**Juglanconis gen. nov. on Juglandaceae, and the new family Juglanconidaceae (Diaporthales)**

H. Voglmayr¹, L.A. Castlebury², W.M. Jaklitsch¹,³

---

**Key words**

Ascomycota  
Diaporthales  
molecular phylogeny  
new species  
pathogen  
systematics  

---

**Abstract**

Molecular phylogenetic analyses of ITS-LSU rDNA sequence data demonstrate that Melanconis species occurring on Juglandaceae are phylogenetically distinct from Melanconis s.str., and therefore the new genus Juglanconis is described. Morphologically, the genus Juglanconis differs from Melanconis by light to dark brown conidia with irregular verrucae on the inner surface of the conidial wall, while in Melanconis s.str. they are smooth. Juglanconis forms a separate clade not affiliated with a described family of Diaporthales, and the family Juglanconidaceae is introduced to accommodate it. Data of macro- and microscopic morphology and phylogenetic multilocus analyses of partial nuSSU-ITS-LSU rDNA, cal, his, ms204, rpb1, rpb2, tef1 and tub2 sequences revealed four distinct species of Juglanconis. Comparison of the markers revealed that tef1 introns are the best performing markers for species delimitation, followed by cal, ms204 and tub2. The ITS, which is the primary barcoding locus for fungi, is amongst the poorest performing markers analysed, due to the comparatively low number of informative characters. Melanconium juglandinum (= Melanconis carthusiana), M. oblongum (= Melanconis juglandis) and M. petrocareya are formally combined into Juglanconis, and J. appendiculata is described as a new species. Melanconium juglandinum and Melanconis carthusiana are neotypified and M. oblongum and Diaporthe juglandis are lectotypified. A short description and illustrations of the holotype of Melanconium ershadii from Pterocarya fraxinifolia are given, but based on morphology it is not considered to belong to Juglanconis. A key to all treated species of Juglanconis is provided.

**Article info**

Received: 22 November 2016; Accepted: 8 January 2017; Published: 19 January 2017.

---

**INTRODUCTION**

Melanconis is a well-known genus of Diaporthales, being the generic type of the family Melanconidaceae. However, its circumscription has substantially changed over the years. In his monograph of Melanconis, Wehmeyer (1941) used a wide generic concept. He included the genera Macrodiaporthes, Melanconiella, Pseudovalsa and even some species of Pseudostegium and Pseudovalsia, making the genus very heterogeneous. This concept was largely accepted by Müller & Von Arx (1962). Subsequent researchers (e.g. Barr 1978) did not follow this wide concept, restricting the genus Melanconis mostly to Wehmeyer’s (1941) subg. Eumelanconis. In this restricted sense, the genus Melanconis was defined by a distinct ectostromatic disc, more or less well-developed entostroma, two-celled hyaline to brown ascosporae with or without appendages, in combination with melanconium- or discosporium-like asexual morphs (Barr 1978).

In the phylogenetic analyses of Castlebury et al. (2002), several species traditionally classified within the genus Melanconis were shown to be phylogenetically scattered throughout the Diaporthales, demonstrating the need of a critical taxonomic revision of the genus. It became evident that the genus Melanconis, based on the type species M. stibostoma, has to be restricted to only five species (Castlebury et al. 2002, Rossman et al. 2007). All five Melanconis species currently accepted in the genus occur on Alnus and Betula (Betulaceae; Fan et al. 2016).

Following the results of phylogenetic analyses, several genera were recently segregated from Melanconis. Based on detailed molecular phylogenetic and morphological investigations, Voglmayr et al. (2012) re-established the genus Melanconiella, widened its circumscription and transferred several species of Melanconis to Melanconiella. These investigations also revealed an unexpectedly high species biodiversity. As a result, several previously synonymised taxa were recognised as distinct species, and several species were described as new. Another species placed in Melanconis by Wehmeyer (1941), M. appendiculata, has recently been shown to belong to the Diaporthaceae (Voglmayr & Jaklitsch 2014), and the genus Phaeodiaporthe described by Petrak (1919) was re-established. In the phylogenetic analyses of Castlebury et al. (2002), Melanconis desmaziieri was also shown to be unrelated to Melanconis but formed an isolated lineage together with Hecropsora tiliae. When describing Melanconis desmaziieri, Petrak (1938) made the connection with its asexual morph, Melanconium desmaziieri, for which Grove (1937) established the monotypic genus Lamproconium. Following the recent changes of the ICN, Lamproconium desmaziieri is therefore the name to be used for M. desmaziieri. Acknowledging their isolated phylogenetic position, Norphanphoun et al. (2016) placed Lamproconium and Hecropsora in a new family Lamproconiaceae.

These results demonstrate the need of detailed investigations on the remaining Melanconis species for which no sequence data are yet available. In this respect, species on Juglandaceae are of particular interest. This group contains economically important pathogens of Juglans spp., causing black pulsatular dieback disease of walnut (Graves 1923, Belisario 1999). Two species are commonly known on Juglans spp., Melanconis
Table 1 | Strains and NCBI GenBank accessions used in the phylogenetic analyses of the combined multigene matrix of *Juglanconis*. All sequences were generated during the present study.

| Taxon | Strain | Culture | Accession Numbers | Origin | Host | GenBank accession no. |
|-------|--------|---------|-------------------|--------|------|----------------------|
|       |        |         | ITS-LSU           |        |      | nrITS-28S rps16-18S  |
| *Juglanconis appendiculata* | D140 | WU 35956 | Greece | Greece | *Juglans regia* | KY427151 - KY427170 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427138 | – | – | – | – | KY427188 - KY427207 |
|        |        |         |                   |        |      |                      |
| *Juglans nigra* | KY427139 | – | – | – | – | KY427189 - KY427208 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427142 | KY427243 | – | – | – | KY427195 - KY427214 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427143 | KY427244 | – | – | – | KY427195 - KY427214 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427145 | – | – | – | – | KY427195 - KY427214 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427146 | KY427247 | KY427129 | KY427164 | KY427179 | KY427197 - KY427216 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427147 | KY427248 | KY427130 | KY427165 | KY427180 | KY427198 - KY427217 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427148 | KY427249 | KY427131 | KY427166 | KY427181 | KY427199 - KY427218 |
|        |        |         |                   |        |      |                      |
| *Juglans regia* | KY427149 | KY427250 | KY427132 | KY427167 | KY427182 | KY427200 - KY427220 |
|        |        |         |                   |        |      |                      |
| *Melanconis pterocaryae* | ME14 | A.R.4413 | CBS 133344 | – | – | KY427183 - KY427202 |
|        |        |         |                   |        |      |                      |
| *Melanconis pterocaryae* | ME15 | A.R.4529 | CBS 133356 | – | – | KY427183 - KY427202 |
|        |        |         |                   |        |      |                      |
| *Melanconis pterocaryae* | ME16 | A.R.4516 | CBS 133359 | – | – | KY427183 - KY427202 |
|        |        |         |                   |        |      |                      |
| *Melanconis pterocaryae* | ME17 | A.R.4520 | CBS 133433 | – | – | KY427183 - KY427202 |
|        |        |         |                   |        |      |                      |
| *Melanconis pterocaryae* | ME18 | M4-1 MAFF 410216 | TFM FPH 2623 | Japan | *Juglans cinerea* | KY427183 - KY427202 |
|        |        |         |                   |        |      |                      |
| *Melanconis pterocaryae* | ME19 | A.R.4341 | M4-2 MAFF 410217 | TFM FPH 2624 | Japan | KY427183 - KY427202 |
|        |        |         |                   |        |      |                      |
| *Melanconis pterocaryae* | ME20 | LFP-M4-8 MAFF 410079 | TFM FPH 3373 | Japan | *Pterocarya rhoifolia* | KY427183 - KY427202 |
|        |        |         |                   |        |      |                      |
| *Melanconis stilbostoma* | D143 | WU 35970 | Poland | Poland | *Betula pendula* | KY427183 - KY427202 |

The altogether 18 isolates of *Melanconis* from *Juglandaceae* included in this study either originated from ascospores or conidia of fresh specimens or from culture collections. Details of the strains including NCBI GenBank accession numbers of gene sequences used to compute the phylogenetic trees are listed in Table 1. Strain acronyms other than those of official gene sequences 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). Freshly collected specimens have been deposited in the Fungarium of the Department of Botany and Biodiversity Research, University of Vienna (WU).

**Morphology**

Microscopic observations were made in tap water except where noted. Methods of microscopy included stereomicroscopy using a Nikon SMZ 1500 equipped with a Nikon DS-U2 digital camera, and Nomarski differential interference contrast (DIC) using a Zeiss Axio Imager.A1 compound microscope equipped with a Zeiss AxioCam 506 colour digital camera. Images and data were gathered using the NIS-Elements D v. 3.22.15 or Zeiss...
Fig. 1 Phylogram of one of 240 MP trees of 894 steps (CI = 0.41, RI = 0.81, RC = 0.33) revealed by PAUP from an analysis of the LSU matrix of selected consensus of all MP trees. GenBank accession numbers are given following the taxon names; nodes marked by an asterisk (*) collapsed in the strict consensus of all MP trees.
ZEN Blue Edition softwares. For certain images of ascomata the stacking software Zenere Stacker v. 1.04 (Zenere Systems LLC, Richland, WA, USA) was used. Measurements are reported as maxima and minima in parentheses and the range representing the mean plus and minus the standard deviation of a number of measurements given in parentheses. Due to poor or absent sporulation in pure culture, conidial and conidiophore morphology was only studied from natural substrates.

**Culture preparation, DNA extraction, PCR and sequencing**

Single ascospore or conidium isolates were prepared and grown on 2% malt extract agar (MEA), or on 2% corn meal agar plus 2% w/v dextrose (CMD).

Growth of liquid culture and 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) or the modified CTAB method of Riethmüller et al. (2002).

The following loci were amplified and sequenced: the complete internal transcribed spacer region (ITS1-5.8S-ITS2) and a c. 900 bp fragment of the large subunit nuclear ribosomal DNA (nuLSU rDNA), amplified and sequenced as a single fragment with primers V9G (De Hoog & Gertits van den Ende 1999) and LR5 (Vilgalys & Hester 1990); a 450–454 bp fragment of the calmodulin (cal) gene with primers CAL-228F and CAL-737R (Carbone & Kohn 1999); a 441–445 bp fragment of the histone H3 (his) gene with primers CYLH3F (Crous et al. 2004) and H3-1b (Glass & Donaldson 1995); a c. 1 kb fragment of the guanine nucleotide-binding protein subunit beta (ms204) gene with primers MS-E1F1 and MS-ES5R1 (Walker et al. 2012); a 711 bp fragment of the RNA polymerase II subunit 1 (rpb1) gene with primers RPBI-Af and RPBI-1r (Stiller & Hall 1997); a c. 1.3 kb fragment of the RNA polymerase II subunit 2 (rpb2) gene with primers RPBR2-5f and RPBR2-7cr (Li et al. 1999) or DRPB2-5f and dRPB2-7cr (Voglmayr et al. 2016); a c. 1.5 kb fragment of the translation elongation factor 1-alpha (tef1) gene containing introns 4 and 5 and part of the exon with primers EF1-728F (Carbone & Kohn 1999) and TEF1LlErev (Jaklitsch et al. 2005); and a 441–445 bp fragment of the beta-tubulin (tub2) gene with primers T1 (O’Donnell & Cigelnik 1997) and the newly designed BtV2r (5’ CATCCTRGCRTNGGAACT 3’). PCR products were purified using an enzymatic PCR cleanup (Werle et al. 2004) as described in Voglmayr & Jaklitsch (2008). DNA was cycle-sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems, Warrington, UK) and the PCR primers; in addition, primers ITS4 (White et al. 1990) and LR3 (Vilgalys & Hester 1990) were used as internal sequencing primers for the ITS-LSU rDNA region. Sequencing was performed on an automated DNA sequencer (ABI 3730xl Genetic Analyzer, Applied Biosystems).

**Data analysis**

To reveal the phylogenetic position of Melanconis species occurring on Juglandaceae within the Diaporthales, a phylogenetic analysis was performed with nuLSU rDNA sequences. Sequences of representative species were selected from Castelbury et al. (2002) and supplemented with sequences from GenBank. Gaeumannomyces graminis and Kohlmeyeriopsis medullaris (Magnaportheaceae) were included as outgroups. GenBank accession numbers of the sequences selected are given in the phylogenetic tree (Fig. 1). In addition, an ITS-LSU matrix was produced with a subset of taxa according to the results of the LSU analyses, including selected members of Cryphonectriaceae, Gnomoniaceae, Harkesiaceae, Melanconidaceae and Schizoparmaceae; for GenBank accession numbers see Table 1. For detailed investigations of species relationships and delimitation within Melanconis species from Juglandaceae, a combined matrix of eight loci (partial SSU-ITS-LSU rDNA, cal, his, ms204, rpb1, rpb2, teff and tub2) was produced for phylogenetic analyses, with Melanconis stibostoma as the outgroup. The GenBank accession numbers of sequences used in these analyses are given in Table 2.

Sequence alignments for phylogenetic analyses were produced with the server version of MAFFT (www.ebi.ac.uk/Tools/mafft or http://mafft.cbrc.jp/alignment/server/), checked and refined using BioEdit v. 7.0.9.0 (Hall 1999). After exclusion of a 355 bp insertion in the LSU of Ditolpella ditopa, the LSU matrix contained 1 337 characters and the ITS-LSU matrix 1 591 characters. The combined data matrix contained 7 767 characters; viz. 1 600 nucleotides of SSU-ITS-LSU, 455 nucleotides of cal, 449 nucleotides of his, 1 037 nucleotides of ms204, 711 nucleotides of rpb1, 1 150 nucleotides of rpb2, 1 395 nucleotides of teff and 970 nucleotides of tub2. Prior to phylogenetic analyses, the approach of Wiens (1998) was applied to test for significant levels of localised incongruence among the markers used for the combined analysis, using the level of bootstrap support (Sung et al. 2007) as described in Jaklitsch & Voglmayr (2014). For this, the 70% maximum parsimony (MP) bootstrap consensus trees were calculated for each individual partition, using the same parameters given below, were compared. No topological conflicts were observed between these bootstrap trees of the various genes, indicating the absence of significant incongruence and combinability of the eight loci (Wiens 1998).

Maximum parsimony (MP) analyses were performed with PAUP* 4.0a150 (Swoford 2002). All molecular characters wereunordered and given equal weight; analyses were performed with gaps treated as missing data; the COLLAPSE command was set to MINBRLEN. For the LSU and the ITS-LSU matrices, first a parsimony ratchet approach was used. For this, nexus files were prepared using PRAP v. 2.0b3 (Müller 2004), implementing 1 000 ratchet replicates with 25% of randomly chosen positions weighted to 2, which were then run with PAUP. In a second step, the best trees obtained by the parsimony ratchet analyses were loaded in PAUP and subjected to heuristic search using TBR branch swapping (MULTREES option in effect, steepest descent option not in effect). MP analysis of the combined multilocus matrix was done using 1 000 replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, steepest descent option not in effect). Bootstrap analyses with 1 000 replicates were performed in the same way, but using 5 rounds of random sequence addition and subsequent branch swapping during each bootstrap replicate; in addition, each replicate was limited to 1 million rearrangements in the LSU and ITS-LSU matrices.

Maximum likelihood (ML) analyses were performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI v. 1.3 (Silvestro & Michalak 2012), using the ML + rapid bootstrap setting and the GTR+MAI substitution model with 1 000 bootstrap replicates. The matrix was partitioned for the different gene regions included in the combined multilocus analyses.

The sequence markers used for the multilocus analyses were also individually compared for their phylogenetic resolution within Juglanconis. Because several markers were not available for the outgroup taxon (Melanconis stibostoma), only the accesses of Juglanconis were compared. The data matrices of the individual genes were subjected to MP bootstrap analyses with the same settings as in the analyses of the multilocus matrix and the resulting bootstrap support values of species and internal nodes were compared.
RESULTS

Molecular phylogeny

Of the 1 337 characters of the LSU matrix, 219 were parsimony informative. MP analyses revealed 240 MP trees of score 894, one of which is shown in Fig. 1; tree topologies of all MP trees were identical except for some nodes within Gnomoniaceae and some deeper nodes in the tree (see nodes marked by an asterisk in Fig. 1). In both MP and ML analyses, the Juglanconis-Gnomoniaceae-Melanconidaceae clade was highly supported. The subclade containing Melanconis (Melanconidaceae s.str.) and Gnomoniaceae received maximum support, but Melanconidaceae and Gnomoniaceae received only low or insignificant support. The genus Juglanconis was revealed as sister clade to the Gnomoniaceae-Melanconidaceae s.str. clade and received low or insignificant support as well.

Of the 1 591 characters included in the ITS-LSU analyses, 291 were parsimony informative. MP analyses revealed two MP trees 1 156 steps long, one of which is shown in Fig. 2. Tree topologies of the two MP trees differed in an interchanged position of Ophiognomonia rosea and O. nana. The ML tree revealed by RaxML showed the same relationships between the families as the MP trees, but differed in some unsupported nodes within the Gnomoniaceae (not shown). The clade containing Juglanconis, Melanconidaceae and Gnomoniaceae received maximum support in both analyses, and Juglanconis were revealed as sister group to the highly supported clade containing Melanconidaceae and Gnomoniaceae.

Table 2

| Taxon | Isolate No.1 | 2 | Herbarium no.1 | Country | Host | Genbank accession numbers |
|-------|--------------|---|----------------|---------|-----|--------------------------|
|       | ITS          | LSU |                |         |     |                          |
| Ahecium auctum | CBS 124283 T | WU 30206 | Austria | Alnus glutinosus | KF570154 KF570154 |
| Ambarignonima geliotorum | CBS 121227 T | BPI 844274 | USA | Liquidambar styraciflua | EU254748 EU255070 |
| Amphiporthe tiliae | CBS 119298 | BPI 843515 | Austria | Tilia platyphylla | EU199178 EU199122 |
| Apioignomonia hystrix | CBS 911.79 | CBS-H 11343 | Switzerland | Acer pseudoplatanus | DQ133549 EU255180 |
| Apioignomonia veneta | CBS 897.79 | NA | Switzerland | Platanus orientalis | DQ133532 EU255195 |
| Celoporthe dispersa | CBS 118742 | PREM 58896 | South Africa | Syzigium cordatum | NR_119569 HQ730853 |
| Coniella diploidiella | CBS 111858 | NA | France | Vitis vinifera | AY339323 KX833335 |
| Coniella fragariae | CBS 172.49 T | NA | Belgium | Fragaria sp. | AY339317 AY339322 |
| Coniella quercicola | CBS 904.69 T | NA | Netherlands | Quercus robur | KX833385 KX833414 |
| Coniella tibouchinae | CBS 131974 | NA | Brazil | Tibouchina granulosa | JQ281774 KX833318 |
| Crypechnocystis parasitica | ATCC 38755 | NA | USA | Castanea dentata | AY141856 EU199123 |
| Cryptosporella betulae | CBS 109763 | BPI 744484 | Austria | Betula alba | EU199180 AF408375 |
| Cryptosporella hypodermia | CBS 171.69 | NA | Netherlands | Ulmus campestris | EU199225 DO80280 |
| Cryptosporella sulfura | CBS 121077 | BPI 871231 | Austria | Alnus incana | EU199184 EU199124 |
| Discula destructiva | CBS 109771 | BPI 1107757 | USA | Cornus nuttallii | EU199186 AF408359 |
| Ditopella ditopa | CBS 109748 | BPI 748439 | Austria | Alnus glutinosus | DQ233526 AF408360 |
| Gnomonia gnomon | CBS 199.53 | NA | Italy | Corylus avellana | AY186956 AF408361 |
| Gnomonia virginianae | CBS 121913 T | BPI 844264 | USA | Ostrya virginiana | EU254801 EU255105 |
| Gnomoniopsis chamaenomeri | CBS 803.79 | NA | Finland | Rubus chamaemorus | EU254808 EU255107 |
| Gnomoniopsis tormentifoliae | CBS 904.97 | NA | Switzerland | Potentilla erecta | EU254856 EU255133 |
| Harknessia eucalypti | CBS 342.73 | NA | Australia | Eucalyptus regnans | AY720745 AF408363 |
| Harknessia leucospermi | CBS 377.97 | NA | South Africa | Leucospermum sp. | AY720727 AY720824 |
| Harknessia molokaiensis | CBS 114877 T | NA | USA | Eucalyptus robusta | AY720749 AY720842 |
| Harknessia syzygi | CBS 111124 T | NA | South Africa | Syzygium cordatum | AY720738 AY720834 |

1 ATCC: American Type Culture Collection, Manassas, VA, USA; BJFC: Museum of the Beijing Forestry University, Beijing, China; BPI: U.S. National Fungus Collections USDA-ARS MD USA; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CFCC: China Forestry Culture Collection Center, Beijing, China; MAFF: MAFF Genebank, National Institute of Agrobiological Sciences, Ibaraki, Japan; NA: not applicable; PREM: South African National Collection of Fungi, Pretoria, South Africa; WU: Herbarium of the University of Vienna, Austria.

2 T: ex-type strain; ET: ex-epitype strain; NT: ex-neotype strain.
received maximum and medium (70 %) support in MP analyses, respectively. Of the 7 767 characters included in the combined multilocus analyses, 315 were parsimony informative (16 from ITS-LSU, 32 from cal, 10 from his, 52 from ms204, 26 from rpb1, 45 from rpb2, 71 from tef1 and 63 from tub2). The his gene consistently failed to amplify in Juglanconis appendiculata and is therefore missing for this species. The MP analysis revealed five MP trees 907 steps long, one of which is shown in Fig. 3. Tree topologies of all MP trees were identical except for minor differences within J. appendiculata. The ML tree revealed by RAxML was identical to the MP tree shown. All four species of Juglanconis received maximum support in both analyses, as well as the relationships between the species. Juglanconis juglandina and J. oblonga are revealed as closely related but distinct species, and conspecificity of Japanese and North American accessions of J. oblonga is confirmed.

The number of alignment characters, the number and percentage of parsimony informative characters of the different markers and the percentage of MP bootstrap support for species and internal nodes revealed in the phylogenetic analyses are shown in Table 3. A comparison of the markers focusing on bootstrap support shows that the tef1 fragment containing introns 4 and 5 is the best resolving marker with 69 (5.1 %) parsimony informative characters (pic) and all nodes supported by 100 %, followed by cal with 32 (7 %) pic and support at all nodes above 98 %, except for J. oblonga with 94 %. Then followed ms204 and tub2 with 51 (6 %) and 62 (6.4 %) pic, respectively; all nodes were highly supported above 99 %, except for J. oblonga where support decreased to 87 % (ms204) and 86 % (tub2). In the rpb2, with 45 (3.9 %) pic, J. oblonga is supported by 95 %, whereas support of J. juglandina drops to 65 %. In the residual markers (rpb1, ITS and his) support of at least one node is absent.

Fig. 2 Phylogram showing one of two MP trees of 1 156 steps (CI = 0.47, RI = 0.78, RC = 0.36) revealed by PAUP from an analysis of the ITS-LSU matrix of selected Diaporthales, showing the phylogenetic position of Juglanconis. MP and ML bootstrap support above 50 % are given at the first and second position, respectively, above or below the branches. Strain/culture numbers are given following the taxon names. The node marked by an asterisk (*) collapsed in the strict consensus of the two MP trees.
Fig. 3 Phylogram showing one of five MP trees of 907 steps (CI = 0.97, RI = 0.98, RC = 0.95) revealed by PAUP from an analysis of the combined ITS-LSU-cal-his-ms204-rpb1-rpb2-tele-tub2 matrix of Juglanconis, with Melanconis stilbostoma selected as outgroup. MP and ML bootstrap support above 50 % are given at the first and second position, respectively, above or below the branches. Strain numbers are given following the taxon names.

| ITS | LSU | cal | his | ms204 | rpb1 | rpb2 | tele | tub2 |
|-----|-----|-----|-----|-------|------|------|------|------|
| No. of alignment characters | 518 | 910 | 455 | 449 | 1030 | 711 | 1144 | 1361 | 970 |
| No. of variable characters | 15 | 5 | 37 | 31 | 65 | 27 | 55 | 77 | 72 |
| No. of parsimony-informative characters (pic) | 13 | 2 | 32 | 10 | 51 | 26 | 45 | 69 | 62 |
| % parsimony informative characters | 2.5 | 0.2 | 7.0 | 2.2 | 5.0 | 3.7 | 3.9 | 5.1 | 6.4 |
| % bts oblonga | – | – | 94 | 71 | 87 | 95 | 95 | 100 | 86 |
| % bts juglandina | 69 | 63 | 99 | 100 | 99 | – | 65 | 100 | 99 |
| % bts oblonga+juglandina | 84 | 61 | 98 | – | 100 | 100 | 100 | 100 | 100 |
| % bts pterocaryae+oblonga+juglandina | 100 | – | 100 | – | 100 | 100 | 100 | 100 | 100 |

**Table 3** Comparison of the phylogenetic markers used for the multigene analyses of Juglanconis. The markers were compared within Juglanconis. For the MP bootstrap support (% bts) of the respective clades, MP bootstrap analyses of the matrices of the respective markers were performed, applying the same rooting as in the multigene analyses (Fig. 3).

**Taxonomy**

**Juglanconidaceae** Voglmayr & Jaklitsch, fam. nov. — MycoBank MB819587

_Etymology._ Referring to the name of the type genus.

_Type genus._ Juglanconis Voglmayr & Jaklitsch.

Family of Diaphorales. *Pseudostromata* consisting of an inconspicuous ectostromatic disc causing a more or less pustulate bark surface. **Central column** beneath the disc more or less conical. **Stromatic zones** lacking. _Perithecia_ surrounding the ectostromatic disc, with long lateral ostioles that emerge at the margin or within the ectostromatic disc. **Paraphyses** deliquescent at maturity. _Asci_ octosporous, with an apical ring, becoming detached from their base. **Ascospores** hyaline, baccate, with or without gelatinous appendages. _Asexual morph_ melanconium-like. _Conidiomata_ acervular, with ectostromatic disc and central column. **Conidiophores** aseptate or few-celled, smooth, hyaline to brownish. **Conidiogenous cells** annelidic. _Conidia_ brown, with gelatinous sheath. _Conidial wall_ smooth on the outer surface, with inconspicuous to distinct irregular verrucae on the inner surface.

Note — We describe this family, because the genus _Juglanconis_ is consistently placed outside described families of Diaphorales in phylogenetic analyses.

**Juglanconis** Voglmayr & Jaklitsch, gen. nov. — MycoBank MB819582

_Etymology._ Referring to its occurrence on Juglandaceae.

_Type species._ Juglanconis juglandina (Kunze) Voglmayr & Jaklitsch.

Genus of Diaphorales. *Pseudostromata* consisting of an inconspicuous, erumpent, light to dark coloured ectostromatic disc causing a more or less pustulate bark surface. **Ectostromatic disc** convex, flat or concave, greyish to brownish, surrounded by bark flaps. **Central column** beneath the disc more or less conical. **Stromatic zones** lacking. _Perithecia_ inconspicuous at the bark level, surrounding the ectostromatic disc, oblique or horizontal, usually more or less irregularly scattered, sometimes arranged in a circle around the central column, with long lateral ostioles that converge at the margin of the column and emerge at the margin or within the ectostromatic disc. **Ostioles** flat in the disc or slightly projecting, rarely distinctly projecting and cylindrical, often obscuring the disc, sometimes covered by a distinct white crust. **Paraphyses** deliquescent at maturity. _Asci_ oblong or fusoid, octosporous, with a more or less distinct apical ring becoming inconspicuous in old herbarium specimens; _asci_ becoming detached from their base. **Ascospores** hyaline, ellipsoidal, symmetrical to asymmetrical, straight to curved, baccate, with a central or slightly eccentric septum, constricted at the septum, smooth, with or without blunt or pointed appendages.
Fig. 4 Juglanconis appendiculata. a–c. Ectostromatic discs and ostioles in surface view; d. ectostromatic disc in side view showing protruding ostioles; e. pseudostroma in vertical section; f, g. transverse sections below ectostromatic disc; h. pseudostroma in transverse section, showing perithecia and indistinct whitish to light brown entostroma; i–l. mature ascii with apical ascal ring (i, j vital, k, l dead); m, n. ascus apex with apical ring (m vital, n dead); o–u. vital ascospores with cylindrical gelatinous appendages; v–z. dead ascospores (v–x showing gelatinous appendages); a1. conidioma in surface view; b1. transverse section of conidioma, showing central column; c1–e1. conidiophores (annelides) with conidia (c1, d1); f1–o1. conidia (showing gelatinous sheath in f1–k1; f1–j1 vital, k1–o1 dead); p1. detail of verruculose inner conidial wall. All in water, except k, l, n, w, z, c1–e1, l1–p1 in 3 % KOH (a, c–e, h, u, a1, b1: WU 35955; b, g, k, l, n, w–z, c1–e1, j1–o1: WU 32010; f, i, j, o–s, f1–i1: WU 35954 (holotype); m, t: WU 35956; v: WU 35958, p1: WU 29730). — Scale bars: a = 1 mm; b, c, e, h = 0.5 mm; d, f, g, a1, b1 = 300 µm; i–l, c1–e1 = 20 µm; m–z, f1–o1 = 10 µm; p1 = 2 µm.
Asexual morph: melanconium-like. Conidiomata acervular, covered by the bark, erumpent at maturity; possessing the same type of ectostromatic disc and central column as the sexual morph, usually preceding it. Conidiophores branched only at the base, mostly aseptate, sometimes few-celled, smooth, hyaline when young, brownish with age. Conidiogenous cells distinctly annellidic, successively producing several generations of conidia. Conidia brown, variable in shape, subglobose, ellipsoid, elongate piryform, pip-shaped to fusoid, with distinct gelatinous sheath when fresh. Conidiomatal wall smooth on the outer surface, with inconspicuous to distinct, sometimes confluent irregular verrucae on the inner surface.

**Juglanconis appendiculata** Voglmayr & Jaklitsch, sp. nov. — MycoBank MB819583; Fig. 4

**Etymology.** Referring to its gelatinous ascospore appendages.

**Holotype.** AUSTRIA, Niederösterreich, Mühlenitz, Herrnau, on corticated branches of *Juglans nigra*, 28 Feb. 2015, H. Voglmayr (WU 35954; ex-epitype culture D96 (ex sexual morph) and culture D96a (ex asexual morph)).

**Pseudoostromata** 1.5–3 mm diam, typically distinct, circular, projecting up to 0.3 mm beyond the host surface, without perithecial bumps. *Ectostromatic disc* distinct, circular or oblong, dark grey, brown or black, 0.3–2 mm diam, sometimes concealed by densely arranged ostioles, pulvinate. **Central column** yellowish, greenish to brownish grey. *Entostroma* indistinct. Ostioides 1–15 per disc, (80–)92–127–(154) µm diam (n = 34), plane or slightly papillate, black, sometimes covered by distinct white crust. **Perithecia** (380–)420–520–(560) µm diam (n = 20), arranged in various configurations. **Asci** = (121–)131–147–(168) × (19.5–)20.5–24.2–(27.8) µm (n = 58), clavate to fusoid, containing 8 uni- to biseriate ascospores, with distinct funnel-shaped apical ring when fresh. **Conidial wall** = (2–)2.5–3.2–(4) µm high, becoming faint in older herbarium specimens.

**Notes** — *Juglanconis appendiculata* is easily distinguished from the other *Juglanconis* species by its conspicuous cylindrical ascospore appendages; the other species with appendaged ascospores, *J. pterocaryae*, has tapering appendages with rounded to subacute tips and also differs by the hosts. *Pterocarya* spp. Additional differences from the sympatric *J. juglandina* include distinct pseudostromata and light brown, distinctly narrower conidia (typically 8.6–10.2 µm wide, l/w = 2.2–2.9, vs 12.0–14.5 µm, l/w = 1.4–1.8). In contrast to *J. juglandina* its sexual morph is produced abundantly, whereas its asexual morph is inconspicuous. Remarkably, it has remained undetected until now, although it appears to be a common species in Southern Europe where it replaces *J. juglandina*; in eastern and southern Austria it is commonly co-occurring with *J. juglandina* on the same branches. Observational evidence suggests that it is currently expanding its range northwards which could be due to global warming.

**Juglanconis juglandina** (Kunze) Voglmayr & Jaklitsch, comb. nov. — MycoBank MB819584; Fig. 5, 6

**Basionym.** *Melanconium juglandinum* Kunze, in Schubert & Ficinus, Fl. Dresd., 2 Aufl., 2: 480. 1823.

**Synonymy.** *Melanconium juglandinum* juglandinum (Kunze) Kunzke, Revis. Gen. Pl. (Leipzig) 3, 2: 493. 1898.

**Description.** Conidiomata perithecia-like, 0.8–2 mm diam, typically inconspicuous, sometimes distinct, circular, slightly projecting, without perithecial bumps. *Ectostromatic disc* indistinct, circular or oblong, dark grey, brown or black, 0.5–1.2–(2.3) mm diam, often concealed by densely arranged ostioles, often pulvinate. **Central column** yellowish, greenish to brownish grey. *Entostroma* indistinct. Ostioides 1–25 per disc, (94–)129–176–(208) µm diam (n = 30), plane or slightly papillate, black. **Perithecia** (375–)440–565 (–565) µm diam (n = 36), arranged in various configurations. **Asci** = (126–)138–161–(184) × (14.2–)17.3–22.3–(25.0) µm (n = 75), clavate to fusoid, containing 8 uni- to irregularly biseriate ascospores, with indistinct apical ring when fresh 3.7–4.4 µm diam, 3.3–4.1 µm high, ring not visible in older herbarium specimens. **Ascospores** (20.5–)24.3–29.0 (–36.5) × (6.7–)8.5–11.0–(12.7) µm, l/w = (2.0–)2.3–3.2–(4.7) µm (n = 359), hyaline, inequilaterally ellipsoid or broadly fusoid, asymmetric, usually slightly to distinctly curved, distinctly constricted at the septum, without appendages; cells usually distinctly dimorphic, upper cell mostly larger, with rounded to subacute end, lower cell subacute to narrowly rounded, multiguttulate, containing mostly one large and numerous small guttules per cell; wall c. 0.4–0.6 µm thick, not swelling.

**Distribution** — Europe; apparently common in Southern Europe.

**Notes** — *Juglanconis appendiculata* is easily distinguished from the other *Juglanconis* species by its conspicuous cylindrical ascospore appendages; the other species with appendaged ascospores, *J. pterocaryae*, has tapering appendages with rounded to subacute tips and also differs by the hosts. *Pterocarya* spp. Additional differences from the sympatric *J. juglandina* include distinct pseudostromata and light brown, distinctly narrower conidia (typically 8.6–10.2 µm wide, l/w = 2.2–2.9, vs 12.0–14.5 µm, l/w = 1.4–1.8). In contrast to *J. juglandina* its sexual morph is produced abundantly, whereas its asexual morph is inconspicuous. Remarkably, it has remained undetected until now, although it appears to be a common species in Southern Europe where it replaces *J. juglandina*; in eastern and southern Austria it is commonly co-occurring with *J. juglandina* on the same branches. Observational evidence suggests that it is currently expanding its range northwards which could be due to global warming.
Fig. 5 Juglanconis juglandina, sexual morph. a–d. Ectostromatic discs and ostioles in surface view; e. ectostromatic disc in side view showing protruding ostioles; f. pseudostroma in vertical section; g, h. transverse sections below ectostromatic disc; i. pseudostroma in transverse section, showing perithecia and indistinct whitish to light brown entostroma; j–l. mature vital asci with apical ascral ring; m. vital ascus apex with apical ring; n–w. vital ascospores; x–w1. dead ascospores. All in water, except b1–j1, s1–w1 in 3 % KOH (a, f, i, h1–j1: WU 35965 (neotype); b–e, g, x–g1: WU 35961; h: PC 0723585; j–w: WU 35966; k1, l1: WU 35959; m1–t1: WU 35964; u1–w1: BPI 614906). — Scale bars: a = 1 mm; b–i = 0.5 mm; j–l = 20 µm; m–w1 = 10 µm.
Fig. 6 Juglanconis juglandina, asexual morph. a. Conidiomata in surface view; b, c. transverse (b) and vertical (c) sections of conidiomata, showing central column; d–h. conidiophores (annellides) with conidia; i–o. conidia (showing gelatinous sheath in i–q, a1–g1; i–q vital, r–o1 dead; in j1–o1 showing verruculose inner conidial wall); p1–r1. detail of inner conidial wall, showing confluent verrucae. All in 3 % KOH, except d, e, i–q, j1 in water (a–c, f–h, w, x, m1: WU 35961; d, e, i–o, j1: WU 35966; p, q: WU 35960; r–v, k1: PC 0723585; y, z: BPI 614909; a1–e1: WU 35968; f1–i1, q1: WU 35967; i1, p1: PC 0723587; n1: BPI 614907; o1: BPI 614910; r1: BPI 614908). — Scale bars: a = 1 mm; b, c = 0.5 mm; d–o1 = 10 µm; p1–r1 = 2 µm.
Asexual morph. Conidiomata acervular, 1–4 mm diam, blackish, scattered or occasionally confluent, with central or eccentric stromatic column; at maturity covered by black discharged conidial masses; usually conspicuous. Conidiphores (17–)26–37–(45) × (4.0–)4.8–6.5–(7.7) µm (n = 36), cylindrical to lageniform, simple, rarely branched at the base, smooth, subhyaline to pale brown. Conidiogenous cells annellidic with distinct annellations, integrated. Conidia (15–)19–23–(28.5) × (9.5–)12–14.5–(17.2) µm, l/w = (1.2–)1.4–1.8–(2.6) (n = 905), unicellular, hyaline when immature, brown to blackish when mature, narrowly ellipsoid to broadly pip-shaped, truncate with distinct scar at the base, densely multiguttulate, thick-walled; wall 0.7–1.1 µm thick, with distinct ornamentation on the inside of the wall consisting of irregular confluent verrucae 0.5–1.5–(2.6) µm diam, with 0.8–1.1 µm wide gelatinous sheath.

Habitat & Host range — Dead corticated twigs and branches of Juglans spp. attached to the tree.

Distribution — Europe, Asia; common, particularly as asexual morph.

Additional specimens examined (all on corticated branches of Juglans regia except where noted). AUSTRIA, Kärnten, St. Margareten im Rosental, 20 June 2015, H. Voglmayr (WU 39560, culture D142); St. Margareten im Rosental, near Stariwal, 6 Dec. 1998, W. Jaklitsch W.J. 1279 (WU 39561); ibid., 21 July 2000, W. Jaklitsch W.J. 1500 (WU 39590); St. Margareten im Rosental, Wogradna, 16 June 1995, W. Jaklitsch W.J. 647 (WU 39562); ibid., 7 July 2013, W. Jaklitsch W.J. 9543 (WU 39670); St. Margareten im Rosental, Zugland, 21 Apr. 2000, W. Jaklitsch W.J. 1450 (BPI 643222, culture CBS 121083); Niederösterreich, Orth an der Donau, near Uferhaus, on corticated branches of Juglans nigra, soc. J. appendiculata, J. Juglans regia except where noted).

Conidiomata = Mycotheca Rossica 94 (BPI 614908). — Krasnaja Poljana, 6 July 1909, J. Serebrianiko, soc. J. Juglans regia, on branches of Juglans nigra, without date, L. Fuckel 2013, Mycotheca Rossica 94 (BPI 614908). – Kryptogamae exsiccatae 2411 (BPI 614907). – Flora Bohemiae et Moraviae exsiccata 761 (BPI 614909); St. Margareten im Rosental, 7 Aug. 2016, H. Voglmayr, Fungi Rossiae exsiccati 299 (BPI 614902); St. Margareten im Rosental, near Stariwal, 6 Dec. 1998, W. Jaklitsch W.J. 1279 (WU 39561); ibid., 21 July 2000, W. Jaklitsch W.J. 1500 (WU 39590); St. Margareten im Rosental, Wogradna, 16 June 1995, W. Jaklitsch W.J. 647 (WU 39562); ibid., 7 July 2013, W. Jaklitsch W.J. 9543 (WU 39670); St. Margareten im Rosental, Zugland, 21 Apr. 2000, W. Jaklitsch W.J. 1450 (BPI 643222, culture CBS 121083); Niederösterreich, Orth an der Donau, near Uferhaus, on corticated branches of Juglans nigra, soc. J. appendiculata, J. Juglans regia except where noted).

Notes — Melanconium juglandinum is the first epithet unequivocally applicable to this taxon. No type specimen could be traced at B (R. Lücking, pers. comm.), and therefore specimen MBT374387; BPI 616363, NY 00921841, NYS 146304 (isotypes); same data, in Shear, New York Fungi 340 (BPI 616364, isotype).

Corda (1839) nicely illustrated conidiomata, conidia and conidio- phores under Melanconium juglandis, a younger synonym. The annellidic conidiogenesis was studied in detail by Belisario & Onofri (1995) by light and scanning electron microscopy. Juglanconium juglandis has been proven to be a virulent pathogen of Juglans spp. (Belisario 1999), being the causal agent of the European black pustular dieback of walnut. Compared to the asexual morph which is very common and conspicuous, the sexual morph has been infrequently found in fully developed condition.

Juglanconium oblonga (Berk.) Voglmayr & Jaklitsch, comb. nov. — MycoBank MB819585; Fig. 7, 8

Basionym. Melanconium oblongum Berk., Grevillea 2 (no. 22): 153. 1874. = Diaporthe juglandis Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 45: 448. 1893.

Typification. USA, Alabama, on corticated twigs of Juglans cinerea, without date, Peters, Herb. Berkeley no. 5250 (K(M) 200285, lectotype of Melanconium oblongum here designated; MBT374386); Massachusetts, on corticated twigs of Juglans cinerea, without date & collector, Herb. Berkeley no. 3380 (K(M) 200285, syntype of Melanconium oblongum); New York, Alcove, on corticated twigs of Juglans cinerea, 31 Aug. 1893, C.L. Shear, in Ellis & Everhart, North American Fungi 3121 (BPI 616365, lectotype of Diaporthe juglandis here designated; MBT374387; BPI 616363, NY 00921841, NYS 146304 (isotypes); same data, in Shear, New York Fungi 340 (BPI 616364, isotype).

Pseudostromata 1–3 mm diam, usually distinct, circular, projecting up to 0.5 mm, without perithecial bumps. Ectostromatic disc indistinct, usually circular, greyish to brownish or black, 0.4–1.3 (2.7) mm diam, commonly concealed by densely arranged ostioles, often pulvinate. Central column yellowish, greenish to brownish grey. Entostroma indistinct. Ostioli 1–15 (25) per disc, (83–)110–163–(220) µm diam (n = 20), papillate, black, sometimes covered by distinctly white crust. Perithecia (490–)525–725–(780) µm diam (n = 31), arranged in various configurations. Asci (85–)110–132–(140) × (12.5–)14.5–16–(19) µm (n = 27), clavate to fusoid, containing 8 uni- to irregularly biseriate ascospores, ring cylindrical to funnel-shaped according to Kobayashi (1970), not seen in the herbarium specimens examined. Ascospores (17.5–)19.8–24–(28) × (6.7–)8.0–11.5–(17.5) µm, l/w = (1.5–)2.2–2.6–(3.3) (n = 322), hyaline, ellipsoid, broadly ellipsoid or broadly fusoid, symmetric to slightly asymmetric, straight, rarely slightly curved, constricted at the septum, without appendages; cells monomorphic to slightly domorphic with larger upper cell, with broadly rounded to subacute ends, multiguttulate; wall c. 0.4–0.6 µm thick, not swelling.

Asexual morph. Conidiomata acervular, 1–4 mm diam, blackish, scattered or occasionally confluent, with central or eccentric stromatic column; at maturity covered by black discharged conidial masses. Conidiophores (21–)28–44.5–(55) × (4.0–)4.8–6.5–(7.5) µm (n = 30), cylindrical to lageniform, simple, rarely branched at the base, smooth, subhyaline to pale brown. Conidiogenous cells annellidic with distinct annellations, integrated. Conidia (13.7–)18–22.7–(27.7) × (7–)9.2–(12.5) µm, l/w = (1.3–)1.7–2.3–(3.2) (n = 1633), unicellular, hyaline when immature, brown to blackish when mature, ellipsoid, elongate to pip-shaped, sometimes slightly allantoid, truncate with distinct scar at the base, densely multiguttulate, thick-walled; wall c. 0.7–0.9 µm, with distinct ornamentation on the inner side of the wall consisting of irregular confluent verrucae 0.5–2 µm diam, with 0.6–0.8 µm wide gelatinous sheath.

Habitat & Host range — Dead corticated twigs, branches and trunks of Juglans spp. Distribution — North America, Eastern Asia (Japan).
Fig. 7 Juglanconis oblonga, sexual morph. a–g. Ectostromatic discs and ostioles in surface view; h. ectostromatic disc in side view showing protruding ostioles; i. pseudostroma in vertical section; j, k. transverse sections below ectostromatic disc; l, m. pseudostromata in transverse section, showing perithecia and indistinct whitish to light brown entostroma; n–r. mature asci; s. ascus apex; t–z1. dead ascospores. All in 3 % KOH, except t–w in water (a, b: BPI 616364; c, h: BPI 616363; d, m–q, n1–q1: NY 01926933; e, r–a1: WU 35969; f, g, k, v1–z1: TFM FPH2623; i: BPI 614960; j, l, b1–f1: BPI 614954, g1–m1: BPI 616365 (lectotype of Diaporthe juglandis); r1–u1: TFM FPH3601). — Scale bars: a = 1 mm; b–m = 0.5 mm; n–r = 20 µm; s–z1 = 10 µm.
Fig. 8 Juglanconis oblonga, asexual morph. a, b. Conidiomata in surface view; c–e. transverse (c, d) and vertical (e) sections of conidiomata, showing central column; f–h. conidiophores (annelides); i–s1. dead conidia showing gelatinous sheath in j, k, s1; d1–g1; in n1–s1 showing verruculose inner conidial wall; t1–w1. detail of inner conidial wall, showing confluent verrucae. All in 3 % KOH (a, f–h: NY 01926935; b, c, k–o, n1, t1: K(M) 200286 (lectotype); d: NY 01926937; e, d1–h1, r1: WU 35969; i, j: K(M) 200285; p–t, o1, u1: NY 00921841; u–x: TFM FPH3599; y–c1: TFM FPH2623; l1–m1, q1: BPI 614951; p1, v1: TFM FPH3601; s1, w1: BPI 614955). — Scale bars: a = 2 mm; b–e = 200 µm; f–s1 = 10 µm; t1–w1 = 2 µm.
Additional specimens examined (all on corticated twigs of Juglans cinerea except where noted). CARYA, Ontario, Brant Co., E. of Harley, 27 June 1937, R.F. Cain (BPI 614954); Frontenac Co., Kingston, on corticated twigs of Juglans nigra, 8 June 1964, E.D. Taylor (BPI 614961); Lake Erie Dist, Aldso- broough, 19 July 1962, G.R. Inrinnell (BPI 614955); Renford Co., near Braeside, 31 Aug. 1960, G.D. Darker (BPI 614959); W of Richmond Hill, 12 Oct, 1935, H.S. Jackson (NY 01926938), Quebec, Plains d' Abraham, 27 July, 2006, H. van Aarle (WU 39989); Gatineau Park, Nature Trail, 9 Sept. 1958, R. Arnold & J. Malvin (BPI 615124). – Jenavn, Hokkaido, Bibai, Hokkaido Forest Research Institute Experimental Forest, on corticated twigs of Juglans ailanthifolia, 24 Sept. 1964, T. Kobayashi (TFM FPH3373); Iwate-gun, Iwate Pref., Takisawa, on corticated twigs of Juglans ailanthifolia, 5 Nov, 1970, T. Kobayashi (TFM FPH3599, TFM FPH3601, NY 01926932). – USA, Connecticut, Boston, July 1924, A.H. Graves (BPI 615128); Hamden, 16 Sept. 1922, A.H. Graves (BPI 614960); Meriden, 16 Sept. 1922, A.H. Graves (BPI 614957); Maine, North Windham, 23 July 1923, A.H. Graves (BPI 614956); Maryland, Beltsville, North Farm walnut planting, on corticated twigs of Juglans ailanthifolia, 7 July 1953, F.H. Berry (BPI 614842); Massachusetts, Conway, Baptist Hill, 10 Feb. 1980, M.E. Barr (NY 01926937); New York, Highlands of Rockland Co., 16 June 1929, A.H. Graves (BPI 614951); Putnam Co., Carmel, S. of Nichols Rd. between Gypsy Trail and Horsepond Rds., 22 June 1998, R.C. Harris (NY 01926935); Walton, Mountain Home Farm, 1 June 1924, A.E. Jenkins (BPI 614958, NY 01926934); Pennsylvania, Lancaster, on corticated twigs of Juglans nigra, 12 June 1940, J.D. Diller (BPI 614843); Vermont, Lamolle Co., Stone, Loomis Hill Rd., 10 July 1964, H.E. Bigelow & M.E. Barr (NY 01926933); Washington D.C., Ft. Kemble Park, on corticated twigs of Juglans nigra, 8 June 1943, G.F. Gravatt (BPI 614836).

Notes — Two authentic collections of Melanconium oblongum are extant at K, of which KM(200286) is here selected as lectotype. The type collection of Diaportha juglandis has been distributed in two exsiccatas (Ellis & Everhart, North American Fungi 3121) and in Shear, New York Fungi 340, the latter bearing the annotation ‘These specc. are from the same collection as Fungi 3121 and in Shear, New York Fungi 340, the latter bearing distributed in two exsiccates (Ellis & Everhart, North American Fungi 3121, 340).’ Wehmeyer (1941) expressed some doubts about its status as the conidial sizes of the Japanese collection were slightly narrower conidia as main distinctions from the European one. Wehmeyer (1941) suggested that the conidial size overlap in certain collections. No fresh collections were But our investigations confirmed shorter (typically 19.8–24 vs 24.3–29 µm in J. juglandina), mostly symmetric spores with monomorphic to slightly dimorphic cells. In addition, the asci are significantly shorter in J. oblonga. The Japanese collections available for study differed from North American collections by distinctly wider ascospores (11–13 µm) with rounded ends, but the sequence data demonstrated conspecificity with material from eastern North America.

Within Melanconium juglandis, Wehmeyer established var. caraya from Caryya glabra (Wehmeyer 1940), and var. tiliae from Tilia americana (Wehmeyer 1941). The former differs in host and the absence of a melanconium-like asexual morph, and the latter was considered to be synonymous with the European Melanconium (now Lamproconium) desmazeri, although the American collections did not produce a lamproconium-like but a melanconium-like asexual morph. In absence of fresh collections and of DNA data, their status cannot be evaluated, but it is likely that at least the latter does not belong to Juglanconis. They are certainly not conspecific with J. oblonga.

Juglanconis pterocaryae (Kuschke) Voglmiår & Jaklitsch, comb. nov. — MycoBank MB819586; Fig. 9

Basionym. Melanconium pterocaryae Kuschke, Trudy Tifissk. Bot. Sada 28: 25. 1913. Synonymy. Melanconium pterocaryae Tak. Kobay., Bull. Govt. Forest Exp. Stn Meguro 226: 24. 1970.

Typification. Japan, Shizuoka, Fuji, on corticated twigs of Pterocarya rhoifolia, 5 Aug. 1968, T. Kobayashi (TFM FPH2623, holotype of Melanconium pterocaryae).

Pseudostromata 1–2 mm diam, typically distinct, circular, projecting up to 0.3 mm, without perithecial bumps. Ecstroystromatic disc reduced to almost absent, circular, grey or brown, 0.15–0.5 mm diam, concealed by densely arranged ostioles, pulvinate. Central column poorly developed, grey to brownish grey, or absent. Entostroma indistinct. Ostioli 1–9 per disc, (79–)91–123(–135) µm diam (n = 31), plane or slightly papillate, black. Perithecia (410–)470–600(–640) µm diam (n = 14), arranged in various configurations, Asci (67.5–)79–96(–105) × (11.5–)12–14.2(–15.2) µm (n = 25), clavate to fusoid, containing 8 uni- to irregularly biseriate ascospores; ring cylindrical according to Kobayashi (1970), not seen in the herbarium specimen. Ascospores (16.5–)17.5–20(–21.5) × (5.3–)6–7(–7.5) µm, l/w = (2.5–)12.7–3.1(–3.5) (n = 51), hyaline, broadly fusoid to fusoidymmetric to slightly asymmetric, straight or slightly curved, slightly constricted at the septum, with distinct tapering appendages having rounded to subacute tips, (1.6–)2–3.4(–4.6) µm long, (1.9–)2.2–2.5(–2.6) µm wide (n = 42); cells monomorphic to dimorphic with slightly larger upper cell, with narrowly rounded to subacute ends, multiguttulate; wall c 0.5 µm thick, not swelling.

Asexual morph. Conidiomata acervulare. 0.4–1.2 mm diam, dark brown to blackish, inconspicuous, scattered, with central or eccentric greenish yellow to grey stromatic column; at maturity covered by brown to blackish discharged conidial masses. Conidiophores (14–)17–28(–38) × (2.5–)3.5–4.7(–5.5) µm (n = 35), narrowly cylindrical to lageniform, simple or branched at the base, smooth, subhyaline to pale brown. Conidiogenous cells anellidic with distinct annellations, integrated. Conidia (10.8–)14.5–17.5(–20) × (5.2–)6.7–7.7(–8.7) µm, l/w = (1.5–)2.5–3.1(–3) (n = 100), unicellular, hyaline when immature, medium brown when mature, narrowly ellipsoid to elongate, rarely pip-shaped, often truncate with scar at the base, densely multiguttulate, thick-walled; wall c 0.6–0.8 µm, with faint ornamentation on the inside of the wall consisting of small irregular confluent verrucae 0.5–0.8(–1.5) µm diam, with c 0.5–0.9 µm wide gelatinous sheath.

Habitat & Host range — Dead corticated twigs and branches of Pterocarya spp. attached to the tree.

Distribution — Asia (Georgian Republic, Iran, Japan).

Notes — Melanconium pterocaryae was described from the Georgian Republic (Abkrzazia) from Pterocarya fraxinifolia, but no type collection could be traced and no collections from the original host were available for morphological investigations and for DNA sequencing. Kobayashi (1970) described Melanconium pterocaryae from Pterocarya rhoifolia collected in Japan as sexual morph of Melanconium pterocaryae. However, the conidial sizes of the Japanese collection were slightly
Fig. 9 Juglanconis pterocaryae (TFM FPH3373). a, b. Ectostromatic discs and ostioles in surface view; c. ectostromatic disc in side view showing slightly protruding ostioles; d. pseudostromata in vertical section; e, f. transverse sections below ectostromatic disc; g. pseudostrum in transverse section, showing perithecia and indistinct entostroma; h–j. mature asci; k. ascus apex (no apical ring visible); l–z. dead ascospores (l–r with tapering, rounded to subacute gelatinous appendages); a1. conidiomata in surface view; b1. vertical section of conidioma; c1. transverse section of conidioma, showing central column; d1, e1. conidiophores (annelides) with conidia; f1. annelations of conidiophore and young conidium; g1–p1. dead conidia (showing gelatinous sheath in g1–j1; in p1 showing verrucae on inner conidial wall); q1. detail of verruculose inner conidial wall. All in 3 % KOH, except l–r, g1–j1 in water. — Scale bars: a, b, d, g, a1 = 0.5 mm; c, e, f, b1, c1 = 200 µm; h–j = 20 µm; k–z, d1–p1 = 10 µm; q1 = 1 µm.
narrower than those given in the protologue of *Melanconium pterocaryae* (14–21 × 6–10 µm vs 14–19 × 8–12 µm), which was confirmed in the present study. Riedl & Ershad (1977) also reported narrower conidia (12–15.5 × 6.5–9.5 µm) from an Iranian collection on the original host, *Pterocarya fraxinifolia*, and we therefore consider these size differences to be within the range of intraspecific variability.

In the original description of *Melanconis pterocaryae*, Kobayashi (1970) mentioned absence of ascospore appendages. However, re-investigation of the type in water mounts revealed the presence of small tapering appendages with rounded to subacute tips, whereas in KOH the appendages were faint and disappearing quickly.

**Melanconium ershadii** Riedl, in Riedl & Ershad, Sydowia 29 (1–6): 163. 1977 (1976–77). — Fig. 10

*Holotype*. **IRAN**, S Gorgan, Nahār Khorān, on corticated twigs of *Pterocarya rhoifolia*, 21 Apr. 1974 (given as 24 Apr. 1974 in Riedl & Ershad 1977), H. Riedl & D. Ershad (W 1978-03131).

**Sexual morph** unknown. **Conidiomata** acervular, 0.3–0.8 mm diam, dark brown to blackish, flat, inconspicuous, scattered, with small central or eccentric whitish to light grey stromatic column; at maturity sometimes covered by brown to blackish discharged conidial masses. **Conidiophores** (20–)24–39(–46) × (2.5–)3–4(–5) µm (n = 22), narrowly cylindrical to lageniform, simple or branched at the base, smooth, hyaline. **Conidiogenous cells** annellidic with few indistinct annellations, integrated. **Conidia** (7.5–)9.5–11.5 (–13.3) × (4–)4.7–5.7(–6.8) µm, l/w = (1.2–)1.7–2.4 (–3) (n = 100), unicellular, hyaline when immature, pale to medium brown when mature, very variable in shape from subglobose, narrowly ellipsoid, allantoid, pip-shaped to

---

Fig. 10. *Melanconium ershadii* (W 1978-03131, holotype). a, b. Conidiomata in surface view; c. transverse section of conidioma, showing reduced central column; d–g. conidiophores (annelides) with conidia; h–y. dead conidia surrounded by gelatinous sheath. All in 3 % KOH. — Scale bars: a = 1 mm; b = 400 µm; c = 200 µm; d–y = 10 µm.
elongate, often truncate with scar at the base, with few faint guttules, thin-walled; wall smooth, c. 0.4 µm, without ornamentation on the inside of the wall, with c. 0.5 µm wide gelatinous sheath.

Habitat & Host range — Dead corticated twigs of *Pterocarya fraxinifolia*.

Distribution — Only known from Iran.

Notes — *Melanconium ershadii* and *M. pterocarya* share the same host, *Pterocarya fraxinifolia*, and the former was reported to differ from the latter in flatter conidiomata and shorter conidia (10.5–11.5 × 5.5–6.2 µm; Riedl & Ershad 1977). This was confirmed by re-investigation of the type. No sexual morph is known and no cultures and sequence data are available, which currently makes an appropriate phylogenetic placement impossible. Whereas the annelidic conidiation and the unicellular brown conidia are melanconium-like, we do not think that it belongs to *Juglanconis*. Important differences concern the consistently hyaline conidiophores with few indistinct annellations (vs at least partly light brown conidiophores with distinct annellations in *Juglanconis*), the entirely smooth inner conidial wall (vs at least finely verrucose in *Juglanconis*), and the highly variable, and commonly irregular, shape of the conidia. These characters indicate that *Melanconium ershadii* may rather belong to *Melanconis* s.str., which needs to be confirmed by sequence data.

**Key to species of Juglanconis**

NB: For observation of ascospore appendages the ascospores should be mounted in water, as in KOH the appendages usually disappear quickly.

1. Ascospores with hyaline terminal appendages; conidia light brown at maturity, inner surface of conidial wall with finely verrucose ornamentation .......................... 2
2. Ascospores without appendages; conidia dark brown at maturity, inner surface of conidial wall with distinct verrucose ornamentation .................................. 3
3. Ascospores appendages cylindrical with truncate ends; most conidia distinctly longer than 20 µm, variable in shape from pip-shaped, narrowly ellipsoid, elongate to subbaccate; on *Juglans* in Europe ........................................... *J. appendiculata*
4. Ascospores appendages tapering, with rounded to subacute ends; most conidia distinctly shorter than 20 µm, narrowly ellipsoid to elongate; on *Pterocarya* spp. in Asia .......................... *J. pterocarya*
5. Ascospores (20.5–)24.3–29(–36.5) µm long, distinctly inequilateral, commonly curved, cells dimorphic; conidia in average usually wider than 12 µm; on *Juglans* spp. in Europe and Asia .................................
6. *J. juglandina*
7. Ascospores (17.5–)19.8–24–28(–28) µm long, mostly symmetrical, only rarely curved, cells monomorphic to slightly dimorphic; conidia in average usually narrower than 12 µm; on *Juglans* spp. in North America and Eastern Asia (Japan) ................................ .......................... *J. oblonga*

**DISCUSSION**

**Molecular phylogeny, species delimitation and barcoding**

The molecular phylogenetic analyses reveal that *Juglanconis* is a genus distinct from *Melanconis*, which cannot be classified within any existing family (Fig. 1–3). Therefore, we consider it justified to describe the family Juglanconidaceae for it. In the LSU tree (Fig. 1) the genus receives low (52 %) MP and no ML bootstrap support, whereas in the ITS-LSU tree (Fig. 2) bootstrap support rises to 100 % (MP) or 70 % (ML), which shows that the LSU alone does not contain sufficient information for providing a sound resolution of all phylogenetic relationships within *Diaporthales*. This has been also shown for other groups of *Diaporthales* like *Stilbospora* (Voglmayr & Jaklitsch 2014), which appears as paraphyletic in the LSU tree but was resolved as a highly supported monophylum in trees obtained from other markers (ITS, *rpb2*, *tef1*). Similarly, also other families like *Gnomoniaceae* and *Melanconidaceae* receive only low to medium support in the LSU analyses (Fig. 1), but become highly supported in multilocus analyses (Sogonov et al. 2008). Unfortunately, for most representatives of *Diaporthales* no sequence data are available apart from ITS and LSU, therefore it has not been possible to perform a multilocus phylogenetic analyses which includes a representative taxon sampling. However, the genus becomes well supported upon addition of the ITS, and also the similar morphological and ecological traits provide good characters for generic and familial delimitation.

Wehmeyer (1941) questioned the status of *Juglanconis juglandinum* and *J. oblongum* as distinct species, but the molecular phylogenetic analyses of the multilocus matrix (Fig. 3) clearly reveal them as distinct species, which also differ morphologically by ascospore and conidial characters (see notes at the respective variable).

The comparison of the different markers used for multilocus analyses (Table 3) showed that the *tef1* fragment containing introns 4 and 5 is the best suited marker for species resolution within *Juglanconis*, which is in line with other investigations on *Diaporthales* (e.g. Voglmayr et al. 2012, Voglmayr & Jaklitsch 2014, Wang et al. 2014, Udayangana et al. 2014, 2015), and it should be adopted as barcoding marker for the group. On the other hand, the ITS which is the primary barcoding locus for fungi (Schoch et al. 2012) is amongst the poorest performing markers, which is clearly due to the comparatively low number (13) of informative characters. This is in line with what is observed in other ascomycete lineages like *Hypocreales* (e.g. Jaklitsch et al. 2013, Jaklitsch & Voglmayr 2015). In phylogenetic multilocus analyses within closely related species of *Diaporthales*, *tef1* should be combined with other informative markers like *ms204*, *cal* and *tub2*, whereas for higher-level relationships the *rp2* may be more suitable, as the sequenced fragment consists of a coding region, which facilitates a better alignment.

**Host range, distribution and other species**

The genus *Juglanconis* appears to be confined to hosts from *Juglandaceae* (Fagales). Three species (*J. appendiculata*, *J. juglandina* and *J. oblonga*) are so far known from the genus *Juglans* and one (*J. pterocarya*) from *Pterocarya*. In contrast to e.g. *Stegonosporium* (Voglmayr & Jaklitsch 2008, 2014), which is highly host specific and where European plantations of North American *Acer* hosts consistently also harbour the North American *S. acerinum*, the genus *Juglanconis* appears to be less host specific. In Europe, *J. appendiculata* and *J. juglandina* are occurring on the indigenous *Juglans regia* as well as on the introduced North American *J. nigra*, which has been planted and become widely naturalised in Central European alluvial forests. *Juglanconis oblonga* has been confirmed from *J. cinerea* and *J. nigra* in North America and from *J. ailanthifolia* in Japan, and it has been recorded from several additional *Juglans* species (see Farr & Rossman 2016), but these records need to be critically evaluated by morphological and DNA data.

Additional *Juglanconis* species may be hidden within the *Juglandaceae*, especially in America and Eastern Asia, the biodiversity centres of *Juglandaceae*, which are still largely understudied except for the few economically important *Juglans* species. It cannot be ruled out that *Melanconis juglandis* var. *caryae* also belongs to *Juglanconis*, but no specimens were available for study. It has been described from *Carya alba*, and differs from *J. oblonga* primarily in hyaline conidia sized...
10.5–14 × 5–7 µm; in addition, hyaline beta-conidia of size 2–2.5 × 0.8–1 µm were recorded (Wehmeyer 1940). Already Wehmeyer (1940) assumed that Melanconis juglandis var. caryae may represent a distinct species, and considering the results of recent molecular phylogenetic investigations of corticulous Diaporthales with similar ecology (e.g. Mejia et al. 2008, 2011a, b; Vizen, pers. comp.) and Voglmayr et al. 2012, Walker et al. 2014), which revealed a much higher species biodiversity than previously perceived, we are convinced that it represents a distinct species. However, DNA sequence data as well as detailed morphological investigations are necessary to evaluate its generic affiliation. Wehmeyer (1936) also transferred Melanconia pallida, a species growing on Carya spp., to Melanconis. This species differs from all Juglanconis species in dark brown ascospores. We have not been able to investigate this species morphologically, and in the absence of DNA sequence data its generic affiliation cannot be evaluated, but its morphological features indicate that it may not belong to Juglanconis.

The current investigations once again show that the traditional generic classification in Diaporthales needs to be critically re-evaluated by detailed morphological and molecular phylogenetic analyses. Even supposedly well-studied areas and hosts still harbour undescribed, morphologically distinct species. Our results also confirm that the ITS-LSU rDNA region, which has mostly been used for phylogenetic analyses in Diaporthales, commonly does not contain sufficient information for satisfactory phylogenetic resolution, and should be supplemented by additional suitable single-copy markers like tef1, cal, tub2, ms204 and rpb2.

Acknowledgements We thank Enrique Rubio for providing fresh material. Jack Fouriniere for providing his detailed documentation of a French collection of J. appendiculata. Robert Lücking from B for information on specimens of Melanconium juglandinum, and the fungarium curators of BPI, K, NY, NYS, PC, TFM, W, and Walter Till at WU for sending and managing collections. The financial support by the Austrian Science Fund (FWF; project P27645-PC, TFM, T, and Walter Till at WU for sending and managing collections. We thank Enrique Rubio for providing fresh material, and the fungarium curators of BPI, K, NY, NYS, PC, TFM, W, and Walter Till at WU for sending and managing collections.

REFERENCES

Acknowledgements

Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. 1999. Cultural characteristics and pathogenicity of Melanconium juglandinum. European Journal of Forest Pathology 29: 317–322.
Belisario A, Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999a. Conidiogenesis and morphology of Melanconium juglandinum. Mycological Research 99: 1059–1062.
Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999a. Conidiogenesis and morphology of Melanconium juglandinum. Mycological Research 99: 1059–1062.
Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999a. Conidiogenesis and morphology of Melanconium juglandinum. Mycological Research 99: 1059–1062.
Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Belisario A. Onofri S. 1999. A method for designing primer sets for speciation in Diaporthales. Mycologia 94: 1017–1031.
Barr ME. 1978. The Diaporthales in North America, with emphasis on Gnomonia and its segregates. Mycologia Memoir 7: 1–232.
Thiers B. 2016. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. http://sweetgum.nybg.org/ih/.

Tulasne ELR. 1856. Note sur l’appareil reproducteur multiple des Hypoxylées (DC) ou Pyrénomycètes (Fr.). Annales des Sciences Naturelles, Botanique, sér. 4, 5: 107–118.

Tulasne ELR, Tulasne C. 1863. Selecta Fungorum Carpologia: Xylariei-Valsei-Spaeriei. 2. Imperial Typograph, Paris.

Udayanga D, Castlebury LA, Rossman AY, et al. 2014. Insights into the genus Diaportha: phylogenetic species delimitation in the D. eres species complex. Fungal Diversity 67: 203–229.

Udayanga D, Castlebury LA, Rossman AY, et al. 2015. The Diaportha sojae species complex: Phylogenetic re-assessment of pathogens associated with soybean, cucurbits and other field crops. Fungal Biology 119: 383–407.

Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172: 4238–4246.

Voglmayr H, Akulov OY, Jaklitsch WM. 2016. Reassessment of Allantonectria, phylogenetic position of Thyronectroidea, and Thyronectria caraganae sp. nov. Mycological Progress 15: 921.

Voglmayr H, Jaklitsch WM. 2008. Prosthecium species with Stegonsporium anamorphs on Acer. Mycological Research 112: 885–905.

Voglmayr H, Jaklitsch WM. 2011. Molecular data reveal high host specificity in the phylogenetically isolated genus Massaria (Ascomycota, Massariaeae). Fungal Diversity 46: 133–170.

Voglmayr H, Jaklitsch WM. 2014. Stilbosporaceae resurrected: generic re-classification and speciation. Persoonia 33: 61–82.

Voglmayr H, Rossman AY, Castlebury LA, et al. 2012. Multigene phylogeny and taxonomy of the genus Melanconiella (Diaporthales). Fungal Diversity 57: 1–44.

Walker DM, Castlebury LA, Rossman AY, et al. 2012. New molecular markers for fungal phylogenetics: two genes for species-level systematics in the Sordariomycetes (Ascomycota). Molecular Phylogenetics and Evolution 64: 500–512.

Walker DM, Lawrence BR, Wooten JA, et al. 2014. Five new species of the highly diverse genus Plagiostoma (Gnomoniaceae, Diaporthales) from Japan. Mycological Progress 13: 1057–1067.

Wang X, Zang R, Yin Z, et al. 2014. Delimiting cryptic pathogen species causing apple Valsa canker with multilocus data. Ecology and Evolution 4: 1366–1380.

Wehmeyer LE. 1936. Cultural life histories of Melanconis and Pseudovalsa. II. Mycologia 28: 528–541.

Wehmeyer LE. 1940. Cultural histories of Melanconis and Pseudovalsa. IV. Mycologia 32: 321–330.

Wehmeyer LE. 1941. A revision of Melanconis, Pseudovalsa, Prosthecium and Titania. University of Michigan Studies, Scientific Series 14: 1–161.

Werle E, Schneider C, Renner M, et al. 1994. Convenient single-step, one tube purification of PCR products for direct sequencing. Nucleic Acids Research 22: 4354–4355.

White TJ, Bruns T, Lee S, et al. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, et al. (eds), PCR protocols: A guide to methods and applications: 315–322. Academic Press, San Diego.

Wiens JJ. 1998. Combining datasets with different phylogenetic histories. Systematic Biology 47: 568–581.