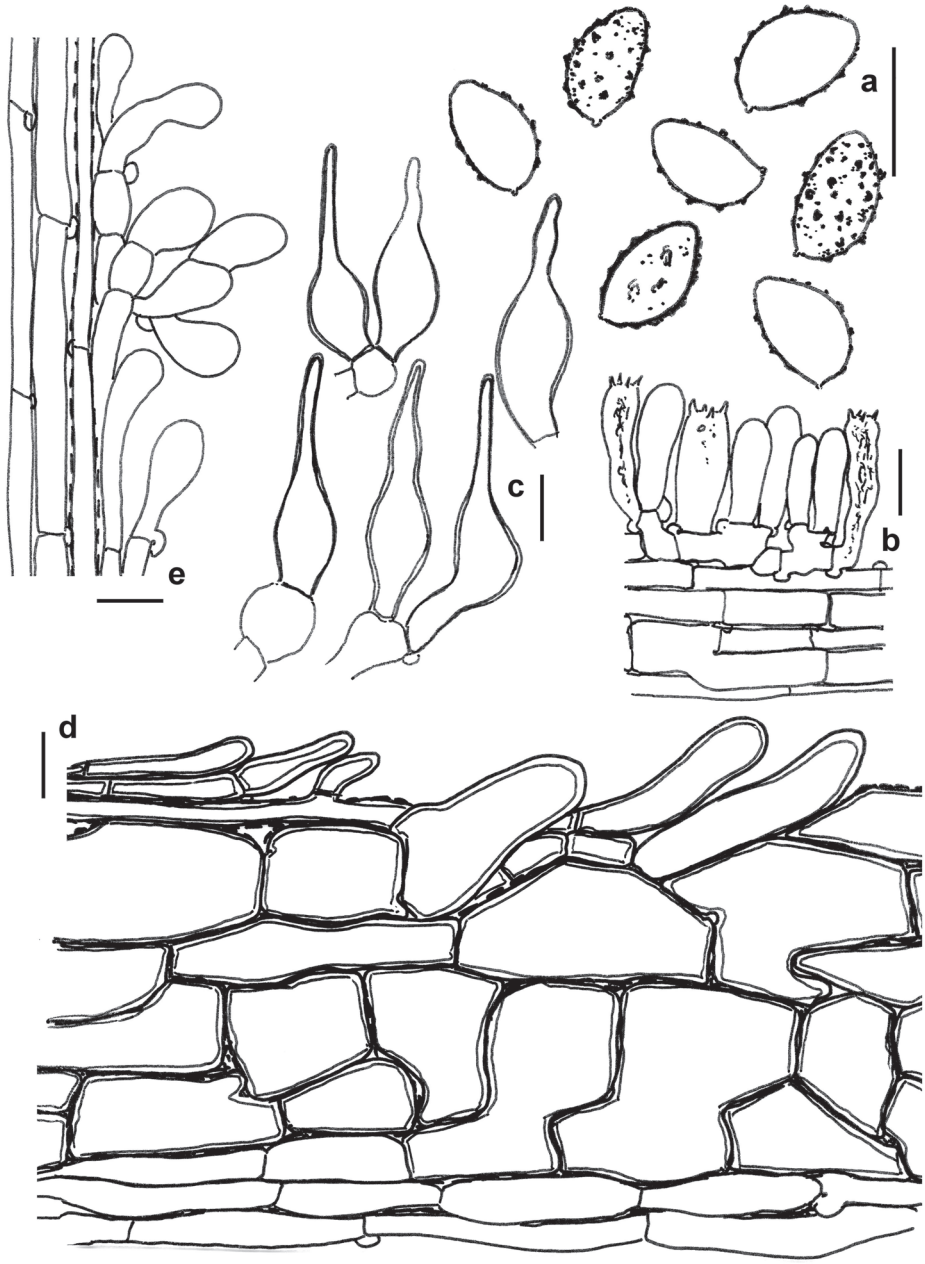

Fig. 4. *Alnicola pallidifolia* P.-A. Moreau & Peintner (from holotype PAM 05082809, LIP). **a**: spores; **b**: hymenium and subhymenium; **c**: cheilocystidia; **d**: pileipellis, radial cut; **e**: stipitipellis, radial cut. Scale: bar = 10 µm.

stratis intermissis hypharum cylindricarum ab obscure flavis ad rubras. Species reperta tantum sub Alnus alnobetula, super substratum minerale.

Holotypus: Austria, Obergurgl, 28.VIII.2005, sub Alno alnobetula subsp. alnobetula, in herb. P.-A. Moreau n° 05082809 (LIP) depositus. Isotypi in herb. IB n° 20050250, ZT depositis.

Portrait: a dirty-looking, unattractive species, devoid of veil, with pale colours except at disc (margin distinctly paler), characterized by an early cracked pileus surface, microscopically easily separated from *A. badia* by absence of necked caulocystidia and pleurocystidia.

Description: **Pileus** 1-2,5 cm, hemispherical to convex-obtuse then flattened, without umbo, first dull fulvous-ochre at disc (duller than M 10YR5/4), with pale yellowish margin, never striate, densely covered by imbricate small yellowish-white squamules when young, early glabrescent and almost smooth, only fibrillose-pruinose at margin when old, often cracked at disc with age, not hygrophanous, drying by opacification from margin, when dry foxy-ochre at disc, pale ochre to somewhat olivaceous elsewhere. **Lamellae** crowded, almost free then widely emarginated when mature, broad, at first whitish, then gradually pale yellowish, finally rather pale rusty ochre; edge convex, white, smooth to minutely pruinose. **Stipe** 2.5-5 × 0.1-0.2 cm, equal, fibrillose-floccose at apex, not pruinose, below slightly fibrillose to somewhat wicked in some specimens, hyaline whitish to pale yellowish, early darkening into ochre brown from basis, without trace of veil. **Context** pale to ± greyish ochre in pileus, dirty brown in stipe base, a bit elastic; smell strongly earthy-raphanoid (of *Lepista nuda* according to Kühner, unpublished notes on coll. 63.325, G); taste raphanoid, mild to exceptionally bitterish.

Pileipellis a hyphoepithelium made of a *thin suprapellis* 10-25 µm thick, especially towards margin, of 1-3 layers of slender cylindrical hyphae 3-6 µm wide with smooth to incrusted wall, deep yellow-ochre to reddish ochre in KOH, often strongly collapsed with age or at disc and then indistinctly covering the subpellis like a yellow-brown mucus, more persistent towards margin with numerous terminal articles 25-35 × 7-14 µm, cylindrical to slightly clavate, wall reddish-ochre in KOH, 1 µm thick, easily seen on scalp. Subpellis 70-100 µm thick, strongly developed especially towards disc, of 4-6 layers of short, cylindrical to subglobose or puzzle-shaped articles 10-25 (30) µm, more isodiametric towards disc, cylindrical-elongate towards margin, with *yellow incrusted wall up to 1.5 µm thick*. **Pileus trama** pale, made of slender and inflate articles mixed, wall 0,5-1 µm thick, smooth, with locally incrusted parts of hyphae (especially septa). Gloeoplerous hyphae rare, a few observed at mid thickness, tortuous, 3-6 µm wide, deep yellow with thick wall (2 µm thick), reddish-brown in melzer on fresh material (hardly visible on exsiccatum). **Stipitipellis** at very apex with some clusters of basidia and spindle-shaped cystidia (hymenium), below with sparse clusters of caulocystidia articulate, globose to clavate, 11-28 × 9-13 (16) µm, not appendiculate, mixed with long cylindro-clavate articles, with yellow smooth wall up to 1 µm thick, in lower half with only long clavate and adpressed to mixed terminal hyphae issued from mycelial hyphae. **Basidiospores** (4 collections, 200 measurements) : (8.3) 8.9-***9.95***-11.0 (13,1) × (4.9) 5.5-***5.96***-6.4 (7.1) µm, Q = 1.50-***1.67***-1.86, amygdaliform with acute but not distinctly umbonate apex, light yellow in KOH and melzer, not dextrinoid, with low ornamentation less than 0.2 µm high, irregularly punctuate to almost echinulate by place, somewhat darker in melzer, mostly not equally distributed on the spores and especially developed on back side, warts punctiform, not confluent. Content homogenous to granular, not guttulate in KOH. **Basidia** 22-32 × 6.5-8.5 µm, shortly cylindrical, sessile or with more or less rooting base,

4-spored (a few 2-spored seen), at first hyaline then yellowish-guttulate when mature, necrobasidia abundant with yellow-brown content. Subhymenium weakly developed, 6-9 µm thick, ramose with slender ± furcate or contorted hyphae. Hymenial trama (mediostratum) regular, pale yellowish a bit more ochre by places, made of cylindrical hyphae 3.5-9 µm wide, with yellowish wall up to 1 µm thick, smooth, a few with deep ochre-yellow wall. **Lamella edge** sterile; **cheilocystidia** spindle-shaped with ampullaceous base, 26-40 × 8.5-9.5 µm (base) × 2.5-3 µm (neck), often septate at base, issued from a vesicular article up to 9 µm wide or catenulate by 2-3, neck usually abruptly differentiated from base, conical, sometimes inflate at base, 6-18 µm long, wall thickened up to 0,5 µm and yellowish especially in base, some entirely ochre-yellow and ± collapsed. **Pleurocystidia** completely absent; cheilocystidia not transgressing on sides more than 10-20 µm far from the edge. **Clamps** present at all septa.

Specimens examined. AUSTRIA: Tirol, Obergurgl, under *Alnus alnobetula* on schist, U. Peintner, 27 Aug. 2005, P.-A. Moreau 05082715 and 05082717 (LIP); M. Floriani, 27 Aug. 2005, P.-A. Moreau 05082716 (LIP); 28 Aug. 2005, P.-A Moreau 05082809 (LIP, holotype; IB and ZT, isotypes), 05082810 and 05082810b (LIP); U. Peintner & P.-A. Moreau, 29 Aug. 2006, P.-A. Moreau 06082902 and 06082903 (LIP); FRANCE: Alpes-Maritimes, Saint-Martin-Vésuby, Parc National du Mercantour, on a dry calcareous slope with sparse *Alnus alnobetula* shrubs, J.-C. Déiana & P.-A. Moreau, 21 Oct. 2003, P.-A. Moreau 03102186 (LIP); Savoie, Bozel, below the Dent-du-Villard, 31 Aug. 1927, two fragmented specimens, R. Kühner V85 p4 (G, as "*Naucoria melinoides*!"); not precised, 13 Sept. 1927, R. Kühner III 98bis (G, as "*Naucoria melinoides*"); Saint-Bon-Tarentaise, Prés de Saix, 11 Sept. 1958, R. Kühner (G, "*A. phaea*" in sched.); Pralognan-la-Vanoise, Sentier Manette, in and on mosses under *Alnus alnobetula*, 5 Sept. 1964, R. Kühner 11-28 (G); 15 Sept. 1963, R. Kühner 63.325 (G); 1964, herb. R. Kühner 64.20 (G); Beaufort, cormet d'Arèches, 26 Aug. 2010, P.-A. Moreau 10082615 (LIP). SWITZERLAND: Graubünden, Bergün, above the Palpuogna lake, under *Alnus alnobetula* on acidic ground along a stream, 14 Aug. 2003, P.-A. Moreau 03081405 (LIP); 3 Sept. 2004, P.-A. Moreau 04090301 (LIP); *idem*, wet mineral slope under *Alnus alnobetula* and *Pinus cembra*, 3 Sept. 2004, P.-A. Moreau 04090302 (LIP).

Ecology and distribution: An uncommon species, of scattered distribution, but gregarious and abundant in its localities; apparently typical of *Alnus alnobetula* stands developed on mineral, non-calcareous substrates (schist, gypsum). Known from France (Northern and Southern Alps, Corsica), Austria, Switzerland, and Northern Italy (Jamoni, 2008).

Observations: *Alnicola pallidifolia* is easily overlooked because of lack of macroscopic peculiarities, but is easily distinguished from *A. badia* and *A. badiofusca* which can co-occur on the same localities (Fig. 6e-f). Pileus of *A. pallidifolia* is bicolour like *A. badia* with same dirty brownish tones, but not hygrophanous. Surface of pileus excoriates early and often forms a crown at disc, a character related to the mainly cellular pileipellis when *A. badia* and *A. badiofusca* have a dense trichodermic structure and becomes squamulose instead of cracking with age. Nevertheless in R. Kühner's unpublished notes (G) *A. badia* and *A. pallidifolia* were confused under various provisional names, and indeed DNA analyses were a great support for ascertaining the differences between both species.

Absence of pleurocystidia and caulocystidia in *A. pallidifolia*, and large spores with blunt apex and contrasted ornamentation in melzer are the most useful characters for a quick identification, but *A. pallidifolia* can already be

suspected in the field by its brittle consistency, pileus margin often eroded and fimbriate, and a contrast between pale young specimens and old, ± reddish-brown specimens within the same collection. In all locations known by us the species fruits abundantly and dominates all other species of *Alnicola*.

Old specimens can evoke old specimens of *A. luteolofibrillosa*, immediately recognized by its strongly bitter taste (mild to occasionally bitterish in *A. pallidifolia*) and different shape of cheilocystidia. It has also been confused by Kühner (1926) and Jamoni (2006) with a very similar species: *A. citrinella* P.-A. Moreau & A. de Haan (de Haan & Moreau, 2012), under the name *Alnicola melinoides*; *A. citrinella* is a common species under *Alnus* sect. *Alnus* in Europe, not confirmed under *Alnus alnobetula*, characterized by a strongly bitter taste and cheilocystidia with a vesiculose body and long neck.

Note on Naucoria cedriolens *Bresinsky* – Because no original material is available at M (D. Triebel, comm. pers.; Moreau, 2005; Moreau *et al.*, 2012) and seems to have been lost (A. Bresinsky, comm. pers.), this taxon is today only documented by the protologue (Schmid-Heckel, 1985: 162-163). Some aspects of this description evoke *A. pallidifolia*: our last collection (PAM10082615) showed a weak cedroid smell and bitterish taste, not perceived in our abundant Austrian collections, and morphological description is compatible with *A. pallidifolia* (pale colours, pileus not hygrophanous, not striate). However the following points are not compatible with our observations: 1) Lamellae "*ochraceae vel pallido-brunneae*" (only lately pale ochre in *A. pallidifolia*); 2) pileus is described smooth to fibrillose but not typically cracking as *A. pallidifolia*; 3) spores cited as "*polymorphic*" but anyway much smaller, 8-10 (11) × (4) 4.5-5.5 (6) µm (in average 10.6 × 6.3 µm in *A. pallidifolia*); 4) caulocystidia are cited rarely similar to cheilocystidia (exceptional at the very apex in *A. pallidifolia*). A verification of presence of pleurocystidia and more precise information on pileipellis structure are crucial information missing in the protologue. We currently interpret this description as based on an old collection of *A. badia*, already dried out when studied (Moreau *et al.*, 2012), but we cannot exclude other interpretations. Schmid-Heckel (1985) only cites three "*Naucoria*" species under *Alnus alnobetula*: *N. cedriolens*, *N. escharoides*, and *N. scolecina*; the most common species under *Alnus alnobetula* being *Alnicola badia*, *A. luteolofibrillosa* and *A. badiofusca* we suspect that most of these collections should be referred to these species, however we have not attempted to revise this material.

3. *Alnicola spectabilis* P.-A. Moreau & Peintner, *sp. nov.* **Figs 5, 6g-h**

Mycobank: MB 561710

= *Alnicola pseudosalabertii ad int.* in Rochet *et al.*, *BMC Evol. Biol.* 11: 40.

Species notata aspectu praecipue robusto, pileo convexo obscure brunneo-rubro, subtiliter furfuraceo, lamellis albidis initio, stipite pruinoso apice et fibrilloso infra sine vestigio veli, odore haud raphanoideo, sporis pallidis subtiliter punctatis, et absentia pleurocystidiorum. Sporae 8.2-10.9 × 4.4-5.4 µm, anguste amygdaliformes apice attenuato. Cheilocystidia breviter a lageniformibus ad fusiformia. Pileipellis sicut epithelium spissum superatum aliquibus hyphis brevibus levibusque, incrustatis vel contento subflavo. Caulocystidia sparsa multis pilis apice mixta. Species reperta tantum sub Alnus alnobetula, supra schistos, rarissima in Alpis.

Holotypus: Austria, Obergurgl, sub Alno alnobetula subsp. alnobetula, 28.VIII.2005, in herb. P.-A. Moreau n° 05082811 (LIP) depositus. Isotypi in herb. IB n° 20050251, ZT depositis.

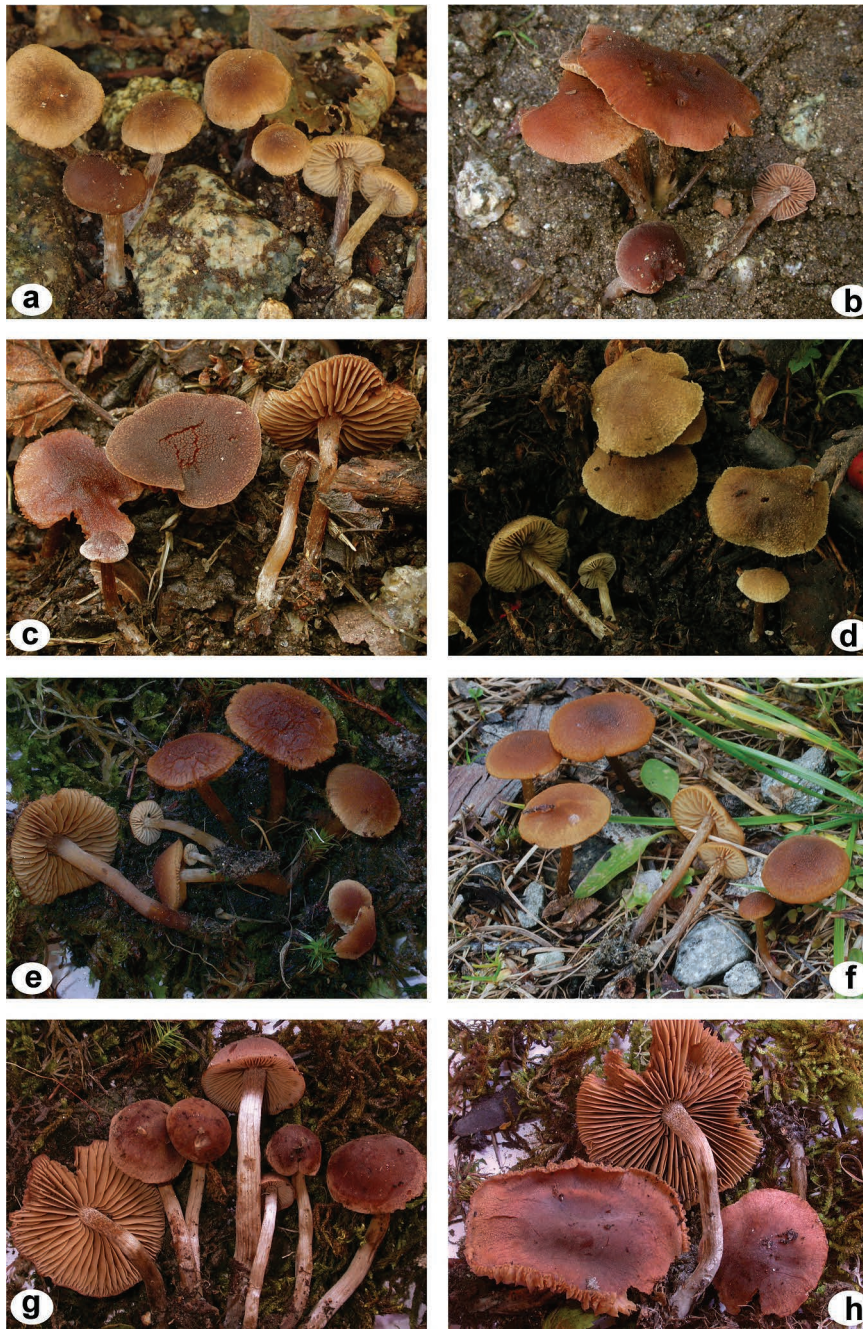

Fig. 5. Basidiomata *in situ*. *Alnicola badia* **a**: PAM07082637. *Alnicola badiofusca*. **b**: PAM 05091023 (holotype); **c**: PAM 050907. *Alnicola* aff. *badiofusca.* **d**: PAM 05091004. *Alnicola pallidifolia*. **e**: PAM 05082809 (holotype); **f**: PAM05082716. *Alnicola spectabilis*. **g-h**: PAM05082811 (holotype). Photos P.-A. Moreau, except f: M. Floriani.

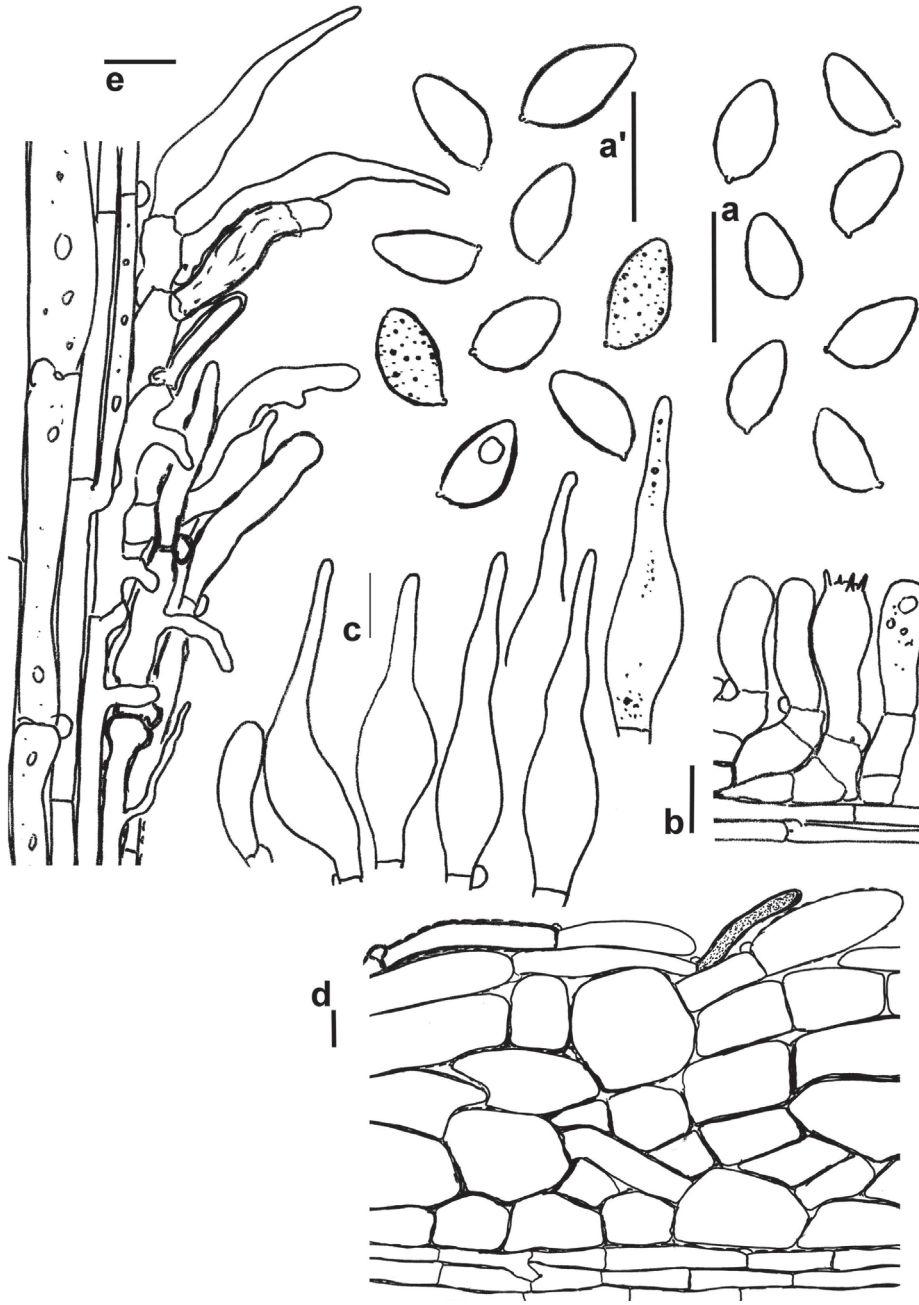

Fig. 6. *Alnicola spectabilis* P.-A. Moreau & Peintner. (from holotype PAM 05082811, LIP). **a**: spores; **b**: hymenium and subhymenium; **c**: cheilocystidia; **d**: pileipellis, radial cut; **e**: stipitipellis, radial cut. Scale: bar = 10 µm.

Etymology: "remarkable", because of its unusually robust habit in the genus. (*Nota bene*: the provisional name "*Alnicola pseudosalabertii*" initially proposed was finally changed because *A. salabertii* to which it refers is unknown to most mycologists).

Portrait: a relatively stout species with fleshy, warm red-brown pileus, not striate, whitish lamellae at first, and non-raphanoid smell.

Description: **Pileus** 2-6 cm, globose then hemispherical to convex-obtuse, never flattened, without umbo, first dark ferruginous brown, dark red brown (M 5YR2/2) with a distinctly lighter margin, pale ± flesh-coloured on 2-3 mm, minutely furfuraceous at disc and gradually more distinctly towards margin, hygrophanous slowly fading from disc to pale foxy-ochre, slightly wrinkled at disc on larger specimens; margin slightly excedent, without trace of veil. **Lamellae** crowded, 2-3 series of lamellules, almost free then deeply emarginated, white at first then clay ochre grey from the stipe, at last rather bright rusty ochraceous brown; edge serrrulate, whitish. **Stipe** 4-9 × 0,2-0,4 cm, flexuose, equal, densely pruinose at apex, strongly fibrillose-striate below, without veil; at first grey by the fibrillum, then brownish ochre by detersion, entirely so when old; mycelium pale yellowish grey, araneous, adpressed on the stipe up to 3 cm from base. **Context** dark grey-brown on pileus, more ochraceous in stipe, then dark brown with age, pale ochre when dry. Smell fungoid, somewhat earthy, not raphanoid. Taste fungoid, mild.

Pileipellis a hyphoepithelium made of a thin suprapellis of 1-2 discontinuous layers of cylindrical repent hyphae, 4,5-16 µm wide, smooth to incrusted by red-brown pigment, or filled with ± dark yellow pigment in KOH. Subpellis 50-70 µm thick, made of polygonal, subglobose to shortly cylindrical hyphae 12-60 × 7-35 µm, rather thin-walled, with thick red-brown incrustations in KOH. **Pileus trama** pale with yellowish zones, made of cylindrical hyphae 4,5-16 µm wide, wall pale yellow and smooth, some with pale yellow incrustations in KOH. **Stipitipellis** at apex made of fascicles of ± erected superficial hyphae, tortuose-cylindrical often diverticulate, 3-7,5 µm wide, some vermiform 1-1,5 µm wide, locally embedded in an ochre-brown resinoid matrix slowly dissolved in KOH; superficial hyphae smooth, often with guttulate content; caulocystidia sparse to rare, 35-55 × 8-11 µm (base) × 1,8-2,5 µm (apex), with attenuate neck and inflate base, wall yellowish 0,3-0,5 µm thick. Stipe context made of parallel hyphae 4-25 µm wide, cylindrical to inflate, pale, wall pale yellow, granulose-incrusted, locally thickened at septa; gloeoplerous hyphae conspicuous, 4-7 µm wide. **Basidiospores** (2 collections, 84 measurements) (7,3) 8,0-***9,29***-10,6 (11,3) × (3,8) 4,2-***4,80***-5,3 (5,7) µm, Q = 1,79-***1,94***-2,07, narrowly amygdaliform to almost fusiform with acute but not umbonate apex, pale yellow in KOH, slightly dextrinoid in mass, verruculose-spinulose with minute punctiform warts of uniform distribution; epispore not distinct; content usually with 1-2 droplets when mature (in KOH). **Basidia** 19-30 × 7-9 µm, shortly clavate with ± elongate base, colourless, guttulate before maturity, pale yellow after spore discharge; necrobasidia absent. **Subhymenium** distinct, 8-15 µm thick, pseudo-parenchymatous, made of polygonal articles 5-7 µm wide. **Hymenial trama** with a relatively distinct hymenopodium 8-10 µm thick, slightly dextrinoid, made of 3-5 µm wide hyphae; mediostratum regular, pale, made of 3-25 µm wide hyphae, cylindrical-inflate, smooth. **Lamella edge** sterile; **cheilocystidia** fusi-lageniform with progressively attenuate neck and ± inflate base, 32-38 (45) × 6,5-8,5 µm (base) × 1,8-2 µm (apex), wall thickened up to 0,3 µm, colourless; content often guttulate in neck, colourless. **Pleurocystidia** completely absent, cheilocystidia not transgressing on sides. **Clamps** present at all septa.

Material studied : AUSTRIA, Tirol: Kellerjoch, under *Alnus alnobetula*, herb. M. Moser n° IB19820194 (IB)[3]; Obergurgl, a group of 10 subcespitose basidiomata under *Alnus alnobetula* on schists, 28 Aug. 2005, P.-A. Moreau 05082811 (LIP, holotype; IB and ZT, isotypes). FRANCE, Savoie, Beaufort, Cormet d'Arèches towards Lac des Fées, 2 very young basidiomata on schists in a dense sloppy *Alnus alnobetula* thicket, J.-P. Vidonne, 27 Aug. 2009, P.-A. Moreau 09082706 (LIP); 1 mature basidiome, C. Hugouvieux, 27 Aug. 2009, P.-A. Moreau 09082701 (LIP). ITALY, Trentino, Passo Rolle, under *Alnus alnobetula*, M. Moser IB19880234 (IB)[4].

Ecology and distribution: only known from five localities in Savoy, Tirol, and Slovenia (mycorrhizal sampling, L. Tedersoo comm. pers.). Two sites are dense shrubs of *Alnus alnobetula* subsp. *alnobetula* on schist, on unstable, wet and mineral-rich substrate; in these stands *Lactarius lepidotus* is the most abundantly fruiting fungus. *Alnicola spectabilis* seems to be a very rare species, never abundant, but easy to recognize; our first collection (PAM05082811) was a spectacular fascicle of ten very large sporocarps.

Observations: *Alnicola spectabilis* is the largest and most fleshy *Alnicola* species known to us (Fig. 6g-h). By its colours and opacity it is reminiscent of *Alnicola salabertii*, a species only reported with *Alnus cordata*, with strongly bitter taste and pleurocystidia (Moreau & Garcia, 2005). In the field it may remind one of *A. badiofusca*, but differs : 1) morphologically by a less scurfy pileus, thicker stipe pruinose at apex (furfuraceous in *A. badiofusca*), almost white lamellae at first, 2) microscopically by absence of pleurocystidia (abundant around the edge in *A. badiofusca*), narrower and paler spores, and especially a pileipellis without chains of articles, cellular if observed on scalp, and superficial hyphae sparse, most with strongly incrusted brownish wall. In the field the stipe only minutely pruinose towards apex differs from the coarsely pruinose-floccose stipe of *A. badiofusca* covered by caulocystidia at apex. *Alnicola badiofusca* has never been found in the few localities known for *A. spectabilis*.

– Identification key to *Alnicola* species reported under *Alnus alnobetula* in Europe:

1a. Cheilocystidia only or mainly spindle-shaped with distinct neck. Lamellae edge not floccose under lens, not weeping. Pileus surface smooth to slightly wrinkled. Stipe fibrillose or only floccose at apex. Smell never farinaceous . . 2

1b. Cheilocystidia cylindrical to somewhat club-shaped, without neck. Lamellae edge coarsely pruinose to floccose under lens, weeping when fresh. Pileus surface furfuraceous, floccose or excoriated, never strictly smooth under lens. Stipe entirely floccose-pruinose (look at untouched specimens!). Smell sometimes farinaceous "*Alnicola*" subgen. *Submelinoides* (not treated here; see Moreau *et al*., 2011: 36). . . . . .

2a. Veil present, often abundant, fibrillose or floccose on stipe and often hanging from margin of pileus. Taste very bitter. Gill edge heteromorphous with fusiform to clavate ± mucronate cheilocystidia mixed with typically spindle-shaped ones. Very common under *Alnus alnobetula*. . . . . *Alnicola luteolofibrillosa sensu lato* (not treated here)

3 Cited by Moreau *et al.* (2006b) as "*Alnicola* cf. *sphagneti*".

4 Cited by Moreau *et al.* (2006b) as "*Alnicola* cf. *suavis*".

2b. Veil completely absent or inconspicuous even on primordia. Taste always mild. Usually fusiform cheilocystidia with ± long neck (occasionally basidia) on edge 3

3a. Pileus hygrophanous, striate or not, strongly furfuraceous all over when fresh or drying; on scalp a trichodermial suprapellis of long chains of catenulate articles. Caulocystidia lanceolate at least on upper third, mixed or not with rounded to clavate articles. Pleurocystidia usually present on faces at least 100 µm from gill edge 4

3b. Pileus not hygrophanous, not striate, slightly furfuraceous, at most towards margin when drying, excoriate towards disc when mature; on scalp of predominant cellular aspect, only partly covered by slender cylindrical articles. Pleurocystidia completely absent more than 20-30 µm from the edge 5

4a. Superficial hyphae of pileipellis smooth to only locally incrusted. Pileus typically bicolour, hygrophanous, margin pale ochre to pale yellowish, disc reddish-brown when fresh, old specimens yellowish and ± striate with age. Caulocystidia partly lanceolate mixed with catenulate subglobose articles. Lamellae whitish to yellowish, then cinnamon-brown. Smell weakly raphanoid to resinoid or slightly fruity-aromatic. Spores ovoid to slightly amygdaliform with obtuse apex, 7.5-10.5 x 4.5-6.5 µm, Q = 1.51-1.79 . . . . . *Alnicola badia* (see Moreau *et al.*, 2012)

4b. Superficial hyphae of pileipellis entirely and regularly incrustate-punctate, in subpellis with coarse masses of pigment. Caulocystidia spindle-shaped to lanceolate, abundant on top of stipe. Pileus uniformly foxy-ochre, foxy brown, rust-brown, reddish-brown, purplish-brown, monochrome or narrowly paler at margin, never striate. Lamellae cinnamon-brown to purplish at first, then rusty brown. Smell strongly raphanoid. Spores with attenuate to acute apex, 7.8-11.1 × 4.5-6.4 µm, Q = 1.55-1.99. . . . . *Alnicola badiofusca*

5a. Large fleshy species, stipe > 3 mm diam. Pileus dark ferrugineous-brown to red-brown, lighter at margin. Caulocystidia present at apex, mixed with numerous slender (non inflate) erected hyphae. Spores 8.0-10.6 × 4.2-5.3 µm, Q = 1.79-2.07, pale, narrowly amygdaliform with acute apex, minutely punctuate . . . . . *Alnicola spectabilis*

5b. Small brittle species, stipe 1-2 mm diam. Pileus usually bicolour, disc fulvous-ochre at first, margin pale yellowish. Caulocystidia absent (except at the very apex), numerous inflate-catenulate and clavate articles at apex. Spores 8.9-11.1 × 5.5-6.4 µm, Q = 1.50-1.86. Spores broadly amygdaliform with obtuse apex, with low echinulate warts. . . . . *Alnicola pallidifolia*

DISCUSSION

As shown by Rochet *et al.* (2011) host-specificity regarding subgenera of *Alnus* (subgen. *Alnus* versus subgen. *Alnobetula*) is an important specific character, but is not the only factor explaining speciation in *Alnicola*; however, at present only *A. luteolofibrillosa* and *A. escharioides* (clade /luteolofibrillosa) are reported under all species of *Alnus*. Regarding *A. umbrina* and *A. badiofusca*, their genetic similarities (ITS sequences identical, but differences confirmed by other genes) do not reflect consistent morphological differences.

Kühner (1926, 1931), the author of the genus *Alnicola*, based his first observations on collections made under *Alnus alnobetula*, during his summer holidays at La Perrière, near Bozel (Savoy, F). As far as we know Robert Kühner was also the first mycologist who paid attention to naucorioid fungi under *A. alnobetula* in Europe, and therefore the three new species names he published: *Alnicola badia*, *A. luteolofibrillosa*, and *A. submelinoides* (Kühner, 1926) are likely the first available names for species associated with this alder. The identity of *A. badia* is discussed in Moreau *et al.* (2012).

A deep immersion into Kühner's numerous collections and unpublished notes, kindly lent to us by P. Clerc (herb. G), was necessary to determine the identity of these key species. Surprisingly enough, while a number of mycocoenological studies have focused on *Alnus alnobetula* funga (Favre, 1960; Brunner & Horak, 1990; Dorninger, 1993; Lamoure, 1997; Senn-Irlet, pers. comm.), only *Naucoria cedriolens* (Schmid-Heckel, 1985), subordinated to *A. badia*, has been published as new after Kühner (1926). In literature most reports are given names of species known from lowlands, such as *A. sphagneti* (Breitenbach & Kränzlin, 2000) or *A. subconspersa* (Bon & Cheype, 1987; Breitenbach & Kränzlin, 2000), or collective and senseless names such as *A. escharioides* (Schmid-Heckel, 1985) or *A. melinoides* (Kühner, 1926; Jamoni, 2008; see Moreau, 2005). This may explain the necessity of publishing new names for the three species described here, although two of them are frequent under *Alnus alnobetula*.

Description and ecology of *Alnus alnobetula* communities are still insufficiently known; Dorninger (1993) and Lamoure (1997) gave the most extensive list of species associated with the *Alnetum viridis* but do not distinguish species communities according to substrate, moisture, orientation etc. This contribution shows that the number of taxa present in Western Europe is represented by at last the three species described here (with some extralimital collections in need of determination), with addition of *A. badia* (Moreau *et al.*, 2012), *Alnicola luteolofibrillosa* and *A. escharioides* (Moreau *et al.*, 2011), and to the *A. submelinoides*-group which represents an independent lineage (Moreau *et al.*, 2006b). This diversity seems lower to that associated with *Alnus* sect. *Alnus* in Europe (at last seven species of genuine *Alnicola*). Moreover, except *Alnicola escharioides* in Corsica (Rochet *et al.*, 2011; Moreau *et al.*, 2011) and *A. luteolofibrillosa* (unpublished data), no species associated with *Alnus alnobetula* has been proved to occur with trees of sect. *Alnus*, and *vice versa*.

Because *Alnus alnobetula sensu lato* is a cosmopolitan circumpolar species – or, according to other plant taxonomists, a species complex – the above described fungal species should be partly found in the whole distribution area of this tree (Moser, 2003), when some might be endemic to restricted areas; data from North America and Asia, under other subspecies of *A. alnobetula*, should bring important information about biogeography and phylogeny of *Alnus*-associated fungal communities.

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