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-rib2 data set proved the monophyly of *Thyridaria*, and based it on *Thyridaria incrustans* (syn. *T. incrustans*). The genus contains two clades *Nigrograna mycophila* Jaklitsch, Friebes & Voglmayr, *N. norvegica* Jaklitsch & Voglmayr, *N. obliqua* Jaklitsch & Voglmayr, *Parathyridaria ramulicola* Jaklitsch, Fourn. & Voglmayr, *N. fuscidula* (Jacq.) Jaklitsch & Voglmayr, *Nigrograna fuscidula* (Sacc.) Jaklitsch & Voglmayr, *Thyridaria rubronotata* (Berk. & Broome) Jaklitsch & Voglmayr, *Nigrograna fuscidula* (Sacc.) Jaklitsch & Voglmayr, *Parathyridaria percutanea* (S.A. Ahmed, D.A. Stevens, W.J.J. van de Sande & G.S. de Hoog) Jaklitsch & Voglmayr, *Thyridaria acaciae* (Crous & M.J. Wingf.) Jaklitsch & Voglmayr, *Eptypifications* (basionyms): *Cucurbitaria broussonetiae* Sacc., *Sphaeria fuscidula* Sacc., *Melanomma rubronotatum* Berk.

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, Friebes & 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 percutanea (S.A. Ahmed, D.A. Stevens, W.J.J. van de Sande & G.S. de Hoog) Jaklitsch & Voglmayr, Thyridaria acaciae (Crous & M.J. Wingf.) Jaklitsch & Voglmayr, Eptypifications (basionyms): Cucurbitaria broussonetiae Sacc., Sphaeria fuscidula Sacc., Melanomma 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 Mycothesa Veneta and based it on *Cucurbitaria broussonetiae*, giving *Broussonetia* as the specific name. 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 *C. broussonetiae* 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. Chetters (1938) studied type material of *T. rubronotata* and compared morphology, ascus 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 ascomata and found that the asexual morph characterised by pycnidia forming slimy masses of amerosporous conidia on phialides lacking conidiophores, is like the aposphaeria-like morphs of *Melanomma*, only that the conidia turn brownish and are thus coniothyrioid-like. He accepted the name *Cytoplea juglandis*, originally described as *Phoma ulmica* 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 longitudinally septa in the ascospores. *Kalmusia* was further differentiated by scattered perithecia in an effused stroma from *Thyridaria*, which was characterised by aggregated perithecia or isolated lineages with unresolved phylogenetic affinities within the Pleosporales. For *Oleotria* the new family *Oleotriaceae* is established. *Melanomma fuscidulum* belongs to *Nigrograna*, and three new species are described in this genus. *Acer* and *Ulmus* become available for sequencing.
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 *Platycternataceae*. Later (Barr 2003) she referred it to the *Didymosphaeriaceae*. The concept of Kalmusia, which is additionally characterised by long-stipitate ascii, 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 *Roussoellaceae* and in effect the *Thyridariaceae*, is not congeneric with *T. rubronotata*, erect the new generic name *Cyclothryriella* 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 redescriptions 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 phenotype 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 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 LRS (Vilgalys & Hester 1990); a 1.1–1.4 kb fragment of the small subunit nuclear ribosomal DNA (nSSU rDNA) with primers SL1 (Landvik et al. 1997) and NSU1088 (Kauff & Lutzoni 2002), a 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 1.3–1.5 kb fragment of the translation elongation factor 1-alpha (*tef1*) containing two introns and a part of the exon with primers EF1-728F (Carbone & Kohn 1999) and TEF1LREv (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). Ascomata 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 (Welte 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 Worlington 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), *Paradiclypothrininaeae* (Liu et al. 2015) and *Toriaceae* (Crous et al. 2015) were added. *Karstefulna 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 1 484 nucleotide characters from the ITS-LSU rDNA, 995 from the SSU rDNA, 1082 from rpb2 and 1314 from *tef1*.

Maximum parsimony (MP) bootstrap analysis was performed with PAUP v. 4.0a149 (Swoford 2002), with 1 000 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 | rpb2 | tef1 |
| Alternaria alternata   | CBS 916.96  | –       | DQ678082 | KC584507 | KC584375 | DQ677927 |
| Amniculicola lignicola | CBS 123094  | –       | EF493861 | EF493863 | EF493862 | GU546278 |
| Anteaglonium parvulum  | SMH6223     | –       | GQ221909 | –       | –       | GQ221918 |
| Arthopyrenia salis     | CBS 368.94  | KF443410| AY538339 | AY53833  | KF443397 | KF443404 |
| Cyclothyriella rubronotata | CBS 419.85 | –       | GU301875 | GU371728 | GU349002 |
|                        | CBS 121892; TR | WU 3862 | KX650541 | KX650541 | –       | KX650516 |
|                        | TR1         | WU 3863 | KX650542 | KX650542 | –       | KX650572 |
|                        | TR3         | WU 3859 | KX650543 | KX650543 | –       | KX650573 |
|                        | CBS 141486; TR9 | WU 3858 | KX650544 | KX650507 | KX650574 | KX650519 |
|                        | TR9a        | WU 3858 | KX650545 | –       | –       | KX650520 |
| Dendryphion europaeum  | CPC 22943   | KJ869146| KJ869203 | –       | –       | –       |
| Herpotrichia diffusa   | CBS 250.62  | –       | DQ678071 | GU205239 | DQ677968 | DQ77915 |
| Hobus wogradensis       | CBS 141484; TI | WU 3874 | KX650546 | KX650508 | KX650575 | KX650521 |
| Karstenula rhodostoma  | CBS 690.94  | –       | GU301821 | GU296154 | GU371788 |
| Leptosphaeria dolicium  | CBS 505.75  | –       | GU301827 | GU296195 | KT389640 | GU349069 |
| Lophiotrema macrostomum | JCM 13544   | –       | AB619010 | AB618961 | JN993491 | –       |
| Lophiotrema nucula      | CBS 627.86  | –       | GU301837 | GU296196 | GU371792 | GU349073 |
| Massaria campestris     | M28         | –       | HQ599385 | HQ599449 | HQ599459 | HQ599325 |
| M. inquinans            | M19         | –       | HQ599402 | HQ599444 | HQ599460 | HQ599342 |
| Massarina eburnea       | CBS 473.64  | –       | GU301840 | GU296170 | GU371732 | GU349040 |
| Massariosphaeria phaeospora | CBS 611.86 | –       | GU301843 | GU296173 | GU371794 | –       |
| Mauritiana rhizophorae  | BCC 28866   | –       | GU371824 | GU371832 | GU371796 | GU371817 |
| Melanomma pulvis-pyrius | CBS 124080  | –       | GU456323 | GU456302 | GU456350 | GU456265 |
| Neococcusbacusa chiangraiensis | MFLUCC 12-0559 | – | KU712442 | KU764699 | KU712458 | – | KU872761 |
| Neorussouella bambusae  | MFLUCC 11-0124 | – | KJ474827 | KJ474839 | – | KJ474856 | KJ474848 |
| Nigrograna fuscicula    | CBS 14176; MF1 | WU 3881 | KX650547 | KX650547 | KX650509 | KX650576 | KX650522 |
|                        | MF1a        | WU 3881 | KX650548 | KX650548 | – | – | KX650523 |
|                        | MF3         | WU 3880 | KX650549 | KX650549 | – | – | KX650524 |
|                        | CBS 141556; MF7 | WU 3879 | KX650550 | KX650550 | – | – | KX650525 |
|                        | MF8         | WU 3883 | KX650551 | KX650551 | – | – | – |
|                        | MF9         | WU 3884 | KX650552 | KX650552 | – | – | – |
| N. mackinnonii         | CBS 110022  | KF015653| GO387614 | GO387553 | KF015704 | KF407985 |
|                        | CBS 674.75  | NR_130237| GO387613 | GO387552 | KF015703 | KF407986 |
|                        | E9303e      | JN545759| LN626681 | LN626678 | LN626666 | LN626673 |
| N. mycophila           | CBS 141478; MF5 | WU 3886 | KX650553 | KX650553 | – | – | KX650526 |
|                        | MF6         | WU 3887 | KX650554 | KX650554 | – | – | KX650527 |
|                        | CBS 141483; TDK | WU 3888 | KX650555 | KX650555 | KX650510 | KX650577 | KX650528 |
| N. norvegica           | CBS 141485; TR8 | WU 3885 | KX650556 | KX650556 | KX650511 | KX650578 | – |
| N. obliqua             | BW4         | –       | KX650557 | KX650557 | – | – | KX650529 |
|                        | CBS 141475; KE | WU 3876 | KX650558 | KX650558 | KX650512 | KX650579 | KX650530 |
|                        | MF          | WU 3878 | KX650559 | –       | – | – | – |
|                        | CBS 141477; MF2 | WU 3875 | KX650560 | KX650560 | – | – | KX650580 |
|                        | MRP         | WU 3877 | KX650561 | KX650561 | – | – | KX650581 |
| Occultibambusa bambusae | MFLUCC 13-0855 | – | KU940123 | KU863112 | KU872116 | KU940170 | KU940193 |
| O. fusiispora          | MFLUCC 11-0127 | – | KU940125 | KU863114 | – | KU940172 | KU940195 |
| O. pustula             | MFLUCC 11-0502 | – | KU940126 | KU863115 | KU872118 | – | – |

(continued on next page)
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

Table 1. (Continued).

| Taxon                  | Strain | Voucher    | GenBank accession numbers |
|------------------------|--------|------------|---------------------------|
|                        |        |            | ITS | LSU | SSU | rpb2 | tef1 |
| Ohleria modesta        | MGC    | WU 36870   | KX650562 | KX650562 | – | KX650562 | KX650533 |
| CBS 141480; OM         | WU 36873 |           | KX650563 | KX650563 | KX650513 | KX650583 | KX650534 |
| Paradictyoarthrinium diffractum | MFLUCC13-0466 |         | KF744455 | KF744408 | KF753960 | – | – |
| P. tectonica           | MFLUCC 13-0465 |      | KF744456 | KF744500 | KF753961 | – | – |
| Parathyridaria percutanea | CBS 128203 |          | KF322117 | KF366448 | KF366450 | KF366453 | KF407988 |
| CBS 868.95             | KF322118 | KF366449 | KF366451 | KF366452 | KF407987 |
| P. ramulicina          | MF4    | WU 36868   | KX650564 | KX650564 | – | – | KX650535 |
| CBS 141479; MRR1       | WU 36867 |           | KX650565 | KX650565 | KX650514 | KX650584 | KX650536 |
| Pleomassaria siparia   | CBS 279.74 |           | – | DO678078 | DO678027 | DO677976 | DO677923 |
| Roussella angustior     | MFLUCC 15-0186 |         | – | KT281979 | – | – | – |
| R. chiangrana          | MFLUCC 10-0556 |       | KJ474828 | KJ474840 | – | KJ474857 | KJ474849 |
| R. hystericoides        | CBS 546.94 |           | KF443405 | KF443381 | AY642528 | KF443392 | KF443399 |
| R. intermedia          | NBRC 106245 |       | KJ474831 | AB524624 | AB524483 | – | – |
| R. japonensis          | MAFF 239636 |         | KJ474829 | AB524621 | AB524480 | AB539101 | AB539114 |
| R. magnatum            | MFLUCC 15-0185 |          | – | KT281980 | – | – | – |
| R. mexicana            | CPC 25355 |           | KJ474840 | – | – | – | – |
| R. neopustulans         | MFLUCC 11-0609 |        | KJ474833 | KJ474841 | – | KJ474850 |
| R. nitidula            | MFLUCC 11-0182 |         | KJ474835 | KJ474841 | – | KJ474850 |
| R. pustulans            | MAFF 239637 |          | KJ474830 | AB524623 | AB524482 | AB539103 | AB539116 |
| R. scabrispora          | MFLUCC 11-0624 |        | KJ474838 | KJ474844 | – | KJ474860 | KJ474853 |
| R. siamensis           | MFLUCC 11-0149 |         | KJ474837 | KJ474845 | – | KJ474861 | KJ474854 |
| Roussella sp.           | CBS 170.96 |           | KF443407 | KF443382 | KF443390 | KF443394 | KF443398 |
| R. thailandica         | MFLUCC 11-0621 |         | KJ474838 | KJ474846 | – | – | – |
| R. verrucipora         | CBS 125434 |           | KJ474832 | AB524622 | AB524481 | AB539102 | AB539115 |
| Roussellopsis macrospora | MFLUCC 12-0005 |        | KJ396904 | KJ474847 | KJ796908 | KJ474862 | KJ474855 |
| Roussellopsis sp.      | NBRC 106246 |           | – | AB524626 | AB524485 | – | – |
| R. tosaensis           | MAFF 239638 |          | – | AB524625 | AB524484 | AB539104 | AB539117 |
| Seriascoma didymospora | MFLUCC 11-0179 |        | KU940127 | KU863116 | KU872119 | KU940173 | KU940196 |
| T. broussonetiae       | CBS 140730; C134 |        | – | KU601591 | – | KU601600 | KU601601 |
| Tetratosphaeria ascioides | MFLUCC 11-0179 |        | KU940127 | KU863116 | KU872119 | KU940173 | KU940196 |
| Thyndaria acaciae      | CBS 138873 |           | KU940127 | KU863116 | KU872119 | KU940173 | KU940196 |
| T. broussonetiae       | CBS 121895; TB | WU 36865 | KX650567 | KX650567 | – | KX650585 | KX650538 |
| CBS 141481; TB1        | WU 36864 |           | KX650568 | KX650568 | KX650515 | KX650586 | KX650539 |
| TB1a                   | WU 36864 |           | KX650569 | KX650569 | – | KX650587 | KX650540 |
| CBS 141482; TB2        | WU 36866 |           | KX650570 | KX650570 | – | KX650587 | KX650540 |
| Torula herbarum        | CBS 140066 |           | KF443406 | KF443393 | KF443396 | KF443396 | KF443403 |
| Ulospora bilgramii     | CBS 110200 |          | – | DQ870576 | DQ870523 | DQ870571 | DQ870521 |
| Versicilloniopsis triseptatum | JCM 14775 |          | AB365596 | AB330081 | AB524501 | – | – |
| Westerdykella ornata   | CBS 379.55 |           | – | GU301880 | GU296208 | GU371803 | GU349021 |
setting and the GTRGAMMAI substitution model with 1 000 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/phylows/study/TB2:S19648). Of the 4 877 nucleotide characters included in the phylogenetic analyses, 1 495 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 saliscis, Neoroussouella, Roussouella and Roussoue- lopsis received medium support in both analyses (87 % ML and 74 % MP; Fig. 1). Cyclothyrilla 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. mackinnoni 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. Ohteria 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 Cyclothyrilla as new generic name on the basis of the asexual morph name Cyclothyrium, which was originally intended for it (Petra 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 Roussouella- ceae. Due to priority this clade now becomes Thyridariaceae in a new circumscription, with Roussouellaceae in synonymy. The Thyridariaceae contain two subclades which both receive only low to medium support (Fig. 1), the large Roussouella 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. Roussouella acaciae, which was described from leaves of Acacia tortilis in Tanzania, based on its coniothyrium- or cytoplia-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. Roussouella 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 Ohteria 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 Ohteria does not fall into any described family, we describe the new family Ohteriacae, 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 Biatriospora marina, which forms the basis of the Biatriosporaceae (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 Biatriospora (Hyde & Borse 1986). This casts doubt whether the isolate CY 1228 indeed represents Biatriospora marina, therefore we do not include the latter in our tree. On the other hand, Biatriospora mackinnoni, which was combined in this genus due to sequence similarity (Ahmed et al. 2014b), is also part of this clade. For this species Gruytey 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.

Cyclothyrillaceae 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. *Ostolar discis* brightly coloured or black, ostioles periphyllate. *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 Thyriadiaceae, but family names are based on their type genus, which itself is defined by its type species. The family Thyriadiaceae is therefore to be used for Thyridaria broussetonelae, 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 volsoidal configuration within KOH-positive tissue in bark, more or less globose, black, peridium or inconspicuous.

Type species: Cyclothyriella rubronotata (Berk. & Broome) Jaklitsch & Voglmayr

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 ascocoma and/or pycnidia in variable, mostly volsoidal 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. epidemoides of thin-walled cells (2.5−)4.5−15.5(−22) × (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. Ostiolar 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 sporae 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 incrusted 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. Ostiolar canal (156−)205−355(−420) μm long, interior (62−)759−122(−154) μm wide (n = 20), periphysate. Hamathecium of narrow branched and anastomosing, trabeculate pseudo-paraphyses, 1.5−3.5 μm wide pseudoparaphyses and some true paraphyses of similar width with free ends among immature asc. Asci (105−)108−125(−140) × (8.2−)9.7−10.5(−11.5) μm (n = 21), cylindrical, bitunicate, (20−)30(−)40 μm in diameter, with thick endotunica, small ocular chamber, short stipe and cucurbit base, containing 8 uniseriate, partly overlapping ascospores. Ascospores (12.8−)15.0−18.2(−21.2) × (5−)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 verrucose 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 volsoidal configuration, often together with ascocoma in red or orange mycelium, depressed globose to nearly conical. Ostiolar discs as with ascomata, ca. 0.2−0.4 mm diam outside, ostiolar 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) × (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) × (2.7−)3.3−4.7(−5.3) μm (n = 30), producing cylindrical, oblong to ellipsoid, 1-celled conidia (3.5−)5.8−6.7(−7.2) × (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,
purple, vinaceous to violaceous, margin hyaline, thin, odour indistinct to slightly fruity. Hyphae submerged in agar partly 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) × (2.8–) 3.0–4.0(–4.3) μm (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) × (2.0–) 2.7–3.5(–4.0) μm, 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 °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.
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 *Nitschia 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. *Nitschia parasitans*, *Nectria nigrescens*, *Cosmospora* sp., 1 Nov. 2014, W. Jaklitsch & H. Voglmayr (WU 36858; ex-epitype culture CBS 141486 = TR9; culture from conidia: TR9a; MBT372419).

Other material examined: Austria, Niederösterreich, Gießhübl, on *Acer campestre*, partly overgrown by *Nitschia 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, 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 Höhnel (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 diaporthalean 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 Höhnel (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 arundinicolana, has not yet been sequenced. Petrak & Sydow (1927) explicitly used Cyclothyrium for the asexual morph of Thyridia 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 ulmica, and they ignored any possibility of host specificity and the fact that Thyridia rubronotata was described from Ulmus. This was already criticised by Chesters (1938) and Wehmeyer (1941).

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

**Phoma ulmica** Berk., Hook. J. Bot. 5: 40. 1853. Fig. 3M–P. Synonyms: Aposphaeria ulmica (Berk.) Sacc., Syll. fung. 3: 175. 1884. Coniothyrium ulmica (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 ulmica*).

This makes clear that Phoma ulmica cannot be the asexual morph of Thyridia 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 ulmica for the asexual morph of Thyridia rubronotata are erroneous and thus Cyclothyrium cannot be used for *T. rubronotata*, because it is nomenclaturally based on *Phoma ulmica*. On Juglans, the host given as typical for *Thyridia rubronotata* by Petrak & Sydow (1927), we have collected three different but morphologically similar fungi in Austria referable to Thyridia, 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 *Thyridia rubronotata*, but belongs to a different clade of the Pleosporales to be published later on.

We erect Cyclothyriella as a holomorph name for *Thyridia rubronotata*. *Cyclothyriella rubronotata* differs from *Thyridia broussonetiae*, the generic type of *Thyridia*, 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 ostiolum. Below we redescribe a fungus, which may be related to *Cyclothyriella rubronotata*.

**Thyridia 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, subhyphal and even immature asci turning purple to violaceous in 3 % KOH. *Hamathecium* containing 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 biseriately 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). *Thyridia sambuci* is a typical member of *Thyridia* 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., Phytophata 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
disc, black, more or less globose, usually with well-developed ostiolar neck and periphysate ostiole. Peridium brown, pseudo-parenchymatous. Hamathecium consisting of apically free paraphyses and/or trabeculate pseudoparaphyses. Asci cylindrical or clavate, bitunicate. Ascospores yellowish- to dark brown, ellipsoid or fusoid, with transversal eusepta or eu- and distosepta, variously ornamented, sometimes with a sheath. Asexual morphs coelomycetous. Saprobic 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 vallsoid 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, pseudo-parenchymatous. Hamathecium consisting of apically free paraphyses and trabeclate 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. Saprobic 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) μm (n = 31) wide hyphae, one or several, usually less than ten ascomata in vallsoid 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) μm high, (400–)440–580(−665) μm diam (n = 21), depressed globose to globose, usually width exceeding height, dark brown to black; peridium (20–)22–30(−40) μm wide.

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Fig. 4. *Thyridaria sambuci*. A, B, D. Stroma, ascomata and ostiolar apices in face view. C. Stroma hyphae in 3 % KOH. E. Trabeclate 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 μm; D = 0.2 mm; I, J = 7 μm; L, M = 5 μm.
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–)6–16(–21) × (2–)3–5(–7.5) μm (n = 34). Ostiolar necks (335–)390–510(–580) μm long, (107–)133–250 (–312) μm wide outside including encasing tissue, interior (46–)75–148(–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–)5.0–7.3(–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, trabeulate, 1–2.5 wide pseudopara-
physes and acipitely 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 fuscate base and 8 uniseriate (or partly biseriate by pressure in mounts) ascospores; wall thin, endo-
tunica thick at the apex, with a distinct ocular chamber. Asco-
spores (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-de
crusted material and is therefore also illustrated in Fig. 5B, M.

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 003135431), 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 stroma 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. Vogmayer (WU 36864; ex-epitype culture CBS 141481 = TB1; MBT372416).

Other material examined: Croatia, Istria, Opatija, Močenička Draga, in the village heading north, on dead standing branch of Hippocrepis (Coronilla) emerus, 29 Mar. 2007, W. Jaklitsch & H. Vogmayer (WU 36865, culture CBS 121895 = TB). Italy, Veneto, Colli Euganei, Padova, Arqua Petrarca, road-
side, 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 Albizia, 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 ascii. 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 vari-
able, as its ascomata are either arranged in well-defined volsod 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 *Melanconiospis* 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 feltly 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 *C. rubronotata*, 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 ascosporas (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:* Roussoea 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, subicularum absent or inconspicuous. *Peridium* pseudoparenchymatous. *Ostiole* necks discoid, less commonly papillate or short-cylindrical, apices black or light-coloured, ostiolar paraphyses. *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 biseriately 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 darkly, 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.

**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 %
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 × 54–96 μm, black, solitary, globose to subglobose, with thin wall of *t. angularis*. Conidiogenous cells hyaline, phialidic, obclavate. Conidia 1.2–2.0 × 0.7–0.9 μm, 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. Saprobic on wood.

Type genus: *Ohleria* Fuckel.

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

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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. Periphery. 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 μm; C, D = 100 μm; E, G, I, N = 7 μm; F, J, K = 10 μm; H, L, M, O, P = 5 μm.
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. Saprobitic 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, varicose, 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) × (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 biseriate ascospores; *endotunica* wide, swelling in 3 % KOH, ocular chamber minute. Ascospores (13–)14–16.5–(21) μm long, lw (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) × (3.8–)4.1–4.7–(5.7) μm, blunt conical, proximal part (6.6–)7.2–8.7–(11.3) × (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) × (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) × (2.0–)2.5–3.2–(3.5) μm (n = 42), lageniform to cylindrical. *Conidia* (2.3–)2.8–3.8–(4.7) × (1.5–)1.7–2.2–(2.5) μm, lw (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:** saprobitic on decorticated wood.

**Distribution:** Europe, possibly also North America

**Lectotype,** here designated: **Germany**, Hessen, Oestrich, Oes- tricher Wald (Aepfelfbach), on roots of *Fagus sylvatica*, in autumn, L. Fuckel (GL, Fungi Rhenani exsic. 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 MG): San Isidro, 5 Jan. 2005, soc. *Patellaria atrata*, P. Karasch W.J. 2798 (WU 36871); El Paso, soc. *Lophiotoma 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 ascoc- mata 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 semigloubose ascocoma 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), Oes- tricher Wald, on decaying wood of *Carpinus betulus*, in spring (G 00266073, Herb. Barby 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 semigloubose 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–T. 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 μm; P = 100 μm; F–J, Q, R = 10 μm; K–O, T, W–Z = 5 μm; S, U = 3 μm.
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. odubensis* 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. cladophila* 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 Fückel (1970) for *O. rugulosa* by association on the natural host, we interpret the *Monodictys* morph as a synonymorph, as, e.g., described by Gondona 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 disarticulation includes *Ohleriella* (Hafellner 1979) and *Ohleriella* (Carneiro de Almeida 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*.

**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 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 ascospores, 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) 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. *Ostiole* necks often for a large part free or surrounded by stroma, (143–)176–255(–280) μm long (n = 21), (70–)94–160(–230) μm wide (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 biseriately 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–)5.8–6.2(–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*.

**Type species:** *Hobus wogradensis* Jaklitsch & Voglmayr

**Hobus wogradensis** Jaklitsch & Voglmayr, *sp. nov.* MycoBank MB817779. Fig. 8.
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. Ascii (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 μm; F, G = 70 μm; H, M, N = 10 μm; L = 50 μm; O–S, V, W = 7 μm; T, U, X = 5 μm.
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 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 Cyclothyriella rubronotata is confined to the colony, i.e. it does not diffuse into the agar.

Nigorgranaceae 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 ascii, later becoming elongated, branching and anastomosing and appearing as "trabeulate pseudoparaphyses". Asci clavate, bitunicate, fissitunicate, with short stipe and knob-like base, containing 8 biseriately 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.

Pyecnia similar to ascomata. Peridium brown, pseudoparenchymatous. Conidiophores when present filiform, simple to sparsely branched, with pegs and terminal phialides. Phialides amphiphiliform, 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 mycetoma in Mexico and Venezuela, and no sexual morph was known. Here we add the sexual morph and asexual morph from natural substrates. For pyecnia 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 additional septa. In all species of Nigrograna with available sexual morph apically free paraphyses were found among immature ascii, just as in other genera of the Thyridiaceae 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 "Mela-noma 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 pyecnia when young, and both surrounded by brown to olive-ceous, 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 ascii, later.

Asexual morph: Pyecnia 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 amphiphiliform, lageniform, or subcylindrical. Conidia forming on pegs and phialides, oblong, cylindrical or allantoid, sometimes ellipsoid, hyaline or subhyaline, 1-celled, smooth.

Notes: This species is characterised by a well-developed stroma, which is absent in 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 Cyclothyriella rubronotata is confined to the colony, i.e. it does not diffuse into the agar.

Nigorgranaceae 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 ascii, later becoming elongated, branching and anastomosing and appearing as “trabeulate pseudoparaphyses”. Asci clavate, bitunicate, fissitunicate, with short stipe and knob-like base, containing 8 biseriately 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.

Pyecnia similar to ascomata. Peridium brown, pseudoparenchymatous. Conidiophores when present filiform, simple to sparsely branched, with pegs and terminal phialides. Phialides amphiphiliform, 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 ascii, later becoming elongated, branching and anastomosing and appearing as “trabeulate pseudoparaphyses”. Asci clavate, bitunicate, fissitunicate, with short stipe and knob-like base, containing 8 ascospores biseriately 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.
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 μm; C, D = 200 μm; G–K, M, O = 10 μm; L, T–Y = 3 μm; N, P–S = 5 μm.
branching and also anastomosing above asci. Asci (48–)
52–72(–82) × (8.0–)8.3–9.8(–11) μm (n = 38), clavate to
oblong, bitunicate, fissitunicate, with short stipe and simple or
furcate base; endotunica thick, swelling in 3 % KOH, containing
8 biseriate ascospores. Ascospores (10.2–)12–14.5(–18) ×
(3.8–)4.2–5.0(–5.4) μm, l/w (2.2–)2.6–3.3(–4.5) (n = 103),
asymetrically 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 μm
diam, ca. 100–195 μm high, co-occurring with ascomata and
even 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 μm thick,
forming a t. angularis of dark brown, thick-walled 4–10(–11) μm
wide cells. Conidiophores arising from the pycnidial wall, to 55 μm long and mainly 2–3.7 μm wide, simple, only
branched once near the base, with pegs along one or two
sides and solitary phialides terminal. Phialides (5.0–)
6.5–8.7(–10.5) × (2.0–)2.5–3.0(–3.5) μm (n = 34), variable in
shape, ampulliform-lageniform-subcylindrical. Conidia (3.0–)
3.2–4.3(–6.0) × (1.1–)1.3–1.6(–1.8) μm, 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, Pan-
ozzalacke, 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, in or above effete ascomata of Diaporthe sp., 6 Apr. 2016, W. Jaklitsch & H. Voglmayr (WU 36882).

Notes: Melanomma fuscidulum is not congeneric with M. pulvispyrus, the generic type of Melanoma, the type genus of the Melanommateae. All species with sexual morphs here recognised in Nigrograna would earlier have been defined as Melanoma fuscidulum. Most seem to be fungicolous. Chesters (1938) studied Melanoma 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 Para-thyridaria 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 valvoid 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 pseudoparenchymatous widest at their bases. Asci (65–)72–85(–89) × (10.5–)11–13(–14.3) μm (n = 26), clavate, bitunicate, fissitunicate but stable in mounts, with a small ocular chamber, thick endotunic, short stipe and knob-like to furcate base, containing 8 ascospores biseriately arranged, particularly at upper levels. Ascospores (12.7–)14.3–17(–19) × (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 subcyllindrical phialides (4.2–)7.0–10(–10.8) × (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) × (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 Diaportha 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, Kaltenbachergaben, in pseudostromata of Diaportha decidua on twigs of Corylus avellana on the ground, 5 Mar. 2016, G. Friebes (WU 36887, culture MF6). Denmark, Kristiansminde, Sørø 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 Calospora 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 μm; B, F = 100 μm; C = 250 μm; G–K, O = 10 μm; L–N, P–R = 5 μm.
**Nigrogra 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 valvoid groups, (177–)200–285(–320) μm (n = 14) diam, with slightly smaller, 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. **Ostiorial 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) × (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) × (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 slightly wider than others, straight to slightly curved, second cell usually slightly widened, constricted at the junction to Pesenthein, on corticated twigs of various shrubs and trees (known from *Ribes uva-crispa*, *Salix caprea*, *Sambucus nigra*, *S. racemosa*).

**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) × (2.0–)2.2–2.7(–3.0) μm (n = 11), lageniform to cylindrical. **Conidioid** formed on phialides and phialospores, (2.9–)3.2–3.7(–4.1) × (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 *Diaporthe*.

**Distribution:** Norway, only known from the holotype location.

**Holotype:** **Norway**, Aust-Agder, Arendal kommune, Nedenes, Langevoll, in pseudostromata of *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.

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**Nigrogra 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** peripheric. **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 "pseudo-paraphyses" clearly originating in the subhymenium between asci, branched near the bases, also free apices present between immature asci. **Asci** (55–)65–83(–96) × (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) × (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-eusepta, 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 verrucose, 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. *Lophiotoma 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 141477 = MF2).
Fig. 12. Nigrograna norvegica (WU 36885). A. Ostiolar apices in face view (red: Cosmospora sp.). B. Horizontally cut ascomata in a Diaporthe pseudoostroma, surrounded by subicular hyphae. C. Ascoma in vertical section (red: Cosmospora sp.). D. Ascoma and pycnidium in vertical section. E. Ascomatal peridium in section. F. Ascus apex. G. Paraphysis tip. H–J. Ascii (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.

Notes: Nigrograna obliqua has the darkest ascospores of all Nigrograna species treated here. In contrast to other species,
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..."
sequences from a second accession which stem from DNA original source of DNA data for this species is the strain CBS phylogenetic relationships within the taxon and sequence sampling is necessary to clarify theences are unsuitable for generic delimitation. Additional detailed the fact that in salicis Roussoellopsis Roussoella A reason why its species are currently contained within a clade of generic level. Particularly are, however, arguments against lumping to such an extent, we idiaria Roussoella et al. (2016). As a main objective of this work we clarify phylogenetic position 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 Cyclothyrillaeaceae with Cyclothyrilla 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 Cyclothyrilla type to defi-finitely 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 Roussoella and ascospores in long-stipitate asci, to the Roussoellaceae 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.

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 campylosporum (as “vagans”). Based on examination of an authentic specimen in PAD, Thyridaria minor seems to be a synonym of Cyclothyrilla 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. fuscidulum 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 fuscidulum, 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 “pleospor-alean centrum” substantially. This finding can only be observed in immature or young material, when there are only apically free paraphyses present and ascii start to develop or form their spores, but also among mature ascii 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 ascostoma is however difficult. Liew et al. (2000) reported that Pleosporales (having “cellular” pseudoparaphyses) and Melanommateles (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 Roussoella is high stability of the ascal exotunica, particularly in 3 % KOH. This is quite common for nearly all fungi treated here, only in Nigrograna fissitunicata ascus dehiscence can be seen rather frequently.

Other morphological features are shared among genera of the Thyridiariaceae, as far as it appears currently: sexual morphs generally have brown ascospores with transverse septa. Asexual morphs are pyridzial to stromatic and form hyaline or brown unicellular conidia on phialides, sometimes annellides (Roussoella). Three-septate brown ascospores are a story of success in evolution, as they are widely distributed in pyrenomycetes. 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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