

Surprising morphological, ecological and ITS sequence diversity in the *Arrhenia acerosa* complex (Basidiomycota: Agaricales: Hygrophoraceae)

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A molecular genetic study of the *Arrhenia acerosa* complex using the ITS fungal barcoding marker revealed unexpected diversity along a cascading group supporting over 20 lineages. Among these, we identified five previously described species: *A. acerosa* s.str., *A. glauca*, *A. latispora*, *A. subglobisemen*, and *Rhodocybe tillii* (recombined as *A. tillii*). We described four new species: *A. fenicola* from Canadian prairie grasslands, *A. junctorum* and *A. leucotricha*, both on live and dead herbaceous material in European wetlands, and *A. svalbardensis* from the high Arctic. All nine taxa treated here were fixed with sequenced types. In addition, we identified seven other lineages, some only represented by a single collection, requiring further study before description, and four groups of two species or more, also requiring further dissection before circumscription of their constituents. The diversity of the complex with respect to size, colour, habitat, range, distribution, and substrate preference is made more intriguing by the presence of several lineages of brown omphalinoid species, differing from the typically pleurotoid forms in this complex. We generated 97 of the 131 ITS sequences studied, adding 65 new sequences from the *acerosa* complex.

Keywords: ITS, pleurotoid basidiomycota, taxonomy. – 4 new species, 9 typifications.

In the course of a review of the genus *Arrhenia* Fr. in the Canadian province of Newfoundland and Labrador, we noted that the species we had consistently identified as *Arrhenia acerosa* (Fr.) Kühner formed a sister clade with the only collection bearing the same name available in GenBank at the time (Geml et al. 2012b). In an attempt to identify the species in Newfoundland and define the application of the name *A. acerosa*, a broader sampling of this

complex, particularly from North and Central Europe, was undertaken.

For a long time *Arrhenia*, introduced by Fries (1849), was considered a small genus of mostly moss associates producing small dorsally attached or pleurotoid basidiomata with a reduced hymenium, ranging from smooth to veined with low, sinuous, anastomosing folds, similar to its type species, *A. auriscalpium* (Kühner & Lamoure 1972). Two of the

three taxa initially included in *Arrhenia* were later transferred to other genera. Species morphologically similar to *Arrhenia* sensu Fries but with distinct lamellae were assigned to the genus *Phaeotellus* Kühner & Lamoure, with *Agaricus acerosus* Fr., first described in 1821 (Fries 1821), as type species (Kühner & Lamoure 1972). Subsequently Kühner (1980) merged both genera under *Arrhenia*, thereby making *A. acerosa* the first species in the genus with distinct lamellae. Bon & Courtecuisse (1987) added two other lamellate species, *A. glauca* (Batsch) Bon & Courtec. and *A. latispora* (J. Favre) Bon & Courtec., and Watling (1989) assigned *A. griseopallida* (Desm.) Watling and *A. rickenii* (Hora) Watling, the first two omphalinoid species, to this genus. Later, additional omphalinoid species were transferred to *Arrhenia* by Redhead et al. (2002), followed by others, e.g. Moreau & Courtecuisse (Courtecuisse 2008) and Elborne (2008). The diverse phenotypes included in the thus emended genus *Arrhenia* formed a coherent, yet paraphyletic assemblage with pleurotoid and omphalinoid phenotypes occurring in various lineages without forming reciprocally monophyletic clades, eventually leading to the lichenized *Dictyonema* C. Agardh and related basidiolichens (Lawrey et al. 2009, Lodge et al. 2014). Initially included in Pleurotaceae (Kühner & Lamoure 1972) and Tricholomataceae (Kühner 1980), *Arrhenia* was found to be closer to *Omphalina* Quéél. and Hygrophoraceae (Lutzoni 1997, Moncalvo et al. 2002), subsequently confirmed by more detailed phylogenetic studies (Lawrey et al. 2009, Lodge et al. 2014). So far, no broad-scale phylogenetic analysis of *Arrhenia* s.l. has been undertaken, and hence the placement of individual lineages, such as *A. acerosa* and relatives, remains unknown.

Over 50 years after describing the species, Fries (1874a, b) considered *Agaricus acerosus* “maxime variabilis” and nearly a century after that Kühner & Lamoure (1972) suggested that *Phaeotellus acerosus* might be a collective species. Several taxa similar to *A. acerosa* have been described over the years, and a study of the group by molecular genetic methods seems overdue. We shall refer to the group as “the *acerosa* complex”, defined for the purposes of this phylogenetic study to mean species arising from the nearest monophyletic lineage that encompasses all taxa morphologically resembling *A. acerosa*. A brief review of epithets applied to this group, in order of publication, follows.

Schäffer (1774) described *Agaricus tremulus* Schaeff., a gelatinous-leathery and flabellate species; the name has been applied for generations to an *acerosa*-like species as *Pleurotellus tremulus*

(Schaeff.) Konrad & Maubl. Redhead (1984) rejected *P. tremulus* as a separate species, pointing out that none of its identifying characters were unique, due to the range of morphological variation of *A. acerosa*, and argued that its protologue fits better with a species of *Hohenbuehelia* Schulzer. The name has since been applied to a species of *Hohenbuehelia* (Thorn & Barron 1986) and recently epitypified as such (Consiglio 2016), making it unavailable for an *Arrhenia*.

Batsch (1786) described *Agaricus glaucus* Batsch from the Webicht woods near Weimar, Germany. Fries (1874a, b) referred it to *Cantharellus*, starting it on a circuitous journey before reaching *Arrhenia* as a separate species (Bon & Courtecuisse 1987). Most experts have synonymized it with *A. acerosa* (Redhead 1984, Kuyper 1995, Barrasa & Rico 2003), but Pilát & Svrček (1953) provided a personal interpretation of this name based on a collection from the Czech steppes.

The epithet *planus* has been applied to taxa in this group at the form, variety and species level for both pink and non-pink basidiomata. It was first described and illustrated by Bolton (1788) for a non-pink terricolous species, *Ag. planus*. Persoon (1801) used it twice in his Synopsis, first on p. 480 referring to his earlier description (Persoon 1796) of the non-pink *Ag. applanatus* Pers. This makes *Ag. planus* Pers. illegitimate, first because of its earlier use by Bolton for a different taxon, and second, because Persoon introduced it as a superfluous name for the brown-spored species currently known as *Crepidotus applanatus* (Pers.) P. Kumm. Persoon used *planus* a second time on p. 484, where he listed it as a (presumably non-pink) variety of the pink *Ag. depluens* Batsch, this time citing Bolton’s non-pink description. Von Albertini & von Schweinitz (1805) described a pink *acerosa*-like taxon, *Ag. planus* var. *violaceo-ruber* Alb. & Schwein., as a variety of *Ag. planus* Pers., but when Fries (1828) described *Ag. planus* Fr., he based the description on the variety established by von Albertini and von Schweinitz, and specifically excluded the invalid and superfluous Persoon name. Because Fries’ name is considered sanctioned, it has priority over all earlier applications of the epithet “*planus*” in the genus *Agaricus*, making *Ag. planus* the correct name, now at the species level, for the pink variety described by von Albertini and von Schweinitz. Subsequently the species was transferred to *Pleurotus* by Kummer (1871). In his monograph of *Pleurotus*, Pilát (1935) reclassified *P. planus* var. *violaceo-ruber* (Alb. & Schwein.) Kumm. as a pink form of *P. acerosus*, differing from the autonymic form by its pink col-

our only. Hesler (1967) placed the non-pink *Ag. planus* Bolton and the pink *Ag. planus* var. *violaceo-ruber* Alb. & Schwein. in synonymy with *Entoloma depluens* (Batsch) Hesler. The epithet *planus* has not been transferred to *Arrhenia* at the species, form, or variety level for either pink or non-pink basidiomata.

Agaricus acerosus was described by Fries (1821) as a small mushroom with a short eccentric stipe, growing among woody debris in dense coniferous forests. Since then the species has been reported from various habitats and assigned to no less than eight genera, including Kühner's (1980) transfer to its current genus, *Arrhenia*.

Quélet (Le Breton & Quélet "1879" 1880) described *Pleurotus roseolus* as a small conchate pink fungus with a relatively prominent near-central stipe and white sporeprint, growing on *Juncus* or Gramineae. Senn-Irlet (1986) transferred *P. roseolus* Quélet to *Arrhenia*. Quélet's protologue, together with an illustration matching *Deconica phillipsii* (Berk. & Broome) Noordel. lead us to conclude that *roseola* is misapplied to a pink-spored species of *Arrhenia*, and is a later synonym for *Agaricus phillipsii* Berk. & Broome.

While *Ag. acerosus* was classified in *Pleurotellus* Fayod, on the basis of three separate collections Kühner (1954) described a variety, *Pleurotellus acerosus* var. *tenellus* Kühner, which differs by having 2-spored (instead of 4-spored) basidia and larger spores. This variety was transferred to *Arrhenia* (Aronsen 1992). Barrasa & Rico (2003) designated Kühner's first collection (from Algiers) as lectotype for the variety, but thought that more observations were required of it, before deciding to elevate the variety to species level, noting a small amount of 1-, 3- and 4-spored basidia in 2-spored collections, as had been reported by Kühner & Lamoure (1972) and Gulden & Jenssen (1988). The variety was recently raised to species level (Blanco-Dios 2019) as *A. kuehneri*, the epithet "tenella" being occupied in *Arrhenia*.

Favre (1955) described *Pleurotellus acerosus* f. *latisporus*, differing from *P. acerosus* by broader spores. Redhead (1984) placed Favre's form (and by extension the derived varietal and specific taxon) in synonymy with the nominal variety, noting spore size of *A. acerosa* is "extremely variable". Preferring to consider it a separate entity, Bon & Courtecuisse (1987) transferred the taxon to *Arrhenia*, elevating it to species level. Barrasa & Rico (2003) reported that the wide amplitude of spore width for *A. acerosa* did not warrant maintaining a separate variety by this character alone, and synonymized *A. acerosa* var. *latispora* with *A. acerosa* var. *acerosa*.

Since the description of *Rhodocybe/Clitopilus tillii* (Krisai-Greilhuber & Noordeloos 1998, Co-David et al. 2009), some collections initially identified as *Arrhenia roseola* have been referred to that taxon, but the relationship between the two, and other pink *acerosa*-like collections, has not been clear.

Corriol (2016) described *Arrhenia subglobisemen* Corriol, which differs from *A. acerosa* by subglobose spores and more florid lobulation, often producing multicephalic basidiomata in advanced maturity. In his opinion, this is the species previously identified with the name *Pleurotellus tremulus*. A year after publication, the species was also reported from Newfoundland (Voitk 2017).

In addition to the foregoing, among taxa described in *Pleurotus* that may be species of the *acerosa* complex but have not been investigated, are *P. rivulorum* Pat. & Doass. (Doassans & Patouillard 1886) from France, and several from Eastern Europe, described by Velenovský [e.g. *P. diabasicus* Vel., *P. terrestris* Vel., *P. viaticus* Vel. (Velenovský 1920), *P. thuidii* Vel. (Velenovský 1927)] and by Pilát [e.g. *P. arbuticola* Pilát, invalidly published without Latin diagnosis, but validated as *Phaeotellus arbuticola* Pilát ex Bon (Bon & Chevassut 1988) and *P. romellianus* Pilát (Pilát 1935)]. Further, Corriol's (2016) key to *A. acerosa*-like species in Europe included *Gerronema josserandii* Singer and *Arrhenia subglobispora* (Moreno, Heykoop & Horak) Redhead, Luzoni, Moncalvo & Vilgalys.

Given this complex situation, we aimed to i) identify the species in Newfoundland and Labrador, ii) fix the name *A. acerosa* by typification, iii) clarify the phylogenetic relationship of the taxa in the *acerosa* complex, specifically including *A. acerosa*, *A. glauca*, *A. latispora*, *A. subglobisemen*, and *A. acerosa* var. *tenella*, and iv) explore the relationship of *A. subglobispora*, *Gerronema josserandii*, and *Rhodocybe/Clitopilus tillii* to this group.

Materials and methods

Specimens were collected using routine field techniques and air dried with heat <40 °C. To these were added specimens from public herbaria in Austria (WU), Canada (CMMF, DAOM, SWGC, UW), Estonia (TAAM, TU), France (BBF, LIP), Norway (O), Sweden (GB, UPS), and Switzerland (G), private collections of the authors, and selected additional collections. Herbaria are designated with the Index Herbariorum code (Thiers 2020). To examine the relationship of taxa considered similar to *A. acerosa*, we include the type of *Rhodocybe tillii*, one pink

collection identified as *Arrhenia roseola*, one specimen identified as *Arrhenia subglobispora* and one as *Gerronema josserandii*. In addition, both new and existing sequences from other species of *Arrhenia* are used to clarify the place of the *acerosa* complex within the genus. Table 1 summarizes data of collections used for this study, with more complete details recorded in Supplemental Tab. 1. New sequences were deposited in GenBank or UNITE.

Macroscopic descriptions are based on *in situ* specimens. Colour was matched from Cailleux (1981) for *A. acerosa* and *A. svalbardensis*, Munsell Soil Color Charts (Munsell Color Co 2000) for *A. subglobisemen*, and Kornerup & Wanscher (1978) for *A. fenicola* and *A. glauca*. Microscopic examination was done on squash mounts in 2–5 % KOH of both live and dried specimens; Cotton blue in lactic acid and Melzer's Reagent were used to examine slides of *A. acerosa* s. str. and *A. svalbardensis*. Spore sizes reported in the descriptions are from multiple observers. The WU spore measurements were done with a Zeiss Axio Imager.A1 compound microscope with Nomarski differential interference contrast (DIC) using a Zeiss AxioCam 506 colour digital camera and Zeiss ZEN Blue Edition software. Microscopic examination and spore measurements of the Pyrenean collection of *A. subglobisemen* followed the procedure of Corriol (2016), that for the Scandinavian collections followed Gulden (1980) and microscopy of the ON and NL collections followed Thorn et al. (2017).

To construct the phylogeny, all available related sequences deposited in GenBank and UNITE (Köljalg et al. 2013, Nilsson et al. 2019) were added to the analysis. Because there was no extant type material for *A. acerosa*, a similar specimen from the toporegion with similar habitat and substrate as described in the protologue, is proposed below as neotype. Types for both *A. latispora* and *A. subglobisemen* were not available for destructive sampling, so that a sequenced epitype for each is proposed. ITS-DNA processing of specimens deposited in UNITE (with UDB- code) followed Voitk et al. (2017); the WU specimens followed Hahn et al. (2018); all *A. obscurata* specimens in Fig. 1a except TU117230, as well as specimens numbered 10 and 13 in Fig 1b, followed the technique described in Lücking et al. (2017).

For the purpose of discussion, we assign a code name AC-n to identify undescribed potential species in the *acerosa* complex. AC stands for *acerosa* complex and n is a number assigned in consecutive order as these groups appear in our phylogenetic tree (Fig. 1b), starting at the top. Specimens not cir-

cumscribable as species were placed in larger groups, which probably contain more than one species, coded G-n.

Results

We generated the only available sequence of the fungal ITS barcoding marker for a specimen identified as *Gerronema josserandii* and 86 new sequences for species of *Arrhenia* (Figs 1a & b; two not shown in our tree), including several species not sequenced previously (indicated by an asterisk on first mention). Included species of *Arrhenia* (Fig. 1a) form three larger, supported clades. The first comprises taxa identified as *A. epichysium*, *A. velutipes**, *A. sphagnicola* and *A. philonotis* and is a strongly supported sister to a clade including all other species. The second well-supported clade, in a supported sister group relationship with the third, encompasses species identified as *A. auriscalpium*, *A. salina**, *A. lobata*, *A. peltigerina**, *A. elegans*, *A. retiruga* and *A. spathulata**. The third clade consists of two sister pathways, one leading to specimens identified as *A. obscurata* and the other to the *acerosa* complex (Fig. 1b), a long cascading clade of several well-supported clades.

The *acerosa* complex contains collections from Asia, Europe and North and South America, originally identified as *A. acerosa*, *A. acerosa* var. *tenella*, *A. latispora* (*A. acerosa* var. *latispora*), *A. roseola*, *A. subglobisemen*, *Rhodocybe (Clitopilus) tillii* and *A. (Phaeotellus) griseopallida(-us)*. Habitats varied from harsh arctic-alpine to woodland, meadow, prairie, wetland, and littoral sand dune, and substrates varied from soil, wood, bryophytes, live and dead herbaceous material and herbivore dung. Both plesiomorphic and convergent homoplasy is evident in the different subclades of the complex. Basidiomata with 4- and 2-spored basidia, pink, brown, grey or dark violet colour, pink or white sporeprint, wide to narrow spores, and pleurotoid (with or without significant stipe formation) to omphalinoid habitat are distributed throughout. Fig. 1b summarizes available characters for these collections, and Figs. 2–5 give an overview of the morphologic diversity of the group.

As the phylogenetic tree grew with each addition of sequences during the investigation, several well-supported clades appeared. Often additions or different outgroups caused changes in the position of these clades in the tree, but their support and composition remained constant. We recognize five such clades as previously described species, four as new species described here, nine as potential addi-

Tab. 1. Data of collections and specimens used in this study.

Species	Herbarium voucher ^a , copy or strain	Country, Prov/State	CODE:		Reference
			GB (above)	UNITE (below)	
<i>Arrhenia epichysium</i>	LE-262961	Russia	KC237880		Zviagina et al. (2015)
<i>Arrhenia epichysium</i>	WU-21938	Austria	MW113695		this study
<i>Arrhenia epichysium</i> (as <i>Omphalina epichysium</i>)	Redhead 5223	Canada	U66442		Lutzoni (1997)
<i>Arrhenia epichysium</i>	17148	Finland	JF908504		Osmundson et al. (2013)
<i>Arrhenia velutipes</i>	WU-28855	Austria	MW113696		this study
<i>Arrhenia velutipes</i>	WU-22371	Austria	MW113697		this study
<i>Arrhenia sphagnicola</i> (as <i>Omphalina sphagnicola</i>)	Lutzoni 930810-1, DUKE	Greenland	U66453		Lutzoni (1997)
<i>Arrhenia philonotis</i> (as <i>Omphalina philonotis</i>)	Lutzoni 930804-5, DUKE & O	Iceland	U66449		Lutzoni (1997)
<i>Arrhenia philonotis</i>	DAOM-744401	Canada, NL	MH491521		Lickey et al. ^b
<i>Arrhenia philonotis</i>	DAOM-744400	Canada, NL	MH491520		Lickey et al. ^b
<i>Arrhenia auriscalpium</i>	Lutzoni 930731-3, DUKE & O	Iceland	U66428		Lutzoni (1997)
<i>Arrhenia</i> sp.	environmental sample	Canada, NT	KF296806		Timling et al. (2014)
<i>Arrhenia salina</i>	O-260200	Norway, Svalbard	MT967341 UDB024594		this study
<i>Arrhenia lobata</i>	O-73053	Norway, Svalbard	GU234033		Geml et al. (2012b)
<i>Arrhenia lobata</i>	WU-38079	Austria	MW113698		this study
<i>Arrhenia lobata</i>	Lutzoni & Lamoure 910824-1, DUKE	France	U66429		Lutzoni (1997)
<i>Arrhenia lobata</i>	DAOM-981256 (TU-117633)	Canada, NL	MT967332 UDB034988		this study
<i>Arrhenia peltigerina</i>	DAOM-981257 (TU-117595)	Canada, NL	MT967339 UDB034636		this study
<i>Arrhenia peltigerina</i>	TU-111507	Estonia	MT967334 UDB034594		this study
<i>Arrhenia peltigerina</i>	DAOM-981258 (TU-117465)	Canada, NL	MT967337 UDB032197		this study
<i>Arrhenia peltigerina</i>	DAOM-981259 (TU-117594)	Canada, NL	MT967338 UDB034635		this study
<i>Arrhenia peltigerina</i>	DAOM-981260 (TU-117461)	Canada, NL	MT967335 UDB032195		this study
<i>Arrhenia peltigerina</i>	DAOM-981261 (TU-117462)	Canada, NL	MT967336 UDB032196		this study
<i>Arrhenia elegans</i>	WU-36410	Austria	MW113699		this study
<i>Arrhenia subglobispora</i>	BSI 14/8	Switzerland	KR606032		Senn-Irlet ^c
<i>Arrhenia elegans</i>	MCVE-16455	Italy	JF908757		Osmundson et al. (2013)
<i>Arrhenia retirugis</i>	GB-0150441	Sweden	EU118604		Larsson (2007)
<i>Arrhenia retiruga</i>	TU-117227	Estonia	MT967340 UDB024164		this study
<i>Arrhenia spathulata</i>	TU-105605	Estonia	MT967347 UDB024678		this study
<i>Arrhenia spathulata</i>	TAAM-172613	Estonia	MT967343 UDB024233		this study

Species	Herbarium voucher ^a , copy or strain	Country, Prov/State	CODE:	
			GB (above)	Reference
			UNITE (below)	
<i>Arrhenia spathulata</i>	WU-25434	Austria	MW113700	this study
<i>Arrhenia spathulata</i>	TAAM-172614	Estonia	MT967344 UDB024232	this study
<i>Arrhenia spathulata</i>	WU-38990	Austria	MW113701	this study
<i>Arrhenia spathulata</i>	TU-105606	Estonia	MT967348 UDB024321	this study
<i>Arrhenia spathulata</i>	TAAM-185757	Estonia	MT967346 UDB031174	this study
<i>Arrhenia spathulata</i>	TAAM-182905	Estonia	MT967345 UDB024234	this study
<i>Arrhenia spathulata</i>	TAAM-172553	Estonia	MT967342 UDB024231	this study
<i>Arrhenia obscurata</i> (as <i>Omphalina obscurata</i>)	Lutzoni & Lamoure L73-101, polypore culture	France	U66448	Lutzoni (1997)
<i>Arrhenia obscurata</i>	none ^d	Canada, NL	MT998928	this study
<i>Arrhenia obscurata</i>	none ^d	Canada, NL	MT998930	this study
<i>Arrhenia obscurata</i>	none ^d	Canada, NL	MT998929	this study
<i>Arrhenia obscurata</i>	TU-117230	Canada, NL	MT967333 UDB024573	this study
<i>Arrhenia obscurata</i>	none ^d	Canada, NL	MT998927	this study
<i>Arrhenia obscurata</i>	none ^d	Canada, NL	MT998924	this study
<i>Arrhenia obscurata</i>	none ^d	Canada, NL	MT998925	this study
<i>Arrhenia obscurata</i>	none ^d	Canada, NL	MT998923	this study
<i>Arrhenia subglobispora</i>	BBF-JF03212	France	UDB033389	this study; not in tree
<i>Gerronema josserandii</i>	BBF-GC15091302	France	UDB035029	this study; not in tree
<i>Arrhenia latispora</i>	WU-22359	Austria	MW113702	this study
<i>Arrhenia latispora</i>	BBF-GC01082301	France	MT967323 UDB033386	this study
<i>Arrhenia latispora</i> EPITYPUS	LIP-0401569	France	MT967324 UDB033395	this study
AC-1	O-63232	Norway	MT967299 UDB032089	this study
AC-1	O-67900	Norway	MT967301 UDB032091	this study
<i>Arrhenia subglobisemen</i>	DAOM-981251 (TU-117353)	Canada, NL	MT967351 UDB032180	this study
<i>Arrhenia subglobisemen</i>	DAOM-981254 (TU-117355)	Canada, NL	MT967353 UDB032184	this study
<i>Arrhenia subglobisemen</i>	O-291235	Norway	MT967350 UDB032092	this study
<i>Arrhenia subglobisemen</i>	DAOM-981253 (TU-117464)	Canada, NL	MT967354 UDB032725	this study
<i>Arrhenia subglobisemen</i>	none ^d	Canada, NL	MT998926	this study
<i>Arrhenia subglobisemen</i>	DAOM-981252 (TU-117354)	Canada, NL	MT967352 UDB032181	this study

Species	Herbarium voucher ^a , copy or strain	Country, Prov/State	CODE:		Reference
			GB (above)	UNITE (below)	
<i>Arrhenia subglobisemen</i> EPITYUS	BBF-GC15100901	France	MT967349 UDB033382		this study
<i>Arrhenia subglobisemen</i>	DAOM-981255	Canada, NL	MT998922		this study
<i>Arrhenia subglobisemen</i>	TU-120029	Estonia	MT967355 UDB023709		this study
AC-2	TU-120494	Estonia	MT967307 UDB031497		this study
<i>Arrhenia tillii</i> HOLOTYPUS	WU-18120	Austria	MT967360 UDB039744		this study
AC-3	BBF-GC13082701	France	MT967294 UDB033385		this study
G-1	environmental sample	Lithuania	MT237088		Marciulynas et al. (2020)
G-1	WU-8395	Austria	MT967309 UDB039750		this study
G-1	BBF-GC08101503	France	MT967293 UDB033390		this study
G-1	LIP-0401689	Spain	MT952839		this study
G-1	BBF-GC08090407	France	MT967292/ UDB033391		this study
G-1	BBF-GC13082806	France	MT967295 UDB033384		this study
G-1	WU-12194	Netherlands	MT967308 UDB039751		this study
G-1	O-65097	Norway	MT967300 UDB024591		this study
G-1	LD ^h	Sweden	MT967303 UDB038351		this study
G-2	TENN-074409	USA, TN	MH558290		Matheny et al. ^c
G-2	HUH-11394 (TU-117356)	USA, NH	MT967306 ^e UDB032183		this study
G-2	HUH-11394 (TU-117203)	USA, NH	MT967305 ^e UDB024572		this study
G-2	environmental sample	USA, NY	JX030244		Tourtellot et al. ^c
G-2	WU-25862	Austria	MW113703		this study
G-2	QFB-32684	Canada, QC	MW057244		Landry ^f
G-2	TU-109664	Estonia	MT967304 UDB024225		this study
G-2	CORD-X (FLAS-F-64782)	Argentina	KY462678		Truong et al. (2017)
G-2	environmental sample	China	MK342048		Guo et al. ^c
<i>Arrhenia fenicola</i>	environmental sample	Canada, AB	MG417815		Thompson et al. ^b
<i>Arrhenia fenicola</i>	environmental sample	Canada, AB	MG433164		Thompson et al. ^b
<i>Arrhenia fenicola</i> HOLOTYPUS	UWO-F44 (HA10)	Canada, ON	KY706173		this study
<i>Arrhenia glauca</i> EPITYUS	WU-6564	Austria	MT967319 UDB039746		this study
<i>Arrhenia glauca</i>	O-64979	Norway	MT967318 UDB024590		this study

Species	Herbarium voucher ^a , copy or strain	Country, Prov/State	CODE:		Reference
			GB (above)	UNITE (below)	
<i>Arrhenia glauca</i>	O-189477	Norway	MT967317 UDB032088		this study
<i>Arrhenia glauca</i>	LIP-0401688	France	MT952840		this study
<i>Arrhenia glauca</i>	Lueck2	Germany	KP965766		Karich et al. (2015)
<i>Arrhenia glauca</i>	GB-0058858	Sweden	MT967316 UDB032047		this study
<i>Arrhenia glauca</i>	BBF-GC97092813	France	MT967313 UDB033388		this study
<i>Arrhenia glauca</i>	GB-0017687	Sweden	MT967314 UDB032046		this study
<i>Arrhenia glauca</i>	GB-0058855	Sweden	MT967315 UDB032045		this study
<i>Arrhenia glauca</i>	WU-9855	Austria	MT967320 UDB039749		this study
G-3	WU-25471	Austria	MW113704		this study
G-3	environmental sample	Austria	FJ237148		Kuhnert et al. (2012)
G-3	G-00295825	France	MT967297 UDB032043		this study
G-3	environmental sample	USA, CO	MK719126		Bueno de Mesquita et al. (2020)
G-3	environmental sample	USA, CO	MH238865		Bueno de Mesquita et al. (2018)
G-3	environmental sample	Austria	EF635806		Oberkofler & Peintner (2008)
G-3	WU-32560	Austria	MW113705		this study
<i>Arrhenia acerosa</i>	TU-109632	Estonia	MT967311 UDB024210		this study
<i>Arrhenia acerosa</i>	O-189467	Norway	MT967310 UDB032087		this study
<i>Arrhenia acerosa</i> NEOTYPUS	UPS-F151993	Sweden	MT967312 UDB032044		this study
AC- 4	LD ^h	Sweden	MT967302 UDB038352		this study
<i>Arrhenia juncorum</i>	BBF-CH13091225	France	MT967321 UDB033383		this study
<i>Arrhenia juncorum</i> HOLOTYPUS	LIP-0401674	France	MT967322 UDB033394		this study
AC-5	CMMF-003682	Canada, QC	MT967296 UDB035025		this study
AC-6	environmental sample	Canada, NT	KF296989		Timling et al. (2014)
AC-7	environmental sample	Canada, BC	KP889745		Guichon & Simard ^e
<i>Arrhenia svalbardensis</i>	O-195466	Norway, Svalbard	GU234048 ^g		Geml et al. (2012b)
<i>Arrhenia svalbardensis</i> HOLOTYPUS	O-50446	Norway, Svalbard	MT967358 UDB024589		this study
<i>Arrhenia svalbardensis</i>	O-195466	Norway, Svalbard	MT967356 ^g UDB024587		this study

Species	Herbarium voucher ^a , copy or strain	Country, Prov/State	CODE:	
			GB (above)	Reference
			UNITE (below)	
<i>Arrhenia svalbardensis</i>	O-50444	Norway, Svalbard	MT967357 UDB024592	this study
<i>Arrhenia svalbardensis</i>	environmental sample	Canada, NT	KC966345	Timling et al. (2014)
<i>Arrhenia svalbardensis</i>	O-76070	Norway, Svalbard	MT967359 UDB024593	this study
AC-8	GB-0202287	Sweden, Lapland	MT994562	Ellen Larsson ^f
AC-9	Lutzoni & Lamoure 910824-4, DUKE	France	U66436 (as <i>Phaeotellus griseopallidus</i>)	Lutzoni (1997)
AC-9	O-50445	Norway, Svalbard	MT967298 UDB024588	this study
<i>Arrhenia leucotricha</i>	WU-6774	Austria	MT967331 UDB039747	this study
<i>Arrhenia leucotricha</i> HOLOTYPE	LIP-0401673	France	MT967329 UDB033396	this study
<i>Arrhenia leucotricha</i>	BBF-GC98092305	France	MT967328 UDB033387	this study
<i>Arrhenia leucotricha</i>	BBF-GC03091814	France	MT967327 UDB033392	this study
<i>Arrhenia leucotricha</i>	BBF-CH13091220	France	MT967325 UDB033381	this study
<i>Arrhenia leucotricha</i>	BBF-GC03091513	France	MT967326 UDB033393	this study
<i>Arrhenia leucotricha</i>	O-179285	Norway	MT967330 UDB032090	this study

^a Herbarium of primary (larger) collection on top and smaller copy below, in parentheses. For collections split between DAOM and TU, DNA extracted from the TU copy.

^b Direct submission; associated study unpublished, presumed in progress.

^c Direct submission; no associated publication found.

^d Specimens sent for sequencing, but package lost in the return mail, so no voucher tissue remains. Used here because data, usually also photo, and DNA available.

^e Two separate sequences from the same basidioma.

^f Direct submission, made independently for this publication.

^g Same collection sequenced in different laboratories at different times, resulting in two different sequences.

^h In private herbarium of Sve-Åke Hanson. To be deposited to LD after access re-established following pandemic

tional species, codenamed AC-1–AC-9, and four groups of unresolved species, designated G-1–4, probably containing more than one species, where ITS data seemed insufficient to determine species limits with reasonable confidence.

Previously recognized species (in order of first description; more complete treatment under Taxonomy). When Batsch described *Agaricus glaucus* (Batsch 1786) he did not indicate a type but provided an illustration (Fig. 2C), which we designate below as lectotype. Collection WU-6564 (Fig. 2B) is a perfect match for this lectotype, and fits the description in Batsch's protologue. It comes from a similar cen-

tral European woodland habitat, about 400 km from the type location. Below we designate this collection as epitype for the species. It belongs in a large clade with collections from Scandinavia and central Europe, which has enjoyed consistently high support in all our phylogenetic analyses. *Agaricus acerosus* Fr., s. str.* (Fig. 2A), is neotypified below by a collection (UPS-151993) from Femsjö, the type locality, fitting Fries' protologue morphologically, growing on woody debris in similar forest habitat. It was one of three collections from northern Europe, which formed a clade with consistently high support in all our phylogenetic analyses. Three collections of *A.*

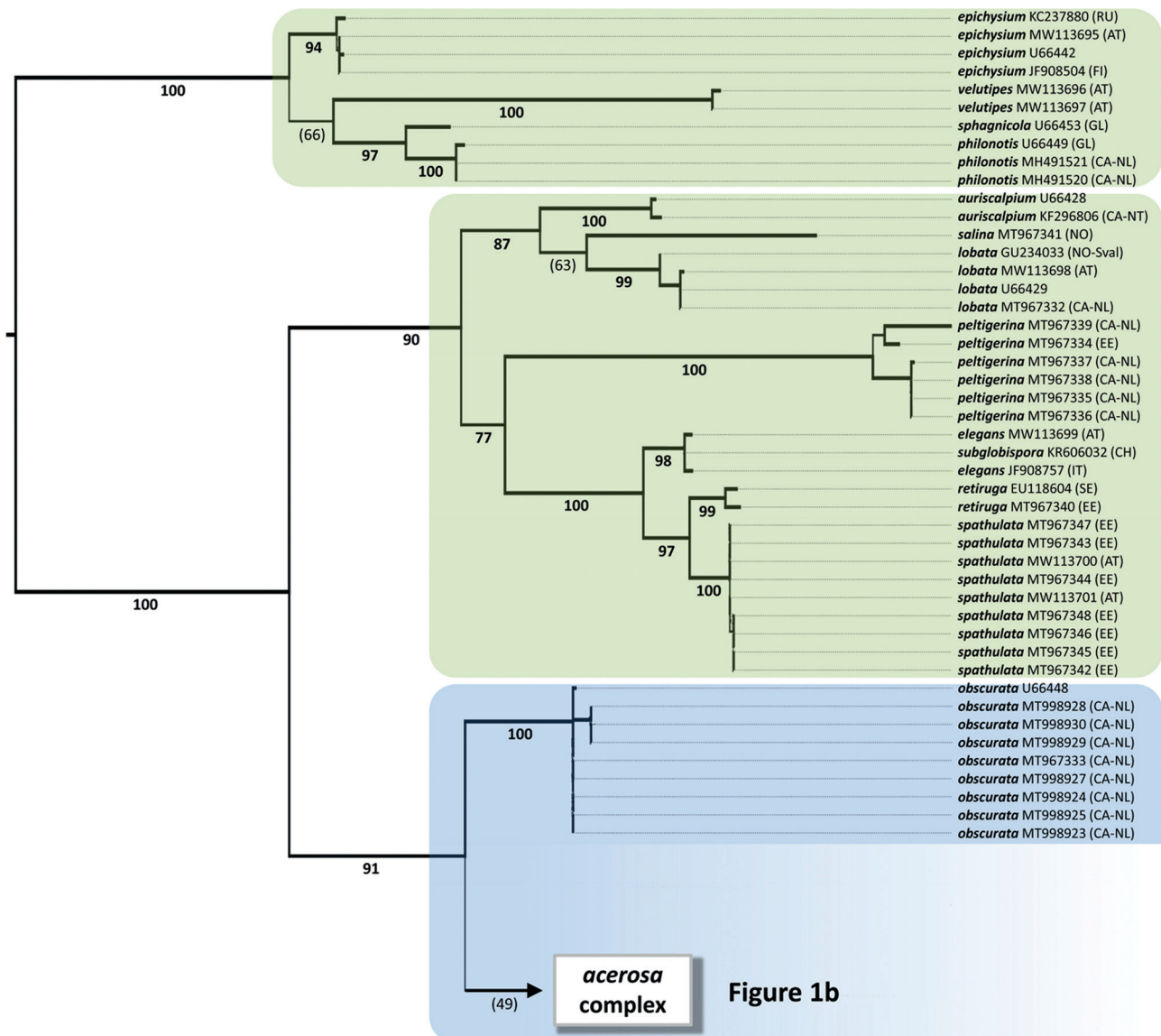


Fig. 1a. The *acerosa* complex within *Acerosa*. Best-scoring maximum likelihood tree of the genus *Arrhenia* based on the fungal ITS barcoding marker. Branch thickness is proportional to bootstrap support and support values for major and species-level clades are given below branches. GenBank accession numbers and geographic origin (as ISO 3166-1 alpha-2 codes) are also given. The branch length scale indicates changes per site.

*latispora** (Fig. 2D, F) from the European Alps agreed morphologically with the holotype, but because it was unavailable for sequencing, a collection from the toporegion (LIP-0401569) is designated as epitype. Although several other species in the complex also produce spores of similar width (e.g. *A. subglobisemen*, *A. svalbardensis*, *A. tillii*), in addition to its ITS sequence data, the species is set apart by its alpine habitat, larger size, *Pelargonium* odour and striking dark bluish-violet colour. Because the holotype for the pink-spored *Rhodocybe tillii* (WU-

18120) fell into the *acerosa* complex it is transferred to *Arrhenia* as the sole representative of *A. tillii** (Krisai & Noordel.) Krisai & I. Saar (Fig. 2J). *Arrhenia subglobisemen** (Fig. 2G, H, I), has the widest distribution of any species of the complex, with collections from Estonia, France, Norway, Newfoundland, and Labrador in arctic-alpine to woodland settings. These agreed morphologically with the type specimen, but because it was not available for sequencing, the species is epitypified below with a collection from the toporegion (BBF-GC15100901).

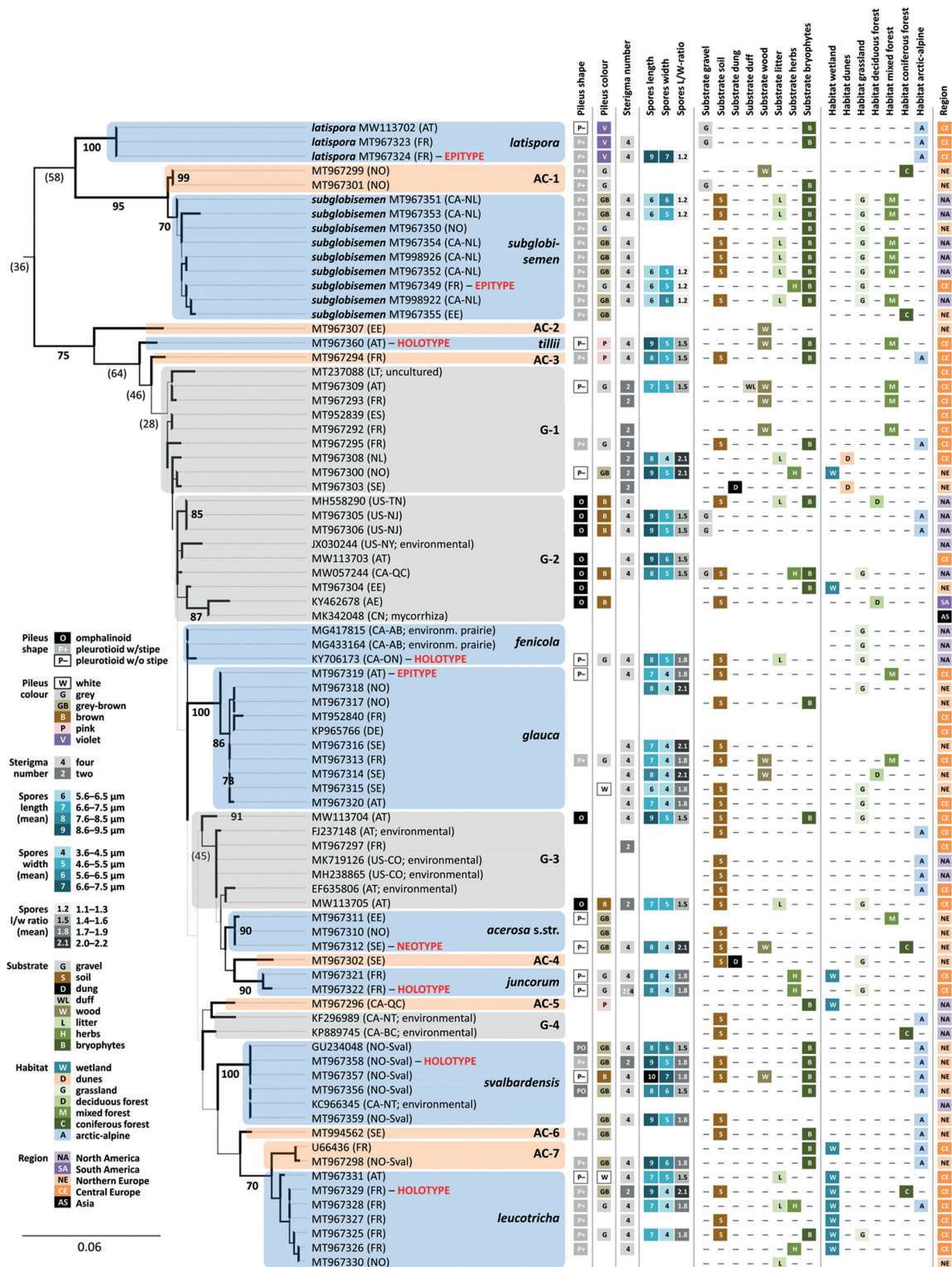


Fig. 1b. The *acerosa* complex. Best-scoring maximum likelihood tree of the *Arrhenia acerosa* complex based on the fungal ITS barcoding marker. Branch thickness is proportional to bootstrap support and support values for major and species-level clades are given below branches. GenBank accession numbers and geographic origin (as ISO 3166-1 alpha-2 codes) are also given. The branch length scale indicates changes per site. Species-level clades and unresolved grades are highlighted in coloured boxes and types are indicated in red. For each terminal, nine characters are mapped, including phenotype, ecology, and distribution.

New species (in order of appearance in our tree; more complete treatment under Taxonomy). Four clades are described as new species, based on stable composition and consistently high support, plus any combination of similar morphology, region, habitat and substrate. *Arrhenia fenicola* Hay & Thorn (Fig. 3A, B) is represented by two collections (one sequenced) found in the course of surveying the macrofungi in the tall grass prairie of Ontario, Canada, and two environmental sequences from the prairies in Alberta, Canada. It forms small grey pleurotoid basiomata with a rudimentary lateral pseudostipe, growing on the ground or on fallen grass litter. *Arrhenia juncorum* P.-A. Moreau & Corriol (Fig. 3C) consists of two collections of light grey astipitate pleurotoid bisporigerous basidiomata from France, growing on dead leaves of live species of *Juncus* in wet subalpine meadows. *Arrhenia svalbardensis* Gulden, I. Saar & Lücking (Fig. 3F, G) consists of four collections of grey-brown pleurotoid collections from Svalbard, and DNA from a soil sample from Prince Patrick Island, Northwest Territories, Canada. Both 2- and 4-spored populations are documented (Fig. 6H, I). *Arrhenia leucotricha* P.-A. Moreau & Corriol (Fig. 3D, E) is a large clade with collections from montane to subalpine Austria, France and Norway, of brown to grey pleurotoid tetrasporigerous basidiomata growing on dead litter of larger wetland herbaceous plants.

Potential additional species (in order of appearance in our tree). We suspect the following are good species, but do not know them well enough to attempt a description here. AC-1, with two Norwegian collections, forms a well-supported sister clade to *A. subglobisemen*. Although the separating branch is short, these two collections differ consistently from *A. subglobisemen* s.str. in two substitutions and eight indels, resulting in a BLAST identity of slightly below the 98.5% level used for species hypotheses in UNITE. We list the clade as a potential species, awaiting further investigation. AC-2 (Fig. 4A) is a singleton from Estonia, found to deviate from its pathway by 25 ITS apomorphies. Unfamiliar with this potential species, we are not able to describe it on the basis of a single collection. AC-3 (Fig. 4B) is a pink terricolous species, seemingly close to the pink *A. tillii*. However, it does not cluster with *A. tillii* s.str., but forms a paraphyletic grade with it. The species is consistently collected on old rotten coniferous wood, which seems to be a required substrate. Despite the pink colour, the 20 substitution and 19 indel phylogenetic difference, based on ITS data, of AC-3 from *A. tillii*, as well as

the apparently different substrate, make us treat this clade as a potentially separate species, pending further investigation. AC-4 is a singleton from Swedish horse pastureland that has remained in a supported sister relationship with the new species *A. juncicola* through all our trees and analyses. We lack sufficient familiarity with it, and treat it as a potential species requiring further investigation. AC-5 (Fig. 4G) is a singleton sequence from a pink basidioma from Québec, Canada. Although it has remained phylogenetically remote from the European pink species, this sequence has not occupied a consistent position in our trees. Yves Lamoureux, who collected the specimen, reports that it was immature, with no spores to be found. We list this very distinct pink North American collection as a potential species, whose nature we are unable to refine further at this point. Its relationship to the two Canadian environmental samples forming grade G-4, from the Northwest Territories and British Columbia, requires further elucidation. AC-6 (Fig. 4H) is a singleton from the Swedish high arctic. Further collections and familiarity are required to define this potential species. AC-7 is made up of two arctic-alpine collections forming a moderately supported sister clade to *A. leucotricha*. The voucher collection for U66436 was collected in the Vanoise National Park in the French Alps as *Phaeotellus griseopallidus*, and O-50445 is a pleurotoid species from Svalbard, the second species in the *acerosa* complex known in the archipelago. Some of our trees have shown this clade apart from *A. leucotricha*, although most place them in a sister relationship, with each arm supported up to 100 %. We present it as a potential species, until additional sequence data clarifies its position, and additional collections permit greater familiarity with it.

Groups of unresolved species (in order of appearance in our tree) consist of one group (G-1) of pleurotoid specimens, two groups (G-2, G-3) of omphalinoid specimens, and one group (G-4) composed of two environmental samples from Canada. The topology of some of these sequences varied widely in different iterations of our trees. We suspect that each group contains more than one species, but ITS data has been insufficient to delimit species in these groups, even with the aid of morphologic and other characters, where available. G-1 contains European collections from Scandinavia to Spain, including highland collections growing on wood (Fig. 4C, D), one on *Ammophila arenaria* in sand dunes of The Netherlands (Fig. 4E) and a Swedish collection (Fig. 4F) growing on horse dung (Hanson 2017). Some of these collections formed an

unsupported cluster on a few Bayesian analyses. Although these specimens are bisporigerous and fruit on cellulose-containing substrate, we suspect that there is more than one species involved. ITS data seems to be inadequate to resolve the species and pending additional studies, we opt to leave this group without designating potential species boundaries. G-2 consists of nine sequences from two environmental samples (from USA and China) and seven terricolous omphalinoid basidiomata, collected in Argentina (Fig. 5E), Austria (Fig. 5D), Estonia, and northeastern North America (Fig. 5A, B, C). The first three sequences come from two collections from northeastern North America, the first from coastal hardwoods and the second from harsh alpine conditions at the summit of Mt Washington, NH. The second specimen was sequenced twice, accounting for three sequences for two specimens. Although we are confident that the first two collections are conspecific, we lack sufficient phylogenetic data to comment on the whole group, and leave the study of the omphalinoid species within the *acerosa* complex for a separate investigation. G-3, somewhat removed from G-2, contains sequences from four European environmental samples and three basidiomata, two of which are documented as omphalinoid, one illustrated (Fig. 5F). No information is available for the remaining basidioma, collected by Kühner, because there is only 1–2 mm of the base of the stipe left in G! The first sequence in the group, from a 4-spored basidioma, has moved to several locations with different iterations of our tree, but the other two non-environmental sequences, both forming 2-spored basidiomata, clustered together throughout with >70 % support, until they parted with the addition of the environmental samples. We are unable to assess G-3 further with available data and leave its elucidation, together with G-2, to future studies of the omphalinoid species within the *acerosa* complex. As mentioned, G-4 consists of two seemingly heterospecific environmental samples from western Canada. The relationship of one of them to AC-5 remains to be determined. Lack of morphologic data prevents further comment, and we leave them to be sorted out in the future.

Other findings. We were unable to study *A. acerosa* var. *tenella* (= *A. kuehneri*), because Kühner's lectotype, curated in G, is not available for loan or destructive sampling needed for molecular genetic studies. It was collected in Algeria, and we found no suitable collection from the toporegion for epitypification. Because of the diversity of parochial species in this complex, we did not consider it appro-

priate to epitypify it with a remote collection. Finally, the specimen we identified as *Arrhenia subglobispora* – not to be confused with *A. subglobisemen* – fell in a different location within *Arrhenia*, well outside the *acerosa* complex (not shown); it did not fall with the specimen identified as *A. subglobispora* in Fig. 1a, which we presume to be a misidentification, because that species with clamp connections is unexpected among its clampless neighbours. Our single specimen identified as *Gerronema josserandii* (UNITE: UDB035029) fell outside *Arrhenia* altogether (not shown).

Taxonomy

Arrhenia acerosa (Fr.) Kühner, Bull. Soc. linn. Lyon, 49: 893, 992. 1980. – Figs. 2A, 6A
Mycobank no.: MBT 393700

Typification. – Holotypus not designated.
Neotypus, here designated: SWEDEN. Småland, Femsjö, Hägnen, close to Bokhultet, “along earthy path amongst twigs, chips, etc.”, 22 August 1943, leg. Seth Lundell (Lundell & Nannfeldt, Fungi exs. Suec. no. 1761), F-151993! (UPS). GenBank/UNITE ITS = MT967312 / UDB032044. UNITE SH1526144.08FU.

= *Agaricus acerosus* Fr. (basionym) Systema mycologicum 1: 191. 1821

= *Pleurotus acerosus* (Fr.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 246. 1872

= *Dendrosarcus acerosus* (Fr.) Kuntze, Revis. gen. pl. (Leipzig) 3(3): 463. 1898

= *Pleurotellus acerosus* (Fr.) Konrad & Maubl., Icon. Select. Fung. 6: 361. 1937

= *Phaeotellus acerosus* (Fr.) Kühner & Lamoure, Botaniste 55(1–6): 25. 1972 (comb. inval.)

= *Leptoglossum acerosum* (Fr.) Parker-Rhodes, Trans. Brit. Mycol. Soc. 37(4): 338. 1954

= *Omphalina acerosa* (Fr.) M. Lange, Nordic J Bot. 1: 695. 1981

= *Panellus acerosus* (Fr.) Z.S. Bi, in Bi, Zheng & Li, Acta Mycol. Sin., Suppl. 1: 285. 1987 (1986)

Description of neotype

Macromorphology. – One larger, one smaller basidioma, and fragments of two smaller basidiomata; some wood fragments attached to one basidioma, no bryophyte remnants. Basidiomata spathulate, fan-shaped to reniform, astipitate. Pileus (as dry) up to 15 mm long from point of attachment to margin and equally wide, thin-fleshed, young margin incurved, becoming straight, lobed, upper side smooth, medium grey brown (N67, 69, 70, P68, 70), white pubescent at point of attachment. Lamellae normally shaped and spaced, not forked,

some lamellulae developed from margin, slightly darker than the pileus (R 69–70).

Micromorphology. – Basidiospores (1 basidioma, 1 collection, 1 observer, n = 50) (5.8)6.8–8.7(9.7) × 3.4–3.9(4.4) μm, average 7.4 × 3.8 μm, Q = 1.4–2.5, Q_{avg} = 2.0; narrowly elliptical to slightly lacrymoid, blunt, with prominent apiculus, hyaline, smooth. Basidia 21–25 × 6–7 μm, 4-spored. Cystidia absent. Hymenophoral trama made of approx. 3–10 μm wide, hyaline hyphae, some with brown incrusting pigment. Pileipellis a cutis of radially repent, 3–10 μm wide, ± cylindrical, thin-walled, yellow brown hyphae with sparse incrustation. Tomentum at the point of attachment to the substrate is made up of smooth, hyaline, cylindrical, long celled hyphae forming bundles. Clamp connections at base of basidia and throughout all tissues. Pigment membranous and incrusting.

Habitat. – Along earthy path, among twigs, chips etc., attached to woody debris.

Comments. – There are two collections of *Pleurotus acerosus* (Fr.) in the Lundell & Nannfeldt exsiccatum. We have chosen no. 1761 as neotype. It contains material collected at Femsjö, the collecting area of Elias Fries (Petersen & Knudsen 2015) and thus the type locality for *Ag. acerosus* s. str., grows in similar habitat and on similar substrate as described in the protologue, and agrees well with the current description and our photo (Fig. 2A) of the species. It differs widely from Fries' (1874a) illustration of *A. acerosa*, which shows yellow-brown, fan-shaped specimens with fairly long, thin, lateral, tapering and strigose pseudostipes attached to moss, which Fries notes shows a dark variety (varietam fuscam) of *Ag. acerosus*, thus already noting the diversity in the complex. This neotype collection, no. 1761 of the Lundell & Nannfeldt exsiccatum, followed their no. 1128 collection from Upland further north in Sweden, which Lundell considered the typical form of the species, and was distributed in order to show the variability of the species. Labels of both collections have references to illustrations by Lange (1936) and pl. 63B is indicated as representative of the material distributed in no. 1761, showing grey, pleurotoid, short stipitate specimens. In the phylogenetic tree (Fig. 1b) the neotype falls in a clade with a specimen from Estonia and one from Norway, Vestfold county in SE Norway. The latter specimen (Fig. 2A) comes from similar habitat (pathside bare earth with moss) and has similar spores (6.8–8.7 × 3.5–4.4 μm, Q_{avg} = 2.1, narrowly elliptical to slightly lacrymoid).

Additional specimens examined. – ESTONIA. Valga County, Ähijärve, 57.685725° N,

26.511601° E, on a sandy forest path, 13 September 2015, leg. Apo Ahola & Kersti Gillen, AA-2015-59, TU-109632. NORWAY. Vestfold, Nøtterøy, Teiesko-gen, 59.2018° N, 10.4861° E, on bare soil by a forest path, 21 September 1987, leg. Arne Aronsen, A60/87, O-189467.

Arrhenia fenicola C.R.J. Hay & Thorn, **sp. nov.** – Figs. 3A–B, 6B
MycoBank no.: MB 836882

Typification. – Holotypus: CANADA. Ontario, Essex County, Windsor, in Herb Gray Parkway, FRS#23, on bare soil in remnant tallgrass prairie, 23 October 2015, leg. Chris Hay, HA10! (UWO-F44). GenBank ITS = KY706173.

Etymology. – Fenicola, from Latin fenum (hay), indicates the habitat in tallgrass or hayfield of this species.

Diagnosis. – A small, grey pleurotoid agaric growing on soil or grass litter in Canadian prairies, with tan to grey lamellae and an eccentric, white-tomentose pseudostipe, elliptical spores and 4-spored basidia. Differs from other species of the *acerosa* complex by its North American distribution, prairie habitat, and diagnostic ITS sequence.

Macromorphology. – Pileus dimidiate, 5–12 mm broad, mouse grey (5E2) to greyish brown (6E2) or smoke grey (5EF1), dry, tomentose, nonhygrophanous, with sharp, incurved, white-rimmed margin. Lamellae sharp, distant, radiating from the eccentric stipe, with two series of lamellulae, at first greyish off-white (5AB1) then yellowish grey (to 4½C3), drying brownish grey (5EF1½), the margins concolorous, with pallid (white to 4½AB1½) context showing between lamellae towards the stipe. Stipe an eccentric pseudostipe, short and stubby, or absent, up to 3 mm in diam and 3 mm long, concolorous with the upper pileus, covered with cottony white tomentum as it descends. Context thin, soft, cottony, white. Taste and smell not noted. Sporeprint white.

Micromorphology. – Basidiospores (1 basidioma, 1 collection, 1 observer, n = 30) 7.3–8.4(9.2) × 4.0–5.0(5.6) μm, average 7.9 × 4.5 μm; Q = 1.6–1.9(2.0), Q_{avg} = 1.8; hyaline, inamyloid, thin-walled, smooth, elliptical, varying from nearly cylindrical to broadly elliptical, a few slightly constricted. Basidia 21–29 × 5.9–6.9 μm, 4-spored, clavate to suburniform. Cystidia absent. Hymenophoral trama made of inflated, thin-walled hyphae, commonly 9–19 μm diam. Pileipellis a loose cutis, with mostly repent, tubular hyphae, 3.4–6.8 μm diam., with both cytoplasmic and incrusting pigments. Pileitrama of hy-



Fig. 2. Previously described species of the *acerosa* complex treated here, in alphabetical order. **A.** *Arrhenia acerosa* s. str., O-189467, Norway, photo: Arne Aronsen. **B–D.** *Arrhenia glauca*. **B.** Epitype, WU-6564, Austria, photo: Anton Hausknecht. **C.** Lectotype, Germany, illustration: August Batsch. **D.** GB-0058855, Sweden, photo: Leif Strindvall. **E–F.** *Arrhenia latispora*. **E.** WU-22359, Austria, photo: Anton Hausknecht. **F.** Epitype, LIP-0401569, France, photo: Pierre-Arthur Moreau. **G–I.** *Arrhenia subglobisemen*. **G.** DAOM-981251, Canada, NL, photo: Andrus Voitk. **H–I.** Epitype, BBF-GC15100901, France, photo: Gilles Corriol. **J.** *Arrhenia tillii*, holotype, WU-18120, Austria, photo: Anton Hausknecht.

aline, tubular to slightly inflated hyphae 3.5–8 µm diam. Clamp connections present at base of basidia and throughout all tissues

Habitat. – On bare soil or grass litter or dead stalks in tallgrass prairies, in late autumn.

Distribution. – Known from prairie in Alberta and Ontario, Canada.

Comments. – Both Ontario collections match each other well, with average spore measurements of 8.1×4.6 µm, $Q_{\text{avg}} = 1.76$, but the second failed to yield amplifiable DNA on two attempts. Two environmental samples from Alberta prairie suggest this small species may have a wider North American prairie distribution.

Additional specimen examined. – CANADA. Ontario, Lambton County, Walpole Island First Nation, on bare soil in remnant tallgrass prairie with *Populus deltoides*, 30 October 2015, leg. Chris Hay, PO21 (UWO-F70).

Arrhenia glauca (Batsch) Bon & Courtec. Doc. Mycol. 18: 70. 1988. Figs. 2B–D, 6C
Mycobank no.: MBT 393701, MBT 393702

Typification. – Holotypus not specifically mentioned in the protologue. **Lectotypus, here designated**, Batsch: Elenchus fungorum, Continuo prima: illustration tab. 24, no 123 a–c. 1786. **Epitypus, here designated**: AUSTRIA. Niederösterreich, Horn, Maissau, Raan, Raanholz, along path on bare soil, 8 Nov 1987, leg. Anton Hausknecht, WU-6564! (WU), GenBank/UNITE MT967319 / UDB039746. UNITE SH1526142.08FU.

≡ *Agaricus glaucus* Batsch (basionym) Elenchus fungorum, Continuo prima: 169, t24:123. 1786

≡ *Agaricus epigaeus* var. *glaucus* (Batsch) Pers., Synopsis methodica fungorum: 484. 1801

≡ *Cantharellus glaucus* (Batsch) Fr., Hymenomyc. eur. (Upsaliae): 460. 1874

≡ *Merulius glaucus* (Batsch) Kuntze, Revis. gen. pl. 2: 862. 1891

≡ *Leptotus glaucus* (Batsch) Maire, Meded. Proefstn W. Java, Kagok-Tegal 15(2): 5. 1933

≡ *Geotus glaucus* (Fr.) Pilát & Svrcek., Česká Mycol. 7(1): 10. 1953

Macromorphology. – Basidiomata spathuliform, astipitate to short laterally stipitate. Pileus 5–10 mm wide, spathuliform, semicircular to almost circular, convex only when very young, soon flattened to even slightly depressed with umbo at insertion point, distinctly whitish tomentose-fibrillose, not striate, tomentum silvery whitish, ground colour under tomentum blue-grey, dark grey (23D1), some parts more watery dull brownish grey (6C1-2)

with age, towards margin whitish, sometimes with a darker submarginal zone; not hygrophanous, slightly fading when drying; surface densely fibrillose-tomentose all over, margin straight, almost not enrolled, white, tomentose. Lamellae a bit distant, narrowly adnate to shortly decurrent, straight, narrow, rarely forked especially when aged, 1–7 lamellulae, light grey to grey (8B-C1, 8C2) with dull brownish shades (8C2); lamellar edge smooth, obtuse, paler than lamellar side. Stipe 1 mm wide, absent to 3 mm long, lateral, densely covered by white tomentum; white hairs at base attached to substratum. Exsiccatum pileus grey-brown (5D3-4), lamellae bronze to dark brown (5E5, 6F6), except still whitish stipe base. Smell and taste not recorded.

Micromorphology. – Basidiospores (1 basidioma, 1 collection, 1 observer, n=60) $(5.3)5.8-7.3(8.1) \times (2.7)3.4-4.5(5.5)$ µm, average 6.6×4.0 µm; $Q = (1.2)1.4-1.9(2.4)$, $Q_{\text{avg}} = 1.7$; lacrymoid to pip-shaped, ovoid, or broadly elliptical, smooth, hyaline, often in tetrads, inamyloid, acyanophilous. Basidia $(17.5)19-25.5(28.7) \times (5.8)6-8(9.5)$ µm, 4-spored, rarely 2-spored, cylindrical to slightly clavate, hyaline. Lamellar trama subregular, similar to pileitrama. Cystidia absent. Pileipellis near insertion point a cutis, a plagiotrichoderm for the rest of the pileus, made up of smooth hyphae, 4–9 µm wide; terminal ends cylindrical or slightly clavate. Pileitrama made up of mostly parallel hyphae, becoming more irregular near the hymenium, made of cylindrical to swollen hyphae 4–7 µm diam, partially distinctly incrustated. Clamp connections at base of basidia and throughout all tissues.

Habitat. – The basidiomata of the epitype collection grew directly on bare organo-mineral soil along a forest path.

Distribution. – In addition to the montane zone of the Bohemian Forest in the granite and gneiss plateau Waldviertel, confirmed from Austria, France, Germany, Norway, and Sweden in our tree (Fig. 1b), additional specimens or soil samples from these countries and Estonia in UNITE SH1526142.08FU.

Comments. – The description is based on WU-6564. *Arrhenia glauca* is characterized by its distinctly pale, blue-grey, very small, spathulate basidiomata covered with a white tomentum, by the greyish lamellae and the thin white tomentose stipe. The habitus of the epitype collection agrees strikingly with Batsch's illustration, i.e. with the lectotype, also from central Europe, supporting the epitypification.

Additional specimens examined. – AUSTRIA. Lower Austria, Wilhelmsburg, Göblas-

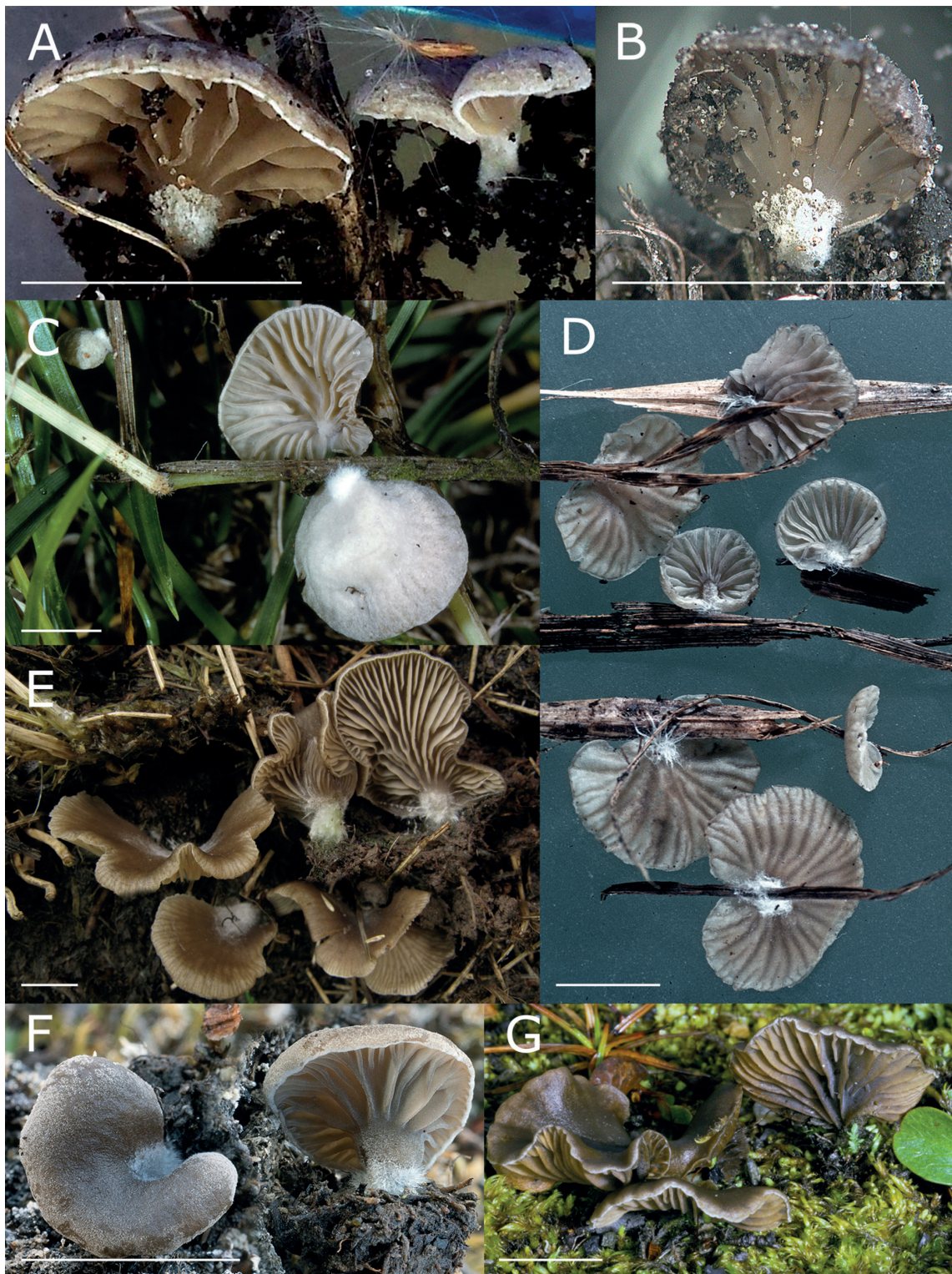


Fig. 3. New species of the *acerosa* complex described here, in alphabetical order. **A–B.** *Arrhenia fenicola* holotype, UWO-F44, Canada, ON, photo: Chris Hay. **C.** *Arrhenia juncorum*, holotype, LIP-0401674, France, photo Pierre-Arthur Moreau. **D–E.** *Arrhenia leucotricha*. **D.** WU-6774, Austria, photo: Anton Hausknecht. **E.** BBF-CH13091220, France, holotype, photo: Gilles Corriol. **F–G.** *Arrhenia svalbardensis*. **F.** O-76070, Norway, Svalbard, photo: Arne Aronsen. **G.** O-50444, Norway, Svalbard, photo: Kolbjørn M. Jenssen.

bruck, 48° 4' 52" N; 15° 35' 36" E, on bare soil in pasture, 13 October 1991, *leg.* Wolfgang Klofac, WU-9855. FRANCE. Pas-de-Calais, Guînes, forêt domaniale de Guînes, on clay soil under *Quercus robur* and *Carpinus betulus*, *leg.* Pierre-Arthur Moreau, 50.8455°N 1.8614°E, PAM06091108, LIP-0401688. Rothreid, Vosges, 48.046078°N, 7.033331°E, on soil and wood debris in beech-fir mountain forest, 28 September 1997, *leg.* Gilles Corriol, GC97092813. GERMANY. Lückendorf, 50.83 N 14.76 E, October 2014, KP-965766. NORWAY. Vestfold, Hof, Rønneberg, 59.5541 °N, 10.0375 °E, wet meadow, on *Carex*, 1989, *leg.* Per Marstad, PM114-89, O-64979. Vestfold, Nøtterøy, Teieskogen, 59.2018 °N, 10.4861 °E, on moss and soil, 2 October 1988, *leg.* Arne Aronsen, A68/88, O-189477. SWEDEN. Västergötland, Vänersborg, Västra Tu4nhem, Hunneberg, Landgedalen, 7 October 2000, on bare soil, *leg.* Leif & Anita Strindvall, LAS00/215, GB-0058858. Skåne, Ignaborga, 56.1217 °N, 13.82703 °E, on rotten deciduous wood in deciduous forest, 15 September 2003, Björn Nordén, GB-0017687. Västergötland, Trollhättan, Jonstorp Ö, on soil in natural meadow, *leg.* Leif & Anita Strindvall, LAS06/149, GB-0058855.

Arrhenia juncorum P.-A. Moreau & Corriol, *sp. nov.*
– Figs. 3C, 6E
Mycobank no.: MB 836883

Typification. – Holotypus: FRANCE. Haute-Loire, Saint-André-en-Vivaraïs, on *Carex rostrata* mixed with *Juncus* spp. in open wetland, 25 September 1998, *leg.* Pierre-Arthur Moreau, PAM98092503 (LIP-0401674). GenBank/UNITE ITS = MT967322 / UDB033394. UNITE SH1526152.08FU

Etymology. – *Juncorum*, from the Latin “*juncus*” (rush), base for the name of the genus *Juncus*, sole or partial host of both collections.

Diagnosis. – A small, astipitate, conchoid species insititious on dead leaves of living *Juncus* and *Carex* species, distinguished by long, somewhat pyriform spores in front view and hyphae that are smooth in the pileipellis but distinctly incrustated in the lamellar trama. Differs from most species in the *acerosa* complex by its lack of stipe, from most wetland species by its substrate, from other herbicolous species by its habitat, and from all by its ITS sequence data.

Macromorphology. – Basidiomata astipitate, conchoid, circular, 0.8–1.8 cm diam., astipitate, attached by a lateral point. Pileus not hygrophalous; surface densely silky, silvery white with light

grey tones towards margin when mature; attachment point thick, white tomentose; margin soon unrolled, smooth, white. Lamellae rather distant (12 reaching the attachment point, 3–5 unequal lamellulae per lamella), not forked, light grey becoming whitish when drying; edge truncate, smooth, greyish. On exsiccatum, pileus and lamellae uniformly ochre-brown. Smell none noted.

Micromorphology. – Basidiospores (2 basiomata, 2 collections, 2 observers, n = 58) (6.5)7.0–9.6(10.1) × (3.2)3.7–5.0(5.9) µm, average 8.3–3.6 µm; Q = 1.6–2.4, Q_{avg} = 2.3; narrowly ellipsoid to slightly lacrymoid, some more ellipsoidal to somewhat pyriform in front view, mostly with adnexed base. Basidia 28–38 × 7.5–8(11) µm, shortly cylindrical, colourless, 4-spored. Cystidia absent. Subhymenium ramose. Hymenophoral trama hyphae 5–12 µm wide, mostly incrustated by a distinct pigment bright yellow in KOH, the longest hyphae slender and smooth. Pileipellis a prostrate trichocutis made of colorless, long hyphae 35–90 × 5–7.5 µm, inflate to lobate at apex, with yellowish intraparietal pigment, not incrustated. Pileitrama thin, made of a few layers of slender hyphae 3.5–5(12) µm wide, irregularly incrustated. Clamp connections present at all septa.

Habitat. – On dead leaves of *Carex* and *Juncus* spp. in open montane wetlands; autumn.

Distribution. – So far only known from France.

Comments. – We suspect that more collections of this uncommon species will reveal a wider European distribution. *Arrhenia fenicola* is a grassland denizen, but neither a montane nor a wetland species, is limited to North America, is terricolous on dead herbaceous litter, has a short pseudostipe, and differs microscopically by a mixed, cytoplasmic and incrusting pigmentation on pileipellis. The more common *A. leucotricha* also grows in montane wetlands, but is bigger, grows on dead herbaceous litter, not dead leaves of living plants, and has a short pseudostipe. Two undescribed herbicolous specimens occur in G-1: WU-1294 grows on living *Ammophila* in sand dunes, not wetland; O-65097 is reported to be morphologically very similar and growing on living *Juncus* in barren coastal wetland (Aronsen 1992). However, the tree topology (Fig. 1b) does not support conspecificity, and sequence diversion from *A. juncorum* reveals 18 differences (mostly substitutions), leaving a 97.2 % similarity. This is one of the many homoplasies in the complex, demonstrating that similar phenotype does not necessarily mean genetic proximity.

Additional specimen examined. – FRANCE. Hautes-Pyrénées, Gaillagos, on *Juncus*



Fig. 4. Undescribed pleurotoid species of the *acerosa* complex, in phylogenetic order, as they appear in our tree (Fig. 1b). **A.** AC-2, TU-120494, Estonia, photo: Vello Liiv. **B1–2.** AC-3, BBF-GC13082701, France, photo: Marcel Vega. **C–F.** G-1. **C.** WU-8395, Austria, photo: Anton Hausknecht. **D.** BBF-GC13082806, France, photo: Gilles Corriol. **E.** WU-12194, Austria, photo: Anton Hausknecht. **F.** LD, Sweden, photo: Sven-Åke Hanson. **G.** AC-5, CMMF-003682, photo: Yves Lamoureux. **H.** AC-8, GB-0202287, Sweden, Lapland, photo: Pierre-Arthur Moreau.

acutiflorus, in semi-shaded wetland, 12 September 2013, *leg.* Carole Hannoire & Gilles Corriol, CH13091225, BBF-CH13091225.

Arrhenia latispora (J. Favre) Bon & Courtec. *Doc. Mycol.* 18(69): 37. 1987. – Figs. 2E–F, 6E
MBT 393703

Typification. – Holotypus: SWITZERLAND. Grisons: Sesvenna Valley, near the Sesvenna upstream toward Marangun, on dead moss, 2400 m a.s.l., 24 August 1943, *leg.* Jules Favre (G13896!).
Epitypus, here designated: FRANCE. Savoie, Bourg-Saint-Maurice, Arc 2000 towards col des Frettes, 2250 m a.s.l., 24 August 1999, *leg.* Pierre-Arthur Moreau PAM99082402 (LIP-0401569!). GenBank/UNITE ITS = MT967324 / UDB033395. UNITE SH1526154.08FU.

= *Pleurotellus acerosus* f. *latisporus* J. Favre, *Ergebn. wiss. Unters. schweiz. Natl Parks* 5: 38, 199. 1955.

= *Phaeotellus acerosus* var. *latisporus* (J. Favre) Jamoni & Bon, *Riv. Micol.* 36(1): 6. 1993.

Macromorphology. – Basidiomata usually 20–30 mm wide, eccentrically stipitate. Pileus 5–30 mm wide, spathuliform to petaloid, convex then flattened, indistinctly striate, bluish-violet dark grey when young, somewhat more brownish with age, lighter towards margin, sometimes with a darker submarginal zone; not hygrophanous, slightly fading when drying; surface densely fibrillose-tomentose all over, becoming glabrous at centre with age; margin wavy, inrolled, white, pruinose. Lamellae crowded, with 2–3 series of lamellulae, adnate to decurrent, not forked, light grey with pinkish shades when aged; lamellar edge smooth, truncate, white at first then concolorous with pileus. Stipe 3–6 × 3 mm, short, lateral to strongly eccentric, densely covered by white tomentum; no rhizomorphs seen. Exsiccatum entirely black except stipe tomentum. Smell distinct of *Pelargonium*. Taste not recorded.

Micromorphology. – Basidiospores (1 basidioma, 1 collection, 1 observer) 7.8–9.5 × 6.3–6.8 µm, spherical in youth becoming pyriform, then lacrymoid at maturity, smooth, hyaline. Basidia 22–28 × 7–8 µm, 4-spored, cylindrical, hyaline. Basidiales and immature basidia often enveloped by colorless mucus. Hymenophoral trama branched, orderly, similar to pileitrama. Cystidia absent. Pileipellis a trichoderm, dense at the margin, thinning out toward the base, made of smooth hyphae, 4–7 µm wide, bulging above septa; terminal ends long, cylindrical or broadly drawn out. Pileitrama

parallel, becoming more intertwined near the hymenium, made of cylindrical to swollen hyphae of 5–11 µm diam, finely but distinctly encrusted; occasional yellow, unbranched, cylindrical, glutinous hyphae seen, 3–4 µm diam. Clamp connections at base of basidia and throughout all tissues.

Habitat. – Bare organo-mineral soil with young mosses.

Distribution. – So far, only confirmed from the lower alpine zone of the Alps.

Additional collections studied. – AUSTRIA. Tirol, Lienz, Nußdorf-Debant, Neualplseen, 46° 43' 52" N; 12° 24' 35" E, on soil among moss, 26 August 2002, *leg.* Anton Hausknecht, WU-22359. FRANCE. Savoie, Bourg-Saint-Maurice, Arc 2000 toward Col des Frettes, 45.561186° N, 6.816898° E, on bryophytes on mineral slope along a road, lower alpine zone, 2250 m a.s.l., basic soil, 23 August 2001, *leg.* Gilles Corriol, GC01082301, BBF-GC01082301.

Comments. – Description based primarily on PAM99082402. It is a seldom-encountered and seemingly regional species, but the name has been misapplied to other wide-spored species in the complex. This is the largest species in the complex, the pileus occasionally exceeding 30 mm in width, thicker and more opaque flesh, dark violet colour (turning black on drying), *Pelargonium* odour and ITS sequences should serve to distinguish it from other species in the complex.

Arrhenia leucotricha P.-A. Moreau & Corriol, *sp. nov.* – Figs. 3D–E, 6F
Mycobank no.: MB 836884

Typification. – Holotypus: FRANCE. Haute-Loire, Saint-André-en-Vivaraire, on bare peat in an acidic peat bog under *Pinus sylvestris*, 25 September 1998, *leg.* Pierre-Arthur Moreau & Pierre Roux, PAM98090107 (LIP-0401673). GenBank/UNITE ITS = MT967329 / UDB033396. UNITE SH1526146.08FU.

Etymology. – *Leucotrichus*: from Greek, λευκο: white, τριχός: hairs, refers to the white hairy tomentum covering the stipe and a part of surface of the pileus.

Diagnosis. – A common European pleurotoid species of montane to alpine wetlands, with a short but distinct lateral white-tomentose pseudostipe found on more or less peaty soil and dead litter of hygrophilous herbaceous species. Differs from most species in the *acerosa* complex by its wetland habitat, from most wetland species by its terricolous litter substrate, and from all by its ITS sequence data.



Fig. 5. Undescribed omphalinoid species of the *acerosa* complex, in phylogenetic order, as they appear in our tree (Fig. 1b). **A–E.** G-2. **A.** TENN-074409, USA, TN, photo: Jacob Kalichman. **B.** HUH-11394, USA, NH, photo: Andrus Voitk. **C.** QFB-32684, Canada, QC, photo: Renée Lebeuf. **D.** WU-25862, Austria, photo: Irmgard Krisai-Greilhuber. **E.** FLAS-F-64782, Argentina, photo: Matthew Smith. **F.** G-2, WU-32560, Austria, photo: Wolfgang Klofac.

Macromorphology. – Basidiomata gregarious, spatulate to flabelliform, substipitate with a lateral bulge or rudimentary pseudostipe, flexuose when old but never lobate. Pileus 10–25 mm long from point of attachment to margin, striate, becoming more conspicuous with age; surface fibrillose with dense to white-silky fibrils, becoming sparse with age, strongly hygrophanous, dark grey-brown towards base and gradually fading to ochraceous-pellucid to almost white all over, whitish and opaque when dried; margin shortly incurved, white pruinose. Lamellae crowded, narrow with straight lamellar edge, 12–20 reaching the base, 3–4 series of lamellulae, occasionally forked, light to dark grey, remaining dark on exsiccata; lamellar edge smooth, narrow, concolourous. Pseudostipe 1–3 mm long, densely covered by a white hairy tomentum usually also covering cap towards base. Flesh with rancid odour on GC98092305, not pelargonium-like. Taste not distinctive. Exsiccatum, uniformly bluish black, with contrasting white tomentum.

Micromorphology. – Basidiospores (3 basidiomata, 3 collections, 2 observers, $n = 103$) (5.9)6.5–9.2(10.1) (3.2)3.6–5.5(5.9) μm , average $4.4 \times 7.5 \mu\text{m}$; $Q = 1.8\text{--}2.4$, $Q_{\text{av}} = 1.7$; narrowly cylindrical to pyriform in front view, usually blunt and broader at apex, often incurved on inner side; base adnexed. Basidia 25–32 (43) \times 6.7–8.5 μm , 4-spored, some with long slender base, wall often thickened and brownish at base on the type collection. Cystidia absent. Subhymenium ramose, a mix of short and long tapering elements, some thick-walled and brownish. Pileipellis 50–60 μm thick, a more or less erect trichocutis; terminal elements 30–55 \times 5–7 μm , cylindrical, clavate to subcapitate, smooth and pale; other elements with a yellow-brown, with zebra pattern incrustation. Pileitrama 60–80 μm thick, made of interwoven hyphae 3.5–10 μm wide, pale brown, mostly smooth, the slenderest coarsely incrustated. Basal tomentum made of long, smooth, hyaline hyphae 4.5–5 μm wide. Clamp connections present at all septa.

Habitat. – Mineralized peat, wet organic soil and damp litter of hygrophilic plants (e.g. *Juncus effusus*), from montane to alpine zones. August–September.

Distribution. – Known from Europe (Austria, France, Norway).

Comments. – *Arrhenia leucotricha*, with its distinct hairy lateral stipe, 4-spored basidia and ellipsoid to subpyriform spores, is one of the most common acerosa-like species in European highland wetlands. See Comments under *A. juncorum* for differences from it and other wetland species. The col-

oured basidia (brownish intraparietal pigment toward the base and in subhymenial hyphae) seem characteristic, but this needs to be confirmed by systematic investigation throughout the complex. The relationship of this species with the putative species AC-9 remains to be elucidated.

Additional specimen examined. – FRANCE. Hautes-Pyrénées, Gaillagos, wetland with *Juncus effusus* in a cow hoof print, 12 September 2013, leg. Carole Hannoire & Gilles Corriol, CH13091220 (in BBF). Haute-Garonne, Cuguron, acid peat-bog, on dead *Juncus* stem, 15 September 2003, leg. Gilles Corriol, GC03091513 (in BBF). Haute-Garonne, Cuguron, acid peat-bog, directly on peaty soil, 15 September 2003, leg. Gilles Corriol, GC03091514 (in BBF). Lozère, Linguas (Mont Aigoual), on dead *Juncus* stem in acid peaty soil, 23 September 1998, leg. Gilles Corriol, GC98092305.

Arrhenia subglobisemen Corriol, Bull. Mycol. Bot. Dauphiné-Savoie 222: 14. 2016. – Figs. 2G–I, 6G MBT 393704

Typification. – FRANCE. Haute-Savoie, La Chapelle-Rambaud, near la Roche-sur-Foron, 23 October 1938, leg. Carlo Poluzzi (Holotypus G, herbier Jules Favre, as *Pleurotellus tremulus*, num. G-9922!) designated in Corriol (2016). **Epitypus here designated:** FRANCE. Vallon de la Prade, plateau de Payolle, Ancizan, Hautes-Pyrénées, October 9, 2015, leg. Gilles Corriol (GC15100901 in BBF!) GenBank/UNITE ITS = MT967349 / UDB033382. UNITE SH1526143.08FU.

Misinterpretations:

= *Pleurotus tremulus* (Schaeff.) P. Kumm., Führ. Pilzk. (Zerbst): 105 (1871). sensu Fries, Gillet, Cooke, Quélet, Saccardo, Rea, Pilát, J. Favre, Lange

= *Pleurotellus tremulus* (Schaeff.) Konrad & Maubl., Encyclop. Mycol. (Paris) 14: 428 (1949) [1948] sensu Konrad & Maublanc, J. Favre, Kühner & Romagnesi

= *Leptoglossum tremulum* (Schaeff.) Singer sensu Singer, Moser

≠ *Hohenbuehelia tremula* (Schaeff.) Thorn & G. L. Barron sensu Thorn & Barron, Consiglio.

Macromorphology. – Basidiomata up to 25 \times 25 mm, with eccentric to lateral rudimentary stipe, at times forming complex multilobular or polycephalic structures up to 30 \times 30 mm, with 4–15 mm wide soft lobes or pilei proliferating in all directions, occasionally hymenium appearing on the superior pileal surface. Pileus rugulose, soft, 1.5 mm thick near stipe, thinning toward margin, pruinose, with fine 0.1–0.3 mm long white tomen-

tum becoming dense near stipe; translucently striate; concentrically hygrophanous, resulting in a zonate aspect during drying; initially dark grey-brown (10YR 4/2–4/3), margin paler (10YR 5/3), becoming light grey-brown when dry (10YR 7/3–8/3); barely darker with 5 % KOH. Lamellae long decurrent, straight, occasionally forked; with time and in complex basidiomata becoming wavy, narrow (about 1–1.5 mm), crowded, with numerous lamellulae; grey-brown, a little lighter than context (10YR 5/3), edge entire, concolorous. Stipe initially broad and short, covered with white tomentum as on pileus; in complex structures reduced to a barely differentiated mass, only a few millimetres high, its upper part covered by decurrent lamellae, and lower part by white tomentum, which may partially cover the base of the hymenium; grey. Context dark grey (10YR 4/2), very aeriferous throughout, lightening when drying; distinct *Pelargonium* smell and taste. Spore-print white.

Micromorphology. – Basidiospores (5 basidiomata, 5 collections, 2 observers, n = 90), (4.8)5.7–7.0(7.8) × (4.3)5.0–6.3(6.7) µm, average 6.5 × 5.5 µm; Q = 1.1–1.3, Q_{avg} 1.3; pip-shaped to subglobose, with prominent apiculus reaching 1 µm, hyaline, smooth, inamyloid, acyanophilous. Basidia 23–35 × 6–8 µm, clavate, 4-spored, sterigmata arched 3–4 µm long. Subhymenial hyphae branched. Lamellar edge fertile. Cystidia absent; some narrow or appendiculate sterile marginal hairs observed. Hymenophoral trama entangled, aeriferous, made of richly branched and anastomosed hyphae with membranal pigment forming dark grey-brown fairly homogeneous patches, irregularly distributed. Pileipellis loose, not gelatinized, with many more or less ascending, cylindrical, 4–8 µm wide, wavy hyphae, with endings quite frequently lobed; in hirsute parts endings fairly dense, well-defined, more elongated and narrower (× 3–4 µm), exceeding 100 µm, with brown pigmented wall, finely incrustated, in some places with granular, refracting, yellow-brown intracellular pigment; subcutis undifferentiated. Pileitrama of branched hyphae, 3–10 µm wide, with brown incrustated membranal pigmentation. Basal mycelium consisting of cylindrical parallel and sparsely branched hyphal bundles, 2.5–5 µm wide, with 80–200 µm spaced septa, with slightly thickened wall (to 0.5 µm), devoid of crystals. Clamp connections at base of basidia and abundant in all tissues.

Habitat. – Growing in both alpine settings and lowlands, but in more sheltered wooded or open grassy areas. Terricolous, gregarious, on cottony mycelium mantles encompassing living stems of

pleurocarpous mosses [e.g. *Hylocomnium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Willd. ex Brid.) Mitt., leaves of surrounding grasses, and surrounding litter.

Distribution. – Known from Europe and North America. The only *acerosa*-like species in NL, to date.

Additional collections studied. – CANADA. NL. Gros Morne National Park, McKenzie's Brook, 49.433318° N, 57.875591° W, 7 m a.s.l., with moss in field by mixed forest, 11 September 2014, *leg.* Renée Lebeuf, GM15a-995, DAOM-981251. Gros Morne National Park, McKenzie's Brook, 49.433318° N, 57.875591° W; 7 m a.s.l., with moss and grass in coniferous forest, 11 September 2014, *leg.* Renée Lebeuf, GM14a-218, DAOM-981254. Gros Morne National Park, Killdevil campgrounds, 49.454057° N, 57.751518° W, 26 m a.s.l., among moss in field beside coniferous forest, 9 September 2014, Renée Lebeuf, GM14a-028, DAOM-981252. Lockston Path Provincial Park, 48.458148° N, 53.456510° W, 119 m a.s.l., on moss in coniferous woods, 28 September 2012, *leg.* Marian Wissinck, TN3-042, DAOM-981255. Labrador, Happy Valley Ski Club, Robin trail, 53.43266° N, 60.38006° W, on soil under *Picea* in coniferous woods, 10 September 2016, *leg.* Emily Hildebrand, GBHV16A-429, DAOM-981253. Labrador, Makkovik Bay, 55.096939° N, 59.180469° W, 62 m a.s.l., among moss and lichens in coniferous woods, 1 August 2010, *leg.* Aare Voitk, 10.08.01.av03, (specimen lost in mail). ESTONIA. Hiiu Co., Kõpu peninsula, 58.9387° N, 22.27957° E, in coniferous forest, 14 October 2014, *leg.* Vello Liiv, TU-120029. NORWAY. Hordaland, Bømlo, Otterøya, 59.7251° N, 5.4333° E, on moss in natural meadow, 1 October 2009, *leg.* Asbjørn Knutsen, John Bjarne Jordal, O-291235.

Comments. – Except when it reaches the florid, multicephalic state, it may be macroscopically indistinguishable from several members of the *A. acerosa* group; other species have broad subglobose spores, but the relatively uniform subglobose shape can be helpful for identification. In a complex of many parochial species, *A. subglobisemen* seems phylogenetically stable across at least two continents, like the circumpolar *Lichenomphalia umbellifera* (Geml et al. 2012a).

Arrhenia svalbardensis Gulden, I. Saar & Lücking, **sp. nov.** – Figs. 3F–G, 6H–I
Mycobank no.: MB 836885

Typification. – Holotypus: NORWAY. Svalbard, Isfjord distr., Hotelneset, N of the airport,

with *Salix polaris* and *Dryas octopetala*, 14 August 1986, *leg.* Gro Gulden & Kolbjørn Mohn Jenssen, GG 411/86, O-50446. GenBank/UNITE ITS = MT967358 / UDB024589. UNITE SH1526148.08FU.

Etymology. – *Svalbardensis* refers to Svalbard, where the species was discovered and is quite common.

Diagnosis. – Brown-grey basidiomata, pilei under 25 mm diam, pleurotooid, with or without a lateral stipe under 2.5 mm long, 2- or 4-spored, growing in arctic heaths. Distinguished from other members of the complex by larger spores and ITS sequence data.

Holotype collection. – Three small basidiomata and some fragments, one apparently of a short stipe. Pilei dry, semiorbicular, up to 7 mm wide with incurved margin and a smooth, dark grey brown surface. Lamellae rather distant and narrow, dark grey. A short, cylindrical, solid, lateral stipe, up to 1.5 mm, pale grey and basally white tomentose in one specimen, lacking in others. Basidia 25–30 × 7.3–8.0(8.7) µm, 4-spored, with walls becoming ± brown with age. Basidiospores (1 basidioma, 1 collection, 1 observer, n = 30) 7.8–10.6 × 4.3–6.3 µm, Q = 1.3–2.2, Q_{avg} = 1.7, broadly elliptical to slightly lacrymoid, hyaline, inamyloid, acyanophilous. Cystidia absent. Hymenophoral trama made of ca 4–10 µm wide hyphae, ± brown. Pileipellis a cutis made of radial, 4–10 µm wide, medium celled hyphae, ± zebroid. Clamp connections at base of basidia and throughout all tissues. Pigment membranous and incrusting.

Macromorphology. – Pileus 5–22 mm, semiorbicular, fan-shaped, thin-fleshed, incurved with white pubescent margin when young, becoming straight to reflexed and ± crenulate to lobed, depressed at stipe attachment; white pubescent in youth, gradually becoming smooth except at stipe attachment, where a white tomentum often persists, matte to slightly greasy, azonate, not striate, hygrophanous, evenly dark olive brown to dark grey brown (T51, T71), drying to grey brown or pale grey with a tinge of yellow (N50, P67, 69, M70, L90). Lamellae adnexed to decurrent, subdistant to distant, occasionally forked or with 1–3 lamellulae, up to 1.5 mm high, thin to slightly thickened, grey ± like the pileus (P91, 92). Stipe, if present, up to 2.5 mm long, 1–2.5 mm thick, lateral to central, cylindrical or somewhat tapering downwards, solid, white pubescent. Context pale grey in pileus centre, dark grey in stipe cortex. No particular smell noted; taste not tested.

Micromorphology. – Basidiospores, 4-spored (4 basidiomata, 4 collections, 1 observer, n = 60) 7.8–

10.6(12.6) × 4.3–6.3 µm, Q = 1.3–2.2, Q_{avg} = 1.7; 2-spored (1 basidioma, 1 collection, 1 observer, n = 17) 9.7–18(23) × 6.3–8.0(9.5) µm, Q = 1.3–2.3, Q_{avg} = 1.8; elliptical to slightly lacrymoid, blunt, with prominent apiculus, hyaline, smooth, inamyloid, acyanophilous. Basidia 25–30 × 7.3–8.0(8.7) µm, 4-spored basidiomata; 30–41 × 6.8–10 µm, (1)2-spored basidiomata. Cystidia absent. Hymenophoral trama made of ca 3–10 µm wide, ± brown incrusting hyphae. Pileipellis a cutis made of radially repent, 3–10 µm wide, cylindrical, thin-walled, ± brown incrusting hyphae. Stipitipellis made of thin-walled, cylindrical or inflated 2–22 µm wide hyphae, evenly brown or zebroid; tomentum at base of stipe made of cylindrical, thin-walled, hyaline hyphae, 2.5–5 µm wide. Dermatocystidia absent. Clamp connections present at base of basidia and throughout all tissues. Pigment membranous and incrusting.

Habitat. – On almost bare soil and among moss in arctic heath vegetation with *Salix polaris* and *Dryas*; autumn.

Distribution. – Sporadic in Svalbard, but not the only species there (see Comments). Confirmed by environmental sampling (KC966345) from Prince Patrick Island in the Northwest Territories of Canada.

Additional collections studied. – NORWAY. Svalbard. Gluudneset, with *Salix polaris* and *Dryas octopetala*, 12 August 1988, *leg.* Gro Gulden, GG31/88, O-195466. Ny-Ålesund, near the Cambridge lab, in yard with moss and *Salix polaris*, 4 August 1986, *leg.* Gro Gulden, Kolbjørn Mohn Jenssen, GG159/86, O-50444. Endalen, W side, on bare soil in a depression, 10 August 2015, *leg.* Sten Svantesson, GG25/15, O-76070.

Comments. – Description based on notes of fresh material from O-50446, O-76070, O-195466 (4-spored), and O-50444 (2-spored). The latter has been described with a photograph by Gulden & Jenssen (1988). A single basidioma of the similar AC-7 (O-50445) comes from a bird-cliff habitat in Svalbard. It has a short eccentric stipe and large spores in the range of *A. svalbardensis*, 8.7–10.6(12.6) × 4.8–6.8, Q_{avg} = 1.8 (n=20).

Arrhenia tillii (Krisai & Noordel.) Krisai & I. Saar, **comb. nov.** – Figs. 2J, 6J
Mycobankno.: MB836886, UNITE SH2713468.08FU.

≡ *Rhodocybe tillii* Krisai & Noordel., Öst. Z. Pilzk. 7: 264 (1998) (basionym)

≡ *Clitopilus tillii* (Krisai & Noordel.) Noordel. & Co-David, Persoonia: 23: 164. 2009

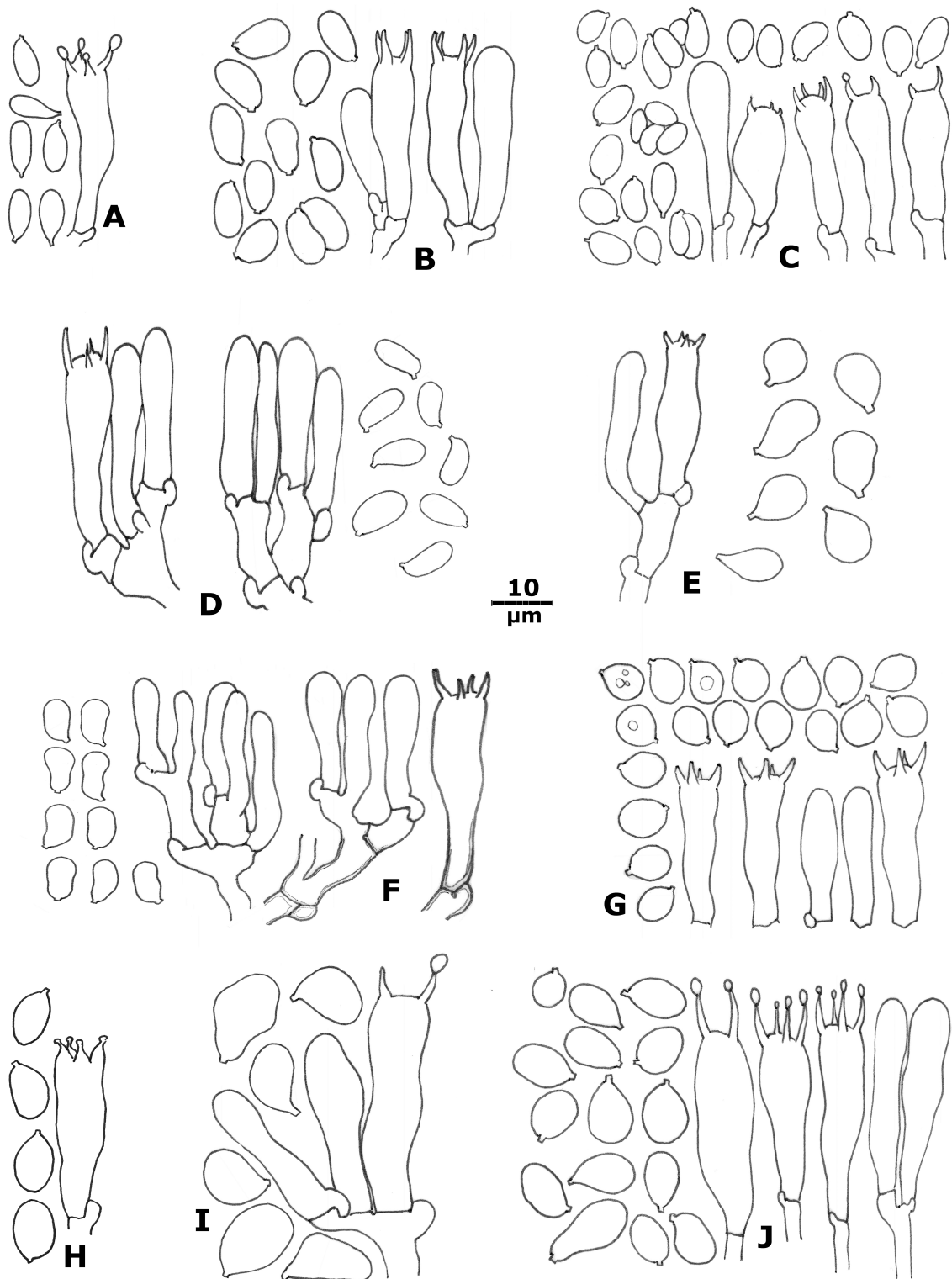


Fig. 6. Line drawings of spores and basidia of treated species, in alphabetical order. Bar 10 µm for all. **A.** Neotype for *Arrhenia acerosa* s. str., UPS-F151993. **B.** Holotype for *A. fenicola*, UWO-F44. **C.** Epitype for *A. glauca*, WU-6564. **D.** Holotype for *A. junctorum*, LIP-0401674. **E.** Epitype for *A. latispora*, LIP-0401569. **F.** Holotype for *A. leucotricha*, BBF-CH13091220. **G.** Epitype for *A. subglobisemen*, BBF-GC15100901. **H.** Holotype for *A. svalbardensis*, O-50446, 4-spored collection. **I.** 2-spored collection of *A. svalbardensis*, O-50444. **J.** Holotype for *A. tillii*, WU-18120.

Misinterpretations:

≠ *Pleurotus roseolus* Quél. Bull. Soc. Amis Sci. Nat. Rouen, Sér II:15: 155. (1879)1880

≠ *Arrhenia roseola* sensu Senn-Irlet 1986 (≡ *Phaeotellus roseolus* (Quél.) Horak 2005;

≡ *Pleurotellus roseolus* (Quél.) Kühner, based on *Pleurotus roseolus* Quél.)

Comment. – *Arrhenia tillii* differs from AC-3 (Fig. 4B₁₋₂) by a rudimentary or lacking stipe, lateral attachment, pink sporeprint and coniferous substrate. Additional finds of *Arrhenia tillii* in France and Switzerland share the same substrate (*Pinus nigra*) as the Austrian collections (Senn-Irlet 1986, Francini 2000). A pink specimen from Quebec (Ac-5, Fig 4G; Lamoureux 2015), identified as *Clitopilus tillii*, proved to be quite distant in the ITS tree (see discussion). The subglobose, obovoid to broadly elliptical spores make a striking discriminating character of *A. tillii*: seemingly smooth under the light microscope, but pustular-wavy in lateral and slightly angular-wavy in pole view with a large hilar apiculus under SEM, characters that previously led to its inclusion in the former genus *Rhodocybe*. Gröger (2006) also suspected parasitic growth on liverworts, which is not the case with the Austrian findings.

Discussion

All but one of our aims were met. We confirmed that the *Arrhenia acerosa*-like species native to NL is *A. subglobisemen*, typified the name with a sequenced specimen, and circumscribed the species. We were fortunate to find a suitable collection to neotypify and circumscribe *A. acerosa* s. str. We agree with Redhead (1984) that Batsch's (1786) protologue for *A. glauca* fits *Arrhenia acerosa* (or at least a species in the *acerosa* complex), and lectotypified the illustration. The habitus of *Arrhenia lobata*, *A. spathulata* and *A. auriscalpium* may resemble that illustration somewhat, but all have a reduced hymenium with sinuous, forked ridges joined by smaller anastomosing intervenose ridges, whereas Batsch's illustration clearly shows sharp, straight, unforked lamellae. Through good fortune we found a collection morphologically matching the lectotype from the same habitat and region, enabling us to epitypify *A. glauca*. The good fit with a robust modern collection seemed like too good an opportunity for preserving Batsch' epithet to miss. One of our more gratifying results was the ability to secure the concept of *A. latispora*. Likely, mycologists unfamiliar with the species, living outside its range, have been misled by the stress on spore width in the

epithet and protologue, a character we now know to be common to many species in the *acerosa* complex, causing them to synonymize these with *A. acerosa*.

Once discrete well-supported clusters developed in our phylogenetic tree, authors familiar with some were able to recognize them as distinct species. For example, *A. svalbardensis* with its wide spores was familiar to one of us from repeated study, and *A. fenicola* had been studied formally in the course of an MSc project (Hay 2016) by both student and supervisor. An additional consideration for describing *A. fenicola* now was that it seems to be restricted to unpopulated Canadian prairieland, a region not studied as commonly by mycologists as the Alps, central Europe and Scandinavia. Others among the author group recognized as discrete species the clades now bearing the names *A. juncorum* and *A. leucotricha*.

To us, far more significant than the treatment of nine taxa or description of four new ones, was the discovery of an unexpected number of undescribed species to which the name *Arrhenia acerosa* has been applied in the past. These and some other questions raised by our enquiry are left for future investigations. This includes our circumscription of the species we have treated. As with most first investigations, our limited experience may have made our circumscriptions overly narrow (e.g. *A. tillii*, *A. leucotricha*), or overly wide (e.g. *A. glauca*); more experience, coupled to more definitive technology may find that lumping some species and splitting others is more appropriate.

The only aim we were unable to meet was to circumscribe *A. acerosa* var. *tenella* s. str. Sterigma count did not seem to correlate with phylogenetic ranking for *A. svalbardensis*, but we are unable to say whether this applies to *A. acerosa* var. *tenella*. When Aronsen (1992) transferred *P. acerosa* var. *tenella* to *Arrhenia* he based his description on three 2-spored Norwegian collections growing on *Juncus*, not type material for *A. acerosa* var. *tenella*. One of these specimens, resembling *A. juncorum* but distant from it phylogenetically, is in our tree (G-1, O-65097), and it would be tempting to typify the taxon with that collection, but Kühner's lectotype was collected in Algeria, differing significantly in climate and habitat from Norway. In view of the diversity and parochial nature of species in the *acerosa* complex, it seems more prudent to leave securing of the name *tenella* to future investigations.

Despite having robust herbarium specimens, good photos (Fig. 4) and/or collecting notes, microscopic findings and phylogenetic ranking for some potential species, we lack sufficient experience with

them as separate entities with unique appearance and behaviour in their own environment to be able to describe them as distinct organisms among their peers. Future observations to gain sufficient knowledge of them in their habitat, as well as definitive resolution of all phylogenetic nodes with multilocus analysis, are bound to be rewarded by the description of several new species. Figure 1b is our attempt to correlate ranking with characters gleaned retrospectively from records accompanying the studied collections. Records may be erroneous and observations fortuitous or skewed. For example, it is easy to omit or include soil, earth, bryophytes or duff because these are virtually omnipresent in most habitats where species in this complex are found. Clearly, this character list is only a modest beginning, to be refined or replaced by more detailed observation, as more experience with these species accumulates. At the end of this Discussion section, we provide a preliminary key for the pleurotooid species. Like the character list, this is a preliminary attempt, which should be improved with more experience with this diverse group.

One of the interesting projects that may come from this work is the study of pink-spored, pink species within this white-spored grey to brown genus. That the pink *Clitopilus tillii* turned out to be a species of *Arrhenia* should not have been entirely unexpected, because pink species have been referred to the genus in the past. (As mentioned in the introduction, we consider *roseola* misapplied to a pink species of *Arrhenia*). Krieglsteiner (2011) reports two sites for a pink *acerosa*-like species, one near Schweinfurt, Germany, on a species of *Molinia* on calcareous soil in a dry warm area, and the other near Bachaue, Germany, on *Phalaris arundinaceae*. If these species are substrate specific, then graminicolous collections may differ from the Austrian *A. tillii* on coniferous wood. AC-3, a French terricolous collection identified earlier as "*A. roseola*", falls in proximity to *A. tillii* in our tree, suggesting that they may be closely related, but the substantial differences in the ITS do not allow treating them as conspecific. The North American pink species, AC-5, is quite remote from *A. tillii*, another example of homoplasy in this complex.

Molecular genetic studies revealed that in addition to the diverse morphology of the pleurotooid habitus, the omphalinoid habitus has found repeated expression in the cascading *acerosa* complex throughout a wide geographic range, so far documented from both Hemispheres, four continents and eight countries. In our current tree these are found in G-2, a group of 4-spored basidiomata, and

G-3, a group containing both 2- and 4-spored basidiomata. Many of these specimens were identified as *A. griseopallida* (Desm.) Watling, but the epithet was also applied to several pleurotooid collections, suggesting a very varied interpretation of the name. Kühner & Lamoure (1972) observed that the stipe of *P. acerosus* starts centrally, soon ceases to elongate, and because of inequilateral growth, ends up eccentric or lateral. Such transition from a central to lateral stipe within the *acerosa* complex was noted in *A. svalbardensis*, and is suggested by comparing the collection from northern Québec (Fig. 5C) and *A. subglobisemen* in Fig. 2G. The thick stipe and incomplete pileus of at least one Québec basidioma approaches the pleurotooid habitus and lateral stipe of the latter. Study of these omphalinoid species of the *acerosa* complex is an interesting and significant project, requiring, among other things, typification of *A. griseopallida* and study of its relationship to the *acerosa* complex.

Most species of the *acerosa* complex seem to be parochial. So far, *A. subglobisemen* seems to have a wide distribution across two continents; *A. svalbardensis* has also been recorded from two continents, but the seriously understudied Canadian north may hide further contributions to this complex. In addition to very varied morphology, habitat and distribution preferences, collecting records indicate this group also occupies diverse substrates. A few are recorded to grow on bare soil or gravel, and a small number are noted to have an apparent association with bryophytes, generally thought to be the lifestyle for arrhenias. The majority is documented to grow on rotten deciduous and coniferous wood, wood chips, conifer duff, herbaceous litter (including live or dead *Ammophila*, *Juncus* and *Carex*), peat and herbivore dung (horse, sheep, and reindeer have been recorded). Significantly, most wood-associated collections do not grow on large boles of rotten wood, which may be acting as water banks rather than nutritional substrate, but chips (Figs. 4A, C) or small debris, often with no visible bryophytes on them, as is seen with true lignicolous species. This preponderance of woody or herbaceous substrates suggests a saprobic lifestyle with an affinity for a cellulose-containing material, rather than the moss-association generally accepted for species of *Arrhenia*. Elucidating the lifestyle of the members of this complex seems like another worthwhile undertaking.

We have raised far more questions than we have answered. The answers to most of these, including the placement of Pilát's (1935) and Velenovský's (1920, 1927) taxa, lie outside the scope of this study

or outside our ability at this time. It is our hope that awareness of these questions will promote productive future investigations.

Tentative key to pleurotoid members of the *Arrhenia acerosa* complex

1. a) Basidiomata pink or pinkish 2
1. b) Basidiomata without pink tones; white or pale, grey, brown or violaceous 4
2. a) Fruiting on rotted coniferous wood, sometimes with bryophytes; central Europe *Arrhenia tillii*
2. b) Fruiting on soil, sometimes with bryophytes; Europe or North America 3
3. a) Arcto-alpine, in central Europe AC3
3. b) In temperate forests, North America AC5
4. a) Basidiomata large (2–3 cm broad), dark violaceous; lower alpine zone in Europe; on soil, often with bryophytes, basidiospores large, $7.8\text{--}9.5 \times 6.3\text{--}6.8 \mu\text{m}$ *Arrhenia latispora*
4. b) Basidiomata smaller and not violaceous 5
5. a) Basidiospores broad ($Q_{\text{avg}} < 1.5$), pip-shaped to subglobose, $5.7\text{--}7.0 \times 5.0\text{--}6.3 \mu\text{m}$; basidiomata grey to grey-brown; on soil or associated with bryophytes or herbaceous litter in mixed forests or grasslands, Europe and North America *Arrhenia subglobisemen* (if basidiospores plump but most less than $5 \mu\text{m}$ broad, see *A. leucotricha*)
5. b) Q_{avg} of basidiospores > 1.5 6
6. a) Basidiospores narrowly elliptical to slightly lacrymoid, $6.8\text{--}8.7 \times 3.4\text{--}3.9 \mu\text{m}$; basidiomata grey-brown, on soil or wood in north Europe..... *Arrhenia acerosa* s.str.
6. b) Basidiospores broader, many $> 4 \mu\text{m}$ broad .7
7. a) Most basidiospores $> 5 \mu\text{m}$ broad, $7.7\text{--}10.7 \times 4.8\text{--}6.8 \mu\text{m}$ (4-spored; broader in 2-spored); in Svalbard and the Canadian arctic; basidiomata grey-brown to brown ... *Arrhenia svalbardensis* (if some basidiospores broader than $5 \mu\text{m}$ but habitat in North American grasslands, see *A. fenicola*)
7. b) Most basidiospores $< 5 \mu\text{m}$ broad 8
8. a) On soil or associated with grass or herbaceous litter in North American grasslands *Arrhenia fenicola*
8. b) European; habitats various9
9. a) Basidia consistently 2-spored; basidiospores $6\text{--}9 \times 3.6\text{--}5.1 \mu\text{m}$; basidiomata on various substrates and varied habitats in central and northern Europe G1
9. b) Basidia 4-spored or occasionally 2-spored 10
10. a) Fruiting on soil or wood debris in woodland or grassland (mesic) habitats; basidiomata distinctly pale blue-grey, white-tomentose; lamellae greyish; pseudostipe white-tomentose *Arrhenia glauca*
10. b) Fruiting in wetland habitats 11
11. a) Fruiting directly on dead leaves of wetland graminoids *Arrhenia juncorum*
11. b) Fruiting on wet organic soil in montane or arcto-alpine habitats *Arrhenia leucotricha*

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