Alternaria redefined

J.H.C. Woudenberg[1,2*], J.Z. Groenewald[1], M. Binder[1], and P.W. Crous[1,2,3]

[1]*CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands;* [2]*Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands;* [3]*Utrecht University, Department of Biology, Microbiology, Padualaan 8, 3584 CH Utrecht, The Netherlands*

*Correspondence: Joyce H.C. Woudenberg, j.woudenberg@cbs.knaw.nl

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 nrDNA, 28S nrDNA, 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*, *Brachycladium*, *Chalastospora*, *Chmelia*, *Crivellia*, *Embellisia*, *Lewia*, *Nimbya*, *Sinomyces*, *Teretispora*, *Ulocladium*, *Undifilum* 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 *Paradendryphiella*. 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*. *Paradendryphiella* 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*, *Paradendryphiella, Sinomyces*, systematics, *Teretispora*, *Ulocladium*, *Undifilum*.
Taxonomic novelties: New combinations – *Alternaria abundans* (E.G. Simmons) Woudenb. & Crous, *Alternaria alternariae* (Cooke) Woudenb. & Crous, *Alternaria atra* (Preuss) Woudenb. & Crous, *Alternaria bornmuelleri* (Magnus) Woudenb. & Crous, *Alternaria botrytis* (Preuss) Woudenb. & Crous, *Alternaria caespitosa* (de Hoog & C. Rubio) Woudenb. & Crous, *Alternaria cantlous* (Yong Wang bis & X.G. Zhang) Woudenb. & Crous, *Alternaria caricis* (E.G. Simmons) Woudenb. & Crous, *Alternaria cinerea* (Baucom & Creamer) Woudenb. & Crous, *Alternaria didymospora* (Munt.-Cvetk.) Woudenb. & Crous, *Alternaria fulva* (Baucom & Creamer) Woudenb. & Crous, *Alternaria hyacinthi* (de Hoog & P.J. Mull. bis) Woudenb. & Crous, *Alternaria indefessa* (E.G. Simmons) Woudenberg & Crous, *Alternaria leptinellae* (E.G. Simmons & C.F. Hill) Woudenb. & Crous, *Alternaria lolii* (E.G. Simmons & C.F. Hill) Woudenb. & Crous, *Alternaria multiformis* (E.G. Simmons) Woudenb. & Crous, *Alternaria obclavata* (Crous & U. Braun) Woudenb. & Crous, *Alternaria obovoidea* (E.G. Simmons) Woudenb. & Crous, *Alternaria oudemansii* (E.G. Simmons) Woudenb. & Crous, *Alternaria oxytropis (Q. Wang, Nagao & Kakish.)* Woudenb. & Crous, *Alternaria penicillata* (Corda) Woudenb. & Crous, *Alternaria planifunda* (E.G. Simmons) Woudenb. & Crous, *Alternaria proteae* (E.G. Simmons) Woudenb. & Crous, *Alternaria scirpinfestans* (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, *Alternaria scirpivora* (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, *Alternaria septospora* (Preuss) Woudenb. & Crous, *Alternaria slovaca* (Svob.-Pol., L. Chmel & Bojan.) Woudenb. & Crous, *Alternaria subcucurbitae* (Yong Wang bis & X.G. Zhang) Woudenb. & Crous, *Alternaria tellustris* (E.G. Simmons) Woudenb. & Crous, *Alternaria tumida* (E.G. Simmons) Woudenb. & Crous, *Paradendryphiella salina* (G.K. Sutherl.) Woudenb. & Crous, *Paradendryphiella arenariae* (Nicot) Woudenb. & Crous. **New names –** *Alternaria aspera* Woudenb. & Crous, *Alternaria botryospora* Woudenb. & Crous, *Alternaria brassicae-pekinensis* Woudenb. & Crous, *Alternaria breviramosa* Woudenb. & Crous, *Alternaria chlamydosporigena* Woudenb. & Crous, *Alternaria concatenata* Woudenb. & Crous, *Alternaria embellisia* 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 cucurbitae* Letendre & Roum., *Alternaria dennisii* M.B. Ellis, *Alternaria eureka* E.G. Simmons, *Alternaria gomphrenae* Togashi, *Alternaria malorum* (Ruehle) U. Braun, Crous & Dugan, *Alternaria phragmospora* Emden, *Alternaria scirpicola* (Fuckel) Sivan. **New sections, all in *Alternaria* –** sect. *Chalastospora* Woudenb. & Crous, sect. *Cheiranthus* Woudenb. & Crous, sect. *Crivellia* Woudenb. & Crous, sect. *Dianthicola* Woudenb. & Crous, sect. *Embellisia* Woudenb. & Crous, sect. *Embellisioides* Woudenb. & Crous, sect. *Eureka* Woudenb. & Crous, sect. *Infectoriae* Woudenb. & Crous, sect. *Japonicae* Woudenb. & Crous, sect. *Nimbya* Woudenb. & Crous, sect. *Phragmosporae* Woudenb. & Crous, sect. *Pseudoulocladium* Woudenb. & Crous, sect. *Teretispora* Woudenb. & Crous, sect. *Ulocladioides* Woudenb. & Crous, sect. *Ulocladium* Woudenb. & Crous, sect. *Undifilum* Woudenb. & Crous. **New genus –** *Paradendryphiella* 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. alternantherae* (Lawrence *et al.* 2012) and three new genera, *Crivellia* (Inderbitzin *et al.* 2006), *Undifilum* (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*, *Undifilum* 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 ºC. 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 ºC) 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 RPB2–5F2 (Sung *et al.* 2007) and fRPB2–7cR (Liu *et al.* 1999) and the TEF1 gene with the primers EF1-728F 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., Veenendaal, The Netherlands) in a total volume of 12.5 µL. The SSU and LSU PCR mixtures consisted of 1 µL genomic DNA, 1´ GoTaq® Flexi buffer (Promega, Madison, WI, USA), 2 µM $MgCl_2$, 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 $MgCl_2$, 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 35 cycles of 30 s at 94 ºC, 30 s at 48 ºC and 90 s at 72 ºC for SSU, LSU, ITS and 40 cycles of 30 s at 94 ºC, 30 s at 52 ºC / 59 ºC and 45 s at 72 ºC for TEF1 using respectively EF2 or EF1-986R as reverse primer and a final elongation step of 7 min at 72 ºC. 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 2 min at 72 ºC, followed by 5 cycles with a 58 ºC annealing temperature and 30 cycles with a 54 ºC annealing temperature. 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).

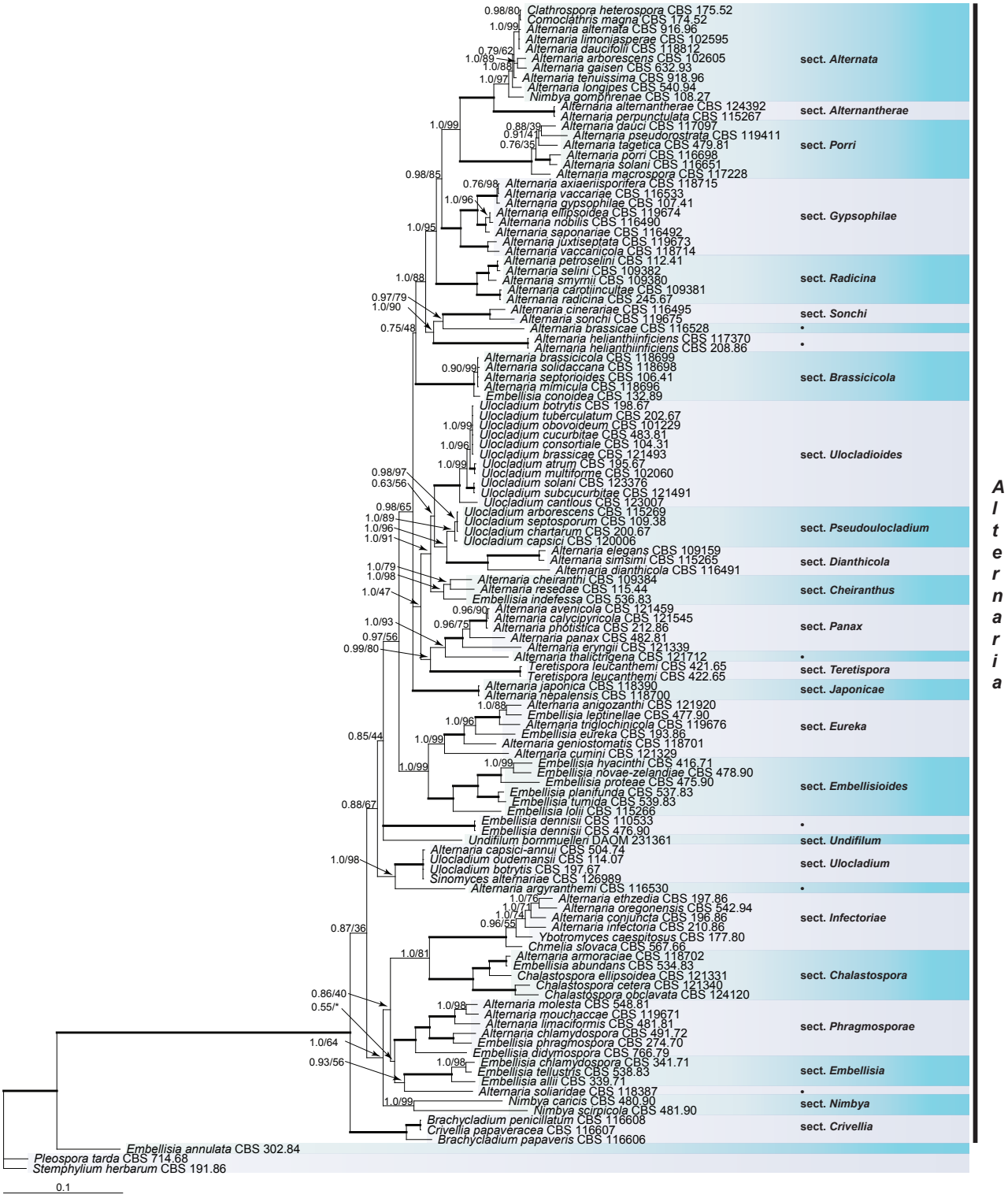

Fig. 1. Bayesian 50 % majority rule consensus tree based on the GAPDH, RPB2 and TEF1 sequences of 121 strains representing the *Alternaria* complex. The Bayesian posterior probabilities (PP) and RAxML bootstrap support values (ML) are given at the nodes (PP/ML). Thickened lines indicate a PP of 1.0 and 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 focusses on the *Alternaria* complex, the second one was produced to place the genera *Comoclathris*, *Clathrospora* and *Alternariaster* 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

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[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Alternaria alternantherae	*Alternaria alternantherae*	*Althernantherae*	CBS 124392		*Solanum melongena*	China	HSAUP2798	KC584506	KC584251	KC584374	KC584179	KC584096	KC584633
Alternaria alternata	*Alternaria alternata*	*Alternata*	CBS 916.96	T	*Arachis hypogaea*	India	EGS 34.016	KC584507	**DQ678082**	KC584375	**AF347031**	**AY278808**	KC584634
Alternaria anigozanthi	*Alternaria anigozanthi*	*Eureka*	CBS 121920	T	*Anigozanthus* sp.	Australia	EGS 44.066	KC584508	KC584252	KC584376	KC584180	KC584097	KC584635
Alternaria arborescens	*Alternaria arborescens*	*Alternata*	CBS 102605	T	*Lycopersicon esculentum*	USA	EGS 39.128	KC584509	KC584253	KC584377	**AF347033**	**AY278810**	KC584636
Alternaria argyranthemi	*Alternaria argyranthemi*		CBS 116530	T	*Argyranthemum* sp.	New Zealand	EGS 44.033	KC584510	KC584254	KC584378	KC584181	KC584098	KC584637
Alternaria armoraciae	*Alternaria armoraciae*	*Chalastospora*	CBS 118702	T	*Armoracia rusticana*	New Zealand	EGS 51.064	KC584511	KC584255	KC584379	KC584182	KC584099	KC584638
Alternaria avenicola	*Alternaria avenicola*	*Panax*	CBS 121459	T	*Avena sp.*	Norway	EGS 50.185	KC584512	KC584256	KC584380	KC584183	KC584100	KC584639
Alternaria axiaeriisporifera	*Alternaria axiaeriisporifera*	*Gypsophilae*	CBS 118715	T	*Gypsophila paniculata*	New Zealand	EGS 51.066	KC584513	KC584257	KC584381	KC584184	KC584101	KC584640
Alternaria brassicae	*Alternaria brassicae*		CBS 116528	R	*Brassica oleracea*	USA	EGS 38.032	KC584514	KC584258	KC584382	KC584185	KC584102	KC584641
Alternaria brassicicola	*Alternaria brassicicola*	*Brassicicola*	CBS 118699	R	*Brassica oleracea*	USA	EGS 42.002; ATCC 96836	KC584515	KC584259	KC584383	**JX499031**	KC584103	KC584642
Alternaria calycipyricola	*Alternaria calycipyricola*	*Panax*	CBS 121545	T	*Pyrus communis*	China	EGS 52.071; RGR 96.0209	KC584516	KC584260	KC584384	KC584186	KC584104	KC584643
Alternaria capsici-annui	*Alternaria capsici-annui*	*Ulocladium*	CBS 504.74		*Capsicum annuum*	–		KC584517	KC584261	KC584385	KC584187	KC584105	KC584644
Alternaria carotiincultae	*Alternaria carotiincultae*	*Radicina*	CBS 109381	T	*Daucus carota*	USA	EGS 26.010	KC584518	KC584262	KC584386	KC584188	KC584106	KC584645
Alternaria cheiranthi	*Alternaria cheiranthi*	*Cheiranthus*	CBS 109384	R	*Cheiranthus cheiri*	Italy	EGS 41.188	KC584519	KC584263	KC584387	**AF229457**	KC584107	KC584646
Alternaria chlamydospora	*Alternaria chlamydospora*	*Phragmosporae*	CBS 491.72	T	Soil	Egypt	EGS 31.060; ATCC 28045; IMI 156427	KC584520	KC584264	KC584388	KC584189	KC584108	KC584647
Alternaria cinerariae	*Alternaria cinerariae*	*Sonchi*	CBS 116495	R	*Ligularia* sp.	USA	EGS 49.102	KC584521	KC584265	KC584389	KC584190	KC584109	KC584648
Alternaria conjuncta	*Alternaria conjuncta*	*Infectoriae*	CBS 196.86	T	*Pastinaca sativa*	Switzerland	EGS 37.139	KC584522	KC584266	KC584390	**FJ266475**	**AY562401**	KC584649
Alternaria cumini	*Alternaria cumini*	*Eureka*	CBS 121329	T	*Cuminum cyminum*	India	EGS 04.158a	KC584523	KC584267	KC584391	KC584191	KC584110	KC584650
Alternaria dauci	*Alternaria dauci*	*Porri*	CBS 117097	R	*Daucus carota*	USA	EGS 46.006	KC584524	KC584268	KC584392	KC584192	KC584111	KC584651
Alternaria daucifolii	*Alternaria daucifolii*	*Alternata*	CBS 118812	T	*Daucus carota*	USA	EGS 37.050	KC584525	KC584269	KC584393	KC584193	KC584112	KC584652
Alternaria dianthicola	*Alternaria dianthicola*	*Dianthicola*	CBS 116491	R	Dianthus × allwoodii	New Zealand	EGS 51.022	KC584526	KC584270	KC584394	KC584194	KC584113	KC584653
Alternaria elegans	*Alternaria elegans*	*Dianthicola*	CBS 109159	T	*Lycopersicon esculentum*	Burkina Faso	EGS 45.072; IMI 374542	KC584527	KC584271	KC584395	KC584195	KC584114	KC584654
Alternaria ellipsoidea	*Alternaria ellipsoidea*	*Gypsophilae*	CBS 119674	T	*Dianthus barbatus*	USA	EGS 49.104	KC584528	KC584272	KC584396	KC584196	KC584115	KC584655
Alternaria eryngii	*Alternaria eryngii*	*Panax*	CBS 121339	R	*Eryngium* sp.	–	EGS 41.005	KC584529	KC584273	KC584397	**JQ693661**	**AY562416**	KC584656
Alternaria ethzedia	*Alternaria ethzedia*	*Infectoriae*	CBS 197.86	T	*Brassica napus*	Switzerland	EGS 37.143	KC584530	KC584274	KC584398	**AF392987**	**AY278795**	KC584657
Alternaria gaisen	*Alternaria gaisen*	*Alternata*	CBS 632.93	R	*Pyrus pyrifolia* cv. Nijiseiki	Japan	EGS 90.512	KC584531	KC584275	KC584399	KC584197	KC584116	KC584658

Table 1. (Continued).

Old species name	New species name	*Alternaria* Section	Strain number[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Alternaria geniostomatis	*Alternaria geniostomatis*	*Eureka*	CBS 118701	T	*Geniostoma* sp.	New Zealand	EGS 51.061	KC584532	KC584276	KC584400	KC584198	KC584117	KC584659
Alternaria gypsophilae	*Alternaria gypsophilae*	*Gypsophilae*	CBS 107.41	T	*Gypsophila elegans*	–	EGS 07.025; IMI 264349	KC584533	KC584277	KC584401	KC584199	KC584118	KC584660
Alternaria helianthiinficiens	*Alternaria helianthiinficiens*		CBS 117370	R	*Helianthus annuus*	UK	EGS 50.174; IMI 388636	KC584534	KC584278	KC584402	KC584200	KC584119	KC584661
Alternaria helianthiinficiens	*Alternaria helianthiinficiens*		CBS 208.86	T	*Helianthus annuus*	USA	EGS 36.184	KC584535	KC584279	KC584403	**JX101649**	KC584120	**EU130548**
Alternaria infectoria	*Alternaria infectoria*	*Infectoriae*	CBS 210.86	T	*Triticum aestivum*	UK	EGS 27.193	KC584536	KC584280	KC584404	**DQ323697**	**AY278793**	KC584662
Alternaria japonica	*Alternaria japonica*	*Japonicae*	CBS 118390	R	*Brassica chinensis*	USA	EGS 50.099	KC584537	KC584281	KC584405	KC584201	KC584121	KC584663
Alternaria juxtiseptata	*Alternaria juxtiseptata*	*Gypsophilae*	CBS 119673	T	*Gypsophila paniculata*	Australia	EGS 44.015; DAR 43414	KC584538	KC584282	KC584406	KC584202	KC584122	KC584664
Alternaria limaciformis	*Alternaria limaciformis*	*Phragmosporae*	CBS 481.81	T	Soil	UK	EGS 07.086; IMI 052976; QM 1790	KC584539	KC584283	KC584407	KC584203	KC584123	KC584665
Alternaria limoniasperae	*Alternaria limoniasperae*	*Alternata*	CBS 102595	T	*Citrus jambhiri*	USA	EGS 45.100	KC584540	KC584284	KC584408	**FJ266476**	**AY562411**	KC584666
Alternaria longipes	*Alternaria longipes*	*Alternata*	CBS 540.94	R	*Nicotiana tabacum*	USA	EGS 30.033; QM 9589	KC584541	KC584285	KC584409	**AY278835**	**AY278811**	KC584667
Alternaria macrospora	*Alternaria macrospora*	*Porri*	CBS 117228	T	*Gossypium barbadense*	USA	EGS 50.190	KC584542	KC584286	KC584410	KC584204	KC584124	KC584668
Alternaria mimicula	*Alternaria mimicula*	*Brassicicola*	CBS 118696	T	*Lycopersicon esculentum*	USA	EGS 01.056; QM 26a	KC584543	KC584287	KC584411	**FJ266477**	**AY562415**	KC584669
Alternaria molesta	*Alternaria molesta*	*Phragmosporae*	CBS 548.81	T	*Phocaena phocaena*	Denmark	EGS 32.075	KC584544	KC584288	KC584412	KC584205	KC584125	KC584670
Alternaria mouchaccae	*Alternaria mouchaccae*	*Phragmosporae*	CBS 119671	T	Soil	Egypt	EGS 31.061	KC584545	KC584289	KC584413	KC584206	**AY562399**	KC584671
Alternaria nepalensis	*Alternaria nepalensis*	*Japonicae*	CBS 118700	T	*Brassica* sp.	Nepal	EGS 45.073; IMI 374543	KC584546	KC584290	KC584414	KC584207	KC584126	KC584672
Alternaria nobilis	*Alternaria nobilis*	*Gypsophilae*	CBS 116490	R	*Dianthus caryophyllus*	New Zealand	EGS 51.027; NZMAF Lynfield 743	KC584547	KC584291	KC584415	KC584208	KC584127	KC584673
Alternaria oregonensis	*Alternaria oregonensis*	*Infectoriae*	CBS 542.94	T	*Triticum aestivum*	USA	EGS 29.194	KC584548	KC584292	KC584416	**FJ266478**	**FJ266491**	KC584674
Alternaria panax	*Alternaria panax*	*Panax*	CBS 482.81	R	*Aralia racemosa*	USA	EGS 29.180	KC584549	KC584293	KC584417	KC584209	KC584128	KC584675
Alternaria perpunctulata	*Alternaria perpunctulata*	*Althernantherae*	CBS 115267	T	*Alternanthera philoxeroides*	USA		KC584550	KC584294	KC584418	KC584210	KC584129	KC584676
Alternaria petroselini	*Alternaria petroselini*	*Radicina*	CBS 112.41	T	*Petroselinum sativum*	–	EGS 06.196	KC584551	KC584295	KC584419	KC584211	KC584130	KC584677
Alternaria photistica	*Alternaria photistica*	*Panax*	CBS 212.86	T	*Digitalis purpurea*	UK	EGS 35.172	KC584552	KC584296	KC584420	KC584212	KC584131	KC584678
Alternaria porri	*Alternaria porri*	*Porri*	CBS 116698	R	*Allium cepa*	USA	EGS 48.147	KC584553	KC584297	KC584421	**DQ323700**	KC584132	KC584679

Table 1. (Continued).

Old species name	New species name	*Alternaria* Section	Strain number[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Alternaria pseudorostrata	*Alternaria pseudorostrata*	*Porri*	CBS 119411	T	*Euphorbia pulcherrima*	USA	EGS 42.060	KC584554	KC584298	KC584422	**JN383483**	**AY562406**	KC584680
Alternaria radicina	*Alternaria radicina*	*Radicina*	CBS 245.67	T	*Daucus carota*	USA	EGS 03.145; ATCC 6503; IMI 124939; QM 1301; QM 6503	KC584555	KC584299	KC584423	KC584213	KC584133	KC584681
"Alternaria resedae"	*Alternaria* sp.	*Cheiranthus*	CBS 115.44		*Reseda odorata*	–	EGS 07.030	KC584556	KC584300	KC584424	KC584214	KC584134	KC584682
Alternaria saponariae	*Alternaria saponariae*	*Gypsophilae*	CBS 116492	R	*Saponaria officinalis*	USA	EGS 49.199	KC584557	KC584301	KC584425	KC584215	KC584135	KC584683
Alternaria selini	*Alternaria selini*	*Radicina*	CBS 109382	T	*Petroselinum crispum*	Saudi Arabia	EGS 25.198; IMI 137332	KC584558	KC584302	KC584426	**AF229455**	**AY278800**	KC584684
Alternaria septorioides	*Alternaria septorioides*	*Brassicicola*	CBS 106.41	T	*Reseda odorata*	Netherlands	EGS 52.089; MUCL 20298	KC584559	KC584303	KC584427	KC584216	KC584136	KC584685
Alternaria simsimi	*Alternaria simsimi*	*Dianthicola*	CBS 115265	T	*Sesamum indicum*	Argentina	EGS 13.110	KC584560	KC584304	KC584428	**JF780937**	KC584137	KC584686
Alternaria smymii	*Alternaria smyrnii*	*Radicina*	CBS 109380	R	*Smyrnium olusatrum*	UK	EGS 37.093	KC584561	KC584305	KC584429	**AF229456**	KC584138	KC584687
Alternaria solani	*Alternaria solani*	*Porri*	CBS 116651	R	*Solanum tuberosum*	USA	EGS 45.020	KC584562	KC584306	KC584430	KC584217	KC584139	KC584688
Alternaria soliaridae	*Alternaria soliaridae*		CBS 118387	T	Soil	USA	EGS 33.024	KC584563	KC584307	KC584431	KC584218	KC584140	KC584689
Alternaria solidaccana	*Alternaria solidaccana*	*Brassicicola*	CBS 118698	T	Soil	Bangladesh	EGS 36.158; IMI 049788	KC584564	KC584308	KC584432	KC584219	KC584141	KC584690
Alternaria sonchi	*Alternaria sonchi*	*Sonchi*	CBS 119675	R	*Sonchus asper*	Canada	EGS 43.131; IMI 366167	KC584565	KC584309	KC584433	KC584220	KC584142	KC584691
Alternaria tagetica	*Alternaria tagetica*	*Porri*	CBS 479.81	R	*Tagetes erecta*	UK	EGS 33.081	KC584566	KC584310	KC584434	KC584221	KC584143	KC584692
Alternaria tenuissima	*Alternaria tenuissima*	*Alternata*	CBS 918.96	R	*Dianthus* sp.	UK	EGS 34.015	KC584567	KC584311	KC584435	**AF347032**	**AY278809**	KC584693
Alternaria thalictrigena	*Alternaria thalictrigena*		CBS 121712	T	*Thalictrum* sp.	Germany		KC584568	KC584312	KC584436	**EU040211**	KC584144	KC584694
Alternaria triglochinicola	*Alternaria triglochinicola*	*Eureka*	CBS 119676	T	*Triglochin procera*	Australia	EGS 41.070	KC584569	KC584313	KC584437	KC584222	KC584145	KC584695
Alternaria vaccariae	*Alternaria vaccariae*	*Gypsophilae*	CBS 116533	R	*Vaccaria hispanica*	USA	EGS 47.108	KC584570	KC584314	KC584438	KC584223	KC584146	KC584696
Alternaria vaccariicola	*Alternaria vaccariicola*	*Gypsophilae*	CBS 118714	T	*Vaccaria hispanica*	USA	EGS 46.003; ATCC 26038	KC584571	KC584315	KC584439	KC584224	KC584147	KC584697
Alternariaster helianthi	*Alternariaster helianthi*		CBS 119672	R	*Helianthus* sp.	USA	EGS 36.007	KC584626	KC584368	KC584493			
Alternariaster helianthi	*Alternariaster helianthi*		CBS 327.69		*Helianthus annuus*	–		KC584627	KC584369	KC584494			
Ascochyta pisi	*Ascochyta pisi*		CBS 126.54		*Pisum sativum*	Netherlands		**EU754038**	**DQ678070**	**DQ677967**			
Boeremia exigua	*Boeremia exigua*		CBS 431.74		*Solanum tuberosum*	Netherlands	PD 74/2447	**EU754084**	**EU754183**	**GU371780**			
Brachycladium papaveris	*Alternaria papavericola*	*Crivellia*	CBS 116606	T	*Papaver somniferum*	USA		KC584579	KC584321	KC584446	**FJ357310**	**FJ357298**	KC584705
Brachycladium penicillatum	*Alternaria penicillata*	*Crivellia*	CBS 116608	T	*Papaver rhoeas*	Austria	DAOM 230457	KC584572	KC584316	KC584440	**FJ357311**	**FJ357299**	KC584698

Table 1. (Continued).

Old species name	New species name	*Alternaria* Section	Strain number[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Chaetodiplodia sp.	*Chaetodiplodia* sp.		CBS 453.68		*Halimione portulacoides*	Netherlands		**DQ678001**	**DQ678054**	KC584499			
Chaetosphaeronema hispidulum	*Chaetosphaeronema hispidulum*		CBS 216.75		*Anthyllis vulneraria*	Germany		**EU754045**	**EU754144**	**GU371777**			
Chalastospora cetera	*Alternaria cetera*	*Chalastospora*	CBS 121340	T	*Elymus scabrus*	Australia	EGS 41.072	KC584573	KC584317	KC584441	**JN383482**	**AY562398**	KC584699
Chalastospora ellipsoidea	*Alternaria breviramosa*	*Chalastospora*	CBS 121331	T	*Triticum* sp.	Australia		KC584574	KC584318	KC584442	**FJ839608**	KC584148	KC584700
Chalastospora obclavata	*Alternaria obclavata*	*Chalastospora*	CBS 124120	T	Air	USA	EGS 12.128	KC584575	**FJ839651**	KC584443	KC584225	KC584149	KC584701
Chmelia slovaca	*Alternaria slovaca*	*Infectoriae*	CBS 567.66	T	Human	Slovakia	ATCC 24279	KC584576	KC584319	KC584444	KC584226	KC584150	KC584702
Clathrospora elynae	*Clathrospora elynae*		CBS 161.51		*Carex curvula*	Switzerland		KC584628	KC584370	KC584495			
Clathrospora elynae	*Clathrospora elynae*		CBS 196.54		*Carex curvula*	Switzerland		KC584629	KC584371	KC584496			
Clathrospora heterospora	*Alternaria* sp.	*Alternata*	CBS 175.52		*Juncus mertensianus*	USA	EGS 35.1619; IMI 068085; QM 1277	KC584577	KC584320	KC584445	KC584227	KC584151	KC584703
Cochliobolus heterostrophus	*Cochliobolus heterostrophus*		CBS 134.39		*Zea mays*	–	DSM 1149	**AY544727**	**AY544645**	**DQ247790**			
Cochliobolus sativus	*Cochliobolus sativus*		DAOM 226212		*Hordeum vulgare*	Canada		**DQ677995**	**DQ678045**	**DQ677939**			
Comoclathris magna	*Alternaria* sp.	*Alternata*	CBS 174.52		*Anemone occidentalis*	USA	EGS 39.1613; IMI 068086; QM 1278	KC584578	**DQ678068**	**DQ677964**	KC584228	KC584152	KC584704
Comoclathris compressa	*Comoclathris compressa*		CBS 156.53		*Castilleja miniata*	USA	EGS No. C-20285-l	KC584630	KC584372	KC584497			
Comoclathris compressa	*Comoclathris compressa*		CBS 157.53		*Ligusticum purpureum*	USA	EGS No. 1952a-1633	KC584631	KC584373	KC584498			
Coniothyrium palmarum	*Coniothyrium palmarum*		CBS 400.71		*Chamaerops humilis*	Italy		**EU754054**	**EU754153**	**DQ677956**			
Crivellia papaveracea	*Alternaria penicillata*	*Crivellia*	CBS 116607	T	*Papaver rhoeas*	Austria	DAOM 230456	KC584580	KC584322	KC584447	KC584229	KC584153	KC584706
Dendryphiella arenariae	*Paradendryphiella arenariae*		CBS 181.58	T	Coastal sand	France	DAOM 63738; IMI 067735; MUCL 4129	KC793336	KC793338	**DQ470924**			
Dendryphiella salina	*Paradendryphiella salina*		CBS 142.60		*Spartina* sp.	UK	MUCL 9639	KC793337	KC793339	KC793340			
Embellisia abundans	*Alternaria abundans*	*Chalastospora*	CBS 534.83	T	*Fragaria* sp.	New Zealand	EGS 29.159	KC584581	KC584323	KC584448	**JN383485**	KC584154	KC584707
Embellisia allii	*Alternaria embellisia*	*Embellisia*	CBS 339.71	R	*Allium sativum*	USA	ATCC 22412; IMI 155707; MUCL 18571; QM 8609	KC584582	KC584324	KC584449	KC584230	KC584155	KC584708
Embellisia annulata	*Cicatricea salina*		CBS 302.84	T	*Cancer pagurus*	North Sea, Skagerrak		KC584583	KC584325	KC584450	**JN383486**	**JN383467**	KC584709

Table 1. (Continued).

Old species name	New species name	*Alternaria* Section	Strain number[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Embellisia chlamydospora	*Alternaria chlamydosporigena*	*Embellisia*	CBS 341.71	R	Air	USA	EGS 10.073; ATCC 22409; IMI 155709; MUCL 18573; QM 7287	KC584584	KC584326	KC584451	KC584231	KC584156	KC584710
Embellisia conoidea	*Alternaria conoidea*	*Brassicicola*	CBS 132.89		*Ricinus communis*	Saudi Arabia		KC584585	KC584327	KC584452	**AF348226**	**FJ348227**	KC584711
Embellisia dennisii	*Alternaria dennisii*		CBS 110533		*Senecio jacobaea*	New Zealand		KC584586	KC584328	KC584453	KC584232	KC584157	KC584712
Embellisia dennisii	*Alternaria dennisii*		CBS 476.90	T	*Senecio jacobaea*	Isle of Man	IMI 151744	KC584587	KC584329	KC584454	**JN383488**	**JN383469**	KC584713
Embellisia didymospora	*Alternaria didymospora*	*Phragmosporae*	CBS 766.79		Seawater	Adriatic Sea		KC584588	KC584330	KC584455	**FJ357312**	**FJ357300**	KC584714
Embellisia eureka	*Alternaria eureka*	*Eureka*	CBS 193.86	T	*Medicago rugosa*	Australia	IMI 273162	KC584589	KC584331	KC584456	**JN383490**	**JN383471**	KC584715
Embellisia hyacinthi	*Alternaria hyacinthi*	*Embellisioides*	CBS 416.71	T	*Hyacinthus orientalis*	Netherlands	EGS 19.102; IMI 279179	KC584590	KC584332	KC584457	KC584233	KC584158	KC584716
Embellisia indefessa	*Alternaria indefessa*	*Cheiranthus*	CBS 536.83	T	Soil	USA	EGS 30.195	KC584591	KC584333	KC584458	KC584234	KC584159	KC584717
Embellisia leptinellae	*Alternaria leptinellae*	*Eureka*	CBS 477.90	T	*Leptinella dioica*	New Zealand	EGS 39.101	KC584592	KC584334	KC584459	KC584235	KC584160	KC584718
Embellisia lolii	*Alternaria lolii*	*Embellisioides*	CBS 115266	T	*Lolium perenne*	New Zealand		KC584593	KC584335	KC584460	**JN383492**	**JN383473**	KC584719
Embellisia novae-zelandiae	*Alternaria botryospora*	*Embellisioides*	CBS 478.90	T	*Leptinella dioica*	New Zealand	EGS 39.099	KC584594	KC584336	KC584461	**AY278844**	**AY278831**	KC584720
Embellisia phragmospora	*Alternaria phragmospora*	*Phragmosporae*	CBS 274.70	T	Soil	The netherlands	EGS 27.098; ATCC 18914	KC584595	KC584337	KC584462	**JN383493**	**JN383474**	KC584721
Embellisia planifunda	*Alternaria planifunda*	*Embellisioides*	CBS 537.83	T	*Triticum aestivum*	Australia	IMI 115034	KC584596	KC584338	KC584463	**FJ357315**	**FJ357303**	KC584722
Embellisia proteae	*Alternaria proteae*	*Embellisioides*	CBS 475.90	T	*Protea* sp.	Australia	IMI 320290; IMI 341684	KC584597	KC584339	KC584464	**AY278842**	KC584161	KC584723
Embellisia tellustris	*Alternaria tellustris*	*Embellisia*	CBS 538.83	T	Soil	USA	EGS 33.026	KC584598	KC584340	KC584465	**FJ357316**	**AY562419**	KC584724
Embellisia tumida	*Alternaria tumida*	*Embellisioides*	CBS 539.83	T	*Triticum aestivum*	Australia		KC584599	KC584341	KC584466	**FJ266481**	**FJ266493**	KC584725
Heterospora chenopodii	*Heterospora chenopodii*		CBS 115.96		*Chenopodium album*	Netherlands	PD 94/1576	**EU754089**	**EU754188**	**GU371775**			
Julella avicenniae	*Julella avicenniae*		BCC 18422		Mangrove wood	Thailand		**GU371831**	**GU371823**	**GU371787**			
Leptosphaerulina australis	*Leptosphaerulina australis*		CBS 317.83		*Eugenia aromatica*	Indonesia		**GU296160**	**GU301830**	**GU371790**			
Loratospora aestuarii	*Loratospora aestuarii*		JK 5535B		*Juncus roemerianus*	USA		**GU296168**	**GU301838**	**GU371760**			
Neophaeosphaeria filamentosa	*Neophaeosphaeria filamentosa*		CBS 102202		*Yucca rostrata*	Mexico		**GQ387516**	**GQ387577**	**GU371773**			
Nimbya caricis	*Alternaria caricis*	*Nimbya*	CBS 480.90	T	*Carex hoodii*	USA	EGS 13.094	KC584600	KC584342	KC584467	**AY278839**	**AY278826**	KC584726
"Nimbya gomphrenae"	*Alternaria sp.*	*Alternata*	CBS 108.27		*Gomphrena globosa*	–		KC584601	KC584343	KC584468	KC584236	KC584162	KC584727
Nimbya scirpicola	*Alternaria scirpicola*	*Nimbya*	CBS 481.90	R	*Scirpus* sp.	UK	EGS 19.042	KC584602	KC584344	KC584469	KC584237	KC584163	KC584728

Table 1. (Continued).

Old species name	New species name	*Alternaria* Section	Strain number[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Ophiosphaerella herpotricha	*Ophiosphaerella herpotricha*		CBS 620.86		*Bromus erectus*	Switzerland	ETH 9373	**DQ678010**	**DQ678062**	**DQ677958**			
Paraleptosphaeria dryadis	*Paraleptosphaeria dryadis*		CBS 643.86		*Dryas octopetala*	Switzerland	ETH 9446	KC584632	**GU301828**	**GU371733**			
Peyronellaea glomerata	*Peyronellaea glomerata*		CBS 528.66		*Chrysanthemum* sp.	Netherlands	PD 63/590	**EU754085**	**EU754184**	**GU371781**			
Peyronellaea zeae-maydis	*Peyronellaea zeae-maydis*		CBS 588.69	T	*Zea mays*	USA		**EU754093**	**EU754192**	**GU371782**			
Phaeosphaeria ammophilae	*Phaeosphaeria ammophilae*		CBS 114595		*Ammophila arenaria*	Sweden	UPSC 3568	**GU296185**	**GU304859**	**GU371724**			
Phaeosphaeria avenaria	*Phaeosphaeria avenaria*		DAOM 226215		*Avena sativa*	Canada	OSC 100096	**AY544725**	**AY544684**	**DQ677941**			
Phaeosphaeria eustoma	*Phaeosphaeria eustoma*		CBS 573.86		*Dactylis glomerata*	Switzerland	ETH 9239	**DQ678011**	**DQ678063**	**DQ677959**			
Phoma complanata	*Phoma complanata*		CBS 268.92		*Anglica sylvestris*	Netherlands	PD 75/3	**EU754081**	**EU754180**	**GU371778**			
Phoma herbarum	*Phoma herbarum*		CBS 276.37		Wood pulp	Sweden		**DQ678014**	**DQ678066**	**DQ677962**			
Plenodomus lingam	*Plenodomus lingam*		DAOM 229267		*Brassica sp.*	France		**DQ470993**	**DQ470946**	**DQ470894**			
Pleospora betae	*Pleospora betae*		CBS 109410		*Beta vulgaris*	Netherlands	PD 77/113	**EU754079**	**EU754178**	**GU371774**			
Pleospora calvescens	*Pleospora calvescens*		CBS 246.79		*Atriplex hastata*	Germany	PD 77/655	**EU754032**	**EU754131**	KC584500			
Pleospora chenopodii	*Pleospora chenopodii*		CBS 206.80		*Chenopodium quinoa*	Bolivia	PD 74/1022	**JF740095**	**JF740266**	KC584501			
Pleospora fallens	*Pleospora fallens*		CBS 161.78		*Olea europaea*	New Zealand		**GU238215**	**GU238074**	KC584502			
Pleospora halimiones	*Pleospora halimiones*		CBS 432.77		*Halimione portulacoides*	Netherlands	IMI 282137	**JF740096**	**JF740267**	KC584503			
Pleospora incompta	*Pleospora incompta*		CBS 467.76		*Olea europaea*	Greece		**GU23822**	**GU238087**	KC584504			
Pleospora tarda	*Pleospora tarda*		CBS 714.68	T	*Medicago sativa*	Canada	EGS 04.118C; IMI 135456; MUCL 11717; QM 1379	KC584603	KC584345	**AF107804**	KC584238	**AF443881**	KC584729
Pleospora typhicola	*Pleospora typhicola*		CBS 132.69		*Typha angustifolia*	Netherlands		**JF740105**	**JF740325**	KC584505			
Pyrenochaeta nobilis	*Pyrenochaeta nobilis*		CBS 407.76	T	*Laurus nobilis*	Italy		**EU754107**	**DQ678096**	**DQ677991**			
Pyrenophora phaeocomes	*Pyrenophora phaeocomes*		DAOM 222769		*Calamagrostis villosa*	Switzerland		**DQ499595**	**DQ499596**	**DQ497614**			
Saccothecium sepincola	*Saccothecium sepincola*		CBS 278.32		*Ribes nigrum*	USA		**GU296195**	**GU301870**	**GU371745**			
Setomelanomma holmii	*Setomelanomma holmii*		CBS 110217		*Picea pungens*	USA		**GU296196**	**GQ37633**	**GU371800**			

Table 1. (Continued).

Old species name	New species name	*Alternaria* Section	Strain number[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Sinomyces alternariae	*Alternaria alternariae*	*Ulocladium*	CBS 126989	T	*Daucus carota*	USA	EGS 46.004	KC584604	KC584346	KC584470	**AF229485**	**AY278815**	KC584730
Stemphylium herbarum	*Stemphylium herbarum*		CBS 191.86	T	*Medicago sativa*	India	EGS 36.138; IMI 276975	**GU238232**	**GU238160**	KC584471	KC584239	**AF443884**	KC584731
Teretispora leucanthemi	*Alternaria leucanthemi*	*Teretispora*	CBS 421.65	T	*Chrysanthemum maximum*	Netherlands	ATCC 16028; IFO 9085; IMI 111986; QM 7227	KC584605	KC584347	KC584472	KC584240	KC584164	KC584732
Teretispora leucanthemi	*Alternaria leucanthemi*		CBS 422.65	R	*Chrysanthemum maximum*	USA	EGS 17.063; ATCC 16029; IMI 111987; QM 8579	KC584606	KC584348	KC584473	KC584241	KC584165	KC584733
Ulocladium arborescens	*Alternaria aspera*	*Pseudoulocladium*	CBS 115269	T	*Pistacia vera*	Japan	IMI 369777	KC584607	KC584349	KC584474	KC584242	KC584166	KC584734
Ulocladium atrum	*Alternaria atra*	*Ulocladioides*	CBS 195.67	T	Soil	USA	ATCC 18040; IMI 124944; QM 8408	KC584608	KC584350	KC584475	**AF229486**	KC584167	KC584735
Ulocladium botrytis	*Alternaria botrytis*	*Ulocladium*	CBS 197.67	T	Contaminant	USA	ATCC 18042; IMI 124942; MUCL 18556; QM 7878	KC584609	KC584351	KC584476	KC584243	KC584168	KC584736
Ulocladium botrytis	*Alternaria* sp.	*Ulocladioides*	CBS 198.67	R	Soil	USA	ATCC 18043; IMI 124949; MUCL 18557; QM 8619	KC584610	KC584352	KC584477	**AF229487**	KC584169	KC584737
Ulocladium brassicae	*Alternaria brassicae-pekinensis*	*Ulocladioides*	CBS 121493	T	*Brassica pekinensis*	China	HSAUPwy0037	KC584611	KC584353	KC584478	KC584244	KC584170	KC584738
Ulocladium cantlous	*Alternaria cantlous*	*Ulocladioides*	CBS 123007	T	*Cucumis melo*	China	HSAUP0209	KC584612	KC584354	KC584479	KC584245	KC584171	KC584739
Ulocladium capsici	*Alternaria concatenata*	*Pseudoulocladium*	CBS 120006	T	–	–	$HSAUPIII_0$0035	KC584613	KC584355	KC584480	KC584246	**AY762950**	KC584740
Ulocladium chartarum	*Alternaria chartarum*	*Pseudoulocladium*	CBS 200.67	T	*Populus* sp.	Canada	ATCC 18044; DAOM 59616b; IMI 124943; MUCL 18564; QM 8328	KC584614	KC584356	KC584481	**AF229488**	KC584172	KC584741
Ulocladium consortiale	*Alternaria consortialis*	*Ulocladioides*	CBS 104.31	T	–	–		KC584615	KC584357	KC584482	KC584247	KC584173	KC584742
Ulocladium cucurbitae	*Alternaria cucurbitae*	*Ulocladioides*	CBS 483.81	R	*Cucumis sativus*	New Zealand	EGS 31.021; LEV 7067	KC584616	KC584358	KC584483	**FJ266483**	**AY562418**	KC584743
Ulocladium multiforme	*Alternaria multiformis*	*Ulocladioides*	CBS 102060	T	Soil	Canada		KC584617	KC584359	KC584484	**FJ266486**	KC584174	KC584744
Ulocladium obovoideum	*Alternaria obovoidea*	*Ulocladioides*	CBS 101229		*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 septosporum	*Alternaria septospora*	*Pseudoulocladium*	CBS 109.38		Wood	Italy		KC584620	KC584362	KC584487	**FJ266489**	**FJ266500**	KC584747

Table 1. (Continued).

Old species name	New species name	*Alternaria* Section	Strain number[1]	Status[2]	Host / Substrate	Country	Other collection number[1]	GenBank accession numbers					
								SSU	LSU	RPB2	ITS	GAPDH	TEF1
Ulocladium solani	*Alternaria heterospora*	*Ulocladioides*	CBS 123376	T	*Lycopersicon esculentum*	China	HSAUP 0521	KC584621	KC584363	KC584488	KC584248	KC584176	KC584748
Ulocladium subcucurbitae	*Alternaria subcucurbitae*	*Ulocladioides*	CBS 121491	T	*Chenopodium glaucum*	China		KC584622	KC584364	KC584489	KC584249	**EU855803**	KC584749
Ulocladium tuberculatum	*Alternaria terricola*	*Ulocladioides*	CBS 202.67	T	Soil	USA	ATCC 18048; IMI 124947; MUCL 18560; QM 8614	KC584623	KC584365	KC584490	**FJ266490**	KC584177	KC584750
Undifilum bornmuelleri	*Alternaria bornmuelleri*	*Undifilum*	DAOM 231361	T	*Securigera varia*	Austria	DAOM 231361	KC584624	KC584366	KC584491	**FJ357317**	**FJ357305**	KC584751
Ybotromyces caespitosus	*Alternaria caespitosa*	*Infectoriae*	CBS 177.80	T	Human	Spain		KC584625	KC584367	KC584492	KC584250	KC584178	KC584752

[1] ATCC: American Type Culture Collection, Manassas, VA, USA; BCC: BIOTEC Culture Collection, Thailand; CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands; DAOM: Canadian Collection of Fungal Cultures, Ottawa, Canada; DAR: Plant Pathology Herbarium, Orange Agricultural Institute, Australia; DSM: German Collection of Microorganisms and Cell Cultures, Leibniz Institute, Braunschweig, Germany; EGS: Personal collection of Dr. E.G. Simmons; ETH: Swiss Federal Institute of Technology, Switzerland; HSAUP: Department of Plant Pathology, Shandong Agricultural University, China; IFO: Institute for Fermentation Culture Collection, Osaka, Japan; IMI: Culture collection of CABI Europe UK Centre, Egham UK; JK: Personal collection of Dr. J. Kohlmeyer; LEV: Plant Health and Diagnostic Station, Levin, New Zealand; MUCL: (Agro)Industrial Fungi and Yeast Collection of the Belgian Co-ordinated Collections of Micro-organisms (BCCM), Louvain-la Neuve, Belgium; NZMAF: New Zealand Ministry of Agriculture and Forestry; OSC: Oregon State University Herbarium, USA; PD: Plant Protection Service, Wageningen, The Netherlands; RGR: Personal collection of Dr. R.G. Roberts; UPSC: Uppsala University Culture Collection, Sweden; QM: Quarter Master Culture Collection, Amherst, MA, USA.

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

species (Table 1) for which the SSU, LSU and RPB2 sequence data set was present or could be completed. Blast searches with *Embellisia annulata* gave hits with two marine *Dendryphiella* species, *Dendryphiella arenariae* and *Dendryphiella salina*, which we also included. Phylogenetic analyses of the sequence data consisted of Bayesian and Maximum likelihood analyses of both the individual data partitions as well as the combined aligned dataset. Bayesian analyses were performed with MrBayes v. 3.2.1 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). The Markov Chain Monte Carlo (MCMC) analysis used four chains and started from a random tree topology. The sample frequency was set at 100 and the temperature value of the heated chain was 0.1. The temperature value was lowered to 0.05 when the average standard deviation of split frequencies did not fall below 0.01 after 5M generations (RPB2 and *Pleosporineae* phylogeny). Burn-in was set to 25 % after which the likelihood values were stationary. Maximum likelihood analyses including 500 bootstrap replicates were run using RAxML v. 7.2.6 (Stamatakis & Alachiotis 2010). The online tool Findmodel (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html) was used to determine the best nucleotide substitution model for each partition. For the SSU (*Pleosporineae* family tree), LSU, ITS, RPB2 and TEF1 partitions a GTR model with a gamma-distributed rate variation was suggested, and for the SSU (*Alternaria* complex) and GAPDH partitions a TrN model with gamma-distributed rate variation. Sequences of *Stemphylium herbarum* (CBS 191.86) were used as outgroup in the *Alternaria* phylogeny and those of *Jullella avenicae* (BCC 18422) in the *Pleosporineae* phylogeny. The resulting trees were printed with TreeView v. 1.6.6 (Page 1996) and together with the alignments deposited into TreeBASE (http://www.treebase.org).

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 of 1.0, RAxML Maximum Likelihood support value of 100) in all phylogenies separates *Embellisia annulata* CBS 302.84 and the *Pleospora*/*Stemphylium* clade from the *Alternaria* complex (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 boostrap support values per *Alternaria* section.

	1-region						2-region			3-region	6-region
	SSU	LSU	ITS	GAPDH	RPB2	TEF	GAPDH RPB2	GAPDH TEF1	RPB2 TEF1	GAPDH RPB2 TEF1	SSU LSU ITS GAPDH RPB2 TEF1
Aligned length	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
No. of sampled trees (post burnin)	39002	31578	75002	23702	56028	12452	10128	13728	44852	5778	16278
	Bayesian Posterior Probabilities										
Sect. *Alternantherae*		*									
Sect. *Alternata*											
Sect. *Brassicicola*											
Sect. *Chalastospora*	*										
Sect. *Cheiranthus*	*		*	*				*			
Sect. *Crivellia*			*								
Sect. *Dianthicola*	*	*									
Sect. *Embellisia*		*									
Sect. *Embellisioides*	*	*			*						
Sect. *Eureka*			*		*	*					
Sect. *Gypsophilae*			*								
Sect. *Infectoriae*	*	*									
Sect. *Japonicae*											
Sect. *Nimbya*											
Sect. *panax*	*										
Sect. *Phragmosporae*		*	*								
Sect. *Porri*		*									
Sect. *Pseudoulocladium*	*	*			*		*				
Sect. *Radicina*											
Sect. *Sonchi*	*	*									
Sect. *Teretispora*											
Sect. *Ulocladioides*	*	*									
Sect. *Ulocladium*			*								

1.00	0.95–0.99	0.90–0.94	0.80–0.89	0.70–0.79
0.50–0.69	0.25–0.49	0.01–0.24	no support	
*= section not complete				

	1-region						2-region			3-region	6-region
	SSU	LSU	ITS	GAPDH	RPB2	TEF	GAPDH RPB2	GAPDH TEF1	RPB2 TEF1	GAPDH RPB2 TEF1	ALL LSU ITS GAPDH RPB2 TEF1
Aligned length	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
	RAxML bootstrap support										
Sect. *Alternantherae*		*									
Sect. *Alternata*											
Sect. *Brassicicola*											
Sect. *Chalastospora*	*										
Sect. *Cheiranthus*	*		*	*				*			
Sect. *Crivellia*			*								
Sect. *Dianthicola*	*	*									
Sect. *Embellisia*		*									
Sect. *Embellisioides*	*	*			*						
Sect. *Eureka*			*		*	*					
Sect. *Gypsophilae*			*								
Sect. *Infectoriae*	*	*									
Sect. *Japonicae*											
Sect. *Nimbya*											
Sect. *panax*	*										
Sect. *Phragmosporae*		*	*								
Sect. *Porri*		*									
Sect. *Pseudoulocladium*	*	*			*						
Sect. *Radicina*											
Sect. *Sonchi*	*	*									
Sect. *Teretispora*											
Sect. *Ulocladioides*	*	*									
Sect. *Ulocladium*			*								

100	95–99	90–94	80–89	70–79
50–69	25–49	1–24	no support	
*= section not complete				

Table 3. Coded inserts in the TEF1 sequence alignment.

Species	Nt position	Coded	Nt position	Coded
Alternaria elegans	23 to 39	TC		
Alternaria simsimi	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 tegetica	186 to 205	C	221 to 269	CACAC

low resolution, which reflects in poor to no support of the sections. Therefore, we chose not to include them in the multi-gene alignments, except in the all-gene alignment. In the GAPDH phylogenies, sect. *Cheiranthus*, sect. *Nimbya* and sect. *Pseudoulocladium* are poorly supported and "*A. resedae*" clusters separate from sect. *Cheiranthus*. In the RPB2 phylogenies the support values for sect. *Alternata*, sect. *Embellisioides* and sect. *Eureka* are relatively low; *A. cumini* clusters in sect. *Embellisioides* instead of sect. *Eureka* and *U. capsici* clusters separate from sect. *Pseudoulocladium*. The TEF1 phylogenies did not support sect. *Nimbya* and show relative low support for sect. *Cheiranthus*, sect. *Dianthicola*, sect. *Embellisioides*, sect. *Panax*, sect. *Phragmosporae* and sect. *Radicina*, and *A. cumini* clusters outside sect. *Eureka*. In the 2-region phylogenies *U. capsici* clusters outside sect. *Pseudoulocladium* based on GAPDH and RPB2, *E. indefessa* clusters outside sect. *Cheiranthus* based on GAPDH and TEF1, and sect. *Eureka* is poorly supported based on RPB2 and TEF1. The combined phylogeny based on the GAPDH, RPB2 and TEF1 sequences (Fig. 1) is displayed, as these are the genes with the best resolution.

The final *Pleosporineae* alignment included 74 strains, representing six families, and consisted of 2 506 characters (SSU 935, LSU 796, RPB2 775) of which 700 were unique site patterns (SSU 111, LSU 145, RPB2 444). In the SSU alignment a large insertion at position 446 in the isolates *Chaetosphaeronema hispidulum* CBS 216.75, *Pleospora fallens* CBS 161.78, *Pleospora flavigena* CBS 314.80 and *Ophiosphaerella herpotrichia* CBS 620.86 was excluded from the phylogenetic analyses. A total of 43 202 trees were sampled after the burn-in. The type species of *Clathrospora*, *C. elynae*, forms a well-supported clade, located basal to the *Pleosporaceae* (Fig. 2), outside the *Alternaria* complex. The type species of *Comoclathris*, *C. lanata*, was not available for study but the two *Comoclathris compressa* strains cluster in a well-supported clade within the *Pleosporaceae* outside *Alternaria s. str*. The genus *Alternariaster*, with *Alternariaster helianthi* as type and only species, also clusters outside the *Alternaria* complex and even outside *Pleosporaceae*; it belongs to the *Leptosphaeriaceae* instead (Fig. 2). *Embellisia annulata* is identical to *Dendryphiella salina*, and forms a well-supported clade in the *Pleosporaceae* together with *Dendryphiella arenariae*. As the type species of *Dendryphiella*, *D. vinosa*, clusters outside the *Pleosporineae* (dela Cruz 2006, Jones *et al.* 2008), *Dendryphiella salina* and *D. arenariae* are placed in a new genus, *Paradendryphiella*, below.

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*, *Brachycladium*, *Chalastospora*, *Chmelia*, *Crivellia*, *Embellisia*, *Lewia*, *Nimbya*, *Sinomyces*, *Teretispora*, *Ulocladium*, *Undifilum* 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.

Alternaria Nees, Syst. Pilze (Würzburg): 72. 1816 [1816–1817].

= *Elosia* Pers., Mycol. Eur. (Erlanga) 1: 12. 1822.
= *Macrosporium* Fr., Syst. Mycol. (Lundae) 3: 373. 1832.
= *Rhopalidium* Mont., Ann. Sci. Nat., Bot., Sér. 2, 6: 30. 1836.
= *Brachycladium* Corda, Icon. Fungorum hucusque Cogn. (Prague) 2: 14. 1838.
= *Ulocladium* Preuss, Linnaea 24: 111. 1851.
= *Chmelia* Svob.-Pol., Biologia (Bratislava) 21: 82. 1966.
= *Embellisia* E.G. Simmons, Mycologia 63: 380. 1971.
= *Trichoconiella* B.L. Jain, Kavaka 3: 39. 1976 [1975].
= *Botryomyces* de Hoog & C. Rubio, Sabouraudia 20: 19. 1982. (nom. illegit.)
= *Lewia* M.E. Barr & E.G. Simmons, Mycotaxon 25: 289. 1986.
= *Ybotromyce*s Rulamort, Bull. Soc. Bot. Centre-Ouest, Nouv. Sér. 17: 192. 1986.
= *Nimbya* E.G. Simmons, Sydowia 41: 316. 1989.
= *Allewia* E.G. Simmons, Mycotaxon 38: 260. 1990.
= *Crivellia* Shoemaker & Inderb., Canad. J. Bot. 84: 1308. 2006.
= *Chalastospora* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.
= *Teretispora* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 674. 2007.
= *Undifilum* B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 190. 2009.
= *Sinomyces* Yong Wang bis & X.G. Zhang, Fungal Biol. 115: 192. 2011.

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 *hyphopodia* absent. *Conidiophores* macronematous, mononematous, simple or irregularly and loosely branched, pale brown or brown, solitary or in fascicles. *Conidiogenous cells* integrated, terminal becoming intercalary, polytretic, sympodial, or sometimes monotretic, cicatrized. *Conidia* catenate or solitary, dry, ovoid, obovoid, cylindrical, narrowly ellipsoid or obclavate, beaked or non-beaked, pale or medium olivaceous-brown to brown, smooth or verrucose, with transverse and 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 pedicel. *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.

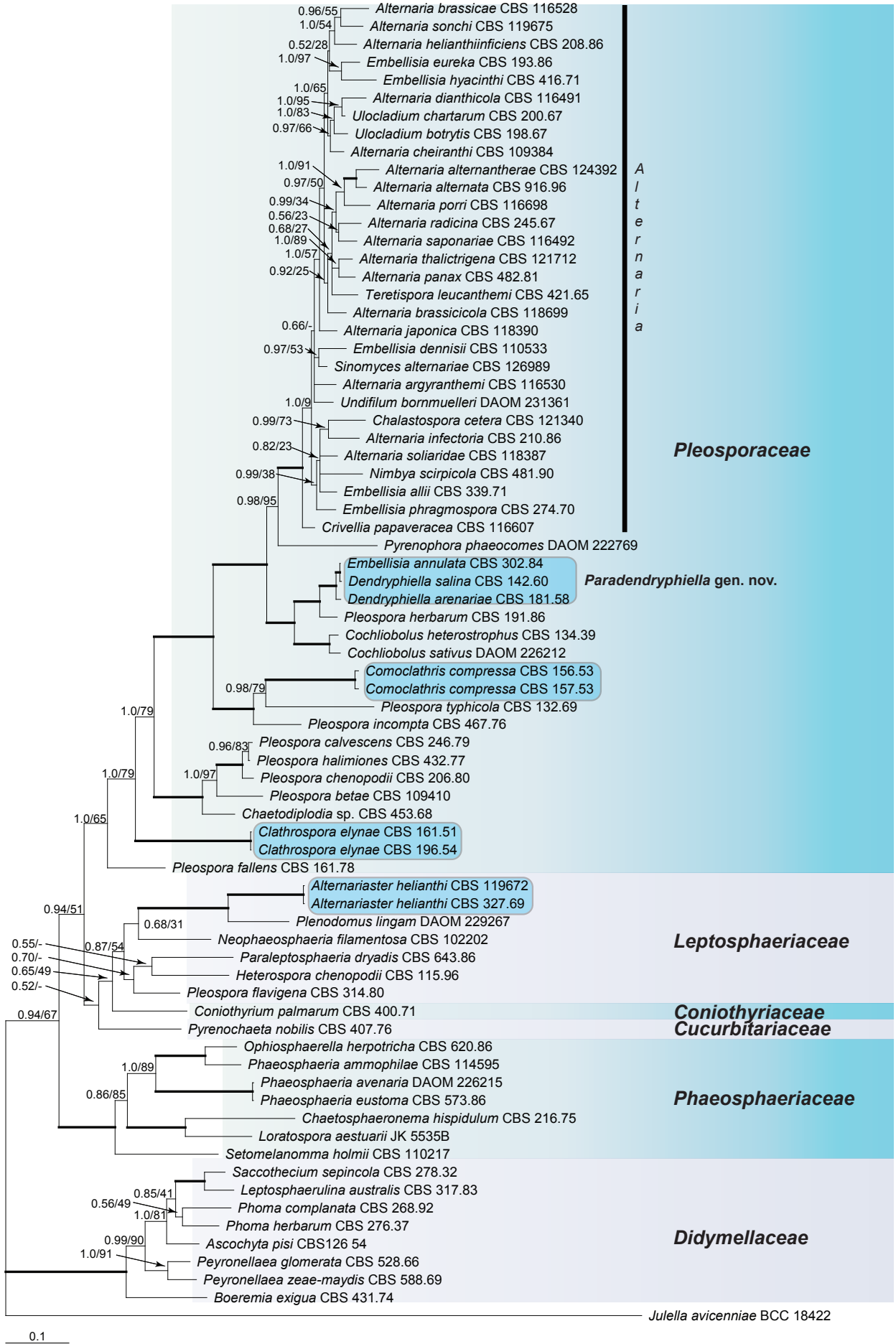

Fig. 2. Bayesian 50 % majority rule consensus tree based on the SSU, LSU and RPB2 sequences of 74 strains representing the *Pleosporineae*. The Bayesian posterior probabilities (PP) and RAxML bootstrap support values (ML) are given at the nodes (PP/ML). Thickened lines indicate a PP of 1.0 and ML of 100. The tree was rooted to *Julella avicenniae* (BCC 18422).

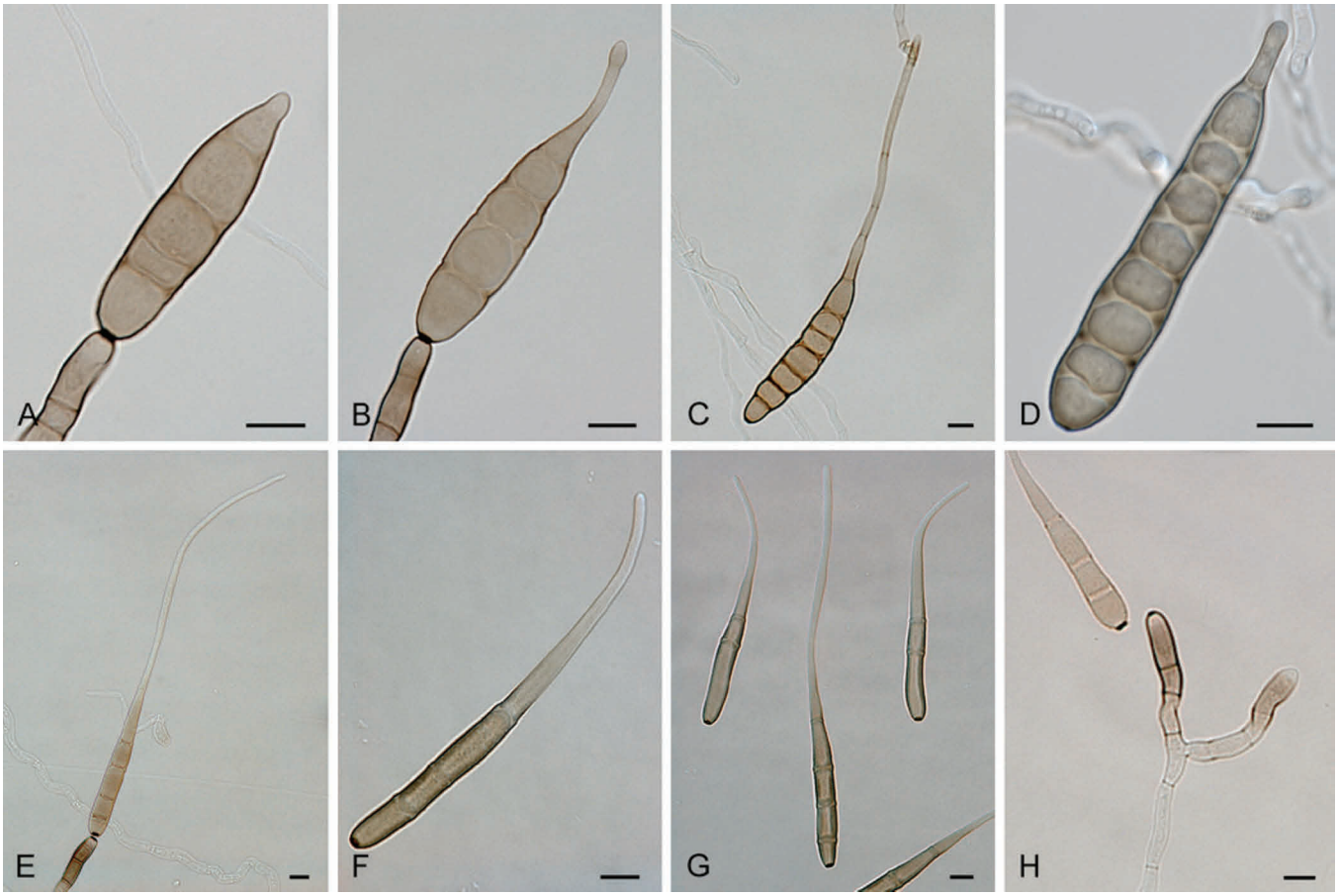

Fig. 3. *Alternaria* sect. *Alternantherae*: conidia and conidiophores. A–D. *A. alternantherae*. E–H. *A. perpunctulata*. Scale bars = 10 µm.

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.

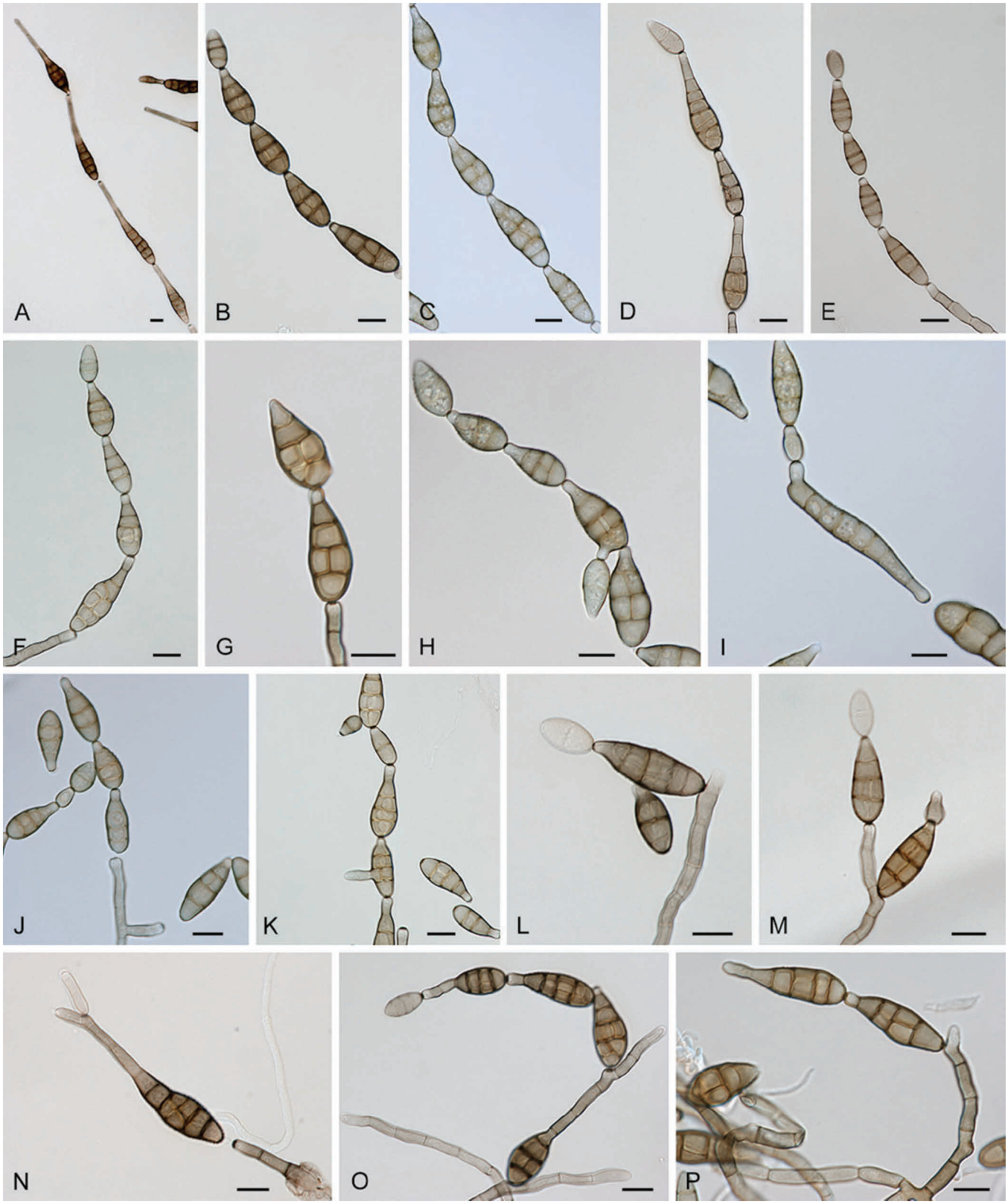

Fig. 4. *Alternaria* sect. *Alternata*: conidia and conidiophores. A, N. *A. daucifolii*. B, L–M. *A. arborescens*. C, H–J. *A. alternata*. D, O. *A. gaisen*. E. *A. limoniasperae*. F, K. *A. tenuissima*. G, P. *A. longipes*. Scale bars = 10 µm.

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.).

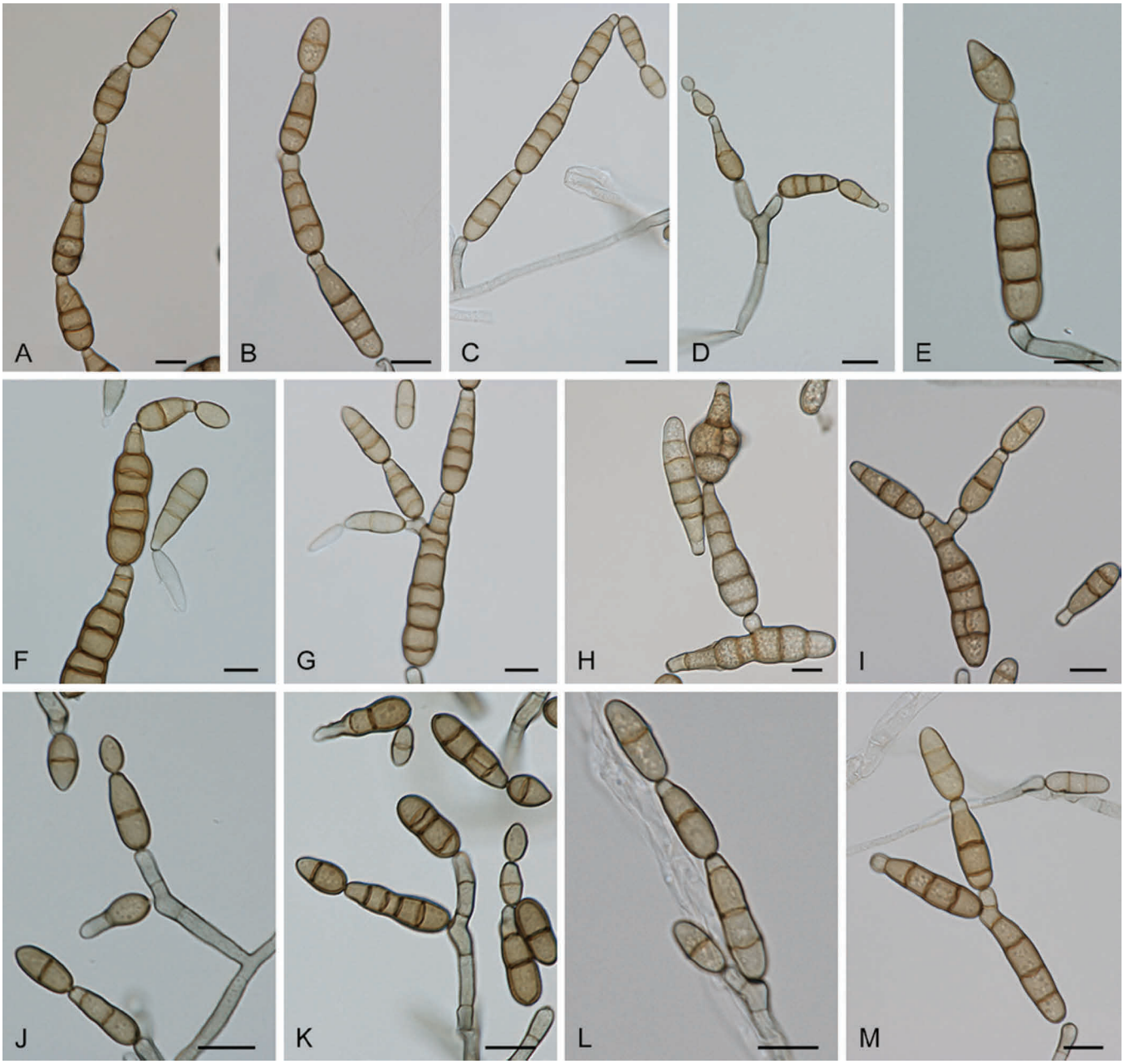

Fig. 5. *Alternaria* sect. *Brassicicola*: conidia and conidiophores. A, H. *A. brassicicola*. B, I, L–M. *A. mimicola*. C, G. *A. solidaccana*. D, J–K. *A. conoidea*. E–F. *A. septorioides*. Scale bars = 10 µm.

= *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 citriarbusti 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 daucifollii 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.

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

Alternaria herbiphorbicola 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: *Macrosporium longipes* Ellis & Everh., J. Mycol. 7: 134. 1892.

= *Alternaria brassicae* var. *tabaci* Preissecker, 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.

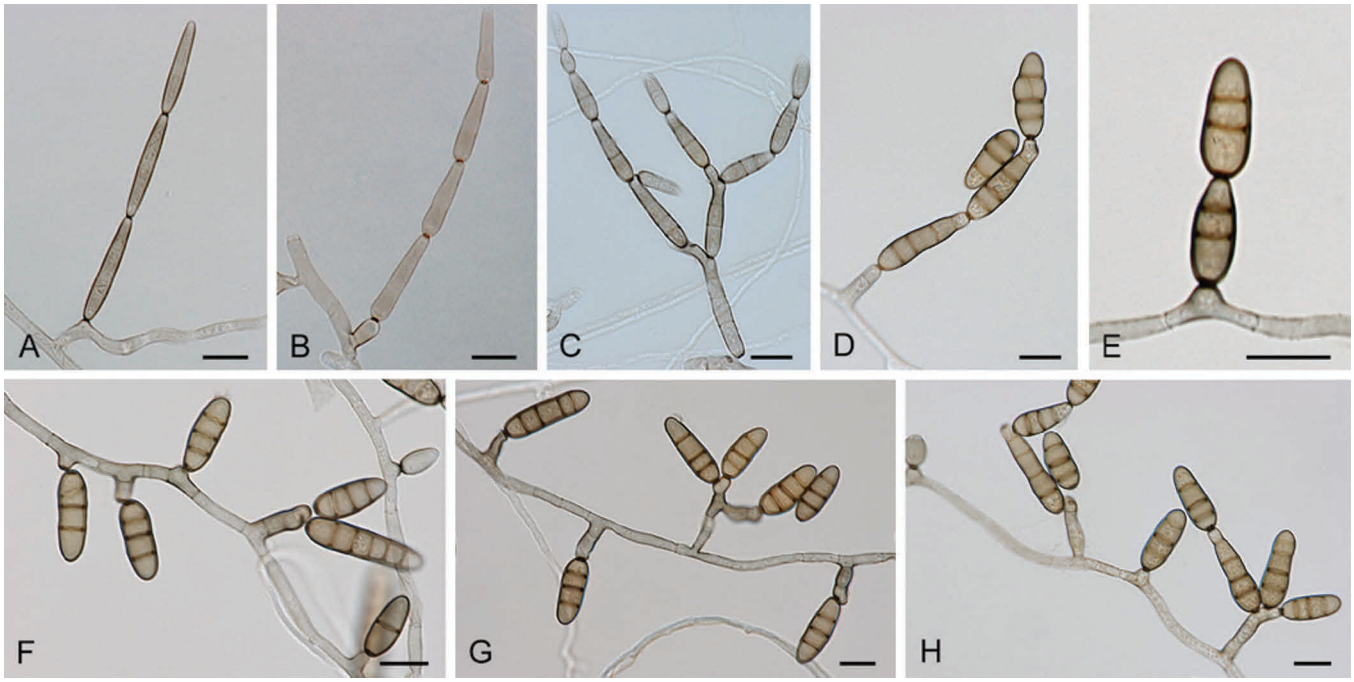

Fig. 6. *Alternaria* sect. *Chalastospora*: conidia and conidiophores. A. *A. cetera*. B. *A. obclavata*. C. *A. breviramosa*. D, H. *A. armoraciae*. E–G. *A. abundans*. Scale bars = 10 µm.

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.
Additional synonyms listed in Simmons (2007)
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. Ohlsens 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) Woudenb. & 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.

Fig. 7. *Alternaria* sect. *Cheiranthus*: conidia and conidiophores. A–B. *A. indefessa*. B–C. *A. cheiranthi*. Scale bars = 10 µm.

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) Woudenb. & 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 Woudenb. & Crous, **nom. nov.** MycoBank MB803690.
Basionym: *Chalastospora ellipsoidea* Crous & U. Braun, Persoonia 22: 145. 2009, non *Alternaria ellipsoidea* E.G. Simmons, 2002.
Etymology: Name refers to the short lateral branches.
Alternaria cetera E.G. Simmons, Mycotaxon 57: 393. 1996.
≡ *Chalastospora cetera* (E.G. Simmons) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.
Alternaria malorum (Ruehle) U. Braun, Crous & Dugan, Mycol. Progr. 2: 5. 2003.
Basionym: *Cladosporium malorum* Ruehle, Phytopathology 21: 1146. 1931.
= *Cladosporium gossypii* Jacz., Khlopkovoe Delo, 1929 (5–6): 564. 1929, non *Alternaria gossypii* (Jacz.) Y. Nisik., K. Kimura & Miyaw., 1940.
≡ *Chalastospora gossypii* (Jacz.) U. Braun & Crous, Persoonia 22: 144. 2009.
= *Cladosporium malorum* Heald, Wash. State Agric. Exp. Sta. Bull., Special Ser. 245: 48. 1930. (nom. nud.)
Additional synonyms in Crous *et al.* (2009c).
Alternaria obclavata (Crous & U. Braun) Woudenb. & Crous, **comb. nov.** MycoBank MB803689.
Basionym: *Chalastospora obclavata* Crous & U. Braun, Persoonia 22: 146. 2009.

Section Cheiranthus Woudenb. & 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: Next to *Alternaria cheiranthi* and *Embellisia indefessa*, sect. *Cheiranthus* contains a non-sporulating strain formerly known as *Alternaria resedae*, CBS 115.44. Because *Alternaria resedae* is synonymised with *Alternaria septorioides* (Simmons 2007), which clusters in section *Brassisicola*, CBS 115.44 will be treated as "*Alternaria* sp.". *Alternaria cheiranthi* and *E. indefessa* have been linked to *Ulocladium* (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Hong *et al.* 2005, Pryor *et al.* 2009, Runa *et al.* 2009, Lawrence *et al.* 2012), but based on morphology could not be placed here. Our extensive dataset showed that they form a sister section to section *Ulocladioides*.

Alternaria cheiranthi (Lib.) P.C. Bolle, Meded. Phytopathol. Lab. "Willie Commelin Scholten" 7: 43. 1924.
Basionym: *Helminthosporium cheiranthi* Lib. [as "*Helmisporium*"], in Desmazières, Plantes Cryptogames du Nord de la France, edn 1: 213. 1827.
≡ *Macrosporium cheiranthi* (Lib.) Fr., Syst. Mycol. (Lundae) 3: 374. 1832.
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.) Woudenb. & Crous, **comb. et stat. nov.** MycoBank MB803735. Fig. 8.

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

Type species: *Alternaria penicillata* (Corda) Woudenb. & 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

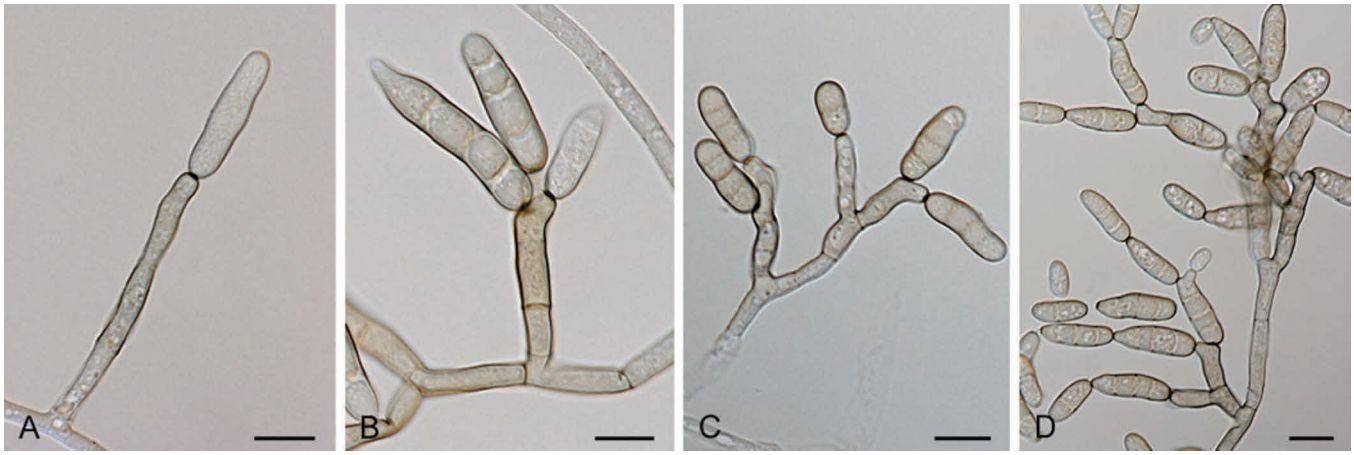

Fig. 8. *Alternaria* sect. *Crivellia*: conidia and conidiophores. A–B. *A. papavericola*. C–D. *A. penicillata*. Scale bars = 10 µm.

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* asexual morph, and *Brachycladium papaveris.* The genus was established by Inderbitzin *et al.* (2006) based on the finding that *C. papaveraceae*, 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. Condia 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.

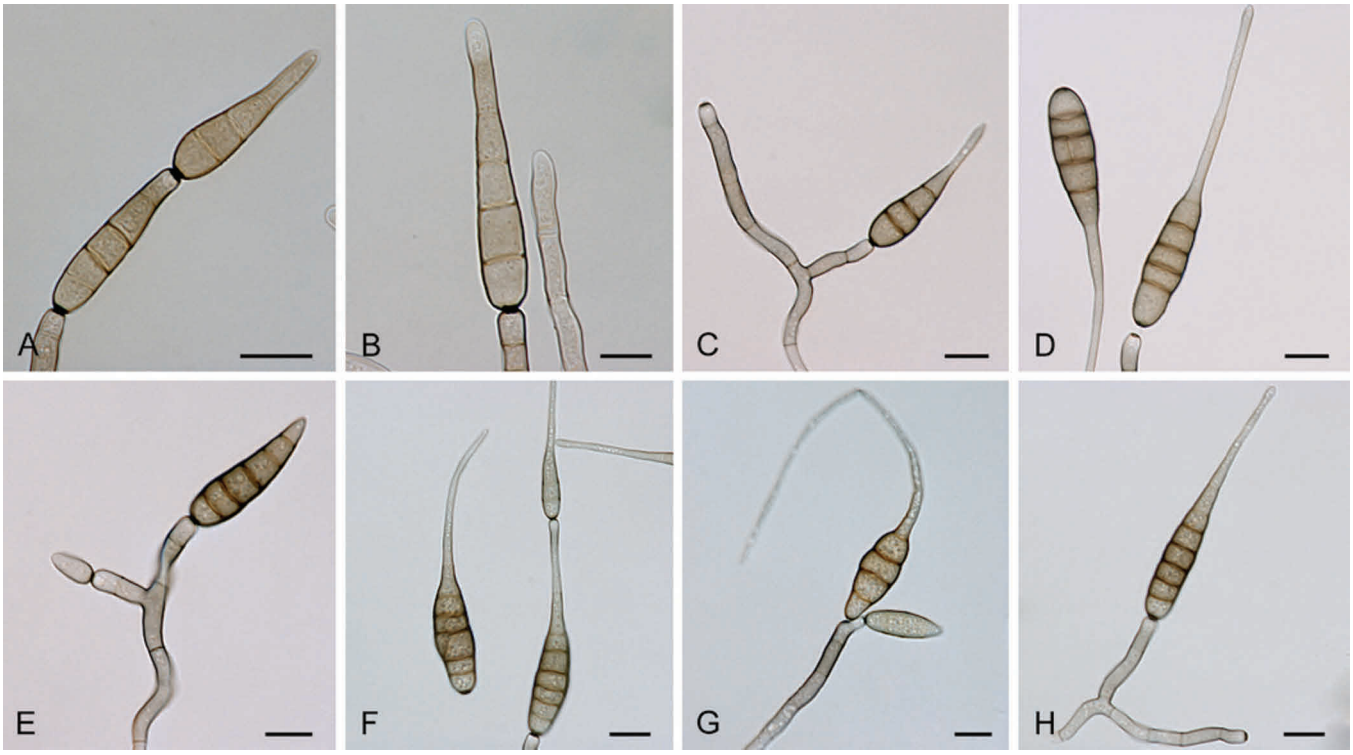

Fig. 9. *Alternaria* sect. *Dianthicola*: conidia and conidiophores. A–B. *A. dianthicola*. C–E. *A. simsimi*. F–H. *A. elegans*. Scale bars = 10 µm.

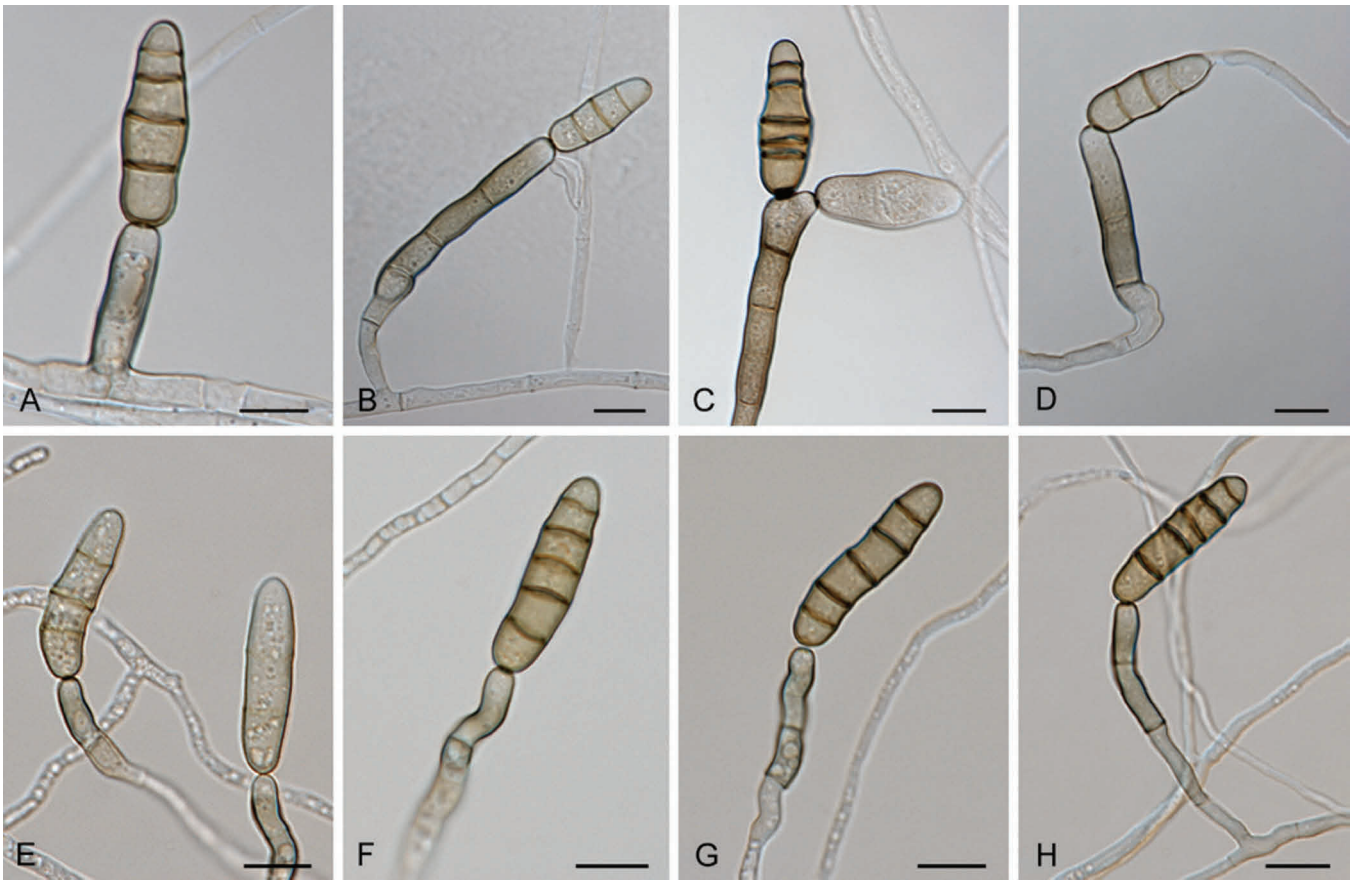

Fig. 10. *Alternaria* sect. *Embellisia*: conidia and conidiophores. A–D. *A. embellisia*. E–H. *A. tellustris*. Scale bars = 10 µm.

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.

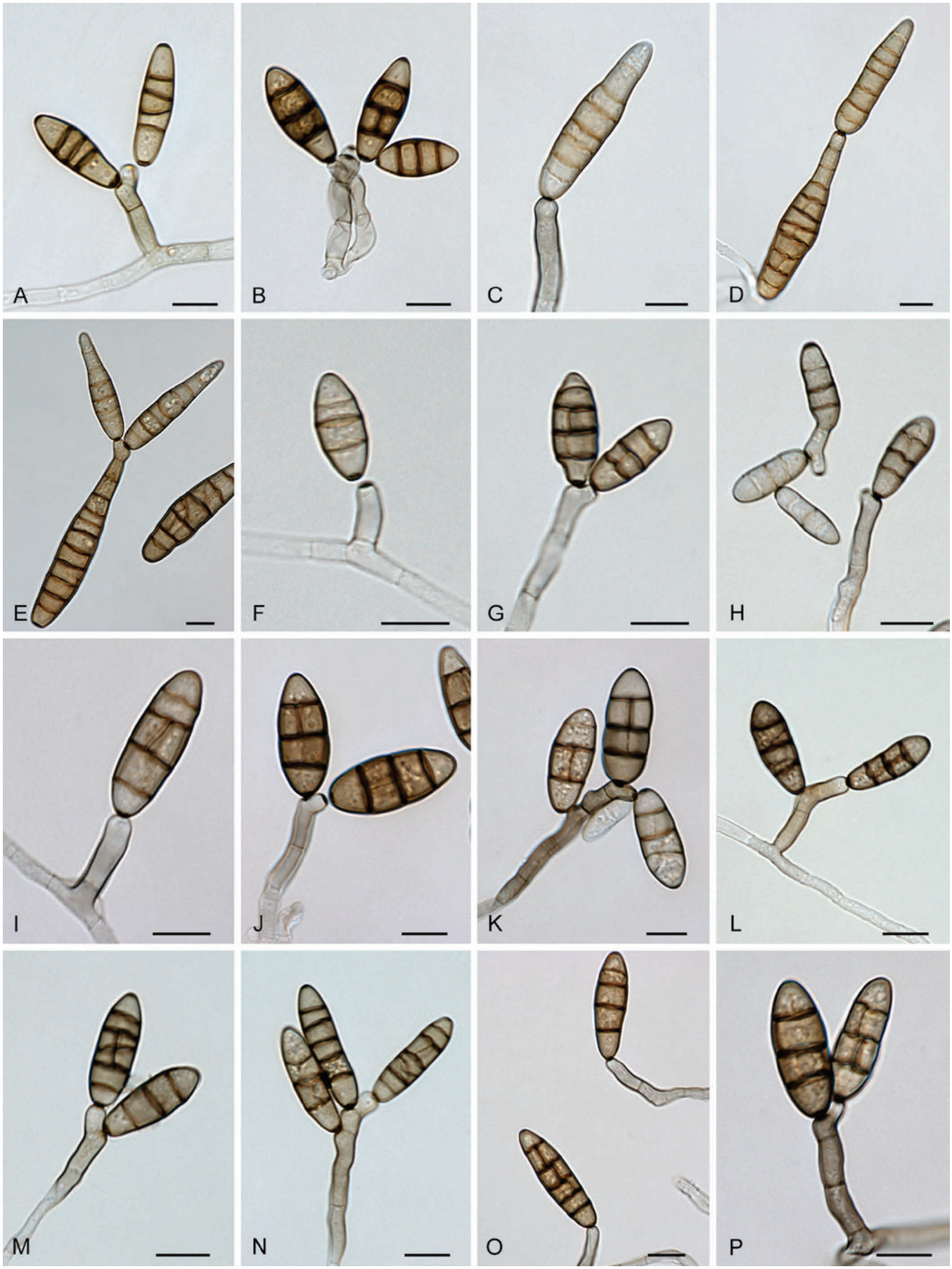

Fig. 11. *Alternaria* sect. *Embellisioides*: conidia and conidiophores. A–B. *A. hyacinthi*. C–E. *A. lolii*. F–H. *A. botryospora*. I–K. *A. planifunda*. L–N. *A. proteae*. O–P. *A. tumida*. Scale bars = 10 µm.

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 multiple, geniculate, sympodial proliferations. Apical or lateral, short secondary conidiophores may occur. Condia are solitary or in short chains, obovoid 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, Mycotaxon 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, c**omb. 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.
= *Allewia proteae* E.G. Simmons, Mycotaxon 38: 262. 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. Condia are solitary or in short chains, narrowly ellipsoid to cylindrical, with transverse and longitudinal septa, slighty 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. 1986.
≡ *Embellisia eureka* (E.G. Simmons) E.G. Simmons, Mycotaxon 38: 260. 1990.
= *Lewia eureka* E.G. Simmons, Mycotaxon 25: 304. 1986.
≡ *Allewia eureka* (E.G. Simmons) E.G. Simmons, Mycotaxon 38: 264. 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 *Gypsophilae* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 13

Type species: *Alternaria gypsophilae Neerg.*

Diagnosis: Section *Gypsophilae* 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 *Gypsophilae* was recently established by Lawrence et al. (2013) containing the four *Alternaria* species, *A. gypsophilae*, *A. nobilis*, *A. vaccariae* and *A. vaccariicola*. Our dataset adds four *Alternaria* species, *A. axiaeriisporifera*, *A. ellipsoidea*, *A. saponariae*, and *A. juxtiseptata* to this section. Simmons (2007) noted the similarity of the primary conidia of *A. ellipsoidea* to *A. gypsophilae*, *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 axiaeriisporifera E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 662. 2007.
Alternaria ellipsoidea E.G. Simmons, Mycotaxon 82: 31. 2002.
Alternaria gypsophilae Neerg., Danish species of *Alternaria* & *Stemphylium*: 207. 1945.
Alternaria juxtiseptata E.G. Simmons, Mycotaxon 82: 32. 2002.
Alternaria nobilis (Vize) E.G. Simmons, Mycotaxon 82: 7. 2002.
Basionym: *Macrosporium 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: *Macrosporium saponariae* Peck, Rep. (Annual) NewYork State Mus. Nat. Hist. 28: 62. 1876 [1875].

Fig. 12. *Alternaria* sect. *Eureka*: conidia and conidiophores. A–B. *A. anigozanthi*. C–D. *A. cumini*. E–F. *A. leptinellae*. G–H. *A. triglochinicola*. I–J. *A. geniostomatis*. K–L. *A. eureka*. Scale bars = 10 µm.

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* Woudenb. & 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*.

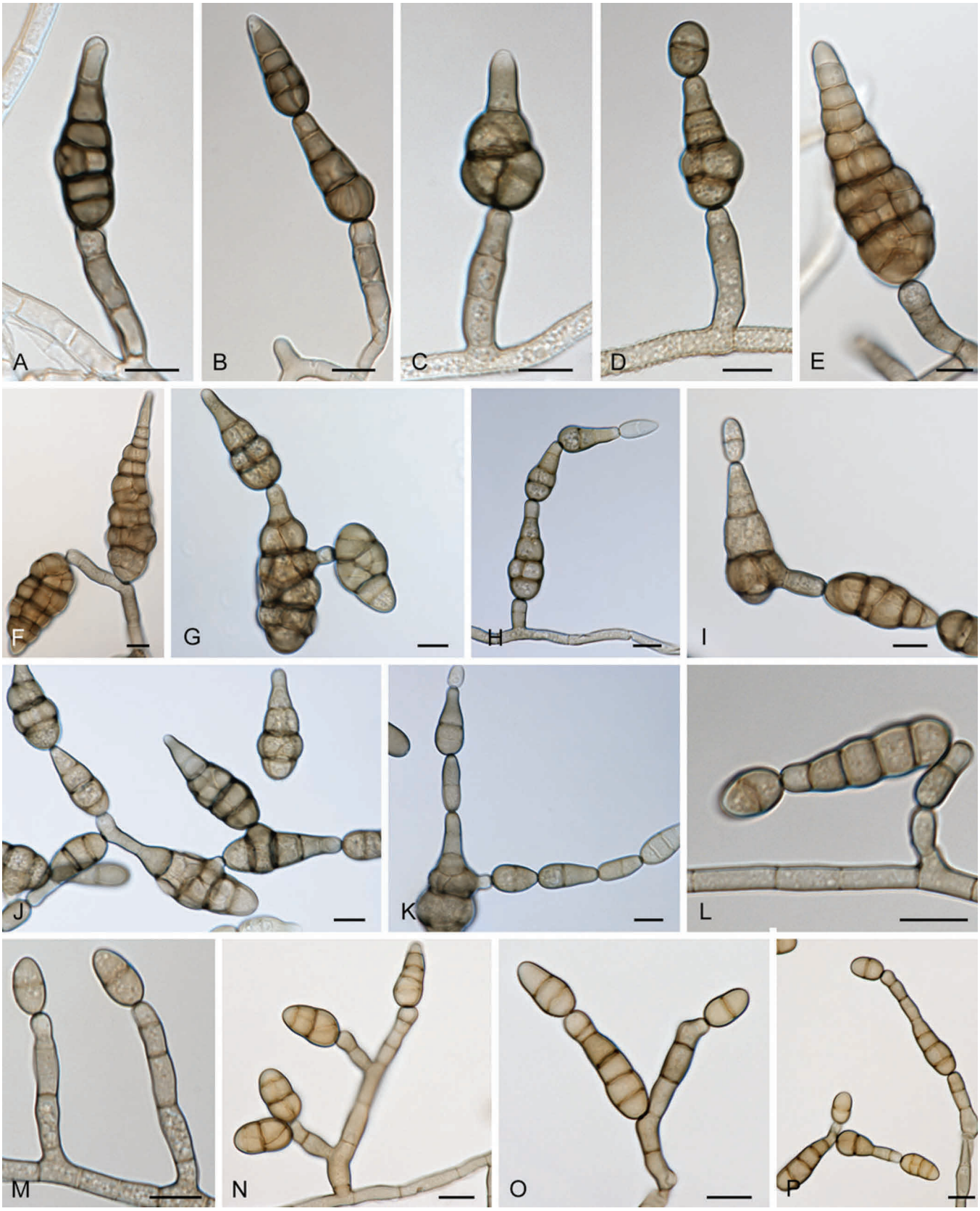

Fig. 13. *Alternaria* sect. *Gypsophilae*: conidia and conidiophores. A–B. *A. axiariisporifera*. C–D. *A. ellipsoidea*. E–G. *A. saponariae*. H–I. *A. vaccariae*. J–K. *A. nobilis*. L–M. *A. juxtiseptata*. N–P. *A. vaccariicola*. Scale bars = 10 µm.

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) Woudenb. & 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.

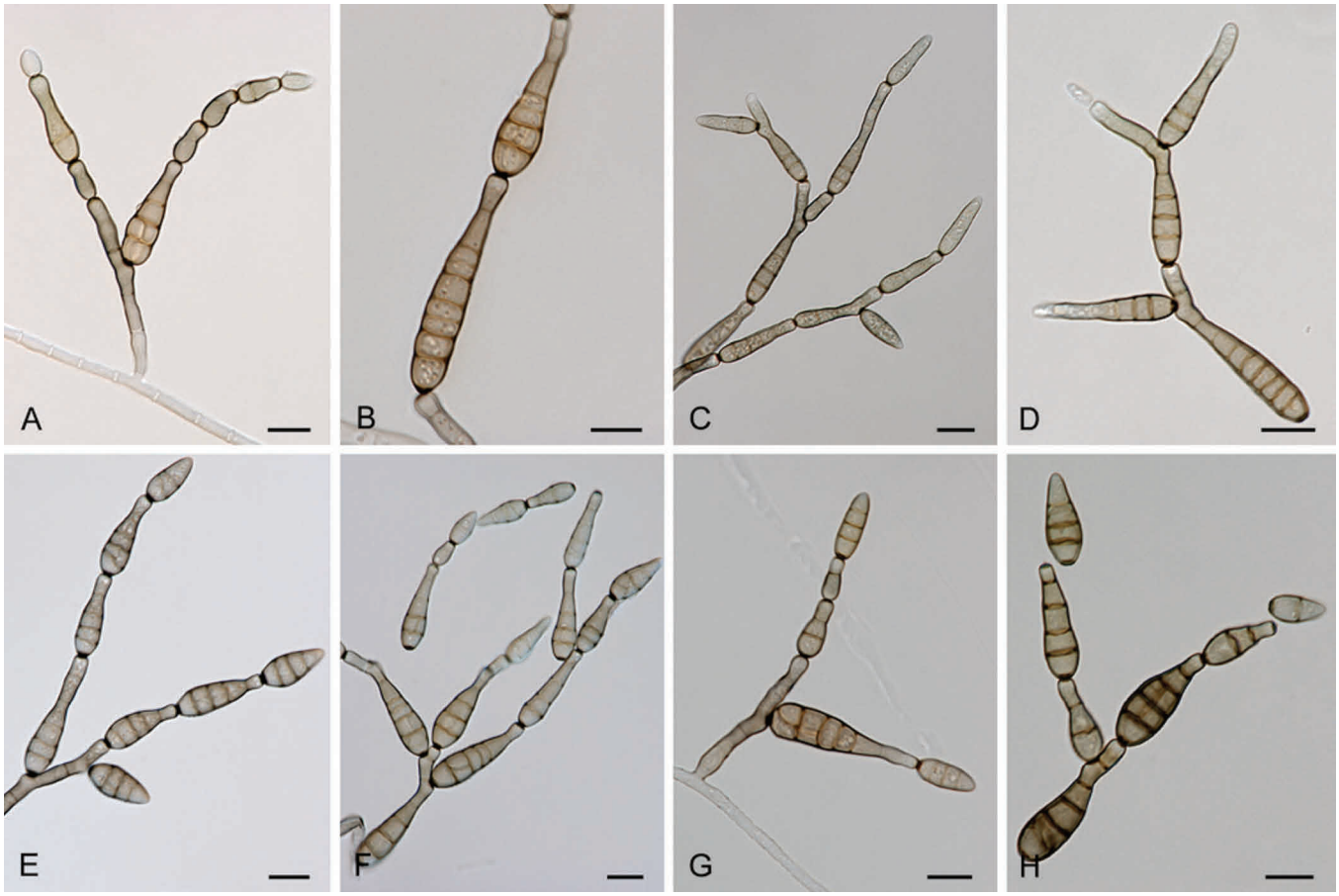

Fig. 14. *Alternaria* sect. *Infectoriae*: conidia and conidiophores. A–B. *A. ethzedia*. C–D. *A. infectoria*. E–F. *A. conjuncta*. G–H. *A. oregonensis*. Scale bars = 10 µm.

Alternaria californica E.G. Simmons & S.T. Koike, CBS Biodiversity Ser. (Utrecht) 6: 602. 2007.

Alternaria conjuncta E.G. Simmons, Mycotaxon 25: 294. 1986.

= *Sphaeria scrophulariae* Desm., Ann. Sci. Nat., Bot., Sér. 2, 6: 245. 1836.

≡ *Leptosphaeria scrophulariae* (Desm.) Sacc., Syll. Fungorum (Abellini) 2: 57. 1883.

≡ *Heptameria scrophulariae* (Desm.) Cooke, Grevillea 18(no. 86): 31. 1889.

≡ *Pleospora scrophulariae* (Desm.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 126(4–5): 374. 1917.

≡ *Lewia scrophulariae* (Desm.) M.E. Barr & E.G. Simmons, Mycotaxon 25: 294. 1986.

Alternaria daucicaulis E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 640. 2007.

= *Lewia daucicaulis* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 640. 2007.

Alternaria ethzedia E.G. Simmons, Mycotaxon 25: 300. 1986.

= *Lewia ethzedia* E.G. Simmons, Mycotaxon 25: 299. 1986.

Alternaria frumenti E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 620. 2007.

Alternaria graminicola E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 626. 2007.

Alternaria hordeiaustralica E.G. Simmons & Alcorn, CBS Biodiversity Ser. (Utrecht) 6: 614. 2007.

= *Lewia hordeiaustralica* E.G. Simmons & Alcorn, CBS Biodiversity Ser. (Utrecht) 6: 614. 2007.

Alternaria hordeicola E.G. Simmons & Kosiak, CBS Biodiversity Ser. (Utrecht) 6: 630. 2007.

= *Lewia hordeicola* Kwaśna & Kosiak, Mycologia 98: 663. 2006.

Alternaria humuli E.G. Simmons, Mycotaxon 83: 139. 2002.

Alternaria incomplexa E.G. Simmons, Mycotaxon 57: 394. 1996.

Alternaria infectoria E.G. Simmons, Mycotaxon 25: 298. 1986.

= *Pleospora infectoria* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 132. 1870 [1869–70].

≡ *Sphaeria infectoria* (Fuckel) Cooke, Handb. Brit. Fungi 2: 897. 1871.

≡ *Pleospora phaeocomoides* var. *infectoria* (Fuckel) Wehm., A World Monograph of the Genus *Pleospora* and its Segregates: 121. 1961.

≡ *Lewia infectoria* (Fuckel) M.E. Barr & E.G. Simmons, Mycotaxon 25: 296. 1986.

Alternaria intercepta E.G. Simmons, Mycotaxon 83: 134. 2002.

= *Lewia intercepta* E.G. Simmons & McKemy, Mycotaxon 83: 133. 2002.

Alternaria merytae E.G. Simmons, Mycotaxon 83: 136. 2002.

Alternaria metachromatica E.G. Simmons, Mycotaxon 50: 418. 1994.

Alternaria novae-zelandiae E.G. Simmons, Mycotaxon 83: 142. 2002.

Alternaria oregonensis E.G. Simmons, Mycotaxon 50: 417. 1994.

Alternaria slovaca (Svob.-Pol., L. Chmel & Bojan.) Woudenb. & Crous, **comb. nov.** MycoBank MB803699.

Basionym: *Aureobasidium slovacum* Svob.-Pol., L. Chmel & Bojan., Conspect. Verruc. 5: 116. 1966.

≡ *Chmelia slovaca* (Svob.-Pol., L. Chmel & Bojan.) Svob.-Pol., Biologia (Bratislava) 21: 83. 1966.

Alternaria triticimaculans E.G. Simmons & Perelló, Mycotaxon 50: 413. 1994.

Alternaria triticina Prasada & Prabhu, Indian Phytopathol. 15 (3–4): 292. 1963. [1962]

Alternaria ventricosa R.G. Roberts, Mycotaxon 100: 164. 2007.

Alternaria viburni E.G. Simmons, Mycotaxon 83: 132. 2002.

= *Lewia viburni* E.G. Simmons & McKemy, Mycotaxon 83: 130. 2002.

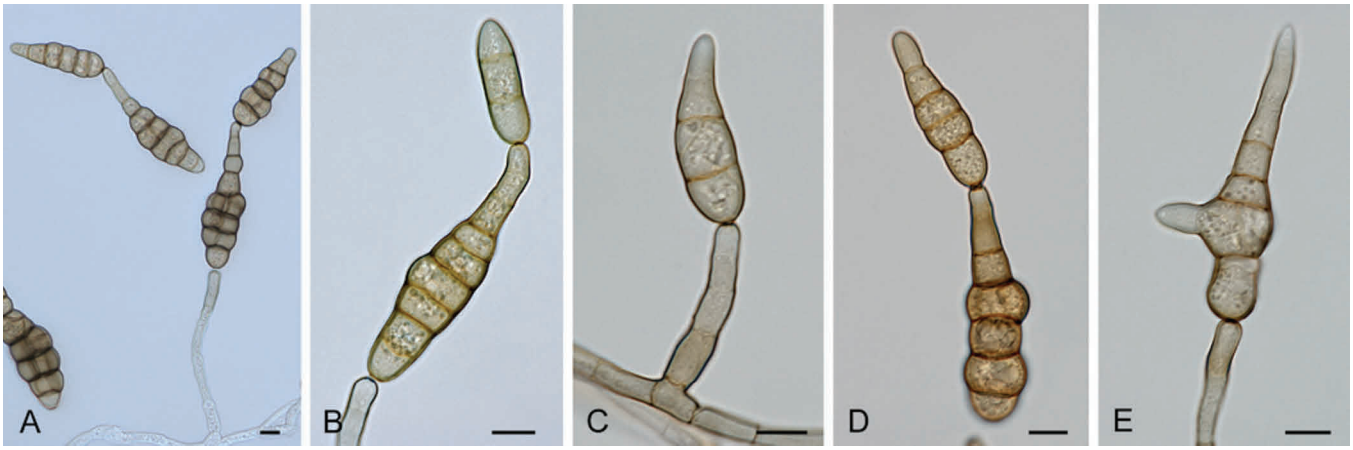

Fig. 15. *Alternaria* sect. *Japonicae*: conidia and conidiophores. A–B. *A. japonica*. C–E. *A. nepalensis*. Scale bars = 10 µm.

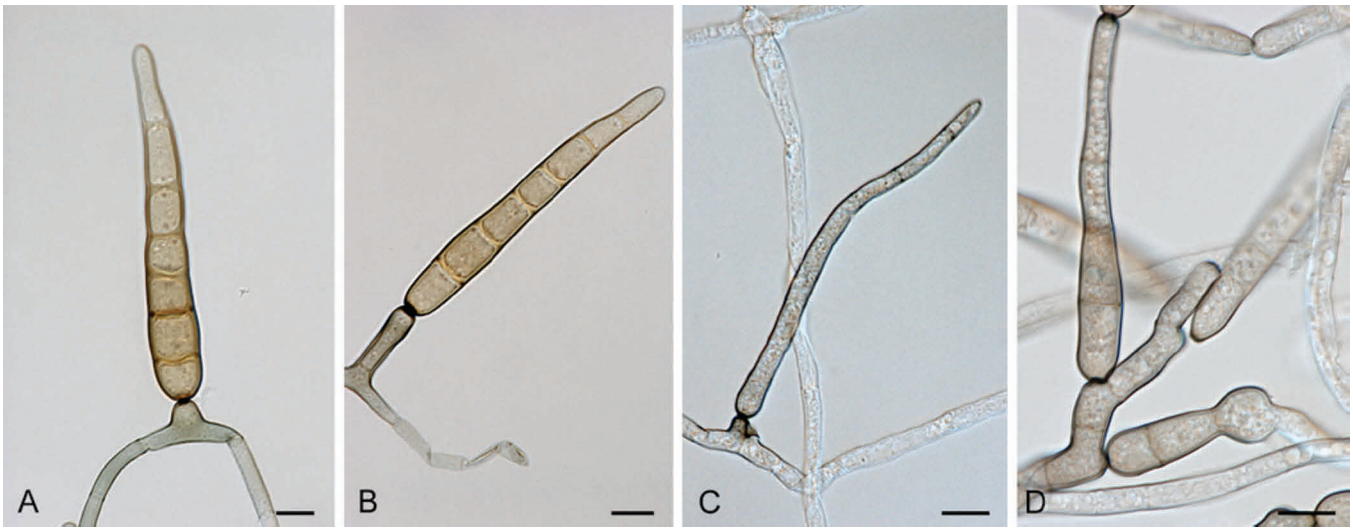

Fig. 16. *Alternaria* sect. *Nimbya*: conidia and conidiophores. A–B. *A. caricis*. C–D. *A. scirpicola*. Scale bars = 10 µm.

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 condiophores 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. scirpinfestans* 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.

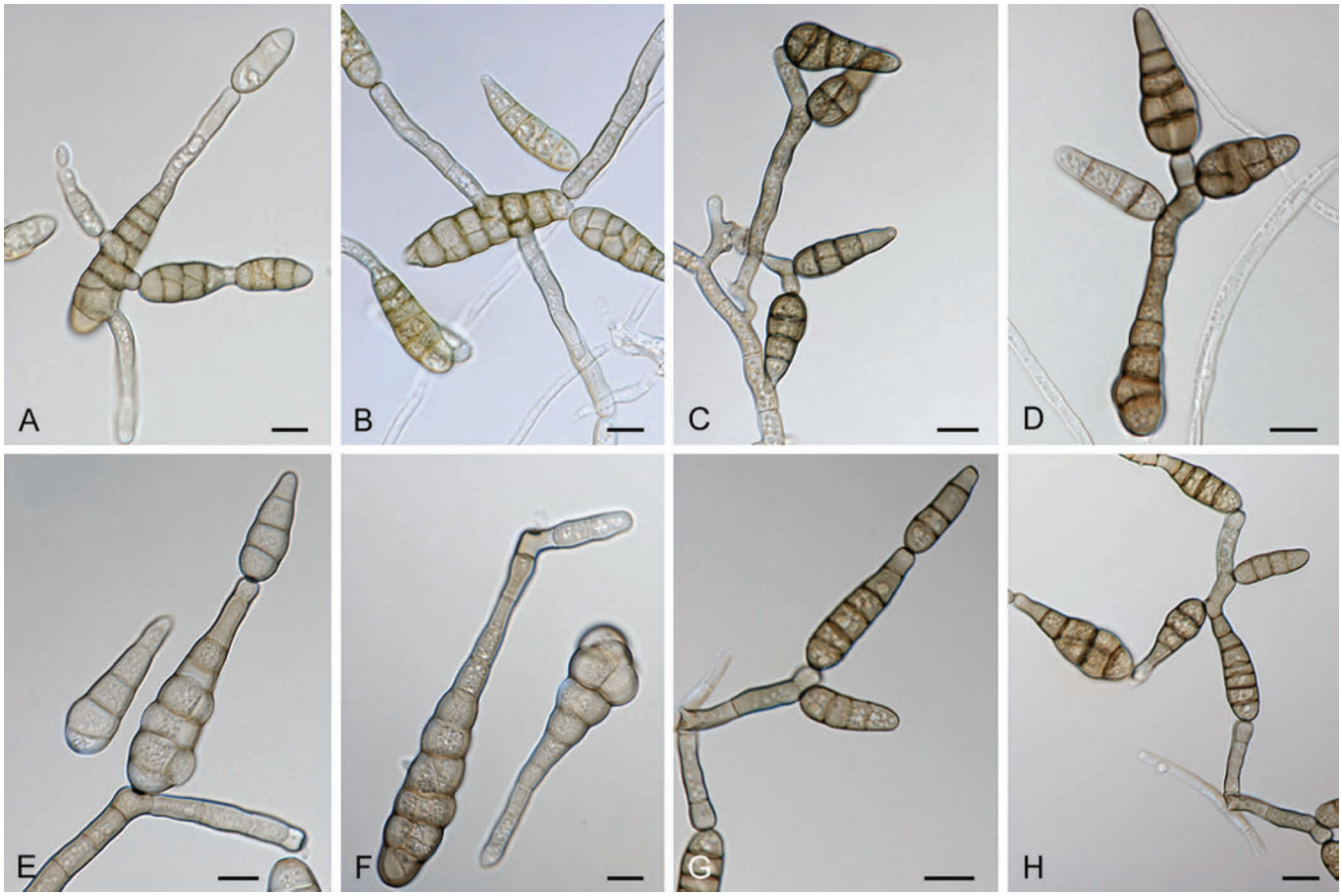

Fig. 17. *Alternaria* sect. *Panax*: conidia and conidiophores. A–B. *A. avenicola*. C–D. *A. calycipyricola*. E–F. *A. panax*. G–H. *A. photistica*. Scale bars = 10 µm.

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.

≡ *Cercospora scirpicola* (Fuckel) Zind.-Bakker, Rev. Mycol. (Paris) 5: 66. 1940.

≡ *Alternaria scirpicola* (Fuckel) M.T. Lucas & J. Webster, Čas. Slez. Mus., Ser. A, Hist. Nat. 23: 151. 1974 (nom. inval.).

≡ *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.

≡ *Clathrospora scirpicola* (DC.) Höhn., Ann. Mycol. 18(1/3): 77. 1920.

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

≡ *Pyrenophora scirpicola* (DC.) E. Müll., 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).

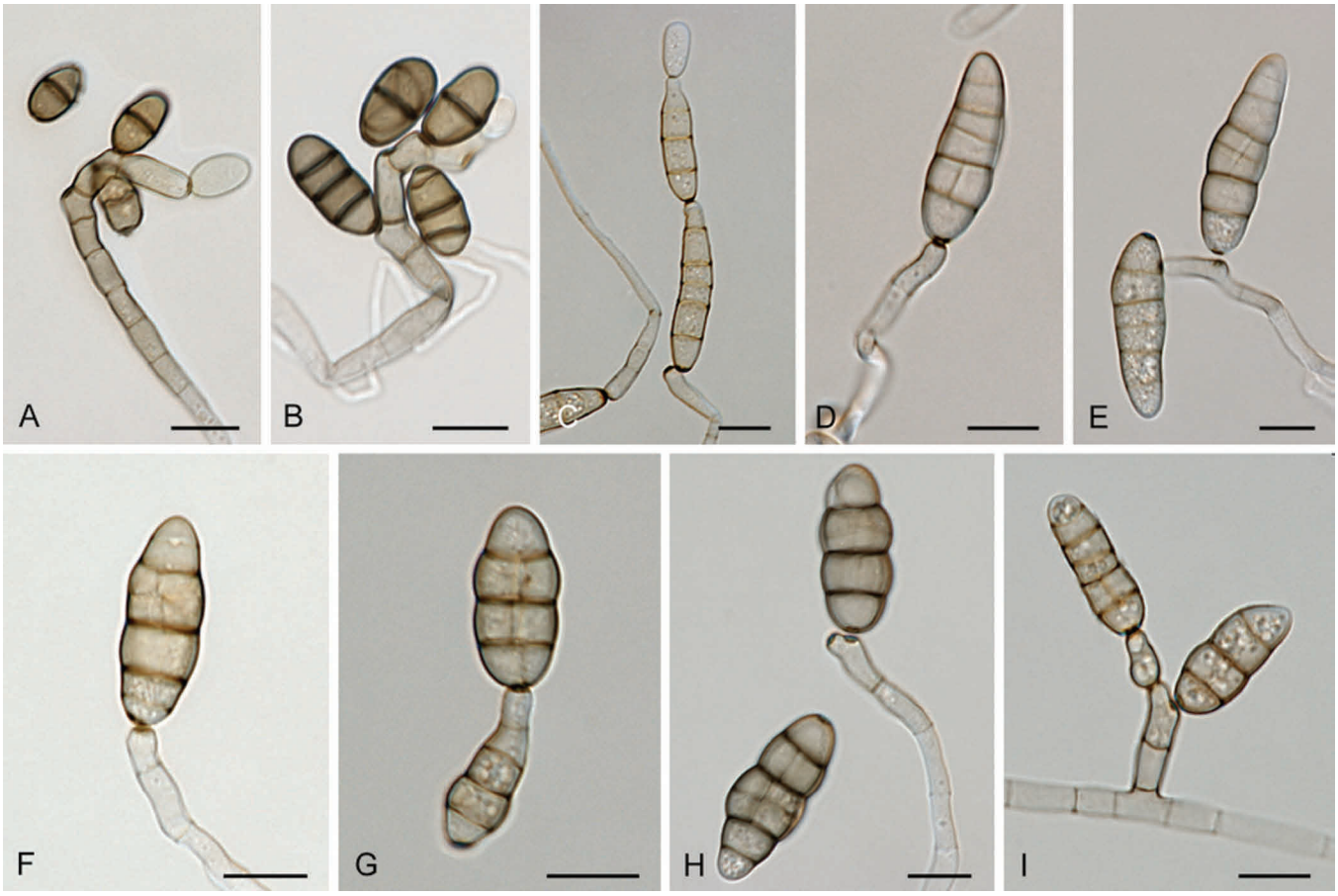

Fig. 18. *Alternaria* sect. *Phragmosporae*: conidia and conidiophores. A–B. *A. didymospora*. C. *A. phragmospora*. D–E. *A. limaciformis*. F–G. *A. molesta*. H–I. *A. mouchaccae*. Scale bars = 10 µm.

Alternaria avenicola E.G. Simmons, Kosiak & Kwaśna, in Simmons, CBS Biodiversity Ser. (Utrecht) 6: 114. 2007.
= *Lewia avenicola* Kosiak & 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.
Basionym: *Conoplea eryngii* Pers., Mycol. Eur. (Erlanga) 1: 11. 1822.
≡ *Exosporium eryngianum* (Pers.) Chevall., Flore Générale des Environs de Paris 1: 39. 1826.
≡ *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.
= *Macrosporium araliae* Dearn. & 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.
Basionym: *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.

Alternaria mouchaccae E.G. Simmons, Mycotaxon 13: 18. 1981.
≡ *Ulocladium chlamydosporum* Mouch., Rev. Mycol. (Paris) 36: 114. 1971, non *Alternaria chlamydospora* Mouch., 1973.

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.

Fig. 19. *Alternaria* sect. *Porri*: conidia and conidiophores. A–C. *A. daucii*. D–F. *A. pseudorostrata*. G–H. *A. solani*. Scale bars = 10 µm.

Diagnosis: Section *Porri* is characterised by broadly ovoid, obclavate, ellipsoid, 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. 88(2): 108. 1977 (nom. illegit., 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* (Natrass) 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.

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 dichondrae Gambogi, Vannacci & Triolo, Trans. Brit. Mycol. Soc. 65(2): 323. 1975.
Alternaria euphorbiicola E.G. Simmons & Engelhard, Mycotaxon 25: 196. 1986.
≡ *Macrosporium euphorbiae* 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.
≡ *Macrosporium 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 [1926].
Alternaria multirostrata E.G. Simmons & C.R. Jacks., Phytopathology 58: 1139. 1968.
Alternaria nitrimali E.G. Simmons & M.E. Palm, Mycotaxon 75: 93. 2000.
Alternaria passiflorae J.H. Simmonds, Proc. Roy. Soc. Queensland. 49: 151. 1938.
Alternaria poonensis Ragunath, Mycopathol. Mycol. Appl. 21: 315. 1963.
Alternaria porri (Ellis) Cif., J. Dept. Agric. Porto Rico 14: 30. 1930 [1929].
Basionym: *Macrosporium porri* Ellis, Grevillea 8 (no. 45): 12. 1879.
Alternaria protenta E.G. Simmons, Mycotaxon 25: 207. 1986.
Alternaria pseudorostrata E.G. Simmons, Mycotaxon 57: 398. 1996.
Alternaria ricini (Yoshii) Hansf., Proc. Linn. Soc. Lond. : 53. 1943.
Basionym: *Macrosporium ricini* Yoshii, Bult. Sci. Fak. Terk. Kjusu Imp. Univ. 3(4): 327. 1929.
Alternaria rostellata E.G. Simmons, Mycotaxon 57: 401. 1996.
Alternaria scorzonerae (Aderh.) Loer., Netherlands J. Pl. Pathol. 90(1): 37. 1984.
Basionym: *Sporidesmium scorzonerae* Aderh.,Arbeiten Kaiserl. Biol. Anst. Land-Forstw . 3: 439. 1903.
Alternaria sesami (E. Kawam.) Mohanty & Behera, Curr. Sci. 27: 493. 1958.
Basionym: *Macrosporium sesami* E. Kawam., Fungi 1(2): 27. 1931.
Alternaria solani Sorauer, Z. Pflanzenkrankh. Pflanzenschutz 6: 6. 1896.
= *Macrosporium solani* Ellis & G. Martin, Amer. Naturalist 16(12): 1003. 1882
≡ *Alternaria solani* (Ellis & G. Martin) L.R. Jones & Grout, Vermont Agric. Exp. Sta. Annual Rep. 9: 86. 1896.
Additional synonyms in Simmons (2007).
Alternaria solani-nigri R. Dubey, S.K. Singh & Kamal [as "*solani-nigri*"], Microbiol. Res. 154(2): 120. 1999.
Alternaria steviae Ishiba, T. Yokoy. & Tani, Ann. Phytopathol. Soc. Japan 48(1): 46. 1982.
Alternaria subcylindrica E.G. Simmons & R.G. Roberts, Mycotaxon 75: 62. 2000.
Alternaria tagetica S.K. Shome & Mustafee, Curr. Sci. 35: 370. 1966.
Alternaria tomatophila E.G. Simmons, Mycotaxon 75: 53. 2000.
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: Section *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.
Etymology: 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, Mycologia 59: 88. 1967.
= *Alternaria stemphylioides* Bliss, Mycologia 36: 538. 1944.
≡ *Alternaria chartarum* f. *stemphylioides* (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 "*capsicuma*"], 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.
≡ *Macrosporium septosporum* (Preuss) Rabenh., Bot. Zeitung 9: 454. 1851.
≡ *Ulocladium septosporum* (Preuss) E.G. Simmons, Mycologia 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: Section *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

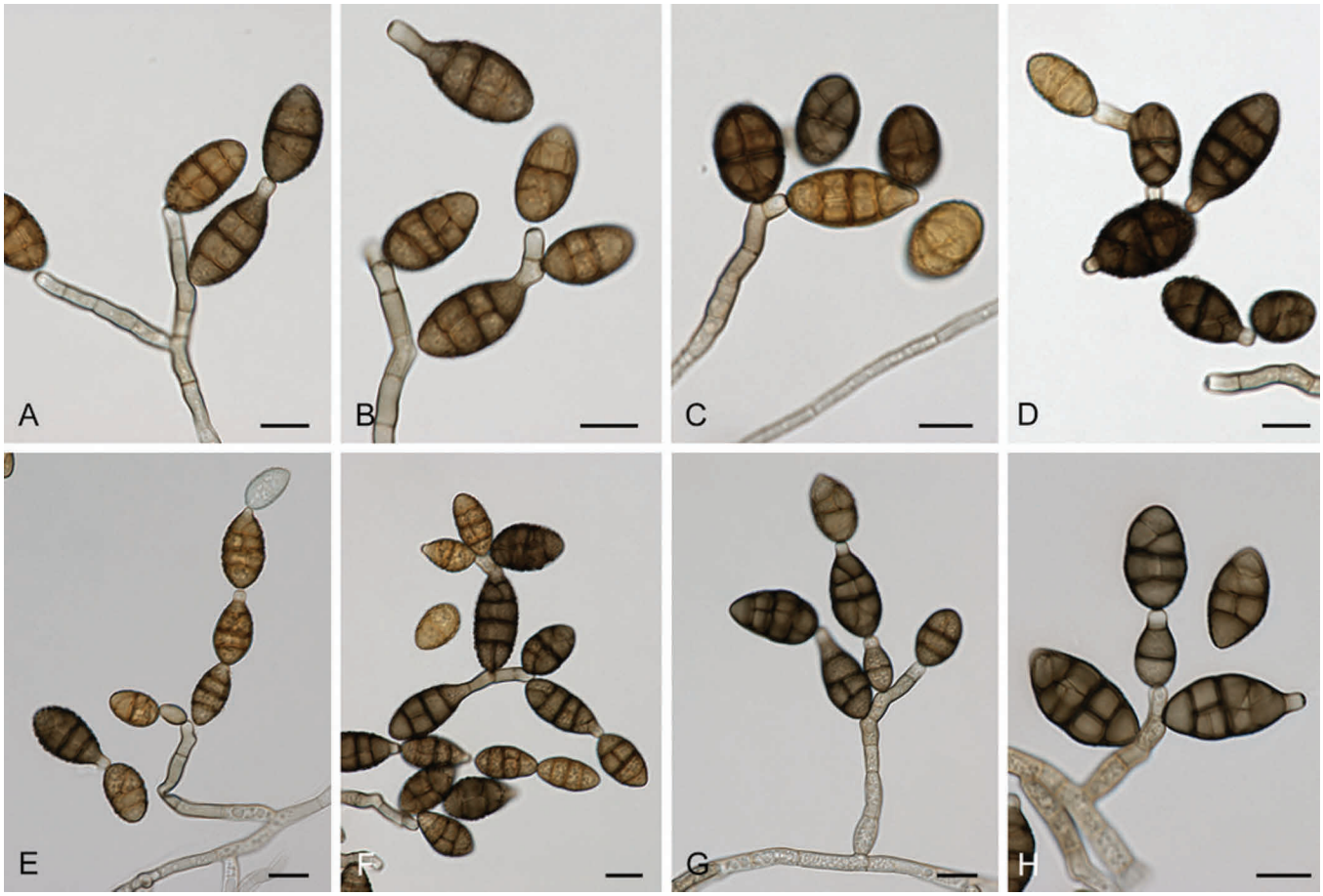

Fig. 20. *Alternaria* sect. *Pseudoulocladium*: conidia and conidiophores. A–B. *A. aspera*. C–D. *A. concatenata*. E–F. *A. chartarum*. G–H. *A. septospora*. Scale bars = 10 µm.

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 carotiincultae 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., Danish species of *Alternaria* & *Stemphylium*: 357. 1945.

≡ *Alternaria radicina* var. *petroselini* (Neerg.) Neerg., Encycl. Mycol. 33: 123. 1964.

Alternaria radicina Meier, Drechsler & E.D. Eddy, Phytopathology 12: 157. 1922.

≡ *Stemphylium radicinum* (Meier, Drechsler & E.D. Eddy) Neerg., Annual Rep. Phytopathol. Lab. J.E. Ohlsens Enkes, Seed Growers, Copenhagen 4: 14. 1939.

≡ *Thyrospora radicina* (Meier, Drechsler & E.D. Eddy) Neerg., Bot. Tidsskr. 44: 361. 1939.

≡ *Pseudostemphylium radicinum* (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.

≡ *Macrosporium smyrnii* (P. Crouan & H. Crouan) Sacc., Syll. Fungorum (Abellini) 4: 527. 1886.

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. carotiincultae*. 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.

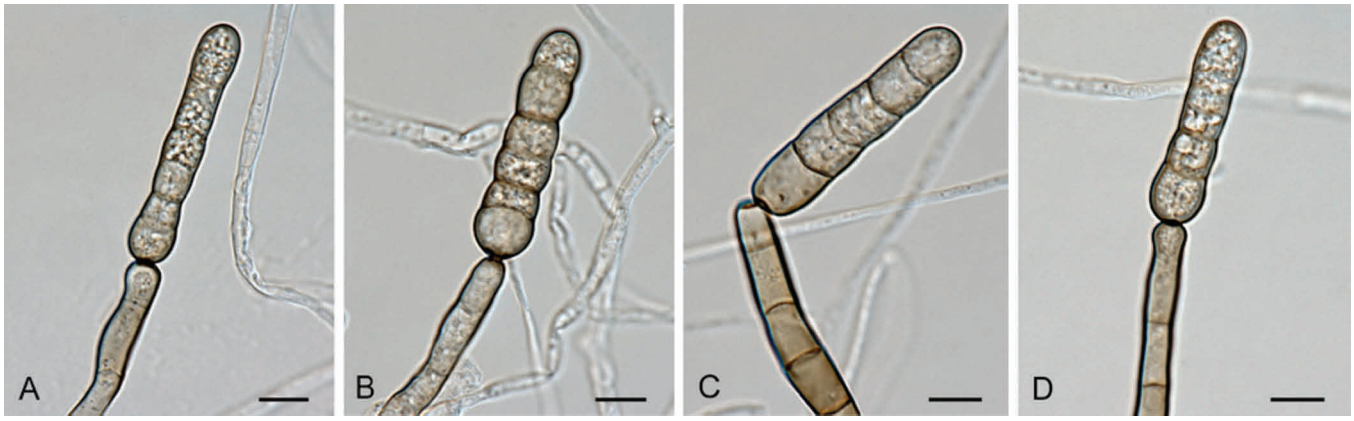

Fig. 23. *Alternaria* sect. *Teretispora*: conidia and conidiophores. A–D. *A. leucanthemi*. Scale bars = 10 µm.

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) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 674. 2007.

= *Alternaria 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 obovoid, 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 atrum* Preuss, Linnaea 25: 75. 1852.

≡ *Stemphylium atrum* (Preuss) Sacc., Syll. Fungorum (Abellini) 4: 520. 1886.

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

Basionym: *Ulocladium brassicae* Yong Wang bis & 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 bis & X.G. Zhang) Woudenb. & Crous, **comb. nov.** MycoBank MB803719.

Basionym: *Ulocladium cantlous* Yong Wang bis & 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.

≡ *Stemphylium consortiale* (Thüm.) J.W. Groves & Skolko, Canad. J. Res., Sect. C, Bot. Sci.: 196. 1944.

≡ *Pseudostemphylium consortiale* (Thüm.) Subram., Curr. Sci. 30: 423. 1961.

≡ *Ulocladium consortiale (Thüm.)* E.G. Simmons, Mycologia 59: 84. 1967.

= *Stemphylium ilicis* Tengwall, Meded. Phytopathol. Lab. "Willie Commelin 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 bis & 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 bis & X.G. Zhang) Woudenb. & Crous, **comb. nov.** MycoBank MB803722.

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

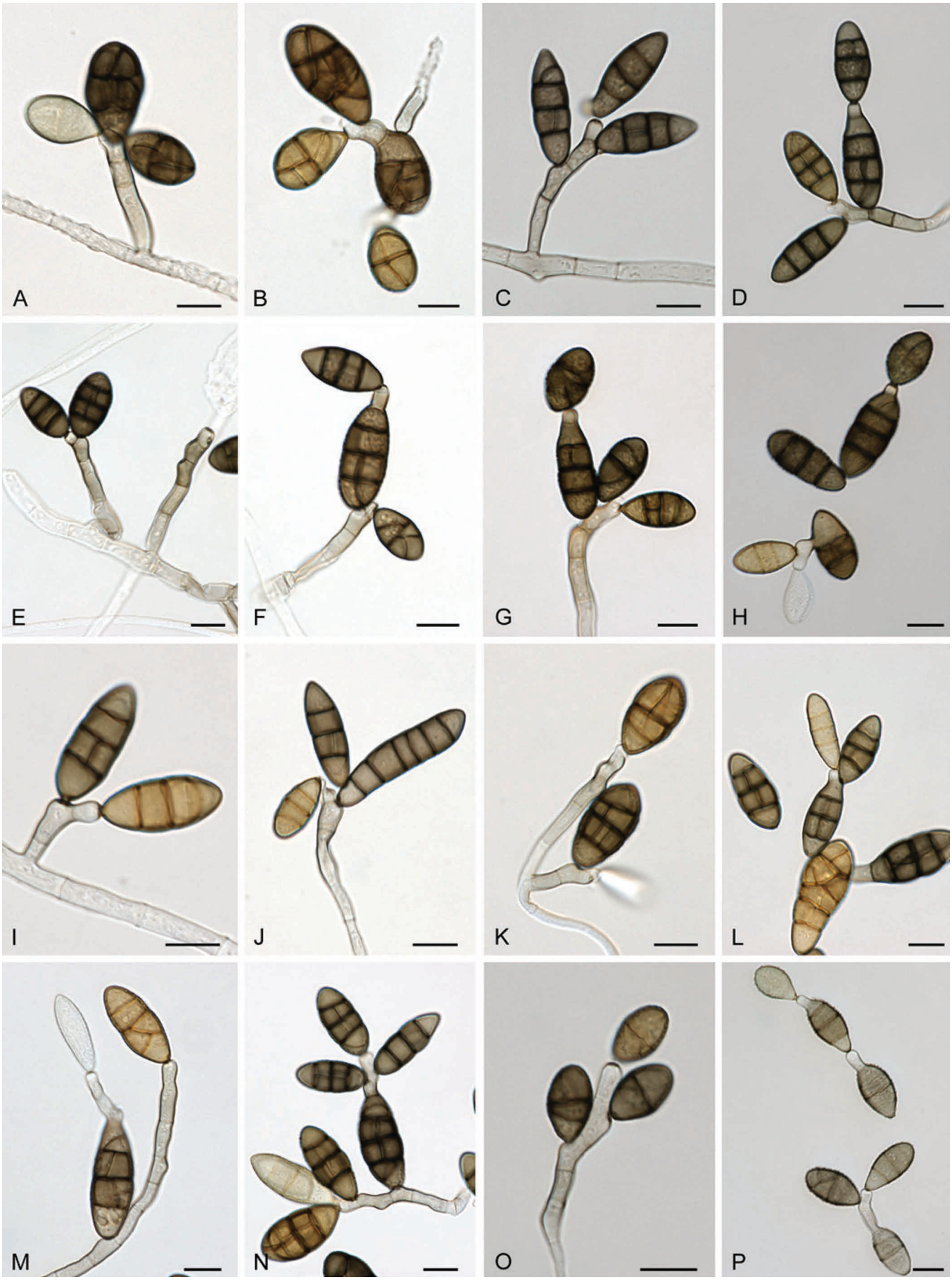

Fig. 24. *Alternaria* sect. *Ulocladioides*: conidia and conidiophores. A–B. *A. atra*. C–D. *A. brassicae-pekinensis*. E–F. *A. cantlous*. G–H. *A. multiformis*. I–J. *A. obovoidea*. K–L. *A. heterospora*. M–N. *A. subcucurbitae*. O–P. *A. terricola*. Scale bars = 10 µm.

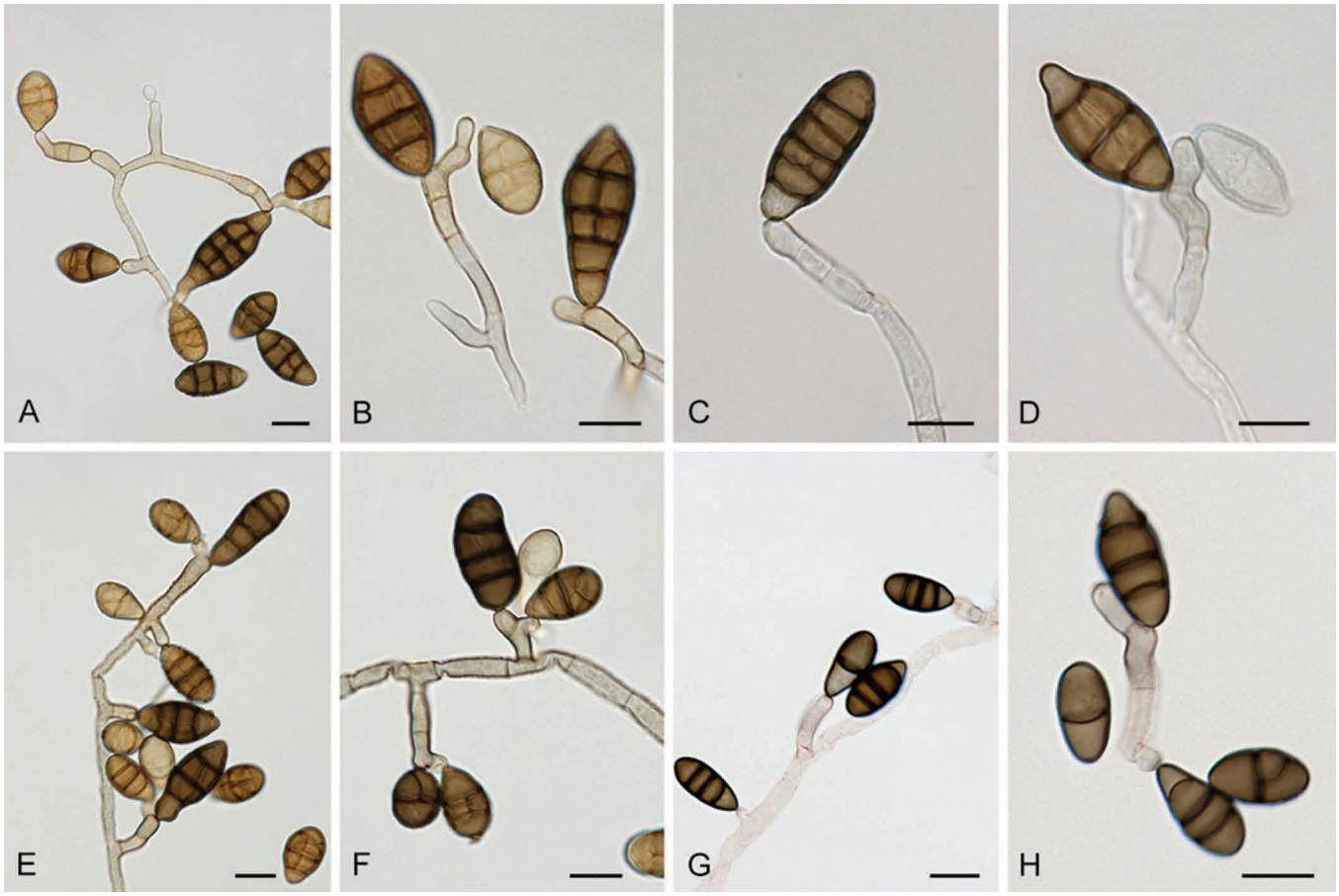

Fig. 25. *Alternaria* sect. *Ulocladium*: conidia and conidiophores. A–B. *A. capsici-annui*. C–D. *A. oudemansii*. E–F. *A. alternariae*. G–H. *A. botrytis*. Scale bars = 10 µm.

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;

Fig. 26. *Alternaria* sect. *Undifilum*: conidia and conidiophores. A–D. *A. bornmuelleri*. 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.

Alternaria brassicae (Berk.) Sacc., Michelia 2(no. 6): 129. 1880.
Basionym: *Macrosporium brassicae* Berk., Engl. Fl., Fungi (Edn 2) (London) 5: 339. 1836.
Additional synonyms listed in Simmons (2007).
Alternaria dennisii M.B. Ellis, Mycol. Pap. 125: 27. 1971.
≡ *Embellisia dennisii* (M.B. Ellis) E.G. Simmons, Mycotaxon 38: 257. 1990.
Alternaria helianthiinficiens E.G. Simmons, Walcz & R.G. Roberts [as "*helianthinficiens*"], Mycotaxon 25: 204. 1986.
Alternaria soliaridae E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 374. 2007.
Alternaria thalictrigena K. Schub. & Crous, Fungal Planet No. 12: 2. 2007.

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.

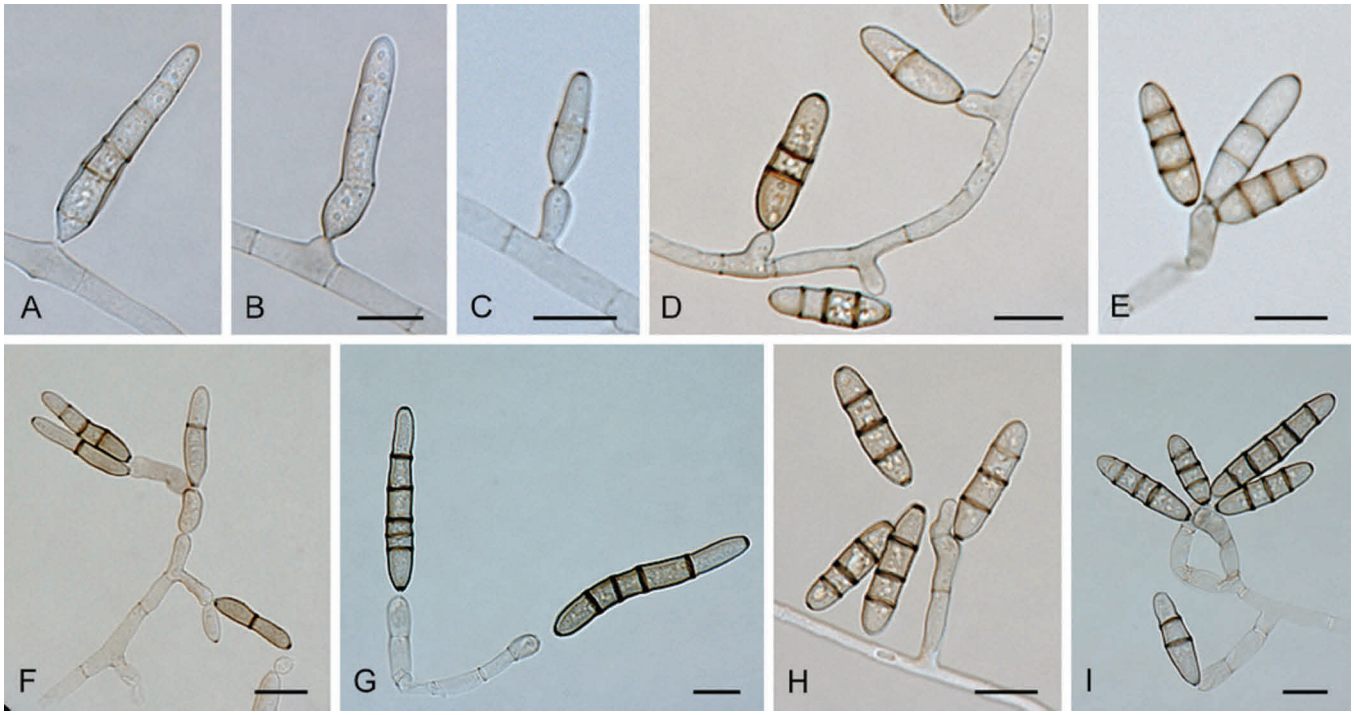

Fig. 27. *Paradendryphiella* gen. nov.: conidia and conidiophores. A–B, D–E, G–I. *P. salina*. C, F. *P. arenariae*. Scale bars = 10 µm.

= *Embellisia annulata* de Hoog, Seigle-Mur., Steiman & K.-E. Erikss., Antonie van Leeuwenhoek J. Microbiol. Serol. 51: 409. 1985.

Paradendryphiella arenariae (Nicot) Woudenb. & Crous, **comb. nov.** MycoBank MB803752.

Basionym: *Dendryphiella arenariae* Nicot, [as "arenaria"] Rev. Mycol. (Paris) 23: 93. 1958.

≡ *Scolecobasidium 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. *Ulocladioides* 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*, *Undifilum* 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. cumini*, 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

with *Dendryphion* (Ellis 1971), was resurrected for the non-sexual stage based on polyphyly within *Dendryphion* and morphological distinction from its type species, *D. comosum*. The type species of *Brachycladium*, *B. penicillatum*, 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. ellipsoidea* 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 *A. armoraciae* are ovoid, but vary from being narrow to broadly ovoid and ellipsoid, with 3–5 transverse septa and a single longitudinal septum in up to four of the transverse segments (Simmons 2007). *Embellisia abundans* was already mentioned as part of the *Chalastospora* clade (Andersen *et al.* 2009, Lawrence *et al.* 2012), and has long ovoid or obclavate conidia with 3–6 transverse septa and rarely any longitudinal septa (Simmons 1983). 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 *Stemphylium* 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. *Embellisioides*) 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 dennissii* is resurrected. Furthermore, the clustering of *E. conoidea* within the *A. brassicicola* species-group and *E. annulata* close to *Stemphylium*, 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 ***Allewia*** (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*. *Allewia* only contains two species of which one resides in sect. *Eureka* and one in sect. *Embellisioides*. 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 synonymised *Lewia* and *Allewia* 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. scirpicola* together with *N. scirpinfestans*, *N. scirpivora* and *N. caricis.* The *N. scirpicola* 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. caricis*. 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. *Alternantherae*. 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 amidst the *Alternaria* species-groups. Based on the data from Chou & Wu (2002), the name *Alternaria gomphrenae* is resurrected and placed in sect. *Alternantherae*.

The genus ***Sinomyces*** was described in by Wang *et al.* (2011) to accommodate *Ulocladium alternariae* and two new species from China, *S. obovoideus* and *S. fusoides* (type). The genus was differentiated 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. obovoideus*) 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* (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Hong *et al.* 2005, Xue & Zhang 2007, Pryor *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 *Sinomyces* 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 Simmons (1967). The suggestion to synonymise *Ulocladium* with *Alternaria* has been made several times in the past (Pryor & 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, Pryor & 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* (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Hong *et al.* 2005, Pryor *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 Pryor *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 (Pryor *et al.* 2009). A recent study on fungal endophytes in locoweeds 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, Pryor & Bigelow 2003, Hong *et al.* 2005, Pryor *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, RPB2 (dela Cruz 2006) gene regions. The transfer of the marine *Dendryphiella* species to *Scolecobasidium* (Ellis 1976), was also disputed. *Scolecobasidium* does not belong to the *Pleosporales* based on ITS, TEF1, and RPB2 sequences (dela Cruz 2006) and the morphology of the two *Dendryphiella* species does not fit the generic circumscription of *Scolecobasidium* (dela Cruz 2006, Jones *et al.* 2008). Ellis (1976) described denticles on the conidiogenous cells when the conidia become detached. However other observers describe a marginal basal 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 asci (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, Schoch *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*

(Fig. 2), outside the *Alternaria* complex. The type species of *Comoclathris*, *Comoclathris lanata*, was not available to us, but the two *Comoclathris compressa* strains cluster together in a well-supported clade within the *Pleosporaceae*, also outside the *Alternaria* complex, which we believe to be the correct phylogenetic placement of the genus. Two other strains, named *Comoclathris magna* (CBS 174.52) and *Clathrospora heterospora* (CBS 175.52) by Shoemaker and Babcock (1992), cluster amidst sect. *Alternata*. Culture studies performed by Simmons (1952) showed the presence of alternaria-like conidia in these cultures and no (mature) ascospore formation. Presumably the species observed by Shoemaker and Babcock (1992) on plant material were lost during cultivation and became replaced by *A. alternata* species-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***, ***Briansuttonia*** 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 rhexolytic conidial liberation and proliferating conidiophores with both phragmosporous and dictyosporous conidia. *Briansuttonia* was described in 2004 to accommodate *Corynespora alternarioides* (Castañeda Ruiz *et al.* 2004). The distoseptate muriform conidia of *Briansuttonia* do resemble *Alternaria* and *Stemphylium*, but the conidiogenous loci and euseptate conidia of *Alternaria* and holoblastic conidial ontogeny and euseptate muriform 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 muriform 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 *Alternaria* 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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