**Alternaria redefined**

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Abstract: Alternaria is a ubiquitous fungal genus that includes saprobic, endophytic and pathogenic species associated with a wide variety of substrates. In recent years, DNA-based studies revealed multiple non-monophyletic genera within the Alternaria complex, and Alternaria species clades that do not always correlate to species-groups based on morphological characteristics. The Alternaria complex currently comprises nine genera and eight Alternaria sections. The aim of this study was to delineate phylogenetic lineages within Alternaria and allied genera based on nucleotide sequence data of parts of the 18S rDNA, 28S rDNA, ITS, GAPDH, RPB2 and TEF1-alpha gene regions. Our data reveal a Pleospora/Stemphylium clade sister to Embellisia annulata, and a well-supported Alternaria clade. The Alternaria clade contains 24 internal clades and six monotypic lineages, the assemblage of which we recognise as Alternaria. This puts the genera Allewia, Brachycladum, Chalastospora, Chmelia, Crivellia, Embellisia, Lewia, Nimbya, Synomyces, Teretispora, Ulocladium, Undilium and Ybotromyces in synonymy with Alternaria. In this study, we treat the 24 internal clades in the Alternaria complex as sections, which is a continuation of a recent proposal for the taxonomic treatment of lineages in Alternaria. Embellisia annulata is synonymised with Dendryphiella salina, and together with Dendryphiella arenariae, are placed in the new genus Parandephylia. The sexual genera Clathrospora and Comoclathris, which were previously associated with Alternaria, cluster within the Pleosporaceae, outside Alternaria s. str., whereas Alternariaster, a genus formerly seen as part of Alternaria, clusters within the Leptosphaeriaceae. Parandephylia is newly described, the generic circumscription of Alternaria is emended, and 32 new combinations and 10 new names are proposed. A further 10 names are resurrected, while descriptions are provided for 16 new Alternaria sections.

Key words: Allewia, Chalastospora, Crivellia, Embellisia, Lewia, Nimbya, Parandephylia, Synomyces, systematics, Teretispora, Ulocladium, Undilium.

Taxonomic novelties: New combinations – Alternaria abundans (E.G. Simmons) Woudenb. & Crous, Alternaria alternateae (Cooke) Woudenb. & Crous, Alternaria atrata (Preuss) Woudenb. & Crous, Alternaria borrhmeuileri (Mergus) Woudenb. & Crous, Alternaria botyris (Preuss) Woudenb. & Crous, Alternaria caespitosa (de Hoog & C. Rubio) Woudenb. & Crous, Alternaria candlous (Yong Wang bis & X.G. Zhang) Woudenb. & Crous, Alternaria canticis (E.G. Simmons) Woudenb. & Crous, Alternaria cinerea (Bacoom & Creaner) Woudenb. & Crous, Alternaria didymopsora (Munt-Cvetk.) Woudenb. & Crous, Alternaria fulva (Bacoom & Creaner) Woudenb. & Crous, Alternaria hyacinthi (de Hoog & P.J. Mull. bis) Woudenb. & Crous, Alternaria indefessa (E.G. Simmons) Woudenb. & Crous, Alternaria leptinellae (E.G. Simmons & C.F. Hill) Woudenb. & Crous, Alternaria kili (E.G. Simmons & C.F. Hill) Woudenb. & Crous, Alternaria multiformis (E.G. Simmons) Woudenb. & Crous, Alternaria obovoides (Cooke & U. Braun) Woudenb. & Crous, Alternaria obovoides (E.G. Simmons) Woudenb. & Crous, Alternaria odena (E.G. Simmons) Woudenb. & Crous, Alternaria oxytripus (Q. Wang, Nagao & Kakish) Woudenb. & Crous, Alternaria penicillata (Preuss) Woudenb. & Crous, Alternaria planifunda (E.G. Simmons) Woudenb. & Crous, Alternaria proteae (E.G. Simmons) Woudenb. & Crous, Alternaria scripstandeas (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, Alternaria septospora (Preuss) Woudenb. & Crous, Alternaria slovacca (Svob.-Pol., L. Chmel & Bojan.) Woudenb. & Crous, Alternaria subcubticae (Yang Wang bis & X.G. Zhang) Woudenb. & Crous, Alternaria tellustis (E.G. Simmons) Woudenb. & Crous, Alternaria tuntida (E.G. Simmons) Woudenb. & Crous, Parandephylia salina (G.K. Sutherl.) Woudenb. & Crous, Parandephylia arenariae (Nicot) Woudenb. & Crous, **New names** – Alternaria aspera Woudenb. & Crous, Alternaria botyrospora Woudenb. & Crous, Alternaria brassicae-pekinensis Woudenb. & Crous, Alternaria breviramosa Woudenb. & Crous, Alternaria chlamydosporigena Woudenb. & Crous, Alternaria concatenata Woudenb. & Crous, Alternaria embelisia Woudenb. & Crous, Alternaria heterospora Woudenb. & Crous, Alternaria papavericola Woudenb. & Crous, Alternaria terricola Woudenb. & Crous, **Resurrected names** – Alternaria cetera E.G. Simmons, Alternaria chartarum Preuss, Alternaria consortialis (Thüm.) J.W. Groves & S. Hughes, Alternaria cubitiae Letendre & Roum., Alternaria demniai M.B. Ellis, Alternaria eurea E.G. Simmons, Alternaria gomphrenae Tagoshi, Alternaria malorum (Ruehle) U. Braun, Crous & Dugan, Alternaria phragmospora Emden, Alternaria scippica (Fuckel) Sivan, **New sections** – all in Alternaria – sect. Chastostospora Woudenb. & Crous, sect. Chelieanthus Woudenb. & Crous, sect. Crivellia Woudenb. & Crous, sect. Diaphanocola Woudenb. & Crous, sect. Embelisia Woudenb. & Crous, sect. Embeliosidae Woudenb. & Crous, sect. Eurekia Woudenb. & Crous, sect. Infectiose Woudenb. & Crous, sect. Japonicae Woudenb. & Crous, sect. Nimbya Woudenb. & Crous, sect. Phragmospora Woudenb. & Crous, sect. Pseudolocusa Woudenb. & Crous, sect. Terrกลับsidae Woudenb. & Crous, sect. Ulocladioidae Woudenb. & Crous, sect. Undilium Woudenb. & Crous, **New genus** – Parandephylia Woudenb. & Crous.

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**INTRODUCTION**

**Alternaria** is a ubiquitous fungal genus that includes saprobic, endophytic and pathogenic species. It is associated with a wide variety of substrates including seeds, plants, agricultural products, animals, soil and the atmosphere. Species of **Alternaria** are known as serious plant pathogens, causing major losses on a wide range of crops. Several taxa are also important postharvest pathogens, causative agents of phaeohyphomycosis in immuno-compromised patients or airborne allergens. Because of the significant negative health effects of **Alternaria** on humans and their surroundings, a correct and rapid identification of **Alternaria** species would be of great value to researchers, medical mycologists and the public alike.

**Alternaria** was originally described by Nees (1816), based on **A. tenuis** as the only species. Characteristics of the genus included the production of dark-coloured phaeodictyospores in chains, and a beak of tapering apical cells. Von Keissler (1912) synonymised both **A. tenuis** and **Torula alternata** (Fries 1832) with **Alternaria alternata**, due to ambiguities in Nees's description of **A. tenuis**. Two additional genera, **Stemphylium** (Wallroth 1833) and **Ulocladium** (Preuss 1851) were subsequently described for phaeodictyosporic

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hyphomycetes, further complicating the taxonomic resolution in this group of fungi. Several re-descriptions and revised criteria of these genera (Saccardo 1886, Elliot 1917, Wiltshire 1933, 1938, Joly 1964) resulted in a growing number of new species. Results of a lifetime study on Alternaria taxonomy based upon morphological characteristics were summarised in Simmons (2007), in which 275 Alternaria species were recognised. One species was transferred to the genus Prathoda and three new genera, Alternariaster, Chalastospora and Teretispora, were segregated from Alternaria.

Molecular studies revealed multiple non-monophyletic genera within the Alternaria complex and Alternaria species clades, which do not always correlate to species-groups based upon morphological characteristics (Pryor & Gilbertson 2000, Chou & Wu 2002, de Hoog & Horré 2002, Pryor & Bigelow 2003, Hong et al. 2005, Inderbitzin et al. 2006, Pryor et al. 2009, Runa et al. 2009, Wang et al. 2011, Lawrence et al. 2012). The A. alternata, A. brassicicola, A. infectoria, A. porri and A. radicina species-groups were strongly supported by these studies and two new species-groups, A. sonchi (Hong et al. 2005) and A. alterantergae (Lawrence et al. 2012) and three new genera, Crivellia (Inderbitzin et al. 2006), Undifillum (Pryor et al. 2009) and Sinomyces (Wang et al. 2011), were described. The latest molecular revision of Alternaria (Lawrence et al. 2013) introduced two new species groups, A. panax and A. gypsophilae, and elevated eight species-groups to sections within Alternaria. The sexual phylogenetic Alternaria lineage, the A. infectoria species-group, did not get the status of section, in contrast to the eight asexual phylogenetic lineages in Alternaria. The Alternaria complex currently comprises the genera Alternaria, Chalastospora (Simmons 2007), Crivellia, Embellisia, Nimbya, Stemphylium, Ulocladium, Undifillum and the recently described Sinomyces together with eight sections of Alternaria and the A. infectoria species-group.

The aim of the present study was to delineate the phylogenetic lineages within Alternaria and allied genera, and to create a robust taxonomy. Phylogenetic inferences were conducted on sequence data of parts of the 18S nrDNA (SSU), 28S nrDNA (LSU), the internal transcribed spacer regions 1 and 2 and intervening 5.8S nrDNA (ITS), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), RNA polymerase second largest subunit (RPB2) and translation elongation factor 1-alpha (TEF1) gene regions of ex-type and reference strains of Alternaria species and all available allied genera.

**MATERIAL AND METHODS**

**Isolates**

Based on the ITS sequences of all ex-type or representative strains from the Alternaria identification manual present at the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, The Netherlands (data not shown), 66 Alternaria strains were included in this study together with 61 ex-type or representative strains of 16 related genera (Table 1). Alternaria is represented by the ex-type or representative strains of the seven species-groups and species that clustered outside known Alternaria clades. Because of the size and complexity of the A. alternata, A. infectoria and A. porri species-groups, we only included known species; the complete species-groups will be treated in future studies.

Freeze-dried strains were revived in 2 mL malt/peptone (50 % / 50 %) and subsequently transferred to oatmeal agar (OA) (Crous et al. 2009a). Strains of the CBS collection stored in liquid nitrogen were transferred to OA directly from -80 °C. DNA extraction was performed using the UltraClean Microbial DNA Isolation Kit (MoBio laboratories, Carlsbad, CA, USA), according to the manufacturer’s instructions.

**Taxonomy**

Morphological descriptions were made for isolates grown on synthetic nutrient-poor agar plates (SNA, Nirenberg 1976) with a small piece of autoclaved filter paper placed onto the agar surface. Cultures were incubated at moderate temperatures (~ 22 °C) under CoolWhite fluorescent light with an 8 h photoperiod for 7 d. The sellotape technique was used for making slide preparations (Crous et al. 2009a) with Shear’s medium as mounting fluid. Photographs of characteristic structures were made with a Nikon Eclipse 80i microscope using differential interference contrast (DIC) illumination. Growth rates were measured after 5 and 7 d. Colony characters were noted after 7 d, colony colours were rated according to Rayner (1970). Nomenclatural data were deposited in MycoBank (Crous et al. 2004).

**PCR and sequencing**

The SSU region was amplified with the primers NS1 and NS4 (White et al. 1990), the LSU region with LSU1Fd (Crous et al. 2009b) and LR5 (Vilgalys & Hester 1990), the ITS region with V9G (De Hoog & Gerrits van den Ende 1998) and ITS4 (White et al. 1990), the GAPDH region with gpd1 and gpd2 (Berbee et al. 1999), the RPB2 region with RPB2–9RF (Sung et al. 2007) and RPB2–7CR (Liu et al. 1999) and the TEF1 gene with the primers EF1-728EF and EF1-986R (Carbone & Kohn 1999) or EF2 (O’Donnell et al. 1998). The PCRs were performed in a MyCycler™ Thermal Cycler (Bio-Rad Laboratories B.V., Veendael, The Netherlands) in a total volume of 12.5 µL. The SSU and LSU PCR mixtures consisted of 1 µL genomic DNA, 1 µL GoTaq® Flexi buffer (Promega, Madison, WI, USA), 2 µM MgCl₂, 40 µM of each dNTP, 0.2 µM of each primer and 0.25 Unit GoTaq® Flexi DNA polymerase (Promega). The ITS and GAPDH PCR mixtures differed from the original mix by containing 1 µM MgCl₂, the RPB2 and TEF1 PCR mixtures differed from the original mix by containing 2 µL genomic DNA and the RPB2 mixture differed from the original mix by containing 0.5 U instead of 0.25 U GoTaq® Flexi DNA polymerase. Conditions for PCR amplification consisted of an initial denaturation step of 5 min at 94 ºC followed by 25 cycles of 94 ºC for 1 min, 50 ºC for 1 min and 72 ºC for 1 min. The partial RPB2 gene was obtained by using a touchdown PCR protocol of 5 cycles of 45 s at 94 ºC, 45 s at 60 ºC and 5 min at 72 ºC followed by 20 cycles of 50 ºC for 50 s, 60 ºC for 30 s and 72 ºC for 30 s. The PCR products were sequenced in both directions using the PCR primers and the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA), according to the manufacturer’s recommendations, and analysed with an ABI Prism 3730XL Sequencer (Applied Biosystems) according to the manufacturer’s instructions. Consensus sequences were computed from forward and reverse sequences using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium). All generated sequences were deposited in GenBank (Table 1).
Fig. 1. Bayesian 50% majority rule consensus tree based on the GAPDH, RPB2 and TEF1 sequences of 121 strains representing the Alternaria complex. The Bayesian posterior probabilities (PP) and RAxML bootstrap support values (ML) are given at the nodes (PP/ML). Thickened lines indicate a PP of 1.0 and ML of 100. The tree was rooted to Stemphylium herbarum (CBS 191.86). The monotypic lineages are indicated by black dots.

Phylogenetic analyses

Multiple sequence alignments were generated with MAFFT v. 6.864b (http://mafft.cbrc.jp/alignment/server/index.html), and adjusted by eye. Two different datasets were used to estimate two phylogenies; an Alternaria complex phylogeny and a Pleosporineae family tree. The first tree focuses on the Alternaria complex, the second one was produced to place the genera Comoclathris, Clathrospora and Alternateaster in the context of the Alternaria complex. The relatives of the three genera were determined with standard nucleotide blast searches, with both the SSU and LSU sequences, against the nucleotide database in GenBank. This resulted in a selection of 35

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Table 1. Isolates used in this study and their GenBank accession numbers. Bold accession numbers were generated in other studies.

| Old species name | New species name | Alternaria Section | Strain number<sup>1</sup> | Status<sup>2</sup> | Host / Substrate | Country | Other collection number<sup>3</sup> | GenBank accession numbers |
|------------------|------------------|-------------------|-------------------|-----------------|----------------|---------|--------------------------|------------------------|
| Alternaria alternantherae | Alternaria alternantherae | Althernantherae | CBS 124392 | T | Solanum melongena | China | HSAUP2798 | KC584505; KC584251; KC584374; KS84179; KS84096; KS84633 |
| Alternaria alternata | Alternaria alternata | Alternata | CBS 916.96 | T | Arachis hypogaea | India | EGS 34.016 | K584507; DQ678082; KS84173; AF347031; KY277908 | KS84634 |
| Alternaria alpinogastri | Alternaria alpinogastri | Eureka | CBS 121920 | T | Arachis hypogaea | Australia | EGS 44.066 | KS84508; KS84252; KS84376; KS84180; KS84097 | KS84635 |
| Alternaria arborescens | Alternaria arborescens | Alternata | CBS 102605 | T | Lycopericon esculentum | USA | EGS 39.128 | KS84509; KS84253; KS84377 | AF347033; KY277908 | KS84636 |
| Alternaria argyranthemi | Alternaria argyranthemi | Chalastospora | CBS 116500 | T | Arachis hypogaea | New Zealand | EGS 44.033 | KS84510; KS84254; KS84378; KS84181; KS84098 | KS84637 |
| Alternaria armoricana | Alternaria armoricana | Chalastospora | CBS 118702 | T | Arachis hypogaea | New Zealand | EGS 31.060 | KS84511; KS84255; KS84379; KS84182; KS84099 | KS84638 |
| Alternaria avernicola | Alternaria avernicola | Parax | CBS 121499 | T | Avena sp. | Norway | EGS 50.185 | KS84512; KS84256; KS84380; KS84183; KS84100 | KS84639 |
| Alternaria axiaeriisporifera | Alternaria axiaeriisporifera | Gypsyphiella | CBS 118715 | T | Gypsyphiella paniculata | New Zealand | EGS 51.066 | KS84513; KS84257; KS84381; KS84184; KS84101 | KS84640 |
| Alternaria brassicae | Alternaria brassicae | Brassicae | CBS 116528 | R | Brassica oleracea | USA | EGS 38.032 | KS84514; KS84258; KS84382; KS84185; KS84102 | KS84641 |
| Alternaria brassicicola | Alternaria brassicicola | Brassicicola | CBS 118699 | R | Brassica oleracea | USA | EGS 42.002 | KS84515; KS84259; KS84383; JX499031 | KS84642 |
| Alternaria calycypyllica | Alternaria calycypyllica | Panax | CBS 121545 | T | Pyrus communis | China | EGS 52.071; RGR 96.0209 | KS84516; KS84260; KS84384; KS84186; KS84104 | KS84643 |
| Alternaria capsici-anuus | Alternaria capsici-anuus | Ulocladium | CBS 50.47 | T | Capsicum annuum | – | EGS 26.010 | KS84517; KS84261; KS84385; KS84187; KS84105 | KS84644 |
| Alternaria carolinicolae | Alternaria carolinicolae | Radicina | CBS 109381 | T | Daucus carota | USA | EGS 41.188 | KS84518; KS84262; KS84386; KS84188; KS84106 | KS84645 |
| Alternaria cheiranthi | Alternaria cheiranthi | Cheiranthus | CBS 109384 | R | Cheiranthus cheiri | Italy | EGS 41.188 | KS84519; KS84263; KS84387; AF229457 | KS84646 |
| Alternaria chlamydospora | Alternaria chlamydospora | Phragmosporae | CBS 491.72 | T | Soil | Egypt | EGS 31.060; ATCC 28045; IMI 156427 | KS84520; KS84264; KS84388; KS84189; KS84108 | KS84647 |
| Alternaria cinerariae | Alternaria cinerariae | Sonchi | CBS 116495 | R | Ligularia sp. | USA | EGS 49.102 | KS84521; KS84265; KS84389; KS84190; KS84109 | KS84648 |
| Alternaria conjuncta | Alternaria conjuncta | Infectoriae | CBS 196.86 | T | Pastinaca sativa | Switzerland | EGS 37.139 | KS84522; KS84266; KS84390; FJ266475; A526401 | KS84649 |
| Alternaria cumini | Alternaria cumini | Eureka | CBS 121329 | T | Cuminum cyminum | India | EGS 04.185a | KS84523; KS84267; KS84391; KS84191; KS84110 | KS84650 |
| Alternaria dauci | Alternaria dauci | Poni | CBS 117097 | R | Daucus carota | USA | EGS 46.006 | KS84524; KS84268; KS84392; KS84192; KS84111 | KS84651 |
| Alternaria daucifolii | Alternaria daucifolii | Daucus | CBS 118812 | T | Daucus carota | USA | EGS 37.050 | KS84525; KS84269; KS84393; KS84193; KS84112 | KS84652 |
| Alternaria dianthicola | Alternaria dianthicola | Dianthicola | CBS 116491 | R | Dianthus × allwoodii | New Zealand | EGS 51.022 | KS84526; KS84270; KS84394; KS84194; KS84113 | KS84653 |
| Alternaria elegans | Alternaria elegans | Dianthicola | CBS 109169 | T | Lycopericon esculentum | Burkina Faso | EGS 43.072; IMI 37642 | KS84527; KS84271; KS84395; KS84195; KS84114 | KS84654 |
| Alternaria ellipsoides | Alternaria ellipsoides | Gypsyphiella | CBS 119674 | T | Dianthus barbatus | USA | EGS 49.104 | KS84528; KS84272; KS84396; KS84196; KS84115 | KS84655 |
| Alternaria eryngii | Alternaria eryngii | Parax | CBS 121339 | R | Eryngium sp. | – | EGS 41.005 | KS84529; KS84273; KS84397; J069360; A526416 | KS84656 |
| Alternaria ethzedia | Alternaria ethzedia | Infectoriae | CBS 197.86 | T | Brassica napus | Switzerland | EGS 37.143 | KS84530; KS84274; KS84398; AF392897; AT278795 | KS84657 |
| Alternaria gaisen | Alternaria gaisen | Alternata | CBS 632.93 | R | Pyrus pyrifolia cv. Nijessiki | Japan | EGS 69.0512 | KS84531; KS84275; KS84399; KS84197; KS84116 | KS84658 |
| Table 1. (Continued). | Old species name | New species name | Section | Strain number | Status | Host / Substrate | Country | Other collection number | GenBank accession numbers |
|------------------------|------------------|------------------|---------|---------------|--------|------------------|---------|------------------------|--------------------------|
| Alternaria genistomatii | Alternaria geniostomatis | Alternaria geniostomatis | Eureka | CBS 118701 R | Netherlands | Genisteum | Germany | EGS 51.001 | KC584427 KC584430 KC584417 KC584418 KC584419 KC584420 |
| Alternaria helianthiinficiens | Alternaria helianthiinficiens | Alternaria helianthiinficiens | CBS 117370 R | 1 | USA | Helianthus annuus | USA | EGS 50.150 | KC584484 KC584485 KC584486 KC584487 KC584488 |
| Alternaria infectoria | Alternaria infectoria | Alternaria infectoria | CBS 210.86 T | 1 | UK | Triticum aestivum | UK | EGS 27.193 | KC584457 KC584458 KC584459 KC584460 KC584461 |
| Alternaria japonica | Alternaria japonica | Alternaria japonica | CBS 118390 R | 1 | USA | Brassica chinensis | USA | EGS 50.099 | KC584489 KC584490 KC584491 KC584492 KC584493 |
| Alternaria juxtiseptata | Alternaria juxtiseptata | Alternaria juxtiseptata | CBS 119673 T | 1 | Australia | Gypsophila paniculata | Australia | EGS 44.015 | KC584494 KC584495 KC584496 KC584497 KC584498 |
| Alternaria limaciformis | Alternaria limaciformis | Alternaria limaciformis | CBS 481.81 T | 1 | UK | Soil | UK | EGS 07.086 | KC584516 KC584517 KC584518 KC584519 KC584520 |
| Alternaria limoniasperae | Alternaria limoniasperae | Alternaria limoniasperae | CBS 102595 T | 1 | USA | Citrus jambhiri | USA | EGS 45.100 | KC584531 KC584532 KC584533 KC584534 KC584535 |
| Alternaria longipes | Alternaria longipes | Alternaria longipes | CBS 540.94 R | 1 | USA | Nicotiana tabacum | USA | EGS 30.033 | KC584546 KC584547 KC584548 KC584549 KC584550 |
| Alternaria macrospora | Alternaria macrospora | Alternaria macrospora | CBS 117228 T | 1 | USA | Gossypium barbadense | USA | EGS 07.127 | KC584555 KC584556 KC584557 KC584558 KC584559 |
| Alternaria molesta | Alternaria molesta | Alternaria molesta | CBS 548.81 T | 1 | Denmark | Phragmosporae | Denmark | EGS 32.075 | KC584564 KC584565 KC584566 KC584567 KC584568 |
| Alternaria nepalensis | Alternaria nepalensis | Alternaria nepalensis | CBS 118700 T | 1 | Nepal | Brassica sp. | Nepal | EGS 01.056 | KC584573 KC584574 KC584575 KC584576 KC584577 |
| Alternaria nobilis | Alternaria nobilis | Alternaria nobilis | CBS 116490 R | 1 | New Zealand | Dianthus caryophyllus | New Zealand | EGS 51.027 | KC584582 KC584583 KC584584 KC584585 KC584586 |
| Alternaria oregonensis | Alternaria oregonensis | Alternaria oregonensis | CBS 542.94 T | 1 | USA | Triticum aestivum | USA | EGS 29.194 | KC584591 KC584592 KC584593 KC584594 KC584595 |
| Alternaria parvella | Alternaria parvella | Alternaria parvella | CBS 482.81 T | 1 | USA | Allium cepa | USA | EGS 21.194 | KC584600 KC584601 KC584602 KC584603 KC584604 |
| Alternaria perpunctulata | Alternaria perpunctulata | Alternaria perpunctulata | CBS 115267 T | 1 | USA | Alternanthera philoxeroides | USA | EGS 13.125 | KC584615 KC584616 KC584617 KC584618 KC584619 |
| Alternaria petroselini | Alternaria petroselini | Alternaria petroselini | CBS 112.41 T | 1 | USA | Petroselinum sativum | USA | EGS 06.196 | KC584624 KC584625 KC584626 KC584627 KC584628 |
| Alternaria photistica | Alternaria photistica | Alternaria photistica | CBS 212.86 T | 1 | UK | Digitalis purpurea | UK | EGS 35.172 | KC584633 KC584634 KC584635 KC584636 KC584637 |
| Alternaria porri | Alternaria porri | Alternaria porri | CBS 116698 R | 1 | USA | Allium cepa | USA | EGS 48.147 | KC584644 KC584645 KC584646 KC584647 KC584648 |
| Alternaria pumila | Alternaria pumila | Alternaria pumila | CBS 16580 T | 1 | USA | Digitalis purpurea | USA | EGS 32.135 | KC584651 KC584652 KC584653 KC584654 KC584655 |
| Alternaria pseudocostata | Alternaria pseudocostata | Alternaria pseudocostata | CBS 112.41 T | 1 | USA | Digitalis purpurea | USA | EGS 13.125 | KC584662 KC584663 KC584664 KC584665 KC584666 |
| Alternaria pseudophlebia | Alternaria pseudophlebia | Alternaria pseudophlebia | CBS 116888 R | 1 | USA | Allium cepa | USA | EGS 44.147 | KC584671 KC584672 KC584673 KC584674 KC584675 |
| Alternaria portei | Alternaria portei | Alternaria portei | CBS 11650 R | 1 | USA | Allium cepa | USA | EGS 34.172 | KC584681 KC584682 KC584683 KC584684 KC584685 |
| Alternaria pseudopallida | Alternaria pseudopallida | Alternaria pseudopallida | CBS 11650 R | 1 | USA | Allium cepa | USA | EGS 34.172 | KC584686 KC584687 KC584688 KC584689 KC584690 |
| Alternaria pseudopallida | Alternaria pseudopallida | Alternaria pseudopallida | CBS 11650 R | 1 | USA | Allium cepa | USA | EGS 34.172 | KC584686 KC584687 KC584688 KC584689 KC584690 |
Table 1. (Continued).

| Old species name | New species name | Alternaria Section | Strain number1 | Status2 | Host / Substrate | Country | Other collection number3 | GenBank accession numbers |
|------------------|------------------|--------------------|----------------|---------|-----------------|---------|--------------------------|--------------------------|
| Alternaria pseu| porstrostrata     | Porri              | CBS 119411      | T       | Euphorbia pulcherrima | USA     | EGS 42.000               | K5S4554 K5S45298 K5S4422 JN338403 AY62406 K5S4580 |
| Alternaria radic| ina               | Radicina           | CBS 245.67      | T       | Daus carota      | USA     | EGS 0:145; ATCC 6503; IMI 124939; QM 1301; QM 6503 | K5S4555 K5S45299 K5S4423 K5S4213 K5S48133 K5S4881 |
| Alternaria sapo| nariae             | Gypsophilae        | CBS 116492      | R       | Saponaria officinalis | USA     | EGS 49.199               | K5S4557 K5S45301 K5S4425 K5S4215 K5S48135 K5S4883 |
| Alternaria sali| ni                 | Radicina           | CBS 109382      | T       | Petriellum crispum | Saudi Arabia | EGS 25.198; IMI 137332  | K5S4558 K5S45302 K5S4426 AF229455 AY278800 K5S4884 |
| Alternaria sepo| tioroideos         | Brassicola         | CBS 106.41      | T       | Reseda odorata    | Netherlands | EGS 52.099; MUCL 20298 | K5S4559 K5S45303 K5S4427 K5S4216 K5S48136 K5S4885 |
| Alternaria sim| simi               | Dianthicola        | CBS 115265      | T       | Sesamum indicum   | Argentina  | EGS 13.110               | K5S4560 K5S45304 K5S4428 JF780337 K5S48137 K5S4886 |
| Alternaria sim| nii                | Radicina           | CBS 109380      | R       | Smyrnium olusatrum | UK       | EGS 37.093               | K5S4561 K5S45305 K5S4429 AF229456 K5S48138 K5S4887 |
| Alternaria sol| ani                 | Saponaria          | CBS 116561      | R       | Solanum tuberosum | USA     | EGS 45.020               | K5S4562 K5S45306 K5S4430 K5S4217 K5S48139 K5S4888 |
| Alternaria soli| liaridae            | Alternaria         | CBS 118387      | T       | Soil             | USA     | EGS 33.024               | K5S4563 K5S45307 K5S4431 K5S4218 K5S48140 K5S4889 |
| Alternaria soli| dicanna             | Brassicola         | CBS 118968      | T       | Soil             | Bangladesh | EGS 36.158; IMI 04798 & | K5S4564 K5S45308 K5S4432 K5S4214 K5S48141 K5S4890 |
| Alternaria son| chi                 | Sonchi             | CBS 119675      | R       | Sonchus asper     | Canada   | EGS 43.131; IMI 366167   | K5S4565 K5S45309 K5S4433 K5S4220 K5S48142 K5S4891 |
| Alternaria tag| etica               | Sonchi             | CBS 479.81      | R       | Tagesect erecta  | UK       | EGS 33.081               | K5S4566 K5S45310 K5S4434 K5S4221 K5S48143 K5S4892 |
| Alternaria tenu| issima              | Alternata          | CBS 918.96      | R       | Dianthus sp.      | UK       | EGS 34.015               | K5S4567 K5S45311 K5S4435 AF347032 AY278809 K5S4893 |
| Alternaria thal| ictigena            | Thalictrum         | CBS 121712      | T       | Thalictrum sp.    | Germany  | EGS 41.070               | K5S4568 K5S45312 K5S4436 EU040211 K5S48444 K5S4894 |
| Alternaria tro| gichnica            | Eureka             | CBS 119676      | T       | Triglochin procera | Australia | EGS 51.070               | K5S4569 K5S45313 K5S4437 K5S4222 K5S48145 K5S4895 |
| Alternaria vac| ccariae             | Gypsophilae        | CBS 116533      | R       | Vaccaria hispanica | USA     | EGS 47.108               | K5S4570 K5S45314 K5S4438 K5S4223 K5S48146 K5S4896 |
| Alternaria vac| caricola            | Gypsophilae        | CBS 118714      | T       | Vaccaria hispanica | USA     | EGS 46.003; ATCC 26038   | K5S4571 K5S45315 K5S4439 K5S4224 K5S48147 K5S4897 |
| Alternaria str| aster helianthi     | Helianthus         | CBS 119672      | R       | Helianthus sp.    | USA     | EGS 36.007               | K5S4562 K5S45326 K5S4438 K5S48439 K5S4898 |
| Alternaria str| aster helianthi     | Helianthus         | CBS 327.69      | R       | Helianthus annus  | –        | –                        | K5S4627 K5S45396 K5S444 K5S48449 K5S4899 |
| Ascochyta pisi  | Apis                | Pismum sativum     | CBS 126.54      | R       | Pismum sativum    | Netherlands | PD 74/2447              | EU754038 DQ678070 DQ677967 EU754038 EU754183 GJ371780 |
| Boeremia exigua | Asperula            | Solarium tuberosum | CBS 431.74      | T       | Solarium tuberosum | Netherlands | PD 74/2447              | EU754038 DQ678070 DQ677967 EU754038 EU754183 GJ371780 |
| Brachycladium   | papavericola        | Crivellia          | CBS 116606      | T       | Papaver somniferum | USA     | EGS 36.007               | K5S4579 K5S45321 K5S4446 FJ357310 FJ357298 K5S4705 |
| Brachycladium   | penicillatum        | Crivellia          | CBS 116608      | T       | Papaver rhoas     | Austria  | DAOM 230457              | K5S4572 K5S45316 K5S4440 FJ357311 FJ357299 K5S4898 |
| Old species name | New species name | Alternaria Section | Country | Other collection number | GenBank accession numbers | LSU | ETS | ITS | GAPDH | TEF1 | Strain number | Status2 | Host / Substrate |
|-----------------|------------------|--------------------|---------|-------------------------|--------------------------|-----|-----|-----|-------|------|---------------|---------|----------------|
Table 1. (Continued).

| Old species name | New species name | Alternaria Section | Strain number | Status | Host / Substrate | Country | Other collection number | GenBank accession numbers |
|------------------|------------------|--------------------|---------------|--------|------------------|---------|------------------------|--------------------------|
| Embellisia chlamydospora | Alternaria chlamydosporigena | Embellisia | CBS 341.71 | R | Air | USA | EGS 10.073; ATCC 22409; IMI 159709; MUQ. 16573; QM 7287 | KJ584584 KJ584326 KJ584451 KJ584231 KJ584156 KJ584710 |
| Embellisia concidea | Alternaria concidea | Brassicicola | CBS 132.89 | | | Saudi Arabia | KA584585 KJ584327 KJ584452 KJ584232 KJ584157 KJ584711 |
| Embellisia dennisii | Alternaria dennisii | Senecio jacobaea | CBS 476.90 | T | Seawater | Adriatic Sea | FJ357312 FJ357310 | KJ584585 KJ584326 KJ584451 KJ584231 KJ584156 KJ584710 |
| Embellisia didymospora | Alternaria didymosporae | Phragmosporae | CBS 768.79 | | | | | |
| Embellisia eureka | Alternaria eureka | Eureka | CBS 193.86 | T | Medicago rugosa | Australia | KJ584586 KJ584327 KJ584452 | AY278844 AY278843 |
| Embellisia hyacinthi | Alternaria hyacinthi | Embellisioides | CBS 416.71 | T | Hyacinthus orientalis | The Netherlands | KJ584590 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia indefessa | Alternaria indefessa | Cheiranthus | CBS 536.83 | T | Soil | USA | KJ584591 KJ584326 KJ584452 KJ584232 KJ584157 KJ584712 |
| Embellisia leptinellae | Alternaria leptinellae | Eureka | CBS 477.90 | T | Leptinella dioica | New Zealand | KJ584592 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia lolii | Alternaria lolii | Senecio jacobaea | CBS 110533 | T | Leptinella dioica | New Zealand | KJ584593 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia novae-zelandiae | Alternaria novae-zelandiae | Cheiranthus | CBS 478.90 | T | Leptinella dioica | New Zealand | KJ584594 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia phragmospora | Alternaria phragmospora | Phragmosporae | CBS 274.70 | T | Soil | The Netherlands | KJ584595 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia planifunda | Alternaria planifunda | Triticum aestivum | CBS 537.83 | T | Triticum aestivum | Australia | KJ584596 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia proteae | Alternaria proteae | Protea sp. | CBS 475.90 | T | Protea sp. | Australia | KJ584597 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia tellustris | Alternaria tellustris | Embellisia | CBS 538.83 | T | Soil | USA | KJ584598 KJ584326 KJ584452 | AY278844 AY278843 |
| Embellisia tumida | Alternaria tumida | Embellisioides | CBS 539.83 | T | Trinicum aestivum | Australia | KJ584599 KJ584326 KJ584452 | AY278844 AY278843 |
| Heterospora chenopodii | Heterospora chenopodii | Chenopodium album | CBS 115.96 | | | Netherlands | KJ584600 KJ584326 KJ584452 | AY278844 AY278843 |
| Julella avicenniae | Julella avicenniae | Mangrove wood | BCC 184.22 | | | Thailand | KJ584601 KJ584326 KJ584452 | AY278844 AY278843 |
| Leptosphaerulina australis | Leptosphaerulina australis | Eugenia aromatica | CBS 317.83 | | | Indonesia | KJ584602 KJ584326 KJ584452 | AY278844 AY278843 |
| Loratospora aestuarii | Loratospora aestuarii | Juncus roemerianus | JK 5535B | | | USA | KJ584603 KJ584326 KJ584452 | AY278844 AY278843 |
| Nimbya caridis | Nimbya caridis | Caricae hoodii | CBS 481.90 | R | Scirpus sp. | UK | EGS 19.042 | KJ584604 KJ584326 KJ584452 |
| Nimbya gomphrenae | Nimbya gomphrenae | Gomphrena globosa | CBS 108.27 | | | | | |
| Nimbya scirpiola | Nimbya scirpiola | Scirpus sp. | CBS 481.90 | R | | | | |
| Old species name            | New species name            | Alternaria Section | Strain number | Status | Host / Substrate                  | Country | Other collection number | GenBank accession numbers |
|-----------------------------|-----------------------------|--------------------|---------------|--------|-----------------------------------|---------|-------------------------|---------------------------|
| Alternaria herpotricha      | Ophiosphaerella herpotricha | CBS 620.86         | Bromus erectus | Switzerland | ETH 9373                          | DQ678010 DQ678062 DQ677958 |
| Alternaria dryads           | Paraleptosphaeria dryads    | CBS 643.86         | Dryas octopetala | Switzerland | ETH 9446                          | KC584632 GU301828 GU371733 |
| Alternaria glomerata        | Peyronellaea glomerata      | CBS 528.66         | Chrysanthemum sp. | Netherlands | PD 63/590                         | EU754085 EU754184 GU371781 |
| Alternaria zeae-maydis      | Peyronellaea zeae-maydis    | CBS 588.69         | Zea mays | USA | GU294185 GU304859 GU371724 |
| Phaeosphaeria ammophilae    | Phaeosphaeria ammophilae    | CBS 114.956        | Ammophila arenaria | Sweden | UPS3 3668                         | AY534725 AY544684 DQ677941 |
| Phaeosphaeria avenaria      | Phaeosphaeria avenaria      | DAOM 226215        | Avena sativa | Canada | OSC 100096                         | DQ678011 DQ678063 DQ677959 |
| Phaeosphaeria eustoma       | Phaeosphaeria eustoma       | CBS 572.36         | Dactylis glomerata | Switzerland | ETH 9239                          | DQ678014 DQ678966 DQ677962 |
| Phoma complanata            | Phoma complanata            | CBS 286.92         | Angelica sylvestra | Netherlands | PD 75/3                          | EU754081 EU754180 GU371778 |
| Phoma herbarum              | Phoma herbarum              | CBS 276.37         | Wood pulp | Sweden | DQ678014 DQ678966 DQ677962 |
| Pleodoromus lingam          | Pleodoromus lingam          | DAOM 229267        | Brassica sp. | France | DQ470946 DQ470946 DQ470894 |
| Pleospora betae             | Pleospora betae             | CBS 1094.10        | Beta vulgaris | Netherlands | PD 77/113                          | EU754079 EU754178 GU371774 |
| Pleospora calvescens        | Pleospora calvescens        | CBS 246.79         | Atriplex hastata | Germany | PD 77/665                        | EU754038 EU754131 KC584500 |
| Pleospora chenopodi         | Pleospora chenopodi         | CBS 206.80         | Chenopodium quinoa | Bolivia | PD 74/1022                        | JF740095 JF740266 KC584501 |
| Pleospora fallens           | Pleospora fallens           | CBS 161.78         | Olea europaea | New Zealand | IMI 282137                        | JF740096 JF740267 KC584503 |
| Pleospora halimiones        | Pleospora halimiones        | CBS 432.77         | Halimione portulacoides | Netherlands | IMI 282137                        | GU238215 GU238574 KC584502 |
| Pleospora incompta          | Pleospora incompta          | CBS 467.76         | Olea europaea | Greece | GU238215 GU238574 KC584504 |
| Pleospora tarda             | Pleospora tarda             | CBS 714.68         | Medicago sativa | Canada | EGS 04.119C; IMI 135496; MUC1 11717; QM 1379 | KC584603 KC584345 AF107804 KC584238 AF443881 KC584729 |
| Pleospora typhicola         | Pleospora typhicola         | CBS 132.69         | Typha angustifolia | Netherlands | JF740105 JF740325 KC584505 |
| Pyenochaeata nobilis        | Pyenochaeata nobilis        | CBS 407.76         | Laurus nobilis | Italy | EU754014 DQ678096 DQ677991 |
| Pyenophora phaeocomes       | Pyenophora phaeocomes       | DAOM 222769        | Calamagrostis vilosa | Switzerland | DQ499595 DQ499596 DQ497614 |
| Saccothecium sepincola      | Saccothecium sepincola      | CBS 278.32         | Ribes nigrum | USA | GU236195 GU238187 GU371745 |
| Setomelanomma holmii        | Setomelanomma holmii        | CBS 110217         | Picea pungens | USA | GU236196 GQ37633 GU371800 |
Table 1. (Continued).

| Old species name | New species name | Alternaria Section | Strain number | Status | Host / Substrate | Country | Other collection number | GenBank accession numbers |
|------------------|------------------|--------------------|--------------|--------|------------------|---------|-------------------------|--------------------------|
| Synnyces alternariae | Alternaria alternariae | Ulocladium | CBS 126989 | T | Daucus carota | USA | EGS 46.04 | KC584604 KC584346 KC584470 KC584770 |
| Stemphylium herbarum | Stemphylium herbarum | CBS 191.86 | T | Medicago sativa | India | EGS 36.138; IMI 27979 | GU238232 GU238160 KC584471 KC584771 |
| Teretispora leucanthemi | Alternaria leucanthemi | CBS 421.65 | T | Chrysanthemum maximum | Netherlands | ATCC 16028; IFO 9085; IMI 111986; QM 7227 | KC584609 KC584347 KC584472 KC584240 KC584166 KC584732 |
| Teretispora leucanthemi | Alternaria leucanthemi | CBS 422.65 | R | Chrysanthemum maximum | USA | EGS 17.063; ATCC 16029; IMI 111987; QM 8579 | KC584660 KC584348 KC584473 KC584241 KC584167 KC584733 |
| Ulocladium arborescens | Alternaria aspera | Pseudoulocladium | CBS 115269 | T | Pistacia vera | Japan | IMI 369777 | KC584607 KC584349 KC584474 KC584242 KC584168 KC584734 |
| Ulocladium atenum | Alternaria atra | Ulocladium | CBS 195.67 | T | Soil | USA | ATCC 18040; IMI 124944; QM 8408 | KC584608 KC584350 KC584475 KC584243 KC584169 KC584735 |
| Ulocladium botrytis | Alternaria botrytis | Ulocladium | CBS 197.67 | T | Contaminant | USA | ATCC 18042; IMI 124942; MUCL 18556; QM 7878 | KC584609 KC584351 KC584476 KC584244 KC584170 KC584736 |
| Ulocladium botrytis | Alternaria sp. | Ulocladium | CBS 198.67 | R | Soil | USA | ATCC 18043; IMI 124943; MUCL 18557; QM 8619 | KC584610 KC584352 KC584477 KC584245 KC584171 KC584737 |
| Ulocladium brassicae | Alternaria brassicae-pekinensis | Ulocladium | CBS 121493 | T | Brassica pekinensis | China | HSAUPw0303 | KC584611 KC584353 KC584478 KC584244 KC584170 KC584738 |
| Ulocladium cantlouis | Alternaria cantlouis | Ulocladium | CBS 123007 | T | Cucumis melo | China | HSAUP0209 | KC584612 KC584354 KC584479 KC584245 KC584171 KC584739 |
| Ulocladium capsici | Alternaria concatenata | Pseudoulocladium | CBS 120006 | T | – | – | – | KC584613 KC584355 KC584480 KC584246 AY762950 KC584740 |
| Ulocladium chartarum | Alternaria chartarum | Pseudoucladium | CBS 200.67 | T | Populus sp. | Canada | ATCC 18044; DAOM 596116; IMI 124943; MUCL 18594; QM 8328 | KC584614 KC584356 KC584481 KC584172 KC584741 |
| Ulocladium consortiale | Alternaria consortialis | Ulocladium | CBS 104.31 | T | – | – | – | KC584615 KC584357 KC584482 KC584247 KC584173 KC584742 |
| Ulocladium cucurbitae | Alternaria cucurbitae | Ulocladium | CBS 483.81 | R | Cucumis sativus | New Zealand | EGS 31.021; LEV 7067 | KC584616 KC584358 KC584483 FJ266483 AY562418 KC584743 |
| Ulocladium multifiorum | Alternaria multiflorum | Ulocladium | CBS 102090 | T | Soil | Canada | – | KC584617 KC584359 KC584484 FJ266486 KC584174 KC584744 |
| Ulocladium obvoidea | Alternaria obvoidea | Ulocladium | CBS 101229 | T | Cucumis sativus | New Zealand | – | KC584618 KC584360 KC584485 FJ266487 FJ266498 KC584745 |
| Ulocladium oudemansii | Alternaria oudemansii | Ulocladium | CBS 114.07 | T | – | – | ATCC 18047; IMI 124940; MUCL 18563; QM 1744 | KC584619 KC584361 KC584486 FJ266488 KC584175 KC584746 |
| Ulocladium sepsosporum | Alternaria sepsospora | Pseudoulocladium | CBS 109.38 | T | Wood | Italy | – | KC584620 KC584362 KC584487 FJ266489 FJ266500 KC584747 |
### Table 1: Continued.

| Strain number | Host / Substrate | Country | Other collection number | GenBank accession numbers | Status2 | Host / Substrate | SSU | LSU | ITS | GAPDH | TEF1 |
|---------------|------------------|---------|-------------------------|--------------------------|---------|------------------|-----|-----|-----|-------|-----|
| 1             | Soil             | USA     | ATCC 18048; IMI 124947; MUCL 18560; QM 8614 | KC584621 | China | HSAUP 0521 | KC584622 | KC584364 | KC584488 | KC584248 | KC584176 |
| 2             | Lycopersicon esculentum | Austria | DAOM 231361 | KC584624 | China | HSAUP 0521 | KC584366 | KC584491 | KC584250 | KC584178 |
| 3             | Ulocladioides CBS 123376 T | Soil | China | KC584752 | Spain | DAOM 231361 | KC584365 | KC584489 | KC584249 | KC584177 | KC584750 |
| 4             | Alternaria terricola Ulocladioides CBS 121491 T | Soil | USA | ATCC 18048; IMI 124947; MUCL 18560; QM 8614 | KC584621 | China | HSAUP 0521 | KC584622 | KC584364 | KC584488 | KC584248 | KC584176 |
| 5             | Alternaria bornmuelleri Undifilum bornmuelleri DAOM 231361 T | Soil | Austria | DAOM 231361 | KC584624 | China | HSAUP 0521 | KC584366 | KC584491 | KC584250 | KC584178 |
| 6             | Alternaria subcucurbitae | Soil | China | KC584752 | Spain | DAOM 231361 | KC584365 | KC584489 | KC584249 | KC584177 | KC584750 |
| 7             | Ulocladioides CBS 121491 T | Soil | USA | ATCC 18048; IMI 124947; MUCL 18560; QM 8614 | KC584621 | China | HSAUP 0521 | KC584622 | KC584364 | KC584488 | KC584248 | KC584176 |
| 8             | Alternaria bornmuelleri Undifilum bornmuelleri DAOM 231361 T | Soil | Austria | DAOM 231361 | KC584624 | China | HSAUP 0521 | KC584366 | KC584491 | KC584250 | KC584178 |
| 9             | Alternaria subcucurbitae | Soil | China | KC584752 | Spain | DAOM 231361 | KC584365 | KC584489 | KC584249 | KC584177 | KC584750 |
| 10            | Ulocladioides CBS 121491 T | Soil | USA | ATCC 18048; IMI 124947; MUCL 18560; QM 8614 | KC584621 | China | HSAUP 0521 | KC584622 | KC584364 | KC584488 | KC584248 | KC584176 |
| 11            | Alternaria bornmuelleri Undifilum bornmuelleri DAOM 231361 T | Soil | Austria | DAOM 231361 | KC584624 | China | HSAUP 0521 | KC584366 | KC584491 | KC584250 | KC584178 |
| 12            | Alternaria subcucurbitae | Soil | China | KC584752 | Spain | DAOM 231361 | KC584365 | KC584489 | KC584249 | KC584177 | KC584750 |
| 13            | Ulocladioides CBS 121491 T | Soil | USA | ATCC 18048; IMI 124947; MUCL 18560; QM 8614 | KC584621 | China | HSAUP 0521 | KC584622 | KC584364 | KC584488 | KC584248 | KC584176 |
| 14            | Alternaria bornmuelleri Undifilum bornmuelleri DAOM 231361 T | Soil | Austria | DAOM 231361 | KC584624 | China | HSAUP 0521 | KC584366 | KC584491 | KC584250 | KC584178 |
| 15            | Alternaria subcucurbitae | Soil | China | KC584752 | Spain | DAOM 231361 | KC584365 | KC584489 | KC584249 | KC584177 | KC584750 |

2 T: ex-type strain; R: representative strain.

Table 1: Strain number (Continued).

For defining the taxonomy of *Alternaria* and allied genera, 121 strains were included in the *Alternaria* complex alignment. The alignment length and unique site patterns of the different genes and gene combinations are stated in Table 2. The original ITS alignment consisted of 577 characters of which the first 78 are excluded as this contained a non-alignable region. In the original TEF1 alignment (375 characters) we coded the major inserts (Table 3), which otherwise would negatively influence the phylogeny, resulting in a TEF1 alignment of 269 characters. All phylogenies, different phylogenetic methods and gene regions or gene combinations used on this dataset (data not shown, trees and alignments lodged in TreeBASE), show a weak support at the deeper nodes of the tree. The only well-supported node (Bayesian posterior probability value of 1.0, RAxML Maximum Likelihood support value of 100) in all phylogenies separates *Embellisia annulata* CBS 302.84 and *Pleosporales* (Fig. 1). In the *Alternaria* clade, six monotypic lineages and 24 internal clades occur consistently in the individual and combined phylogenies, although positions vary between the different gene regions or combinations used. The support values for the clades within *Alternaria* (called sections) are plotted in a heat map (Table 2) per gene and phylogenetic method used. The support values for the different phylogenetic methods vary, with the Bayesian posterior probabilities being higher than the RAxML bootstrap support values (Table 2). The SSU, LSU and ITS phylogenies display a

### RESULTS

**Phylogeny**

For defining the taxonomy of *Alternaria* and allied genera, 121 strains were included in the *Alternaria* complex alignment. The alignment length and unique site patterns of the different genes and gene combinations are stated in Table 2. The original ITS alignment consisted of 577 characters of which the first 78 are excluded as this contained a non-alignable region. In the original TEF1 alignment (375 characters) we coded the major inserts (Table 3), which otherwise would negatively influence the phylogeny, resulting in a TEF1 alignment of 269 characters. All phylogenies, different phylogenetic methods and gene regions or gene combinations used on this dataset (data not shown, trees and alignments lodged in TreeBASE), show a weak support at the deeper nodes of the tree. The only well-supported node (Bayesian posterior probability value of 1.0, RAxML Maximum Likelihood support value of 100) in all phylogenies separates *Embellisia annulata* CBS 302.84 and *Pleosporales* (Fig. 1). In the *Alternaria* clade, six monotypic lineages and 24 internal clades occur consistently in the individual and combined phylogenies, although positions vary between the different gene regions or combinations used. The support values for the clades within *Alternaria* (called sections) are plotted in a heat map (Table 2) per gene and phylogenetic method used. The support values for the different phylogenetic methods vary, with the Bayesian posterior probabilities being higher than the RAxML bootstrap support values (Table 2). The SSU, LSU and ITS phylogenies display a
Table 2. Summary of locus and phylogenetic results as well as a heat map of the Bayesian posterior probabilities and RAxML bootstrap support values per Alternaria section.

| Region 1 | Region 2 | Region 3 | Region 6 |
|----------|----------|----------|----------|
| SSU      | LSU      | ITS      | GAPDH    |
| RPB2     | TEF      | GAPDH    | RPB2     |
| TEF      | GAPDH    | RPB2     | TEF      |
| GAPDH    | RPB2     | TEF      | GAPDH    |
| RPB2     | TEF      | GAPDH    | RPB2     |
| TEF      | GAPDH    | RPB2     | TEF      |
| GAPDH    | RPB2     | TEF      | GAPDH    |
| RPB2     | TEF      | GAPDH    | RPB2     |
| TEF      | GAPDH    | RPB2     | TEF      |
| GAPDH    | RPB2     | TEF      | GAPDH    |
| RPB2     | TEF      | GAPDH    | RPB2     |
| TEF      | GAPDH    | RPB2     | TEF      |
| GAPDH    | RPB2     | TEF      | GAPDH    |
| RPB2     | TEF      | GAPDH    | RPB2     |
| TEF      | GAPDH    | RPB2     | TEF      |
| GAPDH    | RPB2     | TEF      | GAPDH    |
| RPB2     | TEF      | GAPDH    | RPB2     |

Aligned length: 1021 851 499 573 786 269 1359 842 1055 1628 3999 1021 851 499 573 786 269 1359 842 1055 1628 3999

Unique site patterns: 45 57 148 272 296 224 568 496 520 792 1042 45 57 148 272 296 224 568 496 520 792 1042

No. of sampled trees (post burnin): 300/02 31578 75002 23702 56028 12452 10128 13728 44852 5778 16278

Bayesian Posterior Probabilities

| Sect. Alternantherae | Sect. Alternata | Sect. Brassiccola | Sect. Chalastospora | Sect. Cheiranthus | Sect. Citella | Sect. Dianthicola | Sect. Embellsia | Sect. Embellsioides | Sect. Eureka | Sect. Infectoriae | Sect. Japonicae | Sect. Nimbya | Sect. panax | Sect. Phragmosporae | Sect. Porri | Sect. Pseudoulocladium | Sect. Radicina | Sect. Sunchi | Sect. Teretispora | Sect. Ulocladioides | Sect. Ulocladium |
|---------------------|-----------------|-------------------|---------------------|------------------|---------------|------------------|-----------------|-------------------|--------------|-----------------|-----------------|----------------|--------------|---------------------|-------------|---------------------|-----------------|-------------|---------------------|----------------|---------------------|
| 1.00                | 0.95–0.99       | 0.90–0.94         | 0.80–0.89           | 0.70–0.79        | 100           | 95–99            | 90–94           | 80–89             | 70–79        | 50–69           | 25–49           | 1–24           | 0.50–0.69    | 0.25–0.49           | 0.01–0.24 | 50–69               | 25–49           | 1–24     | 0.50–0.69           | 0.25–0.49    | 0.01–0.24           | 50–69               | 25–49               | 1–24     | 0.50–0.69           | 0.25–0.49    | 0.01–0.24           |

RAxML bootstrap support

| Sect. Alternantherae | Sect. Alternata | Sect. Brassiccola | Sect. Chalastospora | Sect. Cheiranthus | Sect. Citella | Sect. Dianthicola | Sect. Embellsia | Sect. Embellsioides | Sect. Eureka | Sect. Infectoriae | Sect. Japonicae | Sect. Nimbya | Sect. panax | Sect. Phragmosporae | Sect. Porri | Sect. Pseudoulocladium | Sect. Radicina | Sect. Sunchi | Sect. Teretispora | Sect. Ulocladioides | Sect. Ulocladium |
|---------------------|-----------------|-------------------|---------------------|------------------|---------------|------------------|-----------------|-------------------|--------------|-----------------|-----------------|----------------|--------------|---------------------|-------------|---------------------|-----------------|-------------|---------------------|----------------|---------------------|
| *                   | *                | *                 | *                   |                  |               |                  |                 |                   |              |                 |                 |               |              | *                    | *           | *                   |                 |            | *                    | *             | *                   |

*sect. not complete

*= section not complete
Alternaria redefined

Table 3. Coded inserts in the TEF1 sequence alignment.

| Species               | Nt position | Coded | Nt position | Coded |
|-----------------------|-------------|-------|-------------|-------|
| Alternaria elegans    | 23 to 39    | TC    |             |       |
| Alternaria simimi     | 23 to 39    | TCC   |             |       |
| Alternaria dauci      | 186 to 205  | C     | 221 to 269  | TACTT |
| Alternaria macrospora | 186 to 205  | C     | 221 to 269  | TCCCC |
| Alternaria porri       | 186 to 205  | C     | 221 to 269  | ACTTA |
| Alternaria pseudorostrata | 186 to 205  | C     | 221 to 269  | TGGTA |
| Alternaria solani      | 186 to 205  | C     | 221 to 269  | -AAGG |
| Alternaria tegeticula  | 186 to 205  | C     | 221 to 269  | CACAC |

Colonies effuse, usually grey, dark blackish brown or black. Mycelium immersed or partly superficial; hyphae colourless, olivaceous-brown or brown. Stroma rarely formed. Setae and hypothecium absent. Conidiophores macronematous, mononematous, simple or irregularly and loosely branched, pale brown or brown, solitary or in fascicles. Conidigenous cells integrated, terminal becoming intercalary, polytretic, sympodial, or sometimes monotropic, cicatrized. Conidia catenate or solitary, dry, ovoid, obvoid, cylindrical, narrowly ellipsoid or obclavate, beaked or non-beaked, pale or medium olivaceous-brown to brown, smooth or verrucose, with or without oblique or longitudinal septa. Septa can be thick, dark and rigid and an internal cell-like structure can be formed. Species with meristematic growth are known. Ascomata small, solitary to clustered, erumpent to (nearly) superficial at maturity, globose to ovoid, dark brown, smooth, apically papillate, ostiolate. Papilla short, blunt. Peridium thin. Hamathecium of cellular pseudoparaphyses. Asci few to many per ascoma, (4–6–8)-spored, basal, bitunicate, fissitunicate, cylindrical to cylindro-clavate, straight or somewhat curved, with a short, furcate pedicle. Ascospores muriform, ellipsoid to fusoid, slightly constricted at septa, yellow-brown, without guttules, smooth, 3–7 transverse septa, 1–2 series of longitudinal septa through the two original central segments, end cells without septa, or with 1 longitudinal or oblique septum, or with a Y-shaped pair of septa.

Type species: Alternaria alternata (Fr.) Keissl.

Taxonomy

Based on DNA sequence data in combination with a review of literature and morphology, the species within the Alternaria clade are all recognised here as Alternaria (Fig 1). This puts the genera Allewia, Brachychladium, Chalastospora, Chmelia, Crivellia, Embelisia, Lewia, Nimbya, Synomyces, Teretispora, Ulocladium, Undifillum and Ybotromyces in synonymy with Alternaria, resulting in the proposal of 32 new combinations, 10 new names and the resurrection of 10 names. Species of Alternaria were assigned to 24 Alternaria sections, of which 16 are newly described, and six monotypic lineages. The (emended) description of the genus Alternaria, the Alternaria sections and monotypic lineages with new Alternaria names and name combinations are treated below in alphabetical order. Finally the description of the new genus Paradendryphiella is also provided.
Fig. 2. Bayesian 50% majority rule consensus tree based on the SSU, LSU and RPB2 sequences of 74 strains representing the Pleosporineae. The Bayesian posterior probabilities (PP) and RAxML bootstrap support values (ML) are given at the nodes (PP/ML). Thickened lines indicate a PP of 1.0 and ML of 100. The tree was rooted to Julelia avicenniae (BCC 18422).
**Alternaria Sections**

**Section Alternantherae** D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 540. 2013. Fig. 3.

*Type species:* *Alternaria alternantherae* Holcomb & Antonop.

*Diagnosis:* Section *Alternantherae* contains short to moderately long conidiophores with a conidiogenous tip which can be enlarged. Conidia are narrowly ellipsoid or ovoid, sometimes subcylindrical, solitary or rarely paired, sometimes slightly constricted near some septa, longitudinal or oblique septa occasionally occur, disto- and euseptate, with a long apical narrow beak. The conidial beak is unbranched, septate or aseptate, long filiform, and sometimes swollen at the end. Internal compartmentation occurs, cell lumina tend to be broadly octagonal to rounded.

*Notes:* Section *Alternantherae* was recently established by Lawrence et al. (2013) after first being described as species-group *A. alternantherae* (Lawrence et al. 2012). The described section consists of three former *Nimbya* species which formed a separate clade amidst the *Alternaria* species-groups based on sequences of the GAPDH, ITS and Alt a 1 genes (Lawrence et al. 2012). *Nimbya celosiae* is placed in this section based on the data of Lawrence et al. (2012), while *N. gomphrenae* is placed in the section based on ITS sequence data from Chou & Wu (2002).

*Alternaria alternantherae* Holcomb & Antonop., Mycologia 68: 1126. 1976.

≡ *Nimbya alternantherae* (Holcomb & Antonop.) E.G. Simmons & Alcorn, Mycotaxon 55: 142. 1995.

*Alternaria celosiicola* Jun. Nishikawa & C. Nakash., J. Phytopathol.: doi: 10.1111/jph.12108 (p. 3). 2013. *Basionym:* *Nimbya celosiae* E.G. Simmons & Holcomb, Mycotaxon 55: 144. 1995.

≡ *Alternaria celosiae* (E.G. Simmons & Holcomb) D.P. Lawr., M.S. Park & B.M. Pryor, Mycol. Progr. 11: 811. 2012. (nom. illegit., homonym of *Alternaria celosiae* (Tassi) O. Savul. 1950).

*Alternaria gomphrenae* Togashi, Bull. Imp. Coll. Agric. 9: 6. 1926.

≡ *Nimbya gomphrenae* (Togashi) E.G. Simmons, Sydowia 41: 324. 1989.

*Alternaria perpunctulata* (E.G. Simmons) D.P. Lawr., M.S. Park & B.M. Pryor, Mycol. Progr. 11: 811. 2012. *Basionym:* *Nimbya perpunctulata* E.G. Simmons, Stud. Mycol. 50: 115. 2004.

**Section Alternata** D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 538. 2013. Fig. 4.

*Type species:* *Alternaria alternata* (Fr.) Keissl.

*Diagnosis:* Section *Alternata* contains straight or curved primary conidiophores, short to long, simple or branched, with one or several apical conidiogenous loci. Conidia are obclavate, long ellipsoid, small or moderate in size, septate, slightly constricted near some septa, with few longitudinal septa, in moderately long to long, simple or branched chains. The conidium body can narrow gradually into a tapered beak or secondary conidiophore. Secondary conidiophores can be formed apically or laterally with one or a few conidiogenous loci.
Notes: Next to the species that are displayed in our phylogeny, 14 more are included in sect. *Alternata* based on the study of Lawrence et al. (2013) and confirmed by our molecular data (not shown). We chose not to include 11 species from the study of Lawrence et al. (2013). The species *A. gossypina*, *A. grisae*, *A. grossulariae*, *A. iridis*, *A. lini*, *A. maritima* and *A. nelumbii* were not recognised by Simmons (2007) and the strains of *A. malvae*, *A. rhadina*, *A. resedae* and *A. tomato* used by Lawrence et al. (2013) were not authentic. Section *Alternata* comprises almost 60 *Alternaria* species based on ITS sequence data (data not shown). The molecular variation within this section is low.

*Alternaria alternata* (Fr.) Keissl., Beih. Bot. Centralbl., Abt. 2, 29: 434. 1912.

Basionym: *Torula alternata* Fr., Syst. Mycol. (Lundae) 3: 500. 1832 (nom. sanct.).
Alternaria redefined

= Alternaria tenuis Nees, Syst. Pilze (Würzburg): 72. 1816 [1816–1817].
Additional synonyms listed in Simmons (2007)

Alternaria angustiovoidea E.G. Simmons, Mycotaxon 25: 198. 1986.

Alternaria arborescens E.G. Simmons, Mycotaxon 70: 356. 1999.

Alternaria burnsii Uppal, Patel & Kamat, Indian J. Agric. Sci. 8: 49. 1938.

Alternaria cerealis E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 600. 2007.

Alternaria citriarbuski E.G. Simmons, Mycotaxon 70: 287. 1999.

Alternaria citrimacularis E.G. Simmons, Mycotaxon 70: 277. 1999.

Alternaria colombiana E.G. Simmons, Mycotaxon 70: 298. 1999.

Alternaria daucifolii E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 518. 2007.

Alternaria destruens E.G. Simmons, Mycotaxon 68: 419. 1998.

Alternaria dumosa E.G. Simmons, Mycotaxon 70: 310. 1999.

Alternaria gaisen Nagano ex Hara, Sakumotsu Byorigaku, Edn 4: 263. 1928.

= Alternaria gaisen Nagano, J. Jap. Soc. Hort. Sci. 32: 16–19. 1920. (nom. illegit.)

= Alternaria kikuchiana S. Tanaka, Mem. Coll. Agric. Kyoto Univ., Phytopathol. Ser. 28: 27. 1933.

= Macrosorum nashi Miura, Flora of Manchuria and East Mongolia, Part III Cryptogams, Fungi: 513. 1928.

Alternaria herbiphoricola E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 608. 2007.

Alternaria limoniasperae E.G. Simmons, Mycotaxon 70: 272. 1999.

Alternaria longipes (Ellis & Everh.) E.W. Mason, Mycol. Pap. 2: 19. 1928.

Basionym: Macrosorum longipes Ellis & Everh., J. Mycol. 7: 134. 1892.

= Alternaria brassicae var. tabaci Priessecker, Fachliche Mitt. Österr. Tabakregie 16: 4. 1916.

Alternaria perangusta E.G. Simmons, Mycotaxon 70: 303. 1999.

Alternaria postmessia E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 598. 2007.

Fig. 5. Alternaria sect. Brassicicola: conidia and conidiophores. A, H. A. brassicicola. B, I, L–M. A. mimicola. C, G. A. solidaccana. D, J–K. A. conoidea. E–F. A. septorioides. Scale bars = 10 µm.

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Alternaria tangelonis E.G. Simmons, Mycotaxon 70: 282. 1999.

Alternaria tenuissima (Nees & T. Nees : Fr.) Wiltshire, Trans. Brit. Mycol. Soc. 18: 157. 1933.
Basionym: Macrosporium tenuissimum (Nees & T. Nees) Fr., Syst. Mycol. (Lundae) 3: 374. 1832 (nom. sanct.).
≡ Helminthosporium tenuissimum Kunze ex Nees & T. Nees, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 9: 242. 1818.
Additional synonyms listed in Simmons (2007).

Alternaria toxicogenica E.G. Simmons, Mycotaxon 70: 294. 1999.

Alternaria turkisafria E.G. Simmons, Mycotaxon 70: 290. 1999.

Section Brassicicola D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 5.

Type species: Alternaria brassicicola (Schwein.) Wiltshire

Diagnosis: Section Brassicicola contains short to moderately long, simple or branched primary conidiophores with one or several apical conidiogenous loci. Conidia are ellipsoid, ovoid or somewhat obclavate, small or moderate in size, septate, slightly or strongly constricted at most of their transverse septa, with no to many longitudinal septa, in moderately long to long, simple or branched chains, with dark septa and cell walls. Secondary conidiophores can be formed apically or laterally with one or a few conidiogenous loci. Chlamydospores may occur.

Notes: Our molecular data support the morphological placement of A. septorioides and A. solidaccana in section Brassicicola (Simmons 2007). The other three species were already assigned to this section based on previous molecular studies (Pryor et al. 2009, Runa et al. 2009, Lawrence et al. 2012). Alternaria japonica was previously linked to the A. brassicicola species-group (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Lawrence et al. 2013), but this association was questioned by Hong et al. (2005). In our analyses, A. japonica clustered in sect. Japonicae.

Alternaria brassicicola (Schwein.) Wiltshire, Mycol. Pap. 20: 8. 1947.
Basionym: Helminthosporium brassicicola Schwein., Trans. Amer. Philos. Soc., Ser. 2, 4: 279. 1832.

Alternaria conoidea (E.G. Simmons) D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 542. 2013.
Basionym: Embellisia conoidea E.G. Simmons, Mycotaxon 17: 226. 1983.

Alternaria mimicula E.G. Simmons, Mycotaxon 55: 129. 1995.

Alternaria septorioides (Westend.) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 570. 2007.
Basionym: Sporidesmium septorioides Westend., Bull. Acad. Roy. Sci. Belgique., Cl. Sci., Sér. 2, 21: 236. 1854.
≡ Alternaria resedae Neerg., Annual Rep. Phytopathol. Lab. J.E. Ohlens Enkes, Seed Growers, Copenhagen 7: 9. 1942 (nom. nud.).
≡ Alternaria resedae Neerg., Danish species of Alternaria & Stemphylium: 150. 1945.

Alternaria solidaccana E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 572. 2007.

Section Chalastospora (E.G. Simmons) Woudenburg & Crous, comb. et stat. nov. MycoBank MB803733. Fig. 6.
Basionym: Chalastospora E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.

Type species: Alternaria cetera E.G. Simmons

Diagnosis: Section Chalastospora contains short to long, simple or branched primary conidiophores with one or several conidiogenous loci. Conidia are pale to medium brown, narrowly ellipsoid to ellipsoid or ovoid, beakless, with no to multiple transverse eusepta and rarely longitudinal septa, solitary or in chains. Secondary conidiophores can be formed apically or laterally with one or a few conidiogenous loci.
Our study also placed *Alternaria armoraciae* in this section, while Crous et al. (2009c) showed that *Chalastospora gossypii*, formerly *Alternaria malorum*, belonged to this section based on sequences of the ITS and LSU genes.

*Alternaria abundans* (E.G. Simmons) Woudenberg. & Crous, *comb. nov*. MycoBank MB803688.

*Basionym*: *Embellisia abundans* E.G. Simmons, Mycotaxon 17: 222. 1983.

*Alternaria armoraciae* E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 660. 2007.

*Alternaria breviramosa* Woudenberg. & Crous, *nom. nov*. MycoBank MB803690.

*Basionym*: *Chalastospora ellipoidea* Crous & U. Braun, Persoonia 22: 145. 2009, non *Alternaria ellipoidea* E.G. Simmons, 2002.

*Embellisia indefessa* (Simmons & C.F. Hill) Woudenberg & Crous, *sect. nov.* MycoBank MB803735. Fig. 7.

*Basionym*: *Chalastospora indefessa* (E.G. Simmons) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.

*Alternaria cetera* E.G. Simmons, Mycotaxon 57: 393. 1996.

*Alternaria cheiranthi* (Lib.) P.C. Bolle, Meded. Phytopathol. Lab. “Willie Commmelin Scholten” 7: 43. 1924.

*Alternaria indefessa* (E.G. Simmons) Woudenberg & Crous, *comb. nov*. MycoBank MB803691.

*Basionym*: *Embellisia indefessa* E.G. Simmons, Mycotaxon 17: 228. 1983.

**Section Cheiranthus** Woudenberg. & Crous, *sect. nov*. MycoBank MB803734. Fig. 7.

*Type species*: *Alternaria cheiranthi* (Lib.) P.C. Bolle

*Diagnosis*: Section *Cheiranthus* contains short to moderately long, simple or branched primary conidiophores with one or several conidiogenous loci. Conidia are ovoid, broadly ellipsoid with transverse and longitudinal septa, slightly or strongly constricted at the septa, in short to long, simple or branched chains. Secondary conidiophores can be formed apically or laterally with a single conidiogenous locus.

*Notes*: Previous studies already placed *E. abundans* in the *Chalastospora-clade* (Andersen et al. 2009, Lawrence et al. 2012). Our study also placed *Alternaria armoraciae* in this section, while Crous et al. (2009c) showed that *Chalastospora gossypii*, formerly *Alternaria malorum*, belonged to this section based on sequences of the ITS and LSU genes.

*Alternaria abundans* (E.G. Simmons) Woudenberg. & Crous, *comb. nov*. MycoBank MB803688.

*Basionym*: *Embellisia abundans* E.G. Simmons, Mycotaxon 17: 222. 1983.

*Alternaria armoraciae* E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 660. 2007.

*Alternaria breviramosa* Woudenberg. & Crous, *nom. nov*. MycoBank MB803690.

*Basionym*: *Chalastospora ellipoidea* Crous & U. Braun, Persoonia 22: 145. 2009, non *Alternaria ellipoidea* E.G. Simmons, 2002.

*Embellisia indefessa* (Simmons & C.F. Hill) Woudenberg & Crous, *sect. nov.* MycoBank MB803735. Fig. 7.

*Basionym*: *Chalastospora indefessa* (E.G. Simmons) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.

*Alternaria cetera* E.G. Simmons, Mycotaxon 57: 393. 1996.

*Alternaria cheiranthi* (Lib.) P.C. Bolle, Meded. Phytopathol. Lab. “Willie Commmelin Scholten” 7: 43. 1924.

*Alternaria indefessa* (E.G. Simmons) Woudenberg & Crous, *comb. nov*. MycoBank MB803691.

*Basionym*: *Embellisia indefessa* E.G. Simmons, Mycotaxon 17: 228. 1983.

**Section Crivellia** (Shoemaker & Inderb.) Woudenberg. & Crous, *comb. et stat. nov*. MycoBank MB803735. Fig. 8.

*Basionym*: *Crivellia* Shoemaker & Inderb., Canad. J. Bot. 84: 1308. 2006.

*Type species*: *Alternaria penicillata* (Corda) Woudenberg. & Crous (≡ *Cucurbitaria papaveracea* De Not.).

*Diagnosis*: Section *Crivellia* is characterised by straight or curved, simple or branched primary conidiophores, with geniculate, sympodial proliferations. Conidia are cylindrical, straight to curved to inequilateral, with transverse eusepta, rarely constricted at
septa, single or in short, simple or branched chains. Secondary conidiophores are formed apically or laterally. Microsclerotia or chlamydospores may occur. Sexual morphs observed.

Notes: Section Crivellia contains the type species of the sexual morph Crivellia, C. papaveracea, with Brachycladium penicillatum sexual morph, and Brachycladium papaveris. The genus was established by Inderbitzin et al. (2006) based on the finding that C. papaveracea, formerly Pleospora papaveraceae, belonged to the Alternaria-complex instead of Pleospora s. str. based on ITS, GAPDH and TEF1 sequences.

Alternaria papavericola Woudenb. & Crous, nom. nov. MycoBank MB803749.
Basionym: Helminthosporium papaveris Sawada, J. Nat. Hist. Soc. Formosa 31: 1. 1917. ≡ Dendryphion papaveris (Sawada) Sawada, Special Publ. Coll. Agric. Natl. Taiwan Univ. 8: 200. 1959, non Alternaria papaveris (Bres.) M.B. Ellis, 1976. ≡ Brachycladium papaveris (Sawada) Shoemaker & Inderb., Canad. J. Bot. 84: 1310. 2006.
Etymology: Name refers to the host.

Alternaria penicillata (Corda) Woudenb. & Crous, comb. nov. MycoBank MB803692.
Basionym: Brachycladium penicillatum Corda, Icon. Fungorum hucusque Cogn. (Prague) 2: 14. 1838. ≡ Dendryphion penicillatum (Corda) Fr., Summa Veg. Scand., Sect. Post. (Stockholm) 504. 1849. ≡ Cucurbitaria papaveracea De Not., Sferiacei Italici: 62. 1863. ≡ Pleospora papaveracea (De Not.) Sacc., Syll. Fungorum (Abellini) 2: 243. 1883. ≡ Crivellia papaveracea (De Not.) Shoemaker & Inderb., Canad. J. Bot. 84: 1308. 2006.
Note: The asexual name, Brachycladium penicillatum is older than the sexual name, Cucurbitaria papaveracea, and therefore the species epithet penicillatum is chosen above papaveracea.

Section Dianthicola Woudenb. & Crous, sect. nov. MycoBank MB803736. Fig. 9.
Type species: Alternaria dianthicola Neerg.
Diagnosis: Section Dianthicola contains simple or branched primary conidiophores, with or without apical geniculate proliferations. Conidia are narrowly ovoid or narrowly ellipsoid with transverse and few longitudinal septa, slightly constricted at the septa, with a long (filamentous) beak or apical secondary conidiophore, solitary or in short chains.

Note: Based on the ITS sequence, Alternaria dianthicola clustered near Ulocladium (Chou & Wu 2002). Our extensive dataset places it in a sister section to section Ulocladioides.

Alternaria dianthicola Neerg., Danish species of Alternaria & Stemphylium: 190. 1945.
Alternaria elegans E.G. Simmons & J.C. David, Mycotaxon 75: 89. 2000.
Alternaria simsimi E.G. Simmons, Stud. Mycol. 50: 111. 2004.

Section Embellisia (E.G. Simmons) Woudenb. & Crous, comb. et stat. nov. MycoBank MB803737. Fig. 10.
Basionym: Embellisia E.G. Simmons, Mycologia 63: 380. 1971.
Type species: Alternaria embellisia Woudenb. & Crous (≡ Helminthosporium allii Campan., Embellisia allii (Campan.) E.G. Simmons).
Diagnosis: Section Embellisia contains simple, septate conidiophores, straight or with geniculate sympodial proliferation. Conidia are solitary, ovoid to subcylindrical, straight to inequilateral, transseptate; septa can be thick, dark and rigid in contrast to the external wall. Chlamydospores may occur.

Notes: Section Embellisia contains the first two species described in the genus Embellisia, Embellisia allii (type species) and Embellisia chlamydospora (Simmons 1971) together with Embellisia tellustris. This clade is also resolved in the latest molecular revision of Embellisia based on sequences of the GAPDH, ITS and Alt a 1 genes as Embellisia group I (Lawrence et al. 2012).

Alternaria chlamydosporigena Woudenb. & Crous, nom. nov. MycoBank MB803694.
Basionym: Pseudostemphylium chlamydosporum Hoes, G.W. Bruehl & C.G. Shaw, Mycologia 57: 904. 1965, non Alternaria chlamydospora Mouch., 1973. ≡ Embellisia chlamydospora (Hoes, G.W. Bruehl & C.G. Shaw) E.G. Simmons, Mycologia 63: 384. 1971.
Etymology: Name refers to the formation of chlamydospores during growth.

Fig. 8. Alternaria sect. Crivellia: conidia and conidiophores. A–B. A. papavericola. C–D. A. penicillata. Scale bars = 10 µm.
**Alternaria embellisia** Woudenb. & Crous, nom. nov. MycoBank MB803693.

*Basionym*: *Helminthosporium allii* Campan., Nuovi Ann. Agric. Roma 4: 87. 1924, non *Alternaria allii* Nolla, 1927.

≡ *Embellisia allii* (Campan.) E.G. Simmons, Mycologia 63: 382. 1971.

**Etymology**: Name refers to the genus *Embellisia* for which it served as type species.

**Alternaria tellustris** (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803695.

*Basionym*: *Embellisia tellustris* E.G. Simmons [as “telluster”], Mycotaxon 17: 234. 1983.

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**Fig. 9.** Alternaria sect. Dianthicola: conidia and conidiophores. A–B. *A. dianthicola*. C–E. *A. simsimi*. F–H. *A. elegans*. Scale bars = 10 µm.

**Fig. 10.** Alternaria sect. *Embellisia*: conidia and conidiophores. A–D. *A. embellisia*. E–H. *A. tellustris*. Scale bars = 10 µm.
Fig. 11. *Alternaria* sect. *Embellisioides*: conidia and conidiophores. A–B. *A. hyacinthi*. C–E. *A. lolii*. F–H. *A. botryospora*. I–K. *A. planifunda*. L–N. *A. proteae*. O–P. *A. tumida*. Scale bars = 10 µm.
Section *Embellisioides* Woudenb. & Crous, sect. nov. MycoBank MB803738. Fig. 11.

**Type species**: *Alternaria hyacinthi* (de Hoog & P.J. Mull. bis) Woudenb. & Crous

**Diagnosis**: Section *Embellisioides* contains simple, septate conidiophores, straight or with geniculate, sympodial proliferations. Apical or lateral, short secondary conidiophores may occur. Conidia are solitary or in short chains, obvoid to ellipsoid, with transverse and longitudinal septa; transverse septa can be thick, dark and rigid in contrast to the external wall. Chlamydospores and a sexual morph may occur.

**Note**: In Lawrence et al. (2012) the section is named *Embellisia* group III.

*Alternaria botryospora* Woudenb. & Crous, nom. nov. MycoBank MB803705.
**Basionym**: *Embellisia novae-zelandiae* E.G. Simmons & C.F. Hill, Mycologia 38: 252. 1990, non *Alternaria novae-zelandiae* E.G. Simmons, 2002.

**Etymology**: Name refers to the clusters of conidia.

*Alternaria hyacinthi* (de Hoog & P.J. Mull. bis) Woudenb. & Crous, comb. nov. MycoBank MB803703.
**Basionym**: *Embellisia hyacinthi* de Hoog & P.J. Mull. bis, Netherlands J. Pl. Pathol. 79: 85. 1973.

*Alternaria lolii* (E.G. Simmons & C.F. Hill) Woudenb. & Crous, comb. nov. MycoBank MB803704.
**Basionym**: *Embellisia lolii* E.G. Simmons & C.F. Hill, Stud. Mycol. 50: 113. 2004.

*Alternaria planifunda* (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803706.
**Basionym**: *Embellisia planifunda* E.G. Simmons, Mycotaxon 17: 233. 1983.

*Alternaria proteae* (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803707.
**Basionym**: *Embellisia proteae* E.G. Simmons, Mycotaxon 38: 258. 1990.

*Alternaria tumida* (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803708.
**Basionym**: *Embellisia tumida* E.G. Simmons, Mycotaxon 17: 236. 1983.

Section *Eureka* Woudenb. & Crous, sect. nov. MycoBank MB803739. Fig. 12.

**Type species**: *Alternaria eureka* E.G. Simmons

**Diagnosis**: Section *Eureka* contains simple, septate conidiophores, straight or with geniculate, sympodial proliferations. Apical or lateral, short secondary conidiophores may occur. Conidia are solitary or in short chains, narrowly ellipsoid to cylindrical, with transverse and longitudinal septa, slightly constricted at the septa, with a blunt rounded apex. Chlamydospores and a sexual morph may occur.

**Notes**: Section *Eureka* contains four *Alternaria* species and two former *Embellisia* species. From the *Alternaria* species only the ITS sequence of *A. geniostomatis* was previously used in a molecular study (Toth et al. 2011), showing it to cluster separate from the other *Alternaria* spp. The two *Embellisia* species were included in the latest molecular-based revision of *Embellisia* (Lawrence et al. 2012) where they formed *Embellisia* group IV. A sexual morph is known for the type species of this section.

*Alternaria anigozanthi* Priest, Australas. Pl. Pathol. 24: 239. 1995.

*Alternaria cumini* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 664. 2007.

*Alternaria eureka* E.G. Simmons, Mycotaxon 25: 306. 1990.

*Alternaria eureka* (E.G. Simmons) E.G. Simmons, Mycotaxon 38: 260. 1990.

*Alternaria geniostomatis* E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 412. 2007.

*Alternaria leptinellae* (E.G. Simmons & C.F. Hill) Woudenb. & Crous, comb. nov. MycoBank MB803696.
**Basionym**: *Embellisia leptinellae* E.G. Simmons & C.F. Hill, Mycotaxon 38: 254. 1990.

*Alternaria triglochinicola* Alcorn & S.M. Francis, Mycotaxon 46: 359. 1993.

Section *Gysposphila* D.P. Lawr., Cannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 13

**Type species**: *Alternaria gysposphila Neerg.*

**Diagnosis**: Section *Gysposphila* contains simple, or occasionally branched, primary conidiophores, with one or a few conidiogenous loci. Conidia are ellipsoid to long ovoid, with multiple transverse and longitudinal septa, conspicuously constricted near some transverse septa, solitary or in short chains. Secondary conidiophores are formed apically with one or two conidiogenous loci or laterally with a single conidiogenous locus. Species from this section occur on *Caryophyllaceae*.

**Notes**: Section *Gysposphila* was recently established by Lawrence et al. (2013) containing the four *Alternaria* species, *A. gysposphila*, *A. nobilis*, *A. vaccariae* and *A. vaccanicola*. Our dataset adds four *Alternaria* species, *A. axiaeriisporfera*, *A. ellipsoidea*, *A. saponariae*, and *A. juxtiseptata* to this section. Simmons (2007) noted the similarity of the primary conidia of *A. ellipsoidea* to *A. gysposphila*, *A. nobilis*, *A. saponariae* and *A. vaccariae*. This section contains all *Alternaria* species that occur on *Caryophyllaceae* (Simmons 2002), except *A. dianthicola* which resides in sect. *Dianthicola*.

*Alternaria axiaeriisporfera* E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 662. 2007.

*Alternaria ellipsoidea* E.G. Simmons, Mycotaxon 82: 31. 2002.

*Alternaria gysposphila* Neerg., Danish species of *Alternaria* & *Stemphylium*: 207. 1945.

*Alternaria juxtiseptata* E.G. Simmons, Mycotaxon 38: 32. 2002.

*Alternaria nobilis* (Vize) E.G. Simmons, Mycotaxon 82: 7. 2002.
**Basionym**: *Macrosporum nobile* Vize, Grevillea 5(35): 119. 1877.

*Alternaria saponariae* (Peck) Neerg., Annual Rep. Phytopathol. Lab. J.E. Ohlsens Enkes, Seed Growers, Copenhagen 3: 6. 1938 [1937–1938].
**Basionym**: *Macrosporum saponariae* Peck, Rep. (Annual) NewYork State Mus. Nat. Hist. 28: 62. 1876 [1875].
Alternaria vaccariae (Săvul. & Sandu) E.G. Simmons & S.T. Koike, Mycotaxon 82: 21. 2002.
Basionym: Macrosporium vaccariae Săvul. & Sandu, Hedwigia 73: 130. 1933.

Alternaria vaccariicola E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 594. 2007.

Section Infectoriae Woud. & Crous, sect. nov. MycoBank MB803740. Fig. 14.

Type species: Alternaria infectoria E.G. Simmons

Diagnosis: Section Infectoriae contains short to long, simple or branched primary conidiophores with one or several conidiogenous loci. Conidia are obclavate, long-ellipsoid, small or moderate in size, septate, slightly constricted near some septa, with few longitudinal septa, in moderately long to long, branched chains. Long, geniculate, multi-locus secondary conidiophores can be formed apically or laterally. Sexual morphs are known, and meristematic growth has been reported.

Notes: In addition to the six species that are displayed in our phylogeny, 19 more are included based on the study of Lawrence et al. (2013), confirmed with our molecular data (not shown). From these 25 species, nine species have a known sexual morph in Lewia. Three species from the study of Lawrence et al. (2013) are not included; A. photistica (sect. Panax) and A. dianthicola (sect. Dianthicola) cluster elsewhere in our phylogenies and A. peglionii is marked as a taxon incertae sedis by Simmons (2007). The human pathogenic genera Ybotromyces and Chmelia are also embedded in sect. Infectoriae.
**Alternaria alternarina** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 644. 2007.

≡ Pyrenophora alternarina M.D. Whitehead & J. Dicks., Mycologia 44: 748. 1952.

≡ Lewia alternarina (M.D. Whitehead & J.G. Dicks.) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 644. 2007.

**Alternaria arbusti** E.G. Simmons, Mycotaxon 48: 103. 1993.

**Alternaria caespitosa** (de Hoog & C. Rubio) Woudenh. & Crous, comb. nov. MycoBank MB803698.

Basionym: Botryomyces caespitosus de Hoog & C. Rubio, Mycotaxon 14: 19. 1982.

≡ Ybotromyces caespitosus (de Hoog & C. Rubio) Rulamort, Bull. Soc. Bot. Centre-Ouest, Nouv. Sér. 21: 512. 1990.

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Fig. 13. *Alternaria* sect. Gypsophilae: conidia and conidiophores. A–B. *A. axiantisporifera*. C–D. *A. ellipsoidae*. E–G. *A. saponariae*. H–I. *A. vaccariae*. J–K. *A. nobilis*. L–M. *A. juxtiseptata*. N–P. *A. vaccanicola*. Scale bars = 10 µm.
Fig. 14. Alternaria sect. Infectoriae: conidia and conidiophores. A–B. A. ethzedia. C–D. A. infectoria. E–F. A. conjuncta. G–H. A. oregonensis. Scale bars = 10 μm.
Section Japonicae Woudenb. & Crous, sect. nov. MycoBank MB803741. Fig. 15.

Type species: Alternaria japonica Yoshii

Diagnosis: Section Japonicae contains short to long, simple or occasionally branched primary conidiophores with a single conidiogenous locus. Conidia are short, to long-ovoid with transverse and longitudinal septa, conspicuously constricted at most of the transverse septa, in short chains. Apical secondary conidiophores are produced with a single conidiogenous locus. The species within this section occur on Brassicaceae.

Note: Alternaria japonica was previously connected to the A. brassicicola species-group (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Lawrence et al. 2013), but this association was questioned by Hong et al. (2005).

Alternaria japonica Yoshii, J. Pl. Protect. 28: 17. 1941.
= Alternaria matthiolae Neerg., Danish species of Alternaria and Stemphylium: 184. 1945.

Alternaria nepalensis E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 480. 2007.

Section Nimbya (E.G. Simmons) Woudenb. & Crous, comb. et stat. nov. MycoBank MB803742. Fig. 16.

Basionym: Nimbya E.G. Simmons, Sydowia 41: 316. 1989.

Type species: Alternaria scirpicola (Fuckel) Sivan.

Diagnosis: Section Nimbya contains simple, short to moderately long conidiophores, which may form one or a few short to long, geniculate, sympodial proliferations. Conidia are narrowly elongate-obclavate, gradually tapering apically, solitary or in short chains, with transverse disto- and eusepta, sometimes slightly constricted near eusepta. Apical conidiophores with a single conidiogenous locus can be formed. Internal compartmentation occurs, cell lumina tend to be broadly octagonal to rounded. A sexual morph may occur.

Notes: Section Nimbya contains the type species of Nimbya, N. scirpicola, and N. caricis (Simmons 1989). A more extensive study on Nimbya (Lawrence et al. 2012) found that N. scirpifestans and N. scirpivora also belonged to this section based on sequences of the GAPDH, ITS and Alt a 1 genes.

Alternaria caricis (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803700.
Basionym: Nimbya caricis E.G. Simmons, Sydowia 41: 328. 1989.
**Alternaria scirpicola** (Fuckel) Sivan., Bitunicate Ascomycetes and their Anamorphs (Vaduz): 526. 1984.

**Basionym:** Sporidesmium scirpicola Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 140. 1870 [1869–70].

≡ Clasterosporium scirpicola (Fuckel) Sacc., Syll. Fungorum (Abellini) 4: 393. 1886.

≡ Nimbya scirpicola (Fuckel) E.G. Simmons, Sydowia 41: 316. 1989.

≡ Sphaeria scirpicola DC., in Lamarck & de Candolle, Fl. Franç., Edn 3 (Paris) 2: 300. 1805.

≡ Macrospora scirpicola (DC.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 139. 1870 [1869–70].

≡ Pyrenophora scirpicola (DC.) E. Mühl., Sydowia 5(3–6): 256. 1951.

**Note:** Although Sphaeria scirpicola DC. (de Candolle 1805) predates Sporidesmium scirpicola Fuckel (Fuckel 1870), a valid combination in Alternaria already exists, thus we choose to retain Alternaria scirpicola (Fuckel) Sivan., which is also a well-established name.

**Alternaria scirpinfestans** (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, **comb. nov.** MycoBank MB803701.

**Basionym:** Nimbya scirpinfestans E.G. Simmons & D.A. Johnson, Mycotaxon 84: 420. 2002.

≡ Macrospora scirpinfestans E.G. Simmons & D.A. Johnson, Mycotaxon 84: 417. 2002.

**Alternaria scirpivora** (E.G. Simmons & D.A. Johnson), Woudenb. & Crous, **comb. nov.** MycoBank MB803702.

**Basionym:** Nimbya scirpivora E.G. Simmons & D.A. Johnson, Mycotaxon 84: 424. 2002.

≡ Macrospora scirpivora E.G. Simmons & D.A. Johnson, Mycotaxon 84: 422. 2002.

**Section Panax** D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 17.

**Type species:** Alternaria panax Whetzel

**Diagnosis:** Section Panax contains simple or branched, short to moderately long primary conidiophores, with one or a few conidiogenous loci. Conidia are obclavate to ovoid, with multiple transverse and longitudinal septa, conspicuously constricted near several transverse septa, solitary or in simple or branched, short chains. Apical secondary conidiophores are formed with one or several conidiogenous loci, multiple lateral secondary conidiophores with a single conidiogenous locus may occur.

**Notes:** Section Panax was recently described by Lawrence et al. (2013) and consists of A. calycipyricola, A. eryngii and A. panax. Our extended dataset added the species A. avenicola and A. photistica to this section. Three species, A. avenicola, A. calycipyricola, and A. photistica have earlier been placed in the A. infectoria species-group based on their morphological characters (Simmons 2007), and two of them have a known sexual morph; Lewia avenicola (Simmons 2007) and Lewia photistica (Simmons 1986). A phylogenetic study based on Alt a 1 and GAPDH sequences placed A. photistica in the A. infectoria species-group (Hong et al. 2005) but an extensive study on the A. infectoria species-group (Andersen et al. 2009) confirmed our finding, and placed this species outside the A. infectoria species-group. Additional research performed on multiple A. photistica strains support our sequence data (data not shown).
**Alternaria avenicola** E.G. Simmons, Kosia & Kwaśna, in Simmons, CBS Biodiversity Ser. (Utrecht) 6: 114. 2007.
\[= Lewia avenicola Kosia & Kwaśna, Mycol. Res. 107: 371. 2003.\]

**Alternaria calycipyricola** R.G. Roberts, Mycotaxon 100: 162. 2007.

**Alternaria eryngii** (Pers.) S. Hughes & E.G. Simmons, Canad. J. Bot. 36: 735. 1958.
\[= Exosporium eryngii (Pers.) Duby, Bot. Gallicum., Edn 2 (Paris) 2: 882. 1830.\]
\[= Helminthosporium eryngii (Pers.) Fr., Syst. Mycol. (Lundae) 3: 361. 1832.\]

**Alternaria panax** Whetzel, Bull. U.S.D.A. 250: 11. 1912.
\[= Macrosorum araliae Deam. & House, Circ. New York State Mus. 24: 58. 1940.\]
\[= Alternaria araliae H.C. Greene, Trans. Wisconsin Acad. Sci. 42: 80. 1953.\]

**Alternaria photistica** E.G. Simmons, Mycotaxon 25: 304. 1986.
\[= Lewia photistica E.G. Simmons, Mycotaxon 25: 302. 1986.\]

**Section Phragmosporae** Woudenb. & Crous, sect. nov. MycoBank MB803743. Fig. 18.

**Type species:** Alternaria phragmospora Emden

**Diagnosis:** Section *Phragmosporae* contains simple, short to moderately long, primary conidiophores, with one or multiple geniculate, sympodial proliferations. Conidia are (broad) ovoid to long ovoid, ellipsoid, curved, or limaciform, with multiple transverse and few to multiple longitudinal septa, some septa darkened, slightly to conspicuously constricted near several transverse septa, solitary or in simple short chains. Apical secondary conidiophores are formed with one or several conidiogenous loci. All species within the section are known from soil and seawater environments.

**Note:** Section *Phragmosporae* contains six species of which two were linked to *Embellisia*.

**Alternaria chlamydospora** Mouch. [as “chlamydosporum”], Mycopathol. Mycol. Appl. 50: 217. 1973.

**Alternaria didymospora** (Munt.-Cvetk.) Woudenb. & Crous, comb. nov. MycoBank MB803709.
\[= Embellisia didymospora Munt.-Cvetk., Mycologia 68: 49. 1976.\]

**Alternaria limaciformis** E.G. Simmons, Mycotaxon 13: 24. 1981.

**Alternaria molesta** E.G. Simmons, Mycotaxon 13: 17. 1981.
\[= Ulocladium chlamydosporum Mouch., Rev. Mycol. (Paris) 36: 114. 1971, non Alternaria chlamydospora Mouch., 1973.\]

**Alternaria mouchaccae** E.G. Simmons, Mycotaxon 13: 18. 1981.
\[= Embellisia phragmospora (Emden) E.G. Simmons, Mycotaxon 17: 232. 1983.\]

**Alternaria phragmospora** Emden, Acta Bot. Neerl. 19: 393. 1970.
\[= Embellisia phragmospora (Emden) E.G. Simmons, Mycotaxon 17: 232. 1983.\]

**Section Porri** D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 19

**Type species:** Alternaria porri (Ellis) Cif.
Diagnosis: Section *Porri* is characterised by broadly ovoid, obclavate, subcylindrical or obovoid (medium) large conidia, disto- and euseptate, solitary or in short to moderately long chains, with a simple or branched, long to filamentous beak. Conidia contain multiple transverse and longitudinal septa and are slightly constricted near some transverse septa. Secondary conidiophores can be formed apically or laterally.

Notes: In addition to the six species that are displayed in our phylogeny, 40 more are included based on the study of Lawrence et al. (2013), confirmed with own molecular data (not shown). With almost 80 species section *Porri* is the largest *Alternaria* section (data not shown). The section displays a higher level of genetic variation than the second largest section; section *Alternata*.

*Alternaria acalyphicola* E.G. Simmons, Mycotaxon 50: 260. 1994.

*Alternaria agerati* Sawada ex E.G. Simmons, Mycotaxon 65: 63. 1997.

≡ *Alternaria agerati* Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 86: 165. 1943. (nom. inval., Art. 36.1)

*Alternaria agripestis* E.G. Simmons & K. Mort., Mycotaxon 50: 255. 1994.

*Alternaria anagallidis* A. Raabe, Hedwigia 78: 87. 1939.

*Alternaria aragakii* E.G. Simmons, Mycotaxon 46: 181. 1993.

*Alternaria argyroxiphii* E.G. Simmons & Aragaki, Mycotaxon 65: 40. 1997.

*Alternaria bataticola* Ikata ex W. Yamam., Trans. Mycol. Soc. Japan 2(5): 89. 1960.

≡ *Macrosporium bataticola* Ikata, Agric. Hort. (Tokyo) 22: 241. 1947 (nom. inval., Art. 36.1).

*Alternaria blumeae* E.G. Simmons & Sontirat, Mycotaxon 65: 81. 1997.

*Alternaria calendulae* Ondřej, Čas. Slez. Mus. v Opavě, Ser. A, Hist. Nat. 23(2): 150. 1974.

≡ *Alternaria calendulae* W. Yamam. 1939 (nom. nud.).

≡ *Macrosporium calendulae* Nelen, Bull. Centr. Bot. Gard. (Moscow) 35: 90. 1959 (nom. inval., Art. 36.1).

≡ *Macrosporium calendulae* Nelen, Bot. MATER. Otd. Sporov. Rast. Bot. Inst. Akad. Nauk S.S.S.R. 15: 144. 1962.

≡ *Alternaria calendulae* Nirenberg, Phytopathol. Z. 86(2): 108. 1977 (nom. illegil., Art. 53.1).

*Alternaria capsici* E.G. Simmons, Mycotaxon 75: 84. 2000.

*Alternaria carthami* S. Chowdhury, J. Indian Bot. Soc. 23: 65. 1944.

≡ *Macrosporium anatolicum* A. Săvul., Bull. Sect. Sci. Acad. Roumaine 26: 709. 1944.

*Alternaria cassiae* Jurair & A. Khan, Pakistan J. Sci. Industr. Res. 3(1): 72. 1960.

*Alternaria cichorii* Nattrass, First List of Cyprus Fungi: 29. 1937.

≡ *Alternaria porri* f.sp. cichorii (Nattrass) T. Schmidt, Pflanzenschutz-berichte 32: 181. 1965.

≡ *Macrosporium cichorii* (Nattrass) Gordenko, Mikol. Fitopatol. 9(3): 241. 1975.

*Alternaria cirsinoxia* E.G. Simmons & K. Mort., Mycotaxon 65: 72. 1997.

*Alternaria crassa* (Sacc.) Rands, Phytopathology 7: 337. 1917. Basionym: *Cercospora crassa* Sacc., Michelia 1(no. 1): 88. 1877.

*Alternaria cretica* E.G. Simmons & Vakal., Mycotaxon 75: 64. 2000.

*Alternaria cucumerina* (Ellis & Everh.) J.A. Elliott, Amer. J. Bot. 4: 472. 1917. Basionym: *Macrosporium cucumerinum* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 47: 440. 1895.

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**Fig. 19.** *Alternaria* sect. *Porri*: conidia and conidiophores. A–C. *A. daucii*. D–F. *A. pseudostrata*. G–H. *A. solani*. Scale bars = 10 µm.
**Alternaria cyphomandrae** E.G. Simmons, Mycotaxon 75: 86. 2000.

**Alternaria danida** E.G. Simmons, Mycotaxon 65: 78. 1997.

**Alternaria dauci** (J.G. Kühn) J.W. Groves & Skolko, Canad. J. Res., Sect. C, Bot. Sci. 22: 222. 1944.

Basionym: Sporidesmium exitiosum var. dauci J.G. Kühn, Hedwigia 1: 91. 1855.

Additional synonyms in Simmons 2007.

**Alternaria dichordae** Gambogi, Vannacci & Triolo, Trans. Brit. Mycol. Soc. 65(2): 323. 1975.

**Alternaria euphoribicola** E.G. Simmons & Engelhard, Mycotaxon 25: 196. 1986.

≡ Macrosporum euphoriae Reichert, Bot. Jahrb. Syst. 56: 723. 1921. (nom. illegit., Art 53.1).

**Alternaria grandis** E.G. Simmons, Mycotaxon 75: 96. 2000.

**Alternaria hawaiiensis** E.G. Simmons, Mycotaxon 46: 184. 1993.

**Alternaria limicola** E.G. Simmons & M.E. Palm, Mycotaxon 37: 82. 1990.

**Alternaria linicola** J.W. Groves & Skolko, Canad. J. Res., Sect. C, Bot. Sci. 22: 223. 1944.

**Alternaria macrospora** Zimm., Ber. Land-Forstw. Deutsch-Ostafrika 2: 24. 1904.

≡ Macrosporum macrosporum (Zimm.) Nishikado & Oshima, Agric. Res. (Kurashiki) 36: 391. 1944.

≡ Sporidesmium longipedicellatum Reichert, Bot. Jahrb. Syst. 56: 723. 1921.

≡ Alternaria longipedicellata (Reichert) Snowden, Rep. Dept. Agric. Uganda: 31. 1927 [1928].

**Alternaria multirostrata** E.G. Simmons & C.R. Jacks., Phytopathology 58: 1139. 1968.

**Alternaria nitrimalia** E.G. Simmons & M.E. Palm, Mycotaxon 75: 62. 2000.

**Alternaria pseudorostrata**

**Alternaria protenta**

**Alternaria ragunathi** E.G. Simmons & R.G. Roberts, Mycotaxon 75: 53. 2000.

**Alternaria solani-nigriii**

**Alternaria solani-nigriii**

**Alternaria steviae**

**Alternaria tropica** E.G. Simmons, Mycotaxon 46: 187. 1993.

**Alternaria zinniae** H.Pape ex M.B. Ellis, Mycol. Pap. 131: 22. 1972.

≡ Alternaria zinniae H. Pape, Angew. Bot. 24: 61. 1942. (nom. inval., Art. 36.1)

Section **Pseudoulocladium** Woudenb. & Crous, *sect. nov.* MycoBank MB803744. Fig. 20.

Type species: *Alternaria chartarum* Preuss

Diagnosis: *Pseudoulocladium* is characterised by simple or branched conidiophores with short, geniculate, sympodial proliferations. Conidia are obovoid, non-beaked with a narrow base, in simple or (mostly) branched chains. Apical secondary conidiophores with multiple conidiogenous loci and lateral secondary conidiophores with a single conidiogenous locus can be formed.

Note: It forms a sister clade to section *Ulocladioides*.

**Alternaria aspera** Woudenb. & Crous, *nom. nov.* MycoBank MB803712.

Basionym: Ulocladium arborescens E.G. Simmons, Stud. Mycol. 50: 117. 2004, non *Alternaria arborescens* E.G. Simmons, 1999.

Eymology: Name refers to the conspicuously ornamented conidia.

**Alternaria chartarum** Preuss, Bot. Zeitung 6: 412. 1848.

≡ Sporidesmium polymorphum var. chartarum (Preuss) Cooke, Fungi Brit. Exs., ser. 2: 329. 1875.

≡ Ulocladium chartarum (Preuss) E.G. Simmons, Mycolgia 59: 88. 1967.

≡ Alternaria stenophylodea Bliss, Mycologia 36: 538. 1944.

≡ Alternaria chartarum f. stenophylodea Bliss (Bliss) P. Joly, Encycl. Mycol. (Paris) 33: 161. 1964.

**Alternaria concatenata** Woudenb. & Crous, *nom. nov.* MycoBank MB803713.

Basionym: Ulocladium capsici F. Xue & X.G. Zhang [as *capsicum*], Sydowia 59: 174. 2007, non *Alternaria capsici* E.G. Simmons, 2000.

Eymology: Name refers to the concatenated conidia.

**Alternaria septospora** (Preuss) Woudenb. & Crous, *comb. nov.* MycoBank MB803714.

Basionym: Helminthosporium septosporum Preuss, Linnaea 24: 117. 1851.

≡ Macrosporum septosporum (Preuss) Rabenh., Bot. Zeitung 9: 454. 1851.

≡ Ulocladium septosporum (Preuss) E.G. Simmons, Mycolgia 59: 87. 1967.

Section **Radicina** D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 21.

Type species: *Alternaria radicina* Meier, Drechsler & E.D. Eddy

Diagnosis: *Radicina* contains straight, simple or branched, short or long, primary conidiophores with multiple, short geniculate, sympodial proliferations with single or a few conidiogenous loci at the apex. Sporulation resembles a cluster or clumps of conidia. Conidia are widely ovoid to narrowly...
ellipsoid, moderate in size, beakless, with several transverse and longitudinal septa, solitary or in short chains. Solitary, short, apical secondary conidiophores may occur. The species from this section occur on *Umbelliferae*.

Note: This section was first recognised by Pryor & Gilbertson (2000) based on sequence data of the ITS and mitochondrial SSU.

**Alternaria carotinincultae** E.G. Simmons, Mycotaxon 55: 103. 1995.

**Alternaria petroselini** (Neerg.) E.G. Simmons, More dematiaceous hyphomycetes (Kew): 417. 1976.  
Basionym: *Stemphylium petroselini* Neerg., Zentralbl. Bakteriol., 2. Abt., 104: 411. 1942.  
≡ *Stemphylium radicinum* var. *petroselini* (Neerg.) Neerg., Encycl. Mycol. 33: 123. 1964.  
≡ *Alternaria radicina* var. *petroselini* (Neerg.) Neerg., Encycl. Mycol. 33: 123. 1964.  
≡ *Stemphylium radicinum* (Meier, Drechsler & E.D. Eddy) Neerg., Annual Rep. Phytopathol. Lab. J.E. Ohlensens Enkes, Seed Growers, Copenhagen 4: 14. 1939.  
≡ *Thyrospora radicina* (Meier, Drechsler & E.D. Eddy) Neerg., Bot. Tidsskr. 44: 361. 1939.  
≡ *Pseudostemphylium radicum* (Meier, Drechsler & E.D. Eddy) Subram., Curr. Sci. 30: 423. 1961.

**Alternaria selini** E.G. Simmons, Mycotaxon 55: 109. 1995.

**Alternaria smyrnii** (P. Crouan & H. Crouan) E.G. Simmons, Mycotaxon 55: 41. 1995.  
Basionym: *Helminthosporium smyrnii* P. Crouan & H. Crouan, Florule Finistère (Paris): 11. 1867.

**Section Sonchi** D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 542. 2013. Fig. 22.

Type species: *Alternaria sonchi* Davis

Diagnosis: Section *Sonchi* is characterised by subcylindrical, broadly ovoid, broadly ellipsoid or obclavate, (medium) large conidia, single or in short chains, with multiple transverse and few longitudinal septa, slightly constricted at the septa, with a blunt taper which can form secondary conidiophores.

Notes: The species-group was described by Hong et al. (2005) based on molecular data of the GAPDH and Alt a 1 regions. Lawrence et al. (2013) included *A. brassicae* as a basal lineage in sect. *Sonchi*, which is supported as a monotypic lineage in our analyses. The species from section *Sonchi* occur on multiple hosts within the Compositae.

**Alternaria cinerariae** Hori & Enjoji, J. Pl. Protect. 18: 432. 1931.  
**Alternaria sonchi** Davis, in Elliott, Bot. Gaz. 62: 416. 1916.

**Section Teretispora** (E.G. Simmons) Woudenb. & Crous, comb. et stat. nov. MycoBank MB803745. Fig. 23.
Fig. 21. Alternaria sect. Radicina: conidia and conidiophores. A–C. A. carotinincultae. D–E. A. petroselini. F–G. A. radicina. H–I. A. selini. J–L. A. smyrnii. Scale bars = 10 µm.

Fig. 22. Alternaria sect. Sonchi: conidia and conidiophores. A–B. A. cinerariae. C–D. A. sonchi. Scale bars = 10 µm.
Basionym: Teretispora E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 674. 2007.

Type species: Alternaria leucanthemi Nelen

Diagnosis: Section Teretispora is characterised by simple conidiophores, sometimes extending at the apex with one or two, geniculate, sympodial proliferations, bearing single, long cylindrical mature conidia lacking a beak portion, with many transverse and a few longitudinal septa, constricted at most of the transverse septa. Secondary conidiophores with a single conidium are rarely formed at the apex; instead, they may form from the base of the primary conidium.

Notes: The genus Teretispora had Teretispora leucanthemi, formerly Alternaria leucanthemi (= Alternaria chrysanthemi), as type and only species (Simmons 2007). We choose to treat this as a section, which retains the name Teretispora, rather than a monotypic lineage.

Alternaria leucanthemi Nelen, in Nelen & Vasiljeva, Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Akad. Nauk S.S.S.R. 15: 148. 1962. ≡ Teretispora leucanthemi Nelen, Bull. Centr. Bot. Gard. (Moscow) 35: 83. 1959. (nom. inval., Art. 36.1) ≡ Alternaria chrysanthemi E.G. Simmons & Crosier, Mycologia 57: 142. 1965.

Section Ulocladioides Woudenb. & Crous, sect. nov. MycoBank MB803746. Fig. 24.

Type species: Alternaria cucurbitae Letendre & Roum.

Diagnosis: Section Ulocladioides is characterised by conidiophores with short, geniculate, sympodial proliferations. Conidia are obvoid, non-beaked with a narrow base, single or in chains, which may form secondary conidiophores at the apex.

Note: Section Ulocladioides resembles section Ulocladium and contains the majority of the species included in this study from the genus Ulocladium (11/17).

Alternaria atra (Preuss) Woudenb. & Crous, comb. nov. MycoBank MB803717.

Basionym: Ulocladium atra Preuss, Linnaea 25: 75. 1852. ≡ Stempyltium atra (Preuss) Sacc., Syll. Fungorum (Abellini) 4: 520. 1886.

Alternaria brassicae-pekinesis Woudenb. & Crous, nom. nov. MycoBank MB803723.

Basionym: Ulocladium brassicae Yong Wang bi & X.G. Zhang, Mycologia 100: 457. 2008, non Alternaria brassicae (Berk.) Sacc., 1880.

Etymology: Name refers to the host from which it was originally isolated.

Alternaria cantlous (Yong Wang bi & X.G. Zhang) Woudenb. & Crous, comb. nov. MycoBank MB803719.

Basionym: Ulocladium cantlous Yong Wang bi & X.G. Zhang, Mycologia 102: 376. 2010.

Alternaria consortialis (Thüm.) J.W. Groves & S. Hughes [as “consortiale”], Canad. J. Bot. 31: 636. 1953.

Basionym: Macrosporium consortiale Thüm., Herb. Mycol. Oecon. 9: no. 450. 1876. ≡ Stempnylum consortiale (Thüm.) J.W. Groves & Skolko, Canad. J. Res., Sect. C, Bot. Sci.: 196. 1944. ≡ Pseudostempnylum consortiale (Thüm.) Subram., Curr. Sci. 30: 423. 1961. ≡ Ulocladium consortiale (Thüm.) E.G. Simmons, Mycologia 59: 84. 1967. ≡ Stempnylum ilicis Tengwall, Meded. Phytopathol. Lab. “Willie Commmelin Scholten” 6: 44. 1924.

Alternaria cucurbitae Letendre & Roum., in Roumeguère, Rev. Mycol. (Toulouse) 8 (no. 30): 93. 1886. ≡ Ulocladium cucurbitae (Letendre & Roum.) E.G. Simmons, Mycotaxon 14: 48. 1982.

Alternaria heterospora Woudenb. & Crous, nom. nov. MycoBank MB803724.

Basionym: Ulocladium solani Yong Wang bi & X.G. Zhang, Mycol. Progr. 8: 209. 2009, non Alternaria solani Sorauer, 1896.

Etymology: Name refers to the various conidial morphologies observed during growth.

Alternaria multiformis (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803720.

Basionym: Ulocladium multiforme E.G. Simmons, Canad. J. Bot. 76: 1537. 1999 [1998].

Alternaria obovoidea (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803721.

Basionym: Ulocladium obovoideum E.G. Simmons, Mycotaxon 37: 104. 1990.

Alternaria subcucurbitae (Yong Wang bi & X.G. Zhang) Woudenb. & Crous, comb. nov. MycoBank MB803722.

Basionym: Ulocladium subcucurbitae Yong Wang bi & X.G. Zhang, Mycologia 100: 456. 2008.

Fig. 23. Alternaria sect. Teretispora: conidia and conidiophores. A–D. A. leucanthemi. Scale bars = 10 µm.
Fig. 24. Alternaria sect. Ulocladioides: conidia and conidiophores. A–B. A. atra. C–D. A. brassicae-pekinensis. E–F. A. canthous. G–H. A. multiformis. I–J. A. obovoidea. K–L. A. heterospora. M–N. A. subcucurbitae. O–P. A. terricola. Scale bars = 10 µm.
**Alternaria terricola** Woudenb. & Crous, nom. nov. MycoBank MB803725.

*Basionym:* *Ulocladium tuberculatum* E.G. Simmons, Mycologia 59: 83. 1967, non *Alternaria tuberculata* M. Zhang & T.Y. Zhang, 2006.

*Etymology:* Name refers to soil from which it was originally isolated.

*Section Ulocladium* (Preuss) Woudenb. & Crous, comb. et stat. nov. MycoBank MB803747. Fig. 25.

*Basionym:* *Ulocladium* Preuss, Linnaea 24: 111. 1851.

*Type species:* *Alternaria botrytis* (Preuss) Woudenb. & Crous

*Diagnosis:* Section *Ulocladium* is characterised by simple conidiophores, or with one or two short, geniculate, sympodial proliferations, with (mostly) single, obovoid, non-beaked conidia with a narrow base.

*Notes:* Section *Ulocladium* resembles sect. *Ulocladioides.* The epitype of *Ulocladium,* *U. botrytis* CBS 197.67, and the isotype of *U. oudemansii* (CBS 114.07) cluster with the *Sinomyces* representative, as do many other strains stored as *U. botrytis* in the CBS collection (data not shown). Furthermore, a strain stored as *A. capsici-annui* (CBS 504.74) in the CBS collection clusters within the *Sinomyces* clade and displays identical morphological features.

*Alternaria alternariae* (Cooke) Woudenb. & Crous, comb. nov. MycoBank MB803716.

*Basionym:* *Sporidesmium alternariae* Cooke, Handb. Brit. Fungi 1: 1440. 1871.

≡ *Stemphylium alternariae* (Cooke) Sacc., Syll. Fungorum (Abellini) 4: 523. 1886.

≡ *Ulocladium alternariae* (Cooke) E.G. Simmons, Mycologia 59: 82. 1967.

≡ *Sinomyces alternariae* (Cooke) Yong Wang bis & X.G. Zhang, Fungal Biol. 115: 194. 2011.

*Alternaria botrytis* (Preuss) Woudenb. & Crous, comb. nov. MycoBank MB803718.

*Basionym:* *Ulocladium botrytis* Preuss, Linnaea 24: 111. 1851.

≡ *Stemphylium botryosum* var. *ulocladium* Sacc. (nom. nov.), Syll. Fungorum (Abellini) 4: 522. 1886.

≡ *Stemphylium botryosum* var. *botrytis* (Preuss) Lindau, Rabenhorst's. Kryptog.-Fl., Edn 2 (Leipzig) 1(9): 219. 1908.

*Alternaria capsici-annui* Săvul. & Sandu, Hedwigia 75: 228. 1936.

*Alternaria oudemansii* (E.G. Simmons) Woudenb. & Crous, comb. nov. MycoBank MB803715.

*Basionym:* *Ulocladium oudemansii* E.G. Simmons, Mycologia 59: 86. 1967.

*Section Undifilum* (B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl.) Woudenb. & Crous, comb. et stat. nov. MycoBank MB803748. Fig. 26.

*Basionym:* *Undifilum* B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 190. 2009.

*Type species:* *Alternaria bornmuelleri* (Magnus) Woudenb. & Crous

*Diagnosis:* Section *Undifilum* is characterised by ovate to obclavate to long ellipsoid, straight to inequilateral, single, transseptate conidia;

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**Fig. 25.** Alternaria sect. Ulocladium: conidia and conidiophores. A–B. *A. capsici-annui.* C–D. *A. oudemansii.* E–F. *A. alternariae.* G–H. *A. botrytis.* Scale bars = 10 µm.
septa can be thick, dark and rigid, and form unique germ tubes, which are wavy or undulate until branching. Species of this section occur on Fabaceae and almost all produce the toxic compound swaisonine.

Notes: Section Undifilum shares morphological features with section Embellisia, but is characterised by the formation of a wavy germ tube upon germination (Pryor et al. 2009). Based on previous studies, the swaisonine producing species U. oxytropis (Pryor et al. 2009, Lawrence et al. 2012), U. fulvum and U. cinereum (Baucom et al. 2012) also belong to this section, although the type species, A. bornmuelleri, does not produce swaisonine.

**Alternaria bornmuelleri** (Magnus) Woudenb. & Crous, **comb. nov.** MycoBank MB803726.
Basionym: Helminthosporium bornmuelleri Magnus, Hedwigia 38 (Beibl.): 73. 1899.
≡ Undifilum bornmuelleri (Magnus) B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 190. 2009.

**Alternaria cinerea** (Baucom & Creamer) Woudenb. & Crous, **comb. nov.** MycoBank MB803731.
Basionym: Undifilum cinereum Baucom & Creamer, Botany 90: 872. 2012

**Alternaria fulva** (Baucom & Creamer) Woudenb. & Crous, **comb. nov.** MycoBank MB803732.
Basionym: Undifilum fulvum Baucom & Creamer, Botany 90: 871. 2012

**Alternaria oxytropis** (Q. Wang, Nagao & Kakish.) Woudenb. & Crous, **comb. nov.** MycoBank MB803727.
Basionym: Embellisia oxytropis Q. Wang, Nagao & Kakish., Mycotaxon 95: 257. 2006.
≡ Undifilum oxytropis (Q. Wang, Nagao & Kakish.) B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 191. 2009.

Monotypic lineages

The following six species are not assigned to one of the 24 above described Alternaria sections and are treated as separate, single species, lineages in this study. Future studies, including more and/or new Alternaria species, might eventually give rise to the formation of new sections, when these new species show to be closely related to one of these monotypic lineages.

**Alternaria argyranthemi** E.G. Simmons & C.F. Hill, Mycotaxon 65: 32. 1997.

**Paradendryphiella** Woudenb. & Crous, **gen. nov.** MycoBank MB803750. Fig. 27.

Colonies on SNA effuse, entire, velvety, olivaceous. Reverse olivaceous-grey to iron-grey. Mycelium consisting of branched, septate hypha, (sub)hyaline, smooth. Conidiophores subhyaline, simple or branched, septate or not, straight or flexuous, often nodose with conspicuous, brown pigmentation at the apical region; at times reduced to conidiogenous cells. Conidiogenous cells terminal or lateral, with denticles aggregated at apex, with prominent conidial scars, thickened but not darkened; sometimes proliferating with a new head or a short, inconspicuous sympodial rachis. Conidia produced holoblastically, on narrow denticle, smooth, cylindrical to obclavate, straight or slightly flexuous, 1–7 transverse septa, pale to medium brown, often with dark septa (often constricted), and a darkened zone of pigmentation at the apex, and at the hilum, which is thickened, and somewhat protruding, with a minute marginal frill. Chlamydospores and sexual state not observed.

Type species: Paradendryphiella salina (G.K. Sutherl.) Woudenb. & Crous

**Paradendryphiella salina** (G.K. Sutherl.) Woudenb. & Crous, **comb. nov.** MycoBank MB803751.
Basionym: Cercospora salina G.K. Sutherl., New Phytol. 15: 43. 1916.
≡ Dendryphiella salina (G.K. Sutherl.) Pugh & Nicot, Trans. Brit. Mycol. Soc. 47(2): 266. 1964.
≡ Scolecobasidium salinum (G.K. Sutherl.) M.B. Ellis, More dematiaceous hyphomycetes (Kew): 192. 1976.
to be described of which three would be monotypic; to create a stable phylogenetic taxonomy, seven new genera need internal clades (sections) and three monotypic lineages. In order in our phylogenies, this would leave an Alternaria. If we take this node as cut-off for the genus, (2013) elevated the asexual species-groups to sections within A. infectoria together with Alternaria clade. By resolving these eight asexual phylogenetic lineages of Ulocladium groups and an clade A by the authors, supports eight “asexual” ATPase and calmodulin (Lawrence et al. 2003, Inderbitzin 2006, Pryor et al. 2009, Runa et al. 2009, Wang et al. 2011, Lawrence et al. 2012). The only phylogenetic study which displays a second fully supported node is based on a five-gene combined dataset of GAPDH, Alt a 1, actin, plasma membrane ATPase and calmodulin (Lawrence et al. 2013). This node, called clade A by the authors, supports eight “asexual” Alternaria species-groups and an Ulocladium (sect. Ulocladioideae in our phylogenies) clade. By resolving these eight asexual phylogenetic lineages of Alternaria together with Ulocladium, which is sister to the sexual A. infectoria species-group and other sexual genera, Lawrence et al. (2013) elevated the asexual species-groups to sections within Alternaria. If we take this node as cut-off for the genus Alternaria in our phylogenies, this would leave an Alternaria clade with 14 internal clades (sections) and three monotypic lineages. In order to create a stable phylogenetic taxonomy, seven new genera need to be described of which three would be monotypic; E. dennissii, A. argyranthemi and A. soliaridae. Embellisia species would be assigned to five different genera of which four would be new, leaving only E. allii, E. chlamydospora and E. tellustris in the genus Embellisia. The well-known (medical) A. infectoria species-group would also have to be transferred to a new genus. This node is not supported in our study (0.98 PP /65 ML Fig 1) and also the strict asexual/sexual division is not supported as two sexual morphs are found in section Panax. This approach would therefore give rise to multiple small genera, and would not end up in a logical and workable situation.

Based on our phylogenetic study on parts of the SSU, LSU, ITS, GAPDH, RPB2 and TEF1 gene regions of ex-type and reference strains of Alternaria species and all available allied genera, we resolved a Pleospora/Stemphylium-clade sister to Embellisia annulata, and a well-supported Alternaria clade. The Alternaria clade contains 24 internal clades and six monotypic lineages. In combination with a review of literature and morphology, the species within the Alternaria clade are all recognised here as Alternaria s. str. This puts the genera Allewia, Brachycladium, Chalastospora, Chmelia, Crivellia, Embellisia, Lewia, Nimbya, Sinomyces, Teretispora, Ulocladium, Undilium and Ybotromyces in synonymy with Alternaria.

The support values for the different sections described in this study are plotted in a heatmap per gene/gene combination and phylogenetic method used (Table 2). This shows that the Bayesian method provides greater support than the Maximum Likelihood bootstrap support values, which is in congruence with previous reports (e.g. Douady et al. 2003). The sections Cheiranthus, Eureka and Nimbya have the lowest support values. For sect. Eureka this is mainly caused by the position of A. cuminii, which clusters within sect. Embellisioides based on its RPB2 sequence and as a monotypic lineage based on its TEF1 sequence. Section Cheiranthus and Nimbya are small sections, with relative long branches. Future studies, including more strains and/or species in these sections, are necessary to check the stability of these long branches.

The sexual genus Crivellia with its Brachycladium asexual morph was described by Inderbitzin et al. (2006) with Crivellia papaveraceae (asexual morph Brachycladium penicillatum) as type species and B. papaveris, with an unnamed sexual morph, as second species. The genus Brachycladium, which was synonymised

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\[ \text{Paradendryphiella arenariae} \ (\text{Woudenb. & Crous, comb. nov. MycoBank MB803752. Basionym: Dendryphiella arenariae Nicot, [as “arenaria”] Rev. Mycol. (Paris) 23: 93. 1958.} \]

\[ \equiv \text{Scolecosbasidium arenarium (Nicot) M.B. Ellis, More dematiaceous hyphomycetes (Kew): 194. 1976.} \]

DISCUSSION

The well-supported node for the Alternaria clade obtained in the present study, and the low bootstrap support at the deeper nodes within the Alternaria complex is also consistently seen in previous phylogenetic studies published on these genera (Pryor & Bigelow 2003, Inderbitzin et al. 2006, Pryor et al. 2009, Runa et al. 2009, Wang et al. 2011, Lawrence et al. 2012). The only phylogenetic study which displays a second fully supported node is based on a five-gene combined dataset of GAPDH, Alt a 1, actin, plasma membrane ATPase and calmodulin (Lawrence et al. 2013). This node, called clade A by the authors, supports eight “asexual” Alternaria species-groups and an Ulocladium (sect. Ulocladioideae in our phylogenies) clade. By resolving these eight asexual phylogenetic lineages of Alternaria together with Ulocladium, which is sister to the sexual A. infectoria species-group and other sexual genera, Lawrence et al. (2013) elevated the asexual species-groups to sections within Alternaria. If we take this node as cut-off for the genus Alternaria in our phylogenies, this would leave an Alternaria clade with 14 internal clades (sections) and three monotypic lineages. In order to create a stable phylogenetic taxonomy, seven new genera need to be described of which three would be monotypic; E. dennissii, A. argyranthemi and A. soliaridae. Embellisia species would be assigned to five different genera of which four would be new, leaving only E. allii, E. chlamydospora and E. tellustris in the genus Embellisia. The well-known (medical) A. infectoria species-group would also have to be transferred to a new genus. This node is not supported in our study (0.98 PP /65 ML Fig 1) and also the strict asexual/sexual division is not supported as two sexual morphs are found in section Panax. This approach would therefore give rise to multiple small genera, and would not end up in a logical and workable situation.

Based on our phylogenetic study on parts of the SSU, LSU, ITS, GAPDH, RPB2 and TEF1 gene regions of ex-type and reference strains of Alternaria species and all available allied genera, we resolved a Pleospora/Stemphylium-clade sister to Embellisia annulata, and a well-supported Alternaria clade. The Alternaria clade contains 24 internal clades and six monotypic lineages. In combination with a review of literature and morphology, the species within the Alternaria clade are all recognised here as Alternaria s. str. This puts the genera Allewia, Brachycladium, Chalastospora, Chmelia, Crivellia, Embellisia, Lewia, Nimbya, Sinomyces, Teretispora, Ulocladium, Undilium and Ybotromyces in synonymy with Alternaria.

The support values for the different sections described in this study are plotted in a heatmap per gene/gene combination and phylogenetic method used (Table 2). This shows that the Bayesian method provides greater support than the Maximum Likelihood bootstrap support values, which is in congruence with previous reports (e.g. Douady et al. 2003). The sections Cheiranthus, Eureka and Nimbya have the lowest support values. For sect. Eureka this is mainly caused by the position of A. cuminii, which clusters within sect. Embellisioides based on its RPB2 sequence and as a monotypic lineage based on its TEF1 sequence. Section Cheiranthus and Nimbya are small sections, with relative long branches. Future studies, including more strains and/or species in these sections, are necessary to check the stability of these long branches.

The sexual genus Crivellia with its Brachycladium asexual morph was described by Inderbitzin et al. (2006) with Crivellia papaveraceae (asexual morph Brachycladium penicillatum) as type species and B. papaveris, with an unnamed sexual morph, as second species. The genus Brachycladium, which was synonymised

Fig. 27. Paradendryphiella gen. nov.: conidia and conidiophores. A–B, D–E, G–I. P. salina. C, F. P. arenariae. Scale bars = 10 µm.

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with Dendryphion (Ellis 1971), was resurrected for the non-sexual stage based on polyphly within Dendryphion and morphological distinction from its type species, D. conosum. The type species of Brachycladium, B. penicillum, resides in Alternaria sect. Crivellia, which places Brachycladium in synonymy with Alternaria instead of Dendryphion.

The genus Chalastospora was established by Simmons (2007) based on Chalastospora cetera, formerly Alternaria cetera. Two new Chalastospora species, C. ellipsoidae and C. obclavata, and A. malorum as C. gossypii were later added to the genus, based on sequence data of the ITS and LSU regions (Crous et al. 2009c). The genus is characterised by conidia which are almost always narrowly ellipsoid to narrowly ovoid with 1–6 transverse eusepta, generally lacking oblique or longitudinal septa (Crous et al. 2009c). Our study shows that Alternaria armoraciae and Embellisia abundans also belong to this clade. Juvenile conidia of Alternaria armoraciae lacking oblique or longitudinal septa (Crous et al. 2009c). The description of sect. Chalastospora does therefore not completely follow the original description of the genus Chalastospora.

The genus Embellisia is characterised by the thick, dark, rigid conidial septa and the scarcity of longitudinal septa (Simmons 2007). It was first described by Simmons (1971), with Embellisia allii as type and E. chlamydospora as second species. Multiple Embellisia species followed after the description of the genus, which was later linked to the sexual genus Allewia (Simmons 1990). The latest molecular-based revision was performed based on sequences of the GAPDH, ITS and Alt a 1 genes (Lawrence et al. 2012). They found that Embellisia split into four clades and multiple species, which clustered individually amidst Alternaria, Ulocladium or Stemphyllium spp. Our results mostly support these data, but with the inclusion of more ex-type/representative strains of Alternaria some additions were made to the different Embellisia groups mentioned by Lawrence et al. (2012). Group I (sect. Embellisia) and III (sect. Embellisioideae) are identical to the treatment of Lawrence et al. (2012) but group II (section Phragmosporae) and IV (section Eureka) are both expanded with four Alternaria species. As not all species from group II and IV display the typical morphological characters of Embellisia, we chose to name these Alternaria sections based on the oldest species residing in the respective sections. Embellisia abundans was already mentioned as being part of the Chalastospora-clade and E. indefessa formed a clade close to Ulocladium, which we now assign to sect. Cheiranthus. Embellisia dennisii also forms a separate lineage in our phylogenies; therefore the old name Alternaria dennisii is resurrected. Furthermore, the clustering of E. conoidea within the brassicicola species-group and E. annulata close to Stemphyllium, now assigned as Paradendryphiella gen. nov., is confirmed by our phylogenetic data. The morphological character of thick, dark, rigid septa seems to have evolved multiple times and does not appear to be a valid character for taxonomic distinction at generic level.

The sexual morphs Lewia (Simmons 1986) and Alleria (Simmons 1990) were linked to Alternaria and Embellisia respectively, with the only difference between these genera being the morphology of their asexual morphs. Lewia chlamidosporiformans and L. sauropodis are transferred to the genus Leptosphaerulina (Simmons 2007), which leaves 11 Lewia species with a known Alternaria anamorph. Most of them (9/11) reside in sect. Infectoriae, the others are found in sect. Panax. Alleria only contains two species of which one resides in sect. Eureka and one in sect. Embellisioidei. With the establishment of the new International Code of Nomenclature for algae, fungi and plants (ICN), the dual nomenclature system for sexual and asexual fungal morphs was abandoned and replaced by a single-name nomenclature (Hawksworth et al. 2011, Norvell 2011). In order to implement the new rules of the ICN, we synonymized Lewia and Alleria with Alternaria.

Although multiple molecular studies included Nimbya isolates in their phylogenies (Chou & Wu 2002, Pryor & Bigelow 2003, Hong et al. 2005, Inderbitzin et al. 2006, Pryor et al. 2009), a more extensive molecular-based study was recently published by Lawrence et al. (2012). Based on sequences of the GAPDH, ITS and Alt a 1 genes, the authors found a Nimbya clade which contained the type species N. scirpifera together with N. scirpifera, N. scirpifera and N. carica. The N. scirpifera isolate which we included in our study, was assigned to this genus by Simmons (1989) based on morphological characters, as is the one used in other molecular studies (Pryor & Bigelow 2003, Hong et al. 2005, Lawrence et al. 2012). The sequences of the ITS, GAPDH and Alt a 1 genes of these isolates are however not identical, but do cluster in the same clade in the two phylogenies (data not shown), together with the isolate of N. carica. The N. gomphrenae isolate we included in our phylogeny was not representative of the name. Simmons mentioned in 1989 that Togashi (1926) described two different fungi and deposited the small-spored species in the CBS collection, instead of the large-spored N. gomphrenae isolate. Nimbya gomphrenae CBS 108.27, which does not sporulate anymore, will therefore be treated as “Alternaria sp.”, and resides in sect. Alternata. The ITS sequence of N. gomphrenae from Chou & Wu (2002) actually clusters within sect. Alternariae. This section was described by Lawrence et al. (2012) and consists of three Nimbya species, which they renamed to Alternaria based on the position of the clade amid the Alternaria species-groups. Based on the data from Chou & Wu (2002), the name Alternaria gomphrenae is resurrected and placed in sect. Alternariae.

The genus Sinomyces was described in by Wang et al. (2011) to accommodate Ulocladium alternariae and two new species from China, S. obovoieae and S. fusioideae (type). The genus was differentiating from Ulocladium based on its simple conidiophores with a single apical pore or 1–2 short, uniperforate, geniculate sympodial proliferations. Unfortunately, our DNA sequence analyses of the ex-type cultures of the two new species from China (CBS 124114 and CBS 123375) were not congruent with the GAPDH (both species) and Alt a 1 (S. obovoieae) sequences deposited in GenBank (data not shown), leading us to doubt the authenticity of these strains. This matter could not be resolved in spite of contacting the original depositors. The ex-type strain of S. alternariae (CBS 126989) was therefore included as representative of the genus Sinomyces. The presence of the epitype of Ulocladium, U. botrytis CBS 197.67, in this section resulted in us rejecting the name Sinomyces, and calling this sect. Ulocladium. In addition, the presence of U. oudemansii in this section, with conidiophores with 1–5 uniperforate geniculations (Simmons 1967), also disagrees with the mentioned differentiation of Sinomyces from Ulocladium.

The type species of Ulocladium, U. botrytis, was typified by two representative strains QM 7878 (CBS 197.67) and QM 8619 (CBS 198.67) (Simmons 1967). Molecular studies performed afterwards showed that these strains are not identical (de Hoog & Horré 2002). Most molecular studies performed used CBS 198.67
as representative of *U. botrytis* (Pyror & Gilbertson 2000, Pyror & Bigelow 2003, Hong et al. 2005, Xue & Zhang 2007, Pyror et al. 2009, Runa et al. 2009, Wang et al. 2010, Wang et al. 2011, Lawrence et al. 2012), which clusters in section Ulocladioides. However, de Hoog & Horré (2002) epitypified *U. botrytis* with CBS 197.67, which clusters with Synomyces strains, as does *Ulocladium oudemansii*, now named sect. *Ulocladium*. Extended phylogenetic analyses on all *U. botrytis* strains present in the CBS culture collection (16 isolates) also highlight this issue as they cluster either within sect. *Ulocladium* or sect. *Ulocladioides* (data not shown), both with one of the representative strains described by Simmonds (1967). The suggestion to synonymise *Ulocladium* with *Alternaria* has been made several times in the past (Pyror & Gilbertson 2000, Chou & Wu 2002). The latest systematic revision of the genus *Ulocladium* (Runa et al. 2009) based on sequences from the ITS, GAPDH and Alt a 1 genes supported previous findings of poly- and paraphyletic relationships of *Ulocladium* among *Alternaria*, *Embellisia* and *Stemphylium* spp. (de Hoog & Horré 2002, Pyror & Bigelow 2003, Hong et al. 2005). *Ulocladium alternariae* and *U. oudemansii*, now known as sect. *Ulocladium*, cluster separately. The core *Ulocladium* clade, containing the two sister clades now called sect. *Ulocladioides* and sect. *Pseudoulocladium*, was confirmed by later studies (Wang et al. 2010, Lawrence et al. 2012). *Alternaria cheiranthi* and *Embellisia indefessa* have been linked to *Ulocladium* (Pyror & Gilbertson 2000, Pyror & Bigelow 2003, Hong et al. 2005, Pyror et al. 2009, Runa et al. 2009, Lawrence et al. 2012), but missed the diagnostic feature of *Ulocladium*. Our study showed that they form a sister section, sect. *Cheiranthus*, to sect. *Ulocladioides*. The confusing taxonomy in this genus strengthens our decision to reduce *Ulocladium* to synonymy with *Alternaria*. The characteristics of the former genus *Ulocladium* are added to the new broader *Alternaria* generic circumscription.

The genus *Undifilum* was described by Pyror et al. (2009) to accommodate the species *U. oxytropis* and *U. bornmuelleri*. It shares the morphological feature of thick, dark and rigid septa with the genus *Embellisia*, but was characterised by the formation of a wavy germ-tube upon germination (Pyror et al. 2009). A recent study on fungal endophytes in locoweed in the US described two new *Undifilum* species (Baucom et al. 2012). Both new species produce the toxic compound swaisonine, which is also produced by *U. oxytropis*. Swaisonine is the cause of a neurological disease, locism, of grazing animals, resulting in economic losses in livestock (James & Panter 1989). The production of swaisonine seems to be related to this section, although the type-species, *U. bornmuelleri*, does not produce this toxin.

The genus *Ybotromyces* contains one species, *Y. caespitosus* (originally *Botryomyces caespitosus*), which was isolated from a skin lesion of a human patient (de Hoog & Rubio 1982). De Hoog et al. (1997) discovered a high similarity to *Alternaria* spp. based on restriction patterns of the ITS and SSU rDNA. A phylogeny study of melanised meristematic fungi based on their SSU and ITS rDNA sequences (Sterflinger et al. 1999) placed *Y. caespitosus* within the *Pleosporales* together with *Alternaria* and *Pleospora*. De Hoog & Horré (2002) hypothesized that the ex-type strain of *Y. caespitosus*, CBS 177.80, is likely a synanamorph of a yet undescribed *Alternaria* species. Our phylogeny supports this hypothesis, and places the genus in sect. *Infectoriae*.

*Chmelia slovaca*, described from dermatic lesions of a human (Svobodová 1966), also clusters with sect. *Infectoriae* as was shown previously (de Hoog & Horré 2002). The genus produces different types of chlamydospores and sporadically blastospores, but no conidia or conidiophores, which makes it difficult to identify based on morphology. De Hoog & Horré (2002) were confident that *Chmelia* is a sterile member of *A. infectoria*, which is in agreement with our results.

**Genera unrelated to Alternaria**

The placement of the sexual genus *Pleospora* (1863) with *Stemphylium* (1833) asexual morphs as basal sister clade to the *Alternaria* complex is well-documented in multiple molecular studies (Chou & Wu 2002, Pyror & Bigelow 2003, Hong et al. 2005, Pyror et al. 2009, Lawrence et al. 2012). Therefore, we only included the type species of both genera in our phylogenies and used them as outgroup in the *Alternaria* phylogeny. *Pleospora herbarum* with its *Stemphylium herbarum* (CBS 191.86) asexual morph is the type species of the genus *Pleospora*. *Stemphylium botryosum* with its *Pleospora tarda* (CBS 714.68) sexual morph is the type species of the genus *Stemphylium*.

*Embellisia annulata* proved to be identical to the marine species *Dendryphiella salina*, and forms a well-supported clade in the *Pleosporaceae* together with *D. arenariae*. Several DNA-based studies ( dela Cruz 2006, Jones et al. 2008, Zhang et al. 2009) concluded that the marine *Dendryphiella* species, *D. arenariae* and *D. salina*, belonged to the *Pleosporaceae* as sister clade to the *Pleospora/Stemphylium* complex. Furthermore, they showed the type species of *Dendryphiella*, *D. vinosa*, to be only distantly related, based on sequences of the ITS, SSU, LSU (Jones et al. 2008) and ITS, TEF1, and RP1B2 (dela Cruz 2006) gene regions. The transfer of the marine *Dendryphiella* species to *Scolecosbasidium* (Ellis 1976), was also disputed. *Scolecosbasidium* does not belong to the *Pleosporales* based on ITS, TEF1, and RP1B2 sequences (dela Cruz 2006) and the morphology of the two *Dendryphiella* species does not fit the generic circumscription of *Scolecosbasidium* (dela Cruz 2006, Jones et al. 2008). Ellis (1976) described denticles on the conidigenous cells when the conidia become detached. However other observers describe a marginal basillar frill on the conidia after detachment, leaving a scar on the conidiophore. We propose to place the two species in the new genus *Paradendryphiella* as *C. arenariae* and *C. salina*. The need for a new genus to accommodate the two species was already suggested by Jones et al. (2008).

A recent study on *Diademaceae*, a family which is characterised by a flat circular operculum and bitunicate asc (Shoemaker & Babcock 1992), excluded the sexual genera *Comoclathris* and *Clathrospora*, and ( provisionally) placed them in the *Pleosporaceae* with alternaria-like asexual morphs (Zhang et al. 2011). Molecular data of two strains (Dong et al. 1998, Sich et al. 2009) placed them within the *Pleosporaceae*. A confusing factor is that Dong et al. (1998) use the name *Comoclathris baccata* in their paper for strain CBS 175.52, but submitted their sequences under the name *Clathrospora diplospora* to GenBank. Shoemaker & Babcock (1992) synonymised *Clathrospora diplospora* with *Comoclathris baccata*, which renders *Comoclathris* as the correct generic name. The confusion around these genera is illustrated by the fact that the CBS collection currently harbours six strains named as *Clathrospora* species of which four were renamed by Shoemaker & Babcock in 1992 based on morphological studies, and three of these four strains were even transferred to the genus *Comoclathris*. The type species of *Clathrospora*, *C. elynae* is represented by two strains of which one, CBS 196.54, was also studied morphologically by Shoemaker and Babcock (1992). They form a well-supported clade, located basal to the *Pleosporaceae*.
Alternaria redefined

In the type species, Pantospora guazumae, Pantospora belongs to the complex and that this genus is clearly not part of the Helminthosporium helianthi group isolates. Both strains will be treated as "Alternaria sp."

The genus Alternariaster was first described by Simmons (2007) with Alternariaster helianthi, formerly Alternaria helianthi or Helminthosporium helianthi, as type and only species. It is distinct from Alternaria by the lack of a pigmented conspicuous internal, circumhilar ring in its conidia and conidiophores. Our study showed that this genus is clearly not part of the Alternaria complex and belongs to the Leptosphaeriaceae (Fig. 2) (Alves et al. 2013). In the recently published book "The genera of Hyphomycetes" (Seifert et al. 2011) three more genera are linked to Alternaria, namely Pantospora, Brianutonia and Rhexoprolifer. A recent study on Pantospora included ITS and LSU sequence data of the type species Pantospora guazumae, which placed the genus in Mycosphaerellaceae (Minnis et al. 2011). This refutes the link with Alternaria. The genus Rhexoprolifer was described in 1996 by Matsushima with R. variabilis as type and only species, isolated from South Africa. Rhexoprolifer variabilis has rhexolitic conidial liberation and proliferating conidiophores with both phragmosporous and dictyosporous conidia. Brianutonia was described in 2004 to accommodate Corynespora alternariae (Castañeda Ruiz et al. 2004). The distoseptate murriform conidia of Brianutonia do resemble Alternaria and Stemphylium, but the conidioconidiogenous loci and euseptate conidia of Alternaria and holoblastic conidial ontogeny and euseptate murriform conidia of Stemphylium were enough for the authors to regard their taxon as a different genus. Both asexual genera presently lack molecular data, and we were unable to obtain any living specimens of these taxa. It would be valuable to include both genera in a future study to resolve the connection among genera with murriform conidia and Alternaria.

The description of Alternaria s. str. in the present study is supported by i) a well-supported phylogenetic node in multiple analyses, ii) high similarity of clades within Alternarioidea based on SSU, LSU and ITS data, and iii) variation in the order of the clades between the different gene phylogenies, which is in congruence with low support values at these deeper nodes. We follow the precedence introduced by Lawrence et al. (2013) to assign the taxonomic status of sections of Alternaria for the different clades found, thus allowing us to retain the former generic names but associated with a different taxonomic status. For end-users, this also results in a more stable and understandable taxonomy and nomenclature.

DEDICATION

We would like to dedicate this manuscript to the late Dr E.G. Simmons, who spent over 50 years of his life researching the systematics of the genus Alternaria. Without the time EGS spent on characterising the species included in this study, and his impeccable strain collection, which he placed in CBS for preservation and further study, the present study would not have been possible.

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