

Hidden diversity in *Thyridaria* and a new circumscription of the *Thyridariaceae*

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Abstract: A multigene analysis of a combined ITS-LSU-SSU-*rpb2-tef1* sequence data matrix was applied to infer the phylogenetic position of the genus *Thyridaria* in the Pleosporales. The generic type of *Thyridaria*, *T. broussonetiae* (syn. *T. incrustans*), is situated in a clade currently named *Rousoellaceae*, which becomes a synonym of *Thyridariaceae*. However, *Thyridaria rubronotata* does not belong to this clade, but is here recognised as *Cyclothyriella rubronotata* in its own family *Cyclothyriellaceae*. The *Thyridariaceae* contain the genera *Thyridaria*, *Rousoella*, *Rousoellopsis*, *Neorousoella* and the new genus *Parathyridaria*. *Rousoella acaciae* is combined in *Thyridaria* and *Rousoella percuteana* in *Parathyridaria*. *Ohleria modesta* and an additional new thyridaria-like genus, *Hobus*, are found to represent isolated lineages with unresolved phylogenetic affinities within the Pleosporales. For *Ohleria* the new family *Ohleriaceae* is established. *Melanomma fuscidulum* belongs to *Nigrograna*, and three new species are described in this genus. A strain named *Biatrispora marina* clusters with *Nigrograna*. Based on the newly recognised species in *Nigrograna*, morphology and ecology do in no way correlate among these genera, therefore we erect the new family *Nigrogranaceae* for *Nigrograna* and recommend to discontinue the use of the family name *Biatrisporaceae* until fresh material of *B. marina* becomes available for sequencing.

Key words: Ascomycota, *Cyclothyrium*, *Dothideomycetes*, *Melanomma*, Phylogenetic analysis, *Pleosporales*.

Taxonomic novelties: **New families:** *Cyclothyriellaceae* Jaklitsch & Voglmayr, *Nigrogranaceae* Jaklitsch & Voglmayr, *Ohleriaceae* Jaklitsch & Voglmayr; **New genera:** *Cyclothyriella* Jaklitsch & Voglmayr, *Hobus* Jaklitsch & Voglmayr, *Parathyridaria* Jaklitsch & Voglmayr; **New species:** *Hobus wogradensis* Jaklitsch & Voglmayr, *Nigrograna mycophila* Jaklitsch, Friebe & Voglmayr, *N. norvegica* Jaklitsch & Voglmayr, *N. obliqua* Jaklitsch & Voglmayr, *Parathyridaria ramulicola* Jaklitsch, Fourn. & Voglmayr; **New combinations:** *Cyclothyriella rubronotata* (Berk. & Broome) Jaklitsch & Voglmayr, *Nigrograna fuscidula* (Sacc.) Jaklitsch & Voglmayr, *Parathyridaria percuteana* (S.A. Ahmed, D.A. Stevens, W.W.J. van de Sande & G.S. de Hoog) Jaklitsch & Voglmayr, *Thyridaria acaciae* (Crous & M.J. Wingf.) Jaklitsch & Voglmayr; **Epitypifications (basionyms):** *Cucurbitaria broussonetiae* Sacc., *Sphaeria fuscidula* Sacc., *Melogramma rubronotatum* Berk..

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INTRODUCTION

Besides *Thyronectria* (Jaklitsch & Voglmayr 2014, Checa *et al.* 2015), *Thyridaria* is another genus that Saccardo derived and separated from *Thyridium*. In order to clarify the concept of the genus, the identity and history of its generic type has to be evaluated: *Cucurbitaria broussonetiae* was described by Saccardo (1873). In 1875 (Saccardo 1875a) he described *Thyridaria incrustans* in the schedae of his Mycotheca Veneta and based it on *Cucurbitaria broussonetiae*, giving *Broussonetia* as the exclusive host. In the same year (Saccardo 1875b) he established the genus *Thyridaria* with *T. incrustans* as its generic type and *C. broussonetiae* as its synonym. Later, he (Saccardo 1883) listed many different hosts for *T. incrustans* and thus produced a collective name rather than a well-defined name for a single species (see below). As *C. broussonetiae* is older than *T. incrustans*, Traverso (1906, p. 302) noted that Berlese (1894) and Saccardo (1875b) preferred the name *Thyridaria incrustans* contrary to nomenclatural rules and combined *C. broussonetiae* in *Thyridaria* with *T. incrustans* as a synonym. Traverso's (1906) treatment is nomenclaturally correct.

Several authors studied *Thyridaria* or selected members of this genus. Chesters (1938) studied type material of *T. rubronotata* and compared morphology, ascoma ontogeny and a putative asexual morph of fresh material of *T. rubronotata*

collected and isolated from *Acer* and *Ulmus* with *Melanomma pulvis-pyrius* and *M. fuscidulum*. He also recognised conspecificity of *T. delognensis* (originally described from *Acer pseudoplatanus*) and *Massaria lateritia* Tul. (described from *Aesculus*) with *T. rubronotata* (originally described from *Ulmus*). He reported synchronous development of pycnidia with ascospores and found that the asexual morph characterised by pycnidia forming slimy masses of asexual spores, is like the aposphaeria-like morphs of *Melanomma*, only that the conidia turn brownish and are thus coniothyrium-like. He accepted the name *Cytoplea juglandis*, originally described as *Phoma ulmicola* Berk., for it. Wehmeyer (1941) monographed *Thyridaria*, accepted fifteen species in the genus and excluded nine species. He examined type material of *T. incrustans* extant in PAD. He reported on the difficulty to distinguish *Thyridaria* from *Kalmusia*, noting that both *Thyridaria* and *Kalmusia* differed from *Thyridium* only in the lack of longitudinal septa in the ascospores. *Kalmusia* was further differentiated by scattered perithecia in an effused stroma from *Thyridaria*, which was characterised by aggregated perithecia or valsoid stromata. However, the latter difference was hampered by an extremely wide variation in the aggregation of the perithecia within the genus *Thyridaria* such as in *T. rubronotata*, where ascospores may be definitely aggregated in numerous small eruptive pustules, densely crowded in extensive layers or

scattered singly. Oddly enough, he accepted *T. incrustans* instead of *T. broussonetiae* as the generic type of *Thyridaria*. Barr (1990) recognised *T. broussonetiae* as the generic type of *Thyridaria* and placed the genus in the *Platystomaceae*. Later (Barr 2003) she referred it to the *Didymosphaeriaceae*. The concept of *Kalmusia*, which is additionally characterised by long-stipitate asci, was recently stabilised by neotypification of the type species *K. ebuli* (Zhang *et al.* 2014), albeit with a specimen not collected from the type host genus *Sambucus* but from *Populus*.

We studied many specimens having thyridaria-like morphology and found that they are distributed among at least nine clades of the *Pleosporales*. We treat here taxa of four unrelated clades. Below we report that *Thyridaria* is polyphyletic, that *T. broussonetiae*, which belongs to a clade encompassing the *Rousoellaceae* and in effect the *Thyridariaceae*, is not congeneric with *T. rubronotata*, erect the new generic name *Cylothryiella* for the latter, which forms a family of its own, and describe some other thyridaria-like fungi in different new or known genera. We provide also DNA data and a redescription of *Ohleria modesta*.

MATERIALS AND METHODS

Isolates and specimens

All newly prepared isolates used in this study originated from ascospores or conidia of fresh specimens. Strain numbers 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 CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands (CBS). Details of the specimens used for morphological investigations are listed in the Taxonomy section under the respective descriptions. Herbarium acronyms are according to Thiers (2016). Specimens have been deposited in the Herbarium of the Institute of Botany, University of Vienna (WU).

Culture preparation, growth rate determination and phenotypic analysis

Cultures were prepared and maintained as described previously (Jaklitsch 2009). Microscopic observations were made in tap water except where noted. Morphological analyses of microscopic characters were carried out as described earlier (Jaklitsch 2009). Methods of microscopy included stereomicroscopy using a Nikon SMZ 1500 and Nomarski differential interference contrast (DIC) using the compound microscope Nikon Eclipse E600. Images and data were gathered using a Nikon Coolpix 4500 or a Nikon DS-U2 digital camera and measured with NIS-Elements D v. 3.0. Measurements are reported as maximum and minimum 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 complete internally transcribed spacer region (ITS1-5.8S-ITS2) and a ca. 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 ca. 1.1–1.4 kb fragment of the small subunit nuclear ribosomal DNA (nSSU rDNA) with primers SL1 (Landvik *et al.* 1997) and NSSU1088 (Kauff & Lutzoni 2002), a ca. 1.2 kb fragment of the RNA polymerase II subunit 2 (*rpb2*) with primers fRPB2-5f and fRPB2-7cr (Liu *et al.* 1999); and a ca. 1.3–1.5 kb fragment of the translation elongation factor 1- α (*tef1*) containing two introns and a part of the exon with primers EF1-728F (Carbone & Kohn 1999) and TEF1LLErev (Jaklitsch *et al.* 2005). For a herbarium specimen of *Nigrograna obliqua* (MF), the ITS was directly amplified from ascomatal contents according to a modified protocol described in Jaklitsch & Voglmayr (2012). Ascospores were cut with a sterile razor blade, the content transferred with a sterile forceps first to 1× TE buffer, and then to a reaction tube containing the PCR master mix with primers V9G and ITS5 (White *et al.* 1990). PCR products were purified using an enzymatic PCR cleanup (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, the primers ITS4 (White *et al.* 1990) and LR3 (Vilgalys & Hester 1990) were used for the ITS-LSU region. Sequencing was performed with an automated DNA sequencer (3730xl Genetic Analyzer Applied Biosystems).

Analysis of sequence data

For phylogenetic analyses, a combined matrix of ITS-LSU, SSU, *rpb2* and *tef1* sequences was produced. According to results of BLAST searches of the LSU and the tree topology of Hyde *et al.* (2013), GenBank sequences of selected *Pleosporales* (Table 1) were included to reveal the phylogenetic relationships of the taxa treated here. In addition, selected members of the families *Occultibambusaceae* (Dai *et al.* 2016), *Paradictyoarthriaceae* (Liu *et al.* 2015) and *Torulaceae* (Crous *et al.* 2015) were added. *Karstenula rhodostoma* was included as a member of *Didymosphaeriaceae* according to Tanaka *et al.* (2015). Two species of *Massaria* (*Massariaceae*) were selected as outgroup according to Voglmayr & Jaklitsch (2011) and Hyde *et al.* (2013). All alignments were produced with the server version of MAFFT 7 (<http://mafft.cbrc.jp/alignment/server/>), using the default settings for the SSU rDNA and the *rpb2*; for the ITS-LSU and the *tef1* the E-INS-i and the G-INS-i iterative refinement methods were implemented, respectively, with a gap opening penalty of 1.0. The resulting alignments were checked and refined using BioEdit v. 7.0.4.1 (Hall 1999). For phylogenetic analyses, all sequence alignments were combined. After exclusion of ambiguously aligned regions from the ITS1 (the first 262 characters) and *tef1* introns (418 characters) and large insertions from the SSU, the final matrix contained 1484 nucleotide characters from the ITS-LSU rDNA, 995 from the SSU rDNA, 1082 from *rpb2* and 1316 from *tef1*.

Maximum parsimony (MP) bootstrap analysis was performed with PAUP v. 4.0a149 (Swofford 2002), with 1000 bootstrap replicates using 5 rounds of heuristic search replicates with

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

Taxon	Strain	Voucher	GenBank accession numbers				
			ITS	LSU	SSU	<i>rpb2</i>	<i>tef1</i>
<i>Alternaria alternata</i>	CBS 916.96		–	DQ678082	KC584507	KC584375	DQ677927
<i>Amniculicola lignicola</i>	CBS 123094		–	EF493861	EF493863	EF493862	GU456278
<i>Anteaglonium parvulum</i>	SMH5223		–	GQ221909	–	–	GQ221918
<i>Arthopyrenia salicis</i>	CBS 368.94		KF443410	AY538339	AY53833	KF443397	KF443404
<i>Cylothyriella rubronotata</i>	CBS 419.85		–	GU301875	–	GU371728	GU349002
	CBS 121892; TR	WU 36862	KX650541	KX650541	–	KX650571	KX650516
	TR1	WU 36863	KX650542	KX650542	–	KX650572	KX650517
	TR3	WU 36859	KX650543	KX650543	–	KX650573	KX650518
	CBS 141486; TR9	WU 36858	KX650544	KX650544	KX650507	KX650574	KX650519
	TR9a	WU 36858	KX650545	KX650545	–	–	KX650520
<i>Dendryphion europaeum</i>	CPC 22943		KJ869146	KJ869203	–	–	–
<i>Herpotrichia diffusa</i>	CBS 250.62		–	DQ678071	GU205239	DQ677968	DQ677915
<i>Hobus wogradensis</i>	CBS 141484; TI	WU 36874	KX650546	KX650546	KX650508	KX650575	KX650521
<i>Karstenula rhodostoma</i>	CBS 690.94		–	GU301821	GU296154	GU371788	–
<i>Leptosphaeria doliolum</i>	CBS 505.75		–	GU301827	GU296159	KT389640	GU349069
<i>Lophiostoma macrostomum</i>	JCM 13544		–	AB619010	AB618691	JN993491	–
<i>Lophiotrema nucula</i>	CBS 627.86		–	GU301837	GU296167	GU371792	GU349073
<i>Massaria campestris</i>	M28		–	HQ599385	HQ599449	HQ599459	HQ599325
<i>M. inquinans</i>	M19		–	HQ599402	HQ599444	HQ599460	HQ599342
<i>Massarina eburnea</i>	CBS 473.64		–	GU301840	GU296170	GU371732	GU349040
<i>Massariosphaeria phaeospora</i>	CBS 611.86		–	GU301843	GU296173	GU371794	–
<i>Mauritiana rhizophorae</i>	BCC 28866		–	GU371824	GU371832	GU371796	GU371817
<i>Melanomma pulvis-pyrius</i>	CBS 124080		–	GU456323	GU456302	GU456350	GU456265
<i>Neococcitibambusa chiangraiensis</i>	MFLUCC 12-0559		KU712442	KU764699	KU712458	–	KU872761
<i>Neorousoella bambusae</i>	MFLUCC 11-0124		KJ474827	KJ474839	–	KJ474856	KJ474848
<i>Nigrograna fuscidula</i>	CBS 141476; MF1	WU 36881	KX650547	KX650547	KX650509	KX650576	KX650522
	MF1a	WU 36881	KX650548	KX650548	–	–	KX650523
	MF3	WU 36880	KX650549	KX650549	–	–	KX650524
	CBS 141556; MF7	WU 36879	KX650550	KX650550	–	–	KX650525
	MF8	WU 36883	KX650551	KX650551	–	–	–
	MF9	WU 36884	KX650552	KX650552	–	–	–
<i>N. mackinnonii</i>	CBS 110022		KF015653	GQ387614	GQ387553	KF015704	KF407985
	CBS 674.75		NR_132037	GQ387613	GQ387552	KF015703	KF407986
	E9303e		JN545759	LN626681	LN626678	LN626666	LN626673
<i>N. mycophila</i>	CBS 141478; MF5	WU 36886	KX650553	KX650553	–	–	KX650526
	MF6	WU 36887	KX650554	KX650554	–	–	KX650527
	CBS 141483; TDK	WU 36888	KX650555	KX650555	KX650510	KX650577	KX650528
<i>N. norvegica</i>	CBS 141485; TR8	WU 36885	KX650556	KX650556	KX650511	KX650578	–
<i>N. obliqua</i>	BW4	–	KX650557	KX650557	–	–	KX650529
	CBS 141475; KE	WU 36876	KX650558	KX650558	KX650512	KX650579	KX650530
	MF	WU 36878	KX650559	–	–	–	–
	CBS 141477; MF2	WU 36875	KX650560	KX650560	–	KX650580	KX650531
	MRP	WU 36877	KX650561	KX650561	–	KX650581	KX650532
<i>Occultibambusa bambusae</i>	MFLUCC 13-0855		KU940123	KU863112	KU872116	KU940170	KU940193
<i>O. fusispora</i>	MFLUCC 11-0127		KU940125	KU863114	–	KU940172	KU940195
<i>O. pustula</i>	MFLUCC 11-0502		KU940126	KU863115	KU872118	–	–

(continued on next page)

Table 1. (Continued).							
Taxon	Strain	Voucher	GenBank accession numbers				
			ITS	LSU	SSU	<i>rpb2</i>	<i>tef1</i>
<i>Ohleria modesta</i>	MGC	WU 36870	KX650562	KX650562	–	KX650582	KX650533
	CBS 141480; OM	WU 36873	KX650563	KX650563	KX650513	KX650583	KX650534
<i>Paradictyoarthrinium diffractum</i>	MFLUCC13-0466		KP744455	KP744498	KP753960	–	–
<i>P. tectonica</i>	MFLUCC 13-0465		KP744456	KP744500	KP753961	–	–
<i>Parathyridaria percutanea</i>	CBS 128203		KF322117	KF366448	KF366450	KF366453	KF407988
	CBS 868.95		KF322118	KF366449	KF366451	KF366452	KF407987
<i>P. ramulicola</i>	MF4	WU 36868	KX650564	KX650564	–	–	KX650535
	CBS 141479; MRR1	WU 36867	KX650565	KX650565	KX650514	KX650584	KX650536
<i>Pleomassaria siparia</i>	CBS 279.74		–	DQ678078	DQ678027	DQ677976	DQ677923
<i>Roussoella angustior</i>	MFLUCC 15-0186		–	KT281979	–	–	–
<i>R. chiangraina</i>	MFLUCC 10-0556		KJ474828	KJ474840	–	KJ474857	KJ474849
<i>R. hysteroioides</i>	CBS 546.94		KF443405	KF443381	AY642528	KF443392	KF443399
<i>R. intermedia</i>	NBRC 106245		KJ474831	AB524624	AB524483	–	–
<i>R. japonensis</i>	MAFF 239636		KJ474829	AB524621	AB524480	AB539101	AB539114
<i>R. magnatum</i>	MFLUCC 15-0185		–	KT281980	–	–	–
<i>R. mexicana</i>	CPC 25355		KT950848	KT950862	–	–	–
<i>R. neopustulans</i>	MFLUCC 11-0609		KJ474833	KJ474841	–	–	KJ474850
<i>R. nitidula</i>	MFLUCC 11-0182		KJ474835	KJ474843	–	KJ474859	KJ474852
	MFLUCC 11-0634		KJ474834	KJ474842	–	KJ474858	KJ474851
<i>R. pustulans</i>	MAFF 239637		KJ474830	AB524623	AB524482	AB539103	AB539116
<i>R. scabrispora</i>	MFLUCC 11-0624		KJ474836	KJ474844	–	KJ474860	KJ474853
	RSC	WU 33540	KX650566	KX650566	–	–	KX650537
<i>R. siamensis</i>	MFLUCC 11-0149		KJ474837	KJ474845	–	KJ474861	KJ474854
<i>Roussoella</i> sp.	CBS 170.96		KF443407	KF443382	KF443390	KF443394	KF443398
<i>R. thailandica</i>	MFLUCC 11-0621		KJ474838	KJ474846	–	–	–
<i>R. verrucispora</i>	CBS 125434		KJ474832	AB524622	AB524481	AB539102	AB539115
<i>Roussoellopsis macrospora</i>	MFLUCC 12-0005		KJ739604	KJ474847	KJ739608	KJ474862	KJ474855
<i>Roussoellopsis</i> sp.	NBRC 106246		–	AB524626	AB524485	–	–
<i>R. tosaensis</i>	MAFF 239638		–	AB524625	AB524484	AB539104	AB539117
<i>Seriascoma didymospora</i>	MFLUCC 11-0179		KU940127	KU863116	KU872119	KU940173	KU940196
<i>Teichospora trubicola</i>	CBS 140730; C134		–	KU601591	–	KU601600	KU601601
<i>Tetraplophaeria sasicola</i>	MAFF 239677		–	AB524631	AB524490	–	–
<i>Thyridaria acaciae</i>	CBS 138873		KP004469	KP004497	–	–	–
<i>T. broussonetiae</i>	CBS 121895; TB	WU 36865	KX650567	KX650567	–	KX650585	KX650538
	CBS 141481; TB1	WU 36864	KX650568	KX650568	KX650515	KX650586	KX650539
	TB1a	WU 36864	KX650569	KX650569	–	–	–
	CBS 141482; TB2	WU 36866	KX650570	KX650570	–	KX650587	KX650540
<i>Torula herbarum</i>	CBS 140066		KR873260	KR873288	–	–	–
	CBS 111855		KF443409	–	KF443391	KF443396	KF443403
<i>T. hollandica</i>	CBS 220.69		KF443406	KF443384	KF443389	KF443393	KF443401
<i>Trematosphaeria pertusa</i>	CBS 122368		–	FJ201990	FJ201991	FJ795476	KF015701
<i>Ulospora bilgramii</i>	CBS 110020		–	DQ678076	DQ678025	DQ677974	DQ677921
<i>Versicolorisporium triseptatum</i>	JCM 14775		AB365596	AB330081	AB524501	–	–
<i>Westerdykella ornata</i>	CBS 379.55		–	GU301880	GU296208	GU371803	GU349021

random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, steepest descent option not in effect) during each bootstrap replicate, with each replicate limited to 1 million rearrangements. All molecular characters were unordered and given equal weight; analyses were

performed with gaps treated as missing data; the COLLAPSE command was set to minbrlen.

Maximum likelihood (ML) analyses were performed with RAXML (Stamatakis 2006) as implemented in raxmlGUI 1.3 (Silvestro & Michalak 2012), using the ML + rapid bootstrap

setting and the GTRGAMMAI substitution model with 1000 bootstrap replicates. The matrix was partitioned for the individual gene regions, and substitution model parameters were calculated separately for them. Bootstrap support of <70 % was considered low, between 70–90 % medium, and > 90 % high.

RESULTS

Molecular phylogeny

The final alignment and the tree obtained were deposited in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19648>). Of the 4877 nucleotide characters included in the phylogenetic analyses, 1495 are parsimony informative (435 of ITS-LSU, 112 of SSU, 550 of *rpb2*, 398 of *tef1*).

The best ML tree (lnL = -47750.4257) revealed by the RAxML analysis is shown as phylogram in Fig. 1. The *Thyridariaceae* are highly supported in both MP and ML analyses (100 % ML and 98 % MP). Sister group relationship of *Thyridaria* to *Parathyridaria* received low (65 %) and medium (82 %) bootstrap support in ML and MP analyses, respectively, while the subclade containing *Arthopyrenia salicis*, *Neoroussoella*, *Roussoella* and *Roussoelopsis* received medium support in both analyses (87 % ML and 74 % MP; Fig. 1). *Cyclothyriella rubronotata*, formerly classified in *Thyridaria*, is phylogenetically remote from *T. broussonetiae*, the generic type. The genus *Nigrograna* received maximum bootstrap support in both analyses, and sister group relationship of *N. fuscidula* to *N. mackinnonii* and of *N. obliqua* to *N. mycophila* received maximum support as well. *Nigrograna* is not closely related to *Melanomma*, within which *N. fuscidula* was formerly classified, but sister clade to *Occultibambusaceae* with high (99 % ML) and medium (77 % MP) bootstrap support. *Ohleria* and *Hobus* formed an isolated unsupported clade within *Pleosporales* with uncertain phylogenetic affinities.

Taxonomy

Contrary to, e.g., *Teichospora* (Jaklitsch *et al.* 2016), which forms a highly supported monophyletic lineage but where the partial lack of internal support of the tree backbone and morphological features currently do not support recognition of separate genera, thyridaria-like fungi are much more complex. The taxa studied here are treated below according to the phylogenetic clades (see Fig. 1) as follows:

1) As revealed by the molecular phylogenetic results, *Thyridaria rubronotata* forms a stable clade of its own, together with only one additional taxon, *Massariosphaeria phaeospora*. *Thyridaria rubronotata* is neither congeneric nor confamilial with *T. broussonetiae*, therefore it needs a different name. We chose *Cyclothyriella* as new generic name on the basis of the asexual morph name *Cyclothyrium*, which was originally intended for it (Petraik 1923). However, the latter cannot be used due to nomenclatural and taxonomic reasons (for details, see below).

2) The generic type of *Thyridaria*, *T. broussonetiae*, is contained within a highly supported clade until now named *Roussoellaceae*. Due to priority this clade now becomes *Thyridariaceae* in a new circumscription, with *Roussoellaceae* in synonymy. The *Thyridariaceae* contain two subclades which both receive only

low to medium support (Fig. 1), the large *Roussoella* sensu lato subclade, and a subclade containing *Thyridaria* sensu stricto and the new genus *Parathyridaria*. The latter remotely resembles *Thyridaria* or *Melanomma*, but differs from the type species of both genera in several features. *Roussoella acaciae*, which was described from leaves of *Acacia tortilis* in Tanzania, based on its coniothyrium- or cytoplea-like asexual morph forming clustered pycnidia producing unicellular pale brown conidia (Crous *et al.* 2014), is part of the first subclade and therefore combined in *Thyridaria*. *Roussoella percutanea*, which was isolated as an opportunistic pathogen of humans causing subcutaneous mycosis and is characterised by pycnidia forming minute unicellular hyaline conidia (Ahmed *et al.* 2014a), is part of the second subclade and therefore combined in *Parathyridaria*.

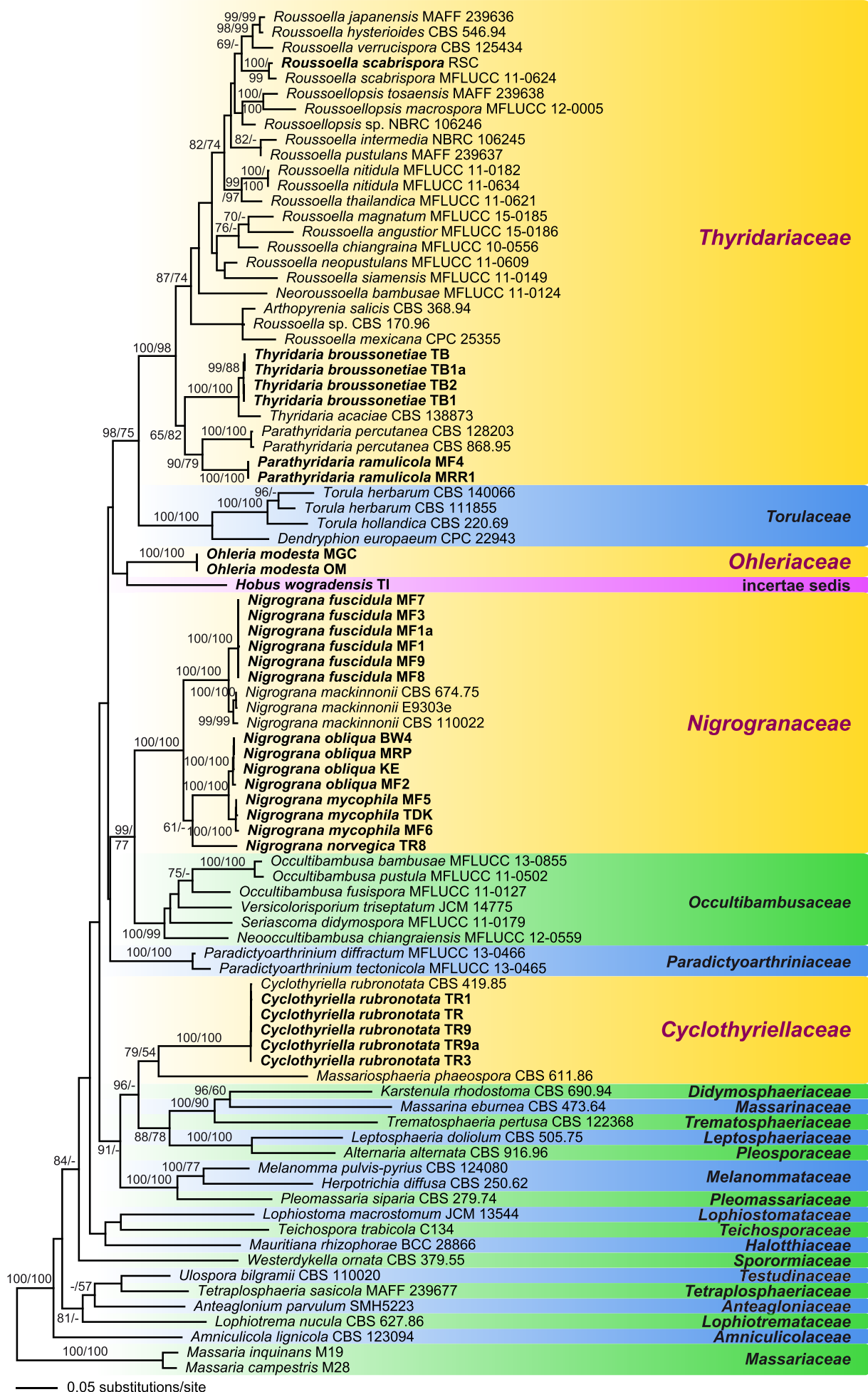
3) An unsupported clade with uncertain affinities consists of *Ohleria modesta* and a thyridaria-like fungus from *Juglans*, which clusters with *O. modesta* but differs substantially from this fungus morphologically and ecologically and is therefore described in the new genus *Hobus*, as *H. wogradensis*. As *Ohleria* does not fall into any described family, we describe the new family *Ohleriaceae*, which does not encompass *Hobus* due to its unstable affiliation, for it.

4) The fourth and last clade is phylogenetically highly supported, but does not belong to any family recognised in phylogenetic trees of the *Pleosporales*. It basically consists of four more or less cryptic species difficult to distinguish morphologically. Thus they are representatives of a single genus. One of these species is *Melanomma fuscidulum*, which thus is not congeneric with the type species of *Melanomma*, *M. pulvis-pyrius*, and does not belong to the *Melanommataceae*. NCBI GenBank sequences of the isolate CY 1228 labelled *Biatrispora marina*, which forms the basis of the *Biatrisporaceae* (Hyde *et al.* 2013), cluster in this clade. All other species in this clade differ substantially in ascospore morphology, ecology and other features from the mangrove-inhabiting *Biatrispora* (Hyde & Borse 1986). This casts doubt whether the isolate CY 1228 indeed represents *Biatrispora marina*, therefore we do not include the latter in our tree. On the other hand, *Biatrispora mackinnonii*, which was combined in this genus due to sequence similarity (Ahmed *et al.* 2014b), is also part of this clade. For this species Gruyter *et al.* (2012) described the genus *Nigrograna* with uncertain familial affinity. Therefore we combine *Melanomma fuscidulum* in *Nigrograna*, describe the three additional species in this genus and recognise this highly supported clade as the new family *Nigrogranaceae*.

Cyclothyriellaceae Jaklitsch & Voglmayr, **fam. nov.** MycoBank MB817772.

Etymology: Referring to the name of the type genus.

Ascomata and/or pycnidia scattered or more commonly clustered in valsoid configuration within KOH-positive tissue or in purple-coloured plant tissue, immersed-erumpent, more or less globose, black, *peridium* pseudoparenchymatous. *Ostiole* discs brightly coloured or black, ostioles periphysate. *Hamathecium* of apically free paraphyses and narrow branched and anastomosing, trabeculate pseudoparaphyses. *Asci* cylindrical to clavate, bitunicate, 8-spored. *Ascospores* ellipsoid to fusoid, with several eusepta, brown, thick-walled, with or without a sheath.



Asexual morph pycnidial, historically called aposphaeria-like. *Peridium* pseudoparenchymatous, dark. *Conidiophores* absent or inconspicuous. *Conidiogenous cells* phialidic. *Conidia* cylindrical, oblong to ellipsoid, 1-celled, hyaline or brown, smooth.

Type genus: *Cyclothyriella* Jaklitsch & Voglmayr

Second genus: *Massariosphaeria* (E. Müll.) Crivelli

Notes: We instate this family name, because the respective clade has proven to be stable (see e.g. Hyde *et al.* 2013). It has been called *Thyridariaceae*, but family names are based on their type genus, which itself is defined by its type species. The family *Thyridariaceae* is therefore to be used for *Thyridaria broussonetiae*, if no other family name applies in the respective clade, depending on priority.

Cyclothyriella Jaklitsch & Voglmayr, **gen. nov.** MycoBank MB817773.

Etymology: In analogy to the generic name *Cyclothyrium*.

Ascomata and pycnidia clustered in valsoid configuration within KOH-positive tissue in bark, more or less globose, black, peridium pseudoparenchymatous. Brightly coloured *ostiole discs* present, ostioles periphysate. *Hamathecium* of apically free paraphyses and narrow branched and anastomosing, trabeculate pseudo-paraphyses. *Asci* cylindrical, bitunicate, fissitunicate but relatively stable in water mounts, with thick endotunica, small ocular chamber, short stipe and furcate base, containing 8 uniseriate to overlapping ascospores. *Ascospores* ellipsoid, oblong to fusoid, with several thick and dark eusepta, straight or curved, dark brown when mature, verruculose. *Asexual morph* pycnidial, morphologically similar to ascomata. *Conidiophores* absent. *Conidia* cylindrical, oblong to ellipsoid, 1-celled, hyaline when immature, turning dark brown, smooth, produced on variously shaped phialides.

Type species: *Cyclothyriella rubronotata*.

Cyclothyriella rubronotata (Berk. & Broome) Jaklitsch & Voglmayr, **comb. nov.** MycoBank MB817803. Figs 2, 3A–L.

Basionym: *Melogramma rubronotatum* Berk. & Broome, Ann. Mag. nat. Hist. Ser. 3, 3: 375. 1859.

Synonyms: *Thyridaria rubronotata* (Berk. & Broome) Sacc., Syll. fung. 2: 141, pl. III, figs. 1–4. 1883.

Thyridaria delognensis Speg. & Roum., Revue mycol. Toulouse 2: 21. 1880.

Kalmusia delognensis (Speg. & Roum.) Wint. in Rab., Krypt.-Fl. 1(2): 764. 1887.

Massaria lateritia Tul., in sched., vide Tul., sel. fung. carp. 2: 244. 1863.

? *Thyridaria minor* (Sacc.) Sacc., Syll. fung. 24(2): 769. 1928.

Stromata 0.5–6.5 mm long, 0.6–1.5 mm high, variable, with an inconspicuous or conspicuous ectostroma projecting up to 1 mm from the host surface, consisting of dark red or orange (2.0–) 3.0–5.2(–7.0) μm ($n = 54$) wide, thin-walled hyphae, turning

purple in 3 % KOH and bright yellow in lactic acid and 40 % glycerol; containing ascomata and/or pycnidia in variable, mostly valsoid configuration. *Ascomata* (330–)380–550(–630) μm high, (340–)380–550(–615) μm wide ($n = 20$), globose or depressed globose, black. *Peridium* (26–)34–51(–60) μm ($n = 20$) wide, comprising a *t. angularis* to *t. epidermoidea* of thin-walled cells (2.5–)4.5–15.5(–22) \times (1.5–)3.0–8.2(–12.5) μm ($n = 30$), compressed inside, becoming more isodiametric, thicker-walled and darker towards the surface, surrounded by a layer of dark brown hyphae followed by red stromal hyphae. *Ostiole discs* (140–)155–343(–415) μm wide, bright to dull red or orange, paler to greenish-yellow with age, not projecting, with a radial to stellate structure in surface view, sometimes with a black pulvinate spore deposit; consisting of small-celled, hyaline to pale brownish *t. angularis* terminating in short, vertically arranged, thick-walled hyaline hyphae, in the central upper area incrustated by yellow to orange-brown pigment dissolving and diffusing in 3 % KOH and lactic acid, purplish in the former and bright yellow in the latter; often surrounded by yellowish, whitish, orange or pale brownish mycelium. *Ostiole canal* (156–)205–355(–420) μm long, interior (62–)759–122(–154) μm wide ($n = 20$), periphysate. *Hamathecium* of narrow branched and anastomosing, trabeculate, 1.5–3.5 μm wide pseudoparaphyses and some true paraphyses of similar width with free ends among immature asci. *Asci* (105–)108–125(–140) \times (8.2–)8.7–10.5(–11.5) μm ($n = 21$), cylindrical, bitunicate, fissitunicate, but relatively stable in water mounts, with thick endotunica, small ocular chamber, short stipe and furcate base, containing 8 uniseriate, partly overlapping ascospores. *Ascospores* (12.8–)15.0–18.2(–21.2) \times (5.0–) 5.7–6.7(–7.2) μm , l/w (2.1–)2.4–3(–3.5) ($n = 91$), narrowly ellipsoid or oblong with narrowly or broadly rounded ends and second cell sometimes slightly widened, 3 thick and dark eusepta, slightly constricted at all septa, straight or slightly curved, yellowish brown when young, turning dark chocolate to blackish brown upon maturation, multiguttulate, with finely verruculose perispore, sheath absent, unchanged in 3 % KOH.

Asexual morph on the natural host: *Pycnidia* (290–) 430–695(–840) μm high, (335–)500–930(–1210) μm diam ($n = 20$), immersed in valsoid configuration, often together with ascomata in red or orange mycelium, depressed globose to nearly conical. *Ostiole discs* as with ascomata, ca. 0.2–0.4 mm diam outside, ostiole canal ca. 0.2–0.4 mm long. *Pycnidial wall* similar to the ascomatal wall, (20–)26–42(–47) μm ($n = 20$) thick, comprising a dark brown *t. angularis* of thick-walled, inhomogeneously pigmented cells (3.0–) 4.0–9.5(–13.0) \times (2.7–)3.0–6.8(–9.6) μm ($n = 40$); surface turning purple in 3 % KOH. Interior lined by hyaline thin-walled isodiametric cells, giving rise to highly variable, ampulliform to lageniform, cylindrical or oddly shaped hyaline *phialides* (5.7–) 7.3–11.8(–15.0) \times (2.7–)3.3–4.7(–5.3) μm ($n = 30$), producing cylindrical, oblong to ellipsoid, 1-celled *conidia* (5.3–) 5.8–6.7(–7.2) \times (2.8–)3.0–3.2(–3.5) μm l/w (1.7–) 1.9–2.2(–2.4) ($n = 30$), first hyaline, turning dark brown, smooth.

Cultures and asexual morph in culture: On CMD at 22 °C colony radius 13–18 mm after 1 mo, colony with irregular outline,

Fig. 1. Phylogram of the best maximum likelihood tree (InL = -47750.4257) revealed by RAxML from an analysis of the combined ITS-LSU-SSU-*rpb2-tef1* sequence data matrix of selected *Pleiosporales* to reveal the phylogenetic position of the genera *Cyclothyriella*, *Hobus*, *Nigrograna*, *Ohleria*, *Parathyridaria* and *Thyridaria*. ML and MP bootstrap support above 50 % are given above or below the branches. The tree was rooted with two species of *Massaria*. Taxa in bold were sequenced in the present study. Familial classification follows Hyde *et al.* 2013, with updates from Crous *et al.* (2015), Dai *et al.* (2016), Liu *et al.* (2015), Tanaka *et al.* (2015).



Fig. 2. *Cyclothyriella rubronotata*, sexual morph. **A–C.** Ostiolar discs and stroma surface in face view (**A.** showing pulvinate spore deposits). **D.** Ostiolar disc in vertical section. **E, G.** Ascomata in vertical section. **F.** Peridium and stroma hyphae in section. **H, I.** Stroma hyphae. **J, K.** Apical ostiolar hyphae. **L.** Trabeculate pseudoparaphyses. **M.** Tip of immature ascus showing ocular chamber. **N.** Apically free paraphysis. **O–Q.** Asci (**O.** immature). **R–X.** Ascospores (**S.** showing verruculose surface). **D, E, J.** in 40 % glycerol; **F, G, I, K, Q, T–X.** in 3 % KOH; **H, I.** in lactic acid. **A, L, X.** WU 36859; **B–K, M–P, R–T, W.** WU 36858; **Q.** WU 36863. **U, V.** holotype. Scale bars: **A–C** = 200 μ m; **D, E, G** = 100 μ m; **F, L** = 20 μ m; **H–J, M–Q** = 10 μ m; **K, R–V** = 7 μ m; **W, X** = 5 μ m.

purple, vinaceous to violaceous, margin hyaline, thin, odour indistinct to slightly fruity. Hyphae submerged in agar partly orange or dark red; pigment encrusted, turning purple to violaceous and dissolving in 3 % KOH leaving hyphae smooth and colourless. Depending on the isolate, *pycnidia* absent or forming after 1–2 mo, 0.3–0.8 mm diam, globose with a prominent papilla releasing olivaceous or brown conidial drops, black, densely surrounded by radial orange hairs. *Peridium* dark brown, pseudoparenchymatous, inhomogeneously pigmented, containing dark brown granules. *Phialides* originating on more or less

globose hyaline cells, (8–)9–14.5(–16) \times (2.8–)3.0–4.0(–4.3) μ m ($n = 13$), mostly lageniform to cylindrical, often with a swollen base, sometimes on an intercalary, more or less cylindrical cell. *Conidia* (2.0–)4.5–6.0(–6.5) \times (2.0–)2.7–3.5(–4.0) μ m, l/w (1.0–)1.4–2.1(–2.5) ($n = 41$), first hyaline, turning medium brown, oblong, ellipsoid, subglobose or rhomboid with one end often truncate, smooth, with 1–3 guttules. On MEA at 22 $^{\circ}$ C colony radius up to ca. 25 mm within 1 mo, colony vinaceous and covered with a whitish mat of aerial hyphae; odour mushroomy; no *pycnidia* produced after 1–2 mo.

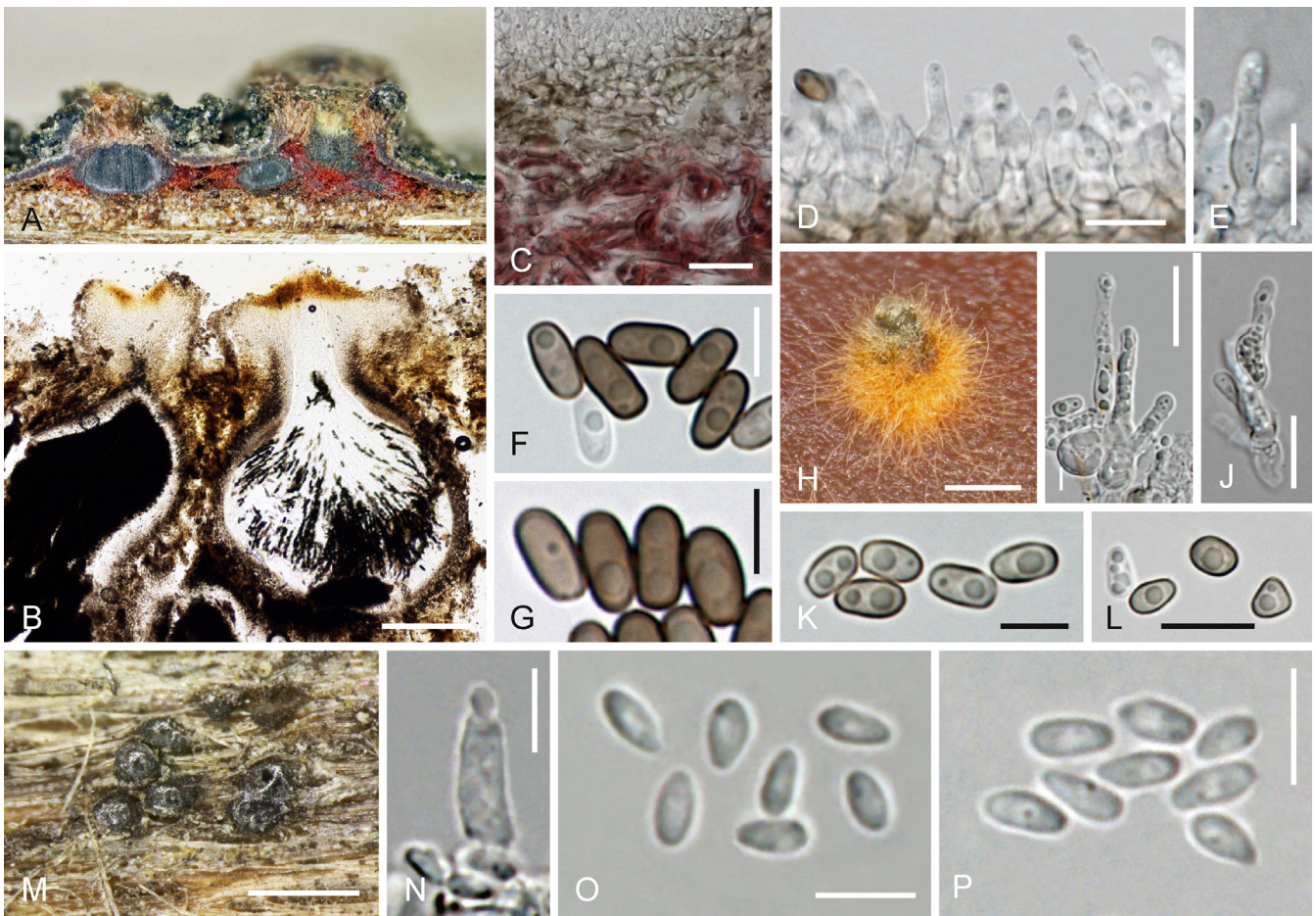


Fig. 3. A–L. *Cyclothyriella rubronotata*, asexual morph. A–G. On the natural host. A. Pycnidia in red hyphal stroma in vertical section. B. Part of pycnidium (left side) adjacent to an ascoma (right side). C. Pycnidial wall and stroma hyphae. D, E. Phialides. F, G. Conidia. H–L. In culture. H. Pycnidium. I, J. Phialides. K, L. Conidia. M–P. *Phoma (Aposphaeria) ulmicola*. M. Pycnidia. N. Phialide. O, P. Conidia. B. in lactic acid; C–G, I–L, N–P. in 3 % KOH. A–G. WU 36858; H–L. culture TR9a; M–P. holotype of *Phoma ulmicola*. Scale bars: A, H, M = 400 µm; B = 150 µm; C, I = 15 µm; D, E, J, L = 10 µm; F, G, K, N–P = 5 µm.

Habitat: in bark of moderately decayed twigs, particularly of *Acer* spp., *Aesculus hippocastanum* and *Ulmus* spp., often on and in association with other fungi, frequently parasitised by *Nitschkia parasitans*.

Distribution: Europe, possibly also North America.

Holotype: UK, Northamptonshire, Peterborough, King's Cliffe, in bark of *Ulmus*, 24 Dec. 1852, M. J. Berkeley (K(M) 202878!, as *Melogramma rubro-notatum*).

Epitype, here designated due to possible confusion with other similar fungi: **Austria**, Niederösterreich, Gießhübl, on branches of *Ulmus glabra* on the ground, soc. *Nitschkia parasitans*, *Nectria nigrescens*, *Cosmospora* sp., 1 Nov. 2014, W. Jaklitsch & H. Voglmayr (WU 36858; **ex-epitype** culture CBS 141486 = TR9 from ascospores; culture from conidia: TR9a; MBT372419).

Other material examined: **Austria**, Niederösterreich, Gießhübl, on *Acer campestre*, partly overgrown by *Nitschkia parasitans*, soc. *Diplodia* sp., *Thyronectria rhodochlora*, 18 Mar. 2012, H. Voglmayr (WU 36859; culture TR3); Vienna, 19th district, Himmelstraße, grid square 7763/2, on branch of *Acer pseudoplatanus* on the ground, 14 Oct. 1995, W. Jaklitsch W.J. 746 (WU 36860); near parking place at Schloß Cobenzl, grid square 7763/2, on branch of *Acer campestre* lying on the ground, 27 Jun. 1999, W. Jaklitsch W.J. 1332 (WU 36861); at the base of the Kahlenberg, grid square 7763/2, on branches of *Acer pseudoplatanus* on the ground, 25 May 2006, W. Jaklitsch W.J. 2916

(WU 36862, culture CBS 121892 = TR); Vienna, 21st district, at the eastern base of the Bisamberg, on branches of *Acer pseudoplatanus* on the ground, 25 Feb. 2012 W. Jaklitsch (WU 36863, culture TR1).

Nomenclatural background and additional notes: The fungus redescribed above was originally described from *Ulmus* and has been known under the name *Thyridaria rubronotata*. However, it is not congeneric with *T. broussonetiae*, the generic type of *Thyridaria*, and therefore requires a different generic name.

The conidial stage of the fungus was referred to *Phoma ulmicola* Berk. by Saccardo (1883) and was redescribed and erroneously referred to as *P. ulmigenum* Berk. by Tulasne & Tulasne (1863, p. 243). This wrongly spelled name was taken up by von Höhnelt (1917), who combined it as *Melanconiopsis ulmigena* (Berk.) Höhn. As already pointed out by Petrak (1923), it is very unlikely that *Melanconiopsis* fits for these fungi, as its generic type, *Melanconiopsis inquinans* Ellis & Everh., was described as a "*Melanconium* with a *Cytospora* stroma" for asexual morphs of diarthalean fungi such as *Melanconis* or *Massariovalsa*. Its conidia are quite different and very large, given as 20–30 × 12–15 µm in the protologue. Petrak (1923) erected *Cyclothyrium* for the asexual morphs of *Thyridaria*, viz. *C. ulmigenum* (generic type) and *C. incrustans*, those species, which, according to Petrak (1923), von Höhnelt (1917) had erroneously treated under *Melanconiopsis*. In a later publication, Petrak & Sydow (1927) treated *Cyclothyrium* preliminarily as a

subgenus of *Cytoplea* Bizz. & Sacc., a genus apparently similar to *Cyclothyrium*, the generic type of which, *Cytoplea arundinicola*, has not yet been sequenced. Petrak & Sydow (1927) explicitly used *Cyclothyrium* for the asexual morph of *Thyridaria rubronotata* but stated that the latter is most common on *Juglans*, and therefore the type species must be called *C. juglandis*, based on *Naemospora juglandis* Schum. Thus they synonymised several names including *Cyclothyrium ulmigenum* with *Cytoplea juglandis*, although they only studied own material from *Juglans*. They did not study *Naemospora juglandis* nor *Phoma ulmicola*, and they ignored any possibility of host specificity and the fact that *Thyridaria rubronotata* was described from *Ulmus*. This was already criticised by Chesters (1938) and Wehmeyer (1941).

We examined the holotype of *Phoma ulmicola* and give a short description here:

Phoma ulmicola Berk., Hook. J. Bot. 5: 40. 1853. Fig. 3M–P. Synonyms: *Aposphaeria ulmicola* (Berk.) Sacc., Syll. fung. 3: 175. 1884. *Coniothyrium ulmicola* (Berk.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 459. 1898.

Pycnidia 100–250 µm diam, erumpent from decorticated wood, scattered to aggregated in small numbers, black, globose, flattened above (by pressure); *peridium* pseudoparenchymatous, bearing some rounded, dark unicellular protruding cells, surrounded by some dark brown hyphae not reacting in 3 % KOH. *Phialides* lageniform to cylindrical, (6.8–) 7.0–9.2(–10.5) × (1.8–)2.0–3.0(–3.5) µm (n = 17). *Conidia* (2.2–)3.0–4.0(–4.8) × (1.1–)1.5–2.0(–2.3) µm, l/w (1.6–) 1.7–2.4(–3.8) (n = 46), narrowly ellipsoid to fusoid or drop-like, 1-celled, hyaline, often truncate at one end, smooth.

Holotype: UK, England, King's Cliffe, in wood of *Ulmus*, 25 Nov. 1851 (Herb. Berk. in Kew, K(M) 201530!, as *Aposphaeria ulmicola*).

This makes clear that *Phoma ulmicola* cannot be the asexual morph of *Thyridaria rubronotata*, as it differs from the latter by smaller pycnidia, smaller and hyaline conidia, by lack of flattened orange to red ostiolar discs and colour reactions in KOH, and by a different ecology, i.e. growth in weathered decorticated wood vs. bark. For this reason, earlier applications of Berkeley's name *Phoma ulmicola* for the asexual morph of *Thyridaria rubronotata* are erroneous and thus *Cyclothyrium* cannot be used for *T. rubronotata*, because it is nomenclaturally based on *Phoma ulmicola*. On *Juglans*, the host given as typical for *Thyridaria rubronotata* by Petrak & Sydow (1927), we have collected three different but morphologically similar fungi in Austria referable to *Thyridaria*, but none of them is conspecific neither with *T. rubronotata* nor with *T. broussonetiae*. One of them has reddish hyphae and reddish pulvinate ostioles and might be the same fungus that Petrak studied. However, the latter is not *Thyridaria rubronotata*, but belongs to a different clade of the Pleosporales to be published later on.

We erect *Cyclothyriella* as a holomorphic name for *Thyridaria rubronotata*. *Cyclothyriella rubronotata* differs from *Thyridaria broussonetiae*, the generic type of *Thyridaria*, in several respects: in the latter the secondary septa are distosepta and appear incomplete when young, the subiculum is KOH-negative

and only the tissue in the ostiolar region reacts to KOH, and there are no elongate hyphal elements present in the ostiolium. Below we redescribe a fungus, which may be related to *Cyclothyriella rubronotata*:

Thyridaria sambuci (P. Karst.) Sacc., Syll. fung. 2: 141. 1883. Fig. 4.

Basionym: *Kalmusia sambuci* P. Karst., Meddeland Soc. Fauna Flora fenn. 6: 54. 1880.

On bark roundish to longish *stromata* of 1.3–5 mm length or diam, erumpent to 1.3 mm, compact, irregularly tuberculate, with distinctly projecting cylindrical ostiolar necks; stroma substance between necks partly orange to reddish. On wood *ascomata* scattered to densely aggregated, with only ostiolar necks visible between wood fibres or erumpent to superficial, usually with the base immersed, covered by a yellow-brown to rust tomentum. *Ostiolar necks* papillate, conical or cylindrical; apices (50–)52–112(–187) µm (n = 24) wide, often flat, yellow, pale orange to black or black with orange centre, contents at upper levels yellow to orange. *Ascomata* (224–) 325–527(–583) µm (n = 14) diam, (245–)300–440(–493) µm (n = 12) high, subglobose. *Peridium* brown, inhomogeneously pigmented, comprising a rather thin-walled *t. angularis* of 3–10 µm wide cells. Stromatic tissue, part of the peridium, subhymenium and even immature asci turning purple to violaceous in 3 % KOH. *Hamathecium* comprising 1–2.5 µm wide branched trabeculate pseudoparaphyses. *Asci* (66–) 68–91(–108) × (9.0–)9.5–12.0(–13.0) µm (n = 12), clavate, bitunicate, fissitunicate, with endotunica swelling in 3 % KOH, containing 8 ascospores biserially arranged in the upper part, with short stipe and simple base. *Ascospores* (12.0–) 13.5–16.0(–18.8) × (3.7–)4.3–5.2(–5.6) µm, l/w (2.6–) 2.9–3.5(–4.1) (n = 51), fusoid, symmetrical or inequilateral, straight to slightly curved, (1–)3-euseptate, slightly to distinctly constricted at the median septum, second cell slightly wider than others, pale to medium brown, not darkening in 3 % KOH, smooth, collapsing upon access of air.

Habitat: on branches of *Sambucus racemosa*.

Distribution: Finland, only known from type material.

Material examined: Finland, Kanta-Häme ("Travastia australis"), Tammela, Mustiala, on *Sambucus racemosa*, 16 Apr. 1872, P.A. Karsten (H 1180); *ibid.*, 17 Apr. 1872 (H 1179), syntypes of *Kalmusia sambuci*. **Lectotype**, here designated: H 1179 (MBT372889).

Notes: This species may be related to *Cyclothyriella rubronotata*, but for the determination of phylogenetic affinities fresh material is necessary. This material was examined also to compare with similar fungi on *Sambucus racemosa* such as *Nigrograna obliqua* (see below). *Thyridaria sambuci* is a typical member of *Thyridaria* in the sense of Wehmeyer (1941).

Thyridariaceae Q. Tian & K.D. Hyde, Fungal Diversity 63: 254. 2013, emend.

Synonym: *Roussoellaceae* J.K. Liu *et al.*, Phytotaxa 181: 7. 2014.

Ascomata immersed-erumpent to superficial, scattered or aggregated under a clypeus or in a subiculum, sometimes with yellowish or reddish pigments around the ostiolar neck forming a

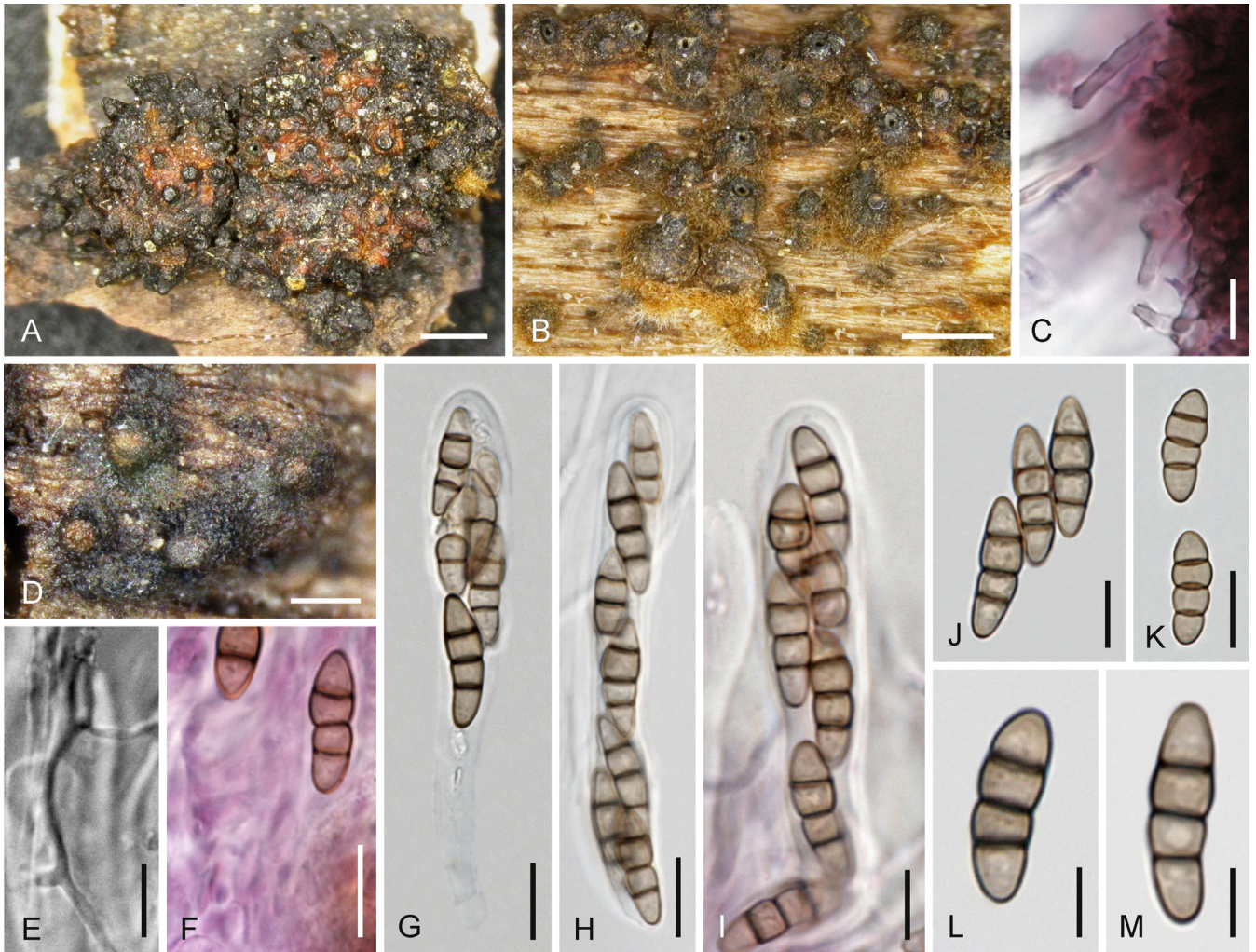


Fig. 4. *Thyridaria sambuci*. **A, B, D.** Stroma, ascomata and ostiolar apices in face view. **C.** Stroma hyphae in 3 % KOH. **E.** Trabeculate pseudoparaphysis. **F.** Ascospore and part of hymenium in 3 % KOH. **G–I.** Asci (**G.** young, **I.** in 3 % KOH). **J–M.** Ascospores. **C, F, H, I, M.** in 3% KOH. **A, C, E–G, I, L.** H 1180; **B, D, H, J, K, M.** lectotype H 1179. Scale bars: **A, B** = 0.5 mm; **C, E–H, K** = 10 μ m; **D** = 0.2 mm; **I, J** = 7 μ m; **L, M** = 5 μ m.

disc, black, more or less globose, usually with well-developed ostiolar neck and periphysate ostiole. *Peridium* brown, pseudoparenchymatous. *Hamathecium* consisting of apically free paraphyses and/or trabeculate pseudoparaphyses. *Asci* cylindrical or clavate, bitunicate. *Ascospores* yellowish- to dark brown, ellipsoid, oblong or fusoid, with transversal eusepta or eu- and distosepta, variously ornamented, sometimes with a sheath. *Asexual morphs* coelomycetous. Saprobiic on leaves and branches of woody plants including monocotyledons such as bamboos and palms, sometimes human pathogenic.

Type genus: *Thyridaria* Sacc.

Thyridaria Sacc., *Grevillea* 4(no. 29): 21. 1875.

Ascomata immersed-erumpent, separate or gregarious in valsoid groups in brown prosenchymatous tissue, sometimes with yellowish or reddish pigments around the ostiolar neck forming a disc, black, more or less globose, with well-developed ostiolar neck; ostiole periphysate. *Peridium* brown, pseudoparenchymatous. *Hamathecium* consisting of apically free paraphyses and trabeculate pseudoparaphyses. *Asci* cylindrical, bitunicate. *Ascospores* yellowish- to dark brown, ellipsoid or fusoid, symmetric, with transversal eu- and distosepta, verruculose. *Asexual morphs* coelomycetous, forming simple or compound pycnidia.

Saprobiic on branches of woody plants, asexual morph also known from leaves.

Type species: *Thyridaria broussonetiae* (Sacc.) Traverso

Thyridaria broussonetiae (Sacc.) Traverso, *Fl. ital. crypt., Pyrenomycetae* (Florence) 1(1): 301. 1906. [Fig. 5.](#)

Basionym: *Cucurbitaria broussonetiae* Sacc., *Mycologiae Venetae specimen. Atti della Società Veneto-Trentina di Scienze Naturali* 2: 166, pl. XII, f. 12–17. 1873.

Synonym: *Thyridaria incrustans* Sacc., *Mycotheca Veneta* II, no. 170. 1875, in sched.

Stromata ca. 0.6–1.5 mm diam, more or less conical to pulvinate, scattered or aggregated in variable numbers, consisting of loosely or densely intertwined brown, (2.5–)3.0–4.5(–5.3) μ m ($n = 31$) wide hyphae, one or several, usually less than ten ascomata in valsoid configuration, standing on the wood, and a pruinose layer of yellow to reddish or orange-brown material forming a circular to elongate flat to convex disc or pulvillus 0.2–0.7 mm diam around the apices of the ostiolar necks; discs sometimes confluent to ca. 2 mm. *Ascomata* (280–)330–450(–495) μ m high, (400–)440–580(–665) μ m diam ($n = 21$), depressed globose to globose, usually width exceeding height, dark brown to black; *peridium* (20–)22–30(–40) μ m wide

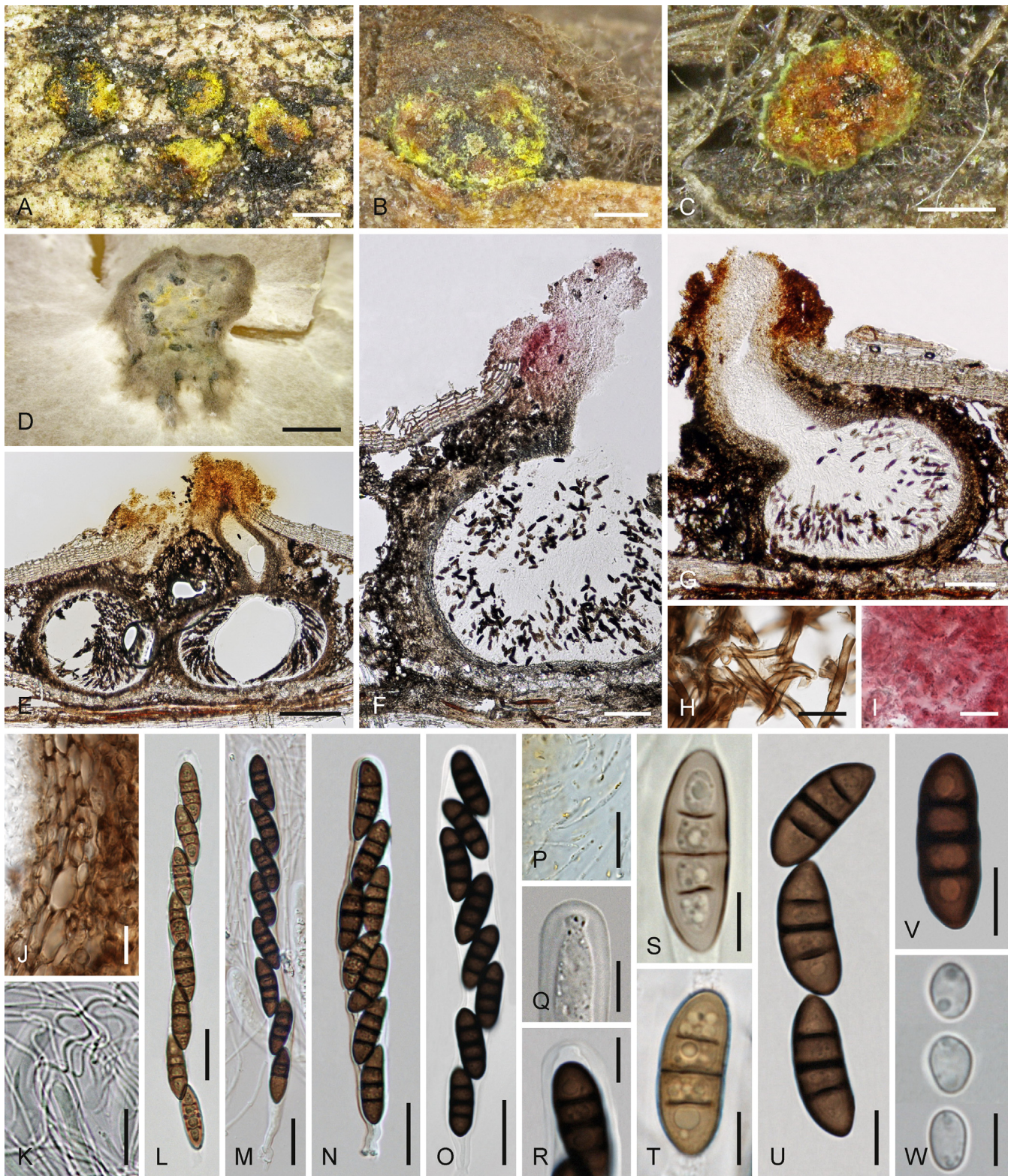


Fig. 5. *Thyridaria broussetiae*. **A–C.** Ostiolar discs and cushions in face view (**B, C.** showing surrounding hyphae). **D.** Stroma in culture at plug side (2 % MEA, 22 °C, 97 d). **E–G.** Ascomata in vertical section (**E.** Valsoid group of ascomata in lactic acid, **F.** in 3% KOH, **G.** in 50% glycerol). **H.** Stroma hyphae. **I.** Ostiolar tissue in 3 % KOH. **J.** Peridium in section. **K.** Trabeculate pseudoparaphyses. **L–O.** Asci (**L.** immature). **P.** Periphyses. **Q, R.** Ascus apices (**Q.** immature). **S–V.** Ascospores (**S, T.** immature). **W.** Conidia. **A, E–L, N–P, R, S, U.** WU 36864; **B, M.** PAD 1876; **C, Q, T, V.** WU 36866; **D, W.** culture TB2. Scale bars: **A** = 300 µm; **B, C, E** = 200 µm; **D** = 2 mm; **F, G** = 100 µm; **H, K–P** = 20 µm; **I, J, U, V** = 10 µm; **Q–T** = 7 µm; **W** = 5 µm.

($n = 21$), but usually appearing thicker due to the often tightly adhering subiculum, pseudoparenchymatous, of thin-walled compressed basally more isodiametric, pale to medium brown cells $(4\text{--}6\text{--}16\text{--}21) \times (2\text{--}3\text{--}5\text{--}7.5)$ µm ($n = 34$). *Ostiolar necks* $(335\text{--}390\text{--}510\text{--}580)$ µm long, $(107\text{--}133\text{--}250$

$\text{--}312)$ µm wide outside including encasing tissue, interior $(46\text{--}75\text{--}148\text{--}178)$ µm wide ($n = 20$), containing 0.5–2 µm wide periphyses, cylindrical, upright or oblique and converging in a common disc, straight or curved, consisting of thin-walled light coloured cells $(3.8\text{--}5.0\text{--}7.3\text{--}8.5)$ µm ($n = 25$); tissue encasing

the ostiolar necks consisting of an amorphous substance, reddish- to orange-brown in 50 % glycerol, yellow and releasing yellow pigment in lactic acid (after 1 d nearly colourless) and turning pink and releasing pinkish to purple pigment in 3 % KOH, ostiolar cells in KOH hyaline but those situated close to the venter remaining dark; ostiolar apices inconspicuous in the disc or appearing as dark spots or slightly projecting dots. *Hama-thecium* of branched, trabeculate, 1–2.5 wide pseudoparaphyses and apically free paraphyses. *Asci* (109–) 124–160(–183) × (12–)13–16(–19) μm ($n = 33$), bitunicate, stable in microscopic mounts, cylindrical with a short stalk to ca. 20 μm , a simple or furcate base and 8 uniseriate (or partly biseriate by pressure in mounts) ascospores; wall thin, endotunica thick at the apex, with a distinct ocular chamber. *Ascospores* (18.3–)22.5–27.8(–33.3) × (6.6–)8.0–9.7(–11.0) μm , l/w (2.0–)2.5–3.2(–3.8) ($n = 122$), oblong, narrowly ellipsoid to fusoid, ends narrowly rounded, straight or curved, pale or yellowish brown when young, dark to blackish brown at maturity, 3-septate with one median euseptum and 2 additional incomplete septa, the latter developing to distosepta when mature, not constricted at the septa, containing several guttules, end cells often slightly longer, sheath absent, surface finely punctate to verruculose. No asexual morph seen in nature.

Cultures and asexual morph: Colony radius on CMD at 22 °C ca. 50 mm after 1 mo; colony first hyaline or whitish, turning dull yellowish green to olivaceous from the centre, centre either dull brown or yellow with yellow crystals forming on the surface; aerial hyphae sometimes amassing at the margin, sometimes *pycnidia* ca. 0.2–0.5 mm diam with pseudoparenchymatous wall formed, but remaining sterile; odour indistinct. Colony radius on MEA at 22 °C after 1 mo ca. 35 mm; colony zonate, brown, with narrow prominent whitish rings of aerial hyphae; odour indistinct, sometimes *pycnidia* with pseudoparenchymatous wall formed, but usually remaining sterile, only once hyaline to pale greyish brown, 1-celled, ellipsoid-oval-oblong, smooth *conidia* (4.3–) 4.8–6(–6.5) × (3–)3.3–3.7(–4) μm . l/w (1.2–)1.3–1.7(–1.9) ($n = 42$), with few small guttules, found in the periphery of a compound stroma after 97 d in an ill-defined stroma ca. 6.4 × 4.7 mm developing at one side of the inoculation plug. *Stroma* soft, surface dull olive-brown with yellow dots (as in ostiolar discs of naturally grown stromata), containing several locules either of immature ascomata or *pycnidia*; no conidiogenous cells seen.

Habitat: in bark of various shrubs; confirmed for *Amorpha fruticosa*, *Broussonetia papyrifera* and *Hippocrepis emerus*.

Distribution: Southern Europe.

Typification: **Lectotype**, here designated: **Italy**, Padua, on *Broussonetia papyrifera*, soc. *Diplodia* sp., Mar. 1873, P.A. Saccardo, distributed as Mycotheca Veneta 170 (W 2009-01175!; MBT372890).

Notes: Mycotheca Veneta 170, where Saccardo (1875a) based *T. incrustans* on *Cucurbitaria broussonetiae*, was wrongly labelled by Saccardo himself for the latter name as Mycol. ven. Spec, pag. 118 (see also Saccardo 1883). The correct page is 166. Isotypes of Mycotheca Veneta 170 (as *Thyridaria*

incrustans) in FH (FH 00313543!), K (K(M) 202716!), PAD, UPS (F-736475!; material overmature). All these materials were examined and apparently represent parts of the original collection of *Thyridaria (Cucurbitaria) broussonetiae*. In the lectotype material one twig contains mature material, all others contain immature stromata with the characteristic yellow to reddish brown ostiolar tops. *Diplodia* is also tightly associated in this specimen. For the FH material the identity is deduced from the received slide, which shows typical ascospores and asci. At PAD there are two specimens from *Broussonetia*, the isotype from March 1873 (a small packet on the second sheet of the *T. incrustans* folder) and an authentic specimen from May 1876 (larger packet on the first sheet); the latter contains better material and is therefore also illustrated in Fig. 5B, M.

Epitype here designated: **Hungary**, south of Eger, 47°51'16" N 20°22'00" E, elev. 235 m, on twigs of *Amorpha fruticosa*, soc. *Valsaria robiniae*, 30 May 2014, W. Jaklitsch & H. Voglmayr (WU 36864; **ex-epitype** culture CBS 141481 = TB1; MBT372416).

Other material examined: **Croatia**, Istrija, Opatija, Mošćenička Draga, in the village heading north, on dead standing branch of *Hippocrepis (Coronilla) emerus*, 29 Mar. 2007, W. Jaklitsch & H. Voglmayr (WU 36865, culture CBS 121895 = TB). **Italy**, Veneto, Colli Euganei, Padova, Arqua Petrarca, roadside, on a dead branch of *Broussonetia papyrifera*, 1 Nov. 2015, W. Jaklitsch (WU 36866, culture CBS 141482 = TB2).

Notes: Apart from the specimens collected from *Broussonetia*, the *Thyridaria incrustans* folder at PAD contains specimens, labelled either as *Thyridaria incrustans* or *Cucurbitaria broussonetiae*, from *Albizzia*, *Calycanthus*, *Chimonanthus*, *Colutea*, *Fagus sylvatica*, *Juglans regia*, *Morus*, *Prunus padus*, *Rhus* and *Robinia*, as Saccardo (1875a) and Traverso (1906) had (at least in part) reported. Only few of them show a yellow substance around the ostiolar tops. These specimens contain at least two species, which corroborates that widening of the concept of *Cucurbitaria broussonetiae* to *Thyridaria incrustans* by Saccardo produced a collective species name, which is besides priority another argument not to use *T. incrustans*. In the PAD specimen from *Juglans* the fungus is overmature with many aberrant ascospores, thus the identity is questionable, and the fungus on *Prunus padus* is different, with smaller euseptate ascospores, (14.5–)16.7–20.5(–22.5) × (5.8–)6.7–7.8(–8.2) μm , l/w (2.1–) 2.3–2.8(–3.1) ($n = 30$), uniseriately arranged in cylindrical asci. Ascospore sizes given by Saccardo on the label for his *Colutea* specimen are 15–24 × 4 (and 17–19 × 4.5) μm and on the *Fagus* specimen 15–18 × 5–6 μm , i.e., they are also different species. Traverso (1906) noticed that the species is very variable, as its ascomata are either arranged in well-defined valsoid groups or in irregular aggregations. Below the cortex and on the wood a black effuse pseudostromatic layer is formed, which was also seen in the sectioned sample. A good character for recognition is the yellow to reddish brown furfuraceous layer which envelops the upper part of the ostiolar necks, and in particular also the secondary distosepta in the ascospores.

Frequent and tight association of ascomata with *Diplodia* *pycnidia* led to the view that the latter is an asexual morph of *T. broussonetiae*, named *Diplodia incrustans* by Saccardo (1883), who had earlier (Saccardo 1875c) identified another asexual morph as *Coniothyrium incrustans* Sacc., both by

association with the sexual morph on the natural hosts. Petrak (1921) classified the asexual morph in *Melanconiopsis* and compared its morphology with that of in his opinion very similar asexual morphs of *Valsaria* (compare Jaklitsch *et al.* 2015). His conclusions were based on material from *Juglans*, a host, on which we have seen at least three different thyridaria-like fungi but not *T. broussonetiae*. Petrak's (1921) description suggests that he had collected *Cyclothyriella rubronotata* (*Thyridaria rubronotata*) rather than *T. broussonetiae*, as he characterised the fungus as a cluster of 2–6 irregular pycnidial chambers imbedded in a loose felty brownish stroma in the surface layers of the bark, containing numerous one-celled, brown, ellipsoid to cylindrical conidia 4–7×2–3 µm. We have not seen a *Coniothyrium*, but plenty of *Diplodia* tightly associated with *T. broussonetiae* particularly between ostiolar necks on *Broussonetia* (WU 36866) and a *Botryosphaeria* morph with pale brown unicellular ascospores (19–)23–29(–30) × (6.0–)7.5–10.0 µm (n = 20) in the epitype material on *Amorpha* (WU 36864). In MEA culture we found conidia only once in a stroma on the plug; unfortunately we could not repeat this result. Fully mature conidia may be brown.

Thyridaria acaciae (Crous & M.J. Wingf.) Jaklitsch & Voglmayr, **comb. nov.** MycoBank MB817774.

Basionym: *Rousoella acaciae* Crous & M.J. Wingf., *Persoonia* 33: 259. 2014.

Notes: For this species only the asexual morph is known, which occurs on leaves of *Acacia tortilis* collected in Tanzania (Crous *et al.* 2014). Brown 1-celled conidia formed on phialides in multilocular conidiomata of this species may be typical for asexual morphs of *Thyridaria*.

Parathyridaria Jaklitsch & Voglmayr, **gen. nov.** MycoBank MB817775.

Etymology: The generic name is based on the phylogenetic vicinity to *Thyridaria broussonetiae*, the generic type of *Thyridaria*.

Ascomata more or less globose, black, immersed in wood and bark, wood surface stromatised, grey to black, subiculum absent or inconspicuous. *Peridium* pseudoparenchymatous. *Ostiolar necks* discoid, less commonly papillate or short-cylindrical, apices black or light-coloured, ostioles periphysate. *Hamathecium* of numerous sparsely branched, trabeculate pseudoparaphyses. *Asci* bitunicate, fissitunicate, narrowly clavate, with a small but distinct ocular chamber, a short stipe and simple or furcate base, containing 8 ascospores biserially arranged at upper levels. *Ascospores* fusoid, with several eusepta and rarely a longitudinal septum, pale to greyish brown, not darkening in 3 % KOH, upper part or second cell often slightly broader than lower part, smooth, guttulate, sheath absent.

Asexual morph (deduced from cultures of *P. percutanea*): *Pycnidia* black, globose to subglobose, with thin pseudoparenchymatous wall. *Conidiogenous cells* hyaline, phialidic. *Conidia* small, ellipsoid, unicellular, hyaline to pale brown.

Habitat: on plant substrates (e.g., decaying twigs), sometimes human pathogenic.

Type species: *Parathyridaria ramulicola* Jaklitsch & Voglmayr

Parathyridaria ramulicola Jaklitsch, Fourn. & Voglmayr, **sp. nov.** MycoBank MB817776. Fig. 6.

Etymology: ramulicola = dwelling on branches and twigs.

Ascomata (200–)260–400(–460) µm (n = 24) diam, (200–)210–335(–375) µm (n = 9) high, globose to subglobose, black, immersed in wood and bark, becoming visible in bark fissures, solitary or aggregated into clusters up to ca. 50 individuals, on wood upper half often becoming erumpent. Wood surface typically stromatised in irregular patches, grey to black. *Peridium* 15–30 µm thick, consisting of a thin dark brown layer and a thin hyaline layer, both of angular thin-walled cells (3.5–)5.5–10.0(–13.5) × (2.0–)3.3–7.2(–9.3) µm (n = 37), sometimes inconspicuous and sparse brown, 1–3 µm wide hyphae present between ascomata. *Ostioles* (25–)35–100(–110) µm diam (n = 20) outside, typically discoid with a flat or concave surface, less commonly papillate or short-cylindrical, usually projecting to less than 200 µm, with a black, whitish to pale brownish, rarely orange-reddish top, interior periphysate. *Hamathecium* of numerous sparsely branched, trabeculate, 1–2.5(–3.5) µm wide pseudoparaphyses. *Asci* (67–)75–89(–96) × (9.2–)10.0–11.7(–12.7) µm (n = 37), bitunicate, fissitunicate, narrowly clavate, with a small but distinct ocular chamber, a short stipe and simple or furcate base, containing 8 ascospores biserially arranged at upper levels. *Ascospores* (12.7–)14.0–16.2(–19.5) × (3.8–)4.8–5.6(–6.0) µm, l/w (2.3–)2.6–3.2(–3.9) (n = 120), fusoid, with (2–)3(–4) darker, slightly constricted eusepta at approximately equal distances, rarely with a longitudinal septum in one cell, pale to greyish brown, not darkening in 3 % KOH, straight or slightly curved, upper part or second cell often slightly broader than lower part, ends narrowly rounded, smooth, guttulate, sheath absent.

Cultures: Colony radius on CMD at 22 °C after 1 mo 17–22 mm, colony deep dark or olive-brown, with light aerial hyphae in the centre, sometimes with a radial segmentation; odour indistinct; no asexual morph detected.

Habitat: On decaying twigs, known from *Ribes rubrum* and *Sambucus nigra*.

Distribution: France, Germany.

Holotype: Germany, Nordrhein-Westfalen, Velen, Geeste 133, on twigs of *Ribes rubrum*, soc. pycnidia with hyaline rod-like conidia, 2 Dec. 2013, K. Siepe (WU 36867; **ex-type** culture CBS 141479 = MRR1).

Other material examined: France, Ariège, Rimont, Las Muros, elev. 480 m, on decorticated twigs of *Sambucus nigra*, 19 Feb. 2016, J. Fournier JF 16002 (WU 36868; culture MF4); *ibid.*, same host, 12 Apr. 2016, J. Fournier JF 16012 and JF 16015 (WU 36869).

Notes: The typical feature of this fungus is the discoid ostiolar apices, which are always present, even if some in a specimen may be cylindrical and projecting. Also characteristic are the pale to greyish brown ascospores, which do not become darker in 3 %

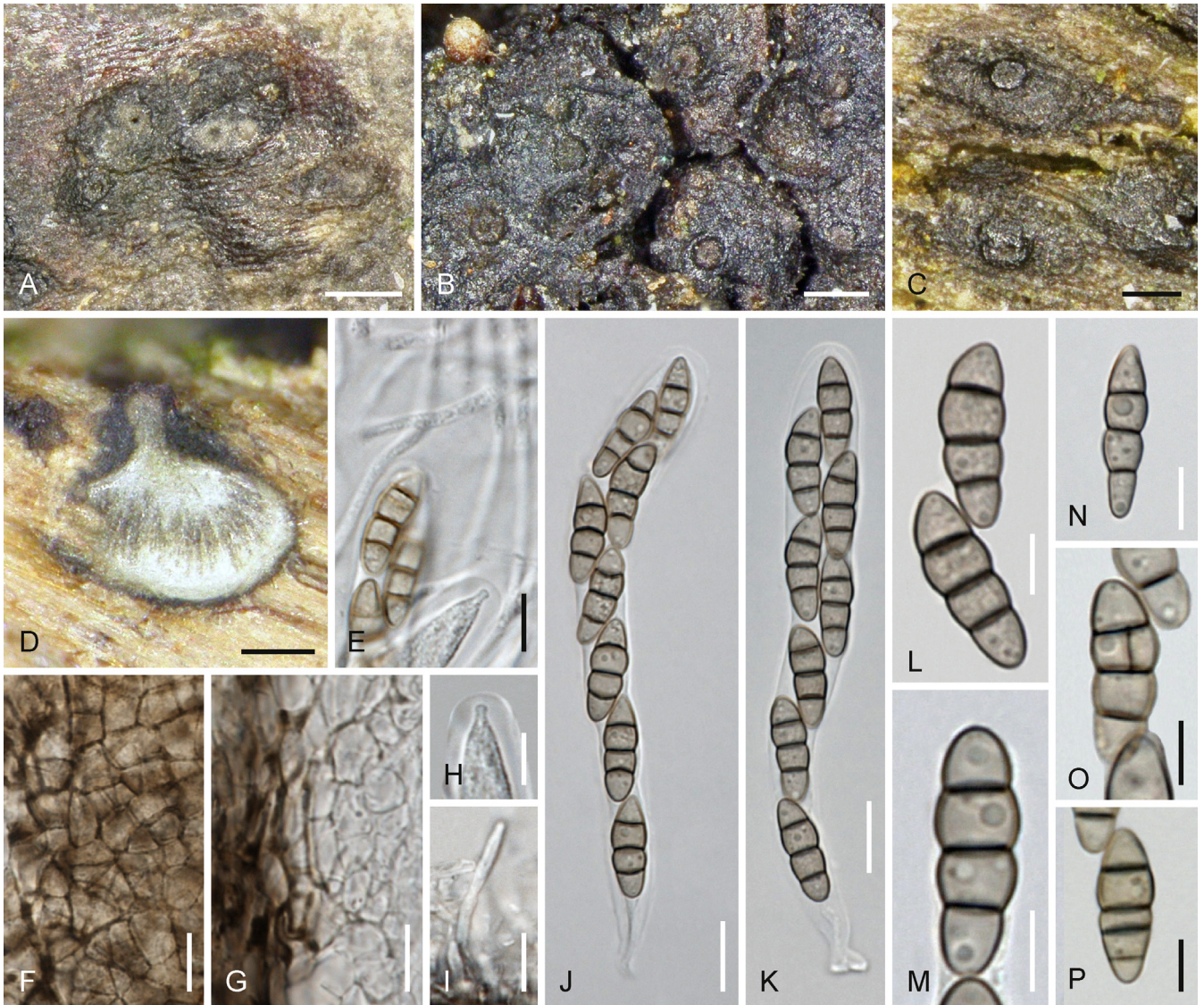


Fig. 6. *Parathyridaria ramulicola*. **A–C.** Ostiolar apices and upper part of ascomata in face view (**A** with whitish ostioles in bark, **B** in bark fissure, **C** in stromatised wood). **D.** Ascoma with short-cylindrical ostiole in vertical section. **E.** Ascus apices and hamathecium. **F, G.** Peridium (**F** in face view, **G** in vertical section). **H.** Apex of immature ascus. **I.** Periphysis. **J, K.** Asci. **L–P.** Ascospores (**O** muriform; **P** with 4 septa). **A, B, D–L, N.** WU 36867; **C, M, O.** WU 36868; **P.** JF16012. Scale bars: **A, B** = 150 μ m; **C, D** = 100 μ m; **E, G, I, N** = 7 μ m; **F, J, K** = 10 μ m; **H, L, M, O, P** = 5 μ m.

KOH. A subiculum is usually absent or confined to very inconspicuous hyphae.

Parathyridaria percutanea (S.A. Ahmed *et al.*) Jaklitsch & Voglmayr, **comb. nov.** MycoBank MB817777.

Basionym: *Roussoella percutanea* S.A. Ahmed *et al.*, Medical Mycology 52(7): 696. 2014.

This species was based on two clinical isolates obtained from human subcutaneous mycoses (Ahmed *et al.* 2014a, 2014b). No sexual morph is known. ITS sequence JX951180 of an Indian isolate from roots of *Tinospora cordifolia* (*Menispermaceae*) also represents this species, indicating that its primary ecology is endophytic or saprobic on plants.

Description (adapted from Ahmed *et al.* 2014a, 2014b): Colonies on oatmeal agar floccose, dark greyish green, with pale grey margin. Hyphae turning dark brown with age. Pycnidia observed after 8 wk, 59–102 \times 54–96 μ m, black, solitary, globose to subglobose, with thin wall of *t. angularis*. Conidiogenous cells hyaline, phialidic, obclavate. Conidia

1.2–2.0 \times 0.7–0.9 μ m, hyaline to pale brown, unicellular, ellipsoid.

Ohleriaceae Jaklitsch & Voglmayr, **fam. nov.** MycoBank MB817828.

Etymology: Referring to the name of the type genus.

Ascomata scattered or aggregated, erumpent-superficial on wood or black crusts, globose to subconical, ostiolate, black. **Peridium** pseudoparenchymatous, dark. **Hamathecium** of narrow pseudoparaphyses. **Asci** cylindrical, 8-spored, bitunicate, fissitunicate. **Ascospores** brown, fusoid or ellipsoid, transversely septate, often disarticulating into two parts. **Asexual morphs** coelomycetous where known; syanamorphs possibly monodictys-like. Saprobian on wood.

Type genus: *Ohleria* Fuckel.

Notes: We describe this family, because the application of various phylogenetic methods on the sequence dataset of *Ohleria*

modesta always resulted in a position, which has no affinity to any other family. The genus *Hobus* is here only tentatively included, as clustering with *Ohleria* does not receive significant support.

Ohleria Fuckel, Fungi rhenani exsic. suppl., fasc. 7, no. 2173. 1868.

Ascomata scattered to aggregated in large numbers, superficial with base or venter embedded in a black crust or wood, globose to subconical, papillate, black. *Peridium* pseudoparenchymatous, dark. *Hamathecium* of narrow pseudoparaphyses. *Asci* cylindrical, 8-spored, bitunicate, fissitunicate. *Ascospores* brown, fusoid to narrowly ellipsoid, 3-septate, disarticulating into two parts at the median primary septum. *Asexual morph* phoma-like, synanamorph presumably monodictys-like. Saprobiic on wood.

Type species: Ohleria modesta Fuckel.

Ohleria modesta Fuckel, Fungi rhenani exsic. suppl., fasc. 7, no. 2173. 1868. Fig. 7.

Ascomata superficial with their bases immersed in a grey to black crust or wood, loosely or densely aggregated, sometimes fusing laterally, often in large numbers, variable in shape, subglobose, semiglobose, pyriform to nearly conical, shiny greyish black, (177–)220–335(–372) μm high, (180–)230–350(–440) μm diam ($n = 30$); surface smooth or variously warted or wrinkled. Apex variable, usually obtuse or broadly papillate, sometimes conical and pointed or laterally compressed, (45–)68–132(–185) μm ($n = 60$) diam. *Peridium* dark brown, (20–)30–65 μm thick, usually thinner at the base, comprising an inner, often degenerated, pale brown amorphous layer, sometimes also containing thin-walled cells, and an outer *textura angularis* of cells (1.5–)2.5–7(–12) μm ($n = 57$) tending to be smaller, darker brown and thick-walled towards the outside, at the base or lower levels surrounded by a dense crust of dark brown, thick-walled compacted, up to 6 μm wide hyphae with various inclusions including ejected ascospores. *Hamathecium* comprising 1–2.5 μm wide, branched and anastomosing trabeculate pseudoparaphyses. *Asci* (80–)92–115(–120) \times (6.2–)6.8–8.3(–9.0) μm ($n = 18$), cylindrical, bitunicate, fissitunicate, with short stipe and simple or furcate base, containing 8 overlapping uni-, partly biserial ascospores; endotunica wide, swelling in 3% KOH, ocular chamber minute. *Ascospores* (13–)14–16.5(–21) μm long, l/w (2.8–)3.2–3.8(–4.8) ($n = 86$), fusoid, with three thick and dark eusepta, pale brown when young, turning dark brown, biconical, disarticulating inside the asci at the middle septum to form two conical, 2-celled parts; parts dimorphic, distal part (6.2–)6.7–8.1(–9.8) \times (3.8–)4.1–4.7(–5.7) μm , blunt conical, proximal part (6.6–)7.2–8.7(–11.3) \times (3.4–)3.7–4.3(–5.5) μm ($n = 86$), narrowly conical, smooth.

Cultures and asexual morph in culture: Hyphae very thin, moderately growing, entirely covering laterally inoculated plates on CMD at 25 °C after ca. 2 mo. *Colony* circular, dull or olive-brown, centre black, cottony mat of aerial hyphae forming (particularly thick on PDA), first white, turning greyish- or olive-brown, after ca. 1 month black conical or subglobose ostiolate pycnidia appearing in the mat and immersed in agar, surrounded by 2–4.5 μm wide in part moniliform brown hyphae with drop-like mucous deposits, extruding hyaline mucous mass of conidia

through the ostiole. *Pycnidia* 70–125(–150) μm high and wide ($n = 20$), up to 200 μm high including conidial mass, ostiole (43–)47–70(–84) μm long, 15–27(–38) μm wide ($n = 16$); peridium thin, comprising a *t. angularis* in face view, olive-brown to dark brown, consisting of cells (3.5–)5.0–8.8(–15) \times (2.7–)4.0–6.5(–13) μm ($n = 35$), dark and thick-walled outside, lighter and thinner-walled inside. Inside lined by hyaline cells giving rise to parallel phialides. *Phialides* (5.5–)6.5–10(–12.5) \times (2–)2.5–3.2(–3.5) μm ($n = 42$), lageniform to cylindrical. *Conidia* (2.3–)2.8–3.8(–4.7) \times (1.5–)1.7–2.2(–2.5) μm , l/w (1.3–)1.5–2.1(–2.4) ($n = 70$), oblong to ellipsoid, 1-celled, hyaline, smooth, with 1–3 guttules, agglutinated in very pale brownish masses. *Pycnidia* also numerous on PDA.

Habitat: saprobiic on decorticated wood.

Distribution: Europe, possibly also North America

Lectotype, here designated: **Germany**, Hessen, Oestrich, Oestricher Wald (Aepfelbach), on roots of *Fagus sylvatica*, in autumn, L. Fuckel (GI, Fungi Rhenani exsicc. 2173; MBT372891; given as holotype by [Samuels \(1980\)](#); isotype in W: W2016-02664!).

Other material examined (all from branches of *Chamaecytisus proliferus*): **Spain**, Canarias, La Palma, El Paso, 30 Dec. 2003, P. Karasch W.J. 2805 (WU 36870; culture MGC); San Isidro, 5 Jan. 2005, soc. *Patellaria atrata*, P. Karasch W.J. 2798 (WU 36871); El Paso, soc. *Lophiostoma macrostomoides*, 15 Jan. 2005, P. Karasch W.J. 2804 (WU 36872); opposite the old chestnut plantation at the road LP 301 heading north, close to the crossing with LP 3, 2 Dec. 2010, W. Jaklitsch (WU 36873; culture CBS 141480 = OM).

Notes: Although we are convinced about the identity of our material, we do not designate an epitype, because of different host (*Chamaecytisus proliferus*) and different region (Canary Islands). At first sight, *Ohleria modesta* looks macroscopically much like *Melanomma pulvis-pyrius*. In all specimens from La Palma most of the material collected is overmature. The ascomata are mostly densely crowded and more or less superficial. In the lectotype of *O. modesta* most ascomata are scattered, but on one piece of wood they are very densely crowded and for a large part immersed in a thick dark hyphal crust. The surface of the ascomata is generally rough and often concentrically ridged or variably tuberculate. As ascospores disarticulate early in the ascus, we calculated their length by addition of each part and the l/w ratio by length divided by the width of the broader distal part. This procedure yields a more reliable size range. *Ohleria rugulosa* was reported by [Fuckel \(1870\)](#) to differ from *O. modesta* by larger semiglobose ascomata and late disarticulation of the ascospores of similar size. We examined type material of *O. rugulosa* from G: **Lectotype**, here designated: **Germany**, Hessen, Oestrich (Nassau), Oestricher Wald, on decaying wood of *Carpinus betulus*, in spring (G 00266073, Herb. Barbey Boissier: MBT 373517). Several differences from *O. modesta* were given on the annotation label of the latter written by Gary Samuels, and by [Samuels \(1980\)](#). We agree with several arguments and summarise the more important ones and add others. While the size of ascomata with *O. modesta* has never been found to exceed a width of 450 μm , those of *O. rugulosa* may reach 780 μm ; they are in comparison with *O. modesta* more amorphous, globose to subglobose or semiglobose or grossly tubercular. No asci were found in the type material in G, but ejected ascospores, of which still many are entire, i.e. they disarticulate late. Their end cells are

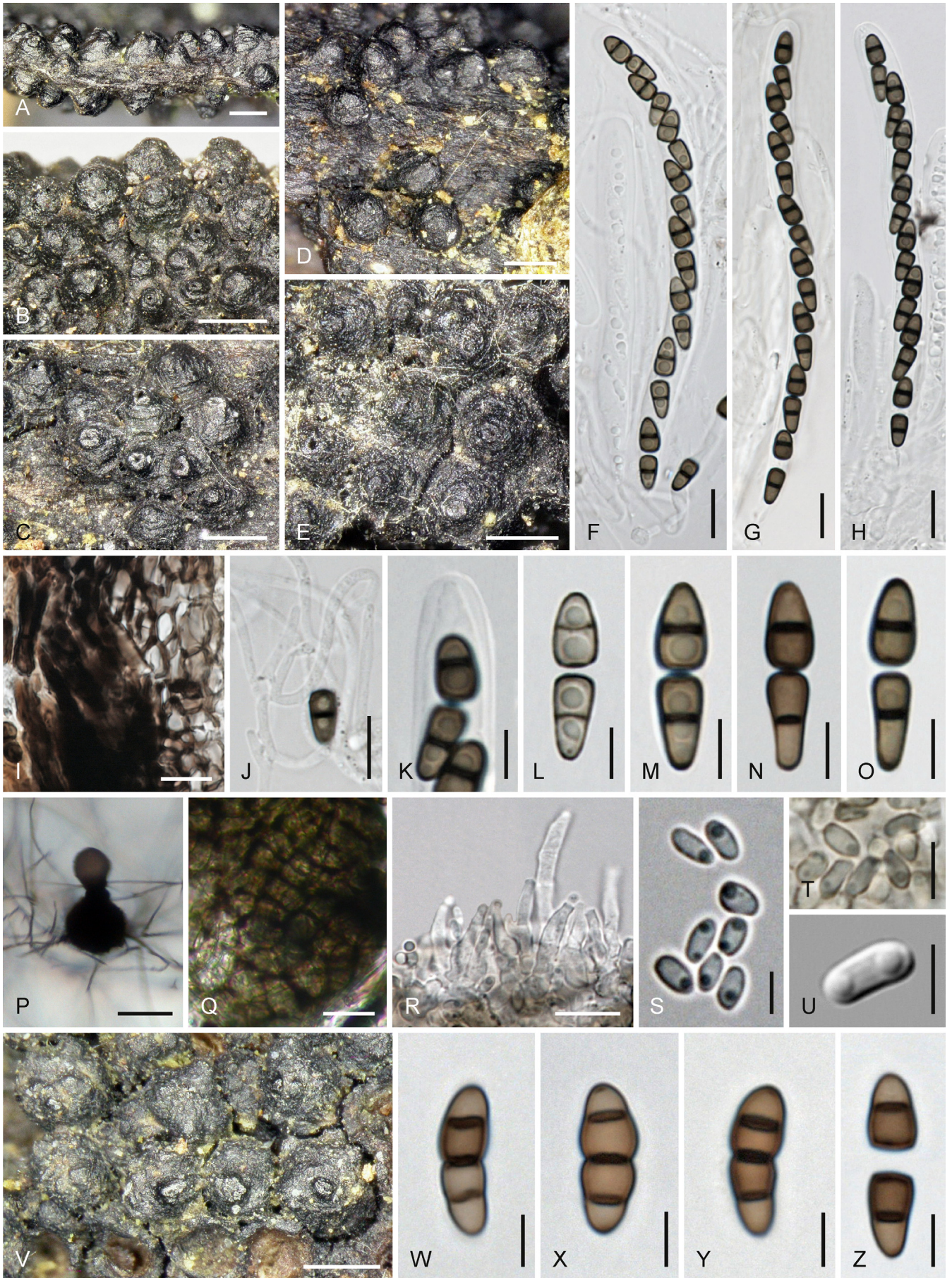


Fig. 7. A–U. *Ohleria modesta*. A–E. Ascomata in face view. F–H. Asci. I. Peridium in section, including hyphae of surrounding crust. J. Trabeculate pseudoparaphyses. K. Ascus apex. L–O. Ascospores (L. young). P–U. Asexual morph. P. Pycnidium with conidial drop. Q. Pycnidial peridium in face view. R. Phialides. S–U. Conidia. A, F, I, J, L, M, O. WU 36873; B. WU 36870; C, E. lectotype G; D, G, H, K. WU 36872; N. isotype W; P, Q, U. culture MGC; R–T. culture OM. V–Z. *Ohleria rugulosa* (lectotype G). V. Ascomata in face view. W–Z. Ascospores. Scale bars: A–E, V = 300 μ m; P = 100 μ m; F–J, Q, R = 10 μ m; K–O, T, W–Z = 5 μ m; S, U = 3 μ m.

paler than the median cells and the ascospores and its parts are curved, with more rounded sides, in contrast to *O. modesta*. Species of *Ohleria* are saprobes on dead wood and thus unlikely to be host-specific. They are rarely collected and this may be the reason that every mycologist described his own species in the nineteenth century. No convincing differences can be found in the descriptions of several species. Therefore and based on examination of available types, [Samuels \(1980\)](#) synonymised *Ohleria adjecta* Pass., *O. obducens* G. Winter, *O. quercicola* Fabre and *O. ulmi* Fabre with *O. modesta* and accepted the two additional species *O. rugulosa* and *O. brasiliensis* in the genus. He determined that *O. clematidis* Fautrey is a species of *Passeriniella*. Other species he referred to *Sporormia* or *Preussia* based on ascospore features. For *O. brasiliensis* Starbäck, [Samuels \(1980\)](#) described a hyphomycetous asexual morph in *Monodictys*. As we have shown that *Ohleria* forms an aposphaeria- or phoma-like asexual morph and a similar asexual morph was described by [Fuckel \(1870\)](#) for *O. rugulosa* by association on the natural host, we interpret the *Monodictys* morph as a synanamorph, as, e.g., described by [Grondona et al. \(1997\)](#) for *Pyrenochaeta dolichi* (now a species of *Coniothyrium*; [Gruyter et al. 2012](#)). Alternatively, *O. brasiliensis* may not be congeneric with *Ohleria*. See also [Karasch et al. \(2005\)](#) and [Zhang et al. \(2012\)](#) for descriptions of *Ohleria modesta*.

Disarticulation of the brown ascospores is diagnostic for this genus. Other dothideomycetous genera with brown disarticulating ascospores are the representatives of the *Sporormiaceae* including *Ohleriella*, the patellariaceous apothecial *Colensoniella* ([Hafellner 1979](#)) and *Glyphium* ([Boehm et al. 2015](#)), also *Delitschia* ([Luck-Allen & Cain 1975](#)) and *Hypsostroma* ([Huhndorf 1992](#)), but most similar although much larger are the ascospores of *Hysterodiffractum* ([Carneiro de Almeida et al. 2014](#)), which forms hysterothecia. Phylogenetically, *Ohleria* is neither closely related to *Melanomma* nor *Trematosphaeria* ([Samuels 1980](#)), nor to the *Sporormiaceae*.

Hobus Jaklitsch & Voglmayr, **gen. nov.** MycoBank MB817778.

Etymology: The generic name is the southern Carinthian word for fungus, with the masculine Latin ending -us.

Sexual morph erumpent from bark through fissures as groups of black, papillate or cylindrical ostiolar necks, free to nearly completely incorporated by stromatic tissue. *Stroma* compact, forming a *t. oblita*, at upper levels a *t. intricata* of densely interwoven, thick-walled, hyaline to brownish hyphae and roundish cells, delimited by a brown subiculum. *Ascomata* scattered to more commonly aggregated in variable numbers within stromatic tissue. *Peridium* carbonaceous, brittle, complex, pseudoparenchymatous, not clearly delimited outside, dark reddish brown in glycerol, black in KOH. *Ostioles* periphysate. *Hamathecium* of numerous narrow pseudoparaphyses and apically free paraphyses. *Asci* clavate, fissitunicate, thick-walled, with a small ocular chamber, 8 biserially arranged ascospores, an up 30 µm long stipe and a furcate base with croziers. *Ascospores* fusoid with the second cell slightly enlarged, with several slightly constricted eusepta, dark brown, end cells sometimes slightly paler; wall thick, verruculose.

Type species: *Hobus wogradensis* Jaklitsch & Voglmayr

Hobus wogradensis Jaklitsch & Voglmayr, **sp. nov.** MycoBank MB817779. [Fig. 8](#).

Etymology: The epithet reflects the collection site “Wograda”, which is an old southern Carinthian word for pasture, in this case reflecting a defined site.

Sexual morph erumpent from bark through fissures as inconspicuous and roundish or large and conspicuous, narrow and longish, 0.2–8.6 mm long and 0.2–1.8 mm broad groups of black, papillate or cylindrical ostiolar necks, variably surrounded, rarely nearly completely incorporated by stromatic tissue. *Stroma* compact, forming a *t. oblita*, at upper levels a *t. intricata* of densely interwoven, thick-walled refractive, (1.5–) 1.8–3.5(–4.5) µm (n = 40) wide hyphae and roundish cells (1.8–)2.8–5.2(–7.5) µm (n = 55) diam, hyaline to brownish, often with some darker inclusions, often thick and present below and around ascomata, outside variably delimited by a layer of (1.8–)2.2–4.2(–6.3) µm (n = 30) wide brown hyphae, sometimes reduced to the latter; stroma surface therefore appearing pale brown to greyish or dark brown to nearly black. *Ascomata* scattered to mostly closely aggregated in variable numbers (up to 80 per group when well-developed) in stromatic tissue below the host epidermis, standing on the wood; often lifting and disintegrating the epidermis and projecting up to ca. 1.4 mm above the bark surface, globose to subglobose, often slightly higher than broad, (230–)250–315(–353) µm high, (174–) 200–300(–332) µm diam (n = 22). *Peridium* (14.5–) 29–56(–82) µm wide (n = 21), carbonaceous, brittle, often thickened and opaque at the base of the ostiolar neck, consisting of an inconspicuous narrow compressed hyaline tissue inside, a layer of brownish angular more or less thin-walled cells (5–) 6–14(–20) × (3.5–)4–8.5(–12) µm (n = 40), and at the outside a poorly defined, not clearly delimited, inhomogeneously pigmented, dark to blackish brown amorphous layer of small particles, cells and hyphae partially peeling off, dark reddish brown in 40 % glycerol, dark brown in LA, black in KOH. *Ostiolar necks* often for a large part free or surrounded by stroma, (143–) 176–255(–280) µm long (n = 21), (70–)94–160(–230) µm (n = 67) wide outside, (40–)51–77(–88) µm (n = 21) wide inside, filled with periphyses of the same width as the pseudoparaphyses, apically partially forming brownish, apically rounded, to 3.5 µm wide hyphae originating from the interior, outside cellular; apex flat or rounded, rough or glabrous and shiny. *Hamathecium* of numerous branched, 1–2.5(–3) µm wide pseudoparaphyses and some apically free paraphyses. *Asci* (58–) 76–99(–106) × (10.2–)10.8–13.2(–14.2) µm (n = 21), clavate, fissitunicate, with thick walls, a small ocular chamber, 8 biserially arranged ascospores, an up 30 µm long stipe and a furcate base with croziers. *Ascospores* (13.8–) 15.7–19.2(–22.5) × (4.5–)5.2–6.2(–6.5) µm, l/w (2.5–) 2.7–3.4(–4.3) (n = 62), fusoid, with the second cell slightly enlarged, with 3 slightly constricted eusepta in ca. equal distances, straight or slightly curved, yellowish to pale brown when young, dark to blackish brown when fully mature, end cells sometimes slightly paler; wall thick, verruculose.

Cultures: On MEA colony radius 26 mm after 7 wk at 22 °C, colony dark brown, mat of aerial hyphae grey to greyish brown, containing numerous droplets, reverse black. On CMD colony radius 14 mm after 1 mo at 22 °C, blackish brown with yellow tint. Dilute reddish pigment diffusing through the agar (particularly on MEA and PDA); odour indistinct. No asexual morph detected.

Habitat: on dead logs and branches of *Juglans regia*.

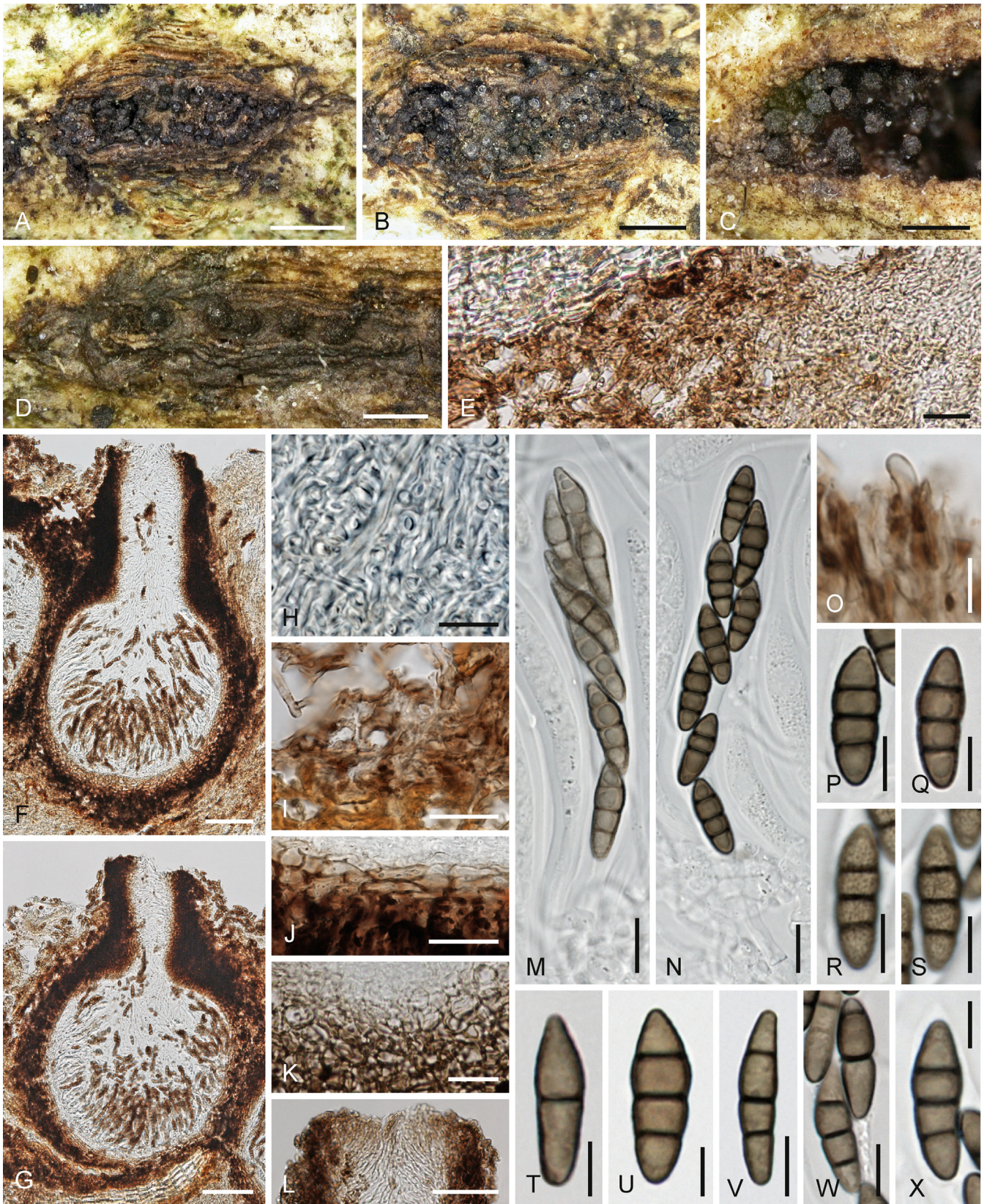


Fig. 8. *Hobus wogradensis* (WU 36874). **A–D.** Ostiolar apices and stroma surface in face view in bark fissures. **E.** Stroma tissue in vertical section (note epidermis cells at upper left, brown hyphae left and compact stroma right). **F, G.** Ascomata in vertical section. **H.** Section through compact hyaline stroma. **I.** Brown hyphae and amorphous tissue above lower bark tissue at the margin of the compact stroma. **J, K.** Basal peridium in section (**J.** median section, **K.** peripheral section). **L.** Ostiolar apex in vertical section. **M, N.** Asci (**M.** young). **O.** Apical ostiolar hypha. **P–X.** Ascospores (**R, S.** showing verruculose surface; **R** is the same ascospore as **P**). Scale bars: **A** = 1 mm; **B** = 0.7 mm; **C, D** = 0.4 mm; **E, I–K** = 20 μ m; **F, G** = 70 μ m; **H, M, N** = 10 μ m; **L** = 50 μ m; **O–S, V, W** = 7 μ m; **T, U, X** = 5 μ m.

Distribution: Central Europe (Austria), only known from the holotype.

Holotype: Austria, Kärnten, St. Margareten im Rosental, Wograda, grid square 9 452/3, on a fallen log of *Juglans regia*, 14 Apr. 2006, W. Jaklitsch W.J. 2902 (WU 36874, **ex-type** culture CBS 141484 = TI).

Notes: This species is characterised by a well-developed stroma, which is absent in all other species studied here. Notable is also the formation of a diffusing reddish pigment in fresh cultures, particularly on MEA and PDA. In contrast, the purple pigment in cultures of *Cylothryiella rubronotata* is confined to the colony, i.e. it does not diffuse into the agar.

Nigrogranaceae Jaklitsch & Voglmayr, **fam. nov.** MycoBank MB817780.

Etymology: Referring to the name of the type genus.

Ascomata immersed-erumpent from wood and bark, sometimes superficial, scattered or aggregated, more or less globose, black, usually seated on or surrounded by a subiculum. *Ostiolar necks* papillate to cylindrical; *ostioles* periphysate. *Peridium* pseudoparenchymatous. *Hamathecium* consisting of apically free paraphyses originating in the subhymenium between developing asci, later becoming elongated, branching and anastomosing and appearing as “trabeculate pseudoparaphyses”. *Asci* clavate, bitunicate, fissitunicate, with short stipe and knob-like base, containing 8 biserially arranged ascospores. *Ascospores* asymmetric, fusoid to narrowly ellipsoid with the second cell slightly wider than others, straight or curved, 1–3-euseptate, pale to chocolate brown, smooth or faintly verruculose.

Pycnidia similar to ascomata. *Peridium* brown, pseudoparenchymatous. *Conidiophores* when present filiform, simple to sparsely branched, with pegs and terminal phialides. *Phialides* ampulliform, lageniform, or subcylindrical. *Conidia* forming on pegs and phialides, rod-like to ellipsoid, 1-celled, hyaline or subhyaline, sometimes pale brown in mass, smooth.

Type genus: *Nigrograna* Gruyter *et al.*

Nigrograna Gruyter *et al.*, Stud. Mycol. 75: 31. 2012, emend.

Sexual morph: **Ascomata** depressed globose to globose, immersed in wood and bark, erumpent, less commonly superficial, scattered or aggregated in small groups, black, seated on or surrounded by olivaceous or brown, KOH-negative subiculum. *Ostiolar necks* papillate to cylindrical; *ostioles* periphysate. *Peridium* pseudoparenchymatous, cells thin-walled and lighter at the inner side, thick-walled and darker at the outer side, usually covered by hyphae. *Hamathecium* consisting of apically free paraphyses originating in the subhymenium between developing asci, later becoming elongated, branching and anastomosing and appearing as “trabeculate pseudoparaphyses”. *Asci* clavate, bitunicate, fissitunicate, with short stipe and knob-like base, containing 8 ascospores biserially arranged in the upper part. *Ascospores* asymmetric, fusoid to narrowly ellipsoid with the second cell slightly wider than others, straight or curved, 1–3-euseptate, pale to chocolate brown, smooth or faintly verruculose.

Asexual morph: **Pycnidia** similar to ascomata and usually co-occurring with them. *Peridium* brown, pseudoparenchymatous. *Conidiophores* filiform, simple to sparsely branched, with pegs along one or two sides and solitary terminal phialides; reduced in culture (from clinical isolates). *Phialides* ampulliform, lageniform, or subcylindrical. *Conidia* forming on pegs and phialides, oblong, cylindrical or allantoid, sometimes ellipsoid, hyaline or subhyaline, 1-celled, smooth.

Habitat: in bark of moderately decayed twigs of shrubs and trees, often in old fructifications of pyrenomycetes, sometimes human pathogenic.

Type species: *Nigrograna mackinnonii* (Borelli) Gruyter *et al.*

Notes: *Nigrograna* was described by Gruyter *et al.* (2012) as a monotypic genus. *Nigrograna mackinnonii* was isolated from human mycetomata in Mexico and Venezuela, and no sexual morph was known. Here we add the sexual morph and asexual morph from natural substrates. For pycnidia of *Nigrograna mackinnonii* in culture no conidiophores were described. Absence of conidiophores may be an adaptive reduction from the natural situation.

All species of *Nigrograna* are morphologically very similar and may be interpreted as cryptic species. As Chesters (1938) noted for *N. fuscidula* (as *Melanomma fuscidulum*), ascospores first develop their median primary septum and consecutively the two 2 additional septa. In all species of *Nigrograna* with available sexual morph apically free paraphyses were found among immature asci, just as in other genera of the *Thyridariaceae* or in *Teichospora* (Jaklitsch *et al.* 2016).

Nigrograna fuscidula (Sacc.) Jaklitsch & Voglmayr, **comb. nov.** MycoBank MB817787. Figs 9, 10.

Basionym: *Sphaeria fuscidula* Sacc., Myc. Ven. II, No. 159. 1875, in sched.

Synonyms: *Melanomma fuscidulum* (Sacc.) Sacc. [as “*Melanoma fuscidula*”], Hedwigia 14: 73. 1875.

Aposphaeria fuscidula (Sacc.) Sacc., Syll. fung. (Abellini) 3: 173. 1884.

Ascomata (180–)215–405(–570) μm (n = 45) diam, (160–)175–260(–340) μm (n = 33) high, depressed globose to globose, grey to black, variable in size and appearance depending on the specimen; immersed in bark and wood with only ostiolar necks visible on the host surface or immersed-erumpent, only rarely becoming superficial, scattered to aggregated in numbers of up to 10, often associated with pycnidia when young, and both surrounded by brown to olivaceous, branched, cylindrical, 2–4 μm wide subicular hyphae. *Subiculum* often concentrated below the epidermis on the host or occurring as mats or extending in patches on decorticated wood. *Peridium* to 35 μm thick, pseudoparenchymatous, consisting of a subhyaline to pale brown inner layer of small thin-walled angular cells and an outer dark brown *t. angularis* of thick-walled cells 3–11 μm diam. *Ostiolar necks* (31–)52–86(–125) μm (n = 53) diam, ca 90–480 μm long, black, protruding up to 0.4 mm from the host surface, short-papillate to long-cylindrical, rounded or angular in section, erect or oblique, central or eccentric, apex rounded or flattened, black. True and distinct hymenium present, apically free, 1–3.5 μm wide unbranched *paraphyses* present among initial stages of asci, later

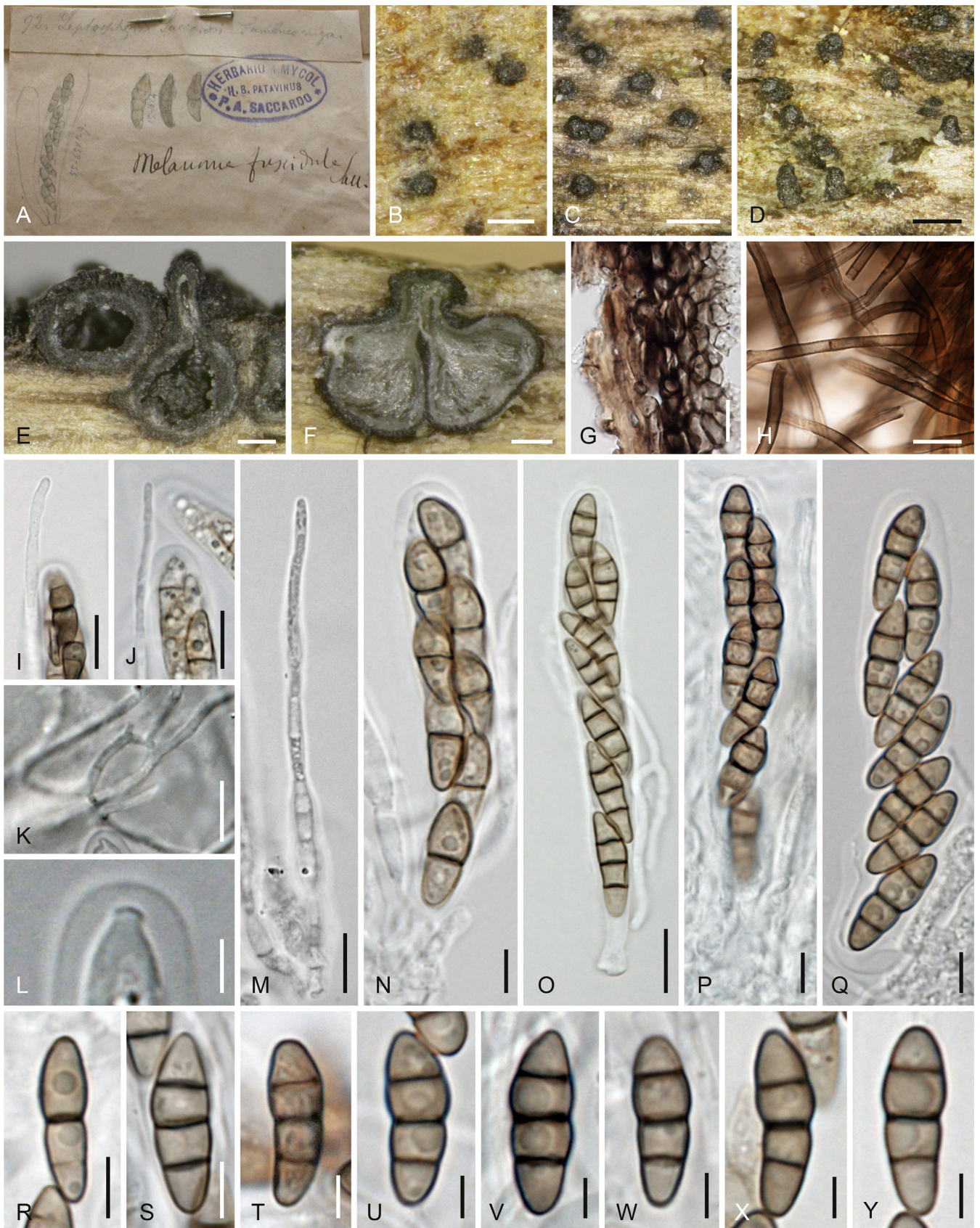


Fig. 9. *Nigrograna fuscidula*, sexual morph. **A.** Specimen label. **B–D.** Ostiolar necks on the host surface. **E, F.** Ascomata in vertical section. **G.** Peridium in section. **H.** Subicular hyphae. **I, J.** Free ends of paraphyses among ascus tips. **K.** Branched (?pseudo)paraphyses above asci. **L.** Ascus tip. **M.** Paraphysis in young hymenium (asci at initial stage). **N–Q.** Asci (**N, O.** young). **R–Y.** Ascospores (**R, S.** young). **G, H, J–L, O, R, S, U, V, X, Y.** in 3% KOH. **A.** isotype (PAD); **B, K, O, P, S, T.** lectotype K(M) 202882; **C–F, R, U, V.** WU 36879; **G–J, L, N.** WU 36881; **M, Q, Y.** WU 36880; **W.** WU 36884; **X.** WU 36883. Scale bars: **B, E, F** = 100 μ m; **C, D** = 200 μ m; **G–K, M, O** = 10 μ m; **L, T–Y** = 3 μ m; **P–S** = 5 μ m.

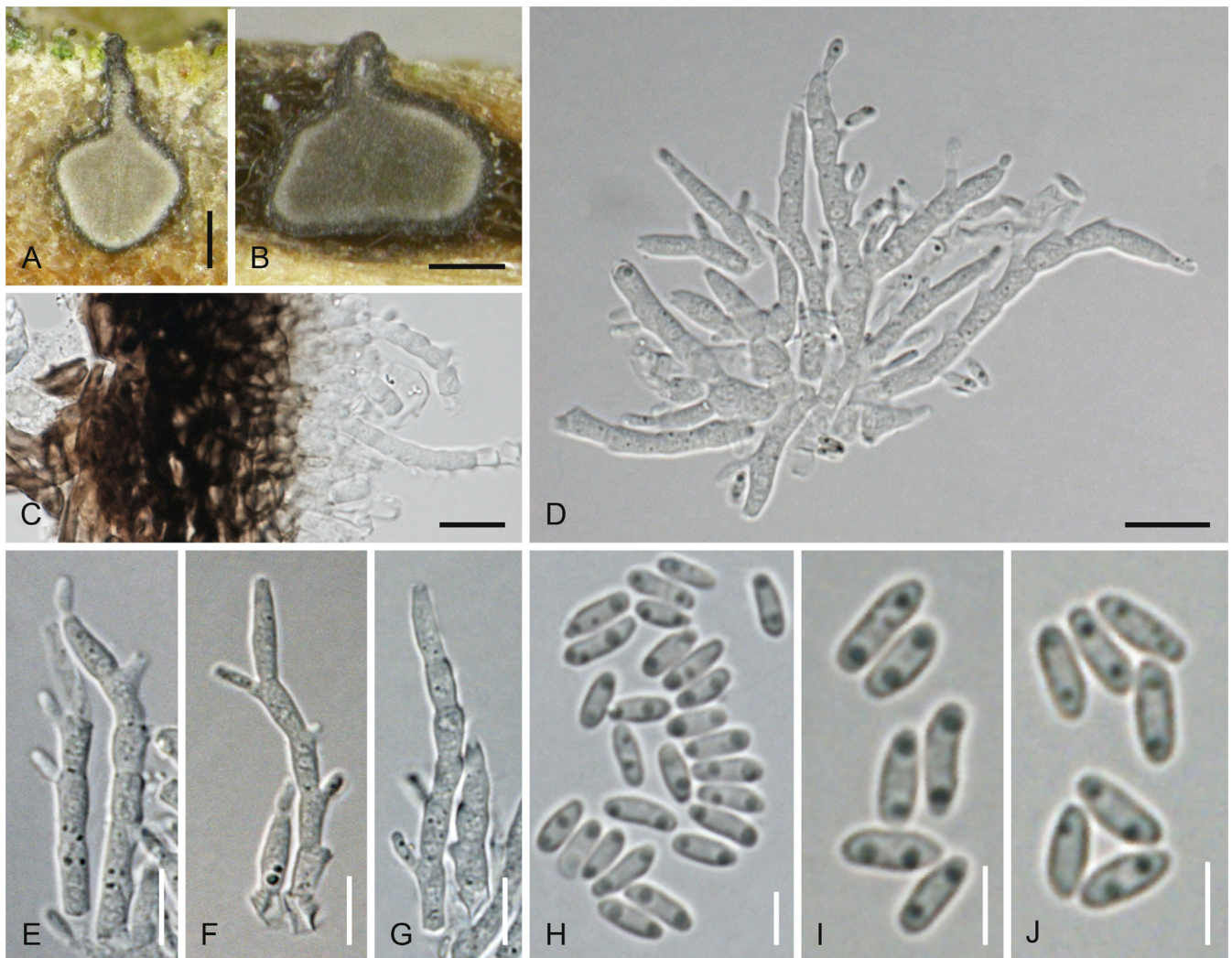


Fig. 10. *Nigrograna fuscidula*, asexual morph on the natural host. **A, B.** Pycnidia in vertical section. **C.** Pycnidial wall, subicular hyphae and old conidiophores. **D–G.** Conidiophores with pegs and phialides. **H–J.** Conidia. **A, B.** WU 36880; **B, D–I.** WU 36882; **C, J.** WU 36881. Scale bars: A, B = 100 μ m; C, D = 10 μ m; E–G = 7 μ m; H–J = 3 μ m.

branching and also anastomosing above asci. *Asci* (48–)52–72(–82) \times (8.0–)8.3–9.8(–11) μ m ($n = 38$), clavate to oblong, bitunicate, fissitunicate, with short stipe and simple or furcate base; endotunica thick, swelling in 3% KOH, containing 8 biseriolate ascospores. *Ascospores* (10.2–)12–14.5(–18) \times (3.8–)4.2–5.0(–5.4) μ m, l/w (2.2–)2.6–3.3(–4.5) ($n = 103$), asymmetrically fusoid with upper part or second cell slightly wider, often slightly curved, thick-walled, 1-septate in young asci, becoming 3-euseptate, slightly constricted at the primary median septum, first pale greyish brown, turning medium to dark grey-brown, not or slightly and slowly darkening in 3% KOH, smooth.

Asexual morph on the natural host: *Pycnidia* ca. 140–340 μ m diam, ca. 100–195 μ m high, co-occurring with ascomata and very similar to them, but contents grey or greyish brown, interior filled with conidia and a whitish conidiophore layer between the peridium and the conidial mass. *Peridium* 20–35 μ m thick, forming a *t. angularis* of dark brown, thick-walled 4–10(–11) μ m wide cells. *Conidiophores* arising from the pycnidial wall, to 55 μ m long and mainly 2–3.7 μ m wide, simple, only branched once near the base, with pegs along one or two sides and solitary phialides terminally. *Phialides* (5.0–)6.5–8.7(–10.5) \times (2.0–)2.5–3.0(–3.5) μ m ($n = 34$), variable in shape, ampulliform-lageniform-subcylindrical. *Conidia* (3.0–)

3.2–4.3(–6.0) \times (1.1–)1.3–1.6(–1.8) μ m, l/w (2–)2.2–3(–3.8) ($n = 72$), rod-like, oblong to cylindrical or allantoid, brownish in mass, individually subhyaline to hyaline, 1-celled, containing 2 guttules, smooth.

Cultures: On CMD at 22 °C colony radius 13–17 mm after 1 mo, colony circular, pale to dull brown, darkening with time, distinctly or indistinctly zonate due to aerial hyphae, centre often darker, white aerial hyphae spreading from the centre, containing numerous minute drops, odour often unpleasant, reminiscent of dental clinics; no asexual morph detected.

Habitat: in bark and wood of branches and logs of *Sambucus nigra*.

Distribution: Europe.

Lectotype, here designated: **Italy**, Treviso, Vittorio, on branches of *Sambucus nigra*, Oct. 1873, P.A. Saccardo Mycotheca Veneta No. 159 (K(M) 202882!; MBT372892. PAD: isotype). **Epitype**, here designated: **Austria**, Vienna, 22nd district, Lobau, Panzallacke, on dead branches and twigs of *Sambucus nigra* lying on the ground, ascomata in wood, 27 Mar. 2016, W. Jaklitsch (WU 36879; **ex-epitype** culture CBS 141556 = MF7; MBT372418). Designation of an epitype is necessary due to

easy mix-up with other species. The Austrian material is selected, because the specimens collected in Italy are for the most part overmature.

Other material examined: **Austria**, Niederösterreich, close to the highway exit Bad Vöslau, on dead branches of *Sambucus nigra* attached to the shrub, 22 Feb. 2016, W. Jaklitsch & H. Voglmayr (WU 36880; culture MF3); Vienna 22nd district, Lobau, Panozzalacke, on dead branches of *Sambucus nigra* attached to the shrub, holomorph, ascomata mainly in bark, often immature, 21 Mar. 2015, W. Jaklitsch (WU 36881; culture from ascospores CBS 141476 = MF1; culture from conidia MF1a); ibidem, same substrate, same collector, 20 Feb. 2016, W. Jaklitsch (WU 36882). **France**, Ariege, Rimont, Las Muros, elev. 480 m, on decorticated twigs of *Sambucus nigra*, 12 Apr. 2016, J. Fournier JF 16013 (WU 36890). **Italy**, Veneto, Padua, Colli Euganei, Arqua Petrarca, on branches of *Sambucus nigra* on the ground, ascomata mostly overmature, mostly in wood, soc. old *Diaporthe* sp., 6 Apr. 2016, W. Jaklitsch & H. Voglmayr (WU 36883; culture MF8). Veneto, Treviso, colle Montello, on branches of *Sambucus nigra* on the ground, ascomata in bark and wood, mostly overmature, 8 Apr. 2016, W. Jaklitsch & H. Voglmayr (WU 36884; culture MF9).

Notes: *Melanomma fuscidulum* is not congeneric with *M. pulvispyrius*, the generic type of *Melanomma*, the type genus of the *Melanommataceae*. All species with sexual morphs here recognised in *Nigrograna* would earlier have been identified as *Melanomma fuscidulum*. Most seem to be fungicolous. **Chesters (1938)** studied *Melanomma fuscidulum* in detail. However, his descriptions and conclusions regarding the asexual morph were from material collected on *Ulmus* and thus, in light of the molecular diversification of species having similar morphology, he most probably studied a different species. We have detected *N. fuscidula* only on its original host *Sambucus nigra*. Ascomata may be found on attached branches. In this case they are usually immersed in bark, asci are often immature and contain 2-celled, sometimes even 1-celled spores; also associated pycnidia are more common in such specimens. On twigs on the ground the fungus usually occurs in wood and bark. Interestingly, in wood ascomata sometimes tend to be larger and ascospores smaller and darker. Culture preparation from both forms yielded the same DNA data. *Nigrograna fuscidula* may be mistaken for *Parathyridaria ramulicola*, which may occur on the same host, but differs by short discoid ostioles, distinctly stromatised wood around ascomata, absence of a subiculum and by pale greyish brown ascospores, which do not darken in 3 % KOH. Darkening around ostioles of *N. fuscidula* may be due to the upper part of erumpent ascomata or subiculum, or by other fungi. A differentiation from *N. obliqua*, which may also occur on *Sambucus nigra* is difficult, but the latter has slightly larger, esp. wider and very dark ascospores when mature. The dark brown ascospores including the ascus shown from the slide of the *M. fuscidulum* lectotype have not been effectively reconstituted and may therefore appear too dark.

Nigrograna mycophila Jaklitsch, Friebes & Voglmayr, **sp. nov.** MycoBank MB817781. Fig. 11.

Etymology: *mycophila* for its occurrence on other fungi, particularly *Diaporthales*.

Ascomata immersed in bark, in or above effete ascomata of *Diaporthales*, singly or arranged in valsoid groups, globose to subglobose, (172–)213–336(–380) μm wide and high (n = 16), variably surrounded by olivaceous to brown subiculum, the latter also ascending ostiolar necks as stiff seta-like hairs. *Ostiolar*

neck (57–)65–124(–159) μm (n = 20) diam, cylindrical, black, straight or obliquely emerging, apex rounded or flat, concolorous or more frequently lighter in colour, whitish, yellowish, olivaceous or brownish, not or only slightly projecting beyond the bark level. *Peridium* pseudoparenchymatous, consisting of (3–) 3.5–7(–11) μm (n = 30) wide cells, thin-walled and pale brown at the interior, becoming darker and thicker-walled to the outside; there wall densely covered by 2–4 μm wide smooth subicular hyphae making width determination difficult. *Hamathecium* consisting of numerous 1–3.5 μm wide paraphyses with free ends visible among immature asci and apparently trabeculate pseudoparaphyses widest at their bases. *Asci* (65–) 72–85(–89) \times (10.5–)11–13(–14.3) μm (n = 26), clavate, bitunicate, fissitunicate but stable in mounts, with a small ocular chamber, thick endotunica, short stipe and knob-like to furcate base, containing 8 ascospores biserially arranged, particularly at upper levels. *Ascospores* (12.7–)14.3–17(–19) \times (5.0–) 5.5–6.3(–6.9) μm , l/w (2.3–)2.4–2.9(–3.2) (n = 80), fusoid to narrowly ellipsoid, with the second cell or the upper part slightly enlarged, straight or curved, 2-celled and pale brown when young, 3-euseptate and dark brown at maturity, slightly constricted at the median septum, thick-walled, smooth, not or only slightly darker in 3 % KOH.

Asexual morph on the natural host: *Pycnidia* similar to ascomata but smaller, ca. 100–220 μm diam, immersed in perithecia of the host fungus, with a dark brown pseudoparenchymatous wall, surrounded by olivaceous to brown subiculum, containing simple, sparsely branched, up to 50 μm long *conidiophores*. Solitary minute *pegs* and lageniform to subcylindrical *phialides* (4.2–) 7.0–10(–10.8) \times (1.8–)2.0–2.5(–2.7) μm (n = 16) inserted along and terminally on the *conidiophores* producing oblong to cylindrical, 1-celled, hyaline, smooth *conidia* (3.0–)3.5–4.2(–5.7) \times (1.3–) 1.5–1.9(–2.1) μm , l/w (1.6–)1.9–2.5(–3) (n = 51).

Cultures: On CMD growth radius at 22 °C ca. 10 mm after 18 d and 15–17 mm after 37 d; colony circular, dark and deep brown or with an olivaceous tinge, with radial texture, indistinctly zonate, with light aerial hyphae in the centre, odour indistinct. On MEA growth radius 18 mm after 41 d at 22 °C (TDK), light grey, turning dark brown with time, with a thick pale (greyish) brown mat of aerial hyphae, reverse dark brown to black, odour indistinct. No asexual morph detected.

Habitat: in ascomata and pseudostromata of *Diaporthales* on corticated twigs of various shrubs and trees (known from *Acer campestre*, *Acer pseudoplatanus* and *Corylus avellana*).

Distribution: Europe (Austria, Denmark)

Holotype: **Austria**, Burgenland, Oberwart, Althodis, near parking place of the Baumwipfelweg, in pseudostromata of *Diaporthe* sp. on twigs of *Acer campestre* attached to the tree, 27 Feb. 2016, G. Friebes (WU 36886, **ex-type** culture CBS 141478 = MF5).

Other material examined: **Austria**, Steiermark, Bruck an der Mur, Kaltenbachergraben, in pseudostromata of ?*Diaporthe decedens* on twigs of *Corylus avellana* on the ground, 5 Mar. 2016, G. Friebes (WU 36887, culture MF6). **Denmark**, Kristiansminde, Sorö Sønderskov, close to the field centre, in ascomata of *Calospora innesii* on twigs *Acer pseudoplatanus*, 27 May 2007, W. Jaklitsch W.J. 3095 (WU 36888, culture CBS 141483 = TDK).

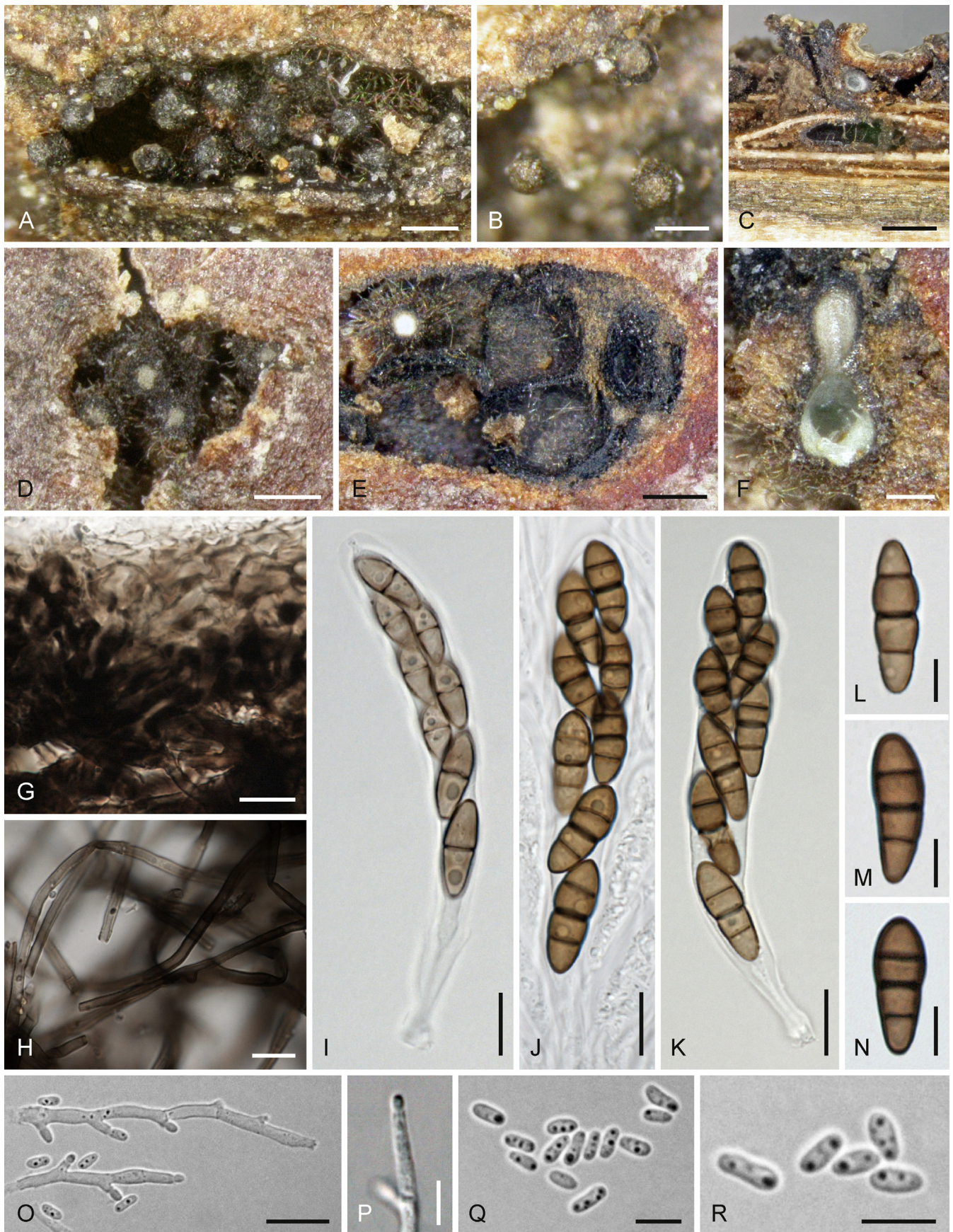


Fig. 11. *Nigrograna mycophila*. **A, B, D.** Ostiolar necks in face view. **C.** Laterally cut ascoma above an effete ascoma of a *Diaporthe* sp. (note the grey stromatic zone of the *Diaporthe* in the wood). **E.** Horizontally cut pycnidium surrounded by subicular hyphae in an ascoma of *Calosporella innesii*. **F.** Young ascoma in vertical section, surrounded by subicular hyphae. **G.** Peridium in section (subicular hyphae in the lower part). **H.** Subicular hyphae. **I–K.** Asci (**I.** immature). **L–N.** Ascospores. **O.** Conidiophores with phialides and conidia. **P.** Phialide. **Q, R.** Conidia. **I, J, O, Q, R.** in 3% KOH. **A, L.** WU 36887; **B, C, J, K.** WU 36886; **D–I, M–R.** WU 36888. Scale bars: **A, D, E** = 150 μ m; **B, F** = 100 μ m; **C** = 250 μ m; **G–K, O** = 10 μ m; **L–N, P–R** = 5 μ m.

Nigrograna norvegica Jaklitsch & Voglmayr, **sp. nov.** MycoBank MB817782. Fig. 12.

Etymology: *norvegica*, due to its occurrence in Norway.

Ascomata immersed in ascomata and pseudostromata of *Diaporthe* sp. singly or in valsoid groups, (177–)200–285(–320) μm ($n = 14$) diam, with slightly smaller height, globose to depressed globose, black, surrounded by a *subiculum* of brown to olivaceous, 2–5 μm wide hyphae; *subiculum* also concentrated between wood and bark. *Ostiolar necks* (50–)51–75(–88) μm ($n = 21$) diam, black, cylindrical or papillate-conical with rounded top, central or eccentric, vertical or oblique and convergent. *Peridium* 10–30 μm thick, pseudoparenchymatous, consisting of (2.5–)3.5–7.5(–11.5) μm ($n = 64$) wide cells, tending to be larger, paler and more thin-walled inside, and smaller, darker reddish brown and thick-walled outside. *Hamathecium* consisting of apically free paraphyses and possibly trabeculate pseudoparaphyses, branched, anastomosing, 1–3 μm wide. *Asci* (50–)61–77(–85) \times (7.2–)7.5–9(–10) μm ($n = 23$), oblong to clavate, fissitunicate but with high stability in mounts, thick-walled, with small but distinct ocular chamber, a stipe to ca. 35 μm long and knob-like base, containing 8 ascospores biseriately arranged at upper levels. *Ascospores* (8.6–)10.8–13.5(–16.5) \times (3.3–)3.8–4.4(–4.8) μm , l/w (2.3–)2.7–3.3(–3.8) ($n = 80$), fusoid to clavate, with 3 eusepta, apical cell often acute, second cell usually slightly widened, constricted at the medium, only slightly at other septa, straight or curved, terminal cells often slightly longer than mid cells, pale to medium brown, slowly turning dark brown in 3 % KOH, smooth.

Asexual morph on the natural host: *Pycnidia* associated with and of similar size and shape as ascomata, white inside; *peridium* 20–30 μm thick, pseudoparenchymatous, of brown cells 2–7 μm diam. *Conidiophores* arising from the wall in palisadic arrangement, filiform, septate, 1- to several-celled, hyaline, to ca. 60 μm long and 3 μm wide, not or sparsely branched, with pegs along one side and a terminal phialide. *Phialides* (8.2–)8.4–10.5(–11.6) \times (2.0–)2.2–2.7(–3.0) μm ($n = 11$), lageniform to cylindrical. *Conidia* formed on phialides and pegs, (2.9–)3.2–3.7(–4.1) \times (1.5–)1.6–1.8(–2.0) μm , l/w (1.6–)1.8–2.2(–2.6) ($n = 50$), oblong to cylindrical, unicellular, with 1–2 small guttules, smooth.

Growth on CMD at 22 °C slow, growth radius reaching up to 33 mm after 70 d; colony dark brown with a paler ring around the centre, internally lobed, aerial hyphae forming a loose reticulum; odour indistinct. No asexual morph detected.

Habitat: in pseudostromata of *Diaporthales*.

Distribution: Norway, only known from the holotype location.

Holotype: Norway, Aust-Agder, Arendal kommune, Nedenes, Langevoll, in pseudostromata of a *Diaporthe* sp. soc. *Cosmospora* (s. lato) sp. on a twig of *Tilia platyphyllos* lying on the ground, 4 Oct. 2014, W. Jaklitsch & H. Voglmayr (WU 36885; **ex-type** culture CBS 141485 = TR8).

Note: This species is known from a single collection, therefore no prediction about variation of morphological features is possible.

Nigrograna obliqua Jaklitsch & Voglmayr, **sp. nov.** MycoBank MB817783. Fig. 13.

Etymology: *obliqua* owing to the oblique position of its ascomata with respect to the host surface.

Ascomata (210–)275–435(–495) μm ($n = 22$) diam, ca. 240–400 μm high, globose to subglobose, immersed in bark, sometimes erumpent, becoming visible in bark fissures, standing on wood or inner bark, scattered or in small groups to 5 forming 0.5–2 mm wide irregular pustules, often lying singly parallel or oblique to the bark or wood surface and then with a cylindrical ostiolar neck to 0.5 mm long; often surrounded by an olivaceous to dark brown *subiculum* of 1.5–5 μm wide brown hyphae, sometimes inflated up to 8.5 μm , unchanged in 3 % KOH. *Apex* blunt or papillate, black, sometimes apically flattened, (45–)67–120(–150) μm ($n = 62$) wide; *ostioles* periphysate. *Peridium* ca. 20–40 μm wide, often appearing thicker due to densely adhering hyphae, dark brown, turning olivaceous to black in 3 % KOH, pseudoparenchymatous, comprising (4–)5.5–11(–15.5) μm ($n = 43$) wide cells, thin-walled and lighter at the inner side, thick-walled and darker at the outer side, usually covered by hyphae; the latter remaining dark brown in 3 % KOH. *Hamathecium* comprising 1–3.5 μm wide trabeculate “pseudoparaphyses” clearly originating in the subhymenium between asci, branched near the bases, also free apices present between immature asci. *Asci* (55–)65–83(–96) \times (8.2–)9.5–12.2(–14.5) μm ($n = 56$), clavate, bitunicate, fissitunicate, with short stipe and knob-like base, with 8 ascospores biseriately arranged in the upper part. *Ascospores* (11.2–)13.0–17.0(–19.8) \times (3.8–)4.5–5.8(–7) μm , l/w (2.3–)2.6–3.2(–4.3) ($n = 162$), fusoid to narrowly ellipsoid with the second cell slightly wider than others, straight to slightly curved, (1–)3-euseptate, slightly constricted at the median septum, pale brownish to yellow-brown when young, turning dark to chocolate brown upon maturation (in water and 3 % KOH), faintly verruculose, with irregularly arranged verrucae (best seen in young ascospores) and one or few guttules in each cell.

Cultures: Growth on CMD at room temperature slow, colony radius 20–25 mm after 2 mo, brown, with a radial texture, margin lighter and wavy, odour indistinct; no asexual morph detected. Colonies on MEA thick, dense, light grey-brown, with a thick mat of aerial hyphae.

Habitat: in bark of moderately decayed twigs of various shrubs and trees (known from *Ribes uva-crispa*, *Salix caprea*, *Sambucus nigra*, *S. racemosa*)

Distribution: Europe (Austria, France, UK).

Holotype: Austria, Kärnten, Millstatt am See, Lammersdorf, at the junction to Pesenthein, on corticated twigs of *Salix caprea*, soc. *Lophiostoma compressum*, 2 Nov. 2015, W. Jaklitsch & H. Voglmayr (WU 36875; **ex-type** culture CBS 141477 = MF2).

Other material examined: Austria, Niederösterreich, Altmelon, Altmeloner Au, on *Sambucus racemosa*, soc. *Diaporthe* sp. in excess, 11 Jul. 2015, W. Jaklitsch, H. Voglmayr & I. Greilhuber (WU 36876; culture CBS

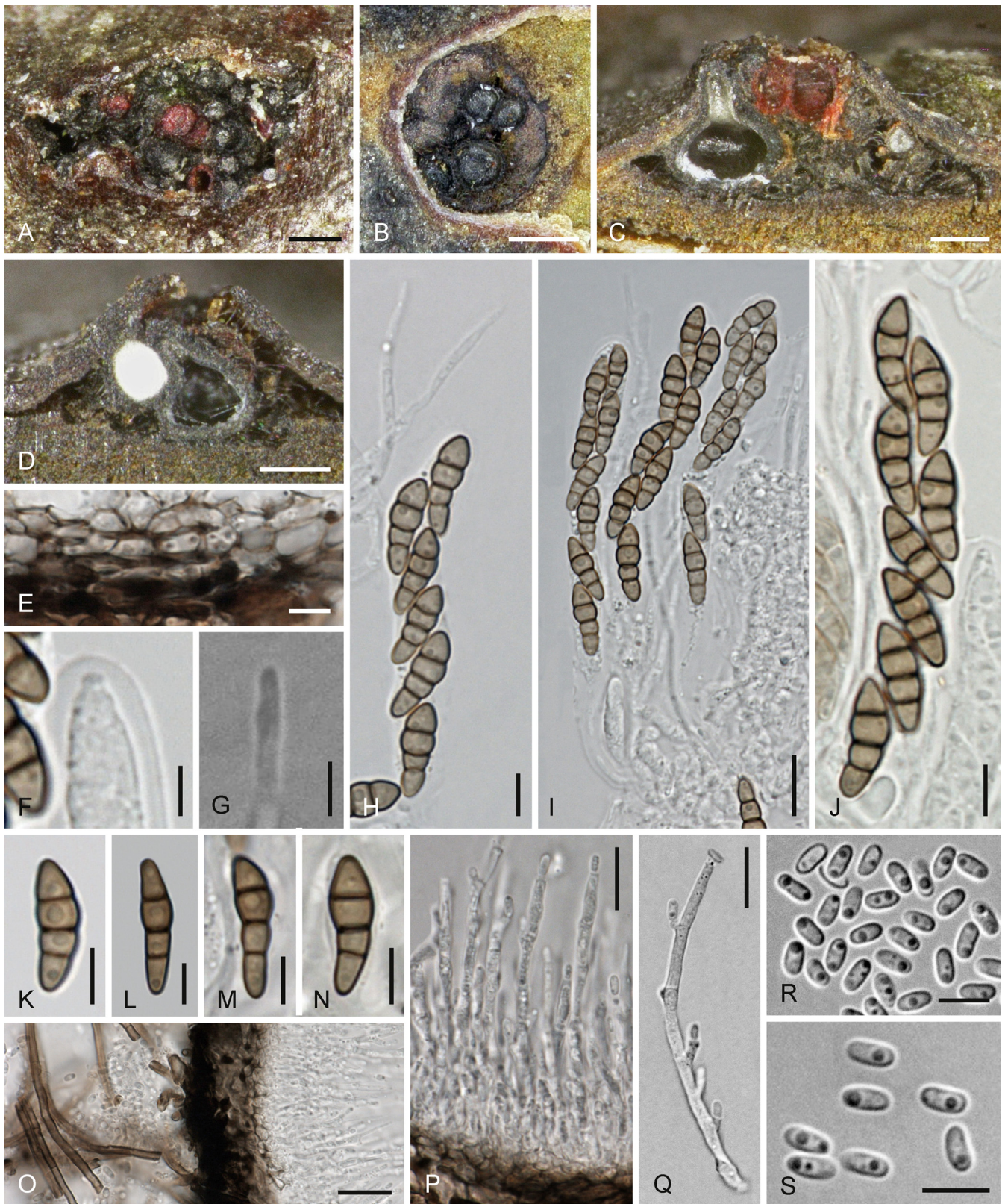


Fig. 12. *Nigrograna norvegica* (WU 36885). **A.** Ostiolar apices in face view (red: *Cosmospora* sp.). **B.** Horizontally cut ascomata in a *Diaporthe pseudostroma*, surrounded by subicular hyphae. **C.** Ascoma in vertical section (red: *Cosmospora* sp.). **D.** Ascoma and pycnidium in vertical section. **E.** Ascumatal peridium in section. **F.** Ascus apex. **G.** Paraphysis tip. **H–J.** Asci (**H.** with apically free paraphyses). **K–N.** Ascospores. **O.** Section through pycnidium showing peridium, subicular hyphae and conidiophores. **P, Q.** Conidiophores and phialides. **R, S.** Conidia. **G, K–M.** in 3% KOH. Scale bars: A, C, D = 150 µm; B = 400 µm; E, H, J–N, R, S = 5 µm; F, G = 3 µm; I, P, Q = 10 µm; O = 15 µm.

141475 = KE); Osttirol, Prägraten am Großvenediger, Umbalfälle, on *Ribes uva-crispa*, soc. *Arthopyrenia* sp., *Capronia* sp., 17 Jun. 2015, W. Jaklitsch & H. Voglmayr (WU 36877; culture MRP). Steiermark, Weiz, Ratten, Kirchenriegel: Bretterhoferwald, 47.482928, 15.711746, 850 m, on a twig of *Sambucus racemosa*, 21 Nov. 2015, B. Wergen (specimen lost, culture BW4). **France**, Ariege, Rimont, Las Muros, elev. 480 m, on decorticated twig of *Sambucus nigra*, 12 Apr. 2016, J. Fournier JF 16011 (WU 36889; culture

MF10). **UK**, England, Devon, Exeter, Killerton Park, on branch of *Sambucus nigra*, 8 Sep. 2004, W. Jaklitsch, H. Voglmayr & J. Webster W.J. 2689 (WU 36878 = MF; identity confirmed by ITS amplified directly from the specimen).

Notes: *Nigrograna obliqua* has the darkest ascospores of all *Nigrograna* species treated here. In contrast to other species,

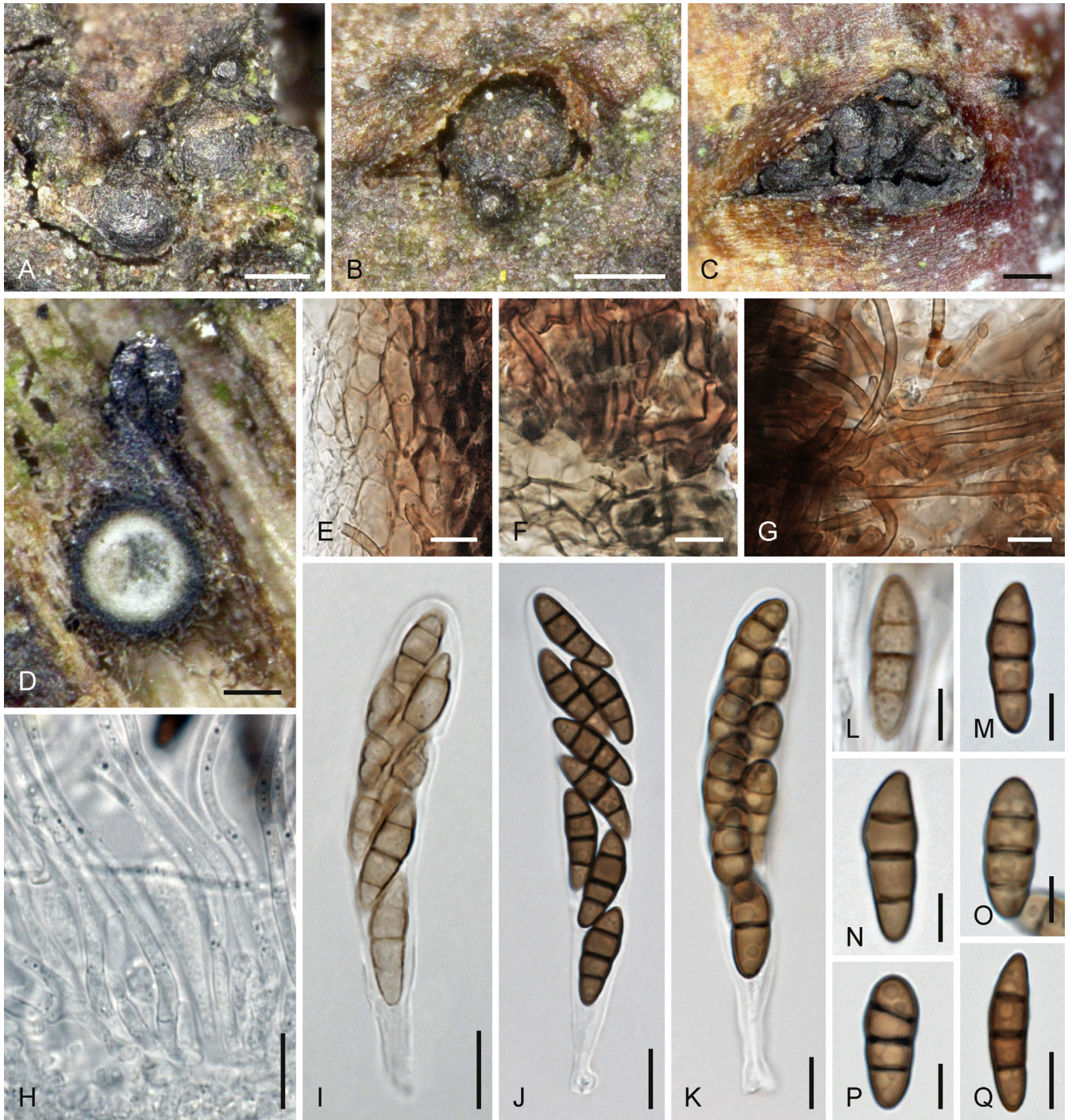


Fig. 13. *Nigrograna obliqua*. **A–C.** Ascomata and ostiolar apices in face view. **D.** Ascoma in section, with eccentric, obliquely ascending ostiolar neck. **E, F.** Peridium in section (**F.** subicular hyphae in upper part). **G.** Subicular hyphae. **H.** Young hymenium with basal part of paraphyses. **I–K.** Asci (**I.** immature). **L–Q.** Ascospores (**L.** young, in face view showing warts). **F, M, N, P, Q.** in 3% KOH. **A, B, K, O, P.** WU 36875; **C.** WU 36878; **N.** WU 36877; **D–J, L, M, Q.** WU 36876. Scale bars: **A, B** = 200 μ m; **C** = 400 μ m; **D** = 100 μ m; **E–J** = 10 μ m; **K, Q** = 7 μ m; **L–P** = 5 μ m.

ascomata frequently become superficial and are situated obliquely to the host surface, often with eccentric ostiolar necks. This fungus differs from *Thyridaria sambuci*, which also occurs on *Sambucus racemosa*, by a number of features: it is inconspicuous, has no orange ostiolar apices, no reaction in 3% KOH, and mature ascospores are dark brown in water and verruculose. Another similar but unrelated fungus occurring on the same host has slightly larger, yellow-brown ascospores, which may become up to 5-septate and are formed in long cylindrical asci.

DISCUSSION

Thyridaria-like fungi are characterised by somehow crowded or clustered perithecioid ascomata with bitunicate asci containing brown phragmospores, often surrounded by subicular hyphae, and they often have a bright-coloured ostiolar area. As indicated in the introduction, already [Wehmeyer \(1941\)](#) pointed out that there is a large number of species of thyridaria-like fungi “with many-celled brown ascospores and numerous filiform

paraphyses which are now scattered through such genera as *Thyridaria*, *Kalmusia*, *Melanomma*, *Leptosphaeria*, *Cucurbitaria* etc., which must undergo a careful comparative study before any usable generic lines can be drawn". Based on our collections, such fungi occur in at least nine lineages within *Pleosporales*. Some belonging to *Teichospora* were treated by Jaklitsch *et al.* (2016). As a main objective of this work we clarify phylogenetic position and morphology of the generic type of *Thyridaria*, which has to be called *T. broussonetiae*, not *T. incrustans*, contrary to previous practice.

The "probably best known species of *Thyridaria*", *T. rubronotata*, does not belong to the genus. It has taken a stable place in phylogenetic trees of the *Pleosporales*. This clade is now named *Cylothryiellaceae* with *Cylothryiella rubronotata* as its type.

Wehmeyer (1941) noted that *Thyridaria rubronotata* is "extremely variable in its stromatic configuration, as even the type collection of *Melogramma rubronotata* shows all transitions from free scattered or crowded perithecia of the *Melanomma* type through widely effuse crust-like masses or smaller erumpent clusters of crowded perithecia of the *Cucurbitaria* type to definitely stromatic pustules with erumpent discs of the *Thyridaria incrustans* type. It illustrates the difficulty of delimiting this genus and seems to represent a species complex which includes a variety of forms on different hosts which will be difficult to separate". He also discussed putative synonyms of this species, but in light of the remarkable phylogenetic divergence of similar fungi, this has little significance from current view.

The generic type of *Thyridaria*, *T. broussonetiae*, is part of a highly supported clade that includes *Roussoella*. This clade becomes the family *Thyridariaceae* with *Roussoellaceae* as a younger synonym. All species of this clade could be interpreted as species of *Thyridaria*, supported on one hand by medium statistical support of its largest subclade (*Roussoella* *sensu lato*), which contains species of *Roussoella*, *Roussoellopsis*, *Neoroussoella* (see Ju *et al.* 1996, Liu *et al.* 2014) and *Arthopyrenia salicis*, and on the other hand there is morphological support by the fact that in *Roussoella* *sensu lato* ascomata are scattered or clustered in or beneath some stromatic tissue and that the asci are usually very stable in microscopic mounts, just as in *Thyridaria*, and that asexual morphs are similar in all genera. There are, however, arguments against lumping to such an extent, we therefore treat the subclades taxonomically separately at the generic level. Particularly *Roussoellopsis* differs from *Roussoella* in ascospore features and especially in different asexual morphs. A reason why its species are currently contained within a clade of *Roussoella* spp. may be incompleteness of the DNA data matrix; e.g., ITS of two species labelled *Roussoellopsis* is lacking. However, it may also turn out that these morphological differences are unsuitable for generic delimitation. Additional detailed taxon and sequence sampling is necessary to clarify the phylogenetic relationships within the *Roussoella* subclade.

Arthopyrenia salicis appears in the *Roussoella* subclade. The original source of DNA data for this species is the strain CBS 368.94. This was collected and isolated from *Salix* bark in the Netherlands in 1994. LSU (AY607730) and SSU (AY607742) sequences from a second accession which stem from DNA extracts from an apparently correctly identified herbarium specimen collected in Scotland (1994 Coppins) are identical to those of CBS 368.94. Two additional strains were only labelled with this name due to sequence similarity. As documented in GenBank, one (strain NRRL 62788) came from crop field soil

plating in Illinois, USA and another (strain CBMA11330) was isolated from the marine sponge *Drumacidon reticulatum* in Brazil. Remarkably, also the ITS sequence (KT270306) of a root endophyte isolated from *Microthlaspi perfoliatum* (*Brassicaceae*) is identical to that of *Arthopyrenia salicis* strain CBS 368.94, as well as the ITS sequence of another strain, CBS 170.96, which was isolated from bamboo collected in Papua New Guinea and initially identified as *Roussoella intermedia* (included as *Roussoella* sp. in our analyses; see Table 1 and Fig. 1). *Arthopyrenia salicis* is apparently not congeneric with *Arthopyrenia* *sensu stricto*, as it differs from other species of the genus by a different hamathecium, which is confined to periphysoids (Coppins 1988). Absence of interascal filaments does not support an affiliation to the *Thyridariaceae*. In addition, ascospores of *Arthopyrenia* spp. do not germinate on artificial media in our experience. In light of this evidence, we suspect that the isolates and correspondent sequences labelled *Arthopyrenia salicis* rather represent a species of *Roussoella*. As the generic type of *Arthopyrenia* has not been sequenced, its phylogenetic position remains obscure.

Ariyawansa *et al.* (2015) added the monotypic *Elongatopedicellata*, a wood saprobe with fusiform, 1-septate hyaline ascospores in long-stipitate asci, to the *Roussoellaceae*, but no DNA data are available for this fungus.

At present a revision of the genus *Thyridaria* is impossible or at least extremely difficult. Index Fungorum lists 57 taxa in *Thyridaria*. After exclusion of forms, varieties and those referred to other groups, 37 names still remain for further study. Berlese (1894) identified *Thyridaria lateritia* (Ellis) Sacc. and *T. myriangioides* (Berk. & Ravenel) Sacc. as *Melogramma campylosporium* (as "vagens"). Based on examination of an authentic specimen in PAD, *Thyridaria minor* seems to be a synonym of *Cylothryiella rubronotata* as already pointed out by Wehmeyer (1941) and Barr (1990). The latter referred *Thyridaria* to the *Platystomaceae* and combined several species of *Lophiostoma* in *Thyridaria*. Probably none of those will remain in this genus. Later she (Barr 2003) changed her concept and referred *Thyridaria* to the *Didymosphaeriaceae*. It seems that most species of *Thyridaria* will find a different generic home. Particularly *Melanomma* epithets need also to be considered, as we have seen that *M. fuscicululum* neither belongs to *Melanomma* nor to the *Melanommataceae*.

Species of *Nigrograna* may be interpreted as a result of cryptic speciation, as morphologically they show only subtle differences. All of them would have morphologically been identified as *Melanomma fuscicululum*, due to its broad definition (see Chesters 1938). We expect many more species in *Nigrograna* yet to be detected, which will not be possible to be identified without gene sequences.

Important to note is the finding already reported for *Teichospora* (Jaklitsch *et al.* 2016) that nearly all species treated here in detail form a true hymenium, i.e. they differ from the "pleosporalean centrum" substantially. This finding can only be observed in immature or young material, when there are only apically free paraphyses present and asci start to develop or form their spores, but also among mature asci apically free paraphyses can be observed. We think that the so-called narrowly cellular or "trabeculate" pseudoparaphyses are true paraphyses, which become considerably elongated, branch and anastomose after ascus maturation. A meaningful study of the hamathecium in fully mature ascomata is however difficult. Liew *et al.* (2000) reported that *Pleosporales* (having "cellular" pseudoparaphyses) and *Melanommatales* (having "trabeculate" pseudoparaphyses) are

not separable as monophyla using SSU sequences. However, they did not study ascoma ontogeny and hamathecial features in detail, but rather reviewed findings of earlier workers, who had apparently studied only a small number of genera not being representative for the whole order *Pleosporales*.

Another feature reported for the genus *Rousoella* is high stability of the ascus exotunica, particularly in 3 % KOH. This is quite common for nearly all fungi treated here, only in *Nigrograna* fissitunicate ascus dehiscence can be seen rather frequently.

Other morphological features are shared among genera of the *Thyridariaceae*, as far as it appears currently: sexual morphs generally have brown ascospores with transverse septa. Asexual morphs are pycnidial to stromatic and form hyaline or brown unicellular conidia on phialides, sometimes annellides (*Rousoellopsis*). Three-septate brown ascospores are a story of success in evolution, as they are widely distributed in pyrenomyces. Ascospore features alone seem therefore not to be very useful for classification.

Ecology: Most species of this clade grow on plants, especially wood and bark, sometimes, leaves, some also on other fungi, and few have been isolated as opportunistic pathogens from human tissue, which appears rather an exception from the natural habitat of these fungi.

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