Colletotrichum species with curved conidia from herbaceous hosts

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Colletotrichum (*Glomerellaceae*, *Sordariomycetes*) species with dark setae and curved conidia are known as anthracnose pathogens of a number of economically important hosts and are often identified as *C. dematium*. *Colletotrichum dematium* has been synonymised with many species, including the type of the genus, *C. lineola*. Since there is no living strain of the original material of either species available, we re-collected *C. lineola* from the original location to serve as an epitype of that name, and chose an appropriate epitype specimen and associated strain of *C. dematium* from the CBS collection. A multilocus molecular phylogenetic analysis (ITS, ACT, Tub2, CHS-1, GAPDH, HIS3) of 97 isolates of *C. lineola*, *C. dematium* and other *Colletotrichum* species with curved conidia from herbaceous hosts resulted in 20 clades, with 12 clades containing strains that had previously been identified as *C. dematium*. The epitype strains of *C. lineola* and *C. dematium* reside in two closely related clades. Other clades represent four previously undescribed species, *C. anthrisci*, *C. liriopes*, *C. rusci* and *C. verruculosum*, isolated respectively from *Anthriscus* in the Netherlands, *Liriope* in Mexico, *Ruscus* in Italy and *Crotalaria* in Zimbabwe. The new combinations *C. spaethianum* and *C. tofieldiae* are made. *Colletotrichum truncatum* is epitypified, as well as *C. circinans*, *C. curcumae* and *C. fructi*. Three further unidentified *Colletotrichum* taxa were detected in the phylogenetic analysis, which may require description after further research. Each species is comprehensively described and illustrated.

Key words: *Ascomycota*, *Colletotrichum*, epitypification, *Glomerella*, phylogeny, systematics.

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Introduction

The genus *Colletotrichum* (*Glomerellaceae*, *Sordariomycetidae*, *Sordariomycetes*, *Ascomycota*) was described in 1831 by Corda, who provided drawings of *C. lineola* on a stem of an unidentified host belonging to the *Apiaceae* found in late autumn near Prague, Czech Republic (Corda, 1831). According to his description, *C. lineola* forms linear acervuli (Latin: *lineolae* = parallel lines) with fusiform, curved, hyaline conidia with acute ends and brown, opaque, subulate setae with acute tips.

Other species were incorporated subsequently into *Colletotrichum* that were originally described as members of *Sphaeria* Haller or *Vermicularia* Tode. Both of these taxa have complex nomenclature, but that of *Vermicularia* is directly relevant to this paper. *Vermicularia* was originally described by Tode (1790) for three species, *V. pseudosphaeria*, *V. pubescens* and *V. hispida*. The identity of all three is obscure, but they clearly have no close relationship with *Colletotrichum*. Fries adopted Tode's name in the *Systema orbis vegetabilium* (Fries, 1825) for a group of species including those now referred to *Colletotrichum dematium* and *C. trichellum*, but although he did not mention any of Tode's species, he did not explicitly exclude them. In the *Elenchus fungorum*, Fries (1828) indicated that he accepted the genus *Vermicularia* Tode in the text relating to *Sphaeria dematium*, and as this is one of the sanctioning works cited in the ICBN, the genus name is available because it was validly published and takes precedence over the homonymous plant genus *Vermicularia* Moench (1802) because it has priority (1790 vs 1802).

Duke (1928) published a detailed discussion of the genera *Vermicularia* and

Colletotrichum, in the course of which she typified *Vermicularia* with *Sphaeria dematium* Pers. This is now considered to be acceptable practice even though it was not one of the original species included in *Vermicularia* by Tode, as the genus was sanctioned by Fries. Duke appreciated the close similarity of the two genera, and observed that technically the name *Vermicularia* should be adopted if they are considered synonyms. She indicated that it would be advisable to conserve the name *Colletotrichum* over *Vermicularia*, but this appears never to have been carried out. The name *Vermicularia* was used subsequently by some authors for species with curved spores (Wollenweber and Hochapfel, 1949; Vassiljevski and Karakulin, 1950), but the name fell out of use following von Arx's revision (von Arx, 1957). In this seminal work, von Arx substantially reduced the number of species accepted in *Colletotrichum*, and synonymised *C. lineola* and many other *Colletotrichum* species with curved conidia with *C. dematium*. Sutton (1980) largely followed von Arx's synonymy, but there has not been a modern assessment of that arrangement.

The original description of *Sphaeria dematium* by Persoon (1801) comprises only a few observations: slightly flattened spheres on grey spots, in the centre with erect, stiff, diverging, monochromatic hairs/setae. The fungus was stated to be common on dead, dry herbaceous stems, especially on *Solanum tuberosum* (Persoon 1801). While later descriptions of *Colletotrichum dematium* all include characters such as the dark, stiff setae, the curved/falcate conidia and the circular or elliptical appressoria, there are considerable differences concerning size and shape of conidia (von Arx, 1957; Sutton, 1980, 1992; Baxter *et al*., 1983). According to Sutton (1980) conidia of *C. dematium* are strongly curved and less than 3 µm wide, features used to distinguish the species from *C. capsici*. However, in drawings of Baxter *et al*. (1983) one side of the conidia of *C. dematium* is nearly straight. The figures of two different strains exhibit different conidium shapes, which was regarded as an indication of the variability of the species. Drawings in Wollenweber and Hochapfel (1949) display a diverse range of variation for *C. dematium* on various host plants and media. Von Arx (1957) lists 88 synonyms of *C. dematium*. For most he did not study the original material, including *C. capsici*, *C. lineola* and *C. trichellum*. The last-named species had been shown to be different from *C. dematium* by Sutton (1962), while *C. capsici* has been epitypified recently (Shenoy *et al*., 2007). Many species have never been recollected and few have living cultures available that are derived from type material.

While *C. lineola* was described by Corda from a specimen on an "Umbelliferen" (=*Apiaceae*) stem, Grove (1937) combined that species name into *Vermicularia* with a description based on a specimen from *Dactylis glomerata* (*Poaceae*), though he indicated that *V. dematium* occurred on all kinds of herbaceous stems, including *Heracleum* (*Apiaceae*). That probably led to many grass-inhabiting collections being identified as *C. dematium* (e.g. Farr *et al*. 2009), which are now mostly if not all accommodated elsewhere. Wollenweber and Hochapfel (1949) and Feige and Ale-Agha (2004) mention *C. dematium* on *Heracleum sphondylium*, *H. pubescens* and *H. mantegazzianum* in Germany.

Colletotrichum dematium is now considered to be polyphagous, occuring on stems of various herbaceous hosts, but with a number of host-restricted parasitic forms. According to von Arx (1957), *C. dematium* is a widespread saprobe on dead leaves, onion peel, twigs and rotting fruits, only occasionally found as a parasite causing fruit rots, leaf spots and anthracnose, for example of *Fragaria* (*Rosaceae*), *Raphanus sativus* var. *hortensis* (*Brassicaceae*) *Rhododendron* (*Ericaceae*), *Morus* (*Moraceae*), *Goniolimon tataricum* (*Plumbaginaceae*), *Vigna unguiculata* (*Fabaceae*) and *Polygonatum falcatum* (*Liliaceae*) (Beraha and Wright, 1973; Smith *et al*., 1999; Yoshida and Shirata, 1999; Vinnere *et al*., 2002; Sato *et al*., 2005; Babu *et al*., 2008; Tomioka *et al*., 2008; Bobev *et al*., 2009). The species can also be associated with infections of humans, most often as keratitis (Mendiratta *et al*., 2005). While there is, as far as we know, no authentic strain of *C. lineola* available in any culture collection, there are numerous *C. dematium* strains from many hosts available, including on *Eryngium campestre* (*Apiaceae*).

Apart from *C. lineola* and *C. dematium*, many other *Colletotrichum* species with curved conidia are known as pathogens of different herbaceous plants, for example *C. truncatum* on *Glycine max* (Backman *et al*., 1982), *C. capsici* on *Capsicum* (*Solanaceae*) (Than *et al*., 2008) and *C. lilii* on *Lilium longiflorum* (Plakidas, 1944). *Colletotrichum* species with curved conidia on grass hosts have been studied recently with the addition of seven new species (Crouch *et al*., 2009a,b). A group of species that are sometimes mentioned as slightly curved, such as *C. fuscum*, *C. higginsianum* and *C. lini* (Sutton, 1980), seem to be closely related to each other according to preliminary phylogenies, and are excluded here. *Colletotrichum trichellum* is excluded in the morphological analysis, and will be the subject of a separate paper.

The *C. dematium* group has been largely overlooked in modern phylogenetic studies. The first rDNA-based studies (Sherriff *et al*., 1994; Sreenivasaprasad *et al*., 1996) included strains identified as *C. capsici* (treated as a synonym of *C. truncatum* in this paper), *C. dematium*, *C. trichellum* and *C. truncatum*, although the identification of some of the strains is doubtful. Both papers suggested that *C. capsici* was related to the *C. gloeosporioides* aggregate rather than the *C. dematium* group, and Sreenivasaprasad and co-workers detected a close relationship between *C. dematium*, *C. trichellum* and *C. truncatum*, though *C. coccodes* was also found in that clade. Moriwaki *et al*. (2002) came to broadly similar conclusions, and established that *C. circinans* also belonged in that aggregate based on studies of rDNA. More recent studies (e.g. Crouch *et al*., 2009c) concur that rDNA data alone are inadequate to detect relationships between *Colletotrichum* spp. except at the species aggregate level. Some studies (e.g. Lubbe *et al*., 2004; Cannon *et al*., 2008) have included strains from the *C. dematium* aggregate to place other studies in a phylogenetic context. A number of strains of *C. capsici* were included in the study that led to epitypification of that name (Shenoy *et al*., 2007), but no attempt was made to elucidate relationships between that taxon and other non-graminicolous falcate-spored species. Ford *et al*. (2004) included strains identified as *C. truncatum* from a range of host plants in their study of populations of that species on lentil in Canada. They detected a number of clades based on rDNA data including those accepted in this paper as *C. spaethianum* and *C. tofieldiae*, but the strains from lentil seem to belong to a separate taxon. We have not studied cultures from this source, but ITS sequences (see also Latunde-Dada and Lucas 2007) indicate strongly that they belong to the *C. destructivum* rather than the *C. dematium* clade. This is of particular concern as the teleomorph name *Glomerella truncata* (Armstrong-Cho and Banniza 2006) is based on a cross between two of the lentil strains.

In preliminary phylogenies using ITS sequence data (unpublished data), strains from the CBS culture collection that had been previously identified as *C. dematium* formed several clades, suggesting that *C. dematium* is polyphyletic in its current circumscription. The scope of this paper is therefore to clarify the identity of *C. dematium* and to epitypify this species, and to reveal the phylogenetic relationships of *C. dematium* and other allied species with curved conidia from herbaceous hosts.

Materials and methods

Isolates

Decayed or recently dead stems of *Apiaceae* were collected near Prague (Czech Republic), in Utrecht (Netherlands) and Hannover (Germany). Type specimens of the species studied were located in the Herbarium of the Royal Botanic Gardens in Kew, UK (K), Corda's herbarium in the Mycological Department of the National Museum in Prague, Czech Republic (PRM), herbarium of the Botanische Staatssammlung München (M), and the Farlow Herbarium, Harvard University, Cambridge, MA, USA (FH). The lectotype of *Sphaeria dematium* was chosen from original material in Persoon's herbarium, specimens from which are preserved in the National Herbarium in Leiden (L), the Netherlands. The epitype specimens of *C. circinans*, *C. curcumae*, *C. dematium*, *C. fructi*, *C. lilii*, *C. spaethianum*, *C. spinaciae*, *C. tofieldiae* and *C. truncatum* were selected from the culture collections of the Centraalbureau voor Schimmelcultures (CBS) Utrecht, The Netherlands and CABI Europe-UK, Egham, Surrey, UK (IMI) and are

preserved as dried cultures in the CBS herbarium. All descriptions are based on the ex-type, ex-epitype or ex-neotype culture as appropriate. Features of other strains are added if deviant. Subcultures of the types and epitypes, respectively, as well as all other isolates used for morphological and sequence analyses are maintained in the culture collection of CBS and/or CABI (IMI) and presented in Table 1.

Morphological analysis

To enhance sporulation, autoclaved filter paper and double-autoclaved stems of *Anthriscus sylvestris* were placed onto the surface of synthetic nutrient-poor agar medium (SNA; Nirenberg 1976). SNA, OA, PDA and MEA cultures incubated at 20 °C under near UV light with 12 h photoperiod or permanent near UV light for 10 d. Measurements and photographs of characteristic structures were made according to Damm *et al*. (2007). Appressoria on hyphae were observed on the undersurface of the SNA cultures. Microscopic preparations were made in clear lactic acid or water, with 30 measurements per structure and observed with a Nikon SMZ1000 dissecting microscope (DM) or with a Nikon Eclipse 80i microscope using differential interference contrast (DIC) illumination. Colony characters and pigment production on malt extract agar (MEA, 2 % malt extract, Oxoid Ltd., England; 1.5 % agar, Difco, USA) and 2 % potato-dextrose agar (PDA; Crous *et al*., 2009) incubated at 20°C were noted after 1 wk. Colony colours were rated according to Rayner (1970). Growth rates were measured after 5, 7 and 10d.

Phylogenetic analysis

Genomic DNA of the isolates was extracted using the method of Damm *et al*. (2008). The 5.8S nuclear ribosomal gene with the two flanking internal transcribed spacers (ITS), a 200-bp intron of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH), a partial sequence of the actin (ACT), chitin synthase 1 (CHS-1), beta-tubulin (Tub2) and of the histone3 (HIS3) gene were amplified and sequenced using the primer pairs V9G (de Hoog and Gerrits van den Ende 1998) + ITS-4 (White *et al*., 1990), GDF1 + GDR1 (Guerber *et al*., 2003), ACT-512F + ACT-783R (Carbone and Kohn, 1999), CHS-354R + CHS-79F (Carbone and Kohn 1999), BT2Fd + BT4R (Woudenberg *et al*., 2009) or T1 (O'Donnell and Cigelnik, 1997) + Bt-2b (Glass and Donaldson 1995) and CYLH3F + CYLH3R (Crous *et al*., 2004b), respectively. The PCRs were per-formed in a 2720 Thermal Cycler (Applied Biosystems, Foster City, California) in a total volume of 12.5 µl. The GAPDH, ACT, CHS-1, Tub2 and HIS3 PCR mixture contained 1 µl 20x diluted genomic DNA, 0.2 µM of each primer, 1x PCR buffer (Bioline, Luckenwalde, Germany), 2 mM $MgCl_2$, 20 µM of each dNTP, 0.7 µl DMSO and 0.25 U Taq DNA poly-merase (Bioline). Conditions for amplification were an initial denaturation step of 5 min at 94°C, followed by 40 cycles of 30 s at 94°C, 30 s at 52°C and 30 s at 72°C, and a final denaturation step of 7 min at 72°C. The ITS PCR was performed as described by Wouden-berg *et al*. (2009). The DNA sequences ob-tained from forward and reverse primers were used to obtain consensus sequences using Bionumeris v. 4.60 (Applied Maths, St-Marthens-Lathem, Belgium) which were added to the outgroup (*C. lindemuthianum* CBS 315.28) and the alignment assembled and manually adjusted using Sequence Alignment Editor v. 2.0a11 (Rambaut, 2002).

A maximum parsimony analysis was performed on the multilocus alignment (ITS, ACT, Tub2, CHS-1, GAPDH, HIS3) with PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford, 2000) using the heuristic search option with 100 random sequence additions and tree bisection and reconstruction (TBR) as the branch-swapping algorithm. Alignment gaps were treated as missing and all characters were unordered and of equal weight. The robustness of the trees obtained was evaluated by 500 bootstrap replications with 2 random sequence additions (Hillis and Bull 1993). Tree length, consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were calculated for the resulting tree. A maximum likelihood phylogenetic analyses of the dataset was performed with RAxML on the Cipres Web Portal (http://www.phylo.org/sub_sections/portal/), with a GTR model of molecular evolution (selected by the program) and 1000 bootstrap replicates using RAxML VI-HPC (Stamatakis *et al*., 2008). Sequences

Table 1. Strains of *Colletotrichum* studied in this paper with details about host/substrate and location, and GenBank accessions of the sequences generated.

Species	Accession number[1]	Host/substrate	Country	GenBank accessions					
				ITS	ACT	Tub2	CHS-1	GAPDH	HIS3
C. anthrisci	CBS 125334*	*Anthriscus sylvestris*, dead stem	Netherlands	GU227845	GU227943	GU228139	GU228335	GU228237	GU228041
	CBS 125335	*Anthriscus sylvestris*, dead stem	Netherlands	GU227846	GU227944	GU228140	GU228336	GU228238	GU228042
C. chlorophyti	IMI 103806*	*Chlorophytum* sp.	India	GU227894	GU227992	GU228188	GU228384	GU228286	GU228090
	CBS 142.79	*Stylosanthes hamata*	Australia	GU227895	GU227993	GU228189	GU228385	GU228287	GU228091
C. circinans	CBS 111.21	*Allium cepa*, smudge	USA	GU227854	GU227952	GU228148	GU228344	GU228246	GU228050
	CBS 221.81*	*Allium cepa*	Serbia	GU227855	GU227953	GU228149	GU228345	GU228247	GU228051
	CBS 123.25 / ATCC 26388	*Allium cepa*, bulb	USA	GU227856	GU227954	GU228150	GU228346	GU228248	GU228052
	CBS 117546	*Allium porrum*	Netherlands	GU227857	GU227955	GU228151	GU228347	GU228249	GU228053
	CBS 351.73 / ATCC 24488	*Beta vulgaris*, pathogenic	New Zealand	GU227858	GU227956	GU228152	GU228348	GU228250	GU228054
	CBS 123885	*Viola hirta*, leaf spot	Czech Republic	GU227859	GU227957	GU228153	GU228349	GU228251	GU228055
	CBS 123886	*Viola hirta*, leaf spot	Czech Republic	GU227860	GU227958	GU228154	GU228350	GU228252	GU228056
	CBS 125331	*Anthriscus sylvestris*, dead stem	Germany	GU227861	GU227959	GU228155	GU228351	GU228253	GU228057
C. curcumae	IMI 288937*	*Curcuma longa*	India	GU227893	GU227991	GU228187	GU228383	GU228285	GU228089
C. dematium	CBS 125.25*	*Eryngium campestre*, dead leaf	France	GU227819	GU227917	GU228113	GU228309	GU228211	GU228015
	CBS 125340	*Apiaceae*, dead stem	Czech Republic	GU227820	GU227918	GU228114	GU228310	GU228212	GU228016
	CBS 125341	*Apiaceae*, dead stem	Czech Republic	GU227821	GU227919	GU228115	GU228311	GU228213	GU228017
	IMI 350847	*Solanum tuberosum*, stem, pathogenic	Australia	GU227825	GU227923	GU228119	GU228315	GU228217	GU228021
	CBS 123728	*Genista tinctoria*, leaf spot	Czech Republic	GU227822	GU227920	GU228116	GU228312	GU228214	GU228018
	CBS 123729	*Genista tinctoria*, leaf spot	Czech Republic	GU227823	GU227921	GU228117	GU228313	GU228215	GU228019
	CBS 125346 / DAOM 212643	*Xanthium sp.*	unknown	GU227824	GU227922	GU228118	GU228314	GU228216	GU228020

Table 1 (continued). Strains of *Colletotrichum* studied in this paper with details about host/substrate and location, and GenBank accessions of the sequences generated.

Species	Accession number[1]	Host/substrate	Country	GenBank accessions					
				ITS	ACT	Tub2	CHS-1	GAPDH	HIS3
	CBS 115524 / STE-U 4078	*Vitis vinifera*, endophyte	South Africa	GU227826	GU227924	GU228120	GU228316	GU228218	GU228022
C. fructi	CBS 346.37 / CCT 4806*	*Malus sylvestris*, fruit	USA	GU227844	GU227942	GU228138	GU228334	GU228236	GU228040
C. lilii	CBS 109214 / BBA 62147	*Lilium* sp.	Japan	GU227810	GU227908	GU228104	GU228300	GU228202	GU228006
	CBS 186.30	*Lilium* sp., bulb	Netherlands	GU227811	GU227909	GU228105	GU228301	GU228203	GU228007
C. lineola	CBS 125337*	*Apiaceae*, dead stem	Czech Republic	GU227829	GU227927	GU228123	GU228319	GU228221	GU228025
	CBS 125339	*Apiaceae*, dead stem	Czech Republic	GU227830	GU227928	GU228124	GU228320	GU228222	GU228026
	CBS 125332	*Anthriscus* sp.	Netherlands	GU227831	GU227929	GU228125	GU228321	GU228223	GU228027
	CBS 125333	*Heracleum* sp.	Netherlands	GU227832	GU227930	GU228126	GU228322	GU228224	GU228028
	CBS 125329	*Astrantia major*	Zimbabwe	GU227833	GU227931	GU228127	GU228323	GU228225	GU228029
	CBS 125344 / DAOM 190485	*Fragaria* sp., petiole	Canada	GU227834	GU227932	GU228128	GU228324	GU228226	GU228030
	CBS 125351 / CCF 2425	*Prunus domestica*, rotten fruit	Czech Republic	GU227841	GU227939	GU228135	GU228331	GU228233	GU228037
	CBS 125345 / DAOM 212586	*Tussilago farfara*	Canada	GU227839	GU227937	GU228133	GU228329	GU228231	GU228035
	CBS 125348 / DAOM 214578	*Euphorbia esula*, in a pasture	Canada	GU227840	GU227938	GU228134	GU228330	GU228232	GU228036
	CBS 147.34	*Clarkia elegans*, seed, pathogenic	unknown	GU227838	GU227936	GU228132	GU228328	GU228230	GU228034
	CBS 109228 / BBA 71528	*Lupinus polyphyllus*	Germany	GU227835	GU227933	GU228129	GU228325	GU228227	GU228031
	CBS 124959	*Symplocarpus foetidus*, leaf	USA	GU227842	GU227940	GU228136	GU228332	GU228234	GU228038
	CBS 124.25	*Trillium* sp., leaf spot	USA	GU227836	GU227934	GU228130	GU228326	GU228228	GU228032
	CBS 282.85	*Allium giganteum*, dead stem	Netherlands	GU227843	GU227941	GU228137	GU228333	GU228235	GU228039
	CBS 661.94	old herbaceous stem	Netherlands	GU227837	GU227935	GU228131	GU228327	GU228229	GU228033
C. liriopes	CBS 119444*	*Lirope muscari*	Mexico	GU227804	GU227902	GU228098	GU228294	GU228196	GU228000
	CBS 122747	*Liriope muscari*	Mexico	GU227805	GU227903	GU228099	GU228295	GU228197	GU228001
***C. phaseolorum* 1**	CBS 157.36	*Phaseolus radiatus* var. *aureus*	Japan	GU227896	GU227994	GU228190	GU228386	GU228288	GU228092

Table 1 (continued). Strains of *Colletotrichum* studied in this paper with details about host/substrate and location, and GenBank accessions of the sequences generated.

Species	Accession number[1]	Host/substrate	Country	GenBank accessions					
				ITS	ACT	Tub2	CHS-1	GAPDH	HIS3
***C. phaseolorum* 2**	CBS 158.36	*Vigna sinensis*	Japan	GU227897	GU227995	GU228191	GU228387	GU228289	GU228093
C. rusci	CBS 119206*	*Ruscus*, stem	Italy	GU227818	GU227916	GU228112	GU228308	GU228210	GU228014
C. spaethianum	CBS 167.49 / BBA 4804*	*Hosta sieboldiana*, dead stem	Germany	GU227807	GU227905	GU228101	GU228297	GU228199	GU228003
	CBS 100063	*Lilium* sp., infected leaves	South Korea	GU227808	GU227906	GU228102	GU228298	GU228200	GU228004
	CBS 101631	*Hemerocallis* sp., leaf spot	New Zealand	GU227809	GU227907	GU228103	GU228299	GU228201	GU228005
C. spinaciae	CBS 128.57	*Spinacia oleracea*	Netherlands	GU227847	GU227945	GU228141	GU228337	GU228239	GU228043
	CBS 108.40	*Spinacia oleracea*, seed	Netherlands	GU227848	GU227946	GU228142	GU228338	GU228240	GU228044
	CBS 150.35	*Spinacia oleracea*, seed	Netherlands	GU227849	GU227947	GU228143	GU228339	GU228241	GU228045
	IMI 104607	*Spinacia* sp.	Italy	GU227850	GU227948	GU228144	GU228340	GU228242	GU228046
	CBS 125349 / DAOM 214579	*Chenopodium album*	USA	GU227852	GU227950	GU228146	GU228342	GU228244	GU228048
	CBS 125347 / DAOM 212662	*Portulaca oleracea*	Canada	GU227851	GU227949	GU228145	GU228341	GU228243	GU228047
	CBS 129.57	*Medicago sativa*	Netherlands	GU227853	GU227951	GU228147	GU228343	GU228245	GU228049
C. tofieldiae	CBS 495.85	*Tofieldia calyculata*	Switzerland	GU227801	GU227899	GU228095	GU228291	GU228193	GU227997
	CBS 168.49	*Lupinus polyphyllus*, dead stem	Germany	GU227802	GU227900	GU228096	GU228292	GU228194	GU227998
	IMI 288810	*Dianthus* sp.	UK	GU227803	GU227901	GU228097	GU228293	GU228195	GU227999
C. trichellum	CBS 118198	*Hedera* sp., living leaves	Guatemala	GU227813	GU227911	GU228107	GU228303	GU228205	GU228009
	CBS 217.64 / IMI 84989	*Hedera helix*, leaf	UK	GU227812	GU227910	GU228106	GU228302	GU228204	GU228008
	CBS 448.90	*Hedera helix*, stems	Germany	GU227814	GU227912	GU228108	GU228304	GU228206	GU228010
	CBS 180.52	*Hedera* sp.	Netherlands	GU227815	GU227913	GU228109	GU228305	GU228207	GU228011
	CBS 102642	*Hedera helix*, leaf	New Zealand	GU227816	GU227914	GU228110	GU228306	GU228208	GU228012
	CBS 125343 / DAOM 188792	*Hedera helix*	Canada	GU227817	GU227915	GU228111	GU228307	GU228209	GU228013
C. truncatum	CBS 151.35*	*Phaseolus lunatus*	USA	GU227862	GU227960	GU228156	GU228352	GU228254	GU228058
	CBS 119189	*Phaseolus lunatus*	USA	GU227863	GU227961	GU228157	GU228353	GU228255	GU228059
	CBS 710.70	*Phaseolus vulgaris*	Brazil	GU227864	GU227962	GU228158	GU228354	GU228256	GU228060
	CBS 195.32	*Glycine max*, anthracnose	USA	GU227865	GU227963	GU228159	GU228355	GU228257	GU228061
	CBS 182.52	*Glycine max*	USA	GU227866	GU227964	GU228160	GU228356	GU228258	GU228062

Table 1 (continued). Strains of *Colletotrichum* studied in this paper with details about host/substrate and location, and GenBank accessions of the sequences generated.

Species	Accession number[1]	Host/substrate	Country	GenBank accessions					
				ITS	ACT	Tub2	CHS-1	GAPDH	HIS3
	CBS 345.70	*Glycine max*, seed	Denmark	GU227867	GU227965	GU228161	GU228357	GU228259	GU228063
	CBS 669.71	*Medicago sativa*	Israel	GU227868	GU227966	GU228162	GU228358	GU228260	GU228064
	CBS 112998	*Arachis hypogaea*	Gambia	GU227869	GU227967	GU228163	GU228359	GU228261	GU228065
	CBS 113117	*Arachis hypogaea*	Tanzania	GU227870	GU227968	GU228164	GU228360	GU228262	GU228066
	CBS 506.97	*Vigna unguiculata*	Burkina Faso	GU227871	GU227969	GU228165	GU228361	GU228263	GU228067
	CBS 356.72	*Vigna sinensis*	Pakistan	GU227872	GU227970	GU228166	GU228362	GU228264	GU228068
	CBS 141.79	*Stylosanthes hamata*	Australia	GU227873	GU227971	GU228167	GU228363	GU228265	GU228069
	IMI 135524	*Clitoria ternatea*, seed	Sudan	GU227874	GU227972	GU228168	GU228364	GU228266	GU228070
	CBS 260.85	*Crotalaria spectabilis*, pathogenic	USA	GU227875	GU227973	GU228169	GU228365	GU228267	GU228071
	CBS 136.30	*Crotalaria juncea*	Trinidad and Tobago	GU227876	GU227974	GU228170	GU228366	GU228268	GU228072
	CBS 120709	*Capsicum frutescens*	India	GU227877	GU227975	GU228171	GU228367	GU228269	GU228073
	CBS 172.48	unknown	India	GU227878	GU227976	GU228172	GU228368	GU228270	GU228074
	CBS 335.75	*Capsicum annuum*, seed	Indonesia	GU227879	GU227977	GU228173	GU228369	GU228271	GU228075
	CBS 371.67	*Capsicum annuum*	India	GU227880	GU227978	GU228174	GU228370	GU228272	GU228076
	CBS 125328	*Capsicum annuum*	Mexico	GU227885	GU227983	GU228179	GU228375	GU228277	GU228081
	CBS 170.59	*Brassica* sp., stump	Netherlands	GU227881	GU227979	GU228175	GU228371	GU228273	GU228077
	IMI 63597	*Peperomia magnoliifolia*	India	GU227886	GU227984	GU228180	GU228376	GU228278	GU228082
	CBS 127.57 / IMI 80025	*Peperomia magnoliifolia*	India	GU227888	GU227986	GU228182	GU228378	GU228280	GU228084
	IMI 61677	*Corchorus capsularis*	Bangladesh	GU227882	GU227980	GU228176	GU228372	GU228274	GU228078
	CBS 125327	*Bougainvillea* sp., stem, necrotic spots	Netherlands	GU227887	GU227985	GU228181	GU228377	GU228279	GU228083
	CBS 714.95	*Limonium* sp.	Israel (imported in the Netherlands)	GU227883	GU227981	GU228177	GU228373	GU228275	GU228079
	CBS 146.32	*Opuntia* sp.	USA, Texas	GU227884	GU227982	GU228178	GU228374	GU228276	GU228080
	CBS 125330	*Basella rubra*	Laos	GU227889	GU227987	GU228183	GU228379	GU228281	GU228085
	CBS 667.88	unknown plant species, leaf	Martinique	GU227891	GU227989	GU228185	GU228381	GU228283	GU228087
	CBS 711.70	*Cyperus rotundus*	Brazil	GU227892	GU227990	GU228186	GU228382	GU228284	GU228088
	IMI 266002	*Homo sapiens*, eye, corneal ulcer	Nepal	GU227890	GU227988	GU228184	GU228380	GU228282	GU228086
C. verruculosum	IMI 45525*	*Crotalaria juncea*	Zimbabwe	GU227806	GU227904	GU228100	GU228296	GU228198	GU228002

Table 1 (continued). Strains of *Colletotrichum* studied in this paper with details about host/substrate and location, and GenBank accessions of the sequences generated.

Species	Accession number[1]	Host/substrate	Country	GenBank accessions					
				ITS	ACT	Tub2	CHS-1	GAPDH	HIS3
***Colletotrichum* sp. 1**	CBS 125326	*Rubus idaeus*	Canada	GU227827	GU227925	GU228121	GU228317	GU228219	GU228023
***Colletotrichum* sp. 2**	CBS 125338 / DAOM 147549	*Hemerocallis fulva*, old flower stalk	Canada	GU227828	GU227926	GU228122	GU228318	GU228220	GU228024
***C. lindemuthianum* (outgroup)**	CBS 151.28	*Phaseolus vulgaris*	UK	GU227800	GU227898	GU228094	GU228290	GU228192	GU227996

[1]CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands; IMI: Culture collection of CABI Europe UK Centre, Egham, UK; ATCC: American Type culture collection; DAOM: National Mycological Herbarium, Ottawa, Canada; STE-U: Culture collection of the Department of Plant Pathology, University of Stellenbosch, South Africa; CCT: Colecao de Culturas Tropical, Sao Paulo, Brazil; BBA: Culture collection of the Biologische Bundesanstalt für Landund Forstwirtschaft**,** *Berlin*, Germany; CCF: Culture Collection of Fungi, Prague, Czech Republic;. * ex-type and ex-epitype cultures.

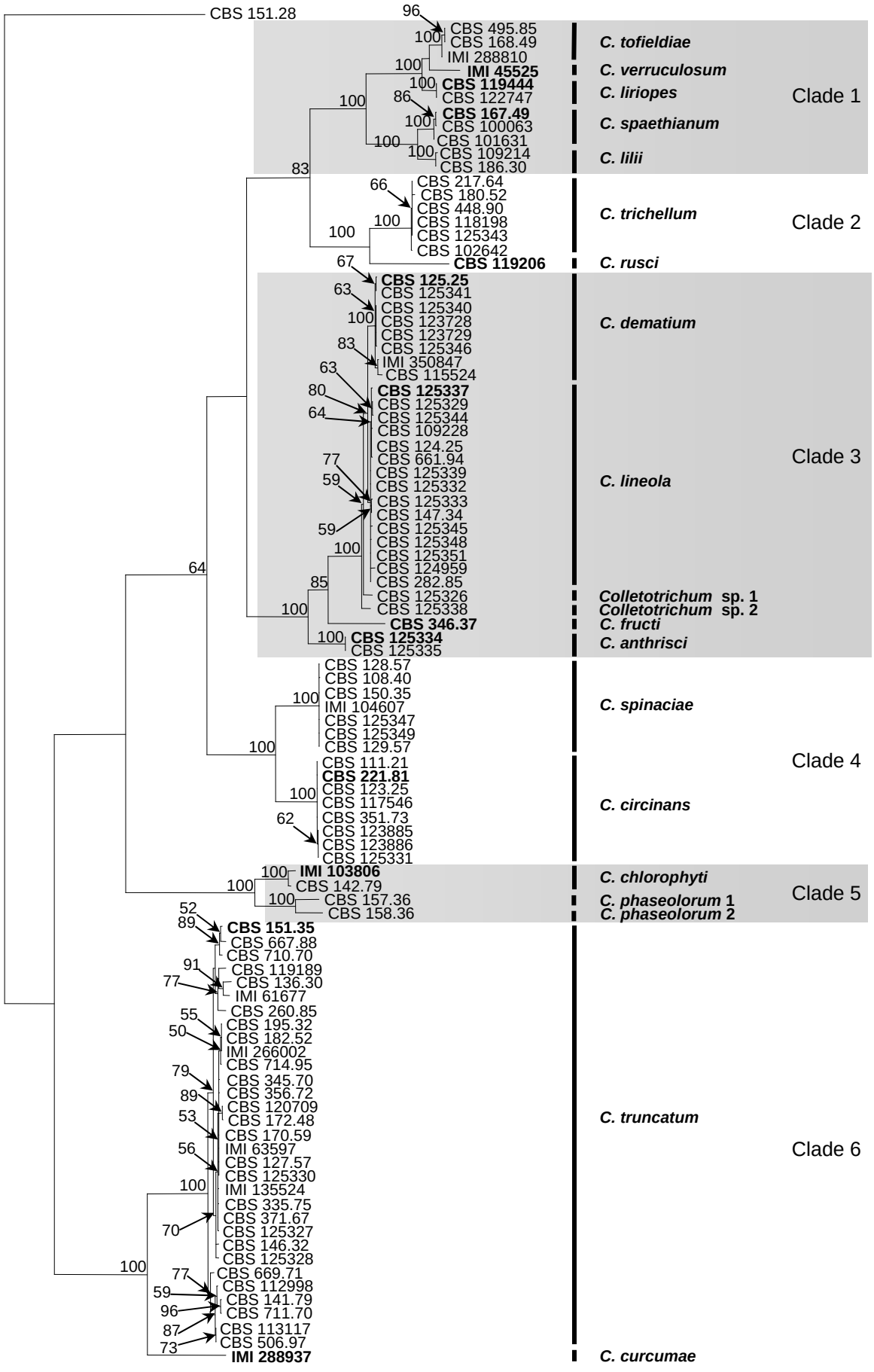
CBS 151.28
CBS 495.85
CBS 168.49
IMI 288810
IMI 45525
CBS 119444
CBS 122747
CBS 167.49
CBS 100063
CBS 101631
CBS 109214
CBS 186.30
C. tofieldiae
C. verruculosum
C. liriopes
C. spaethianum
C. lilii
Clade 1
CBS 217.64
CBS 180.52
CBS 448.90
CBS 118198
CBS 125343
CBS 102642
CBS 119206
C. trichellum
C. rusci
Clade 2
CBS 125.25
CBS 125341
CBS 125340
CBS 123728
CBS 123729
CBS 125346
IMI 350847
CBS 115524
CBS 125337
CBS 125329
CBS 125344
CBS 109228
CBS 124.25
CBS 661.94
CBS 125339
CBS 125332
CBS 125333
CBS 147.34
CBS 125345
CBS 125348
CBS 125351
CBS 124959
CBS 282.85
CBS 125326
CBS 125338
CBS 346.37
CBS 125334
CBS 125335
C. dematium
C. lineola
Colletotrichum sp. 1
Colletotrichum sp. 2
C. fructi
C. anthrisci
Clade 3
CBS 128.57
CBS 108.40
CBS 150.35
IMI 104607
CBS 125347
CBS 125349
CBS 129.57
C. spinaciae
CBS 111.21
CBS 221.81
CBS 123.25
CBS 117546
CBS 351.73
CBS 123885
CBS 123886
CBS 125331
C. circinans
Clade 4
IMI 103806
CBS 142.79
CBS 157.36
CBS 158.36
C. chlorophyti
C. phaseolorum 1
C. phaseolorum 2
Clade 5
CBS 151.35
CBS 667.88
CBS 710.70
CBS 119189
CBS 136.30
IMI 61677
CBS 260.85
CBS 195.32
CBS 182.52
IMI 266002
CBS 714.95
CBS 345.70
CBS 356.72
CBS 120709
CBS 172.48
CBS 170.59
IMI 63597
CBS 127.57
CBS 125330
IMI 135524
CBS 335.75
CBS 371.67
CBS 125327
CBS 146.32
CBS 125328
CBS 669.71
CBS 112998
CBS 141.79
CBS 711.70
CBS 113117
CBS 506.97
IMI 288937
C. truncatum
C. curcumae
Clade 6
10 changes

Fig. 1. One of 8735 most parsimonious trees obtained from heuristic searches of ITS, ACT, BT, CHS-1, GAPDH and HIS3 gene sequences of *Colletotrichum* species (length = 2141 steps, CI = 0.632, RI = 0.948, RC = 0.599, HI = 0.368). Bootstrap support values (500 replicates) above 50 % are shown at the nodes. *Colletotrichum lindemuthianum* CBS 151.28 is used as outgroup. Numbers of ex-type and ex-epitype strains are emphasised in bold.

derived in this study were lodged at GenBank, the alignment in TreeBASE (http://www.treebase.org/treebase/index.html), and taxonomic novelties in MycoBank (Crous *et al*., 2004a).

Results

Phylogeny

In the multigene analyses (ITS, ACT, Tub2, CHS-1, HIS3, GAPDH) of 98 isolates of *C. dematium* and other *Colletotrichum* species with curved conidia including the outgroup, 2333 characters including the alignment gaps were processed, of which 740 characters were parsimony-informative, 157 parsomony-uninformative and 1436 constant. For the individual alignments of the six genes, the obtained trees were compared by eye and the tree topology of the individual data sets was found to be similar to each other and to the tree obtained from the combined alignment. However some clades, e.g. *C. circinans* and *C. spinaciae* were very short-branched in the ITS phylogeny and some, e.g. *C. dematium* and *C. lineola* were only distinguished in three (Actin, HIS3 and GAPDH) of the six phylogenies. After a heuristic search using PAUP, 8735 most parsimonious trees were retained (length = 2141 steps, CI = 0.632, RI = 0.948, RC = 0.599, HI = 0.368) of which one is shown in Fig. 1. The topology of the 8735 trees was similar, which was verified for a large selection of trees. They differed in the position of taxa within the subclades.

The analyses resulted in detection of 6 clades and 20 subclades, presumably representing different *Colletotrichum* species. Clade 1 (100 % bootstrap support) is divided into five subclades, of which four subclades (*C. tofieldiae*, *C. liriopes*, *C. spaethianum* and *C. lilii*) are well supported (100 %) and contain two or tree strains each, including at least one strain previously identified as *C. dematium*. The fifth subclade (*C. verruculosum*) is represented by a single strain, IMI 45525 that groups with the *C. tofieldiae* and the *C. liriopes* subclades (100 %), while *C. spaethianum* and *C. lilii* form a sisterclade (100 %). The second clade (100 %) consists of two subclades, *C. trichellum* (100 %) and *C. rusci* (CBS 119206), a single-strain clade. The six strains of the *C. trichellum* clade, all from *Hedera* sp., have little variability. Clade 1 and clade 2 are sisterclades (83 %). Clade 3 (100 %) contains 6 subclades. Two of these clades, the *C. dematium* (100 %) and the *C. lineola* clade (77 %), are closely related to each other, contain both many strains from diverse host plants, and group with two single-strain clades belonging to unidentified taxa (100 %). These clades group with the subclade formed by one strain of *C. fructi* (85 %) of which *C. anthrisci* formes a sisterclade (100 %). The two subclades in clade 4 (100 %) represent *C. spinaciae* (100 %) and *C. circinans* (100 %), have little intraspecific variability and contain 4 strains from *Spinacia* and *Allium*, respectively. Clade 5 consists of *C. chlorophyti* (100 %) and *C. phaseolorum* is represented by two single strain clades, which cluster with each other (100 %). Clade 6 (100%) consists of one clade formed by a single strain (IMI 288937) representing *C. curcumae* and the *C. truncatum* clade (100 %), which is very heterogenous and contains strains from many different host plants, with the majority from *Fabaceae* and *Capsicum* spp., that had been identified as *C. dematium*, *C. capsici* (including the epitype strain), *C. truncatum*, *C. curvatum* (authentic material), *Glomerella glycines*, *C. corchori* and *C. dematium* f. sp. *clitoriicola* before. In the single gene phylogenies (not shown) there was, however, no consistency in subgrouping that would support distinguishing further taxa within this subclade.

The maximum likelihood phylogenetic analyses with RAxML resulted in a similar phylogeny, with the same 20 clades as in the parsimony analyses and similar bootstap supports (not shown).

Taxonomy

The 97 strains studied (Table 1) could be assigned to 20 species based on DNA sequence data and morphology, including four species, *C. anthrisci*, *C. liriopes, C. rusci* and *C. verruculosum*, that proved to be new to science, two

needing new combinations (*C. spaethianum and C. tofieldiae*), and six epitypifications have been made. All 15 species studied in culture are characterised below.

Colletotrichum anthrisci Damm, P.F. Cannon & Crous, **sp. nov.** (Fig. 2)
MycoBank: 514641

Etymology: Named after its host, *Anthriscus*.

Colletotrichi lineolae simile, sed setis ad basim constrictis, conidiis ad apicem valde acutis, in vitro (SNA) (23–)25–27.5(–29) x 3–3.5 µm, in cultura cum caulibus Anthrisci (22–)24–27(–28.5) x (3–)3.5(–4) µm, appressoriis (7.5–)11–23.5(–35) x (4.5–)5.5–8.5(–10) µm.

On SNA: *Vegetative hyphae* 1–8 µm diam, hyaline or pale brown, smooth-walled to finely verruculose, septate, branched. *Conidiomata* acervular, conidiophores and setae formed on a basal cushion of roundish brown cells, 5–15 µm diam. *Setae* very dark brown, concoloured, opaque, septation hardly visible, 2- to 4-septate, 80–220 µm long, base constricted, sometimes slightly inflated above the constriction, 4–10 µm at the widest part, tip acute, smooth to finely verruculose. *Chlamydospores* not observed. *Conidiophores* pale brown, septate, branched, 25–40 µm long. *Conidiogenous cells* enteroblastic, pale brown, cylindrical to elongate ampulliform, 6–18 × 3–6.5 µm, opening 1.5–2 µm diam, collarette 0.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, central part of conidia usually almost straight with parallel walls, bent apruptly to the acute apex and truncate base, giving the conidia an almost angular shape, (23–)25–27.5(–29) × 3–3.5 µm, mean ± SD = 26.3 ± 1.4 × 3.4 ± 0.2 µm, L/W ratio = 7.8. *Appressoria* solitary, in chains or in loose groups, pale to medium brown, aseptate, smooth-walled, navicular, bullet-shaped to clavate, (7.5–)11–23.5(–35) × (4.5–)5.5–8.5(–10) µm, mean ± SD = 17.3 ± 6.1 × 7.0 ± 1.3 µm, L/W ratio = 2.5.

On Anthriscus stem Conidiomata: acervular, conidiophores and setae formed from a cushion of brown, angular cells, 5–10 µm diam. *Setae* very dark brown, opaque, septation hardly visible, 90–350 µm long, base cylindrical, inflated, constricted or both, 6–18 µm wide, tip acute, smooth to finely verruculose. *Conidiophores* pale brown, septate, branched, 30–50 µm long. *Conidiogenous cells* enteroblastic, pale brown, cylindrical, 5–15 (2.5–3.5) µm, opening 1.5–2 µm diam, collarette 0.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, central part of conidia usually almost straight with parallel walls, bent apruptly to the acute apex and truncate base, giving the conidia an almost angular shape, (22–)24–27(–28.5) × (3–)3.5(–4) µm, mean ± SD = 25.4 ± 1.5 × 3.5 ± 0.2 µm, L/W ratio = 7.3.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, the medium pigmented cinnamon. Acervuli aggregated around the *Anthriscus* stem and filter paper, extending over the agar surface with a lower density, olivaceous-grey to iron-grey; colonies 26–28 mm after 7 d (38–39 mm in 10 d). Colonies on OA flat with entire margin, aerial mycelium sparse, short, pale olivaceous-grey, the colony surface buff, some sectors dark grey-olivaceous to dark-olivaceous, covered with pale olivaceous-grey, olivaceous-grey to iron-grey acervuli, reverse smoke-grey, pale olivaceous-grey to olivaceous-grey; 24–25 mm in 7 d (38 mm in 10 d). *Conidia in mass* white to pale grey.

Materials examined: NETHERLANDS. Utrecht, isolated from dead stems of *Anthriscus sylvestris*, 12 Sep. 2009, U. Damm, (CBS H-20355, **holotype**, culture ex-type CBS 125334).

Notes: Among the species with angular conidia, conidia of *C. anthrisci* have the highest L/W ratio (7–8) and the apex is strongly pointed. *Colletotrichum anthrisci* differs from all other species studied here by the constricted base of setae and very long (L/W ratio = 2.5), navicular appressoria. The species is known only from two isolates made from stems of *Anthriscus* sp. originating from the Utrecht area, the Netherlands. *C. lineola*, also isolated from *Anthriscus*, has much more complex appressoria, and colours the medium red rather than cinnamon. *Colletotrichum anthrisci* was found in association with stem lesions, as well as on dead stems, which makes conclusions about its lifestyle difficult.

Colletotrichum chlorophyti S. Chandra & Tandon [as 'chlorophytumi'], *Current Science* 34: 565 (1965) (Fig. 3)

On SNA: *Vegetative hyphae* hyaline, septate, branched 1.5–7 µm diam. *Chlamydospores* dark brown, thick-walled, verruculose,

Fig. 2. *Colletotrichum anthrisci* (from ex-type strain CBS 125334). a–b. acervuli; c. tip of a seta; d–e. conidiophores; f. conidiophores and setae; g–i. appressoria; j–k.conidia; all from ex-type culture CBS 125334. a, c–e, j: from *Anthriscus* stem; b,f, g, k: from SNA. a–b: DM; c–k: DIC. — Scale bars: a = 200 µm; e = 10 µm; a applies to a–b; e applies to c–k.

in chains and clusters, globose to subglobose, 6–12 µm diam. *Conidiomata* acervular, no compact fruiting structures, often no or few setae and few conidiophores, appearing just as accumulations of conidia on the surface of the medium. *Sporulation* abundant. *Setae* scattered or in small groups, straight or bent at the base, 2- to 4-septate, brown, basal cell pale brown, 80–120 µm long, base more or less inflated, 4–8 µm diam, tip usually acute, finely verruculose. *Conidiophores* hyaline to pale brown, simple or septate, occasionally branched, smooth-walled, up to 50 µm long. *Conidiogenous cells* enteroblastic, hyaline to pale brown, ampulliform to elongate ampulliform, 7–33 × 3.5–5.5 µm, opening 1.5–2.5 µm diam, collarette distinct, 1.5–2.5 µm long, periclinal thickening sometimes visible. *Conidia* hyaline, aseptate, smooth or verruculose, curved, base truncate, apex acute, more tapered and stronger curved than base, guttulate, guttules of different size, (10.5–)16–21.5(–37) × (3–)3.5–4.5(–5) µm, mean ± SD = 18.7 ± 2.8 × 4.1 ± 0.4 µm, L/W ratio = 4.6. *Appressoria* not observed.

On Anthriscus stem: *Chlamydospores* dark brown, thick-walled, in clusters within plant cells, subglobose, 5–15 µm diam. *Conidiomata* as on SNA. *Setae* straight, brown, 2- to 4-septate, 60–110 µm long, base inflated, ca. 4 µm diam, tip acute. *Conidia* hyaline, aseptate, smooth-walled, curved, base truncate, apex acute, more tapered and stronger curved than base, guttulate, guttules of different size, (16–)19–21.5(–22) × 4–5 µm, mean ± SD = 20.1 ± 1.3 × 4.5 ± 0.3 µm, L/W ratio = 4.4.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, no pigments; strain CBS 142.79 differs in partly grey discolouration of filter paper with black acervuli; 24–26 mm in 7 d (38–40 mm in 10 d). Colonies on OA flat with entire margin, no aerial mycelium, surface flat slimy, olivaceous-grey with small black structures, centre salmon due to sporulation, reverse pale olivaceous-grey, centre vinaceous-

Fig. 3. *Colletotrichum chlorophyti* (from ex-type strain IMI 103806). a–b. acervuli; c. seta; d. conidiophores; e. conidiophores; f. conidiophores and setae; g–i. appressoria; j. conidia; k. conidia; all from ex-type culture CBS 125334. a, c–j: from SNA; b, k: from *Anthriscus* stem. a–b: DM; c–l: DIC. — Scale bars: a = 100 µm; d = 10 µm; a applies to a–b; d applies to c–l.

buff. *Conidia in masse* white to salmon; strain CBS 142.79 olivaceous-grey to iron-grey and with greyish white conidia masses; 24–27 mm in 7 d (35–40 mm in 10 d).

Materials examined: INDIA. Allahabad, Alfred Park, on leaves of *Chlorophytum* sp., Oct. 1963, S. Chandra (IMI 103806 – **holotype**; K(M) – **isotype**, culture ex-type IMI 103806); AUSTRALIA. Queensland, Townsville, on *Stylosanthes hamata*, isolated 1978 by W.A. Shipton (living culture CBS 142.79).

Notes: *Colletotrichum chlorophyti* was described as causing a leaf spot of *Chlorophytum* sp. from India (Chandra and Tandon, 1965). Strain CBS 142.79 from *Stylosanthes hamata*, originally identified as *C. truncatum*, has only a few bp differences in the sequences and is therefore regarded as *C. chlorophyti* as well. Chandra and Tandon (1965) gave conidial measurements on host tissue as 16.4–26.2 × 3.5 µm (av. 20.4 × 3.1 µm), and in (unknown medium) culture 20.8–30.2 × 3.2–5.6 µm (av. 24.2 × 4.1 µm), which correspond well with those from our studies.

Morphological diagnostic features include the dark brown chlamydospores in chains and clusters. No appressoria were found using the standard methods for this paper. Based on molecular evidence, *C. chlorophyti* is most closely related to *C. phaseolorum*, but more research is needed to characterise that taxon (see below).

Colletotrichum circinans (Berk.) Voglino, *Annali della Reale Accademia d'Agricoltura di Torino* 49:175 (1907) (Fig. 4)

Basionym: *Vermicularia circinans* Berk., *The Gardeners' Chronicle*, London: 595 (1851)

≡ *Volutella circinans* (Berk.) F. Stevens & E.Y. True, *University of Illinois Agricultural Experimental Station, Bulletin* 220: 530 (1919)

≡ *Colletotrichum dematium* f. *circinans* (Berk.) Arx, *Phytopathologische Zeitschrift* 29: 461 (1957)

On SNA: *Vegetative hyphae* hyaline, smooth, septate, branched, 1–8 µm diam. *Conidiomata* acervular, compact fruiting structures composed of cushions of pale brown angular

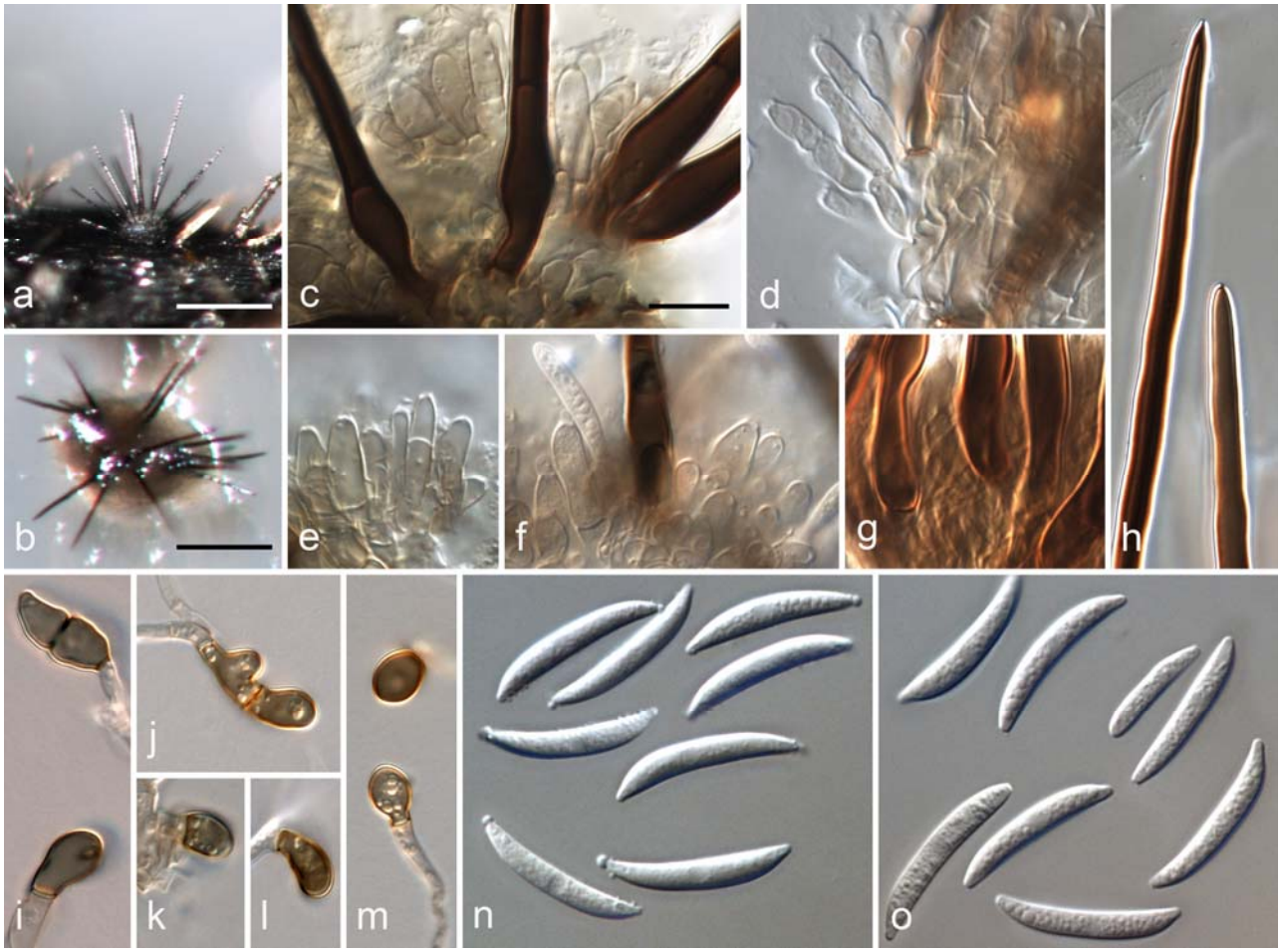

Fig. 4. *Colletotrichum circinans* (from ex-epitype strain CBS 221.81). a–b. acervuli; c. conidiophores with basal parts of setae; d–f. conidiophores; g. basal parts of setae; h. tips of setae; i–m. appressoria; n–o. conidia; a, c, e, f, n: from *Anthriscus* stem; b, d, g–m, o: from SNA. a–b: DM; c–o: DIC. — Scale bars: a = 200 µm; b = 100 µm; c = 10 µm; c applies to c–o.

cells from which setae and conidiophores are produced. *Setae* dark brown, concoloured, smooth-walled to finely verruculose, 2- to 4-(5-) septate, (70–)100–180(–290) µm long, irregular in length within acervulus, often one or few long setae with the rest much shorter, base constricted, sometimes slightly inflated above the constriction or cylindrical, 3.5–6(–9) µm diam, tip somewhat acute. *Chlamydospores* not observed. *Conidiophores* hyaline to pale brown, septate, branched, to 80 µm long. *Conidiogenous cells* enteroblastic, hyaline to pale brown, cylindrical to clavate, 5–16 × 3–5 µm, opening 1–2 µm wide, collarette distinct, 1–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, little curved, the central part often with nearly parallel walls, at one side more strongly curved towards base and apex than in the central part, apex acute, base truncate, (15–)19–23(–23.5) × (2.5–)3–3.5(–4) µm, mean ± SD = 21.0 ± 1.8 × 3.4 ± 0.3 µm, L/W ratio = 6.2. *Appressoria* solitary, elongate elliptical to clavate, sometimes crenate or slightly lobed, smooth-walled, one- or two-celled, pale to mid brown, (7–)7–16(–24) × (3.5–)5–7.5(–11) µm, mean ± SD = 11.6 ± 4.4 × 6.1 ± 1.3 µm, L/W ratio = 1.9.

On Anthriscus stem: *Conidiomata* acervular, compact fruiting structures composed of cushions of pale brown angular cells from which setae and conidiophores are produced. *Setae* dark brown, concoloured, smooth to verruculose, 1- to 6-septate, 45–340 µm long, setae with very variable lengths within acervulus, base cylindrical or constricted, often inflated shortly above the constriction, 4–8 µm wide, tip somewhat acute. *Conidiophores* pale brown, simple to 2-septate, usually not branched, 10–30 µm long. *Conidiogenous cells* enteroblastic, pale brown, cylindrical to clavate,

8–14 × 4–5 µm, opening 1.5–2 µm wide, collarette 1–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, little curved, central part usually with nearly parallel walls, at one side more strongly curved towards base and apex than in the central part, apex acute, base truncate, (18.5–)19.5–23(–25.5) × 3–3.5 µm, mean ± SD = 21.4 ± 1.8 × 3.2 ± 0.2 µm, L/W ratio = 6.6.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, whitish to buff, filter paper, *Anthriscus* stem and medium partly greyish due to tiny acervuli, on medium growing in growth rings. Colonies on OA flat with entire margin, surface buff to umber, with dark grey to black acervuli, no aerial mycelium, reverse greyish sepia, pale olivaceous-grey to olivaceous-grey. Colonies on PDA flat with entire margin, surface dark grey-olivaceous to olivaceous-black, white margin, covered by short floccose whitish aerial mycelium, reverse grey-olivaceous to iron-grey. Colonies on MEA slightly raised with entire to slightly undulate margin, surface radially folded, olivaceous black with white margin, covered with restricted aerial mycelium and exudate, conidial masses pale luteous, reverse iron-grey with pale luteous margin. *Conidia in mass* whitish, buff to greyish, but strain CBS 125331 salmon.

Materials examined: UNITED KINGDOM, England, Northamptonshire, King's Cliff, on bulb scales of *Allium cepa*, 23 Aug. 1851, M.J. Berkeley (K (M) 121469– **holotype** of *Vermicularia circinans*); SERBIA, Novi Sad, on *Allium cepa*, isolated 1980 by Z. Klocokar-Smit (CBS H-20356 [dried culture] **epitype** here designated, culture ex-epitype CBS 221.81); GERMANY, Hannover, on dead stem of *Anthriscus sylvestris*, collected 19 July 2009 by U. Damm (living culture CBS 125331).

Notes: *Colletotrichum circinans* was originally described from diseased onion bulbs grown from seed originating from the Paris area (Berkeley, 1851); it is not clear whether the fungus was seed-borne, and therefore it is unknown which country the fungus Berkley described originates from. According to the strains studied, *C. circinans* is not restricted to a specific country or continent, but appears to be common in temperate regions. An epitype is designated above as no culture was made from the original material; it conforms very well in morphological terms to the holotype specimen. *C. circinans* has traditionally been considered to be a pathogen of onions (*Allium* spp.), often described as causing "smudge" disease of bulbs (e.g. Walker, 1921; von Arx, 1957; Hall *et al*., 2007) but our work has shown that it has a less pronounced host preference. *C. circinans* is a sister group to another temperate species, *C. spinaciae* which seems primarily to be associated with *Amaranthaceae*. Morphological differences of the two closely related species include the different shapes of conidia and setae observed on both media. Conidia of *C. circinans* are more strongly curved towards the truncate base and acute apex, while conidia of *C. spinaciae* taper gradually towards the round or truncate base and the round apex. Setae of *C. circinans* are dark brown, concoloured, often constricted and sometimes inflated above the constriction, while setae of *C. spinaciae* are often pale brown, with a paler tip and/or base, the latter being cylindrical or conical.

Little molecular work has been done on this species. Martín and García-Figueres (1999) and Abang *et al*. (2002) could not separate *C. circinans* from *C. coccodes* using RFLPs of rDNA, but Fagbola and Abang (2004) could distinguish the two taxa using DGGE. None of these studies used sequence data for the species in question. Zeng *et al*. (2004) used RAPD analysis to separate a number of falcate-spored species of *Colletotrichum* including *C. circinans*, but that method is of limited value in investigation of relationships.

Colletotrichum curcumae (Syd.) E.J. Butler & Bisby, *The Fungi of India*: 153 (1931)

(Fig. 5)

Basionym: *Vermicularia curcumae* Syd., *Annales Mycologici* 11: 329 (1913)

On SNA: *Vegetative hyphae* hyaline, septate, branched, 1.5–8 µm diam. *Chlamydospores* globose or elongate, pale to dark brown, in branched chains, smooth-walled, 5–25 × 3–8 µm. *Conidiomata* acervular, conidiophores either directly in rows on brown, verruculose hyphae or on a stroma formed by roundish brown cells. *Setae* dark brown up to the tip, verruculose, 50–200 µm long and 4-10 µm diam, 2- to 3-septate, tapering only little towards the slightly acute to roundish tip, the base inflated. *Conidiophores* septate, rarely branched, pale brown, verruculose, becoming lighter towards the tip, 10–35 µm long. *Conidiogenous cells* enteroblastic, hyaline to

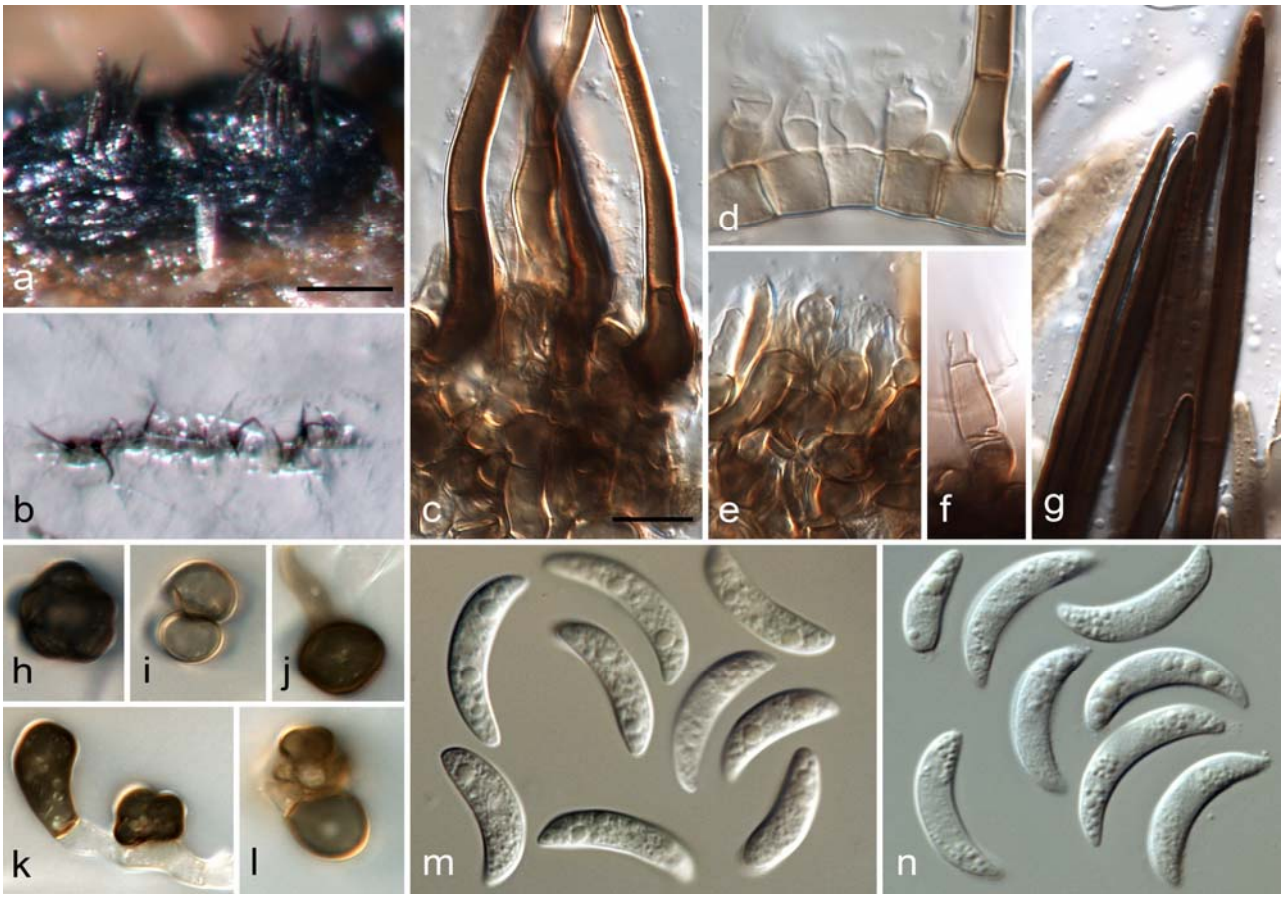

Fig. 5. *Colletotrichum curcumae* (from ex-epitype strain IMI 288937). a–b. acervuli; c. basal parts of setae; d. conidiophores with basal parts of setae; e–f. conidiophores; g. tips of setae; h–l. appressoria; m–n. conidia; a, g, m: from *Anthriscus* stem; b–f, h–l, n: from SNA. a–b: DM; c–n: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–n.

pale brown, smooth-walled to verruculose, cylindrical to conical, disintegrating fast, 5–15 × 2–4.5 µm, collarette sometimes visible, periclinal thickening observed. *Conidia* hyaline, smooth-walled, aseptate, strongly curved, widest in the centre or close to the base, which is round and more or less truncate, tapering much more towards the apex, which is more or less acute, guttulate, some of the guttules yellowish, (13.5–)17.5–21.5(–22.5) × (3.5–)4–5(–5.5) µm, mean ± SD = 19.4 ± 2 × 4.6 ± 0.4 µm, L/W ratio = 4.2. *Appressoria* solitary, sometimes in groups of two, pale to dark brown, globose to subglobose, sometimes clavate, the edge entire, sometimes slightly lobed, smooth-walled, (4–)6–13.5(–20.6) × (4–)5.5–9.5(–11.5) µm, mean ± SD = 9.7 ± 3.6 × 7.6 ± 2.1 µm, L/W ratio = 1.3.

On Anthriscus stem: *Conidiomata* acervular, big brown structures (stroma/sclerotia) formed by olive-brown, roundish cells, with converging setae in the centre only, hardly sporulating. *Setae* uniformly dark brown, converging, verruculose to verrucose, 90–160 µm long, 1- to 4-septate, tip acute or round, base cylindrical to wedge-shaped, 5–10 µm wide. *Conidiophores* septate, not branched, pale brown, verruculose, 15–20 µm long. *Conidiogenous cells* enteroblastic, pale brown, 5–20 × 2.5–3 µm, collarette sometimes visible. *Conidia* hyaline, smooth-walled, aseptate, strongly curved, widest in the centre or close to the base, which is round and more or less truncate, tapering more towards the apex, which is more or less acute, guttulate, some of the guttules yellowish, (16–)17.5–20.5(–22) × 4.5–5(–5.5) µm, mean ± SD = 18.9 ± 1.4 × 4.8 ± 0.4 µm, L/W ratio = 3.9.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, black streaking on surface and inside medium and black spots on *Anthriscus* stemdue to acervuli formation. Colonies on OA flat with entire margin, surface granular due to production of acervuli, with few aerial hyphae, dark olivaceous, iron-grey to black, reverse

pale olivaceous-grey to iron-grey. *Conidia in mass* white, greyish, yellowish to pale salmon.

Materials examined: INDIA. Tamil Nadu, Kistna, Angalur, on leaves of *Curcuma longa*, 24 Dec. 1912, W. McRae 24 (IMI 20994, K(M) – **isotypes** of *Vermicularia curcumae* Syd.); INDIA. Maharashtra, Warora, isol. ex *Curcuma longa*, 22 Aug. 1984, M.Y. Palarpawar 1 (IMI 288937 [dried culture], **epitype** here designated, culture ex-epitype IMI 288937). There is further material in IMI identified as this species isolated from leaves of *Curcuma longa* from Bangladesh and India (Uttar Pradesh, West Bengal).

Notes: *Colletotrichum curcumae* differs from all other species studied here by forming big brown flattened stromata on *Anthriscus* stems with straight setae that are aggregated in the centre and with little sporulation; in other species setae are diverging and formed all over the acervulus/stroma, and usually sporulation is abundant on that host material. The species appears to be at least largely confined to turmeric (*Curcuma longa*) but few strains have been sequenced of the *C. dematium* aggregate from South Asia. Palarpawar and Ghurde (1988) isolated strains that confirmed to *C. curcumae* in morphological features from plants surrounding turmeric fields including *Brachiaria reptans*, *Cynodon dactylon*, *Solanum xanthocarpum* and *Colocasia esculenta*, and demonstrated their pathogenicity to *Curcuma*.

Colletotrichum dematium (Pers.) Grove, *Journal of Botany*, British and Foreign, London 56: 341 (1918)

(Fig. 6)

Basionym: *Sphaeria dematium* Pers., *Synopsis methodica fungorum* (Göttingen) 88 (1801)

≡ *Exosporium dematium* (Pers.) Link, in Willdenow, *Willd., Sp. pl.*, Edn 4 6(2): 122 (1825)

≡ *Vermicularia dematium* (Pers.) Fr., *Summa Vegetabilium Scandinaviae*, Sectio Posterior: 420 (1849)

≡ *Lasiella dematium* (Pers.) Quél. *Mémoires de la Société d'Émulation de Montbéliard,* 2e Série, 5: 518 (1875)

= *Vermicularia eryngii* Desm., *Plantes Cryptogames du Nord de la France*, fasc. 11: 542 (1831)

≡ *Colletotrichum eryngii* (Desm.) Duke, *Transactions of the British Mycological Society* 13: 170 (1928)

On SNA: *Vegetative hyphae* <1–7 µm diam, hyaline, smooth-walled, septate, branched. *Chlamydospores* in old cultures observed, in branched chains, dark brown, verrucose, single cells 6–13 × 5–8 µm, but not observed in other strains. *Conidiomata* acervular, conidiophores formed directly on hyphae. *Setae* not observed. *Conidiophores* hyaline to pale brown, septate, branched. *Conidiogenous cells* enteroblastic, hyaline to pale brown, cylindrical, 7–17 × 3–4 µm, opening 1–1.5 µm wide, collarette 0.5 µm long, periclinal thickening not observed. *Conidia* hyaline, smooth-walled, sometimes finely verruculose, aseptate, central part of conidia usually almost straight with parallel walls, bent apruptly to the roundish to acute apex and truncate base, giving the conidia an almost angular shape, (18–)20–23(–24) × 3–4(–5.5) µm, mean ± SD = 21.3 ± 1.5 × 3.5 ± 0.4 µm, L/W ratio = 6.1; other isolates form longer conidia, e.g. IMI 350847: 22.5–27.5 × 3–3.5 µm, while CBS 125340 did not sporulate on SNA. *Appressoria* solitary, elliptical to clavate or slightly lobed, brown, smooth-walled, aseptate, rarely septate, (2.5–)5–12(–18.5) × (2–)3–6.5(–8.5) µm, mean ± SD = 8.5 ± 3.5 × 4.8 ± 1.5 µm, L/W ratio = 1.8.

On Anthriscus stem: *Conidiomata* acervular, consisting of dark brown roundish cells from which setae (usually one seta per acervulus) and conidiophores develop. *Setae* straight, dark brown, 30-140 µm long, 3- to 8-septate, base cylindrical, conical or slightly inflated, 7–12 µm diam, tip acute. *Conidiophores* hyaline to pale brown, septate, up to 20 µm long. *Conidiogenous cells* enteroblastic, hyaline to pale brown, cylindrical to elongate ampulliform, 4–15 × 3–5 µm, opening 0.5–1 µm wide, collarette or periclinal thickening not observed. *Conidia* hyaline, smooth-walled, aseptate, central part of conidia usually almost straight with parallel walls, bent apruptly to the roundish to acute apex and truncate base, giving the conidia an almost angular shape, (18.5–)20–22.5(–23.5) × 3–4 µm, mean ± SD = 21.3 ± 1.3 × 3.6 ± 0.3 µm, L/W ratio = 6.0; other isolates form longer conidia, e.g. IMI 350847: 21–26.5 × 3–4 µm and CBS 125340 12.5–26.5 × 3–4 µm.

Culture characteristics: Colonies on SNA flat with entire margin, surface of *Anthriscus* stem and filter paper partly covered by floccose white aerial mycelium, medium close to stem stained pale honey, margins of filter paper grey, 27–29 mm in 7 d at 20 °C. OA flat with entire margin, no aerial mycelium, surface

Fig. 6. *Colletotrichum dematium* (a, b, e, f from lectotype LO117771, c, g from CBS H-20358, d from CBS 125340 (culture ex CBS H-20358), h–z from ex-epitype strain CBS 125.25). a, c, e, g. acervuli on host tissue; b. tip of a seta; d. conidia; f. conidiophores; h, n, acervuli; i–j. tips of setae; k, p. basal parts of setae; l–m, q–r. conidiophores; o. chlamydospore; s–x. appressoria; y–z. conidia; a–c, e–g: from host tissue; d, i–k, n, p–q, y: from *Anthriscus* stem; h, l–m, o, r–x, z: from SNA. a, c, e, g, h, n: DM; b, d, f, i–m, o–z: DIC. — Scale bars: a = 1 mm; c = 1 mm; d = 10 µm; e = 200 µm; g = 100 µm; h = 100 µm; j = 10 µm; d applies to b, d and f; h applies to h and n; j applies to i–m and o–z.

buff with fine greyish lines arranged in concentrical rings, reverse buff, 27–29 mm in 7d at 20 °C. PDA flat with entire margin, surface grey-olivacious, partly covert with floccose white aerial mycelium, reverse olivaceous-grey becoming smoke-grey with olivaceous-grey concentrical rings towards the margin, 30 mm in 7 d at 20°C. MEA flat with entire margin, colony radially folded, surface covered by floccose to felty white aerial mycelium, reverse pale luteous to luteous (medium not stained), radial folds visible

delimited by whitish lines, 25 mm in 7 d at 20 °C. *Conidia in mass* greyish white.

Materials examined: FRANCE, on stem of *Eryngium* sp. (L 0117771 – **syntype** of *Sphaeria dematium*, here designated as **lectotype**); FRANCE, from dead leaf of *Eryngium campestre*, deposited in CBS by C. Killian in Dec. 1925 (CBS H-20357 [dried culture] **epitype** here designated, culture ex-epitype CBS 125.25); ITALY, Piemonte, unknown host (L 011772 **syntype** of *Sphaeria dematium*); UNKNOWN LOCATION, on stems of *Solanum tuberosum* (L 011772 **syntype** of *Sphaeria dematium*); UNKNOWN LOCATION, unknown host (K(M) **syntype** of *Sphaeria dematium*), CZECH REPUBLIC, Central Bohemia, Celakovice ca 30 km E of Prague, sandpits Malviny, on dead stem of *Apiaceae*, 20 Sept. 2009, M. Reblová (CBS H-20358, living culture CBS 125340); CZECH REPUBLIC, Central Bohemia, Celakovice ca 30 km E of Prague, sandpits Malviny, on dead stem of *Apiaceae*, 20 Sept. 2009, M. Reblová (CBS H-20359, living culture CBS 125341). AUSTRALIA, Northern Tasmania, from stem of *Solanum tuberosum*, deposited 1991 by L. Ransom (living culture IMI 350847); UNKNOWN LOCATION, unknown host (K(M) **isotype** of *Vermicularia eryngii* Desm.).

Notes: The original description of *Sphaeria dematium* by Persoon (1801) comprises only a few observations: tiny, slightly flattened spheres on grey spots covered in the centre with erect, stiff, diverging, homochromatic hairs/setae. The fungus is common on dead dry herbaceous stems, especially on *Solanum tuberosum*, while variety *capreae* occurs on *Salix caprea.* No type specimen was designated by Persoon. There are 20 specimens of *Sphaeria dematium* in the Persoon Herbarium in Leiden, 15 of them with Persoon's handwriting, and two of them annotated with Syn. Fung. (= *Synopsis Methodica Fungorum*), where the description was published. With one of these two collections, specimen L0117771, host and locality was mentioned, *Eryngium* Gallia (Persoon wrote: *Sphaeria dematium* Syn. Fung., *Eryngium* Gallia, *Exosporium dematium* Link). There were no conidia found on the holotype material of *Sphaeria dematium*, but all structures observed, e.g. setae and conidiogenous cells, resemble those of the epitype, which is from the same host and location, and new collections of *C. dematium* from other *Apiaceae* from the Czech Republic. The symptoms found on the type material, on other herbarium specimens of *S. dematium* and of the new collections is similar (Fig. 6a, c) and differ from the symptoms caused by *C. lineola* (Fig. 9a, h). A further specimen labelled as *Sphaeria dematium* in Persoon's handwriting is stored in K(M) and could be part of the type material, but a note in another hand states that it contains "no fruit". Examination of isotype material of *Colletotrichum eryngii* (Desm.) Duke (*Vermicularia eryngii* Desm.) from K shows a very similar fungus to *C. dematium* and the two taxa are almost certainly synonymous. However, there is no living culture associated with authentic material of *C. eryngii* and epitypification would serve little purpose.

Typical features include the angular conidia, the production in many fresh cultures of red pigment, and the well-developed sclerotium-like conidiomata. There has been much confusion in the past regarding the separation of this species from *Colletotrichum capsici*, with differential characters cited by some authors (e.g. Sutton 1980) including conidial width but with others (e.g. von Arx 1957; Baxter *et al*., 1983) accepting a broader species concept. Mordue (1971) separated the two taxa using presence or absence of sclerotial structures. Its distribution is difficult to assess due to differing species concepts, but there is some suggestion that it occurs primarily in temperate rather than tropical zones. Some authors (e.g. Sutton 1962) maintain that the species is not a pathogen, developing exclusively on dead plant material from a wide range of species.

Colletotrichum dematium is claimed to cause several economically important diseases, such as leaf blight of Japanese radish (*Raphanus sativus* var. *hortensis*) seedlings (Sato *et al*., 2005), mulberry (*Morus* spp.) and cowpea (*Vigna unguiculata*) anthracnose (Smith *et al*., 1999; Yoshida and Shirata, 1999; Babu *et al*., 2008), spotting, blight and drop of leaves on potted plants of *Polygonatum falcatum* (Tomioka *et al*., 2008), and anthracnose of statice (*Goniolimon tataricum)* (Bobev *et al*., 2009). However, comparisons of ITS sequences of the causal organisms with sequences generated in this study (not shown) revealed that at least most of them do not belong to *C. dematium* as defined here. ITS sequences from a strain associated with *Raphanus sativus* var. *hortensis* (AB196295-AB196301) are identical to those of *C. spaethianum*; ITS sequences of a fungus associated

with *Polygonatum falcatum* (AB334523) differ in two nucleotides from *C. spaethianum* sequences; ITS sequences of a fungus associated with *Goniolimon tataricum* (FJ236461-FJ236463) are similar to those of *C. tofieldiae*, while sequences of a fungus associated with *Morus* spp. (EU554165, EU4173) are different from the species studied here. One Canadian strain from strawberry (CBS 125344) belongs to *C. lineola*. However, it still needs to be confirmed that the causal organisms of strawberry anthracnose in the USA and India (Beraha and Wright, 1973; Singh *et al*., 2003) belong to the same species. There is no sequence from cowpea anthracnose from South Africa available, but strains from *Vigna* that were included in our study, belong either to *C. truncatum* or to *C. phaseolorum* as it is originally described.

Few molecular studies have been published that include strains identified as *C. dematium*. Vinnere *et al*. (2002) included two strains in their study of *Colletotrichum* diseases of *Rhododendron* in Sweden, using sequences from rDNA, mtDNA and β-tubulin genes, but no attempt was made to establish the precise phylogeny. Their ITS sequences submitted to GenBank (AF411770, AF411773) suggest that the species they were studying was either *C. dematium sensu stricto* or *C. lineola* in our interpretations. Cano *et al*. (2004) investigated the relationships of *Colletotrichum* species associated with clinical cases, which included sequences from two strains initially identified as *C. dematium*. One of these clustered with a sequence from CBS 351.73, identified at that time as *C. truncatum* but re-determined in this paper as *C. circinans*. The other is derived from a strain that is here designated as epitype of *C. spaethianum* (CBS 167.49). While the *C. dematium* strains used in that study originated from plants, there was one strain from a corneal ulcer of a human eye included in our study, that belongs to *C. truncatum*. Figures from case studies (Joseph *et al*., 2004; Kaliamurthy *et al*., 2004) might suggest the same species, but this needs to be examined more carefully. A study of five *Colletotrichum* species from India using RAPDs included strains identified as *C. dematium* and *C. capsici* (Wijesekara *et al*., 2005). The two taxa clustered together in their study, but the true identity of their strains needs confirmation and RAPDs is not a good method for assessing relationships.

Colletotrichum dematium sensu stricto comprises only a few of the strains originally identified as *C. dematium* in our study, which could be assigned to 12 different species, namely *C. circinans*, *C. dematium*, *C. lilii*, *C. lineola*, *C. liriopes*, *C. spaethianum*, *C. spinaciae*, *C. tofieldiae*, *C. trichellum*, *C. truncatum* and two unidentified species. But even with the reduced number of strains that could be shown to represent *C. dematium* in this study, it can be confirmed that *C. dematium* has a wide host range and can have pathogenic, saprobic and endophytic lifestyles.

Colletotrichum fructi (F. Stevens & J.G. Hall) Sacc. [as '*fructus*'], *Sylloge fungorum* (Abellini) 22: 1201 (1913) (Fig. 7)

Basionym. Volutella fructi F. Stevens & J.G. Hall, *Journal of Mycology* 13: 97 (1907)

≡ *Vermicularia fructi* (F. Stevens & J.G. Hall) Vassiljevsky [as '*fructus*'], *Fungi Imperfecti Parasitici* 2: 351 (1950)

On SNA: *Vegetative hyphae* hyaline, septate, branched, smooth, 1.5–6 µm diam. *Conidiomata* acervular, with small clusters of hyaline to pale brown, roundish to angular cells, 3–6 µm diam, from which conidiophores and conidia are produced. *Setae* not (or rarely) formed on SNA. *Chlamydospores* not observed. *Conidiophores* hyaline, simple or septate, rarely branched, up to 30 µm. *Conidiogenous cells* enteroblastic, hyaline, cylindrical, occasionally ampulliform, 5–15 × 2–4(–10) µm, opening 0.5–1 µm diam, with collarette 1-2 µm long, periclinal thickening not observed. *Conidia* hyaline, aseptate, smooth-walled, central part of conidium almost straight with parallel walls, often bent apruptly to the apex giving the conidia an almost angular shape, apex narrow and acute, base usually broader and truncate (16.5–)20.5–24(–24.5) × (3–)3.5–4(–4.5) µm, mean ± SD = 22.3 ± 1.8 × 3.7 ± 0.3 µm, L/W ratio = 6.0. *Appressoria* solitary, elliptical to clavate, pale brown, smooth-walled, aseptate, (3.5–)5.5–8.5(–10.5) × (2–)3–4.5(–5) µm, mean ± SD = 6.9 ± 1.5 × 3.8 ± 0.7 µm, L/W ratio = 1.8.

On Anthriscus stem: *Conidiomata* acervular, forming roundish cushions of pale brown

Fig. 7. *Colletotrichum fructi* (from ex-epitype strain CBS 346.37). a–b. acervuli; c. seta; d–g. conidiophores; h. acervulus; i–n. appressoria; o–p. conidia; a, c–e, o: from *Anthriscus* stem; b, f–n, p: from SNA. a–b: DM; c–p: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–p.

angular cells 3–7 µm diam, from which setae and conidiophores are produced, 50–150 µm diam. *Setae* 60–90 µm long, 4–9 µm at the base, 1- to 4-septate, brown usually up to the tip, sometimes paler towards the tip, base cylindrical, conical or slightly attenuated, often zig-zag-shaped, tip acute to roundish. *Conidiophores* pale brown, septate, rarely branched, up to 30 µm long. *Conidiogenous cells* enteroblastic, pale brown, cylindrical, 6–15× 3–3.5 µm µm, opening 0.5–1 µm diam, collarette not seen, periclinal thickening visible. *Conidia* hyaline, in masses greyish white, aseptate, smooth-walled, central part of conidium usually almost straight with parallel walls, often bent apruptly to the apex or to both ends, giving the conidia an almost angular shape, apex narrow and acute, base either the same or broader and truncate (18–)23.5–29(–30) × (3–)3.5–4(–5) µm, mean ± SD = 26.3 ± 2.7 × 3.8 ± 0.4 µm, L/W ratio = 7.0.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, medium not stained, filter paper partly pale salmon and partly covered by tiny black acervuli. Colonies on OA flat with entire margin, surface buff to olivaceous, partly covered with very short aerial mycelium, reverse buff to olivaceous-grey. Colonies on PDA flat with entire margin, surface dark olivaceous, partly covered with very short aerial mycelium, reverse pale to dark olivaceous-grey. Colonies on MEA flat with entire margin, surface covered by floccose white, pale olivaceous grey to olivaceous-grey aerial mycelium, margin saffron to pale luteous, reverse dark olivaceous-grey, saffron towards the margin, margin pale luteous. *Conidia in mass* greyish white to pale salmon.

Materials examined: USA, North Carolina, West Raleigh, on *Pyrus malus* (syn. *Malus* × *domestica*), 9 Feb. 1907, F.L. Stevens & J.G. Hall 780 (Bartholomew, Fungi Columbiani no. 2500; K(M), presumed **isotype**); USA, Rhode Island, Kingston, on fruit of *Malus sylvestris* (syn. *Malus* × *domestica*), deposited in CBS collection Feb. 1937 by C.J. Alexopoulos (CBS H-20360 [dried culture] **epitype** here designated, culture ex-

epitype CBS 346.37 = CCT 4806).

Notes: Walker (1925) noticed the difference in conidium shape between *C. circinans* and *C. fructi*, which forms slightly angular conidia. The conidium shape is similar to that of *C. dematium*, however *C. fructi* is slower growing. The species has rarely been referred to in the literature, and it seems likely that any disease caused is of little economic importance. It was not investigated by Gonzalez *et al*. (2006) in their study of *Colletotrichum* species causing leaf spot and fruit rot of apple in North and South America.

Probable type material of *C. fructi* is stored in BPI; its status is doubtful as although the collection number is correctly cited, the collection date is after that given on the original publication (Stevens and Hall, 1907). No living culture is associated with that specimen, and according to WFCC World Federation for Culture Collections, (http://www.wfcc.info/datacenter.html) strain CBS 346.37 is the only strain of *C. fructi* in any public culture collection. The morphological characteristics of that strain are in concord with the illustration given in the original publication, and it originates from a closely related species in the same geographical region as the type. It is therefore an appropriate choice as epitype.

Colletotrichum lilii Plakidas ex Boerema & Hamers, *Netherlands Journal of Plant Pathology* 94(suppl. 1): 12 (1988) (Fig. 8)

"*Colletotrichum lilii*" Plakidas, *Phytopathology* 34: 568 (1944), nom. inval. (Vienna Code, Art. 36.1).

≡. *Vermicularia lilii* (Plakidas ex Boerema & Hamers) Vassiljevsky, *Fungi Imperfecti Parasitici* 2: 346 (1950)

On SNA: *Vegetative hyphae* 1.5–5 µm diam, hyaline or pale brown, smooth-walled, septate, branched. *Conidiomata* acervular, conidiophores loosely arranged, no compact fruiting structures formed, with masses of pale salmon conidia. *Setae* smooth to finely verruculose, 1- to 3-septate, 20–70 µm long, base cylindrical to conical, 3–5 µm diam, pale to medium brown up to the tip, tip acute to roundish. *Chlamydospores* not observed. *Conidiophores* brown or very pale brown, septate, branched, filiform, up to 50 µm long. *Conidiogenous cells* enteroblastic, long cylindrical to elongate ampulliform, 7.5–20 × 2–3.5 µm, opening 1.5–2 µm diam, collarette distinct, 1.5 (–2) µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled or verruculose, aseptate, very variable in size and shape: some strongly curved, more strongly curved towards the (often broadly) rounded apex than towards the truncate base, some small conidia almost straight, (9.5–)13–19.5(–33.5) × 3–4(–4.5) µm, mean ± SD = 16.2 ± 4.6 × 3.4 ± 0.4 µm, L/W ratio = 5.6. *Appressoria* solitary or in loose groups, 1-, sometimes 2-celled, dark brown, irregularly shaped, but often with clavate to somewhat triangular outline, strongly lobed, smooth-walled, (7.5–)10.5–19(–28.5) × (4.5–)6–10(–14) µm, mean ± SD = 14.7 ± 4.4 × 8 ± 2.2 µm, L/W ratio = 1.8.

On Anthriscus stem: *Conidiomata* few, composed of pale brown angular cells, 4–7 µm diam. *Setae* pale to medium brown up to the tip, but often paler basal cell, verruculose, 30–150 µm, (mostly 50–100 µm) long, 1- to 4- (to 5-) septate, base cylindrical, conical, sometimes slightly inflated, 3–7 µm wide, tip more or less acute to roundish. *Conidiophores* pale brown, septate, branched, up to 50 (–80) µm long, smooth to verruculose. *Conidiogenous cells* enteroblastic, pale brown, cylindrical, occationally ellipsoidal, smooth to finely verruculose, 9–20 (–38) × 3.5–6 µm, opening 1.5–2 µm wide, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, aseptate, smooth-walled curved, more strongly curved towards the more or less acute apex than towards the truncate base, (14.5–)16.5–19(–20) × 3–3.5(–4) µm, mean ± SD = 17.6 ± 1.3 (3.4 ± 0.3 µm, L/W ratio = 5.1.

Culture characteristics: Colonies on SNA flat with entire margin, short hyaline aerial mycelium on filter paper, *Anthriscus* stem, medium close to stem and under filter paper yellowish brown. Colonies on OA flat with entire margin, surface moist, no aerial mycelium, honey to isabelline with tiny darker brown dots, reverse hazel. *Conidia in* mass salmon.

Materials examined: JAPAN, unlocalised, on *Lilium* sp., deposited in CBS collection Jan. 2001 by H. Nirenberg (CBS H-20361 [dried culture], living culture CBS 109214 = BBA 62147).

Notes: This appears to be a host-specific pathogen of *Lilium* species, causing black scale disease of bulbs. It was originally described

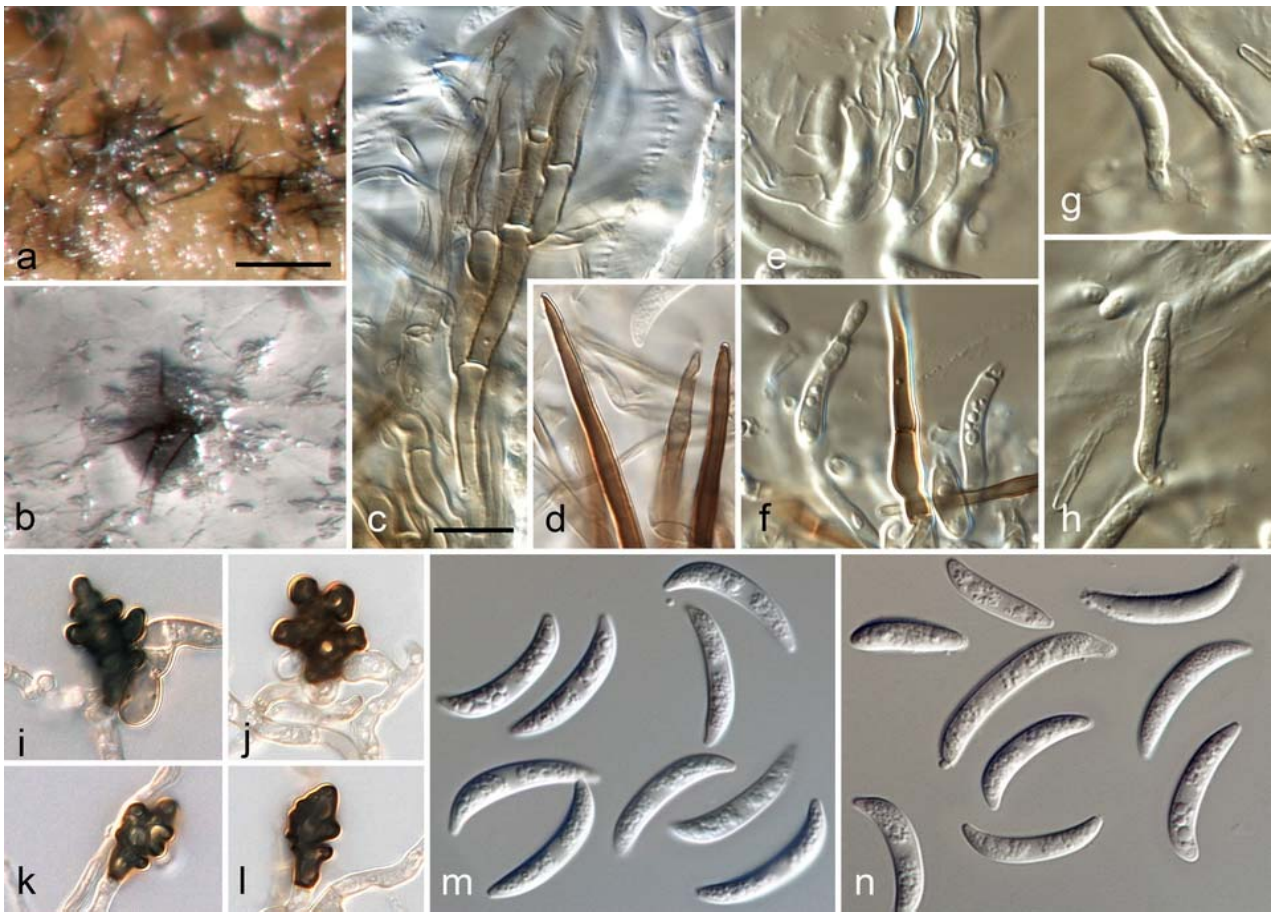

Fig. 8. *Colletotrichum lilii* (from ex-epitype strain CBS 109214). a–b. acervuli; c. conidiophore; d. tips of setae; e. conidiophores; f. conidiophores and basis of a seta. g. tip of conidiogenous cell with conidium; h. conidiophore; i–l. appressoria; m–n. conidia; a, c, d, m: from *Anthriscus* stem; b, e–l, n: from SNA. a–b: DM; c–n: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–n.

from cultivated bulbs of *Lilium longiflorum* in Louisiana, but the species was probably imported from Japan (Plakidas, 1944; Sobers and Plakidas, 1962). It has also repeatedly been isolated from *Lilium* bulbs in the Netherlands (Boerema and Hamers, 1988) though it does not cause disease in that country as symptoms become apparent only at soil temperatures ≥ 22 °C. The two strains we have studied (from Japan and the Netherlands) agree with the original description in morphology and ecology.

Sobers and Plakidas (1962) compared *Colletotrichum lilii* with a number of other *Colletotrichum* strains isolated from *Lilium* and *Hemerocallis* species. Some of these had somewhat larger conidia and setae and were considered by them to belong to *C. liliacearum*, here treated as a probable synonym of *C. spaethianum*. No sequences from either taxon have previously been submitted to GenBank; our studies suggest that they are closely related but phylogenetically distinct.

Colletotrichum lineola Corda, in Sturm, *Deutschlands Flora* (Nürnberg) 3: 41 (1831) (Fig. 9)

≡ *Vermicularia lineola* (Corda) Grove, *British Stem- and Leaf-Fungi (Coelomycetes)* (Cambridge) 2: 241 (1937)

≡ *Ellisiellina lineola* (Corda) Bat., *Anais da Sociedade de Biologia de Pernambuco* 14(1/2): 18 (1956)

On SNA: *Vegetative hyphae* hyaline or pale brown, smooth-walled, septate, branched, 1–9 µm diam. *Chlamydospores* not observed. *Conidiomata* acervular, poorly developed, conidiophores and setae formed on a base of brown angular cells 4–15 µm diam. *Sporulation* abundant. *Setae* straight or ± bent, dark brown up to the tip, opaque, septa difficult to distinguish, 2- to 4-septate, sometimes branched at the base, 50–150 µm long, smooth-walled, base cylindrical, 3–7 µm diam, tip acute. *Conidiophores* medium brown, septate, branched, smooth-walled, to 130 µm long. *Conidiogenous cells* enteroblastic, pale brown, smooth-walled, cylindrical, 5.5–16 × 3–4 µm,

Fig. 9. *Colletotrichum lineola* (a–g,i from holotype PRM 155463, h,j from epitype CBS H-20361, k–x from ex-epitype strain CBS 125337). a, h. vascular stripes on host surface; b–f. conidia; g. seta; i–j. acervuli apearing from vascular stipes; k–l. acervuli; m–n. tips of setae; o–p. conidiophores; q–r. bases of setae; s. conidiophores; t–v. appressoria; w–x. conidia; a–j: from host tissue; k, m, p–r, w: from *Anthriscus* stem; l, n–o, s–v, x: from SNA. a, h, i–l: DM; b–g, m–x: DIC. — Scale bars: a = 1 mm; f = 10 µm; h = 1 mm; i = 100 µm; j = 100 µm; k = 200 µm; m = 10 µm; f applies to b–g; k applies to k–l; m applies to m–x.

opening 1–2 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, central part of conidia usually almost straight with parallel walls, bent apruptly to the roundish to acute apex and truncate base giving the conidia an

almost angular shape, (21.5–)22.5–24.5(–25.5) × 3–3.5 (–4) µm, mean ± SD = 23.4 ± 0.9 × 3.4 ± 0.2 µm, L/W ratio = 6.8; strain CBS 125351 forms shorter conidia: 19–23 × 3–3.5 µm. *Appressoria* solitary, in small groups or short chains, medium to dark brown, smooth-walled, ellipsoidal to clavate, sometimes crenate or slightly lobed, (7.5–)7.5–16.5(–26) × (4–)5–9.5(–14) µm, mean ± SD = 12.0 ± 4.3 × 7.3 ± 2.1 µm, L/W ratio = 1.6.

On Anthriscus stem: *Conidiomata* acervular, conidiophores and setae formed on cushions of brown, angular cells, 3–9 µm diam. *Setae* straight, hyaline, pale to medium brown, hyaline towards the tip, smooth-walled or verruculose, 1- to 3-septate, often only septate at the base, 50–160 µm long, base cylindrical, conical or slightly inflated, 4–8 µm diam, tips of brown setae ± acute, tips of hyaline setae rounded. *Conidiophores* brown, septate, branched, smooth-walled, to 30 µm long. *Conidiogenous cells* enteroblastic, pale brown, smooth-walled, cylindrical, 10–16 × 3–4 µm, opening 1.5–2 µm diam, collarette distinct, 0.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, central part of conidia usually almost straight with parallel walls, bent apruptly to the acute apex and truncate base giving the conidia an almost angular shape, (21.5–)23–25(–25.5) × (3–)3.5–4 µm, mean ± SD = 23.9 ± 1.1 × 3.6 ± 0.2 µm, L/W ratio = 6.6; strain CBS 125351 forms shorter conidia: 18–23 × 3–4 µm.

Culture characteristics: Colonies on SNA flat with entire margin, medium hyaline slightly pale olivaceous to cinnamon, filter paper and *Anthriscus* stem covered with short olivaceous grey aerial mycelium and olivaceous grey to iron grey acervuli; 36–37 mm in 7 d. Colonies on OA flat with entire margin, surface smoke-grey to olivaceous-buff, covert with short, felty, pale olivaceous-grey aerial mycelium and iron-grey acervuli, reverse smoke-grey to olivaceous-buff; 33 mm in 7 d. *Conidia in mass* white, greyish white to salmon.

Materials examined: CZECH REPUBLIC, close to Prague, from stem of *Apiaceae* plant, late autum/winter 1829, A. J. Corda (PRM 155463, **holotype** of *Colletotrichum lineola)*; CZECH REPUBLIC, Central Bohemia, Lazne Tousen (ca 25 km E of Prague), left bank of river Labe, from dead stem of *Apiaceae* plant, 20 Sep. 2009, M. Reblová (CBS H-20362 [dried specimen] **epitype** here designated, culture ex-epitype CBS 125337); CZECH REPUBLIC, same location, from dead stem of *Apiaceae* plant, 20 Sep. 2009, M. Reblová (CBS H-20363, living culture CBS 115339).

Notes: The structures found on the newly collected material designated as epitype and the ex-epitype strain (described above) resemble those on the holotype material, including a few conidia, measuring 15–23 × 3–4(–4.5) µm, setae and conidiogenous cells (Fig. 9a–g, i).

Based on our research, *C. lineola* is a widespread, primarily temperate species associated with a very wide range of plant species. It is characterised by small compressed acervuli emerging in rows/lines ("*lineola*") on stems of the type host plant associated with short brown vascular stripes, while *C. dematium* forms big black spherical ("*Sphaeria dematium*") stromatic acervuli in irregular groups on the host surface. Apart from these host-related differences we did not find consistent morphological distinctions between these two species, though red pigmentation in culture was only observed in *C. lineola*. Several strains (e.g. CBS 125339, CBS 109228, CBS 124959) released an apricot to coral pigment into the medium. Wollenweber and Hochapfel (1949) isolated single-spore strains of *C. dematium s.l.* from *Heracleum pubescens* with and without a red pigment that corresponded in all other features; these are likely to belong to *C. lineola*. The two species are however clearly divergent in sequence and occupy separate clades. Therefore we prefer to retain them as separate taxa, awaiting more detailed population studies verify if they represent two populations or two distinct species.

Colletotrichum lineola is the type species of the genus *Colletotrichum*, collected in late autumn 1829 on stems of a species of *Apiaceae* near Prague (Corda, 1831). The publication was issued in parts, and despite the title page of the volume bearing the date of 1837, the part containing *Colletotrichum* had already been indexed in the journal *Flora* in November 1831 (Stafleu and Cowan, 1986). The genus name was actually cited as *Colletothrichum*, and as the name is spelled in this way in the index and the following genus (*Aseimothrichum*) is formed in a similar manner, it would not be appropriate to assume that the spelling results from a misprint. There is an overwhelming

case for conservation, and we do not recommend adoption of the original spelling.

Corda indicated that *C. lineola* had conidiomata in groups in a linear arrangement, setae and conidia in slime. No measurements were given. Grove (1937) transferred the species name to *Vermicularia*, based on a collection from sheaths and culms of *Dactylis glomerata* in Warwickshire, England. Although the name *V. lineola* is nomenclaturally an authentic homotypic synonym of *C. lineola*, Grove's description of the *Dactylis* fungus is ambiguous in some respects and its taxonomic identity is in doubt.Batista (1956) transferred *C. lineola* to the genus *Ellisiellina* Sousa de Câmara, which is based on the species now commonly treated as *Colletotrichum caudatum*.

Colletotrichum liriopes Damm, P.F. Cannon & Crous, **sp. nov.** (Fig. 10)
MycoBank: 514642

Etymology: Named after its host, *Liriope.* Colletotrichi tofieldiae simile, sed cellulis conidiogenis saepe valde inflatis, celeriter fatiscentibus, conidiis maioribus, in vitro (SNA) (10.5–)16–23.5(–25.5) x (2.5–) 3.5–4.5(–5) µm, in cultura cum caulibus Anthrisci (19–) 21.5–24.5(–27) x 3.5–4.5(–5) µm, appressoriis crenatioribus et lobatioribus, (9.5–)10.5–15(–17.5) x (6–) 7.5–11.5(–16) µm.

On SNA: *Vegetative hyphae* 1.5–5 µm diam, hyaline, smooth-walled, septate, branched. *Conidiomata* acervular, conidiophores and rarely setae formed directly on hyphae. *Setae* brown up to the tip, 2- to 3-septate, 50–80 µm long, base conical to slightly inflated, 4–7 µm diam, tip acute. *Chlamydospores* not observed. *Conidiophores* hyaline to pale brown, septate, branched. *Conidiogenous cells* enteroblastic, hyaline, ampulliform or cylindrical, the cells often strongly inflated, disintegrating quickly, 8–15 × 3.5–5.5 µm, collarette 0.5–1.5 µm long, opening 1–2 µm diam, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, rarely finely verruculose, aseptate, slightly curved, both sides gradually tapering towards the round to slightly acute apex and truncate base, (10.5–)16–23.5(–25.5) × (2.5–) 3.5–4.5(–5) µm, mean ± SD = 19.7 ± 3.6 × 4 ± 0.5 µm, L/W ratio = 5.0. *Appressoria* solitary or in loose groups, irregularly shaped, but often with a somewhat circular to elliptical outline, crenate to lobed, smooth-walled, aseptate, dark brown, (9.5–)10.5–15(–17.5) × (6–)7.5–11.5(–16) µm, mean ± SD = 12.9 ± 2.3 × 9.4 ± 2.1 µm, L/W ratio = 1.4.

On Anthriscus stem. Conidiomata acervular, hyaline to pale brown cells, 3–7 µm diam, roundish to more or less globose, from which setae (few setae per acervulus) and conidiophores are produced. *Setae* light to medium brown, finely verruculose, 70–110 µm long, 2- to 4- septate, base conical to inflated, 4–7 µm diam, tip acute. *Conidiophores* hyaline to pale brown, not differentiated from basal cells. *Conidiogenous cells* enteroblastic, hyaline to pale brown, conical, subglobose to ellipsoidal, 3–10 × 2.5–5 µm, opening 1–2 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, slightly curved, both sides gradually tapering towards the round to slightly acute apex and truncate base, (19–)21.5–24.5(–27) × 3.5–4.5(–5) µm, mean ± SD = 23.1 ± 1.6 × 4.1 ± 0.4 µm, L/W ratio = 5.6.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, no pigmentation. Colonies on OA flat with entire margin, surface moist, no aerial mycelium, smoke-grey, honey to rosy-buff, reverse buff to very pale smoke-grey. *Conidia in mass* salmon.

Materials examined: MEXICO, APHIS interception Houstan 057263, on *Liriope muscari*, collected 29 Nov. 2000 by M.J. Segall, isolated 2000 by A.Y. Rossman (CBS H-20364, **holotype**, culture ex-type CBS 119444 = AR 3563).

Notes: This species is known only from two duplicate strains isolated from *Liriope muscari*, originating from Mexico and the result of a quarantine interception in Houston, USA. It belongs to a major clade that is almost completely confined to petaloid monocotyledon plants from the *Liliales*, primarily characterised morphologically by its appressoria with complex outlines that are similar to those of *C. lilii*, but differs from it by the often strongly inflated conidiogenous cells. The same strain was included in a phylogenetic analysis of *Colletotrichum* species from *Agavaceae* by Farr *et al*. (2006), identified there as *C. dematium*.

Colletotrichum phaseolorum S. Takim., *Annals of the Phytopathological Society of Japan* 5: 21 (1934).

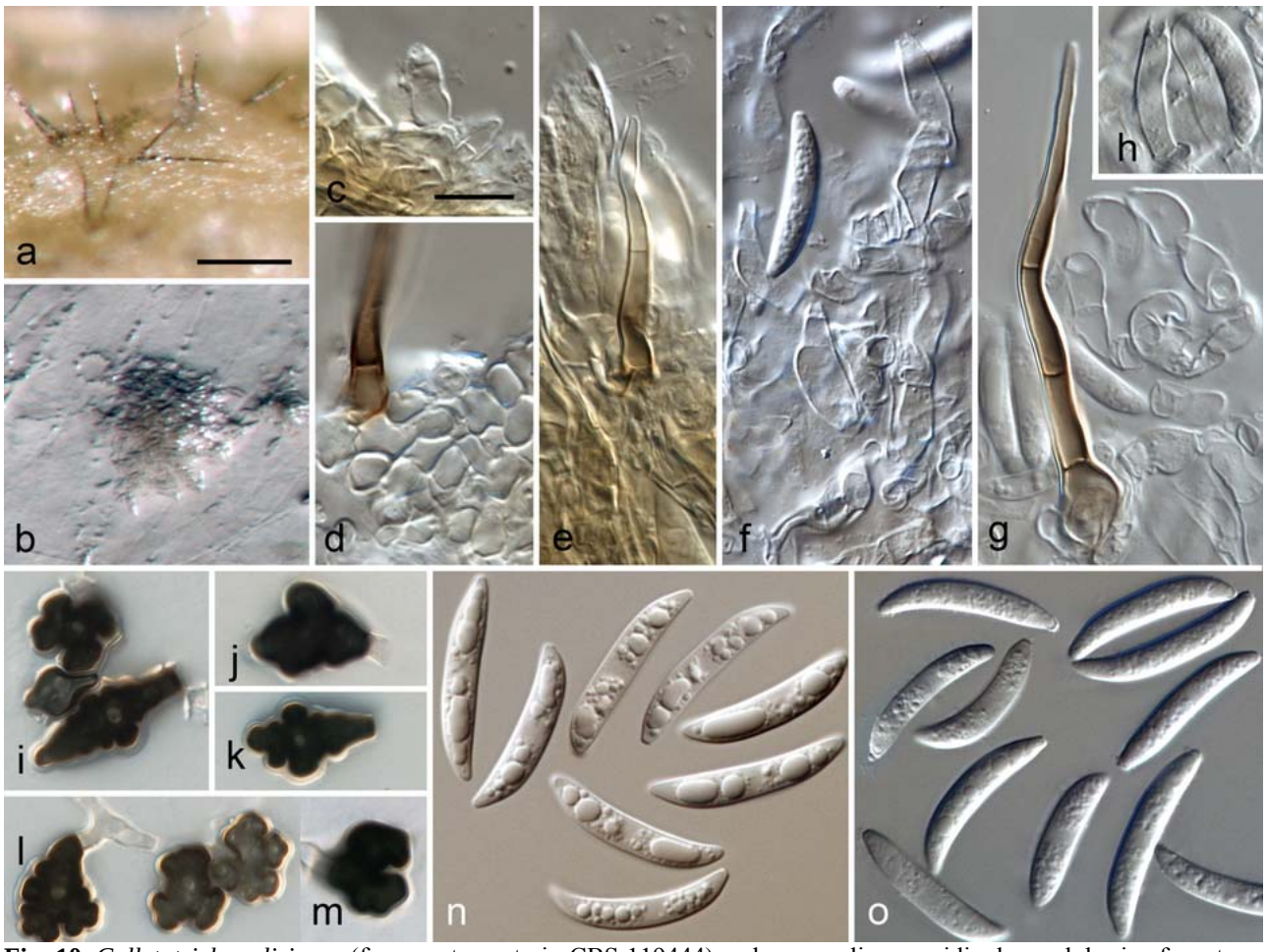

Fig. 10. *Colletotrichum liriopes* (from ex-type strain CBS 119444). a–b. acervuli; c. conidiophore; d. basis of a seta; e. seta; f–h. conidiophores; g. conidiophores and seta; l–m. appressoria; n–o. conidia; a, c–e, n: from *Anthriscus* stem; b, f–m, o: from SNA. a–b: DM; c–o: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–o.

Notes: *Colletotrichum phaseolorum* is known only from the original collections in Japan. In June 1936 Takimoto deposited two cultures in CBS, CBS 157.36 from *Vigna angularis* (syn. *Phaseolus radiatus* var. *aureus*), which is kept as an authentic strain of *C. phaseolorum* in the collection, and CBS 158.36 from *Vigna sinensis* with no further information. Takimoto did not designate one specimen as holotype in the publication, but lists three syntypes, two on *V. angularis* and one on *V. sinensis*. We have been unable to locate the type specimens cited in the original paper, and the two strains in CBS are not identical genetically and form distinct lineages, although they occupy the same subclade (labelled as *C. phaseolorum* 1 and 2). However, neither is an ideal choice for neotype as they do not sporulate under our conditions. The description below is derived from the original publication (Takimoto 1934).

"Acervuli which are imperfect and subepidermal rupture and compose irregular or hemispherical mycelial mass in which setae surrounded by conidia are formed. Conidia are mostly fusiform, 17-20 × 3-7 µm in size, rarely cylindrical or spindle-shaped. Conidiophores are short; setae are dark brown, one to three celled, 60–110 × 3–4 µm (on *Phaseolus radiatus* var. *aureus*), 60–120 × 3–4 µm (on *Vigna catjang* var. *sinensis*)." The illustration shows conidia that are distinctly curved.

Colletotrichum rusci Damm, P.F. Cannon & Crous, **sp. nov.** (Fig. 11)
MycoBank: 514643

Etymology: Named after its host, *Ruscus*. Colletotrichi trichelli simile, sed conidiis brevioribus et latioribus, laevibus, hilis prominentibus, in vitro (SNA) (16–)17.5–21(–23) x 4–4.5(–5) µm, in cultura cum caulibus Anthrisci (16–)17.5–21(–23.5) x 4–5 µm, appressoriis (5–)8–17(–21) x (3–)4–7.5(–10.5) µm.

On SNA: *Vegetative hyphae* 1–6 µm diam, hyaline or pale brown, smooth-walled, septate, branched. *Conidiomata* acervular, conidiophores formed directly on hyphae. *Setae* not observed. *Chlamydospores* not observed. *Coni-*

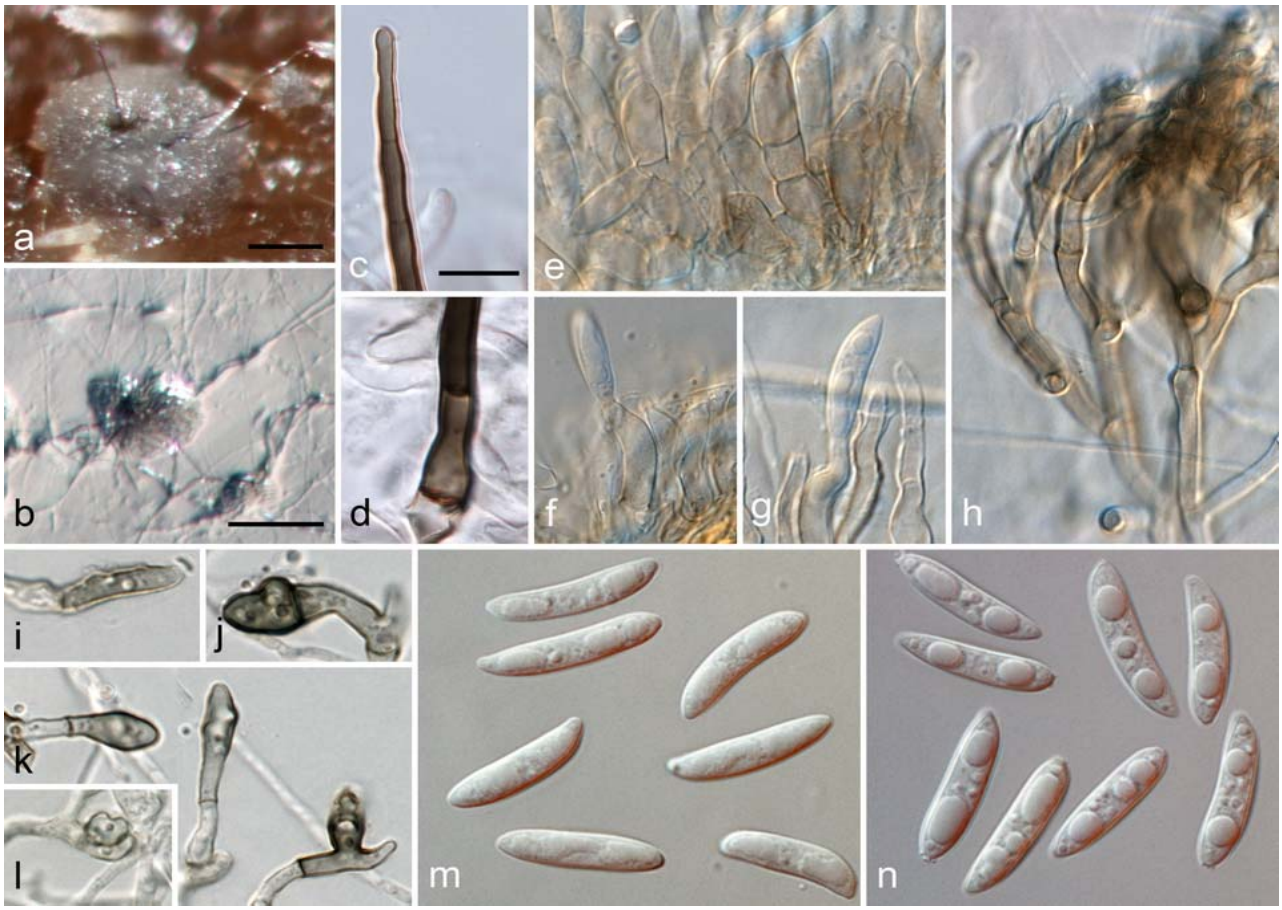

Fig. 11. *Colletotrichum rusci* (from ex-type strain CBS 119206). a–b. acervuli; c. tip of a seta; d. basis of a seta; e–h. conidiophores; i–l. appressoria; m–n. conidia; a, c–f, m: from *Anthriscus* stem; b, g–l, n: from SNA. a–b: DM; c–n: DIC. — Scale bars: a = 100 µm; b = 100 µm; c = 10 µm; c applies to c–n.

diophores light to medium brown, septate, branched, up to 110 µm long. *Conidiogenous cells* enteroblastic, pale brown, cylindrical to elongate ampulliform, 6–18 x 3–4 µm, opening 1.5–2 µm diam, collarette 0.5 µm long, periclinal thickening not observed. *Conidia* hyaline, smooth-walled, aseptate, hardly curved, base usually broader than apex, truncate and with a prominent hilum, apex somewhat acute, contens with (often two) big guttules, (16–) 17.5–21(–23) × 4–4.5(–5) µm, mean ± SD = 19,4 ± 1.8 × 4.4 ± 0.3 µm, L/W ratio = 4.4. *Appressoria* solitary, in chains or in loose groups, light to medium brown, aseptate, smooth-walled, clavate or slightly lobed, (5–) 8–17(–21) × (3–)4–7.5(–10.5) µm, mean ± SD = 12.5 ± 4.6× 5.8 ± 2.0 µm, L/W ratio = 2.2.

On Anthriscus stem: *Conidiomata* acervular, conidiophores and sparse setae formed from a cushion of brown, angular cells, 4–6 µm diam. *Setae* dark brown up to the tip, basal cell pale brown, 70–130 µm long, 3- to 4- septate, base inflated, 4.5–7 µm diam, tip round. *Conidiophores* pale brown, septate, branched, up to 50 µm long. *Conidiogenous cells* enteroblastic, pale brown, cylindrical to elongate ampulliform, 8–17 × 4–5 µm, opening 1–1.5 µm diam, collarette 1–2 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, hardly curved, base often broader than apex, truncate, apex somewhat acute, contens with big guttules, (16–)17.5–21(–23.5) × 4–5 µm, mean ± SD = 19.2 ± 1.8 × 4.5 ± 0.3 µm, L/W ratio = 4.2.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, medium hyaline, filter paper partly covered with grey acervuli; 18 mm in 7 d (27 mm in 10 d). Colonies on OA flat with entire margin, surface buff (no pigmentation), partly covert with short, filty, grey aerial mycelium, reverse buff; 19 mm in 7 d (29 mm in 10 d). *Conidia in mass* white to pale grey.

Materials examined: ITALY, intercepted JFKIA 151256, on stem of *Ruscus*, collected 26 Jul. 2002 by A. Towson (CBS H-20365, **holotype**, culture ex-type CBS 119206 = MEP 1530).

Notes: *Colletotrichum rusci* apparently differs from *C. erumpens*, described on *Ruscus aculeatus* from France (Saccardo, 1880, 1884) in having smaller conidia, measuring 19.4 x 4.4 µm (SNA) and 19.2 x 4.5 µm (*Anthriscus* stem), while those of *C. erumpens* measure 25 x 5 µm. Conidiogenous cells are pigmented and cylindrical to elongate ampulliform, while those of *C. erumpens* are hyaline with brown bases and conical. The type of *C. erumpens* has not been located; it is not present in Saccardo's herbarium (Gola, 1930) and while the original paper dealt with fungi from France sent to Saccardo by Roumeguère, there was no specimen number given. As there is considerable doubt that the two species on *Ruscus* are synonymous, we prefer to describe a new taxon rather than neotypify the old name. The same strain was included in a phylogenetic analysis of *Colletotrichum* species from *Agavaceae* by Farr *et al*. (2006).

Colletotrichum spaethianum (Allesch.) Damm, P.F. Cannon & Crous, **comb. nov.** (Fig. 12)
MycoBank: 514644

Basionym: *Vermicularia spaethiana* Allesch., in Sydow, *Beiblatt zur Hedwigia* 36: 161 (1897)

On SNA: *Vegetative hyphae* 1.5–7 µm diam, hyaline, smooth-walled, septate, branched. *Conidiomata* acervular, conidiophores and setae formed directly on hyphae. *Setae* medium brown up to the tip, basal cell often paler, smooth to finely verruculose, (2- to) 3-septate, 30–90 µm long, base cylindrical to conical, 3–6 µm diam, tip more or less acute. *Chlamydospores* not observed. *Conidiophores* hyaline, septate, branched, up to 60 µm long. *Conidiogenous cells* enteroblastic, hyaline, cylindrical, sometimes slightly inflated, 6–16 × 3–4 µm, opening 1–2 µm diam, collarette distinct, 1–2 µm diam, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, curved, slightly curved, more towards the round or somewhat acute apex, base truncate, (13.5–)17–22.5 (–29) × (3–)3.5– 4(–4.5) µm, mean ± SD = 19.7 ± 2.7 × 3.6 ± 0.3 µm, L/W ratio = 5.4. *Appressoria* single or in loose groups, dark brown, irregular shapes, sometimes more or less lobed, smooth-walled, (5–)7–9.5(–12) × 5–7.5(–9) µm, mean ± SD = 8.1 ± 1.3 × 6.4 ± 1.3 µm, L/W ratio = 1.3; appressoria of strain CBS 100063: 6–18.5 × 4–16.5 µm and deeply lobed.

On Anthriscus stem: *Conidiomata* acervular, conidiophores and setae formed on a cushion of pale brown, angular cells, 3–6 µm diam. *Setae* medium to dark brown, smooth to finely verruculose, 40–100 µm long, 2- to 4-septate, often bend at the base or in the middle, base cylindrical, 3–5 µm diam, tip acute. *Conidiophores* pale brown, septate, branched, sometimes filiform, up to 70 µm long. *Conidiogenous cells* enteroblastic, pale brown, cylindrical, sometimes more or less inflated, 6–17 × 2.5–3.5 µm, opening 1–1.5 µm diam, collarette 0.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, slightly curved, more towards the round or somewhat acute apex, base truncate (11.5–)17–22.5(–24.5) × 3–3.5(–4) µm, mean ± SD = 19.7 ± 2.7 × 3.2 ± 0.3 µm, L/W ratio = 6.1.

Culture characteristics: Colonies on SNA flat with entire margin, short greyish white aerial mycelium on *Anthriscus* stem, tiny dark grey to salmon acervuli on filter paper and in a lesser extent on the surrounding medium. Colonies on OA flat with entire margin, surface moist, aerial mycelium absent, buff to honey, partly salmon to orange due to sporulation, reverse same colours. *Conidia in mass* salmon to orange.

Materials examined: GERMANY, Berlin, Spaeth'sche Baumschule, on dead stems of *Funkia univittata* [syn. *Hosta sieboldiana*] , Oct. 1895, P. Sydow (Sydow, Mycotheca Marchica no. 4486; M-0155529 **holotype** of *Vermicularia spaethiana*, K - **isotype**); GERMANY, Berlin-Zehlendorf, on a dead stem of *Funkia sieboldiana* [syn. *Hosta sieboldiana*] , isolated Oct. 1932 by H. Richter (CBS H-20369 [dried culture] **epitype** here designated, culture ex-epitype CBS 167.49); SOUTH KOREA, infected leaves of *Lilium* sp., deposited Sep. 1997 by Y.S. Lee (living culture CBS 100063).

Notes: There are four species described on *Hemerocallis*, *Hosta* (= *Funkia*) and *Lilium*: *C. lilii* Plakidas ex Boerema & Hamers (on *Lilium*), *C. liliacearum* Ferraris (on *Hemerocallis*) and *V. spaethiana* and *C. omnivorum* Halst. on *Hosta*. *C. lilii* is represented in this paper by strains CBS 109214 and 186.30 (see above). The type of *C. omnivorum* has not been examined, but it is described as having much longer conidia (20–28 × 3–5 µm), and no cultures are available for this species. Of the remaining two potential names for this species,

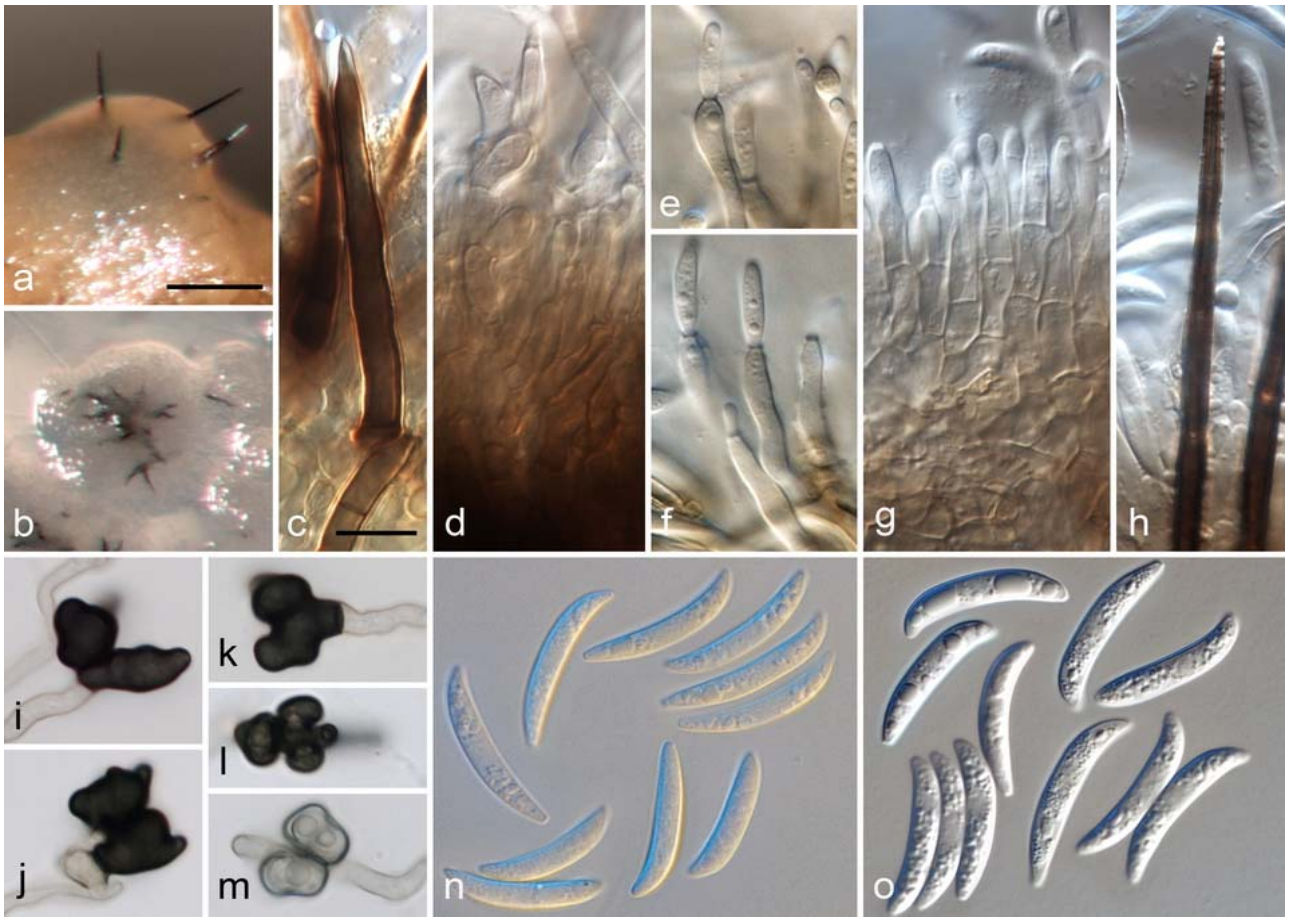

Fig. 12. *Colletotrichum spaethianum* (b, n–o. from ex-epitype strain CBS 167.49, a, c–n. from CBS 1100063). a–b. acervuli; c. seta; d–g. conidiophores; h. tip of a seta: i–m; appressoria; n–o. conidia; a, c–f, n: from *Anthriscus* stem; b, g–m, o: from SNA. a–b: DM; c–o: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–o.

V. spaethiana (Sydow 1897) was described before *C. liliacearum* Ferraris (1902). There is in addition a homonym of *C. liliacearum* Ferraris; *C. liliacearum* Duke, nom. nov., nom. illegit. (Duke, 1928), and *V. liliacearum* Schwein. (as *"liliaceorum"*; Schweinitz, 1832) could also be synonymous with *C. spaethianum*. *C. liliacearum* Duke, nom. nov., nom. illegit. has been used quite widely for species on *Liliaceae* but it has not been studied in any detail in modern times and no type material has been examined.

The characters of the type of *Vermicularia spaethiana*, including conidia, agree in most respects with those of the material illustrated here. As far as we can tell, *V. spaethiana* represents the earliest legitimate name for this species, so we make the necessary new combination and epitypify the name with a dried specimen for which a living culture is available. *C. spaethianum* was described from dead stems of *Hosta sieboldiana* in Berlin, Germany; strain 167.49 was collected from dead stems of the same host in the same city.

This species differs from the other four closely related species, which have also similar conidia shapes, mainly in setae that usually have an acute tip and cylindrical to conical base and appressoria with irregular outline that are more or less lobed but not crenate.

Colletotrichum spinaciae Ellis & Halst., *Journal of Mycology* 6: 34 (1890) (Fig. 13)

≡ *Vermicularia spinaciae* (Ellis & Halst.) Vassiljevsky, *Fungi imperfecti Parasitici* 2: 339 (1950)

≡ *Colletotrichum dematium* f. *spinaciae* (Ellis & Halst.) Arx, *Phytopathologische Zeitschrift* 29(4): 460 (1957)

On SNA: *Vegetative hyphae* hyaline, smooth or verrucose, septate, branched, 1–8 µm diam. *Conidiomata* acervular, forming irregular masses of pale brown angular cells from which setae and conidiophores are produced, only a few acervuli on surface of medium, usually with no setae or only one seta per acervulus. *Setae* pale to medium brown, sometimes dark brown, base and tip sometimes lighter, finely verruculose, 30–90(–200) µm long, 2- to 3- septate, base cylindrical to

Fig. 13. *Colletotrichum spinaciae* (from ex-epitype strain CBS 128.57). a–b. acervuli; c. tips of setae; d. bases of conidiophores; e–f. conidiophores; g. tip of a seta: h basis of a seta; i–j. conidiophores; k–o; appressoria; p–q. conidia; a, c–f, p: from *Anthriscus* stem; b, g–o, q: from SNA. a–b: DM; c–q: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–q.

conical, 3–7 µm diam, tip round or acute. *Chlamydospores* not observed. *Conidiophores* hyaline to pale brown, filiform, septate, branched at the base, 40–70 µm long. *Conidiogenous cells* enteroblastic, (usually monophialidic, but one polyphialide observed) hyaline to pale brown, cylindrical, 15–20 × 2–4 µm, opening 1.5–2 µm diam, collarette distinct, 1–2 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, hardly curved, both sides gradually tapering towards the round apex and round or truncate base, (14–)18–23(–32) × 3–3.5(–4) µm, mean ± SD = 20.4 ± 2.5 × 3.4 ± 0.3 µm, L/W ratio = 6.0. *Appressoria* solitary, ellipsoidal to clavate, pale brown, entire edge, smooth-walled, aseptate, rarely septate, (4.5–)4.5–11(–21.5) × (3–)4.5–6(–6.5) µm, mean ± SD = 7.8 ± 3.2 × 5.1 ± 0.8 µm, L/W ratio = 1.5.

On Anthriscus stem: *Conidiomata* acervular, compact fruiting structures composed of irregular masses of pale brown angular cells from which setae and conidiophores are produced. *Setae* pale brown, some dark brown setae in between, basal cell often lighter brown, smooth to verruculouse, up to 4-septate, (50–)70–120(–270) µm long, irregular length within acervulus, most setae short but with one or few very long setae, base cylindrical to conical, 3.5–6 µm diam. *Conidiophores* hyaline to pale brown, simple to 2-septate, usually not branched, 10–25 µm long. *Conidiogenous cells* enteroblastic, hyaline to pale brown, clavate to cylindrical, 5.5–15 × 2.5–5 µm, opening 1–1.5 µm diam, collarette 0.5–1 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, hardly curved, both sides gradually tapering towards the round apex and round or truncate base, (15.5–)19–24(–25) × (2.5–)3–3.5 µm, mean ± SD = 21.6 ± 3 × 3.2 ± 0.3 µm, L/W ratio = 6.8.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, whitish to buff, filter paper, *Anthriscus* stem and medium partly greyish through production of tiny acervuli. Colonies on OA

flat with entire margin, surface salmon to olivaceous, white margin, no aerial mycelium, reverse rosy-buff, pale olivaceous-grey to olivaceous-grey. Colonies on PDA flat with entire margin, surface dark grey-olivaceous to olivaceous-black, white margin, covered by very short whitish aerial mycelium, reverse grey-olivaceous to olivaceous-grey. Colonies on MEA slightly raised with entire margin, surface radially folded, iron-grey with white margin, partly covert by salmon conidial masses (in the centre) and paches of felty whitish aerial mycelium (towards the margin), reverse olivaceous-grey with buff margin. *Conidia in mass* whitish, buff to greyish.

Materials examined: NETHERLANDS, on *Spinacia oleracea*, isolated Dec. 1957 by G. van den Ende (living culture CBS 128.57).

Notes: *C. spinaciae* was treated as a minor variant of *C. dematium* by von Arx (1957), but is here confirmed as a distinct species that is most closely related to *C. circinans*. It has been widely reported as a pathogen of spinach and beet (e.g. Correll *et al*. 1994), and research indicates that individual strains can be highly host-specific (Washington *et al*., 2006). However, our studies suggest that the species as a whole is not specific to *Chenopodiaceae*, and the apparent preference may well be due to sampling bias.

Colletotrichum tofieldiae (Pat.) Damm, P.F. Cannon & Crous, **comb. nov.** (Fig. 14)
MycoBank: 514645

Basionym: *Vermicularia tofieldiae* Pat., *Revue mycologique* 8: 83 (1886)

= *Colletotrichum dematium* var. *minus* Wollenw., *Zeitschrift für Parasitenkunde* 14: 206 (1949)

On SNA. Vegetative hyphae hyaline, smooth, septate, branched, 1–7 µm diam. *Conidiomata* acervular, conidiophores and rarely setae directly formed on hyphae. *Setae* medium brown, basal cell sometimes paler, smooth to verruculose, 1- to 3- septate, 40–60 µm long, base conical to slightly inflated, 4–5.5 µm diam, apex more or less rounded. *Chlamydospores* not observed. *Conidiophores* hyaline to pale brown, septate, branched, up to 50 µm long. *Conidiogenous cells* enteroblastic, hyaline, cylindrical to ellongate ampulliform, 6–18 × 2.5–5 µm, opening 1.5–2.5 µm diam, collarette distinct, 1–2 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, usually whole conidia distinctly curved, both sides gradually tapering towards the round apex and round or truncate base, sometimes less curved towards the base, (12–)17–21(–23) × 3–3.5(–4) µm, mean ± SD = 19.1 ± 2.0 × 3.4 ± 0.3 µm, L/W ratio = 5.7. *Appressoria* solitary or in loose groups, ellipsoidal to clavate, entire edge, crenate or more or less lobed, smooth-walled, aseptate, medium brown or dark brown to almost black, 4–7.5(–22.5) × (4.5–)6–9.5(–11) µm, mean ± SD = 11.5 ± 4.0 × 7.9 ± 1.8 µm, L/W ratio = 1.5.

On Anthriscus stem: *Conidiomata* acervular, conidiophores and setae formed on a cushion of light brown angular cells, 4–9 µm diam. *Setae* medium brown, base often paler, smooth to verruculose, (setae of CBS 168.49 verrucose), 40–100 µm long, 2- to 4-septate, base cylindrical to conical or inflated, 3.5–7 µm diam, tip round to more or less acute. *Conidiophores* hyaline to pale brown, septate, sometimes branched, up to 25 µm long, smooth-walled. *Conidiogenous cells* enteroblastic, hyaline to pale brown, ellipsoidal, ampulliform to short cylindrical, 4–12 × 3–6 µm, opening 1–2 µm diam, collarette distinct, 0.5–1.5 µm long, periclinal thickening distinct. *Conidia* hyaline, smooth-walled, aseptate, whole conidia distinctly curved, both sides gradually tapering towards the round to somewhat acute apex and round or truncate base, (12.5–)16–23(–26) × 3.5–4 µm, mean ± SD = 19.5 ± 3.4 × 3.8 ± 0.2 µm, L/W ratio = 5.2.

Culture characteristics: Colonies on SNA flat with entire margin, very short white aerial mycelium on filter paper and *Anthriscus* stem, filter paper, and in a lesser extent, *Anthriscus* stem and surrounding medium covert with black or orange acervuli. Colonies on OA flat with entire margin, surface moist, aerial mycelium absent, buff to honey, partly salmon to orange due to sporulation, reverse same colours. *Conidia in mass* orange.

Materials examined: THIBET ORIENTAL prov. de Moupin, now in southern Sichuan (CHINA), on dead leaves of *Tofieldia* sp., collected by Abbé David (FH-**holotype** of *Vermicularia tofieldiae*); SWITZERLAND. Graubünden, from *Tofieldia calyculata*, isolated July 1985 by J.A. von Arx (CBS H-20367 [dried culture], living culture CBS 495.85); GERMANY, Berlin-Dahlem, on dead stem of *Lupinus polyphyllus*, collected Oct. 1

Fig. 14. *Colletotrichum tofieldiae* (a–b, l–m. from ex-epitype strain CBS 495.85, c–k. from CBS 168.49). a–b. acervuli; c. setae; d–g. conidiophores; h. seta; i–k. appressoria; l–m. conidia; a, c–d, l: from *Anthriscus* stem; b, i–k, m: from SNA. a–b: DM; c–m: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–m.

932 by H. Richter (ex-type strain of *Colletotrichum dematium* var. *minus* CBS 168.49); UNITED KINGDOM, from Dianthus sp., isolated 1985 by T.D. Godson (living culture IMI 288810)

Notes: The type of *Vermicularia tofieldiae* was collected from dead leaves of a *Tofieldia* species by Abbé David (Armand David, a Catholic priest, missionary and biologist most well known for introducing the Western world to the giant panda and for ensuring survival of the Père David's Deer). The collection locality was described by Patouillard (1886) as "Thibet Oriental, prov. de Moupin", which is now situated in southern Sichuan (China). Type material is present in Patouillard's herbarium (FH).

Vermicularia tofieldiae Pat. was described as forming small, scattered, superficial acervuli, filiform black setae twice as long as the acervuli and hyaline, curved, aseptate conidia, measuring 21 µm (Patouillard, 1886). It forms a subclade of a species aggregate that is almost exclusively composed of monocot-associated strains. However, we have examined two other strains that could be identified as *C. tofieldiae*, isolated from *Lupinus* (Fabaceae) and *Dianthus* (*Caryophyllaceae*), so the specificity may be artefactual. The *Lupinus* strain was derived from type material of *C. dematium* var. *minus* Wollenw.

Colletotrichum truncatum (Schwein.) Andrus & W.D. Moore, *Phytopathology* **25**: 122 (1935). (Fig. 15)

Basionym: *Vermicularia truncata* Schwein., Transactions of the American Philosophical Society 4(2): 230 (1832)

≡ *Colletotrichum dematium* f. *truncatum* (Schwein.) Arx [as 'truncata'], Phytopathologische Zeitschrift 29(4): 459 (1957)

= *Vermicularia capsici* Syd. Annales Mycologici 11: 329 (1913)

≡ *Steirochaete capsici* (Syd.) Sacc. Philippine Journal of Science, Section C, Botany 18: 605 (1921)

≡ *Colletotrichum capsici* (Syd.) E.J. Butler & Bisby The Fungi of India: 152 (1931)

= *Colletotrichum curvatum* Briant & E.B. Martyn Tropical Agriculture 6:258 (1929)

On SNA: *Vegetative hyphae* hyaline, septate, branched, 1–8 µm diam. *Chlamydospores* not observed. *Conidiomata* acervular,

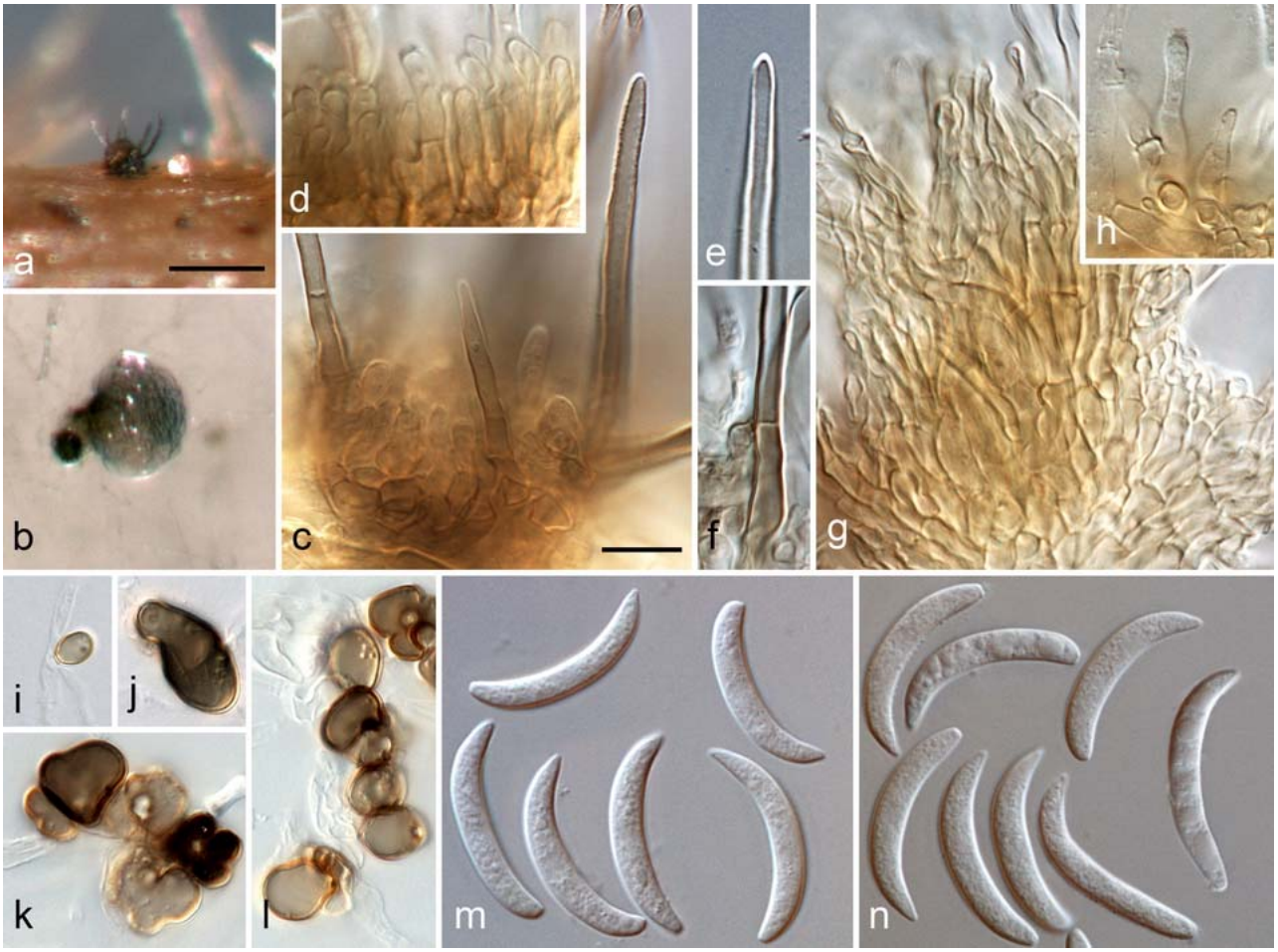

Fig. 15. *Colletotrichum truncatum* (a–h, m–n. from ex-epitype strain CBS 151.35, i–l. from CBS 120709). a–c. acervuli; d. conidiophores; e. tip of a seta; f. basis of a seta; g–h. conidiophores; i–l. appressoria; m–n. conidia; a, c–d, m: from *Anthriscus* stem; b, e–l: from SNA. a–b: DM; c–n: DIC. — Scale bars: a = 100 µm; c = 10 µm; a applies to a–b; c applies to c–n.

conidiophores and setae formed directly on hyphae. *Setae* hyaline to pale brown, smooth to verruculose, 80–150 µm long, 2- to 5-septate, tapering only little towards the slightly acute to roundish tip, base cylindrical to conical, 4–6 µm diam. *Conidiophores* hyaline to pale brown, septate, strongly branched, densely clustered, up to 90 µm long. *Conidiogenous cells* enteroblastic, hyaline to pale brown, cylindrical, 6–20 × 2.5–4 µm, opening 1.5–2 µm diam, collarette rarely visible, 0.5 µm long, periclinal thickening not observed. *Conidia* hyaline, smooth-walled to verruculose, aseptate, long central part of conidia usually slightly curved with parallel walls, ending abruptly at the round and truncate base, while tapering towards the acute and more strongly curved apex, with granular content, (16.5–)20–23.5(–26) × (3–)3.5–4(–4.5) µm, mean ± SD = 21.8 ± 1.9 × 3.8 ± 0.3 µm, L/W ratio = 5.7; other isolates form smaller conidia, e.g. CBS 120709: 15–20 × 3.5–4.5 µm, or larger conidia, e.g. CBS 112998: 24–27 × 3–4 µm. *Appressoria* solitary, in groups or dense clusters, light to medium brown, entire edge to lobed, outline roundish to ellipsoidal or clavate, contact point of hyphae often above the appressorium, (4–)6.5–13(–19) × (4–)5.5–7.5(–10) µm, mean ± SD = 9.8 ± 3.5 × 6.4 ± 1.2 µm, L/W ratio = 1.5.

On Anthriscus stem: *Conidiomata* acervular, conidiophores and setae formed on a cushion of pale brown angular cells 3–5 µm diam. *Setae* pale brown to medium brown up to the tip, smooth to verruculose, 45–100(–170) µm long, 1- to 3- (to 5-)septate, tapering only slightly towards the slightly acute to roundish tip, base cylindrical to conical, 4–8 µm diam. *Conidiophores* pale brown, septate, branched, densely clustered, up to 30 µm long. *Conidiogenous cells* enteroblastic, hyaline to pale

brown, cylindrical, 5–12 × 2.5–3.5 µm, opening 1–1.5 µm diam, collarette 0.5 µm long, periclinal thickening visible. *Conidia* hyaline, smooth-walled, aseptate, long central part of conidia usually slightly curved with parallel walls, ending abruptly at the round and truncate base, while tapering towards the acute and more strongly curved apex, with granular content, (18–)21.5–24.5(–26) × (3.5–)4–4.5 µm, mean ± SD = 22.9 ± 1.6 × 4.1 ± 0.2 µm, L/W ratio = 5.6; other isolates form smaller conidia, e.g. CBS 120709: 15–22.5 × 3–4 µm, or larger conidia, e.g. CBS 112998: 25–28 × 3.5–4 µm.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, filter paper stained partly saffron, 14 mm in 7 d (23 mm in 10 d). Colonies on OA flat with entire margin, no aerial mycelium, surface buff, covered with olivaceous-grey to iron-grey acervuli, reverse buff to pale olivaceous-grey, 19 mm in 7 d (28 mm in 10 d). *Conidia in mass* whitish, buff to pale saffron.

Materials examined: USA, Pennsylvania, Bethlehem, on pods of *Phaseolus* sp. (K probably **isotype** *Vermicularia truncata* ex herb Berkeley (K).); USA, Pennsylvania, Bethlehem, on pods of *Phaseolus lunatus*, isolated by C.F. Andrus (CBS H-20368 [dried culture] **epitype** here designated, culture ex-epitype CBS 151.35); INDIA, Tamil Nadu, Coimbature, on fruits of *Capsicum frutescens*, Ar. 2006, D.J. Bhat (CBS 120709 = HKUCC 10928 culture ex-epitype of *C. capsici*); GAMBIA, on *Arachis hypogaea*, P. Cannon (living culture CBS 112998 = IMI 217517)

Notes: There is no living strain available from Schweinitz's collections of *Vermicularia truncata*. The new combination of *V. truncata* into *Colletotrichum* by Andrus & Moore (1935) was based on observations of specimens from lima bean pods (*Phaseolus lunatus*) gathered in Mississippi, USA. They examined type material of *V. truncata* from *Phaseolus* sp. collected in Bethlehem, Pennsylvania, eastern USA that is now included in the Michener collection of Schweinitz type specimens (BPI), and recognised the host as probably *P. lunatus*. They did not find conidia on the specimen, but all visible characters (conidiomata, setae) agreed with the specimens they received from Mississippi. A specimen identified as this species from Schweinitz's collection was sent to Berkeley in the mid 1800s and this is preserved in Berkeley's herbarium at K. It is certainly authentic material and could be part of the type collection, but unfortunately it too lacks conidia. As discussed below, the strain CBS 151.35 (from *Phaseolus lunatus* in the USA) is an appropriate choice for epitype and is so designated here.

One culture of *C. truncatum* that Andrus & Moore (1935) had received from T.D. Persons of the State Plant Board of Mississippi, southern USA was deposited at CBS in April 1935 by Andrus (CBS 151.35). The dried sample of that strain is therefore an obvious choice as epitype. Further supporting evidence for the identity of *C. truncatum* as defined here is the inclusion of a second strain from *P. lunatus* in the *C. truncatum* clade of our multigene analyses (CBS 119189 from Maryland, Eastern USA), which originates from close to the site where the original type material of *V. truncata* had been collected.

The *C. truncatum* clade also contains the epitype strain of *C. capsici* (CBS 120709) from *Capsicum frutescens* in India (Shenoy *et al*., 2007), a strain from the original collection of *C. curvatum* (CBS 136.30) from *Crotalaria juncea* in Trinidad and Tobago (Briant and Martyn 1929), and strains originally identified as *C. dematium*, *C. dematium* f. sp. *clitoriicola*, *C. corchori* and *Glomerella glycines*. *Colletotrichum dematium* is a distinct species. Since *Vermicularia truncata* (= *C. truncatum*) was described prior to *C. capsici* and *C. curvatum*, both species are regarded as synonyms of *C. truncatum*. Type material of *C. corchori* (Ikata and Yoshida, 1940) has not been studied, but the description in Sutton (1980) matches our concept of *C. truncatum* well, and it is likely that the culture we have studied is correctly identified. The identity of *Glomerella glycines* needs further study. It was described by Lehman and Wolf (1926) as the teleomorph of *Colletotrichum glycines* Hori ex Hemmi (Hemmi, 1920), which Manandhar *et al*. (1986) treated as *Colletotrichum destructivum* O'Gara, 1915. Molecular studies have shown that *C. destructivum* belongs to a different clade to the entire *C. dematium* aggregate (Latunde-Dada and Lucas, 2007). It appears that the strains from lentil in Canada identified as *C. truncatum* by Ford *et al*. (2004) (and accepted as that species by Latunde-Dada and Lucas) actually belong to the *C. destructivum* clade, though probably not actually to *C. destructivum* itself (Gossen *et al*., 2009). This is

particularly unfortunate as a teleomorph formed by mating two of those strains was given the name *Glomerella truncata* (Armstrong-Cho and Banniza 2006). According to the current nomenclatural rules, that name could not be used for a genuine teleomorph of *C. truncatum* without invoking conservation legislation.

Colletotrichum truncatum causes economically important anthracnose diseases of many leguminous and solanaceous plants (e.g. Sutton, 1992; Shenoy *et al*., 2007 as *C. capsici*). According to our data, *C. truncatum* occurs on many host species all over the world, with the biggest group belonging to the *Fabaceae*. Almost all plant families are dicotyledons, with only two exceptions: CBS 711.70 from *Cyperus rotundus* (*Cyperaceae*) in Brazil and IMI 266002, isolated from a human corneal ulcer in Nepal. Cultural and microscopical characters are very variable. According to our molecular data, however, the species does not form any intraspecific groups (not shown).

Colletotrichum verruculosum Damm, P.F. Cannon & Crous, **sp. nov.** (Fig. 16)
MycoBank: 514646

Etymology: Named after the surface texture of its conidia, that are verruculose when formed on SNA medium.

Colletotrichi lilii simile, sed conidiis semper verruculosis, in vitro (SNA) leviter maioribus, (15–) 16.5–19(–20.5) x (3–)3.5–4(–4.5) µm, in cultura cum caulibus Anthrisci (14.5–)16–20.5(–23.5) x 3.5–4.5(–5) µm, appresoriis non crenatis et leviter lobatis, (8–)8.5–12.5(–16.5) x 4.5–6(–7.5) µm.

On SNA: *Vegetative hyphae* hyaline, verruculose, septate, branched, 1.5–6 µm diam. *Chlamydospores* not observed. *Conidiomata* acervular, no compact fruiting structures, conidiophores with few setae. *Sporulation* abundant. *Setae* separately and scattered or in small groups, straight or bent at base, 2- to 4-septate, brown, paler at the base, 70–160 µm long, base cylindrical, conical or slightly inflated, 3–6 µm diam, tip more or less rounded, finely verruculose. *Conidiophores* pale brown, septate, strongly branched, smooth-walled or verruculose, to 110 µm long. *Conidiogenous cells* enteroblastic, pale brown, smooth-walled or verruculose, cylindrical to elongate ampulliform, 10–25 × 3–5 µm, opening 1.5–2 µm diam, collarette distinct, 1–2 µm long, periclinal thickening visible. *Conidia* hyaline, verruculose, aseptate, base rounded and truncate, apex rounded to slightly acute, more tapered and stronger curved than base, (15–) 16.5–19(–20.5) × (3–)3.5–4(–4.5) µm, mean ± SD = 17.7 ± 1.1 × 3.8 ± 0.3 µm, L/W ratio = 4.6. *Appressoria* solitary, medium to dark brown, smooth-walled, entire edge, ellipsoidal to clavate, sometimes curved or slightly lobed, (8–)8.5–12.5(–16.5) × 4.5–6(–7.5) µm, mean ± SD = 10.5 ± 2.2 × 5.4 ± 0.8 µm, L/W ratio = 1.9.

On Anthriscus stem: *Chlamydospores* not observed. *Conidiomata* acervular, conidiophores and setae formed on poorly defined cushions of cells. *Setae* straight, hyaline, pale to medium brown, hyaline towards the tip, smooth-walled or verruculose, 1- to 3-septate, often only septate at the base, 50–160 µm long, base cylindrical, conical or slightly inflated, 4–8 µm diam, tip of brown setae more or less rounded, tip of hyaline setae broadly rounded. *Conidiophores* pale brown, septate, branched, smooth-walled, to 50 µm long. *Conidiogenous cells* enteroblastic, pale brown, smooth-walled, cylindrical to elongate ampulliform, 8–35 × 3–4 µm, opening 1–2 µm diam, collarette distinct, 0.5–1.5 µm long, periclinal thickening visible. *Conidia* hyaline, aseptate, smooth-walled, base rounded and truncate, apex rounded to slightly acute, more tapered and stronger curved than base, (14.5–)16–20.5(–23.5) × 3.5–4.5(–5) µm, mean ± SD = 18.3 ± 2.1 × 4.0 ± 0.4 µm, L/W ratio = 4.6.

Culture characteristics: Colonies on SNA flat with entire margin, no aerial mycelium, no pigments in medium, filter paper with black acervuli; 15 mm in 7 d (26 mm in 10 d). Colonies on OA flat with entire margin, no aerial mycelium, surface flat, granular, buff to honey becoming iron-grey due to development of acervuli, centre salmon due to sporulation, reverse pale olivaceous-grey to olivaceous-grey; 14 mm in 7 d (23 mm in 10 d). *Conidia in mass* salmon.

Materials examined: Zimbabwe, isolated from *Crotalaria juncea*, 1951 (IMI 45525 **holotype**, culture ex-type IMI 45525).

Notes: Several species have been described on *Crotalaria*: *Colletotrichum curvatum* Briant & E.B. Martyn, described from *Crotalaria juncea* in Trinidad and Tobago (Briant and Martyn 1929), is synonymous with

Fig. 16. *Colletotrichum verruculosum* (from ex-type strain IMI 45525). a–b. acervuli; c. conidiophores; d. conidiophores with bases of setae; e. tips of setae; f. basis of a seta; g. conidiophores; h–j. appressoria; k–l. conidia; a, c–e, k: from *Anthriscus* stem; b, f–j, l: from SNA. a–b: DM; c–l: DIC. — Scale bars: a = 200 µm; c = 10 µm; a applies to a–b; c applies to c–l.

C. truncatum as shown in this study. *Colletotrichum crotalariae-junceae* Sawada, 1959, described on *Crotalaria juncea* in Taiwan, could be a synonym of *C. truncatum* as well: conidia measure 18–26 x 3–4.8 µm; conidia in the drawing resemble those of *C. truncatum* in having long parallel walls from shortly after the base (Sawada, 1959), while those of *C. verruculosum* are shorter and differ in shape. Conidia of *C. gangeticum* Pavgi & U.P. Singh, 1965, described on *Crotalaria medicaginea* in India (Pavgi and Singh 1965), are very small (14.3–17.1 x 2.8–4.3 µm) and have pointed ends and setae are dark brown and broad up to the tip, while conidia of *C. verruculosum* have rounded ends and setae, if brown, become very thin towards the apex (Fig. 16). *Colletotrichum crotalariae* Petch 1917, described on *Crotalaria striata* from Sri Lanka has straight conidia (Saccardo *et al*., 1931) and is regarded as a synonym of *C. coccodes* (Index Fungorum).

Sequences of the six genes studied for *Colletotrichum verruculosum* differ from those of other *Colletotrichum* species with curved conidia from herbaceous plants (Fig. 1). It clusters within a group of species from monocot hosts and is most similar in phylogenetic terms to *C. tofieldiae*, but the conidia are verruculose as the name suggests. Additionally, setae formed on *Anthriscus* stem are often hyaline and and appressoria are solitary and have a rather simple shape, while the four closely related species *C. liriopes*, *C. tofieldiae*, *C. lilii* and *C. spaethianum* have strongly crenate and/or strongly lobed appressoria.

Discussion

While graminicolous species with curved conidia have few morphological features for differentiation (Crouch *et al*., 2009a), species from herbaceous hosts differ not only in shape

and size of appressoria, but also in shapes of conidia and conidiophores, chlamydospores, setae and colony growth. In some cases it is possible to identify species with some confidence based on morphological features and knowledge of the host plant, but many of the differential characters are subtle and the majority of the species studied only show limited host specificity. The apparent host preferences for species based on the strains studied may be artefactual and subject to sampling bias.

The large degree of infraspecific morphological variation in comparison to differences between species may partially be due to strain variability (colony colour, aerial mycelium and sporulation, size of conidia) which result at least partly from degeneration during repeated subculturing; the strains used here range up to 88 years old with an unknown frequency of transferral especially in the early years. Even freshly collected strains differ significantly, and there is evidence (e.g. Guerber and Correll, 2001) in other *Colletotrichum* species of small genetic change resulting in large cultural differences. Because of the high variability of the morphological features, even in this group, the most certain identification is by sequencing of at least one of the genes used here in addition to ITS.

Since many previous descriptions of *C. dematium* and other *Colletotrichum* species with curved conidia are uninformative and sampling has rarely been adequate before the description of new taxa, the assumption by many plant pathologists has been that host identity is a key diagnostic feature. This means that the applied literature is peppered with accounts of diseases caused by *Colletotrichum* species with the causal organism identified only (or almost only) by the host. This lack of investment over the years in diagnostic systems has now led to a situation where a high proportion of published literature on *Colletotrichum* must be interpreted with extreme caution. A good recent example of this is the confusion caused by misidentification of the Canadian strains from lentil described above in the account of *C. truncatum*, but this is only one of a whole series of situations where good science is let down by what is subsequently found to be inaccurate identification. Recent molecular tools are of very substantial use in untangling these confusions.

The interpretation of host specificity in *Colletotrichum* may be more appropriately addressed using information on pathogenicity rather than simple occurrence; this is clearly the case for endophytic strains where the identity of the host may be incidental (e.g. Lu *et al*., 2004). Our studies indicate that all (or almost all) strains of *Colletotrichum* with curved conidia causing leaf spot of *Hedera* species are referable to *C. trichellum*, those causing disease of spinach and sugar beet are almost certainly *C. spinaciae* and those causing disease of onion bulbs are likely to be *C. circinans*. However, in many, if not most cases of apparent host specificity a proportion of strains are found associated with the "wrong" host. In some instances this may be linked to the ease with which *Colletotrichum* species survive in soil and may subsequently cause non-debilitating infections of subsequent crops, but we are not aware of research that documents this process in any detail. Other species of *Colletotrichum* (notably *C. lineola*, *C. dematium*, and *C. truncatum*) occur on many different hosts and at least in some cases include strains that are pathogenic to quite unrelated plants. We are now starting to understand species of *Colletotrichum* in phylogenetic terms, but much remains to be studied in terms of the variety of host-pathogen interactions.

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