**Linoprosorisis, a new leaf-inhabiting scolesporous genus in Xylariaceae**

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**Abstract**

Based on molecular phylogenetic and morphological evidence, the new genus *Linoprosorisis* (Xylariales) is established for several species previously classified within *Linoprosorisis* (Diaporthales). Fresh collections of *Linoprosorisis ischnotheca* from dead overwintered leaves of *Fagus sylvatica* and of *L. ochracea* from dead overwintered leaves of *Malus domestica*, *Pyrus communis*, and *Sorbus intermedia*, respectively, were isolated in pure culture, and molecular phylogenetic analyses of a multi-locus matrix of partial nuITS-LSU rDNA, *RPB2* and *TUB2* sequences as well as morphological investigations revealed that both species are unrelated to the diaporthalean genus *Linoprosorisis*, but belong to Xylariaceae sensu stricto. The new combinations *Linoprosorisis ischnotheca* and *L. ochracea* are proposed, the species are described and illustrated, and their basionyms lecto- and epitypified. *Linoprosorisis faginea* is synonymized with *L. ischnotheca*. Based on similar morphology and ecology, *Linoprosorisis carpini* and *Linoprosorisis magnagutiana* from dead leaves of *Carpinus betulus* and *Sorbus torminalis*, respectively, are also combined in *Linoprosorisis*. The four accepted species of *Linoprosorisis* are illustrated, a key to species is provided and their ecology is discussed.

**Keywords** Ascomycota · Diaporthales · Leaf endophytes · *Linoprosorisis* · Molecular phylogeny · Systematics · Xylariaceae · 4 new combinations · 1 new name

**Introduction**

The genus *Linoprosorisis* was established by Fuckel (1870) for five species growing on dead leaves of Salicaceae. He did not designate a generic type, but Clements and Shear (1931) selected *Linoprosorisis capreae*, which grows on *Salix caprea*, as lectotype. The genus is characterized by long, filiform ascospores arranged in a single fascicle within the ascus, and by reduced black stromata embedded in dead leaf tissue containing usually one (in *L. ceuthocarpa* up to six) perithecia with laterally inserted ostioles. The black stromata appear in spring and are noticeable as black dots of ca. 0.5–1 mm diam on both sides of the dead, usually bleached leaves. The characteristics of ascomata and asci are clearly diaporthalean, and its classification within Gnomoniaceae (Monod 1983; Barr 1990) has also been corroborated by molecular phylogenetic analyses (Mejía et al. 2008). So far, the about eight accepted species of *Linoprosorisis* inhabit leaves of *Salix* or *Populus* spp. (Salicaceae), but morphological evidence suggests the presence of additional undescribed species on Salicaceae (Monod 1983).

Soon after its description, additional species with long filiform ascospores and black ascomata or stromata embedded in leaf tissues were added to *Linoprosorisis*. However, critical morphological re-investigations by Monod (1983) revealed that many of these are not diaporthalean and therefore unrelated to the generic type. Five of them, *L. carpini* from leaves of *Carpinus betulus*; *L. faginea*, and *L. ischnotheca* from leaves of *Fagus sylvatica*; *L. magnagutiana* from leaves of *Sorbus torminalis* and *L. ochracea* from leaves of various other rosaceous hosts from subtribe Pyrinae, were considered to be synonymous and to belong to the genus *Ophiodothella*...
(Phyllachoraceae), but Monod (1983) neither provided a detailed reasoning nor proposed a formal combination. Thus, in the lack of additional detailed studies, the nomenclature, systematic affiliation and taxonomic status of these five species remained unresolved.

Recent fresh collections of *L. ischnotheca* and *L. ochracea* provided the opportunity to study their morphology in detail and to isolate them in pure culture for sequencing. Molecular phylogenetic analyses of a multi-locus matrix of nuITS-LSU rDNA, *RPB2* and *TUB2* sequences and morphological studies including type material enabled us to resolve their systematic affiliation, to evaluate their species status and taxonomy, and to propose a revised classification, the results of which we report here.

### Materials and methods

#### Sample sources

All isolates included in this study originated from ascospores of freshly collected specimens. 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 culture collections are noted. Methods of microscopy included stereomicroscopy and microscopy equipped with a Zeiss Axiocam 506 color digital camera. Images and data were gathered using the NIS-Elements D v. 3.22.15 or Zeiss ZEN Blue Edition software packages. 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.

Isolates were prepared from ascospores as described in Jaklitsch (2009) and grown on 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 and 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 internal transcribed spacer region (ITS1–5.8S–ITS2) and a ca. 0.9-kb fragment of the large subunit nuclear ribosomal DNA (nuLSU rDNA), amplified and sequenced as a single fragment with primers V9G (de Hoog and Gerrits van den Ende 1998) and LR5 (Vilgalys and Hester 1990); a ca. 1.2-kb fragment of the RNA polymerase II subunit 2 (*RPB2*) gene with primers dRPB2-5f and dRPB2-7r (Voglmayr et al. 2016a); and a ca. 1.6-kb fragment of the beta-tubulin (*TUB2*) gene with primers T1D and T22D (Voglmayr et al. 2019). PCR products were purified using an enzymatic PCR cleanup (Werle et al. 1994) as described in Voglmayr and 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), LR2R-A (Voglmayr et al. 2012) and LR3 (Vilgalys & Hester 1990) were used as internal sequencing primers for the ITS-LSU rDNA region, and BtHV2r (Voglmayr et al. 2016b, 2017) and BtHVf (Voglmayr & Mehrabi 2018) for *TUB2*. Sequencing was performed on an automated DNA sequencer (ABI 3730xl Genetic Analyzer, Applied Biosystems).

### Data analysis

The newly generated sequences were aligned to the sequence alignments of Voglmayr et al. (2018), and GenBank sequences of four taxa of Diaporthales (*Gnomonia gnomon, Juglanconis juglandina, Limospora capreae*, and *Melanconis stilbostoma*) were added as the outgroup. Some taxa included in the matrix of Voglmayr et al. (2018) which contained poor or incomplete sequence data and which were not relevant for this study were removed from the matrices. The GenBank accession numbers of sequences used in these analyses are given in Table 1.

Sequence alignments for phylogenetic analyses were produced with the server version of MAFFT (http://mafft.cbrc.jp/alignment/server/), checked and refined using BioEdit v. 7.2.6 (Hall 1999). The ITS-LSU rDNA, *RPB2* and *TUB2* matrices were combined for subsequent phylogenetic analyses. After exclusion of ambiguously aligned regions and long gaps, the final combined data matrix contained 4718 characters (622 nucleotides of ITS, 1355 nucleotides of LSU, 1169 nucleotides of *RPB2* and 1572 nucleotides of *TUB2*). Familial
### Table 1  
Isolates and accession numbers used in the phylogenetic analyses. Isolates/sequences in bold were isolated/sequenced in the present study.

| Species                  | Specimen or strain number | Origin | Status | GenBank accession numbers | References                                                                 |
|--------------------------|----------------------------|--------|--------|--------------------------|-----------------------------------------------------------------------------|
| **Amphirosellinia fushanensis** | HAST 91111209               | Taiwan | HT     | GU339496 N/A QG48339 QG499590 | Hsieh et al. (2010)                                                         |
| **Amphirosellinia nigrospora** | HAST 91092308               | Taiwan | HT     | GU222457 N/A QG48340 QG499591 | Hsieh et al. (2010)                                                         |
| **Annulohypoxylon annulatum** | CBS 140775                  | Texas   | ET     | KY610418 KY610418 KY624263 KY276353 | Kuhnert et al. (2014), Wendt et al. (2018)                                  |
| **Annulohypoxylon aroroseum** | ATCC 76051                  | Thailand | A390397 KY610422 KY2423 KY640083 | Kuhnert et al. (2014), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY62434 KY272139 | Kuhnert et al. (2014), Wendt et al. (2018)                                  |
| **Annulohypoxylon moniforme** | CBS 123579                  | Martinique | KX376321 KY610425 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon nitens** | MFLUCC 12–0823             | Taiwan | HT     | KY610409 KY610429 KY272163 | Wendt et al. (2018)                                                         |
| **Annulohypoxylon atroroseum** | ATCC 76081                  | Thailand | KY610419 KY610419 KY24277 KY276352 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| **Annulohypoxylon michelianum** | CBS 119993                  | Spain   | KX37632 KX610423 KY24289 KY272161 | Kuhnert et al. (2017), Wendt et al. (2018)                                  |
| Species                        | Specimen or strain number<sup>a</sup> | Origin         | Status<sup>b</sup> | GenBank accession numbers<sup>c</sup> | References                  |
|-------------------------------|--------------------------------------|----------------|-------------------|--------------------------------------|-----------------------------|
| Diatrype disciformis          | CBS 197.49                           | Netherlands    | N/A               | DQ470964 DQ470915 N/A               | Zhang et al. (2006)         |
| Entoleuca mammuta             | J.D.R. 100                           | France         | N/A               | GU300072 N/A                        | Hisch et al. (2010)         |
| Entosordaria perfílosa        | CBS 142773                           | Austria        | ET                | MF488993 MF488993 MF489003 MF489021 | Voglmayr et al. (2018)     |
| Entosordaria quercina         | CBS 142774                           | Greece         | HT                | MF488994 MF488994 MF489004 MF489022 | Voglmayr et al. (2018)     |
| Euepixylon sphaeriostomum     | J.D.R. 261                           | USA            | N/A               | GU300072 N/A                        | Hsieh et al. (2010)         |
| Gnomonia gnomon               | CBS 199.53                           | Italy          | N/A               | AY818956 AF408361 EU219295 EU219148 | Castlebury et al. (2002),  |
|                              |                                      |                |                   |                                      | Sogonov et al. (2005, 2008) |
| Hypocreodendron sanguineum    | J.D.R. 169                           | Mexico         | N/A               | GU300072 N/A                        | Wendt et al. (2018)         |
| Hypomontagnella monticulosa   | MUCL 54604                           | French Guiana  | ET                | KY610404 KY610487 KY624305 KY271273 | Wendt et al. (2018)         |
| Hypomontagnella               | CBS 115280                           | France         | N/A               | KY610400 KY610457 KY624226 KY77267  | Kuhnert et al. (2014),     |
| Hypoxylon carpum              | MUCL 54177                           | France         | N/A               | KY610400 KY610480 KY624297 KY271270 | Wendt et al. (2018)         |
| Hypoxylon cerecicola          | CBS 119009                           | France         | N/A               | KC968908 KY610444 KY624254 KY77263  | Kuhnert et al. (2014),     |
| Hypoxylon crocopedum          | CBS 119904                           | France         | N/A               | KC968907 KY610445 KY624255 KY77268  | Kuhnert et al. (2014),     |
| Hypoxylon fendleri            | MUCL 54792                           | French Guiana  | N/A               | KY610481 KY624298 KY300547           | Kuhnert et al. (2014),     |
| Hypoxylon fragiforme          | MUCL 31264                           | Germany        | ET                | KM186295 KM186296 KM271282          | Kuhnert et al. (2014),     |
| Hypoxylon fusciach             | CBS 113049                           | France         | N/A               | KY610401 KY610482 KY624299 KY271271 | Wendt et al. (2018)         |
| Hypoxylon grisoebrumetum      | CBS 211.72                           | India          | HT                | KY610402 KY610483 KY624300 KY77260  | Kuhnert et al. (2014),     |
| Hypoxylon haematoxaster       | MUCL 53301                           | Martinique     | N/A               | KY610439 KY610456 KY624298 KY77267  | Kuhnert et al. (2014),     |
| Hypoxylon hoveanae            | MUCL 47599                           | Germany        | N/A               | KY610400 KY610480 KY624297 KY271270 | Wendt et al. (2018)         |
| Hypoxylon hypomutum            | MUCL 51845                           | Guadeloupe     | N/A               | KY610400 KY610480 KY624297 KY271270 | Wendt et al. (2018)         |
| Hypoxylon investiens           | CBS 118183                           | Malaysia       | HT                | KY610486 KY610486 KY271249           | Wendt et al. (2018)         |
| Hypoxylon lateripigmentum     | MUCL 53304                           | Martinique     | N/A               | KY610483 KY624298 KY77270           | Kuhnert et al. (2014),     |
| Hypoxylon lenormandii         | CBS 100                              | Ecuador        | N/A               | KY610483 KY610483 KY624298 KY77270  | Kuhnert et al. (2014),     |
| Hypoxylon muscum              | MUCL 53765                           | Guadeloupe     | N/A               | KY610483 KY610483 KY624298 KY77270  | Kuhnert et al. (2014),     |
| Hypoxylon ochraceum           | MUCL 54625                           | Martinique     | N/A               | KY610483 KY610483 KY624298 KY77270  | Kuhnert et al. (2014),     |
| Hypoxylon papillatum          | ATCC 58729                           | USA            | N/A               | KY610483 KY610483 KY624298 KY77270  | Kuhnert et al. (2014),     |
| Hypoxylon perforatum          | CBS 115281                           | France         | N/A               | KY610405 KY610491 KY624279 KY271274 | Wendt et al. (2018)         |
| Hypoxylon phaeotherme         | CBS 118183                           | Malaysia       | HT                | KY610412 KY610412 KY624308 KY624315 | Wendt et al. (2018)         |
| Hypoxylon petriaceae          | CBS 114746                           | France         | N/A               | KY610405 KY610491 KY624279 KY271274 | Wendt et al. (2018)         |
| Hypoxylon pilgeranium         | STMA 13455                           | Martinique     | N/A               | KY610405 KY610491 KY624279 KY271274 | Wendt et al. (2018)         |
| Hypoxylon porphyreum          | CBS 119002                           | France         | N/A               | KY610456 KY624225 KY77264           | Kuhnert et al. (2014),     |
| Hypoxylon pulicicidum         | CBS 119004                           | Martinique     | N/A               | KY610492 KY624280 KY183072          | Bills et al. (2012),       |
| Hypoxylon rickii              | MUCL 53309                           | Martinique     | N/A               | KY610416 KY624281 KY77288           | Wendt et al. (2018)         |
| Hypoxylon rubiginosum         | MUCL 52887                           | Germany        | ET                | KM186295 KM186296 KM271282          | Wendt et al. (2018)         |
| Hypoxylon samuelstii          | MUCL 51843                           | Guadeloupe     | HT                | KY610466 KY624269 KY77286           | Wendt et al. (2018)         |
| Hypoxylon ticinense           | CBS 115271                           | France         | N/A               | KY610471 KY624272 KY951757          | Hisch et al. (2005),       |
| Hypoxylon trigodea            | MUCL 54794                           | Sri Lanka      | ET                | KY610493 KY624282 KY300547           | Kuhnert et al. (2014),     |
| Hypoxylon Vogesiacum          | CBS 115272                           | France         | N/A               | KY610417 KY624283 KY271275          | Kuhnert et al. (2014),     |
| Jackrogersella cohaerens      | CBS 119126                           | Germany        | N/A               | KY610497 KY624270 KY624314          | Wendt et al. (2018)         |
| Species | Specimen or strain number<sup>a</sup> | Origin | Status<sup>b</sup> | GenBank accession numbers<sup>c</sup> | References |
|---------|----------------------------------|--------|-----------------|----------------------------------|------------|
| Jackrogersella minutella | CBS 119015 | Portugal | | KY610381 KY610424 KY624235 KX271240 | Kuhnert et al. (2017), Wendt et al. (2018) |
| Jackrogersella multiformis | CBS 119016 | Germany | ET | KC477234 KY610473 KY624290 KX271262 | Kuhnert et al. (2014), Kuhnert et al. (2017), Wendt et al. (2018) |
| Juglanconis juglandina | CBS 133343 | Austria | | KY427149 KY427149 KY427199 KY427234 | Voglmayr et al. (2017) |
| Kretzschmaria deusta | CBS 163.93 | Germany | | KY774570 KY774570 MF489025 | Stadler et al. (2013), Wendt et al. (2018) |
| Liriope capreae | CBS 372.69 | Netherlands | | EU199194 EU255199 EU199152 | Mejia et al. (2008) |
| Liriope ischnotheca | LIF1 = CBS 145761 | Switzerland | ET | MN818952 MN818952 MN820708 MN820715 | This study |
| Liriope ischnotheca | LIF2 | Switzerland | ET | MN818953 MN818953 MN820709 MN820716 | This study |
| Liriope ischnotheca | LIF3 | Switzerland | MN818954 MN818954 MN820710 MN820717 | This study |
| Liriope ochracea | LIO = CBS 145999 | Switzerland | ET | MN818955 MN818955 MN820711 MN820718 | This study |
| Liriope ochracea | LIO1 | Switzerland | ET | MN818956 MN818956 MN820712 MN820719 | This study |
| Liriope ochracea | LIO2 | Switzerland | ET | MN818957 MN818957 MN820713 MN820720 | This study |
| Liriope ochracea | LIO3 = CBS 145999 | Switzerland | ET | MN818958 MN818958 MN820714 MN820721 | This study |
| Lopadostoma dryophilum | CBS 133213 | Austria | ET | KY610414 KY610414 N/A | Wendt et al. (2018) |
| Lopadostoma turgidum | CBS 133207 | Austria | ET | KY610414 KY610414 N/A | Wendt et al. (2018) |
| Melanconis stilbostoma | TSTMA 0419 = J.F. 03075 | France | | KY610414 KY610414 | Wendt et al. (2018) |
| Nemania abortiva | HAST 467 | USA | HT | GU292816 N/A GQ844768 GQ702019 | Hisieh et al. (2010) |
| Nemania beaumontii | HAST 405 | Martinique | GU292816 N/A GQ844772 GQ702022 | Hisieh et al. (2010) |
| Nemania bipapillata | HAST 90080610 | Taiwan | GU292816 N/A GQ844771 GQ702021 | Hisieh et al. (2010) |
| Nemania maritima | HAST 89120401 | Taiwan | ET | N/A N/A GQ844775 GQ702025 | Hisieh et al. (2010) |
| Nemania maritima | HAST 89120401 | France | ET | KY610414 KY610414 | Wendt et al. (2018) |
| Nemania primolutea | HAST 1112001 | France | | EF026121 N/A GQ844767 EF025607 | Hisieh et al. (2010) |
| Obolokera dryophila | MUCL 49882 | France | WSP | GU324762 N/A GQ853039 GQ844840 | Hisieh et al. (2010) |
| Podosordaria mexicana | MUCL 13307 | Mexico | WSP | GU324762 N/A GQ853039 GQ844839 | Hisieh et al. (2010) |
| Poronia pileiformis | WSP 88113001 | Taiwan | ET | GU324760 N/A GQ853037 GQ502720 | Hisieh et al. (2010) |
| Poronia punctata | CBS 656.78 | Australia | HT | KY610496 KY610496 KY624278 KX271281 | Senanayake et al. (2015), Wendt et al. (2018) |
| Pyrenoporypora huntei | MUCL 52673 | Ivory Coast | KY610421 KY610421 | KU159530 KU159530 | Wendt et al. (2017), Wendt et al. (2018) |
| Pyrenoporypora laminosus | MUCL 53305 | Martinique | KY610485 KY610485 | K677292 K677292 | Wendt et al. (2014), Wendt et al. (2018) |
| Pyrenoporypora nicaraguensis | CBS 117739 | Burkina Faso | AM749922 KY610489 KY610489 | KX271277 KX271277 | Bitzer et al. (2008), Kuhnert et al. (2014), Wendt et al. (2018) |
| Rhopalostroma angolese | CBS 126414 | Ivory Coast | KY610420 KY610420 | KX271277 KX271277 | Wendt et al. (2018) |
| Rosellinia aquila | MUCL 51703 | France | | KY610392 KY610460 KY624285 KY624285 | Wendt et al. (2018) |
| Rosellinia buxi | MUCL 51693 | France | | KY610393 KY610393 | Wendt et al. (2018) |
| Rosellinia corticium | MUCL 51693 | France | | GU300070 N/A GQ844780 | Wendt et al. (2018) |
| Rosellinia necatrix | CBS 349.36 | Argentina | Ay909001 KF719204 KY624275 KY624275 | Pelaez et al. (2008), Wendt et al. (2018) |
| Rostrohypoxylon terebratum | CBS 19134 | Thailand | KT281903 KT281903 | KX271280 KX271280 | Wendt et al. (2018) |
| Sarcozystis pseudonannulata | MUCL 51394 | D. R. Congo | KY610406 KY610406 | KY624286 KY624286 | Wendt et al. (2018) |
| Stilbophytoporus elaeiocola | CBS 359.61 | South Africa | KY610406 KY610406 | KY624286 KY624286 | Senanayake et al. (2015), Wendt et al. (2018) |
| Stilbophytoporus quinquangularis | CBS 123557 | France | | KY624281 KY624281 | Wendt et al. (2018) |
| Thamnomyces dendroidea | CBS 590650506 | Thailand | | GU322432 N/A GQ844818 | Hisieh et al. (2010) |
| Xylaria acuminatilongissima | J.D.R. 99 | France | | KY610393 KY610393 | Wendt et al. (2018) |

<sup>a</sup> Species Specimen or strain number<sup>a</sup>
<sup>b</sup> Origin Status<sup>b</sup>
<sup>c</sup> GenBank accession numbers<sup>c</sup>
<sup>d</sup> References
classification of Xylariaceae and pylogenetically related families follows Voglmayr et al. (2018) and Wendt et al. (2018).

Maximum parsimony (MP) analyses were performed with PAUP v. 4.0a165 (Swofford 2002). 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. MP analysis of the combined multilocus matrix was done using 1000 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 1000 replicates were performed in the same way, but using 5 rounds of random sequence addition and subsequent branch swapping during each bootstrap replicate.

Maximum likelihood (ML) analyses were performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI 1.3 (Silvestro and Michalak 2012), using the ML + rapid bootstrap setting and the GTR+GAMMA substitution model with 1000 bootstrap replicates. The matrix was partitioned for the different gene regions. For evaluation and discussion of bootstrap support, values below 70% were considered low, between 70 and 90% medium/moderate and above 90% high.

Results

Molecular phylogeny

The combined multilocus matrix used for phylogenetic analyses comprised 4718 characters, of which 2129 were parsimony informative (360 from ITS, 273 from LSU, 658 from RPB2 and 838 from TUB2). Figure 1 shows a simplified phylogram of the best ML tree (lnL = \(-131,936.737\)) obtained by RAxML. Maximum parsimony analyses revealed four MP trees 31,692 steps long, which were identical except for slightly different positions of \(Daldinia andina\) and \(Stilbohypoxylon quisquiliarum\) (not shown). The backbone of the MP trees was similar to the ML tree, except for a few minor topological differences of unsupported nodes within the Barrmaeliaceae, Graphostromataceae, Hypoxylaceae and Xylariaceae (not shown). \(Linospora ischnotheca\) and \(L. ochracea\) were revealed as closely related but distinct species with maximum support (Fig. 1). They were placed remotely from \(Linospora capreae\) (Diaporthales) in a basal position within Xylariaceae sensu

Fig. 1 Simplified phylogram of the best ML trees (lnL = \(-131,936.737\)) revealed by RAxML from an analysis of the combined ITS-LSU-\(RPB2-TUB2\) matrix of selected Xylariales, showing the position of \(Linospora ischnotheca\) and \(L. ochracea\) were revealed as closely related but distinct species with maximum support (Fig. 1). They were placed remotely from \(Linospora capreae\) (Diaporthales) in a basal position within Xylariaceae sensu

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| Species               | Origin                  | Status     | GenBank accession numbers | References               |
|-----------------------|-------------------------|------------|---------------------------|--------------------------|
|                       |             | ITS        | LSU          | RPB2     | TUB2   |                       |
| \(Xylaria arbuscula\) | Germany     | HT         | KY631036     | KY623882 | KY634857 | Fournier et al. (2011), Wendt et al. (2018) |
| \(Xylaria bambusicola\) | Taiwan      | HT         | KY631037     | N/A       | GQ844802 | Hsieh et al. (2010)   |
| \(Xylaria brunneovinosa\) | Martinique | HT         | EU173921     | N/A       | GQ502706 | Hsieh et al. (2010)   |
| \(Xylaria curta\)     | Martinique   | ET         | KY624231     | N/A       | GQ487706 | Hsieh et al. (2010)   |
| \(Xylaria discolor\)  | USA          | HT         | KY631035     | N/A       | GQ487706 | Hsieh et al. (2010)   |
| \(Xylaria hypoxylon\) | Sweden       | ET         | KY616070     | N/A       | GQ487706 | Hsieh et al. (2010)   |
| \(Xylaria multiplex\) | Martinique   | HB         | KY631035     | N/A       | GQ487706 | Hsieh et al. (2010)   |
| \(Xylaria polymorpha\) | France       | HB         | KY616070     | N/A       | GQ487706 | Hsieh et al. (2010)   |
| \(Xylaria polyphyla\) | France       | HB         | KY616070     | N/A       | GQ487706 | Hsieh et al. (2010)   |

\(^a\) ATCC, American Type Culture Collection, Manassas, USA; \(^b\) BISH, Bishop Museum, Honolulu, USA; \(^c\) CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; \(^d\) GZU H, Guizhou University, Guiyang, China; \(^e\) HAST, Academia Sinica, Taipei, Taiwan; \(^f\) J.D.R., Jack D. Rogers, Washington State University, Pullman, USA; \(^g\) J.F., Jacques Fournier, Rimont, France; \(^h\) MFLUCC, Mae Fah Luang University, Chiang Rai, Thailand; \(^i\) MUCL, Universiteit Catholique de Louvain, Louvain-la-Neuve, Belgium; \(^j\) STMA, STMA, Antwerp, Belgium; \(^k\) UCR, University of California, Riverside, USA; \(^l\) Y.-M.J., Yu-Ming Ju, Academia Sinica, Taipei, Taiwan; \(^m\) WSP, Washington State University, Pullman, USA

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Fig. 1 Simplified phylogram of the best ML trees (lnL = \(-131,936.737\)) revealed by RAxML from an analysis of the combined ITS-LSU-\(RPB2-TUB2\) matrix of selected Xylariales, showing the position of \(Linospora ischnotheca\) and \(L. ochracea\) were revealed as closely related but distinct species with maximum support (Fig. 1). They were placed remotely from \(Linospora capreae\) (Diaporthales) in a basal position within Xylariaceae sensu
stricto. A sister-group relationship with the highly (100%, ML) to moderately (89%, MP) supported Clypeosphaeria mamillana-Anthostomelloides krabienensis clade (Fig. 1) received high (98%, ML) or low (53%, MP) bootstrap support. The sequences of Linospora ochracea accessions from Malus domestica, Pyrus communis, and Sorbus intermedia were almost identical, confirming conspecificity of the accessions from these hosts.

**Taxonomy**

**Linosporopsis** Voglmayr & Beenken, gen. nov.

*MycoBank*: MB 833894.

*Etymology*: referring to its similarity to *Linospora*.

*Type species*: *Linosporopsis ischnotheca* (Desm.) Voglmayr & Beenken.

Mycelium in dead overwintered leaves, strongly bleaching the host tissue. Pseudostromata immersed in dead leaves, reduced, forming a distinct black clypeus-like structure on both sides of the leaf above and below the single perithecium, composed of dark brown, septe hyphae in dead host epidermis cells and forming a textura epidermoidea-intricata. Ascomata perithelial, scattered, solitary, immersed in dead leaf tissue, globose to ellipsoid, with a distinct central apical papilla 70–140(–185) μm wide at the base. Peridium not observed. Paraphyses unbranched, septe, thin-walled, collabent, 107–120 μm long, 3–5 μm wide at the base and gradually tapering to 1–1.2 μm at the tips. Asci (118–)135–160(–165) × (3.5–)3.7–4.5(–5.0) μm (n = 30), unitunicate, long-cylindrical, with a short stipe, with eight ascospores arranged in a single fascicle, with an indistinct inamyloid apical apparatus. Ascospores (120–)136–158(–162) × 0.7–1.1 μm, l/w = (110–)145–201(–230) (n = 30), filiform, with rounded ends, hyaline, without visible septa, without sheath or appendages.

No cultures available. No asexual morph observed.

*Habitat and host range*: Dead overwintered leaves of *Carpinus betulus*.

*Distribution*: Europe; only known from southwestern Germany and northern Italy.

*Isotypes*: Germany, Baden-Württemberg, Rastatt, Apr. 1876, J. Schröter, in Rabenhorst, Fungi Eur. Exs. 2132 (M-0304424, M-0304425, W 2019–02783).

*Notes*: Although no DNA data are yet available, morphology of ascocarps, asci and ascospores leave no doubt that the species belongs to *Linosporopsis*, and considering the high host specificity of the genus, we recognize *L. carpini* as a distinct species. Apart from the type collection, this species is to our knowledge only known from an additional collection in northern Italy (Veneto, near Conegliano), which was collected in the same year as the type (Saccardo 1877). On the herbarium label of the type collection, it was stated to be common in the forests around Rastatt; however, we are not aware of any recent collections. The type collection has been edited and distributed in numerous copies in Rabenhorst, Fungi Eur. Exs. 2132, but we have investigated in detail only the copy deposited in W, that consists of a single leaf with a few perithecia. To save material, no sections were performed, and only a microscope preparation for documentation and measurements of asci, ascospores, paraphyses and clypeus hyphae was done. Our measurements revealed distinctly longer asci and ascospores than reported in the original description (118–165 μm vs. 70–80 μm in Rabenhorst 1876), which therefore is within the range of the other accepted *Linosporopsis* species.

**Linosporopsis carpini** (J. Schrö.) Voglmayr & Beenken, comb. nov. Fig. 2.

*MycoBank*: MB 833896.

*Basionym*: *Linospora carpini* J. Schrö., Hedwigia 15: 119. 1876.

Pseudostromata immersed in dead overwintered leaves, reduced, forming a distinct black clypeus (353–)384–463(–507) μm wide (n = 17) on both sides of the leaf, consisting of a textura epidermoidea-intricata composed of thick-walled, dark brown, septe hyphae 1.5–3 μm wide in dead host epidermis cells. Ascomata perithelial, scattered, solitary, immersed in dead leaf tissue, globose to ellipsoid, with a distinct central apical papilla 70–140(–185) μm wide at the base. Peridium not observed. Paraphyses unbranched, septe, thin-walled, collabent, 107–120 μm long, 3–5 μm wide at the base and gradually tapering to 1–1.2 μm at the tips. Asci (118–)135–160(–165) × (3.5–)3.7–4.5(–5.0) μm (n = 30), unitunicate, long-cylindrical, with a short stipe, with eight ascospores arranged in a single fascicle, with an indistinct inamyloid apical apparatus. Ascospores (120–)136–158(–162) × 0.7–1.1 μm, l/w = (110–)145–201(–230) (n = 30), filiform, with rounded ends, hyaline, without visible septa, without sheath or appendages.

No cultures available. No asexual morph observed.

*Habitat and host range*: Dead overwintered leaves of *Carpinus betulus*.

*Distribution*: Europe; only known from southwestern Germany and northern Italy.

*Isotypes*: Germany, Baden-Württemberg, Rastatt, Apr. 1876, J. Schröter, in Rabenhorst, Fungi Eur. Exs. 2132 (M-0304424, M-0304425, W 2019–02783).

*Notes*: Although no DNA data are yet available, morphology of ascocarps, asci and ascospores leave no doubt that the species belongs to *Linosporopsis*, and considering the high host specificity of the genus, we recognize *L. carpini* as a distinct species. Apart from the type collection, this species is to our knowledge only known from an additional collection in northern Italy (Veneto, near Conegliano), which was collected in the same year as the type (Saccardo 1877). On the herbarium label of the type collection, it was stated to be common in the forests around Rastatt; however, we are not aware of any recent collections. The type collection has been edited and distributed in numerous copies in Rabenhorst, Fungi Eur. Exs. 2132, but we have investigated in detail only the copy deposited in W, that consists of a single leaf with a few perithecia. To save material, no sections were performed, and only a microscope preparation for documentation and measurements of asci, ascospores, paraphyses and clypeus hyphae was done. Our measurements revealed distinctly longer asci and ascospores than reported in the original description (118–165 μm vs. 70–80 μm in Rabenhorst 1876), which therefore is within the range of the other accepted *Linosporopsis* species.
Pseudostromata immersed in dead overwintered leaves, forming a distinct black clypeus (107–145–247(--315) μm wide (n = 88) on both sides of the leaf, consisting of a textura epidermoidea-intricata composed of thick-walled, dark brown, septate hyphae 1.5–3 μm wide in dead host epidermis cells. Ascomata perithecial, scattered, solitary, immersed in dead leaf tissue, globose to ellipsoid, 230–340 μm diam., with a distinct central apical papilla 100–145(--160) μm wide at the base. Peridium (19–)22–32(--38) μm wide (n = 23), hyaline, pseudoparenchymatous, of hyaline isodiametric to elongate cells, marginal peridium cells (4.5–)7–13.5(--17) × (1.5–)2.5–4.5(--6.5) μm (n = 46), basal peridium cells smaller, (3–)4–9 (--10) × 1.5–2.3(--2.7) μm (n = 16). Paraphyses unbranched, septate, thin-walled, collabent, 74–110 μm long, 4.0–7.5 μm wide at the base and gradually tapering to 2–4.5 μm at the tips (n = 20). Ascii (94–)122–153(--175) × (2.8–)3.4–4.3(--5.2) μm (n = 98), unitunicate, long-cylindrical, with a short stipe, with eight ascospores arranged in a single fascicle, with an indistinct base.

**Fig. 2** *Linusporopsis carpini* (W 2019-02783, isotype). a Colonies (bleached patches) on dead overwintered leaf of *Carpinus betulus*. b Close up of a colony with black clypeus-like uniperitheciate pseudostromata. c–f Uniperitheciate pseudostromata from above (c, d) and in side view (e, f). g Host epidermis cells with dark brown, septate, branched hyphae forming a textura epidermoidea-intricata. h, i Ascus apices. j–l Asci. m Paraphyses. All in 3% KOH. Scale bars a 10 mm; b 400 μm; c 200 μm; d–f 100 μm; g, j–m 10 μm; h, l 5 μm.
Fig. 3  *Linosporopsis ischnotheca*.  

a Colonies (bleached patches) on dead overwintered leaves of *Fagus sylvatica* with scattered black, clypeus-like uniperitheciate pseudostromata.  

b-d Close up of colonies with black clypeus-like uniperitheciate pseudostromata.  

e-g Uniperitheciate pseudostromata from above (e), in side view (f), and in transverse section (g).  

h Host epidermis cells with dark brown, septate, branched hyphae forming a textura intricata.  

i Uniperitheciate pseudostroma in transverse section.  

j Pseudoparenchymatous, hyaline peridium and adjacent host tissue in section.  

k-o Asci (o immature).  

p-r Ascus apices.  

s Paraphysis.  

All in 3% KOH, except i, j, p, s in water; r in Lugol after KOH pre-treatment (a, e–g, m, n WU 40027; b PC0706583, isotype; c PC0706584, isotype; d PAD, holotype of *Linospora magnagutiana* subsp. *faginea*; h K(M) 206638, isotype; i, j, p, s WU 40026; o, q, r K(M) 206636, lectotype). Scale bars a, d 10 mm; b 1 mm; c, e 200 μm; f, g, i 100 μm; h, j–o, s 10 μm; p–r 5 μm.
inamylloid apical apparatus. Ascospores (84–)118–149(–170) × (0.6–)0.8–1.0(–1.3) μm, l/w = (35–)119–175(–205) (n = 55), filiform, with rounded ends, hyaline, without visible septa, without sheath or appendages.

Colonies on CMD and MEA white; aerial hyphae abundant.

Habitat and host range: Dead overwintered leaves of Fagus sylvatica and F. orientalis; rarely also on Quercus sp.

Distribution: Europe; known from France, Germany, Italy, Spain, and Switzerland.

Typification: France, without place, date and collector, on dead leaves of Fagus sylvatica, in Desmazières, Pl. Crypt. N. France, Ed. 1, no. 2098 (K(M) 206636, lectotype of Sphaeria ischnotheca here designated, MBT 390204; PC 0706583, isotype); same collection, in Desmazières, Pl. Crypt. N. France, Ed. 1, no. 1798 (K(M) 206635, PC 0706584, isolatypes). Italy, Veneto, Treviso, near Conegliano, spring 1877, C.L. Spegazzini (PAD, holotype of Linospora faginea). Switzerland, Zürich, Thuraue near Flaach, 13 May 2017, L. Beenken (WU 40024, epitype of Sphaeria ischnotheca here designated, MBT 390205; ex epitype culture CBS 145761 = LIF1).

Other specimens examined: France, Calvados (14), Caen, on dead leaves of Fagus sylvatica, without date, M.R. Roberge (M-0304427, ? syntype). Landes, Lussagnet, 43.763725° N, −0.223289° E, 140 m, 16 May 2017, A. Gross (ZT Myc 59965). Germany, Bavaria, Freising, Kranzberger Forst, Weltwald, on dead leaves of Fagus orientalis, 30 Apr. 2019, L. Beenken (WU 40033). Spain, Asturias, Gijón, on dead leaves of Fagus sylvatica, 16 Apr. 2015, Enrique Rubio Domínguez ERD 6431 (WU 40027). Ibid., on dead leaves of Fagus sylvatica and Quercus robur, 16 Apr. 2015, Enrique Rubio Domínguez (WU 40026; culture LIF3). Switzerland, Zürich, Ellikon am Rhein, 20 May 2017, L. Beenken (WU 40025, ZT Myc 59966; culture LIF2). Zürich, Winterthur, Eschenberg, 47°28′58″ N, 8°43′24″ E, 530 m, 16 May 2015, L. Beenken (ZT Myc 59967).

Notes: DNA sequence data and morphology place the species within Xylariaceae, as closest relative of L. ochracea. Desmazières (1851) first included specimens from leaves of Fagus sylvatica in his Sphaeria ochracea, but soon thereafter, he described them as a distinct species, S. ischnotheca (Desmazières 1852). In the protologue, he mentioned that the type collection contained only immature asci without spores, which was confirmed for all syntypes investigated in our study. The type collection was edited and distributed in two sets as Pl. Crypt. N. France, Ed. 1, nos. 1798 and 2098, which is also mentioned in the protologue. Neither locality nor collector are mentioned on the herbarium labels and in the original description of the species, and no original notes of Desmazières are attached to the two copies present in PC. However, the herbarium labels of a specimen in M, probably also a syntype, indicates that it was collected by M.R. Roberge in Caen, i.e. the same place and collector as the type of L. ochracea (see below), which appears plausible considering that material of Fagus was mentioned in the original description of L. ochracea. As the type collection of Sphaeria ischnotheca is immature, we here designate a recent mature collection, for which a culture and DNA sequences are available, as epitype to stabilize the species nomenclature.

Linospora faginea, which was also described from dead leaves of Fagus sylvatica, is obviously a synonym of L. ischnotheca; the protologue in Saccardo (1878) fully matches our material. As Saccardo material of PAD is not sent out on loan, we have not been able to investigate the type in detail, but the illustrations of the specimen and label kindly provided by the Erbario dell’Università di Padua show that it agrees with L. ischnotheca (see Fig. 3d).

The inamylloid apical apparatus of L. ischnotheca is usually indistinct, and only well-seen in IKI (Fig. 3r) or cotton blue. For beautiful additional illustrations of the Spanish specimen ERD 6431, see also http://www.ascofrance.com/search_forum/35346.

Linosporopsis magnagutiana (Sacc.) Voglmayr & Beenken, comb. nov. Fig. 4.

MycoBank: MB 833897.

Basionym. Linospora magnagutiana Sacc., Michelia 1(no. 1): 45. 1877.

Pseudostromata immersed in dead overwintered leaves, reduced, forming a distinct black clypeus (109–)126–203(–294) μm wide (n = 42) on both sides of the leaf, consisting of a texture epidermoidea-intricata composed of thick-walled, dark brown, septate hyphae 2–4 μm wide mostly in dead host epidermis cells. Ascomata perithecial, scattered, solitary, immersed in dead leaf tissue, globose to depressed globose, ca. 150–170 μm diam., with a distinct central apical papilla 30–65 μm wide at the base. Paraphyses unbranched, septate, thin-walled, collaret, (73–)81–100(–111) μm long, (3.5–)4–5.5(–6) μm wide at the base and gradually tapering to (1.2–)1.6–2.3(–2.6) μm wide at the tips (n = 23). Ascii (79–)94–121(–137) × (3.5–)4.2–5.3(–6.2) μm (n = 96), uniseriate, long-cylindrical, with a short stipe, with eight ascospores arranged in a single fascicle, with an indistinct inamyloid apical apparatus. Ascospores (73–)90–116(–132) × (0.7–)0.8–1(–1.3), l/w = (74–)94–137(–174) (n = 89), with rounded ends, hyaline, without visible septa, without sheath or appendages.

No cultures available. No asexual morph observed.

Habitat and host range: Dead overwintered leaves of Sorbus torminalis.

Distribution: Europe; only known from northern Italy.

Holotype: Italy, Veneto, Mantova, Bosco della Fontana, on dead leaves of Sorbus torminalis, Apr. 1873, A. Magnaguti-Rondini (PAD, not seen).

Specimens examined: Italy, Veneto, Conegliano, on dead leaves of Sorbus torminalis, summer 1878, C. Spegazzini, in
**Fig. 4** Linosporopsis magnagutiana.  

a Colonies on dead overwintered bleached leaf of *Sorbus torminalis*.  
b Close up of a colony with black clypeus-like uniperitheciate pseudostromata.  
c–f Uniperitheciate pseudostromata from above (c, d), in side view (e) and in transverse section (f).  
g Host epidermis cells with dark brown, septate, branched hyphae forming a textura epidermoidea-intricata.  
h–l Asci with paraphyses (h, j, l).  
m Paraphysis.  
n, o Ascus apices with slightly amyloid ring.  
All in 3% KOH, except k, n, o Lugol after KOH pre-treatment (a–m Thümen, Mycoth. Univ. 1454 (a M s.n., b–m WU s.n.); n, o Saccardo, Mycoth. Ven. 1352 (WU s.n.)).  
*Scale bars* a 10 mm; b 1 mm; c–f 100 μm; g–i 10 μm; j–m 5 μm; n, o 2 μm.
Saccardo, Mycoth. Ven. 1352 (WU s.n.). Same place, May 1878, C. Spezegazzini, in Baglietto, Cesati & Notarist, Erb. Critt. Ital. Ser. II 727 (M-0304429, Z Myc 8040). Same place, Apr. 1879, C. Spezegazzini, in Thümen, Mycoth. Univ. 1454 (M-0304428, WU s.n., ZT Myc 60357).

Notes: Due to the lack of fresh specimens, no cultures and sequence data are available for L. magnagutiana, but its morphology clearly places it in Linosporopsis. Only few historic records from northern Italy, all collected in the 1870ies, are known. We have not been able to investigate the type from PAD, which is not sent out on loan, but two additional authentic collections from the same area were available for study. As the historic material is very brittle, no useful section of the peridium could be prepared. The rosaceous host, Sorbus terminalis, and similar morphology indicates that L. magnagutiana may be conspecific with L. ochracea. However, in one locality (Bayerisches Landesarboretum “Weltwald”), where leaves of Pyrus domestica and Sorbus latifolia were heavily infected by L. ochracea, no Linosporopsis could be found on leaves of directly close-by Sorbus terminalis, indicating that they are distinct. In addition, the asci and ascospores of L. magnagutiana are slightly shorter than those of L. ochracea ((79–94)–121–(137) and (73)–90–116–(132) μm vs. (91)–108–130–(153) and (88)–103–126–(149) μm, respectively), and also its clypei are somewhat smaller ((109)–126–203–(294) vs. (97)–172–276–(355) μm). Therefore, for the time being, we argue for maintaining them as distinct species.

Linosporopsis ochracea (Sacc.) Voglmayr & Beenken, comb. nov. Fig. 5.

MycoBank: MB 833898.
Basionym. Linospora ochracea Sacc., Syll. fung. (Abellini) 2: 355. 1883.
Replaced synonym. Sphaeria ochracea Desm., Annls Sci. Nat., Bot., sér. 3 16: 317. 1851, nom. illegit. Art. 53.1, non Sphaeria ochracea Pers., Syn. meth. fung. (Göttingen) 1: 18. 1801.

Pseudostromata immersed in dead overwintered leaves, reduced, forming a distinct black clypeus (97–172–276–(355) μm wide (n = 143) on both sides of the leaf, consisting of a textura epidermoidea-intricata composed of thick-walled, dark brown, septate hyphae 1.5–3.7 μm wide mostly in dead host epidemic cells. Ascoma perithecial, scattered, solitary, immersed in dead leaf tissue, globose to depressed globose, 180–260 μm diam., with a distinct central apical papilla (45–60–89–(114) μm wide at the base (n = 88). Peridium (22)–26–37–(41) μm wide (n = 20), hyaline, pseudoparenchymatous, of hyaline isodiametric to elongate cells, marginal peridium cells (6.2–)8.5–14.8–(17.3) × (3.7–)4.8–7.7–(10) μm (n = 25), basal peridium cells smaller, (4)–5–9.5–(11.3) × (1.7–)2.5–4.2–(5) μm (n = 26). Paraphyses unbranched, septate, thin-walled, collabent, 75–160 μm long, 3–6(–9.7) μm wide at the base and gradually tapering to 1–2 μm at the tips (n = 34). Ascii (91)–108–130–(153) × (3–)4–5.5–(6.7) μm (n = 205), uniloculate, long-cylindrical, with a short stipe, with eight ascospores arranged in a single fascicle, with an indistinct inamyloid or slightly amyloid apical apparatus. Ascospores (88–)103–126–(149) × (0.8–)0.9–1.3–(1.6) μm, l/w = (62–)87–132–(174) (n = 139), filiform, with rounded ends, hyaline, without visible septa, without sheath or appendages.

Colonies on CMD and MEA white; aerial hyphae abundant. No asexual morph observed.

Habitat and host range: Dead overwintered leaves of various Rosaceae, subtribus Pyrinae; e.g., Crataegus spp., Cydonia oblonga, Malus domestica, Mespilus germanica, Pyrus spp. and Sorbus spp.

Distribution: Europe; known from Austria, France, Germany, Italy and Switzerland.

Typification: France, Calvados (14), Caen, Hérouville-Saint-Clair, Parc de Lébisey, on dead leaves of Crataegus monogyna and Sorbus latifolia, May 1850, M.R. Roberge, in Desmazières, Pl. Crypt. N. France, Ed. 1, no. 2099 (PC 0706581, lectotype of Linospora ochracea here designated, MBT 390206; K(M) 206803, K(M) 206804, K(M) 206805, K(M) 206,806, PC 0706579, isotypes). Germany, Bavaria, Freising, Kranzberger Forst, Bayerisches Landesarboretum “Weltwald”, on dead leaves of Sorbus intermedia, 30 Apr. 2019, L. Beenken (WU 40031, epitype of Linospora ochracea here designated, MBT 390207, isotype ZT Myc 59968; ex epitype culture CBS 145999 = LIO3).

Other specimens examined: Austria, Niederösterreich, Marchegg, at the railroad embankment near the river March, on dead leaf of Malus domestica, 1 May 2019, H. Voglmayr (WU 40032); Oberösterreich, Raab, Wetzlbach, on dead leaves of Pyrus communis, 23 Mar. 2019, H. Voglmayr (WU 40029; culture LIO1). France, Calvados (14), Caen, Hérouville-Saint-Clair, Parc de Lébisey, on dead leaves of Pyrus argentea, Apr. 1851, M.R. Roberge (K(M) 206645, PC 0706580); same collection data, in Desmazières, Pl. Crypt. N. France, Ed. 1, no. 2100 (K(M) 206641, K(M) 206642, K(M) 206644, PC 0706582); same collection data, in Desmazières, Pl. Crypt. N. France, Ed. 2, Ser. 1, no. 1800 (K(M) 206643); same place, collector and host, without date (M-0304431); same place and collector, on dead leaves of Sorbus sp., without date (M-0304430). Germany, Bavaria, Freising, Kranzberger Forst, Weltwald, on dead leaves of Pyrus communis, 30 Apr. 2019, L. Beenken (WU 40030, ZT Myc 59969; culture LIO2). Switzerland, Zürich, Henggart, on dead leaves of Malus domestica, 13 May 2017, L. Beenken (WU 40028, ZT Myc 59970; culture CBS 145760 = LIO).
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Notes: DNA sequence data and morphology place the species within Xylariaceae, as closest relative of *L. ischnotheca*. It was first described as *Sphaeria ochracea* by Desmazières (1851), but the name is illegitimate as it is a younger homonym of *Sphaeria ochracea* Pers. (1801). Therefore, *Linospora ochracea* Sacc., originally established as a new combination of *Sphaeria ochracea* Desm., is to be treated as a replacement name and represents the valid basionym.

In the protologue, Desmazières (1851) listed leaves of *Crataegus*, *Cydonia*, *Mespilus*, *Sorbus* and also *Fagus* as hosts; however, no collection or specimen data were given. For the specimens on *Fagus*, Desmazières (1852) subsequently described a distinct species, *Sphaeria ischnotheca* (see above). As concluded from the original material of Desmazières in PC and K, and from his notes attached to the specimen PC 0706581, the species was based on material collected by M.R. Roberge in Hérouville-Saint-Clair near Caen in May 1850, which Desmazières edited in his Pl. Crypt. N. France, Ed. 1, no. 2099. This exsiccatum contains material from *Crataegus monogyna* and *Sorbus latifolia*. From the same locality, Desmazières also distributed material from *Pyrus argentea* (as Pl. Crypt. N. France, Ed. 1, no. 2100 and Pl. Crypt. N. France, Ed. 2, Ser. 1, no. 1800), under the unpublished name *Sphaeria ochracea l. pyrina*, which, however, does not qualify for the type, as this host is not listed in the protologue; in addition, it was collected one year later (Apr. 1851) than the type, which may be a reason why this host was not cited in the protologue.

Unlike all other accessions of *L. ochracea* investigated by us, which had an indistinct, inamyloid apical apparatus, the Swiss collection WU 40028 from *Malus domestica* showed a tiny, wedge-shaped, slightly amyloid apical apparatus after KOH pre-treatment (see Fig. 5). However, the sequences obtained from this accession fully matched the other collections, indicating a variable iodine reaction that probably depends on the maturity and preservation of the specimen.

Key to the species of *Linosporopsis*

- 1. On leaves of Rosaceae ..................................................2
- 2. On leaves of Fagaceae (*Fagus, Quercus*) or Betulaceae (*Carpinus*) .................................................................3

Discussion

The results of our molecular phylogenetic investigations confirmed the conclusions of Monod (1983) that the species treated here are not congeneric with *Linospora* and do not belong to Diaporthales. However, while he assumed that they belong to *Ophiadothella*, currently classified within Phyllachoraceae (Phyllachorales), our phylogenetic analysis placed them in a basal clade of Xylariaceae sensu stricto (Xylariales). Based on the presence of an amyloid apical ascus ring, conidia resembling Diatrypaceae and a single nuSSU rNDa sequence, Hanlin et al. (2002) assumed xylarialean affinities of *Ophiadothella*; however, these conclusions were based on non-type species and need to be verified by re-investigation of the generic type. No type material of the generic type, *O. atromaculans* (Henn.) Höhn., is extant in B where the material of Hennings is kept (R. Lücking, personal communication). However, even if xylarialean, the following features do not support that *Ophiadothella* is congeneric with the species treated here: an obligate parasitic lifestyle in living leaves, a tropical to subtropical distribution almost exclusively in the New World, formation of pycnidial or acervular conidiomata, lack of distinct bleaching of the substrate and morphological differences of the ascomata (Hanlin et al. 1992, 2002, 2018). Particularly the generic type, *O. atromaculans*, deviates significantly from our species by an extended effuse, black stromatic crust (Hennings 1904; Hanlin et al. 1992). Additional genera with solitary clypeate ascomata and filiform ascospores that were previously attributed to Xylariales include *Linocarpon* and *Neolinocarpon*; however, these have been shown to belong to Chaetosphaeriales by sequence data (Konta et al. 2017). As no suitable described genus is available within Xylariaceae, we establish the new genus *Linosporopsis* for them.

Sister group relationship of *Linosporopsis* to the *Clryasphaeria mamillana-Anthostomelloides krabiensis* clade is highly supported in the ML analyses, but receives only low support in the MP analyses. *Linosporopsis* is similar to the latter species in solitary ascomata of similar size that are
embedded in a reduced pseudostroma within the host tissue and shares a distinct clypeus and apical papilla with *Clpeosphaeria mamillana*. However, marked differences to *Linosporopsis* include ellipsoid to oblong brown ascospores; a large, wedge-shaped, strongly amyloid apical ascus apex; and, in *A. krabiensis*, the lack of a clypeus and of an apical papilla (Jaklitsch et al. 2016; Tibpromma et al. 2017).

Ecologically, there is evidence that *Linosporopsis* occupies a niche as a leaf endophyte, and there is so far no indication of parasitism. Observations in Austrian and Swiss sites with abundant sporulation of *Linosporopsis ochracea* on dead overwintered *Pyrus* and *Malus* leaves revealed no obvious symptoms on living *Pyrus* and *Malus* leaves during the following summer. Evidently, the life cycle of *Linosporopsis* is connected with that of their hosts, as the short-lived ascospores are only produced briefly after their hosts unfold their new leaves in spring. These young leaves are then infected by the ascospores to complete the life cycle, with the living leaf tissue remaining asymptomatic during the growing season. After leaf abscission, the mycelium continues growth on the fallen leaves during the winter season, causing a distinctive bleaching of the decaying leaves, and finally ascomata and ascospores are produced again in the following spring.

The filiform, hyaline ascospores of *Linosporopsis* are very unusual for Xylariaceae, which mostly have more or less ellipsoid, brown ascospores, and therefore, the placement of *Linosporopsis* within Xylariaceae sensu stricto is somewhat surprising. However, ascospore morphology has proven not to be a good character for family segregation in the Xylariales, while the asexual morphs seem to agree better with the phylogeny (Ju and Rogers 1996, 2002; Wendt et al. 2018). So far, no asexual morph is known for *Linosporopsis*. The hyaline, filiform spores are likely an adaptation to colonization and infection of living leaves of trees. While little understood and investigated in detail, there is strong evidence that long, curved spores are effective adaptations to facilitate attachment on vertical or otherwise challenging exposed surfaces and are therefore advantageous for successful germination and establishment on aerial plant parts (Calhim et al. 2018). It is therefore not surprising that filiform ascospores have independently evolved in leaf-inhabiting species of various ascomycete lineages. This also provides an explanation for the morphological similarities to the unrelated diaporthalean genus *Linospora*, which has a similar ecology.

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