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Taxonomy and systematics of *Hyaloscyphaceae* and *Arachnopezizaceae*

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Key words

Arachnoscypha
epibryophytic
genealogical species
Helotiales
subiculum
type studies

Abstract The circumscription and composition of the *Hyaloscyphaceae* are controversial and based on poorly sampled or unsupported phylogenies. The generic limits within the hyaloscyphoid fungi are also very poorly understood. To address this issue, a robust five-gene Bayesian phylogeny (LSU, *RPB1*, *RPB2*, *TEF-1α*, mtSSU; 5521 bp) with a focus on the core group of *Hyaloscyphaceae* and *Arachnopezizaceae* is presented here, with comparative morphological and histochemical characters. A wide representative sampling of *Hyaloscypha* supports it as monophyletic and shows *H. aureliella* (subgenus *Eupezizella*) to be a strongly supported sister taxon. Reinforced by distinguishing morphological features, *Eupezizella* is here recognised as a separate genus, comprising *E. aureliella*, *E. britannica*, *E. roseoguttata* and *E. nipponica* (previously treated in *Hyaloscypha*). In a sister group to the *Hyaloscypha-Eupezizella* clade a new genus, *Mimicoscypha*, is created for three seldom collected and poorly understood species, *M. lacrimiformis*, *M. mimica* (*nom. nov.*) and *M. paludosa*, previously treated in *Phialina*, *Hyaloscypha* and *Eriopezia*, respectively. The *Arachnopezizaceae* is polyphyletic, because *Arachnoscypha* forms a monophyletic group with *Polydesmia pruinosa*, distant to *Arachnopeziza* and *Eriopezia*; in addition, *Arachnopeziza variepilosa* represents an early diverging lineage in *Hyaloscyphaceae* s.str. The hyphae originating from the base of the apothecia in *Arachnoscypha* are considered anchoring hyphae (vs a subiculum) and *Arachnoscypha* is excluded from *Arachnopezizaceae*. A new genus, *Resinoscypha*, is established to accommodate *Arachnopeziza variepilosa* and *A. monoseptata*, originally described in *Protounguicularia*. *Mimicoscypha* and *Resinoscypha* are distinguished among hyaloscyphoid fungi by long tapering multiseptate hairs that are not dextrinoid or glassy, in combination with ectal excipulum cells with deep amyloid nodules. Unique to *Resinoscypha* is cyanophilous resinous content in the hairs concentrated at the apex and septa. Small intensely amyloid nodules in the hairs are furthermore characteristic for *Resinoscypha* and *Eupezizella*. To elucidate species limits and diversity in *Arachnopeziza*, mainly from Northern Europe, we applied genealogical concordance phylogenetic species recognition (GCPSR) using analyses of individual datasets (ITS, LSU, *RPB1*, *RPB2*, *TEF-1α*) and comparative morphology. Eight species were identified as highly supported and reciprocally monophyletic. Four of these are newly discovered species, with two formally described here, viz. *A. estonica* and *A. ptilidiophila*. In addition, *Belonium sphagnisedum*, which completely lacks prominent hairs, is here combined in *Arachnopeziza*, widening the concept of the genus. Numerous publicly available sequences named *A. aurata* represent *A. delicatula* and the confusion between these two species is clarified. An additional four singletons are considered to be distinct species, because they were genetically divergent from their sisters. A highly supported five-gene phylogeny of *Arachnopezizaceae* identified four major clades in *Arachnopeziza*, with *Eriopezia* as a sister group. Two of the clades include species with a strong connection to bryophytes; the third clade includes species growing on bulky woody substrates and with pigmented exudates on the hairs; and the fourth clade species with hyaline exudates growing on both bryophytes and hardwood. A morphological account is given of the composition of *Hyaloscyphaceae* and *Arachnopezizaceae*, including new observations on vital and histochemical characters.

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INTRODUCTION

Helotiales is one of the remaining unsolved pieces in the great puzzle of *Leotiomycetes* systematics. Depending on the taxonomic concept, the number of recognised species ranges from c. 2360 (Baral 2016) to 3881 (Kirk et al. 2008). There are no recent speculations on the total number of existing species, but e.g., Hawksworth (2001) gives an estimate of c. 70000 species. Members of *Helotiales* are morphologically very variable and exhibit saprobic, parasitic as well as mycorrhizal life strategies.

Hyaloscyphaceae in the traditional wide sense (Nannfeldt 1932) is the largest and most diverse family in the order (Kirk et al. 2008, Baral 2016 as Lineage D/*Hyaloscyphaceae* s.lat. with 68 genera and 673 species).

When Nannfeldt (1932) introduced the concept of *Hyaloscyphaceae*, it included three tribes, i.e., *Arachnopezizeae*, *Hyaloscypheae* and *Lachneae*, and altogether 13 genera. Nannfeldt emphasized especially the shape and structure of the excipular cells as a delimiting character at the family-level. *Lachneae* included species with lanceolate paraphyses and multiseptate granulate hairs and *Arachnopezizeae* species with a subiculum surrounding the apothecia. The species of *Hyaloscypheae* were not united by any unique combination of characters, but the majority of genera had cylindrical paraphyses and hairs of very diverse shapes and size.

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Hyaloscyphaceae received growing attention during the following years and the systematics of the whole group was treated in studies by Dennis (1949, 1962, 1981), Raitviir (1970, 1987), Spooner (1987) and Svrček (1987). Although only a few monographs on hyaloscyphaceous genera have been published so far (Korf 1951b, Zhuang 1988, Huhtinen 1989), various authors contributed in documenting the diversity of the hairy *Helotiales*, e.g., Korf (e.g., 1951a, 1978, 1981, 2007), Haines (1974, 1989), Raschle (1977), Svrček (e.g., 1977, 1984, 1985), Korf & Kohn (1980), Raitviir & Sharma (1984), Baral & Krieglsteiner (1985), Spooner & Dennis (1985), Raitviir & Galán (1986), Baral (e.g., 1987, 1993), Huhtinen (e.g., 1987a, b, 1993a), Galán & Raitviir (1994, 2004), Cantrell & Hanlin (1997), Hosoya & Otani (1997), Raitviir & Huhtinen (1997), Leenurm et al. (2000), Zhuang (2000), Raitviir (2001), Quijada et al. (2014), and Baral & Rämä (2015). The number of recognised genera today is c. 70 and the number of species c. 1 000 (Kirk et al. 2008, Baral 2016).

There were no major revisions to the higher-level systematics until the 21st century. In his revised synopsis of the *Hyaloscyphaceae* s.str., Raitviir (2004) concluded that the morphological differences between the core members of the two largest tribes, *Hyaloscypheae* and *Lachneae* were 'strictly contrasting'. With evidence on the ultra-structural differences in the hair wall layers (Leenurm et al. 2000) and the first phylogenetic analyses of the ITS region available (Cantrell & Hanlin 1997), Raitviir (2004) emended *Hyaloscyphaceae* to conform to the tribe *Hyaloscypheae*, and elevated *Lachneae* to the rank of family.

Recent multi-gene phylogenetic analyses have clearly shown that *Hyaloscyphaceae* sensu Raitviir (2004) is polyphyletic (Han et al. 2014, Johnston et al. 2019). The species occur in six or more clades, spread among other clades of *Helotiales*. These hyaloscyphoid clades correspond to emended tribes/subfamilies/families, and to two newly described families (*Arachnopezizaceae*, *Hyaloscyphaceae* s.str., *Lachnaceae*, *Pezizellaceae*, *Vandijckellaceae*), as well as to unnamed groups (Raitviir 2004, Han et al. 2014, Crous et al. 2017, Johnston et al. 2019). The sampling of taxa or molecular characters is, however, very limited in the molecular studies (Han et al. 2014, Johnston et al. 2019), and the evolutionary history of these fungi is still poorly understood. In this study, we focus specifically on taxa closely related to *Arachnopezizaceae*, and the core group of *Hyaloscyphaceae*.

Arachnopezizaceae

Of the three original tribes, *Arachnopezizeae* comprised only a small number of species. Nannfeldt (1932) was unsure about the status of the tribe and gave only a provisional description. Korf (1951b) validated the tribe and stressed the significance of subiculum together with septate spores as the key morphological characters defining a natural group. Subiculum refers to the protruding hyphal elements forming an interconnected web-like structure on the substratum surrounding the apothecia (Kirk et al. 2008, see also Fig. 1). Korf (1951b) defined the tribe further as having septate hairs and partially thick-walled excipular cells. He included the genera *Arachnopeziza*, *Eriopezia* and *Tapesina* in *Arachnopezizeae* and placed *Arachnoscypha* in synonymy with *Arachnopeziza*. Dennis (1949, 1981) still recognised *Arachnoscypha* (for *A. aranea*), but did not comment on the close relationship between *A. aranea* and *Arachnopeziza eriobasis* shown by Korf (1951b). Raitviir (1970) removed *Arachnopezizeae* from *Hyaloscyphaceae*, emphasizing the similarities in the excipular structure to *Durelloideae* and *Phialeoideae* (*Helotiaceae*); he thought these three tribes should be placed in a separate family. Doing this, Raitviir gave less weight to the presence or absence of hairs in the overall systematics, suggesting that the presence of 'true hairs' is a polyphyletic character within *Helotiales*. Korf (1978) recognised *Arachnopezizeae* as a subfamily within *Hyaloscyphaceae*. At the same time he divided *Arachnopezizoideae* into two tribes: *Arachnopezizeae* including *Arachnopeziza* and provisionally *Velutaria*; and *Polydesmiaeae*, including *Eriopezia*, *Parachnopeziza* and *Polydesmia*. Later, a newly established genus *Proliferodiscus* was placed in *Polydesmiaeae* (Haines & Dumont 1983).

Han et al. (2014) addressed the delimitation and relationship between *Hyaloscyphaeae* and *Arachnopezizeae* using phylogenetic analyses of the ITS, partial LSU rDNA, mtSSU and *RPB2* sequences. *Polydesmia* and *Proliferodiscus* were suggested not to be close relatives of *Arachnopeziza*. Eventually, the rank of *Arachnopezizeae* was raised to its present status as a family including the genera *Arachnopeziza*, *Arachnoscypha*, *Austropezia*, *Eriopezia* and *Parachnopeziza* (Baral 2015). Although many species in *Arachnopeziza* are relatively conspicuous and new species have continued to be described, the number of *Arachnopeziza* sequences available is still relatively low as is the number of species sampled. A phylogenetic approach to clarify the family limits of *Arachnopezizaceae*, and the generic limits of the largest genus *Arachnopeziza*, is lacking.

Two different species have been interpreted as the type species of *Arachnopeziza*: *A. aurata* and *A. aurelia*. We follow here Korf (1951b: 132–133, 152) who concluded that *A. aurata* is the type species, as indicated by Saccardo (1884) when he combined *Arachnopeziza* as a subgenus in *Belonidium*. In his synopsis of the discomycete genera, Saccardo (1884) listed in general only one species per genus or subgenus that appear to have been selected as typical for them. Korf (1951b) also found it unfortunate if *A. aurelia* was to be considered the type species, because Fuckel (1872) excluded it from *Arachnopeziza* shortly after he described the genus. Several databases (e.g., MycoBank, Index Fungorum and Index Nominum Genericorum) list *A. aurelia* as the type species. Either they follow Clements & Shear (1931), who applied the 'first species rule' (*A. aurelia* is the first species listed by Fuckel (1870) in his description of *Arachnopeziza*), or Cannon et al. (1985) who first cite Korf (1951b) and then (erroneously!) list *A. aurelia* as the type species. The likeness of the epithets '*aurelia'* and '*aurata'* possibly contributed to that error.

Towards Hyaloscyphaceae sensu stricto

The disciplined use of histochemical methods and the reintroduction of vital taxonomy resulted in novel insights in inoperculate discomycetes systematics throughout the later part of the 20th century. The variation in iodine reactions and the significance of KOH pretreatment and its implications to taxonomy was observed and reviewed by Kohn & Korf (1975) and further explored by Baral (1987) resulting in the concept of hemiamyloidity. Nevertheless, the reactions in the cells produced by Melzer's reagent were often reported inaccurately and an effort was made to distinguish between amyloid and dextrinoid reactions (Huhtinen 1987b, 1989, 1993b). The importance of studying living material was underlined by the works of Baral & Krieglsteiner (1985) and Baral (1992), showing the cells contained taxonomically valuable characters, changing or disappearing upon drying and/or using various reagents.

The type genus *Hyaloscypha*, as well as *Phialina* and *Hamatocanthoscypha*, were treated in detail by Huhtinen (1989). Many hyaloscyphaceous genera are characterised by a substance in the hair wall filling the space inside the hair partially or completely, giving it a glassy appearance. Several authors paid special attention to this character and proposed generic limits based on the morphology and chemical properties of the hairs (Raschle 1977, Korf & Kohn 1980, Huhtinen 1987b,

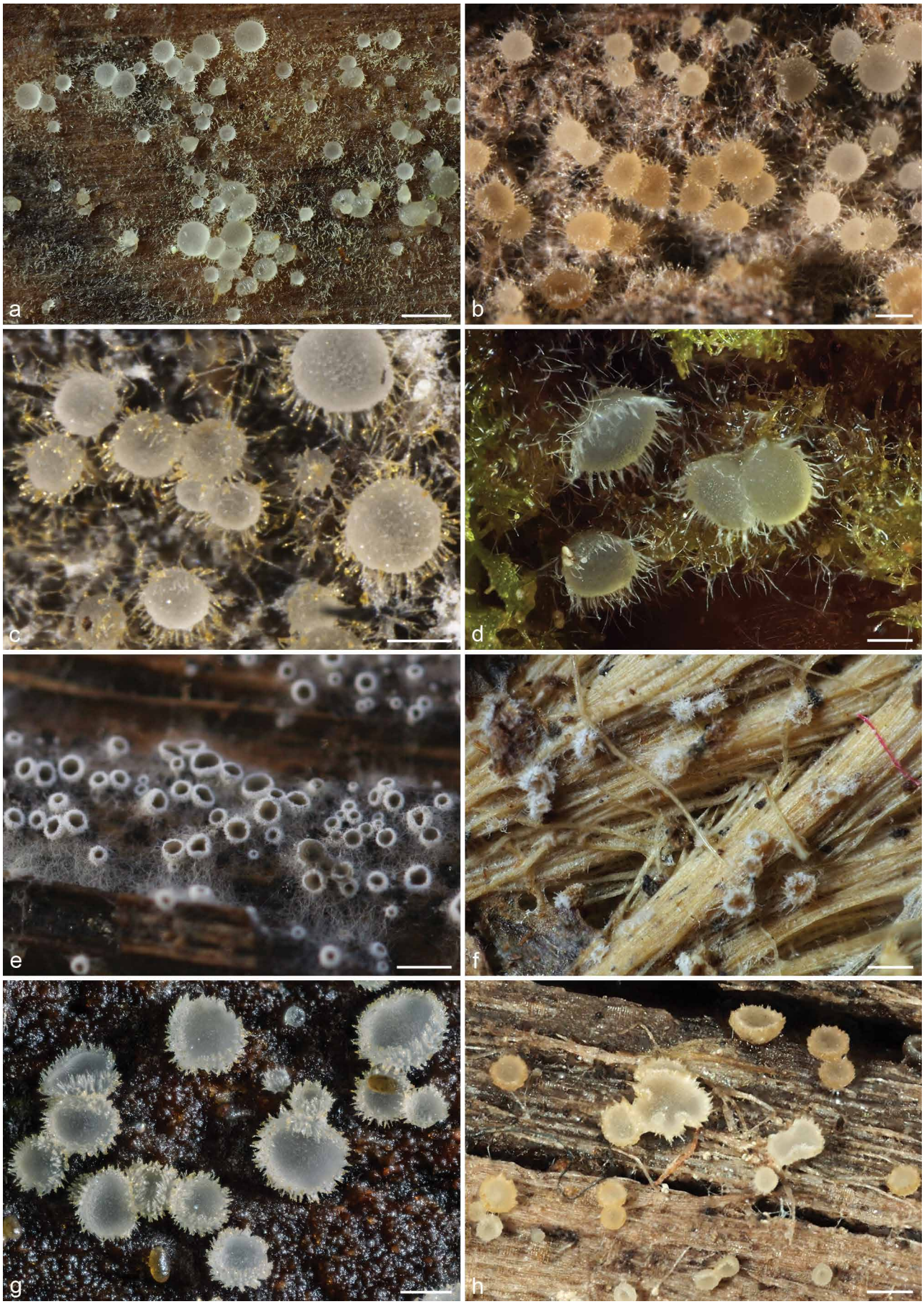


Fig. 1 Examples of apothecia and habitats in *Arachnopezizaceae*, *Arachnoscypha* and *Hyaloscyphaceae*. a–c. *Arachnopeziza leonina*, showing hairs with crystals and subiculum; d. *Arachnopeziza ptilidiophila*; e. *Eriopezia caesia*; f. *Arachnoscypha araneа*†; g. *Eupezizella aureliella*; h. *Olla transiens* (a: *T. Kosonen* 7294; b: *S. Huhtinen* 16/42; c: *S. Huhtinen* 16/58; d: *T. Kosonen* 7289; e: *T. Kosonen* 7005; f: DPP-11788; g: DMS-9189563; h: *T. Kosonen* 7017). — Scale bars: a, e–f, h = 0.5 mm; b–d, g = 0.25 mm; † dried material. — Photos: a, d, f, h. N. Llerena; b–c. K. Hansen; e. T. Kosonen; g. J.H. Petersen.

1989). Despite many advances, *Hyaloscyphaceae* remained essentially a combination of genera without a clear concept on their evolutionary relationship.

Combining the first phylogenetic results (Han et al. 2014) and vital taxonomy, Baral (2016) resurrected the family *Pezizellaceae* for 18 hyaloscyphaceous genera. The unifying morphological character is the frequent presence of vacuolar bodies (VB) in the cells of fresh specimens and a *Chalara* or similar asexual morph (Baral 2016). The family is supported as a distinct lineage in a recent study employing genome scale data (Johnston et al. 2019). In the systematic arrangement of the helotialean genera (Baral 2016), 26 genera representing c. 220 species were left in a restricted *Hyaloscyphaceae*, although the available phylogenetic evidence suggested it may still be polyphyletic (Han et al. 2014). As such, the family is delimited without any unique combination of characters, becoming distinguished rather by the lack of specific characters (i.e., the absence of *Chalara* asexual morph and VB's). As a result, several taxa are included in *Hyaloscyphaceae* merely because no better placement is known.

Recent evidence shows, contrary to the traditional view, that at least some species of *Urceolella* and *Cistella* belong to a monophyletic clade *Vandijckellaceae*, distantly related to *Hyaloscypha* (Crous et al. 2017, Johnston et al. 2019). Han et al. (2014) proposed a very narrow concept of *Hyaloscyphaceae*, including only the genus *Hyaloscypha*. In their analyses of a dataset (the 'inter-set') including representatives from other families of *Helotiales*, *Hyaloscypha* formed a well-supported monophyletic group, resolved as a sister group to a clade including species of *Olla*, *Hyalopeziza*, *Vibrisseaceae*, *Dermateaceae* and *Loramycetaceae*. Johnston et al. (2019) showed that *Amicodisca castanea* and *Dematioscypha* are likely sisters to *Hyaloscyphaceae* s.str. However, many hyaloscyphoid genera have not been included in molecular phylogenetic studies and several might be non-monophyletic. Fehrer et al. (2018) provided some new samples, but most importantly broadened the view on the ecology of *Hyaloscyphaceae* by showing the connection between several well-known or new mycorrhizal-forming sterile, asexual or sexual morphs (including the *Rhizoscyphus* (*Hymenoscyphus*) *ericae* aggregate) and sexual *Hyaloscypha* species. The need to investigate the composition and circumscription of *Hyaloscyphaceae* is evident.

In the present study, we considerably expand the number of molecular characters, through the addition of sequence data from three protein-coding genes (*RPB1*, *RPB2*, *TEF-1α*), mitochondrial SSU and LSU rDNA, 5 521 bp in total. The ITS region was sequenced and used to aid in species identification or delimitation. With our observations of less known and novel species, together with phylogenetic analyses of sequences, we address the circumscription and relationships of *Hyaloscyphaceae* and *Arachnopezizaceae*. In *Hyaloscyphaceae*, we examine the delimitation of *Hyaloscypha* and the phylogenetic relationships of closely related taxa. In *Arachnopezizaceae* we investigate the phylogenetic placement and status of *Arachnoscypha*, and clarify species boundaries within *Arachnopeziza*, with a focus on Northern Europe, using genealogical concordance and comparative morphological studies, including the description of two new species and several new combinations.

MATERIALS AND METHODS

Material studied

This study is mainly based on samples collected by the authors in Estonia, Finland and Sweden during 2014–2018. These specimens are deposited in S and TUR. Several samples were collected as part of the project 'Epibryophytic and lichenicolous fungi in Finland' in 2003–2008 (Stenroos et al. 2010). In addition, we received both fresh and dry material from mycologists from Europe and North America (USA). From all of these, 69 samples were chosen for molecular phylogenetic study (Table 1). Fungarium material from CUP, H, K, NMNS, PRM, S, TAAM, TNS and TUR were studied.

Fungal cultures

Fresh collections were cultured on malt-agar plates in order to ensure ample living material for DNA extraction. Depending on the size of the collection, 4–10 small pieces of substratum (c. 2 × 2 mm) with fresh apothecia were cut under a dissecting microscope and placed on moist paper tissue of a slightly larger size. In cases where apothecia from different species were growing intermixed, the apothecia of the untargeted species were removed. A 50 mm Petri dish, half filled with growth media, was placed upside down on top of each piece of apothecia assembly. The growth media consisted of sterile ion-exchanged water with 2 % (w/v) malt, glucose, agar, 0.1 % peptone and 0.01 % chloramphenicol. Spore release was triggered by altering the air pressure inside the Petri dish by carefully lifting it partially for 1–2 s. After 12–24 h, the Petri dish was closed and sealed. Similar hyphal growth pattern, on the 4–10 plates made from one collection, was used as an indication of the target species being successfully isolated. Cultures were grown for 3–6 mo at room temperature prior to DNA extraction. We observed no asexual reproductive structures during the first 3 mo when cultures were under consistent observation. Fungal cultures will be deposited in the Westerdijk Fungal Biodiversity Institute (CBS-KNAW collection).

Morphological methods

The material was studied with Olympus BX53 and Nikon i80 microscopes with bright field optics. Measurements were made using a 1 000× magnification. Fresh samples were first studied in tap water. Other mounting media used were: Melzer's reagent (MLZ), IKI solution (LUG), Cotton blue (CB), ammoniacal Congo red (CR) and c. 5 % potassium hydroxide (KOH). The formulas for reagents follow Huhtinen (1989). Large apothecia were cut in half or sectioned for mounting, whereas minute and fragile apothecia were squash mounted. Thirty discharged spores were measured, when possible, from each population. Dimensions were recorded subjectively at the accuracy of 0.1 µm. The mean spore Q values were calculated separately from the individual Q values. The total number of spores measured is given (n), followed by the number of populations used as a source. Spore sizes include 90 % of the measured variation; the smallest and the largest 5 % of the values are excluded, although the largest measured value is given in parentheses. Colours, when accurately described, are given according to Cailleux (1981). Line drawings were made using a drawing tube and when present, photographs of vital characters were used as an aid. The exclamation mark (!) indicates that we examined type or other original.

Molecular techniques

DNA was isolated from fresh mycelia scraped from the agar plates, or in cases of unsuccessful culturing from fresh or very recently dried apothecia. In the latter case, 10–30 apothecia were handpicked to a sterile Eppendorf tube. The material was shaken in a cell disrupter Mini-BeadBeater™ (BioSpec Products, Bartlesville, Oklahoma) with 1.2 mm disposable steel beads in a 2 mL screw-cap microvial, at 4 200 rpm for 20 s. If necessary, shaking was repeated once after allowing the sample to cool down for 2–3 min. Alternatively, fresh mycelia were ground in an Eppendorf tube with a pestle together with a tiny amount of sterilized sea sand. DNA was extracted using the

Table 1 Collections used in the molecular phylogenetic analyses, with voucher information and GenBank accession numbers. The number in parenthesis following a species name indicates the specific collection of a species (used in Fig. 2–4). Some GenBank sequences are re-identified by us and the names originally used in GenBank are listed after the taxon names ('as'). Accession numbers in **bold** are sequences generated in this study. Sequences marked with 'not used' are available in GenBank but they were not used in the analyses. Unavailable sequence marked with an n-dash (–).

Taxon	Voucher or culture[1]	Origin, year, collector	GenBank accession number[2]					
			ITS	LSU	*TEF-1α*	*RPB1*	*RPB2*	mtSSU
Amicodisca svrcekii	TK7157 (S, TUR)	Sweden, 2016, T. Kosonen	**MT231647**	**MT231647**	**MT434824**	**MT216583**	**MT228637**	**MT231568**
A. virella	SBRH828 (S, TUR)	Netherlands, 2015, S. Helleman	**MT231648**	**MT231648**	**MT254577**	**MT216584**	**MT228638**	**MT231569**
Arachnopeziza araneosa (1)	ICMP 21731	New Zealand, NA, NA	genome	genome	genome	genome	genome	genome
A. araneosa (2)	PDD 59117 /IMCP 22836	New Zealand, 1991, P.R. Johnston	MH578555	–	–	–	–	–
A. araneosa (3)	PDD 69076 /IMCP 22837	New Zealand, 1994, P.R. Johnston	MH578556	–	–	–	–	–
A. araneosa (4)	PDD 74085 /IMCP 22838	New Zealand, 2001, P.R. Johnston & S. Whitton	MH578557	–	–	–	–	–
A. aurata (1)	TUR 179456	Denmark, 2007, J. Fournier	**MT231649**	**MT231649**	**MT241676**	–	**MT228639**	–
A. aurata (2)	CBS 116.54	France, F. Mangenot	–	MH878241	–	–	–	–
A. aurelia (1)	KUS-F51520	Korea, 2007	JN033409	JN086712	–	–	–	not used
A. aurelia (2)	CBS 117.54	France, F. Mangenot	MH857261	MH868796	–	–	–	–
A. aurelia (3)	TNS-F-11211 / NBRC 102330	Japan, 2003	JN033435	AB546937	–	–	not used	not used
A. aurelia (4)	CBS 127675	Japan, O. Izumi, single spore isolation	MH864618	MH876056	–	–	–	–
A. delicatula (1)	TNS-F-12770	Japan, 2004, T. Hosoya	JN033433	JN086736	–	–	JN086877	JN086802
A. delicatula (2)	TK7076 (S, TUR)	Finland, 2015, T. Kosonen	**MT231650**	**MT231650**	**MT254567**	**MT216585**	**MT228640**	**MT231570**
A. delicatula (3)	JK14051801 (S, TUR)	USA, 2014, J. Karakehian	**MT231651**	**MT231651**	**MT241687**	**MT216586**	**MT228641**	**MT231571**
A. delicatula (4)	JP6655 (S, TUR)	Finland, 2013, J. Purhonen	**MT231652**	**MT231652**	**MT241688**	**MT216587**	**MT228642**	–
A. delicatula (5)	TK7036 (S, TUR)	Finland, 2015, T. Kosonen	**MT231653**	**MT231653**	**MT241689**	**MT216588**	**MT228643**	**MT231572**
A. delicatula (6) as '*A. aurata*'	TNS-F-11212	Japan, 2003, T. Hosoya	JN033436	AB546936	–	–	JN086881	JN086806
A. delicatula (7)	TK7115 (S, TUR)	Finland, 2015, T. Kosonen	**MT231654**	**MT231654**	–	–	–	–
A. delicatula (8)	TK7127 (S, TUR)	Sweden, 2015, T. Kosonen	**MT231655**	**MT231655**	–	–	–	–
A. delicatula (9)	TK7152 (S, TUR)	Sweden, 2016, T. Kosonen	**MT231656**	**MT231656**	–	–	–	–
A. delicatula (10) *as 'A. aurata'*	TENN 074424	USA, SC, 2018, D. Newman & K. Fleming	MH558278	–	–	–	–	–
A. delicatula (11) *as 'A. aurata'*	Isolate CL0301_4_1	South Africa	KY228700	–	–	–	–	–
A. delicatula (12) *as 'A. aurata'*	JHH 2210 (NYS)	USA, MA	U57496	–	–	–	–	–
A. delicatula (13) *as 'A. aurata'*	CBS 127674	Japan	MH864617	MH876055	–	–	–	–
A. delicatula (14) *as 'A. aurata'*	KUS-F52038	South Korea, 2008	JN033393	JN086696	–	–	not used	not used
A. estonica (1)	SH15/38 (S, TUR)	Estonia, 2015, S. Huhtinen	**MT231657**	**MT231657**	**MT241693**	**MT216589**	**MT228644**	**MT231573**
A. estonica (2)	TL210 (TUR)	Finland, 2005, T. Laukka	**MT231658**	**MT231658**	**MT241677**	**MT216590**	**MT228645**	–
A. estonica (3)	TL245 (TUR)	Finland, 2005, T. Laukka	**MT231659**	**MT231659**	**MT241678**	**MT216591**	**MT228646**	–
A. estonica (4)	TL253 (TUR)	Finland, 2005, T. Laukka	**MT231660**	**MT231660**	**MT241679**	**MT216592**	**MT228647**	–
A. japonica (1)	SH06/03 (TUR)	Sweden, 2006, S. Huhtinen	**MT231661**	**MT231661**	**MT241683**	**MT216593**	**MT228648**	–
A. japonica (2)	RI194 (TUR)	Finland, 2006, R. Ilmanen	**MT231662**	**MT231662**	**MT241684**	**MT216594**	**MT228649**	–
A. japonica (3)	RI239 (TUR)	Finland, 2006, R. Ilmanen	**MT231663**	**MT231663**	**MT241685**	**MT216595**	**MT228650**	–
A. japonica (4)	TL267 (TUR)	Finland, 2006, T. Laukka	**MT231664**	**MT231664**	**MT241686**	**MT216596**	**MT228651**	–
A. leonina (1)	KH.15.23 (S, TUR)	Estonia, 2015, K. Hansen	**MT231665**	**MT231665**	**MT254566**	**MT216597**	**MT228652**	**MT231574**
A. leonina (2)	TK7101 (S, TUR)	Estonia, 2015, T. Kosonen	**MT231666**	**MT231666**	**MT241694**	**MT216598**	**MT228653**	**MT231575**
A. leonina (3)	SH16/42 (S, TUR)	Sweden, 2016, T. Kosonen & S. Huhtinen	**MT231667**	**MT231667**	**MT241695**	**MT216599**	**MT228654**	**MT231576**
A. leonina (4)	JYV 11610	Finland, 2013, J. Purhonen	**MT277004**	–	–	–	–	–
A. obtusipila (1)	TNS-F-12768	Japan, 2006, T. Hosoya	JN033445	JN086746	–	–	JN086890	JN086815
A. obtusipila (2)	TNS-F-12769	Japan, 2006, T. Hosoya	JN033446	JN086747	–	–	not used	not used
A. ptilidiophila (1)	TK7287 (S, TUR)	Finland, 2018, T. Kosonen	**MT231668**	**MT231668**	–	**MT216600**	**MT228655**	**MT231577**
A. ptilidiophila (2)	TK7289 (S, TUR)	Finland, 2018, T. Kosonen	**MT231669**	**MT231669**	–	**MT216601**	**MT228656**	**MT231578**
A. ptilidiophila (3)	TK7290 (S, TUR)	Finland, 2018, T. Kosonen	**MT231670**	**MT231670**	–	–	**MT228657**	**MT231579**
A. ptilidiophila (4)	AL51 (TUR)	Finland, 2005, A. Lesonen	**MT231671**	**MT231671**	**MT241680**	**MT216602**	**MT228658**	–
A. sp. 'a' (1)	RI199 (TUR)	Finland, 2006, R. Ilmanen	**MT435517**	**MT435517**	**MT241681**	**MT216603**	**MT228659**	–
A. sp. 'a' (2)	TL260 (TUR)	Finland, 2006, T. Laukka	**MT231672**	**MT231672**	**MT241682**	**MT216604**	**MT228660**	–
A. sp. 'a' (3) as 'uncultured fungus'	OTU19 (environ.)	n/a	EF521221	–	–	–	–	–
A. sp. 'a' (4) as 'uncultured fungus'	SG031 E06 (environ.)	n/a	KP889888	–	–	–	–	–
A. sp. 'a' (5) as 'uncultured fungus'	OTU18 (environ.)	n/a	EF521220	–	–	–	–	–
A. sp. 'b' (1)	TK7223 (S, TUR)	Sweden, 2017, T. Kosonen	**MT231673**	**MT231673**	**MT241696**	**MT216605**	**MT228661**	–

Table 1 (cont.)

Taxon	Voucher or culture[1]	Origin, year, collector	GenBank accession number[2]					
			ITS	LSU	*TEF-1α*	*RPB1*	*RPB2*	mtSSU
A. sp. 'b' (2)	TK7286 (S, TUR)	Finland, 2018, J. Purhonen	**MT231674**	**MT231674**	–	**MT216606**	**MT228662**	**MT231580**
A. sp. (1)	L30_2013 /JCM 31955	Japan, 2013, N. Nakamura	LC190976	–	–	–	–	–
A. sp. (2) as 'uncultured fungus'	c19 (environ.)	USA, NC	HM030576	–	–	–	–	–
A. sp. (3) as '*Arachnopeziza* sp.'	PDD 112237 /ICMP 22830	New Zealand, 2008, P.R. Johnston & P. White	MH578548	–	–	–	–	–
A. sp. (4) as '*Helotiales*'	EXP-0411F	n/a	DQ914728	–	–	–	–	–
A. sp. (5) as 'fungal sp.'	Strain Mh859.5.8	USA, NC	GQ996153	–	–	–	–	–
A. sp. (6)	PDD 112226	New Zealand, 2018, P.R. Johnston	MH578523	–	–	–	–	–
A. sp. (7)	PDD 111524 /IMCP 22834	Australia, 2009, P.R. Johnston	MH578552	–	–	–	–	–
A. sp. (8)	PDD 105290 /IMCP 22833	New Zealand, 1994, P.R. Johnston	MH578551	–	–	–	–	–
A. sp. (9)	PDD 105289 /IMCP 22832	New Zealand, 2008, P.R. Johnston & P. White	MH578550	–	–	–	–	–
A. sphagniseda (1)	RI226 (TUR)	Finland, 2006, R. Ilmanen	**MT231675**	**MT231675**	–	**MT216607**	**MT228663**	–
A. sphagniseda (2)	RI267 (TUR)	Finland, 2006, R. Ilmanen	**MT231676**	**MT231676**	–	**MT216608**	–	–
A. sphagniseda (3)	TUR 178046	Finland, 2006, S. Huhtinen	**MT231677**	**MT231677**	–	–	–	–
A. sphagniseda (4)	TL268 (TUR)	Finland, 2006, T. Laukka	**MT231678**	**MT231678**	–	–	–	–
A. trabinelloides (1)	GJO 0071771	Austria, 2014, I. Wendelin	**MT231679**	**MT231679**	**MT241697**	**MT216609**	**MT228664**	**MT231581**
A. trabinelloides (2)	JK14030203 (S, TUR)	USA, MA, 2014, J. Karakehian	**MT252825**	–	–	–	–	–
Arachnoscypha aranea (1)	SH15/44 (S)	Finland, 2015, S. Huhtinen	**MT231680**	**MT231680**	**MT241698**	**MT216610**	**MT228665**	**MT231582**
A. aranea (2)	TK7129 (S)	Sweden, 2015, T. Kosonen	**MT231681**	**MT231681**	**MT254568**	**MT216611**	**MT228666**	**MT231583**
Ascocoryne sarcoides	NRRL 50072	Chile, 2003	not used	genome	genome	genome	genome	genome
Calycellina leucella	MP150937 (S, TUR)	Finland, 2015, M. Pennanen	**MT231682**	**MT231682**	**MT241672**	**MT216612**	**MT228667**	–
Calycina citrina	CBS 139.62	France	–	FJ176871	–	–	FJ238354	FJ176815
Cenangiopsis quercicola	TAAM:178677	Denmark	not used	KX090811	KX090663	KX090760	KX090713	–
Chlorociboria aeruginascens	TAAM:198512	Germany	not used	LT158419	KX090657	KX090752	KX090706	–
C. aeruginosa	OSC 100056	n/a	not used	AY544669	DQ471053	DQ471125	DQ470886	AY544734
Ciborinia camelliae	ICMP 19812	New Zealand, 2012, M. Denton-Giles	not used	genome	genome	genome	genome	genome
Cudoniella clavus	OSC 100054	n/a	not used	DQ470944	DQ471056	DQ471128	DQ470888	DQ470992
Cyathicula microspora	TF2006-BI (TUR)	Sweden, 2006	EU940165	EU940088	–	–	EU940304	EU940240
Dematioscypha delicata	TK7123 (S, TUR)	Sweden, 2015, T. Kosonen	**MT231683**	**MT231683**	**MT254569**	**MT216613**	**MT228668**	**MT231584**
D. richonis	TK7082 (S, TUR)	Finland, 2015, T. Kosonen	**MT231684**	**MT231684**	**MT254576**	**MT216614**	**MT228669**	**MT231585**
Dermea acerina	CBS 161.38	Canada, 1936	–	DQ247801	DQ471091	DQ471164	DQ247791	DQ247809
Eriopezia caesia	TK7005 (S, TUR)	Finland, 2014, S. Huhtinen	**MT231685**	**MT231685**	**MT241673**	**MT216615**	**MT228670**	**MT231586**
Eupezizella aureliella (1)	TK7300 (S, TUR)	Sweden, 2016, T. Kosonen & S. Huhtinen	**MT231686**	**MT231686**	**MT241699**	**MT216616**	**MT228671**	**MT231587**
E. aureliella (2)	s.n. (S, TUR)	Finland, 2016, O. Miettinen	**MT231687**	**MT231687**	**MT241700**	**MT216617**	**MT228672**	**MT231588**
Hamatocanthoscypha straminella	JHP-15.170 (S, TUR)	Estonia, 2015, J.H. Petersen	**MT231688**	**MT231688**	**MT254565**	**MT216618**	**MT228673**	**MT231589**
Hyalopeziza alni	TK7210 (S, TUR)	Sweden, 2016, T. Kosonen	**MT231689**	**MT231689**	**MT241701**	**MT216619**	**MT228674**	**MT231590**
H. nectrioidea (1)	CBS 597.77	Switzerland, 1973, P. Raschle	JN033381	JN086684	–	–	JN086836	JN086761
H. nectrioidea (2)	ES-2016.35 (S, TUR)	Switzerland, 2016, E. Stöckli	**MT231690**	**MT231690**	–	**MT216620**	–	**MT231591**
Hyaloscypha fuckelii (1)	AMFB1780 (S, TUR)	Belgium, 2016, B. Clesse	**MT231691**	**MT231691**	**MT254571**	**MT216621**	**MT228675**	**MT231592**
H. fuckelii (2)	TK7053 (S, TUR)	Finland, Åland, 2015, T. Kosonen	**MT231692**	**MT231692**	**MT254572**	**MT216622**	**MT228676**	**MT231593**
H. hepaticola	MK37 (TUR)	Finland, 2006, M. Kukkonen	JN943614	EU940150	–	JN985233	EU940359	EU940290
H. herbarum	MP150945 (S, TUR)	Finland, 2015, M. Pennanen	**MT231693**	**MT231693**	**MT241674**	**MT216623**	**MT228677**	**MT231594**
H. intacta	TK7111 (S, TUR)	Estonia, 2015, T. Kosonen	**MT231694**	**MT231694**	**MT241675**	**MT216624**	**MT228678**	**MT231595**
H. leuconica var. *leuconica*	TK7014 (S, TUR)	Finland, 2014, T. Kosonen	**MT231695**	**MT231695**	**MT254573**	**MT216625**	**MT228679**	**MT231596**
H. occulta as '*Hyaloscypha* sp.'	TNS-F-31287	Japan, 2007, T. Hosoya	JN033454	JN086754	–	–	JN086900	JN086825
H. usitata	TK7083 (S, TUR)	Finland, 2015, T. Kosonen	**MT231696**	**MT231696**	**MT254574**	**MT216626**	**MT228680**	**MT231597**
H. vitreola	SH14/10 (S, TUR)	Finland, 2014, S. Huhtinen	**MT231697**	**MT231697**	**MT254575**	**MT216627**	**MT228681**	**MT231598**
Hyaloscyphaceae sp.	SH16/40 (S, TUR)	Sweden, 2016, T. Kosonen & S. Huhtinen	**MT231698**	**MT231698**	**MT241702**	**MT216628**	**MT228682**	**MT231599**
Hymenoscyphus caudatus	KUS-F52291	Korea, 2008	not used	JN086705	–	–	JN086856	JN086778
H. fraxineus	CBS 133217 (MNHNL)	Luxembourg, 2012, G. Marson	not used	genome	genome	genome	genome	genome
H. fructigenus	TNS-F-44644	Japan, 2011, T. Hosoya	AB926057	AB926144	–	–	AB926189	–
H. infarciens	CBS 122016	France, 2001, G. Marson	not used	genome	genome	genome	genome	genome
Lachnum imbecille	TK7121 (S, TUR)	Finland, 2015, T. Kosonen	**MT231699**	**MT231699**	**MT254570**	**MT216629**	**MT228683**	**MT231600**
Leotia lubrica	OSC 100001	n/a	–	AY544644	DQ471041	DQ471113	DQ470876	AY544746

Table 1 (cont.)

Taxon	Voucher or culture[1]	Origin, year, collector	GenBank accession number[2]					
			ITS	LSU	*TEF-1α*	*RPB1*	*RPB2*	mtSSU
Meria laricis	CBS 298.52	Switzerland, 1952, E.Müller	MH857046	DQ470954	DQ842026	DQ471146	DQ470904	DQ471002
Mimicoscypha lacrimiformis (1)	SH17/8 (S, TUR)	Sweden, 2017, S. Huhtinen	**MT231700**	**MT231700**	**MT241703**	**MT216630**	**MT228684**	**MT231601**
Mimicoscypha lacrimiformis (2)	TK7224 (S, TUR)	Sweden, 2017, T. Kosonen	**MT231701**	**MT231701**	–	–	–	–
Mimicoscypha lacrimiformis (3)	SH17/6 (S, TUR)	Sweden, 2017, S. Huhtinen	**MT231702**	**MT231702**	–	–	**MT228685**	**MT231602**
Mimicoscypha lacrimiformis (4)	SH17/7 (S, TUR)	Sweden, 2017, S. Huhtinen	**MT231703**	**MT231703**	**MT434823**	**MT216631**	**MT228686**	**MT231603**
Mimicoscypha lacrimiformis (5)	KH.17.02 (S)	Sweden, 2017, K. Hansen	**MT231704**	**MT231704**	–	–	**MT228687**	–
Neobulgaria pura	CBS 477.97	USA, 1996, K. Cameron	–	FJ176865	FJ238397	FJ238434	FJ238350	–
Olla millepunctata	TK7167 (S, TUR)	Sweden, 2016, T. Kosonen	**MT231705**	**MT231705**	**MT241705**	**MT216632**	**MT228688**	**MT231604**
O. transiens	TK7125 (S, TUR)	Sweden, 2015, T. Kosonen	**MT231706**	**MT231706**	**MT241706**	**MT216633**	**MT228689**	**MT231605**
Pezicula carpinea	CBS 282.39	Canada, 1932, H.S. Jackson	–	DQ470967	DQ479932	DQ842032	DQ479934	DQ471016
Polydesmia pruinosa (1)	TK7139 (S, TUR)	Sweden, 2015, T. Kosonen	**MT231707**	**MT231707**	**MT241707**	**MT216634**	**MT228690**	**MT231606**
P. pruinosa (2)	TK7236 (S, TUR)	Finland, 2017, T. Kosonen	**MT231708**	**MT231708**	**MT241708**	–	**MT228691**	**MT231607**
Proliferodiscus sp.	KUS-F52660	Korea, 2010	not used	JN086730	–	–	JN086871	JN086796
Resinoscypha variepilosa	SH16/41 (S, TUR)	Sweden, 2016, T. Kosonen & S. Huhtinen	**MT231709**	**MT231709**	**MT241709**	**MT216635**	**MT228692**	**MT231608**
Rustroemia firma	CBS 341.62	France	–	DQ470963	DQ471082	DQ471155	DQ470912	DQ471010
Sclerotinia sclerotiorum	1980_UF70	n/a	not used	genome	genome	genome	genome	genome
Scutoscypha fagina	TK7178 (S, TUR)	Sweden, 2016, T. Kosonen	**MT231710**	**MT231710**	**MT241710**	**MT216636**	**MT228693**	**MT231609**
Solenopezia solenia	SH17/18 (S, TUR)	Sweden, 2017, S. Huhtinen	**MT231711**	**MT231711**	**MT241711**	**MT216637**	**MT228694**	**MT231610**
Trichopeziza sp.	s.n. (S, TUR)	Spain, 2016, J. Castillo	**MT427744**	**MT427744**	**MT241712**	**MT216638**	–	**MT231611**
Vibrissea truncorum	CBS 258.91	Canada, 1987, R.G. Thorn	not used	FJ176874	FJ238405	FJ238438	FJ238356	FJ190635

[1] In personal collection numbers names have been shortened and only the initials are given. Herbaria are cited according to acronyms in Index Herbariorum (http://sweetgum.nybg.org/ih/).

[2] ITS: Internal transcribed spacers (ITS1 and ITS2) and the 5.8S gene of the nrDNA; LSU: 28S large subunit of the nrRNA gene; TEF-1α: Translation elongation factor 1-alpha; RPB1: RNA polymerase II largest subunit; RPB2: RNA polymerase II second largest subunit.

DNeasy® Plant Mini Kit (Qiagen), following the standard protocol for fresh plant material. In the final step, the DNA extract was eluted with the provided elution buffer in a volume of 200 µL. A 1 : 10 dilution of the DNA with sterile DNase-free water was used as template for the polymerase chain reaction (PCR). The DNA extract from scanty specimens was (in the final step) eluted in only a volume of 100 µL or less, and without further dilution used for PCR. For a small (random) part of the material, DNA was extracted using the Promega Wizard® Genomic DNA purification kit, following the provided protocol for filamentous fungi. The brightness of ITS-LSU PCR bands was used as an initial indication of the concentration of the DNA that was diluted even further, if necessary, for subsequent reactions.

Six different gene regions were amplified: rDNA ITS1–5.8S–ITS2 and the D1–D2 regions of LSU, c. 1300–1400 bp; mitochondrial small subunit (mtSSU), regions U2–U6, c. 800–1000 bp; RNA polymerase I (*RPB1*), A–C region, c. 700 bp; RNA polymerase II (*RPB2*), 5–11 regions, c. 1800 bp; and translation elongation factor 1-alpha (*TEF-1α*), c. 1000–1300 bp. The respective primers used were: ITS1, ITS4, LR0R, LR3 and LR5 (White et al. 1990); mrSSU1 and mrSSU3R (Zoller et al. 1999); RPB1A, RPB1C (Matheny et al. 2002); 5F, 6F, 7R, 7F, 11aR (Liu et al. 1999) and both RPB2-9R (Taşkin et al. 2010, referred as 'RPB2-9f' in the article) and RPB2-9mR (ATY AAA TGD GCA ATN GTC ATR CG), a modification of the RPB2-9R primer; 526F, 2F, 1567R and 2218R (S. Rehner unpubl., Rehner & Buckley 2005) and EF–3AR (Taşkin et al. 2010). Generally, the gene regions were PCR amplified in one piece. If unsuccessful, the genes were PCR amplified in two or more overlapping pieces. A standard approach for the *RPB2* and *TEF-1α* genes was to use primers 5F and 9mR (*RPB2*) and 526F and EF-3AR (*TEF-1α*). This resulted in strong target product without multiple bands in 80–90 % of the sampled species. PCR amplifications were done using Illustra™ Hot Start Mix RTG PCR beads (GE Healthcare, UK) in a volume of 25 µL. All PCR programs included an initial hot start at 95 °C for 5 min and a final incubation at 72 °C for 7 min. The actual cycles were as follows: ITS and LSU regions of rDNA: 35 cycles of denaturation at 95 °C for 30 s, annealing at 58 °C for 45 s and extension at 72 °C for 1–1.5 min; for mtSSU the program was identical, except that the annealing was at 56 °C for 1 min; for *RPB1*: 35 cycles at 95 °C for 1 min, annealing at 52 °C with 1 °C increase every 5 s until 72 °C and extension at 72 °C for 1.5 min; for *RPB2*: 34–40 cycles of denaturation at 95 °C for 1 min, annealing at 55–58 °C for 1 min and extension at 72 °C 1 min with an increase of 1 s each cycle; for *TEF-1α* a touchdown program: 9 cycles of denaturation at 95 °C for 30 s, annealing at 66 °C for 30 s with temperature reduced 1 °C every cycle and extension at 72 °C for 1 min followed by an additional 30–33 cycles with denaturation at 95 °C, annealing at 56 °C for 30 s and extension at 72 °C for 1 min. PCR products were examined on 1 % agarose gel and either purified directly using ExoSap–IT (Thermo Fisher Scientific) to remove excess primers and nucleotides. In the case of multiple bands, the total volume of PCR was run on a 1.5 % agarose gel and the band of correct size was excised and retained using the Gel Extraction Kit (Qiagen). Purified PCR products were sequenced by Macrogen Inc. (the Netherlands). The primers used for PCR (listed above) were also used for sequencing. Two internal primers were in addition used for sequencing long PCR products (> 1 000 bp), to produce multiple overlapping sequences.

Alignment, data-partitioning and phylogenetic analyses

Sequences were assembled and edited using Sequencher v. 4.10 (Gene Codes Corporation, Ann Arbor, MI, USA). Nucleotide sequences were aligned manually using Se-Al v. 2.0a11 (Rambaut 2002). Each alignment of the protein-coding genes

was translated to amino acids using MacClade v. 4.08 (Maddisson & Maddisson 2000) to verify the alignment and determine the intron positions. The introns were too variable to align unambiguously and were therefore excluded from the analyses. All gene regions were analysed using the nucleotides. Two multi-gene datasets were assembled:

1. the *Helotiales* dataset, to resolve the boundaries and relationships of *Arachnopezizaceae* and *Hyaloscyphaceae* (including also representatives of other *Helotiales*); and
2. the *Arachnopezizaceae* dataset, to delimit species and elucidate the relationships in *Arachnopeziza* (including *Arachnopezizaceae* s.str. as delimited from analyses of the *Helotiales* dataset).

Leotia lubrica was used as an outgroup for the *Helotiales* dataset based on its placement outside *Helotiales* in various studies (Spatafora et al. 2006, Johnston et al. 2019). *Amicodisca virella* was used as an outgroup for the *Arachnopezizaceae* dataset, based on our results from analyses of the *Helotiales* dataset. *Arachnopeziza aurelia* (TNS-F11211) was not included in the final multi-gene *Arachnopezizaceae* dataset, because of missing data (no *RPB1* and *TEF-1α* sequences are available and the *RPB2* sequence is short (716 bp) compared to our sequences) and because it in preliminary analyses was found to be divergent from the other species sampled by us. The combination of lack of characters and closely related species (occurring on a very long branch) resulted in loss of resolution in the backbone of the multi-gene Bayesian and ML phylogenies (in the relationships among the *Arachnopeziza* clades). *Arachnopeziza obtusipila* was included, despite missing similar data, because it is closely related to another taxon (*A. leonina*) and the impediment of the missing data appeared to have no (or less) effect on the analyses. For each dataset the single gene regions were analysed separately and combined. Each of the three protein coding gene regions (*RPB1*, *RPB2* and *TEF-1α*) were analysed with two distinct partitions:

1. first and second codon positions; and
2. third codon positions.

The LSU rDNA and mtSSU were each analysed as one distinct partition. Thus, the combined five-gene datasets were analysed with eight partitions.

The ITS was too variable to align across *Helotiales* and it was therefore not included in the *Helotiales* dataset. For the *Arachnopezizaceae* dataset, the ITS sequences were alignable. Analyses of the six-gene dataset, including the ITS region, improved the support values for the *Arachnopeziza leonina* clade, but weakened the support values for some of the backbone nodes. Also, we observed that analyses including the ITS were very sensitive to minor, but equally justified alterations in the ITS alignment. As a result, we did not include the ITS in the combined *Arachnopezizaceae* dataset. Nevertheless, to provide further insight into the species and ecological diversity and geographical distributions of *Arachnopeziza*, a third dataset was assembled that included additional *Arachnopeziza* species and collections with only ITS and, if available, LSU sequences (from GenBank and our own data). For an improved alignment, no outgroup was included in the analyses of this dataset and the phylogenies were rooted along the branch leading to *A. sphagniseda*. The beginning and tail of the mtSSU sequences were highly variable and not possible to align, and were not included in the *Helotiales* or *Arachnopezizaceae* datasets. Alignments of the combined five-gene *Helotiales* and *Arachnopezizaceae* datasets, and the more inclusive ITS-LSU alignment of *Arachnopeziza*, are available at TreeBASE under accession number S25441.

Individual and combined analyses of the six different gene regions were performed using Metropolis-coupled Markov chain Monte Carlo (MCMCMC) in MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003) and Maximum Likelihood-based inference (ML) in RAxML-HPC2 v. 8.2.10 (Stamatakis 2014). All analyses were run on CIPRES science Gateway (Miller et al. 2010). The Bayesian analyses were run in parallel using model jumping (/mixed models) (Ronquist et al. 2012), and with all parameter values, except branch length and tree topologies, unlinked. The analyses consisted of four parallel searches, with four chains each, initiated with random trees. For the single gene datasets the analyses were run for 5 M generations and the combined five-gene datasets for 10 M generations. The chains were sampled every 500 generations in the 5 M generation runs and every 1 K generations in the 10 M runs. A majority rule consensus tree was assembled and the posterior probabilities (PP) were calculated from the last 75 % of the posterior tree samples. The ML analyses used a GTRGAMMA model for the rate heterogeneity with all free model parameters estimated by the program. Maximum likelihood bootstrap analyses (ML-BP) were performed using 1 000 rapid bootstrap replicates from random starting trees, followed by a thorough ML search similarly using 1 000 replicates to find the best tree.

We applied the concept of Genealogical Concordance Phylogenetic Species Recognition (GCPSR) (Taylor et al. 2000) to delimit species in *Arachnopeziza*. To identify independent evolutionary lineages using genealogical concordance we employed two criteria based on Dettman et al. (2003):

1. the clade had to be present in the majority (3/4) of the single-gene phylogenies; and
2. the clade was well supported in at least one single-gene phylogeny (as judged by both PP ≥ 0.95 and ML-BP ≥ 75 %), and if its existence was not contradicted by any of the other single-gene phylogenies at the same level of support.

The ITS, LSU, *RPB1*, *RPB2* and *TEF-1α* genealogies were visually compared to find concordance.

RESULTS

Sequences produced, congruence and data partitions

Altogether 346 sequences from 69 samples were produced in this study. GenBank accession numbers for the specific gene regions are listed in Table 1. In addition, 126 sequences of 28 samples were retrieved from GenBank. The concatenated datasets for *Helotiales* and *Arachnopezizaceae* contained 5 521 and 5 124 characters, respectively. The *Arachnopeziza* ITS-LSU dataset had 1 045 characters. All Bayesian analyses converged: the average standard deviation of split frequencies reached values below 0.01, except in the individual analysis of *RPB2* in the *Helotiales* dataset, which reached a value of c. 0.013 after 5 M generations. In all analyses, the Potential Scale Reduction Factor values stabilized at 1.000. In the ML analyses of the combined *Helotiales* and *Arachnopezizaceae* datasets, the single best scoring trees were recovered with –InL = 73800.332097 and –InL = 18838.975670, respectively. In the ML analyses of the *Arachnopeziza* ITS-LSU dataset, the single best scoring tree was recovered with –InL = 3423.787414. Individual trees for each gene marker for both concatenated datasets were studied for conflicts. There were no supported (PP ≥ 0.95 and ML-BP ≥ 75 %) conflicts between the individual gene trees of the *Helotiales* dataset.

The major lineages and relationships of Arachnopezizaceae, Hyaloscyphaceae s.str. and related genera

Bayesian and ML analyses of the five-gene *Helotiales* dataset produced topologies with identical deeper branching patterns. The back-bone nodes are supported by Bayesian analysis

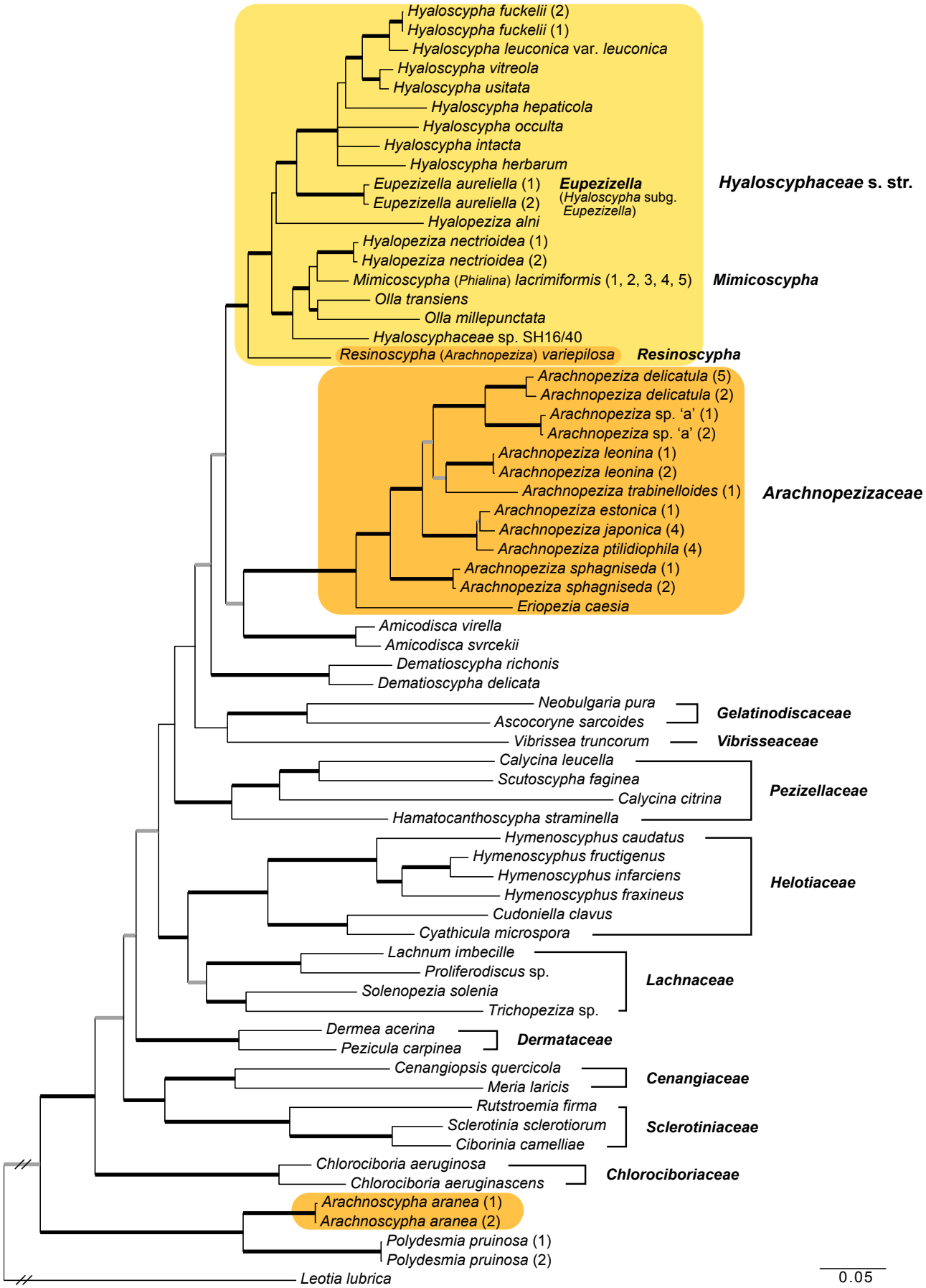


Fig. 2 Phylogenetic relationships of *Arachnopezizaceae* (orange square) and *Hyaloscyphaceae* (yellow square) among members of *Helotiales* based on Bayesian analyses of combined LSU, *RPB1*, *RPB2*, *TEF-1α* and mtSSU loci. *Arachnoscypha aranea* and *Resinoscypha variepilosa* (orange squares) were previously treated in *Arachnopezizaceae*. Thick black branches received both Bayesian posterior probabilities (PP) ≥ 0.95 and maximum likelihood bootstrap value (ML-BP) ≥ 75 %. Thick grey branches received support by either PP ≥ 0.95 or ML-BP ≥ 75 %. The number in parenthesis after a species name refers to an exact collection (see Table 1).

(PP values ≥ 0.95, Fig. 2), except for two nodes that have low support (both PP 0.73) i.e., in the placement of *Pezizellaceae*, *Vibrissea(ceae) and Gelatinodiscaceae*. The *Arachnopezizaceae* is polyphyletic, because *Arachnoscypha* forms a highly supported monophyletic group with *Polydesmia pruinosa* as a sister group to the rest of the *Helotiales* (PP 1.00, ML-BP 91 %), very distant to *Arachnopeziza* and *Eriopezia*. Eight species of *Arachnopeziza* and *Eriopezia caesia* form a highly supported monophyletic group (PP 1.00, ML-BP 100 %). *Arachnopeziza variepilosa* is supported as a separate distinct lineage. *Hyaloscyphaceae (Hyaloscypha* and closely related taxa) is supported as a sister group to a clade of *Arachnopezizaceae* and *Amicodisca* in Bayesian analyses (PP 0.96), with *Dematioscypha* as a sister group to all of those (PP 0.96) (Fig. 2). The ML analysis, however, resolves *Dematioscypha* and *Amicodisca* as successive sister taxa to *Hyaloscyphaceae*, but without support (ML-BP below 50 %). The placement of *Gelatinodiscaceae* and *Vibrissea* differs likewise in the ML phylogeny, but also without support. The *Hyaloscyphaceae* s.str. here includes novel sequences of poorly understood hyaloscyphoid taxa. All other families, as represented here, are supported as monophyletic in both Bayesian and ML analyses, except *Lachnaceae* that is resolved as two successive sister lineages to members of *Helotiaceae* in the ML-analysis but without support (ML-BP 59 %). Members of *Lachnaceae* and *Helotiaceae* form a highly supported monophyletic group (PP 1.00, ML-BP 94 %) as do members of *Cenangiaceae* and *Sclerotiniaceae* (PP 1.00, ML-BP 94 %).

Generic relationships in Hyaloscyphaceae s.str.

The nine selected species of *Hyaloscypha* form a highly supported monophyletic clade (Fig. 2). *Hyaloscypha aureliella* is strongly supported as a sister lineage to all other *Hyaloscypha* species (PP 1.00, ML-BP 99 %), confirming that it is distinct; Huhtinen (1989) recognised it within *Hyaloscypha* in subgenus *Eupezizella*. It is here accepted in the separate genus *Eupezizella* (see Taxonomy). The relationships within *Hyaloscypha* s.str. are not fully resolved (Fig. 2). Two species of *Olla*, *O. transiens* and *O. millepunctata* (type species of *Olla*), form a monophyletic group (PP 1.00, ML-BP 81 %). Two species of *Hyalopeziza*, *H. alni* and *H. nectrioidea*, do not form a monophyletic group. Our preliminary results on the type species of *Hyalopeziza* (*H. ciliata*) indicate that it belongs in *Pezizellaceae* (not shown) and that it is not closely related to any of the other sequenced *Hyalopeziza* species. *Hyalopeziza alni* forms a separate distinct lineage within *Hyaloscyphaceae* s.str., but its placement is without support. *Hyalopeziza nectrioidea* forms a monophyletic group with *Olla* and *Mimicoscypha* (*Phialina*) *lacrimiformis*. The relationships of *M. lacrimiformis* are resolved differently between the two analyses and with only low support from Bayesian PP and ML bootstrap analyses, but it is clearly distinct morphologically from *Olla* and from the two *Hyalopeziza* species (see Taxonomy) and therefore we erect a new genus *Mimicoscypha* for this taxon. Based on morphology this is not a species of *Phialina*. Other species of *Phialina* or *Calycellina* are placed in *Pezizellaceae* (Han et al. 2014, Baral 2016, Johnston et al. 2019).

A possible new species or genus constitutes a distinct lineage (*Hyaloscyphaceae* sp., SH 16/40), sister to the *Mimicoscypha-Olla* clade. Additional material is needed to fully understand and describe this taxon. *Arachnopeziza variepilosa* is highly supported as a sister group to all other *Hyaloscyphaceae* s.str. representatives. It is clearly distant from other species of *Arachnopeziza* and a new genus, *Resinoscypha*, is therefore created (Fig. 2, see Taxonomy).

Phylogenetic species recognition and diversity in Arachnopeziza

Eight terminal independent evolutionary lineages were identified in *Arachnopeziza*, using the two grouping criteria for GCPSR (see Materials and Methods), and these are inferred as phylogenetic species (marked by a triangle on the node in Fig. 3). All of the species were strongly supported as monophyletic by Bayesian PP (≥ 0.95) and ML-BP (≥ 75 %) in at least two of the single gene trees (Table 2). Four of them present newly discovered species of which two are formally described in the present paper, *A. estonica* and *A. ptilidiophila*. Analyses of the LSU did not resolve *A. delicatula* and *A. estonica* as monophyletic, but their monophyly was not significantly contradicted in the LSU genealogies. Bayesian and ML analyses of the combined LSU, *RPB1*, *RPB2*, and *TEF-1α* data supported all eight species as monophyletic (PP 1.00, ML-BP 100 %). The monophyly of four putative species (*A. araneosa*, *A. aurata*, *A. obtusipila* and *A. trabinelloides*), represented by only single collections, could not be tested, but they were considered to be distinct because they were genetically divergent from their sisters (Fig. 3). ITS and LSU sequences were available in GenBank from one to three additional collections of these four species and our analyses of the taxon-expanded ITS-LSU dataset support them as monophyletic groups (Fig. 4). The two collections each of *A. aurata* (from Denmark and France), *A. obtusipila* (Japan) and *A. trabinelloides* (Austria and USA, MA) showed identical ITS and/or LSU sequences. *Arachnopeziza delicatula* showed internal phylogenetic structure in analyses of the five-gene dataset, with two subgroups: *A. delicatula* (4) and (5) (PP 1.00) and *A. delicatula* (2) and (6) (ML-BP 88 %) (Fig. 3), but these groupings were strongly contradicted among the single genealogies suggesting recent recombination within a single

Table 2 Support values for *Arachnopeziza* species recognised by genealogical concordance in the analysis of individual gene regions and in the combined dataset (LSU, *RPB1*, *RPB2*, *EF-1α* and mtSSU[3]): Maximum Likelihood values (RAxML) and Bayesian posterior probabilities (PP). NA, only one or no sequences available. Limits of these species correspond to the nodes with triangles in Fig. 3.

Species[1]	ITS ML-BP / PP	LSU ML-BP / PP	*RPB1* ML-BP / PP	*RPB2* ML-BP / PP	*TEF-1α* ML-BP / PP	Combined five-gene data
A. delicatula	87 / 0.82	–[2] / –	96 / 1.00	100 / 1.00	100 / 1.00	100 / 1.00
A. estonica	100 / 1.00	– / –	100 / 1.00	100 / 1.00	99 / 1.00	100 / 1.00
A. japonica	100 / 1.00	95 / 1.00	100 / 1.00	100 / 1.00	100 / 1.00	100 / 1.00
A. leonina	100 / 1.00	97 / 0.96	100 / 1.00	98 / 0.99	100 / 1.00	100 / 1.00
A. ptilidiophila	97 / 0.68	64 / 0.84	100 / 1.00	100 / 1.00	NA	100 / 1.00
A. sphagniseda	100 / 1.00	100 / 1.00	99 / 1.00	NA	NA	100 / 1.00
A. sp. 'a'	99 / 1.00	77 / 0.84	97 / 1.00	92 / 1.00	NA	100 / 1.00
A. sp. 'b'	98 / 0.97	100 / 1.00	100 / 1.00	100 / 1.00	99 / 1.00	100 / 1.00

[1] Support values not available for the following species represented by a single collection: *A. aurata*, *A. araneosa*, *A. obtusipila* and *A. trabinelloides*.
[2] –, the clade was not resolved as monophyletic.
[3] Support values based on mtSSU alone are not given due to the limited taxon sampling.

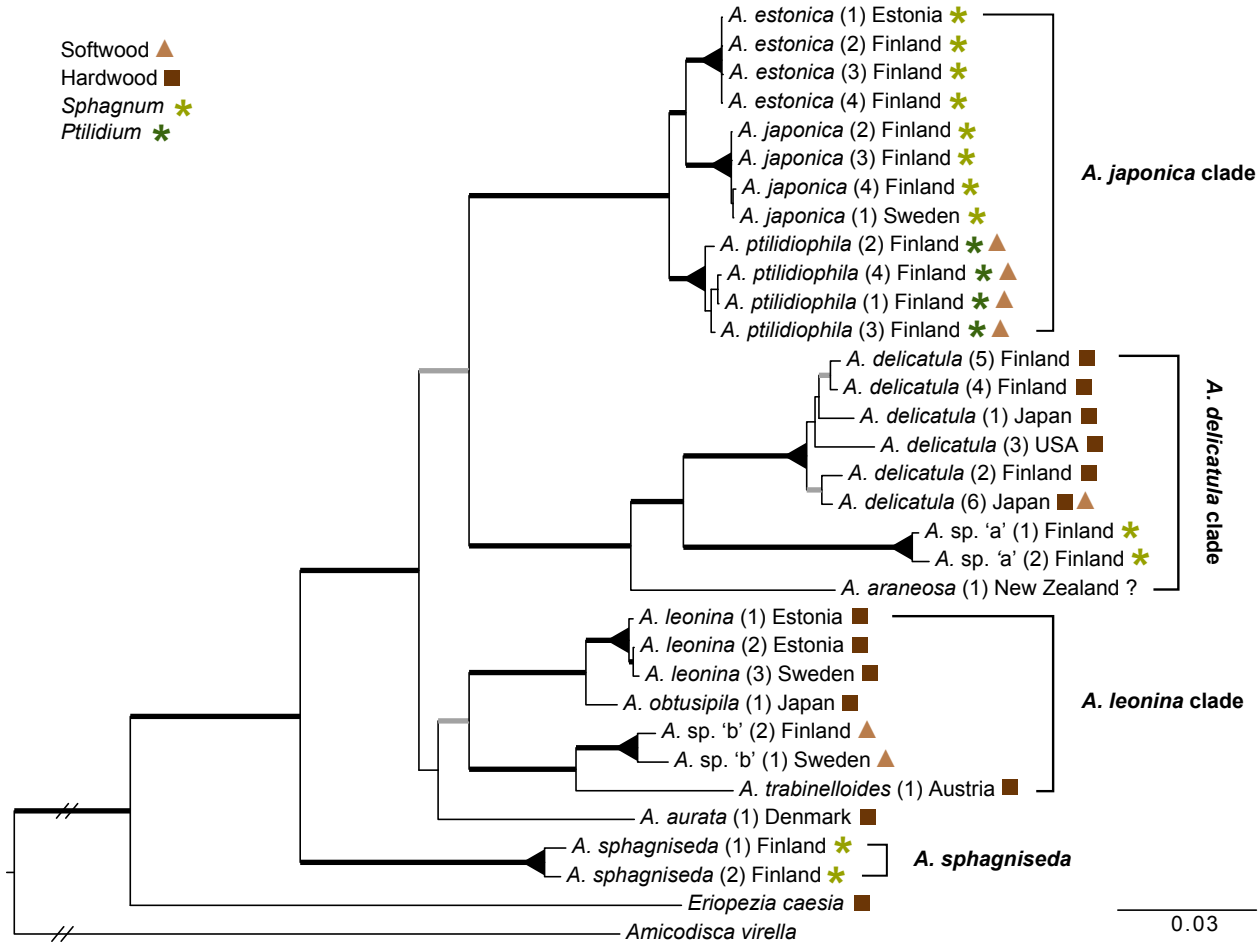


Fig. 3 Phylogenetic tree based on Bayesian analysis of the *Arachnopezizaceae* dataset (combined LSU, *RPB1*, *RPB2*, *TEF-1α* and mtSSU loci). *Amicodisca virella* was used as an outgroup in the analysis and for rooting the tree. Thick black branches received both Bayesian posterior probabilities (PP) ≥ 0.95 and maximum likelihood bootstrap value (ML-BP) ≥ 75 %. Thick grey branches received support by either PP ≥ 0.95 or ML-BP ≥ 75 %. The triangles at the nodes indicate eight species recognised by genealogical concordance phylogenetic species recognition. The number in parenthesis after a species name refers to an exact collection (see Table 1). Four clades are named for discussion.

lineage/species. The *A. delicatula* populations sampled for multiple gene analyses were from three different continents, Japan, Northern Europe and USA, and did not show any geographical pattern.

Bayesian and/or ML analyses of the taxon-expanded ITS-LSU dataset supported all of the species recognised using GCPSR or genetic divergence, except for *A. delicatula* (Fig. 4). In addition to the six collections included in our multi-gene analyses (Fig. 3), nine other *A. delicatula* collections were included in the ITS-LSU dataset. Six of these were retrieved from GenBank as *A. aurata*, but are for the time being referred to the *A. delicatula* lineage, because they had ITS (± LSU) sequences that were identical to ITS and LSU sequences of *A. delicatula* studied by us (Fig. 4). They include populations from four different continents, i.e., Northern Europe, Eastern North America, South Africa and East Asia. *Arachnopeziza aurata*, the type species of *Arachnopeziza*, forms a separate distinct lineage (Fig. 3, 4). Included in the ITS-LSU phylogeny is one species not represented in our five-gene phylogeny, *A. aurelia*, which is supported as a distinct lineage (PP 1.00, ML-BP 99 %). Three undetermined sequences of *Arachnopeziza* are closely related or conspecific with *A. araneosa*, originating from apothecia on hardwood or softwood from Australia and New Zealand (*A.* sp. 7, 8, 9). Three environmental ITS sequences from clones originating from mesh bag in spruce forest and soil, i.e., *A.* sp. 'a' (3, 4, 5) (Fig. 4), were 100 % identical or nearly so to our two ITS sequences from *A.* sp. 'a' (1, 2) collections from Finland on *Sphagnum*, and are considered conspecific. Another four undetermined ITS sequences are likely closely related or conspecific with *A.* sp. 'a' based on ML analyses (ML-BP 75 %): three are environmental sequences from plant leaves (*A.* sp. 4, 5) and from soil (*A.* sp. 2), and one from apothecia on *Phormium* (*A.* sp. 3) (Fig. 4).

Relationships among phylogenetic species in Arachnopeziza

No supported conflict (PP ≥ 0.95, ML-BP ≥ 75 %) was detected between the single gene *Arachnopezizaceae* phylogenies in terms of relationships among the twelve species recognised. The five-gene phylogeny of *Arachnopezizaceae* is fully resolved and highly supported in all branches as inferred from Bayesian PP and/or ML-BP, except for the node joining *A. aurata* and the *A. leonina* clade, which has no support (Fig. 3). *Eriopezia caesia* is placed as the earliest diverging lineage in *Arachnopezizaceae* (as also found in the five-gene *Helotiales* phylogeny, Fig. 2). Four major clades are identified in *Arachnopeziza* and to facilitate results and discussion we have named these as indicated on Fig. 3. These clades receive high support from Bayesian PP (1.00) and ML-BP (100 %) except for the *A. leonina* clade that is supported only by Bayesian PP 0.99 (ML-BP 37 %).

The *A. japonica* clade consists of three closely related species with a lifestyle connected to bryophytes. *Arachnopeziza estonica* and *A. japonica* are morphologically very alike and they both form apothecia on stems and branches of *Sphagnum*. They are strongly supported as sister species in the five-gene phylogeny (Fig. 3); although Bayesian and ML analysis of

Fig. 4 The best scoring maximum likelihood phylogeny of *Arachnopeziza* based on ITS-LSU. Thick black branches received both Bayesian posterior probabilities (PP) ≥ 0.95 and maximum likelihood bootstrap value (ML-BP) ≥ 75 %. Thick grey branches received support by either PP ≥ 0.95 or ML-BP ≥ 75 %. The analyses were run without an outgroup. The tree was rooted on the branch leading to *A. sphagniseda*. All sequences are derived from ascomata or cultures derived from ascomata, unless marked as environmental samples. The number in parenthesis after a species name refers to an exact collection (see Table 1).

RPB1 resolve *A. ptilidiophila* and *A. japonica* as sister species (PP 0.92, ML-BP 70 %), analysis of *RPB2* and *TEF-1α* strongly supports *A. japonica* and *A. estonica* as sisters (PP 1.00, ML-BP 98 % and PP 0.53, ML-BP 87 %). *Arachnopeziza ptilidiophila* is associated with *Ptilidium* spp. and *Pinus sylvestris*, forming apothecia both on wood and *Ptilidium* shoots. Its connection to *Ptilidium* is unclear, not least because *Ptilidium* is omnipresent on *Pinus sylvestris* trunks. The *A. japonica* clade forms a highly supported monophyletic group with the *A. delicatula* clade as inferred from ML-BP 78 % (PP 0.86). The *A. delicatula* clade is composed of *A. delicatula*, *A. araneosa* and a newly discovered species *A.* sp. 'a' (to be described later when more material has been collected, including observations on vital morphological features). *Arachnopeziza delicatula* and *A.* sp. 'a' form a monophyletic group (PP 1.00, ML-BP 83 %). The *A. leonina* clade includes two highly supported subclades: *A. leonina* and *A. obtusipila*; and *A. trabinelloides* and a newly discovered species *A.* sp. 'b'. *Arachnopeziza* sp. 'b' is morphologically difficult to distinguish from *A. leonina*, but appears to be restricted to *Picea abies*. The two records from Sweden and Finland show marked variation in all the studied gene regions and additional material is needed to explore this further. The *A. leonina* clade (and *A. aurata*) is placed as sister to the *A. japonica* and *A. delicatula* clades (PP 1.00, ML-BP 88 %). *Arachnopeziza sphagniseda* (previously *Belonium sphagnisedum*) constitutes a distinct separate clade, strongly supported as sister to the rest of *Arachnopeziza* in the five-gene phylogeny (PP = 1.00, ML-BP = 98 %, Fig. 3).

TAXONOMY

Based on GCPSR or genetic divergence using five loci (Fig. 3, Table 2), we delimited 12 species within *Arachnopeziza*, and with newly collected material from Northern Europe, nine of these are treated and discussed below. Based on the five-gene Bayesian phylogeny (Fig. 2) and morphological and histochemical characters, the two new genera within *Hyaloscyphaceae*, *Mimicoscypha* and *Resinoscypha*, are described with two and three species, respectively, that are combined in the genera. Updated descriptions or notes are given for all of these. *Eupezizella* is recognised as a separate genus for four species that are combined in the genus. *Hyaloscypha usitata* is reported for the first time from Europe. An account is given for *Arachnoscypha* that is removed from *Arachnopezizaceae* and placed in the *Arachnoscypha-Polydesmia* clade.

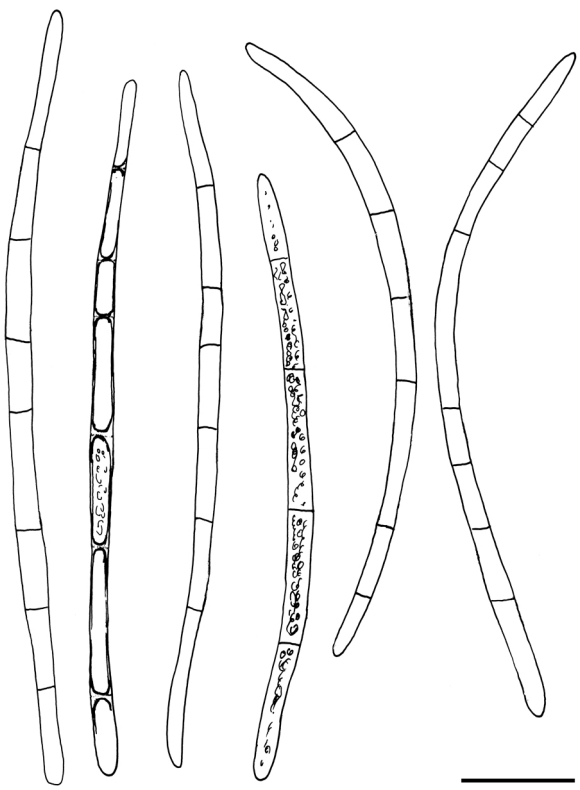


Fig. 5 *Arachnopeziza aurata*. Spores in water (TUR 179456). — Scale bar = 10 µm. — Drawings: T. Kosonen.

Arachnopeziza aurata Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 304. 1870 — Fig. 5

Original material. Germany, Oestrich, on very moist inner bark of *Populus pyramidalis*, in the autumn, Fuckel (no date) (S-F92643, ex Herb. Fuckel 1894, ex Herb. Barbey-Boissier 1266) ! (duplicate S-F92641).

Specimen examined. Denmark, Sjælland, Allindelille Fredskov, on hardwood, 26 May 2007, *J. Fournier* (TUR 179456).

Notes — We apply the name *A. aurata* to a collection from Denmark and, based on identical LSU sequences, to CBS 116.54 from France (Fig. 4). It is a distinct, well-delimited species based on our multi-gene phylogenetic analyses and morphology (Fig. 3, 5). In his monograph, Korf (1951b) distinguished *A. aurata* and *A. delicatula* primarily on spore measurements and septation: *A. aurata* with longer, (43–)48–73(–80) × 1.4–2.7(–3.4) µm, 7-septate spores; and *A. delicatula* with shorter, (24–)28–40(–48) × 2–2.7(–3.4) µm, 3–5 septate spores. Based on our molecular results using GCPSR, *A. delicatula* populations have often longer and up to 6–7-septate spores thus overlapping with *A. aurata* (see further under *A. delicatula*). We suggest that *A. aurata* is distinguished from *A. delicatula* by narrower, pointed and straight or curved spores, with regularly 6–7 septa. The spore measurements for the studied material are: 51.8–70.6(–78.3) × 1.7–2.7(–2.9) µm, mean 61.1 × 2.2 µm (n = 30), Q = 21.4–34.0, mean Q = 28.7. The apothecia of the Danish collection are intensively yellow orange. Resin is present on the hairs, among the excipulum cells as large droplets and on the subicular hyphae. No resin was observed on the paraphyses, but the exact placement of the pigment should be studied from fresh material.

Arachnopeziza aurata is resolved as a sister species to the *A. leonina* clade (Fig. 3), characterized by ample resin depositions on the hairs and in the excipulum. *Arachnopeziza delicatula*, although with overlapping spore morphology, belongs to a separate clade. Since the large material studied and referred to *A. aurata* by Korf (1951b) may include collections representing *A. delicatula*, the reported variation in morphology is possibly variation between *A. delicatula* and *A. aurata* populations. The distribution and ecological range of *A. aurata* is thus also unclear, and will need further study. It is interesting that the collections of *A. aurata* sensu Korf were not only from various decaying hardwood trees, but also from herbaceous plants, i.e., *Typha* and *Andromeda* (Korf 1951b), a substrate not commonly reported for *Arachnopeziza* species. We made no observations of *A. aurata* from Estonia, Finland and Sweden during forays in a wide range of habitats, whereas *A. delicatula* was observed continuously.

Arachnopeziza delicatula Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 304. 1870 — Fig. 6

Original material. Germany, Eberbach, Eichberg forest, on *Quercus* sp., Fuckel, no date (S-F153832, Fuckel Fungi Rhen. Exs. 2384) !

Specimens examined. Canada, Yukon, Kluane Lake, NW of Sulphur Lake, on *Populus tremuloides*, 22 Sept. 1987, *S. Huhtinen* 87/145 (TUR). – Finland, Varsinais-Suomi, Turku, Piipanoja, 14 May 2015, *T. Kosonen* 7036 (S, TUR); Etelä-Häme, Urjala, Raikonkulma, Rantakaski, on a fallen trunk of *Betula*, 25 Sept. 2015, *T. Kosonen* 7115 (S, TUR); same date and location, *T. Kosonen*

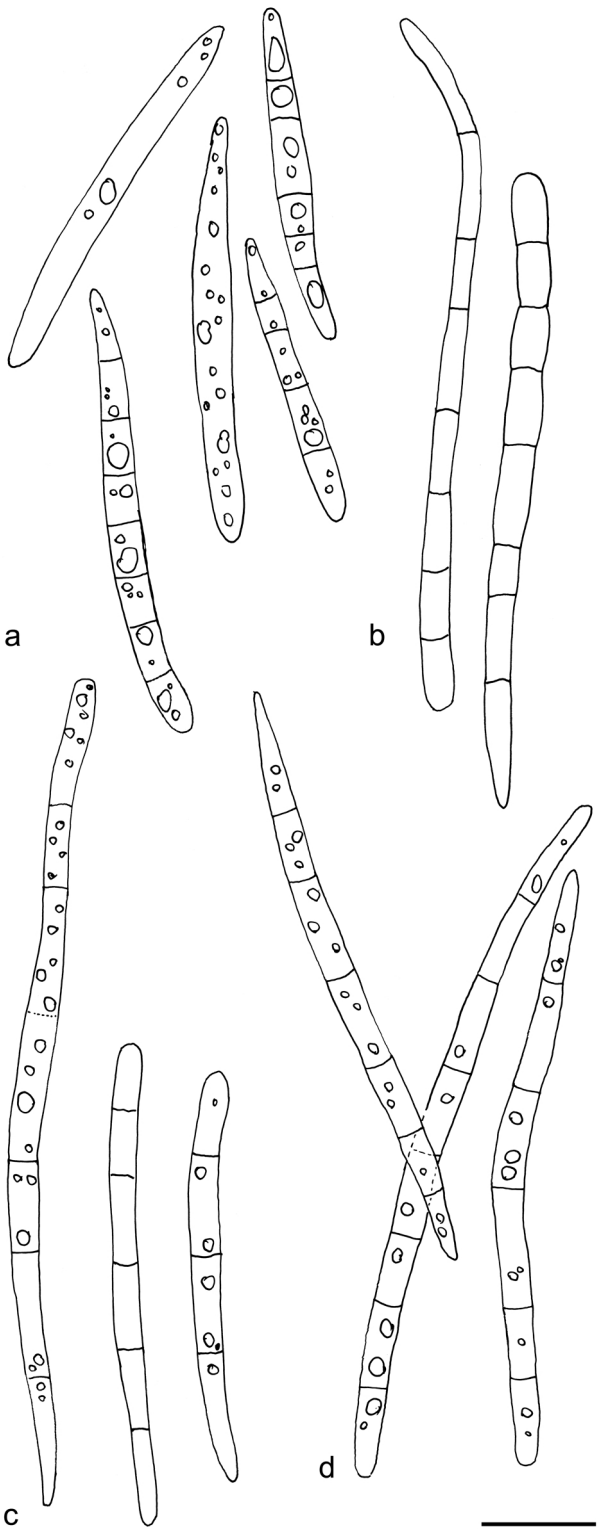


Fig. 6 *Arachnopeziza delicatula*. Spores in CR (a: TNS-F12770; b: *T. Kosonen* 7036; c: *T. Kosonen* 7076; d: *T. Kosonen* 7127). — Scale bar = 10 µm. — Drawings: T. Kosonen.

7116 (S, TUR); Pohjois-Savo, Suonenjoki, Viippero, Ilmakkamäki, on a trunk of *P. tremula*, 23 Sept. 2013, *J. Purhonen* 6655 (JYV 11610); Muurame, Kuusimäki, 25 Aug. 2015, *T. Kosonen* 7076 (S, TUR). – Japan, Hokkaido, Iwamizawa-shi, Tonebetsu, 25 July 2004, *T. Hosoya* (TNS-F12770). – Sweden, Dalsland, Håverud, Forsbo Nature Reserve, on a trunk of *Betula*, 23 Sept. 2016, *S. Huhtinen* 16/54 (S, TUR); Västergötland, Falköping, Forentorpa ängars Nature Reserve, on a trunk of *Betula*, 15 Oct. 2015, *T. Kosonen* 7127 (S, TUR); Kinnekulle, Munkängerna, on *Ulmus*, 17 Oct. 2015, *K. Hansen* & *T. Kosonen* 7132 (S, TUR); Öland, Byxelkrok, Trollskogen, on a trunk of *Betula*, 29 Mar. 2016, *T. Kosonen* 7152 (S, TUR). – USA, Massachusetts, Bristol County, North Easton, Borderland State Park, on the underside of a decayed hardwood log, 19 May 2012, *J. Karakehian* 12051901 (S, TUR).

Notes — *Arachnopeziza delicatula* appears to be a phylogenetically and morphologically diverse species. Both Fuckel (1870) in the original description and Korf (1951b) in his monograph describe *A. delicatula* spores being on average less than 50 µm long and with up to 5 septa. Such populations exist in the material reported here, but using GCPSR they do not represent a distinct species from those populations with on average longer spores (above 50 µm). Instead, our results suggest that *A. delicatula* have spores with a wide range in length: 30–61.0(–63.5) × 2.4–3.8(–4.0) µm in CR, mean 47.6 × 2.9 µm, Q = 9.7–23.8(–25.7), mean Q = 16.5 (n = 35, from three populations). It can be distinguished from *A. aurata* by the width of the spores that are on average wider in *A. delicatula* (3–3.5 µm wide in the longest spores) and by the Q-value that is in average less than 20 in *A. delicatula* and above 20 in *A. aurata.* Most likely this is the main reason for the numerous ITS and LSU sequences deposited in GenBank under the name *A. aurata*, which we consider to represent *A. delicatula* (see Fig. 4). Despite the wide range in spore size and high divergence in ITS sequences we found no support for delimiting further species based on GCPSR or on geographical origin (Fig. 3, Table 2). All the samples studied by us were from hardwood and most of the ITS and LSU sequences retrieved from GenBank originated from apothecia on wood (if specified, on hardwood). One GenBank ITS sequence is from a plant root (CL0301_4_1 from South Africa) (Fig. 4). It is identical to an ITS sequence of a North American collection (*J. Karakehian* 12051901), which is also represented in our multi-gene analyses (*A. delicatula* 3, Fig. 3). There are earlier reports of *A. delicatula* from softwood (e.g., Korf 1951b), as well as some more recent collections in TAAM. Our preliminary morphological study of the TAAM *A. delicatula* collection (TAAM062455) from softwood, found it conforms to the other *A. delicatula* material examined here. This could well be a demonstration of a broad ecology, but there are no sequences available from material on softwood.

Arachnopeziza estonica T. Kosonen, Huhtinen, K. Hansen, *sp. nov*. — MycoBank MB835728, Fig. 7

Etymology. Referring to the geographical origin of the holotype.

Holotype. Estonia, Otepää, Kääriku, NE of lake Kääriku, on *Sphagnum squarrosum*, in a boggy mixed forest, 13 Sept. 2015, *S. Huhtinen* 15/38 (S-F399746); Isotype (TUR 212780) !

Apothecia 0.2–0.5 mm diam, hyaline to white when fresh, white with a yellow hue when dry, on leaves of *Sphagnum*, narrowly attached, often only with a few visible long hairs originating from the margin and upper flanks, subiculum present but indistinct to naked eye. *Ectal excipulum* in the upper flanks of *textura prismatica*, cells c. 15–20 × 5 µm, below and towards the base of *textura angularis* to *globulosa*, cells c. 5–10 µm diam. *Hairs* 50–90 × 3–4 µm, with 3–5 septa, cylindrical, thin-walled, but moderately to clearly thick-walled in the basal parts, uppermost cell tapering distinctly, smooth, hyaline resin present on the outside. *Asci* 70–90 × 6–10(–14) µm, cylindrical to clavate, apical pore MLZ+, arising from croziers. *Ascopores* 15.6–23.2(–24.2) × 2.8–4.4(–5.2) µm, mean 18.8–3.7 µm, Q = 3.9–8.3, mean Q = 5.2 (n = 55, from two populations), cylindrical, often narrowing more prominently towards basal end, with characteristic angular appearance, usually with 0–1 septa, or more rarely with two. *Paraphyses* cylindrical, regularly branched at the basal cell, smooth and without content in CR. *Subicular hyphae* 3–5 µm wide, thick-walled, finely warted.

Specimens examined. Finland, Varsinais-Suomi, Turku, Kuhankuono, on *Sphagnum*, 13 Nov. 2005, *T. Laukka* 253 (TUR); Etelä-Häme, Tammela, Liesjärvi, on *Sphagnum*, 4 July 2005, *T. Laukka* 210 (TUR); Pohjois-Häme, Ruovesi, Siikaneva National Park, on *Sphagnum squarrosum*, 7 Sept. 2005, *T. Laukka* 245 (TUR).

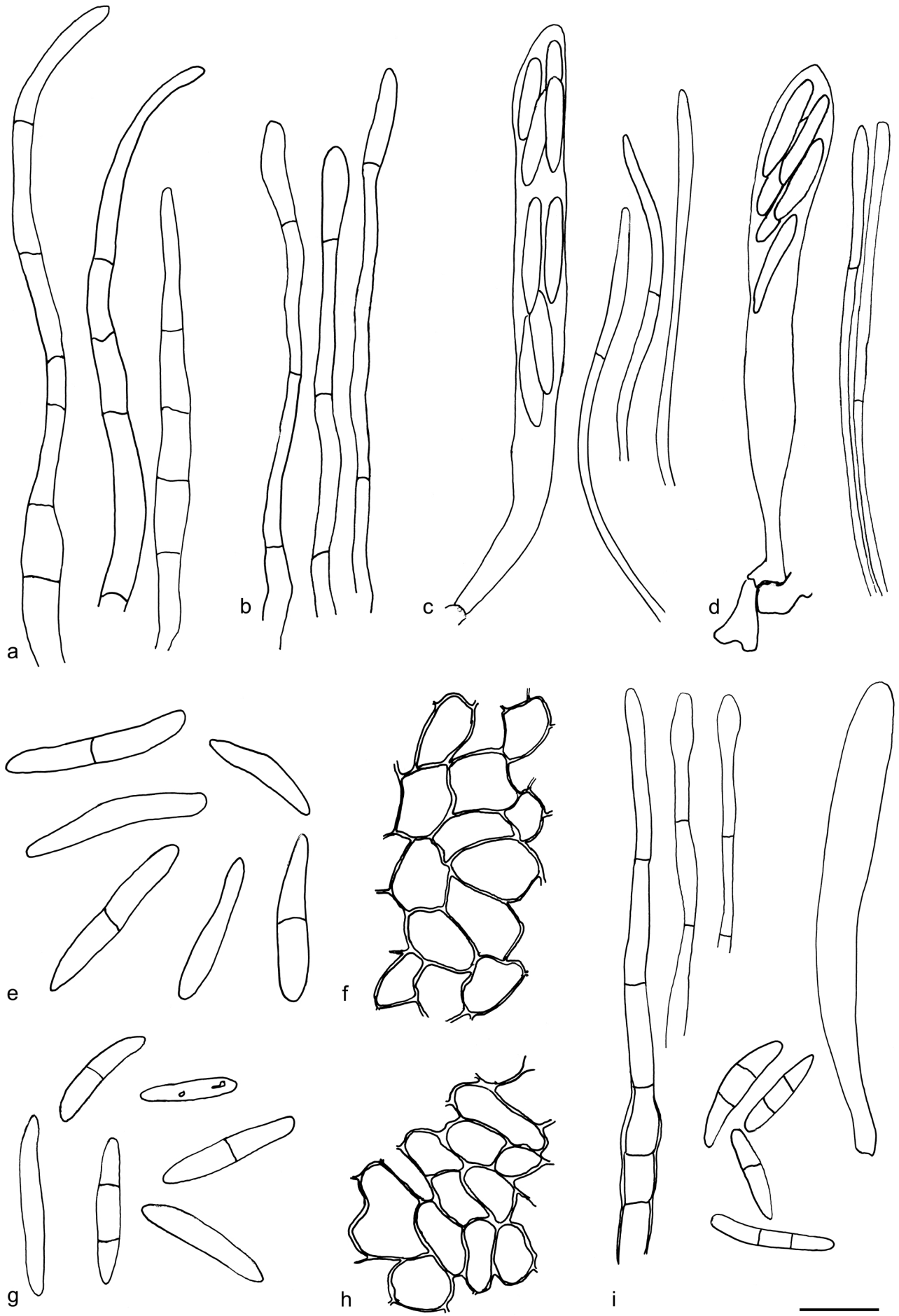


Fig. 7 a, c, e–f. *Arachnopeziza estonica* (holotype) and b, d, g–i. *A. japonica*. All in CR. a–b. Hairs; c–d. asci and paraphyses; e–f. spores; g–h. excipulum; i. hairs, asci and spores (a, c, e–f: *S. Huhtinen* 15/38; b, d, g–h: *T. Laukka* 267; i: holotype). — Scale bar = 10 µm. — Drawings: T. Kosonen.

Notes — This species is very closely related to *A. japonica* and morphologically very similar. It is supported as a separate species using GCPSR (Fig. 3, Table 2) and it can be distinguished by the on average larger spores and wider hairs as compared to *A. japonica*. The hair apices are slightly inflated in *A. japonica*, whereas in *A. estonica* the hairs taper evenly and no apical widening is observed. All observations are from *Sphagnum* and often from *Sphagnum squarrosum*. The two close species, *A. japonica* and *A. estonica*, appear to have very similar ecology at least in Scandinavia.

Arachnopeziza japonica Korf, Bull. Natl. Sci. Mus., Tokyo 44: 392. 1959 — Fig. 7

Holotype. Japan, Kyushu, Miyazaki prefecture, Yabitsu valley, Kijomura village, on leaves, leaf-galls and debris, 6 Nov. 1957, *S. Imai* et al. (CUP-JA-422) !

Apothecia 0.2–0.6 mm diam, hyaline to whitish when fresh, white with a yellow hue when dry, at margin distinctly hairy, broadly attached, subiculum present, scanty. *Ectal excipulum* of firm walled *textura prismatica*, cells c. 18 × 5 µm in the upper flanks, somewhat thick-walled *textura angularis* – *textura globulosa* towards the base, cells 3.5–10 µm wide. *Hairs* 50–80 × 2–3 µm, cylindrical, with 3–5 septa, thin-walled, in the basal parts with moderately to clearly thickened walls, apices typically widened, smooth, hyaline resin present, only partly soluble in MLZ or lactic acid, hairs often tightly glued together in dry material. *Asci* 70–90 × 6–10(–14) µm, cylindrical to clavate, apical pore clearly MLZ+, arising from croziers. *Ascospores* 12.5–21.6(–23.2) × 2.7–4.1(–4.4) µm, mean 16.3 × 3.3 µm (n = 60, from two populations), Q = 3.9–7.9, mean Q = 5.1, cylindrical, but usually narrowing more prominently towards the basal end, slightly angular, usually with 1–2 septa, the 2-septate spores are relatively common, rarely with 3 septa. *Paraphyses* regularly branched at the basal cell, smooth and without content in CR, with a round apex. *Subicular hyphae* 3–5 µm wide, thick-walled, warted.

Specimens examined. All specimens on *Sphagnum*. Finland, Varsinais-Suomi, Nousiainen, Pukkipalo, 26 May 2006, *R. Ilmanen* 194 (TUR); Parainen, Kirjalansaari, 22 Sept. 2006, *R. Ilmanen* 239 (TUR); same location, 22 Sept. 2006, *T. Laukka* 267 (TUR). – Sweden, Söderåsen Nature Park, 5 June 2006, *S. Huhtinen* 06/3 (TUR).

Notes — *Arachnopeziza japonica* is recorded for the first time from Europe. The four collections from Finland and Sweden agree well with the original description and our study of the holotype. In spore size, the holotype (CUP-JA-422, spores: 11.5–16.0 × 2.7–3.0, n = 4) represents the smaller-spored part of the variability, but the observed range is relatively wide and the number of measured spores from the scanty specimen is very small. New observations include a population (*R. Ilmanen* 194) with a roughly similar average spore size and variation as the holotype. Spores with 3 septa are rare and usually then clearly overmature. Spores with 2 septa are relatively common and have the same size and shape as spores with one or no septa. The original description was based on only the holotype from forest litter without any mention of bryophytes or mires. The four recent collections are from *Sphagnum* from paludified forest habitats. *Arachnopeziza japonica* belongs to a clade of three closely related species sharing a connection to bryophytes. Often apothecia of these *Arachnopeziza* species were found by studying randomly picked *Sphagnum* tuffs under a dissecting microscope. Based on the frequently found (single) apothecia on *Sphagnum*, we conclude that the species are relatively common (on *Sphagnum*), but the limits of their ecological niche are poorly known. Larger groups of apothecia of these species were found less often.

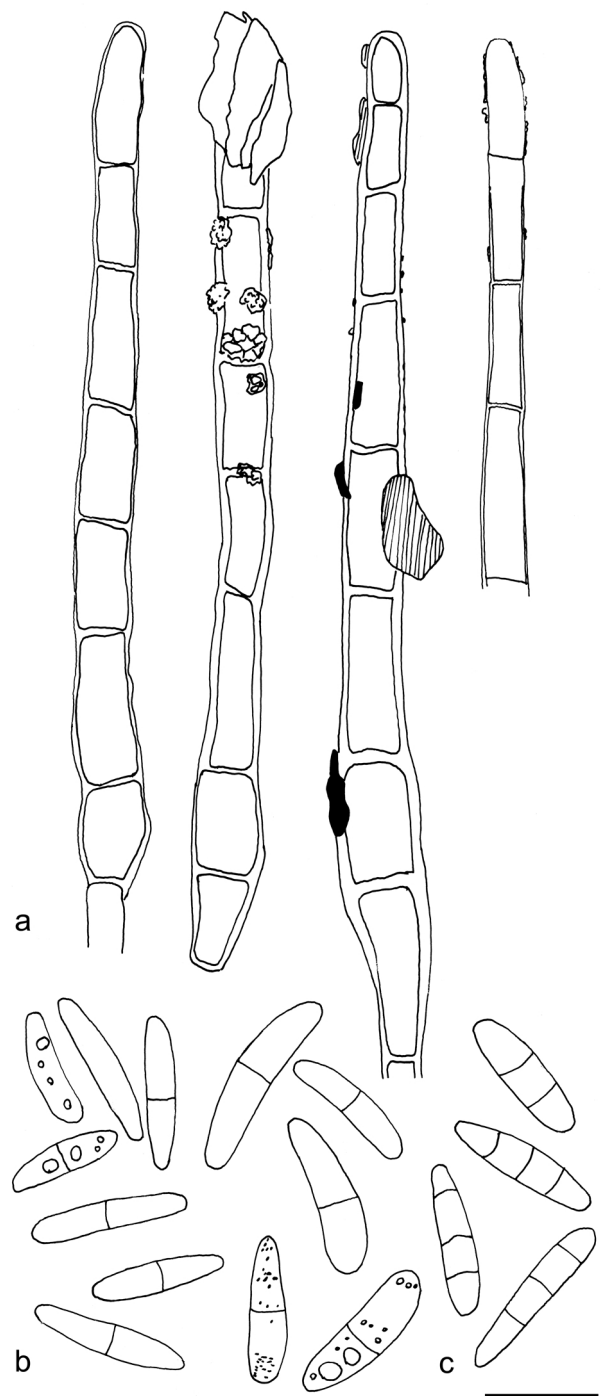


Fig. 8 *Arachnopeziza leonina*. a. Hairs in water; b. spores in water; c. four spores with multiple septa in CR (a–b: GJO 0071770; c: KH.15.23). — Scale bar = 10 µm. — Drawings: T. Kosonen.

Arachnopeziza leonina (Schwein.) Dennis, Kew Bull. 17: 351. 1963 — Fig. 1a–c, 8

Basionym. Peziza leonina Schwein., Schr. Naturf. Ges. Leipzig 1: 93. 1822.

Synonym. *Arachnopeziza candido-fulva* (Schwein.) Korf, Lloydia 14: 163. 1951.

Specimens examined. Austria, Steiermark, Graz, Andritz, near the church of St. Ulrich, on hardwood, 1 Mar. 2014, *I. Wendelin* (GJO 0071770). – Estonia, Valga, Sangaste, Lauküla, Keesliku forest, on a trunk of *Populus tremula*, 12 Sept. 2015, *T. Kosonen* 7101 (S, TUR); same date and location, *K. Hansen*, KH.15.23 (S, TUR). – Finland, Pohjois-Häme, Muurame, Kuusimäki, on a trunk of *Betula* sp., 25 Aug. 2015, *T. Kosonen* 7078 (S, TUR); same date and location, on a trunk of *P. tremula*, *T. Kosonen* 7091 (S, TUR); on a trunk of *Betula* sp., *T. Kosonen* 7092 (S, TUR); on trunk of *Betula* sp., 14 May 2018, *J. Purhonen* & *T. Kosonen* 7294 (S, TUR). – Slovakia, Chorvátsky Grob, Čierna voda, National Nature Reserve Šúr, on a decayed hardwood trunk,

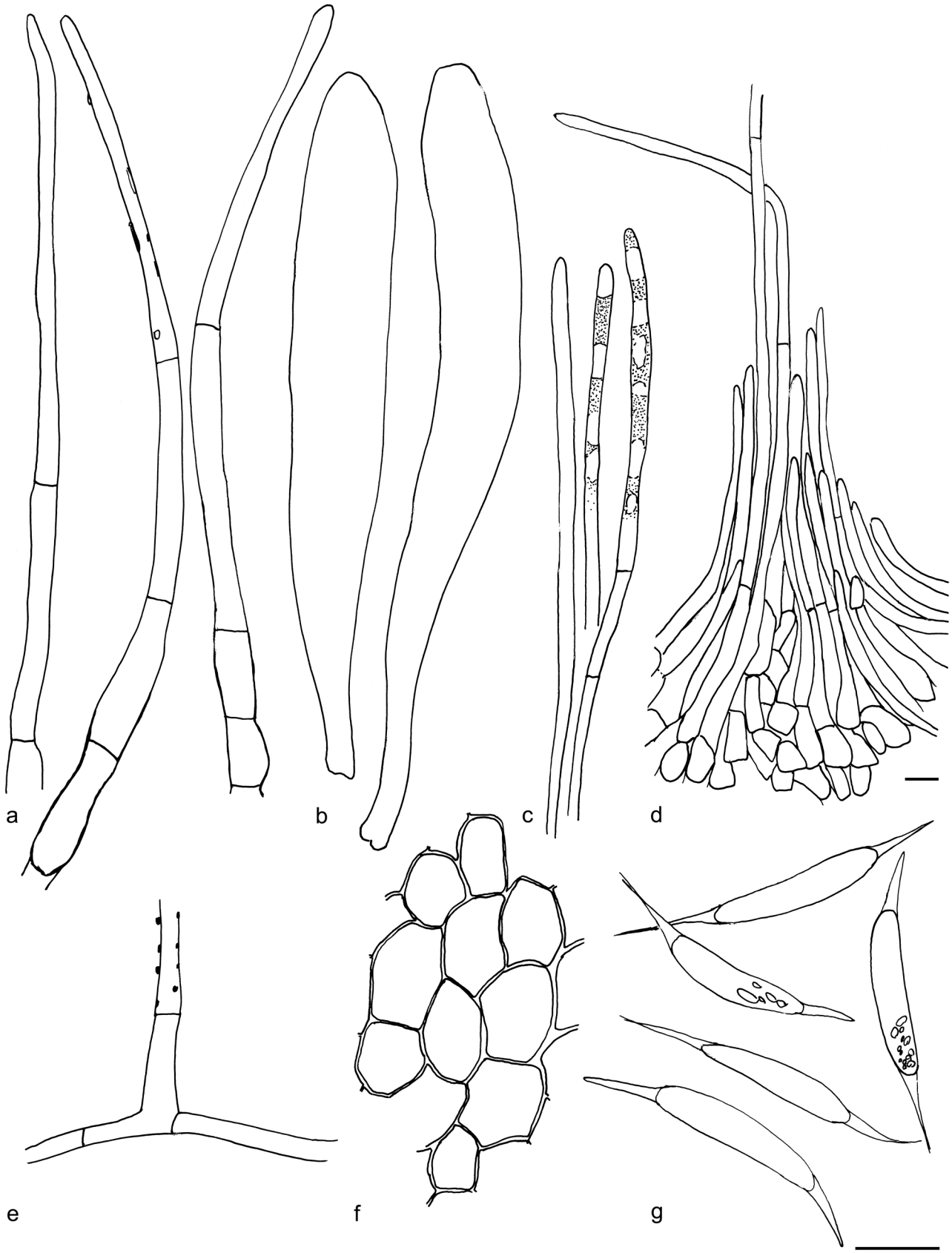


Fig. 9 *Arachnopeziza ptilidiophila* (*T. Kosonen* 7291). All in water. a. Hairs; b. asci; c. paraphyses; d. multiple hairs glued together; e. subicular hypha; f. excipulum; g. spores. — Scale bars: a–c, e–g = 10 µm, d = 10 µm. — Drawings: T. Kosonen.

22 Nov. 2017, *A. Polhorský* 18/26 (S, TUR). – Sweden, Stockholm, Haninge, Tyresta National Park, on a trunk of *P. tremula*, 1 June 2016, *T. Kosonen & S. Huhtinen* 16/42 (S, TUR); Västra Götaland, Falköping, Forentorpa ängars Nature Reserve, 15 Oct. 2015, *T. Kosonen* 7128 (S, TUR).

Notes — *Arachnopeziza leonina* is a phylogenetically distinct species. It is best characterised by the less than 18 µm long, relatively wide spores with three or less septa and by the yellow resin on the hairs and between the excipular cells. It appears to be restricted to decayed hardwood trunks (*Populus*, *Betula* and *Quercus)* or to very coarse debris. No observations were made from recently (< 5 yr) fallen trunks. Morphologically, it overlaps with *Arachnopeziza* sp. 'b' found on softwoods (*Picea abies*). *Arachnopeziza trabinelloides* can often be distinguished from *A. leonina* by the abundant resin on the hairs and the practically non-existent subiculum, but herbarium specimens of *A. trabinelloides* with little resin can be morphologically inseparable from *A. leonina* samples with (for that species) ample resin. We found very little help, if any, in the number of septa in the spores since mature spores seem to have 1–3 septa in both *A. leonina* and *A. trabinelloides*. Fresh samples of *A. leonina* do not react in MLZ as *A. trabinelloides* (see notes under *A. trabinelloides*). For herbarium material we found the best delimiting character to be the lower part of the hairs: in *A. trabinelloides* hairs are fairly cylindrical and of even width for the whole length, whereas in *A. leonina* the hairs are slightly, but clearly, basally widened. In Scandinavia *A. leonina* has an ecology similar to *A. delicatula*; both are regularly present on fallen trunks of hardwood (*Betula* or *Populus tremula*) already in the early stages of decomposition. In his monograph, Korf (1951b) missed the older description by Schweinitz (1822) and applied the name *A. candido-fulva* instead. This was pointed out by Dennis (1963) and later accepted by Korf (Korf & Gruff 1981). *Arachnopeziza leonina* is a relatively common species in the boreal and temperate zones, with observations from Europe and North America. Observations from the southern hemisphere are lacking.

Arachnopeziza ptilidiophila T. Kosonen, Huhtinen, K. Hansen, *sp. nov*. — MycoBank MB835729, Fig. 1d, 9

Etymology. Referring to co-occurrence with *Ptilidium*.

Holotype. Finland, Pohjois-Häme, Muurame, Kuusimäki, on decayed, still quite hard *Pinus sylvestris* trunk, beside or directly on *Ptilidium* shoots, 14 May 2018, *J. Purhonen & T. Kosonen* 7287 (S-F399747) !

Apothecia 0.2–0.7 mm diam, hyaline when fresh, white to yellow when dry, narrowly attached, hymenium flat, hairs concolorous with the receptacle surface, protruding c. 50–70 µm above the hymenium, hairs often slightly bent at upper-third and attached to each other giving a shaggy appearance, subiculum distinct but sparse. *Ectal excipulum* of *textura prismatica*, cells slightly rounded, c. 12–20 × 5 µm in the upper flanks, excipulum below of *textura angularis* – *textura globulosa*, cells c. 10–13 × 6–10. *Hairs* 80–130 × 3–5 µm, cylindrical, thin-walled, basal cells more thick-walled, slightly widened, usually 1–3-septate, apical cell c. one third of the whole length, resin present as small hyaline droplets on the hairs. *Asci* 70–100 × 6–12 µm, clavate, apical pore MLZ+, arising from croziers. *Ascospores* 15.7–23.4(–25.6) × 3.9–5.3(–5.5) µm, mean = 20.1 × 4.6 µm, Q = 3.3–6.1, mean Q = 4.4 (n = 60, from two populations), inequilateral, freshly released spores with 0–1 septa, aseptate spores dominating, most spores with c. 6–10 µm long, hyaline, thin, slender, gel-like polar appendages, tapering to a very sharp end. *Paraphyses* filiform, 1.5–2.5 µm wide. *Subicular hyphae* c. 1.5–3 µm wide, thick-walled, smooth or minutely warted.

Specimens examined. Finland, Satakunta, Yläne, Vaskijärvi Nature Protection Area, Kuusela, on *Ptilidium pulcherrimum*, 15 Apr. 2005, *T. Laukka* & *A. Lesonen* 51 (TUR); Pohjois-Häme, Muurame, Kuusimäki, on *Pinus sylvestris* trunk and on *Ptilidium* shoots, 14 May 2018, *T. Kosonen* 7287 (S, TUR); same date and location, *T. Kosonen* 7289 (S, TUR); same date and location, *T. Kosonen* 7291 (S, TUR).

Notes — The most striking feature of *A. ptilidiophila* is the long and slender polar spore appendages (Fig. 9g). The character is only visible in living material; already more than 1-mo-old dried specimens failed to show the appendages in various rehydration trials with different reagents. Although gelatinous appendages are rare in hyaloscyphoid fungi, they seem to be less so in *Arachnopeziza*. Spore appendages have also been observed in *A. aurelia*, *A. cornuta* and *A. floriphila*. Boudier (1910: Plate 520, n°. 530) illustrated *A. aurelia* with similar spore appendages to those in *A. ptilidiophila*, but in *A. aurelia* the appendages are often shorter and more blunt. *Arachnopeziza floriphila* has also similar spore appendages to *A. ptilidiophila*, but it differs in spore size and by the thick-walled multiseptate hairs (Baral 1989). In his monograph, Korf (1951b) did not observe the appendages in (dried) specimens of *A. cornuta*, but according to the original description (Ellis 1882) spores have 'short, blunt polar appendages'. Spore size (less than 15 µm long) and hair morphology (distinctly multiseptate and thick-walled) distinguish *A. cornuta* from *A. ptilidiophila*. Another noteworthy feature are the thin-walled hairs attached to each other forming 'teeth'. This is rare in *Arachnopeziza* with only *A. fitzpatrickii* sharing the character. We observed *A. ptilidiophila* growing directly on liverwort shoots as well as on barkless softwood, but always with liverwort shoots or protonema in the immediate vicinity. Many of the observed populations were often relatively small, comprising less than five apothecia in a small notch on the *Pinus* bark. The specimens examined by us are of populations with more (> 10) apothecia. *Ptilidium ciliare* and *P. pulcherrimum* are ubiquitous liverworts growing as epiphytes on a range of softwood and hardwood. Further sampling of *Arachnopeziza* species on *Ptilidium* growing on non-coniferous or non-woody substrates should elucidate the more specific ecological niche of this species. All the observations are from sites with relatively undisturbed continuity of dead wood and with large dead *Pinus sylvestris* trunks.

Arachnopeziza sphagniseda (Velen.) T. Kosonen, Huhtinen & K. Hansen, *comb. nov.* — MycoBank MB835730; Fig. 10

Basionym. Belonium sphagnisedum Velen., Monogr. Discom. Bohemiae Pars. 1: 179, pl. iv, f. 16. 1934.

Synonym. Hymenoscyphus sphagnisedus (Velen.) Svrček, Česká Mykol. 33: 200. 1979.

Holotype. Czech republic, Krkonoše Mountains, on *Sphagnum*, Aug. 1927, *K. Cejp* (PRM 149855) ! (the convolute is empty).

Lectotype designated here: pl. IV, f. 16 in Velenovsky 1934: Monogr. Discom. Bohemiae Pars. 1. MycoBank MBT392710.

Superseded neotype. Designated by Svrček 1979 in Česká Mykol. 33: 200. Czech Republic, Southern Bohemia, Třeboň, 'Hrádeček', in a ditch on living *Sphagnum* sp., 18 May 1964, *M. Svrček* (PRM 611379) !

Apothecia 0.2–2 mm diam, discoid to cupulate, smooth, white, apricot when dry, sessile to subsessile with scanty subicular hyphae around the base. *Ectal excipulum* of *textura oblita* to *textura prismatica*, more globose below, cells relatively thick-walled. *Margin* with cylindrical-clavate 2–3 µm wide hyphal ends forming a smooth rim, thin-walled to somewhat thick-walled, varying between the populations, no true hairs observed. *Asci* 49–67 × 5.6–8.0 µm in CR, mean 52.2 × 7.0 µm (n = 10, from six populations), cylindrical, in *neotype* often clearly widened, maximally to 14 µm, characterized by an abruptly narrowed apex, apical pore blue both in MLZ and LUG, arising from croziers. *Ascospores* 8.6–13.2(–14.0) × 2.0–3.0 µm in CR, mean 10.6 × 2.4 µm, Q = 3.0–5.8(–6.0), mean Q = 4.4 (n = 38, from six populations), in *neotype* 9.3–15.2(–16.6) × 2.0–2.8 µm in CR, mean 12.3 × 2.5 µm, Q = 4.0–6.0(–7.5), mean Q = 5.1,

ellipsoid to narrowly ellipsoid to subfusoid, septation varying from aseptate to sparsely 1-septate populations, to populations where 1-septate free spores are a majority, 2–3-septate spores rare. *Paraphyses* cylindrical, obtuse, 2–3 um wide, unbranched, not exceeding the asci. *Subicular hyphae* hardly observable under dissecting microscope but always present in a mount, 3–4 µm wide, smooth to minutely warty, thick-walled.

Specimens examined. All on *Sphagnum*. Finland, Varsinais-Suomi, Kaarina, Kuusisto, 10 June 2003, *T. Laukka* 06 (TUR 165732); Lieto, Mellilä, Liedonperäntie 294, 5 Sept. 2007, *R. Ilmanen* 338 (TUR 179358); Nousiainen, Kurjenrahka National Park, 11 July 2006, *T. Laukka* et al. (TUR 174929); Parainen, Kirjalansaari, 22 Sept. 2006, *R. Ilmanen* 246 (TUR); same date and location, *T. Laukka* 268 (TUR); Turku, Ruissalo, Choraeuksen lähde, 26 May 2004, *M. Paajanen* 804 (TUR 173706); same date and location, *M. Paajanen* 805 (TUR 173700); Satakunta, Luvia, Rekojärvi, 13 Aug. 2006, *R. Ilmanen* 224 (TUR 174912); same date and location, *R. Ilmanen* 226 (TUR 174911); Rekojärvi, 28 Oct. 2006, *R. Ilmanen* 267 (TUR 178007); same date and location, *R. Ilmanen* 269 (TUR 178009); Pohjois-Karjala, Kitee, 15 Sept. 2006, *S. Huhtinen* 06/18 (TUR); same date and location, *S. Huhtinen* 06/20 (TUR).

Notes — The presence of a subiculum and relatively big, septate spores are typical characters of an *Arachnopeziza*. Most likely it was the presence of a subiculum that prompted Velenovský to name the single collection initially as '*Arachnopeziza sphagnicola*' in his fungarium notes on the original convolute. In 1934 the collection was described as *Belonium*, most likely owing to the lack of hairs. Due to the missing holotype collection (thereafter found by us in PRM, but only as an empty convolute), Svrček (1979) designated a neotype. This was, however, superfluous since there is a plate to choose as lectotype (Velenovský 1934). As Svrček stated, this 'neotype' is a perfect

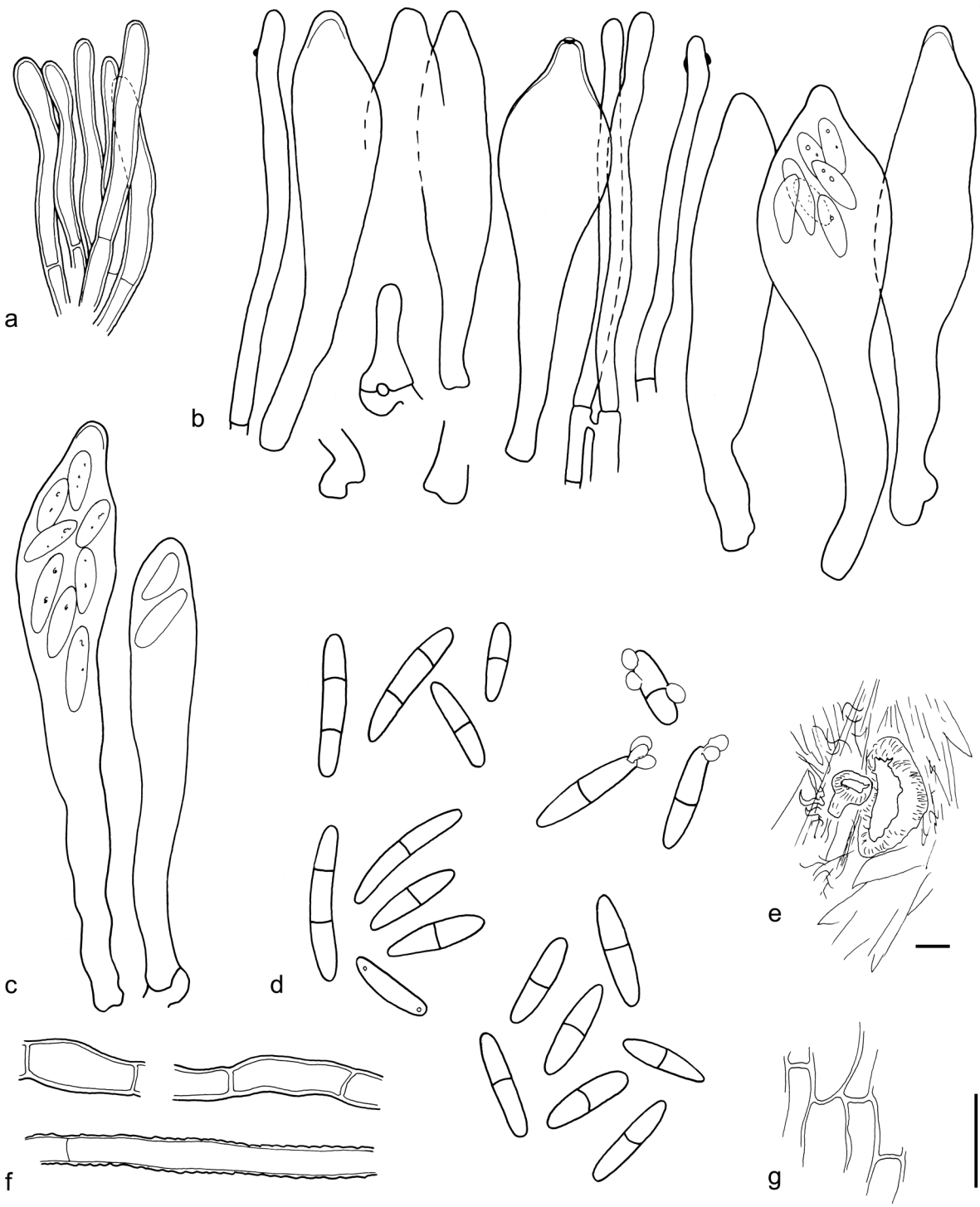


Fig. 10 *Arachnopeziza sphagniseda* (PRM611379). a. Detail from margin; b. asci and paraphyses in CR; c. asci in CR; d. spores, including rare spores producing conidia; e. dry apothecia; f. subicular hyphae; g. ectal excipulum. — Scale bars: a–d, f–g = 10 µm, e = 100 µm. — Drawings: S. Huhtinen.

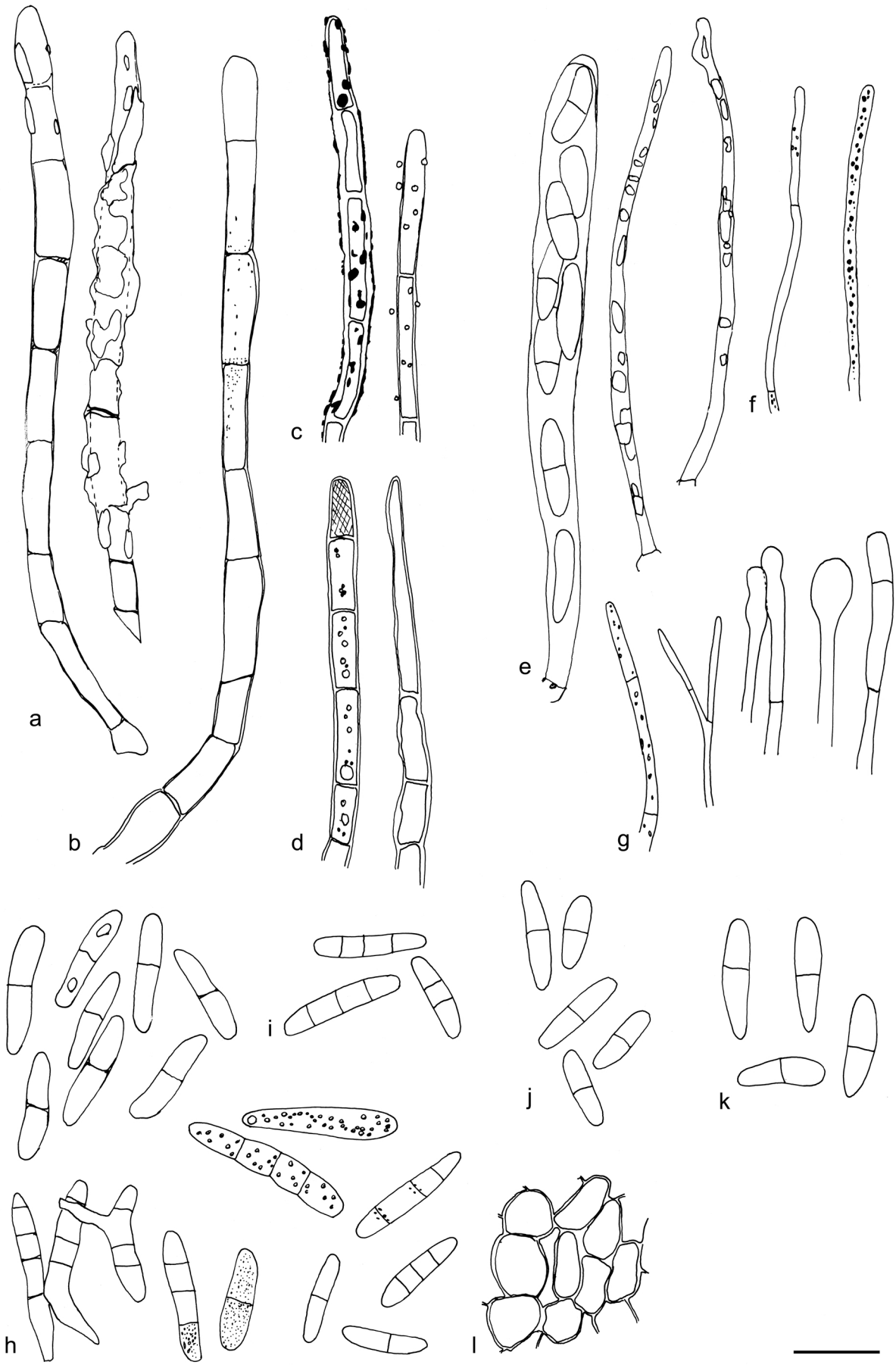


Fig. 11 *Arachnopeziza trabinelloides*. a. Hairs in water, hair on the right almost totally covered by resin; b. hair in CR; c. upper part of hairs in water, loose resin around the hair on the right; d. upper part of hairs in CR; e. asci and paraphyses with pigmented resin in water; f. paraphyses in CR; g. paraphyses apex variation in CR; h. spores of different maturity in water; i. spores in MLZ; j–k. spores in CR; l. ectal excipulum in water (a, c, e, h–i, l: GJO 0071771; b, g, k: holotype; d, f, j: DHP-02493). — Scale bar = 10 µm. — Drawings: T. Kosonen.

match to Velenovský's description, and therefore we use it as a reference collection. We, nevertheless, refrain from selecting it as an epitype, because it is a very scanty specimen and it is not suitable for DNA extraction and sequencing. Our material is from a totally different biogeographical area, although also from *Sphagnum*. This species seems to be relatively easily found, so a new collection from the Czech Republic (with photographs and DNA sequences) would make the most suitable epitype. Our material fits well both the original diagnosis and Svrček's collection. Although there is substantial morphological variation among our material, there is no variation in the sequence data and the growth form in culture was also identical. We did not obtain *TEF-1α* or mtSSU sequences for *A. sphagniseda*, but the four ITS and LSU rDNA sequences were 100 % identical, and the two *RPB1* sequences had identical amino acid translation and differed only by six base pairs. In the superseded neotype, especially the subtruncate apex and width of the asci are prominent (Fig. 10b), and represent the extreme end of the observed overall variation.

Only one species of *Arachnopeziza* known, *A. nuda*, resembles *A. sphagniseda* in lacking distinct apothecial hairs. It is also described as having asci with an abruptly narrowed and thickened apex. *Arachnopeziza nuda* has, however, short clavately enlarged cells, i.e., hairs, 9–18 µm long, arising from the outermost cells of the ectal excipulum (Korf 1959). It also has longer and broader spores than *A. sphagniseda* and occurs on decorticated wood. We were not able to sample *A. nuda* for molecular phylogenetic study, but our five-gene phylogeny suggests *A. sphagniseda* is sister to all other *Arachnopeziza* species sampled (Fig. 3).

Arachnopeziza trabinelloides (Rehm) Korf, Lloydia 14: 169. 1952 — Fig. 11

Basionym. Helotium trabinelloides Rehm, Hedwigia 26 (3): 82. 1887.

Holotype. Romania [former Austria-Hungary], Caraș-Severin, Băile Herculane, on a fallen decorticated trunk of *Fagus*, Apr. 1885, *Lojka* (S F7139) !

Specimens examined. Austria, Steiermark, Graz, Andritz, Reinerkogel N-side, near the church of St. Ulrich, on deciduous wood, 1 Mar. 2014, *I. Wendelin* (GJO 0071771). – United States, Massachusetts, Princeton, Fay Lane, a trunk of *Acer rubrum*, 1 Apr. 2002, *J. Choiniere*, DHP-02493 (TUR); Wachusett Meadow Wildlife Sanctuary, West Trail, on decayed wood (white-rot), 2 Mar. 2014, *J. Karakehian* 14030203 (S, TUR).

Notes — A well annotated and illustrated collection of this relatively rarely collected and documented *Arachnopeziza* species was recently reported from Austria (Friebes & Wendelin 2014). Its morphological similarities to *A. leonina* are commented on under that species. A unique character of *A. trabinelloides* is the rapidly disappearing colour reaction, where MLZ turns the resinous exudates and oily pigments in the hymenia blue. The reaction, that is only visible in fresh samples, was already observed by Rehm (1887) and part of the original description. As noted by Korf (1951b), the variation in the shape of the paraphyses apices is high in *A. trabinelloides* compared to other species of *Arachnopeziza* (Fig. 11f, g). Typically, the hairs of *A. trabinelloides* have abundant resin expanding more or less the whole length of the hair, much more than in any other *Arachnopeziza* species known to us (Fig. 11a, c). In the field it is easily recognised by the large (often > 1 mm diam), bright yellow-orange apothecia and the scanty or nearly non-existing subiculum. *Arachnopeziza trabinelloides* belongs to the *A. leonina* clade (Fig. 3) of wood inhabiting *Arachnopeziza* species with substantial pigmented resin. We made no observations of *A. trabinelloides* during numerous forays in Estonia and Fennoscandia in this project. It appears to be restricted to *Quercus*, *Fagus*, *Castanea* and other hardwoods in the temperate region. It is strongly supported as a sister species to *Arachnopeziza* sp. 'b', an undescribed *Arachnopeziza* species on softwood (Fig. 3).

***Arachnopeziza* sp. 'a'** — Fig. 12

Apothecia on *Sphagnum* shoots, c. 0.3–0.5 mm diam, sessile, narrowly attached, margin hairy, white to hyaline when fresh, yellow when dry, subiculum not observed. *Ectal excipulum* of *textura prismatica* to *textura angularis*. *Hairs* 80–140 × 3–5 µm, cylindrical, thin-walled, with 2–5 septa, tapering, apex obtuse, c. 2 µm wide, fragile appearance, occasionally with small hyaline resinous exudates. *Asci* 50–65 × 5–8 µm, thin-walled, cylindrical, apical pore MLZ+, arising from croziers. *Ascospores* 18.3–23.7(–25.4) × 2.6–3.0 µm in CR, mean = 20.6 × 2.8 µm, Q = 6.0–8.5, mean Q = 7.4 (n = 17, from two populations), ellipsoid, unevenly cylindrical, tapering towards the somewhat angular ends, usually with one septum. *Paraphyses* filiform, occasionally bifurcate, no septa observed, 1–2 µm wide, smooth.

Specimens examined. Finland, Varsinais-Suomi, Turku, Kohmo, 20 June 2006, *R. Ilmanen* 199 (TUR); Pääskyvuori, on *Sphagnum*, 6 July 2006, *T. Laukka* 260 (TUR).

Notes — We have found no published name for this species that is easily distinguished by the large spores, long slender multiseptate hairs and occurrence on *Sphagnum* shoots. The two samples were collected less than 2 km apart, although on different forays, and it may be rare. The collections are relatively small and documentation of characters from fresh apothecia is incomprehensive and therefore we refrain from formally describing this novel species. The ecology appears similar to that of the species in the *A. japonica* clade (e.g., *A. japonica* and *A. estonica*) (Fig. 3). Based on our phylogenetic analysis, however, it is a sister species to *A. delicatula* and not a member of the *A. japonica* clade. There are three identical or nearly identical ITS sequences in GenBank (EF521221, KP889888, EF521220) obtained from environmental samples from soil and mesh bag in spruce forest. In addition, four other samples form a group with *A.* sp. 'a', as supported by ML-BP 75 % (Fig. 4), but it is uncertain if these are conspecific, differing in 5–10 base pairs.

Arachnoscypha Boud., Bull. Soc. Mycol. France 1: 118. 1885

Type species. *Arachnoscypha aranea* (De Not.) Boud. ex Dennis.

Notes — The genus *Arachnoscypha* was erected with a single species listed ('L'espèce typique'), *Peziza aranea*, by Boudier (1885). Later, however, Boudier (1907) treated and combined *P. aranea* in *Arachnopeziza*. Korf (1951b) agreed on placing *Arachnoscypha* in synonymy with *Arachnopeziza*, based on morphological similarities, i.e., the multiseptate hairs, septate spores and the existence of a subiculum. Korf (1951b) also noted that since 1-septate spores are not uncommon in *Arachnopeziza*, *Arachnoscypha* (*aranea*) should not be separated based on this. Our molecular phylogenetic results, placing *Arachnoscypha aranea* as a sister taxon to *Polydesmia*, are somewhat surprising. When compared, *Arachnoscypha* and *Polydesmia* show some similarities in morphological characters. Both the type species of *Polydesmia* (*P. pruinosa*) and *Arachnoscypha* have apothecia with hairs on the flanks. However, in *P. pruinosa* the hairs are regarded as undifferentiated (Korf 1978, Verkley 2005) and undulating. In *Arachnoscypha*, especially on the upper flanks, there are relatively straight multiseptate hairs (Fig. 13a). Also, *P. pruinosa* and *A. aranea* both have long hyphal structures arising from the base of the apothecia. In *A. aranea* these hyphae are often bent, giving them a characteristic angular appearance (Fig. 13b). We consider the hyphae originating at the base of the apothecia

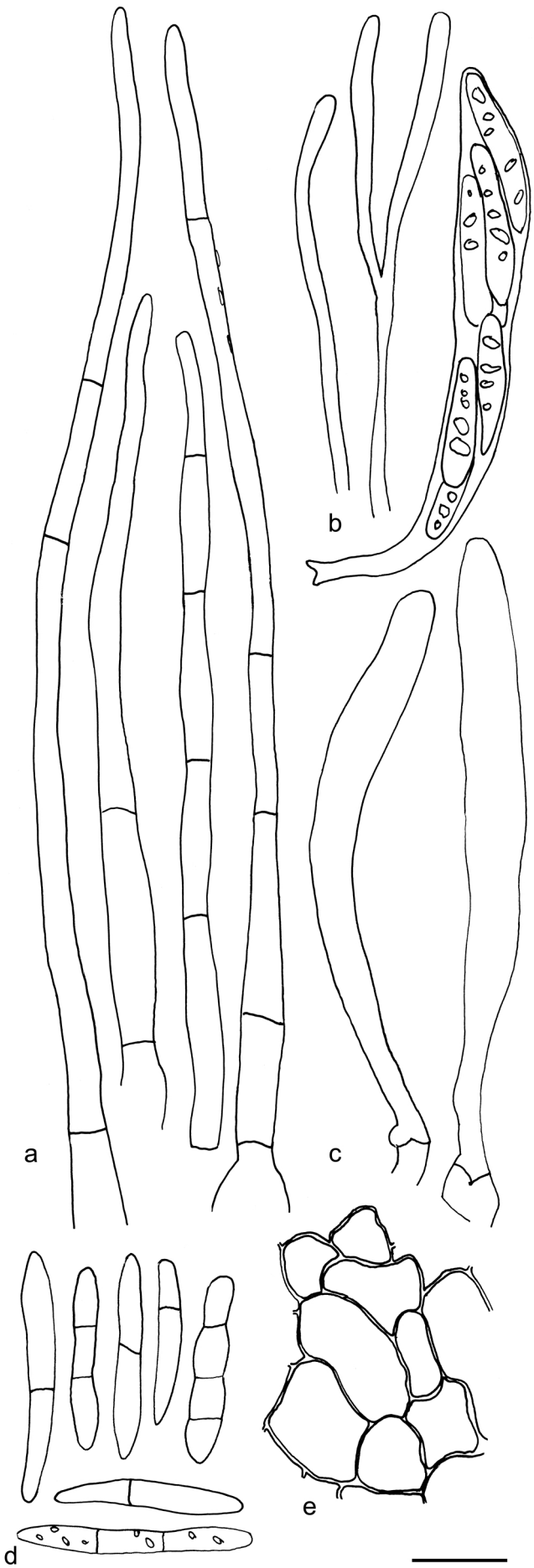


Fig. 12 *Arachnopeziza* sp. 'a' (*T. Laukka* 260). All in CR. a. Hairs; b. paraphyses and ascus; c. asci; d. spores; e. excipulum. — Scale bar = 10 µm. — Drawings: T. Kosonen.

in *Arachnoscypha* to be anchoring hyphae (as opposed to subicular hyphae, see further under Discussion). The branched and twisted paraphysis apices protruding above the asci in *Polydesmia*, giving the apothecia the characteristic pruinose appearance is a unique feature. The paraphyses in *Arachnoscypha* are bifurcate and undulating as in *Polydesmia*, but in *Arachnoscypha* they undulate more irregularly. This is also observed from fresh material. In *Polydesmia* the paraphyses have exudates somewhat like the exudates on *Arachnoscypha* hairs and hyphae at the apothecial base.

Arachnoscypha aranea (De Not.) Boud. ex Dennis, Mycol. Pap. 32: 87. 1949. — Fig. 1f, 13

Basionym. Peziza aranea De Not., Mem. Reale Accad. Sci. Torino, Ser. 2, 3: 57. 1841.

Synonym. Arachnopeziza aranea (De Not.) Boud. Icon. Mycol. livr. 14: n°. 236, pl. 521. 1907.

Apothecia up to 0.4–0.6 mm diam, white to pale yellow, narrowly attached, no visible stipe, surrounded by a 'mesh' of undulating hairs originating from the flanks and by superficially similar anchoring hyphae originating from the base. Hymenium clearly yellow when fresh. *Ectal excipulum* of *textura prismatica* with variable wall thickness, towards inner parts of gelatinized *textura prismatica*, cells c. 8–12 µm long. *Hairs* 40–100 × 4–6 µm with 2–4 septa, with clearly widened, bulbous, relatively short basal cell, thin-walled and often covered with crystalline exudates; numerous elongated hairs, reaching several hundred µm in length, slightly varying in width, but usually less than 5 µm wide, sparsely septate, with crystalline exudates, tapering towards a 1–2 µm wide apex, often bent at irregular intervals. *Asci* 40–60 × 5–7 µm, cylindrical to clavate, apical pore MLZ+, arising from distinct croziers. *Ascospores* 6.8–12.7(–12.9) × 2.0–3.2(–3.3) µm, mean = 10.4 × 2.7 µm, Q = 3.2–4.8(–5.2), mean Q = 3.8 (n = 38, from three populations), cylindrical, subfusoid to slightly allantoid, occasionally with one septum. *Paraphyses* simple or bifurcate near the apice, c. 1–2 µm wide, irregularly undulating. *Anchoring hyphae* 3–6 µm wide, slightly to clearly thick-walled, with crystalline exudates similar to hairs, sparsely branched.

Specimens examined. Finland, Varsinais-Suomi, Salo, Perniö, Lampyöli, on a leaf of a deciduous tree in a ditch, 28 Sept. 2015, *S. Huhtinen* 15/44 (TUR); Etelä-Häme, Jämsä, Kalmavirta, Hallinmäki, Sammalsuo Nature Reserve, on a large trunk of *Populus tremula*, 18 Sept. 2013, *J. Purhonen* 6063 (JYV). – Sweden, Västergötland, Skövde, Silverfallet-Karlsfors Nature Reserve, on fallen *Acer platanoides* leaves, 16 Oct. 2015, *T. Kosonen* 7129 (S, TUR); same location, 6 Oct. 2017, *S. Huhtinen* 17/52 (S, TUR). – USA, New York, Ithaca, Cascadilla Creek woods, on wood, 28 Sept. 1947, *R. Korf* 913 (CUP-K-0237) (sub *Arachnopeziza eriobasis*); Coy Glen, 3 Oct. 1902, *H. Whetzel* (DPP 563); Lower Six Miles Creek, on hull of *Carya*, 2 Oct. 1949, *C. Rogerson & R. Korf* (CUP-K-0239) (sub *A. eriobasis*); Ithaca, old burrs of *Castanea dentata*, c. 1929, *H. Whetzel* (DPP 11788).

Notes — In the monograph of *Arachnopeziza*, including both North American and European material, Korf (1951b) considered *A. aranea* to be a rare species restricted to *Castanea*. This strict ecology was the main character delimiting *A. aranea* from *Arachnopeziza eriobasis*, a species combined into *Arachnopeziza* in the same study. Korf (1951b) considered these as two closely related species, but *A. eriobasis* having a less specific ecology. Dennis (1981) recognised *Arachnoscypha* for *A. aranea*, but refrained from combining *Arachnopeziza eriobasis* into *Arachnoscypha*, although he considered it appropriate. He also considered *A. eriobasis* as 'not uncommon' occurring on various decaying substrates and *A. aranea* as 'uncommon' and restricted to *Castanea*. His descriptions of the two species are overlapping, as are Korf's. We were not able to distinguish two species among the material studied here using morphology and therefore we choose to refer our material

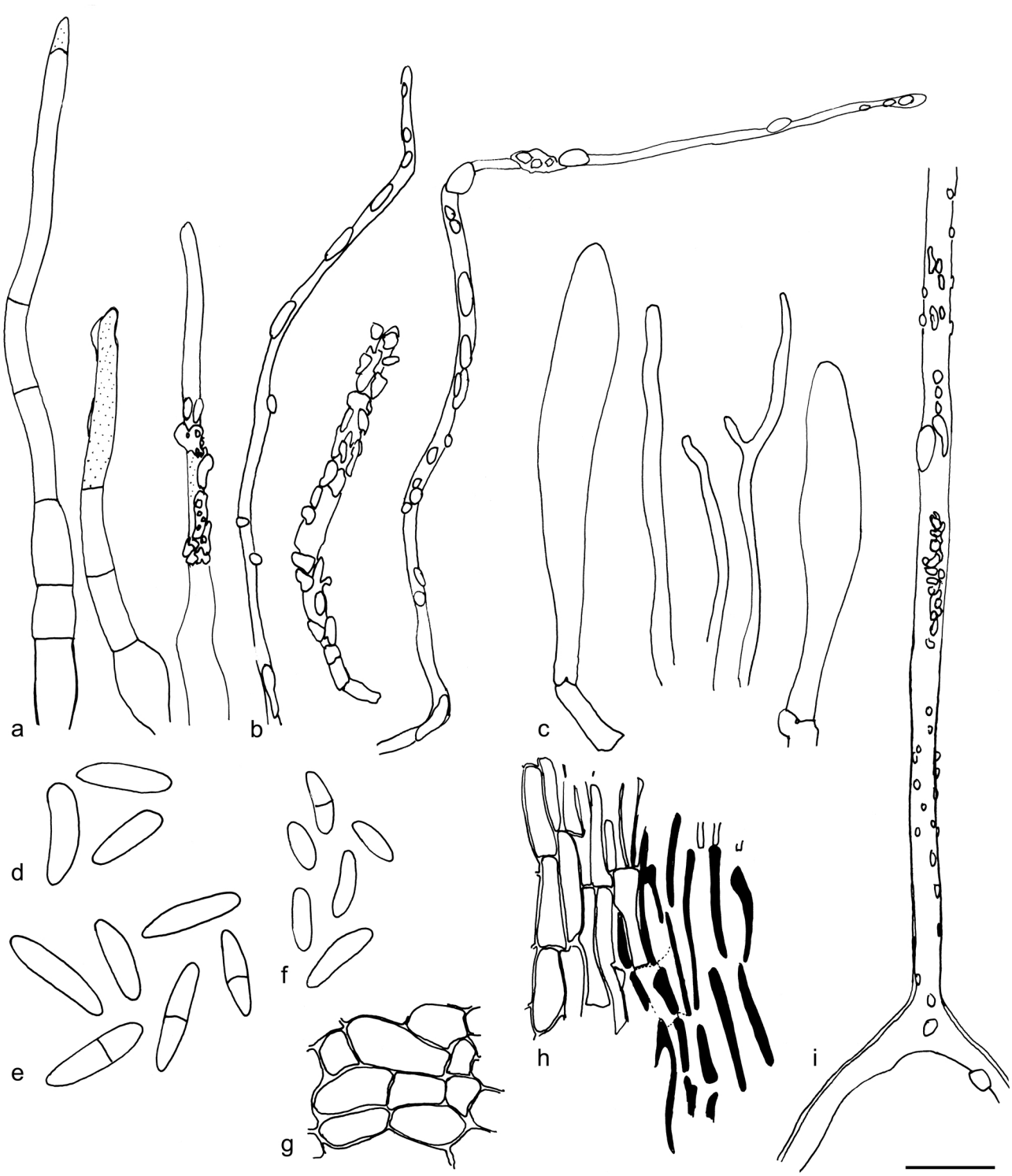


Fig. 13 *Arachnoscypha aranea*. All in CR. a–b. Hairs with crystals; c. asci and paraphyses; d–f: spores; g. basal ectal excipulum; h. excipulum with gelatinized *textura prismatica*; i. anchoring hypha showing the thick-walled base not present in the hairs (a, c, e: *T. Kosonen* 7129; b, f–i: *J. Purhonen* 6063-B1; d: DPP-563). — Scale bar = 10 µm. — Drawings: T. Kosonen.

to *A. aranea*. None of our recent collections from Finland and Sweden, from which we obtained 100 % identical sequences, were from *Castanea*. Such a specific ecology is uncommon, but of course not impossible among helotialean fungi. If recent material from *Castanea* becomes available in future studies it should be further explored if two species exist.

Eupezizella Höhn., Mitt. Bot. Inst. Techn. Hochsch. Wien 3: 61. 1926

Type species. *Eupezizella candida* (Starbäck) Höhn., Mitt. Bot. Inst. Techn. Hochsch. Wien 3: 61. 1926.

Basionym. *Pezizella candida* Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21: 30, pl. 1: 16a–c. 1895; non *Pezizella candida* Velen., Opera Bot. Cech. 4: 117. 1947, nom. illeg. (Art. 53.1).

Synonym. *Hyaloscypha candida* (Starbäck) Boud., Hist. Classific. Discomyc. Europe: 127. 1907.

Included species: *Eupezizella aureliella*, *E. britannica*, *E. candida*, *E. nipponica*, *E. roseoguttata*.

Notes — The genus *Eupezizella* conforms here to *Hyaloscypha* subgenus *Eupezizella* (Huhtinen 1989). It is distinguished from *Hyaloscypha* by the abundant resinous exudates (Fig. 1g), the predominantly blunt and aseptate hairs and by the lack of overall dextrinoid reactions. Some species and populations

show deep amyloid nodules in the hairs and/or in the excipular cells. In very rare cases these nodules may be dextrinoid (Fig. 14b). Contrary to *Hyaloscypha*, *Eupezizella* is almost exclusively known from softwoods. Two Japanese collections of *E. nipponica* Huhtinen (1989; as *Hyaloscypha nipponica*) originate from hardwood. In the same study, the third cited specimen under *H. nipponica* seems to represent an unknown species of the new genus *Resinoscypha*.

Starbäck (1895) described *Eupezizella* as a subgenus in *Pezizella*, which makes the name invalid (Art. 21.3). He included three species: *Pezizella candida*, *P. atomaria* (= *Hyaloscypha aureliella*) and *P. minor* (= *Phialina lachnobrachya*). When *Hyaloscypha* was monographed, *Eupezizella* was combined at subgeneric level under *Hyaloscypha*, as well as lectotypified (Huhtinen 1989). The taxa included in the subgenus were: *Hyaloscypha aureliella*, *H. britannica*, *H. britannica* var. *roseoguttata*, *H. candida*, *H. nipponica* and *H. strobilicola*. They are here all, with the exception of *H. strobilicola*, combined into the genus *Eupezizella.* Our phylogenetic analyses strongly support the placement of *H. aureliella* as a sister group to *Hyaloscypha* s.str. (Fig. 2), confirming the results of Huhtinen (1989). Some of the morphological features of *Eupezizella* are also characteristic for the new genera *Resinoscypha* and *Mimicoscypha*, but the aseptate hairs are a consistent feature distinguishing *Eupezizella*.

In previous molecular phylogenetic studies *H. aureliella* has been considered to be nested within *Hyaloscypha*, because two collections (TNS-F17137 and TNS-F11213) published as *H. albohyalina* var. *albohyalina* (Han et al. 2014), formed a sister group to *Hyaloscypha* including *H. aureliella* (see also Fehrer et al. 2018). Our morphological studies of TNS-F17137 have, however, convinced us that these do not represent *H. albohyalina* sensu Huhtinen (1989). Instead they represent a distinct species and genus to be described later when more material becomes available. We refer to Huhtinen (1989) for full descriptions and illustrations of all species here combined in *Eupezizella*, including their type specimens, because very little additional data has emerged.

Recently, the generic name *Cheiromycella* was proposed to be used for *E. aureliella* and closely related species through the synonymy of *C. microscopica* and *E. aureliella* (Fehrer et al. 2018). Since there is no sequence material available from either of the generic types (*C. speiroidea* and *E. candida*) we find it most appropriate, for the time being, to keep the name *Eupezizella* for this group of species.

Eupezizella aureliella (Nyl.) T. Kosonen, Huhtinen & K. Hansen, *comb. nov.* — MycoBank MB835731

Basionym. Peziza aureliella Nyl., Not. Sallsk. Fauna Fl. Fenn. Forh. 10: 49. 1869.

Eupezizella britannica (Huhtinen) T. Kosonen, Huhtinen & K. Hansen, *comb. nov.* — MycoBank MB835732

Basionym. Hyaloscypha britannica Huhtinen, Karstenia 29: 113. 1990.

Eupezizella nipponica (Huhtinen) T. Kosonen, Huhtinen & K. Hansen, *comb. nov.* — MycoBank MB835733

Basionym. Hyaloscypha nipponica Huhtinen, Karstenia 29: 155. 1990.

Eupezizella roseoguttata (Huhtinen) T. Kosonen, Huhtinen & K. Hansen, *comb. & stat. nov.* — MycoBank MB835734

Basionym. Hyaloscypha britannica var. *roseoguttata* Huhtinen, Karstenia 29: 116. 1990.

Notes — We recognise *E. roseoguttata* as a distinct species based on morphology. The type collection of *H. britannica* var. *roseoguttata* can be distinguished by the combination of two independent morphological characters: the rosy-coloured exudates at the margin and the MLZ-ascal pore. The culture (strain CBS 251.90) of the type is reddish orange, a colour not present in other cultures of *Eupezizella* (only obtained from *E. aureliella* so far) (Huhtinen 1989). Also, the single available sequence in GenBank of *E. roseoguttata* (ITS, MH862208) differs in 20 bp from the ITS sequences of *E. aureliella*, supporting it as a distinct species. A direct comparison between the ITS and LSU sequences of *E. roseoguttata* and *E. britannica* is not possible, because so far only an LSU sequence is available for *E. britannica*. The LSU region of *E. britannica* and *E. aureliella* differs in 10 base pairs. The available sequences strongly suggest *E. aureliella*, *E. britannica* and *E. roseoguttata* to be congeneric.

Hyaloscypha usitata Huhtinen, Karstenia 29: 173. 1990

Holotype. Colombia, Dpto, Antipquia, Medellin, Forest research station Piedras Blancas, on wood, 19 July 1974, *Dumont*, *Haines & Velasquez*, *Dumont-Co* 1591 (NY).

Specimens examined. Finland, Pohjois-Häme, Toivakka, Vuorilampi, on a trunk of *Betula*, 27 Aug. 2015, *T. Kosonen* 7083 (TUR). – Sweden, Härjedalen, Hamrafjällen, a trunk of *Betula*, 4 Aug. 2015, *S. Huhtinen* 15/25 (S); Södermanland, Haninge, Tyresta National Park, on a small hardwood trunk, 1 June 2016, *S. Huhtinen* 16/47 (S); Västra Götland, Falköping, Tidaholm, Forentorpa nature reserve, on a trunk of *Betula*, 15 Oct. 2015, *S. Huhtinen* 15/54 (S); Skara, Vadet, on a trunk of *Betula* or *Alnus*, 14 Oct. 2015, *T. Kosonen* 7122 (TUR).

Notes — *Hyaloscypha usitata* was described from fungarium material from Colombia and Venezuela (Huhtinen 1989). It is here reported for the first time from Europe. The material of *H. usitata* and *H. vitreola* studied so far indicate that these two are phylogenetically and morphologically clearly defined, but closely related sister species. The vital characters of *H. usitata* differ from most other *Hyaloscypha* species in that the hairs and especially the paraphyses have usually one distinct VB in each cell. This feature was observed in all material studied fresh.

Mimicoscypha T. Kosonen, Huhtinen & K. Hansen, *gen. nov*. — MycoBank MB835735; Fig. 14f–h, 15–18

Etymology. For mimicking two other genera, *Eupezizella* and *Resinoscypha*.

Type species. Mimicoscypha lacrimiformis (Hosoya) T. Kosonen, Huhtinen & K. Hansen.

Included species: *M. lacrimiformis*, *M. mimica*, *M. paludosa*.

A genus with light-coloured, hairy apothecia on wood, bryophytes and plant debris. *Hairs* with 1–3 septate, thin- to somewhat thick-walled, hyaline, mostly smooth, sometimes with hyaline to yellowish, superficial resin; inside the hairs hyaline, refractive globules variably present in living, occasionally in dried material, amyloid nodules not present. *Ectal excipulum* of *textura angularis – prismatica*, typically without dextrinoid reactions, but may show strongly amyloid nodules inside the cells. *Asci* arising from croziers or simple septa, apical pore MLZ+, 8-spored. *Ascospores* ellipsoid to oblong-ellipsoid, aseptate to 1-septate. *Paraphyses* cylindrical.

Notes — *Mimicoscypha* earns its name by sharing morphological features with both *Eupezizella* and *Resinoscypha*, despite it is clearly distinct from these genera based on our multi-gene data (Fig. 2). Delimitation may prove difficult if only morphological features are used. It differs from *Eupezizella* in the septate hairs, and from both *Eupezizella* and *Resinoscypha* in not showing amyloid nodules in the hairs (see further in Notes under *Resinoscypha* below). These blunt-haired, hyaloscyphaceous

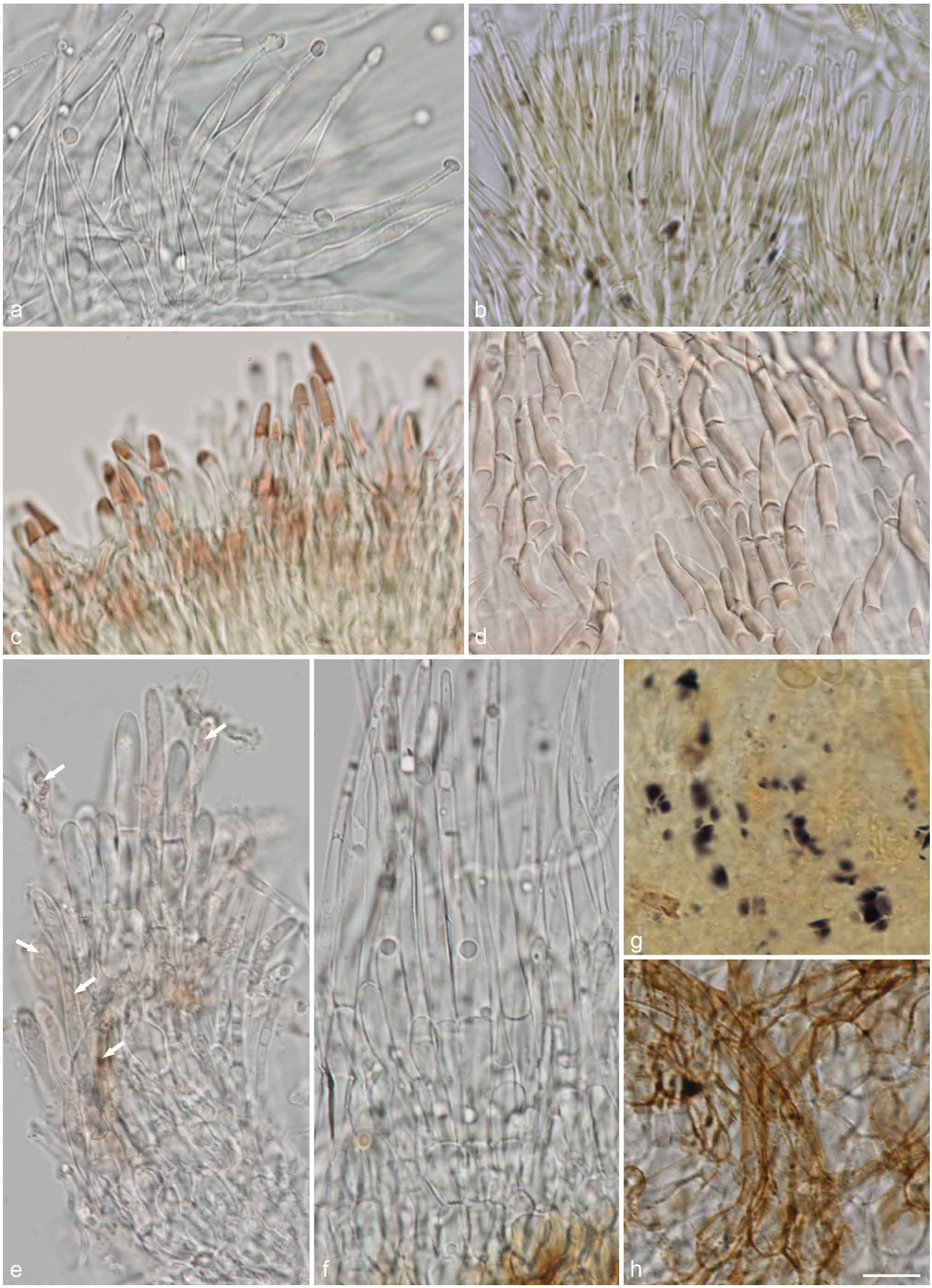


Fig. 14 Examples of hair shapes, inclusions and reactions, and of amyloid nodules in excipulum cells, in *Hyaloscyphaceae*. a. Thin-walled aseptate hairs, *Hyaloscypha spiralis* (in water); b. hairs showing amyloid and dextrinoid nodules, *Eupezizella aureliella* (in MLZ); c–d. dextrinoid glassy hairs in *Olla* (in MLZ): c. *Olla transiens*; d. *Olla millepunctata*; e. septate hairs showing resinous matter inside the hairs (arrows), *Resinoscypha variepilosa* (in water); f–h. *Mimicoscypha lacrimiformis*: f. septate hairs with refractive globules; g. purple nodules in ectal excipulum cells (in MLZ); h. bulbous basal cells of hairs with exudates (in water) (a: KH.16.02; b: *T. Kosonen* 7296; c: *U. Söderholm* 4829; d: *T. Kosonen* 7155; e: *S. Huhtinen* 16/41; f–h. KH.17.02). — Scale bars = 10 µm. — All from fresh material. — Photos: a, e–h. K. Hansen; b–d. T. Kosonen.

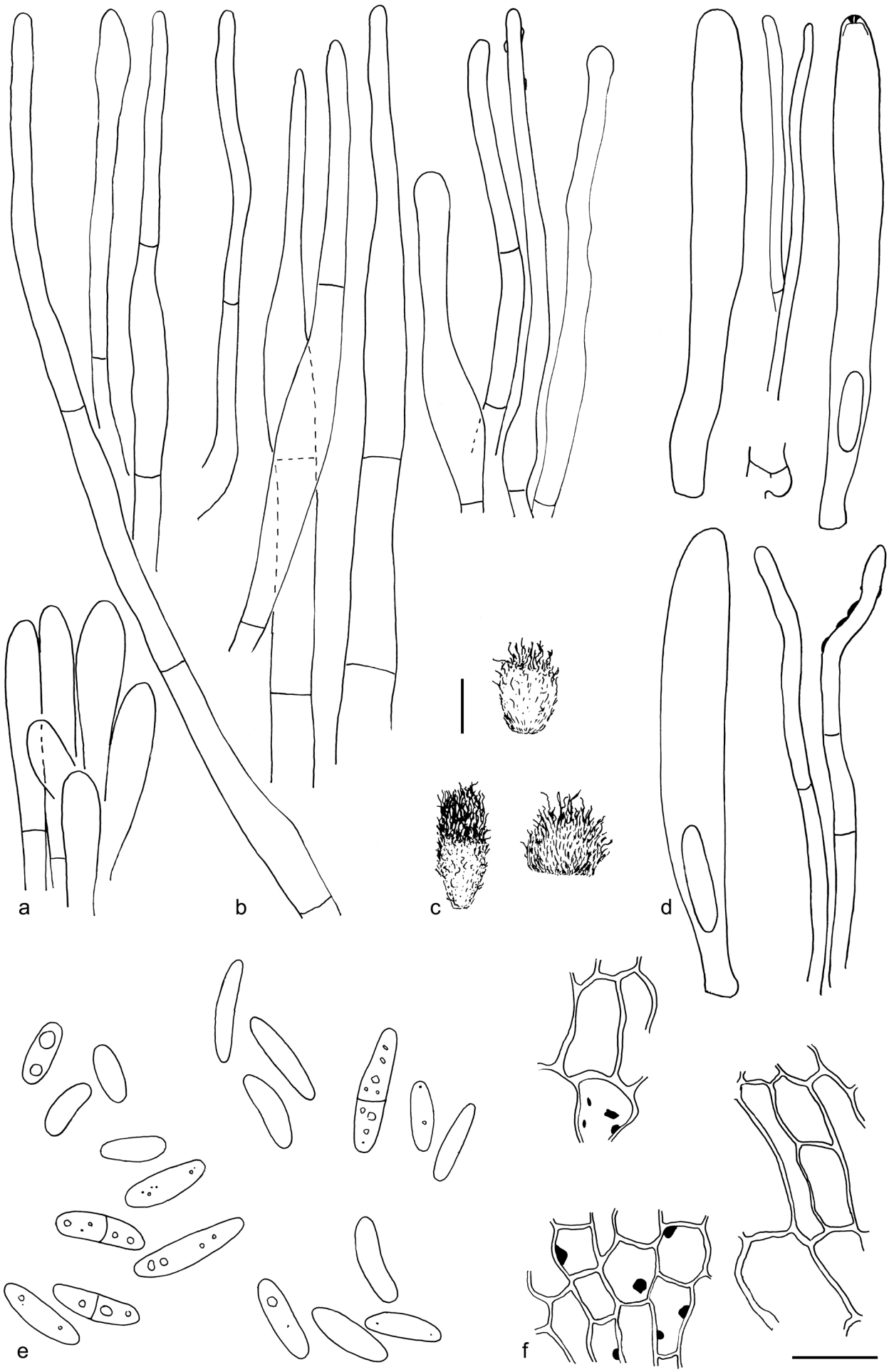


Fig. 15 *Mimicoscypha lacrimiformis* (holotype). a. Marginal end cells; b. marginal hairs in CR, the four on right in KOH; c. dry apothecia; d. asci and paraphyses; e. spores; f. ectal excipulum in MLZ showing the amyloid nodules. — Scale bars: a–b, d–f = 10 µm, c = 100 µm. — Drawings: S. Huhtinen.

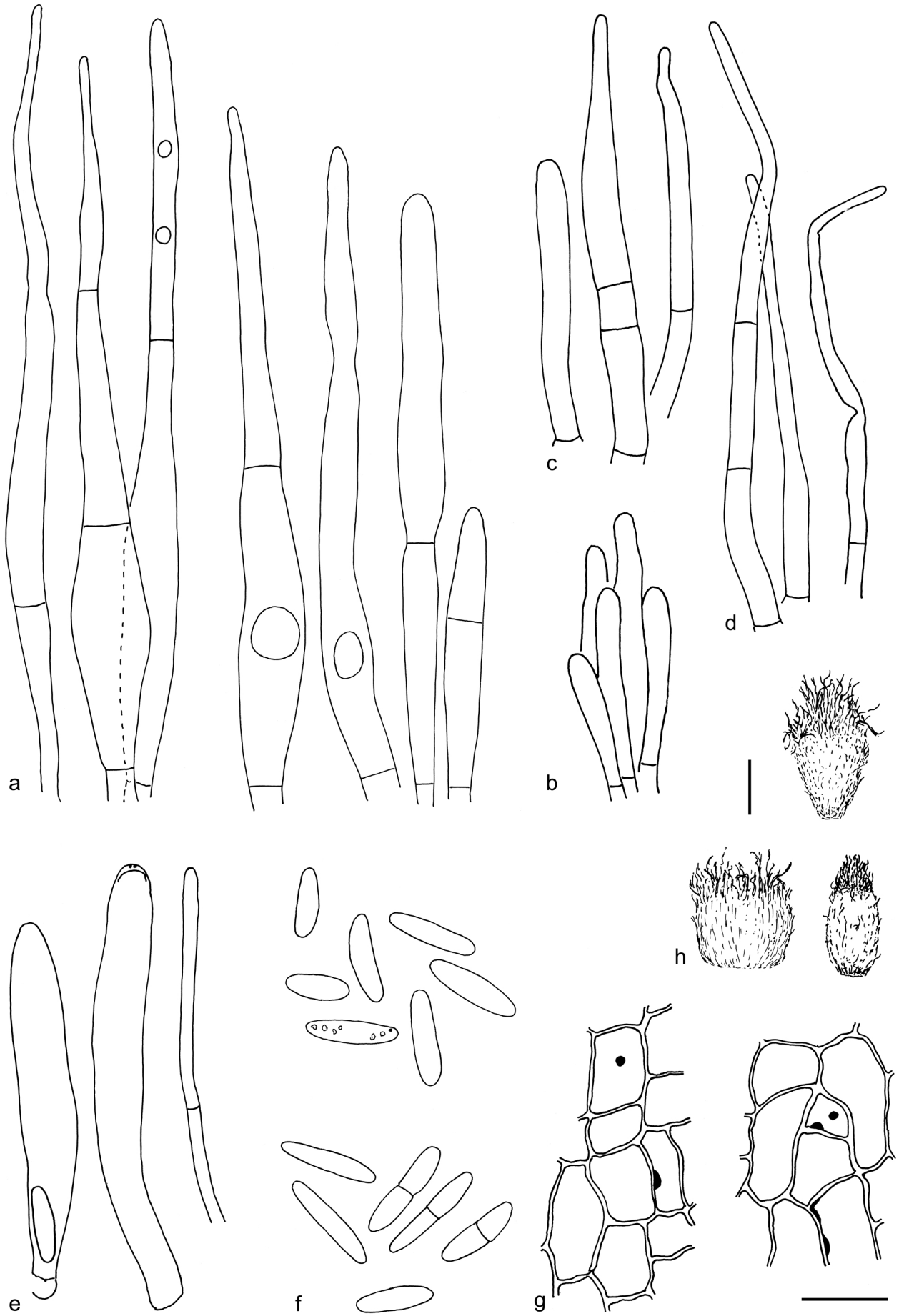


Fig. 16 *Mimicoscypha lacrimiformis*. a. Marginal hairs in CR showing several months old refractive globules; b. marginal end cells; c–d. marginal hairs in CR; e. asci and paraphysis; f. ascospores in CR; g. ectal excipulum in MLZ showing the amyloid nodules; h. dry apothecia (a, f: *T. Kosonen* 7224; b, d, g–h: *S. Huhtinen* 17/6; c, e: *Huhtinen* 17/8). — Scale bars: a–g = 10 µm, h = 100 µm. — Drawings: S. Huhtinen.

taxa have been vaguely placed for decades and a strongly supported placement has not been offered until now. Our solution is based on a combination of morphological characters and molecular phylogenetic results. *Mimicoscypha* is closely related to the genus *Olla* and *Hyalopeziza nectrioidea* (Fig. 2) although species of *Olla* and *H. nectrioidea* have very different excipular hairs (see Fig. 14c–d, f). The long slender, thin- to somewhat thick-walled, hyaline hairs, without glassy elements (typical for *Olla*) or a dextrinoid reaction (typical for both *Olla* and *H. nectrioidea*), supports the creation of this new genus.

Mimicoscypha lacrimiformis (Hosoya) T. Kosonen, Huhtinen & K. Hansen, *comb. nov.* — MycoBank MB835736; Fig. 14f–h, 15, 16

Basionym. Phialina lacrimiformis Hosoya, Mycoscience 38: 181. 1997.

Holotype. Japan, Nagano Pref., Sanada-cho, Daimyojin water fall, on decaying wood, 24 May 1993, *T. Hosoya* (TNS-F-181594) !

Apothecia 0.2–0.5 mm diam, white, disc-shaped and broadly attached, to shallowly cupulate, to shortly stipitate, prominently hairy at the margin. *Ectal excipulum* of *textura prismatica* to *textura angularis*, cell walls thickened, with abundant amyloid nodules in the basal excipulum cells, sometimes present also in cells closer to the margin, basal excipulum covered with brown, crustose resin, not changing in MLZ. *Hairs* up to 150 µm long, narrowly to broadly conical, straight, thin-walled and hence tardily reviving to their original shape, apex blunt or tapering to 1–2 µm wide, close to base 4–8 µm wide, smooth, without apical solidifications, regularly with 1–2 septa, rarely up to 6–7 septa, occasionally with solitary refractive vacuoles inside, the amount varying between populations from prominent to lacking, external resinous matter gluing hairs together, present in water mounts or totally lacking, on lower flanks hairs occasionally completely covered in similar brown crustose resin as basal excipular cells. *Asci* 40–55 × 4–8 µm, cylindrical, 8-spored, apical pore MLZ+, arising from croziers. *Ascospores* 7.2–12.6(–14) × 2.0–3.0 µm, mean 9.9 × 2.5 µm, Q = 3.2–4.8, mean Q = 4.0 (n = 28, from 3 populations), ellipsoid to oblong-ellipsoid to cylindrical, often slightly allantoid, aseptate, more rarely 1-septate, with or without refractive vacuoles when fresh in water. *Paraphyses* cylindrical, 1–2 µm wide.

Specimens examined. Sweden, Östergötland, Ödeshög, Mörkahålkärrets Nature Reserve, on man-made coarse, coniferous wood chips, 26 Apr. 2017, *S. Huhtinen* 17/6 (S, TUR); same date, ecology and location, *S. Huhtinen* 17/7 (S, TUR); same date, ecology and location, *S. Huhtinen* 17/8 (S, TUR); same date, ecology and location, *K. Hansen* KH.17.02 (S, TUR); on a decayed trunk of *Picea abies*, *T. Kosonen* 7224 (S, TUR).

Notes — The absence of bright yellow pigment, typical for the genus *Phialina* (Huhtinen 1989), excludes its original placement by Hosoya (Hosoya & Otani 1997). In some populations from Sweden there were clear refractive globules in the hairs when studied in fresh condition (e.g., Fig. 14f, 16a), whereas other populations, collected simultaneously from the same locality, lacked the character completely. The four collections sequenced by us, had all identical ITS and LSU sequences. The *RPB1*, *RPB2* and *TEF-1α* regions were in addition sequenced from two of these populations (*S. Huhtinen* 17/8, with refractive vacuoles and *S. Huhtinen* 17/7, without the vacuoles). All the sequences were identical between the two populations. The presence of amyloid nodules in the ectal excipulum (Fig. 14g, 15f, 16g) is a character common with *Eupezizella* and *Resinoscypha*. Swedish material of *M. lacrimiformis* shows marked variation in the amount of crustose, brown resin present on basal excipulum cells and basal hairs (Fig. 14h). Even in the same collection the apothecia vary from faintly coloured (as in the holotype) to basally dark brown. The species is new to Europe.

Mimicoscypha mimica T. Kosonen, Huhtinen & K. Hansen, *nom. nov.* — MycoBank MB835737; Fig. 17

Etymology. For mimicking *Mimicoscypha paludosa*.

Synonym. Hyaloscypha paludosa Dennis, Kew Bull. 16: 325. 1962, non *Hyaloscypha paludosa* Velen. 1934, Monogr. Discom. Bohemiae Pars. 2: pl. xiv, f. 25, nom. illeg. (Art. 33.1, lapsus calami pro *Eriopeziza paludosa*).

Holotype. UK, Derbyshire, Kinder Scout, Ashop Clough, on dead culms of *Cyperaceae*, 9 July 1960, *J.T. Palmer* (K) !

Apothecia 0.2–0.5 mm diam, 0.2–0.4 mm high, cupulate, narrowing towards base, with amber yellow (Cailleux K87) flanks and disc when dry, hair cover prominent, white. *Ectal excipulum* of *textura prismatica*, with small, deep amyloid nodules in the cells, walls thickened, at places up to 2 µm, walls CB-, MLZ-, CR-. *Hairs* 80–150 × 3–4 µm, cylindrical-conical with a blunt apex, 1–5-septate, somewhat firm-walled, smooth or bearing very small amount of yellowish brown, resinous substance seen in a water mount, lost in MLZ and CR, walls CB-, MLZ-, CR+. *Asci* cylindrical-clavate, 8-spored, 70–83 × 5.0–5.7 µm, apical pore deep MLZ+ even without KOH pretreatment, arising from croziers. *Ascospores* 8.5–14.0 × 2.0–3.0 µm in MLZ, mean 10.6 × 2.4 µm (n = 14), Q = 3.5–5.4, mean Q = 4.5, oblong-ellipsoid, slightly bent, narrowly tapering towards the ends, multiguttulate, often with one septum, sometimes already in asci. *Paraphyses* cylindrical, 2 µm wide.

Notes — Describing *Hyaloscypha paludosa*, Dennis (1962) missed the frequent septa in the hairs (Fig. 17a). As he also overemphasized the narrowness of the hairs, it is understandable that he placed the new taxon in the genus *Hyaloscypha*. This placement was later followed by Raitviir (1970), but criticized by Huhtinen (1989). This taxon has seldom been collected. Dennis (1962) mentioned another collection from UK. One additional collection from the Netherlands (leg. Rommelaars in herb. S. Helleman) may belong here, but it shows dextrinoid nodules (or wall thickenings) in the excipulum cells. This variation between dextrinoid and amyloid has proved to be very rare. For example, in *E. aureliella* c. 29 % of the populations studied showed the deep amyloid nodules and only 3 % dextrinoid (Huhtinen 1989).

Mimicoscypha paludosa (Velen.) T. Kosonen, Huhtinen & K. Hansen, *comb. nov*. — MycoBank MB835738; Fig. 18

Basionym. *Eriopezia paludosa* (as *Eriopeziza paludosa*) Velen., Monogr. Discom. Bohemiae Pars. 1: 266. 1934.

Synonym. *Hyaloscypha paludosa* Velen., Monogr. Discom. Bohemiae Pars. 2: pl. xiv, f. 25. 1934. nom. illeg. (Art. 33.1., lapsus calami pro *Eriopezia paludosa*).

Lectotype designated here: Czech republic, Mnihovice, Svojětice, 11 July 1927, *J. Velenovský* (PRM 147457) ! MycoBank MBT392711.

Apothecia 0.2–0.4 mm diam, shortly stipitate to seemingly sessile, stipe hidden below the disc, ochraceous yellow when dry (between L80 and L87), hair cover white. *Ectal excipulum* of *textura prismatica-angularis*, lacking MLZ+ nodules. *Hairs* 60–130 × 2–3.5 µm, regularly reaching 100 µm in length, cylindrical, tapering to a blunt apex, thin-walled, ranging from aseptate to more often 1–3-septate, rarely up to 5-septate, basally widened up to 5–6 µm, in water often tightly glued together, hyaline resin sometimes present, hard to notice even in a water mount where hairs mainly smooth and empty, as well as in MLZ, CB and CR, rarely some hair contents and resin cover CB+ and CR+. *Asci* cylindrical, 40–60 × 4–6 µm, 8-spored, apical pore clearly MLZ+, arising from simple septa. *Ascospores* (6.8–)7.7–9.7(–10.0) × 1.9–2.2 µm, mean 9.1 × 2.2 µm, Q = 3.3–5.0, mean Q = 4.1 (n = 50, from three populations), ellipsoid to oblong-ellipsoid, aseptate, rarely 1-septate, eguttulate to guttulate. *Paraphyses* mainly cylindrical, 1–2 µm

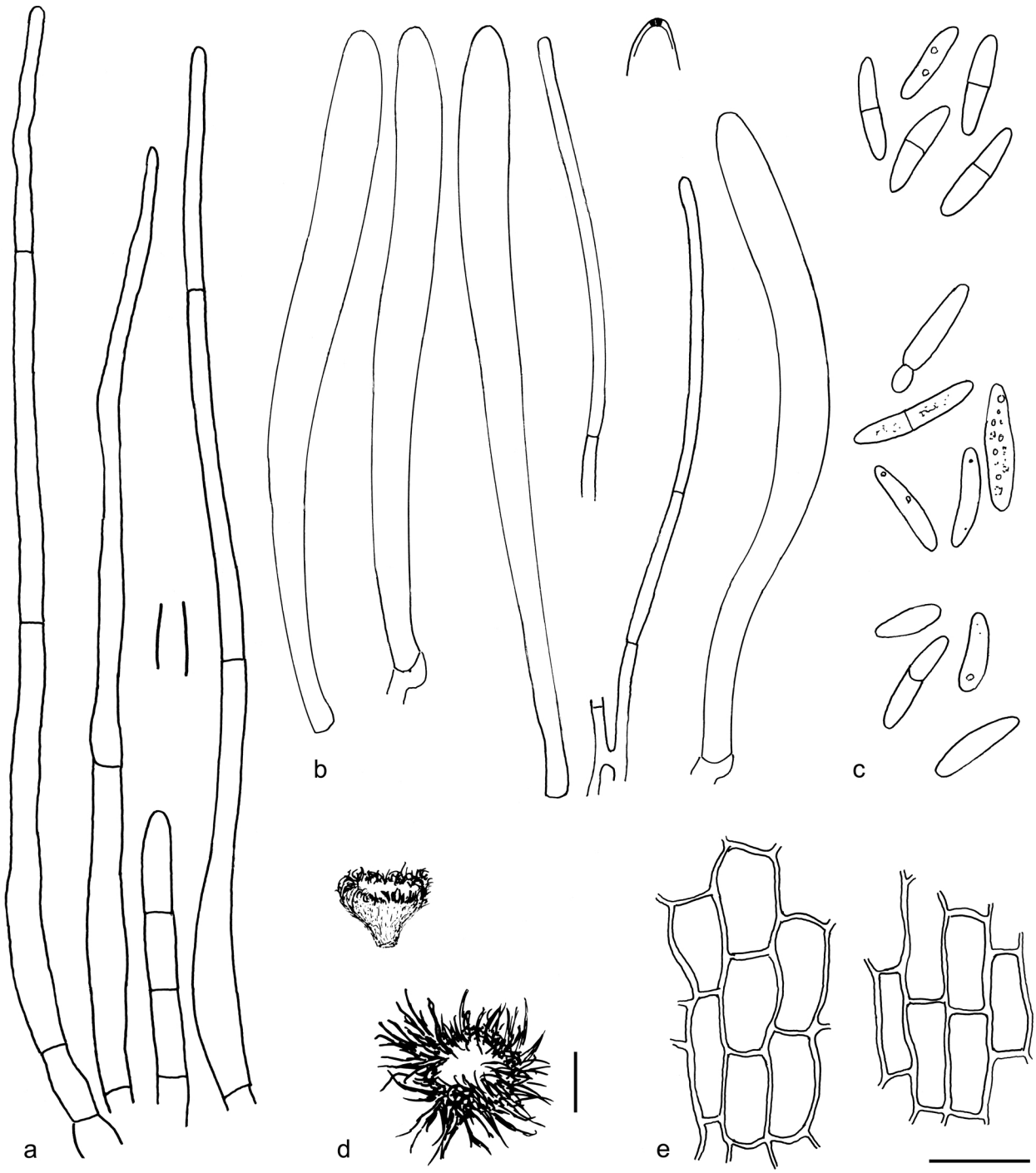


Fig. 17 *Mimicoscypha mimica* (holotype). a. Marginal hairs, detail showing maximal wall thickness in CR; b. asci and paraphyses; c. ascospores; d. dry apothecia; e. ectal excipulum in CB. — Scale bars: a–c, e = 10 µm, d = 100 µm. — Drawings: S. Huhtinen.

wide, but in one specimen also moniliform and subcapitate paraphyses are common.

Specimens examined. Czech Republic, Bohemia, Revnice, amongst pine needles buried in *Sphagnum*, 10 Oct. 1948, *M. Svrček* (PRM 817288). – Finland, Varsinais-Suomi, Nauvo, Seili, seashore thicket with *Phragmites*, on debris, 17 Aug. 1980, *J. Vauras & S. Huhtinen* s.n. (TUR). – UK, Yorkshire, Skipwith, on *Juncus* stem, 11 Sept. 1983, *M.C. Clark* s.n. (K).

Notes — *Mimicoscypha paludosa* is distinguished from *M. mimica* by asci that arise from simple septa and on average smaller spores. The wall of the hairs also differs, being somewhat thick-walled and CR+ in *M. mimica*. All observations are from wet environments, from e.g., *Sphagnum*, *Juncus* and dead bryophytes.

Apparently, this species has been overlooked in the literature and the few reports have been hiding under the later homonym *Hyaloscypha paludosa* Dennis (1962) (= *M. mimica*). The cited, abundant type in PRM has markings by Prof. Svrček, indicating it as a syntype and hence valid for lectotypification, although the exact collection locality, mentioned in the protoloque, seems to be different. But as many collection sites were included in the protoloque by Velenovský and all with 'pr.' (prope = near) and Svojětice is a neighbouring municipality to, e.g., Struharov and Ondřejov (mentioned in the protoloque) we feel it safe enough to validate Svrček's selection.

The name *Hyaloscypha paludosa* was not explicitly accepted by Velenovský (1934) (Art. 33.1.). The proof of this is rather obvious. Under *Eriopeziza paludosa*, Velenovský refers to his plate 14: 25, where the legend erroneously bears the name *Hyaloscypha paludosa*. But only *E. paludosa* is listed in the index. Furthermore, *H. paludosa* is not treated in the texts on

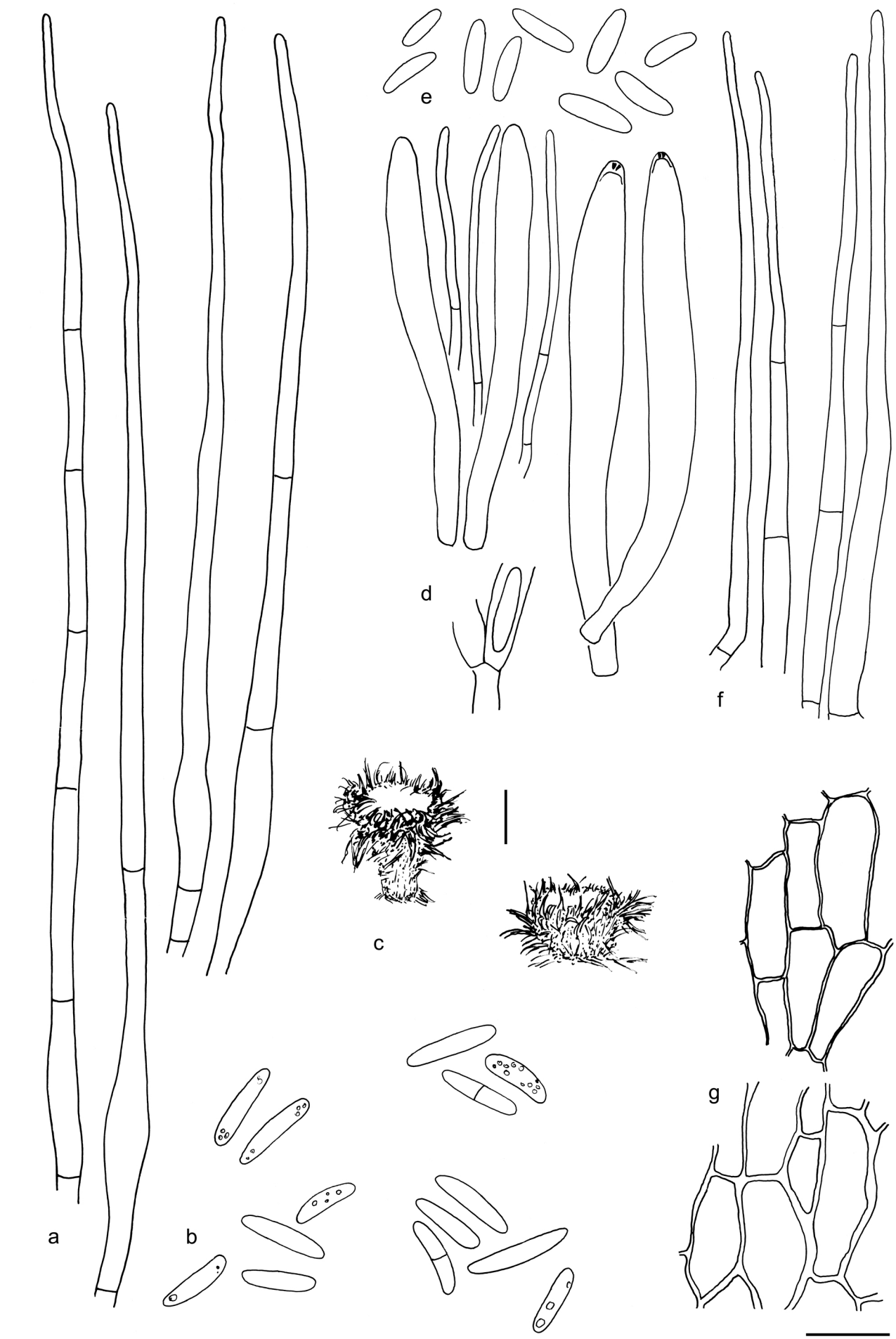


Fig. 18 *Mimicoscypha paludosa*. a. Marginal hairs in CR; b. ascospores; c. dry apothecia; d. asci and paraphyses; e. ascospores; f. marginal hairs; g. ectal excipulum in CR (a, g: PRM 817288; b–c, f (right): *Clark* 11 Sept. 1983; d–f (left): lectotype). — Scale bars: a–b, d–g = 10 µm, c = 100 µm. — Drawings: S. Huhtinen.

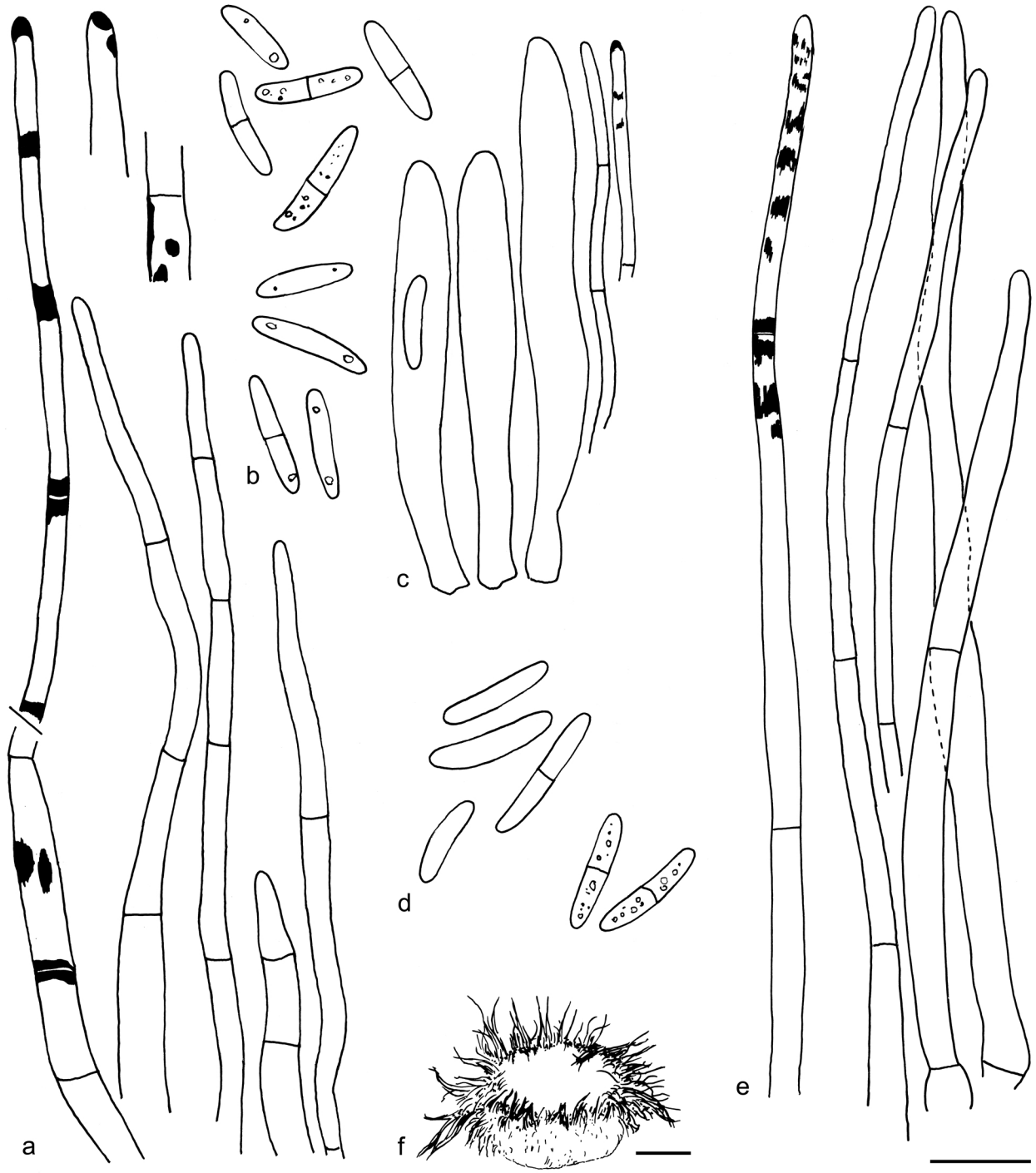
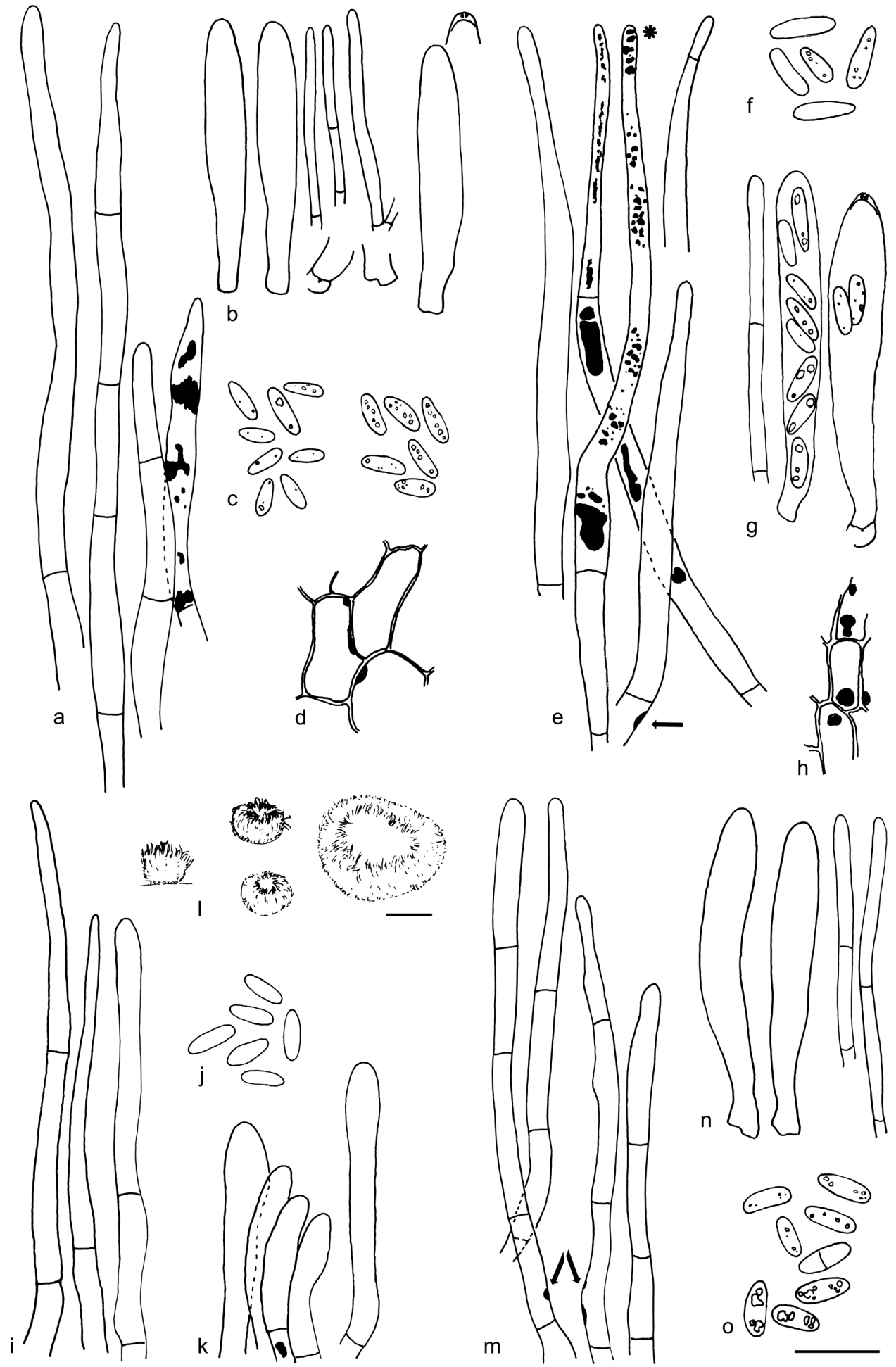


Fig. 19 *Resinoscypha monoseptata*. a. Marginal hairs in lactic acid, leftmost in CB showing the CB+ resinous substance, the two details in MLZ showing deep amyloid nodules; b. spores, upper five in CB, lower four in lactic acid; c. asci and paraphyses in lactic acid, paraphyse on right in CB showing the scanty resinous substance; d. spores, upper four in CB, lower two in MLZ; e. marginal hairs in lactic acid, leftmost in CB showing the CB+ resin; f. dry apothecium (a–c: isotype, Herb. Galán 6154; d–f: CUP 59279). — Scale bars: a–e = 10 µm, f = 100 µm. — Drawings: S. Huhtinen.

→

Fig. 20 *Resinoscypha variepilosa*. a. Marginal hairs in CR, rightmost in CB showing the CB+ resinous contents; b. asci and paraphyses; c. spores in CB (left) and CR (right); d. ectal excipulum showing the amyloid nodules; e. marginal hairs showing the brown resinous substance inside, in MLZ, hair with asterisk (*) in water, one hair with basal amyloid nodule (arrow); f. spores in MLZ; g. asci and paraphysis; h. ectal excipulum showing the amyloid nodules; i. marginal hairs in CR, rightmost hair in water; j. spores in CR; k. short marginal hairs in MLZ showing one rare amyloid nodule; l. dry apothecia; m. marginal hairs in MLZ, some showing the amyloid nodules (arrows); n. asci and paraphyses; o. spores in CB, three lower in KOH (a–d: holotype; e–h: *S. Huhtinen* 87/131; i–k: *S. Huhtinen* 16/41; l–o: *S. Huhtinen* 86/60). — Scale bars: a–k, m–o = 10 µm, l = 100 µm. — Drawings: S. Huhtinen.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Hyaloscypha (Velenovský 1934). Looking at the lectotype cover markings of *E. paludosa* in PRM, made by Svrček, one can see that he was of the same opinion. In this case he had added to the lectotype: '*Hyaloscypha paludosa* Vel. in herb. = *Eriopeziza paludosa*', so apparently he also thought that Velenovský had changed his mind of the placement at some point, but forgot to change it in the legend of plate 14.

Resinoscypha T. Kosonen, Huhtinen & K. Hansen, *gen. nov.* — MycoBank MB835739; Fig. 14e, 19, 20

Etymology. Referring to the cyanophilous resinous substance inside the hairs.

Type species. *Resinoscypha variepilosa* (R. Galán & Raitv.) T. Kosonen, Huhtinen & K. Hansen.

Included species. *R. monoseptata*, *R. variepilosa.*

A light-coloured, hairy, lignicolous genus characterised by long, smooth, hyaline, thin-walled, regularly somewhat flexuous, cylindrical to narrowly conical *hairs* with 1–4 septa, tapering towards a blunt apex and showing cyanophilous, non-glassy resinous substance especially inside, shorter marginal hairs very variable in shape, refractive globules lacking. *Excipulum* of *textura angularis-prismatica*, without dextrinoid reactions, but both hairs and excipular cells may contain strongly amyloid nodules. *Asci* arising from croziers, apical pore MLZ+, 8-spored. *Ascospores* ellipsoid to oblong-ellipsoid, aseptate to 1-septate. *Paraphyses* cylindrical.

Notes — Emended descriptions of both included species were provided by Huhtinen (1993b) and also earlier by Huhtinen (1987b) and are therefore not reproduced here, but new additional illustrations are provided (Fig. 14e, 19, 20). *Resinoscypha* is phylogenetically a distinct genus, sister to all other taxa in the *Hyaloscyphaceae* s.str. clade (Fig. 2). The two species, originally described in *Protounguicularia* by Raitviir & Galán (1986), were separated from the type species, *P. brevicapitata* (now *Olla transiens*), mainly based on the notable differences in hair inclusions (Huhtinen 1987a). In *O. transiens* the material inside the hairs is glassy and strongly dextrinoid (Fig. 14c). The true glassiness is verified by observations in CB, where the colour does not penetrate the glassy substance. The two *Resinoscypha* species have resinous material concentrated at the apex of the hairs and at septal areas (Fig. 14e, 19a, e, 20a, e). These inclusions are MLZ- and strongly CB+. The taxonomic value of these differences, as well as the differences in ascal development (arising from simple septa in the type species versus from clear croziers in the others), passed largely unnoticed by the original authors. The characteristic CB+ resin inside the hairs, combined with the variably shaped and septate hairs, delimit this new genus from *Eupezizella* and *Mimicoscypha*, which both may have a variable number of amyloid nodules in the excipula.

When combining the two species to *Arachnopeziza*, Huhtinen (1987a) emphasized the cylindrical septate hairs. It was suggested, however, that these species occupy 'a transitional position' between *Arachnopezizoideae* and *Hyaloscyphaceae* and the author contemplated on alternative solutions (e.g., a separate genus).

Resinoscypha monoseptata (R. Galán & Raitv.) T. Kosonen, Huhtinen & K. Hansen, *comb. nov.* — MycoBank MB835741; Fig. 19

Basionym. Protounguicularia monoseptata R. Galán & Raitv., Int. J. Mycol. Lichenol. 2: 224. 1986.

Synonym. Arachnopeziza monoseptata (R. Galán & Raitv.) Huhtinen, Mycotaxon 30: 18. 1987.

Holotype. Spain, Malaga, Ronda, Sierra de las Nieves, 1500 m a.s.l., decorticated wood of *Abies pinsapo*, 2 Apr. 1984, *R. Galán* (TAA; Isotype in Herb. Galán 6154) !

Specimens examined. Finland, Inarin Lappi, Utsjoki, Kevo, on an old coniferous board lying in a collapsed cellar, 8 Aug. 1991, *S. Huhtinen* 91/29 (TUR 105080, sub *A. cf. monoseptata*). – Norway, Finnmark, Karasjåkka, near old customs house, on a coniferous board with *Tomentella* sp., 22 Aug. 1978, *S. Sivertsen et al.* s.n. (CUP 59279); Spitsbergen, Ny-Ålesund, old mining area near the village, on a coniferous board, 11 Aug. 1988, *S. Huhtinen* 88/10 (TUR 107784, sub. *A.* cf. *monoseptata*).

Notes — We have no sequences of this species, but it is clearly congeneric with *R. variepilosa*. The very obvious morphological features of the type specimens (the CB+ inclusions in the hairs and the variable hair morphology) linking the two taxa have been discussed before (e.g., Huhtinen 1987a, b). Some variability has since been observed, as summarized by Huhtinen (1993b). *Resinoscypha monoseptata* differs from the generic type species by longer (8.6–13.6 × 2–3 µm) and occasionally 1-septate spores (Raitviir & Galán 1986, see also our Fig. 19b, d, 20c, j, o). Interestingly, all four collections of *R. monoseptata* were collected from arctic/alpine to subarctic areas and always on decorticated softwood, especially construction timber. *Resinoscypha variepilosa* shows more variability, growing both on hardwood and softwood.

Resinoscypha variepilosa (R. Galán & Raitv.) T. Kosonen, Huhtinen & K. Hansen, *comb. nov.* — MycoBank MB835740; Fig. 14e, 20

Basionym. Protounguicularia variepilosa R. Galán & Raitv., Int. J. Mycol. Lichenol. 2: 223. 1986.

Synonym. Arachnopeziza variepilosa (R. Galán & Raitv.) Huhtinen, Mycotaxon 30: 14. 1987.

Holotype. Spain, Cádiz, Grazalema, Sierra del Pinar de Grazalema, 1200 m a.s.l., on dead wood of *Abies pinsapo*, 27 Nov. 1982, *R. Galán* (Herb. Galán 6117) !

Specimens examined. Canada, Yukon, Kluane Lake, Outpost Mountain, on fallen, decayed trunk of Picea glauca, 19 Aug. 1987, *S. Huhtinen* 87/131 (TUR 99569). – Denmark, Zealand, Sorø, Suserup forest reserve, on decorticated trunk of *Fagus*, 8 May 1994, *J. Heilmann-Clausen* 04-035 (TUR 124469). – Slovakia, Bratislava Forest Park, along river Vydrica, on decorticated hardwood, 4 Aug. 1986, *P. Lizon & S. Huhtinen* 86/60 (TUR 92119). – Sweden, Upland, Haninge, Tyresta National Park, Bylsjöbäcken, on coniferous trunk, 1 June 2016, *T. Kosonen & S. Huhtinen* 16/41 (S, TUR). – UK, England, Hertfordshire, Wadesmill, on decayed wood of *Ulmus*, 24 Nov. 2010, *K. Robinson* (TUR 193603); Gloucestershire, Forest of Dean, Coalpit Hill, on a trunk of *Betula pendula*, 18 Apr. 2012, *K. Robinson* (TUR 196799).

Notes — This is a distinct but rarely collected species with collections from two continents. Based on morphology alone it is difficult to assign a suitable genus to this species. However, in addition to the CB+ resin (Fig. 20a), also the very variable shape of (especially the shorter marginal) hairs is a characteristic feature, already shown by Raitviir & Galán (1986: f. 8–11 of the holotype). The two collections, *S. Huhtinen* 87/131 and *S. Huhtinen* 16/41, from Canada and Sweden (Fig. 20e–k), have identical ITS and LSU sequences. The amount of resin on and in the hairs is highly variable even within one population, ranging from hairs practically without resin to hairs densely covered in resin (Fig. 20a, e, i). An ITS-LSU sequence of the Canadian sample has been previously deposited to GenBank (isolate M337 / collection *S. Huhtinen* 87/131: ITS, EU940163 and LSU, EU940086) (Stenroos et al. 2010). It was an erroneously annotated combination of two different species, the ITS presenting the correct species and the LSU apparently that of *Pezoloma ciliifera* of uncertain origin. The correct sequences were obtained by re-sequencing the original extraction of the isolate M337. The two sequenced samples were both from softwood.

DISCUSSION

The composition of the family Arachnopezizaceae

Our datasets included multiple sequences of *Arachnopeziza* species, the monotypic *Eriopezia* and *Arachnoscypha aranea*. Of these, *Arachnoscypha* is clearly shown to be distant to *Arachnopezizaceae*. *Eriopezia* forms a robust monophyletic group with species of *Arachnopeziza* and these two genera constitute, with the current sampling, the core *Arachnopezizaceae*. The included species produce a subiculum and usually apothecial hairs that are thin- to thick-walled and multiseptate. The ectal excipulum is mostly of *textura angularis* with somewhat thick to thick walls. Reinforcing the results by Han et al. (2014), our five-gene analyses suggest that the subiculum is a shared derived character for *Arachnopezizaceae*. It excludes species lacking a subiculum, such as *A. variepilosa* and *A. monoseptata*, now placed in *Resinoscypha*.

To our knowledge, a close relationship between *Arachnoscypha* and *Polydesmia* has not been proposed previously. Earlier authors have treated *Polydesmia* as a monogeneric unit without a well-established placement within *Helotiales* (Dennis 1960, 1968, Verkley 2005). At one point, *Polydesmia* was assigned to *Arachnopezizoideae* in the tribe *Polydesmieae* together with *Eriopezia* and *Parachnopeziza* (Korf 1978). The main point was, however, to include *Polydesmia* in *Hyaloscyphaceae* and no specific arguments were given for a close relationship of *Polydesmia* and *Arachnopeziza*, which, at that time, included *Arachnoscypha* (Korf 1978). Our results confirm, with high support, the recent multi-gene phylogenetic results by Johnston et al. (2019) that resolves *Polydesmia* as a sister taxon to *Chlorociboria*(*ceae*).

Two of the genera included in the recent description of *Arachnopezizaceae* (Baral 2015), *Austropezia* and *Parachnopeziza*, have not been included in robust molecular phylogenies. Based on analysis of the ITS-region across all of the *Leotiomycetes*, Johnston et al. (2019) suggested that *A. samuelsii* (the type species of *Austropezia*) does not belong in *Arachnopezizaceae*. There are some recent observations of other taxa that are, in preliminary analyses, early diverging in a monophyletic clade including *Arachnopezizaceae*. For example, Sokolski et al. (2006) have reported a black spruce (*Picea mariana*) needle endophyte with an aquatic stage, which, based on ITS/LSU sequences, appears to be related to *Arachnopeziza*. Moreover, the ITS/LSU sequences from *Durella melanochlora* and *D. macrospora* suggest that these are related to *Arachnopezizaceae* (Johnston et al. 2019). In addition to these, we have made some collections of herbicolous helotioid populations (unpubl. data) without distinctive morphological characters to assign them to known genera, but which likewise show strong phylogenetic affinity to *Arachnopezizaceae*.

Morphological characters and diversity in Arachnopeziza

The fact, that apothecia of *A. sphagniseda* have no true hairs, underlines the significance of the somewhat thick-walled subiculum as a unifying character among the members of *Arachnopeziza*. It is often less obvious among the species producing apothecia on bryophytes, but still regularly observed at least in mounts of apothecia. A subiculum is also produced in other groups of ascomycetes, for example, in *Mollisia* (*Helotiales*) as well as in *Pyronema* and *Byssonectria* (*Pezizomycetes*), but appears to be a result of convergent evolution. The subicular hyphae in *Arachnopeziaceae* are characteristic. The hyphae are thick-walled compared to the apothecial cells, but less than 2 µm wide and hyaline. The surface of the hyphae bears minute warts and is often partly covered with exudates similar to those on the apothecial hairs. In the literature, apothecia are sometimes described as being seated on the subiculum (Korf 1978). This is related to the idea of a 'false' and 'true' subiculum, where apothecia are borne on a 'true' subiculum, and a 'false' subiculum is a hyphal mat only surrounding the base of the apothecia. We find this kind of terminology problematic. The ontogeny of subicular hyphae in different genera has not been studied comprehensively and compared. There is large variation in the amount of subiculum produced among species of *Arachnopeziza*, but it is fairly constant for a given species. For example, *A. trabinelloides* has often very little subiculum, whereas *A. aurelia* or *E. caesia* always have copious subiculum.

Although *Arachnoscypha* is considered to have a subiculum there are some distinct differences between the aerial hyphae surrounding or connected to apothecia of *Arachnoscypha* and members of *Arachnopezizaceae*. Based on observations on fresh and dried material, we conclude that in *Arachnoscypha* the hyphae originate mainly from the lower part of the apothecia and there is no 'hyphal web' (i.e., subiculum) arising from the substrate surface even in the immediate vicinity of the apothecia as in *Arachnopeziza.* The subicular hypha in *Arachnopeziza* is of fairly even width and relatively thick-walled for the whole length and thus easily distinguishable from other apothecial elements. In *Arachnoscypha*, the basal parts of the hypha are thick-walled and branch as in *Arachnopeziza*, but towards the apices of the hypha are thin-walled, tapering and thoroughly covered in exudates and morphologically inseparable from the hairs. Based on these differences, we consider the thick-walled hyphae originating from the base of the apothecia in *Arachnoscypha* to be anchoring hyphae or simply basal mycelium.

All the species currently recognised in *Arachnopeziza*, including the species accepted in this study, have asci arising from croziers. The feature is mentioned in the description of the family (Baral 2015), but deserves to be noted, because in many species-rich helotialean genera there is variability in ascus development between species (e.g., in *Hyaloscypha*, *Hymenoscyphus*). The spore and excipulum characters show variation, but spores with at least one septum exist in most of the populations and the excipulum is at least partly thick-walled.

Using genealogical concordance (GCPSR), we recognise eight species within *Arachnopeziza* (indicated with triangles at the nodes in Fig. 3, Table 2). An additional four species are recognised based on single collections, because these are genetically divergent from their sisters (Fig. 3). Based on ITS (± LSU) sequences available in GenBank, we accept an additional species, *A. aurelia* (Fig. 4). However, the genetic exclusivity of this species still needs to be tested. To fully resolve the *Arachnopeziza* species limits and diversity requires further sampling. Several morphologically established species were lacking in our study and some were likely too narrowly sampled geographically, with our focus in Northwestern Europe. Species described from North America, such as *A. cornuta*, *A. fitzpatrickii* and *A. major*, treated in the *Arachnopeziza* monograph (Korf 1951b), should be recollected and investigated. Furthermore, three species of *Arachnopeziza* have been described fairly recently from subtropical Asia: *A. colachna*, *A. hiemalis* and *A. subnuda* (Korf & Zhuang 1985, Yu & Zhuang 2002, Wang 2009), and no sequences are available for these. Based on the descriptions and available literature, our estimate is that on top of the species treated in this study, there are c. 10–20 species described and assigned to *Arachnopeziza* that should be investigated and included in molecular studies to confirm their identity and phylogenetic relationships. Based on documents of *Arachnopeziza* species on softwood (Korf 1951b), together with our observations and some of Raitviir's unpublished collections (in TAAM) from Siberia, we suggest that conifers are likely to harbour some undiscovered *Arachnopeziza* species that should be further searched for and studied.

Of the four clades in *Arachnopeziza* supported by our five-gene phylogeny (Fig. 3), two are composed solely of species with a strong association to bryophytes, i.e., the *A. japonica* clade and *A. sphagniseda*. The *A. delicatula* clade has also at least one species producing apothecia on *Sphagnum*. Our observations show that in *Arachnopeziza* a substantial proportion of the known species grow on or in bryophytes and sequences from environmental sampling indicates an unrecognised diversity (Fig. 4, around *Arachnopeziza* sp. 'a'). The relationship of bryophytes and these fungi is not fully understood (e.g., Stenroos et al. 2010).

The *A. leonina* clade appears to be composed solely of species forming apothecia on wood (Fig. 3). Many of the wood-associated species produce excessive amounts of resin especially on the hairs, resulting in apothecia with a strong, yellow-orange overall appearance (Fig. 1b, c). The ecological spectrum of the studied species is relatively wide. Species such as, for example, *A. floriphila* (Baral 1989; on dead flowers of *Fagus sylvaticus*) or *A. groenlandica* (Raitviir 2003; dead branches of *Salix glauca*) expand the spectrum even further. *Arachnopeziza* is also one of the inoperculate genera that have unrecognised species present in the rhizobiome of woody plants (GenBank: LC190976, see also Fig. 4).

For barcoding purposes the ITS-region in *Arachnopeziza* has enough variation to provide a good estimate on the species identity. The LSU-region is conservative, and sequences differ often in only few single nucleotides between species and do not offer a reliable mean for species identification. *RPB1* proved to have a strong species recognition power, resolving all species with high support values (Table 2). Due to missing data we were not able to fully judge the *RPB2* and *TEF-1α* as barcoding regions, but both regions seem promising. With the high amplification success of the short *RPB1* region, we suggest it may serve as the best barcoding locus for *Arachnopeziza* species.

Towards a natural Hyaloscyphaceae

Based on our results *Hyaloscyphaceae* s.str. embraces *Hyaloscypha*, *Eupezizella*, *Olla*, *Mimicoscypha* and *Resinoscypha*. In addition, several species currently accepted in *Hyalopeziza* belong to this clade. The genera included have hyaline or whitish to greyish apothecia, and they all have hairs, which are often dextrinoid. The hair morphology varies, from cylindrical to tapering, from aseptate to multiseptate, as well as ranging from thin-walled to thick-walled or to solidified ('glassy'). The ectal excipulum is of predominantly thin-walled *textura prismatica*, which is occasionally dextrinoid or has small amyloid inclusions. Most species have been considered saprobic, but recent molecular phylogenetic studies and *in vitro* re-synthesis experiments (Fehrer et al. 2018) have shown some species to have the ability to form ericoid mycorrhizae, ectomycorrhizae, and/or to grow in rhizoids of liverworts. The majority of the species are lignicolous or herbicolous, and some occur on bryophytes. Strictly foliicolous species are rare.

Our strongest estimate of the phylogeny suggests *Hyaloscyphaceae* s.str. is sister to a clade of *Arachnopezizaceae* and *Amicodisca* (Fig. 2). Based on analyses of 3156 single copy genes, but with a very limited taxon sampling, Johnston et al. (2019) recently suggested that the closest sister group to *Arachnopezizaceae* is *Erysiphaceae*. We did not include members of *Erysiphaceae* in our analyses, but otherwise our results are in general consistent with those of Johnston et al. (2019).

Hyaloscypha encompass c. 35 recognised species (Huhtinen 1989, Fehrer et al. 2018). It is the most species-rich genus in the family. Based on our analyses, including nine species selected from a larger (unpublished) sampling, *Hyaloscypha* species form a monophyletic clade. The genus is well defined morphologically: the hairs of *Hyaloscypha* species do not have septa in the protruding part, i.e., the hairs are aseptate. There are taxa, closely related to *Hyaloscypha*, that have caused confusion in the delimitation of the genus. For example, the undescribed taxon represented by TNS-F-17137 (as *H. albohyalina* in Han et al. 2014; see our Taxonomy section under *Eupezizella*) has thin-walled, cylindrical hairs as in *Hyaloscypha*, but they are multiseptate, unlike in *Hyaloscypha* or in *Eupezizella*.

Another example is *Hyaloscypha leuconica* var. *leuconica* and var. *bulbopilosa* that were combined into *Hyalopeziza* (Raitviir 2004) based on partially thick, glassy walls typical in many populations (Huhtinen 1989). Most likely, material matching Raitviir's description is represented by for example KUS-F-52474 (Han et al. 2014). We have, however, sequences of populations that fit the morphological concept of *Hyaloscypha leuconica* var. *leuconica* (asci arising from simple septa) as well as *H. leuconica* var. *bulbopilosa* (asci arising from croziers). Based on our phylogenetic analyses, these are members of *Hyaloscypha* (results not shown for var. *bulbopilosa*). Our preliminary phylogenetic analyses also suggest that these varieties represent separate species. In Huhtinen (1989) the morphological concept of *Hyaloscypha leuconica* var. *leuconica* hairs was wide and included also collections with relatively thick glassy walls, perhaps morphologically close to KUS-F-52474. We have not been granted a study of the KUS-material, but it most likely represents an undescribed species related to species in the clade of *Hyalopeziza nectrioidea*, *Mimicoscypha* and *Olla* (Fig. 2).

The morphological delimitation of *Eupezizella* largely follows Huhtinen (1989; as a subgenus). *Hyaloscypha* and *Eupezizella* both have aseptate apothecial hairs, but in *Eupezizella* the hairs are always blunt and are never dextrinoid. The occasional amyloid nodules in the excipulum of *Eupezizella* have not been observed in *Hyaloscypha*. The latter character is shared with some of the other members of *Hyaloscyphaceae* s.str. (e.g., *Mimicoscypha*). *Eupezizella* is highly supported as a sister group to *Hyaloscypha*.

The erection of a new genus, *Mimicoscypha*, solves some long-lasting taxonomic questions among the hyaloscyphoid taxa. The species, *Mimicoscypha paludosa* and *M. mimica* were previously considered to belong to *Hyaloscypha* (Velenovský 1934, Dennis 1962). Although the multiseptate hairs indicate that these species do not belong to *Hyaloscypha* or *Eupezizella*, there has been no suitable genus for these species with long (sparsely) multiseptate thin-walled tapering hairs (Huhtinen 1989). The observed variation in vital taxonomy of *M. lacrimiformis* is interesting, but it should be interpreted with caution. Vacuolar bodies in paraphyses and often in hairs have been suggested as a character for several members of *Pezizellaceae* (Baral 2016) and there are only few observations of vacuolar bodies in strictly hyaloscyphoid genera. *Mimicoscypha* is forming a group with *Olla* and *Hyalopeziza nectrioidea* (Fig. 2). They all have multiseptate hairs, but *Olla* and *H. nectrioidea* differ from *Mimicoscypha* in having dextrinoid hairs. Since the type species of *Hyalopeziza*, *H. ciliata*, is not related to the species of *Hyalopeziza* nested within *Hyaloscyphaceae* s.str. (unpubl. data), eventually a new genus is needed for these. *Hyalopeziza alni* has similarly dextrinoid, multiseptate hairs, but it is resolved outside the *Mimicoscypha-Olla* clade (Fig. 2). Also, for example Han et al. (2014) have two species identified as '*Hyalopeziza* sp.' in their analyses that are possibly related to this clade. Based on morphological characters, *Hyalopeziza corticicola* with dextrinoid hairs, is most likely another closely related species. In our five-gene phylogeny the type species of *Olla* (*O. millepuctata*) and *Protounguicularia* (*P. brevicapitata* = *O. transiens*) form a supported monophyletic group and there-

fore we follow here Baral (1993) and treat *Protounguicularia* as a synonym of *Olla*. Nevertheless, it should be noted that these two representatives of *Olla* are morphologically very different (see Fig. 14c, d for their apothecial hairs) and the long branches leading to these species suggest they diverged a long time ago (Fig. 2). '*Hyaloscyphaceae* sp.' (SH 16/40) presents an undescribed lignicolous species. It has multiseptate, thin-walled hairs, no dextrinoid reactions and the spores are characteristically large, measuring close to 20 µm in length. We have no suggestion for a genus that could host such a species. It could be described as a monotypic genus, but with a single collection only, we refrain from doing so.

The dextrinoid reaction of hairs and excipulum cells appears to be a unique character for *Hyaloscyphaceae* s.str. As discussed above, some genera lack the reaction completely and there is also variation inside some genera, e.g., in *Hyaloscypha*, Huhtinen (1989) lists nine species with dextrinoid hairs, five without, and eight occasionally with dextrinoid hairs. Importantly, in *Hyaloscyphaceae*, species with solidified hair walls always show a dextrinoid reaction. *Resinoscypha* has some unique features within *Hyaloscyphaceae*, i.e., the CB+ resinous inclusions in the hairs (Fig. 19, 20) and our results suggest it is an early diverging lineage within the family.

Other genera and species associated with Hyaloscyphaceae s.str.

Our datasets did not include recognised members of *Psilocistella*. However, based on our preliminary analyses of the ITS/LSU region, *P. quercina* and *P. vernalis* belong to *Hyaloscyphaceae* s.str. As long as the generic type *P. obsoleta* is unavailable for phylogenetic analysis, it is difficult to treat the morphologically rather diverse genus with necessary certainty. *Psilocistella obsoleta*, with the relatively short, aseptate hairs, resembles morphologically *P. quercina*, whereas *P. vernalis* has relatively long multiseptate hairs (Svrček 1977, 1985, Huhtinen 1993a, Quijada et al. 2014). We have observations on taxa that based on phylogenetic analyses, nest in *Hyaloscyphaceae* s.str., close to *Hyaloscypha* and *Eupezizella*. They are morphologically similar to *Cistella*, with short, thin-walled lageniform hairs with small spines. The type of *Cistella* (*C. dentata*) has not been sequenced, but sequences available from other species of *Cistella* indicate these do not belong to *Hyaloscyphaceae* s.str., but are more closely related to *Urceolella* (Han et al. 2014, Johnston et al. 2019).

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