



# Fenestelloid clades of the *Cucurbitariaceae*

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## Key words

*Cucurbitaria*  
*Dothideomycetes*  
multigene phylogenetic analysis  
new taxa  
*Phoma*  
*Pleosporales*  
*Pyrenochaeta*

**Abstract** Fresh collections and their ascospore and conidial isolates backed up by type studies and molecular phylogenetic analyses of a multigene matrix of partial nuSSU-, complete ITS, partial LSU rDNA, *rpb2*, *tef1* and *tub2* sequences were used to evaluate the boundaries and species composition of *Fenestella* and related genera of the *Cucurbitariaceae*. Eight species, of which five are new, are recognised in *Fenestella* s.str., 13 in *Parafenestella* with eight new species and two in the new genus *Synfenestella* with one new species. *Cucurbitaria crataegi* is combined in *Fenestella*, *C. sorbi* in *Synfenestella*, *Fenestella faberi* and *Thyridium salicis* in *Parafenestella*. *Cucurbitaria subcaespitosa* is distinct from *C. sorbi* and combined in *Neocucurbitaria*. *Fenestella minor* is a synonym of *Valsa tetratrupha*, which is combined in *Parafenestella*. *Cucurbitaria marchica* is synonymous with *Parafenestella salicis*, *Fenestella bavarica* with *S. sorbi*, *F. macrospora* with *F. media*, and *P. mackenziei* is synonymous with *P. faberi*, and the latter is lectotypified. *Cucurbitaria sorbi*, *C. subcaespitosa* and *Fenestella macrospora* are lecto- and epitypified, *Cucurbitaria crataegi*, *Fenestella media*, *F. minor* and *Valsa tetratrupha* are epitypified in order to stabilise the names in their phylogenetic positions. A neotype is proposed for *Thyridium salicis*. A determinative key to species is given. Asexual morphs of fenestelloid fungi are phoma-like and do not differ from those of other representatives of the *Cucurbitariaceae*. The phylogenetic structure of the fenestelloid clades is complex and can only be resolved at the species level by protein-coding genes, such as *rpb2*, *tef1* and *tub2*. All fungal species studied here occur, as far as has been possible to determine, on members of *Diaporthales*, most frequently on asexual and sexual morphs of *Cytospora*.

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## INTRODUCTION

Phylogenetic assignment of non-lichenised pyrenocarpous ascomycetes forming brown muriform ascospores is a complex and ongoing task. While fungi with such ascospores are rather rare in *Sordariomycetes*, e.g., *Dictyoporthe* s.lat. (Jaklitsch & Barr 1997), *Stegonsporium* (Voglmayr & Jaklitsch 2008, 2014) in *Diaporthales*, *Strickeria* (*Xylariales*; Jaklitsch et al. 2016a), *Thyronectria* (*Hypocreales*; Jaklitsch & Voglmayr 2014, Voglmayr et al. 2016a) or *Thyridium* (Spatofora et al. 2006), they are common in many families of *Dothideomycetes*, particularly in several of the *Pleosporales* (Jaklitsch et al. 2016b). The *Cucurbitariaceae* is one of these families. In contrast to genera like, e.g., *Thyronectria* (*Hypocreales*; Jaklitsch & Voglmayr 2014, Voglmayr et al. 2016a) or *Teichospora* (*Pleosporales*; Jaklitsch et al. 2016c), where both phragmospores and dictyospores cluster in the same genus, all sexual morphs of the *Cucurbitariaceae* (*Pleosporales*) have dictyospores (Jaklitsch et al. 2018). Other characters shared by all representatives of this family are the presence of a subiculum and phoma- or pyrenochaeta-like asexual morphs, although these characters may occur in several other families, too (Jaklitsch et al. 2018, Valenzuela-Lopez et al. 2018). Several species of *Cucurbitaria* with no or other asexual morphs have been recently removed to different families of *Pleosporales*, e.g., *Coniothyriaceae* (*Cucurbitaria varians*; Crous & Groenewald 2017), *Camarosporidiella-*

*ceae* (most cucurbitaria-like species on fabaceous hosts; Wanasinghe et al. 2017a), *Melanommataceae* (e.g., *C. obducens*; Jaklitsch & Voglmayr 2017) or *Nectriaceae* (*C. bicolor* in *Thyronectria*; Checa et al. 2015). In a foregoing publication, Jaklitsch et al. (2018) redefined the scope of the *Cucurbitariaceae* and included the generic type of *Fenestella*, *F. fenestrata*, by redescription, illustration, lecto- and epitypification and DNA data. Other fenestella-like species were included in that work as the new genera *Cucitella*, *Parafenestella*, *Protofenestella* and *Seltsamia*.

After the original publication of *Fenestella* by Tulasne & Tulasne (1863), who recognised three species in the genus including *F. princeps*, a synonym of *F. fenestrata* (see Jaklitsch et al. 2018), 52 additional species names were created in the genus. Eleven names including *Fenestella bipapillata* (Jaklitsch & Barr 1997) and *Fenestella frit* (see Jaklitsch et al. 2018) have been removed to other genera or they, among others, are not interpretable, because no type material exists (for more data see notes to species and Discussion). Barr (1990) recognised eight species in *Fenestella* occurring in North America, which she keyed out and described morphologically. She also gave a detailed diagnosis of the genus *Fenestella* recognising its fungicolous habit. However, she subsumed American fungi under European *Fenestella* names without having seen type material of most of them. As a result, several of her taxonomic interpretations and conclusions are either erratic or too broad. A definition of what fenestelloid fungi are is difficult, particularly when compared to other members of the *Cucurbitariaceae*. The main character apart from a more marked tendency to form valloid groups or pseudostromatic pustules, are the ascospores, whose septa are variable in number and often difficult to count due to incompleteness, dense insertion and apparent oblique or shifted superposition in sectional view. This character is

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**Table 1** Isolates and accession numbers used in the phylogenetic analyses. Isolates/sequences in **bold** were isolated/sequenced in the present study.

Taxon	Host/substrate	Strain	Ex-type status	GenBank accession numbers					
				ITS	LSU	SSU	rpb2	tef1	tub2
<i>Allocurbitaria botulispora</i>	Superficial tissue	CBS 142452	holo	LT592932	LN907416	–	LT593070	–	LT593001
<i>Astragalicola amorpha</i>	<i>Astragalus angustifolius</i>	CBS 142999 = C227a	holo	MF795753	MF795753	–	MF795795	MF795842	MF795883
<i>Cucitella opali</i>	<i>Acer opalus</i>	CBS 142405 = FV	holo	MF795754	MF795754	MF795837	MF795796	MF795843	MF795884
<i>Cucurbitaria berberidis</i>	<i>Berberis vulgaris</i> ssp. <i>atropurpurea</i>	C39	–	MF795755	MF795755	–	MF795797	MF795844	MF795885
	<i>Berberis vulgaris</i>	CB	–	MF795757	MF795757	–	MF795799	MF795846	MF795887
	<i>Berberis vulgaris</i>	CBS 130007 = CB1	epi	MF795758	MF795758	–	MF795800	–	–
	<i>Berberis</i> sp.	CBS 142401 = C241	–	MF795756	MF795756	–	MF795798	MF795845	MF795886
	<i>Berberis aethnensis</i>	C265	–	MF795762	MF795762	–	MF795804	MF795850	MF795891
<i>Cucurbitaria oromediterranea</i>	<i>Berberis hispanica</i>	C29	–	MF795759	MF795759	–	MF795801	MF795847	MF795888
	<i>Berberis hispanica</i>	C86	–	MF795760	MF795760	–	MF795802	MF795848	MF795889
	<i>Berberis hispanica</i>	CB2	–	MF795763	MF795763	–	MF795805	MF795851	MF795892
	<i>Berberis hispanica</i>	CB3	–	MF795764	MF795764	–	MF795806	MF795852	–
	<i>Berberis cretica</i>	CBS 142399 = C229	holo	MF795761	MF795761	–	MF795803	MF795849	MF795890
<i>Fenestella crataegi</i>	<i>Crataegus monogyna</i>	<b>C287</b>	–	<b>MK356281</b>	<b>MK356281</b>	–	–	<b>MK357554</b>	<b>MK357598</b>
	<i>Crataegus monogyna</i>	<b>CBS 144857 = C314</b>	epi	<b>MK356282</b>	<b>MK356282</b>	–	<b>MK357512</b>	<b>MK357555</b>	<b>MK357599</b>
<i>Fenestella fenestrata</i>	<i>Alnus glutinosa</i>	CBS 143001 = FP9	epi	MF795765	MF795765	–	MF795807	MF795853	MF795893
<i>Fenestella gardiennetii</i>	<i>Acer glutinosum</i>	<b>CBS 144859 = FM</b>	holo	<b>MK356283</b>	<b>MK356283</b>	–	<b>MK357513</b>	<b>MK357556</b>	<b>MK357600</b>
<i>Fenestella granatensis</i>	<i>Acer granatense</i>	<b>CBS 144854 = C279</b>	holo	<b>MK356284</b>	<b>MK356284</b>	–	<b>MK357514</b>	<b>MK357557</b>	<b>MK357601</b>
<i>Fenestella media</i>	<i>Corylus avellana</i>	<b>CBS 144860 = FP</b>	epi	<b>MK356285</b>	<b>MK356285</b>	<b>MK356326</b>	<b>MK357515</b>	<b>MK357558</b>	<b>MK357602</b>
	<i>Carpinus orientalis</i>	FCO	–	<b>MK356286</b>	<b>MK356286</b>	–	<b>MK357516</b>	<b>MK357559</b>	–
	<i>Corylus avellana</i>	FP1	–	<b>MK356287</b>	<b>MK356287</b>	–	<b>MK357517</b>	<b>MK357560</b>	<b>MK357603</b>
	<i>Acer pseudoplatanus</i>	FP3	–	<b>MK356288</b>	<b>MK356288</b>	–	<b>MK357518</b>	<b>MK357561</b>	<b>MK357604</b>
	<i>Castanea sativa</i>	FP7	–	<b>MK356289</b>	<b>MK356289</b>	–	<b>MK357519</b>	<b>MK357562</b>	<b>MK357605</b>
	<i>Tilia cordata</i>	FP10	–	<b>MK356290</b>	<b>MK356290</b>	–	<b>MK357520</b>	<b>MK357563</b>	<b>MK357606</b>
<i>Fenestella parafenestrata</i>	<i>Quercus robur</i>	<b>CBS 144856 = C306</b>	holo	<b>MK356291</b>	<b>MK356291</b>	–	<b>MK357521</b>	<b>MK357564</b>	<b>MK357607</b>
	<i>Salix</i> sp.	C317	–	<b>MK356292</b>	<b>MK356292</b>	–	<b>MK357522</b>	<b>MK357565</b>	<b>MK357608</b>
<i>Fenestella subsymetrica</i>	<i>Acer campestre</i>	<b>CBS 144861 = FP6</b>	holo	<b>MK356293</b>	<b>MK356293</b>	–	<b>MK357523</b>	<b>MK357566</b>	<b>MK357610</b>
	<i>Juglans regia</i>	C285	–	<b>MK356293</b>	<b>MK356293</b>	–	–	<b>MK357566</b>	–
	<i>Juglans regia</i>	C286	–	<b>MK356294</b>	<b>MK356294</b>	–	–	<b>MK357567</b>	–
	<i>Juglans regia</i>	<b>C286x</b>	–	<b>MK356295</b>	<b>MK356295</b>	–	–	–	–
	<i>Corylus avellana</i>	FP4	–	<b>MK356296</b>	<b>MK356296</b>	–	<b>MK357524</b>	<b>MK357568</b>	<b>MK357609</b>
	<i>Salix caprea</i>	FP8	–	<b>MK356298</b>	<b>MK356298</b>	–	<b>MK357526</b>	<b>MK357570</b>	<b>MK357611</b>
<i>Fenestella viburni</i>	<i>Viburnum lantana</i>	<b>CBS 144863 = FVL</b>	holo	<b>MK356300</b>	<b>MK356300</b>	–	<b>MK357528</b>	<b>MK357613</b>	<b>MK357612</b>
	<i>Viburnum lantana</i>	FP2	–	<b>MK356299</b>	<b>MK356299</b>	–	<b>MK357527</b>	<b>MK357571</b>	<b>MK357612</b>
<i>Neocucurbitaria acanthocladae</i>	<i>Viburnum lantana</i>	CBS 142398 = C225	holo	MF795766	MF795766	–	MF795808	MF795854	MF795894
<i>Neocucurbitaria acerina</i>	<i>Genista acanthoclada</i>	C26a	–	MF795767	MF795767	–	MF795809	MF795855	MF795895
	<i>Acer pseudoplatanus</i>	CBS 142403 = C255	holo	MF795768	MF795768	–	MF795810	MF795856	MF795896
<i>Neocucurbitaria aethnensis</i>	<i>Acer pseudoplatanus</i>	CBS 142404 = C261	holo	MF795769	MF795769	–	MF795811	MF795857	MF795897
	<i>Genista aethnensis</i>	C270	–	MF795770	MF795770	–	MF795812	MF795858	MF795898
<i>Neocucurbitaria aquatica</i>	Sea water	CBS 297.74	holo	LT623221	EU754177	–	LT623278	–	LT623238
<i>Neocucurbitaria cava</i>	Unknown	CBS 115979	–	AY853248	EU754198	–	LT623273	–	LT623234
	Wheat-field soil	CBS 257.68	epi	JF740260	EU754199	–	LT171681	–	KT389844
<i>Neocucurbitaria cinerea</i>	<i>Genista cinerea</i>	CBS 142406 = KU9	holo	MF795771	MF795771	–	MF795813	MF795859	MF795899
<i>Neocucurbitaria cisticola</i>	<i>Cistus monspeliensis</i>	CBS 142402 = C244	holo	MF795772	MF795772	–	MF795814	MF795860	MF795900
<i>Neocucurbitaria hakeae</i>	<i>Hakea</i> sp.	CBS 142109 = CPC 28920	holo	KY173436	KY173526	–	KY173593	–	KY173613
<i>Neocucurbitaria irregularis</i>	Subcutaneous tissue	CBS 142791	holo	LT592916	LN907372	–	LT593054	–	LT592985
<i>Neocucurbitaria juglandicola</i>	<i>Quercus rubra</i>	<b>C316</b>	–	<b>MK356301</b>	<b>MK356301</b>	–	<b>MK357529</b>	<b>MK357573</b>	<b>MK357614</b>
	<i>Juglans regia</i>	CBS 142390 = BW6	holo	MF795773	MF795773	–	MF795815	MF795861	MF795901
<i>Neocucurbitaria keratinophila</i>	Man corneal scrapings	CBS 121759	holo	EU885415	LT623215	–	LT623275	–	LT623236
<i>Neocucurbitaria populi</i>	<i>Populus</i> sp.	CBS 142393 = C28	holo	MF795774	MF795774	–	MF795816	MF795862	MF795902
<i>Neocucurbitaria quercina</i>	<i>Quercus robur</i>	CBS 115095	neo	LT623220	GO387619	GO387558	LT623277	–	LT623237

Table 1 (cont.)

Taxon	Host/substrate	Strain	Ex-type status	GenBank accession numbers						
				ITS	LSU	SSU	rpb2	tef1	tub2	
<i>Neocucurbitaria rhamni</i>	<i>Rhamnus frangula</i>	CBS 142391 = C1	epi	MF795775	MF795775	MF795838	MF795817	MF795863	–	
	<i>Rhamnus frangula</i>	C112		MF795776	MF795776	–	MF795818	MF795864	MF795903	
	<i>Rhamnus frangula</i>	C133		MF795777	MF795777	–	MF795819	MF795865	MF795904	
	<i>Rhamnus frangula</i>	C190		MF795778	MF795778	–	MF795820	MF795866	–	
	<i>Rhamnus saxatilis</i>	C277		MF795779	MF795779	–	MF795821	MF795867	MF795905	
<i>Neocucurbitaria rhamnicola</i>	<i>Rhamnus lycioides</i>	CBS 142396 = C185	holo	MF795780	MF795780	–	MF795822	MF795868	MF795906	
	<i>Rhamnus alaternus</i>	KRx		MF795781	MF795781	–	MF795823	MF795869	MF795907	
	<i>Rhamnus saxatilis</i> ssp. <i>prunifolius</i>	C222		MF795783	MF795783	MF795839	MF795825	MF795871	MF795909	
	<i>Rhamnus saxatilis</i> ssp. <i>prunifolius</i>	C223		MF795784	MF795784	–	MF795826	MF795872	MF795910	
	<i>Rhamnus myrtifolius</i>	CBS 142395 = C118	holo	MF795782	MF795782	–	MF795824	MF795870	MF795908	
<i>Neocucurbitaria ribicola</i>	<i>Ribes rubrum</i>	CBS 142394 = C55	holo	MF795785	MF795785	MF795840	MF795827	MF795873	MF795911	
	<i>Ribes rubrum</i>	C155		MF795786	MF795786	–	MF795828	MF795874	MF795912	
	<i>Agropomus</i> sp. Lung	CBS 111112	holo	LT623222	GQ387623	–	LT623279	–	LT623239	
	<i>Vachellia gummifera</i>	CBS 142397 = C192	holo	MF795787	MF795787	EU754077	MF795829	MF795875	MF795913	
	<i>Olea europaea</i>	CBS 234.92	holo	LT623219	EU754176	–	LT623274	–	LT623235	
<i>Paracucurbitaria vachelliae</i>	<i>Fraxinus excelsior</i> with bacterial canker	CBS 248.79	holo	LT903672	GQ387608	–	LT903673	–	LT900365	
	<i>Cotoneaster integerrimus</i>	CBS 145263 = C198	holo	MK356302	MK356302	–	MK357530	MK357574	MK357615	
	<i>Salix appendiculata</i>	C249		MK356303	MK356303	–	MK357531	MK357575	MK357616	
	<i>Rosa canina</i>	CBS 145262 = C152	holo	MK356304	MK356304	–	MK357532	MK357576	MK357617	
	<i>Corylus avellana</i>	CBS 145267 = C307	holo	MK356305	MK356305	–	MK357533	MK357577	MK357618	
<i>Parafenestella parasalicum</i>	<i>Salix cinerea</i>	CBS 145271 = C318	holo	MK356306	MK356306	–	MK357534	MK357578	MK357619	
	<i>Acer pseudoplatanus</i>	CBS 142392 = C26	holo	MF795788	MF795788	–	MF795830	MF795876	MF795914	
	<i>Salix cf. alba</i>	CBS 145264 = C301	holo	MK356307	MK356307	–	MK357535	MK357579	MK357620	
	<i>Pyracantha coccinea</i>	CBS 145268 = C309	holo	MK356311	MK356311	–	MK357539	MK357583	MK357624	
	<i>Pyrus communis</i>	C203		MK356308	MK356308	–	MK357536	MK357580	MK357622	
<i>Parafenestella rosacearum</i>	<i>Crataegus monogyna</i>	C269		MK356309	MK356309	–	MK357537	MK357581	MK357622	
	<i>Pyrus communis</i>	C283		MK356310	MK356310	–	MK357538	MK357582	MK357623	
	<i>Rosa canina</i>	C315		MK356312	MK356312	–	MK357540	MK357584	MK357625	
	<i>Sorbus aria</i>	C320		MK356315	MK356315	–	MK357543	MK357587	–	
	<i>Prunus domestica</i>	CBS 145272 = FP11	neo	MK356314	MK356314	–	MK357542	MK357586	MK357627	
<i>Parafenestella salicis</i>	<i>Rosa canina</i>	FM1		MK356313	MK356313	MK356327	MK357541	MK357585	MK357626	
	<i>Salix alba</i>	CBS 145270 = C313		MK356317	MK356317	–	MK357545	MK357589	MK357629	
	<i>Salix alba</i>	C303		MK356316	MK356316	–	MK357544	MK357588	MK357628	
	<i>Salix alba</i>	CBS 145269 = C311	holo	MK356318	MK356318	–	MK357546	MK357590	MK357630	
	<i>Alnus glutinosa</i>	CBS 145266 = C304	epi	MK356319	MK356319	–	MK357547	MK357591	MK357631	
<i>Parafenestella vindobonensis</i>	<i>Salix babylonica</i>	CBS 145265 = C302	holo	MK356320	MK356320	–	MK357548	MK357592	MK357632	
	<i>Ulmus minor</i>	CBS 143000 = FP5	holo	MF795791	MF795791	–	MF795833	MF795879	MF795915	
	<i>Laurus nobilis</i> leaves	CBS 407.76 = AFTOL-ID 1856	neo	MF795792	MF795792	DQ988287	MF795834	MF795880	MF795916	
	Unknown	UTHSC D116-225	holo	LT592912	LN907368	–	LT593050	–	LT592981	
	Respiratory tract	CBS 142458	holo	LT592946	LN907441	–	LT593085	–	LT593015	
<i>Pyrenochaetopsis confliuens</i>	Deep tissue/fluids	CBS 142459	holo	LT592950	LN907446	–	LT593089	–	LT593019	
	Superficial tissue	CBS 143034	holo	LT592934	LN907418	–	LT593072	–	LT593003	
	<i>Secale cereale</i>	CBS 101635	epi	MF795793	MF795793	MF795841	MF795835	MF795881	MF795917	
	Superficial tissue	CBS 142461	holo	LT592935	LN907420	–	LT593074	–	LT593004	
	<i>Ulmus glabra</i>	CBS 143002 = L150	holo	MF795794	MF795794	MF795794	MF795836	MF795882	MF795918	
<i>Sytnestella pyri</i>	<i>Pyrus communis</i>	CBS 144855 = C297	holo	MK356321	MK356321	–	MK357549	MK357593	MK357633	
	<i>Sorbus aucuparia</i>	C298		MK356325	MK356325	–	MK357553	MK357597	MK357636	
	<i>Sorbus aucuparia</i>	CBS 144858 = C196	holo	MK356324	MK356324	–	MK357552	MK357596	MK357635	
	<i>Sorbus aucuparia</i>	CBS 144862 = FR	epi	MK356322	MK356322	MK356328	MK357550	MK357594	MK357634	
	<i>Sorbus aucuparia</i>	FRa		MK356323	MK356323	–	MK357551	MK357595	–	

shared with the morphologically rather pleomassariaceous genus *Seltsamia* (Jaklitsch et al. 2018), whose ascospores have an indefinitely swelling, bipartite sheath. A similar situation is found in *Fenestella* as shown below for *F. granatensis*, where the ascospore sheath swells however in a limited manner. Other unrelated, non-lichenised pyrenocarpous fungi on or in wood and bark having ascospores with many transverse and longitudinal eusepta in more or less cylindrical, fissitunicate asci are *Aigialus*, differing from fenestelloid fungi, e.g., in different ecology, as ascomata are immersed in submerged wood of mangroves in marine environments (Kohlmeyer & Schatz 1985), *Decaisnella* and *Karstenula* in the very wide concept of Barr (1990), which, e.g., lack a subiculum and are not associated with *Diaporthales*, or *Ostreichnion*, which produces conchate, superficial ascomata on wood (Boehm et al. 2009).

Here we take a detailed look into the taxonomy and phylogenetic structure of fenestelloid fungi described from Europe on woody hosts, from which fresh material was available for study. These fungi include several species originally described in *Fenestella*, *Cucurbitaria* or *Thyridium*, and cluster in three clades representing the three genera *Fenestella*, *Parafenestella* and *Synfenestella*.

## MATERIALS AND METHODS

### Isolates and specimens

All isolates used in this study originated from ascospores or conidia (where noted) of fresh specimens. Numbers of strains including NCBI GenBank accession numbers of gene sequences used to compute the phylogenetic trees are listed in Table 1. Strain acronyms other than those of official culture collections are used here primarily as strain identifiers throughout the work. Representative isolates have been deposited at the Westerdijk Fungal Biodiversity Centre, Utrecht, The Netherlands (CBS culture collection). Details of the specimens used for morphological investigations are listed in the Taxonomy section under the respective descriptions. Herbarium acronyms are according to Thiers (2018). Freshly collected specimens have been deposited in the Fungarium of the Department of Botany and Biodiversity Research, University of Vienna (WU).

### Culture preparation and phenotype analysis

Cultures were prepared and maintained as described previously (Jaklitsch 2009) except that CMD (CMA; Sigma, St Louis, Missouri; supplemented with 2 % (w/v) D(+)-glucose-monohydrate) or 2 % malt extract agar (MEA; 2 % w/v malt extract, 2 % w/v agar-agar; Merck, Darmstadt, Germany) was used as the isolation medium. Cultures used for the study of asexual morph micro-morphology were grown on CMD or 2 % MEA at 22 ± 3 °C in darkness. Microscopic observations were made in tap water except where noted. Morphological analyses of microscopic characters were carried out as described by Jaklitsch (2009). Methods of microscopy included stereomicroscopy using a Nikon SMZ 1500 and Nomarski differential interference contrast (DIC) using the compound microscopes Nikon Eclipse E600 or Zeiss Axio Imager.A1 equipped with a Zeiss AxioCam 506 colour digital camera. Images and data were gathered using a Nikon Coolpix 4500 or a Nikon DS-U2 digital camera and measured by using the NIS-Elements D v. 3.0 or 3.22.15 or Zeiss ZEN Blue Edition software packages. Some images obtained by using the Nikon interference contrast may be slightly too dark. For certain images of ascomata the stacking software Zerene Stacker v. 1.04 (Zerene Systems LLC, Richland, WA, USA) was used. Measurements are reported as maxima and minima in parentheses and the mean plus and minus the standard deviation of a number of measurements given in parentheses.

## DNA extraction and sequencing methods

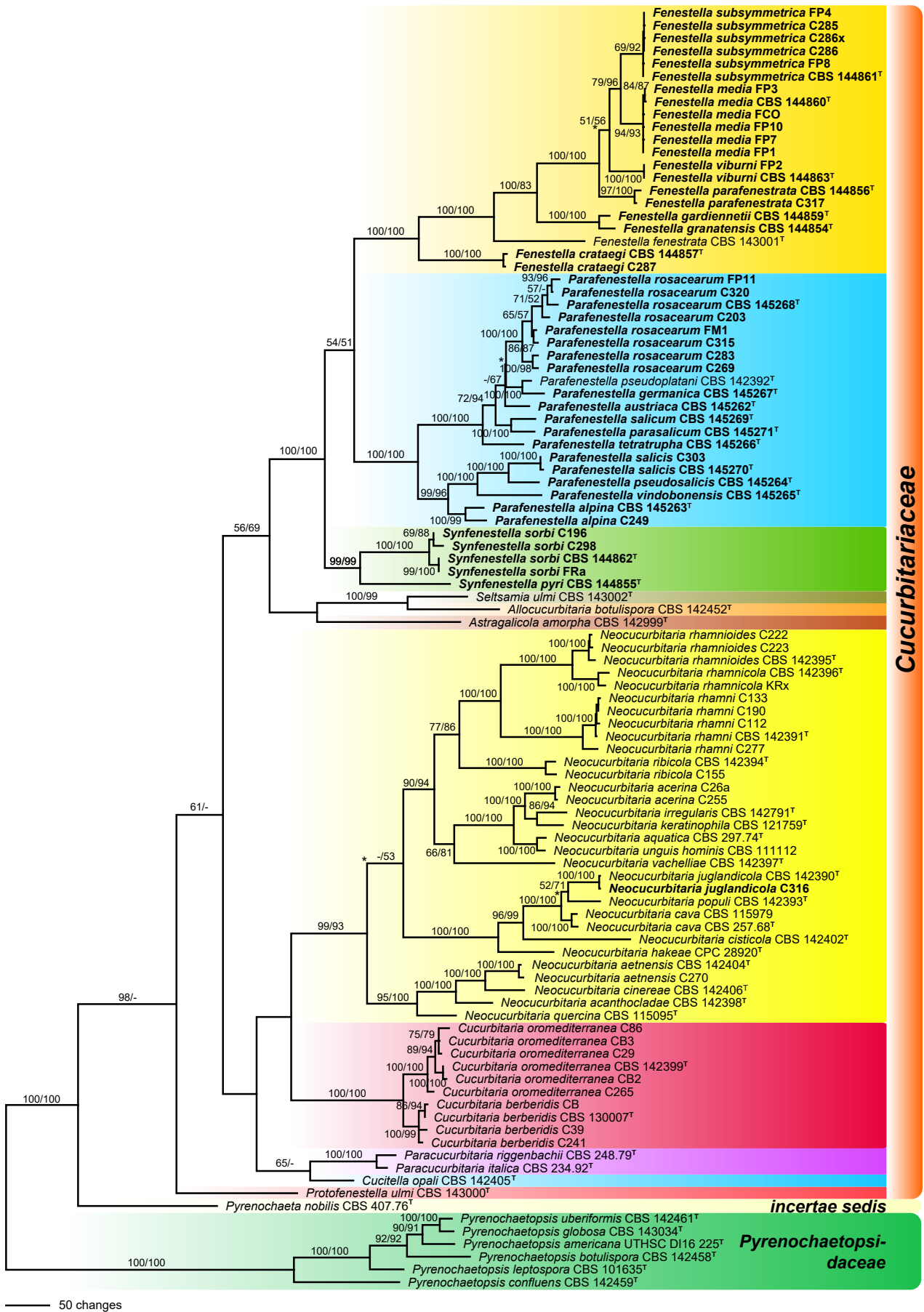
The extraction of genomic DNA was performed as reported previously (Voglmayr & Jaklitsch 2011, Jaklitsch et al. 2012) using the DNeasy Plant Mini Kit (QIAGEN GmbH, Hilden, Germany). The following loci were amplified and sequenced: the terminal 3' end of the small subunit nuclear ribosomal DNA (nSSU rDNA), the complete internally transcribed spacer region (ITS1-5.8S-ITS2) and a c. 900 bp fragment of the large subunit nuclear ribosomal DNA (nLSU rDNA), amplified and sequenced as a single fragment with primers V9G (De Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990); a c. 1.0–1.4 kb fragment at the 5' end of the nSSU rDNA with primers SL1 (Landvik et al. 1997) and NSSU1088 (Kauff & Lutzoni 2002); a c. 1.2 kb fragment of the RNA polymerase II subunit 2 (*rpb2*) gene with primers fRPB2-5f and fRPB2-7c (Liu et al. 1999) or dRPB2-5f and dRPB2-7r (Voglmayr et al. 2016a); a c. 1.3–1.5 kb fragment of the translation elongation factor 1-alpha (*tef1*) gene with primers EF1-728F (Carbone & Kohn 1999) and TEF1LLErev (Jaklitsch et al. 2005) or EF1-2218R (Rehner & Buckley 2005); and a c. 0.7 kb fragment of the beta tubulin (*tub2*) gene with primers T1 (O'Donnell & Cigelnik 1997) or T1HV (Voglmayr et al. 2016b) and BtHV2r (Voglmayr et al. 2016b, 2017). PCR products were purified using an enzymatic PCR clean-up (Werle et al. 1994) as described in Voglmayr & Jaklitsch (2008). DNA was cycle-sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems, Warrington, UK) with the same primers as in PCR; in addition, primers ITS4 (White et al. 1990), LR2R-A (Voglmayr et al. 2012) and LR3 (Vilgalys & Hester 1990) were used for the ITS-LSU region. In some cases the *tef1* was cycle-sequenced with internal primers TEF1\_INTF (forward; Jaklitsch 2009) and TEF1\_INT2 (reverse; Voglmayr & Jaklitsch 2017). Sequencing was performed on an automated DNA sequencer (3730xl Genetic Analyzer, Applied Biosystems).

### Analysis of sequence data

For the phylogenetic analyses, a combined matrix of nSSU-ITS-LSU rDNA, *rpb2*, *tef1* and *tub2* sequences was produced. The newly generated sequences were complemented with GenBank sequences of *Cucurbitariaceae* from Jaklitsch et al. (2018), and sequences of six taxa of *Pyrenochaetopsis* (*Pyrenochaetopsidaceae*) were added as outgroup according to the results of the phylogenetic analyses of Jaklitsch et al. (2018). All alignments were produced with the server version of MAFFT ([www.ebi.ac.uk/Tools/mafft](http://www.ebi.ac.uk/Tools/mafft)), checked and refined using BioEdit v. 7.2.6 (Hall 1999). Large insertions sometimes present in the SSU and at the terminal 3' end of the SSU of the partial SSU-ITS-LSU fragment were removed from the alignments.

The combined matrix contained 5707 nucleotide characters, represented by 1688 from the partial SSU-ITS-LSU, 999 from the SSU, 1067 from *rpb2*, 1258 from *tef1* and 695 from *tub2*.

Maximum parsimony (MP) analysis was performed using a parsimony ratchet approach. For this, a nexus file was prepared using PRAP v. 2.0b3 (Müller 2004), implementing 1000 ratchet replicates with 25 % of randomly chosen positions upweighted to 2, which was then run with PAUP v. 4.0a164 (Swofford 2002). The resulting best trees were then loaded in PAUP and subjected to heuristic search with TBR branch swapping (MULTREES option in effect, steepest descent option not in effect). Bootstrap analysis with 1000 replicates was performed using 5 rounds of replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, steepest descent option not in effect) during each bootstrap replicate. In all MP analyses molecular characters were unordered and given equal weight; analyses were performed with gaps treated as missing data; the COLLAPSE



**Fig. 1** Phylogram of one of 33 MP trees 6241 steps long (CI = 0.386, RI = 0.817), obtained by PAUP from an analysis of the combined matrix (SSU-ITS-LSU, *rpb2*, *tef1*, *tub2*) of Cucurbitariaceae and Pyrenochaetopsidaceae, with the latter selected as outgroup. MP and ML bootstrap support above 50 % are given at the first and second position, respectively, above or below the branches. Strains formatted in **bold** were isolated and sequenced in the current study; ex-type strains are indicated by a superscript T. Nodes collapsed in the strict consensus of the 33 MP trees are marked by an asterisk (\*).

command was set to minbrlen. Maximum likelihood (ML) analyses were performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI 1.5 (Silvestro & Michalak 2012), using the ML + rapid bootstrap setting and the GTRGAMMA substitution model with 1000 bootstrap replicates. The matrix was partitioned for the individual gene regions, and substitution model parameters were calculated separately for them. For evaluation and discussion of bootstrap support, values below 70 % were considered low, between 70 and 90 % medium/moderate and above 90 % high.

## RESULTS

### Phylogenetic analyses

Of the 5707 nucleotide characters of the combined matrix, 1266 are parsimony informative (283 of ITS-LSU, 5 of SSU, 423 of *rpb2*, 302 of *tef1* and 253 of *tub2*). Maximum parsimony analyses revealed 33 MP trees 6241 steps long, one of which is shown as Fig. 1. Topologies of the MP trees were identical except for one backbone node each within the *Fenestella* and *Parafenestella* clades, and two backbone nodes within the *Neocucurbitaria* clade (marked by asterisks in Fig. 1).

Like in the previous phylogenetic analyses of Jaklitsch et al. (2018), many of the deeper nodes within *Cucurbitariaceae* were unsupported or received only low support, while the genera *Cucurbitaria* and *Neocucurbitaria* were highly supported. The fenestelloid clade received maximum support and contained three highly supported subclades here recognised as three distinct genera: *Fenestella*, *Parafenestella* (both with maximum support in MP and ML analyses) and *Synfenestella* (99 % MP and ML bootstrap support). The sister group relationship of *Fenestella* and *Parafenestella* received only low support (54 % MP and 51 % ML), while most backbone nodes within the three genera received high to maximum support (Fig. 1).

### Taxonomy

***Fenestella*** Tul. & C. Tul., Select. Fung. Carpol. (Paris): Xylariei-Valsei-Spaeriei 2: 207. 1863, emend.

*Type species. Fenestella fenestrata* (Berk. & Broome) J. Schröt.

***Fenestella fenestrata*** (Berk. & Broome) J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.2(4): 435. 1897 (1908)

*Basionym. Valsa fenestrata* Berk. & Broome, Ann. Mag. Nat. Hist., ser. III 3: 366. 1859.

*Synonym. Fenestella princeps* Tul. & C. Tul., Select. Fung. Carpol. (Paris) 2: 207. 1863.

Notes — See Jaklitsch et al. (2018) for description and typification of the genus and its type species. In that work it was stated that all materials of *F. fenestrata* available for study were more or less overmature, which made identification of the fungal host difficult. The black encasement of ascomata was interpreted as belonging to a *Diaporthe* sp. Considering that all other species of the genus occur on *Cytospora* spp. (see below), it appears probable that the stromatic encasement belonged to a *Cytospora* sp. having a *Leucostoma* sexual morph.

The second specimen given in the protologue of *F. fenestrata* was examined: England, Leicestershire, Orton Wood, on dead twigs of *Quercus robur*, Mar. 1859, A. Bloxam (K(M) 233193; as *Valsa fenestrata*). Although the plant host would suggest *Fenestella parafenestrata* (see below), the fungus in this specimen is morphologically indistinguishable from *F. fenestrata*: Pseudostromatic pustules are 1–4 mm diam, brown to black, outside limited by a black stromatic line, ascomata 400–770 µm diam, ostiolar areas 180–420 µm diam, asci are cylindrical and

ascospores (35–)43–61(–74) × (14.5–)16.5–22.5(–27) µm, l/w (2–)2.3–3.1(–3.5) (n = 30), ellipsoid to fusoid, very dark brown, symmetric or asymmetric, with up to 16 distinct transverse and 7 longitudinal septa and up to 4 µm long hyaline apiculi. See Fig. 6b1 for the illustration of an ascospore.

***Fenestella crataegi*** (Niessl) Jaklitsch & Voglmayr, *comb. nov.* — MycoBank MB829741; Fig. 2

*Basionym. Cucurbitaria crataegi* Niessl, Verh. Naturf. Vereins Brünn 10: 199. 1872.

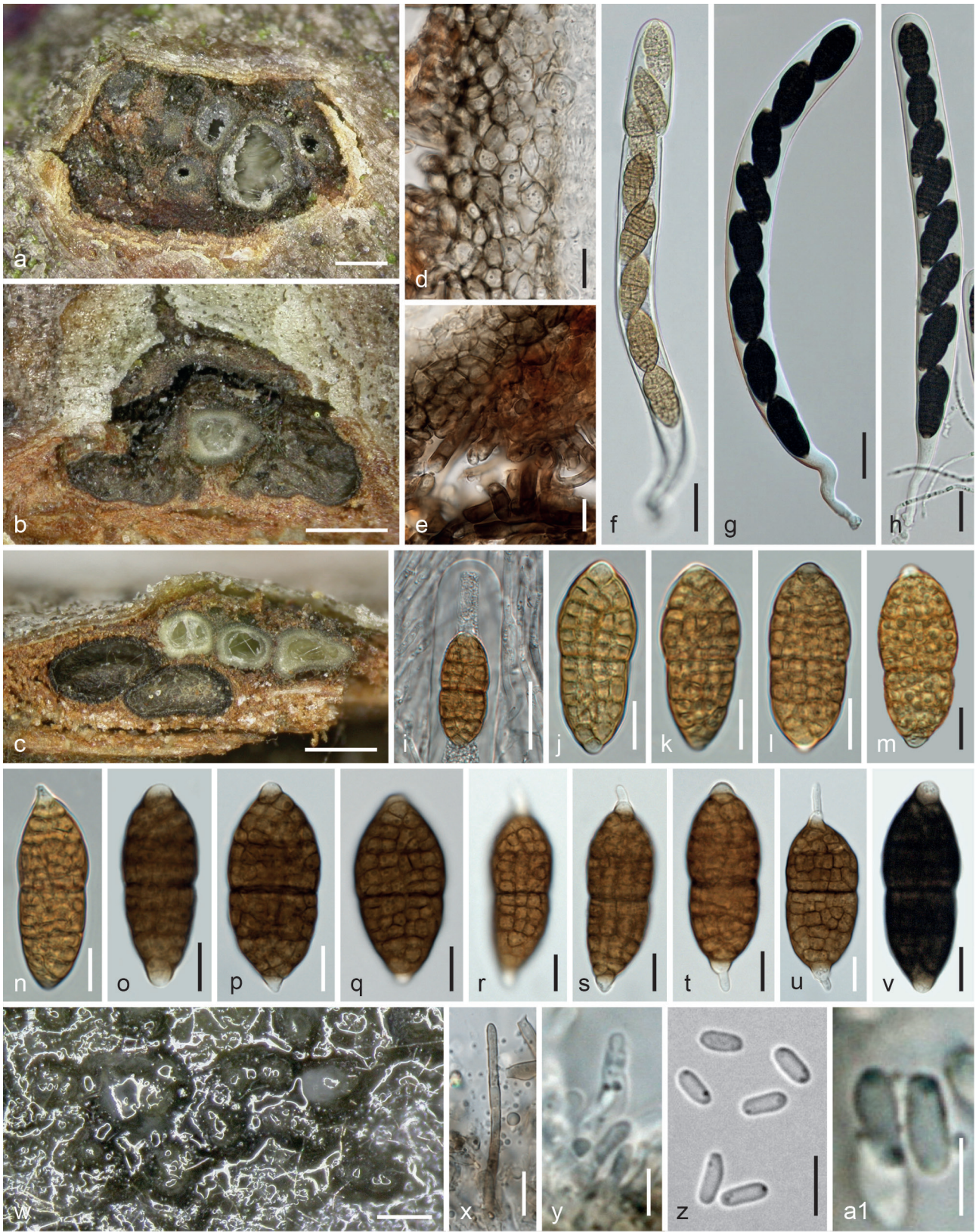
*Holotype.* CZECH REPUBLIC, near Brno, on dry branches of *Crataegus oxyacanthae* (used at that time for *C. monogyna*), no date given, G. Niessl (M-0281851). *Epitype*, here designated: AUSTRIA, Burgenland, Purbach, Purbacher Heide, on *Cytospora* sp. on a branch of *Crataegus monogyna*, soc. *Diplodia* sp., 24 Mar. 2018, H. Voglmayr (WU 36987; MBT385683; ex-epitype culture CBS 144857 = C314).

*Ascomata* (330–)368–507(–540) µm (n = 12) diam, globose, subglobose to pyriform, immersed in groups of 0.9–2.4 mm diam or length containing usually less than 10 individuals or solitarily above *Cytospora* (*Valsa*) ascomata or conidiomata in a single or two vertical layers, and erumpent from bark; ascomata individually surrounded by shiny, pale to dark brown, thick-walled, 2–6.5 µm wide subicular hyphae connecting them and sometimes forming pseudostromatic structures. *Ostiolar areas* 90–180 µm diam, black, poorly differentiated from the venter and inconspicuous, less commonly papillate. *Peridium* c. 20–75 µm wide, pseudoparenchymatous, consisting of (3.5–)5.5–10(–14.5) µm (n = 30) wide cells, dark brown outside, gradually paler, larger and thinner-walled to the inside; the innermost layer ill-defined, variably comprising hyaline or pale brown compressed cells. *Hamathecium* consisting of numerous branched, 1–4 µm wide, apically free paraphyses. *Asci* (214–)245–295(–317) × (20–)22–26.7(–28) µm (n = 22), cylindrical to oblong or narrowly clavate, bitunicate, fissitunicate, with an ocular chamber, a short stipe and simple or knob-like base, containing (4–)8 ascospores in (obliquely) uniseriate, sometimes partly biseriate arrangement; unstable in water, stable in 3 % KOH. *Ascospores* (31–)36.5–45.5(–54.5) × (11–)15–19.5(–23) µm, l/w (2–)2.2–2.6(–3) (n = 95), ellipsoid or broadly fusoid, with 11–14(–16) transverse and 2–4 longitudinal septa, constricted at the median or nearly median primary septum with upper part often wider than lower, thick-walled, first hyaline, turning yellowish, finally medium to dark brown, in 3 % KOH blackish brown; terminal part of terminal cells hyaline and broadly or narrowly rounded, projecting to c. 3.5 µm, becoming elongate upon germination.

Culture characteristics and asexual morph in culture — *Colony radius* on CMD at 22 °C in the dark 4 mm after 1 wk, 21 mm after 3 wk; *colony* circular, thick, dense, first white, turning greyish olive, dark grey-brown and finally black, slightly zonate, becoming velvety by aerial hyphae, odour indistinct. *Pycnidia* developing on and around the plug submerged in the agar to superficial, globose, c. 90–300 µm diam, olivaceous to black, aggregating and confluent to large masses; peridium pseudoparenchymatous, bearing hyaline to brown hyphae and dark brown thick-walled setae 10–50 × 1.5–5 µm; releasing conidia as whitish to olivaceous turbid drops. *Phialides* (4.5–)5.7–8.7(–11) × (1.5–)2.2–3.5(–4.2) µm (n = 30), lageniform, ampulliform or subcylindrical, sessile or on short few-celled conidiophores; conidia also formed on lateral pegs. *Conidia* (3.2–)3.5–4.7(–5.6) × (1.2–)1.4–1.8(–2.1) µm, l/w (1.8–)2.2–3.2(–4.3) (n = 51), cylindrical, oblong to ellipsoid, 1-celled, hyaline to pale greyish olivaceous, containing 2 sub-terminal drops, smooth.

*Habitat* — On *Cytospora* sp. (sexual and asexual morphs) on branches and twigs of *Crataegus monogyna*.

*Distribution* — Central Europe (Czech Republic, Austria).



**Fig. 2** *Fenestella crataegi*. a–v. Sexual morph. a. Horizontal section through unevenly immersed ascomata; b–c. Immature ascomata immersed at the ostiolar levels of the *Cytospora* morph (b) and the *Valsa* morph (c); d. peridium in vertical section; e. subicular hyphae below vertically sectioned peridium; f–h. asci (in f young and opening); i. ascus apex surrounded by hamathecial threads; j–v. ascospores (j–n from fresh material; germinating in s–u); w–a1. asexual morph from CMD at 22 °C; w. pycnidia with conidial drops; x. pycnidial seta; y. phialides; z–a1. conidia (greyish olivaceous in a1) (g–h, v. in 3 % KOH). a–i, m, o–a1. WU 36987/CBS 144857 (C314); j–l, n. C287. — Scale bars: a–c = 300 µm; d–e, j–v, x = 10 µm; f–i = 25 µm; w = 150 µm; y–z = 5 µm; a1 = 3 µm.

*Other materials examined.* AUSTRIA, Burgenland, Purbach am See, Purbacher Heide, on branch of *Crataegus monogyna*, 4 Feb. 2017, H. Voglmayr (culture C287; specimen lost); Niederösterreich, Wolfsthal, grid square 7868/3, on corticated twigs of *Crataegus monogyna*, 1 Apr. 2000, W. Jaklitsch W.J. 1434 (WU 37020).

**Notes** — There are two specimens of Niessl labelled *Cu-curbitaria crataegi* in M. Specimen M-0281852 contains a *Parafenestella* with ascospores  $(25\text{--})26\text{--}30\text{--}(31) \times (11.8\text{--})12.3\text{--}14\text{--}(14.3) \mu\text{m}$ , recognised as *P. austriaca* (see below). It was collected in Rosenthal near Hütteldorf (Vienna, Austria), thus it cannot be type material. Specimen M-0281851 was collected at the type locality and contains a *Diplodia* (plus its botryosphaeriaceous sexual morph) in excess and a *Massarina* sp. (s.lat.) with bicellular hyaline ascospores. Also present are a few pycnidia on subiculum, containing rod-like unicellular hyaline conidia  $(3\text{--})3.3\text{--}4\text{--}(4.4) \times (1.2\text{--})1.3\text{--}1.6\text{--}(1.8) \mu\text{m}$ , l/w 2.1–2.9(–3.7) ( $n = 30$ ), on lageniform to subcylindrical phialides. This is presumably the asexual morph of *C. crataegi*. As the sexual morph is apparently used up and the specimen is depauperate, epitypification is essential. Von Niessl's (1872) measurements of ascospores lies at the lower end of our measurements, but his illustrations strongly suggest that our material represents this taxon, therefore we stabilise this name by epitypification rather than describing a new species. He compared his fungus with *C. acervata*, of which he had not seen authentic material.

***Fenestella gardiennetii* Jaklitsch & Voglmayr, sp. nov.** — MycoBank MB829742; Fig. 3

*Etymology.* Named after its collector Alain Gardiennet.

*Holotype.* FRANCE, 21, Longvic, Arboretum, on *Cytospora* sp. on twigs of *Acer saccharum*, soc. *Diplodia* sp., 27 June 2013, A. Gardiennet (WU 36986; ex-type culture CBS 144859 = FM).

*Ascomata*  $(390\text{--})405\text{--}565\text{--}(630) \mu\text{m}$  ( $n = 12$ ) diam, depressed subglobose to globose, immersed in valsoid groups or in lines c. 0.7–2 mm long, also solitarily or in pairs, on and surrounded by subiculum on effete *Cytospora* sp.; ascoma apex mostly flat, black, sometimes partly covered by brown subiculum. *Ostioles* 55–150  $\mu\text{m}$  diam, central, papillate to conical, black, periphysate. *Subiculum* consisting of subhyaline to dark brown, thick-walled, 2–6  $\mu\text{m}$  wide hyphae. *Peridium* 20–75  $\mu\text{m}$ , apically to 110  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of thick-walled, dark brown cells  $(5\text{--})7.5\text{--}14\text{--}(17) \mu\text{m}$  ( $n = 45$ ) diam becoming gradually lighter towards the interior, sometimes terminated inside by pale brown compressed cells. *Hamathecium* consisting of richly branched 1–3.5  $\mu\text{m}$  wide threads in a gel matrix. *Asci*  $(176\text{--})202\text{--}243\text{--}(263) \times (20.5\text{--})21\text{--}25.5\text{--}(30) \mu\text{m}$  ( $n = 25$ ), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a usually short stipe and simple or knob-like base, containing 4–8 ascospores in (obliquely) uniseriate, sometimes partly biseriate arrangement. *Ascospores*  $(34\text{--})36.5\text{--}45\text{--}(49) \times (13.5\text{--})15\text{--}19\text{--}(22.5) \mu\text{m}$ , l/w  $(1.9\text{--})2.2\text{--}2.6\text{--}(2.8)$  ( $n = 50$ ), broadly ellipsoid to clavate, thick-walled, first hyaline with 1–4 main transverse septa, usually distinctly asymmetric with submedian primary septum and smaller lower part, developing additional septa and turning dark brown, when mature with 11–16 distinct transverse and



**Fig. 3** *Fenestella gardiennetii* (WU 36986, CBS 144859 = FM). a–o. Sexual morph. a. Ascomata in face view; b. vertical section of ascoma on a *Cytospora* pseudostroma; c. peridium in vertical section; d. subicular hyphae; e. ascus apex; f–h. asci; i–o. ascospores (i. initial stage); p. conidia from CMD at 22 °C; (n–o. in 3% KOH). — Scale bars: a = 300  $\mu\text{m}$ ; b = 500  $\mu\text{m}$ ; c–d, f–h = 25  $\mu\text{m}$ ; e, i–o = 10  $\mu\text{m}$ ; p = 5  $\mu\text{m}$ .



3–5 longitudinal septa, distinctly constricted at the primary septum; surface verruculose; ends of terminal cells concolorous or hyaline, often narrowed and projecting as 1–2 µm long apiculi; in 3% KOH ascospores turning blackish brown when mature, apiculi remaining hyaline.

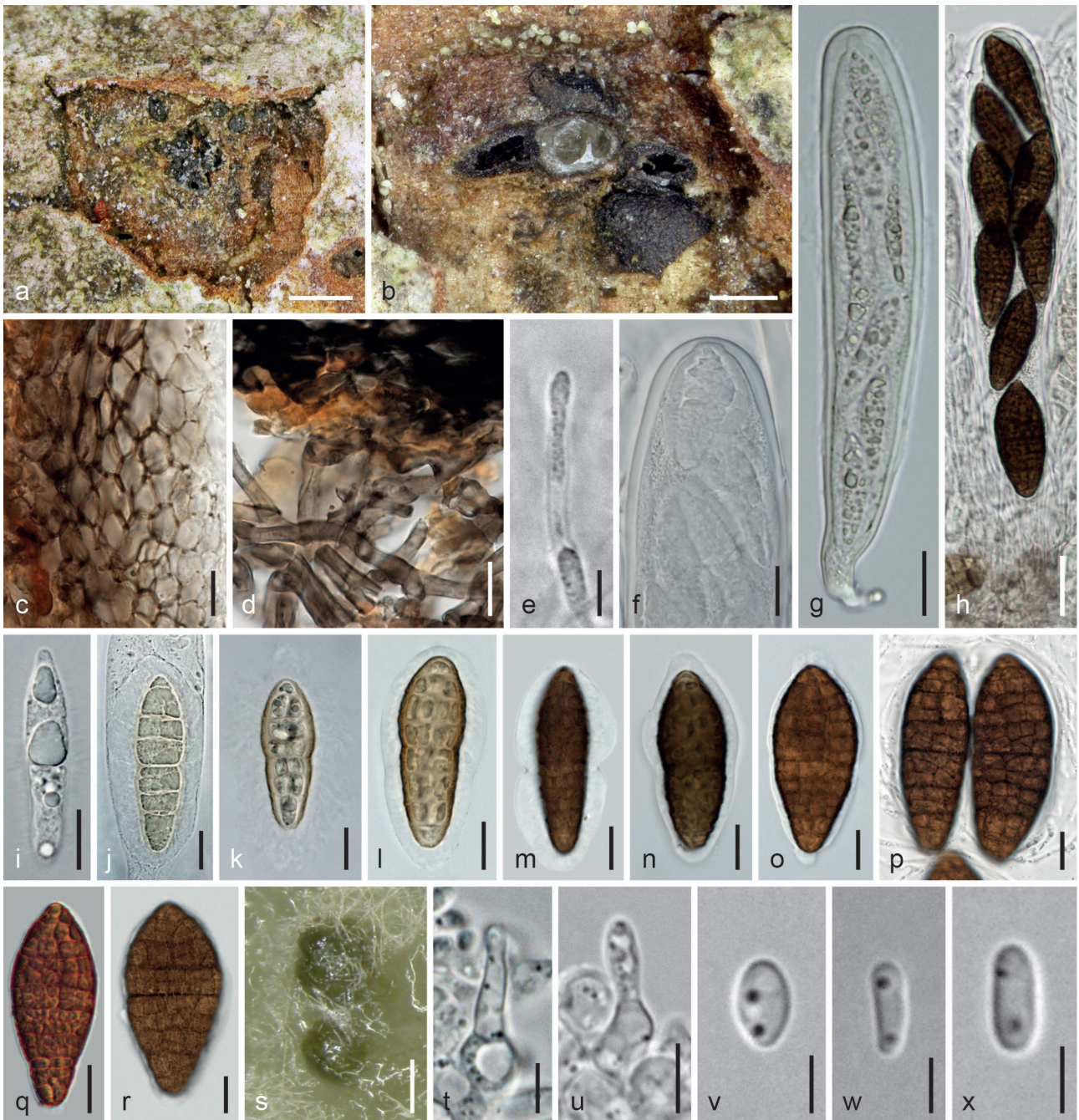
Culture characteristics and asexual morph in culture — Ascospores germinating simultaneously from many cells. *Colony radius* on CMD at 22 °C in the dark 10 mm after 1 wk, 35 mm after 4 wk; *colony* circular, thick and dense, first white, turning dull olivaceous brown to brownish grey from the centre, zonate; aerial hyphae forming loose grey mesh; reverse dark grey to black; odour indistinct. *Pycnidia* formed after 4 d, mostly remaining submerged in agar and densely aggregated on and around the inoculation plug, globose, 120–210 µm diam, greenish, turning black; peridium pseudoparenchymatous, consisting

of isodiametric cells with irregularly distributed dark brown pigment, surrounded by brown hyphae. *Conidia* amassing in pale greyish mucous drops, (3.3–)3.5–4.5(–5) × (1.1–)1.2–1.5(–1.7) µm, l/w (2–)2.5–3.4(–4.4) (n = 30), cylindrical, straight to slightly curved, 1-celled, smooth, containing 2 minute guttules.

Habitat — On *Cytospora* sp. (sexual and asexual morphs) on *Acer saccharum*.

Distribution — Europe (France), only known from the type locality; possibly occurring also in North America.

Notes — *Fenestella gardiennetii* may have travelled on its host from North America and may thus occur also there. It is closely related to *F. granatensis*, which occurs on *Acer granatense* and differs from the former by more distinctly clavate ascospores that are surrounded by a mucous sheath.



**Fig. 4** *Fenestella granatensis*. a–r. Sexual morph (WU 36985). a. *Cytospora* (*Valsa*) pseudostroma with laterally inserted ascoma; b. vertical section of 3 ascomata sitting on a *Cytospora* (*Valsa*) ascoma; c. peridium in vertical section; d. subicular hyphae; e. free end of a paraphysis with sheath; f. apex of immature ascus; g–h. asci (immature in g); i–r. ascospores (i. initial stage; j–l. young; r. compressed); s–x. asexual morph (CBS 144854 (C279) from CMD at 22 °C); s. pycnidia; t–u. phialides; v–x. conidia (d, h, k–l. in 3% KOH). — Scale bars: a = 500 µm; b = 300 µm; c–d, f, i–r = 10 µm; e, t–u = 5 µm; g–h = 20 µm; s = 150 µm; v–x = 3 µm.

***Fenestella granatensis*** Jaklitsch & Voglmayr, *sp. nov.* — MycoBank MB829743; Fig. 4

*Etymology.* Referring to the place of its occurrence, Granada, and its host *Acer granatense*.

*Holotype.* SPAIN, Andalusia, Granada, La Zubia, Cerro del Trevenque, near the Jardín Botánico de la Cortijuela, elev. 1600 m, on *Cytospora* sp. on twig of *Acer granatense*, soc. *Dictyosporthe* sp., a melanommataceous fungus, and *Myriangium durieui*, 14 May 2014, W. Jaklitsch & S. Tello (WU 36985; ex-type culture CBS 144854 = C279).

*Ascomata* (330–)358–636(–900)  $\mu\text{m}$  ( $n = 20$ ) diam, globose, depressed subglobose to subpyriform, immersed and erumpent through bark fissures, in valsoid groups of 1–10 typically around ostiolar necks of *Cytospora* (*Valsa*) ascomata, forming pustules 0.9–2 mm diam; individually surrounded by whitish to dark brown *subiculum* consisting of thick-walled, 2–7  $\mu\text{m}$  wide hyphae. *Ostiolar structures* short-cylindrical, hardly noticeable on the surface or appearing as black dots 75–170(–210)  $\mu\text{m}$  diam; interior periphysate. *Peridium* c. 30–65  $\mu\text{m}$ , apically to 100  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of thick-walled, dark brown cells (4.5–)6–11.5(–16)  $\mu\text{m}$  ( $n = 40$ ) diam becoming gradually lighter towards the interior, sometimes terminated inside by pale brown compressed cells. *Hamathecium* consisting of numerous, richly branched, 1–3  $\mu\text{m}$  wide, apically free paraphyses in a dense matrix. *Asci* (195–)222–265(–284)  $\times$  (28.5–)31–34(–34.5)  $\mu\text{m}$  ( $n = 15$ ), cylindrical, oblong or clavate, bitunicate, fissitunicate, with an ocular chamber, a usually short stipe and simple or knob-like base, containing 4–8 ascospores in (obliquely) uni- to biseriolate arrangement. *Ascospores* (36.5–)43–53.5(–60)  $\times$  (13–)17–22.5(–28.5)  $\mu\text{m}$ , l/w (1.9–)2.2–2.7(–3.4) ( $n = 100$ ), clavate, fusoid to subellipsoid with the upper part always wider than the lower, when young hyaline to yellowish and with 1–7 transverse and 1–2 longitudinal septa, eventually dark brown, with 12–17 transverse and 4–5 longitudinal septa; usually slightly constricted at the nearly median primary septum; tips of end cells slightly lighter or concolorous; cells filled with oil drops, surface warted and appearing fissured; surrounded by a bipartite, 1–2  $\mu\text{m}$  wide gelatinous sheath swelling in water and terminally fraying out at as variably shaped, appendage-like distortions or protuberances; in 3% KOH blackish brown, primary septum appearing more distinct, other septa becoming less distinct, sheath swelling indefinitely. *Pycnidia* of the presumed asexual morph with minute rod-like hyaline unicellular conidia on lageniform to subulate phialides on filiform conidiophores also present between ostiolar necks of the *Cytospora* (*Valsa*) host.

Culture characteristics and asexual morph in culture — *Colony radius* on CMD at 22 °C in the dark 10–13 mm after 1 wk, 33 mm after 3 wk; *colony* circular, thick, dense, first white to yellowish, later turning dark olivaceous brown to dark grey, reverse black; aerial hyphae forming a dense brownish mat; odour indistinct. *Pycnidia* appearing after 4 d in the colony centre, numerous, separate or aggregating to larger complexes, globose, 150–270  $\mu\text{m}$  diam, first hyaline to greenish, turning olivaceous to black; conidia becoming released in whitish turbid drops. *Phialides* sessile or formed terminally on cylindrical to globose intercalary cells, (2.7–)5–9(–11.3)  $\times$  (1.5–)2.3–4(–5)  $\mu\text{m}$  ( $n = 20$ ), lageniform, ampulliform to subglobose with a long neck. *Conidia* formed on phialides and lateral pegs, (3–)3.5–4.8(–6)  $\times$  (1.4–)1.6–2.1(–2.7)  $\mu\text{m}$ , l/w (1.5–)2–2.7(–3.1) ( $n = 25$ ), oblong, allantoid or narrowly ellipsoid, 1-celled, with usually 2 subterminal drops, smooth.

*Habitat* — On *Cytospora* sp. (sexual and asexual morphs) on *Acer granatense*.

*Distribution* — Europe (Spain), only known from the type locality.

*Notes* — *Fenestella granatensis* is easily recognisable by its clavate pleomassariaceous ascospores having a gelatinous sheath and by its host, *Acer granatense*. As with several other species of the fenestelloid clades, a few pycnidia are present on the fungal host; always discrete, globose and collapsing cupulate.

***Fenestella media*** Tul. & C. Tul., *Select. Fung. Carpol.* (Paris) 2: 208. 1863. — Fig. 5

*Synonym.* *Fenestella macrospora* Fuckel, *Jahrb. Nassauischen Vereins Naturk.* 25–26: 313. 1871.

*Typification.* *Holotype* of *Fenestella media*. FRANCE, Meudon (close to Versailles; in the protologue: circa Versalies), Mar. 1860, parasitizing the *Cytospora* state of *Valsa salicis* (as *Cytospora fagaci* (Bull.), *salicicola*) on *Salix alba* (PC 0706651); donated by L.R. Tulasne to PC in 1873. Another specimen extant in PC (PC 0706650) was collected in 1892, i.e., after its first description. The material of the holotype contains numerous effete *Cytospora* pseudostromata in bark and only few are infected by the *Fenestella* with small pustules containing c. 1–4 ascomata. *Lectotype* of *Fenestella macrospora*, here designated: GERMANY, Hessen, Oestrich-Winkel, Reichartshausen, on twigs of *Corylus avellana*, L. Fuckel (G 00127659, from Herbar Barbey-Boissier, Herbar Fuckel 1894; distributed as Fungi Rhenani 2328; MBT385684). *Epitype* of *Fenestella media* and *F. macrospora*, here designated: AUSTRIA, Kärnten, St. Margareten im Rosental, shrubs between the village and Stariwald, grid square 9452/4, on *Cytospora* sp. on *Corylus avellana*, soc. *Fenestella subsymmetrica*, 10 Jan. 2011, W. Jaklitsch (WU 31641; MBT385685, MBT385686; ex-epitype culture CBS 144860 = FP).

*Pseudostromatic pustules* 0.6–3.6 mm diam or long, with circular, elliptic or oblong outline, lenticular, subglobose or pulvinate, erumpent from bark and projecting to c. 0.6 mm, sometimes confluent to rows of up to 10 mm, often compact; surface convex, plane or with sunken centre, typically with a brittle, pale brown, less commonly yellow- or dark brown disc or crust due to condensed subiculum. *Ascomata* (330–)450–665(–780)  $\mu\text{m}$  ( $n = 40$ ) diam, globose, subglobose to pyriform or distorted by mutual pressure, loosely or densely aggregated in one or two layers, connected by subiculum, also solitary on conidiomata or ascomata of the *Cytospora* host. *Subiculum* dense or scant, present at bases, sides and/or surface of ascomata, consisting of hyaline to dark brown, thick-walled, c. 2.5–6  $\mu\text{m}$  wide hyphae merging into pseudoparenchyma of the outer peridium. *Ostioles* (90–)110–210(–270)  $\mu\text{m}$  ( $n = 47$ ) diam, indistinct at the surface, sometimes discoid or papillate with plane or convex top and more or less circular outline, dark brown to black, often only visible upon injury showing the whitish interior; sometimes mixed with ostioles of the host. *Peridium* 20–90(–120)  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of a dark brown narrow outer and a highly variable glassy hyaline inner layer, the latter often thickened in upper regions particularly when young; cells more or less isodiametric, thick-walled, (4.5–)6–12(–19)  $\mu\text{m}$  ( $n = 110$ ) diam; outermost layer darkening in 3% KOH. *Hamathecium* consisting of often rather sparse, 1.5–2.5(–3)  $\mu\text{m}$  wide, branched and anastomosing ?paraphyses. *Asci* (185–)207–294(–328)  $\times$  (18–)21–26.5(–28)  $\mu\text{m}$  ( $n = 32$ ), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a usually short stipe and simple or knob-like base, containing 8 ascospores in (obliquely) uniseriate, sometimes partly biseriolate arrangement. *Ascospores* (30–)34.5–43.5(–53.5)  $\times$  (12–)14–18(–21)  $\mu\text{m}$ , l/w (1.9–)2.2–2.7(–3.3) ( $n = 304$ ), ellipsoid or broadly fusoid, thick-walled, first hyaline to yellowish with 1–5 transverse septa, asymmetric with submedian primary septum, developing additional septa, turning yellowish brown, when mature with often indistinct, 11–18 transverse and 3–6(–7) longitudinal septa, yellow- to golden brown when fresh, medium to dark brown when dried; surface verruculose; often upper part wider than lower; terminal cells concolorous or hyaline, often narrowed and projecting as 1–2  $\mu\text{m}$  long apiculi, becoming longer (3–4  $\mu\text{m}$ ) when old; germinating from apiculi;



**Fig. 5** *Fenestella media*. a–m1. Sexual morph. a–c. Pseudostromatic pustules in face view (obliquely sectioned to expose ascomata in c); d–e. ascomata in vertical section (e. above peripheral *Cytospora* (*Valsa*) ascomata); f–h. peridium in vertical section; i. subicular hyphae; j–l. asci (j–k. young); m. apex of young ascus; n. section of hamathecium; o–m1. ascospores (o–u. initial and young stages; v–x. from fresh material; g1. germinating); n1–o1. asexual morph from CMD at 22 °C; n1. pycnidia; o1. conidia (f–g, j1–m1 in 3 % KOH). a, j, n, q. WU 36970 (FCO); b, h1. WU 36972 (FP3); c, f, i, l, s, e1, j1. lectotype of *F. macrospora* (G 00127659); d, v, w, c1, i1, k1, l1, n1, o1. WU 31641/CBS 144860 (FP); e, z, d1, g1. WU 36967; g, o, t, f1. holotype of *F. media* (PC 0706651); h, p. WU 15513; k, m, u. WU 36974 (FP10); r, m1. WU 36971 (FP1); x. WU 36973 (FP7); y. WU15069; a1. WU 36969; b1. WU 36968. — Scale bars: a–c = 500 µm; d–e = 300 µm; f–i = 20 µm; j–l = 25 µm; m–m1 = 10 µm; n1 = 100 µm; o1 = 5 µm.

in 3 % KOH ascospores turning olivaceous when young and dark to blackish brown when mature, apiculi remaining hyaline.

Culture characteristics and asexual morph in culture — Ascospores germinating simultaneously from many cells. *Colony radius* on CMD at 22 °C in the dark 23 mm after 4 wk; *colony* thick, dense, aerial hyphae forming dense white to pale grey mat on pale brown mycelium, sometimes turning citrine and citrine pigment diffusing into agar, centre turning black by crowded pycnidia amassing from 4 days, eventually entire colony brown, reverse grey, slightly zonate; odour indistinct. On MEA colony soon turning brown, numerous pycnidia formed. *Pycnidia* when formed usually covered by aerial hyphae, 120–210 µm diam, more or less globose, greyish brown to black, discrete, crowded, later fusing and forming clusters or irregular stromatic masses. *Conidia* forming whitish to brown turbid drops, (2.2–)3–4(–4.6) × (1–)1.3–1.6(–2) µm, l/w (1.4–)1.8–2.8(–3.9) µm (n = 70), oblong to narrowly ellipsoid, hyaline, 1-(rarely 2-)celled, smooth, with 1–2 subapical guttules.

Habitat — On *Cytospora* spp. (sexual and asexual morphs) on various deciduous trees and shrubs, particularly common on *Corylus avellana*.

Distribution — Europe, possibly North America; locally common in winter.

*Other materials examined* (all on *Cytospora* spp. on corticated twigs and branches): AUSTRIA, Kärnten, St. Margareten im Rosental, shrubs between the village and Stariwald, grid square 9452/4, on *Corylus avellana*, partly overgrown by *Exidia* sp., 24 Feb. 1992, W. Jaklitsch (WU 15069); *ibid.*, on stem of *Rubus idaeus*, soc. ?*Neocucurbitaria* sp. (possibly on *Apioporthes vepris*), 31 Dec. 1994, W. Jaklitsch W.J. 412 (WU 36965); *ibid.*, on *Corylus avellana*, 31 Dec. 1994, W. Jaklitsch W.J. 413 (WU 36966); *ibid.*, on *Corylus avellana*, 7 Jan. 1994, W. Jaklitsch (WU 15513); *ibid.*, on *Corylus avellana*, 24 Oct. 1993, W. Jaklitsch (WU 15786); *ibid.*, on *Acer pseudoplatanus*, soc. *Thyridaria* sp. s.lat., 28 Dec. 2013, W. Jaklitsch (WU 36972; culture FP3); St. Margareten im Rosental, Gupf, grid square 9452/4, on *Corylus avellana*, soc. *Massarina* s.lat., 15 Apr. 1995, W. Jaklitsch W.J. 564 (WU 36967); Gupf, grid square 9452/2, on *Corylus avellana*, soc. *Fenestella subsymmetrica*, 8 Nov. 2013, W. Jaklitsch (WU 36971; culture FP1); Niederösterreich, Maissau, grid square 7460/2, on *Corylus avellana*, 26 Oct. 1995, W. Jaklitsch W.J. 764 (WU 36968); Mauerbach, close to the cemetery, grid square 7763/1, on *Carpinus betulus*, 28 Sept. 1996, W. Jaklitsch W.J. 964 (WU 36969); Oberösterreich, Schärding, Raab, Rothmayrberg, grid square 7648/1, on *Corylus avellana*, mostly immature, 5 Sept. 2009, H. Voglmayr (WU 32630); Wetzlbach, on *Tilia cordata*, 13 Aug. 2017, H. Voglmayr (WU 36971; culture FP10); Steiermark, Steinberg, on *Castanea sativa*, 3 Nov. 2015, H. Voglmayr & W. Jaklitsch (WU 36970; culture FP7). — CROATIA, Istrija, NE Pula, near Krnica, on *Carpinus orientalis*, 25 Sept. 2010, H. Voglmayr (WU 36970; culture FCO).

Notes — This is one of three cryptic species difficult to identify morphologically. Characteristic for *F. media* is the asymmetric ascospore septation. See also notes under *F. subsymmetrica* and *F. viburni*. As the fungus is not specific for the plant host, we use a specimen on *Corylus* for epitypification. Fructifications of *F. media* can be found particularly in winter, after the *Cytospora* has become old. Size and development of pseudostromata vary considerably. The largest pseudostromata occur on *Corylus* and may be locally very common. In contrast to Barr (1990), who considered *F. macrospora* as a synonym of *F. fenestrata* (as *F. princeps*), *F. macrospora* is clearly a synonym of *F. media*. Nonetheless, morphological identification of some older, non-cultured and non-sequenced specimens here included under examined specimens is not always easy and therefore at least in part, tentative.

***Fenestella parafenestrata* Jaklitsch & Voglmayr, sp. nov.** — MycoBank MB829744; Fig. 6

*Etymology.* Referring to the close relationship with *Fenestella fenestrata*.

*Holotype.* AUSTRIA, Oberösterreich, Raab, Wetzlbach, on *Cytospora* (*Valsa*) sp. on a branch of *Quercus robur*, 24 Feb. 2018, H. Voglmayr (WU 36988; ex-type culture CBS 144856 = C306).

*Ascomata* (420–)460–610(–690) µm (n = 15) diam, globose, subglobose to pyriform, immersed in and erumpent from bark, solitary or in small groups of usually less than 10 individuals forming pustules 0.5–2.2 mm diam on and connected by subiculum on or associated with conidiomata or ascomata of *Cytospora* (*Valsa*) sp. in the ostiolar region of the latter. Pustule surface brownish by compacted subiculum or blackened by spore deposits. *Ostiolar areas* 90–240(–270) µm diam, dark brown, flat or convex disc-like or irregular, sometimes slightly papillate. *Subiculum* consisting of thick-walled, hyaline to greyish or dark brown, 2–7 µm wide hyphae merging with the outer peridial layer. *Peridium* 20–75 µm thick, pseudoparenchymatous, consisting of (5–)7.5–14(–16.5) µm (n = 37) wide cells, dark brown, gradually paler toward the interior, at the ostiole to 100 µm wide and paler with (sub-)hyaline cells toward the interior; inside compressed brownish cells present. *Hamathecium* consisting of numerous richly branched, 1–3 µm wide paraphyses. *Asci* (216–)241–320(–342) × (21–)23–27(–28) µm (n = 20), cylindrical, bitunicate, fissitunicate, with an ocular chamber, a usually short stipe and simple or knob-like base, containing 6–8 ascospores in (obliquely) uniseriate arrangement; unstable in water; biseriate rearrangement and long stipes generated by pressure. *Ascospores* (32–)41.5–52.5(–61) × (13–)15–19(–23) µm, l/w (2.1–)2.4–3.1(–3.6) (n = 100), ellipsoid with upper part usually broader than lower, constricted at the median to submedian primary septum, thick-walled, hyaline to yellowish and with 3–5(–8) transverse septa and 1 longitudinal septum when young, turning yellow-brown to dark brown and with 11–16(–20) transverse and 2–4 longitudinal septa; terminal cells concolorous or hyaline at the tips and often with 1–4 µm long acute apiculi; smooth, containing minute guttules; in 3 % KOH mature spores turning blackish brown. *Pycnidia* of the presumed asexual morph sometimes associated with ascomata on the natural host.

Culture characteristics and asexual morph in culture — *Colony radius* on CMD at 22 °C in the dark 8 mm after 1 wk, 26 mm after 4 wk; *colony* thick, dense, slightly zonate, white, turning cream to pale brownish, releasing bright yellow pigment diffusing into surrounding agar, centre turning olivaceous to dark brown due to pycnidia, surface velvety by a white to pale greyish or brownish mat of aerial hyphae; reverse yellow-brown, dark brown in the centre; odour indistinct to pleasant or leathery. *Pycnidia* appearing after 4 d below white aerial hyphae, (90–)150–330 µm diam, globose, black, first hyaline to greenish, turning olivaceous and eventually black, surrounded by brown hyphal appendages, numerous, tightly aggregated and fusing into stromatic masses to c. 2 mm diam with many ostioles releasing conidia as turbid whitish to olivaceous drops; peridium thin, pseudoparenchymatous. *Phialides* (4–)4.5–6.3(–6.6) × (1.8–)2–3.5(–4) µm (n = 12), sessile, subglobose to ampulliform to conical. *Conidia* (2.5–)3–4(–4.7) × (1–)1.1–1.5(–2) µm, l/w (1.9–)2.4–3.2(–3.9) (n = 65), cylindrical, oblong to suballantoid or narrowly ellipsoid, smooth, with 1–2 subterminal guttules.

Habitat — On *Cytospora* (*Valsa*) spp. on deciduous trees, confirmed for *Quercus* and *Salix*.

Distribution — Europe.

*Other specimens examined.* AUSTRIA, Burgenland, Mattersburg, Staremühl / Rosaliengebirge, on *Cytospora* (*Valsa*) sp. on attached twig of *Quercus petraea*, 1 Oct. 2001, W. Jaklitsch W.J. 1815 (WU 36990); Oberösterreich, Raab, Wetzlbach, on *Cytospora* (*Valsa*) sp. on a branch of *Salix* sp., 31 Mar. 2018, H. Voglmayr (WU 36989; culture C317).

Notes — This species is morphologically intermediate between *F. fenestrata* and the cryptic species *F. media*, *F. subsymmetrica* and *F. viburni*. See also notes under *F. fenestrata*.



**Fig. 6** *Fenestella parafenestrata*. a–w. Sexual morph. a–c. Ascomatal groups connected by subiculum erumpent through bark fissures in face view; d. peridium in vertical section; e–g. asci (e. young, from fresh material); h–i. ascus apices (immature in h); j–w. ascospores (j–k. young; j, l–o. from fresh material); x–a1. asexual morph from CMD at 22 °C; x. pycnidia; y. phialides and conidia; z–a1. conidia; b1. ascospore of *Fenestella* cf. *fenestrata* K(M) 233193 (t, v. in 3 % KOH). a–b, d–j, l–m, p–t, v, x, a1. WU 36988/CBS 144856 (C306); c, n–o, y–z. WU 36989 (C317); k, u, w. WU 36990. — Scale bars: a = 300 µm; b–c = 500 µm; d, h–w, y, b1 = 10 µm; e–g = 30 µm; x = 200 µm; z–a1 = 5 µm.

***Fenestella subsymetrica*** Jaklitsch & Voglmayr, *sp. nov.* —  
Mycobank MB829745; Fig. 7

*Etymology.* Referring to the nearly symmetric shape of ascospores due to the submedian to median insertion of the primary septum.

*Holotype.* AUSTRIA, Vienna, 21st district, at Marchfeldkanalweg near Felix Slavikstraße, on/soc. *Cytospora* holomorph on *Acer campestre*, soc. *Diplodia* sp., *Fusarium* sp., 8 Nov. 2015, W. Jaklitsch (WU 36979; ex-type culture CBS 144861 = FP6).

*Pseudostromatic pustules* 0.7–3.4 mm wide or long, with circular, elliptic or oblong outline, subglobose or pulvinate, erumpent from bark, sometimes confluent; surface usually ill-defined and irregular, convex, plane or with sunken centre, often partly covered by bark fibres or brownish condensed subiculum, pale brown to nearly black. *Ascomata* (300–)370–600(–765)  $\mu\text{m}$  (n = 49) diam, subglobose to pyriform or distorted by mutual pressure, often obliquely oriented and convergent toward the



**Fig. 7** *Fenestella subsymetrica*. a–z. Sexual morph. a. Pseudostromatic pustule in face view; b–c. ascomata in vertical section (b. above *Cytospora* (*Valsa*) ascomata); d. peridium with subicular hyphae in vertical section; e, i–k. ascus apices (e. immature; i. from fresh material); f–h. asci (f. immature; g. from fresh material); l–z. ascospores (l–n. initial and young stages; o. from fresh material); a1–e1. asexual morph from CMD at 22 °C; a1. pycnidia; b1. phialides; c1–e1. conidia (e–f, h, j–k, n, z. in 3 % KOH). a, c, o, y. WU 36978 (FP4); b, d–f, h, j, k, m–n, u, x, z–e1. WU 36979/CBS 144861 (FP6); g, i, p, s–t. WU 36975; l, r, v. WU 36977 (C286); q. WU 36976 (C285); w. WU 36980 (FP8). — Scale bars: a–b = 500  $\mu\text{m}$ ; c, a1 = 200  $\mu\text{m}$ ; d, f–h = 25  $\mu\text{m}$ ; e, i–k, n–z = 10  $\mu\text{m}$ ; l–m, b1 = 5  $\mu\text{m}$ ; c1–e1 = 3  $\mu\text{m}$ .

pustule centre, loosely or densely aggregated in valsoid or ill-defined groups of up to c. 20 individuals on and connected by subiculum, sometimes fusing laterally, also solitary on conidiomata or ascomata of the *Cytospora* host in its ostiolar region. *Subiculum* present at bases, sides and/or surface of ascomata, consisting of mostly pale brown, thick-walled, 2.5–6(–7)  $\mu\text{m}$  wide hyphae. *Ostiolar areas* (75–)85–163(–180)  $\mu\text{m}$  ( $n = 10$ ) diam, ill-defined, irregular, often only visible by spore deposits, sometimes roundish and slightly projecting, black. *Peridium* 20–80(–90)  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of a dark brown narrow outer and a glassy pale brownish to hyaline inner layer, the latter often thickened in upper regions particularly when young; cells more or less isodiametric, thick-walled, (3.5–)5.5–11(–15)  $\mu\text{m}$  ( $n = 82$ ) diam; in 3 % KOH outermost layer turning blackish brown. Innermost part of the inner layer often slightly darker and of distinctly compressed elongate cells. *Hamathecium* consisting of numerous 1–3  $\mu\text{m}$  wide, branched and anastomosing ?paraphyses. *Asci* (182–)207–302(–345)  $\times$  (19–)21.5–25.5(–26.5)  $\mu\text{m}$  ( $n = 32$ ), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a usually short stipe and simple or knob-like base, containing 4–8 ascospores in (obliquely) uniseriate, sometimes partly biserial arrangement. *Ascospores* (28–)34.5–44.5(–54.5)  $\times$  (13–)15.5–19.5(–24.5)  $\mu\text{m}$ , l/w (1.8–)2–2.5(–2.9) ( $n = 201$ ), broadly ellipsoid, oblong or broadly fusoid, thick-walled, first hyaline to yellowish with 1–4 transverse septa, asymmetric to subsymmetric, with submedian to median primary septum, developing additional septa, turning pale brown to olivaceous, when mature with distinct, 11–16(–18) transverse and 3–6 longitudinal septa and yellow- to golden brown when fresh, dark brown when dried; surface verruculose; often upper part wider than lower; terminal cells concolorous or hyaline, often narrowed and projecting as 1–2  $\mu\text{m}$  long apiculi, becoming longer (3–5  $\mu\text{m}$ ) when old; germinating from apiculi; in 3 % KOH ascospores turning olivaceous when young and dark to blackish brown when mature, apiculi remaining hyaline.

Culture characteristics and asexual morph in culture — Ascospores germinating simultaneously from many cells. *Colony radius* on CMD at 22 °C in the dark 6 mm after 1 wk, c. 20 mm after 3–4 wk; *colony* white, centre turning black by pycnidia after 4 d, soon entire colony turning grey, brownish grey to olivaceous, margin often hyaline to white, covered by a white to pale grey mat of aerial hyphae; odour indistinct; no diffusing pigment formed. *Pycnidia* 120–240  $\mu\text{m}$  diam, more or less globose, first hyaline to greenish, turning green to black, numerous, often concentrically and very densely arranged, spreading over entire colony or remaining in the centre; often covered by mats of aerial hyphae; conidia amassing in whitish to greenish turbid drops. *Phialides* 4.5–8  $\times$  2–4  $\mu\text{m}$ , lageniform to subglobose with a long neck. *Conidia* (3.2–)3.5–4.2(–4.5)  $\times$  (1.1–)1.3–2(–2.3)  $\mu\text{m}$ , l/w (1.7–)1.9–3(–3.7) ( $n = 30$ ), cylindrical, oblong to ellipsoid, 1-celled, hyaline, with 1–3 drops, smooth.

Habitat — On *Cytospora* spp. (sexual and asexual morphs) on various deciduous trees and shrubs.

Distribution — Europe, possibly North America; locally common in winter; sometimes co-occurring with *F. media*.

*Other materials examined* (all on or in pseudostromata of *Cytospora* spp. including their *Valsa* sexual morphs): AUSTRIA, Kärnten, St. Margareten im Rosental, Aussicht, grid square 9452/3, on branch of *Corylus avellana*, on *Valsa* morph, soc. *Parafenestella* sp., 8 Jan. 1994, W. Jaklitsch W.J. 91 (WU 15613); Gupf, grid square 9452/2, on *Corylus avellana*, soc. *Fenestella media*, 8 Nov. 2013, W. Jaklitsch (WU 36975; part of WU 36971); Niederösterreich, Bad Vöslau, Grossau, near Haidlhof, on old *Cytospora* holomorph on *Salix caprea*, 22 Feb. 2016, W. Jaklitsch & H. Voglmayr (WU 36980; culture FP8); Oberösterreich, Schärding, Raab, between Riedlhof and Großrotmayr, grid square 7647/2, on branch of *Corylus avellana*, 18 Mar. 2015, H. Voglmayr (WU 36978; culture FP4); Vienna, 22nd district, at AGES, Spargelfeldstraße 191, on *Valsa* morph on cut branches of *Juglans regia*; soc. *Diaporthe* sp., 25 Jan. 2017, R. Moosbeckhofer (WU 36976; culture C285); *ibid.*, other tree of

*Juglans regia*, 25 Jan. 2017, R. Moosbeckhofer (WU 36977; cultures C286, C286x).

Notes — *Fenestella subsymetrica* is hardly distinguishable from *F. media* by morphology alone. Ascospores of *F. subsymetrica* often tend to appear broader, with more distinct septa and a more median primary septum. However, individual specimens pose serious problems in morphological identification. For example, culture C286x derived from distinctly asymmetric ascospores of WU 36977 yielded ITS and LSU sequences, which are identical with those derived from symmetric ascospores. In cultures on CMD no pigment is formed. Mature asci are very unstable in water, therefore they were mostly measured and illustrated in 3 % KOH.

***Fenestella viburni* Jaklitsch & Voglmayr, sp. nov.** — MycoBank MB829746; Fig. 8

*Etymology.* Owing to its occurrence on *Viburnum* spp.

*Holotype.* AUSTRIA, Niederösterreich, Wr. Neustadt, Markt Piesting, on the Hart N Piesting, grid square 8162/2, elev. 500 m, on *Cytospora (Leucostoma)* sp. on *Viburnum lantana*, 12 Oct. 2014, H. Voglmayr (WU 36982; ex-type culture CBS 144863 = FVL).

*Ascomata* (330–)390–600(–720)  $\mu\text{m}$  ( $n = 21$ ) diam, subglobose to subpyriform, immersed singly or in small groups in the ostiolar region above ascomata or in conidiomata of *Cytospora (Leucostoma)* sp., less commonly forming pulvinate *pseudostromatic pustules* 0.7–2.5 mm diam with circular or oblong outline, in loose association with the fungal host, erumpent from bark. *Subiculum* individually surrounding ascomata and connecting them, consisting of thick-walled, pale to dark brown, 2–6  $\mu\text{m}$  wide hyphae, sometimes condensed to brown crusts between ascomata. *Ascomatal apices* obtuse, brown, mostly 90–180  $\mu\text{m}$  diam; *ostioles* 70–150  $\mu\text{m}$  diam, usually inconspicuous, rarely papillate, black, sometimes whitish. *Peridium* 20–60  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of a dark brown narrow outer and a glassy pale brownish to hyaline inner layer; cells more or less isodiametric, thick-walled, (5–)7–13.5(–17)  $\mu\text{m}$  ( $n = 40$ ) diam; innermost part of the inner layer of distinctly compressed brownish cells. *Hamathecium* consisting of numerous, 1–3  $\mu\text{m}$  wide, branched and anastomosing ?paraphyses. *Asci* (247–)258–295(–312)  $\times$  (19–)22–26(–29)  $\mu\text{m}$  ( $n = 34$ ), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a usually short stipe and simple or knob-like base, containing 8 ascospores in uniseriate arrangement. *Ascospores* (29–)38–46(–49.5)  $\times$  (12.5–)15–18(–22)  $\mu\text{m}$ , l/w (2–)2.3–2.8(–3.1) ( $n = 193$ ), ellipsoid or fusoid, sometimes distinctly pointed at the ends, asymmetric to subsymmetric, with submedian to median primary septum, first hyaline to yellowish, turning olivaceous, when mature yellow- to golden brown when fresh, dark brown when dried, with distinct 11–16 transverse and 3–6 longitudinal septa; surface verruculose; upper part often slightly wider than lower; terminal cells concolorous or terminally hyaline and projecting as minute, 1–2  $\mu\text{m}$  long apiculi, becoming slightly longer when old; in 3 % KOH ascospores turning olivaceous when young and darker to blackish brown when mature, apiculi remaining hyaline.

Culture characteristics and asexual morph in culture — Ascospores germinating simultaneously from many cells. *Colony radius* on CMD at 22 °C in the dark 4 mm after 1 wk, 22 mm after 4 wk; *colony* thick, dense, white, turning grey or olivaceous grey with white margin, velvety by a dense whitish to greyish mat of aerial hyphae; odour indistinct. *Pycnidia* appearing after 5 d, globose, 90–250  $\mu\text{m}$  diam, first hyaline to olivaceous, turning black, immersed to superficial, tightly aggregated or fusing in large numbers around the inoculation plug or spreading over the colony, often covered by aerial hyphae, releasing conidia in whitish turbid drops through ostioles lined by clavate

hyaline marginal cells; peridium thin, pseudoparenchymatous, consisting of thin-walled cells (4.5–)6.5–11(–14)  $\mu\text{m}$  ( $n = 30$ ) diam. *Phialides* (3.8–)4.8–7.5(–8.2)  $\times$  (1.7–)2.5–4(–4.2)  $\mu\text{m}$  ( $n = 10$ ), crowded, lageniform to subglobose with long neck or subulate. *Conidia* (3.3–)3.5–5(–6.3)  $\times$  (1.4–)1.7–2.3(–2.7)  $\mu\text{m}$ , l/w (1.6–)1.9–2.5(–3) ( $n = 32$ ), cylindrical, oblong to ellipsoid, sometimes pinched, 1-celled, hyaline, with 2 subterminal drops, smooth.

Habitat — On *Cytospora* spp. (both morphs; sexual morph of the *Leucostoma* type) on *Viburnum* spp.

Distribution — Europe.

*Other materials examined.* AUSTRIA, Kärnten, St. Margareten im Rosental, Aussicht, grid square 9452/3, on *Viburnum lantana*, 8 Jan. 1994, W. Jaklitsch (WU 15341); shrubs between the village and Stariwald, grid square 9452/4, on *Cytospora* sp. on *Viburnum opulus*, 24 Dec. 1995, W. Jaklitsch W.J. 814 (WU 36982); Stariwald, grid square 9452/4, on *Cytospora* sp. on *Viburnum lantana*, 10 Jan. 1995, W. Jaklitsch W.J. 454 (WU 36981). — FRANCE, Aude, Belcaire, chemin du Traouc, elev. 1050 m, on *Cytospora* (*Leucostoma*) sp. on

*Viburnum lantana*, 25 Oct. 2013, J. Fournier J.F.13212 (WU 36981; culture FP2).

Notes — *Fenestella viburni* is one of three cryptic species, morphologically most closely related to *F. subsymmetrica*, but difficult to differentiate. In individual specimens ascospores tend to be distinctly pointed terminally. Formation of pseudostromatic pustules is less pronounced and asci are more stable in water than with *F. media* and *F. subsymmetrica*. Pustules are difficult to assess, as they are usually produced basically by its *Leucostoma* host. Older, not sequenced specimens from *Viburnum* spp. are added tentatively to the list above.

***Neocucurbitaria*** Wanas. et al., Mycosphere 8: 408. 2017, emended by Jaklitsch & Voglmayr in Jaklitsch et al. (2018)

*Type species.* *Neocucurbitaria unguis-hominis* (Punith. & M.P. English) Wanas. et al.



**Fig. 8** *Fenestella viburni*. a–q. Sexual morph. a. Ascomata in face view (inserted right and left in a *Cytospora* (*Leucostoma*) pseudostroma); b. ascomata above *Cytospora* (*Leucostoma*) ascomata in vertical section; c. peridium in vertical section; d–e. ascus apices; f–h. asci (f–g. from fresh material); i–q. ascospores (i–l. from fresh material; m. young); r–u. asexual morph from CMD at 22 °C; r. pycnidia and conidial drops; s. peridium in surface view; t–u. conidia. a, e, h, m, o, q. WU 36983 (FP2); b–c, f–g, i–l, r–u. WU 36984/CBS 144863 (FVL); d, n. WU 36982; p. WU 15341. — Scale bars: a–b, r = 300  $\mu\text{m}$ ; c–e, i–q = 10  $\mu\text{m}$ ; f–h = 25  $\mu\text{m}$ ; s = 15  $\mu\text{m}$ ; t–u = 3  $\mu\text{m}$ .



Notes — *Neocucurbitaria juglandicola* is not host-specific, as it has been recently collected on *Quercus rubra*, too. Cultured and sequenced material: Austria, Oberösterreich, St. Willibald, Große Sallet, on a branch of *Quercus rubra*, 30 Mar. 2018, H. Voglmayr (WU 36984; culture C316).

***Neocucurbitaria subcaespitosa*** (G.H. Otth) Jaklitsch & Voglmayr, *comb. nov.* — MycoBank MB829747; Fig. 9

*Basionym.* *Cucurbitaria subcaespitosa* G.H. Otth, Mitth. Naturf. Ges. Bern 711–744: 103. 1871 ‘1870’.

*Synonym.* *Fenestella subcaespitosa* (G.H. Otth) M.E. Barr, Ann. Univ. Turku., A II 55: 14. 1974.

*Lectotype*, here designated: SWITZERLAND, near Bern, on twigs of *Sorbus aria*, without date, G.H. Otth (B 700016481; transferred from Münster in 1936; MBT385687). On the label Otth noted that he retained this material as No. 10, a rather bad but perhaps not entirely useless part of No. 90. He might have sent No. 90 to Nitschke for inspection. No additional material is extant in B, but according to R. Berndt (pers. comm.) Otth’s material was transferred from Bern to Z, where a part of the type may be present but is currently not accessible. For this reason we designate B 700016481 as lectotype.

*Ascomata* (300–)354–550(–600) µm (n = 20) diam, more or less globose, immersed-erumpent from bark, loosely aggregated on

subiculum in valsoid groups or in rows or firmly united by greyish or brown subiculum forming pseudostromatic pustules 0.5–2.6 mm diam of various shapes containing up to c. 10 ascospores; ascospores also solitary and glabrous or individually covered by brown, crust-like subiculum. *Ostioles* (60–)95–186(–210) µm (n = 21) diam outside, papillate, or cylindrical and projecting to c. 210 µm, sometimes apically flattened, circular, angular or substellate in section, shiny black, whitish inside when injured. *Asci* cylindrical, bitunicate, containing 8 ascospores in uniseriate arrangement. *Ascospores* (20–)21.5–26(–29.5) × (8–)9–11.5(–14) µm, l/w (1.9–)2.1–2.6(–2.9) (n = 81), ellipsoid, with (4–)5–7(–9) distinct transverse and 1–2 longitudinal septa, distinctly constricted at the median primary septum, less distinctly at other septa, pale brown when immature, dark brown when mature, ends rounded, concolorous, surrounded by a narrow hyaline perispore swelling in KOH to 2 µm.

*Habitat* — On dead partly corticated twigs of *Sorbus aria*.

*Distribution* — Europe.

*Other material examined.* AUSTRIA, Kärnten, St. Margareten im Rosental, Schwarzgupf, grid square 9452/4, on branch of *Sorbus aria*, 25 May 1997, W. Jaklitsch W.J. 1072 (WU 36991).



Fig. 9 *Neocucurbitaria subcaespitosa*. a–e. Ascomata in face view; f–l. ascospores (i–l. in 3% KOH). a, d–e, i–l. WU 36991; b–c, f–h. *Cucurbitaria subcaespitosa* holotype B 700016481. — Scale bars: a–e = 300 µm; f–l = 5 µm.



**Fig. 10** *Parafenestella alpina*. a–r. Sexual morph. a. Ascomata in face view; b. vertical section of young ascoma above the perithecial host and one ascoma in horizontal section; c. vertical section of laterally fused ascomata surrounded by subiculum; d–f. asci; g. peridium of laterally fused ascomata in vertical section; h–i. ascus apices (h. immature); j. paraphysis tip near immature ascus apex; k–r. ascospores (k. young; q, r. aberrant); s–v. asexual morph from CMD at 22 °C; s. pycnidia and conidial drops; t–u. phialides; v. conidia (h, j, o. in 3 % KOH). a–m, p–v. WU 36997/CBS 145263 (C198); n–o. WU 36998 (C249). — Scale bars: a–c, s = 200 µm; d–g = 20 µm; h, j, r = 10 µm; i, k–q, v = 7 µm; t–u = 5 µm.

Notes — In both studied specimens ascomata are over-mature, and only fragments of asci allowing interpretations of ascus shape and ascospore arrangement. Our material was neither cultured nor sequenced, therefore relegation to *Neocucurbitaria* is tentative but strongly suggested by the morphology, particularly based on features of ascomata, ascospores and ostioles (compare Jaklitsch et al. 2018). Barr (1990) incorrectly synonymised this species with *Cucurbitaria sorbi* without having seen type material and anticipated occurrence on several *Sorbus* spp. in Europe and North America. However, *N. subcaespitosa* seems to occur only on *Sorbus aria*.

**Parafenestella** Jaklitsch & Voglmayr, in Jaklitsch et al., Stud. Mycol. 90: 108. 2018

*Type species. Parafenestella pseudoplatani* Jaklitsch & Voglmayr.

**Parafenestella alpina** Jaklitsch & Voglmayr, sp. nov. — MycoBank MB829748; Fig. 10

*Etymology.* For its occurrence in subalpine to alpine regions.

*Holotype.* AUSTRIA, Osttirol, Prägraten am Großvenediger, Wallhorn, Bodenalm, elev. c. 2000 m, on dead attached twigs of *Cotoneaster integerrimus*, soc. *Cytospora* (*Leucostoma* morph) sp., *Discostroma* sp. (in excess), *Mollisia* sp., cf. *Nigrograna* sp., cf. *Teichospora* sp., 18 June 2015, W. Jaklitsch & H. Voglmayr (WU 36997; ex-type culture CBS 145263 = C198).

*Ascomata* (180–)240–375(–450)  $\mu\text{m}$  ( $n = 22$ ) diam, globose, subglobose or pyriform, usually tightly aggregated in bark on a perithecial host fungus in small numbers and connected by subhyaline to dark brown, thick-walled, 2–5  $\mu\text{m}$  wide subicular hyphae, dark brown to black; tightly packed ascomata sometimes covered by a brown to black, densely packed mesh of subicular hyphae and ejected ascospores. *Ostiolar areas* (53–)60–105(–135)  $\mu\text{m}$  ( $n = 12$ ) diam, slightly papillate, rounded, black. *Peridium* 15–70  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of isodiametric cells (4–)5–9.5(–12)  $\mu\text{m}$  ( $n = 30$ ) diam, outside moderately thick-walled and dark brown, paler to hyaline in upper regions and thinner-walled to the inside; confluent with tightly appressed ascomata. *Hamathecium* consisting of numerous 0.5–1  $\mu\text{m}$  (to 2.5  $\mu\text{m}$  in 3 % KOH) wide, branched paraphyses with free ends. *Asci* (143–)170–208(–227)  $\times$  (18–)18.5–21.5(–24.5)  $\mu\text{m}$  ( $n = 25$ ), cylindrical to oblong, bitunicate, fissitunicate, with a truncate ocular chamber, a short stipe and simple or knob-like base, containing 6–8 ascospores in uniseriate arrangement. *Ascospores* (19–)24–30.5(–35)  $\times$  (10.5–)12–14(–15.5)  $\mu\text{m}$ , l/w (1.4–)1.8–2.4(–2.9) ( $n = 73$ ), typically ellipsoid to fusoid, often inequilateral, very variable in shape and size, from subglobose to clavate or lower part elongated fusoid, first with 1–5 main septa, constricted at the more or less median primary septum, developing (7–)8–12(–15) transverse and (2–)3–4 longitudinal septa, with upper part often broader, first hyaline to yellowish, turning medium to dark brown, blackish brown when old; ends concolorous; in 3 % KOH turning pale olivaceous when young and dark to blackish brown when mature or old.

Culture characteristics and asexual morph in culture — Ascospores germinating simultaneously from many cells. *Colony radius* on CMD at 22 °C in the dark 8 mm after 1 wk, 25 mm after 3 wk, 38 mm after 5 wk; *colony* dark grey to olivaceous, centre darker; aerial hyphae long, white, forming an initially loose later dense mesh above the colony; odour indistinct. *Pycnidia* 75–170  $\mu\text{m}$  diam, (sub-)globose, papillate with a pale opening, numerous, first appearing after 3 d, hyaline, turning greenish, olivaceous to black, mostly immersed, partially erumpent, solitary and in firm packs, spreading from the centre; conidia emitted as whitish turbid drops. *Peridium* thin, pseudoparenchymatous, olivaceous, surrounded by subhyaline

submoniliform hyphae. *Phialides* 4.8–7.5(–9.3)  $\times$  2–3.5(–4.4)  $\mu\text{m}$  ( $n = 14$ ), sessile, varying from subglobose over ampulliform and lageniform to subulate. *Conidia* (3.4–)3.7–4.3(–4.6)  $\times$  (1–)1.1–1.4(–1.5)  $\mu\text{m}$ , l/w (2.6–)2.9–3.7(–3.9) ( $n = 24$ ), cylindrical to allantoid, less commonly narrowly ellipsoid, 1-celled, hyaline with 2 small drops, smooth.

Habitat — On perithecial fungi on *Cotoneaster integerrimus* and *Salix appendiculata*.

Distribution — Central Europe (Austria).

*Other materials examined.* AUSTRIA, Steiermark, Deutschlandsberg, Korralpe, at the parking place of the walking path to the Grünanger- and Bärenstalhütte; N46°49'44" E15°00'56", elev. c. 1540 m; on dead attached twigs of *Salix appendiculata*, soc. effete *Plagiostoma* sp., *Plenodomus hendersoniae* (in excess), 6 May 2016, G. Friebe (WU 36998; culture C249).

Notes — Due to the rough climate in (sub)alpine regions, asci and ascospores are often aberrantly developed. The fungal host of *P. alpina* may be *Cytospora*, but due to the many other fungi that are present on the specimens, this is uncertain.

**Parafenestella austriaca** Jaklitsch & Voglmayr, sp. nov. — MycoBank MB829749; Fig. 11

*Etymology.* For its occurrence in Austria.

*Holotype.* AUSTRIA, Oberösterreich, Schärding, St. Willibald, Geitzedt, grid square 7648/1, on branch of *Rosa canina*, 19 Mar. 2015, H. Voglmayr (WU 37014; ex-type culture CBS 145262 = C152).

*Ascomata* (270–)295–412(–450)  $\mu\text{m}$  ( $n = 10$ ) diam, subglobose to pyriform, immersed-erumpent from bark, scattered or aggregated in small valsoid groups, often on an effete perithecial fungus, laterally collapsing from above, basally and laterally surrounded by subhyaline to dark brown, thick-walled, 2–5  $\mu\text{m}$  wide, smooth to verruculose subicular hyphae turning olivaceous in 3 % KOH. *Ostiolar area* (60–)75–128(–150)  $\mu\text{m}$  ( $n = 17$ ) diam, convex or papillate with rounded opening, black. *Peridium* 15–85  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of isodiametric cells (3.5–)4–10(–14.5)  $\mu\text{m}$  ( $n = 40$ ) diam, outside thick-walled and dark brown, paler to hyaline in upper regions and thinner-walled to the inside; darkening in 3 % KOH. *Hamathecium* consisting of numerous 1–2.5  $\mu\text{m}$  wide, branched ?paraphyses in a gel matrix. *Asci* (150–)159–205(–237)  $\times$  16–19.5(–24.2)  $\mu\text{m}$  ( $n = 33$ ), cylindrical, bitunicate, fissitunicate, with a distinct ocular chamber, a short stipe and simple or knob-like base, containing 4–8 ascospores in uniseriate arrangement. *Ascospores* (25–)27–32.5(–38.2)  $\times$  (12–)13–15(–16.5)  $\mu\text{m}$ , l/w (1.9–)2–2.3(–2.6) ( $n = 87$ ), broadly ellipsoid with usually broadly rounded ends and upper part often wider, constricted at the median or slightly supra- or submedian primary septum, with 9–13(–14) distantly spaced transverse including v-septa in end cells and 3–4(–5) longitudinal septa, first hyaline to yellowish, with 1–3 main septa, turning yellowish brown, finally medium to dark brown or dark reddish brown with concolorous, sometimes paler to hyaline ends; surface appearing verruculose; in 3 % KOH wall appearing smooth, interior containing numerous minute droplets, turning greenish to yellow-green when immature, dark to blackish brown when mature.

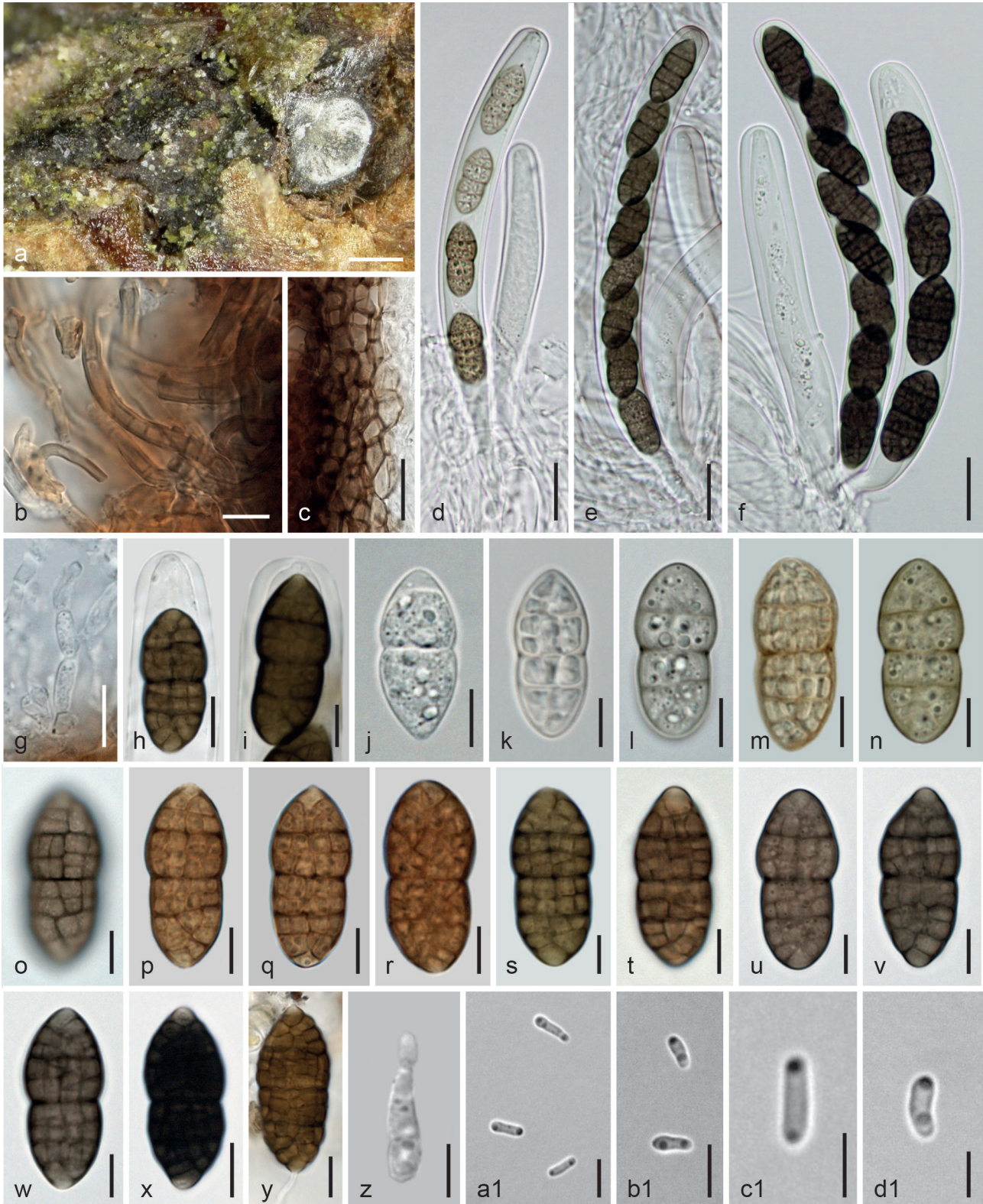
Culture characteristics and asexual morph in culture — *Colony radius* on CMD at 22 °C in the dark 7–8 mm after 1 wk, 16 mm after 2 wk, 26–27 mm after 23 d; *colony* first white, soon turning greyish olivaceous to greyish brown; aerial hyphae forming a dense mesh above the colony hiding pycnidia; reverse dark grey to black; odour indistinct. *Pycnidia* c. 100–200  $\mu\text{m}$  diam, subglobose with papillate to cylindrical ostioles, first appearing after 3 d, hyaline, turning greenish, olivaceous to black, mostly immersed, scattered to densely aggregated, covered by aerial hyphae; conidia emitted as whitish turbid drops.

*Peridium* thin, pseudoparenchymatous, olivaceous. *Phialides* (3.5–)4.2–7(–8.2) × (1.5–)2–3.2(–3.8) μm (n = 16), sessile or formed on short, 1–2 celled conidiophores, varying from subglobose over ampulliform and lageniform to subulate. *Conidia* (3–)3.5–4.2(–5) × 0.9–1.5(–2) μm, l/w (2.1–)2.6–3.7(–4.2) (n = 50), cylindrical to allantoid, less commonly narrowly ellipsoid, 1-celled, hyaline, with 2 small drops, smooth; produced on phialides and pegs. After a few transfers no pycnidia formed.

Habitat — Associated with perithecial fungi on *Rosa canina* and possibly *Crataegus monogyna*.

Distribution — Central Europe (Austria).

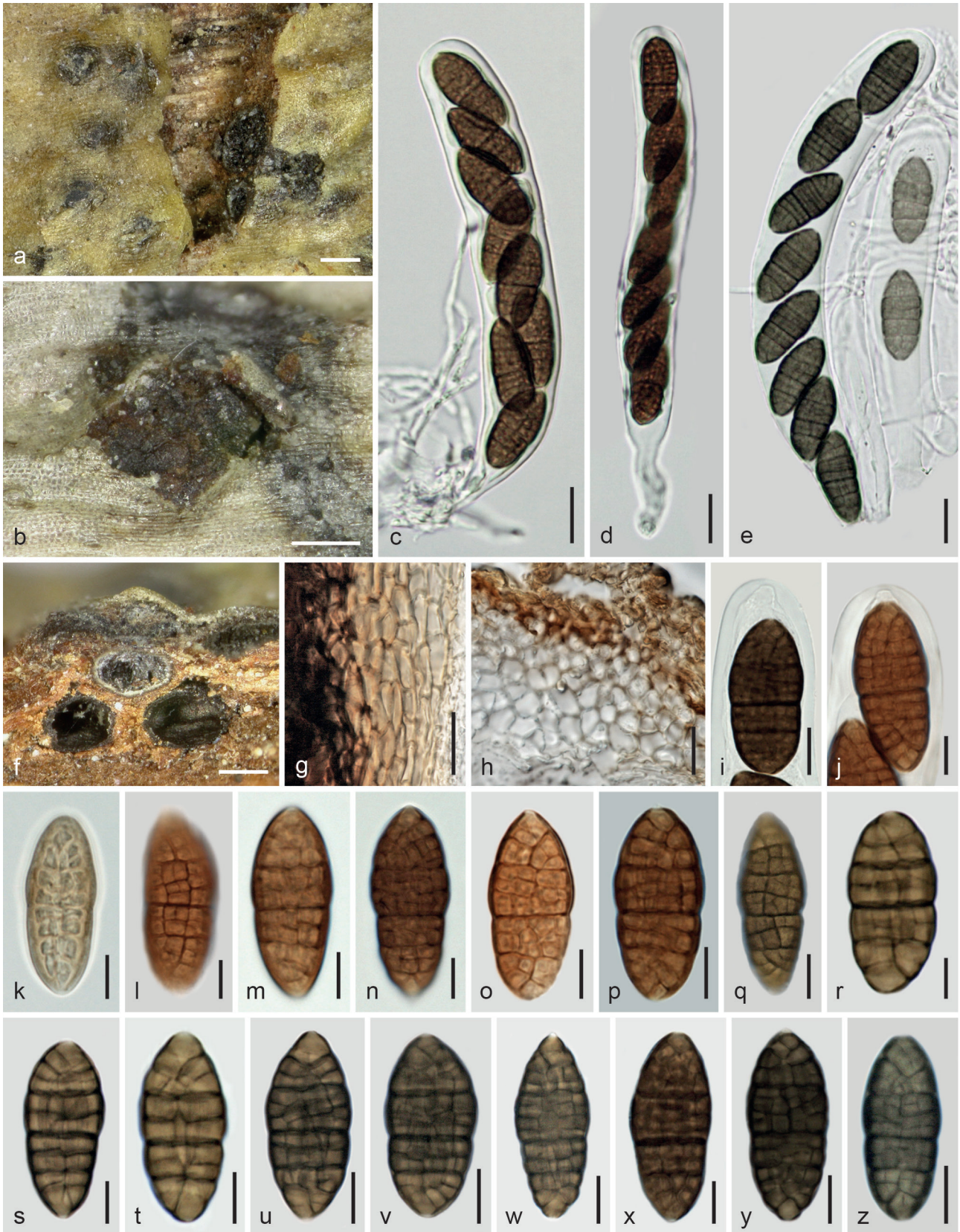
Notes — Von Niessl's Austrian collection from *Crataegus* in Rosenthal bei Hütteldorf, Vienna (M-0281852; as *Cucurbitaria crataegi* Niessl) is morphologically indistinguishable and therefore apparently this species. As we have not seen type material of *Cucurbitaria rosae* G. Winter & Sacc. (none is present in W),



**Fig. 11** *Parafenestella austriaca*. a–y. Sexual morph. a. Ascomata in face view and in vertical section; b. subicular hyphae; c. peridium in vertical section; d–f. asci (d. young, 4-spored); g. periphysis; h–i. ascus apices; j–y. ascospores (j–n. immature; y. germinating); z–d1. asexual morph from CMD at 22 °C; z. phialide; a1–d1. conidia. (d–f, h–i, l, n–o, s, u–x, z. in 3 % KOH). a–l, n–q, s–v, y–d1. WU 37014/CBS 145262 (C152); m, r, w, x. M 0281852. — Scale bars: a = 250 μm; b, g–h, x–y = 10 μm; c–f = 20 μm; i–w = 7 μm; z–b1 = 5 μm; c1–d1 = 3 μm.

its concept is unclear, but its protologue suggests that it may be a synonym of *C. acervata*. However, a fungus matching the description of that species in the sense of Mirza (1968) was found not belong to the *Cucurbitariaceae*. Another species described from *Rosa* is *Cucurbitaria occulta* Fuckel, with ascospores  $16 \times 8 \mu\text{m}$  having 4–5 transverse and 1 longitudinal septa. Its

type material (Germany, Hessen, Oestrich, Oestricher Wald, erumpent on *Rosa canina* in the spring, Fuckel (G 00266382; Fungi rhenani 1279, from Herbarium Boissier, labelled *Agyrium nitidum* Lib.) contains a drawing with a cylindrical ascus  $102 \times 13 \mu\text{m}$  with 8 uniseriate ascospores, one ellipsoid, with 5/1 septa,  $16 \times 8 \mu\text{m}$  and bark fragments containing the asexual



**Fig. 12** *Parafenestella faberi*. a–b. Ascomata in face view (with superficial subiculum in b); c–e. asci; f. ascoma above *Cytospora* (*Valsa*) ascomata in vertical section; g–h. peridium in vertical section (g. from side; h. from top); i–j. ascus apices; k–z. ascospores (k. immature; l, q. surface view (e, q–w, y–z. in 3 % KOH; h, o. in lactoglycerol (from slides prepared by R. Phookamsak). a, c–d, f, h–i, o, q–y. lectotype GZU; b, e, g, j–n, p, z. WU 37022. — Scale bars: a–b, f = 200  $\mu\text{m}$ ; c–e, g–h = 15  $\mu\text{m}$ ; i, q, u–w, y–z = 10  $\mu\text{m}$ ; j–p, r–t, x = 7  $\mu\text{m}$ .

fungus *Agyriella nitida* as black gelatinous drops producing masses of cylindrical to allantoid, 1-celled hyaline conidia on ampulliform phialides, a *Cytospora* (*Valsa* morph) sp. and a *Diplodia* sp. No sexual morph matching *C. occulta* was found. Fuckel (1870) interpreted the *Agyriella* as asexual morph of his *C. occulta*. For comparison with other *Parafenestella* spp. on *Rosaceae* see notes under *P. rosacearum*.

***Parafenestella faberi*** (J. Kunze) Jaklitsch & Voglmayr, *comb. nov.* — MB829750; Fig. 12

*Basionym.* *Fenestella faberi* J. Kunze, *Fung. Sel. Exs.*, Cent. 3: no. 263. 1879.

*Synonyms.* *Fenestella mackenziei* Wanas. et al., *Mycosphere* 8: 407. 2017b.

*Parafenestella mackenziei* (Wanas. et al.) Jaklitsch & Voglmayr, in Jaklitsch et al., *Stud. Mycol.* 90: 109. 2018.

*Lectotype* of *Fenestella faberi*, here designated. GERMANY, Sachsen-Anhalt, Mansfeld-Südharz, Eisleben, Oberrißdorf, on dead corticated sticks of *Rosa canina*, Sept. 1878, J. Kunze (GZU, Inv No. 226, Digi Bota ID 365656; Joannes Kunze, *Fungi Selecti exsiccati, ex museo botanico berlinensi*; as *Thyridium faberi* J. Kunze, nom. nud.; MBT385688). No type material is extant in B, therefore the material in GZU, which was originally received from B, may be the only available type specimen.

*Ascomata* (240–)300–450(–480) µm (n = 14) diam, subglobose to pyriform or subconical, black, tightly or loosely aggregated in small numbers in more or less valsoid configuration below blackened epidermis on inner bark or among ostiolar necks of *Cytospora* (*Valsa*) sp., partly erumpent through bark fissures, surrounded and connected by hyaline to brown, thick-walled, 2–4.5 µm wide subicular hyphae; sometimes subiculum also forming brown discs c. 0.2–1 mm diam at the bark surface. *Ostiolar areas* 50–180 µm diam, inconspicuous, appearing as black dots or blunt black papillae. *Peridium* 15–70 µm thick, thickest around the ostiole, pseudoparenchymatous, consisting of (4–)5.5–10.5(–14.5) µm (n = 54) wide cells, outside thick-walled and very dark brown *textura angularis* with encrusted pigment, gradually paler to hyaline and thinner-walled to the inside, partly terminated at the inner side by a compressed layer of pale brown longish cells; cells more isodiametric at upper levels and sometimes vertically elongated at the sides; in 3 % KOH turning dark olivaceous to dark brown. *Hamathecium* consisting of numerous 1–3 µm wide, branched ?paraphyses. *Asci* (110–)135–180(–200) × (15.5–)18.5–23.5(–26) µm (n = 22), cylindrical to oblong or narrowly clavate, bitunicate, fissitunicate, with a distinct ocular chamber, a short stipe and simple or knob-like base, containing 4–8 ascospores in uniseriate to partly biseriolate arrangement. *Ascospores* (23.5–)28.5–36(–42) × (11–)12.5–16(–17.5) µm, l/w (1.9–)2.1–2.5(–2.8) (n = 103), ellipsoid, sometimes fusoid, with upper part broader than lower, first hyaline, with 1–4 main septa, turning pale or yellowish brown, eventually dark brown, reddish brown in herbarium material, with 7–12(–14) transverse and 1–3(–5) longitudinal septa, slightly constricted at the median to submedian primary septum; end cells broadly or narrowly rounded, concolorous except for a truncate to convex hyaline terminal part of their walls; in 3 % KOH turning olivaceous to grey-brown; surface slightly verruculose.

*Other material examined.* AUSTRIA, Osttirol, Prägraten am Großvenediger, Umbalfälle, grid square 8939/4, on *Cytospora* (*Valsa*) sp. on a branch of *Rosa canina*, soc. *Diplodia* sp., 28 Aug. 2000, W. Jaklitsch W.J. 1539 (WU 37022).

*Notes* — Although ascospore size of *Parafenestella faberi* is in the range of *P. austriaca* and *P. rosacearum* (see below), its ascospores are unique due to the hyaline terminal wall of the terminal cells and a uniform shape. Ascospore septa appear rather distant in surface view, but dense in sectional view due to strong superposition. Ascospore size varies slightly among ascomata and specimens. We found the largest ascospores in the

isotype, and they were even up to 34.7 × 12.4 µm in the slides prepared by R. Phookamsak. We synonymise *P. mackenziei* with *P. faberi* here, as we do not see a difference between them. The authors did not compare their new species with *Fenestella faberi*, although the latter was redescribed by Phookamsak & Hyde (2015); in illustrations of Wanasinghe et al. (2017b) up to 12 transverse septa including incomplete ones are discernible. We give only a morphological account of this species here, as our material was not cultured and sequenced.

***Parafenestella germanica*** Jaklitsch & Voglmayr, *sp. nov.* — MycoBank MB829751; Fig. 13

*Etymology.* For its occurrence in Germany.

*Holotype.* GERMANY, Baden-Württemberg, Hornberg, Am Rubersbach, on *Diaporthe decedens* on a branch of *Corylus avellana*, soc. ?*Cosmospora* sp. and a dothideomycete with minute muriform spores, 18 Feb. 2018, K. Pätzold, comm. B. Wergen (WU 37017; ex-type culture CBS 145267 = C307).

*Ascomata* (195–)230–450(–570) µm (n = 12) diam, globose to subglobose, laterally collapsing from above, black, solitary or in small groups on inner bark or on the ostiolar level of old *Diaporthe decedens*, individually surrounded and connected by hyaline to dark brown, thick-walled, 1.5–6.5 µm wide subicular hyphae with often swollen and sometimes forked attachment cells, near the ostiole often short with rounded ends (blunt setae). *Ostiolar areas* c. 60–160 µm diam, indistinct or slightly papillate, rounded, black, sometimes convergent in clustered ascomata. *Peridium* 10–60 µm thick, pseudoparenchymatous, consisting of (4–)5.5–10.5(–13.5) µm (n = 32) wide cells, outside thick-walled and dark brown, paler to hyaline and thinner-walled to the inside. *Hamathecium* consisting of numerous 1–3 µm wide, branched ?paraphyses; in 3 % KOH swelling to c. 6 µm when old. *Asci* (128–)140–173(–193) × (17–)17.5–22(–24.5) µm (n = 25), cylindrical to oblong, bitunicate, fissitunicate, with a distinct ocular chamber, a short stipe and simple or knob-like base, containing 2–8 ascospores in (obliquely or overlapping) uniseriate arrangement. *Ascospores* (25.5–)29–39.5(–47) × (11–)13–16.5(–19) µm, l/w (1.9–)2.1–2.5(–2.7) (n = 70), ellipsoid to broadly fusoid, symmetric, with the upper part often broader, first hyaline, with 1–3 main septa, more or less constricted at the median or slightly eccentric primary septum, turning yellow to yellow-brown and finally dark brown when mature, with often broadly rounded, paler to hyaline end cells, sometimes larger terminal parts paler than the middle, with (8–)9–13(–15) transverse and 3–6 longitudinal septa; in 3 % KOH turning dark to blackish brown, end cells remaining hyaline.

*Culture characteristics and asexual morph in culture* — *Colony radius* on CMD at 22 °C in the dark up to 10 mm after 1 wk, 18 mm after 2 wk, 25 mm after 3 wk; *colony* first hyaline to whitish, dense, turning olivaceous, later greyish brownish due to a thick mat of aerial hyphae, surface and reverse becoming zonate; reverse dull grey to dark greyish olivaceous; odour indistinct. *Pycnidia* appearing after 4 d, immersed to erumpent, c. 70–200 µm diam, more or less globose, first hyaline, turning olivaceous to black, with whitish conidial drops. *Peridium* thin, pseudoparenchymatous, olivaceous. *Phialides* (3.2–)4.7–7.5(–9) × (1.7–)2–3(–4) µm (n = 30), sessile, subglobose to lageniform. *Conidia* (3.2–)3.5–4.3(–4.7) × (1.1–)1.2–1.4(–1.6) µm, l/w (2.5–)2.7–3.4(–3.8) (n = 50), oblong to ellipsoid, 1-celled, hyaline, with 1–2 minute drops, smooth; also produced on pegs present below phialides. After a few transfers no pycnidia formed.

*Habitat* — On *Diaporthe decedens* on *Corylus avellana*.

*Distribution* — Central Europe (Germany), only known from the type locality.

*Notes* — *Parafenestella germanica* is phylogenetically closely related to *P. pseudoplatani* but has distinctly larger ascospores than the latter species.



**Fig. 13** *Parafenestella germanica*. a–v. Sexual morph (WU 37017). a. Ascomata and subiculum in face view; b. ascoma above *Diaporthe* ascomata in vertical section; c–f. asci (2-, 3-, 4- and 8-spored); g. peridium in vertical section; h. seta-like subicular hypha; i. ascus apex; j–v. ascospores (j–k. immature); w–z. asexual morph in culture (CBS 145267 (C307) from CMD at 22 °C); w. pycnidia; x–y. phialides; z. conidia (d, h–i, u–v. in 3 % KOH). — Scale bars: a–b, w = 150 µm; c–g = 15 µm; h–i, o–v = 10 µm; j–n = 7 µm; x–z = 5 µm.

***Parafenestella parasalicum* Jaklitsch & Voglmayr, sp. nov.** — MycoBank MB829752, Fig. 14

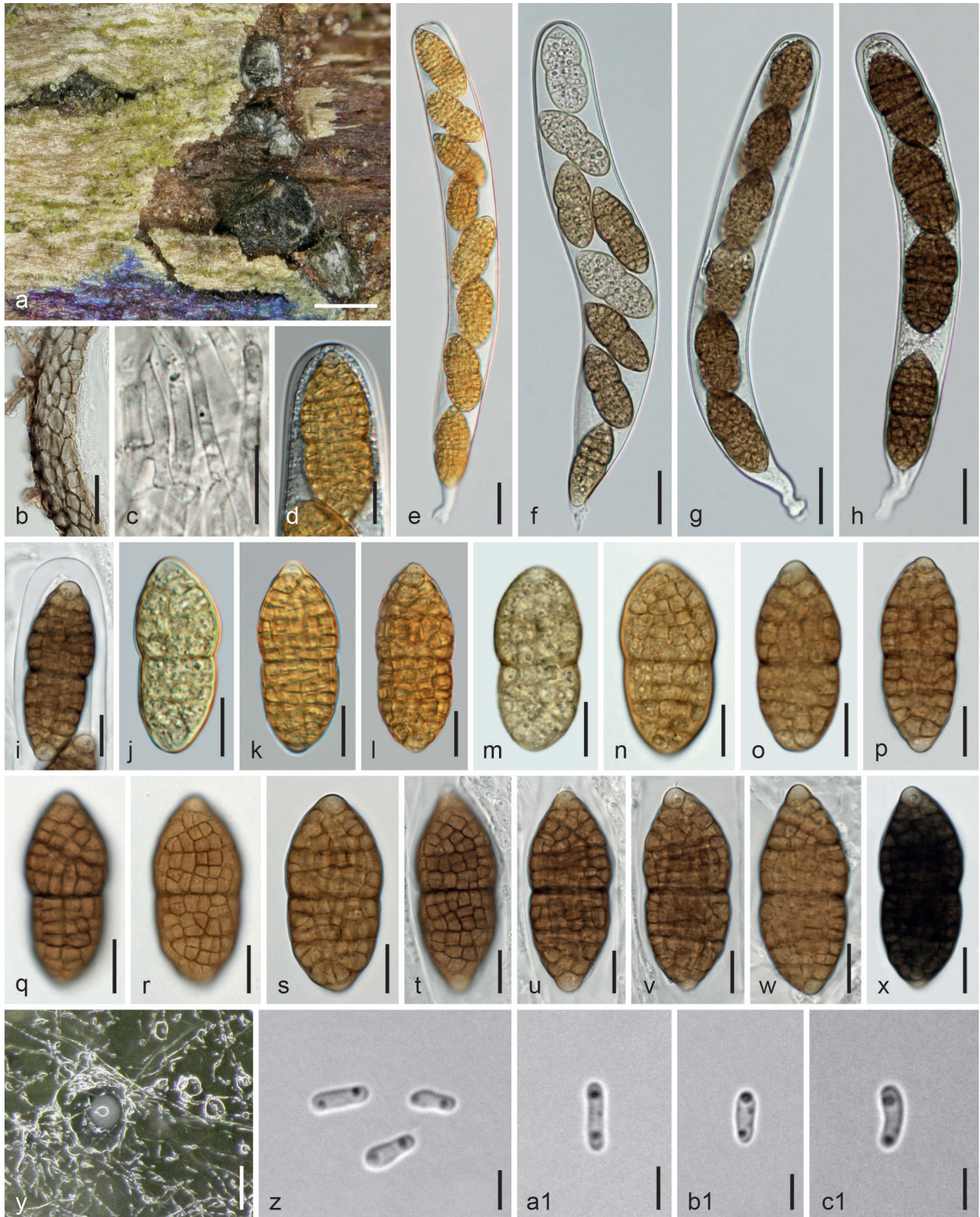
*Etymology.* Para = at, near; the epithet refers to the close phylogenetic relationship with *P. salicum*.

*Holotype.* AUSTRIA, Niederösterreich, Marchauen, Drösing, village area, on branch of *Salix cinerea*, on/soc. *Cytospora (Valsa)* sp., 7 Apr. 2018, H. Voglmayr (WU 37006; ex-type culture CBS 145271 = C318).

*Ascomata* 270–400 µm diam, globose, subglobose or pyriform, black, immersed in bark in the ostiolar region of *Cytospora (Valsa)* morph) or on inner bark, scattered, in valsoid configuration or in rows in small numbers, forming groups 0.5–1.7 mm diam, individually surrounded or connected by pale to dark brown, thick-walled, 1.5–6 µm wide subicular hyphae, the latter widened up to 10 µm at the connection to the peridium; incon-

spicuous at the bark surface, becoming visible in fissures. *Ostiole* areas (70–)75–138(–160)  $\mu\text{m}$  ( $n = 10$ ) diam, flattened, convex or slightly papillate, shiny black, often mixed with minute pycnidia. *Peridium* 15–50  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of isodiametric cells (3.5–)5.5–11(–14)  $\mu\text{m}$  ( $n = 30$ ) diam, outside thick-walled and very dark brown, paler brown to hyaline and thinner-walled toward the inner side and there

also with some brownish compressed elongate cells; darkening in 3% KOH. *Hamathecium* consisting of numerous, 1–4 wide, branched ?paraphyses. *Asci* (176–)185–219(–239)  $\times$  (20–)22–27(–30)  $\mu\text{m}$  ( $n = 12$ ), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a short stipe and simple or knob-like base, containing 4–8 ascospores in (overlapping, obliquely) uniseriate to partly biseriata arrangement. *Asco-*



**Fig. 14** *Parafenestella parasalicum*. a–x. Sexual morph (WU 37006). a. Ascomata in face view and in obliquely vertical section; b. peridium and subiculum hyphae in vertical section; c. hamathecium; d, i. ascus apices; e–h. asci (f. partially developed); j–x. ascospores (j, m. immature); y–c1. asexual morph in culture (CBS 145271 (C318) from CMD at 22 °C); y. pycnidia and conidial drops; z–c1. conidia; d–e, j–l. from fresh material; x. in 3% KOH. — Scale bars: a = 300  $\mu\text{m}$ ; b, e–h = 20  $\mu\text{m}$ ; c–d, i–x = 10  $\mu\text{m}$ ; y = 100  $\mu\text{m}$ ; z–c1 = 3  $\mu\text{m}$ .



spores (33.5–)36–44(–49.5) × (14.5–)15.8–19.3(–22.2) μm, l/w (2–)2.1–2.4(–2.6) (n = 44), fusoid or ellipsoid, first hyaline and 2-celled, developing 2 additional main septa, turning yellowish to yellow-brown and finally dark brown and eventually with 11–16 distinct and densely inserted transverse and 3–5 longitudinal septa; constricted at the primary septum, with the upper part usually broader and often longer than the lower; ends usually broadly rounded, concolorous, sometimes papillate and paler to hyaline, smooth, containing numerous minute droplets; in 3% KOH turning dark to blackish brown.

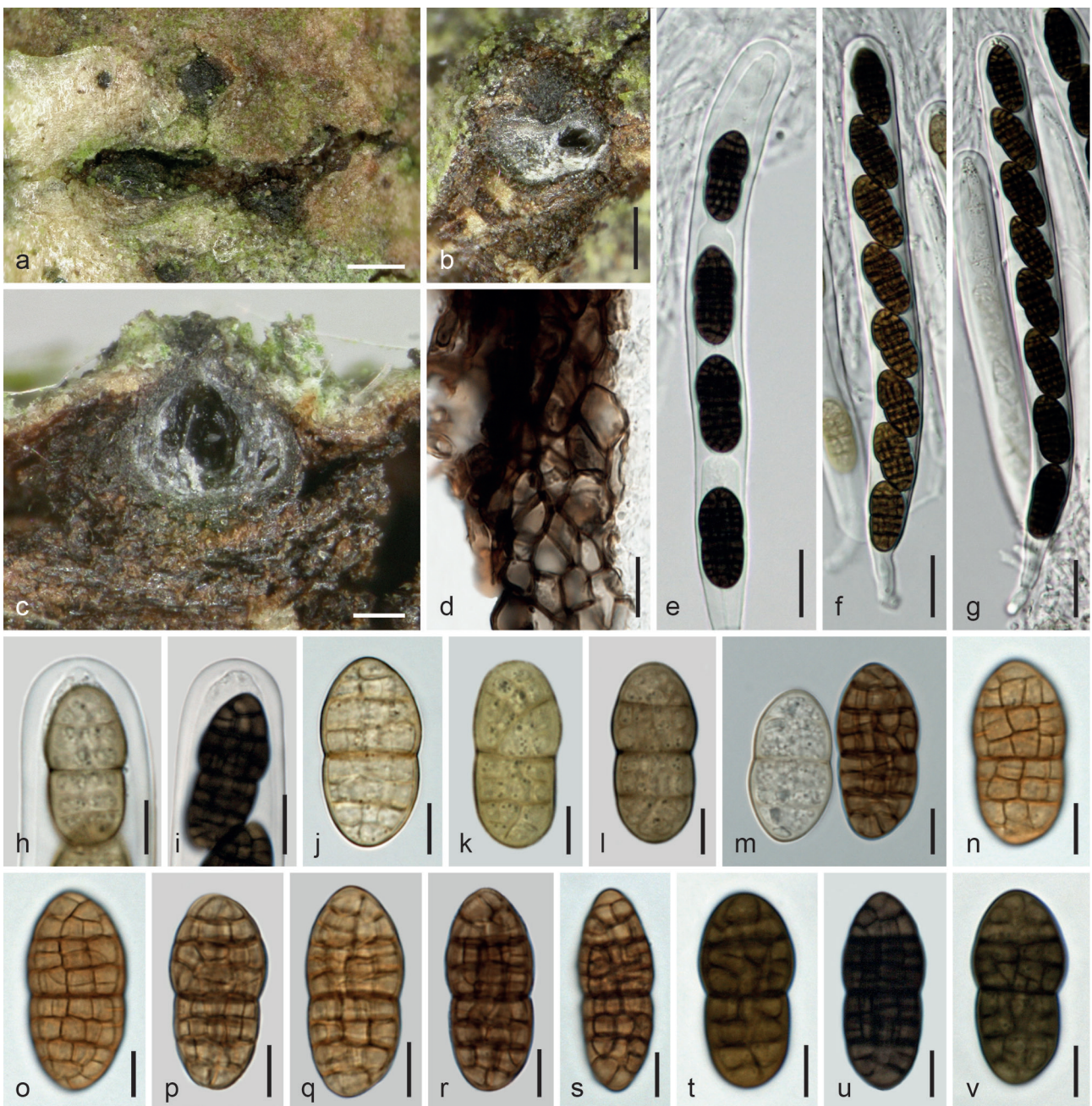
Culture characteristics and asexual morph in culture — *Colony radius* on CMD at 22 °C in the dark 7–8 mm after 1 wk, 22 mm after 22 d; *colony* first pale to medium grey, turning dark olivaceous grey, centre black; aerial hyphae long, white, forming a loose, later dense and thick mesh above the colony; reverse dark grey to black; odour indistinct. *Pycnidia* c. 45–100 μm diam, (sub-)globose, papillate, first appearing after 3–4 d,

hyaline, turning dark olivaceous, mostly immersed, spreading from the centre, solitary or in firm small packs, with whitish turbid conidial drops. *Peridium* thin, pseudoparenchymatous, olivaceous, surrounded by olivaceous, partly submoniliform hyphae. *Phialides* (4–)4.2–6.2(–7) × (1.8–)2.2–3.5(–4) μm (n = 16), sessile, varying from subglobose over ampulliform or lageniform to subulate. *Conidia* (3.3–)3.6–4.4(–4.8) × (1–)1.1–1.5(–1.8) μm, l/w (2.2–)2.6–3.4(–4.1) (n = 24), cylindrical to allantoid, less commonly narrowly ellipsoid, 1-celled, hyaline with 2 small drops, smooth.

Habitat — On both morphs of a *Cytospora* (*Valsa*) sp. on *Salix cinerea*.

Distribution — Central Europe (Austria), only known from the type locality.

Notes — *Parafenestella parasalicum* is phylogenetically and morphologically close to *P. salicum*, but differs from the latter by larger ascospores.



**Fig. 15** *Parafenestella pseudosalicis* (WU 37016/CBS 145264 (C301)). a. Ascomata in bark fissures; b. apically depressed ascoma in oblique face view and in vertical section; c. ascoma in vertical section; d. peridium in vertical section; e–g. asci (e. 4-spored, spore part); h–i. ascus apices (h. immature); j–v. ascospores (j–l. immature; m. immature and mature mixed) (e–i, k–l, t–v. in 3% KOH). — Scale bars: a = 300 μm; b = 200 μm; c = 100 μm; d, i = 10 μm; e–g = 20 μm; h, j–v = 7 μm.

***Parafenestella pseudosalicis* Jaklitsch & Voglmayr, sp. nov.**  
— MycoBank MB829753; Fig. 15

*Etymology.* Pseudo = false; the epithet denotes phylogenetic distinctness from *P. salicis* despite morphological similarity.

*Holotype.* UKRAINE, Ivano-Frankivsk region, Kosiv district, National Nature Park 'Hutsulshchyna' (Carpathians), on twigs of *Salix cf. alba*, soc. *Cytospora* sp., cf. *Keissleriella* sp., 5 Aug. 2017, A. Akulov (WU 37016; ex-type culture CBS 145264 = C301).

*Ascomata* (270–)300–400(–420)  $\mu\text{m}$  ( $n = 11$ ) diam, subglobose to subpyriform, solitary or loosely or tightly aggregated in small numbers, immersed in bark or on ascomata of an effete perithecial fungus, often with concave apex, individually surrounded or connected by rather scant subhyaline to dark brown, thick-walled, 2–5.5  $\mu\text{m}$  wide subcircular hyphae. *Ostiolar areas* (53–)60–116(–142)  $\mu\text{m}$  ( $n = 10$ ) diam, indistinct and inconspicuous, concave or papillate, black. *Peridium* 15–55  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of isodiametric cells (3.5–)4–8(–12)  $\mu\text{m}$  ( $n = 32$ ) diam, outside thick-walled and dark brown, slightly paler and thinner-walled toward the inner side; darkening in 3 % KOH. *Hamathecium* consisting of numerous, 1–4 wide, branched paraphyses. *Asci* (180–)186–215(–220)  $\times$  (17–)17.5–19(–19.5)  $\mu\text{m}$  ( $n = 10$ ), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a short stipe and simple or knob-like base, containing 4–8 ascospores in uniseriate arrangement. *Ascospores* (23–)25–29(–32)  $\times$  (11–)12–14(–15)  $\mu\text{m}$ , l/w (1.9–)2–2.3(–2.7) ( $n = 41$ ), ellipsoid, first hyaline to yellowish, with 1–3 main septa, turning yellow-brown to dark brown, developing 7–10(–11) transverse and 2–4 longitudinal septa, distinct in surface view, in section difficult to count due to oblique superposition; constricted at the median primary septum, upper part often wider, ends concolorous, wall smooth, contents with minute guttules; in 3 % KOH turning very dark to blackish brown, yellow-green to greyish brown when immature.

*Culture characteristics and asexual morph in culture* — *Colony radius* on CMD at 22 °C in the dark 6–7 mm after 1 wk, 15–16 mm after 2 wk; *colony* first hyaline to whitish, thick, dense, turning olivaceous from the centre, becoming grey to greyish brown due to a dense whitish to greyish villose mat of aerial hyphae; reverse dark grey to black; odour indistinct. No asexual morph detected.

*Habitat* — Associated with a perithecial fungus (probably *Cytospora*, *Valsa* morph) on *Salix cf. alba*.

*Distribution* — Europe, only known from the type locality in Ukraine.

*Notes* — *Parafenestella pseudosalicis* is morphologically similar to *P. salicis*, but differs from that species by a more regular, symmetric ascospore shape and more longitudinal septa being visible in surface view. Also, colonies on CMD tend to be more distinctly brown than with other species from *Salix*, which are more grey, and no asexual morph was produced in culture. However, as the species is based on a single species, further material would be necessary to evaluate its natural variation.

***Parafenestella rosacearum* Jaklitsch & Voglmayr, sp. nov.** — MycoBank MB829754; Fig. 16

*Etymology.* For its occurrence on various species of *Rosaceae*.

*Holotype.* AUSTRIA, Vienna, 22nd district, Spargelfeldstraße, on ?*Diaporthe* sp. on a branch of *Pyracantha coccinea*, soc. *Diplodia* sp., 25 Jan. 2018, R. Moosbeckhofer, comm. B. Wergen (WU 37010; ex-type culture CBS 145268 = C309).

*Ascomata* (270–)285–432(–510)  $\mu\text{m}$  ( $n = 42$ ) diam, globose, subglobose to subpyriform, dark brown to black, immersed on often blackened inner bark or at the ostiolar level of *Cytospora* spp. or other perithecial fungi, scattered or in small groups, erumpent through bark fissures, laterally and basally loosely or

tightly connected by hyaline to pale brown, less commonly dark brown, thick-walled, 2–5  $\mu\text{m}$  wide subcircular hyphae. *Ostiolar areas* (53–)73–125(–150)  $\mu\text{m}$  ( $n = 47$ ) diam, inconspicuous or papillate to short-cylindrical, sometimes depressed when immature, sometimes mixed with slender ostiolar necks of the host or often by pycnidia of its presumed asexual morph. *Peridium* 15–50  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of isodiametric cells (2.7–)4–8(–12)  $\mu\text{m}$  ( $n = 30$ ) diam, outside thick-walled and dark brown, paler to hyaline and thinner-walled to the inside; darkening in 3 % KOH. *Hamathecium* consisting of numerous 1–3, basally to 5  $\mu\text{m}$  wide branched paraphyses with free ends. *Asci* (150–)181–240(–290)  $\times$  (17–)19–22(–24)  $\mu\text{m}$  ( $n = 59$ ), cylindrical to oblong, bitunicate, fissitunicate, with a distinct ocular chamber, a short, sometimes contorted stipe and simple or knob-like base, containing (2–)4–8 ascospores in uniseriate, rarely partly biseriate arrangement. *Ascospores* (23.3–)28–35(–44.5)  $\times$  (11–)13.5–16.5(–19.5)  $\mu\text{m}$ , l/w (1.7–)1.9–2.2(–2.6) ( $n = 230$ ), ellipsoid, symmetric to inequilateral, constricted at the more or less median primary septum, initially hyaline to yellowish, with 1–3 main septa, developing (7–)9–13(–15) transverse and 2–4(–5) longitudinal septa and turning yellow-brown, pale-, medium- to dark brown, ends broadly rounded and concolorous, less commonly narrowly rounded and slightly paler, surface appearing slightly verruculose; in 3 % KOH turning olivaceous when young, blackish brown when mature.

*Culture characteristics and asexual morph in culture* — *Ascospores* germinating simultaneously from many cells. *Colony radius* on CMD at 22 °C in the dark 7–9 mm after 1 wk, up to 18 mm after 2 wk, 35 mm after 5 wk; *colony* first hyaline, turning greyish olivaceous, dense, usually becoming thick and pale grey by a dense mesh of white aerial hyphae, long remaining pale greyish brownish olivaceous, finally darkening; reverse dark grey to black; odour indistinct. *Pycnidia* appearing after 4 d, c. 80–200  $\mu\text{m}$  diam, more or less globose, olivaceous, often numerous, aggregated, immersed in the agar and usually completely covered by a dense mat of aerial hyphae, with whitish conidial drops. *Peridium* thin, pseudoparenchymatous, brown to olivaceous, surrounded by submoniliform hyphae. *Phialides* (2.7–)4.7–8.2(–9.7)  $\times$  (2–)2.5–4(–5.2)  $\mu\text{m}$  ( $n = 25$ ), sessile, varying from subglobose over ampulliform or lageniform to subulate; conidia also formed on lateral pegs below phialides. *Conidia* (3–)3.5–4.2(–4.8)  $\times$  (1.1–)1.2–1.5(–1.7)  $\mu\text{m}$ , l/w (2–)2.5–3.3(–4.1) ( $n = 55$ ), cylindrical or oblong, less commonly ellipsoid, 1-celled, hyaline, with 1–3 drops, smooth.

*Habitat* — Associated with *Cytospora* spp. and other perithecial fungi on various species of *Rosaceae*, recorded from *Crataegus*, *Prunus*, *Pyracantha*, *Pyrus*, *Rosa* and *Sorbus aria*.

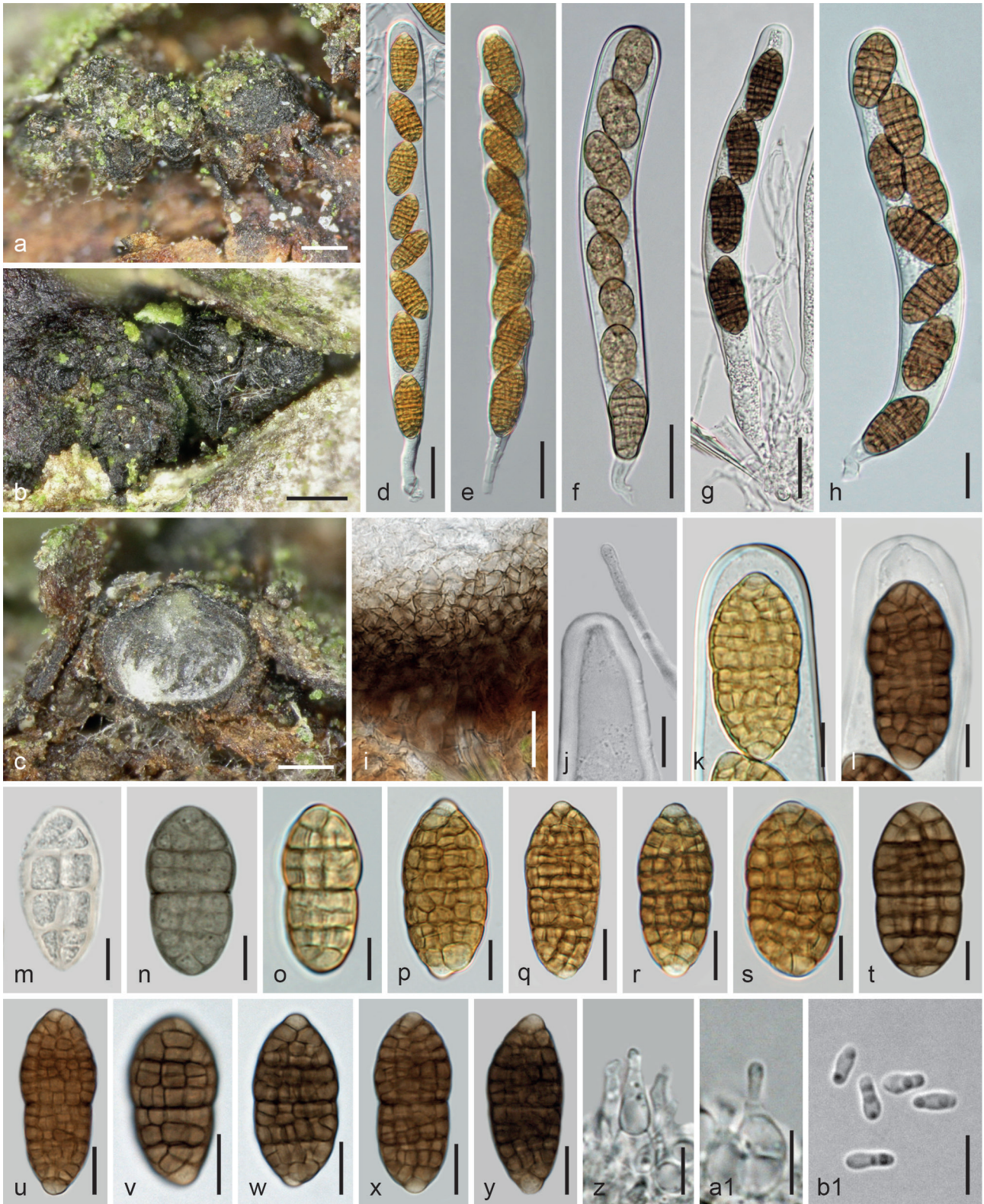
*Distribution* — Central Europe (Austria).

*Other materials examined.* AUSTRIA, Burgenland, Purbach, Purbacher Heide, on *Cytospora* sp. on a branch of *Rosa canina*, 24 Mar. 2018, H. Voglmayr (WU 37011; culture C315); Siegendorf, Königshüßel, on effete perithecia of ?*Diaporthe* sp. on *Crataegus monogyna*, 18 Sept. 2016, W. Jaklitsch & H. Voglmayr (WU 37008; culture C269); Niederösterreich, Ulrichschlag, on *Cytospora* sp. on an attached branch of *Pyrus communis*, soc. *Diplodia* sp., 11 July 2015, W. Jaklitsch & H. Voglmayr (WU 37007; culture C203); Oberösterreich, Schärding, Raab, Wetzlbach, on a branch of *Prunus domestica*, soc. diverse fungi including a *Botryosphaeria* sp., 2 Dec. 2017, H. Voglmayr (WU 37013; culture CBS 145272 = FP11); Steiermark, N Rein, Kaschsteig, on a branch of *Sorbus aria*, 30 June 2018, G. Friebe (WU 37023; culture C320); Ratten, Kirchenviertel, vlg. Kirchenberger, beim 'Dörrofen', on a branch of *Pyrus communis*, soc. *Acanthostigma* sp., '*Cucurbitaria acervata*', a perithecioid fungus with yellow muriform ascospores and diverse pycnidia, 6 Jan. 2017, R. Moosbeckhofer (WU 37009; culture C283); Vienna, 21st district, at Marchfeldkanalweg near Felix Slavikstraße, on *Cytospora* sp. on a branch of *Rosa canina*, soc. *Calosphaeria* sp., *Massaria* sp., 8 Nov. 2015, W. Jaklitsch (WU 37012; culture FM1).

*Notes* — As deduced from the protologue, *P. rosacearum* may be what Saccardo (1884) termed *Cucurbitaria delitescens*

*\*prunorum*. However, we have not seen type material and a varietal name is not binding. *Parafenestella rosacearum* is a complex species. In spite of splitting into two or three groups in multigene analyses (see Fig. 1), we recognise a single species, because there are no morphological differences among those groups and particularly due to the following observations: *tef1* sequences of C203 and C283 are identical and *tef1* of C309 is

nearly identical with them, whereas *rpb2* sequences of C203, C315, FM1 and FP11 are virtually identical, while those of C269 and C283, which are identical, differ from the first group by c. 20 nucleotides. This finding was verified by repetition of DNA amplifications and sequencing. Species of *Parafenestella* on *Rosaceae*, particularly on *Rosa* spp., are difficult to distinguish morphologically; ascospores of *P. faberi* are characteristic due



**Fig. 16** *Parafenestella rosacearum*. a–y. Sexual morph. a–b. Ascomata in face view; c. ascoma in vertical section; d–h. asci (d–e. from fresh material; f. immature); i. basal peridium in vertical section; j. immature ascus apex and apically free paraphysis; k–l. ascus apices (k. from fresh material); m–y. ascospores (m–o. immature; p–s. from fresh material); z–b1. asexual morph from CMD at 22 °C; z–a1. phialides; b1. conidia (j, n. in 3% KOH). a, c, f, z–b1. WU 37010/ CBS 145268 (C309); b, d–e, i–k, p–s, y. WU 37013 (FP11); g, t, w. WU 37008 (C269); h, v. WU 37009 (C283); j, n. WU 37007 (C203); l, m, u, x. WU 37012 (FM1); o. WU 37011 (C315). — Scale bars: a–b = 250 µm; c = 150 µm; d–g = 25 µm; h–i = 15 µm; j, q–r, u–y = 10 µm; k–p, s–t = 7 µm; z–b1 = 5 µm.

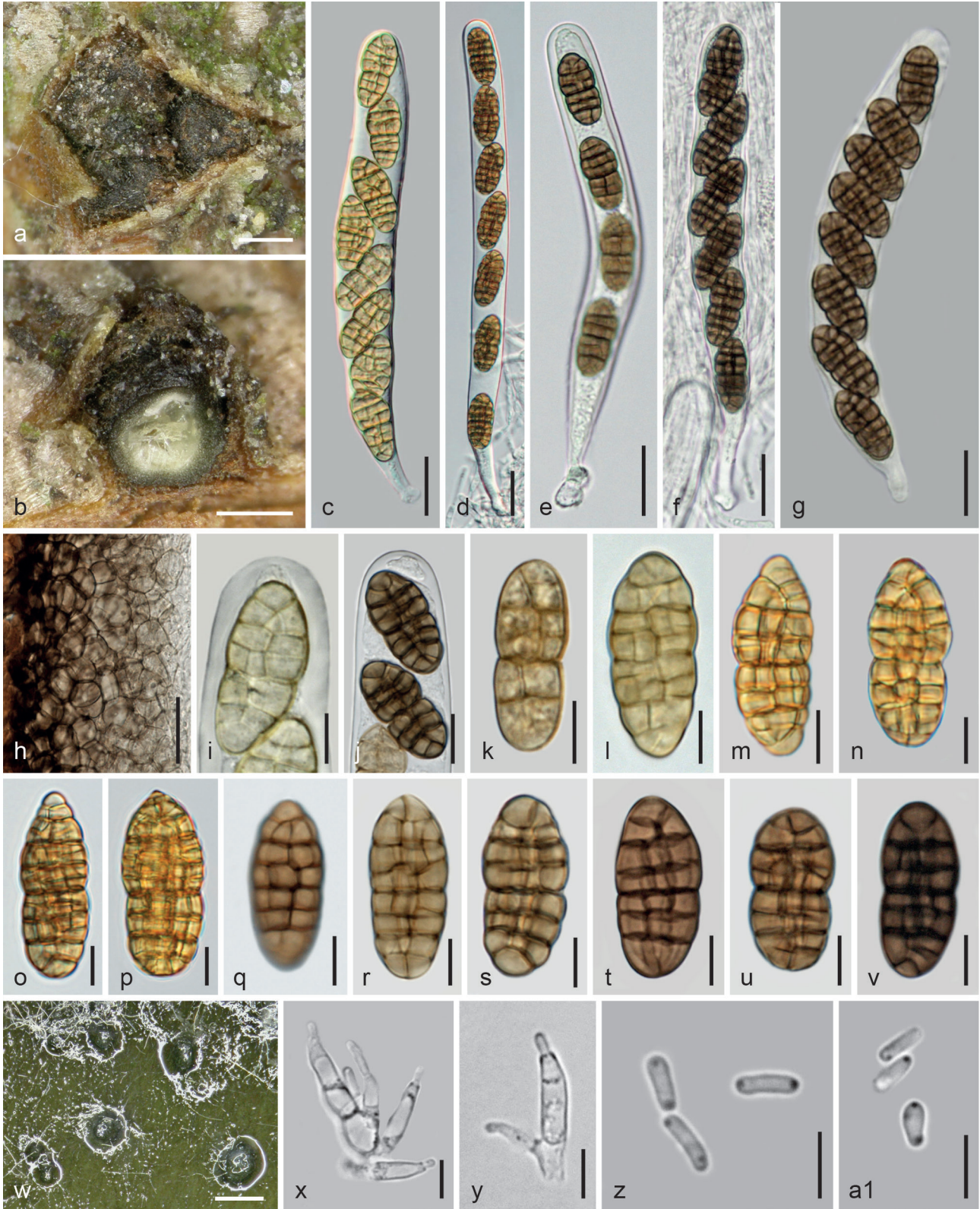
to their often truncate hyaline terminus of the end cells, and *P. austriaca* differs from *P. rosacearum* by a rather invariable ascospore shape. In both of the latter species ascospore end cells are rounded, slightly projecting and may be only diffusely paler to hyaline.

***Parafenestella salicis* (Rehm) Jaklitsch & Voglmayr, comb. nov.** — MycoBank MB829755; Fig. 17

*Basionym.* *Thyridium salicis* Rehm, in Thümen, Beiträge zur Pilzflora Sibiriens IV, Bull. Soc. Imp. Naturalistes Moscou 55 (1–4): 218. 1880.

*Synonyms.* *Fenestella salicis* (Rehm) Sacc., Syll. Fung. (Abellini) 2: 330. 1883.

*Cucurbitaria marchica* Kirschst., Ann. Mycol. 34: 186. 1936.



**Fig. 17** *Parafenestella salicis*. a–v. Sexual morph. a. Ascomata in face view; b. ascoma in oblique view and in vertical section; c–g. asci (c. from fresh material); h. peridium in vertical section; i–j. ascus apices (i. young); k–v. ascospores (k–l. immature / young; m–p. from fresh material); w–a1. asexual morph from CMD at 22 °C; w. pycnidia; x–y. phialides and short conidiophores; z–a1. conidia (g, v. in 3 % KOH). a–f, h, j–k, s, w–a1. WU 37002/CBS 145270 (C313); g, r. K(M) 251618; i, l–n. WU 37003 (C311); o–p, u. WU 37001 (C303); q. part of WU 37015; t, v. *C. marchica* holotype B 700016516. — Scale bars: a–b, w = 250 µm; c–h = 20 µm; i, k–v = 7 µm; j = 10 µm; x–a1 = 5 µm.

**Typification.** According to the herbarium curator of LE, Dr. Olga Morozova, comm. Dr. Eugene Popov, there is only a younger specimen of the original collector, N. Martianov, but not the type, extant in LE. Also, no type material has been found in other herbaria. Therefore we here propose a *neotype* for *Thyridium salicis*: AUSTRIA, Niederösterreich, Marchegg, on *Cytospora* (*Valsa*) sp. on branchlets of *Salix alba*, soc. a coniothyrium-like fungus, 17 Mar. 2018, H. Voglmayr (WU 37002; MBT385689; ex-neotype culture CBS 145270 = C313).

**Ascomata** (255–)275–442(–510)  $\mu\text{m}$  ( $n = 20$ ) diam, globose, subglobose to pyriform or subconical, black, immersed below the epidermis on inner bark or in the ostiolar region of *Cytospora* (*Valsa*) sp., scattered or tightly or loosely aggregated in valsoid or irregular configuration, partly erumpent through bark fissures, surrounded laterally and basally and connected by subhyaline to medium brown, thick-walled, 2–5  $\mu\text{m}$  wide subcircular hyphae. **Ostiolar areas** (35–)55–118(–180)  $\mu\text{m}$  ( $n = 22$ ) diam, usually indistinct, sometimes papillate, rounded or apically flattened or compressed and furrowed, black. **Peridium** 20–80  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of (4–)6–13(–18)  $\mu\text{m}$  ( $n = 30$ ) wide cells, outside thick-walled and very dark brown, gradually paler and thinner-walled to the inside. **Hamathecium** consisting of numerous, 1–3.5  $\mu\text{m}$  wide, branched ?paraphyses; when old widened up to c. 6  $\mu\text{m}$  and submoniliform at their bases. **Asci** (131–)141–188(–220)  $\times$  (14.8–)16–19(–21.5)  $\mu\text{m}$  ( $n = 33$ ), cylindrical to oblong, bitunicate, fissitunicate, with a distinct ocular chamber, a short stipe and simple or knob-like base, containing (1–)4–8 ascospores in (obliquely) uniseriate to partly biseriate arrangement. **Ascospores** (20.5–)23–29(–34)  $\times$  (10–)11–13.5(–15)  $\mu\text{m}$ , l/w (1.5–)1.9–2.3(–2.7) ( $n = 152$ ), ellipsoid to fusoid, slightly to distinctly constricted at the more or less median primary septum, often also at other septa, symmetric to inequilateral, first hyaline to yellowish, with 1–3 main septa, turning bright or golden yellow to yellow-brown (when fresh), eventually dark brown, with (5–6–)7–10(–11) transverse and (1–)2–3 longitudinal septa, the former often with oblique superposition in section, the latter often forming parallel lines; ends broadly rounded and concolorous, less commonly narrowly rounded and only rarely hyaline immediately before germination, smooth. Often tightly accompanied by the presumed asexual morph forming pycnidia with minute cylindrical to allantoid, 1-celled, hyaline conidia.

**Culture characteristics and asexual morph in culture** — **Colony radius** on CMD at 22 °C in the dark 9–11 mm after 1 wk, 22 mm after 2 wk; **colony** dense, first hyaline, turning olivaceous and later pale to dark grey owing to aerial hyphae; reverse dark grey to black; odour indistinct to sour. **Pycnidia** appearing after 3 d, c. 80–200  $\mu\text{m}$  diam, numerous, immersed, partially erumpent, scattered or tightly aggregated to confluent in small numbers, globose or subglobose, papillate, olivaceous to black, with whitish to greyish conidial drops, partly covered by aerial hyphae, surrounded by olivaceous to brown hyphae. **Peridium** thin, pseudoparenchymatous, olivaceous. **Phialides** (4.3–)5.3–9(–10.5)  $\times$  (1.8–)2–3(–3.8)  $\mu\text{m}$  ( $n = 22$ ), subglobose to subcylindrical, sessile or formed on short conidiophores; conidia also formed on pegs. **Conidia** (3.2–)3.7–4.5(–5.2)  $\times$  (1–)1.1–1.5(–1.7)  $\mu\text{m}$ , l/w (2.1–)2.7–3.6(–4.2) ( $n = 64$ ), cylindrical to allantoid, sometimes narrowly ellipsoid, 1-celled, hyaline, with 1–2 subterminal drops, smooth.

**Habitat** — On both morphs of *Cytospora* (*Valsa*) sp(p). on *Salix* spp.

**Distribution** — Europe (Austria, Germany, UK), Russia, etc.

**Other materials examined.** AUSTRIA, Niederösterreich, Orth, on *Cytospora* (*Valsa*) sp. on branchlets of *Salix alba*, soc. *Diplodia* sp., 3 Feb. 2018, H. Voglmayr (WU 37001; culture C303); same area, on *Cytospora* sp. on branches of *Salix alba*, soc. *Coniothyrium* sp., *Parafenestella salicum* (removed as WU 37004), 10 Mar. 2018, W. Jaklitsch & H. Voglmayr (WU 37003). — GERMANY, Westhavelland, Quermathen bei Großbehnitz, Löffelpfuhl, on branches of *Salix cinerea*, 4 Nov. 1935, W. Kirschstein (B 70 0016516; holotype of *Cucurbitaria marchica*). — UK, England, Kew, on twigs of *Salix cinerea*, apparently on *Plagiostoma* sp., May 1887, no collector given (K-M 251618).

**Notes** — Judging on the specimens we have seen, *P. salicis* is the most common species of the genus on *Salix* spp. and occurs often together with other *Parafenestella* species. Counting of ascospore septa in sectional view is particularly difficult in this species, due to conspicuous superposition; they differ from those of *P. salicum* and *P. parasalicum* in less and more widely spaced septa and from the latter also by size. Ascospores are often inequilateral and often slightly constricted at other than the primary septum, traits not seen with *P. pseudosalicis*. Like with other species, mature ascospores are often dark reddish brown in herbarium material.

**Other species/names described on Salix:** *Cucurbitaria salicina* was described from *Salix fragilis* and *S. triandra* with ascospores measuring 22  $\times$  9  $\mu\text{m}$  having 4–5 transverse septa and 1 longitudinal septum. The holotype (Germany, Oestrich, L. Fuckel, G 00127757, ex Herbarium Barbey-Boissier, Nassau's Flora. 6) does not contain a sexual morph but numerous pycnidia with camarosporium-like conidia and a *Diplodia* sp. *Cucurbitaria cinerea*, described from *Salix aurita*, is *Discostroma corticola*, according to Brockmann (1976). *Cucurbitaria rubefaciens*, described from *Salix caprea*, does not belong to the *Cucurbitariaceae* (unpublished results).

***Parafenestella salicum*** Jaklitsch & Voglmayr, sp. nov. — MycoBank MB829756; Fig. 18

**Etymology.** For its occurrence on species of *Salix*.

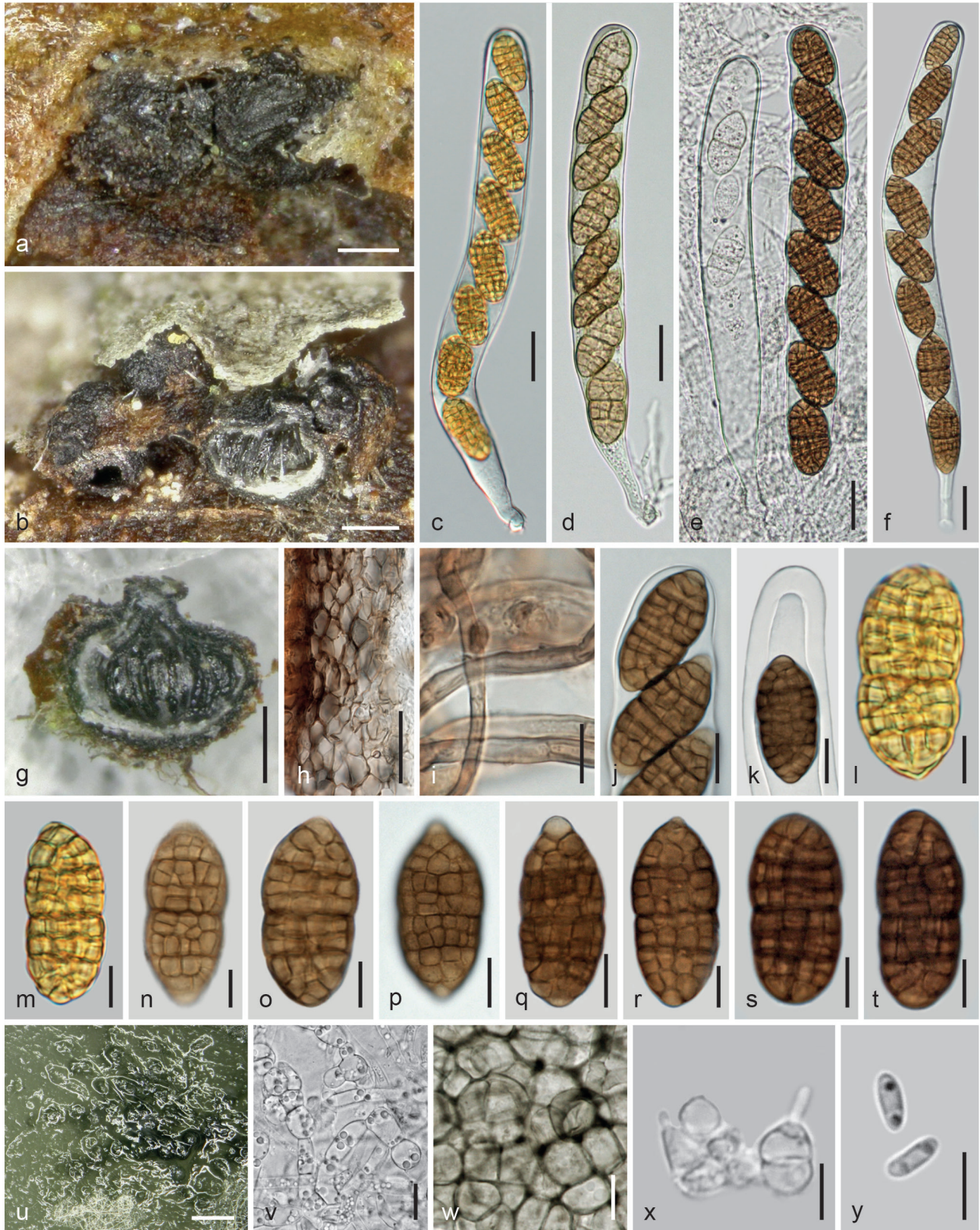
**Holotype.** AUSTRIA, Niederösterreich, Orth, on thin branches of *Salix alba*, soc. effete *Cytospora* sp., *Massarina* sp., *Parafenestella salicis* (removed as WU 37003) and effete *Plagiostoma* sp., 10 Mar. 2018, W. Jaklitsch & H. Voglmayr (WU 37004; ex-type culture CBS 145269 = C311).

**Ascomata** (270–)280–375(–420)  $\mu\text{m}$  ( $n = 11$ ) diam, globose, subglobose or pyriform, black, laterally collapsing, immersed in bark over a perithecial host fungus or firmly connected to the inner bark layers, scattered or aggregated in small numbers in valsoid groups, connected by subhyaline to dark brown, thick-walled, 1.5–5  $\mu\text{m}$  wide subcircular hyphae. **Ostiolar areas** 85–200  $\mu\text{m}$  diam, inconspicuous at the bark surface, roundish to longish, black, often apically flattened, sometimes concave or papillate; sometimes accompanied by pycnidia of the putative asexual morph. **Peridium** 15–65  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of (3.5–)6–10(–12.5)  $\mu\text{m}$  ( $n = 40$ ) wide cells, outside thick-walled and very dark brown and forming a narrow layer, gradually paler to hyaline and thinner-walled to the inside, terminated by a narrow layer of brownish compressed cells. **Hamathecium** consisting of numerous 1–3.5(–4)  $\mu\text{m}$  wide, branched ?paraphyses. **Asci** (172–)181–228(–246)  $\times$  (17.5–)19.5–24(–28)  $\mu\text{m}$  ( $n = 20$ ), cylindrical, bitunicate, fissitunicate, with a distinct ocular chamber, a short stipe and simple or knob-like base, containing 6–8 ascospores in (overlapping) uniseriate arrangement. **Ascospores** (22.5–)27–33(–40)  $\times$  (11–)12.5–16(–18)  $\mu\text{m}$ , l/w (1.7–)1.9–2.3(–2.5) ( $n = 110$ ), broadly ellipsoid to broadly fusoid with broadly rounded ends or one end narrowly rounded, upper part often slightly wider, not or slightly constricted at the median primary septum, first 2-celled and hyaline, turning golden yellow to golden brown, eventually dark brown or dark reddish brown, ends concolorous, only rarely slightly paler and sometimes slightly projecting, with 9–13(–14) transverse and 3–4 longitudinal septa; smooth. Presumed asexual morph forming pycnidia at the apices or sides of ascomata, c. 70–150  $\mu\text{m}$  diam, more or less globose, with masses of oblong, allantoid to narrowly ellipsoid, 1-celled, hyaline conidia typically containing two drops.

**Culture characteristics and asexual morph in culture** — Ascospores germinating simultaneously from many cells. **Colony radius** on CMD at 22 °C in the dark 5–7 mm after 1 wk, 16 mm after 2 wk, 18 mm after 27 d; **colony** pale brownish to pale grey-

ish brown, covered by a dense and thick mat of aerial hyphae; reverse dark grey; odour indistinct to unpleasant. *Pycnidia* appearing after 3 d, numerous, immersed, partially erumpent, 80–180 µm diam, solitary, in lines or tightly aggregated in small numbers, globose, subglobose or vertically elongated, papillate, greenish, olivaceous to black, with narrow periph-

ses in the ostiole; conidial drops whitish to greyish. *Peridium* thin, pseudoparenchymatous, an olivaceous *textura angularis* of (6.5–)8.5–14.5(–19) µm ( $n = 30$ ) wide cells; surrounded by submoniliform hyphae. *Phialides* (4–)4.5–6.2(–7.3) × (1.5–)1.8–3.5(–4.7) µm ( $n = 20$ ), sessile, subglobose, ampulliform, lageniform to subcylindrical. *Conidia* (3.3–)3.5–4(–4.5)



**Fig. 18** *Parafenestella salicum*. a–t. Sexual morph. a. Ascomata in face view; b, g. ascomata in oblique view and in vertical section (detached in g); c–f. asci (c. from fresh material; d. young; e. early stage on the left side); h. peridium in vertical section; i. subicular hyphae; j–k. ascus apices; l–t. ascospores (l–m. from fresh material); u–y. asexual morph from CMD at 22 °C; u. pycnidia; v. submoniliform hyphae; w. peridium in face view; x. phialides; y. conidia. a–g, i–r, u–y. WU 37004/CBS 145269 (C311); h, s–t. WU 37005. — Scale bars: a–b, g = 150 µm; c–f, h = 20 µm; i–k, p–q, v–w = 10 µm; l–o, r–t = 7 µm; u = 300 µm; x–y = 5 µm.

× (0.9–)1.1–1.6(–2) μm, l/w (1.9–)2.4–3.4(–4.1) (n = 42), cylindrical to allantoid, sometimes narrowly ellipsoid, 1-celled, hyaline, with 2 subterminal drops, smooth.

Habitat — On thin branches of *Salix alba*, presumably on both morphs of a *Cytospora* (*Valsa*) sp.

Distribution — Europe (Austria).

*Other material examined.* AUSTRIA, Vienna, 22nd district, Lobau, Panoz-zalacke, grid square 7865/1, on thin branches of *Salix alba*, soc. effete *Cytospora* sp., *Keissleriella holmiorum*, 8 Feb. 1997, W. Jaklitsch W.J. 1015 (WU 37005).

Notes — *Parafenestella salicum* differs from *P. salicis* by larger asci, larger, particularly broader ascospores with a larger number of septa. While phylogenetically closely related to



**Fig. 19** *Parafenestella tetrarupha*. a–y. Sexual morph. a. Ascomata and subiculum in face view; b. cluster of ascomata in conidioma of *Melanconis alni* (grey patches at bottom and left are host conidia); c. young ascomata in conidioma of *Melanconis alni*; d–h. asci (f. upper part, partially developed, apically opening); i. ascomatal setae; j. peridium in vertical section (showing host conidia); k–m. ascus apices; n–y. ascospores (n. immature); z–c1. asexual morph from CMD at 22 °C; z. pycnidia and conidial drops; a1. phialide and basal peg; b1–c1. conidia (d–e, i–j, m, r, x–y. in 3% KOH). a, d–e, i, l–m, w, y. WU 37000; b, g–h, s–v, x. *Valsa tetrarupha* holotype K-M 251617; c, f, j, n–o. *Fenestella minor* holotype PC 0706652; k, p–r, z–c1. WU 36999/CBS 145266 (C304). — Scale bars: a–c, z = 200 μm; d–e, g–j = 20 μm; f, k–m, o–q, t–v, y = 10 μm; n, r–s, w–x = 7 μm; a1–c1 = 5 μm.

*P. parasalicum*, *P. salicum* differs from that species by smaller ascospores, although some old aberrant ascospores may approach those of *P. parasalicum* in size. The fungal host of *P. salicum* is not unequivocally clear. As is usual in the *Cucurbitariaceae*, ascospores are more reddish brown in herbarium material.

***Parafenestella tetratrupha*** (Berk. & Broome) Jaklitsch & Voglmayr, *comb. nov.* — MycoBank MB829757; Fig. 19

*Basionym.* *Valsa tetratrupha* Berk. & Broome, *Ann. Mag. Nat. Hist.*, ser. III, 3: 366. 1859.

*Synonyms.* *Fenestella tetratrupha* (Berk. & Broome) Sacc., *Syll. Fung.* (Abellini) 2: 326. 1883.

*Fenestella minor* Tul. & C. Tul., *Select. Fung. Carp.* 2: 207. 1863.

*Holotype.* UK, England, North Somerset, Batheaston, on conidiomata of *Melanconis alni* on twigs of *Alnus* sp. (probably *A. glutinosa*), Feb. 1852, C.E. Broome (K-M 251617, as *Fenestella minor* written on the outer, *Sphaeria tetratrupha* on the inner label). *Epitype* of *Fenestella minor* and *Valsa tetratrupha*, here designated: AUSTRIA, Kärnten, St. Margareten im Rosental, village area, at the brook Tumpfi, on conidiomata of *Melanconis alni* on a branch of *Alnus glutinosa*, partly overgrown by *Fusarium/Cosmospora* (s.lat.) sp., 4 Feb. 2018, W. Jaklitsch (WU 36999; MBT385691, MBT385690; ex-epitype culture CBS 145266 = C304).

*Ascomata* (240–)300–500(–630)  $\mu\text{m}$  ( $n = 31$ ) diam, globose, subglobose or pyriform, immersed in the ostiolar region of *Melanconis alni* conidiomata singly or in more or less valsoid groups with often convergent ostiolar necks, tightly or loosely aggregated in whitish to dark brown subiculum, forming pustules c. 0.5–2.3 mm depending on the size of the host, projecting up to 0.6 mm from the bark surface. Pustules pulvinate, causing small bumps in elevated bark, erumpent through fissures, outline circular, elliptic or elongate, surface obtuse, dark brown to black, often partly covered by brown subiculum consisting of subhyaline to dark brown, thick-walled, 1.5–6  $\mu\text{m}$  wide hyphae, mixed with dark brown, pointed, thick-walled, up to 60  $\mu\text{m}$  long and 2–6  $\mu\text{m}$  wide setae on the ascomatal surface. *Ostiolar areas* 70–186(–270)  $\mu\text{m}$  ( $n = 17$ ) diam, inconspicuous or papillate, sometimes eccentric and convergent, rounded or flat and angular, brown to black, whitish inside, often mixed with shiny black ostiolar necks of the host. *Peridium* 15–100  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of isodiametric cells (4–)6–11(–13.5)  $\mu\text{m}$  ( $n = 30$ ) diam, outside moderately thick-walled and dark brown, paler and thinner-walled to the inside. *Hamathecium* consisting of numerous 0.5–3.5  $\mu\text{m}$  wide branched paraphyses. *Asci* (141–)154–229(–294)  $\times$  (16.8–)18.5–22.2(–26)  $\mu\text{m}$  ( $n = 50$ ), cylindrical to oblong, bitunicate, fissitunicate, with a truncate ocular chamber, a short stipe and simple or knob-like base, containing 2–8 ascospores in uniseriate arrangement. *Ascospores* (19–)26.5–33.5(–39)  $\times$  (10–)13–16.5(–18)  $\mu\text{m}$ , l/w (1.7–)1.9–2.3(–2.8) ( $n = 120$ ), ellipsoid with broadly rounded ends or upper end narrowly rounded, sometimes broadly fusoid, first hyaline, with 1–3 main septa, turning yellow to yellow- or pale brown and finally reddish brown to dark brown with concolorous, rarely paler ends and 8–14(–17) distinct transverse and 2–4 longitudinal septa; constricted at the median primary septum and upper part often slightly wider; surface finely verruculose; in 3 % KOH becoming dark olivaceous to blackish brown.

*Culture characteristics and asexual morph in culture* — Ascospores germinating simultaneously from many cells. *Colony radius* on CMD at 22 °C in the dark 9 mm after 1 wk, 27 mm after 24 d; *colony* olivaceous, but in face view appearing pale grey to greyish brown due to a thick and dense mat of whitish aerial hyphae; reverse dark grey; odour indistinct. *Pycnidia* c. 100–200  $\mu\text{m}$  diam, subglobose, olivaceous, completely covered by aerial hyphae, scattered, immersed, partly erumpent, with whitish conidial drops; spreading from the centre. *Peridium*

thin, pseudoparenchymatous, olivaceous. *Phialides* (3.5–)4.5–6.7(–7.5)  $\times$  (1.7–)2.2–4(–4.2)  $\mu\text{m}$  ( $n = 21$ ), sessile, varying from subglobose over ampulliform and lageniform to subulate; conidia also formed on lateral pegs. *Conidia* (3.2–)3.5–4.3(–6)  $\times$  (0.9–)1–1.2(–1.4)  $\mu\text{m}$ , l/w (2.8–)3.2–4.1(–4.7) ( $n = 50$ ), cylindrical to allantoid, rarely narrowly ellipsoid, 1-celled, hyaline, with 2 small drops, smooth.

*Habitat* — On or in conidiomata of *Melanconis alni* on *Alnus glutinosa*.

*Distribution* — Europe (Austria, France, UK).

*Other materials examined.* AUSTRIA, Kärnten, St. Margareten im Rosental, village area, at the brook Tumpfi, grid square 9452/4, on conidiomata of *Melanconis alni* on a branch of *Alnus glutinosa*, 17 Dec. 1994, W. Jaklitsch W.J. 377 (WU 37000). — FRANCE, Chaville, on conidiomata of *Melanconis alni* on *Alnus glutinosa*, soc. *Cytospora* sp., Apr. 1860, L.-R. Tulasne (PC 0706652, *holotype* of *Fenestella minor*; donated to PC in 1873 as *Sphaeria fenestrata deminuta* in herb).

*Notes* — The fungal host of *P. tetratrupha* is clearly *Melanconis alni*, usually present as asexual morph and easily identifiable by the white central stromatic column and the brown conidia having a pale median band. Conidia of the host are present directly below ascomata in all studied specimens and usually adhere in masses to the peridium. The holotype of *Fenestella minor* has scant and mostly immature material, whereas the holotype of *Valsa tetratrupha* has well-developed ascomata with mostly 8-spored asci, although 4-spored asci are given in the protologue. The number of ascospores in the ascus depends much of the developmental condition of ascomata.

***Parafenestella vindobonensis*** Jaklitsch & Voglmayr, *sp. nov.* — MycoBank MB829758; Fig. 20

*Etymology.* For its occurrence in Vienna, Austria.

*Holotype.* AUSTRIA, Vienna, 21st district, Wasserpark, on *Cytospora* sp. on *Salix babylonica*, soc. *Massarina* sp., *Parafenestella salicis* and a pycnidial fungus with fusoid, hyaline, 1-celled conidia, 27 Jan. 2018, W. Jaklitsch (WU 37015; ex-type culture CBS 145265 = C302).

*Ascomata* (240–)308–425(–450)  $\mu\text{m}$  ( $n = 13$ ) diam, globose, subglobose or pyriform, black, immersed in bark, partially erumpent, forming more or less valsoid groups in usually loose connection by hyaline to dark brown, thick-walled, 2–5  $\mu\text{m}$  wide subicular hyphae or entirely covered by subiculum, sometimes tightly aggregated in small groups on inner bark and on conidiomata and pseudostromata of a *Cytospora* sp., partly blackening inner bark. *Ostiolar areas* (70–)75–145(–160)  $\mu\text{m}$  ( $n = 11$ ) diam, indistinct or papillate, black, rounded or angular in section. *Peridium* 15–65(–80)  $\mu\text{m}$  thick, pseudoparenchymatous, consisting of (4–)5–10(–12)  $\mu\text{m}$  ( $n = 40$ ) wide cells, outside thick-walled and dark brown, paler and slightly thinner-walled to the inside. *Hamathecium* consisting of numerous 1–3  $\mu\text{m}$  wide, branched paraphyses with free ends. *Asci* (162–)179–214(–228)  $\times$  (12.5–)13.5–15.5(–16)  $\mu\text{m}$  ( $n = 25$ ), cylindrical, bitunicate, fissitunicate, with a distinct ocular chamber, a short stipe and simple or knob-like base, containing 4–8 ascospores in uniseriate arrangement. *Ascospores* (20–)24.5–30.5(–37.5)  $\times$  (8.5–)9.5–11(–13)  $\mu\text{m}$ , l/w (2–)2.4–2.9(–3.4) ( $n = 85$ ), oblong, fusoid or narrowly ellipsoid, first hyaline, with 1–6 main septa, turning yellowish, pale, yellow- to golden or medium brown with concolorous or slightly paler ends, thick-walled, when mature with 7–9(–11) thick transverse and 1–2(–3) septa, constricted at the median or suprmedian primary septum, smooth, containing minute droplets; in 3 % KOH turning greenish to yellow-brown when young, dark olivaceous when mature.

*Culture characteristics and asexual morph in culture* — *Colony radius* on CMD at 22 °C in the dark 7–8 mm after 1 wk, 17–18 mm after 2 wk, 28 mm after 25 d; *colony* first hyaline to





**Fig. 20** *Parafenestella vindobonensis*. a–e1. Sexual morph (WU 37015). a–b. Ascomata in face view; c–d. ascomata in vertical section (with subicular disc in c; on *Valsa* ascomata in d); e–g. asci (note paraphysis in e); h. peridium in vertical section; i. aged hamothecium; j–m. ascus apices (immature in j–l); n–e1. ascospores (n–o. immature); f1–l1. asexual morph in culture (CBS 145265 (C302) from CMD at 22 °C); f1. pycnidia; g1–h1. phialides; i1–l1. conidia (e–g, j–n, y–e1. in 3 % KOH). — Scale bars: a–d = 250 µm; e–h = 20 µm; i, q, s–v, e1 = 10 µm; j–p, r, w, x–d1, g1–h1 = 7 µm; f1 = 150 µm; i1–l1 = 3 µm.

whitish, thick, dense, turning olivaceous, later greyish brown from the centre, covered by a velvety mat of whitish to brownish aerial hyphae; reverse dark grey to black; odour indistinct. *Pycnidia* appearing after 4 d, mostly solitary, greenish; formation of pycnidia not reproducible on CMD. *Colony* on MEA grey, aerial hyphae forming a loose mesh over numerous pycnidia aggregating in dense masses. *Pycnidia* c. 60–130 µm diam, hyaline, turning olivaceous from the base, globose, with grey-

ish olivaceous conidial drops. *Peridium* thin, pseudoparenchymatous, olivaceous, surrounded by submoniliform hyphae. *Phialides* (3.8–)5–7.5(–9.5) × (2–)2.5–4(–4.8) µm (n = 39), sessile, varying from subglobose to lageniform, often with a long neck. *Conidia* (2.8–)3.5–4(–4.7) × (1.1–)1.3–2(–2.7) µm, l/w (1.4–)1.9–2.7(–3) (n = 42), oblong to ellipsoid, 1-celled, hyaline, with two or more minute drops, smooth.



**Fig. 21** *Synfenestella pyri*. a–t. Sexual morph (WU 36996). a. Ascomata in face view; b–c. ascomata in vertical section (c. in a *Cytospora* (*Leucostoma*) pseudostroma); d. hamathecial threads; e–f. ascus apices; g–i. asci (g. immature; note sheaths around ascospores); j. peridium and subiculum in vertical section; k–t. ascospores (k. showing size variation); u–w. asexual morph in culture (CBS 144855 (C297) from CMD at 22 °C); u. pycnidia and conidial drops; v–w. conidia (f, i, t. in 3 % KOH). — Scale bars: a–c, u = 250 µm; d–f, l–t = 10 µm; g–i = 25 µm; j–k = 15 µm; v–w = 3 µm.

Habitat — On both morphs of a *Cytospora* (*Valsa*) sp. on *Salix babylonica*.

Distribution — Central Europe (Austria), only known from the type locality in Vienna.

Notes — This species is well characterised by its narrow ascospores.

***Synfenestella*** Jaklitsch & Voglmayr, *gen. nov.* — MycoBank MB829759

*Etymology.* Syn = together with, for its close phylogenetic relationship with *Fenestella*.

*Type species.* *Synfenestella sorbi* Jaklitsch & Voglmayr.

*Ascomata* 300–1000 µm diam, globose, subglobose or pyriform, ostiolate, dark brown to black, immersed below bark epidermis, scattered, forming inconspicuous valsoid groups or conspicuous pseudostromatic pustules on pseudostromata or conidiomata of *Diaporthales*, surrounded and connected by thick-walled subicular hyphae, the latter sometimes short and subsetose in the ostiolar region. *Peridium* c. 15–130 µm thick, thicker and whitish inside in the apical region, pseudoparenchymatous, dark brown and thick-walled outside and pale to hyaline and thin-walled inside. *Hamathecium* consisting of numerous 1–3.5 µm wide, branched and anastomosing paraphyses with free ends in a matrix. *Asci* cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a short or long undulating stipe and simple or knob-like base, containing 4–8 ascospores in (obliquely) uniseriate arrangement. *Ascospores* ellipsoid, oblong to fusoid, sometimes subglobose, symmetric to slightly curved, with upper part often wider, initially 2-celled, hyaline and surrounded by a swelling sheath, developing additional transverse and longitudinal septa, turning yellow to golden brown (when fresh), finally dark brown with concolorous rounded ends, ends sometimes paler or apiculate upon germination, usually strongly constricted at the primary septum; in 3 % KOH surface smooth; turning dark olivaceous to blackish brown.

Culture characteristics and asexual morph in culture — *Colony* on CMD at 22 °C in the dark typically producing a diffusing yellow pigment. *Pycnidia* more or less globose, green to black, densely aggregating and fusing. *Phialides* lageniform, ampulliform, subglobose or subconical, sessile or produced on short simple conidiophores. *Conidia* cylindrical, oblong to allantoid, less commonly ellipsoid, 1-celled, hyaline, with 2 drops, smooth; produced on phialides and pegs.

Habitat — On or in pseudostromata or conidiomata of *Diaporthales* or in loose association with them on *Rosaceae*.

Distribution — Europe, North America.

***Synfenestella pyri*** Jaklitsch & Voglmayr, *sp. nov.* — MycoBank MB829760; Fig. 21

*Etymology.* Referring to its plant host, *Pyrus communis*.

*Holotype.* AUSTRIA, Niederösterreich, Ottenschlag, on *Cytospora* (*Leucostoma*) sp. on a branch of *Pyrus communis*, 19 Mar. 2017, W. Jaklitsch (WU 36996; ex-type culture CBS 144855 = C297).

*Ascomata* (330–)370–620(–720) µm (n = 21) diam, subglobose to globose, immersed in bark singly or in small groups c. 0.6–1.6 mm diam, on or in loose association with both morphs of a *Cytospora* (*Leucostoma*) sp., on and connected by subhyaline to dark brown, thick-walled, 2–5 µm wide *subicular hyphae*, often only visible on the surface due to spore deposits in bark fissures or slightly erumpent, rarely projecting up to 350 µm above the bark surface. *Ostiolar areas* 90–270 µm diam, concealed by spore deposits or short-papillate, black, shiny. *Peridium* 15–70 µm thick, thicker and whitish inside in the osti-

olar region, pseudoparenchymatous, consisting of isodiametric cells (3.8–)5–9(–11) µm (n = 40) diam, outside thick-walled and dark brown, paler to hyaline and thinner-walled to the inside. *Hamathecium* consisting of numerous 1–3.5 µm wide, branched and anastomosing paraphyses with free ends in a matrix. *Asci* (206–)228–268(–296) × (21–)21.8–23.7(–25) µm (n = 14), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a short to long stipe and simple or knob-like base, containing 4–8 ascospores in (obliquely) uniseriate arrangement; unstable in water. *Ascospores* (27–)31.5–42(–51.5) × (13–)15–19(–22) µm, l/w (1.9–)2–2.4(–3.1) (n = 50), very variable, typically ellipsoid to fusoid, sometimes subglobose, symmetric or inequilateral or slightly curved, initially 2-celled, hyaline and surrounded by a sheath, developing additional septa, turning yellow to golden brown (when fresh), finally dark brown with concolorous ends, with 8–14 distinct transverse and 3–5 longitudinal septa, usually strongly constricted at the primary septum; surface smooth; in 3 % KOH turning blackish brown when mature.

Culture characteristics and asexual morph in culture — *Colony radius* on CMD at 22 °C in the dark 13 mm after 1 wk, 27 mm after 4 wk; *colony* circular, thick by a dense whitish to greyish mat of aerial hyphae, first white, turning dull yellow and later becoming concentrically zonate with medium or greyish brown and dark brown zones and a white margin; producing a yellow diffusing pigment; odour indistinct. After 5 d *pycnidia* densely disposed, appearing on and around the plug or in rings, green, turning black, 120–300 µm diam, becoming fused to larger complexes in aged cultures, emitting conidia in white to olivaceous turbid drops. *Phialides* (4–)4.5–7(–7.8) × (2–)2.3–3.3(–4) µm (n = 19), crowded, sessile or on intercalary cells, mostly lageniform, also subconical, ampulliform to subglobose. *Conidia* (3.5–)4–4.8(–5.5) × (1.2–)1.3–2(–2.5) µm, l/w (2.2–)2.4–3.2(–3.8) (n = 32), cylindrical, oblong or allantoid, 1-celled, smooth, with 2 guttules.

Habitat — On *Cytospora* sp. (both morphs; sexual morph of the *Leucostoma* type) on *Pyrus communis*.

Distribution — Europe (Austria), only known from the type locality.

Notes — *Synfenestella pyri* is an inconspicuous fungus. It differs from *Parafenestella* spp. occurring on *Rosaceae* by the swelling sheath visible in immature ascospores within asci.

***Synfenestella sorbi*** (P. Karst.) Jaklitsch & Voglmayr, *comb. nov.* — MycoBank MB829761; Fig. 22

*Basionym.* *Cucurbitaria sorbi* P. Karst., Bidrag Kannedom Finlands Natur Folk 23(2): 62. 1873.

*Synonyms.* *Gibberidea sorbi* (P. Karst.) Kuntze, Revis. Gen. Pl. (Leipzig) 3(2): 481. 1898.

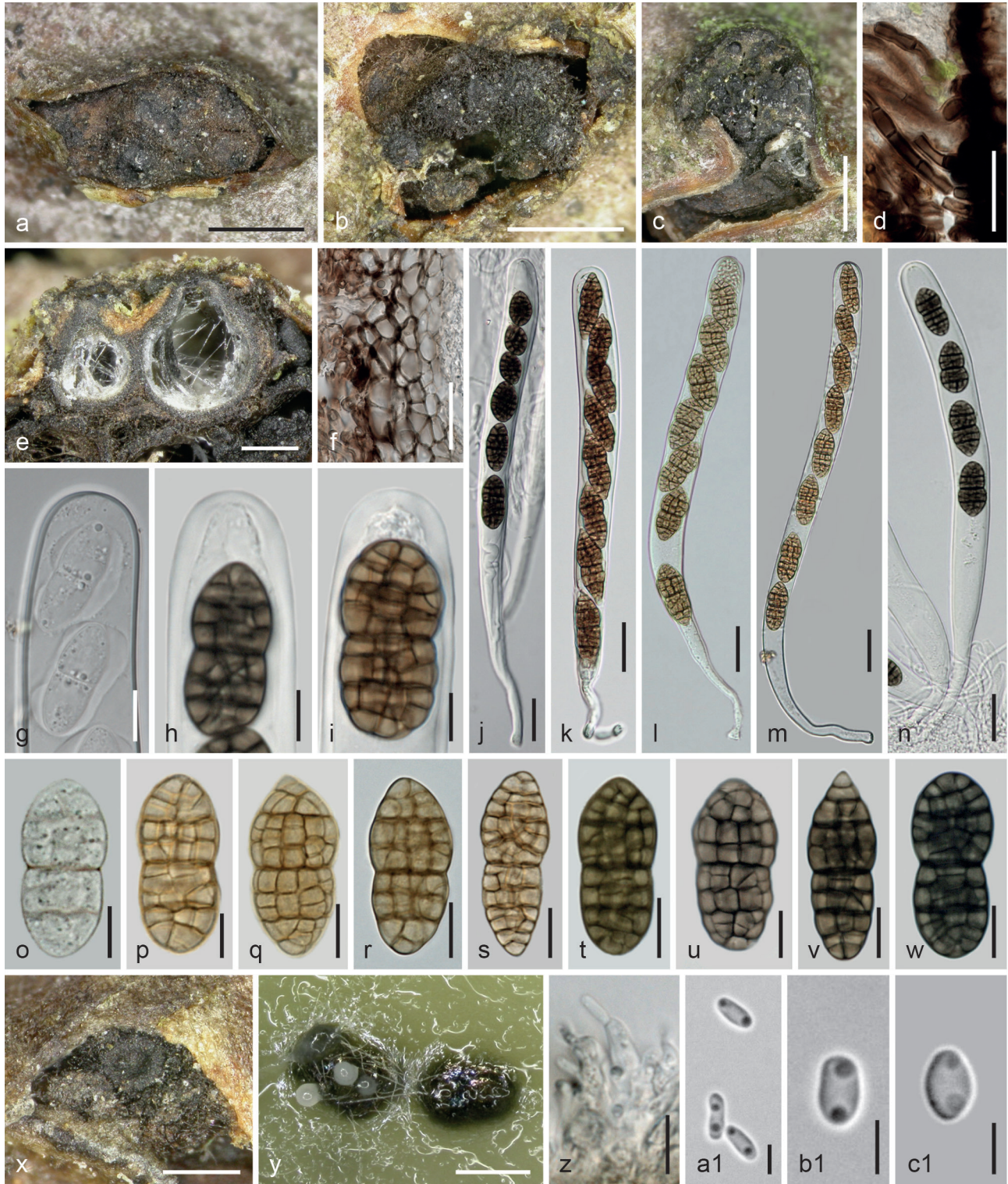
*Fenestella bavarica* Kirschst., Ann. Mycol. 34(3): 193. 1936.

*Lectotype* of *Cucurbitaria sorbi*, here designated. FINLAND, Aboe, on branches of *Sorbus aucuparia*, soc. *Cytospora* (*Leucostoma*) sp., 8 Apr. 1861, P.A. Karsten (H 3686, from the herbarium Karsten; MBT385692). *Epitype* of *Cucurbitaria sorbi*, here designated: AUSTRIA, Niederösterreich, Reichenau, Rax, near Seehütte, on twig of *Sorbus aucuparia*, on/soc. *Cytospora* sp. (*Leucostoma* type; holomorph), 21 Sept. 2014, W. Jaklitsch (WU 36992; MBT385693; ex-epitype culture from ascospores CBS 144862 = FR; culture from conidia = FRa).

*Pseudostromatic pustules* when present 0.9–4.7 mm diam, erumpent from bark and projecting up to 1.5 mm beyond the bark surface, subglobose to pulvinate, roundish to longish in outline; surface brown (compacted subiculum) to dark grey or black (ascomatal apices), sometimes containing also narrow cylindrical ostiolar necks of the *Diaporthe* or *Leucostoma* host. *Ascomata* (330–)425–745(–990) µm (n = 47) diam, globose, subglobose or pyriform, immersed in bark in rows or valsoid configuration, often laterally in the ostiolar region of the fungal

host or inserted in the pustules on a single or two levels upright or obliquely and convergent, singly or up to c. 20 individuals loosely or tightly aggregated and surrounded by usually ample dark brown subiculum, partly directly on the fungal host; subiculum also present below epidermis. *Ascomatal apices* containing inconspicuous ostiolar openings 120–300(–600)  $\mu\text{m}$  ( $n = 46$ ) diam, black, whitish when injured, often flattened. *Subiculum* consisting of hyaline, pale to dark brown, thick-walled, 2–7  $\mu\text{m}$

(widened up to 9.5  $\mu\text{m}$  at points connecting to the peridium) wide hyphae, darker brown, particularly thick-walled, often short and subsetose ('hyphal appendages') near the ascomatal apices. *Peridium* 20–65  $\mu\text{m}$  thick, up to 130  $\mu\text{m}$  at the ostiolar level, pseudoparenchymatous, consisting of cells (4–)7–14(–23)  $\mu\text{m}$  ( $n = 63$ ) diam, outside very dark brown, thick-walled, to the inside gradually paler and thinner-walled and terminated by a narrow layer of pale brownish compressed cells. *Hamathecium*



**Fig. 22** *Synfenestella sorbi*. a–w. Sexual morph. a–b. Ascomata/pseudostromata in face view; c. *Diaporthe impulsa* pseudostroma with a small *S. sorbi* ascoma inserted laterally; d. subsetose subicular hyphae at ascoma apex; e. ascomata above *Diaporthe* ascomata in vertical section; f. peridium and subiculum in vertical section; g–i. ascus apices (g. immature; note sheath around ascospores); j–n. asci; o–w. ascospores (o. immature; p. young); x. pycnidia on the natural host; y–c1. asexual morph from CMD at 22 °C; y. pycnidia and conidial drops; z. phialides; a1–c1. conidia (h, j, n–o, t–w. in 3 % KOH). a, k, u–v. *Cucurbitaria sorbi* lectotype H 3686; b, d–f, l, q–r, z–b1. WU 36994/CBS 144858 (C196); c, i, p, w. WU 36995 (C298); g, m, o, s–t, x–y, c1. WU 36992/CBS 144862 (FR); h, j. *Fenestella bavarica* holotype B 700016482; n. WU 36993. — Scale bars: a–c = 1 mm; d, f, j–n = 25  $\mu\text{m}$ ; e, x–y = 300  $\mu\text{m}$ ; g, q–w = 10  $\mu\text{m}$ ; h–i, o–p, z = 7  $\mu\text{m}$ ; a1–c1 = 3  $\mu\text{m}$ .

consisting of numerous tightly packed, richly branched, 1–3 µm wide paraphyses. Asci (199–)228–297(–377) × (15–)18–21(–23) µm (n = 64), cylindrical to oblong, bitunicate, fissitunicate, with an ocular chamber, a usually long undulating stipe and simple or knob-like base, containing 4–8 ascospores in (obliquely) uniseriate arrangement. Ascospores (22–)28–35(–43.5) × (10–)13–15.5(–18.5) µm, l/w (1.6–)2–2.5(–3.2) (n = 171), very variable in shape, ellipsoid, oblong to fusoid, first hyaline, 2-celled and with a swelling sheath, developing 3–5 main thick septa and later additional thin septa, eventually with 7–13, rarely 15, distinct transverse and (1–)2–4 longitudinal septa, turning golden yellow, yellow brown, pale or reddish brown and finally dark brown; often strongly constricted at the primary septum, upper part often wider, ends usually broadly rounded or upper end narrowly and lower broadly rounded, concolorous, only paler or apiculate upon germination; smooth, containing small droplets, often smaller in the ascus apex, often several in the ascus aborted or aberrant; in 3% KOH turning dark olivaceous to blackish brown. Sexual morph sometimes accompanied by black, shiny, globose, non-papillate, apically collapsing-cupulate pycnidia 90–300 µm diam seated on scant to ample dark brown subiculum on innermost bark layers around old *Leucostoma* pseudostroma (black encasement) and on ?*Diaporthe* ascomata.

Culture characteristics and asexual morph in culture — *Colony radius* on CMD at 22 °C in the dark 8 mm after 1 wk, 21 mm after 3 wk; *colony* circular, thick, dense, first white to bright yellow, aerial hyphae forming a thick white mat, reverse yellow, yellow pigment diffusing into the agar, later colony turning greyish brown from the centre, diffusing pigment turning dull yellow; odour indistinct. After 4 d pycnidia numerous, mostly covered by a white mat of aerial hyphae, 120–330 µm diam, more or less globose, hyaline to greenish olivaceous, turning black, densely aggregating and forming stromatic masses; conidia appearing in whitish turbid drops from many ostioles; peridium pseudoparenchymatous, yellow to dark olivaceous, surrounded by olivaceous to brown hyphae. *Phialides* (4.8–)5–8(–11.5) × 2–4(–5.7) µm (n = 15), very variable, subglobose to ampulliform to lageniform, on short simple conidiophores, also with lateral pegs or on hyaline intercalary cells. *Conidia* (3.3–)4–4.5(–5) × (1.2–)1.5–2(–2.8) µm, l/w (1.5–)2.1–3.1(–3.9) (n = 64), cylindrical, oblong to allantoid, less commonly ellipsoid, 1-celled, hyaline, with 2 drops, smooth.

Habitat — On both morphs of *Cytospora* sp. of the *Leucostoma* type, in pseudostromata on effete ascomata of *Diaporthe impulsula* or in loose association with it on *Sorbus aucuparia*.

Distribution — Europe, North America fide Barr (1990; under *Fenestella subcaespitosa*) and Mirza (1968; under *Cucurbitaria sorbi*).

*Other materials examined.* AUSTRIA, Osttirol, Prägraten am Großvenediger, Hinterbichl, Umbalfälle, on cf. *Diaporthe impulsula* on a dead attached branch of *Sorbus aucuparia*, soc. cf. *Karstenula* sp., *Mollisia caespiticea*, 17 June 2015, H. Voglmayr & W. Jaklitsch (WU 36994; culture CBS 144858 = C196); Steiermark, Deutschlandsberg, Freiländer Alm, W Freiländer Almhütte; E15°02'57" N46°54'47", elev. 1410 m, on *Diaporthe impulsula* on a branch of *Sorbus aucuparia* on the ground, 3 May 2017, G. Friebes (WU 36995; culture C298); highway parking place close to the Pack tunnel, on a branch of *Sorbus aucuparia* attached to the tree, soc. *Diaporthe impulsula*, 17 Feb. 1995, W. Jaklitsch W.J. 499 (WU 36993). — GERMANY, Bavaria, Bayerisch Häusel bei Eisenstein, on *Cytospora (Leucostoma)* on branches of *Sorbus aucuparia*, June 1935, W. Kirschstein (B 700016482, holotype of *Fenestella bavarica*).

Notes — In H two syntypes of *Cucurbitaria sorbi* are extant; No. 3687 (Finland, Vaasa, on *Sorbus*, 12 Aug. 1867, P.A. Karsten) contains mostly *Dothiora pyrenophora*, a fungus with 3-septate ascospores (possibly *Nigrograna* sp.), an immature nectriaceous fungus and only little and old *S. sorbi* (ascospore measurements given on the label: 25–30 × 12–14). In contrast,

No. 3686 contains good material and is thus selected as lectotype. The latter was also examined by M.E. Barr according to the annotation slip. *Synfenestella sorbi* has been found in direct association with both *Cytospora* sp. (*Leucostoma* morph) and *Diaporthe impulsula*. Also other ascomycetes are associated with the fungus, thus parasitism on other fungi may be possible. *Fenestella bavarica* is clearly a synonym of *S. sorbi*. In its holotype, *S. sorbi* grew on *Cytospora (Leucostoma)* morph, has typical long-pedicellate asci with often aberrantly developed ascospores, many aborted or distorted or even globose. At the pustule surface cylindrical *Leucostoma* ostioles peek through brown compacted subiculum of the *Synfenestella*; also a *Tympanis* is present on thin twigs.

*Synfenestella sorbi* is extremely variable in appearance, ranging from solitary ascomata (on *Diaporthe*) to large conspicuous pseudostromata. Hyphal appendages sensu Barr (1990; sub *Fenestella subcaespitosa*) are subcicular hyphae and occur variably in the entire family. In *S. sorbi* they are often but not always differentiated from other hyphae around the ascomatal apices by having a nearly setose appearance, darker colour and slightly thicker walls. The long-pedicellate asci were already described by Mirza (1968; under *Cucurbitaria sorbi*). *Cucurbitaria subcaespitosa* from *S. aria* is clearly a different species and here combined in *Neocucurbitaria*.

There are some sequence differences between isolates derived from specimens containing the fungal host *Cytospora (Leucostoma)* and those growing on *Diaporthe impulsula*. However, as these differences are not convincing and the specimens are morphologically indistinguishable, we do not recognise two separate species. In the lectotype H 3686 *S. sorbi* is associated with *Cytospora*, therefore we epitypify it with material containing the same fungal host.

## KEY TO FENESTELLOID SPECIES

Fungal hosts are only given in the key when different from or additional to *Cytospora* spp. *Parafenestella ostrya* from *Ostrya carpinifolia* (Wanasinghe et al. 2017b) is not included, as we have not seen material of this species. Some species, particularly *Fenestella media* vs *F. subsymmetrica*, *Parafenestella salicis* vs *P. pseudosalicis*, or *P. austriaca* vs *P. rosacearum* cannot be safely distinguished morphologically.

1. Ascospores with a gelatinous sheath . . . . . 2
1. Ascospores lacking a sheath . . . . . 5
2. Sheath persistent during ascospore development. . . . . 3
2. Sheath only present initially in the ascus . . . . . 4
3. Ascospores (52–)58–67(–72) × (16–)19–23(–26) µm, l/w 2.5–3.7, fusoid to subclavate, with c. 17–25 transverse and 3–7 longitudinal septa, surrounded by a sheath around each hemisphere, quickly swelling and losing contours in water; on *Ulmus glabra* . . . . . *Seltsamia ulmi*
3. Ascospores (36–)43–54(–60) × (13–)17–22(–28) µm, l/w 2–3.4, clavate to fusoid, with 12–17 transverse and 4–5 longitudinal septa; on *Acer granatense* . . . . . *Fenestella granatensis*
4. Ascomatal groups inconspicuous, ascospores (27–)32–42(–51) × (13–)15–19(–22) µm, l/w 2–3, typically ellipsoid to fusoid, ends concolorous, with 8–14 distinct transverse and 3–5 longitudinal septa; on *Pyrus* . . . . . *Synfenestella pyri*
4. Ascomata often forming conspicuous pseudostromatic pustules, ascospores (22–)28–35(–44) × (10–)13–16(–19) µm, l/w 1.5–3.2, ellipsoid, oblong to fusoid, with 7–13(–15) transverse and (1–)2–4 longitudinal septa, ends concolorous, only paler or apiculate upon germination; on *Sorbus aucuparia* . . . . . *Synfenestella sorbi*

5. Ascospores immersed evenly or randomly in bark, ascospores (32–)38–52(–63) × (14–)16–21(–25) µm, l/w 1.8–3.3, with 12–18(–20) transverse and 3–7 longitudinal septa, with wall distinctly thicker than septa; ends sometimes apiculate; on *Ulmus* spp. . . . . *Protopenestella ulmi*
5. Ascospores forming inconspicuous groups or well-defined pseudostromatic pustules . . . . . 6
6. Ascospores (36–)49–65(–73) × (14–)18–25(–31) µm, mostly fusoid, with 13–20 transverse and 4–6(–7) longitudinal septa, often with hyaline, 2–7 µm long terminal apiculi; on *Alnus glutinosa* and possibly *Quercus* . . . . . *Fenestella fenestrata*
6. Ascospores smaller . . . . . 7
7. Ascospores (32–)41–53(–61) × (13–)15–19(–23) µm, l/w 2–3.6, with 11–16(–20) transverse and 2–4 longitudinal septa; on *Quercus* and *Salix* . . . . . *Fenestella parafenestrata*
7. Ascospores smaller . . . . . 8
8. Ascospores forming more or less compact pustules, ascospores (28–)32–46(–55) µm long . . . . . 9
8. Ascospores forming inconspicuous groups, ascospores shorter . . . . . 14
9. Ascospores (30–)32–41(–47) × (14–)15–19(–24) µm, l/w 1.8–2.6, with (9–)10–14(–16) transverse and 3–5 longitudinal septa and pale non-apiculate ends; on *Acer opalus* . . . . . *Cucitella opali*
9. Ascospores with apiculate ends . . . . . 10
10. Ascospores (31–)36–46(–55) × (11–)15–20(–23) µm, l/w 2–3, with 11–14(–16) transverse and 2–4 longitudinal septa and usually broad, often hyaline terminal cells sometimes transformed into an ampulliform cellular appendage; on *Crataegus monogyna* . . . . . *Fenestella crataegi*
10. Apiculi not ampulliform, up to 2 µm long, to 5 µm when old . . . . . 11
11. Ascospores with distinctly submedian primary septum, clavate to ellipsoid, (34–)36–45(–49) × (13–)15–19(–22) µm, l/w 2–2.8, with 11–16 distinct transverse and 3–5 longitudinal septa; on *Acer saccharum* . . . . . *Fenestella gardiennetii*
11. Ascospores ellipsoid or fusoid, with submedian to median primary septum . . . . . 12
12. On *Viburnum* spp.; ascospores (29–)38–46(–49) × (12–)15–18(–22) µm, l/w 2–3, with 11–16 transverse and 3–6 longitudinal septa, sometimes distinctly pointed at ends . . . . . *Fenestella viburni*
12. On diverse woody hosts . . . . . 13
13. Ascospores (30–)34–44(–53) × (12–)14–18(–21) µm, l/w 2–3.3, mostly asymmetric, with indistinct 11–18 transverse and 3–6(–7) longitudinal septa . . . . . *Fenestella media*
13. Ascospores (28–)34–44(–55) × (13–)15–20(–25) µm, l/w 1.8–3, asymmetric to subsymmetric, with distinct 11–16 (–18) transverse and 3–6 longitudinal septa . . . . . *Fenestella subsymmetrica*
14. In (sub)alpine regions on *Cotoneaster* and *Salix*; ascospores (19–)24–30.5(–35) × (10.5–)12–14(–15.5) µm, l/w 1.4–2.9, with (7–)8–12(–15) transverse and (2–)3–4 longitudinal septa and concolorous ends . . . . . *Parafenestella alpina*
14. Not exclusively in (sub)alpine regions . . . . . 15
15. On *Melanconis alni* on *Alnus*; ascospores (19–)26–34(–39) × (10–)13–17(–18) µm, l/w 1.7–2.8, with 8–14(–17) distinct transverse and 2–4 longitudinal septa and concolorous, rarely paler ends . . . . . *Parafenestella tetratrupha*
15. On other hosts . . . . . 16
16. On species of *Diaporthe* . . . . . 17
16. Not known to occur on *Diaporthe* . . . . . 18
17. Ascospores (22–)24–30(–32) × (11–)12–14(–16) µm, l/w 1.6–2.5, with (7–)8–12(–13) transverse and 3–4 longitudinal septa and often subacute concolorous, sometimes lighter ends; on *Acer pseudoplatanus* . . . . . *Parafenestella pseudoplatani*
17. Ascospores (26–)29–40(–47) × (11–)13–17(–19) µm, l/w 1.9–2.7, with (8–)9–13(–15) transverse and 3–6 longitudinal septa and often broadly rounded, paler to hyaline end cells; on *Corylus* . . . . . *Parafenestella germanica*
18. On *Salix* spp. . . . . 19
18. On *Rosaceae* . . . . . 23
19. Ascospores (20–)24–31(–38) × (8.5–)9.5–11(–13) µm, l/w 2–3.4, with 7–9(–11) thick transverse and 1–2(–3) longitudinal septa and concolorous or slightly paler ends . . . . . *Parafenestella vindobonensis*
19. Ascospores wider . . . . . 20
20. Ascospores (33–)36–44(–50) × (14–)16–19(–22) µm, l/w 2–2.6, with 11–16 distinct transverse and 3–5 longitudinal septa and mostly concolorous ends . . . . . *Parafenestella parasalicum*
20. Ascospores smaller . . . . . 21
21. Ascospores (22–)27–33(–40) × (11–)13–16(–18) µm, l/w 1.7–2.5, with 9–13(–14) transverse and 3–4 longitudinal septa and concolorous, rarely slightly paler ends . . . . . *Parafenestella salicum*
21. Ascospores with fewer septa . . . . . 22
22. Ascospores (20–)23–29(–34) × (10–)11–14(–15) µm, l/w 1.5–2.7, often inequilateral, with often indistinct (5–6–)7–10(–11) transverse and (1–)2–3 longitudinal septa, the latter often forming parallel lines; ends concolorous, rarely hyaline . . . . . *Parafenestella salicis*
22. Ascospores (23–)25–29(–32) × (11–)12–14(–15) µm, l/w 1.9–2.7, symmetric, with distinct 7–10(–11) transverse and 2–4 longitudinal septa; ends concolorous . . . . . *Parafenestella pseudosalicis*
23. Ascospores (23–)28–36(–42) × (11–)12–16(–18) µm, l/w 1.9–2.8, with 7–12(–14) transverse and 1–3(–5) longitudinal septa; end cells concolorous except for a truncate to slightly convex hyaline terminal part of their walls . . . . . *Parafenestella faberi*
23. Ascospore end cells rounded and concolorous or diffusely to entirely paler to hyaline . . . . . 24
24. Ascospores (25–)27–33(–38) × (12–)13–15(–16) µm, l/w 1.9–2.6, ellipsoid, symmetric, with 9–13(–14) distantly spaced transverse and 3–4(–5) longitudinal septa . . . . . *Parafenestella austriaca*
24. Ascospores (23–)28–35(–45) × (11–)13–17(–19) µm, l/w 1.7–2.6, symmetric to inequilateral, with (7–)9–13(–15) transverse and 2–4(–5) longitudinal septa . . . . . *Parafenestella rosacearum*

## DISCUSSION

### Other species of *Fenestella* (and *Cucurbitaria*)

See notes under the species described in the Taxonomy section above and in Jaklitsch et al. (2018), where many names in *Cucurbitaria* are commented on. In this work we studied particularly European species of *Fenestella* s.lat. with available fresh material. We did not study, e.g., *F. betulae* nor *F. parvula*, because no fresh material from *Betula* was available. No type material of *Fenestella cydoniae* (basinonym *Pleospora cydoniae*) could be located. The protologue may suggest affiliation with *F. media* or a similar species. *Fenestella microspora* was described from *Corylus* in France with ascospores 10–11 × 6–7 µm, thus it is apparently not a member of *Cucurbitariaceae*.

*Fenestella phaeospora* is not a member of the *Cucurbitariaceae* phylogenetically (unpublished results). *Fenestella prunastri* from *Prunus spinosa* in Luxemburg was described with ascospores having 3–4 transverse and 1 longitudinal septa, 20–22 × 8–9 µm, pale yellow, as similar to *F. lycii*, i.e., not a species of *Fenestella*, but possibly rather belonging to *Camarosporidiellaceae* or *Coniothyriaceae*. Species with muriform ascospores on *Lycium* spp. (*Cucurbitaria varians*, *Fenestella lycii*) are referable to *Camarosporium*. *Fenestella subvestita* from *Alnus glutinosa* in Lyngby, Denmark, was described with ascospores 15–19 × 7.5–8.5 µm having 3 transverse and 1 longitudinal septa, i.e., not a species of *Cucurbitariaceae*. The genera *Teichospora* and *Thyridium* may house additional cucurbitariaceous species, but the task to examine all available type materials of these genera is beyond this work.

### Molecular phylogeny

As shown in Fig. 1, there is significant infraspecific variation in taxa of the genera *Parafenestella* and *Synfenestella*. On the other hand, in those *Fenestella* species, where several isolates were available, *F. media*, *F. subsymmetrica* and *F. viburni*, there is no or very little variation in DNA sequences of all markers. This is particularly interesting, as most species of all genera grow on *Cytospora* spp., i.e., they share the same ecology. The reason for the infraspecific variability is unclear but may indicate that these lineages are in the process of ongoing speciation, probably triggered by host specificity on different *Cytospora* hosts. This, however, is difficult to assess, as the identification of the effete *Cytospora* hosts is usually impossible when ascomata are produced.

### Ecology, hosts and development

Fenestelloid fungi produce their ascomata and conidiomata on or in tight association with effete ascomata and conidiomata of mostly if not always *Diaporthales*, in temperate zones mostly in the cold season (late autumn to early spring). This means that climatic conditions have first to be favourable enough to promote development of the fungal host and secondly, the following period must be long and favourable enough to support ascomatal development and maturation. In the cold season such periods are often short and irregular, as temperatures may variably decrease below 0 °C often terminating fungal development, and this may influence development of ascospores dramatically. Moisture is usually not a criterion limiting fungal development in the cold season, but in recent years and decades, even this has changed in many temperate regions, where little precipitation occurs even in winter. At high elevations (montane to alpine levels) impact on development by climatic variation is even more drastic. One example is *Synfenestella sorbi*, whose plant host *Sorbus aucuparia* occurs from lowlands to subalpine levels. As a result, ascospores often vary tremendously with regard to size and shape, even within a single ascus, in this but also other species. Often only one to four ascospores in an ascus are mature and others are aborted. The resulting drastic infraspecific variation of ascospore characters makes species recognition and identification using morphological traits alone extremely difficult.

Also, size and development of ascomatal groups or pseudostromata vary considerably, as they depend on the size and development of the *Cytospora* (and other) hosts, thickness of twigs or branches, and again on (micro-)climatic conditions on twigs and branches determining the magnitude of infection of the present host pseudostromata or conidiomata. As the latter are mostly effete when colonised by the *Fenestella*, we have no information on host identity on the species level, which is difficult also due to the unsettled taxonomy of *Cytospora* and the fact that several *Cytospora* species may occur on a single

host plant. Specificity toward the fungal host is unknown, as, e.g., *Fenestella media* occurs on several plant hosts, which may be substrates of different *Cytospora* spp. Thus, *F. media* either has a wide specificity regarding its *Cytospora* host species or alternatively, it grows on a single *Cytospora* sp., which occurs on many different plants. As species of *Cytospora* are numerous and common, we expect that many more species of fenestelloid fungi will be described in future, at least from temperate zones worldwide.

### Morphological characters

Ascomata of fenestelloid fungi are always immersed in to erumpent from bark and have a marked tendency to form groups, besides forming solitary ascomata in a colony, too. Numbers of ascomata in a group is often less than 10 in *Parafenestella*, but may be much higher in *Fenestella* and *Synfenestella*. A few species of the latter genera may produce conspicuous pseudostromatic pustules. Morphological variation in *Synfenestella* is remarkable, as fructifications of *S. pyri* are very inconspicuous and consist of only few ascomata in a group, and asci are mostly short-stipitate, while in contrast *S. sorbi* often forms large conspicuous pseudostromata and asci are long-stipitate. However, the swelling sheath in young ascospores within asci unites the two species. It should be borne in mind that elongated ascus stipes and partly biseriate arrangement of ascospores in microscopic mounts may also be consequences of exerting pressure on the cover slip in order to free asci from the hymenium. The peridium of *Fenestella* was characterised as 3-layered by Barr (1990; sub *Fenestellaceae*). However, the innermost narrow layer of brownish compressed and elongated cells is not always present and the outer two layers (dark brown, of thick-walled cells outside, followed by thinner-walled and paler brown to hyaline cells) are, after consideration of all species, rather a single layer with internal variation. The outermost region can be narrow and then more easily be interpreted as a layer of its own, particularly when the transition to lighter colour and thin walls, which basically is always gradual, takes place at a short distance. This is especially obvious in *F. fenestrata* and *F. parafenestrata* and in the three sibling species *F. media*, *F. subsymmetrica* and *F. viburni*. The hamathecium has been identified as apically free paraphyses present among immature asci in several species, thus this may be a character common to the entire family *Cucurbitariaceae* (see also Jaklitsch et al. 2018). Morphology and illustration of several species in this work was done using dried material; thus images of fresh vital ascospores are missing. However, ascospores of fenestelloid fungi are mostly yellow-brown or golden-brown when fresh, but turn dark brown upon drying and may often be dark reddish brown in herbarium material. They turn greenish olivaceous when immature to blackish brown when mature in 3 % KOH. Verruculose ornamentation has been seen in many species. This might however be an effect of drying of the perispore.

### Asexual morphs in the *Cucurbitariaceae*

As pointed out by Jaklitsch et al. (2018), asexual morphs of the *Cucurbitariaceae* do not offer sufficient traits for reliable distinction at the species or generic level. As we have seen here, asexual morphs of all fenestelloid fungi are morphologically similar and may be termed phoma-like.

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## REFERENCES

- Barr ME. 1990. Melanommatales (Loculoascomycetes). North American Flora. Series II 13: 1–129.
- Boehm EWA, Mugambi GK, Miller AN, et al. 2009. A molecular phylogenetic reappraisal of the Hysteriaceae, Mytiliniaceae and Gloniaceae (Pleosporomycetidae, Dothideomycetes) with keys to world species. *Studies in Mycology* 64: 49–83.
- Brockmann I. 1976. Untersuchungen über die Gattung *Discostroma* Clements (Ascomycetes). *Sydowia* 28: 275–338.
- Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* 91: 553–556.
- Checa J, Jaklitsch WM, Blanco MN, et al. 2015. Two new species of *Thyronectria* from Mediterranean Europe. *Mycologia* 107: 1314–1322.
- Crous PW, Groenewald JZ. 2017. The genera of fungi – G 4: *Camarosporium* and *Dothiora*. *IMA Fungus* 8: 131–152.
- De Hoog GS, Gerrits van den Ende AHG. 1998. Molecular diagnostics of clinical strains of filamentous basidiomycetes. *Mycoses* 41: 183–189.
- Fuckel L. 1870 '1869–1870'. *Symbolae Mycologicae. Beiträge zur Kenntnis der Rheinischen Pilze. Jahrbücher des Nassauischen Vereins für Naturkunde* 23–24: 1–459.
- Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis, program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Jaklitsch WM. 2009. European species of *Hypocrea* – Part I. *Studies in Mycology* 63: 1–91.
- Jaklitsch WM, Baral HO, Lücking R, et al. 2016b. Syllabus of plant families – A. Engler's Syllabus der Pflanzenfamilien Part 1/2: Ascomycota. 13th edn. Borntraeger, Berlin.
- Jaklitsch WM, Barr ME. 1997. *Dictyoportha bipapillata* – a new combination and a key to the species of *Dictyoportha*. *Österreichische Zeitschrift für Pilzkunde* 6: 45–49.
- Jaklitsch WM, Checa J, Blanco MN, et al. 2018. A preliminary account of the Cucurbitariaceae. *Studies in Mycology* 90: 71–118.
- Jaklitsch WM, Gardiennet A, Voglmayr H. 2016a. Resolution of morphology-based taxonomic delusions: *Acrocordiella*, *Basiseptospora*, *Blogiascospora*, *Clypeosphaeria*, *Hymenoplella*, *Lepteutypa*, *Pseudapiospora*, *Requienella*, *Seiridium* and *Strickeria*. *Persoonia* 37: 82–105.
- Jaklitsch WM, Komon M, Kubicek CP, et al. 2005. *Hypocrea voglmayrii* sp. nov. from the Austrian Alps represents a new phylogenetic clade in *Hypocrea*/*Trichoderma*. *Mycologia* 97: 1365–1378.
- Jaklitsch WM, Olariaga I, Voglmayr H. 2016c. *Teichospora* and the *Teichosporaceae*. *Mycological Progress* 15: 31 (1–20).
- Jaklitsch WM, Stadler M, Voglmayr H. 2012. Blue pigment in *Hypocrea caerulescens* sp. nov. and two additional new species in sect. *Trichoderma*. *Mycologia* 104: 925–941.
- Jaklitsch WM, Voglmayr H. 2014. Persistent hamathecial threads in the Nectriaceae, Hypocreales: *Thyronectria* revisited and re-instated. *Persoonia* 33: 182–211.
- Jaklitsch WM, Voglmayr H. 2017. Three former taxa of Cucurbitaria and considerations on *Petrakia* in the Melanommataceae. *Sydowia* 69: 81–95.
- Kauff F, Lutzoni F. 2002. Phylogeny of Gyalectales and Ostropales (Ascomycota, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. *Molecular Phylogenetics and Evolution* 25: 138–156.
- Kohlmeyer J, Schatz S. 1985. *Aigialus* gen. nov. (Ascomycetes) with two new marine species from mangroves. *Transactions of the British Mycological Society* 85: 699–707.
- Landvik S, Egger K, Schumacher T. 1997. Towards a subordinal classification of the Pezizales (Ascomycota): phylogenetic analyses of SSU rDNA sequences. *Nordic Journal of Botany* 17: 403–418.
- Liu YL, Whelen S, Hall BD. 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16: 1799–1808.
- Mirza F. 1968. Taxonomic investigations on the ascomycetous genus *Cucurbitaria* S.F. Gray. *Nova Hedwigia* 16: 161–213.
- Müller K. 2004. PRAP - calculation of Bremer support for large data sets. *Molecular Phylogenetics and Evolution* 31: 780–782.
- O'Donnell K, Cigelnik E. 1997. Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* 7: 103–116.
- Phookamsak R, Hyde KD. 2015. Fenestellaceae. *Mycosphere* 6: 402–413.
- Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1- $\alpha$  sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84–98.
- Saccardo PA. 1884. *Miscellanea Mycologica I (V)*. *Atti dell'Istituto Veneto di Scienze* 2 (VI): 5 (1–29).
- Silvestro D, Michalak I. 2012. raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution* 12: 335–337.
- Spatafora JW, Sung GH, Johnson D, et al. 2006. A five-gene phylogeny of Pezizomycotina. *Mycologia* 98: 1018–1028.
- Stamatakis E. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Swofford DL. 2002. PAUP\* 4.0b10: phylogenetic analysis using parsimony (\*and other methods). Sinauer Associates, Sunderland, Massachusetts.
- Thiers B. 2018. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>.
- Tulasne LR, Tulasne C. 1863. *Selecta Fungorum Carpologia* 2. Paris.
- Valenzuela-Lopez N, Cano-Lira JF, Guarro J, et al. 2018. Coelomycetous Dothideomycetes with emphasis on the families Cucurbitariaceae and Didymellaceae. *Studies in Mycology* 90: 1–69.
- Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238–4246.
- Voglmayr H, Akulov OY, Jaklitsch WM. 2016a. Reassessment of *Allantonectria*, phylogenetic position of *Thyronectroidea*, and *Thyronectria caraganae* sp. nov. *Mycological Progress* 15: 921.
- Voglmayr H, Castlebury LA, Jaklitsch WM. 2017. *Juglanconis* gen. nov. on Juglandaceae, and the new family Juglanconidaceae (Diaporthales). *Persoonia* 38: 136–155.
- Voglmayr H, Gardiennet A, Jaklitsch WM. 2016b. *Asterodiscus* and *Stigmatodiscus*, two new apothecial dothideomycete genera and the new order Stigmatodiscales. *Fungal Diversity* 80: 271–284.
- Voglmayr H, Jaklitsch WM. 2008. Prosthecium species with *Stegosporium* anamorphs on *Acer*. *Mycological Research* 112: 885–905.
- Voglmayr H, Jaklitsch WM. 2011. Molecular data reveal high host specificity in the phylogenetically isolated genus *Massaria* (Ascomycota, Massariaceae). *Fungal Diversity* 46: 133–170.
- Voglmayr H, Jaklitsch WM. 2014. Stilbosporaceae resurrected: generic reclassification and speciation. *Persoonia* 33: 61–82.
- Voglmayr H, Jaklitsch WM. 2017. *Corynespora*, *Exosporium* and *Helminthosporium* revisited – new species and generic reclassification. *Studies in Mycology* 87: 43–76.
- Voglmayr H, Rossman AY, Castlebury LA, et al. 2012. Multigene phylogeny and taxonomy of the genus *Melanconiella* (Diaporthales). *Fungal Diversity* 57: 1–44.
- Von Niessl G. 1872. Beiträge zur Kenntniss der Pilze. *Verhandlungen des naturforschenden Vereines in Brünn* 10: 153–217, pl. 3–7.
- Wanasinghe DN, Hyde KD, Jeewon R, et al. 2017a. Phylogenetic revision of *Camarosporium* (Pleosporineae, Dothideomycetes) and allied genera. *Studies in Mycology* 87: 207–256.
- Wanasinghe DN, Phookamsak R, Jeewon R, et al. 2017b. A family level rDNA based phylogeny of Cucurbitariaceae and Fenestellaceae with descriptions of new *Fenestella* species and *Neocucurbitaria* gen. nov. *Mycosphere* 8: 397–414.
- Werle E, Schneider C, Renner M, et al. 1994. Convenient single-step, one tube purification of PCR products for direct sequencing. *Nucleic Acids Research* 22: 4354–4355.
- White TJ, Bruns T, Lee S, et al. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, et al. (eds), *PCR protocols: A guide to methods and applications*: 315–322. Academic Press, San Diego.