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## Agarics of alders 1 – the *Alnicola badia* complex

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**ABSTRACT** — Three closely related species in *Alnicola* sect. *Alnicola*, *Alnicola*, are described, illustrated, and compared. *Alnicola badia* is revised based on the type collection and recent collections made under *Alnus alnobetula*. Two species (*A. longicystis*, *A. xanthophylla*) associated with *Alnus glutinosa* and *A. incana* and locally frequent in western and central Europe are described as new.

**KEY WORDS** — Agaricales, Basidiomycota, Hymenogastraceae, *Naucoria*, taxonomy

### Introduction

The agaric genus *Alnicola* Kühner (*Naucoria s. auct.*) was defined by Kühner (1926) as strictly an *Alnus*-associated genus with small-sized basidiomata and rough basidiospores. Four species were cited by Kühner: three of them (*A. badia*, *A. luteolofibrillosa* and *A. submelinoides*) were new to science, all discovered by Kühner under *Alnus alnobetula* (Ehrh.) K. Koch (Moreau 2005).

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This paper is dedicated to the memory of Denise Dailly-Lamouré (26 January 1928 - 26 September 2012), French mycologist, disciple of and successor to Robert Kühner at the University of Lyon.

Although a number of agaricologists studied *Alnicola* species (e.g. Orton 1960, Singer 1978, Reid 1984, Runge 1990, Bon 1992, Ludwig 2000, 2001), each of them presented their own nomenclature and made taxonomy of the genus more and more complex and confusing.

Recent molecular work (Moreau et al. 2006) suggested that species hypotheses in *Alnicola* could be resolved by using several gene sequences to create a robust phylogeny. A four-gene analysis by Rochet et al. (2011) showed that at least 16 phylogenetic *Alnicola* species could be identified in *Alnus*-associated ectomycorrhizal communities in Europe. Most of them could be named according to traditional taxonomy, but some were new to science and given provisional names. Moreover, a complex infrageneric structure of *Alnicola* was suggested in the same study, but no details were given on morphological interpretations of the taxa defined there.

As a first step towards a general taxonomic revision of the genus *Alnicola* in Europe, this article treats the “/badia clade”; a small clade identified by Rochet et al. (2011: fig. 2), which currently encompasses three well-defined species in Europe. Morphological descriptions based on numerous observations of fresh collections and microscopical studies are presented for these three species. One of them, only collected under *Alnus alnobetula* so far, is identified as *Alnicola badia*, the two others, found with *A. incana* and *A. glutinosa*, could not be assigned to any previously described species and are given new names.

## Material & 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

Basidiomata were collected in Austria (Tirol), France (Alps), Italy (Trentino) and Switzerland (Graubünden). Photographs and morphological descriptions were made from specimens soon after sampling; all specimens were cut and air-dried. Additional collections (exsiccata, notes, and pictures) were provided by collaborators from France and various parts of Europe. Also included are collections of R. Kühner (G); D. Dailly-Lamoure, personal herbarium; M. Moser (IB); U. Peintner (IB); L. Tedersoo (TU); and those in the general herbarium of the Kew Botanical Garden (K). Because intraspecific variability is often important in these species, the following descriptions are based on the holotype; species variability is discussed after each description on the basis of all collections studied.

### Descriptions

Morphological descriptions are adapted from notes taken on fresh specimens; colour references (when quoted on fresh material) correspond to Munsell (1975; = M)

TABLE 1: Basidiospores in representative *Alnicola* collections.

COLLECTION	# SPORES	L (µm)	W (µm)	Q
<i>A. badia</i>				
04101206	34	(7.2-)7.5-8.1-8.7(-9.0)	(4.2-)4.3-4.8-5.2(-5.4)	1.58-1.70-1.85(-1.93)
07090905	21	(9.6-)10.3-11.1-12.0(-12.2)	(5.9-)6.0-6.7-7.1(-7.2)	(1.50-)1.55-1.68-1.85(-1.91)
09082204	77	(8.4-)8.8-9.7-10.3(-10.8)	(5.3-)5.6-6.1-6.6(-6.9)	(1.41-)1.47-1.60-1.71(-1.93)
<i>A. longicystis</i>				
04092201	30	(9.4-)9.7-11.1-11.9(-12.2)	(5.4-)5.5-6.2-6.7(-7.0)	(1.57-)1.64-1.79-1.94(-2.09)
04092401	40	(9.0-)9.6-10.9-12.3(-13.2)	(4.8-)5.4-5.9-6.5(-7.0)	(1.58-)1.69-1.86-2.10(-2.24)
05082501 *	120	(9.5-)9.9-10.9-11.9(-14.5)	(5.6-)5.8-6.3-6.8(-8.5)	(1.52-)1.60-1.74-1.88(-2.06)
05082501 **	102	(8.3-)8.8-9.7-10.6(-12.9)	(4.6-)5.0-5.5-5.9(-7.3)	(1.50-)1.64-1.77-1.92(-2.10)
<i>A. xanthophylla</i>				
06090101	40	(9.1-)9.5-10.5-11.7(-12.0)	(5.6-)5.8-6.3-6.8(-6.9)	(1.40-)1.55-1.68-1.88(-2.04)
06090104	32	(9.8-)10.5-12.0-13.5(-14.0)	(5.4-)5.6-6.2-6.8(-7.0)	(1.63-)1.72-1.94-2.21(-2.37)
08110901	32	(11.3-)11.6-12.5-13.3(-14.6)	(6.0-)6.5-6.9-7.4(-7.9)	(1.57-)1.65-1.81-2.01(-2.04)
23_7_04	45	(8.8-)9.2-10.3-11.7(-11.7)	(5.8-)5.9-6.4-6.9(-7.2)	(1.44-)1.47-1.61-1.72(-1.84)

Basidiospores measured from spore deposits on stipe in mature, old\*, and young\*\* sporocarps; dimensions presented as (minimum value-)1st decile-average value-9th decile(-maximum value). L = Length, W = Width, Q = Quotient (L/W).

or Cailleux & Taylor (1963; = C). Microscopical descriptions are based on observations made at the Laboratory of Botany (Lille), with a light microscope Nachet Andromede 018 at  $\times 100$ ,  $\times 400$  and  $\times 1000$  magnifications on hand-sectioned mounts in Melzer's reagent, 5% KOH, and Congo red (1 mg in 10 ml  $\text{NH}_4\text{OH}$ ) after reviving in 10% KOH for a few minutes. For all collections at least 30 basidiospores have been measured from spore prints or from natural deposits on stipe or pileus surfaces. Statistical treatments and notations follow Fannechère (2005) and measurements were made using the software Mycomètre 2.02 (Fannechère 2011). Estimations of spore dimensions for each collection are given in detail separately in TABLE 1. In the corresponding description they are re-calculated for all measurements made on collections attributed to the species. In the following descriptions basidiospore dimensions are given as follows: (minimum value-)1st decile-average value-9th decile(-maximum value), and calculated on all basidiospores measured for each species. Pileipellis structures are described and illustrated from radial sections, additional observations on suprapellis structure are made on tangential cuts (scalps). Descriptive terminology for pileus structures s adapted

from Heilmann-Clausen et al. (1997) – proposed for *Lactarius* but perfectly adapted for the description of structures of *Alnicola* and most agaricales. Stipitipellis structures are described from the upper part of stipe, 1-3 mm below the lamellae.

TABLE 2: Main distinguishing features of *Alnicola badia*, *A. longicystis*, and *A. xanthophylla*.

CHARACTER	<i>A. badia</i>	<i>A. longicystis</i>	<i>A. xanthophylla</i>
PILEUS			
Young color	Bicoloured: pale straw ochre margin, date-brown disc	Bicoloured: dirty yellowish margin, dark brown/± olivaceous disc	Uniformly dull yellowish ochre, aging to ± brownish at disc
Striation	Late in age	To centre even when young	Faintly with age
Surface	Minutely scurfy, then glabrous	Smooth, then fibrillose-silky	Furfuraceous, then glabrous, ± cracking
LAMELLAE	20–30 (1–2), pale gray to pale yellow-ochre	22–24 (2), yellowish ochre	20–26 (2–3), butter yellow
STIPE			
Color	Pale grey ± darker at apex, darkening with age	Purplish black at apex, darkening with age	Dull ochre-yellow, early darkening from base
Apex	± sheathed by caulohymenium, not pruinose	Coarsely floccose	Densely pruinose-floccose
SMELL	Weak, resinous, cold tobacco, cedar oil	Fungoid to raphanoid	Strongly raphanoid
TASTE	Mild	Mild	Mild, ± astringent
CHEILOCYSTIDIA	38–50 × 4.5–8 × 2–2.5 µm, neck 9–26 µm long, with yellow walls	45–55 × 6.5–8 × 1.5–2 µm, neck 18–38 µm long, partly with yellow walls	28–36 × 8–9.5 × 2 µm, neck 10–15 µm long, with bright yellow walls
PLEUROCYSTIDIA	Scattered towards edge	Abundant towards edge	Scattered towards edge
CAULOCYSTIDIA	Scattered at apex, intermixed with clavate elements	Abundant at apex	In dense clusters at apex, intermixed with clavate- catenulate elements
PILEIPELLIS			
Morphology	Oedotrichoderm	Hyphoepithelium	Hyphoepithelium
Subpellis	40–50 µm thick	35–50 µm thick	50–70 µm thick
Hyphal pigments	Smooth to punctuate	Smooth	Incrusted in subpellis, smooth in suprapellis
BASIDIOSPORES	7.5–10.5 × 4.6–6.5 µm Ovo-amygdaliform not papillate	8.8–12.3 × 5.5–6.8 µm Amygdaliform partly subpapillate	9.2–13.5 × 5.6–7.4 µm Amygdaliform ± elongated, not papillate
ALNUS HOST; SUBSTRATE	<i>A. alnobetula</i> , mainly on mineral soil	<i>A. glutinosa</i> , <i>A. incana</i> , on humus-rich or acidic soil	<i>A. glutinosa</i> , <i>A. incana</i> , mainly on bare, ± mineral soil

## Taxonomy

*Alnicola badia* Kühner, Botaniste 17: 176. 1926. FIGS 1–2

= *Naucoria phaea* Maire & Kühner, in Maire, Bull. Inst. Bot. Barcelona 3(4): 101. 1937.

= *Alnicola phaea* (Maire & Kühner) Romagn., Bull. Soc.

Mycol. France 58: 126. 1942, nom. superfl.

?= *Naucoria cedriolens* Bresinsky & Schmid-Heckel, in Schmid-Heckel,

Forschungsber. Nationalpark Berchtesgaden 8: 163. 1985.

= *Alnicola cedriolens* (Bresinsky & Schmid-Heckel) Bon, Doc. Mycol. 21(83): 37. 1991.

“*Alnicola phaeodisca* Kühner in sched. [R. Kühner, unpublished notes, (G)].”

ILLUSTRATED REFERENCE — Moreau et al. (2011: 33).

DESCRIPTION OF HOLOTYPE (adapted from handwritten notes of R. Kühner on the holotype n° 9.100, G) — “Pileus 1.5–2.5 cm, convex-flat ± umbonate, opaque or hardly striolate on one specimen, reddish bistre (margin paler), under whitish pruinose flakes (furfuraceous aspect), then red-brown and pruinose, hygrophanous. Taste mild, odour none. Lamellae 22–23 at stipe, 3–7 lamellules per lamella, almost spaced, cinnamon brownish. Stipe 3.5–4.5 × 0.17–0.25 cm, equal, flexuose, base ± coated with a white cotton-like mycelium; fulvous-brown, glabrescent, slightly pale-fibrillose, with slightly fluffy or minutely pruinose apex, narrowly fistulose; context brown. Spore amygdaliform, 9.5–10.0 × 5.5 (10.5 × 6.0) μm, faintly rugose-punctate, cheilocystidia cuspidate. Cellular cuticle distinctly deviating.<sup>1</sup> Trama regular, made of short hyphae. Basidia 4-spored, 28–29 × 8–9 μm; paraphyses shorter, cylindro-clavate. Subhymenium narrow, cellular-branched.”

DESCRIPTION OF RECENT COLLECTIONS — Pileus 0.8–2.5(–3) cm, early flattened without distinct umbo or lowly convex-flattened, completely scurfy-squamulose at first with pale ochre to whitish squamules, especially towards margin, becoming glabrous towards centre by erosion, never cracked; distinctly bicoloured at first: margin pale straw-ochre (2.5YR2/4, M), centre date brown to dark red-brown (2.5YR5/6), not or hardly striate (only when old and wet), hygrophanous, quickly fading from disc to yellowish ochre slightly darker at centre. Lamellae crowded, 20–30 reaching stipe, 1–2 series of lamellulae, narrow, adnate-subdecurrent to ± emarginate, pale grey-ochre to slightly yellowish ochre, when mature cinnamon ochre (7.5YR6/4, M); edge white pruinose. Stipe 2.5–6(–9) × 0.1–0.2 cm, not pruinose at apex, somewhat sheathed by caulohymenium under lamellae, fibrillose-twisted below, pale greyish, on some collections slightly darker gray at apex, then greying, blackish brown at the

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<sup>1</sup>Kühner frequently used this term for describing pileus structures in naucorioid groups (Kühner 1931, 1942, 1980). A “deviating” structure refers to a basically hymenodermioid structure, more or less “degraded”, i.e. with inflate terminal cells of more or less radial orientation and adpressed (transitions to hyphotrichoderm).

base, with white  $\pm$  strigose mycelium. Smell weak,  $\pm$  resin-like, reminding of cedar oil, cooking oil or cold tobacco; taste mild, insipid to weakly fungoid-raphanoid.

Pileipellis an oedotrichoderm (Heilmann-Clausen et al. 2007) 60–90  $\mu\text{m}$  thick; suprapellis made of 3–5 layers of hyphae, each a long chain of up to 15 catenulate cells, more or less fasciculate and erected, prostrate with age, cells cylindrical to inflate, subterminal cells often constricted, 9–20  $\mu\text{m}$  wide, usually of thin- (<0.2  $\mu\text{m}$  thick) yellowish walls, but some (about 10%) with thicker yellow to brownish walls or thickened only at septa, smooth to locally encrusted; terminal cells frequent, cylindrical to fusiform, 45–70  $\times$  7–15  $\mu\text{m}$ , smooth and thick-walled; rarely with superficial very slender hyphae 2–2.5  $\mu\text{m}$  wide, observed on surface (scalp, sections) with yellow thickened wall and coarsely incrusting yellow pigment; subpellis hardly differentiated from suprapellis, 40–50  $\mu\text{m}$  thick, made of 4–6 layers of short cylindrical to polygonal cells 7–15  $\mu\text{m}$  wide, with yellow walls up to 0.5  $\mu\text{m}$  thick, minutely punctuate to locally distinctly incrusted, not stained by KOH. Pileus trama pale, with somewhat brownish zones, composed of variously shaped hyphae, slender cylindrical hyphae 3–5  $\mu\text{m}$  wide, and cylindrical to ampullaceous hyphae 8–25  $\mu\text{m}$  wide, mostly smooth, some incrusted or with light yellow walls especially at septa. Stipitipellis with sparse clusters of caulocystidia at apex, 45–90  $\times$  6–14  $\mu\text{m}$ , some repent, cylindro-clavate more or less curved, with or without lateral neck, mixed with more typical ampullo-fusiform cystidia, all with yellow thickened walls. Superficial hyphae 4–6  $\mu\text{m}$  wide, wall yellow and coarsely incrusted. Stipe context composed of cylindrical hyphae 5–14  $\mu\text{m}$  wide, with smooth strongly thickened walls up to 1.5  $\mu\text{m}$  thick, yellowish towards cortex, paler in centre.

Basidiospores (5 collections, 196 measurements) (6.7–)7.5–9.02–10.5 (–12.2)  $\times$  (4.2–)4.6–5.48–6.5(–7.2)  $\mu\text{m}$ ,  $Q = 1.51–1.65–1.79$ , ovoid to slightly amygdaliform with obtuse apex, never subpapillate, ochre-yellow in KOH, not dextrinoid, uniguttulate in KOH, ornamentation of low warts less than 0.2  $\mu\text{m}$  long, punctiform-rounded, not confluent, weakly contrasted; episporium not distinct. Basidia 22–26(–32)  $\times$  6.5–8  $\mu\text{m}$ , cylindro-clavate, 4-spored, base variously elongated, before maturity with granular content, sometimes weakly brownish; necrobasidia abundant, deep ochre yellow in KOH. Subhymenium 12–15  $\mu\text{m}$  thick, ramose with short cylindrical articles 3–4.5  $\mu\text{m}$  wide, hyaline. Hymenial trama regular, mediostratum almost colourless to pale brownish zoned, made of short cylindrical hyphae 15–45  $\times$  4–14  $\mu\text{m}$ , with yellowish wall locally thickened (up to 1  $\mu\text{m}$  thick) and incrusted. Lamella edge sterile; cheilocystidia 38–50  $\times$  4.5–8  $\mu\text{m}$  (base),  $\times$  2–2.5  $\mu\text{m}$  (apex), ampullaceous at base, with distinct attenuate neck 9–26  $\mu\text{m}$  long, sometimes obtuse to  $\pm$  inflate at apex (e.g. on holotype, FIG. 1), all with thickened yellowish wall up to 0.5  $\mu\text{m}$  thick, most colourless, scattered ones with deep yellow content. Pleurocystidia

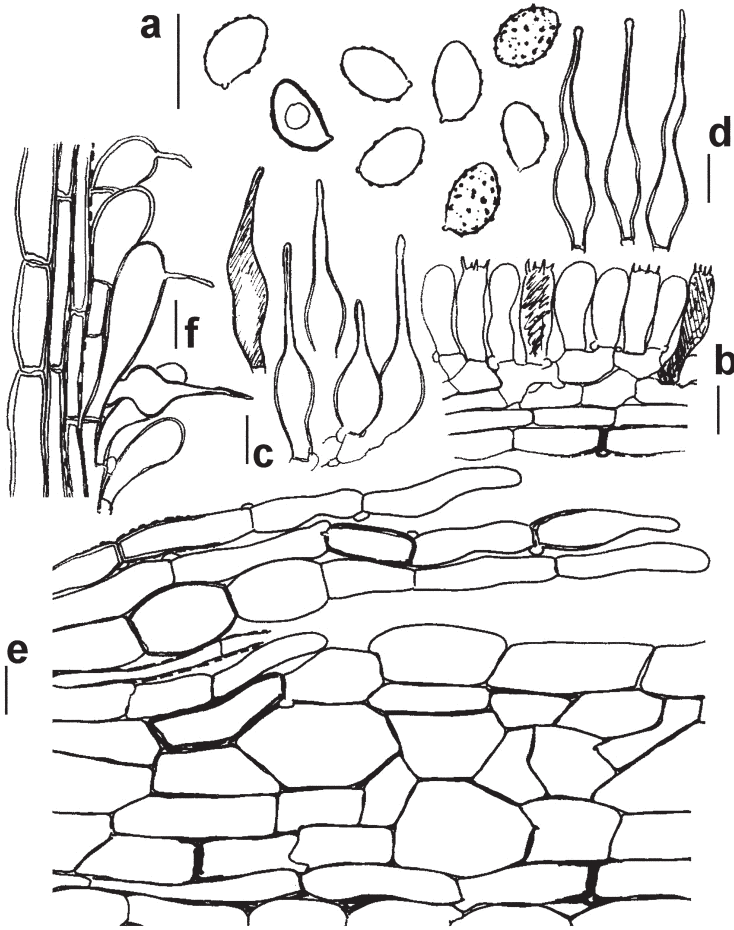


FIGURE 1: *Alnicola badia* (09082204, LIP). a: basidiospores; b: portion of hymenium with basidia and subhymenium; c: cheilocystidia; d: pleurocystidia; e: pileipellis, radial section; f: stiptipellis at stipe apex (longitudinal section.). Scale bar = 10  $\mu$ m.

scattered but not unfrequent towards edge, much rarer 300  $\mu$ m in from the edge, 36–56  $\times$  6–6.5  $\mu$ m (base),  $\times$  2  $\mu$ m (neck), fusiform, neck 22–40  $\mu$ m long and attenuate, occasionally abruptly inflated at apex, walls thickened and yellowish up to 0.3  $\mu$ m thick, originating from deep in subhymenium. Gloeoplerous hyphae absent to very rare, pale yellow, slender, cylindrical, in stipe and pileus context. Clamp connections present at all septa.

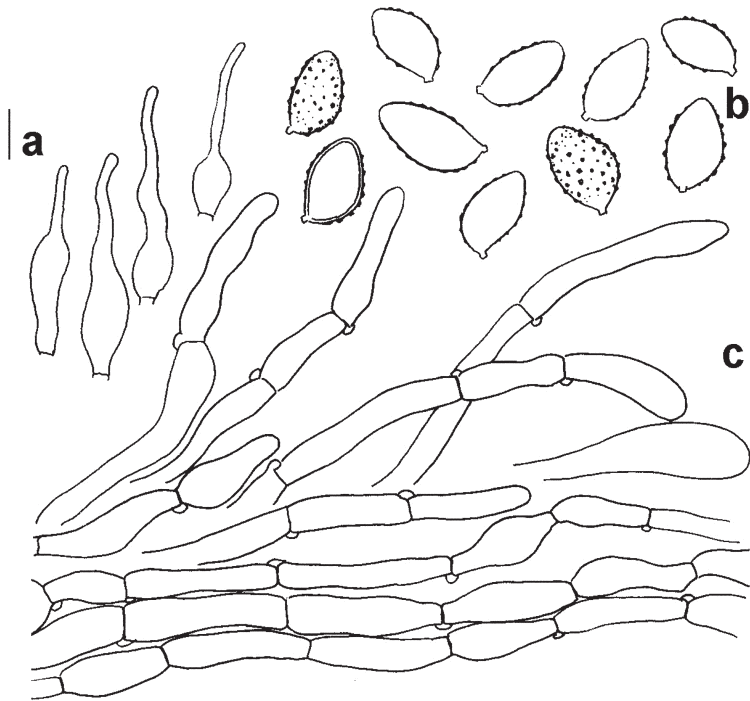


FIGURE 2: *Alnicola badia* (Holotype, R. Kühner 9.100, G). a: basidiospores; b: cheilocystidia; c: pileipellis, radial section. Scale bar = 10  $\mu$ m.

SPECIMENS EXAMINED — AUSTRIA, TIROL, Obergurgl, *Alnus alnobetula*, 25 August 2005, P.-A. Moreau n° 05082717 (LIP); 28 August 2005, P.-A. Moreau 05082808b (LIP). FRANCE, CORSE DU SUD, Bocca Palmente, *Alnus alnobetula* subsp. *suaveolens* along a stream, leg. F. Richard & P.-A. Moreau, 12 October 2004, P.-A. Moreau 04101209 and 04101206 (LIP); Bastelica, val d'Ese, *Alnus alnobetula* subsp. *suaveolens* in sand along a stream, 7 September 2007, P.-A. Moreau 07090822 (LIP); 8 September 2007, P.-A. Moreau 07090905 (LIP); 3 September 2008, P.-A. Moreau 08090340 (LIP; illustrated in Moreau et al. 2011: 33); HAUTE-CORSE, Vizzavona, Monte d'Oro, under *Alnus alnobetula* subsp. *suaveolens* along a stream, leg. F. Richard & P.-A. Moreau, 11 October 2004, P.-A. Moreau 04101101 (LIP); HAUTE-SAVOIE, Samoëns, Collet d'Anterne, 6 September 1958, R. Kühner Sa-58-58 (G, "*Naucoria subescharoides*" in herb., "*Alnicola phaeodisca*" in sched.); SAVOIE, La Perrière, Praz Joseph, 31 August [see note 1], under alders on ground, R. Kühner 9.100 (G, holotype); la Rosière, left side of the road to La Jäiraz below the dam, under *Alnus alnobetula*, 8 September 1942, R. Kühner (G, "*Naucoria (Alnicola) Joniss A*") ; under La Rosière, 10 September 1942, under *Alnus alnobetula*, R. Kühner (G, "*Alnicola [Nauc. pannosa ?] Joniss A*") ; above La Rosière, *Alnus alnobetula*, 18 September 1961, R. Kühner (G, "sp.1961"); Bourg-Saint-Maurice, Arc 1800, above the golf area, in old *Alnus alnobetula* thickets along a stream on acidic soil, 1870 m, 7 September 1993,



P.-A. Moreau n° 93090702 (LIP); ruisseau du Villard, 19 August 2002, J.-C. Deïana, P.-A. Moreau JCD19-8-02; 21 August 2003, P.-A. Moreau 03082102 (LIP); Peisey-Nancroix, Nancroix, les Lanches, under *Alnus alnobetula*, calcareous watercourse, P. Saviuc, 21 October 2003, P.-A. Moreau 03082110 (LIP); Landry, Barmont, under *Alnus alnobetula*, leg. M. Broussal, 23 August 2003, P.-A. Moreau 03082301 (LIP); 26 October 2007, P.-A. Moreau 07082637 (LIP); Bessans, Ecot de Bonneval, under *Alnus alnobetula*, 1 October 2008, leg. M. Durand, M. Durand 08100119 and 08100121 (LIP); Crest-Voland, APPB Tourbière des Saisies, along the Nant Pareu stream, acidic peaty soil under *Alnus alnobetula* subsp. *alnobetula* amongst liverworts (*Pellia* spp.), 22 October 2009, P.-A. Moreau 09082204 (LIP); Beaufort, Cormet d'Arèches above the Lac des Fées, under *Alnus alnobetula* on calciferous schists, 22 October 2008, P.-A. Moreau 08082201 (LIP); leg. C. Hugouvieux, 27 October 2009, P.-A. Moreau 09082703 (LIP); locality unknown (Savoie or Haute-Savoie), 1964, R. Kühner n° 64-20 (G). SWITZERLAND, GRAUBÜNDEN, Davos, leg. H. Gamper, under *Alnus alnobetula* isolated bush in a pasture, 1 August 2003, P.-A. Moreau 03080101 (LIP); Bergün, above the Palpuogna lake, under *Alnus alnobetula* on acidic ground along a stream, 14 August 2003, P.-A. Moreau 03081403 (LIP); 2 September 2006, P.-A. Moreau 06090202 (LIP); Lenzerheide, Parpan, under a thicket of *Alnus alnobetula*, 31 August 2006, P.-A. Moreau 06083102 (LIP).

NOTE 1 — The year of collection of the holotype is neither mentioned in the notes nor in any of Kühner's publications, but the notes (kind of paper, handwritten indications and style) are identical to those on *A. submelinoides* and *A. luteolofibrillosa*. The collection of *A. submelinoides* was dated 1924 by Kühner (1931) himself, therefore 31 August 1924 should be accepted as the date of collection of the original material of *A. badia*.

GENBANK ACCESSION NUMBERS (Moreau et al. 2006, Rochet et al. 2011) — ITS1-5.8S-ITS2: AY900031, AY900032, AY900033, AY900036, AY900037, AY900039, HQ714656, HQ714657, HQ714658, HQ714664, HQ714670, HQ714676, HQ714755, HQ714756, HQ714781, HQ714787. GPD: HQ714896, HQ714597, HQ714598, HQ714599, HQ714603, HQ714608, HQ714614. RPB2: HQ714796, HQ714797, HQ714799, HQ714800, HQ714811, HQ714818. V9: HQ714500, HQ714508.

ECOLOGY AND DISTRIBUTION — Only known with *Alnus alnobetula*, usually on acidic substrate, on wet humus amongst liverworts, more rarely on schists; known from subalpine altitudes of Western and Central Alps (Austria, France, Switzerland) and Corsica. Widespread but usually not abundant, often scattered.

OBSERVATIONS — Kühner (1926, 1931) found his very first collections of *A. badia* and *A. submelinoides* (a species with club-shaped cystidia) together in 1924 at the same locality of Praz Joseph, La Perrière (near Bozel, Savoie). In fact both species often grow together and are easy to mistake in the field. Dry *A. badia* can be detected by darker colours, and especially blackish stipe on mature specimens, while dry basidiomata of *A. submelinoides* remain pale.

It cannot be proved that Heim's (1931) representation of the pileipellis of *A. badia* was based on Kühner's holotype, but we are inclined to think so because: 1) Kühner contributed to Heim's work; 2) Heim does not seem to have collected any agaric himself under *Alnus alnobetula* in the Alps; 3) pileus

structure excludes all species known to us from lowland species of *Alnus*; and 4) at this date Kühner only knew *A. badia* from his type collection. However Heim's figure is a representative – although somewhat stylized – illustration of the oedotrichodermial structure observed on our typical collections of *A. badia*; it is reproduced by Cléménçon (1997: 58, fig. 2.61) who interprets it as “moniliform physalohyphae”.

**VARIABILITY OF THE SPECIES** —The pileus colour of *A. badia* is variable, making identification uncertain in the field. Also, basidiomata are often scattered, intermixed with other species, and young and old specimens can be easily confused with other species without microscopic observations. However, a pale pileus margin with light ochre tones, distinctly bicoloured on darker specimens, and pale browning stipe are apparently constant features distinguishing it from other *Alnicola* species found with *Alnus alnobetula*. The presence of pleurocystidia is usually confined to the vicinity of lamella edge, and sometimes not conspicuous (very scarce on PAM07090905). A spectacular variation is found in spore size within the same otherwise homogenous collection (see TABLE 1), ranging from rather narrow (3.8–4.8  $\mu\text{m}$  wide in average) to widely ovo-amygdaliform (6.0–6.6  $\mu\text{m}$  wide in average), partly attributed to age of specimens; but they are rather well characterized by low, thin punctate ornamentation and obtuse, neither attenuate nor mucronate apex.

**EXTRALIMITAL COLLECTIONS** — 1) A few collections from mineral substrates in Corsica (riverbed) and Savoy (calciferous schists) show a more distinct cedar-like smell; such collections are described in the diagnosis of *A. cedriolens* (Schmid-Heckel 1985). There is no morphological or molecular evidence that this character supports a distinct taxon. The same cedroid smell has also been reported on collections of *A. luteolofibrillosa* (Moreau 2005; E. Campo, pers. com.); 2) two rather poor collections also from Savoy and Corsica are morphologically conform to *A. badia* but have a slight aromatic smell reminiscent of *Inocybe bongardii* (Weinm.) Quél. (or *Alnicola suavis* (Bres.) Kühner); basidiospores are at the larger size limit for *A. badia* (suggesting senescent or damaged specimens) and no sequence could be generated for these collections.

***Alnicola longicystis*** P.-A. Moreau, Bizio & Deparis, **sp. nov.**

FIG. 3

MYCOBANK MB 563643

Similar to *Alnicola badia* and *A. xanthophylla* by cheilocystidia with yellow thickened walls, amygdaliform punctate basidiospores, pleurocystidia, and mild taste. Diagnosed by purplish-black stipe apex when young. Differs from *Alnicola badia* by association with *Alnus glutinosa* and *A. incana*, pileus striate from early stages, and frequent pleurocystidia.

TYPE: Italy, Trentino, Balsega di Pinè, *Alnus incana*, 25.VIII.2005, leg. A. Aiardi & E. Bizio, herb. P.-A. Moreau n° 05082501 (Holotype, LIP; isotypes, IB 20050690, ZT).

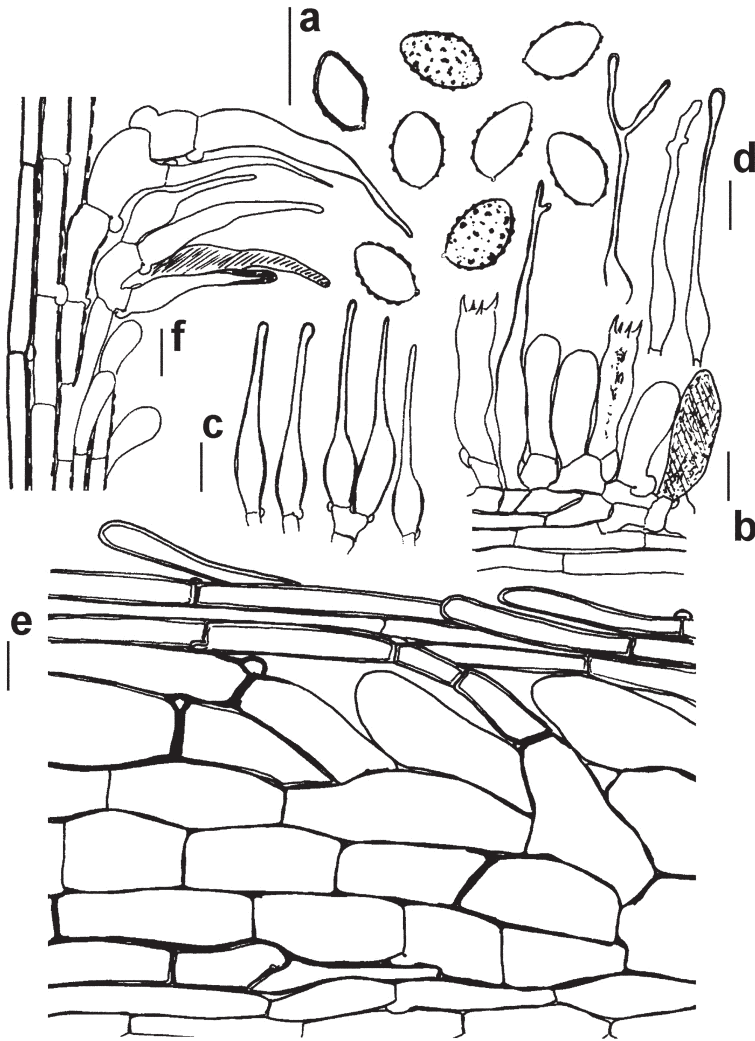


FIGURE 3: *Alnicola longicystis* (Holotype, 05082501, LIP). a: basidiospores; b: portion of hymenium with basidia, pleurocystidia and subhymenium; c: cheilocystidia; d: pleurocystidia; e: pileipellis, radial section; f: stipitipellis at stipe apex, longitudinal section. Scale bar = 10  $\mu$ m.

ETYMOLOGY: “with long cystidia”, referring to the distinctive lanceolate cheilocystidia with elongated neck.

Pileus 0.8–2.5 cm, convex then soon flattened, striate to centre, at first pale yellowish ochre with subpapillate dark brown centre, this dark colour expanding

with age, when old gradually brownish-grey at centre with somewhat olivaceous tones (H63-H64, C) to dirty yellowish at margin (B72), hygrophane, fading uniformly to pale ochraceous (A84), when fresh almost glabrous and smooth, becoming fibrillose-silky from margin when drying. Lamellae crowded, 22–24 reaching the stipe, 2 series of lamellulae, adnexed-horizontal to slightly emarginated, at first yellowish ochre to pale lemon-ochre (A84), darkening slightly with age to dull ochre (C74-D74), rusty ochre when old; edge white, minutely pruinose. Stipe 3–8 × 0.1–0.3 cm, fistulose, slightly enlarged at base, initially dull ochre brown with purplish-black apex, coarsely floccose at apex, below whitish-fibrillose, fading to pale yellowish in lower part with age, apex remaining darker, base darkening on older specimens. Context greyish in pileus, dark grey-brown at apex, yellowish in stipe cortex. Smell strongly fungoid or raphanoid. Taste raphanoid or fungoid, mild.

Basidiospores (3 collections, 292 measurements): 8.8–10.48–12.3 × 5.5–5.97–6.8 μm,  $Q = 1.60–1.79–2.10$ , amygdaliform, dimorphic with a variable proportion of large basidiospores with more elongate to subpapillate apex, rather bright yellow in KOH, not dextrinoid, ornamentation when mature warty-punctate to echinulate, up to 0.3 μm high, warts isolated, irregular in size but rarely confluent, before maturity often as low patches (especially when observed on hymenium); content homogenous, not distinctly guttulate, or with a single irregular drop; epispodium not loosening. Basidia all with 4 sterigmata, strongly heteromorphic: 21–36 × 6.5–8.5 μm, cylindrical, slightly stragulate under apex when mature, with variously elongated base, the longest generating larger basidiospores; necrobasidia with yellowish brown content frequent, collapsed, but also some basidioles and young basidia with yellow cytoplasmic content present, otherwise colourless; most mature basidia with dense colourless granular content. Subhymenium compact and weakly developed, 10–12 μm wide, composed of small short cells forming a thin pseudoparenchymatic tissue. Mediostratum of lamellae regular, pale yellow-brown in KOH, composed of slender and wide hyphae intermixed, 3–14 μm wide, with smooth slightly thickened walls. Lamella edge sterile; cheilocystidia (38–)45–55 × 6.5–8 μm (base), × 1.5–2 μm (neck), all lanceolate with an exceptionally long and slender neck (18–38 μm long), slightly thick-walled (up to 0.3 μm thick), some with the neck filled with yellow pigment towards apex; often with small basidioles intermixed. Pleurocystidia relatively frequent up to 200 μm from the lamella edge, larger and slenderer than cheilocystidia, 55–62 × 5.5 μm (base), × 1.5–2.5 μm (neck), with a long neck often difformed: capitate, inflated, ramose or bifid, often yellow at apex, arising distinctly from hymenium, disappearing early from edge to sinus.

Pileipellis a thick hyphoepithelium (Heilmann-Clausen et al., 2007); suprapellis 12–20 μm thick, distinctly yellowish coloured, made of 2–4 layers

of cylindrical-filamentous hyphae 2.5–7 µm wide, walls yellow, up to 0.5(–1) µm thick, smooth; terminal cells cylindrical with rounded to slightly inflated apex. Subpellis 35–50 µm thick, very distinct, formed of inflated to subglobose cells 25–75 × 6–28 µm, with pale yellow smooth walls, moderately thick-walled except towards septa (up to 1 µm thick). Pileus trama of short, pale and smooth walled hyphae, 3–8 µm wide. Stipitipellis covered by a velipellis of cylindrical, incrusting hyphae 5–6.5 µm diam, with scattered erected clavate cells; at apex intermixed with large clusters of caulocystidia 40–70 × 5.5–11 µm, lanceolate with long neck, most with yellow apex, some collapsed with yellow-brown necropigment. Stipe trama made of parallel hyphae, 3–12 µm diam, with yellowish slightly incrusting wall, often thickened and more brownish at septa; gloeoplerous hyphae very rare, long, sinuous and slender (3–4 µm diam.), with yellow-brown thick walls in KOH. Clamp connections present at all septa.

ADDITIONAL SPECIMENS EXAMINED — ESTONIA, VILJANDI, Songa, 58°18'N 25°22'E, *Alnus glutinosa*, 12 September 2009, L. Tedersoo 110256 and 110257 (TU); LÄÄNE, Vormsi, Fällarna, 59.001°N 23.202°E, *A. glutinosa*, 17 September 2010, L. Tedersoo 110285 (TU); HULLO, 59.008°N 23.2275°E, *A. glutinosa*, 17 September 2010, L. Tedersoo 110300 (TU); SÖDERBY, 59.0049°N 23.3520°E, 18 September 2010, L. Tedersoo 110304 (TU); PÕLVA, Järvselja ürgkvarital, 58°16'N 27°19'E, *A. glutinosa*, 30 September 2010, L. Tedersoo 110343 (TU); TARTU, Haage, 58.363°N 26.63°E, 26 September 2010, L. Tedersoo 110321 (TU); MAKSA, 58°22'N 27°03'E, *A. incana*, 30 September 2010, L. Tedersoo 110344 (TU); PORIJÕE, 58°23'N 26°43'E, *A. incana*, 6 October 2010, L. Tedersoo 110358 (TU). FRANCE, HAUTE-SAVOIE, les Houches, under *A. incana* and *A. alnobetula* intermixed, 22 September 2004, P.-A. Moreau 04092201 (LIP); Argentière, under *A. incana* on acidic peaty ground, 24 September 2004, leg. L. Deparis & P.-A. Moreau, P.-A. Moreau 04092401 (LIP); LANDES, Yrieu, edge of brook with *A. glutinosa*, 29 avril 2000, leg. J. Guinberteau & P.-A. Moreau, P.-A. Moreau 100 and 101 (LIP); PAS-DE-CALAIS, Boulogne-sur-Mer, domanial forest, oceanic deciduous forest on clay soil, under *A. glutinosa* along a rivulet, 10 September 2009, P.-A. Moreau 09091001 (LIP); SAVOIE, Séez, along the Isère river, under *A. incana* in a mixed riparian forest, leg. M. Gardes, J. Rochet & P.-A. Moreau, 28 August 2008, P.-A. Moreau 08082805 (LIP); Bozel, les Perrières, under *A. incana* along a rivulet in a *Fagus* forest, 780 m, 26 August 2010, P.-A. Moreau 10082611 (LIP); Beaufort, Arêches, le Perthuis, wet mesotrophic riparian forest with *A. incana*, 22 August 2011, P.-A. Moreau 11082203 (LIP). SPAIN, CANTABRIA, Ruente, Parque natural, under *A. glutinosa* on acidic peaty soil, 29 October 2011, P.-A. Moreau 11102901 (LIP).

GENBANK ACCESSION NUMBERS (Moreau et al. 2006, Rochet et al. 2011, Tedersoo et al. 2009) — ITS1-5.8S-ITS2: AY900038, AY900075, FM993128, FM993140, FM993256, FM993273, HQ714667, HQ714757, HQ714795, HQ714668: **holotype**; GPD: HQ714605, HQ714606: **holotype**, HQ714641; RPB2: HQ714808, HQ714809: **holotype**, HQ714885; V9: HQ714576: **holotype**.

ECOLOGY AND DISTRIBUTION— With *Alnus glutinosa* and *A. incana*, most often on humus-rich substrates, typically in wet mixed *Alnus*–*Corylus* thickets on acidic ground (often with *Polytrichum* or *Sphagnum* spp.), but also in neutrophilic to slightly basophilic river sides with *A. xanthophylla*, known from

lowland to mountainous altitudes (1000 m); known from siliceous mountains of Western and Southern Europe (Pyrenees, Cantabrian Mountains, Alps; also isolated from mycorrhizae in Corsica, unpublished data) and scattered localities in coastal forests (Aquitaine, North of France), as well as Estonia. Probably widespread in Europe, gregarious but rarely abundant.

OBSERVATIONS — This is one of the most frequent species of *Alnicola* associated with *Alnus incana* in the mountains. It is found on river sides (with *Gyrodon lividus* and *Paxillus filamentosus*) as well as in acidic peaty alder stands amongst *Sphagnum*. It is also present but rare and scattered in coastal peaty forests under *Alnus glutinosa*. In alpine regions it can be found together with *Alnicola xanthophylla*, which differs macroscopically on the field by distinctly striate pileus, yellow lamellae, and the absence of purplish black spot at stipe apex. Because colours evolve strongly with age, old or atypical specimens can be difficult to interpret in the field, but can be recognized easily by long-necked cheilocystidia and pleurocystidia (e.g., most cheilocystidia measuring  $45\text{--}55 \times 6.5\text{--}8 \mu\text{m}$  in *A. longicystis*,  $28\text{--}36 \times 8\text{--}9.5$  in *A. xanthophylla*). *Alnicola badia*, which can show the same characteristic dark tones at stipe apex, differing especially by the host tree and a pileus becoming striate only with age. *Alnicola umbrina* (Maire) Kühner (Kühner 1931: 241) differs by more foxy to brown colours and the fusiform spores and cystidia (Moreau 2005).

*Alnicola xanthophylla* P.-A. Moreau, Peintner & Senn-Irlet, sp. nov.

FIG 4

MYCOBANK MB 563644

Differs from *Alnicola longicystis* by a pileus that is striate only in age, uniform yellowish colors, and shorter cheilocystidia with bright yellow walls and necks  $\leq 15 \mu\text{m}$  long.

TYPE: SWITZERLAND, GRAUBÜNDEN, Rothenbrunnen, leg. P.-A. Moreau & B. Senn-Irlet, 1.IX.2006, herb. P.-A. Moreau 06090101 (Holotype, LIP; isotypes, IB20060540, ZT).

ETYMOLOGY: “with yellow gills”, referring to the characteristic butter-yellow tinges of lamellae.

Pileus 1–2.5 cm diam, soon flattened to slightly obtuse, slightly striate when mature, entirely furfuraceous, glabrescent, often cracked-squamulose when old, dull yellowish ochre (C74-C66, C), subpapillate, brownish at centre, gradually pale yellowish towards margin, when old dark grey, strongly hygrophanous fading to uniformly dull greyish ochre to somewhat more rusty at centre (C72 or a bit darker), slightly fibrillose under a lens, without trace of veil. Lamellae very crowded, 20–26 reaching the stipe, 2(–3) series of lamellulae, adnexed to almost free, initially butter yellow (D68-C68), becoming dull greyish ochre when old, at the end tobacco brown; edge pale yellow, smooth to pruinose-pubescent. Stipe 2–5  $\times$  0.1–0.2 cm, equal or slightly enlarged at base, when very young dark grey-brown at apex, then uniformly dull ochre-yellow (C74),

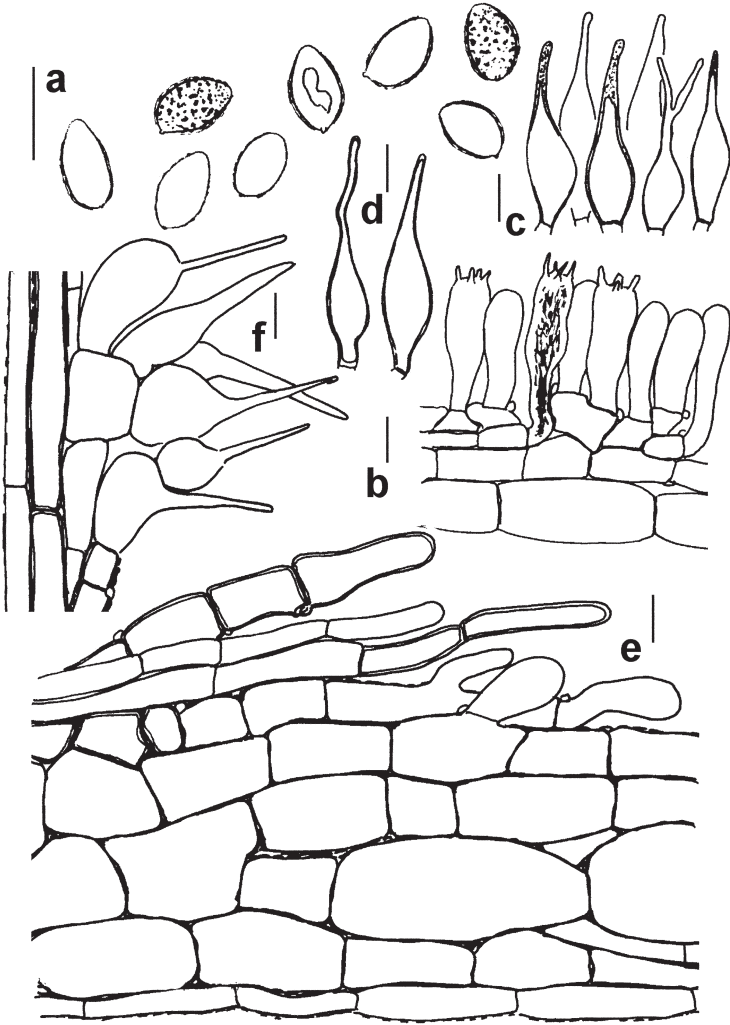


FIGURE 4: *Alnicola xanthophylla* (Holotype, 06090101, LIP). a: basidiospores; b: portion of hymenium with basidia and subhymenium; c: cheilocystidia; d: pleurocystidia; e: pileipellis, radial section; f: stipitipellis at stipe apex, longitudinal section. Scale bar = 10  $\mu$ m.

soon browning from base, at maturity dark grey-brown with yellowish tones at apex, densely pruinose-floccose 2–3 mm under the lamellae, slightly covered

by fibrils more conspicuous on old darkened specimens, without trace of veil; mycelium white hardly visible. Context grey when fresh then whitish, amber-yellow in cortex, when old dirty grey in stipe base. Smell strongly raphanoid. Taste mild, raphanoid, more or less astringent.

Basidiospores (4 collections, 149 measurements):  $9.2-11.20-13.5 \times 5.6-6.46-7.4 \mu\text{m}$ ,  $Q = 1.55-1.76-2.21$ , ovo-amygdaliform, rather polymorphic and partly elongated with acute apex but not distinctly subpapillate (a majority of abnormally elongate basidiospores on coll. PAM06090104), bright yellow in KOH, not dextrinoid, ornamentation when mature warty-punctate, up to  $0.3 \mu\text{m}$  high, warts low and obtuse, irregular in size, punctiform to slightly cristate; content with a large irregular droplet and often granular cytoplasm; epispodium not or only slightly loosening. Basidia all with 4 sterigmata, cylindro-clavate with more or less elongate base,  $22-32 \times 7.5-9.5 \mu\text{m}$ ; necrobasidia abundant, with amber-yellow content, usually collapsed, young and mature basidia usually colourless. Subhymenium thin, filamentous,  $5-8 \mu\text{m}$ , made of slender hyphae  $2-4 \mu\text{m}$  wide, with small, short cells forming a weakly developed pseudoparenchymatic structure. Lamella mediostratum regular,  $80-100 \mu\text{m}$  wide, pale to almost colourless in KOH, made of shortly cylindrical to polygonal or strongly inflated cells  $7-35 \mu\text{m}$  wide, pale yellow, with smooth, slightly thickened walls. Lamella edge sterile; cheilocystidia  $28-36(-40) \times 8-9.5 \mu\text{m}$  (base),  $\times 2 \mu\text{m}$  (neck), shortly fusi-lageniform with strongly inflated base and rather short attenuate neck ( $10-15 \mu\text{m}$  long), apex obtuse to slightly rounded, walls bright yellow, especially thickened, up to  $0.5 \mu\text{m}$  at apex, without basidia found intermixed. Pleurocystidia scattered, only frequent very close to the edge but sometimes up to  $200-300 \mu\text{m}$  from the edge,  $32-40 \times 6-8 \mu\text{m}$  (base),  $\times 2 \mu\text{m}$  (neck), fusiform with longer neck than cheilocystidia ( $15 \mu\text{m}$  long), sometimes tortuous, bright yellow, arising from subhymenium, disappearing towards sinus.

Pileipellis a hyphoepithelium; suprapellis  $20-30 \mu\text{m}$  thick made of  $1-2(-3)$  layers of cylindrical to catenulate hyphae of cells  $18-45 \times 4.5-11(-16) \mu\text{m}$ ,  $\pm$  erected towards centre, terminal cells cylindrical-attenuate; walls yellowish to brownish on some cells, smooth; subpellis  $50-70 \mu\text{m}$  thick, very distinct, reddish ochre in KOH, cellular, with slightly radial-ascendant orientation, made of cylindrical to polygonal or subglobose isodiametric cells,  $15-90 \times 8-30 \mu\text{m}$ , with yellow incrustated walls, especially thickened and brownish at septa. Pileus trama reddish brown in KOH, under subpellis gradually paler, composed of cylindrical hyphae  $4-16 \mu\text{m}$  wide, more inflated towards surface, walls minutely incrustated. Stipitipellis at apex with sparse short catenulate hyphae  $5-8 \mu\text{m}$  wide, dark yellowish, with thickened strongly incrustated walls, intermixed towards apex with dense clusters of caulocystidia  $22-28 \times 10-18 \mu\text{m}$  (base)  $\times 2-2.5 \mu\text{m}$  (neck), strongly inflated with attenuate neck  $12-25 \mu\text{m}$



long, only slightly thick-walled (some with thickened yellow neck). Stipe trama made of parallel hyphae, 3–12 µm wide, with yellowish incrustated walls in cortex, colourless in depth; gloeoplerous hyphae sparse, more frequent towards base, short and rather wide (5–8 µm), dark reddish brown in KOH. Clamp connections present at all septa.

ADDITIONAL SPECIMENS EXAMINED — CZECH REPUBLIC, BOHEMIA, Prague-Radotín, under *Alnus glutinosa*, J. Borovička n° JB2010-2515; Prague, Reporyje, herb. J. Borovička BORE2008-9 (part in LIP). ESTONIA, TARTU, Jänese matkarada/Kvissentali, *Alnus incana*, 24 September 2010, L. Tedersoo 110319 (TU); Lüllü, 58°27.5'N 26°49'E, *Alnus incana*, 2 October 2010, L. Tedersoo 110349 (TU). FRANCE, AIN, Vanchy, calcareous sand pit, under a small *Alnus glutinosa* in a watercourse, R. Fillion & P.-A. Moreau, 1 May 1999, P.-A. Moreau 99050110 (LIP, as “*A. pseudoscolecina*”); NORD, Trélon, *A. glutinosa*, 25 April 1999, J.-J. Wuilbaut 99042503 (LIP); Zuydcoote, fixed dune, under a single *Alnus glutinosa* along a sandy path, 9 November 2008, herb. P.-A. Moreau 08110901 (LIP); PAS-DE-CALAIS, Evin-Malmaison, under *Alnus incana* planted in a periurban park, on wet clay-calcareous soil along a ditch, 30 October 2007, leg. A. Hayet & P.-A. Moreau, P.-A. Moreau 07103002 (LIP); SAVOIE, la Perrière, under *Alnus incana* along a rivulet in a *Fagus* forest, 780 m, 26 August 2010, P.-A. Moreau 10082610 (LIP); Beaufort, la Turnaz, with young *Alnus incana* in a mineral river bed, 1015 m, 28 August 2010, P.-A. Moreau 10082802 (LIP). SLOVENIA, *Alnus incana*, L. Tedersoo L7054 (TU). SWEDEN, JÄMTLAND, Östersund, Rannåson, *Alnus incana* on calcareous gravel, 26 September 2007, leg. H. Lindström, H. Lindström 06.373 (part in LIP); SKÅNE, Ivö, Ivö klack, 56.139766°N 14.403568°E, under *Alnus incana*, *Salix* and *Betula* on calcareous clay, poor in organic matter, 22 October 2010, K. Gillen, K. Hansen, L. Örstadius and I. Olariaga, F-176866 (S, as “*Alnicola* cf. *escharoides*”). SWITZERLAND, GRAUBÜNDEN, Filisur, leg. U. Peintner, 18 September 1998, IB1998/0446 (IB, as “*Alnicola escharoides*”); Rothenbrunnen, under *Alnus incana* on black alluviums, alt. 600 m, leg. P.-A. Moreau & B. Senn-Irlet, 1 September 2006, P.-A. Moreau 06090104; Alvaneu-Bad, under *Alnus incana*, 600 m, 1 September 2006, leg. V. Queloz, P.-A. Moreau 04090104 (LIP); BERN, Kandersteg, Filfalle, 1200 m, *Alnus incana* on calcareous soil, 30 September 2003, leg. H. Woltsche, P.-A. Moreau (LIP); *idem*, *A. incana* along a stream, on black alluviums, 22 July 2004, leg. B. Senn-Irlet & P.-A. Moreau, P.-A. Moreau 04072201 (LIP).

GENBANK ACCESSION NUMBERS (Moreau et al. 2006, Rochet et al. 2011) — ITS1-5.8S-ITS2: AF325630, HQ714705, HQ714709, HQ714765; GPD: HQ714627, HQ714628, HQ714648; RPB2: HQ714839, HQ714844, HQ714889; V9: HQ714530, HQ714534, HQ714581.

ECOLOGY AND DISTRIBUTION— With *Alnus incana*, more rarely *A. glutinosa*, usually on mineral-rich substrates, typically on black alluviums on river banks in alpine valleys (Alps), but also on coastal calcariferous sands (Northern France) or chalk in disturbed continental sites; known from lowland to montane altitudes (1200 m), from France to Estonia. Probably strictly basophilic, widespread in Europe and locally abundant.

OBSERVATIONS — This species is easily recognizable in the field by its general yellow colour when young, persistent in lamellae with age, non-striate pileus (when young), and a preference for basic mineral-rich sedimentary substrates.

It is typically found under *Alnus incana* on river banks in alpine regions, where it seems frequent and locally dominant, but also in plantations on calcareous soil, and a single collection from calcareous sand dunes under *Alnus glutinosa* in Northern France, what suggests an oro-septentrional distribution. It has probably been misidentified as *Alnicola escharoides* by various mycologists, despite the mild taste, and shorter basidiospores and cystidia that are usually described for this variously interpreted species (Moreau 2005; Fernández Sasia & Moreau 2011).

The closest species is *Alnicola longicystis*, which has the same biogeographical distribution but seems to prefer humus-rich or more acidic soils. Macroscopically it can be possible to misidentify old or single specimens of the two species; microscopically cystidia shape and size make a clear distinction between them. Analysis of ITS sequences clearly separate these species (Rochet et al. 2011).

## Discussion

### The identity of *Alnicola badia*

*Alnicola badia* is one of the most common agarics associated with *Alnus alnobetula* and one of the first (with *A. luteolofibrillosa* and *A. submelinoides*) described under this plant, but paradoxically one of the less documented in the difficult genus *Alnicola*. Kühner (1926) described *A. badia* from a single collection, a provision he wrote later (1931: 239): "... récolte unique sur laquelle nous avons cru pouvoir baser une espèce indépendante de *N. escharoides*", with a detailed description of this unique material. "Praz Joseph," now called "Praz Juget," is a locality of the village of La Perrière (Gros 1973), close to Bozel (Savoie), at low subalpine level (1890 m), with a northern exposure; the only alder species found there is *Alnus alnobetula*. In this locality Kühner also found two species exclusively associated with *Alnus alnobetula* (Basso 1999): *Lactarius alpinus* Peck (illustrated by Kühner 1929a as "*L. subalpinus* R. Kühner" [nom. illegit.], also known as *Lactarius kuehneri* Joss) and *L. lepidotus* Hesler & A.H. Sm. (illustrated by Kühner 1929b as "*Lactarius griseus* Peck").

Unfortunately, this single collection did not give the young Kühner a clear concept of his *Alnicola badia*, and at that time he was not experienced in lowland alnicolous fungi. By contrast, his friend Marcel Josserand, an active mycologist familiar with wet lowland forests around Lyon, was experienced in a common species identified by René Maire as *Tubaria umbrina* (Maire 1930), found abundantly under *Alnus glutinosa*. Josserand was convinced that *Alnicola badia* and *Tubaria umbrina* were synonyms, and did his best to convince Maire and Kühner of his opinion (unpublished correspondence, coll. R. Kühner (G), and coll. R. Maire (MPU)). Kühner (1931: 240) hesitated to synonymize these taxa, but finally accepted Josserand's point of view (Kühner 1942: 1). He also rejected his own genus name *Alnicola* under the influence of Maire (Maire

1937), and together they formalized the synonymy between *A. badia* and *A. umbrina* under a new name, *Naucoria phaea*.

Despite his affirmations, Kühner's numerous unpublished notes and collections prove that he had never been really convinced with this synonymy, but failed to define the limits of his *A. badia*. The unpublished names "*A. phaeodisca*," "*A. subescharoides*," "*A. alnobetulae*," "*A. phaea* from 1961," etc. in his abundant notes on collections made after 1954 under *Alnus alnobetula*, show his repeated attempts to compare his collections and to separate them from the common lowland species *A. umbrina*, to which he had become familiar after 1942. But he never completed this challenge (Kühner 1981) and never published any definitive decision about *A. badia* after 1931.

The epithet name *badia* is in fact quite deceptive for a species typically bicoloured when fresh, only turning red brown with age or on drying. We formerly (Moreau 2006a; Moreau et al. 2006) interpreted it erroneously as a dark-coloured species (provisionally named "*A. badiofusca*" in Rochet et al. 2011), before understanding the importance of pileus structure and pigmentation for the distinction of these species. Before clearly separating these two species, we had already intuitively separated them in the field by their general colours and pileus striations under the respective field names "*A. badia* pâle [light]" or "*A. badia* bicolore" (*A. badia*) and "*A. badia* sombre [dark]" or "*A. badia* rouge [red]" (= "*A. badiofusca*"). The type collection of *A. badia* (herb. R. Kühner, G) is small, only made of two fragmented pilei, but fortunately we could precisely observe pileipellis (typically catenulate with mainly smooth pigmentation) and basidiospores, and establish identity with our own collections.

#### **Morphology and ecology in the *Alnicola badia* complex**

*Alnicola badia*, although strictly associated with *Alnus alnobetula*, is morphologically not a very distinctive species. With the two other species described here, both associated with *Alnus glutinosa* and *A. incana*, it forms a small group of mainly orophilic species, sharing the following characteristics: 1) lack of reddish, ferruginous or fulvous tinges, 2) absence of any trace of partial veil, 3) mild taste, 4) abundant necrobasidia, 5) cheilocystidia with thickened wall and neck partly filled with yellow content, 6) pleurocystidia around lamella edge, and 7) medium-sized amygdaliform basidiospores with low punctuate ornamentation. Species in the *Alnicola umbrina* group ("*A. badiofusca*" ad int., *A. sphagneti*, *A. subconspersa*, *A. umbrina*; Rochet et al. 2011) differ by the presence of red-brown colours in lamellae and/or pileus even when young, and spores frequently fusiform. *Alnicola citrinella* P.-A. Moreau & A. de Haan (= *A. escharoides* sensu auct.; de Haan & Moreau 2012), the most common *Alnicola* species under *Alnus glutinosa* and *A. incana*, differs by absence of pleurocystidia, bitter taste, and non-striate pileus.

*Alnicola longicystis* is macroscopically closest to *A. badia*. Its distinctive features include the distinctly bicoloured pileus (especially on young specimens) and distinct yellow tones in young lamellae, contrasting strongly with the typical grey-brown apex of stipe. Its distribution is apparently wide but irregular. It especially frequent under *Alnus incana* in the Alps but also found occasionally under *Alnus glutinosa* on peaty ground in lowlands, and also occurs at montane levels in the Pyrenees where *Alnus glutinosa* fills the natural niche of *A. incana* as known from the Alps. When *Alnus alnobetula* and *A. incana* grow intermixed, as in some localities in the Alps, the grayish to pale cream-yellow colour of lamellae and the very weakly striate pileus of *A. badia* are good field characters as compared to the clearly yellowish lamellae and distinctly striate pileus of young specimens of *A. longicystis*. Old or too wet specimens are almost impossible to recognize without a rigorous microscopic analysis.

*Alnicola xanthophylla* is also a very distinct species, easily separated from *A. longicystis* (with which it can grow closely intermixed in wet peaty *Alnus-Picea* forests on rich ground, as observed in several sites in Savoy) by the uniformly yellow colours of fresh basidiomata, slightly striate pileus, and absence of gray colour on the stipe apex even on youngest stages. Both species should be confused with *Alnicola striatula* (P.D. Orton) Romagn., a species with pale colours (not bright yellow; Orton 1960: 322), striate pileus, “amygdaliform-limoniform” and verrucose basidiospores and lanceolate cystidia, which belongs to the *Alnicola umbrina* complex (see Moreau, 2004, 2006). An updated identification key including the new taxa described here will be the object of a further publication.

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