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Japanese species of *Alternaria* and their species boundaries based on host range

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Abstract: To clarify the diversity of plant-parasitic *Alternaria* species in Japan, diseased samples were collected, and fungal isolates established in culture. We examined 85 isolates representing 23 species distributed in 14 known sections based on conidial morphology and DNA phylogeny. Three species were found to be new, *A. cylindrica, A. paragomphrenae* and *A. triangularis*. Furthermore, a lectotype was designated for *A. gomphrenae*, and epitypes for *A. cinerariae*, *A. gomphrenae*, *A. iridicola*, and *A. japonica*. Species boundaries of isolates were also clarified by studying phenotypes and determining host ranges. *Alternaria gomphrenae* and related species in sect. *Alternantherae* were recognized as distinct species owing to their host specificity. Among the species infecting *Apiaceae*, the pathogenicity of *A. cumini* and a novel species, *A. triangularis* ex *Bupleurum*, were confirmed as host specific. Another novel species, *A. cylindrica,* proved to be host specific to *Petunia*. *Alternaria iridicola* was recognized as a large-spored species in sect. *Alternaria*, being host specific to *Iris* spp. On the other hand, the experimental host ranges of three morphologically and phylogenetically distinct species infecting *Brassicaceae* (*A. brassicae*, *A. brassicicola*, and *A. japonica*) showed almost no differences. *Alternaria brassicicola* and *A. porri* were even found on non-host plants. In general, host ranges of *Alternaria* species correlated with morphology and molecular phylogeny, and combining these datasets resulted in clearer species boundaries.

INTRODUCTION

Alternaria is a genus in the phylum *Ascomycota* (*Pleosporaceae*, *Pleosporales*) characterized by phaeodictyospores or phaeophragmospores (Seifert *et al.* 2011), and is one of the most ubiquitous fungal genera, inhabiting nearly every environmental substrate (atmosphere, soil, litter, and living plants) (Guo *et al.* 2004, Kirk *et al.* 2008). They are often allergenic, and can cause mycoses in humans and insects (Rossmann *et al.* 1996, Christias *et al.* 2001, Downs *et al.* 2001), but most species are plant pathogenic (Yu 2001). *Alternaria* species usually cause leaf spot diseases, especially on vegetables and ornamental flowers. However, it is their seed-borne phase that carries the greatest economic importance (Groves & Skolko 1944, Neergaard 1945, Richardson 1990, Tohyama 1993, Rathod 2012).

Alternaria was established and originally typified by *Alternaria tenuis*, and was redefined as a genus related to *Stemphylium* and *Ulocladium* based on its mode of conidiogenesis (Simmons 1967). Two additional genera, *Embellisia* and *Nimbya*, were subsequently established by Simmons (1971, 1989). The taxonomy of *Alternaria* and allied genera was previously based on conidial morphology, sporulation patterns, and differences in their host plants (mostly at the rank of genus) or substrates (Simmons 2007). However, their morphological variation and fundamental pleomorphism complicated species recognition, and thus host plants played a key role in identification. Due to their ubiquitous nature, this approach led to a false inflation of species numbers, resulting in the genus containing more than 400 species (Nishikawa & Nakashima 2015, Lawrence *et al.* 2016). The introduction of a molecular phylogenetic approach has again helped to clarify their taxonomy, reducing many allied genera into one large genus, *Alternaria* (Woudenberg *et al.* 2013).

Despite the application of molecular phylogenetic analyses, the relationship between taxonomy and plant parasitism remain insufficient to aid the practical recognition of species boundaries, and additional characterization is needed. Many of the phylogenetic species described by Woudenberg *et al*. (2013) were defined without morphological and pathological features able to distinguish closely related species. Therefore, we proposed an integrated species recognition based on morphology, molecular phylogeny, and pathogenicity (Nishikawa & Nakashima 2013). In our previous studies, it was suggested that phenotyping combined with a clarification of the host range via inoculation studies was helpful to resolve species boundaries (Nishikawa & Nakashima 2013, 2015).

During the survey of Japanese species of *Alternaria*, we collected and examined 85 isolates, and applied the integrated species recognition method to all Japanese species. The present study focused on biodiversity and the utility of phenotyping based on systematic experimental host range determination by inoculation tests. In addition, morphological observations and phylogenetic analyses were conducted to distinguish closely related species infecting *Amaranthaceae*, *Apiaceae*, *Brassicaceae*, *Iridaceae*, and *Solanaceae*.

MATERIALS AND METHODS

Fungal collection and isolation

The 85 isolates examined in the present study were obtained from diseased leaves, stems, buds, rhizomes, and seeds of various plants on the basis of field surveys in Japan from 2002 to 2018 (Table 1). Some of the isolates and specimens were obtained from the culture collection at the Genetic Resources Center of the National Agriculture and Food Research Organization (NARO; MAFF), Tsukuba, Japan, and several collaborators who assisted in the acquisition of these specimens are mentioned in the acknowledgements. To establish axenic cultures originating from single conidia, alternarioid conidia from lesions were suspended in sterilized distilled water and spread on 2 % water agar (WA) medium using a flame-sterilized microspatula. After incubation at 20 °C for 24 h, individual germinating conidia were transferred to potato-carrot agar (PCA; Simmons 2007) using a flame-sterilized microtube under a dissecting microscope at ×100 magnification (Nakashima *et al.* 2011). Deposits of the representative isolates from the present study were made in NARO and Mie University (MUCC), Tsu, Mie, Japan. Specimens, including holotype and epitype specimens were deposited in TNS (National Museum of Nature and Science), Tsukuba, Ibaraki, Japan, and/or in TSU (Mie University).

Morphological observation and culture characteristics

For microscopic observations of diagnostic morphology comparable to those of Simmons's standard conditions (2007), sporulation was induced according to methods reported by Nishikawa & Nakashima (2013). After incubation of the isolates at 25 °C in the dark for 7 d on PCA and V8 juice agar (V8; Simmons 2007), the growing colonies were scratched with a flame-sterilized microspatula and the aerial mycelia were removed to observe sporulation. Treated colonies in unsealed Petri dishes were incubated for 12–24 h at 25 °C under blacklight blue fluorescent lamps to induce sporulation, and then the plates were transferred to 20 °C in the dark. Caespituli that formed on the medium 7 d after incubation were mounted with Shear's mounting fluid [300 mL aqueous potassium acetate (2 %), 120 mL glycerin, and 180 mL ethanol (95 %)]. The morphology of 100 conidia and other structures, such as conidiophores and chlamydospores, were examined at ×400 magnification, and sporulation patterns were also observed under a compound microscope. Morphological descriptions were made for examined isolates based on both media; however small-spored species (mostly in sect. *Alternaria*) were based on PCA, and large-spored species (mostly in sect. *Porri*) were based on V8 according to their comparable descriptions in Simmons (2007).

Mycelial discs of 85 isolates were plated onto potato-dextrose agar (PDA; 200 g potato, 20 g dextrose, and 20 g agar in 1.0 L distilled water) plates. The diameter of each of five colonies was measured after incubation in the dark for 7 d at 25 °C, and the mean diameters for a species were calculated with 95 % confidence intervals. Culture characteristics were also rated using the charts of Rayner (1970).

To induce sexual reproduction in our collected species, we applied the rice straw agar (RSA) method reported by Tanaka & Harada (2003). Rice straws 4–5 cm long were soaked in distilled water in a glass vial, autoclaved, and then three pieces of each straw were placed on WA. Mycelial discs of each isolate were plated and pre-incubated at 20 °C in the dark for 2 wk. To induce the production of ascomata, the plates were transferred and incubated under blacklight blue fluorescent lamp irradiation for 3 mo.

DNA extraction and phylogenetic analyses

An UltraClean Microbial DNA isolation kit (MoBio Laboratories, Carlsbad) was used to conduct DNA extraction according with manufacturer's instructions. PCR amplification and sequencing of the rDNA internal transcribed spacer (ITS) region, glyceraldehyde-3-phosphate dehydrogenase (*gapdh*), RNA polymerase second largest subunit (*rpb2*), translation elongation factor 1-alpha (*tef1*), actin (*act*), Alternaria major allergen (*Alt a 1*), and endopolygalacturonase (*endoPG*) genes were conducted at the Mie University Advanced Science Research Promotion Center, according to the procedure described in previous studies (Nishikawa & Nakashima 2013, 2015, 2019). All the newly determined sequences were deposited in the DNA Data Bank of Japan (DDBJ) (Table 2). Complementary strands of the sequences were assembled and concatenated in MEGA v. 7 (Kumar *et al.* 2016) and were aligned using MAFFT v. 7 (Katoh *et al.* 2017; http://mafft.cbrc.jp/alignment/server/index.html). Sequence alignments were deposited in TreeBASE under number S24554.

To analyze the relationships between Japanese isolates and existing species, and to correctly classify them in *Alternaria* sections following Woudenberg *et al*. (2013), maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) analyses were conducted using a combined dataset composed of 80 *gapdh*, *rpb2*, and *tef1* sequences generated from our collected Japanese isolates and other sequences from GenBank (Table 2). Maximum parsimony analyses were performed in PAUP v. 4.0b10 (Swofford 2003) using heuristic searches, each of which consisted of 100 random sequence additions and a tree-bisection-reconnection (TBR) algorithm for branch swapping. All the characters were unordered and unweighted, with alignment gaps treated as missing data. Clade robustness of the obtained trees was assessed using 1 000 bootstrap (BS) replications (Felsenstein 1985). Tree scores, including tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI), were calculated. Maximum likelihood analyses were performed in RAxML-NG v. 0.6.0 BETA (Kozlov *et al.* 2018) using the GTR+FO+G model as the nucleotide substitution model and 100 BS replicates. Bayesian inference analyses were performed in BEAST v. 2.5.1 (Bouckaert *et al.* 2014). A nucleotide substitution model TN93 was selected by Kakusan4 software (Tanabe 2011). To estimate the posterior probabilities (PPs) of tree topologies, Metropolis-Coupled Markov Chain Monte Carlo searches (MCMCMC) were run for 30 M generations with trees sampled and saved every 1 000 generations until the average standard deviation of split frequencies reached 0.01 (stop value), which generated 18 001 trees from which the initial 12 000 trees were discarded as burn-in based on the effective sample size (ESS) calculated by Tracer v. 1.7.1 software package (Rambaut *et al.* 2018). After discarding, PPs were determined from the remaining trees. Sequences of *Paradendryphiella salina* (= *E. annulata*) (CBS 302.84) were used as the outgroup.

To evaluate the validity of ITS as the fungal barcoding gene for *Alternaria*, and to find phylogenetic species boundaries via multi-locus phylogeny, MP, ML, and BI analyses were conducted separately with the ITS dataset, which was composed of 74 sequences generated from our collected Japanese isolates and other sequences from GenBank (Table 2). Maximum parsimony analyses were performed in PAUP v. 4.0b10, with the same procedure and settings. Maximum likelihood analyses were performed in RAxML v. 8.1.17 (Stamatakis 2014), using the GTR+GAMMA model as the nucleotide substitution model and 100 BS replicates. Bayesian inference analyses were performed in BEAST v. 2.5.1, with the HKY+GAMMA model selected by Kakusan4. To estimate the PPs of tree topologies, MCMCMC were run for 20 M generations with trees sampled and saved every 1 000 generations. After discarding the initial 10 000 trees as burn-in, PPs were determined from the remaining trees. Sequences of *P. salina* were used as the outgroup.

To analyze the detailed relationships between Japanese isolates within sect. *Alternaria*, MP, ML, and BI analyses were conducted using a combined dataset of *act*, *Alt a 1*, *endoPG*, *gapdh*, *rpb2*, and *tef1* sequences, which was composed of nine sequences generated from our collected Japanese isolates and other sequences from GenBank (Table 2). Maximum parsimony and ML analyses were performed in PAUP v. 4.0b10 and RAxML v. 8.1.17, respectively, using the same procedure and settings used for ITS analyses. Bayesian inference analyses were performed in BEAST v. 2.5.1 with the GTR+GAMMA model selected by Kakusan4. To estimate the PPs of tree topologies, MCMCMC were run for 10 M generations with trees sampled and saved every 1 000 generations, which generated 9 001 trees from which the initial 1 000 trees were discarded as burn-in. After discarding, PPs were determined from the remaining trees. Sequences of the Japanese isolate of *A. nobilis* (AC1) were also used as the outgroup. The generated trees were printed with FigTree v. 1.4.2 (Institute of Evolutionary Biology, University of Edinburgh, http://tree.bio.ed.ac.uk/software/figtree).

Inoculation tests

To determine the experimental host range of the obtained isolates, conidia produced on V8 medium as described above were washed with sterile distilled water containing 0.02 % polyoxyethylene (20) sorbitan monolaurate (Wako Pure Chemicals, Osaka), and used as inocula (Nishikawa & Nakashima 2013). The concentration of each conidial suspension was adjusted using a hemocytometer, and then each inoculum was sprayed onto mature leaves of potted plants (at least three replicates) until run-off. Closely related plant species from the same family as the original host source of each *Alternaria* species were also inoculated. Furthermore, the unrelated plant species recorded as hosts were also inoculated to confirm potential host species, and to define host range boundaries of *Alternaria* species. Control plants were prepared and sprayed with sterile distilled water. All the inoculated plants were maintained in an incubator under moist conditions at 20 °C.

Virulent phenotypes were evaluated 7 d post-inoculation (dpi) using the index described by Chaerani *et al.* (2007) (0: no visible leaf lesions; 1: up to 10 % of leaf area affected; 2: 11–25 % of leaf area affected; 3: 26–50 % of leaf area affected; 4: 51–75 % of leaf area affected; and 5: more than 75 % of leaf area affected or the leaf abscised), and the means for each inoculated plant species were calculated as disease severity with 95 % confidence intervals. Given the importance of epidemiology to the obtained results, we also focused on whether sporulation was present or absent on the host lesions. Consequently, pathogenicity of examined isolates was determined by the disease severity, symptom, and sporulation on lesions to evaluate host ranges more accurately. Inoculated plants showing no symptoms within 7 dpi were observed continuously until 30 dpi.

Among sect. *Alternantherae*, two species on *Gomphrena*, namely *A. gomphrenae* and MAFF 246768 (*A. paragomphrenae*), were examined to determine host preference within *Amaranthaceae*, and differential plants for both species compared with those of allied taxa in this section. Three species on *Brassicaceae*, which were known to be polyphyletic and morphologically distinguishable from each other (Simmons 2007, Woudenberg *et al*. 2013), were inoculated onto 13 species of *Brassicaceae* (with two varieties of *Brassica oleracea* and four subspecies of *B. rapa*) to compare their host range. Moreover, previously recorded non-*Brassicaceae* host plants, *e.g. Cucumis* and *Beta* for *A. brassicae* (Simmons 2007), including that of closely related species, namely *Solanum* for *A. mimicula*, were also used to verify their validity as true hosts. *Alternaria cumini* and MAFF 246776 (*A. triangularis*) were inoculated onto 13 host species of *Apiaceae*, including *Bupleurum,* comparing the host range of the other pathogenic species on this family. MAFF 246770 (*A. cylindrica*) was inoculated onto *Petunia* and six species of *Solanaceae* to determine its host range compared to those of *A. crassa* and *A. solani*. *Vigna* and *Zea*, which are recorded as host species of *Prathoda longissima* (= *A. longissima*) (Deighton *et al.* 1698), were also used to examine conspecificity with the previously reported pathogen identified as *A. longissima* in Japan (Takano 2005). Two isolates of *A. iridicola* were examined to reveal their host range within *Iridaceae,* including *Gladiolus* and *Iris ensata*, which are additional natural hosts recorded in Korea (Yu 2001), and one of the original host species of *A. iridiaustralis* recorded in China (Luo *et al*. 2018), respectively. Two non-*Iridaceae* species were additionally inoculated because one of these, *Allium*, was regarded as susceptible by Elliot (1917). In addition, *A. porri*-like large-spored isolates obtained from *Calibrachoa* (AC6), *Eustoma* (MUCC 1702), and *Viola* (AC2) were inoculated on each original host and related plant species as well as *Allium* to identify these miscellaneous isolates. Koch’s postulates were also tested for the three novel species described in this study.

RESULTS

Molecular phylogeny

The combined alignment of the *gapdh*, *rpb2*, and *tef1* datasets contained 189 sequences with a total of 1 567 characters. PCR amplification and sequencing from six Japanese isolates, *e.g.* the *gapdh* sequence of *A. petroselini* MAFF 243057, were unsuccessful. The topologies of the resulting trees from MP, ML, and BI analyses were congruent, and Fig. 1 shows the ML tree with BS values (MP and ML) and Bayesian PP. The Japanese *Alternaria* isolates examined were divided into 14 sections and two monotypic lineages as strongly supported clades; The Japanese isolate of *A. petroselini* clustered with species of sect. *Radicina* based on ITS, *tef1*, *rpb2*, *Alt a 1*, and *act*, respectively (data not shown). Five Japanese species clustered respectively in sect. *Alternaria* and *Porri*, and three species in sect. *Alternantherae*.

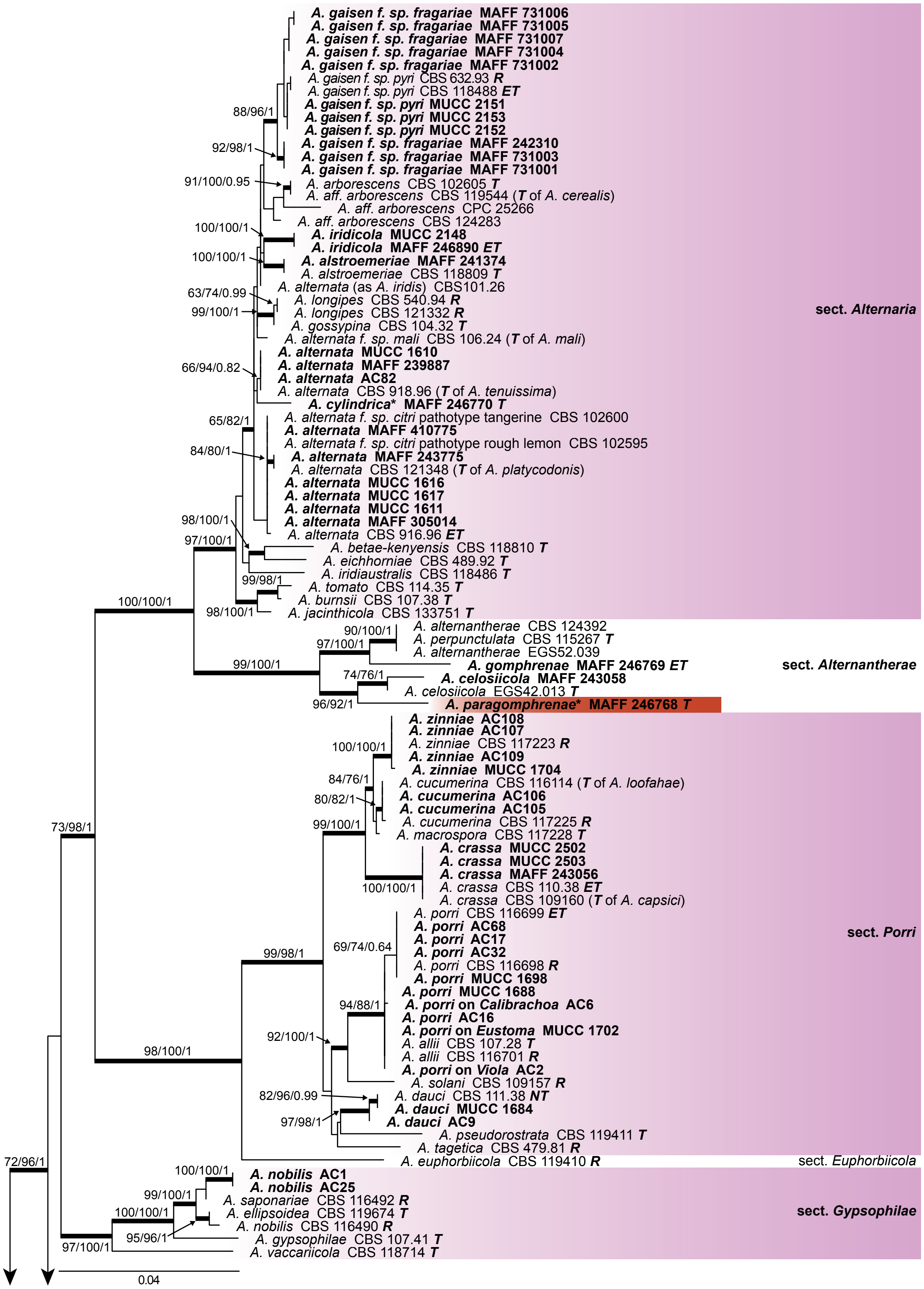

Fig. 1. Maximum likelihood (ML) tree based on the combined dataset of *gapdh*, *rpb2*, and *tef1* sequences from Japanese *Alternaria* isolates. The tree was rooted to *Paradendryphiella salina* (CBS 302.84). Maximum parsimony (MP) and ML bootstrap values and Bayesian posterior probabilities (PP) are given near branches (MP/ML/PP). Thickened nodes indicate significant support by MP/ML/PP (> 70/70/0.95). The scale bar indicates the number of nucleotide substitutions per site. Japanese isolates examined are indicated in bold, and the statuses of reference isolates are indicated in bold and italic. *T*: ex-type, *NT*: ex-neotype, *ET*: ex-epitype, *R*: representative strain assigned by Simmons (2007). Names of sections and monotypic lineages (MTL) for each taxon are given in the right column, and the Japanese isolates examined in the study are also indicated in bold. Resolved novel taxa with an asterisk were indicated as red shadings.

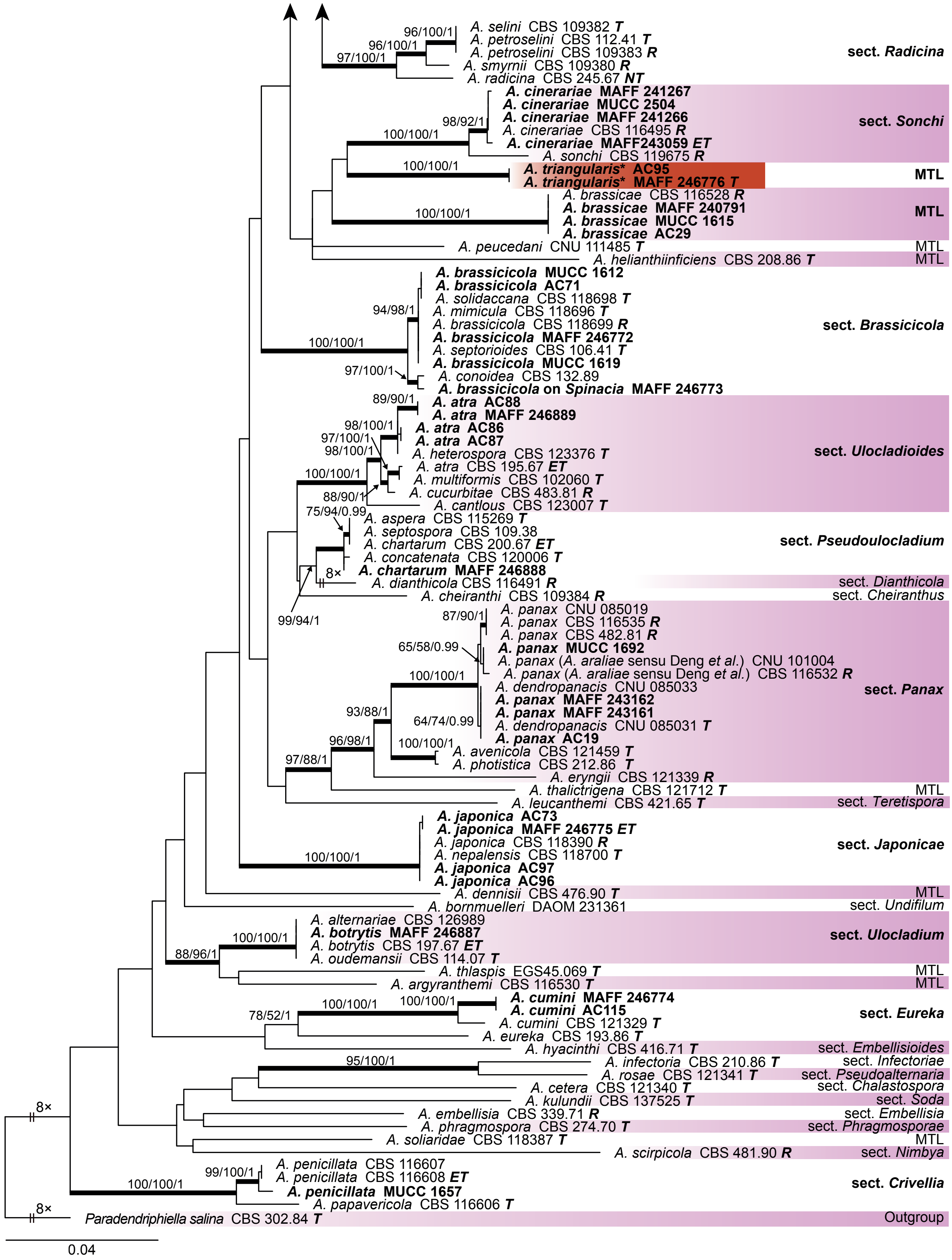

Fig. 1. (Continued).

Table 1. Isolates of Japanese species of *Alternaria* obtained in this study.

Fungal name	***Alternaria*** **section**	Strain number$^{1, 2}$	Host plant	Location; year
Alternaria alstroemeriae	*Alternaria*			
		MAFF 241374	*Alstroemeria* sp.	Nagano Pref., Matsumoto; 2008
Alternaria alternata	*Alternaria*			
		MAFF 239887	*Vigna radiata*	unknown (Japan); 1998
		MUCC 1610	*Impatiens hawkeri*	Nagano Pref., Azumino; 2006
		MUCC 1611	*Antirrhinum majus*	Shizuoka Pref., Kakegawa; 2008
		MUCC 1616	*Pelargonium hortorum*	Kanagawa Pref. Nakai; 2004
		MUCC 1617	*Primula × polyantha*	Shizuoka Pref., Kakegawa; 2004
		AC82	*Solanum lycopersicum*	Shizuoka Pref., Kakegawa; 2011
		MAFF 243775	*Vigna radiata*	Tokyo, Chiyoda; 2012
		MAFF 305014	*Pyrus aromatica*	Kanagawa Pref.; 1958
		MAFF 410775	Unknown (*Pyrus*?)	Unknown (Japan)
Alternaria atra	*Ulocladioides*			
		AC86	*Raphanus sativus*	Tokyo, Setagaya; 2000
		AC87	*Brassica oleracea* var. *capitata*	Tokyo, Setagaya; 2001
		AC88	*Brassica rapa* subsp. *pekinensis*	Tokyo, Setagaya; 2001
		MAFF 246889	*Allium fistulosum*	Tokyo, Setagaya; 2001
Alternaria botrytis	*Ulocladium*			
		MAFF 246887	*Asparagus officinalis*	Shizuoka Pref., Kakegawa; 2008
Alternaria brassicae				
		AC29	*Brassica rapa*	Shizuoka Pref., Kakegawa; 2006
		MAFF 240791	*Raphanus sativus*	Ibaraki Pref., Tsukuba; 2007
		MUCC 1615	*Raphanus sativus*	Chiba Pref. Narita; 2009
Alternaria brassicicola	*Brassicicola*			
		MAFF 246772 = MUCC 1694	*Brassica oleracea* var. *sabellica*	Shizuoka Pref., Kakegawa; 2003
		MAFF 246773	*Spinacia oleracea*	Tokyo, Setagaya; 2002
		MUCC 1612 = AC56	*Brassica rapa* subsp. *pekinensis*	Shizuoka Pref., Kakegawa; 2008
		MUCC 1619 = AC70	*Raphanus sativus*	Tokyo, Setagaya; 2000
		AC71	*Raphanus sativus*	Tokyo, Setagaya; 2000
		AC72	*Brassica oleracea* var. *italica*	Tokyo, Setagaya; 2001
Alternaria celosiicola	*Alternantherae*			
		MAFF 243058	*Celosia argentea* var. *plumosa*	Kanagawa Pref., Fujisawa; 2006
Alternaria chartarum	*Pseudoulocladium*			
		MAFF 246888	*Capsicum annuum*	Tokyo, Setagaya; 2000
Alternaria cinerariae	*Sonchi*			
		MAFF 243059 = MUCC 1701$^{\mathrm{ET}}$	*Pericallis cruenta*	Chiba Pref., Narita; 2002
		MAFF 241266 = MUCC 1613	*Farfugium japonicum*	Ibaraki Pref., Tsukuba; 2008
		MAFF 241267 = MUCC 1614	*Gynura bicolor*	Ibaraki Pref., Tsukuba; 2008
		MUCC 2504	*Jacobaea maritima*	Kanagawa Pref., Atsugi; 2017
Alternaria crassa	*Porri*			
		MAFF 243056	*Datura stramonium*	Tokyo, Kodaira; 2000

Table 1. (Continued).

Fungal name	*Alternaria* section	Strain number[1, 2]	Host plant	Location; year
		MUCC 2502 = 12-M0180	*Datura fastuosa*	Tokyo, Kodaira; 2012
		MUCC 2503 = 12-M0099	*Datura inoxia*	Tokyo, Kodaira; 2012
Alternaria cucumerina	*Porri*			
		AC105	*Cucurbita maxima*	Niigata Pref., Sado; 2010
		AC106	*Cucurbita maxima*	Niigata Pref., Sado; 2010
Alternaria cumini	*Eureka*			
		MAFF 246774	*Cuminum cyminum*	Shizuoka Pref., Kakegawa; 2012
		AC115	*Cuminum cyminum*	Shizuoka Pref., Kakegawa; 2013
*Alternaria cyrindrica**	*Alternaria*			
		MAFF 246770^{T}	*Petunia* × *atkinsiana*	Shizuoka Pref., Kakegawa; 2006
Alternaria dauci	*Porri*			
		MUCC 1684	*Daucus carota*	Shizuoka Pref., Kakegawa; 1998
		AC9	*Daucus carota*	Shizuoka Pref., Kakegawa; 1998
Alternaria gaisen f. sp. fragariae	*Alternaria*			
		MAFF 242310 = MUCC 1609	*Fragaria* × *ananassa* 'HS-138'	Hokkaido, Esashi; 2007
		MAFF 731001	*Fragaria* × *ananassa* 'Morioka-16'	Iwate Pref., Morioka; 1975
		MAFF 731002	*Fragaria* × *ananassa* 'Morioka-16'	Iwate Pref., Morioka; 1975
		MAFF 731003	*Fragaria* × *ananassa* 'Morioka-16'	Iwate Pref., Morioka; 1975
		MAFF 731004	*Fragaria* × *ananassa* 'Morioka-16'	Iwate Pref., Morioka; 1975
		MAFF 731005	*Fragaria* × *ananassa* 'Morioka-16'	Iwate Pref., Morioka; 1975
		MAFF 731006	*Fragaria* × *ananassa* 'Morioka-16'	Iwate Pref., Morioka; 1975
		MAFF 731007	*Fragaria* × *ananassa* 'Morioka-16'	Iwate Pref., Morioka; 1975
Alternaria gaisen f. sp. pyri	*Alternaria*			
		MUCC 2151 = 9901A	*Pyrus pyrifolia* var. *culta* 'Nijisseiki'	Tottori Pref., Tohaku; 1999
		MUCC 2152 = 9903A	*Pyrus pyrifolia* var. *culta* 'Nijisseiki'	Tottori Pref., Tohaku; 1999
		MUCC 2153 = 9904C	*Pyrus pyrifolia* var. *culta* 'Nijisseiki'	Tottori Pref., Tohaku; 1999
Alternaria gomphrenae	*Alternantherae*			
		MAFF 246769 = MUCC 1623^{ET}	*Gomphrena globosa*	Shizuoka Pref., Kakegawa; 2011
Alternaria iridicola	*Alternaria*			
		MUCC 2148	*Iris japonica*	Tokyo, Kodaira; 2010
		MAFF 246890 = MUCC 2149^{ET}	*Iris japonica*	Kanagawa Pref., Kamakura; 2013
		MAFF 246771 = MUCC 2501	*Iris japonica*	Shizuoka Pref., Fukuroi; 2018
Alternaria japonica	*Japonicae*			
		AC73	*Raphanus sativus*	Tokyo, Setagaya; 2000
		MAFF 246775 = MUCC 1622^{ET}	*Raphanus sativus*	Tokyo, Setagaya; 2000
		AC96	*Brassica oleracea* var. *italica*	Shizuoka Pref., Kakegawa; 2010
		AC97	*Brassica oleracea* var. *italica*	Shizuoka Pref., Kakegawa; 2010
Alternaria nobilis	*Gypsophilae*			
		AC1	*Dianthus barbatus*	Shizuoka Pref., Kakegawa; 2003

Table 1. (Continued).

Fungal name	*Alternaria* section	Strain number[1, 2]	Host plant	Location; year
		AC25	*Dianthus caryophyllus*	Miyagi Pref., Sendai; 2002
Alternaria panax	*Panax*			
		MUCC 1692 = PFAlt1-1	*Polyscias fruticosa*	Tokyo, Ogasawara (Bonin Is.); 2003
		AC19 = PGAlt1	*Polyscias guilfoylei*	Tokyo, Ogasawara (Bonin Is.); 2003
		MAFF 243161 = MUCC 1625	*Polyscias fruticosa*	Tokyo, Ogasawara (Bonin Is.); 2011
		MAFF 243162 = MUCC 1626	*Polyscias fruticosa*	Tokyo, Ogasawara (Bonin Is.); 2011
*Alternaria paragomphrenae**	*Alternantherae*			
		MAFF 246768 = MUCC 1683^{T}	*Gomphrena haageana*	Shizuoka Pref., Hamamatsu; 2004
Alternaria penicillata	*Crivellia*			
		MUCC 1657	*Papaver nudicaule*	Tokyo, Tachikawa; 2005
Alternaria petroselini	*Radicina*			
		MAFF 243057	*Petroselinum crispum*	Shizuoka Pref., Kakegawa; 2007
Alternaria porri	*Porri*			
		AC2	*Viola × wittrockiana*	Shizuoka Pref., Kakegawa; 2003
		AC6	*Calibrachoa* sp.	Shizuoka Pref., Kakegawa; 2004
		MUCC 1688	*Allium fistulosum*	Shizuoka Pref., Kakegawa; 2004
		AC15	*Allium fistulosum*	Saitama Pref.; 2004
		AC16	*Allium fistulosum*	Gunma Pref., Takasaki; 2005
		AC17	*Allium fistulosum*	Gunma Pref., Takasaki; 2005
		MUCC 1698	*Allium fistulosum*	Gunma Pref., Tomioka; 2006
		AC32	*Allium fistulosum*	Chiba Pref., Mobara; 2006
		MUCC 1702	*Eustoma exaltatum* subsp. *russellianum*	Shizuoka Pref., Kakegawa; 2007
		AC68	*Allium fistulosum*	Tokyo, Setagaya; 2001
*Alternaria triangularis**				
		MAFF 246776^{T}	*Bupleurum rotundifolium*	Kochi Pref., Konan; 2004
		AC95	*Bupleurum rotundifolium*	Shizuoka Pref., Kakegawa; 2004
Alternaria zinniae	*Porri*			
		MUCC 1704	*Zinnia hybrida*	Nagano Pref., Tomi; 2007
		AC107	*Zinnia hybrida*	Nagano Pref., Azumino; 2010
		AC108	*Zinnia elegans*	Shizuoka Pref., Kakegawa; 2011
		AC109	*Zinnia elegans*	Nagano Pref., Azumino; 2011
Alternaria sp.				
	Alternaria	MAFF 305015	*Pyrus aromatica*	Chiba Pref.; 1959

[1] AC: Personal collection of JN; MAFF: Genetic Resources Center, National Agriculture and Food Research Organization, Tsukuba, Japan; MUCC (Japan): Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Japan.

[2] Ex-type and -epitype strain indicated with T and ET, respectively.

* Novel taxa proposed in the taxonomy section.

Table 2. Isolates and their accession numbers for phylogenetic analyses.

			DDBJ/GenBank/EMBL accession numbers^3						
***Alternaria* section**	**Fungal name and isolate numbers^{1,2}**	**Country, host plant**	**ITS**	***gapdh***	***tef1***	***rpb2***	***Alt a 1***	***endoPG***	***act***
Alternantherae	*Alternaria alternantherae* (= *Nimbya alternantherae*)								
	EGS52.039	Unknown, *Alternanthera philoxeroides*?	JN383496	JN383477	JQ672485	–	JN383511	–	JQ671717
	CBS 124392; HSAUP2798	China, *Solanum melongena*	KC584179	KC584096	KC584633	KC584374	KP123846	–	–
	A. celosiicola (= *A. cristata*)								
	MAFF 243058	**Japan, *Celosia argentea* var. *plumosa***	AB678217	AB744033	**LC480205**	**LC476781**	AB744029	–	AB744036
	EGS42.013^T	USA, *Celosia cristata*	JN383497	JN383478	JQ672483	JQ646495	JN383512	–	JQ671716
	A. gomphrenae (= *N. gomphrenae*)								
	MAFF 246769; MUCC 1623^{ET}	**Japan, *Gomphrena globosa***	**LC440579**	**LC481999**	**LC480206**	**LC476782**	–	–	**LC481857**
	*A. paragomphrenae**								
	MAFF 246768; MUCC 1683^T	**Japan, *Gomphrena haageana***	–	**LC482000**	**LC480207**	**LC476783**	**LC481610**	–	**LC481858**
	A. perpunctulata (= *N. perpunctulata*)								
	CBS 115267; EGS51.130^T	USA, *Alternanthera philoxeroides*	KC584210	KC584129	KC584676	KC584418	JQ905111	–	JQ671718
Alternaria	*A. alstroemeriae*								
	MAFF 241374	**Japan, *Alstroemeria* sp.**	AB678214	AB744034	LC275050	LC275231	AB744031	LC276240	AB744038
	CBS 118809; EGS52.068^T	Australia, *Alstroemeria* sp.	KP124297	KP124154	KP125072	KP124765	–	KP123994	–
	A. alternata								
	MAFF 239887	**Unknown, *Vigna radiata***	**LC440580**	**LC482001**	**LC480208**	**LC476784**	**LC481611**	**LC480946**	**LC481859**
	MUCC 1610	**Japan, *Impatiens hawkeri***	LC269968	LC270135	LC275052	LC275233	LC276230	LC276242	**LC481860**
	MUCC 1611	**Japan, *Antirrhinum majus***	**LC440581**	LC270134	LC275051	LC275232	LC276229	LC276241	**LC481861**
	MUCC 1616	**Japan, *Pelargonium hortorum***	LC269969	LC270136	LC275053	LC275234	LC276231	LC276243	**LC481862**
	MUCC 1617	**Japan, *Primula polyantha***	**LC440582**	**LC482002**	–	**LC476785**	**LC481612**	**LC480947**	**LC481863**
	AC82	**Japan, *Solanum lycopersicum***	**LC440583**	**LC482003**	**LC480209**	**LC476786**	**LC481613**	**LC480948**	**LC481864**
	MAFF 243775	**Japan, *Vigna radiata***	**LC164855**	**LC169124**	**LC167147**	**LC476787**	**LC167084**	–	–
	MAFF 305014	**Japan, *Pyrus aromatica***	**LC164847**	**LC482004**	**LC167153**	**LC476788**	**LC481614**	**LC480949**	–
	MAFF 410775	**Japan, unknown (*Pyrus*?)**	**LC164846**	**LC482005**	**LC167155**	**LC476789**	**LC167089**	**LC480950**	–
	CBS 916.96; EGS34.016^{ET}	India, *Arachis hypogaea*	AF347031	AY278808	KC584634	KC584375	AY563301	JQ811978	JQ671702
	CBS 918.96; EGS34.015 (= *A. tenuissima*^{R})	UK, *Dianthus chinensis*	AF347032	AY278809	KC584693	KC584435	AY563302	KP124026	JQ671703
	CBS 121348; EGS50.070 (= *A. platycodonis*^{T})	China, *Platycodon grandiflorus*	KP124367	KP124219	KP125144	KP124836	KP123915	KP124070	–
	CBS 101.26 (as *A. iridis*)	Unknown	–	JQ646313	JQ672475	JQ646482	JQ646396	–	JQ671694
	A. alternata f. sp. citri pathotype rough lemon (= *A. limoniasperae*^{T})								

Table 2. (Continued).

Alternaria section	Fungal name and isolate numbers[1, 2]	Country, host plant	DDBJ/GenBank/EMBL accession numbers[3]						
			ITS	*gapdh*	*tef1*	*rpb2*	*Alt a 1*	*endoPG*	*act*
	CBS 102595; EGS45.100; BMP0316	USA, *Citrus jambhiri*	FJ266476	AY562411	KC584666	KC584408	AY563306	KP124029	JQ671704
	A. alternata f. sp. citri pathotype tangerine (= *A. toxicogenica*^{T})								
	CBS 102600; EGS39.181; ATCC 38963	USA, *Citrus reticulata*	KP124331	KP124186	KP125107	KP124799	KP123880	KP124033	–
	A. alternata f. sp. mali (= *A. mali*^{T})								
	CBS 106.24; EGS38.029; ATCC 13963	USA, *Malus sylvestris*	KP124298	KP124155	KP125073	KP124766	KP123847	AY295020	–
	A. arborescens species complex								
	CBS 102605; EGS39.128; BMP0308^{T} (= *A. alternata* tomato pathotype)	USA, *Solanum lycopersicum*	AF347033	AY278810	KC584636	KC584377	AY563303	AY295028	JQ671705
	CBS 119544; EGS43.072 (= *A. cerealis*^{T})	New Zealand, *Avena sativa*	KP124408	JQ646321	KP125186	KP124878	KP123955	KP124112	JQ671708
	CBS 124283	Russia, *Oryza* sp.	KP124416	KP124267	KP125194	KP124885	KP123963	KP124120	–
	CPC 25266	Austria, *Pyrus* sp.	KP124418	KP124269	KP125196	KP124887	KP123965	KP124122	–
	A. betae-kenyensis								
	CBS 118810; EGS49.159^{T}	Kenya, *Beta vulgaris* var. *cicla*	KP124419	KP124270	KP125197	KP124888	KP123966	KP124123	–
	A. burnsii								
	CBS 107.38; EGS06.185^{T}	India, *Cuminum cyminum*	KP124420	JQ646305	KP125198	KP124889	KP123967	KP124124	JQ671685
	*A. cylindrica**								
	MAFF 246770^{T}	**Japan, *Petunia × atkinsiana***	**LC440584**	**LC482006**	**LC480211**	**LC476791**	**LC481616**	**LC480951**	**LC481867**
	A. eichhorniae								
	CBS 489.92; ATCC 22255^{T}	India, *Eichhornia crassipes*	KC146356	KP124276	KP125204	KP124895	KP123973	KP124130	–
	A. gaisen f. sp. fragariae (= *A. alternata* strawberry pathotype)								
	MAFF 242310; MUCC 1609	**Japan, *Fragaria × ananassa* ‘HS-138’**	LC269973	LC270141	LC275059	LC275239	LC276237	LC276252	**LC481865**
	MAFF 731001	**Japan, *Fragaria × ananassa* ‘Morioka-16’**	LC164854	LC169125	LC167148	LC169131	LC276235	LC276246	–
	MAFF 731002	**Japan, *Fragaria × ananassa* ‘Morioka-16’**	LC164853	LC169126	LC167149	LC169132	LC276236	–	–
	MAFF 731003	**Japan, *Fragaria × ananassa* ‘Morioka-16’**	LC164852	LC169127	LC167150	LC169133	LC167085	LC276247	–
	MAFF 731004	**Japan, *Fragaria × ananassa* ‘Morioka-16’**	LC164851	LC270140	LC167151	LC275238	–	LC276248	–
	MAFF 731005	**Japan, *Fragaria × ananassa* ‘Morioka-16’**	LC164850	LC169128	LC167152	LC169134	LC167086	LC276249	–
	MAFF 731006	**Japan, *Fragaria × ananassa* ‘Morioka-16’**	LC164849	LC169129	LC275057	LC169135	LC167087	LC276250	–
	MAFF 731007	**Japan, *Fragaria × ananassa* ‘Morioka-16’**	LC164848	LC169130	LC275058	LC169136	LC167088	LC276251	–
	A. gaisen f. sp. pyri (= *A. alternata* Japanese pear pathotype)								

Table 2. (Continued).

Alternaria section	Fungal name and isolate numbers$^{1, 2}$	Country, host plant	DDBJ/GenBank/EMBL accession numbers^{3}						
			ITS	*gapdh*	*tef1*	*rpb2*	*Alt a 1*	*endoPG*	*act*
	CBS 118488; EGS90.0391^{ET}	Japan, *Pyrus pyrifolia* var. *culta* 'Nijisseiki'	KP124427	KP124278	KP125206	KP124897	KP123975	KP124132	–
	CBS 632.93; EGS90.0512^{R}	Japan, *Pyrus pyrifolia* var. *culta* 'Nijisseiki'	KC584197	KC584116	KC584658	KC584399	KP123974	AY295033	–
	MUCC 2151; 9901A	**Japan, *Pyrus pyrifolia* var. *culta* 'Nijisseiki'**	LC269970	LC270137	LC275054	LC275235	LC276232	–	–
	MUCC 2152; 9903A	**Japan, *Pyrus pyrifolia* var. *culta* 'Nijisseiki'**	LC269971	LC270138	LC275055	LC275236	LC276233	LC276244	–
	MUCC 2153; 9904C	**Japan, *Pyrus pyrifolia* var. *culta* 'Nijisseiki'**	LC269972	LC270139	LC275056	LC275237	LC276234	LC276245	–
	A. gossypina								
	CBS 104.32^{T}	Zimbabwe, *Gossypium* sp.	KP124430	JQ646312	KP125209	KP124900	JQ646395	KP124135	JQ671693
	A. iridiaustralis								
	CBS 118486^{T}; EGS43.014	Australia, *Iris* sp.	KP124435	KP124284	KP125214	KP124905	KP123981	KP124140	–
	A. iridicola								
	MUCC 2148	**Japan, *Iris japonica***	LC269974	LC270142	LC275060	LC275240	LC276238	LC276253	–
	MAFF 246890; MUCC 2149^{ET}	**Japan, *Iris japonica***	LC269975	LC270143	LC275061	LC275241	LC276239	LC276254	–
	MAFF 246771; MUCC 2501	**Japan, *Iris japonica***	–	–	**LC480210**	**LC476790**	**LC481615**	–	**LC481866**
	A. jacinthicola								
	CBS 133751^{T}	Mali, *Eichhornia crassipes*	KP124438	KP124287	KP125217	KP124908	KP123984	KP124143	–
	A. longipes (= *A. alternata* tobacco pathotype)								
	CBS 540.94; EGS30.033^{R}	USA, *Nicotiana tabacum*	AY278835	AY278811	KC584667	KC584409	AY563304	KP124147	JQ671689
	CBS 121332; EGS30.048^{R}	USA, *Nicotiana tabacum*	KP124443	KP124292	KP125222	KP124913	KP123989	KP124149	–
	A. tomato								
	CBS 114.35	Unknown, *Solanum lycopersicum*	KP124446	KP124295	KP125225	KP124916	KP123992	KP124152	JQ671686
Brassicicola	*A. brassicicola*								
	MAFF 246772; MUCC 1694	**Japan, *Brassica oleracea* var. *sabellica***	**LC440585**	**LC482007**	**LC480212**	**LC476792**	**LC481617**	–	**LC481868**
	MAFF 246773	**Japan, *Spinacia oleracea***	–	**LC482008**	**LC480213**	**LC476793**	**LC481618**	–	**LC481869**
	MUCC 1612; AC56	**Japan, *Brassica rapa* var. *glabra***	**LC440586**	AB862969	AB862981	AB862975	**LC481619**	–	**LC481870**
	MUCC 1619; AC70	**Japan, *Raphanus sativus***	**LC440587**	AB862968	AB862980	AB862974	**LC481620**	–	**LC481871**
	AC71	**Japan, *Raphanus sativus***	**LC440588**	**LC482009**	**LC480214**	**LC476794**	**LC481621**	–	**LC481872**
	CBS 118699; EGS42.002; ATCC 96836^{R}	USA, *Brassica oleracea*	JX499031	KC584103	KC584642	KC584383	–	–	–
	A. conoidea (= *Embellisia conoidea*)								
	CBS 132.89	Saudi Arabia, *Ricinus communis*	FJ348226	FJ348227	KC584711	KC584452	FJ348228	–	JQ671667
	A. mimicula								

Table 2. (Continued).

			DDBJ/GenBank/EMBL accession numbers[3]						
***Alternaria* section**	**Fungal name and isolate numbers[1, 2]**	**Country, host plant**	**ITS**	***gapdh***	***tef1***	***rpb2***	***Alt a 1***	***endoPG***	***act***
	CBS 118696; EGS01.056; BMP0324^{T}	USA, *Solanum lycopersicum*	FJ266477	AY562415	KC584669	KC584411	AY563310	–	JQ671668
	A. septorioides								
	CBS 106.41; EGS52.089^{T}	Netherlands, *Reseda odorata*	KC584216	KC584136	KC584685	KC584427	–	–	–
	A. solidaccana								
	CBS 118698; EGS36.158^{T}	Bangladesh, soil	KC584219	KC584141	KC584690	KC584432	–	–	–
Chalastospora	*A. cetera* (= *Chalastospora cetera*)								
	CBS 121340; CBS 110898; EGS41.072; BMP0033^{T}	Australia, *Elymus scabrus*	JN383482	AY562398	KC584699	KC584441	AY563278	–	JQ671626
Cheiranthus	*A. cheiranthi*								
	CBS 109384; EGS41.188; BMP0148; BMP0148^{R}	Italy, *Cheiranthus cheiri*	AF229457	KC584107	KC584646	KC584387	JQ905106	–	JQ671656
Crivellia	*A. papavericola* (= *Crivellia homothallica, Brachycladium papaveris*)								
	CBS 116606; P351^{T}	USA, *Papaver somniferum*	FJ357310	FJ357298	KC584705	KC584446	JN383501	–	JQ671608
	A. penicillata (= *Cr. papaveracea, B. penicillatum*)								
	MUCC 1657	**Japan, *Papaver nudicaule***	**LC440589**	**LC482010**	**LC480215**	**LC476795**	–	–	–
	CBS 116608; P354.8^{ET}	Austria, *Papaver rhoeas*	FJ357311	FJ357299	KC584698	KC584440	JN383502	–	JQ671609
	CBS 116607; P354.1	Austria, *Papaver rhoeas*	KC584229	KC584153	KC584706	KC584447	–	–	–
Dianthicola	*A. dianthicola*								
	CBS 116491; EGS51.022^{R}	New Zealand, *Dianthus* × *allwoodii*	KC584194	KC584113	KC584653	KC584394	–	–	–
Embellisia	*A. embellisia* (= *E. allii*)								
	CBS 339.71^{R}	USA, *Allium sativum*	KC584230	KC584155	KC584708	KC584449	–	–	–
Embellisioides	*A. hyacinthi* (= *E. hyacinthi*)								
	CBS 416.71; EGS19.102^{T}	Netherlands, *Hyacinthus orientalis*	KC584233	KC584158	KC584716	KC584457	–	–	–
Euphorbiicola	*A. euphorbiicola*								
	CBS 119410; EGS41.029^{R}	USA, *Euphorbia pulcherrima*	KJ718173	KJ718018	KJ718521	KJ718346	–	–	–
Eureka	*A. cumini*								
	MAFF 246774	**Japan, *Cuminum cyminum***	**LC440590**	**LC482011**	**LC480216**	**LC476796**	**LC481622**	–	**LC481873**
	AC115	**Japan, *Cuminum cyminum***	**LC440591**	**LC482012**	**LC480217**	**LC476797**	**LC481623**	–	–
	CBS 121329; EGS04.1581^{T}	India, *Cuminum cyminum*	KC584191	KC584110	KC584650	KC584391	–	–	–
	A. eureka (= *E. eureka*)								

Table 2. (Continued).

			DDBJ/GenBank/EMBL accession numbers[3]						
***Alternaria* section**	**Fungal name and isolate numbers[1, 2]**	**Country, host plant**	**ITS**	***gapdh***	***tef1***	***rpb2***	***Alt a 1***	***endoPG***	***act***
	CBS 193.86; EGS36.103^{T}	Australia, *Medicago rugosa*	JN383490	JN383471	KC584715	KC584456	JN383507	–	JQ671596
Gypsophilae	*A. ellipsoidea*								
	CBS 119674; EGS49.104^{T}	USA, *Dianthus barbatus*	KC584196	KC584115	KC584655	KC584396	–	–	–
	A. gypsophilae								
	CBS 107.41; EGS07.025^{T}	Unknown, *Gypsophila elegans*	KC584199	KC584118	KC584660	KC584401	KJ718688	–	JQ671682
	A. nobilis								
	AC1	**Japan, *Dianthus barbatus***	**LC440592**	**LC482013**	**LC480218**	**LC476798**	**LC481624**	**LC480952**	**LC481874**
	AC25	**Japan, *Dianthus caryophyllus***	**LC440593**	**LC482014**	**LC480219**	**LC476799**	–	–	–
	CBS 116490; EGS51.027^{R}	New Zealand, *Dianthus caryophyllus*	KC584208	KC584127	KC584673	KC584415	JQ646385	–	JQ671680
	A. saponariae								
	CBS 116492; EGS49.199^{R}	USA, *Saponaria officinalis*	KC584215	KC584135	KC584683	KC584425	–	–	–
	A. vaccariicola								
	CBS 118714; EGS46.003^{T}	USA, *Vaccaria hispanica*	KC584224	KC584147	KC584697	KC584439	JQ646384	–	JQ671679
Infectoriae	*A. infectoria*								
	CBS 210.86; EGS27.193^{T}	UK, *Triticum aestivum*	AF347034	AY278793	KC584662	KC584404	FJ266502	–	JQ671629
Japonicae	*A. japonica*								
	AC73	**Japan, *Raphanus sativus***	**LC440594**	**LC482015**	**LC480220**	**LC476800**	**LC481625**	–	**LC481875**
	MAFF 246775; MUCC 1622^{ET}	**Japan, *Raphanus sativus***	**LC440595**	**LC482016**	**LC480221**	**LC476801**	**LC481626**	–	**LC481876**
	AC96	**Japan, *Brassica oleracea* var. *italica***	**LC440596**	**LC482017**	**LC480222**	**LC476802**	**LC481627**	–	**LC481877**
	AC97	**Japan, *Brassica oleracea* var. *italica***	**LC440597**	**LC482018**	**LC480223**	**LC476803**	**LC481628**	–	**LC481878**
	CBS 118390; EGS50.099^{R}	USA, *Brassica chinensis*	KC584201	KC584121	KC584663	KC584405	–	–	–
	A. nepalensis								
	CBS 118700; EGS45.073^{T}	Nepal, *Brassica* sp.	KC584207	KC584126	KC584672	KC584414	–	–	–
Nimbya	*A. scirpicola* (= *N. scirpicola*)								
	CBS 481.90; EGS19.042^{R}	UK, *Scirpus* sp.	KC584237	KC584163	KC584728	KC584469	–	–	–
Panax	*A. avenicola*								
	CBS 121459; EGS50.185^{T}	Norway, *Avena* sp.	KC584183	KC584100	KC584639	KC584380	–	–	–
	A. dendropanacis								
	CNU 085031^{T}	Korea, *Dendropanax morbifer*	HQ203210	KF516506	KP877992	KP877985	KF516492	–	–
	CNU 085033	Korea, *Aralia elata*	–	KF516507	KP877993	KP877986	KF516493	–	–
	A. eryngii								

Table 2. (Continued).

Alternaria section	Fungal name and isolate numbers^{1,2}	Country, host plant	DDBJ/GenBank/EMBL accession numbers^{3}						
			ITS	*gapdh*	*tef1*	*rpb2*	*Alt a 1*	*endoPG*	*act*
	CBS 121339; EGS41.005; BMP0336^{R}	Unknown, *Eryngium* sp.	JQ693661	AY562416	KC584656	KC584397	AY563313	–	JQ671670
	A. panax								
	MUCC 1692; PFAlt1-1	**Japan, *Polyscias fruticosa***	–	**LC482019**	**LC480224**	**LC476804**	–	–	–
	AC19; PGAlt1	**Japan, *Polyscias guilfoylei***	**LC440598**	**LC482020**	**LC480225**	**LC476805**	–	–	–
	MAFF 243161; MUCC 1625	**Japan, *Polyscias fruticosa***	**LC440599**	AB862972	AB862984	AB862978	–	–	–
	MAFF 243162; MUCC 1626	**Japan, *Polyscias fruticosa***	**LC440600**	**LC482021**	**LC480226**	**LC476806**	–	–	–
	CBS 482.81; EGS29.180^{R}	USA, *Aralia racemosa*	KC584209	KC584128	KC584675	KC584417	JQ646382	–	JQ671672
	CBS 116532; EGS46.157^{R} [as *A. araliae* in Deng *et al.* (2015)]	New Zealand, *Meryta sinclairii*	JF417549	JF417630	JX213321	JF417657	JX213285	–	–
	CBS 116535; EGS48.124^{R}	USA, *Panax quinquefolius*	JF417562	JF417643	JX213334	JF417670	JX213298	–	–
	CNU 085019	Korea, *Panax ginseng*	–	KF516502	KP877988	KP877981	KF516488	–	–
	CNU 101004 [as *A. araliae* in Deng *et al.* (2015)]	Korea, *Aralia continentalis*	–	KF516501	KP877987	KP877980	KF516487	–	–
	A. photistica								
	CBS 212.86; EGS35.172; BMP0041^{T}	UK, *Digitalis purpurea*	KC584212	KC584131	KC584678	KC584420	AY563282	–	JQ671632
Phragmosporae	*A. phragmospora* (= *E. phragmospora*)								
	CBS 274.70; EGS27.098^{T}	Netherlands, soil	JN383493	JN383474	KC584721	KC584462	JN383509	–	JQ671623
Porri	*Alternaria allii*								
	CBS 107.28; EGS48.084^{T}	Puerto Rico, *Allium cepa*	KJ718100	KJ717954	KJ718449	KJ718274	KJ718620	–	–
	CBS 116701; EGS33.134^{R}	USA, *Allium cepa* var. *viviparum*	KJ718103	KJ717957	KJ718452	KJ718277	KJ718623	–	–
	A. crassa								
	MAFF 243056	**Japan, *Datura stramonium***	AB678215	AB744032	**LC480227**	**LC476807**	AB744028	–	AB744035
	MUCC 2502; 12-M0180	**Japan, *Datura fastuosa***	**LC440601**	**LC482022**	**LC480228**	**LC476808**	–	–	–
	MUCC 2503; 12-M0099	**Japan, *Datura inoxia***	–	**LC482023**	**LC480229**	**LC476809**	–	–	–
	CBS 110.38^{ET}	Cyprus, *Datura stramonium*	KJ718147	KJ717997	KJ718495	KJ718320	KJ718665	–	–
	CBS 109160; EGS45.075; BMP0180 (= *A. capsici*^{T})	Australia, *Capsicum annuum*	KJ718148	AY562408	KJ718496	KJ718321	AY563298	–	JQ671747
	A. cucumerina								
	AC105	**Japan, *Cucurbita maxima***	**LC440602**	**LC482024**	**LC480230**	**LC476810**	–	–	–
	AC106	**Japan, *Cucurbita maxima***	**LC440603**	**LC482025**	**LC480231**	**LC476811**	–	–	–
	CBS 117225; EGS41.127^{R}	USA, *Cucumis melo*	KJ718154	KJ718001	KJ718502	KJ718327	KJ718669	–	–

Table 2. (Continued).

			DDBJ/GenBank/EMBL accession numbers[3]						
***Alternaria* section**	**Fungal name and isolate numbers[1, 2]**	**Country, host plant**	**ITS**	***gapdh***	***tef1***	***rpb2***	***Alt a 1***	***endoPG***	***act***
	CBS 116114; EGS35.123 (= *A. loofahae*^{T})	USA, *Luffa acutangula*	KJ718153	KJ718000	KJ718501	KJ718326	KJ718668	–	–
	A. dauci								
	MUCC 1684	**Japan, *Daucus carota***	**LC440604**	**LC482026**	–	**LC476812**	–	–	–
	AC9	**Japan, *Daucus carota***	**LC440605**	**LC482027**	–	**LC476813**	–	–	–
	CBS 111.38^{NT}	Italy, *Daucus carota*	KJ718158	KJ718005	KJ718506	KJ718331	KJ718673	–	–
	A. macrospora								
	CBS 117228; EGS50.190^{T}	USA, *Gossypium barbadense*	KC584204	KC584124	KC584668	KC584410	KJ718702	–	–
	A. porri								
	AC2	**Japan, *Viola × wittrockiana***	**LC440606**	**LC482028**	**LC480232**	**LC476814**	–	–	–
	AC6	**Japan, *Calibrachoa* sp.**	**LC440607**	**LC482029**	**LC480233**	**LC476815**	–	–	–
	MUCC 1688	**Japan, *Allium fistulosum***	**LC440608**	**LC482030**	**LC480234**	–	–	–	–
	AC16	**Japan, *Allium fistulosum***	**LC440609**	**LC482031**	**LC480235**	**LC476816**	–	–	–
	AC17	**Japan, *Allium fistulosum***	–	**LC482032**	**LC480236**	**LC476817**	–	–	–
	MUCC 1698	**Japan, *Allium fistulosum***	**LC440610**	**LC482033**	**LC480237**	**LC476818**	–	–	–
	AC32	**Japan, *Allium fistulosum***	**LC440611**	**LC482034**	**LC480238**	**LC476819**	–	–	–
	MUCC 1702	**Japan, *Eustoma exaltatum* subsp. *russellianum***	**LC440612**	**LC482035**	**LC480239**	**LC476820**	–	–	–
	AC68	**Japan, *Allium fistulosum***	**LC440613**	**LC482036**	**LC480240**	**LC476821**	–	–	–
	CBS 116699; EGS48.152^{ET}	USA, *Allium cepa*	KJ718218	KJ718053	KJ718564	KJ718391	KJ718727	–	–
	CBS 116698; EGS48.147^{R}	USA, *Allium cepa*	DQ323700	KC584132	KC584679	KC584421	KJ718726	–	–
	A. pseudorostrata								
	CBS 119411; EGS42.060; BMP0174^{T}	USA, *Euphorbia pulcherrima*	JN383483	AY562406	KC584680	KC584422	AY563295	–	JQ671737
	A. solani								
	CBS 109157; EGS44.098^{R}	USA, *Solanum tuberosum*	KJ718238	GQ180080	–	KJ718413	KJ718746	–	–
	A. tagetica								
	CBS 479.81; EGS33.081^{R}	UK, *Tagetes erecta*	KC584221	KC584143	KC584692	KC584434	KJ718761	–	–
	A. zinniae								
	MUCC 1704	**Japan, *Zinnia hybrida***	**LC440614**	**LC482037**	**LC480241**	**LC476822**	–	–	–
	AC107	**Japan, *Zinnia hybrida***	**LC440615**	**LC482038**	**LC480242**	**LC476823**	–	–	–
	AC108	**Japan, *Zinnia elegans***	**LC440616**	**LC482039**	**LC480243**	**LC476824**	–	–	–
	AC109	**Japan, *Zinnia elegans***	**LC440617**	**LC482040**	**LC480244**	**LC476825**	–	–	–

Table 2. (Continued).

			DDBJ/GenBank/EMBL accession numbers^{3}						
***Alternaria* section**	**Fungal name and isolate numbers^{1,2}**	**Country, host plant**	**ITS**	***gapdh***	***tef1***	***rpb2***	***Alt a 1***	***endoPG***	***act***
	CBS 117223; EGS44.035^{R}	New Zealand, *Zinnia elegans*	KJ718270	KJ718096	KJ718616	KJ718445	KJ718777	–	–
Pseudoalternaria	*A. rosae*								
	CBS 121341; EGS41.130^{T}	New Zealand, *Rosa rubiginosa*	JQ693639	JQ646279	JQ672414	–	JQ646370	–	JQ671628
Pseudoulocladium	*A. chartarum* (= *Ulocladium chartarum*)								
	MAFF 246888	**Japan, *Capsicum annuum***	**LC440618**	**LC482041**	**LC480245**	**LC476826**	**LC481629**	–	**LC481879**
	CBS 200.67; ATCC 18044; BMP0359^{ET}	Canada, *Populus* sp.	AF229488	KC584172	KC584741	KC584481	AY563319	–	JQ671654
	A. aspera (= *Ul. arborescens*)								
	CBS 115269; EGS44.109^{T}	Japan, *Pistacia vera*	KC584242	KC584166	KC584734	KC584474	KF533899	–	–
	A. concatenata (= *Ul. capsici*)								
	CBS 120006; HSAUPIII$_{0}$0035^{T}	China, *Capsicum annuum*	KC584246	AY762950	KC584740	KC584480	–	–	–
	A. septospora (= *Ul. septosporum*)								
	CBS 109.38	Italy, wood pulp	FJ266489	FJ266500	KC584747	KC584487	–	–	–
Radicina	*A. petroselini*								
	MAFF 243057	**Japan, *Petroselinum crispum***	AB678216	–	**LC480246**	**LC476827**	AB744030	–	AB744037
	CBS 112.41; EGS06.196^{T}	unknown, *Petroselinum sativum*	KC584211	KC584130	KC584677	KC584419	–	–	–
	CBS 109383; EGS09.159; BMP0144^{R}	USA, *Petroselinum crispum*	AF229454	AY278799	JQ672455	JQ646474	AY563288	–	JQ671677
	A. radicina								
	CBS 245.67; EGS03.145; ATCC 6503^{NT}	USA, *Daucus carota*	KC584213	KC584133	KC584681	KC584423	FN689405	–	–
	A. selini								
	CBS 109382; EGS25.198^{T}	Saudi Arabia, *Petroselinum crispum*	AF229455	AY278800	KC584684	KC584426	FJ266504	–	JQ671676
	A. smyrnii								
	CBS 109380; EGS37.093; BMP0147^{R}	UK, *Smyrnium olusatrum*	AF229456	KC584138	KC584687	KC584429	AY563289	–	JQ671675
Soda	*A. kulundii*								
	CBS 137525; M313^{T}	Russia, soil	KJ443262	KJ649618	KJ443219	KJ443176	–	–	–
Sonchi	*A. cinerariae*								
	MAFF 243059; MUCC 1701^{ET}	**Japan, *Pericallis cruenta***	AB906673	AB906670	**LC480247**	**LC476828**	AB906671	–	AB906672
	MAFF 241266; MUCC 1613	**Japan, *Farfugium japonicum***	**LC440619**	AB862970	AB862982	AB862976	**LC481630**	–	**LC481880**
	MAFF 241267; MUCC 1614	**Japan, *Gynura bicolor***	**LC440620**	AB862971	AB862983	AB862977	**LC481631**	–	**LC481881**
	MUCC 2504	**Japan, *Jacobaea maritima***	**LC440621**	**LC482042**	–	**LC476829**	**LC481632**	–	**LC481882**
	CBS 116495; EGS49.102^{R}	USA, *Ligularia* sp.	KC584190	KC584109	KC584648	KC584389	–	–	–

Table 2. (Continued).

Alternaria section	Fungal name and isolate numbers^{1,2}	Country, host plant	DDBJ/GenBank/EMBL accession numbers^{3}						
			ITS	*gapdh*	*tef1*	*rpb2*	*Alt a 1*	*endoPG*	*act*
	A. sonchi								
	CBS 119675; EGS43.131^{R}	Canada, *Sonchus asper*	KC584220	KC584142	KC584691	KC584433	–	–	–
Teretispora	*A. leucanthemi* (= *Teretispora leucanthemi*)								
	CBS 421.65; ATCC 16028; EGS10.059^{T}	Netherlands, *Chrysanthemum maximum*	KC584240	KC584164	KC584732	KC584472	–	–	–
Ulocladioides	*A. atra* (= *Ul. atrum*)								
	AC86	**Japan, *Raphanus sativus***	**LC440622**	**LC482043**	**LC480248**	**LC476830**	**LC481633**	–	**LC481883**
	AC87	**Japan, *Brassica oleracea* var. *capitata***	–	**LC482044**	**LC480249**	**LC476831**	**LC481634**	–	**LC481884**
	AC88	**Japan, *Brassica rapa* subsp. *pekinensis***	**LC440623**	**LC482045**	**LC480250**	**LC476832**	**LC481635**	–	**LC481885**
	MAFF 246889	**Japan, *Allium fistulosum***	**LC440624**	**LC482046**	**LC480251**	**LC476833**	**LC481636**	–	**LC481886**
	CBS 195.67; ATCC 18040; BMP0355^{ET}	USA, soil	AF229486	KC584167	KC584735	KC584475	AY563318	–	JQ671660
	A. cucurbitae (= *Ul. cucurbitae*)								
	CBS 483.81; EGS31.021; BMP0351^{R}	New Zealand, *Cucumis sativus*	FJ266483	AY562418	KC584743	KC584483	AY563315	–	JQ671663
	A. multiformis (= *Ul. multiforme*)								
	CBS 102060; EGS31.005^{T}	Canada, soil	FJ266486	KC584174	KC584744	KC584484	FJ266512	–	JQ671664
	A. cantlous (= *Ul. cantlous*)								
	CBS 123007; HSAUP0209^{T}	China, *Cucumis melo*	KC584245	KC584171	KC584739	KC584479	EU684146	–	–
	A. heterospora (= *Ul. solani*)								
	CBS 123376; HSAUP 0521^{T}	China, *Solanum lycopersicum*	KC584248	KC584176	KC584748	KC584488	EU855805	–	–
Ulocladium	*A. alternariae* (= *Sinomyces alternariae*)								
	CBS 126989; EGS46.004	USA, *Daucus carota*	AY376642	AY376329	KC584730	KC584470	–	–	–
	A. botrytis (= *Ul. botrytis*)								
	MAFF 246887	**Japan, *Asparagus officinalis***	**LC440625**	**LC482047**	**LC480252**	**LC476834**	**LC481637**	–	**LC481887**
	CBS 197.67; ATCC 18042^{ET}	USA, air	KC584243	KC584168	KC584736	KC584476	–	–	–
	A. oudemansii (= *Ul. oudemansii*)								
	CBS 114.07; ATCC 18047; IMI 124940; MUCL 18563; QM 1744^{T}	Unknown	FJ266488	KC584175	KC584746	KC584486	FJ266514	–	–
Undifilum	*A. bornmuelleri* (= *Undifilum bornmuelleri*)								
	DAOM 231361	Austria, *Securigera varia*	FJ357317	FJ357305	KC584751	KC584491	JN383516	–	JQ671610
Monotypic lineage	*A. argyranthemi*								
	CBS 116530; EGS44.033^{T}	New Zealand, *Argyranthemum* sp.	KC584181	KC584098	KC584637	KC584378	–	–	–
	A. brassicae								

Table 2. (Continued).

Alternaria section	Fungal name and isolate numbers[1, 2]	Country, host plant	DDBJ/GenBank/EMBL accession numbers[3]						
			ITS	*gapdh*	*tef1*	*rpb2*	*Alt a 1*	*endoPG*	*act*
	AC29	**Japan, *Brassica rapa***	**LC440626**	AB862967	AB862979	AB862973	**LC481638**	–	**LC481888**
	MAFF 240791	**Japan, *Raphanus sativus***	**LC440627**	**LC482048**	**LC480253**	**LC476835**	**LC481639**	–	**LC481889**
	MUCC 1615	**Japan, *Raphanus sativus***	**LC440628**	**LC482049**	**LC480254**	**LC476836**	**LC481640**	–	**LC481890**
	CBS116528; EGS38.032^{R}	USA, *Brassica oleracea*	KC584185	KC584102	KC584641	KC584382	–	–	–
	A. dennisii (= *E. dennisii*)								
	CBS 476.90; EGS30.121^{T}	Isle of Man, *Senecio jacobaea*	JN383488	JN383469	KC584713	KC584454	JN383505	–	–
	A. helianthiinficiens								
	CBS 208.86; EGS36.184^{T}	USA, *Helianthus annuus*	JX101649	KC584120	EU130548	KC584403	–	–	–
	A. peucedani								
	CNU 111485^{T}	Korea, *Peucedanum japonicum*	KF728231	KF889361	–	–	KF889363	–	–
	A. soliaridae								
	CBS 118387; EGS33.024^{T}	USA, soil	KC584218	KC584140	KC584689	KC584431	–	–	–
	A. thalictrigena								
	CBS 121712; CPC 13410^{T}	Germany, *Thalictrum* sp.	EU040211	KC584144	KC584694	KC584436	–	–	–
	A. thlaspis (= *E. thlaspis*)								
	EGS45.069^{T}	UK, *Thlaspis caerulescentis*	JN383495	JN383476	–	–	JN383510	–	JQ671607
	*A. triangularis**								
	MAFF 246776^{T}	**Japan, *Bupleurum rotundifolium***	**LC440629**	**LC482050**	**LC480255**	**LC476837**	**LC481641**	–	**LC481891**
	AC95	**Japan, *Bupleurum rotundifolium***	**LC440630**	**LC482051**	**LC480256**	**LC476838**	**LC481642**	–	**LC481892**
Out group	*Paradendryphiella salina* (= *E. annulata*)								
	CBS 302.84^{T}	North Sea, *Cancer pagurus*	JN383486	JN383467	KC584709	KC584450	–	–	JQ671591

[1] AC: Personal collection of JN; ATCC: American Type Culture Collection, Virginia, USA; BMP: Personal collection of Dr. B.M. Pryor, School of Plant Sciences, University of Arizona, Arizona, USA; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CNU: Culture Collection of Chungnam National University, Daejeon, Korea; CPC: Personal collection of Dr. P.W. Crous, housed at CBS; DAOM: Canadian Collection of Fungal Cultures, Ottawa, Canada; EGS: Personal collection of Dr. E.G. Simmons; HSAUP: Department of Plant Pathology, Shandong Agricultural University, China; MAFF: Genetic Resources Center, National Agriculture and Food Research Organization, Tsukuba, Japan; MUCC (Japan): Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Japan; P: Personal collection of Dr. P. Inderbitzin, Department of Plant Pathology, Cornell University, New York, USA.

[2] Ex-type, -neotype, and -epitype strain indicated with T, NT, and ET; R: representative strain by Simmons (2007). Fungal names between parentheses refer to the former name or the name under the pathotype concept (Nishimura 1980).

[3] Japanese isolates examined and accession numbers newly generated in this study are indicated in boldface.

* Novel taxa proposed in the taxonomy section.

Among the three novel species identified based on their distinct morphological characteristics, MAFF 246768 ex *G. haageana* (*A. paragomphrenae*) was clearly distinguishable from *A. gomphrenae* and *A. celosiicola* in sect. *Alternantherae*, and two isolates (MAFF 246776 and AC95) ex *Bupleurum* (*A. triangularis*) were also well-resolved as a new monotypic sister lineage to sect. *Sonchi*. However, MAFF 246770 ex *Petunia* (*A. cylindrica*) had a unique sequence with strong BS support in ML but with weak support in MP and BI. The remaining other morphologically distinguishable species were assigned to each valid clade, whereas Japanese isolates of *A. botrytis*, *A. brassicicola*, *A. chartarum*, and *A. japonica* were indistinguishable from closely related taxa, including the ex-type and ex-epitype isolates in each section.

The ITS datasets containing 178 sequences were aligned for a total of 586 characters. The topologies of the resulting trees from MP, ML, and BI analyses were congruent, and Fig. 2 shows one of the MP trees (TL = 600, CI = 0.433, RI = 0.881, RC = 0.382, HI = 0.567) with BS values (MP and ML), and Bayesian PP. Almost all of the examined Japanese species, together with their closely related taxa in phylogenetic trees that were indistinguishable based on the combined *gapdh*, *rpb2*, and *tef1* sequence datasets, were each recognized as separate species. Two isolates (MAFF 246776 and AC95) ex *Bupleurum* (*A. triangularis*) were well-resolved as a distinct new species. However, species in sect. *Alternaria*, and two large-spored species in sect. *Porri* having colored filamentous beaks (*A. cucumerina* and *A. zinniae*), were not recognized as independent species. PCR amplification and sequencing of seven Japanese isolates, *i.e.* MAFF 246768 (*A. paragomphrenae*) and *A. iridicola* MAFF 246771, were unsuccessful.

The combined alignment of *act*, *Alt a 1*, *endoPG*, *gapdh*, *rpb2*, and *tef1* datasets contained 18 sequences with a total of 2 473 characters. PCR amplification and sequencing of the *act* sequence of *A. iridicola* MAFF 246890 was unsuccessful. The topologies of the resulting trees from MP, ML, and BI analyses were congruent, and Fig. 3 shows one of the MP trees (TL = 383, CI = 0.859, RI = 0.783, RC = 0.673, HI = 0.141) with BS values (MP and ML) and Bayesian PP. MAFF 246770 ex *Petunia* (*A. cylindrica*) was identified as a new sister lineage to the *A. arborescens* species complex in this section.

Morphology and growth rate on potato-dextrose agar

Based on their conidial morphology on PCA and V8 media, the Japanese *Alternaria* isolates examined in the present study were recognized as either one of 23 existing species, or one of three novel species. One of the novel taxa, MAFF 246768 (*A. paragomphrenae*) ex *Gomphrena haageana*, produced very similar conidia to those of *A. gomphrenae* and other species in sect. *Alternantherae*; however, they differed in the length and width of their conidial bodies (Table 3). Among their various features, conidiophore width was a defining characteristic of each *Alternaria* section: those of sect. *Alternaria* [*A. alstroemeriae*, *A. alternata*, *A. gaisen*, and MAFF 246770 (*A. cylindrica*)], *Brassicicola*, *Crivellia*, *Japonica*, *Pseudoulocladium*, *Ulocladioides*, *Ulocladium*, and MAFF 246776 (*A. triangularis*) for the most part did not exceed an average of 5 µm (narrow conidiophores); those of sect. *Alternantherae* [*A. celosiicola*, *A. gomphrenae*, and MAFF 246768 (*A. paragomphrenae*)], *Eureka*, *Gypsophilae*, *Panax*, *Porri* (*A. crassa*, *A. cucumerina*, *A. dauci*, *A. porri*, *A. zinniae*), *Sonchi*, and *A. brassicae* usually reached 6–7 µm (thick conidiophores); those of sect. *Radicina* were of an intermediate width, ranging around 5–6 µm; and *A. iridicola* produced mostly narrow, but often thickened, conidiophores. In addition, species in sect. *Porri* were characterized by the morphology of their beaks, especially in color. Those of *A. porri* and *A. dauci* were typically hyaline, whereas those of *A. cucumerina* and *A. zinniae* were always colored. Moreover, *A. crassa* grown on V8 medium commonly also formed colored beaks as cylindrical secondary conidiophores, but not filamentous true beaks. A detailed morphology of each Japanese species examined in the present study follows in the taxonomy section.

Colony diameters of the examined species ranged from 24–87 mm after 7 d incubation at 25 °C, and the mean with 95 % confidence intervals was 61.6 ± 6.3 mm (Fig. 4). Based on the mean colony diameters, the examined species were classified into groups; fast-growing: *A. alstroemeriae*, *A. alternata*, *A. celosiicola*, *A. crassa*, *A. cucumerina*, *A. gaisen*, *A. petroselini*, and *A. porri*; moderate-growing: *A. atra*, *A. botrytis*, *A. brassicicola*, *A. chartarum*, *A. cinerariae*, *A. cumini*, *A. iridicola*, *A. japonica*, *A. zinniae*, MAFF 246768 ex *Gomphrena* (*A. paragomphrenae*), and MAFF 246770 ex *Petunia* (*A. cylindrica*); slow to moderate-growing: *A. dauci*, *A. gomphrenae*, and *A. panax*; slow-growing: *A. brassicae*, *A. nobilis*, *A. penicillata*, and MAFF 246776 ex *Bupleurum* (*A. triangularis*).

Experimental host range

Inoculation tests conducted in this study determined host ranges of each species, as well as species boundaries between closely related species. Moreover, "false" hosts, which were previously recorded as if true hosts or susceptible host plants, were also revealed. Detailed results are described for each host family as follows.

Alternaria gomphrenae *and a novel species infecting* Amaranthaceae

Two *Alternaria* isolates, *A. gomphrenae* MAFF 246769 and MAFF 246768 ex *G. haageana* (*A. paragomphrenae*), were inoculated onto *Amaranthaceae* plants by spraying a conidial suspension concentrated at an average of 2.2 × 10^4 conidia/mL; both isolates had similar aggressiveness toward these hosts, but differed on *Alternanthera* (Table 4).

Distinct reddish spots appeared on *Gomphrena* after 7 dpi with *A. gomphrenae*, leading to defoliation, with poor sporulation on lesions even after 30 dpi (Fig. 5A, B). Almost no distinct symptoms caused by *A. gomphrenae* were observed on the inoculated leaves of *Alternanthera* or the other examined plants – *Amaranthus*, *Celosia*, *Beta*, and *Spinacia* – until 30 dpi (Fig. 5C).

Distinct spots caused by MAFF 246768 similar to those of *A. gomphrenae* were also observed, but were more severe on *Gomphrena* by 10 dpi (Fig. 5D), while no symptoms were observed on control plants. Indistinct spots frequently appeared on the leaves of *Alternanthera* inoculated with MAFF 246768 by 2 dpi, and then the leaves were severely defoliated with sporulation by 10 dpi (Fig. 5E, F). Almost no distinct symptoms were observed on the inoculated leaves of the other examined plants until 30 dpi, though they often showed small necrotic spots without sporulation (Fig. 5G, H).

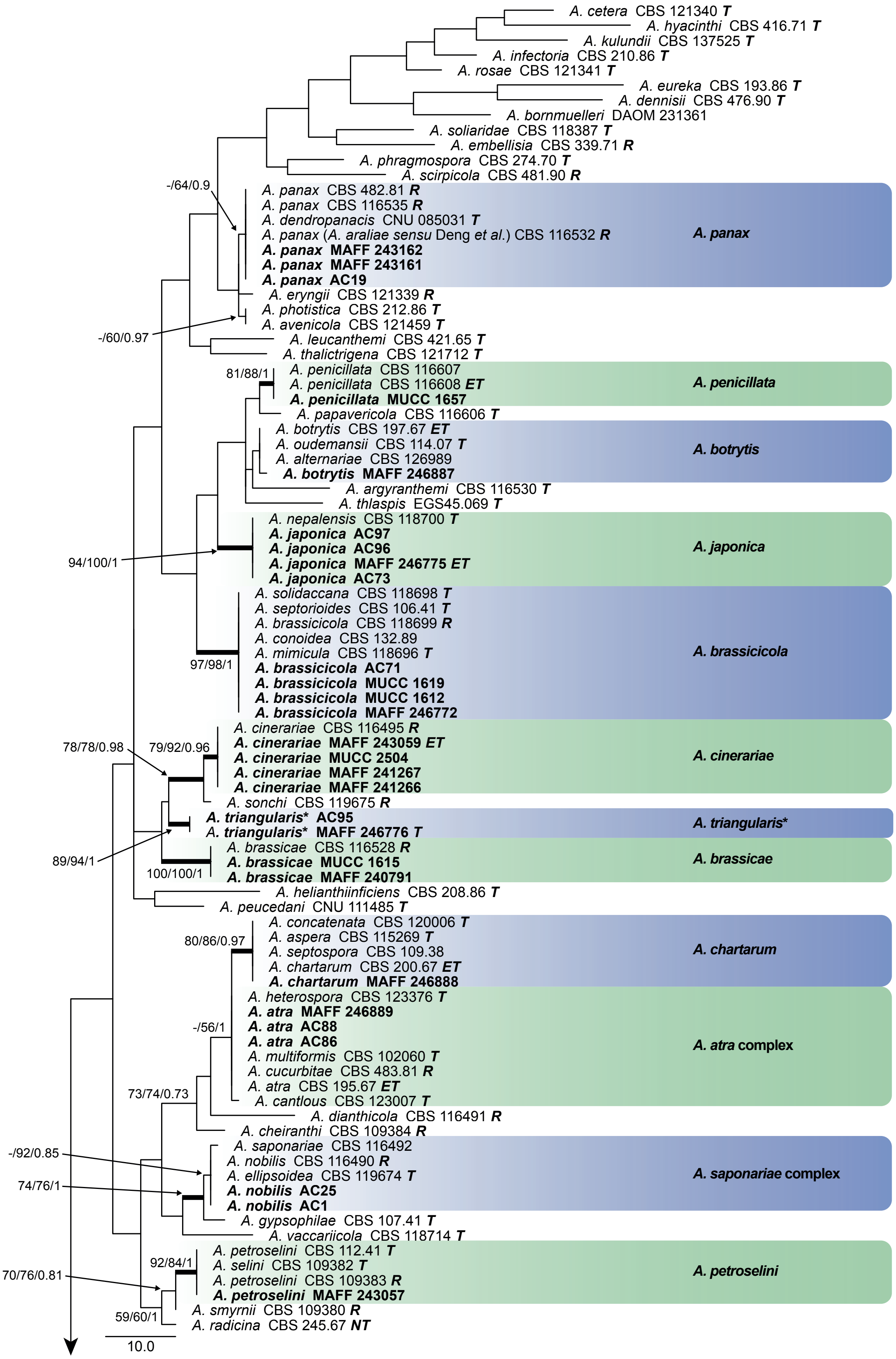

Fig. 2. Phylogenetic tree generated from maximum parsimony (MP) analysis based on the ITS sequences from Japanese *Alternaria* isolates. The tree was rooted to *Paradendryphiella salina* (CBS 302.84). MP and RAxML maximum likelihood (ML) bootstrap values and Bayesian posterior probabilities (PP) are given near branches (MP/ML/PP). Thickened nodes indicate significant support by MP/ML/PP (> 60/60/0.96). Tree length = 600, consistency index = 0.433, homoplasy index = 0.567, retention index = 0.881, and rescaled consistency index = 0.382. The scale bar indicates the number of nucleotide substitutions. Japanese *Alternaria* isolates examined are indicated in bold, and the statuses of reference isolates are indicated in bold and italic. *T*: ex-type, *NT*: ex-neotype, *ET*: ex-epitype, *R*: representative strain assigned by Simmons (2007). Asterisks indicate novel taxa proposed in the taxonomy section.

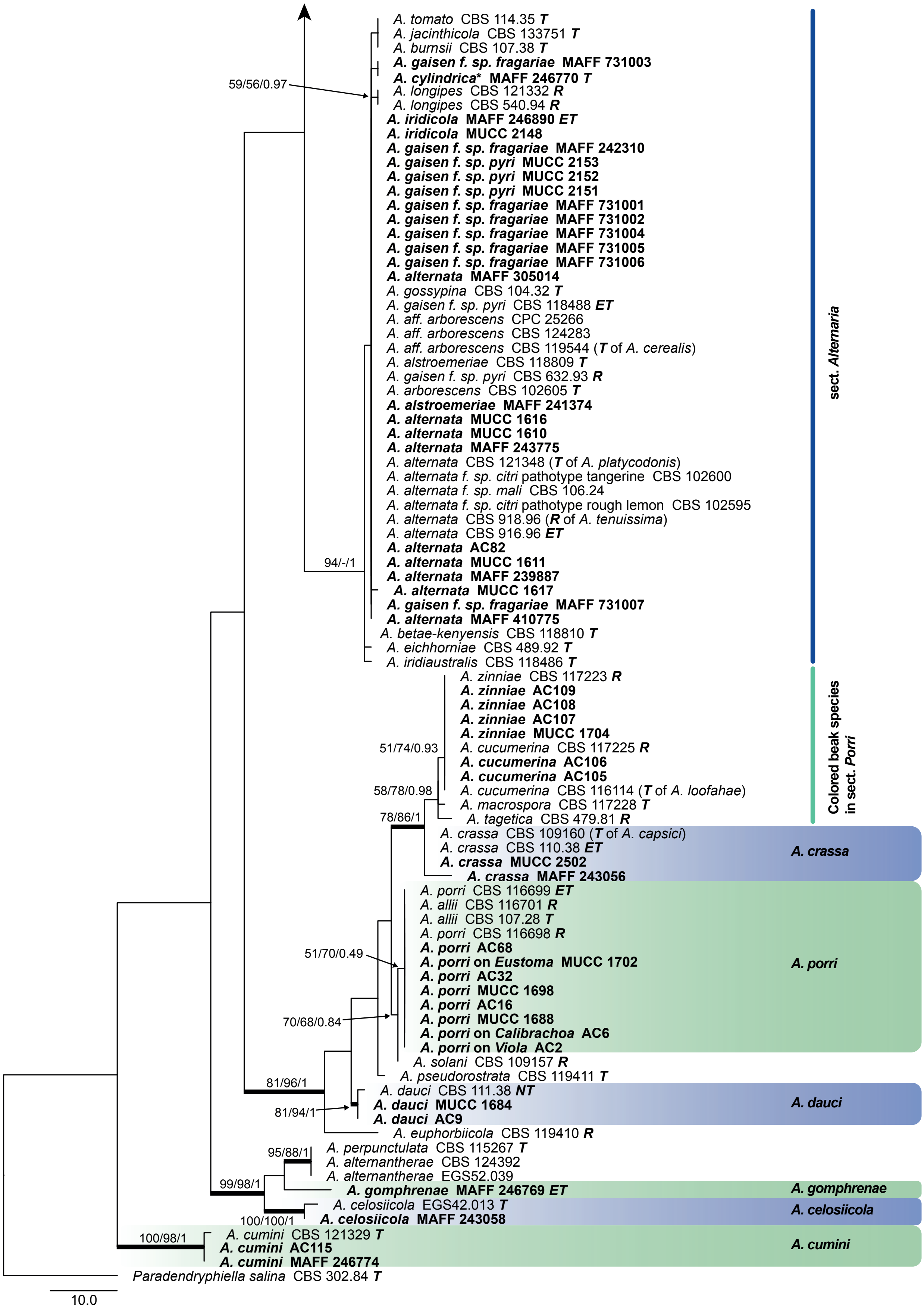

Fig. 2. (Continued).

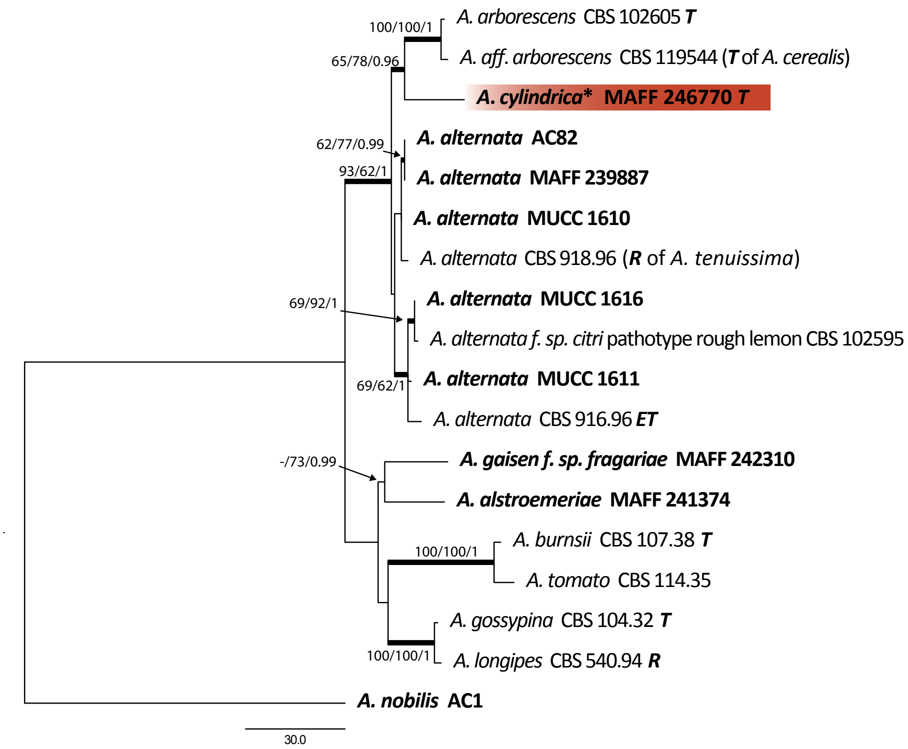

Fig. 3. Phylogenetic tree of sect. *Alternaria* generated from maximum parsimony (MP) analysis based on the combined dataset of *act*, *Alt a 1*, *endoPG*, *gapdh*, *rpb2*, and *tef1* sequences from 17 isolates. The tree was rooted to *Alternaria nobilis* (sect. *Gypsophilae*). MP and RAxML maximum likelihood (ML) bootstrap values and Bayesian posterior probabilities (PP) are given near branches (MP/ML/PP). Thickened nodes indicate significant support by MP/ML/PP (> 60/60/0.96). Tree length = 383, consistency index = 0.859, homoplasy index = 0.141, retention index = 0.783, and rescaled consistency index = 0.673. The scale bar indicates the number of nucleotide substitutions. Japanese isolates examined are indicated in bold, and statuses of reference isolates are indicated in bold and italic. *T*: ex-type, *ET*: ex-epitype, *R*: representative strain assigned by Simmons (2007). Resolved novel taxon with asterisk was indicated as red shadings.

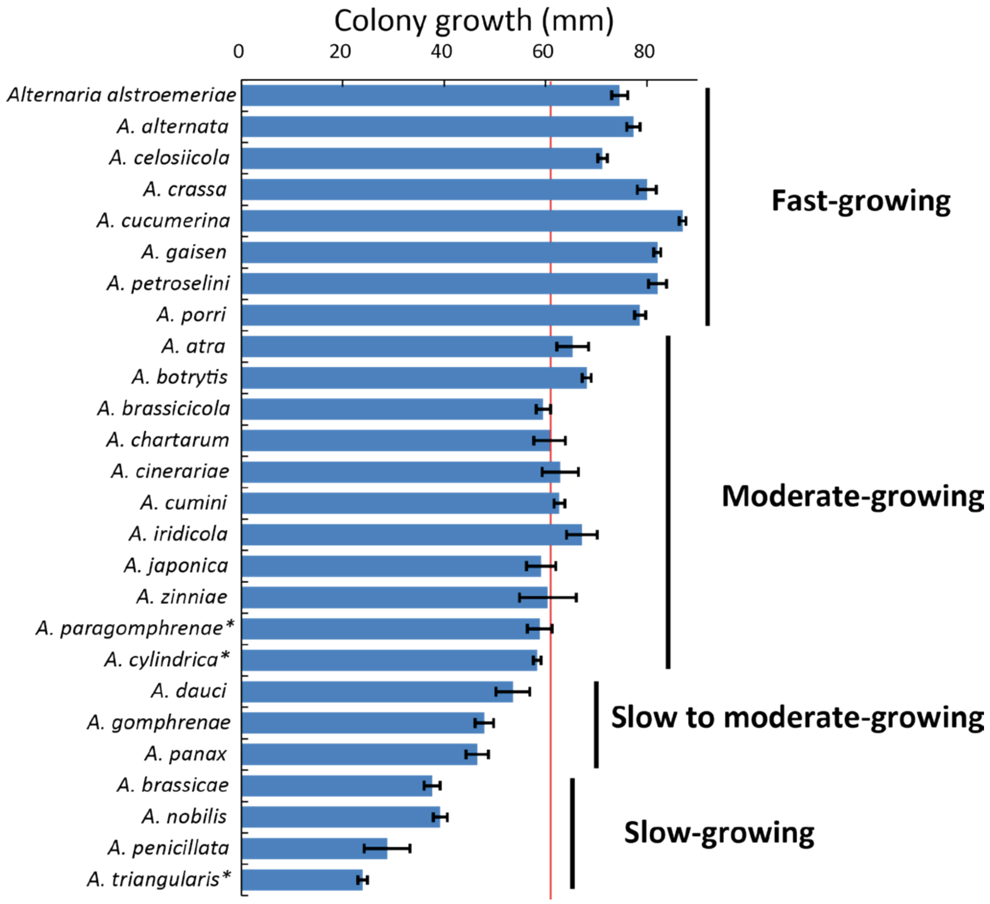

Fig. 4. Mean colony diameters (mm) on potato-dextrose agar medium. The mean for the entire examined species is indicated as a red line at 61.6 mm. Bars indicate the 95 % confidence intervals. Asterisks indicate novel taxa proposed in the taxonomy section.

Table 3. Morphological comparisons among the species of sect. *Alternantherae*.

Fungal species and isolates[1]	**Original host plants**	**Conidial bodies**				**Beaks**		**Substrates**	**References**
		Length × width (µm)	**Average with 95 % CI**	**Transverse septa**	**Longitudinal septa**	**Length × width (µm)**	**Average with 95 % CI**		
Examined species									
Alternaria celosiicola	*Celosia*								
MAFF 243058		36–161 × 8–26	107±7 × 20±1	2–16	0–4	55–670 × 2–3	332±44 × 2±0.1	PCA	Nishikawa & Nakashima (2013)
		42–180 × 10–26	116±7 × 18±1	2–17	0–5	49–575 × 2–4	195±38 × 2±0.1	V8	Nishikawa & Nakashima (2013)
		68–173 × 13–26	119±5 × 20±1	8–15	0(–2)	120–285 × 2–3	197±13 × 2±0.1	Lesion	Nishikawa & Nakashima (2013)
EGS42.013^{T}		50–190 × 7–17	–	11–14	1–3	250–470 × 2–4	–	PCA	Simmons (1995b)
A. gomphrenae	*Gomphrena*								
MAFF 246769^{ET}		46–103 × 11–21	82±4 × 16±1	4–10	0(–1)	18–188 × 2–4	87±10 × 3±0.1	PCA	This study
		35–77 × 10–17	58±2 × 14±0.4	3–9	0–1	13–216 × 2–4	97±14 × 3±0.1	V8	This study
		30–106 × 8–23	67±5 × 12±1	0–13	0	11–163 × 2–5	72±9 × 2±0.2	Lesion	This study
–		46–94 × 10–16	74±3 × 14±0.4	4–10	0	–	–	Lesion	This study, lectotype
–		100 × 15	–	5–14	–	up to 150	–	Lesion	Togashi (1926); Simmons (1989)
EGS40.146		80–100 × 18–20	–	–	–	60–80 × 2	–	PCA	Simmons (1995b)
–		48–105 × 9–18	80 × 14	–	rare	33–111 × 2–3	69 × 3	Lesion	Yoshii (1933)
*A. paragomphrenae**	*Gomphrena*								
MAFF 246768^{T}		60–111 × 15–25	87±3 × 20±1	2–9	0–3	14–208 × 2–5	129±11 × 3±0.1	PCA	This study
		48–98 × 17–33	76±3 × 25±1	3–7	0–4	25–316 × 3–5	150±18 × 3±0.2	V8	This study
		25–99 × 8–26	56±5 × 19±1	1–9	0–2	14–87 × 3–4	55±4 × 3±0.1	Lesion	This study
Comparable species									
A. alternantherae	*Alternanthera*								
EGS39.124^{NT}		50–115 × 8–20	–	6–10	0–2	350–470 × 2–4	–	PCA	Simmons (1995b)
A. crassoides	*Froelichia*								
–		45–90 × 8–20	–	7–9	–	40–60 × 2	–	Lesion	Simmons (1995b), lectotype
A. perpunctulata	*Alternanthera*								
CBS 115267^{T}		80–100 × 10–14	–	10–15	1–2	100–210	–	PCA	Simmons (2004)

[1] CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; EGS: Personal collection of Dr. E.G. Simmons; MAFF: Genetic Resources Center, National Agriculture and Food Research Organization, Tsukuba, Japan. Ex-type, -neotype, and -epitype strain indicated with T, NT, and ET.

* Novel taxa proposed in the taxonomy section.

Table 4. Experimental host ranges of *Alternaria* species infecting *Amaranthaceae*.

Inoculated plants	Disease severity[1] and pathogenicity[2] by inoculation with:				Notes[6]
	Alternaria gomphrenae	***Alternaria paragomphrenae*[3]**	***Alternaria celosiicola*[4]**	***Alternaria alternantherae*[5]**	
	MAFF 246769	MAFF 246768	MAFF 243058		
Amaranthaceae					
Amaranthoideae					No distinct symptoms were observed on the inoculated leaves with *Ago,* while *Apa* often produced small spots without sporulation. *Ace* is pathogenic to plants in *Amaranthoideae*. *Aal* is non-pathogenic to *Amaranthus spinosus*, but to tribe *Celosieae*.
Amarantheae					
Amaranthus tricolor	0	0.1±0.2	4.4±0.6 ***	–	
Celosieae					
Celosia argentea var. *cristata*	0	0.8±0.3 *	**4.6±0.5 *** **	S	
C. argentea var. *plumosa*	0	0.4±0.3	**4.7±0.3 *** **	S	
Betoideae					No distinct symptoms were observed on the inoculated leaves with *Ace*, *Ago*, and *Apa*, but *Aal* was reported as pathogenic to both *Beta* and *Spinacia*.
Beta vulgaris	0.3±0.3	0	0.2±0.3	S	
Chenopodioideae					
Spinacia oleracea	0	0.1±0.2	0.1±0.2	S	
Gomphrenoideae					Distinct leaf spots and defoliations with rich sporulation were observed on *Gomphrena* inoculated with *Ago* isolates by 6 dpi. Leaf spots produced by *Ago* also observed on *Alternanthera* by 7 dpi but fewer with poor sporulation than on *Gomphrena*. *Apa* and *Ace* has distinct pathogenicity to both *Alternanthera* and *Gomphrena*. *Aal* is partially pathogenic to *Alternanthera* species at least but not to *Gomphrena*.
Alternanthera sessilis	0.5±0.7 *	3.3±0.8 **	4.5±0.4 ***	–	
Gomphrena globosa	**2.0±0.5 *** **	**4.6±0.3 *** **	3.0±0.7 **	I	

[1] Mean disease severity at 7 d post-inoculation (dpi) rated on a 0–5 scale (0: no visible lesions, 1: <10 % leaf area affected, 2: 11–25 % leaf area affected, 3: 26–50 % leaf area affected, 4: 51–75 % leaf area affected, and 5: >75 % leaf area affected or defoliation). 95 % confidence intervals are also indicated. –: not available. Results for the original plant source of each *Alternaria* isolate are indicated in bold.

[2] Pathogenicity was evaluated by the presence or absence of distinct lesions and sporulation on lesions, and are indicated with asterisks (***: strongly aggressive, showing distinct lesions with rich sporulation; **: weakly aggressive, showing indistinct or fewer distinct lesions with sporulation; *: weakly aggressive to opportunistic, showing few, indistinct lesions with no to rare sporulation; blank: non-pathogenic, showing no distinct lesions nor sporulation).

[3] Novel taxa proposed in the taxonomy section.

[4] From results reported by Nishikawa & Nakashima (2013).

[5] From results reported by Pomella *et al*. (2007). S: susceptible, I: immune. They also determined *Alternanthera philoxeroides* and *Portulaca halimoides* (*Portulacaceae*) as susceptible hosts, and *Alternanthera ficoidea*, *Amaranthus spinosus*, and *Hebanthe eriantha* (= *Pfaffia paniculata*; *Gomphrenoideae*) as immune plants.

[6] Fungal names are abbreviated as follows; *Ace*: *Alternaria celosiicola*, *Ago*: *A. gomphrenae*, *Apa*: *A. paragomphrenae**, and *Aal*: *A. alternantherae*.

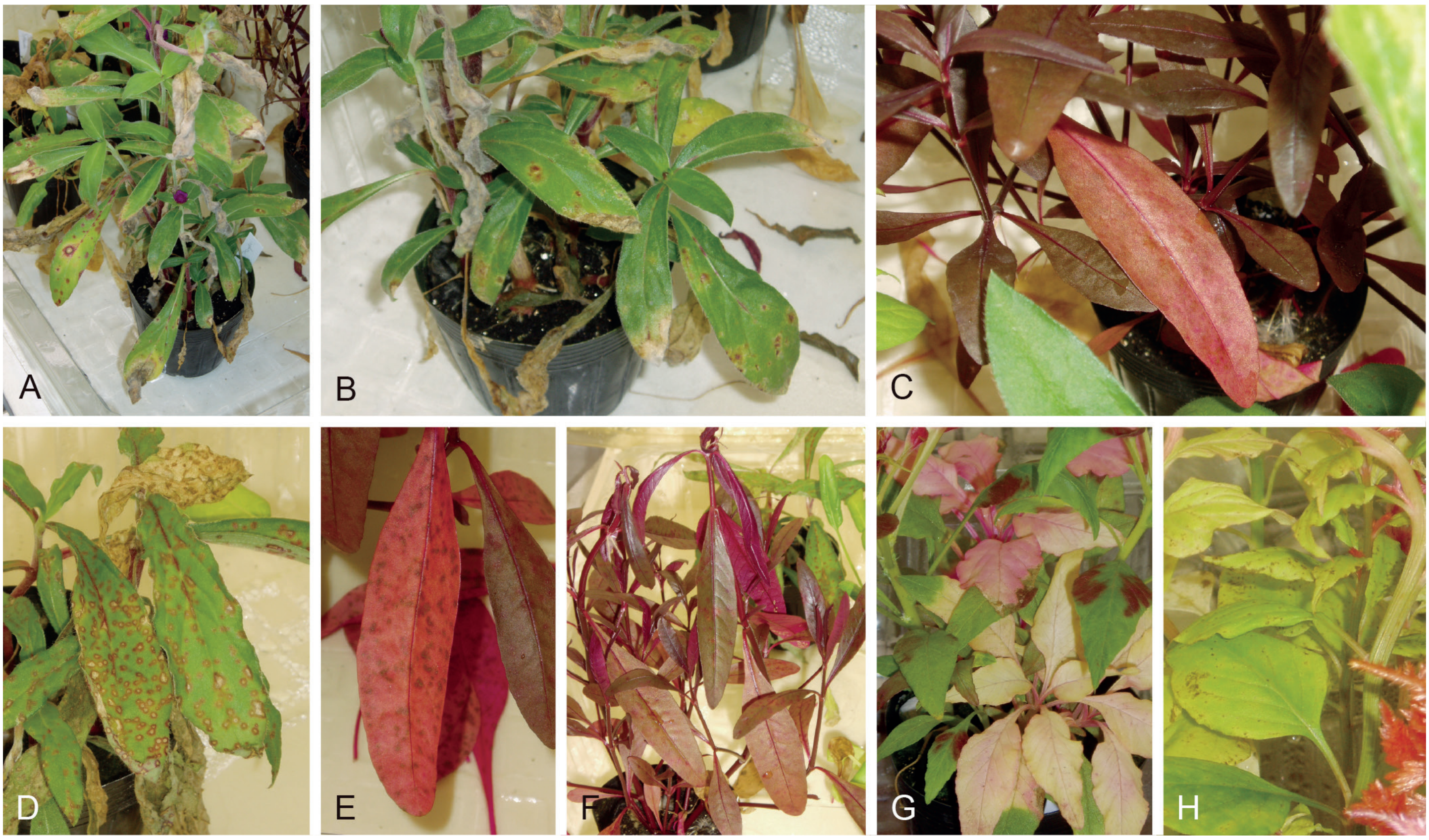

Fig. 5. Pathogenicity of two *Alternaria* species of sect. *Alternantherae*. **A–C.** *Alternaria gomphrenae* (MAFF 246769); **A, B.** On *Gomphrena* at 30 d post-inoculation (dpi). **C.** On *Alternanthera* at 8 dpi. **D–H.** *Alternaria paragomphrenae* (MAFF 246768); **D.** On *Gomphrena* at 10 dpi. **E, F.** On *Alternanthera* at 4–6 dpi. **G.** On *Amaranthus* at 11 dpi. **H.** *Celosia* at 4 dpi.

Species infecting Brassicaceae

Three isolates of *A. brassicae*, MAFF 240791, AC29, and MUCC 1615, were applied by spraying a conidial suspension at an average of 8.4 × 10^4 conidia/mL (Table 5). Distinct black lesions appeared on the inoculated leaves of all *Brassiceae* plants, *Nasturtium*, and *Iberis* within 2 dpi, and inoculated leaves showed severe rot or defoliation with rich sporulation at 7–10 dpi (Fig. 6A–H). Distinct black spots also appeared on *Eutrema* at 7 dpi, although these differed in disease severity between applied isolates (Fig. 6I). Lesions on *Lobularia* and *Matthiola* were usually indistinct; however, severe leaf blight or rot were observed with rich sporulation at 9–10 dpi (Fig. 6J, K). No distinct symptoms were observed on *Aubrieta* and *Capsella* until 30 dpi as on the non-*Brassicaceae* plants, although poor sporulation was sometimes seen on lower, older leaves (Fig. 6L).

Three isolates of *A. brassicicola* (MAFF 246772, MAFF 246773, and MUCC 1619) were applied at an average of 3.2 × 10^6 conidia/mL (Table 5). Results were similar to those of *A. brassicae*, with three isolates of *A. brassicicola* being highly aggressive toward *Brassiceae* plants, *Nasturtium*, *Iberis*, and *Matthiola* (Fig. 7A–G). On the inoculated leaves of *Lobularia*, small spots resulting in indistinct leaf blight were observed but with rich sporulation at 10 dpi (Fig. 7H). On the other hand, inoculated *Eutrema* leaves mostly showed only indistinct tip burn with no to rare sporulation by 18 dpi (Fig. 7I), and the inoculated leaves of *Aubrieta* and *Capsella* showed no distinct symptoms. However, sporulation was often observed on suberized stem surfaces of the former species at 7 dpi, and rarely produced necrotic spots on leaves of the latter without sporulation by 7 dpi (Fig. 7J, K). No distinct symptoms appeared on the non-*Brassicaceae* plants, even on *Spinacia*, which was the original source of MAFF 246773 (Fig. 7L).

Two isolates of *A. japonica* (MAFF 246775 and AC96) were applied at an average of 1.7 × 10^6 conidia/mL (Table 5). Similar results as those observed on the former two species were obtained on *Brassiceae* plants, *Nasturtium*, *Iberis*, *Lobularia*, and *Matthiola* (Fig. 8A–H). The inoculated leaves of *Eutrema*, *Aubrieta*, and *Capsella* showed no distinct symptoms, although necrotic spots without sporulation were rarely produced at 14 dpi (Fig. 8I–K). No distinct symptoms appeared on the non-*Brassicaceae* plants (Fig. 8L).

Alternaria cumini *and a novel species infecting* Apiaceae

An isolate of *A. cumini* (MAFF 246774) was applied at an average of 5.0 × 10^4 conidia/mL (Table 6). Leaf spots on *Cuminum*, which was the original source of the fungus used for inoculation, appeared at 2 dpi; leaves became severely blighted and rotten with rich sporulation within 6 dpi (Fig. 9A). On the inoculated leaves of *Petroselinum* and *Anthriscus*, mostly small spots or tip burn appeared at 7 dpi, with rare sporulation within 30 dpi (Fig. 9B). No distinct symptoms were observed on the other seven *Apiaceae* plants, including *Coriandrum* and *Daucus* at 30 dpi.

A conidial suspension of MAFF 246776 ex *Bupleurum* (*A. triangularis*) was applied at an average of 6.4 × 10^4 conidia/mL (Table 6). The inoculated leaves of *Bupleurum* showed distinct black spots within 5 dpi, and sporulation was abundant on lesions at 7 dpi (Fig. 9C–F); no symptoms were observed on control plants. Small necrotic spots without sporulation were sometimes observed within 30 dpi on the inoculated leaves of *Angelica* (Fig. 9G). No distinct symptoms were observed on the inoculated leaves of the other seven plants at 30 dpi (Fig. 9H).

Table 5. Experimental host ranges of *Alternaria* species infecting *Brassicaceae*.

Inoculated plants	Disease severity[1] and pathogenicity[2] by inoculation with:								Notes[3]
	Alternaria brassicae			*Alternaria brassicicola*			*Alternaria japonica*		
	AC29	**MAFF 240791**	**MUCC 1615**	**MAFF 246772**	**MAFF 246773**	**MUCC 1619**	**MAFF 246775**	**AC96**	
Brassicaceae									
Alysseae									Small black spots and indistinct leaf blight were observed at 7–10 dpi, usually with rich sporulation.
Lobularia maritima	2.4±0.6 **	3.6±0.4 **	3.3±0.7 **	3.5±0.6 **	3.0±1.1 **	2.8±0.8 **	3.1±0.6 **	0.2±0.3 *	
Anchonieae									Black lesions appeared, then whole plants rotted with rich sporulation by 7 dpi, but relatively slight for *Abe*.
Matthiola incana	3.1±0.4 **	3.7±0.5 **	2.6±0.5 **	4.9±0.2 ***	4.9±0.2 ***	4.8±0.3 ***	4.8±0.3 ***	3.8±0.4 ***	
Arabideae									Distinct symptoms were rarely observed. Isolate MAFF 246775 of *Aja* produced necrotic spots without sporulation at 7 dpi, and isolates of *Aba* often reproduced conidia on stem surfaces without distinct symptoms.
Aubrieta sp.	0	0	0.2±0.2	0.3±0.2 *	1.4±0.7 *	0.3±0.2 *	1.9±0.5 *	0.1±0.2 *	
Brassiceae									Black spots were produced on leaves of all *Brassiceae* plants, then whole plants rotted with rich sporulation by 7 dpi. No significant differences were found between inoculated species.
Brassica juncea	4.3±0.6 **	4.2±0.4 ***	3.3±0.5 ***	4.9±0.2 ***	4.4±0.5 ***	3.7±0.7 ***	2.8±0.6 ***	3.3±0.8 ***	
B. oleracea var. *capitata*	4.1±0.4 ***	3.8±0.3 ***	4.0±0.5 ***	**4.9±0.1 *****	4.5±0.6 ***	5.0 ***	5.0 ***	**4.7±0.3 *****	
B. oleracea var. *sabellica*	–	–	–	**4.6±0.2 *****	–	–	–	–	
B. rapa subsp. *chinensis*	–	4.1±0.5 ***	–	4.6±0.3 ***	4.1±0.5 ***	4.1±0.6 ***	4.1±0.7 ***	3.3±0.7 ***	
B. rapa subsp. *nipposinica*	–	3.4±0.4 ***	–	4.7±0.4 ***	5.0 ***	5.0 ***	3.7±0.5 ***	4.5±0.4 ***	
B. rapa subsp. *pekinensis*	**4.1±0.2 *****	4.0±0.3 ***	4.1±0.2 ***	4.3±0.4 ***	4.8±0.3 ***	4.4±0.6 ***	2.7±0.7 ***	3.6±0.6 ***	
B. rapa subsp. *rapa*	**3.4±0.3 *****	4.0±0.7 ***	3.9±0.5 ***	4.6±0.5 ***	5.0 ***	5.0 ***	3.9±0.6 ***	4.1±0.5 ***	
Diplotaxis tenuifolia	2.8±0.3 **	3.4±0.4 ***	3.9±0.5 ***	4.7±0.3 ***	4.4±0.5 ***	–	3.9±0.6 ***	3.9±0.6 ***	
Eruca vesicaria subsp. *sativa*	3.8±0.8 ***	3.2±0.6 ***	3.3±0.4 ***	5.0 ***	4.4±0.4 ***	5.0 ***	4.5±0.4 ***	4.6±0.3 ***	
Raphanus sativus var. *sativus*	3.7±0.9 ***	**3.9±0.5 *****	**4.3±0.4 *****	5.0 ***	4.3±0.4 ***	**5.0 *****	**4.7±0.4 *****	4.8±0.3 ***	
Cardamineae									Black spots were produced on lower leaves, then leaf blight with rich sporulation was observed at 7–10 dpi.
Nasturtium officinale	3.4±0.5 ***	3.4±0.5 ***	3.5±0.3 ***	4.2±0.7 ***	2.2±0.8 **	4.0±0.5 ***	4.8±0.3 ***	1.5±0.6 **	
Eutremeae									Leaves inoculated with *Abe* showed distinct black spots with sporulation at 7 dpi. Leaves inoculated with *Aba* and *Aja* showed mostly indistinct tip burn with no to rare sporulation by 10 dpi.
Eutrema japonicum	1.5±0.6 *	3.0±1.6 ***	3.0 **	1.5±0.4 *	2.0±3.0 **	1.1±0.4 *	1.3±0.7 *	2.0 *	

Table 5. (Continued).

Inoculated plants	Disease severity^1 and pathogenicity^2 by inoculation with:								Notes^3
	Alternaria brassicae			*Alternaria brassicicola*			*Alternaria japonica*		
	AC29	MAFF 240791	MUCC 1615	MAFF 246772	MAFF 246773	MUCC 1619	MAFF 246775	AC96	
Iberideae									Small black spots were produced, then the plant easily defoliated with sporulation by 10 dpi; relatively severe for *Aba*.
Iberis sempervirens	1.6±0.5 **	1.7±0.4 **	3.4±0.5 ***	4.8±0.2 ***	3.6±0.9 ***	2.8±0.6 **	1.9±0.4 **	2.0±0.4 **	
Lepidieae									No distinct symptoms were typically observed; *Aba* isolate MUCC 1619 and *Aja* isolate MAFF 246775 rarely produced necrotic spots without sporulation by 7 dpi.
Capsella bursa-pastoris	0	0	0	0	0	0.6±0.5 *	0.5±0.4 *	0	
Amaranthaceae									No distinct symptoms observed in this test over 14 dpi, even on *Spinacia* inoculated with *Aba* isolate MAFF 246773 ex *Spinacia*.
Beta vulgaris	0	0	0	0	0	–	–	–	
Chenopodium giganteum	0	0	0	–	–	–	–	–	
Spinacia oleracea	–	–	–	0	**0**	0	–	–	
Apiaceae									
Daucus carota	–	0	–	0	0	–	–	–	
Asteraceae									
Callistephus chinensis	–	–	–	0	0.2±0.3	–	–	–	
Lactuca sativa	0	0.3±0.2 *	0	0	0	–	0.2±0.3	0	
Convolvulaceae									
Ipomoea nil	0	0	0.3±0.3 *	–	–	–	–	–	
Cucurbitaceae									
Cucumis sativus	0.5±0.4 *	0	0	0	0	–	–	–	
Cucurbita maxima	0.2±0.3 *	0	0	–	–	–	–	–	
C. pepo	–	–	–	0.2±0.2	0	–	–	–	
Fabaceae									
Phaseolus vulgaris	–	0	–	0	0	–	–	–	
Vicia faba	–	0	–	0	0	–	–	–	
Vigna unguiculata subsp. *unguiculata*	–	–	–	–	–	–	0.2±0.3	0	
Onagraceae									
Clarkia amoena	–	0	–	0	0	–	–	–	
Pedaliaceae									

Table 5. (Continued).

Inoculated plants	Disease severity[1] and pathogenicity[2] by inoculation with:								Notes[3]
	Alternaria brassicae			*Alternaria brassicicola*			*Alternaria japonica*		
	AC29	**MAFF 240791**	**MUCC 1615**	**MAFF 246772**	**MAFF 246773**	**MUCC 1619**	**MAFF 246775**	**AC96**	
Sesamum indicum	–	–	–	0	0	–	0	0	
Solanaceae									
Capsicum annuum	–	0	–	–	–	–	–	–	
Solanum lycopersicum	–	–	–	0.1±0.2	0.3±0.3	–	–	–	
Poaceae									
Zea mays	–	0	–	–	–	–	–	–	

[1] Mean disease severity at 7 d post-inoculation (dpi) rated on a 0–5 scale (0: no visible lesions, 1: <10 % leaf area affected, 2: 11–25 % leaf area affected, 3: 26–50 % leaf area affected, 4: 51–75 % leaf area affected, and 5: >75 % leaf area affected or defoliation). 95 % confidence intervals are also indicated. –: not tested. Results for the original plant sources of each *Alternaria* isolate are indicated in bold.

[2] Pathogenicity was evaluated by the presence or absence of distinct lesions and sporulation on lesions, and are indicated with asterisks (***: strongly aggressive, showing distinct lesions with rich sporulation; **: weakly aggressive, showing indistinct or fewer distinct lesions with sporulation; *: weakly aggressive to opportunistic, showing few, indistinct lesions with no to rare sporulation; blank: non-pathogenic, showing neither distinct lesions nor sporulation).

[3] Fungal names are abbreviated as follows; *Abe*: *Alternaria brassicae*, *Aba*: *A. brassicicola*, and *Aja*: *A. japonica*.

Table 6. Experimental host ranges of *Alternaria* species infecting *Apiaceae*.

Inoculated plants	Disease severity[1] and pathogenicity[2] by inoculation with:			References of host range of the other species on *Daucus carota*			Notes[7]
	Alternaria cumini	***Alternaria triangularis***[3]	***Alternaria petroselini***[4]	***Alternaria carotiincultae***[5]	***Alternaria dauci***[6]	***Alternaria radicina***[5]	
	MAFF 246774	**MAFF 246776**	**MAFF 243057**				
Apiaceae, *Apioideae*							
Apieae							Small spots appeared on leaves of *Petroselinum* inoculated with *Acu*, but no sporulation was observed by 30 dpi. No distinct symptoms were observed on leaves inoculated with *Atr* by 30 dpi. *Ape* and the other three species are widely and partially pathogenic to the tribe, respectively. The host range of *Aca* and *Ara* is identical within the tribe.
Ammi majus	–	0.1±0.2	2.9±1.1 ***	–	–	–	
Anethum graveolens	–	–	4.4±0.7 ***	Weak–Non	HE	Weak–Non	
Apium graveolens	0.1±0.2	0.3±0.3	3.2±1.2 ***	Weak	L	Weak	
Foeniculum vulgare	–	–	3.3±1.1 ***	Weak	HE	Weak	
Petroselinum crispum	0.3±0.3 *	0	**3.8±0.7 *****	Non	L	Non	
Bupleureae							Leaves inoculated with *Atr* showed distinct black spots with sporulation within 7 dpi. *Ape* is also weakly pathogenic.
Bupleurum rotundifolium	0	**3.9±0.7 *****	2.6±1.1 **	–	–	–	

Table 6. (Continued).

Inoculated plants	Disease severity[1] and pathogenicity[2] by inoculation with:			References of host range of the other species on *Daucus carota*			Notes[7]
	Alternaria cumini MAFF 246774	*Alternaria triangularis*[3] MAFF 246776	*Alternaria petroselini*[4] MAFF 243057	*Alternaria carotiincultae*[5]	*Alternaria dauci*[6]	*Alternaria radicina*[5]	
Careae							No distinct symptoms were observed on leaves inoculated with *Acu* and *Atr*, and no other pathogenic species were found.
Carum carvi	0.3±0.6	0.2±0.2	0	Weak–Non	–	Weak–Non	
Coriandreae							No distinct symptoms were observed on the inoculated leaves of the two examined species, while *Ape*, *Aca*, *Ada*, and *Ara* were shown to be pathogenic.
Coriandrum sativum	0	0	3.5±0.7 ***	Weak	Hn	Weak	
Oenantheae							No distinct symptoms were observed on the inoculated leaves.
Cryptotaenia japonica	0	0	0	–	–	–	
Scandiceae							
Daucinae							*Cuminum* leaves inoculated with *Acu* showed severe leaf blight with rich sporulation at 5 dpi, and *Daucus* leaves inoculated with examined three species showed no distinct symptoms at 30 dpi.
Cuminum cyminum	**4.5±0.3 *****	–	5.0 ***	–	–	–	
Daucus carota	0	0	0.6±0.3 *	**HP**	**HE**	**HP**	
Scandicinae							Small spots and tip burn without sporulation was rarely observed on leaves inoculated with *Acu* at 14 dpi, while *Ape* and *Ada* are clearly pathogenic.
Anthriscus cerefolium	0.4±0.4 *	–	3.7±0.7 ***	–	Hn	–	
Selineae							Small necrotic spots without sporulation were observed at 30 dpi on leaves inoculated with *Atr*. Only *Ape* is weakly pathogenic.
Angelica keiskei	0	0.7±1.3 *	2.2±1.0 **	–	–	–	

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[1] Mean disease severity at 7 d post-inoculation (dpi) rated on a 0–5 scale (0: no visible lesions, 1: <10 % leaf area affected, 2: 11–25 % leaf area affected, 3: 26–50 % leaf area affected, 4: 51–75 % leaf area affected, and 5: >75 % leaf area affected or defoliation). 95 % confidence intervals are also indicated. –: not tested. Results for the original plant sources of each *Alternaria* isolate are indicated in bold.

[2] Pathogenicity was evaluated by the presence or absence of distinct lesions and sporulation on lesions, and are indicated with asterisks (***: strongly aggressive, showing distinct lesions with rich sporulation; **: weakly aggressive, showing indistinct or fewer distinct lesions with sporulation; *: weakly aggressive to opportunistic, showing few, indistinct lesions with no to rare sporulation; blank: non-pathogenic, showing neither distinct lesions nor sporulation).

[3] Novel taxa proposed in the taxonomy section.

[4] From results reported by Nishikawa & Nakashima (2013).

[5] From results reported by Pryor & Gilbertson (2002). HP: highly pathogenic, Weak: weakly pathogenic, Non: non-pathogenic. They also determined that *A. carotiincultae*, *A. petroselini*, and *A. radicina* were weakly or non-pathogenic to *Pimpinella anisum* (tribe *Pimpinelleae*) and *Pastinaca sativa* (tribe *Tordylieae*).

[6] From results reported by Boedo *et al.* (2012). HE: species exhibiting a relatively high disease index with expanding lesions, Hn: species showing a relatively high disease index with non-expanding lesions, L: species exhibiting a relatively low disease index with non-expanding lesions. They also noted that the inoculated leaves of *Pastinaca* and non-*Apiaceae* plants (corn salad and leek) showed a low disease index or were symptomless.

[7] Fungal names are abbreviated as follows; *Acu*: *Alternaria cumini*, *Atr*: *A. triangularis**, *Ape*: *A. petroselini*, *Aca*: *A. carotiincultae*, *Ada*: *A. dauci*, *Ara*: *A. radicina*.

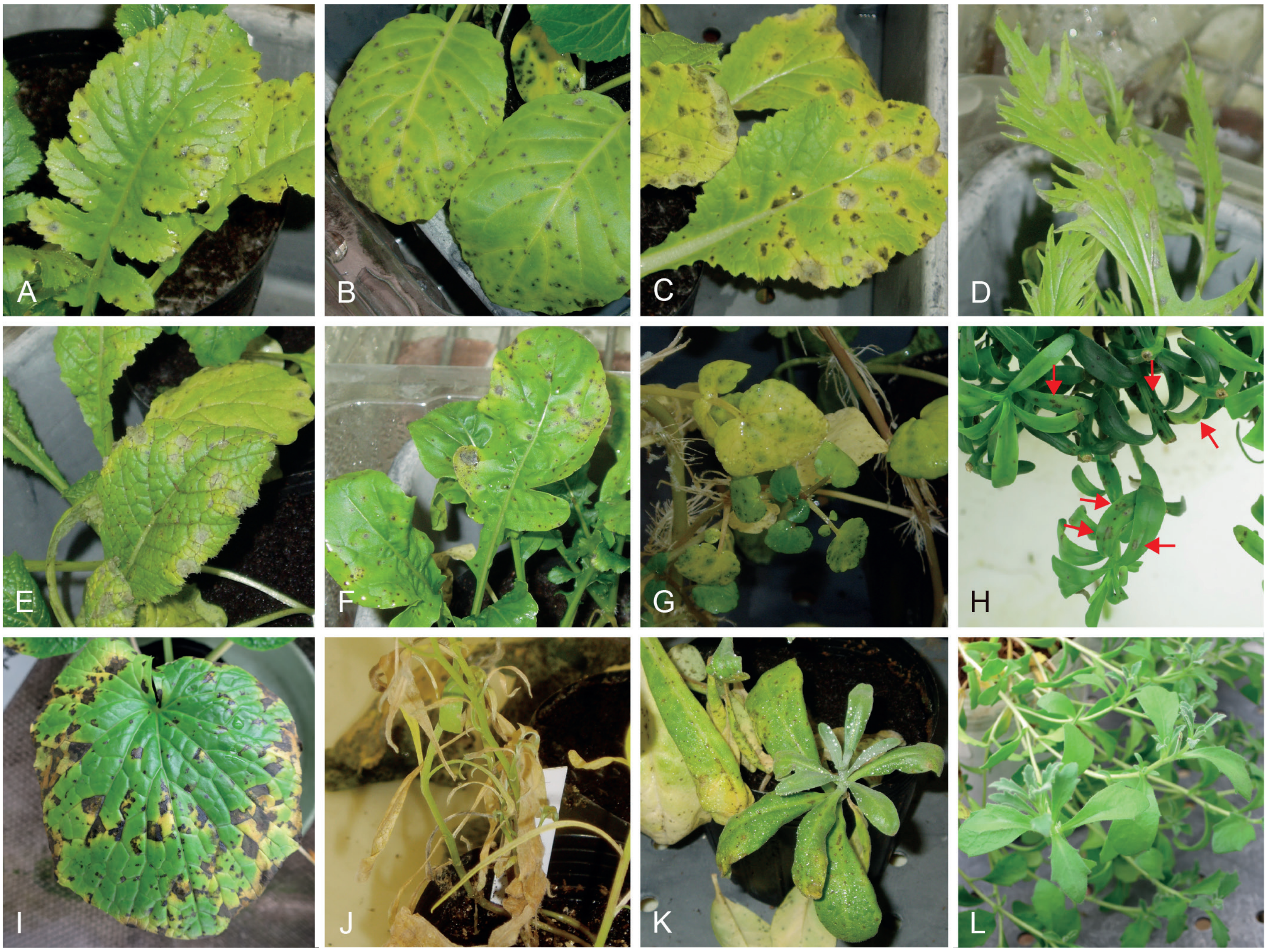

Fig. 6. Pathogenicity of *Alternaria brassicae* (MAFF 240791). **A.** On *Raphanus* at 5 d post-inoculation (dpi). **B.** On *Brassica oleracea* var. *capitata* at 5 dpi. **C.** On *B. rapa* subsp. *pekinensis* at 7 dpi. **D.** On *B. rapa* subsp. *nipposinica* at 5 dpi. **E.** On *B. juncea* at 5 dpi. **F.** On *Eruca* at 7 dpi. **G.** On *Nasturtium* at 2 dpi. **H.** On *Iberis* at 7 dpi. **I.** On *Eutrema* at 10 dpi. **J.** On *Lobularia* at 9 dpi. **K.** On *Matthiola* at 13 dpi. **L.** On *Aubrieta* at 7 dpi.

A novel species ex Petunia *infecting* Solanaceae

A conidial suspension of MAFF 246770 (*A. cylindrica*) was applied at an average of 8.2 × 10^5 conidia/mL (Table 7). Irregular-shaped lesions appeared abundantly on the inoculated *Petunia* leaves at 2 dpi, and then lesions quickly expanded and caused severe rot of the whole plant with rich sporulation (Fig. 10A–C), but no symptoms were observed on control plants. Small necrotic spots were observed on the inoculated leaves of *Solanum lycopersicum* and *S. melongena* at 2 dpi, and were slightly expanded with little sporulation within 7 dpi (Fig. 10D, E). No distinct symptoms were observed on the other three *Solanoideae* plants, *Nicotiana*, and two non-solanaceous plants (Fig. 10F).

Alternaria iridicola *infecting* Iridaceae

Two isolates of *A. iridicola* (MAFF 246890 and MAFF 246771) were applied at an average of 3.2 × 10^5 conidia/mL, and both isolates showed similar results (Table 8). Distinct leaf spots appeared on *Iris* spp., except for *I. ensata*, at 7 dpi, and then the inoculated leaves became severely blighted with rich sporulation (Fig. 11A, B). As for *I. ensata*, neither distinct symptoms nor sporulation were observed within 14 dpi (Fig. 11C). Small yellow spots and slightly yellowing spots with no or poor sporulation were observed at 7 dpi on *Gladiolus* and *Crocus*, respectively (Fig. 11D, E). No distinct symptoms were observed on *Freesia* and *Asparagus*, while yellow spots and tip burn without sporulation were sometimes observed on leaves of *Allium* at 14 dpi (Fig. 11F–H).

Alternaria porri *on non-host plants*

Obtained *A. porri* isolates from non-host plants, such as isolates AC2 ex *Viola* (*Violaceae*), AC6 ex *Calibrachoa* (*Solanaceae*), and MUCC 1702 ex *Eustoma* (*Gentianaceae*), were used to inoculate each original host and related plants by spraying with a conidial suspension concentrated at an average of 2.0 × 10^5 conidia/mL. No isolates showing pathogenicity toward non-alliaceous plants including each source host plant were found.

Taxonomy

Eighty-five Japanese *Alternaria* isolates were collected, and found to represent 26 species, of which three were new to science. Each species is described for each *Alternaria* section in alphabetical order below.

Table 7. Experimental host ranges of *Alternaria* species on *Solanaceae*.

Inoculated plants	Disease severity[1] and pathogenicity[2] by inoculation with:		References of host range of *Alternaria solani*[5]	Notes
	***Alternaria cylindrica*[3]**	***Alternaria crassa*[4]**		
	MAFF 246770	**MAFF 243056**		
Solanaceae				
Nicotianoideae				No distinct symptoms were observed.
Nicotiana tabacum	0.3±0.4	0	Non	
Petunioideae				Severe necrosis appeared on leaves inoculated with MAFF 246770 at 2 dpi, which then became rotten with rich sporulation.
Petunia × atkinsiana	**5.0 *****	0.2±0.3 *	–	
Solanoideae				Small necrotic spots were observed on *Solanum* inoculated with MAFF 246770 at 2 dpi, which occasionally became slightly expanded with sporulation until 7 dpi. MAFF 246770 showed no pathogenicity to the other examined *Solanoideae* plants. Host selectivities of *A. crassa* and *A. solani* are reported as to each original source plant and *Capsicum*.
Capsiceae				
Capsicum annuum	0	4.2±0.7 ***	M	
Datureae				
Brugmansia × candida	0	**2.3±0.7 *****	Non	
Physaleae				
Physalis alkekengi var. *franchetii*	0	0.3±0.4	–	
Solaneae				
Solanum lycopersicum	2.4±0.7 *	1.2±0.3 *	**S**	
S. melongena	2.9±0.9 *	0.4±0.4	**S**	
Fabaceae				No distinct symptoms were observed over 30 dpi on leaves of non-host plants inoculated with MAFF 246770.
Vigna unguiculata	0	–	–	
Poaceae				
Zea mays	0	–	–	

[1] Mean disease severity at 7 d post-inoculation (dpi) rated on a 0–5 scale (0: no visible lesions, 1: <10 % leaf area affected, 2: 11–25 % leaf area affected, 3: 26–50 % leaf area affected, 4: 51–75 % leaf area affected, and 5: >75 % leaf area affected or defoliation). 95 % confidence intervals are also indicated. –: not tested. Results for the original source plant species (or close relatives) of each *Alternaria* species are indicated in bold.

[2] Pathogenicity was evaluated by the presence or absence of distinct lesions and sporulation on lesions, and are indicated with asterisks (***: strongly aggressive, showing distinct lesions with rich sporulation; **: weakly aggressive, showing indistinct or fewer distinct lesions with sporulation; *: weakly aggressive to opportunistic, showing few, indistinct lesions with no to rare sporulation; blank: non-pathogenic, showing neither distinct lesions nor sporulation).

[3] Novel taxa proposed in the taxonomy section.

[4] From results reported by Nishikawa & Nakashima (2013).

[5] From results reported by Cardoso (2014). S: susceptible, M: caused mild symptoms, Non: non-pathogenic (symptoms or pathogen structures absent). Cardoso's results also confirmed virulences of *A. solani* toward three asteraceous species (*Ageratum conyzoides*, *Erigeron bonariensis*, and *Galinsoga parviflora*), and *Rumex acetosa* (*Polygonaceae*).

Table 8. Experimental host range of *Alternaria iridicola*.

Inoculated plants	Disease severity[1] and pathogenicity[2] by inoculation with:		Notes
	MAFF 246890	MAFF 246771	
Amaryllidaceae			Small yellow spots and tip burn without sporulation were rarely observed at 14 dpi.
Allium fistulosum	0.7±0.7 *	0.3±0.3 *	
Asparagaceae			No distinct symptoms observed by 14 dpi.
Asparagus officinalis	0.1±0.3	–	
Iridaceae			
Crocoideae			Slightly yellowing on tips with occasional sporulation were observed.
Crocus sp.	1.0±0.8 *	1.7±0.7 *	
Iridoideae			Leaf spots and sever blight with rich sporulation on *I. laevigata* and *Iris* × *hollandica* were observed at 7 dpi, but *I. ensata* var. *spontanea* never showed any symptoms over 14 dpi.
Iris ensata var. *spontanea*	**0.6±0.5**	**0.3±0.3**	
I. laevigata	**3.5±1.3 *****	**4.0±0.8 *****	
Iris × *hollandica*	**4.1±0.6 *****	**4.4±0.5 *****	
Ixioideae			Small yellow spots were often produced on *Gladiolus* by 14 dpi, but never expanded and sporulated. No distinct symptoms were observed on *Freesia* by 14 dpi.
Freesia refracta	0	0	
Gladiolus sp.	0.3±0.5	0.3±0.3	

[1] Mean disease severity at 7 d post-inoculation (dpi) rated on a 0–5 scale (0: no visible lesions, 1: <10 % leaf area affected, 2: 11–25 %, 3: 26–50 %, 4: 51–75 %, and 5: >75 % or defoliated). 95 % confidence intervals also indicated. –: not tested. Results of the original source plant genus of each *Alternaria* species are indicated in bold.

[2] Pathogenicity was evaluated by presence or absence of distinct lesion and sporulation on lesion, and indicated asterisks (***: strongly aggressive, showing distinct lesions with rich sporulation, **: weakly aggressive, showing indistinct or fewer distinct lesions with sporulation, *: weakly aggressive to opportunistic, showing fewer indistinct lesions with no to rare sporulation, blank: non-pathogenic, showing distinct lesions nor sporulation).

Section *Alternantherae* D.P. Lawr. *et al.*, *Mycologia* **105**: 540. 2013.

Four species were recognized in this section (Lawrence *et al.* 2013, Woudenberg *et al.* 2013), and Gannibal (2018) added two additional species. All taxa and phylogenetically unresolved species (*A. crassoides* and *A. pimpriana*) were former members of the genus *Nimbya,* and parasitic toward *Amaranthaceae* plant hosts (Simmons 1989, 1995b, 2004). In this section, two known species and one novel species were found.

***Alternaria celosiicola* Jun. Nishikawa & C. Nakash., *J. Phytopathol*. 161: 606. 2013. Fig. 12.**
Synonyms: *Nimbya celosiae* E.G. Simmons & Holcomb, *Mycotaxon* **55**: 144. 1995.
Alternaria celosiae (E.G. Simmons & Holcomb) Lawrence, Park & Pryor, *Mycol. Progr.* **11**: 811. 2012, *nom. illeg.* (later homonym; ICN Art. 53.1). *non Alternaria celosiae* (Tassi) O. Săvul., *Herb. Mycol. Rom.*: fasc. **30**, no. 1489. 1950.
Alternaria cristata D.P. Lawr., M.S. Park & B.M. Pryor, *Mycol. Progr.* **13** (2): 259. 2014, *nom. nud.*, ICN Art. 52.1.

Typus: **USA**, Louisiana, on *Celosia cristata*, Jul. 1993, *G.E. Holcomb*, **holotype** BPI 803020, **isotype** IMI 369150 and IMI 369153, culture ex-type EGS42.013.

Specimens and isolates examined: **Japan**, Kanagawa Prefecture, Fujisawa, on leaves of *Celosia argentea* var. *plumosa*, 26 Jun. 2006, *S. Masugi & Y. Makizumi*, MUMH 11676 and MUMH 11701, living culture MAFF 243058.

Morphological characters on V8 medium: Previously reported in Nishikawa & Nakashima (2013). Morphology observed on PCA medium similar to that observed on V8 medium (Table 3).

Colony characteristics on PDA after 7 d at 25 °C: Fast-growing, reaching 71.2 ± 0.9 mm diam; aerial hypha cottony, pale green to grayish green, with white margins; reverse center black to dark green; sporulation sparse; diffusible pigment absent (Nishikawa & Nakashima 2013).

Sexual morph: Not observed.

Natural hosts: Celosia (*Amaranthaceae*).

Symptoms: Leaf spots on *Celosia* are circular to subcircular, 2–10 mm diam, brown to dark brown with distinct reddish margin, and often surrounded by a yellowish halo, becoming confluent (Nishikawa & Nakashima 2013).

Experimental host range: Pathogenic to *Celosia*, *Amaranthus*, *Alternanthera*, and *Gomphrena*, but not to *Beta* and *Spinacia* (Nishikawa & Nakashima 2013).

Distribution: USA (Simmons 1995b), China (Zhao & Zhang 2005), and Japan (Nishikawa & Nakashima 2013).

Distinctive features: Conidia are larger than those of other related species in sect. *Alternantherae*; conidial bodies usually exceeded 100 × 20 µm, and beaks exceed 200 µm long. Conidial bodies commonly consist of a distosepta-like internal wall structure

Fig. 7. Pathogenicity of *Alternaria brassicicola* (MAFF 246772). **A.** On *Brassica oleracea* var. *capitata* at 7 d post-inoculation (dpi). **B.** On *B. rapa* subsp. *chinensis* at 7 dpi. **C.** On *Raphanus* at 7 dpi. **D.** On *Eruca* at 7 dpi. **E.** On *Nasturtium* at 7 dpi. **F.** On *Iberis* at 7 dpi. **G.** On *Matthiola* at 7 dpi. **H.** On *Lobularia* at 18 dpi. **I.** On *Eutrema* at 18 dpi. **J.** On *Aubrieta* at 18 dpi. **K.** On *Capsella* at 7 dpi. **L.** On *Spinacia* at 7 dpi.

with octagonal lumina. This species is widely pathogenic not only to *Celosia*, but also to *Amaranthus*, *Alternanthera*, and *Gomphrena* (Table 4), and is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, and *act* sequence data (data not shown).

Notes: Lawrence *et al*. (2012) transferred this species from the genus *Nimbya* to *Alternaria* based on phylogenetic analysis, but the proposed name – *A. celosiae* (E.G. Simmons & Holcomb) Lawrence, Park & Pryor – resulted in a later homonym of *A. celosiae* (Tassi) O. Săvul. Although Lawrence *et al.* (2014) renamed the epithet of *A. celosiae* to *Alternaria cristata* Lawrence, Park & Pryor (MB 803181), this name is a later synonym of *A. celosiicola* described by Nishikawa & Nakashima (2013).

Alternaria gomphrenae **Togashi, *Bull. Imp. Coll. Agric. Forest. Morioka, Japan* 9: 6. 1926. Figs 13, 14.**

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

Pseudocercospora gomphrenicola Chidd., *Sci. Cult.* (*Calcutta*) **22**: 511. 1957.

Typus: **Japan**, Kyoto Prefecture, Kitashirakawa, on leaves of *Gomphrena globosa* (not specified; syntype specimens are assigned as lectotype and paralectotype, respectively, in this study). **Lectotype designated here**: **Japan**, Kyoto Prefecture, Kitashirakawa, on leaves of *G. globosa*, 24 Aug. 1924, *K. Togashi*, TNS-F-243868 [MBT 385025]; ***Paralectotype***: **Japan**, Kyoto Prefecture, Kitashirakawa, on leaves of *G. globosa*, 5 Aug. 1925, *K. Togashi*, TNS-F-243861; *ibid*., 10 Aug. 1925, *K. Togashi*, TNS-F-243862; *ibid*., 4 Dec. 1925, *K. Togashi*, TNS-F-243866; *ibid*., 19 Aug. 1924, *K. Togashi*, TNS-F-243867; *ibid*., 22 Jun. 1925, *K. Togashi*, TNS-F-243872; *ibid*., 7 Aug. 1924, *T. Hemmi & K. Togashi*, TNS-F-243873; *ibid*., 17 Aug. 1924, *K. Togashi*, TNS-F-243875. **Epitype designated here**: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *G. globosa*, 16 Oct. 2011, *J. Nishikawa*, TNS-F-85451 (dried culture of MAFF 246769) [MBT 385026], isoepitype MUMH 11685, culture ex-isoepitype MAFF 246769.

Additional materials examined: **Japan**, Kyoto Prefecture, Kitashirakawa, on leaves of *G. globosa*, 5 Aug. 1925, *K. Togashi*, TNS-F-243861; *ibid*., 10 Aug. 1925, *K. Togashi*, TNS-F-243862; *ibid*., 4 Dec. 1925, *K. Togashi*, TNS-F-243866; *ibid*., 22 Jun. 1925, *K. Togashi*, TNS-F-243872; *ibid*., 7 Aug. 1924, *T. Hemmi & K. Togashi*, TNS-F-243873; *ibid*., 17 Aug. 1924, *K. Togashi*, TNS-F-243875.

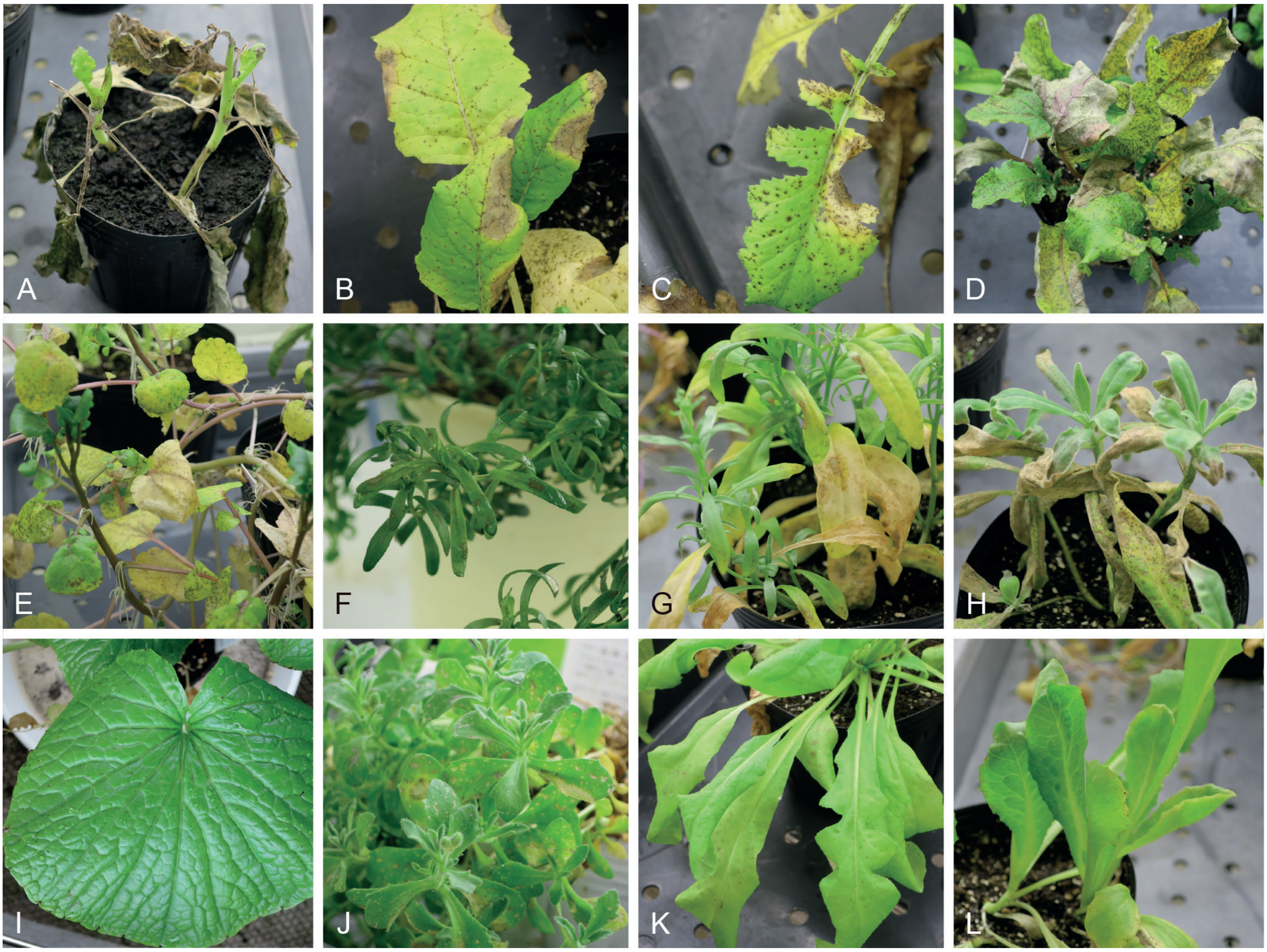

Fig. 8. Pathogenicity of *Alternaria japonica* (MAFF 246775). **A.** On *Brassica oleracea* var. *capitata* at 9 d post-inoculation (dpi). **B.** On *B. rapa* subsp. *rapa* at 10 dpi. **C.** On *Raphanus* at 10 dpi. **D.** On *Eruca* at 4 dpi. **E.** On *Nasturtium* at 4 dpi. **F.** On *Iberis* at 4 dpi. **G.** On *Lobularia* at 9 dpi. **H.** On *Matthiola* at 9 dpi. **I.** On *Eutrema* at 7 dpi. **J.** On *Aubrieta* at 7 dpi. **K.** On *Capsella* at 10 dpi. **L.** On *Lactuca* at 9 dpi.

Morphological characters on V8 medium: *Conidiophores* short and broad, 25–65 × 5–8 µm. *Conidia* usually solitary, brown to dark brown, subcylindrical to long obclavate, 50–287 µm in total length, surface smooth; conidial bodies 35–77 × 10–17 µm, with 3–9 transverse and 0–1 longitudinal septa consisting of distosepta. The lumina usually distinct, octagonal to round; filamentous beaks usually straight, subhyaline to pale brown, sometimes multiseptated, unbranched, conspicuously border the conidial body, often knobbed at the apex, 13–216 × 2–4 µm. Conidial bodies on lectotype specimens (TNS-F-243868) 46–94 × 10–16 µm, with 4–10 transverse and no longitudinal septa. Morphology on PCA medium and lesions similar to those observed on V8 medium (Table 3).

Colony characteristics on PDA after 7 d at 25 °C: Slow to moderate-growing, reaching an average of 48 ± 1.8 mm diam; aerial hypha cottony, grayish green to white, with inconspicuous margins; reverse center pale brown to reddish orange; sporulation sparse.

Sexual morph: Not observed.

Natural hosts: Gomphrena (*Amaranthaceae*).

Symptoms: Leaf and stem spots on *G. globosa* are circular to elliptical, 2–10 mm diam, pale brown with reddish margins, and become enlarged and confluent, resulting in leaf blighting.

Experimental host range: Selectively pathogenic to *Gomphrena*; weakly pathogenic or opportunistic to *Alternanthera*; non-pathogenic to *Celosia* and the other examined *Amaranthaceae* plants (Table 4).

Distribution: In Asia (Cambodia, China, India, Indonesia, Japan, Malaysia, Myanmar, and Sri Lanka), as well as North and Latin America (Cuba, Jamaica, Trinidad and Tobago, and USA) (Yoshii 1933, Ellis 1976, Simmons 1989, Zhao & Zhang 2005).

Distinctive features: Conidia are long obclavate, shorter, and narrower (usually not exceeding 100 × 20 µm) than other species infecting *Amaranthaceae*. They rarely have longitudinal septa, with octagonal lumina and colored beaks. This species is selectively pathogenic to *Gomphrena*, and recognizable phylogenetically via its ITS (Fig. 2), *gapdh*, *rpb2*, and *act* sequences (data not shown).

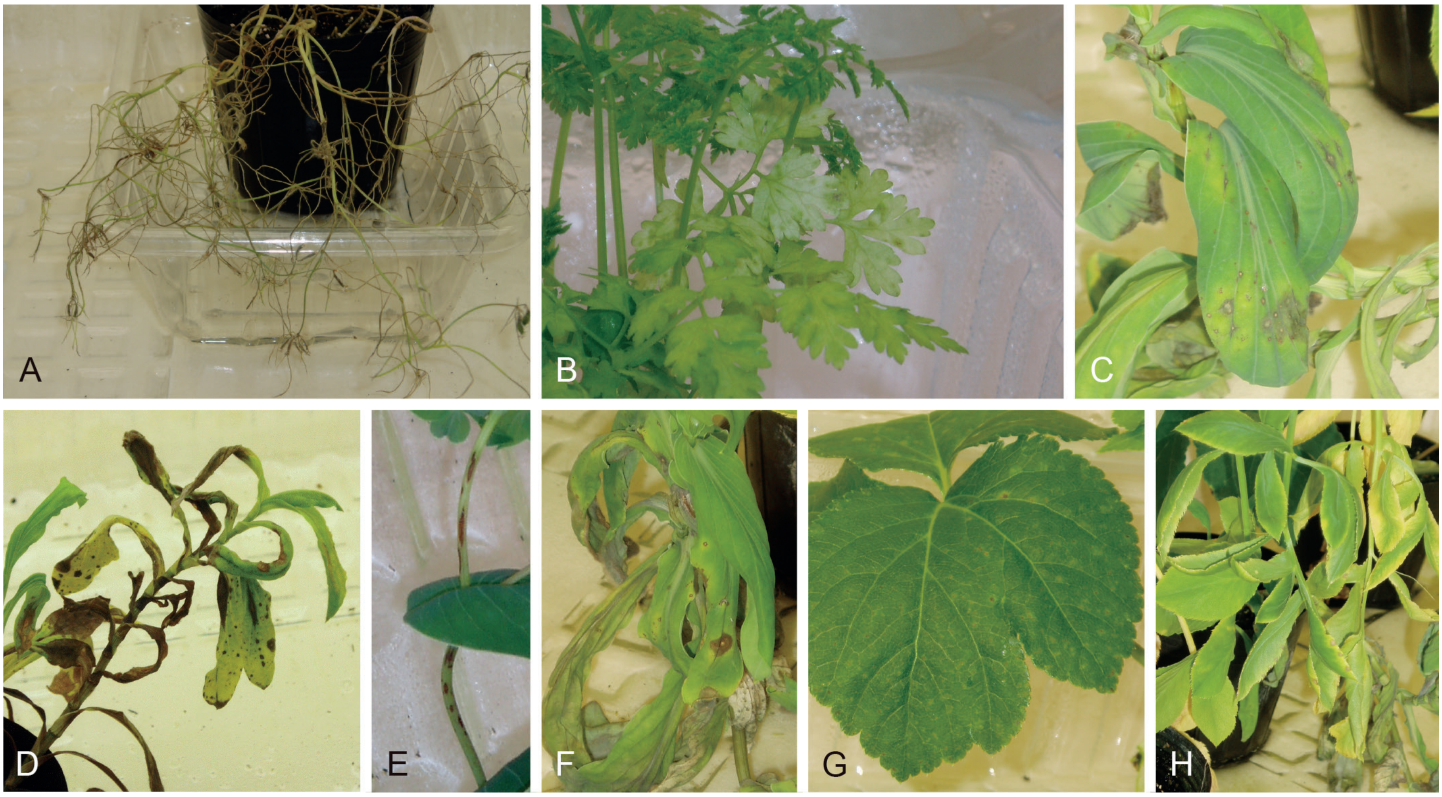

Fig. 9. Pathogenicity of two *Alternaria* species on *Apiaceae*. **A, B.** *Alternaria cumini* (MAFF 246774); **A.** On *Cuminum* at 7 d post-inoculation (dpi). **B.** On *Anthriscus* at 7 dpi. **C–H.** *Alternaria triangularis* (MAFF 246776); **C, D.** On *Bupleurum* at 8 dpi. **E.** On stem of *Bupleurum* at 8 dpi. **F.** On *Bupleurum* at 11 dpi. **G.** On *Angelica* at 10 dpi. **H.** On *Ammi* at 11 dpi.

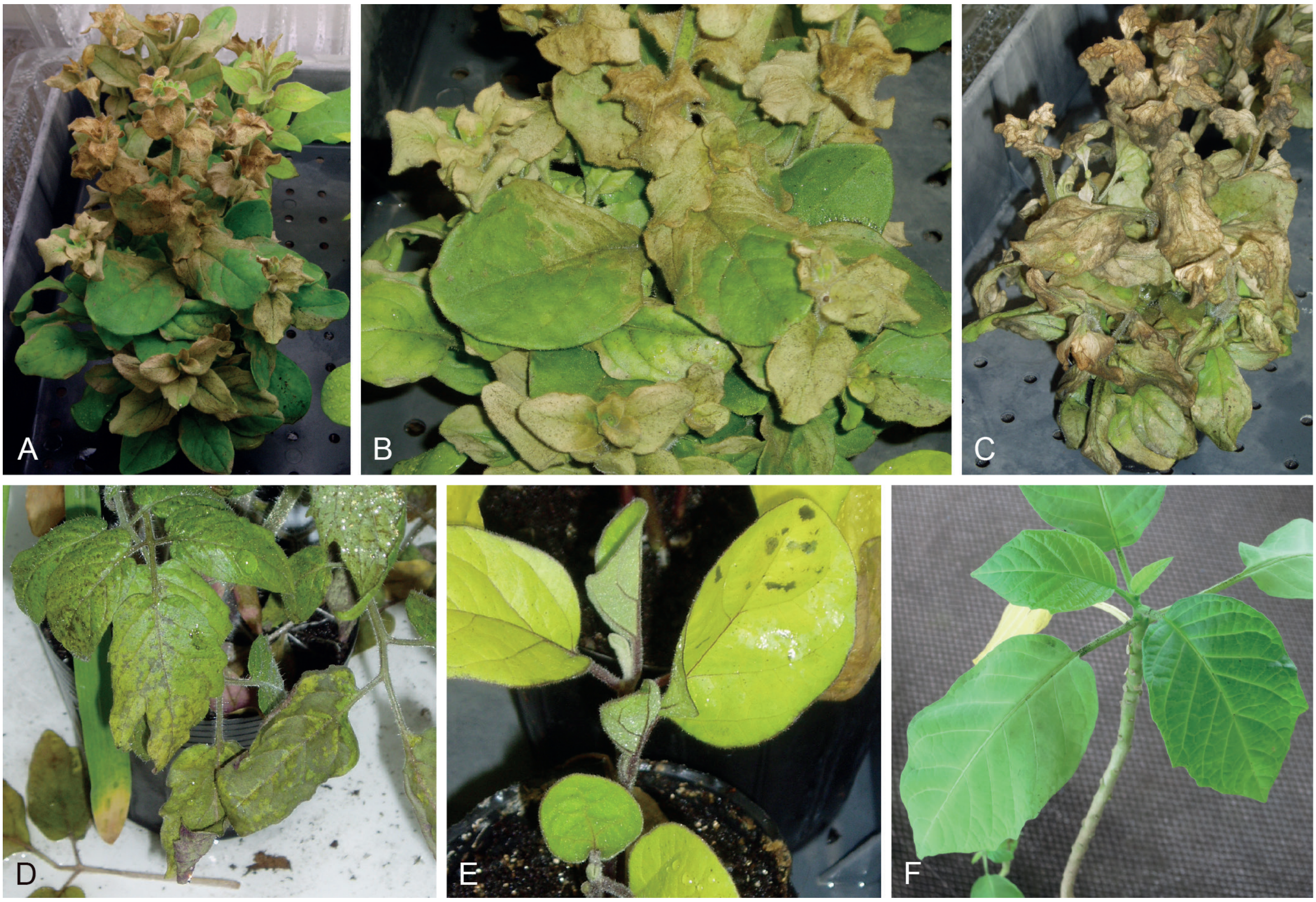

Fig. 10. Pathogenicity of *Alternaria cylindrica* (MAFF 246770). **A–C.** On *Petunia*; **A, B.** At 3 d post-inoculation (dpi). **C.** At 7 dpi. **D.** On *Solanum lycopersicum* at 6 dpi. **E.** On *S. melongena* at 7 dpi. **F.** On *Brugmansia* at 9 dpi.

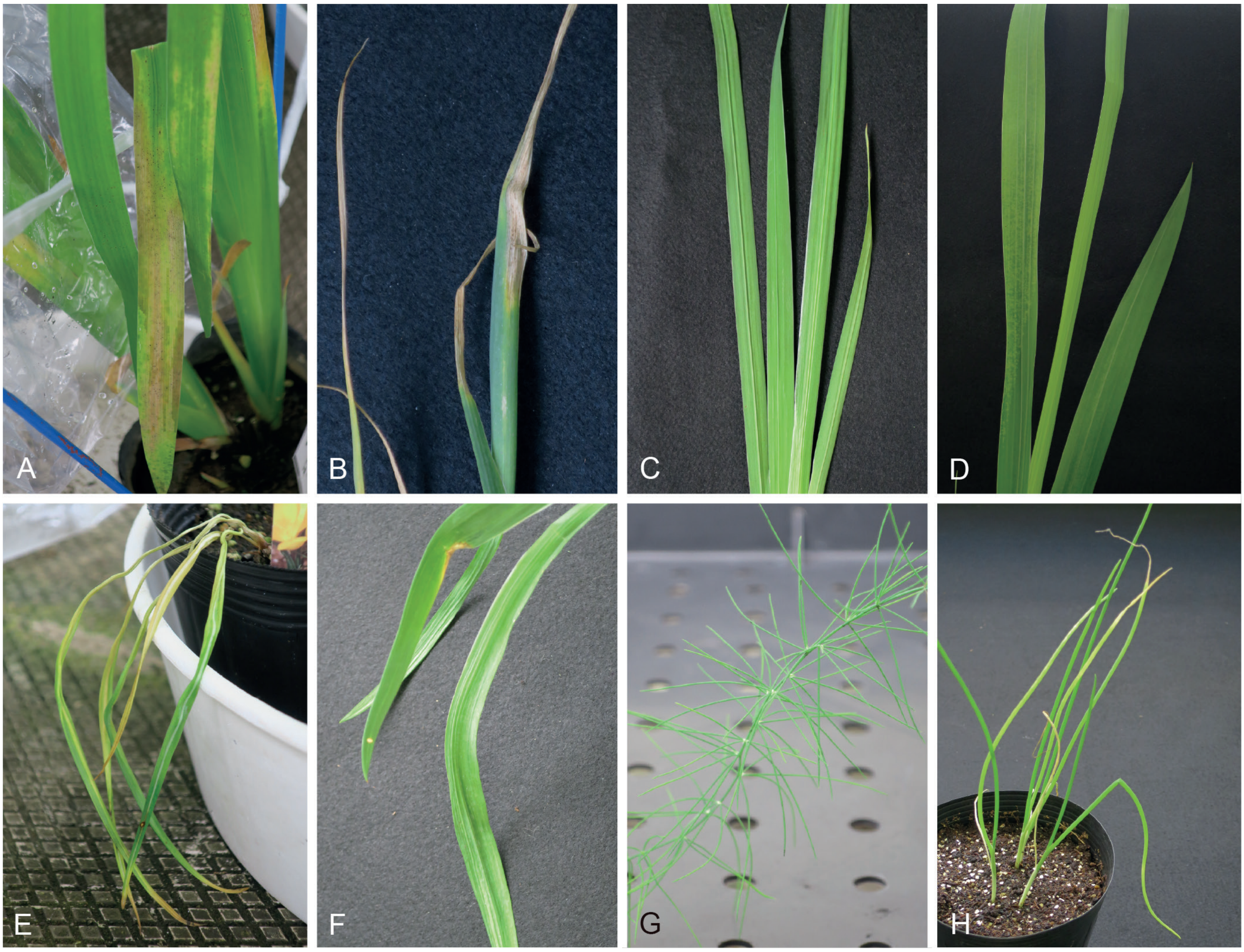

Fig. 11. Pathogenicity of *Alternaria iridicola* (MAFF 246890). **A.** On *Iris laevigata* at 6 d post-inoculation (dpi). **B.** On *Iris* × *hollandica* at 14 dpi. **C.** On *I. ensata* at 14 dpi. **D.** On *Gladiolus* at 14 dpi. **E.** On *Crocus* at 6 dpi. **F.** On *Freesia* at 14 dpi. **G.** On *Asparagus* at 14 dpi. **H.** On *Allium* at 14 dpi.

Notes: This species is the causal pathogen of leaf spot on *Gomphrena*, and was first described by Togashi (1926) in Japan. In this description, Togashi also described 10 specimens, but did not specify the holotype. Fortunately, eight of these specimens were preserved as "TYPUS" in TNS; therefore, we re-examined these syntype specimens and selected TNS-F-243868 as a lectotype in the present study. However, we confirmed rich sporulation of *A. gomphrenae*, often together with those of a small-spored *Alternaria* species, and found that Togashi, in fact, failed to establish pure cultures, much less complete inoculation testing (Togashi 1926, Yoshii 1933, Simmons 1989, 1995b). Therefore, we also designated an epitype specimen.

Alternaria paragomphrenae **Jun. Nishikawa & C. Nakash., *sp. nov*. MycoBank MB829109. Figs 15, 16.**

Etymology: Named because of its close resemblance to *Alternaria gomphrenae*, both in conidial morphology and host range.

Diagnosis: Conidial bodies are cylindrical, commonly less than 100 µm in length and exceeded 20 µm in width, sometimes with longitudinal septa forming octagonal lumina, with colored beaks. Pathogenicity of the species is selective to *Gomphrena* and *Alternanthera*. It is phylogenetically recognizable among sect. *Alternantherae* via *act*, *Alt a 1*, *gapdh*, *rpb2*, and *tef1* sequences.

Leaf and stem spots appear on *G. haageana* (*Amaranthaceae*), and are pale brown with a small, grayish eye in the center surrounded by reddish margins. They are circular to elliptical, 2–6 mm diam, scattered, show water-soaked enlargement, and become confluent resulting in leaf blighting. On V8 medium, *conidiophores* are short and thick, 27–81 × 5–7 µm. *Conidia* usually solitary, pale to brown, ellipsoid to cylindrical, 58–409 µm in total length, with a smooth surface; conidial bodies 48–98 × 17–33 µm, with 3–7 transverse and 0–4 longitudinal septa consisting of distosepta, constricted at each transverse septa. The lumina distinct to indistinct, octagonal to round; filamentous beaks straight to curved, subhyaline to pale brown, sometimes multiseptated, unbranched, conspicuously border the conidial body, 25–316 × 3–5 µm, elongated on cultures rather than on lesions. Morphology on PCA similar to that observed on V8 medium; conidiophores 43–125 × 6–9 µm, conidia 60–294 µm in total length, conidial bodies 60–111 × 15–25 µm, with 2–9 transverse and 0–3 longitudinal septa,

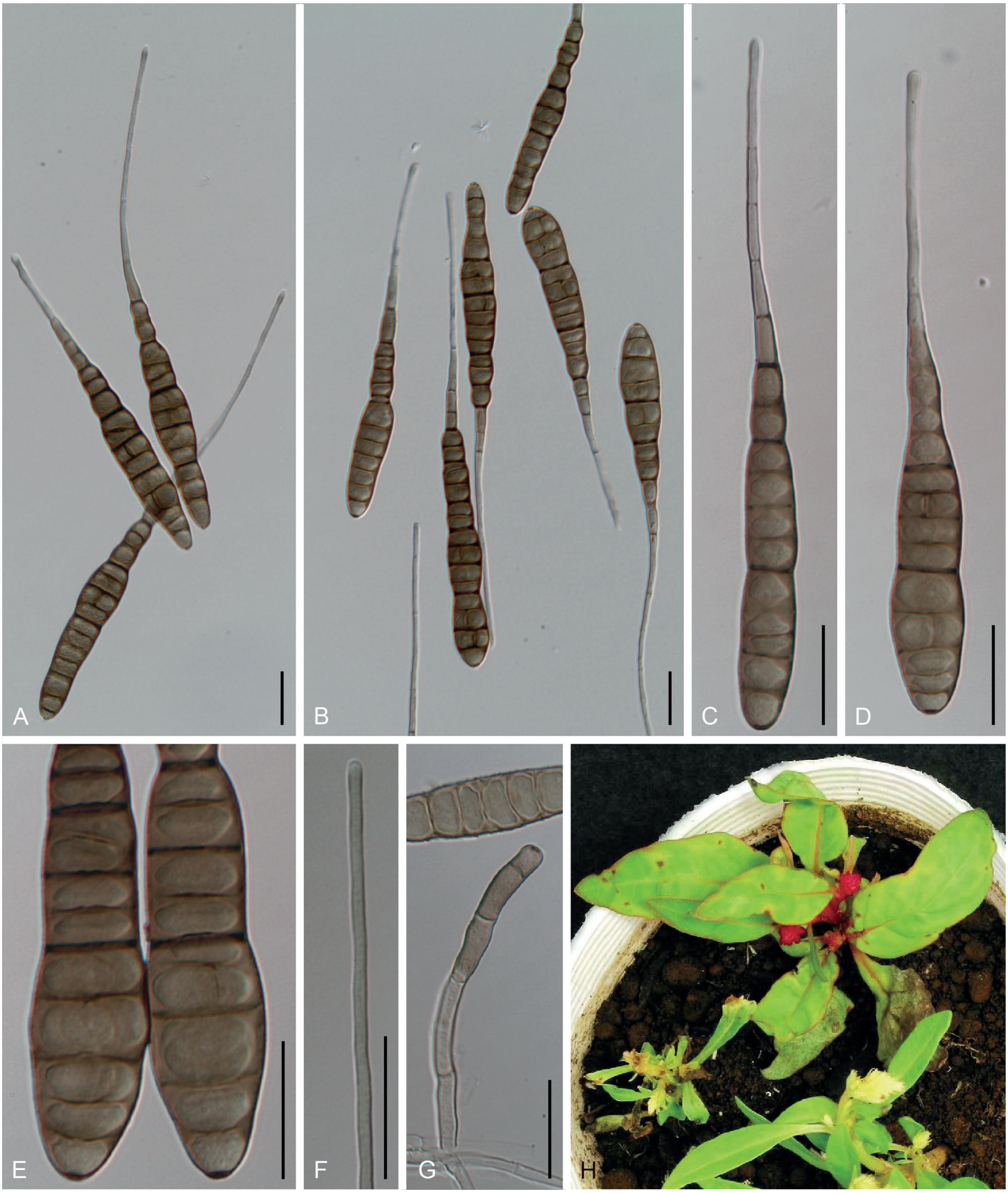

Fig. 12. Morphological features of Japanese isolates of *Alternaria celosiicola* (MAFF 243058) on potato-carrot agar medium. **A–E.** Conidia and lumina. **F.** Colored beak. **G.** Conidiophores. **H.** Natural symptoms on *Celosia*. Scale bars = 25 µm.

beaks 14–208 × 2–5 µm. On lesions, conidiophores 26–99 × 5–7 µm, conidia 35–173 µm in total length, conidial bodies 25–99 × 8–26 µm, with 1–9 transverse and 0–2 longitudinal septa, beaks 14–87 × 3–4 µm.

Typus: **Japan**, Shizuoka Prefecture, Hamamatsu, Hamakita, on leaves of *Gomphrena haageana*, 14 Sep. 2004, *J. Nishikawa*, **holotype** TNS-F-85449 (a dried culture specimen ex MAFF 246768), culture ex-holotype MAFF 246768 = MUCC 1683,

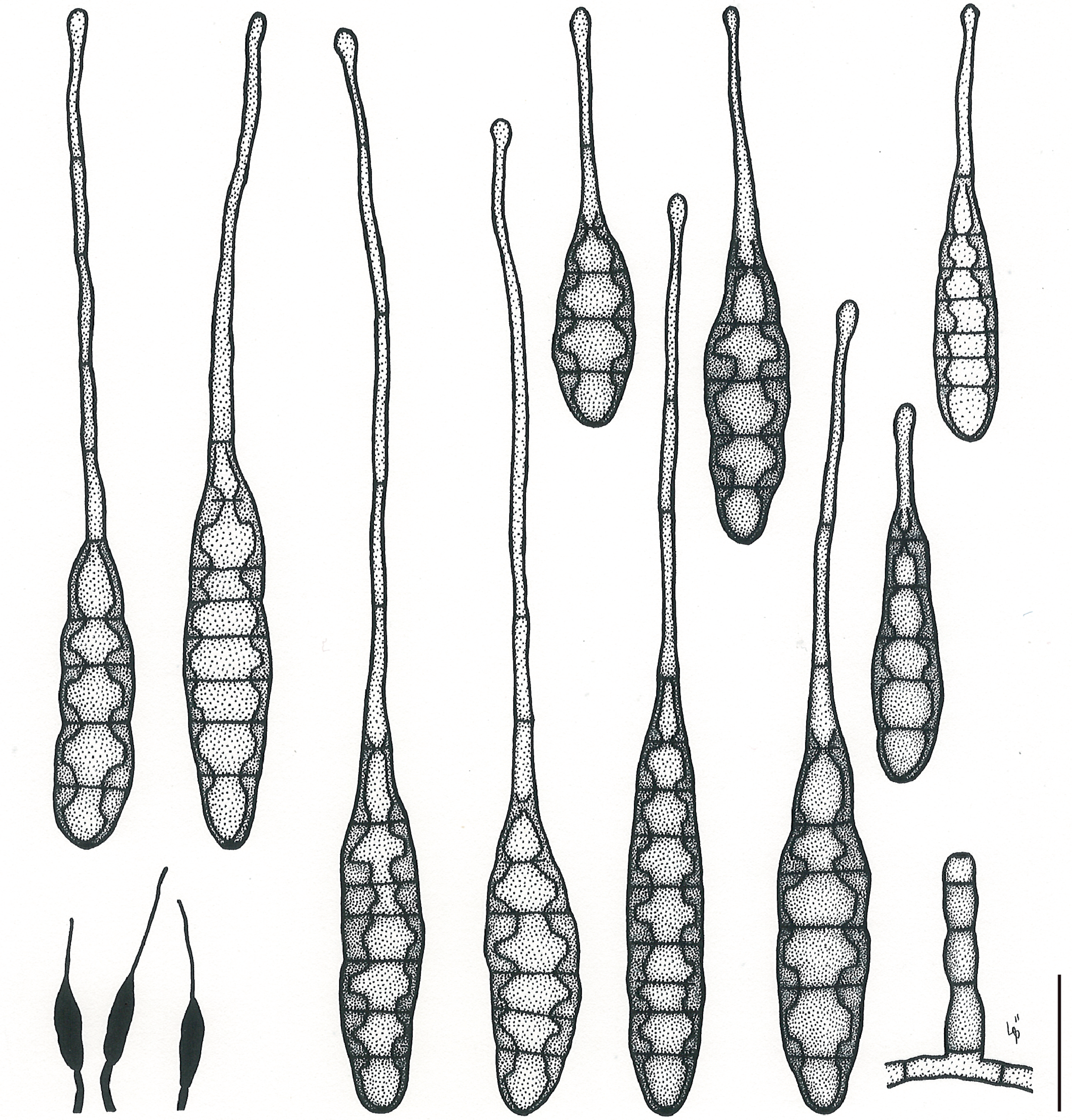

Fig. 13. Illustrations of *Alternaria gomphrenae* (MAFF 246769). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on V8 juice agar medium. Scale bar = 25 µm.

isotype MUMH 242310, GenBank accession number *gapdh*: LC482000, *rpb2*: LC476783, *tef1*: LC480207, *Alt a 1*: LC481610, *act*: LC481858.

Experimental host range: Selectively pathogenic to subfamily *Gomphrenoideae* (*Gomphrena* and *Alternanthera*), but sometimes weakly to *Celosia* and the other examined *Amaranthaceae* plants (Table 4).

Distribution: Only known from the type collection.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 59 ± 2.4 mm diam; aerial hypha cottony, pale gray to white, with inconspicuous margins; reverse center yellowish to reddish orange; sporulation sparse.

Sexual morph: Not observed.

Notes: This species demonstrates specific pathogenicity to *Gomphrena* in common with *A. gomphrenae*, and is also more aggressive to *Alternanthera* than *A. gomphrenae* (Table 4). This species is phylogenetically supported by DNA sequence data

2327 Herb. Kogo Togashi.
No. Type
Alternaria Gomphrenae Togashi
on Gomphrena globosa L.
Kitashirakawa, Kyoto.
Aug. 24, 1924. Leg. K. Togashi
TNS-F-243868
TYPUS

Fig. 14. Morphological features of Japanese isolates of *Alternaria gomphrenae* (MAFF 246769) on V8 juice agar medium. **A–H.** Conidia and lumina. **I.** Colored beak. **J.** Conidiophores. **K.** Dried culture specimen ex MAFF 246769 (epitype: TNS-F-85451). **L.** Natural symptoms on the specimen of *Gomphrena globosa* (isoepitype: MUMH 11685). **M.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **N, O.** Lectotype specimen, TNS-F-243868. **P, Q.** Conidia on lectotype. Scale bars (A–J, P, Q) = 25 µm.

combined with *gapdh*, *tef1*, and *rpb2*, but close to *A. celosiicola* rather than *A. gomphrenae* (Fig. 1). Based on its shorter and wider bodies, this species is morphologically distinct from these two relevant species (Table 3).

Section *Alternaria* D.P. Lawr. *et al.*, *Mycologia* **105**: 538. 2013.

This section was morphologically characterized by catenate, small spores, which were typified by those of *A. alternata* (Lawrence *et al*. 2013, Woudenberg *et al*. 2015). Eleven species with three *formae speciales* of *A. alternata* and one species complex (*A. arborescens*) were recognized by Woudenberg *et al.* (2015). This section also includes important host-selective toxin producers, and they were recognized as distinct species or *formae speciales* of *A. alternata* (Woudenberg *et al*. 2015). Four species with two *formae speciales* and a novel species from Japan are described in the present study. Additionally, *A. iridicola* is newly assigned to this section.

Alternaria alstroemeriae E.G. Simmons & C.F. Hill, in Simmons, *CBS Biodiversity Ser.* (*Utrecht*) 6: 444. 2007. Fig. 17.

Typus: **Australia**, on leaves of *Alstroemeria* sp., Jul. 2005, *C.F. Hill*, **holotype** BPI 877375 (dried culture ex EGS 52.068), culture ex-type CBS 118809 = EGS 52.068.

Additional material examined: **Japan**, Nagano Prefecture, Matsumoto, on leaves of *Alstroemeria* sp., Jan. 2008, *N. Yamagishi*, living culture MAFF 241374.

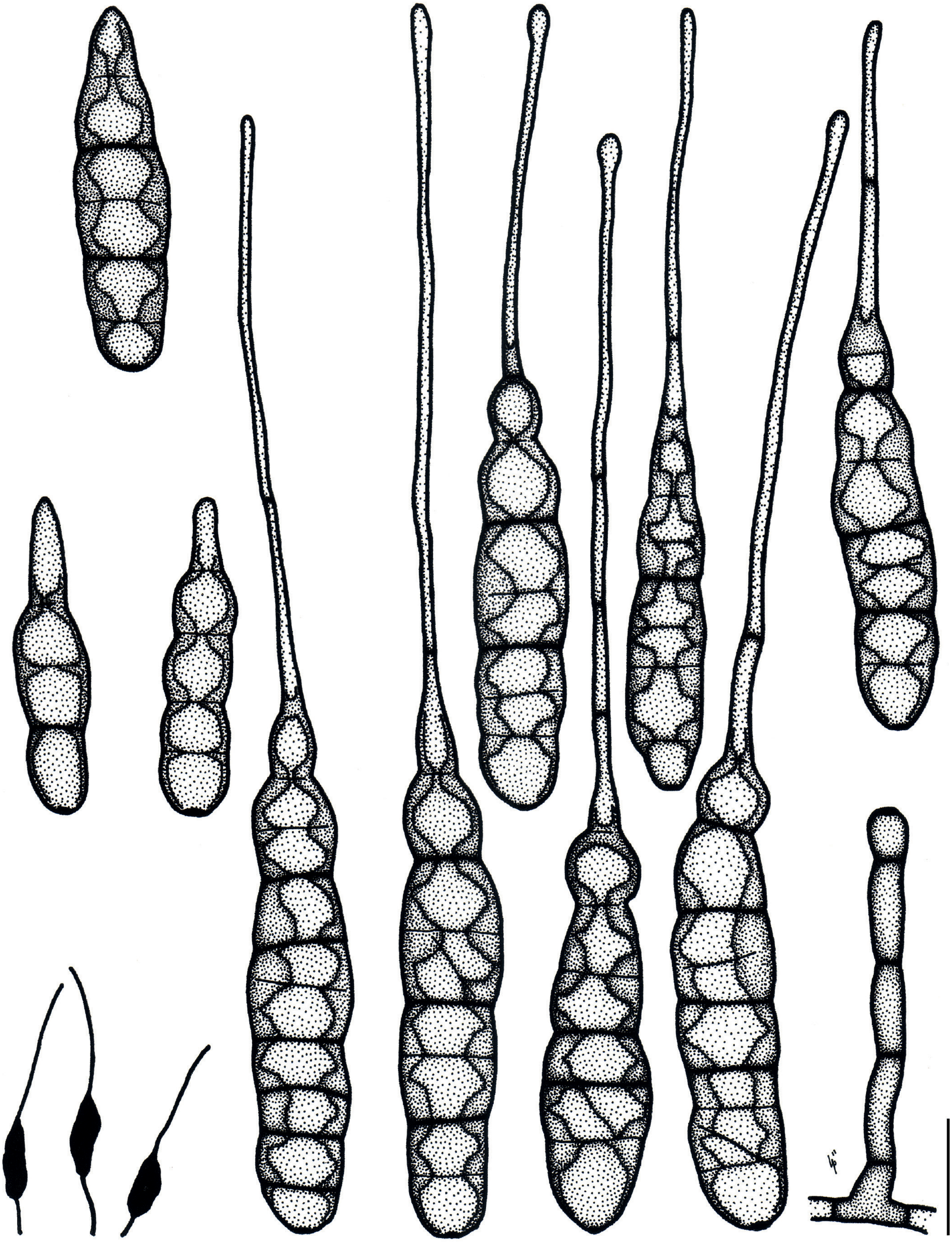

Fig. 15. Illustrations of *Alternaria paragomphrenae* (MAFF 246768). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on V8 juice agar medium. Scale bar = 25 µm.

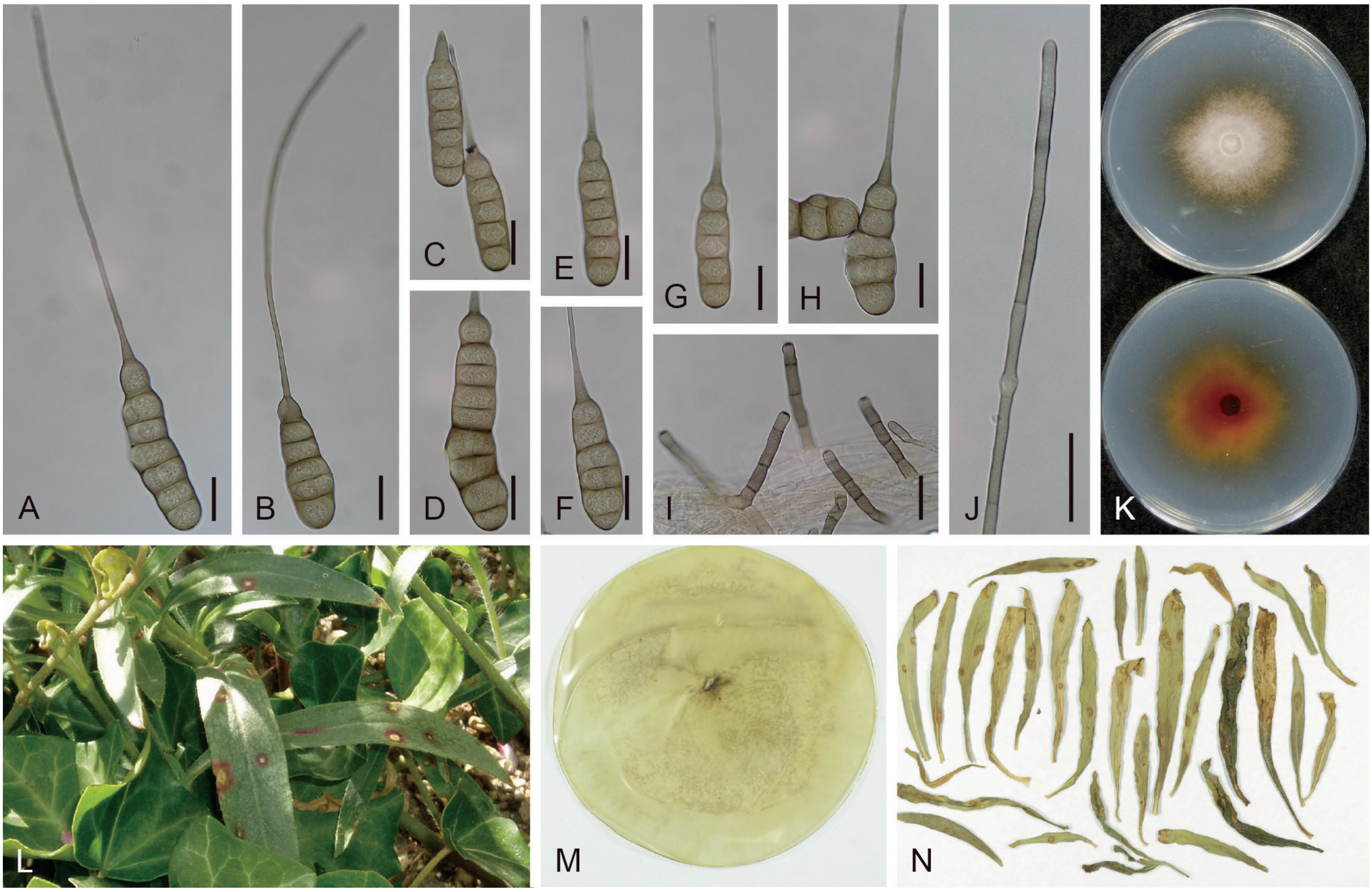

Fig. 16. Morphological features of *Alternaria paragomphrenae* (ex-holotype culture MAFF 246768) on V8 juice agar medium. **A–H.** Conidia and lumina. **I.** Conidiophores. **J.** Colored beak. **K.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **L.** Natural symptoms on *Gomphrena haageana*. **M.** Dried culture specimen ex MAFF 246768 (holotype: TSN-F-85449). **N.** Isotype specimen, MUMH 242310. Scale bars (A–J) = 25 µm.

Morphological characters on PCA medium: Previously reported in Yamagishi *et al*. (2009).

Colony characteristics on PDA after 7 d at 25 °C: Fast-growing, reaching 74.6 ± 1.6 mm diam (Nishikawa & Nakashima 2013); aerial hypha sparse, olive brown to black, with indistinct margins; reverse center black to dark green; sporulation abundant on conidiophores arising from aerial and submerged hypha; diffusible pigment absent.

Sexual morph: Not observed.

Natural host: *Alstroemeria* (*Alstroemeriaceae*).

Symptoms: Leaf spots are circular to subcircular, 3–12 mm diam, and are dark brown to black. The same spots also form on stems, followed by defoliation.

Experimental host range: The Japanese isolate shows a restricted host range; it is pathogenic to *Alstroemeria*, but not to the other plants formerly classified as *Liliaceae*, including *Lilium*, *Tulipa*, *Allium*, *Asparagus*, and *Hyacinthus* (Nishikawa & Nakashima 2013).

Distribution: Limited to Australia (Simmons 2007), and Japan (Yamagishi *et al.* 2009, Nishikawa & Nakashima 2013).

Distinctive features: Mature and basal conidia are often subcylindrical, rarely with longitudinal septa; conidia appear in short chains (never exceeding 10) in 7 d; sporulation occurs in part when submerged in agar substrate. It is phylogenetically distinguishable from the other species of this section via its *gapdh*, *rpb2*, *tef1*, *Alt a 1*, and *endoPG* sequences (Figs 1, 3), but not via ITS (Fig. 2) and *act* sequences (data not shown).

***Alternaria alternata* (Fr.) Keissl., *Beih. Bot. Centralbl., Abt. 2*, 29: 434. 1912. Fig. 18.**

Synonyms: *Torula alternata* Fr., *Syst. Mycol.* (*Lundae*) **3**: 500. 1832, *nom. sanct*.
Alternaria tenuis Nees, *Syst. Pilze* (*Würzburg*): 72. 1817.
Additional synonyms fully provided in Woudenberg *et al*. (2015) although *A. viniferae* was doubtful as described below.

Typus: **Neotype**, on fragments of a pithy stem, *C.G.D. Nees von Esenbeck*, L 910, 262-129 (designated in Simmons 1967); **Epitype**, **India**, on *Arachis hypogaea*, 1 Dec. 1980, *E.G. Simmons*, IMI 254138 (designated in de Hoog & Horré 2002), culture ex-epitype CBS 916.96 = ATCC 66981 = EGS 34.016.

Additional materials examined: **Japan**, from seeds of *Vigna radiata*, 1998, *T. Sato*, MUMH 11693, living culture MAFF 239887; Nagano Prefecture, Azumino, on leaves of *Impatiens hawkeri*, 28 Aug. 2006, *J. Nishikawa*, living culture MUCC 1610; Shizuoka Prefecture, Kakegawa,

Fig. 17. Morphological features of Japanese isolates of *Alternaria alstroemeriae* (MAFF 241374) on potato-carrot agar medium. **A–G.** Conidia. **H.** Submerged sporulation in media. **I.** Conidiophores. Scale bars = 25 µm.

on leaves of *Antirrhinum majus*, 28 May 2008, *J. Nishikawa*, MUMH 11682, living culture MUCC 1611; Kanagawa Prefecture, Nakai, on leaves of *Pelargonium hortorum*, 29 Sep. 2004, *J. Nishikawa*, MUMH 11672, living culture MUCC 1616; Shizuoka Prefecture, Kakegawa, on leaves of *Primula × polyantha*, 6 Nov. 2004, *J. Nishikawa*, MUMH 11674, living culture MUCC 1617; Shizuoka Prefecture, Kakegawa, on leaves of *Solanum lycopersicum*, 28 Jun. 2011, *J. Nishikawa*, living culture AC82; Tokyo, Chiyoda, from seeds of *V. radiata*, Dec. 2012, *T. Sato*, living culture MAFF 243775; Kanagawa Prefecture, on leaves of *Pyrus aromatica*, 1958, *S. Toyota*, living culture MAFF 305014; on leaves of *Pyrus* sp.?, *M. Kusunoki*, living culture MAFF 410775.

Morphological characters on PCA medium: *Conidiophores* solitary, subcylindrical, unbranched, straight or geniculate, thin, 15–93 × 3–5 µm, sometimes proliferating sympodially. *Conidia* form as complex, long chains of 10–22, commonly with lateral branches, highly varied, ovoid to ellipsoid, pyriform or obclavate, pale brown to brown, usually smooth; conidial bodies 11–50 × 7–18 µm and 25 × 12 µm on average, commonly not exceeded 50 µm long, with 1–7 transverse and 0–5 longitudinal septa, slightly constricted at the median and some transverse septa. Secondary conidiophores (false beaks) appear at the apical end of conidia, short and mostly single-celled, but often unstable in length (some in isolate MAFF 239887 elongated, reaching 19–110 µm).

Colony characteristics on PDA after 7 d at 25 °C: Fast-growing, reaching an average of 77.3 ± 1.3 mm diam; aerial hypha cottony, sometimes sparse, variable in color, pale gray, grayish green to dark green, with white margins; reverse center black to dark green; sporulation abundant; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: Multiple genera in multiple families serve as hosts, and it is often saprophytic; 692 host records were found in USDA Fungal databases (Farr & Rossman 2018), and 32 diseases in the database of plant diseases in Japan, including three

Fig. 18. Japanese isolates of *Alternaria alternata*. **A–K.** Conidia and conidiophores on potato-carrot agar medium ex MUCC 1610 (A, B), MUCC 1611 (C, D), MUCC 1616 (E, F), and MAFF 239887 (G–K). **L–O.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse) of MUCC 1610 (L), MUCC 1611 (M), MUCC 1616 (N), and MAFF 239887 (O). **P–R.** Natural symptoms on *Impatiens* (P), *Antirrhinum* (Q), and *Pelargonium* (R). Scale bars (A–J) = 25 µm.

pathotype strains (http://www.gene.affrc.go.jp/databases-micro_pl_diseases_en.php).

Symptoms: Necrotic spots on *Impatiens* are sometimes circular and often irregular, measuring 1–8 mm diam. Leaf spots on *Antirrhinum* are usually fairly circular, measuring 5–10 mm diam, developing into coalesced lesions that are gray with pale brown margins. Leaf and stem spots on *Pelargonium* seedlings are irregular, then represented as leaf blight. As for isolates MAFF 239887 and MAFF 243775 obtained from *Vigna*, lesions appearing from the roots to the hypocotyls of sprouts appear black and rotten (Sato *et al.* 2014, Sato 2015), and angular to irregular spots are produced on inoculated true leaves (Sato, pers. comm.).

Distribution: Ubiquitous.

Distinctive features: Small conidia, conidial bodies rarely exceed 50 µm long, and are formed in long chains (mostly over 20 conidia), frequently with lateral branches. Secondary conidiophores are commonly short, consisting of 1–2 cells.

Notes: Woudenberg *et al.* (2015) synonymized 35 names under this species based on their multi-locus phylogeny. Those synonyms include important host selective species, such as *A. mali*, *A. limoniasperae*, and *A. toxicogenica*, which were newly assigned as *formae speciales* (with pathotypes) of the species: *f. sp. mali*, *f. sp. citri* pathotype rough lemon, and *f. sp. citri* pathotype tangerine, respectively. *Alternaria viniferae* was synonymized by Woudenberg *et al.* (2015); however, this classification is problematic because of the original description using a *gapdh* and *Alt a 1*-based phylogeny, as well as *A. alstroemeriae*-like morphology (Tao *et al.* 2014), which are highly distinguishable from those of *A. alternata*.

Alternaria cylindrica **Jun. Nishikawa & C. Nakash.,** ***sp. nov.*** **MycoBank MB829136. Figs 19, 20.**

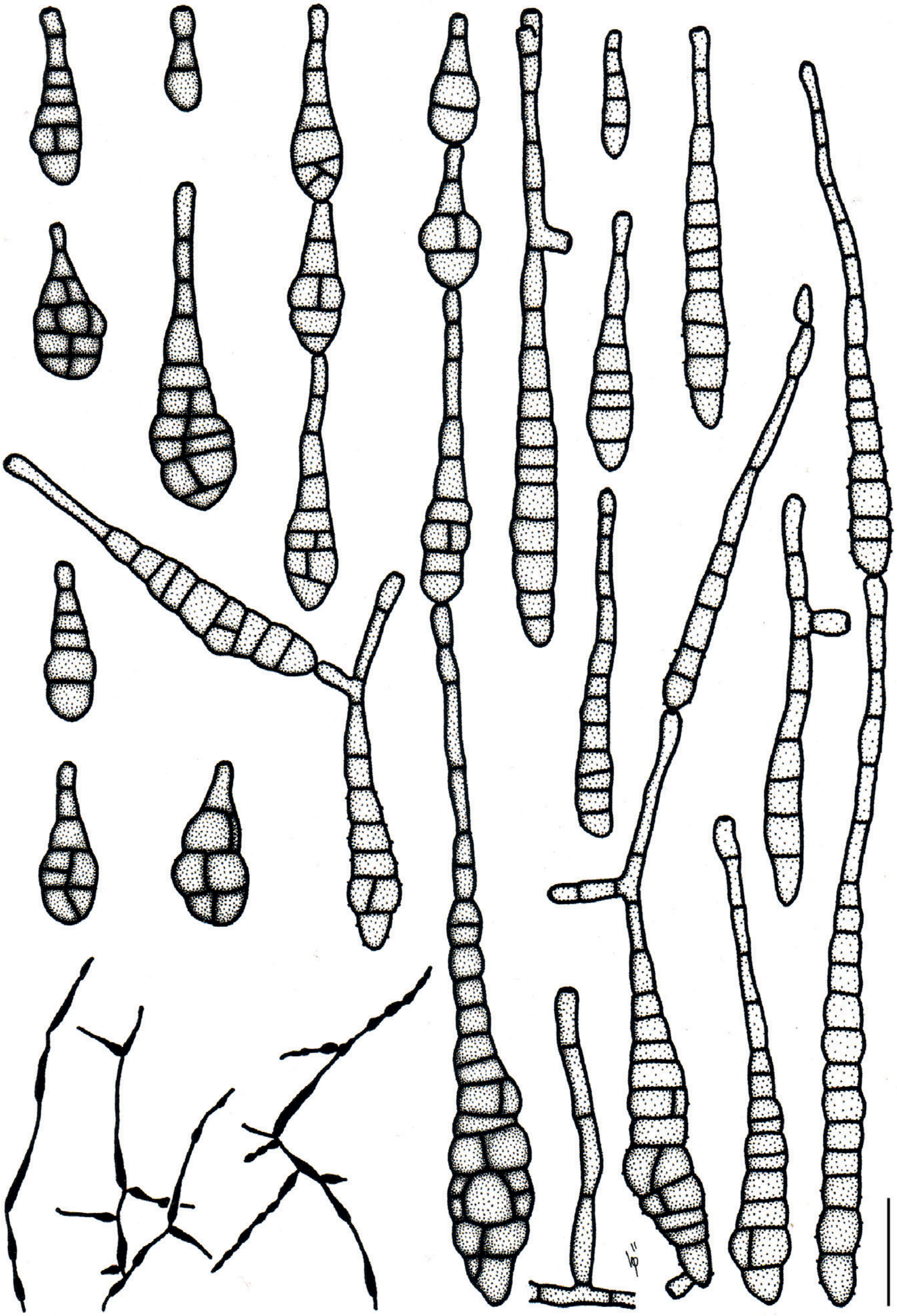

Fig. 19. Illustrations of *Alternaria cylindrica* (ex-holotype culture MAFF 246770). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on V8 juice agar medium. Scale bar = 25 µm.

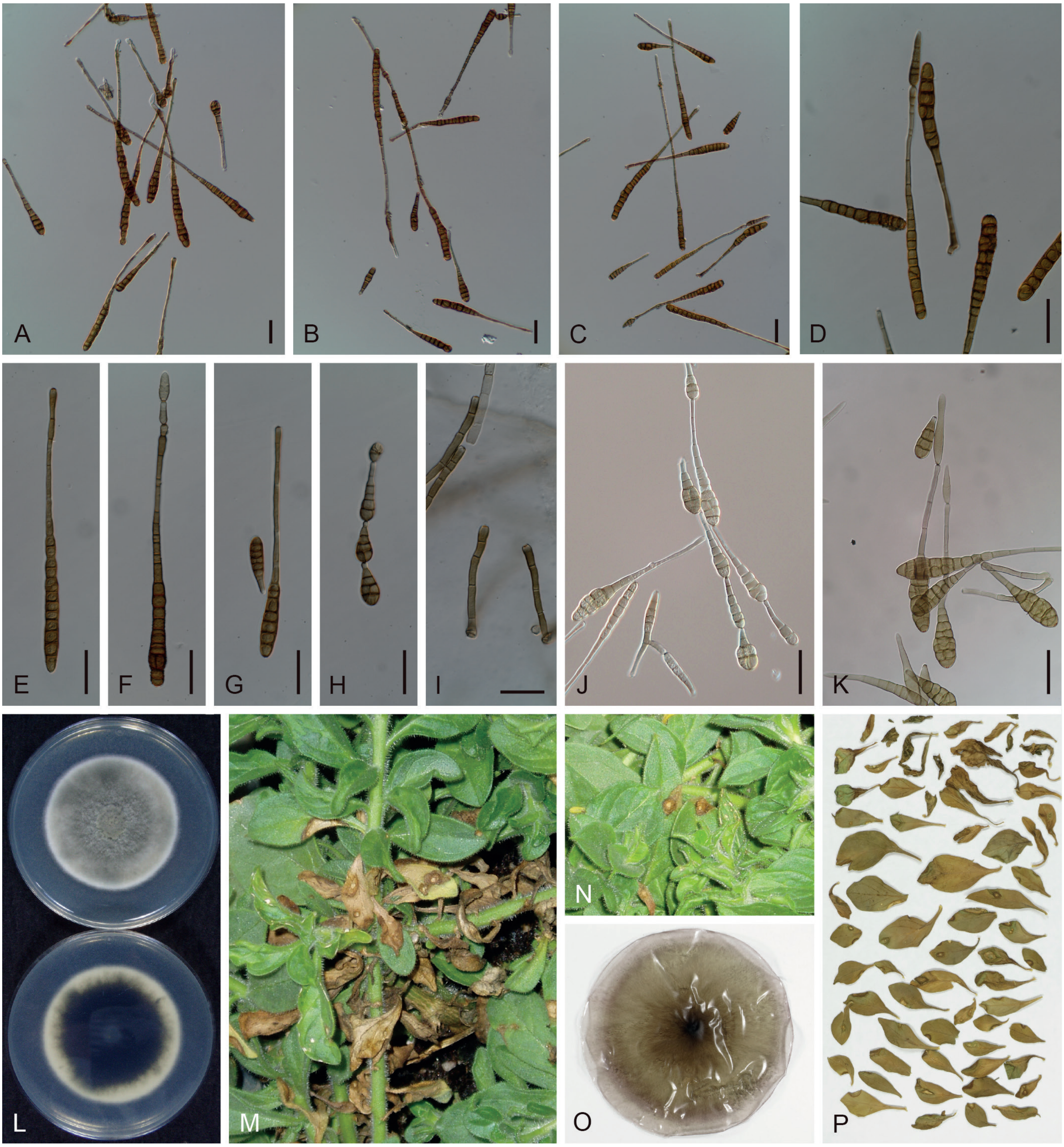

Fig. 20. Morphological features of Japanese isolates of *Alternaria cylindrica* (ex-holotype culture MAFF 246770). **A–I.** Conidia and conidiophores on potato-carrot agar medium. **J.** Conidia on V8 juice agar medium. **K.** Conidia on lesion. **L.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **M, N.** Natural symptoms on *Petunia*. **O.** Dried culture specimen ex MAFF 246770 (holotype: TNS-F-85450). **P.** Isotype specimen. Scale bars (A–K) = 25 µm.

Etymology: Named after the Latin "*cylindricus*", referring to the shape of the conidia, which are cylindrical.

Diagnosis: Long and narrow, cylindrical conidia with few longitudinal septa, which are produced abundantly in long chains and are quite distinctive among members of the genus. Obclavate conidia such as typically seen in sect. *Alternaria* are often produced at the apex and sides of chains. Pathogenicity is selective to *Petunia* among members of the *Solanaceae*. It is phylogenetically close to *A. alternata* and the *A. arborescens* species complex.

Leaf spots appear on *Petunia*, which are dark brown to black with a pale brown eye in the center. They are circular to irregular, measuring 4–7 mm diam, are scattered, and become enlarged and confluent, resulting in blighting of leaves. On V8 medium, *conidiophores* narrow and short to moderately long, 28–90 × 4–6 µm. *Conidia* mostly in chains of 5–9 conidia (moderately long chain), lateral branches frequently present in 5–7 d. Conidia subhyaline to pale brown, obclavate and cylindrical to long and narrow ovoid, 11–214 µm in total length, with 0–21(–33) transverse and 0–7 (relatively uncommon) longitudinal septa. Conidial bodies 11–156 × 5–20 µm with 0–13(–25) transverse and 0–7 (relatively uncommon) longitudinal septa, usually smooth surface but very occasionally faintly rough. Secondary conidiophores (false beaks) elongated up to 120 × 3–6 µm. On lesions, conidiophores 30–79 × 5–7 µm. Conidia typically 21–192 µm in total length; conidial bodies 11–89 × 6–18 µm with 1–14 transverse and 0–7 longitudinal septa; secondary conidiophores up to 121 × 3–6 µm. Morphology grown on PCA medium similar to that observed on V8 medium: conidiophores 29–98 × 3–6 µm; conidia 18–270(–340) µm in total length, with 0–30(–43) transverse and 0–4 longitudinal septa; conidial bodies 10–115 × 5–14 µm, with 0–19 transverse and 0–4 longitudinal septa; secondary conidiophores up to 225 × 3–5 µm.

Typus: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *Petunia* × *atkinsiana*, 16 Dec. 2006, *J. Nishikawa*, **holotype** TNS-F-85450 (a dried culture specimen ex MAFF 246770), **isotype** MUMH 11678 and MUMH 11703, culture ex-holotype MAFF 246770, GenBank accession number ITS: LC440584, *gapdh*: LC482006, *rpb2*: LC476791, *tef1*: LC480211, *Alt a 1*: LC481616, *endoPG*: LC480951, *act*: LC481867.

Experimental host range: Selectively pathogenic to *Petunia* among members of the examined *Solanaceae* plants, but remarkable lesions with no sporulation were frequently observed on the inoculated leaves of *Solanum* (Table 7).

Distribution: Only known from Japan.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching 58.4 ± 0.7 mm diam; aerial hypha cottony, pale gray to grayish or bluish green, with white margins; reverse center dark green to black; sporulation sparse; diffusible pigment absent.

Sexual morph: Not observed.

Notes: Takano (2005) reported a similar disease on *Petunia* in Japan, and he identified the pathogen as *A. longissima*, which was commonly known as a saprophytic fungus of numerous plants and was characterized as having cercosporoid scolecospores with few longitudinal septa (Deighton & MacGarvie 1968, Ellis 1971). *Alternaria longissima* has since been transferred to the genus *Prathoda* by Simmons (2007), which was supported by molecular phylogenetic analysis indicating that the species should not be treated as an *Alternaria* species (Pryor & Gilbertson 2000). Both our examined isolate and those in Takano (2005) were nearly morphologically identical to each other; however, our examined isolate obviously belongs to a species in the sect. *Alternaria* based on phylogenetic analysis (Figs 1–3). Although these isolates need to be re-examined, they were probably previously misidentified.

Alternaria gaisen **Bokura, *J. Pl. Protect.* (*Tokyo*) 11: 490. 1924. Fig. 21.**

Synonyms: *Alternaria gaisen* Nagano, *J. Jpn. Hort. Soc.* (*Nihon Engei Zasshi*) **32** (3): 16. 1920, *nom. inval*. (provisional name; ICN Art. 36.1).
Alternaria gaisen Nagano, in Hara, *Jitsuyo Sakumotsu Byorigaku*: 263. 1925.
Alternaria gaisen Nagano ex Hara, *Sakumotsu Byorigaku*, Edn 4: 263. 1928, in Woudenberg *et al*., *Stud. Mycol.* **82**: 15. 2015, *nom. superfl*.
Alternaria kikuchiana S. Tanaka, *Mem. Coll. Agric. Kyoto Imp. Univ.* **28** (*Phytopathol. Ser.* **6**): 27. 1933.

Typus: **Japan**, Nara Prefecture, on leaves of *Pyrus pyrifolia* var. *culta* 'Nijisseiki' (details unknown; not preserved). **Lectotype**, Nagano K., *J. Jpn. Hort. Soc.* (*Nihon Engei Zasshi*) **32** (3): 17, figures (iconotype, selected by Simmons 2007). **Epitype**, **Japan**, Tottori Prefecture, on *P. pyrifolia* var. *culta*, Jul. 1990, *E.G. Simmons*, dried culture specimen CBS H-22842 (designated in Nishikawa & Nakashima 2019), culture ex-epitype CBS 118488 = EGS 90.0391.

Additional materials examined: **Japan**, Iwate Prefecture, Morioka, on leaves of *Fragaria × ananassa* 'Morioka-16', 1975, *Y. Watanabe*, living cultures M-11 (MAFF 731001), M-14 (MAFF 731002), M-15 (MAFF 731003), M-17 (MAFF 731004), M-20 (MAFF 731005), M-22 (MAFF 731006), M-23 (MAFF 731007); Tottori Prefecture, Tohaku, Hokuei, Horticultural Research Center, on leaves of *P. pyrifolia* var. *culta* 'Nijisseiki', Jul. 1999, *F. Yasuda*, living cultures 9901A (MUCC 2151), 9903A (MUCC 2152), 9904C (MUCC 2153); Hokkaido, Esashi, on leaves of *Fragaria × ananassa* 'HS-138', Aug. 2007, *T. Misawa*, dried culture specimen MUMH 11698, living culture E-11 (MAFF 242310 = MUCC 1609); Hokkaido, Hokuto, on leaves of *Fragaria × ananassa* 'HS-138', 22 May 2008, *T. Misawa*, MUMH 11681 (inoculated leaves with MAFF 242310).

Morphological characters on PCA medium: Previously reported in Nishikawa & Nakashima (2019).

Colony characteristics on PDA after 7 d at 25 °C: Fast-growing, reaching an average of 82.1 ± 0.7 mm diam; aerial hypha cottony, grayish green to dark green, with white margins; reverse center dark green to black; sporulation abundant; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: *Fragaria × ananassa* 'Morioka-16', *P. pyrifolia* var. *culta* 'Nijisseiki', and their related cultivars (*Rosaceae*).

Symptoms: Leaf spots on strawberries are circular, 3–12 mm diam, brown to black with a reddish-brown border and a yellowish halo that is grayish brown at the center, which may be extend by the fungal toxin.

Host range: It is known as a host-selective toxin producer, which is pathogenic to strawberry cultivar 'Morioka-16' and Japanese pear cultivar 'Nijisseiki', and a few of their related lines (Hayashi *et al.* 1992).

Distribution: Limited to Japan (Nagano 1920, Watanabe & Umekawa 1977), New Zealand (Dingley 1970), Korea (Cho & Moon 1980), and Italy (Wada *et al.* 1996).

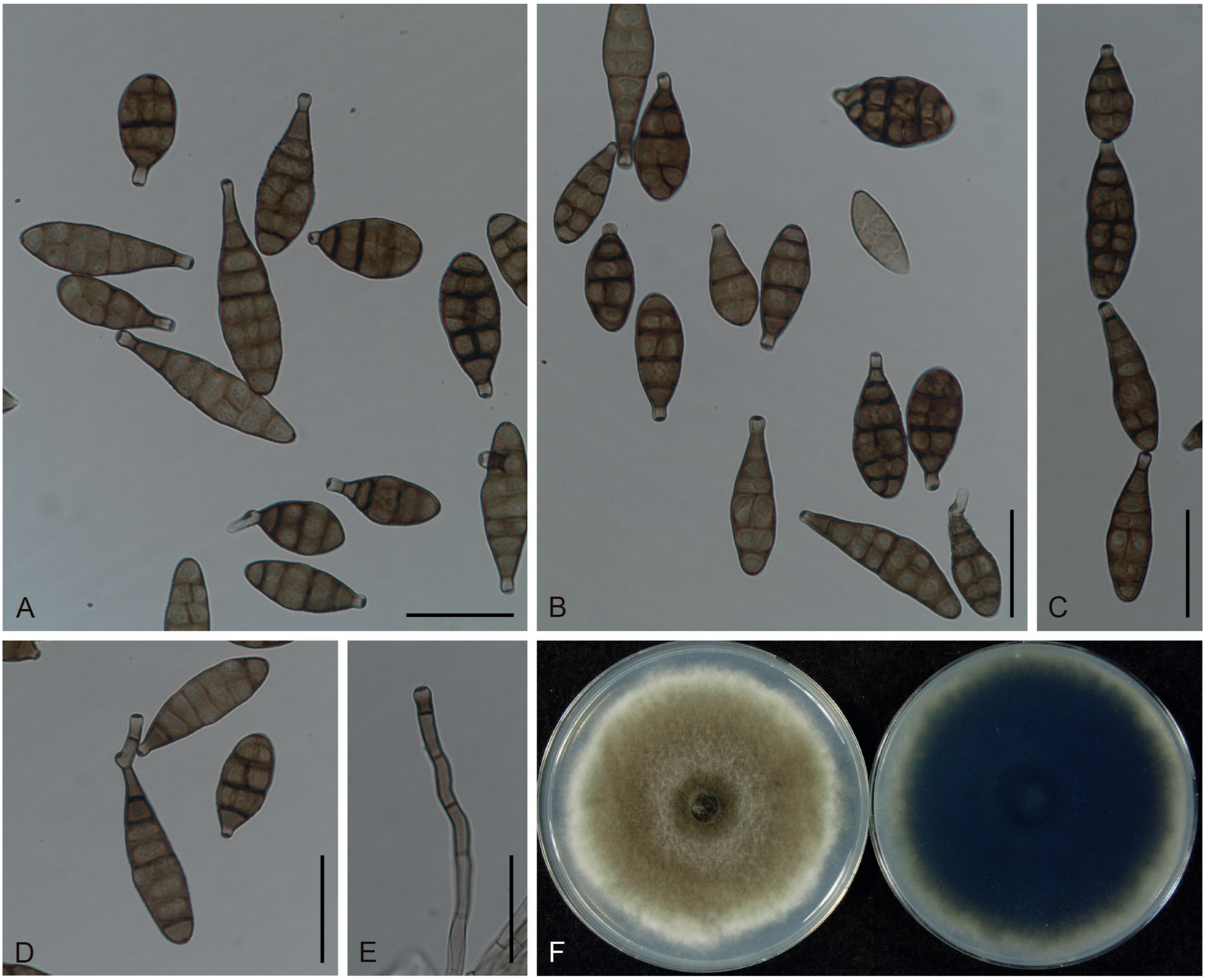

Fig. 21. Morphological features of Japanese isolates of *Alternaria gaisen f. sp. fragariae* (MAFF 242310) on potato-carrot agar medium. **A–D.** Conidia. **E.** Conidiophore. **F.** Culture on potato-dextrose agar medium (left = surface, right = reverse). Scale bars (A–E) = 25 µm.

Distinctive features: Conidia form in short, unbranched chains. It is pathogenic to only a few cultivars of strawberry (cv. Morioka-16) and Japanese pear (cv. Nijisseiki) owing to its production of AF-toxin. Phylogenetically, it is clearly distinguishable from the other species of this section via *gapdh*, *rpb2*, *Alt a 1* and *endoPG* sequences (Figs 1, 3).

Notes: Within the species, *A. gaisen* includes two *formae speciales*, *A. gaisen f. sp. pyri* producing the AK-toxin (toxic to Japanese pear), and *f. sp. fragariae* producing the AF-toxin (toxic to strawberry) (Nishikawa & Nakashima 2019).

Alternaria iridicola **(Ellis & Everh.) J.A. Elliott, *Am. J. Bot.* 4: 450. 1917. Figs 22, 23.**
Basionym: *Macrosporium iridicolum* Ellis & Everh., *Proc. Acad. Nat. Sci. Philad.* **46**(3): 382. 1894.

Typus: **USA**, Idaho, Moscow, on *Iris missouriensis*, 27 May 1894, *Henderson*, **holotype** NY 2640. **Epitype designated here, Japan**, Kanagawa Prefecture, Kamakura, on leaves of *Iris japonica*, 17 Apr. 2013, *H. Horie*, TNS-F-85452 (dried culture specimen of MAFF 246890) [MBT385027], isoepitypes MUMH 11687and MUMH 11739, culture ex-epitype MAFF 246890 = MUCC 2149.

Additional materials examined: **Japan**, Tokyo, Kodaira, on *I. japonica*, 2010, *H. Horie*, living culture MUCC 2148; Shizuoka Prefecture, Fukuroi, Ugari, on *I. japonica*, 24 Mar. 2018, *J. Nishikawa*, MUMH 11690 and MUMH 11697, living culture MAFF 246771 = MUCC 2501.

Morphological characters on PCA medium: *Conidiophores* solitary to fascicular, subcylindrical, unbranched, straight or sometimes geniculate, thin, 23–128 × 4–6 µm. *Conidia* either solitary, or in short chains of 3–4 conidia without lateral branches. Conidia vary in size and appear as distorted, ovoid, ellipsoid to broadly obclavate, or sometimes beakless small oval, pale brown to yellowish brown, 28–311 × 7–38 µm in total. Conidial bodies 21–127 × 7–38 µm, with 2–16 transverse and 0–11 longitudinal septa, constricted at some transverse septa, commonly with distosepta-like internal wall structure. Secondary conidiophores appear at the apical end of conidia, short to long, usually unbranched, often with swollen cells inserted, 6–200

× 2–7 µm. Conidia of ex-epitype culture MAFF 246890 on PCA medium 25–114 × 11–38 µm, with 2–16 transverse and 1–11 longitudinal septa; secondary conidiophores 6–200 × 2–7 µm.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 67.2 ± 3 mm diam, variable among strains; aerial hypha cottony, gray to pale grayish-green,

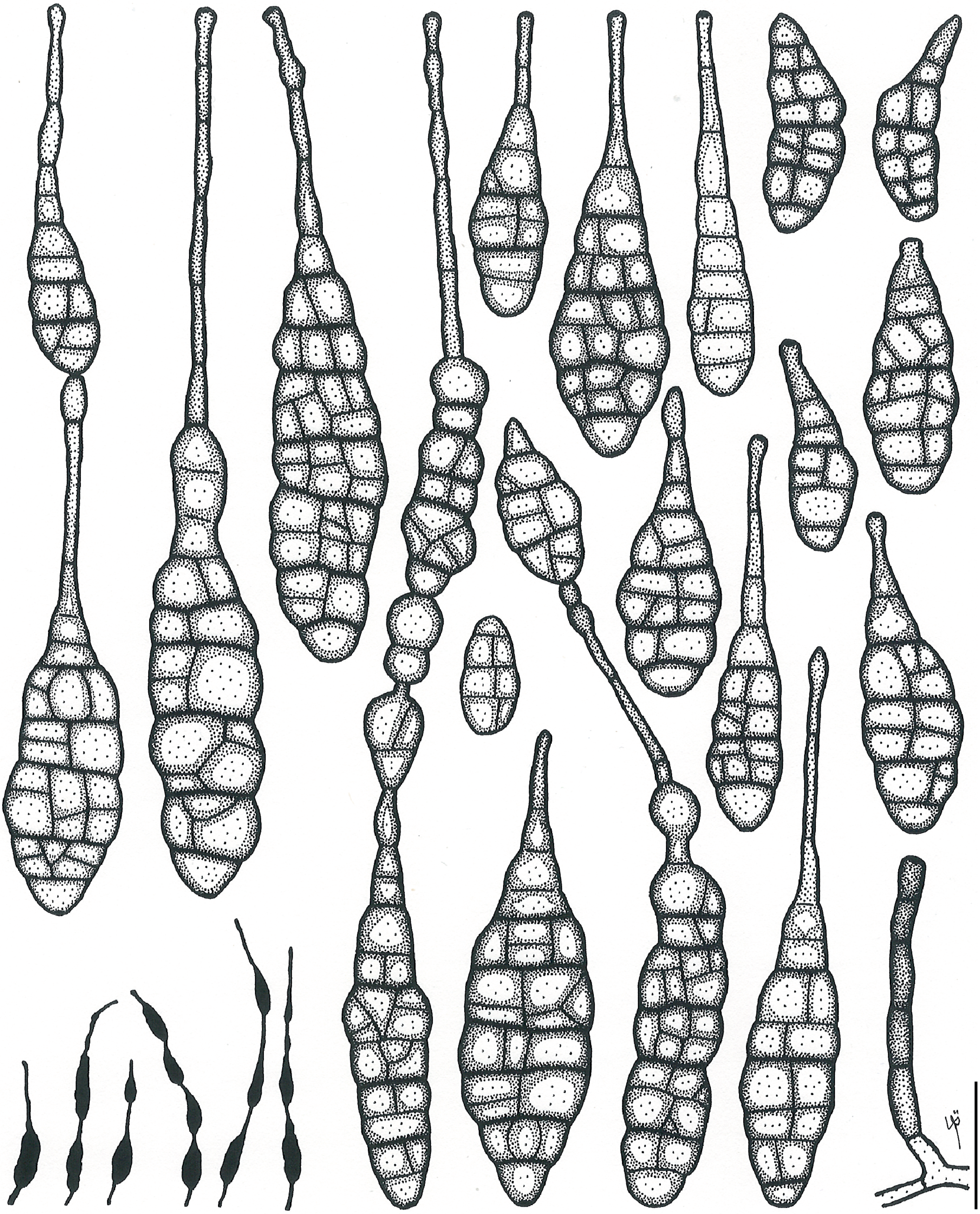

Fig. 22. Illustrations of *Alternaria iridicola* (MAFF 246771). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on potato-carrot agar medium. Scale bar = 25 µm.

Fig. 23. Morphological features of Japanese isolates of *Alternaria iridicola* (MAFF 246890) on potato-carrot agar medium. **A–J.** Conidia. **K.** Conidiophores. **L.** Culture on potato-dextrose agar medium (left = surface, right = reverse). **M.** Dried culture specimen ex MAFF 246890 (epitype: TNS-F-85452). **N.** Specimens of diseased leaves of *Iris japonica* (isoepitype: MUMH 11687). Scale bars (A–K) = 25 µm.

with white margins; reverse center grayish green to dark green; sporulation sparse; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: Iris (including *Belamcanda chinensis*) and *Gladiolus* (*Iridaceae*) (Yu 2001).

Symptoms: Leaf spots on *I. japonica* appear grayish brown surrounded by a yellowish halo. They are distinctly circular, and become enlarged and confluent, with caespituli abundantly formed at the center, and measuring 5–40 mm diam.

Experimental host range: Restricted to *Iris* excluding *I. ensata*, and weakly or non-pathogenic to the other examined plants including *Gladiolus* and *Allium* (Table 8). Similar results on *Allium* were also obtained by Elliot (1917).

Distribution: China, Japan, Korea, and USA (Shimazaki 1930, Tohyama 1993, Yu 2001, Zhang 2003, Simmons 2007).

Distinctive features: Notably large spores among sect. *Alternaria* commonly arising from narrow conidiophores. Conidia often have a long secondary conidiophore with cellular swellings. The pathogenicity of this species is restricted to certain *Iris* spp. with some species-selectivity. Phylogenetically, it is clearly distinguishable from the other species of this section in *gapdh*, *rpb2*, *tef1*, *Alt a 1*, and *endoPG* sequences (Figs 1, 3).

Notes: Based on conidial morphology of the holotype material, Simmons (2007) suggested that previous morphological descriptions of the species by Elliott (1917), Joly (1964), and Zhang (2003), which described conidial chains and long beaked conidia, could be misidentifications of other *A. tenuissima*-like species. However, conidial morphology obtained from fresh Japanese materials was identical with those in the original descriptions (Ellis & Everhart 1894, Elliott 1917), and also contained the unrepresentative beakless conidia illustrated by Simmons (2007) (Fig. 23F–J). Because diagnostic conidia of the species are scarcely present on the holotype, and no reliable living isolates exist in public culture collections, one of the Japanese specimens, TNS-F-85452, was newly designated as epitype in the present study. Although Yu (2001) has added *Gladiolus* as a natural host in Korea, without photos and details, no distinct symptoms and sporulation were observed on the inoculated leaves in this study.

Section *Brassicicola* D.P. Lawr. *et al.*, *Mycologia* **105**: 541. 2013.

Five species were recognized in this section based on the multi-locus phylogeny reported by Woudenberg *et al.* (2013), excluding *A. japonica*. This section was morphologically characterized by ellipsoidal to ovoid conidia formed in long chains, with apical conidiogenous cells and no or a few longitudinal septa (emending the description of sect. *Brassicicola sensu* Lawrence *et al.* 2013). However, neither the morphological nor the pathological differences among these species have been defined.

***Alternaria brassicicola* (Schwein.) Wiltshire, *Mycol. Pap.* 20: 8. 1947. Figs 24, 25.**

Basionym: *Helminthosporium brassicicola* Schwein. (as ‘*brassicola*’), *Trans. Amer. Philos. Soc.* **4**(2): 279. 1832.
Synonyms: *Sporidesmium septorioides* Westend., *Bull. Acad. Roy. Sci. Belgique., Cl. Sci., Sér.* 2, **21**: 236. 1854.
Alternaria septorioides (Westend.) E.G. Simmons, *CBS Biodiversity Ser.* (*Utrecht*) **6**: 570. 2007.
Sporidesmium exitiosum f. alternarioides J.G. Kühn, *Hedwigia* **1**: 91. 1855.
Polydesmus exitiosus f. alternarioides (J.G. Kühn) J.G. Kühn, *Hedwigia* **1**: 165. 1858.
Sporidesmium exitiosum f. luxuriosum J.G. Kühn, *Hedwigia* **1**: 91. 1855.
Polydesmus exitiosus f. luxuriosum (J.G. Kühn) J.G. Kühn, *Die Krankheiten der Kulturgewächse, ihre Ursachen und Verbreitung*: 165. 1858.
Macrosporium circinans Berk. & M.A. Curtis, in Curtis, *N. Carol. Geol. Nat. Hist. Surv.* **3**: 128. 1867, *nom. nud.*
Macrosporium cheiranthi var. *circinans* Berk. & M.A. Curtis, in Berkeley, *Grevillea* **3** (27): 105. 1875.
Macrosporium commune var. *circinans* (Berk. & M.A. Curtis) Sacc., *Syll. Fung.* **4**: 524. 1886.
Alternaria circinans (Berk. & M.A. Curtis) P.C. Bolle, *Meded. Phytopath. Labor. ‘WCS’* **7**: 26. 1924.
Alternaria brassicae var. *minor* Sacc., *Michelia* **2**(6): 172. 1880.
Helminthosporium brassicae Henn., *Hedwigia* **41**: 117. 1902.
Alternaria oleracea Milbr., *Bot. Gaz.* **74**(3): 321. 1922.
Alternaria brassicae var. *microspora* J.A. Elliott, in Neergaard, *Danish species of* Alternaria *and* Stemphylium: 129. 1945.
Alternaria mimicula E.G. Simmons, *Mycotaxon* **55**: 129. 1995.
Alternaria solidaccana E.G. Simmons, *CBS Biodiversity Ser.* (*Utrecht*) **6**: 572. 2007.

Typus: on petioles of *Brassica oleracea* var. *capitata* (details unknown; not preserved). **Lectotype** EGS 05.167, slide glass preparation “*Helminthosporium brassicola* S [sic] / *valde memoria Beth. in cella nostra*”, in the Schweinitz herbarium at PH (designated in Simmons 1995a).

Ex-type culture: Unknown.

Additional materials examined: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *Brassica oleracea* var. *sabellica*, 13 Mar. 2003, *J. Nishikawa*, MUMH 11667, living culture MAFF 246772 = MUCC 1694; Tokyo, Setagaya, from seeds of *Spinacia oleracea*, 13 Feb. 2002, *J. Nishikawa*, living culture MAFF 246773; Shizuoka Prefecture, Kakegawa, on leaves of *Brassica rapa* subsp. *pekinensis*, 5 Nov. 2008, *J. Nishikawa*, MUMH 11683, living culture MUCC 1612 = AC56; Tokyo, Setagaya, from seeds of *Raphanus sativus*, Jul. 2000, *J. Nishikawa*, living culture MUCC 1619 = AC70 and AC71; *ibid*., from seeds of *B. oleracea* var. *italica*, 2001, *J. Nishikawa*, living culture AC72.

Morphological characters on PCA medium: *Conidiophores* solitary, often branched, straight, intermediately broad, 6–60 × 3–6 µm. *Conidia* in chains 7–10 more conidia with frequent lateral branches, resulted in 30 more conidial units from one conidiophore. Conidial bodies, ovoid to ellipsoid, subcylindrical at maturity, brown to dark brown, 8–60 × 6–16 µm, with 0–8 transverse and few longitudinal thicken septa, mostly smooth to occasionally roughened; conidiogenous cell at terminal conidia (secondary conidiophores) short, mostly single-celled. Conidia on lesions also similar but somewhat larger than those on PCA.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 59.5 ± 1.4 mm diam; aerial hypha sparse, dark green to black; reverse center gray; sporulation abundant; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: Brassicaceae. Simmons (2007) and Farr & Rossman (2018) also recorded on *Digitalis* (*Plantaginaceae*) and non-brassicaceous plants.

Symptoms: Leaf spots on *B. oleracea*, gray to brown, circular to zonate, 8–12 mm diam, enlarged and confluent; head rot (pin rot) of broccoli and cauliflower, water-soaked to discolored on buds. Caespituli were frequently observed on lesions.

Experimental host range: Strongly pathogenic to *Brassicaceae* including *Diplotaxis*, *Matthiola*, *Iberis*, and *Nasturtium*; weakly pathogenic *Lobularia*, to *Eutrema* and *Aubrieta*; non-pathogenic to *Capsella* and non-*Brassicaceae* plants (Table 5).

Distribution: Worldwide, including Asia (Bangladesh, Brunei, China, India, Indonesia, Japan, Korea, Malaysia, Mongolia, Myanmar, Nepal, Pakistan, Saudi Arabia, Sri Lanka, Taiwan, Thailand, and Uzbekistan), Europe (Bulgaria, Cyprus, Denmark, France, Greece, Italy, Netherlands, Poland, Romania, Russia, Turkey, and UK), North and Latin America (Barbados, Brazil, Canada, Chile, Cuba, Jamaica, Panama, USA, and Venezuela), Africa (Ethiopia, Ghana, Guinea, Libya, Malawi, Mauritius, Nigeria, Rhodesia, Sierra Leone, South Africa, Sudan, Tanzania, Tunisia, Uganda, Zambia, and Zimbabwe), and the Pacific

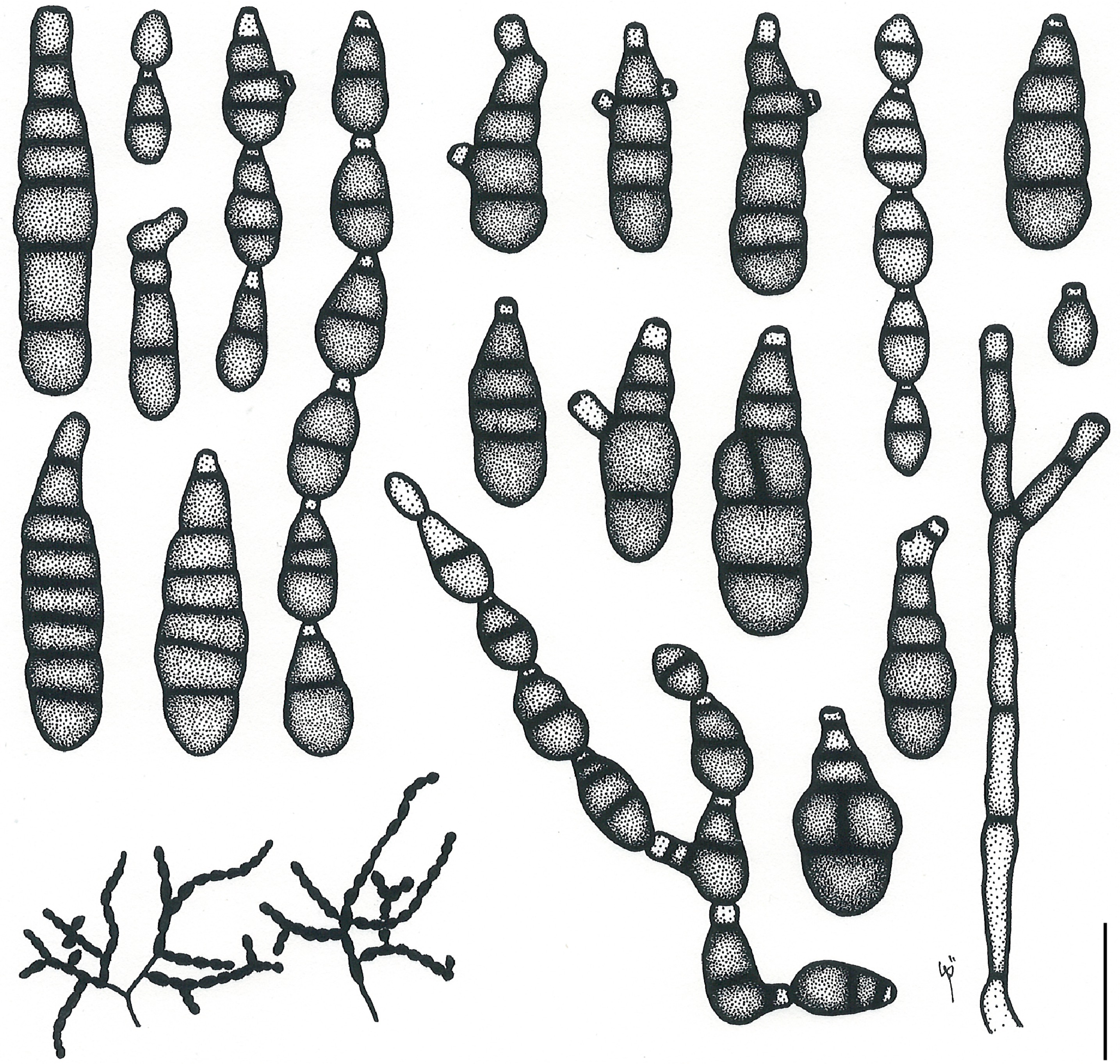

Fig. 24. Illustrations of *Alternaria brassicicola* (MAFF 246772). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on potato-carrot agar medium. Scale bar = 25 µm.

(Australia, Cook Islands, New Caledonia, New Zealand, Papua New Guinea, Samoa, and Tonga) (Yoshii 1941, Ellis 1971, Yu 2001, Zhang 2003, Farr & Rossman 2018).

Distinctive features: Small conidia form in long chains, frequently with lateral branches and rarely with longitudinal septa. Basal conidia form in subcylindrical to oblong. This species was widely pathogenic to *Brassicaceae*, but non- or weakly to *Eutrema*, *Aubrieta* and *Capsella*. It is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: *Alternaria septorioides*, *A. mimicula*, and *A. solidaccana* were synonymized in the present study based on their phylogeny using each ex-type isolate, morphological similarity, restricted host range within *Brassicaceae* plants, and the ubiquitousness and saprophytic habit of the species. Likewise, *A. conoidea* is a possible synonym of the species (CBS 132.89 is not authentic), and, therefore, sect. *Brassicicola* may be a monotypic lineage as supported by the ITS phylogeny (Fig. 2).

Section *Crivellia* (Shoemaker & Inderb.) Woudenb. & Crous, *Stud. Mycol.* **75**: 189. 2013.
Basionym: *Crivellia* Shoemaker & Inderb., *Canad. J. Bot.* **84**: 1308. 2006.

Two species are assigned in this section, which is morphologically characterized by cylindrical conidia forming in chains of geniculate conidiophores and microsclerotial formation (Woudenberg *et al.* 2013). Both of the species are known as

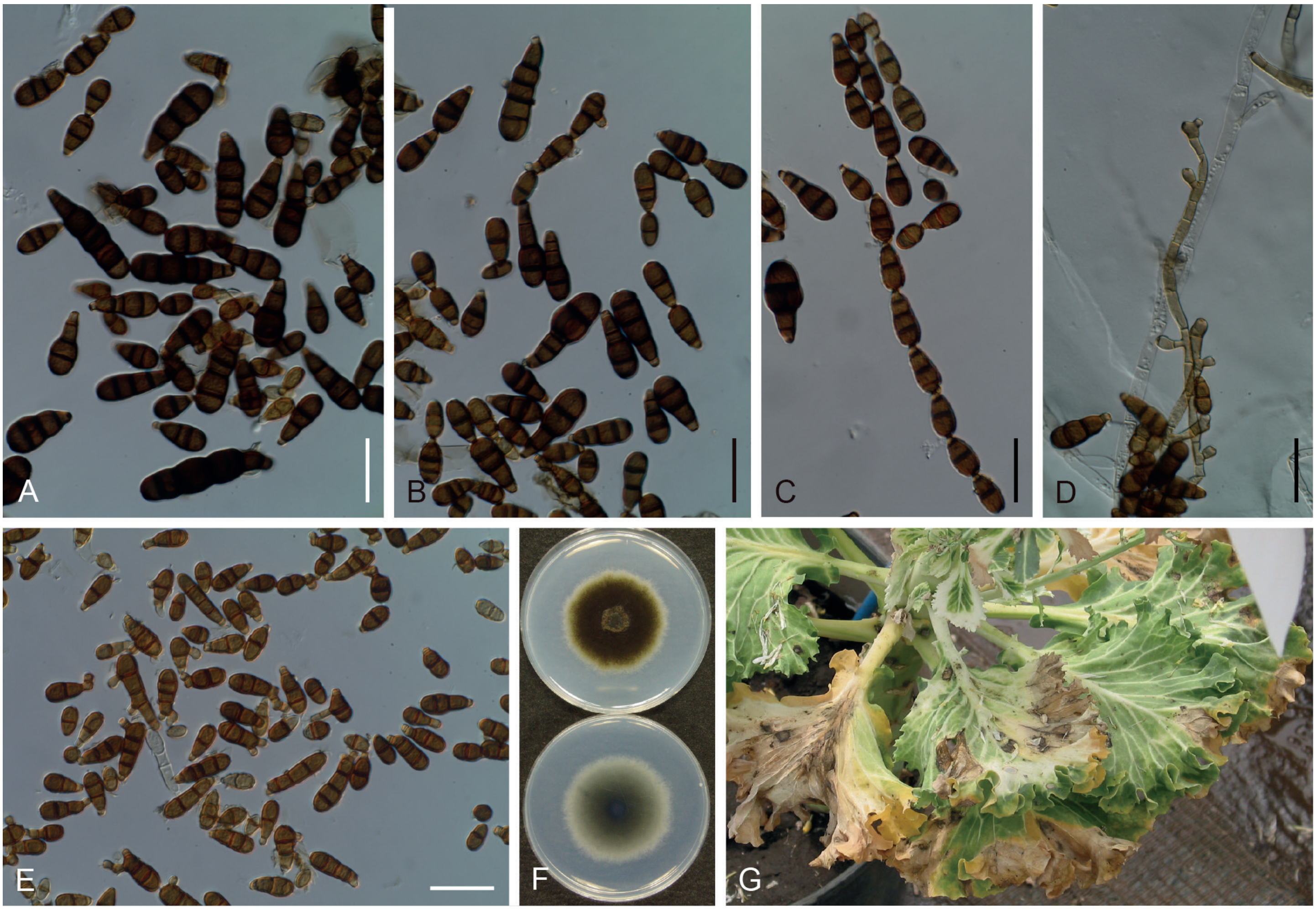

Fig. 25. Morphological features of Japanese isolates of *Alternaria brassicicola* on potato-carrot agar medium. **A–D.** Conidia and conidiophores (MAFF 246772). **E.** Conidia ex MAFF 246773. **F.** Culture on potato-dextrose agar medium (MAFF 246772; left = surface, right = reverse). **G.** Natural symptoms on *Brassica oleracea* var. *sabellica*. Scale bars (A–E) = 25 µm.

pathogenic to *Papaver* spp., having a sexual morph formerly known as *Crivellia* (Inderbitzin *et al.* 2006).

Alternaria penicillata **(Corda) Woudenb. & Crous, *Stud. Mycol.* 75: 190. 2013. Fig. 26.**
Basionym: *Brachycladium penicillatum* Corda, *Icon. Fung.* **2**: 14. 1838.
Synonyms: *Dendryphion penicillatum* (Corda) Fr., *Summa Veg. Scand., Sect. Post.* (*Stockholm*): 504. 1849.
Cucurbitaria papaveracea De Not., *Sferiacei Italici*: 62. 1863.
Pleospora papaveracea (De Not.) Sacc., *Syll. Fung.* **2**: 243. 1883.
Crivellia papaveracea (De Not.) Shoemaker & Inderb., *Canad. J. Bot.* **84**: 1308. 2006.
Dendryphion penicillatum var. *sclerotiale* M.-E. Meffert, *Z. ParasitKde* **14** (5): 462. 1950, *nom. nud.* (ICN Art. 39.1).

Typus: **Czech**, Praha, on *Papaver* sp., 6 Dec. 1837, **holotype** DAOM 49356 in PR. **Epitype**, **Austria**, Vienna, on stems of *Papaver rhoeas*, DAOM 230456 (P354) (designated in Inderbitzin *et al.* 2006), culture ex-epitype P354.8 = CBS 116608.

Additional material examined: **Japan**, Tokyo, Tachikawa, on leaves of *Papaver nudicaule*, 13 Jun. 2005, *Y. Makizumi*, living culture MUCC 1657.

Morphological characters on V8 medium: Globose knotted cells (microsclerotia), brown to dark reddish brown, 30–65 × 25–45 µm. *Conidiophores* arising from stroma (macroconidiophores), brown to reddish brown, straight and long, 128–225 × 8–11 µm, with short and sub-hyaline conidiogenous cells at the apex. Conidiophores arising from aerial mycelia (microconidiophores), geniculate with sympodial proliferation, branches often arboroid, short and narrow, 19–98 × 3–6 µm. *Conidia* commonly in short chains of 2–5, ellipsoid to cylindrical, subhyaline to pale brown, 8–38 × 4–6 µm in total, with 0–6 transverse and no longitudinal septa, remaining as distosepta-like, smooth structures. Intercalary chlamydospore-like cells, dark brown and roughened, in knots or chains, 11–29 × 10–24 µm.

Colony characteristics on PDA after 7 d at 25 °C: Slow-growing, reaching 28.7 ± 4.5 mm diam; aerial hypha cottony, olive brown, with white margins; reverse center dark green to black; sporulation abundant; diffusible pigment absent.

Sexual morph: Known formerly as the genus *Crivellia*, but not observed in the present study.

Natural host: Papaver (*Papaveraceae*).

Distribution: Worldwide, including Asia (Afghanistan, India, Iran, Japan, and Korea), Europe (Austria, Azerbaijan, Czech, Germany, Hungary, Netherlands, Poland, Romania, Russia, Spain, Sweden, Switzerland, Turkey, UK, and Ukraine), North and Latin America

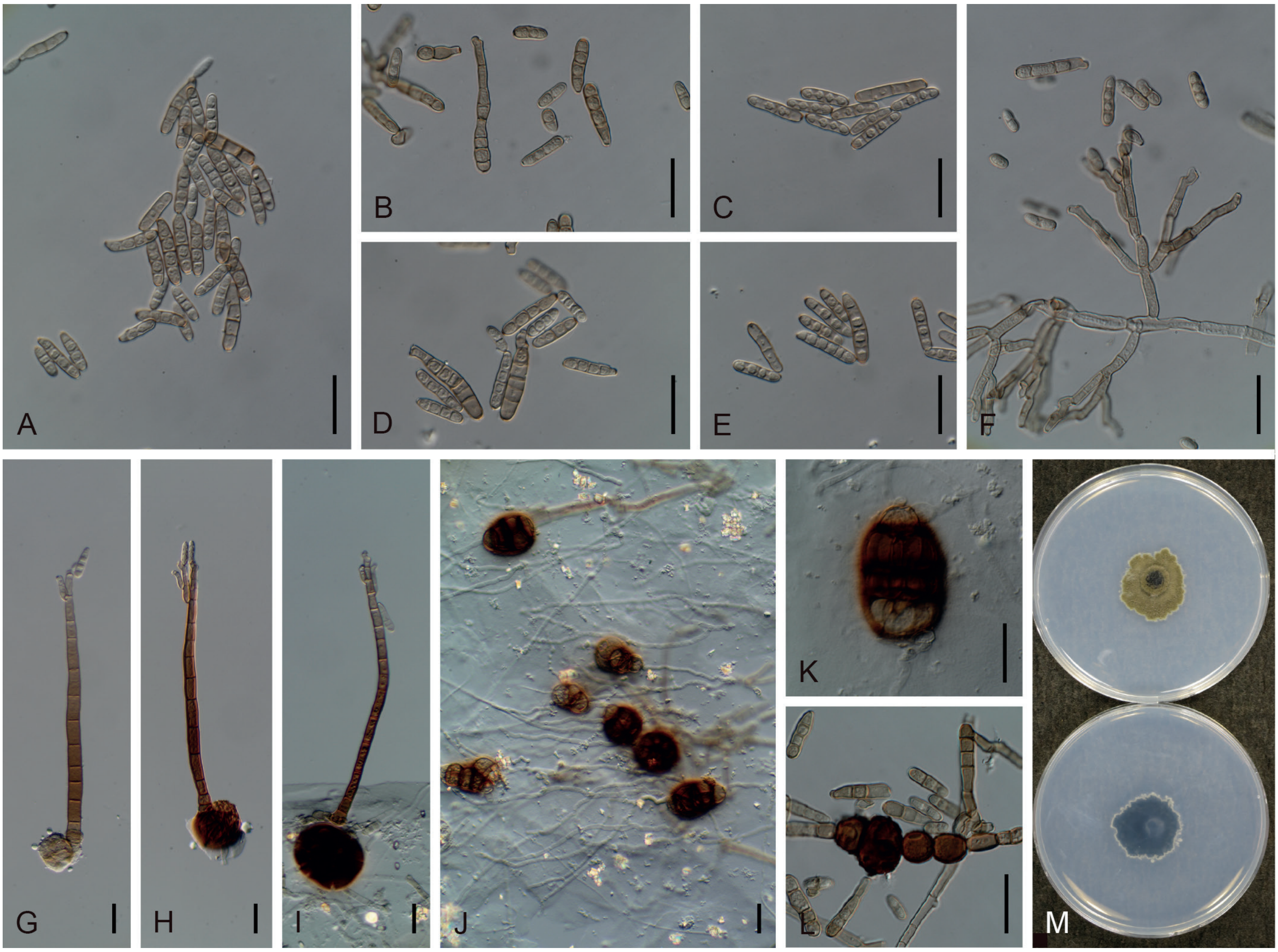

Fig. 26. Morphological features of Japanese isolates of *Alternaria penicillata* (MUCC 1657) on V8 juice agar medium. **A–E.** Conidia. **F.** Conidiophore arising from aerial mycelium (microconidiophores). **G–I.** Conidiophores arising from stroma (macroconidiophores). **J, K.** Globose knotted cells (microsclerotia). **L.** Intercalary chlamydospore-like cells. **M.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). Scale bars (A–L) = 25 µm.

(USA, Colombia, and Venezuela), Australia, and South Africa (Hirayama & Imura 1941, Richardson 1990, Farr *et al.* 2000, Inderbitzin *et al.* 2006, Hyun *et al.* 2012, Gasich *et al.* 2013, Woudenberg *et al.* 2013, Farr & Rossman 2018).

Distinctive features: Subhyaline to pale brown conidia appearing in chains, and macroconidiophores, microconidiophores, and microsclerotia are also present. It is phylogenetically distinguishable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Section *Eureka* Woudenb. & Crous, *Stud. Mycol.* **75**: 193. 2013.

Six species are assigned to this section, which are characterized by simple, short, and broad conidiophores, and ellipsoidal to cylindrical conidia that are either solitary or appear in short chains (Woudenberg *et al.* 2013). As to *A. eureka*, the type species of this section, a sexual morph has been reported (Simmons 1986).

Alternaria cumini **E.G. Simmons, *CBS Biodiversity Ser.* (*Utrecht*) 6: 664. 2007. Figs 27, 28.**

Typus: **India**, Gujarat, Karli, on *Cuminum cyminum*, Jan. 1954, *M.K. Patel*, **holotype** BPI 877406 (dried culture specimen ex CBS 121329), culture ex-holotype CBS 121329 = EGS 04.1581.

Additional materials examined: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *C. cyminum*, 17 May 2012, *J. Nishikawa*, living culture MAFF 246774; *ibid*., 18 May 2013, *J. Nishikawa*, living culture AC115.

Morphological characters on V8 medium: *Conidiophores* erect, short and narrow, 18–60 × 5–7 µm. *Conidia* solitary, rarely in chains, brown to dark brown, obclavate to long ellipsoid, subcylindrical, smooth, 23–76 × 8–26 µm, with 1–9 transverse and 0–5 longitudinal septa, slightly constricted at each transverse segment, beakless, but most with a conical cell at the apex. Morphology on PCA medium similar to that on V8 medium: conidiophores 25–93 × 5–6 µm; conidia 24–61 × 13–25 µm, with 2–7 transverse and 1–5 longitudinal septa.

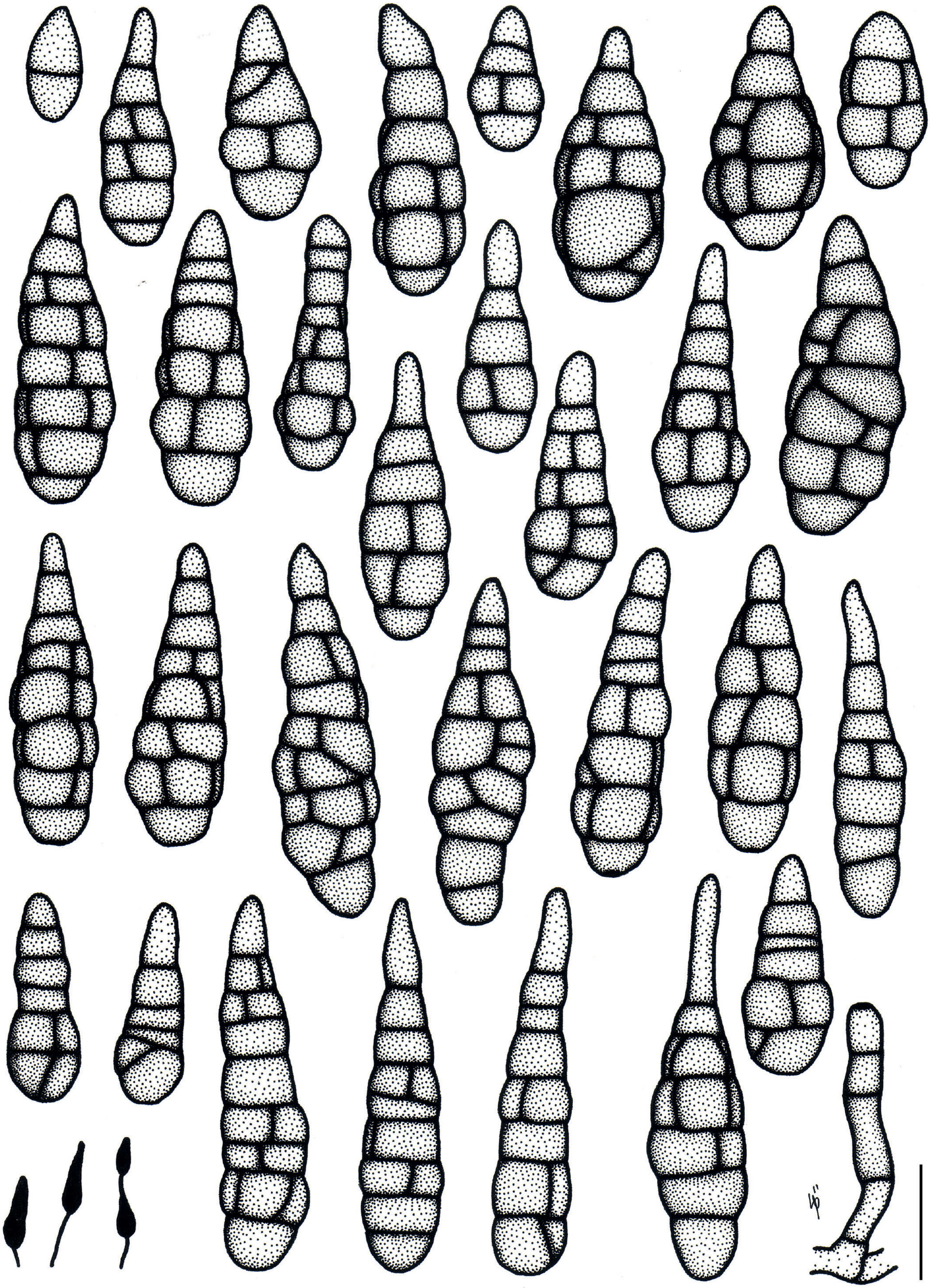

Fig. 27. Illustrations of *Alternaria cumini* (MAFF 246774). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on V8 juice agar medium. Scale bar = 25 µm.

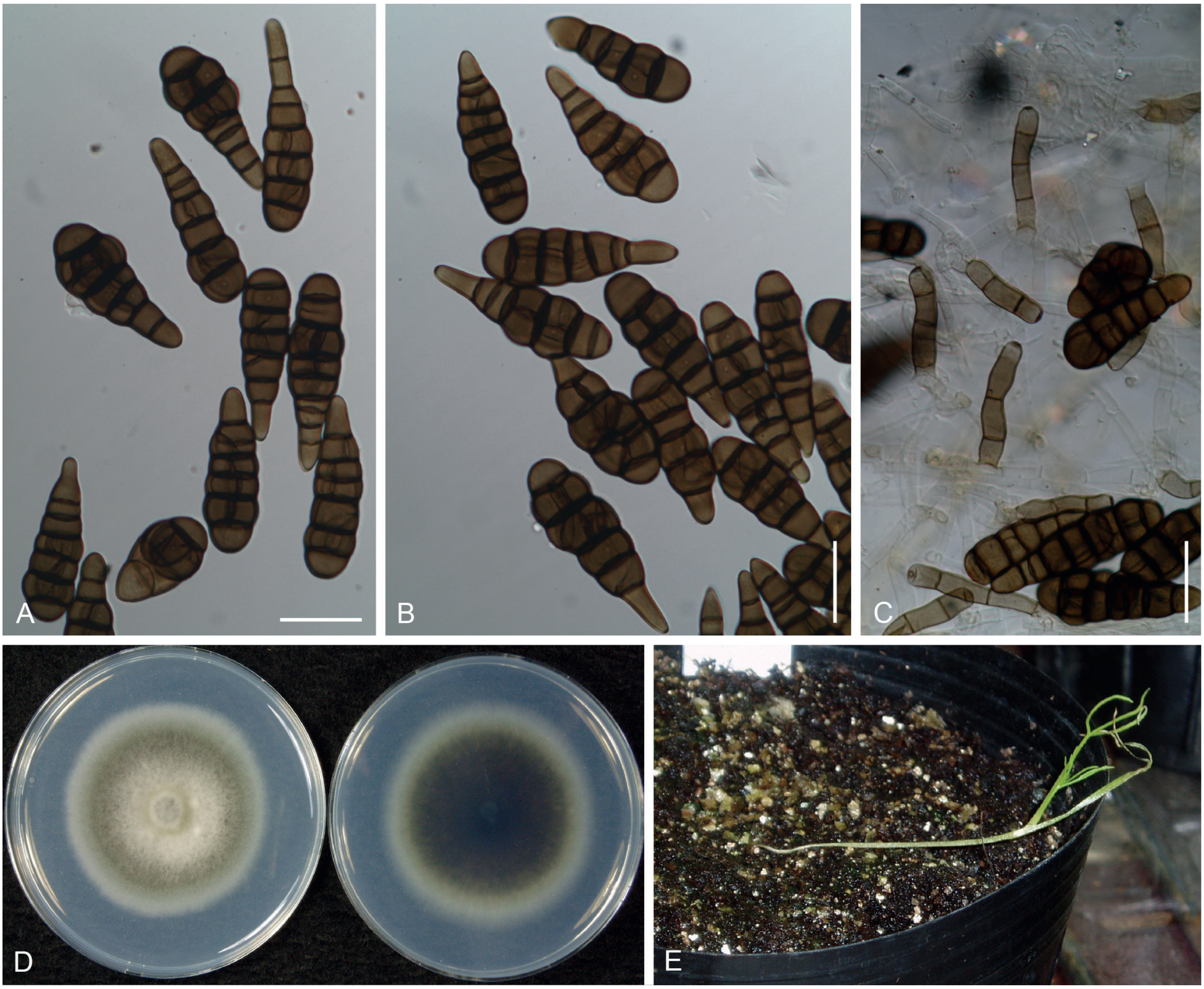

Fig. 28. Morphological features of Japanese isolates of *Alternaria cumini* (MAFF 246774). **A–C.** Conidia and conidiophores on V8 juice agar medium. **D.** Culture on potato-dextrose agar medium (left = surface, right = reverse). **E.** Natural symptoms (damping-off of seedlings and leaf blight) on seedling of *Cuminum*. Scale bars (A–C) = 25 µm.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 62.7 ± 1.1 mm diam; aerial hypha cottony, pale gray to grayish green, with white to pale gray margins; reverse center brownish green to dark green; sporulation sparse; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: Cuminum (*Apiaceae*).

Symptoms: Damping-off of *Cuminum* seedlings, and experimentally-caused leaf blight.

Experimental host range: Strongly pathogenic to *Cuminum*; weakly pathogenic or opportunistic to *Anthriscus* and *Petroselinum*; but non-pathogenic to other *Apiaceae* plants, including *Daucus* (Table 6).

Distribution: Japan and India (Simmons 2007).

Distinctive features: Beakless, solitary conidia with a conical apical cell. Conidiophores are long and broad. Host range of the species is highly selective to *Cuminum*, and it is phylogenetically recognizable via its ITS, *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences based on the DDBJ BLASTn results (data not shown).

Note: This is the first record other than the type locality.

Section *Gypsophilae* D.P. Lawr. *et al.*, *Mycologia* **105**: 541. 2013.

Eight species were assigned to this section (Woudenberg *et al.* 2013). This section is morphologically characterized by large conidia formed in short chains, with a short, blunt-tapered false beak and multiple septa (Lawrence *et al*. 2013). In Russia, Gannibal (2019) proposed an additional species on *Dianthus*, *A. kamtschatica*, based on multi-locus phylogeny using *gapdh*, calmodulin, and *Alt a 1* sequences. All the recognized species in this section occur on *Caryophyllaceae*.

Alternaria nobilis **(Vize) E.G. Simmons, *Mycotaxon* 82: 7. 2002. Fig. 29.**
Basionym: *Macrosporium nobile* Vize, in Cooke, *Grevillea* **5**(35): 119. 1877.
Synonyms: *Alternaria dianthi* F. Stevens & J.G. Hall, *Bot. Gaz.* **47**(5): 413. 1909.
Macrosporium dianthi F. Stevens & J.G. Hall, in Bewley, *Diseases of Glasshouse Plants*: 106. 1923, *nom. illeg.* (later homonym; ICN Art. 53.1). *non Macrosporium dianthi* J.V. Almeida & Sousa da Câmara, *Revista Agron.* **1**: 59. 1903.

Typus: **UK**, Forden, on stems and leaves of *Dianthus caryophyllus*, 1877, *J.E. Vize* (holotype not specified). **Lectotype**, K, EGS 11.014 (designated in Simmons 2002), isolectotype (probable) IMI 57062 (*J.E. Vize*, Micro-Fungi Britannici no. 63, *Macrosporium nobile* Vize 1878).

Ex-type culture: Unknown.

Additional materials examined: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *Dianthus barbatus*, 5 Jun. 2003, *J. Nishikawa*, living culture AC1; Miyagi Prefecture, Sendai, on leaves of *D. caryophyllus*, 12 Nov. 2002, *Y. Makizumi*, living culture AC25.

Morphological characters on V8 medium: *Conidiophores* erect, broad, pale brown to brown, unbranched, 16–60 × 5–9 µm. *Conidia* solitary to commonly in chains of 2–5 conidia, without or rarely with lateral branches, yellowish brown to brown, oblong to long obclavate, with a blunt-tapered false beak, almost straight, not swollen, smooth, clearly constricted at each transverse septa, 14–141 µm in total length. Conidial bodies 14–100 × 6–30 µm, with up to 16 transverse septa and 13 longitudinal septa. False beaks not filamentous, usually unbranched and short, consist of 2–3 cells, 3–52 × 3–6 µm.

Colony characteristics on PDA after 7 d at 25 °C: Slow-growing, reaching an average of 39.2 ± 1.4 mm diam; aerial hypha cottony, dense, grayish green, with white margins; reverse center dark green to black; sporulation sparse; diffusible pigment absent.

Sexual morph: Sexual form not observed.

Natural hosts: Primarily *Dianthus*, *Gypsophila*, *Lychnis*, and *Saponaria* (*Caryophyllaceae*), and also recorded on *Calendula* (*Asteraceae*), *Hibiscus* (*Malvaceae*), *Jasminum* (*Oleaceae*), *Lolium* (*Poaceae*), and *Sesamum* (*Pedaliaceae*) (Rao 1969, Richardson 1990, Garibaldi *et al*. 2013, Farr & Rossman 2018).

Symptom: Leaf spots on *Dianthus* are circular to zonate, grayish brown to brown, and become enlarged and confluent, reaching 4–7 mm with a necrotic eye at the center, and sometimes with a chlorotic halo around the primary lesion.

Distribution: Worldwide, including Asia (China, India, Japan, Korea, Malaysia, Myanmar, Pakistan, and Thailand), Europe (Armenia, Austria, Bulgaria, Croatia, Cyprus, Denmark, France, Germany,

Fig. 29. Morphological features of Japanese isolates of *Alternaria nobilis* (AC1) on V8 juice agar medium. **A–E.** Conidia. **F.** Conidiophores. **G.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **H.** Natural symptoms on *Dianthus*. Scale bars (A–F) = 25 µm.

Greece, Italy, Latvia, Poland, Romania, Russia, Spain, Sweden, Turkey, and UK), North and Latin America (Argentina, Brazil, Canada, Jamaica, Mexico, Puerto Rico, Uruguay, USA, Venezuela, and Virgin Islands), Africa (Malawi, Morocco, Mozambique, South Africa, Tanzania, Zambia, and Zimbabwe), and the Pacific (Australia and New Zealand) (Imai 1914, Rao 1969, Ellis 1971, Richardson 1990, Cho *et al.* 2001, Yu 2001, Garibaldi *et al.* 2013, Woudenberg *et al.* 2013, Farr & Rossman 2018).

Distinctive features: Large conidia, solitary to in short chain with a blunt-tapered false beak and multiple septa. Conidiophores long and broad. This species is pathogenic to *Dianthus*.

Notes: Morphological characteristics of the examined Japanese isolates were identical to those of *A*. *nobilis* described in Simmons (2002). However, these were also similar to those of the other members in sect. *Gypsophilae*: shorter than the conidial length of *A*. *saponariae*; larger than the conidial width of *A*. *ellipsoidea* and *A*. *kamtschatica* according to the criteria in Simmons (2002) and Gannibal (2019). The multi-locus phylogeny conducted in this study showed that examined isolates of this section were divided into five subclades, and Japanese isolates formed a distinct subclade (Fig. 1), while ITS (Fig. 2) as well as *tef1* and *act* phylogeny proposed that Japanese isolates are identical with the representative isolate of *A*. *nobilis* (data not shown). It is still unclear which trait can practically determine species boundaries among them, and therefore, we provisionally identified Japanese isolates as *A*. *nobilis* based on their morphological similarity and original source host, *Dianthus*.

Section *Japonicae* Woudenb. & Crous, *Stud. Mycol.* **75**: 197. 2013.

Woudenberg *et al.* (2013) assigned two species to this section, which is morphologically characterized by short- to long-ovoidal conidia formed in short chains, with constrictions at the septa. However, neither the morphological nor the pathological differences between these two species have been well defined.

***Alternaria japonica* Yoshii, *J. Pl. Protect.* (*Tokyo*) 28: 17. 1941. Figs 30, 31.**
Synonyms: *Alternaria brassicae* (Berk.) Sacc. var. *macrospora* [*non* Sacc.] *sensu* Yoshii, *Bult. Sci. Fak. Terk. Kjusu Imp. Univ.* **5** (3): 224. 1933.
Alternaria raphani J.W. Groves & Skolko, *Canad. J. Res., Sect. C* **22** (5): 227. 1944.
Alternaria matthiolae Neerg., *Danish species of* Alternaria *and* Stemphylium: 184. 1945.
Alternaria nepalensis E.G. Simmons, *CBS Biodiversity Ser.* (*Utrecht*) **6**: 480. 2007.

Typus: **Japan**, on leaves of *Brassica rapa* and *Raphanus sativus* (details unknown, not specified, not preserved). **Lectotype**, IMI 876 (designated in Tohyama & Tsuda 1990; the same specimen was designated as a neotype in Simmons 1995a). **Epitype designated here, Japan**, Tokyo, Setagaya, from seeds of *R. sativus*, 24 Jul. 2000, *J. Nishikawa*, TNS-F-85453 (dried culture specimen of MAFF 246775) (MBT385028), isoepitype MUMH 11696, culture ex-epitype MAFF 246775 = MUCC 1622.

Additional materials examined: **Japan**, Tokyo, Setagaya, from seeds of *R. sativus*, 24 Jul. 2000, *J. Nishikawa*, living cultures AC73; Shizuoka Prefecture, Kakegawa, on buds of *Brassica oleracea* var. *italica*, 7 Jun. 2010, *K. Takebayashi*, living culture AC96; *ibid*., on stem of *B. oleracea* var. *italica*, 7 Jun. 2010, *K. Takebayashi*, living culture AC97.

Morphological characters on PCA medium: *Conidiophores* solitary, short and narrow, 18–80 × 4–6 µm. *Conidia* of ex-epitype solitary or in short chains of 1–2, without lateral branches, 20–84 µm in total length. Conidial bodies ovoid to obclavate, ellipsoid, pale brown to brown and smooth, 20–68 × 8–25 µm, with 2–7 transverse septa and 0–4 longitudinal septa, constricted at some transverse septa. Secondary conidiophores (false beaks) usually short, 1–3 celled, unbranched, 5–20 × 4–10 µm. Intercalary chlamydospores frequently both in air and submerged in agar substrate, either as single spores or in knots or chains, brown to dark brown, 10–21 × 8–16 µm.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 59.1 ± 2.9 mm diam, variable among strains; aerial hypha cottony, white or pale gray to grayish green, with white margins; reverse center dark green to black; sporulation sparse; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: *Brassicaceae*. There are also reported exceptions of *Carya* (*Juglandaceae*), *Kalanchoe* (*Crassulaceae*), *Oryza* (*Poaceae*), *Sesamum* (*Pedaliaceae*), and *Vigna* (*Fabaceae*) serving as hosts (Huang & Hanlin 1975, Farr & Rossman 2018).

Symptoms: Head rot and leaf spot like those caused by *A. brassicicola*, but caespituli appear sparsely on lesions.

Experimental host range: Strongly pathogenic to *Brassicaceae*, including *Diplotaxis*, *Matthiola*, and *Nasturtium*; weakly pathogenic or opportunistic to *Lobularia*, *Eutrema*, *Iberis*, and *Aubrieta*; almost non-pathogenic to *Capsella* and non-*Brassicaceae* plants (Table 5).

Distribution: Worldwide, including Asia (China, India, Japan, Korea, Myanmar, Nepal, Pakistan, Taiwan, and Saudi Arabia), Europe (Austria, Denmark, Finland, Germany, Greece, Italy, Netherlands, Poland, Russia, and Spain), North and Latin America (Barbados, Brazil, Canada, Cuba, and USA), Africa (Egypt, South Africa, Tunisia, and Zimbabwe), and the Pacific (Australia, New Caledonia, New Zealand, and Papua New Guinea) (Yoshii 1941, Rao 1969, Ellis 1971, Richardson 1990, Tohyama & Tsuda 1990, Jasalavich *et al*. 1995, Sharma & Tewari 1998, Yu 2001, Zhang 2003, Su *et al.* 2005, Simmons 2007, Gannibal & Gasich 2009, Ren *et al.* 2012, Bassimba *et al.* 2013, Woudenberg *et al.* 2013, Siciliano *et al.* 2017, Farr & Rossman 2018).

Distinctive features: Small conidia are either solitary or appear in short chains. Intercalary chlamydospores frequently form both in air and submerged in agar substrate. This species is widely pathogenic to *Brassicaceae*, but non- or weakly to *Eutrema*, *Aubrieta* and *Capsella*. It is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: This species is often confused under the names, *A*. *raphani* and *A. matthiolae*. However, *A. japonica* has nomenclatural priority to these two epithets. As for *A. nepalensis* described by Simmons (2007), it was clearly appropriate to synonymize it with *A. japonica* based on its conidial morphology, phylogenetic analysis, and its original source (from seeds of *Brassica* sp.). There are no ex-type living cultures and therefore we designated an epitype herein to provide reference for further molecular studies.

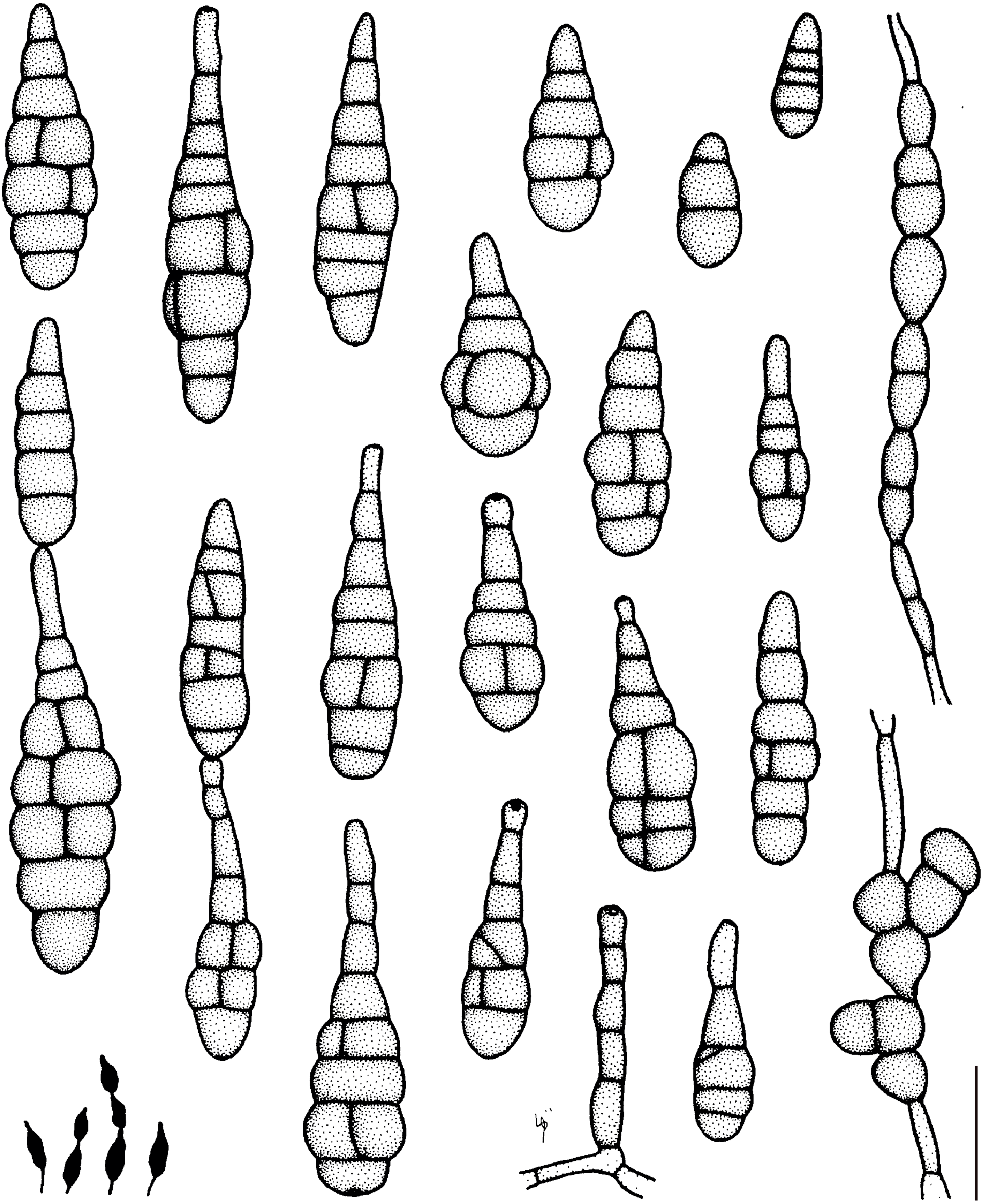

Fig. 30. Illustrations of *Alternaria japonica* (MAFF 246775). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on potato-carrot agar medium. Scale bar = 25 µm.

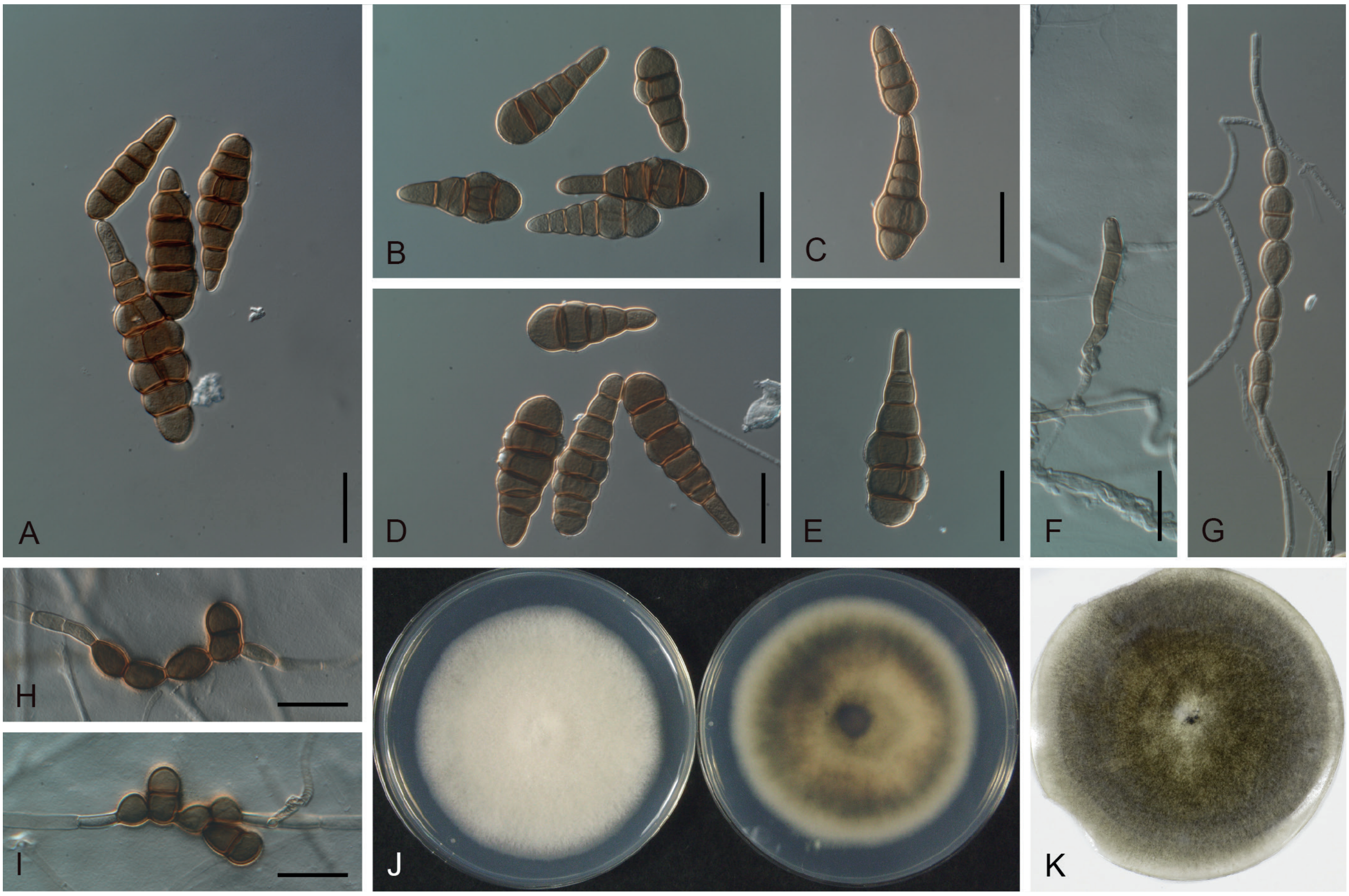

Fig. 31. Morphological features of Japanese isolates of *Alternaria japonica* (MAFF 246775) on potato-carrot agar medium. **A–E.** Conidia. **F.** Conidiophore. **G–I.** Chlamydospores. **J.** Culture on potato-dextrose agar medium (left = surface, right = reverse). **K.** Dried culture specimen ex MAFF 246775 (epitype: TNS-F-85453). Scale bars (A–I) = 25 µm.

Section *Panax* D.P. Lawr. *et al.*, *Mycologia* **105**: 541. 2013.

Woudenberg *et al.* (2013) assigned five species to this section. This was morphologically characterized by small to large conidia with blunt-tapered false beaks and broad conidiophores. Two species, *A. avenicola* and *A. photistica*, have a sexual morph (Simmons 1986, 2007). Only one species, *A. panax*, is distributed in Japan, and was described in the present study.

***Alternaria panax* Whetzel, in Whetzel & Rosenbaum, *Bull. U.S.D.A. Bur. Pl. Industr.* 250: 11. 1912. Fig. 32.**

Synonyms: *Alternaria panax* Whetzel, in Cowles, *Science n. s.* **29**: 912. 1909, *nom. nud.*

Alternaria panacis Whetzel, in Saccardo, *Syll. Fung.* **25**: 864. 1931, citing Rosenbaum & Zinnsmeister, *J. Agric. Res.* **5**: 181. 1915, *nom. illeg*. (orthographic variant; ICN Art. 60.1).

Macrosporium araliae Dearn. & House, *Circ. N.Y. St. Mus.* **24**: 58. 1940, *nom. inval.* (no Latin; ICN Art. 39.1).

Alternaria araliae H.C. Greene, *Trans. Wisc. Acad. Sci.* **42**: 80. 1953. *non Alternaria araliae sensu* Deng *et al.*, *Mycol. Progr.* **14**(31): 4. 2015.

Alternaria actinophylla J.W. Mille, *Fl. Dep. Agr., Div. Pl. Ind., Pl. Pathol. Circ.* **80**: 1969, *nom. nud*. (no Latin and type; ICN Art. 39.1, 40.1).

Typus: **USA**, New York, Fulton, on *Panax quinquefolius*, 15 Jun. 1909, *H.H. Whetzel*, BPI 446440 (**isotype**: fide Simmons 2007) ex CUP 4852; EGS 07.074.

Ex-type culture: Unknown.

Additional materials examined: **Japan**, Tokyo, Ogasawara (Bonin Is.), Chichijima, on leaves of *Polyscias fruticosa*, Jan. 2003, *T. Ono*, living culture PFAlt1-1 (MUCC 1692); *ibid*., on leaves of *Polyscias guilfoylei*, Apr. 2003, *T. Ono*, living culture PGAlt1 (AC19); Tokyo, Ogasawara (Bonin Is.), Hahajima, on leaves of *P. fruticosa*, 28 Oct. 2011, *T. Sato*, MUMH 11686, living cultures MAFF 243161 = MUCC 1625 and MAFF 243162 = MUCC 1626.

Morphological characters on V8 medium: *Conidiophores* broad, brown and unbranched, 55–145 × 7–10 µm. *Conidia* commonly in chains of 2–7, without or rarely with lateral branches, yellowish brown to brown, smooth, oblong to long obclavate, with a blunt-tapered false beak, mostly straight and laterally symmetrical but occasionally excessively swollen, often constricted at each transverse segment, 51–208 µm in total length. Conidial bodies 28–118 × 13–38 µm, with 4–13 transverse septa and up to 9 (often complicated) longitudinal septa; false beaks unbranched and not filamentous, 9–110 × 3–9 µm, pale brown to brown.

Colony characteristics on PDA after 7 d at 25 °C: Slow to moderate-growing, reaching an average of 46.5 ± 2.2 mm diam; aerial hypha cottony, white to pale gray; reverse center dark

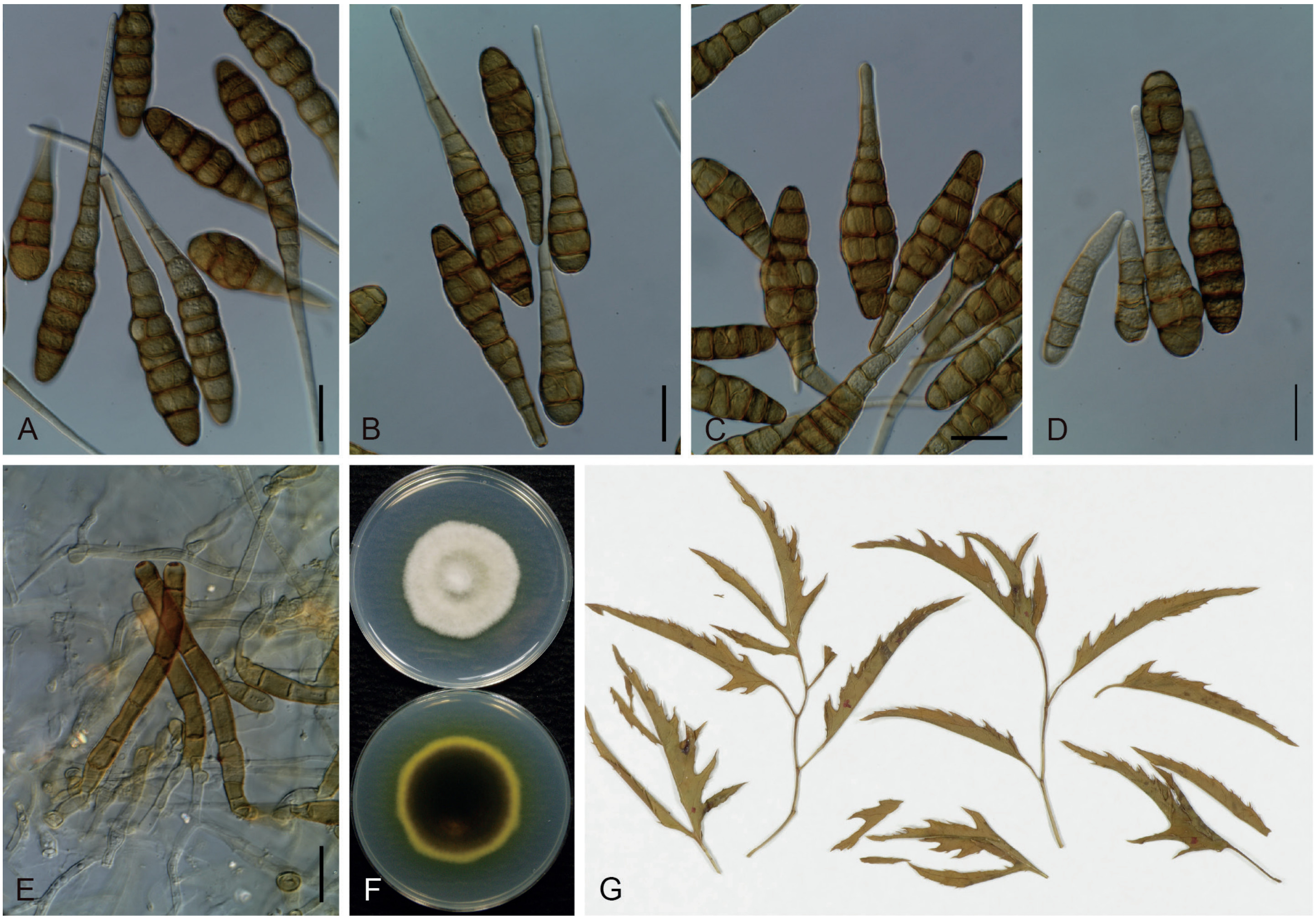

Fig. 32. Morphological features of Japanese isolates of *Alternaria panax* (MAFF 243161) on V8 juice agar medium. **A–D.** Conidia. **E.** Conidiophores. **F.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **G.** Specimens of diseased leaves of *Polyscias* (MUMH 11686). Scale bars (A–E) = 25 µm.

green to black; sporulation sparse; diffusible pigment absent or bright yellow to reddish orange.

Sexual morph: Not observed.

Natural hosts: *Araliaceae* (*Acanthopanax*, *Aralia*, *Brassaia*, *Dendropanax*, *Echinopanax*, *Fatsia*, *Kalopanax*, *Meryta*, *Panax*, *Plerandra*, *Polyscias*, *Pseudopanax*, *Schefflera*, and *Tupidanthus*) (Uchida *et al*. 1984, Yu 2001, Simmons 2007, Deng *et al.* 2010, 2013).

Symptoms: Leaf and petiole spots on *Polyscias*, appearing water-soaked to circular, brown, becoming enlarged and confluent, measuring 2–5 mm diam.

Distribution: Canada, China, Italy, Japan, Korea, New Zealand, and USA (Bokura 1915, Atilano 1983, Uchida *et al.* 1984, Yu 2001, Zhang 2003, Garibaldi *et al.* 2004, Ono 2004, Zhang *et al.* 2009, Deng *et al.* 2010, 2013, Woudenberg *et al.* 2013, Farr & Rossman 2018).

Distinctive features: Small and large conidia develop in short chains, with blunt-tapered false beaks. Colonies grown on PDA release either no pigment or a bright yellow to reddish orange pigment into the medium. This species is widely pathogenic to *Araliaceae*, and is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: Deng *et al.* (2015) split *A. panax* into three species, *A. araliae*, *A. dendropanacis*, and *A. panax* (as *A. panacis*, orthographic variant), based on their culture characteristics, phylogeny (*Alt a 1*, *β-tubulin*, *tef1*, *gapdh*, and *rpb2*), and hosts. However, among these, *A. araliae* sensu Deng *et al.* was unrelated to the type material of *A. araliae* H.C. Greene (BPI 445904). Japanese isolates examined in the present study could not accommodate the definitions of these three species, which focused on pigment production and conidial morphology, as established by Deng *et al.* (2015).

Section *Porri* D.P. Lawr. *et al.*, *Mycologia* **105**: 541. 2013.

This section is the largest and, morphologically, the most confusable section. It was morphologically characterized by large spores that were usually non-catenate with filamentous beaks and broad conidiophores, consisting of 63 species as defined by Woudenberg *et al.* (2014). Among these, only 12 species are distributed in Japan (NIAS Genebank database of plant diseases in Japan: https://www.gene.affrc.go.jp/databases-micro_pl_ diseases_en.php), and five species are described in the present study.

Alternaria crassa **(Sacc.) Rands, *Phytopathology* 7: 337. 1917. Fig. 33.**
Basionym: *Cercospora crassa* Sacc., *Michelia* **1**(1): 88. 1877.
Synonyms: *Cercospora daturae* Peck, *Rep.* (*Annual*) *New York State Mus. Nat. Hist.* **35**: 140. 1884.
Macrosporium cookei Sacc., *Syll. Fung.* **4**: 530. 1886.
Macrosporium solani Cooke, *Grevillea* **12**: 32. 1883. *non M. solani* Ellis & G. Martin, 1882.
Alternaria cookei (Sacc.) Bremer, Işmen, Karel & Özkan & M. Özkan, *Istanbul Univ. Fak. Mecm., B* **13**: 42. 1948.
Macrosporium daturae Fautrey, in Lambottle & Fautrey, *Rev. Mycol.* (*Toulouse*) **16**: 76. 1894.
Alternaria daturae (Fautrey) Bubák & Ranoj., in Kobát & Bubák, *Fungi Imperf. Exsicc.* **14**: 694. 1911.
Alternaria capsici E.G. Simmons, *Mycotaxon* **75**: 84. 2000.

Typus: on leaves of *Datura stramonium* (details unknown; two specimens in PAD). **Lectotype**, PAD, *D. stramonium*, S. [elva] '76. 10. (designated in Simmons 2000). **Epitype**, **Cyprus**, Famagusta, on leaves of *D. stramonium*, Jan. 1936, *R.M. Nattrass*, CBS H-21744 (designated in Woudenberg *et al.* 2014), culture ex-epitype CBS 110.38.

Additional materials examined: **Japan**, Tokyo, Kodaira, on leaves of *D. stramonium*, Jul. 2000, *J. Nishikawa*, living culture MAFF 243056; *ibid.*, on leaves of *Datura fastuosa*, 20 Oct. 2012, *Ichinose et al.*, MUMH 11689, living culture MUCC 2502 (12-M0180); on leaves of *Datura inoxia*, 15 Sep. 2012, *Ichinose et al.*, MUMH 11688, living culture MUCC 2503 (12-M0099).

Morphological characters on V8 medium: Previously reported in Nishikawa & Nakashima (2013) and Ichinose *et al*. (2015).

Colony characteristics on PDA after 7 d at 25 °C: Fast-growing, reaching an average of 80 ± 1.8 mm diam; aerial hypha cottony, grayish green to black, with white margins; reverse center dark green to black; sporulation sparse; diffusible pigment absent.

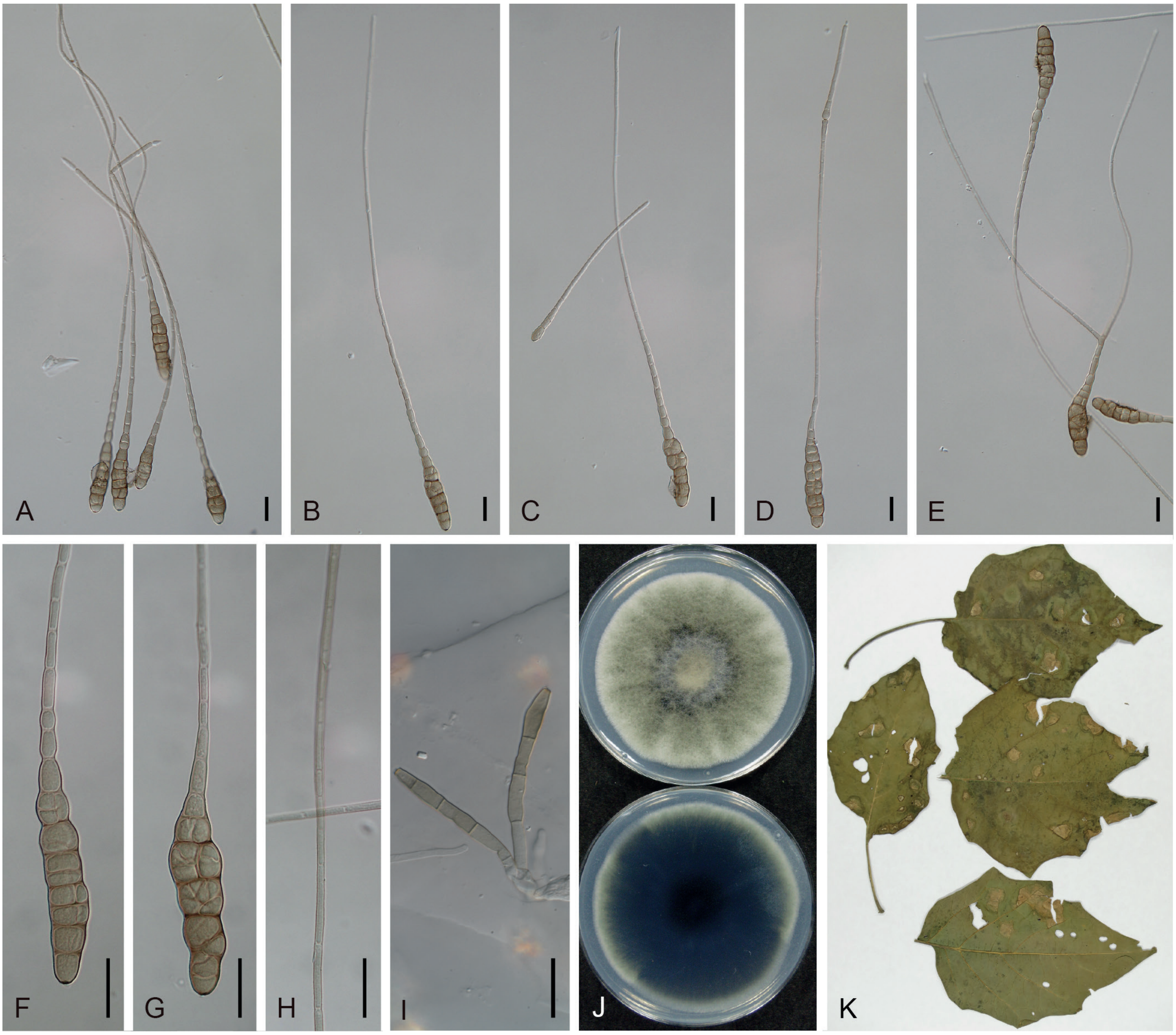

Fig. 33. Morphological features of Japanese isolates of *Alternaria crassa* (MAFF 243056) on V8 juice agar medium. **A–H.** Conidia with colored beaks. **I.** Conidiophores. **J.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **K.** Symptoms on specimens of *Datura* (MUMH 11688). Scale bars (A–I) = 25 µm.

Sexual morph: Not observed.

Natural hosts: *Datura* (including *Brugmansia*), *Capsicum*, *Nicandra*, *Petunia*, and *Solanum nigrum* (*Solanaceae*) (Rao 1969, Zhang 2003, Simmons 2007, Nishikawa & Nakashima 2013).

Symptoms: Leaf spots appear on *Datura*, and are vein-limited circular to irregular, straw-yellow to pale brown with a gray center, distinct at their borders, and are scattered, but become enlarged and confluent (Nishikawa & Nakashima 2013).

Experimental host range: Pathogenic to *Datura* (tribe *Datureae*, *Solanoideae*) and *Capsicum* (tribe *Capsiceae*, *Solanoideae*), and occasionally weakly or opportunistic to *Petunia* and *Solanum* (Nishikawa & Nakashima 2013).

Distribution: Worldwide, including Asia (China, India, Israel, Japan, Myanmar, Nepal, Pakistan, and Taiwan), Europe (Bulgaria, Croatia, Cyprus, Germany, Italy, Latvia, Macedonia, Poland, Portugal, Romania, Serbia, Spain, and Switzerland), North and Latin America (Cuba, El Salvador, USA, and Venezuela), Africa (Ethiopia, Ghana, Kenya, Mozambique, Nigeria, Rhodesia, South Africa, Sudan, Tanzania, Uganda, Zambia, and Zimbabwe), and the Pacific (Australia and New Zealand) (Sawada 1944, Rao 1969, Ellis 1971, Richardson 1990, Crous *et al.* 2000, Zhang 2003, Woudenberg *et al.* 2014, Ichinose *et al.* 2015, Farr & Rossman 2018).

Distinctive features: Large-spored species with filamentous but clear false beaks, which are usually unbranched, colored, significantly elongated, and often exceed 4 µm in width. Conidial bodies are pale brown, with longitudinal septa in common. Colonies on PDA medium released no pigment, which is unique to the species among related species in sect. *Porri*. This species is pathogenic to *Datura* and *Capsicum*, and is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: Woudenberg *et al.* (2014) synonymized *A. capsici* based on the combined phylogeny of its ITS, *gapdh*, *tef1*, *rpb2*, and *Alt a 1* sequences, and then inoculation tests conducted by Nishikawa & Nakashima (2013) also supported this taxonomic classification. In addition, Nishikawa & Nakashima (2013) suggested that *A. daturicola* was also a probable synonym.

Alternaria cucumerina (Ellis & Everh.) J.A. Elliott, _Amer. J. Bot._ 4: 472. 1917. Fig. 34.
Basionym: *Macrosporium cucumerinum* Ellis & Everh., *Proc. Acad. Nat. Sci. Philadelphia* **47**: 440. 1895.
Synonym: *Alternaria loofahae* E.G. Simmons & Aragaki, *CBS Biodiversity Ser.* (*Utrecht*) **6**: 316. 2007.

Typus: **USA**, New Mexico, Las Cruces, on leaves of *Cucumis melo*, Aug. 1895, *E.O. Wooton*. (not specified). **Lectotype**, **USA**, New Mexico, Las Cruces, on leaves of *C. melo*, Aug. 1895, *E.O. Wooton*, PH (designated in Simmons 2007).

Ex-type culture: Unknown.

Additional materials examined: **Japan**, Niigata Prefecture, Sado, on leaves of *Cucurbita maxima*, 27 Jul. 2010, *Y. Makizumi*, living culture AC105; *ibid*., 30 Jul. 2010, *Y. Makizumi*, living culture AC106.

Morphological characters on V8 medium: *Conidiophores* moderately long and broad, 69–109 × 5–7 µm. *Conidia* usually solitary, but occasionally in chains of two, 56–411 µm in total length. Conidial bodies subcylindrical to broadly obclavate and oblong, 36–106 × 13–28 µm, with 4–15 transverse and 2–12 (often complicated) longitudinal septa, brown to dark brown with a smooth surface. Filamentous beaks almost straight, unbranched, 16–305 × 1–2 µm, pale brown and conspicuously distinguishable, bordering the conidial body.

Colony characteristics on PDA after 7 d at 25 °C: Fast-growing, reaching an average of 87 ± 0.7 mm diam; aerial hypha cottony, white to pale gray; reverse center dark green to black; sporulation sparse; diffusible pigment absent to occasionally bright yellow to pale orange.

Sexual morph: Not observed.

Natural hosts: Cucurbitaceae (*Benincasa*, *Citrullus*, *Cucumis*, *Cucurbita*, *Lagenaria*, *Luffa*, and *Sicyos*), as well as occasionally reported on *Asimina* (*Annonaceae*), *Cyamopsis* and *Phaseolus* (*Fabaceae*) (Ellis 1971, Woudenberg *et al*. 2014, Farr & Rossman 2018).

Symptoms: Leaf spots appear on *Cucurbita*, and are dark brown to black with grayish eye at center, subcircular to angular with a distinct border, 1–5 mm diam, becoming confluent.

Distribution: Worldwide, including Asia (China, India, Japan, Korea, Nepal, Pakistan, and Thailand), Europe (Bulgaria, Cyprus, France, Germany, Norway, Romania, Russia, Spain, Switzerland, Turkey, and UK), North and Latin America (Canada, Chile, Cuba, El Salvador, Haiti, Jamaica, Mexico, Peru, Trinidad and Tobago, USA, and Venezuela), Africa (Ghana, Kenya, Libya, Mozambique, Nigeria, Rhodesia, Sierra Leone, South Africa, Sudan, Tanzania, Uganda, Zambia, and Zimbabwe), and the Pacific (Australia and New Zealand) (Benjamin & Slot 1969, Ellis 1971, Yu 2001, Zhang 2003, Gannibal 2011, Woudenberg *et al.* 2014, Farr & Rossman 2018).

Distinctive features: Large-spored species with filamentous colored beaks, which are usually unbranched and do not exceed 3 µm in width. Conidial bodies are broadly obclavate to oblong, often with complicated longitudinal septa. Colonies on PDA often release yellow to pale orange pigment into the medium. This species is generally characterized by pathogenicity to *Cucurbitaceae* (Ellis 1971, Yu 2001, Zhang 2003, Simmons 2007), and is phylogenetically recognizable via *gapdh*, *rpb2*, *tef1* (Fig. 1), and *Alt a 1* sequences (data not shown).

Alternaria dauci (J.G. Kühn) J.W. Groves & Skolko, _Canad. J. Res., Sect. C, Bot. Sci._ 22(5): 222. 1944. Fig. 35.
Basionym: *Sporidesmium exitiosum* var. *dauci* J.G. Kühn, *Hedwigia* **1**: 91. 1855.
Synonyms: *Polydesmus exitiosus* var. *dauci* (J.G. Kühn) J.G. Kühn, *Die Krankheiten der Kulturgewächse, ihre Ursachen und ihre Verhütung*: 165. 1858.
Macrosporium dauci (J.G. Kühn) Rostr., *Tidsskr. Landoekon. ser. 5*, **7**: 385. 1888.
Macrosporium carotae Ellis & Langl., *J. Mycol.* **6**(1): 36. 1890.
Alternaria carotae (Ellis & Langl.) J.A. Stev. & Wellman, *J. Wash. Acad. Sci.* **34**: 263. 1944.
Alternaria brassicae var. *dauci* (J.G. Kühn) Lindau, *Rabenh. Krypt.-*

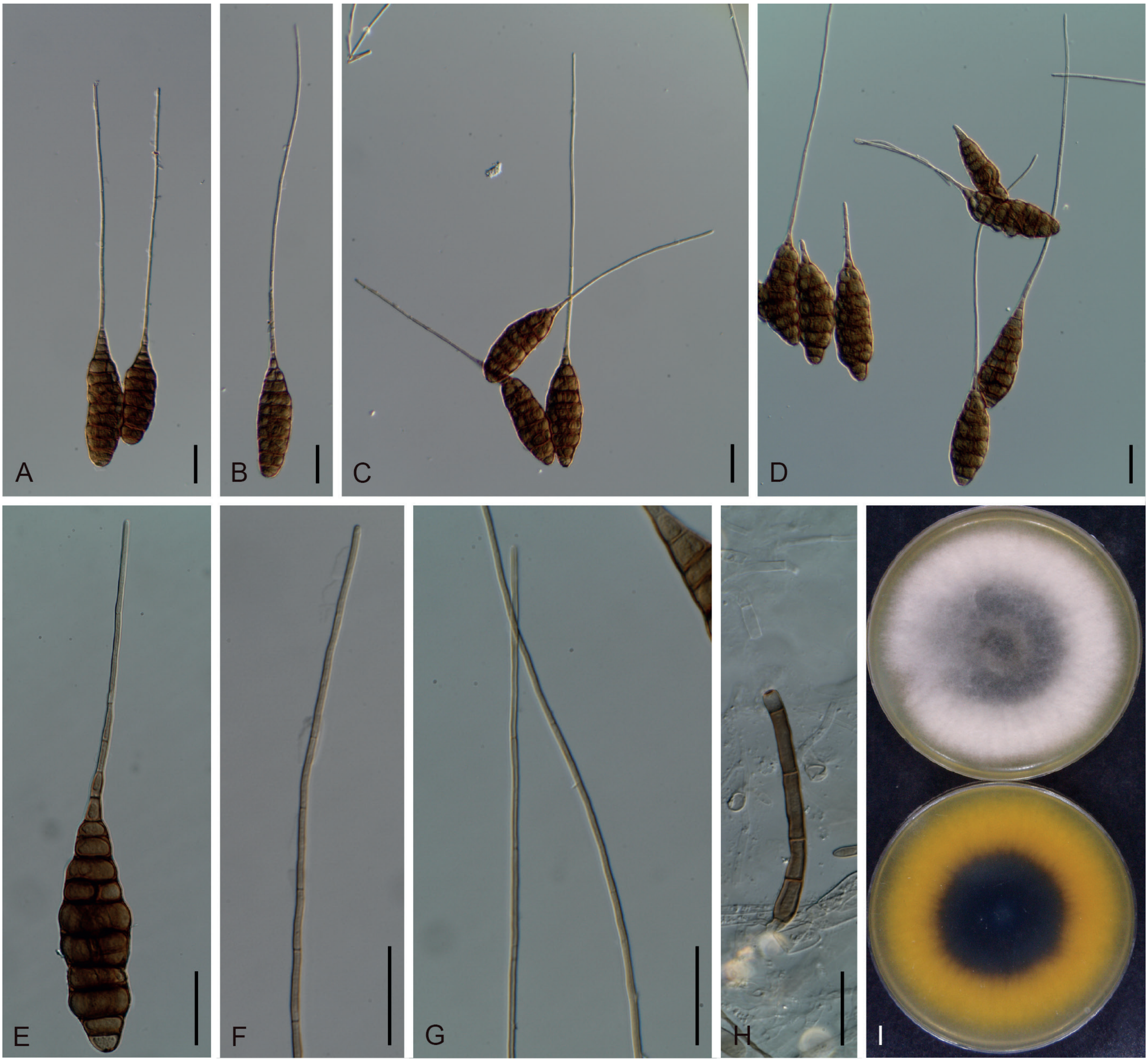

Fig. 34. Morphological features of Japanese isolates of *Alternaria cucumerina* (AC106) on V8 juice agar medium. **A–E.** Conidia. **F, G.** Colored beaks. **H.** Conidiophore. **I.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). Scale bars (A–H) = 25 µm.

Fl., Edn 2 (*Leipzig*) **1**(9): 260. 1908. *non Alternaria brassicae* var. *dauci* (J.G. Kühn) P.C. Bolle, *Meded. Phytopathol. Lab. "Willie Commelin Scholten"* **7**: 42. 1924, later isonym.
Alternaria porri f. sp. dauci (J.G. Kühn) Neerg, *Danish species of* Alternaria *and* Stemphylium: 252. 1945.
Alternaria poonensis Ragunath, *Mycopathol. Mycol. Appl.* **21**: 315. 1963.

Typus: **Lectotype**, B, on leaves of *Daucus carota*, slide glass specimen of *Sporidesmium exitiosum* var. *dauci*, Gross Krausche p. Bunzlau, Jul., *Kühn* (designated in Simmons 1995a; appeared to be lost according to Woudenberg *et al.* 2014). **Neotype**, **Italy**, from seed of *D. carota*, Sep. 1937, *P. Neergaard*, CBS H-21745 (designated in Woudenberg *et al.* 2014), culture ex-neotype CBS 111.38.

Additional material examined: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *D. carota*, Nov. 1998, *K. Takebayashi*, living cultures MUCC 1684 and AC9.

Morphological characters on V8 medium: *Conidiophores* moderately long and broad, 36–94 × 6–8 µm. *Conidia* commonly solitary, 152–448 µm in total length. Conidial bodies oblong to broadly obclavate, 52–100 × 13–31 µm, with 5–11 transverse and 0–8 longitudinal septa, sometimes with distosepta-like structures, brown to dark brown, with a smooth surface. Filamentous beaks straight and elongated, hyaline to subhyaline, unbranched or branched once, septated with distoseptum, 100–368 × 1–3 µm.

Colony characteristics on PDA after 7 d at 25 °C: Slow to moderate-growing, reaching an average of 53.6 ± 3.3 mm diam,

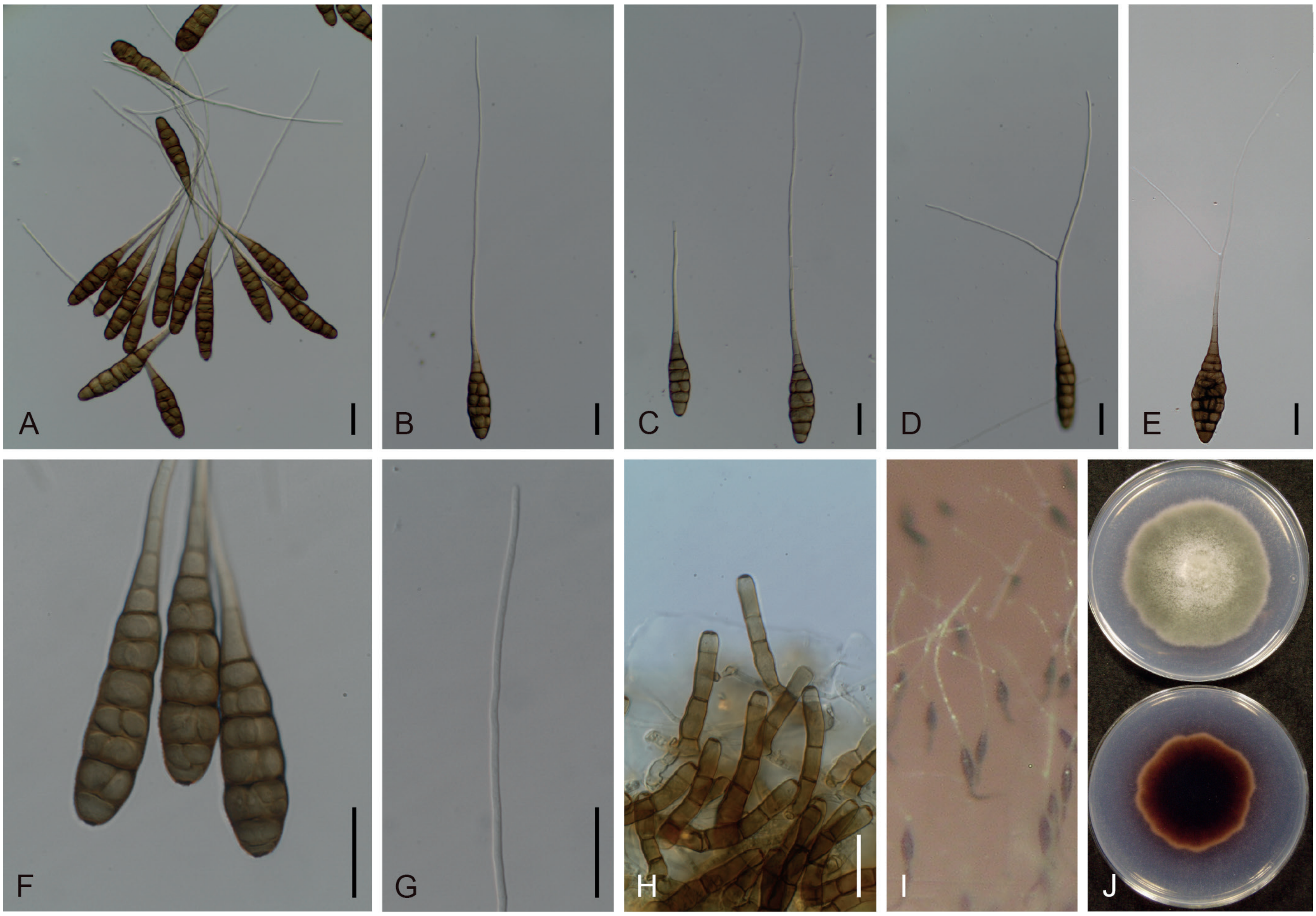

Fig. 35. Morphological features of Japanese isolates of *Alternaria dauci* (MUCC 1684) on V8 juice agar (V8) medium. **A–G.** Conidia with filamentous beaks. **H.** Conidiophores. **I.** Sporulation on surface of V8 medium. **J.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). Scale bars (A–H) = 25 µm.

variable among strains; aerial hypha cottony, grayish green to dark green, with white margins; reverse center dark green to black; sporulation sparse; diffusible pigment red to reddish brown.

Sexual morph: Not observed.

Natural hosts: *Daucus*, *Coriandrum*, *Apium* (*Apiaceae*), and *Cichorium* (*Asteraceae*), as well as some recorded cases infecting non-*Apiaceae* families under heterogeneous names as *forma speciales* of *A. dauci* (Richardson 1990, Simmons 2007, Woudenberg *et al.* 2014, Farr & Rossman 2018, Poudel & Zhang 2018).

Symptoms: Spots appear on the leaves and petioles of *Daucus*, and are circular to subcircular with distinct margins, measuring 1–3 mm diam, which become confluent, resulting in severe leaf blight and causing significant economic losses.

Distribution: Worldwide, including Asia (Cambodia, China, India, Israel, Japan, Korea, Malaysia, Nepal, Pakistan, Philippines, Taiwan, and Thailand), Europe (Austria, Bulgaria, Denmark, Germany, Greece, Finland, France, Italy, Netherlands, Poland, Portugal, Russia, Turkey, and UK), North and Latin America (Barbados, Brazil, Canada, Costa Rica, Cuba, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Peru, Puerto Rico, Trinidad and Tobago, USA, Venezuela, and Virgin Islands), Africa (Algeria, Congo, Ghana, Guinea, Kenya, Malawi, Mauritius, Morocco, Nigeria, South Africa, Tanzania, Zambia, and Zimbabwe), and the Pacific (Australia, Cook Islands, Fiji, New Zealand, Papua New Guinea, Samoa, and Tonga) (Goto 1927, Kranz 1963, Benjamin & Slot 1969, Rao 1969, Richardson 1990, Crous *et al.* 2000, Yu 2001, Zhang 2003, Soylu *et al.* 2004, Lopes & Martins 2008, Delgado 2011, Woudenberg *et al.* 2014, Farr & Rossman 2018, Ozkilinc *et al.* 2018, Poudel & Zhang 2018).

Distinctive features: Conidial bodies are oblong to obclavate, with hyaline filamentous beaks that often have a single branch. The conidial morphology of the species is indistinguishable from those of *A. porri*, but differs in length and width (usually not exceeding 3 µm), and more frequently in their longitudinal septa. Its growth rate on PDA is clearly slower, and colonies produce red pigment. This species is pathogenic to *Daucus* and some other species in *Apiaceae* (Boedo *et al.* 2012), and is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Alternaria porri **(Ellis) Cif., *J. Dept. Agric. Porto Rico* 14(1): 30. 1930. Figs 36, 37.**
Basionym: *Macrosporium porri* Ellis, in Cooke and Ellis, *Grevillea* **8** (45): 12. 1879.

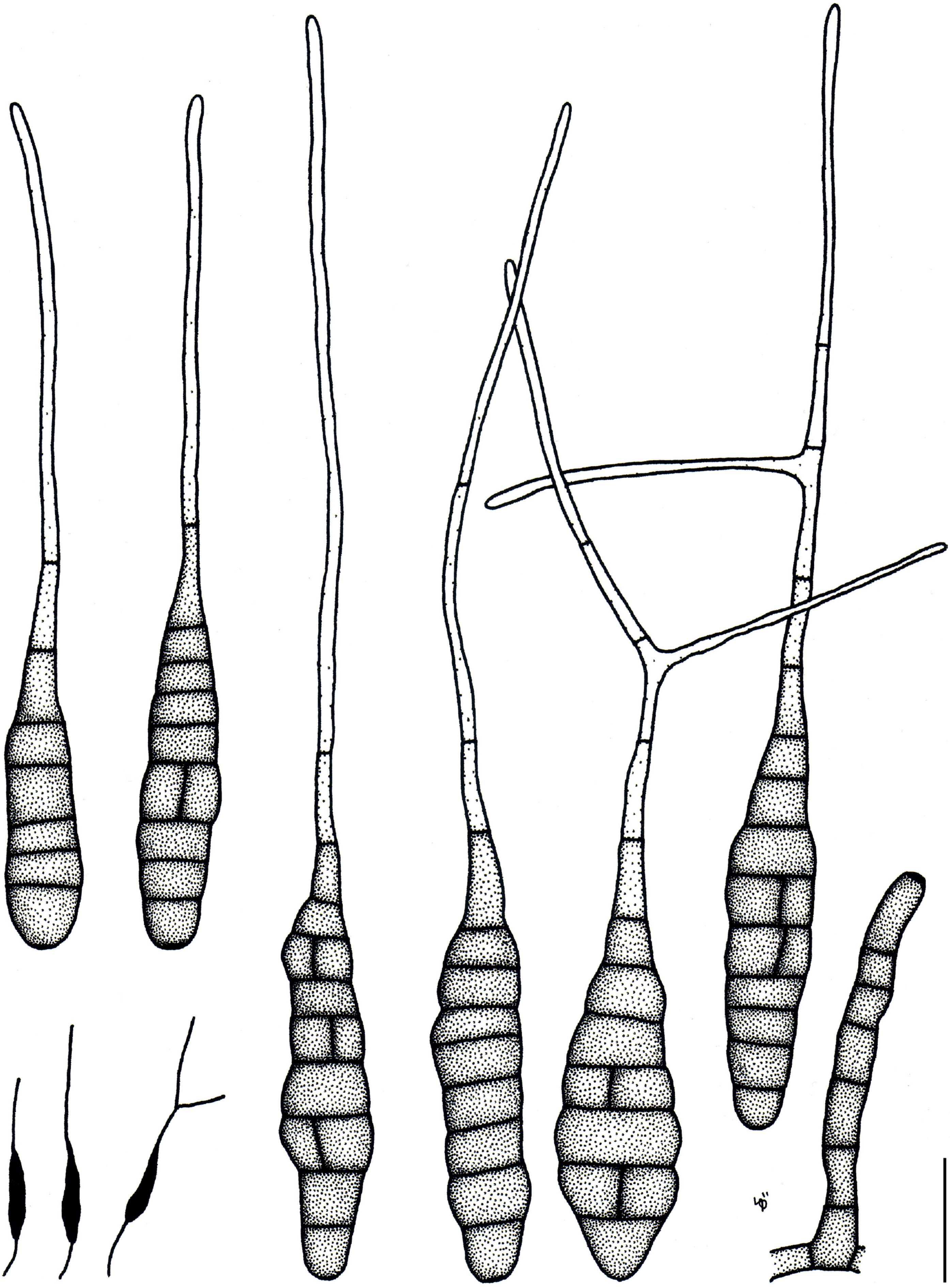

Fig. 36. Illustrations of *Alternaria porri* (AC6). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on V8 juice agar medium. Scale bar = 25 µm.

Fig. 37. Morphological features of Japanese isolates of *Alternaria porri* (MUCC 1688) on V8 juice agar medium. **A–G.** Conidia with filamentous beaks. **H.** Conidiophores. **I.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **J.** Natural symptoms on *Allium*. Scale bars (A–H) = 25 µm.

Synonyms: *Alternaria porri* (Ellis) Sawada, *Rep. Dept. Agric. Gov. Res. Inst. Formosa* **61**: 92. 1930.
Alternaria porri (Ellis) Neerg., *Aarsberet*. *J. E. Ohlsens Enkes Plantepat*. *Lab*. **3**: 5. 1938.
Alternaria allii Nolla, *Phytopathology* **17**: 118. 1927.
Alternaria vanuatuensis E.G. Simmons & C.F. Hill, *CBS Biodiversity Ser.* (*Utrecht*) **6**: 260. 2007.

Typus: on *Allium porrum* (holotype not specified). **Lectotype**, **USA**, New Jersey, Newfield, on leaves of *A. porrum*, Sep. 1878, *Ellis*, NY (designated in Simmons 2007). **Epitype**, **USA**, New York, Orange County, from leaf of *Allium cepa*, 1996, *M.J. Yáñes* Morales, CBS H-21746 (designated in Woudenberg *et al.* 2014), culture ex-epitype CBS 116699 = EGS 48.152.

Additional materials examined: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *Viola × wittrockiana*, 24 Dec. 2003, *J. Nishikawa*, living culture AC2; *ibid*., on leaves of *Calibrachoa* sp., 23 Apr. 2004, *J. Nishikawa*, MUMH 11670 and MUMH 11699, living culture AC6; *ibid*., on leaves of *Allium fistulosum*, 7 Oct. 2004, *J. Nishikawa*, MUMH 11673, living culture MUCC 1688; Saitama Prefecture, on leaves of *A. fistulosum*, 1 Nov. 2004, *J. Nishikawa*, living culture AC15; Gunma Prefecture, Takasaki, on leaves of *A. fistulosum*, 16 Mar. 2005, *J. Nishikawa*, living cultures AC16 and AC17; Gunma Prefecture, Tomioka, on leaves of *A. fistulosum*, 6 Oct. 2006, *J. Nishikawa*, MUMH 11677, living culture MUCC 1698; Chiba Prefecture, Mobara, on leaves of *A. fistulosum*, 24 Oct. 2006, *J. Nishikawa*, living culture AC32; Shizuoka Prefecture, Kakegawa, from seeds of *Eustoma exaltatum* subsp. *russellianum*, 20 Mar. 2007, *Y. Makizumi*, MUMH 11692, living culture MUCC 1702; Tokyo, Setagaya, from seeds of *A. fistulosum*, 7 Jul. 2001, *J. Nishikawa*, living culture AC68.

Morphological characters on V8 medium: *Conidiophores* moderately long and broad, 35–139 × 6–11 µm. *Conidia* commonly solitary, 75–351 µm in total length. Conidial bodies subcylindrical to oblong, pale brown to brown, with smooth surface, 38–114 × 10–26 µm with 3–12 transverse and 0–5 longitudinal septa, sometimes with distosepta-like structures. Filamentous beaks straight to slightly curved, hyaline, 30–248 × 2–4 µm, unbranched or often branched 1–2 times, septated with distoseptum. Conidial morphology on lesions similar to those on V8 medium, though usually short-beaked.

Colony characteristics after 7 d at 25 °C: Fast-growing, reaching an average of 78.6 ± 1.1 mm diam; aerial hypha cottony, white to grayish green, sometimes with white margins; reverse center dark green; diffusible pigment bright yellow to orange or reddish brown.

Sexual morph: Not observed.

Natural hosts: *Allium* spp. (*Amaryllidaceae*) are the most common hosts, although there are reports of the following serving as occasional hosts: *Acalypha* (*Euphorbiaceae*), *Apium* (*Apiaceae*), *Calendula*, *Gerbera*, and *Tagetes* (*Asteraceae*), *Clarkia* (*Onagraceae*), *Dichondra* and *Ipomoea* (*Convolvulaceae*), *Gossypium* and *Mucuna* (*Malvaceae*), *Peganum* (*Nitrariaceae*), *Scabiosa* (*Dipsacaceae*), and *Solanum* (*Solanaceae*) (Kranz 1963, Rao 1969, Richardson 1990, Crous *et al.* 2000, Ye *et al.* 2013, Farr & Rossman 2018).

Symptoms: Leaf spots on *Allium* are circular to long elliptical, distinct sooty spots, often with purple-stained appearance, measuring 7–50 mm diam. Caespituli were frequently observed on lesions.

Experimental host range: Pathogenic to *Allium*, but not to leaves of *Ageratum*, *Calibrachoa*, *Capsicum*, *Gentiana*, *Petunia*, *Solanum*, *Nicotiana*, and *Viola* (data not shown).

Distribution: Worldwide, including Asia (Brunei, China, India, Indonesia, Iraq, Israel, Japan, Korea, Malaysia, Myanmar, Nepal, Pakistan, Philippines, Taiwan, Thailand, Uzbekistan, and Vietnam), Europe (Austria, Bulgaria, Denmark, France, Germany, Greece, Italy, Netherlands, Poland, Portugal, Romania, Russia, Slovakia, and UK), North and Latin America (Argentina, Brazil, Canada, Colombia, Costa Rica, Cuba, Dominican Republic, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Puerto Rico, USA, Venezuela, and Virgin Islands), Africa (Egypt, Ethiopia, Ghana, Guinea, Kenya, Libya, Malawi, Mauritius, Nigeria, Rhodesia, South Africa, Tanzania, Uganda, Zambia, and Zimbabwe), and the Pacific (Australia, Fiji, New Caledonia, New Zealand, Papua New Guinea, Tonga, and Vanuatu) (Yoshii 1929a, Rao 1969, Ellis 1971, Stevenson 1975, Richardson 1990, Aveling & Naude 1992, Koike & Henderson 1998, Crous *et al.* 2000, Yu 2001, Zhang 2003, Hall *et al.* 2007, Simmons 2007, Delgado 2011, Woudenberg *et al.* 2013, 2014, Farr & Rossman 2018).

Distinctive features: Large-spored species with hyaline filamentous beaks, which are often branched and exceeded 3 µm in width. Conidial bodies are subcylindrical, with relatively fewer longitudinal septa. Colonies grown on PDA medium released bright yellow to reddish brown pigment. This species is pathogenic to *Allium*, and is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: Woudenberg *et al.* (2014) recognized *A. allii*, which is a morphospecies with multiple branched beaks (Simmons 2007), as a distinct taxon based on the combined phylogeny of ITS, *gapdh*, *rpb2*, *tef1*, and *Alt a 1* sequences. However, the morphology of isolates that clustered in the *A. allii* clade was not always distinguishable in beak branching (Figs 36, 37), and results of phylogenetic analysis based on ITS, *gapdh*, *tef1*, *Alt a 1*, and *act* sequences individually did not clearly support this species as a unique *Allium* pathogen (data not shown). Therefore, we regarded *A. allii* as a synonym of *A. porri* here. This species is also ubiquitous, and frequently found on non-host plants.

Alternaria zinniae **M.B. Ellis, *Mycol. Pap.* 131: 22. 1972. Fig. 38.**
Synonym: *Alternaria zinniae* H. Pape, *Angew. Bot.* **24**: 61. 1942, *nom. inval*. (no Latin; ICN Art. 39.1).

Typus: holotype specimen not specified. **Lectotype**, **USA**, New York, Ithaca, on *Zinnia elegans*, 28 Sep. 1942, *A.W. Dimock*, IMI 1037 (designated in Simmons 2007; as holotype in Simmons 1997).

Ex-type culture: Unknown.

Additional materials examined: **Japan**, Nagano Prefecture, Tomi, on leaves of *Zinnia* hybr., 6 Jul. 2007, *J. Nishikawa*, MUMH 11680, living culture MUCC 1704; Nagano Prefecture, Azumino, on leaves of *Zinnia* hybr., Aug. 2010, *Y. Makizumi*, living culture AC107; Shizuoka Prefecture, Kakegawa, on *Z. elegans*, 16 Mar. 2011, *Y. Makizumi*, living culture AC108; Nagano Prefecture, Azumino, on *Z. elegans*, 31 May 2011, *Y. Makizumi*, living culture AC109.

Morphological characters on V8 medium: *Conidiophores* moderately long and broad, 60–183 × 6–8 µm. *Conidia* usually solitary, but occasionally in chains of two, 109–318 µm in total length. Conidial bodies subcylindrical to oblong, 74–119 × 20–33 µm, with 9–16 transverse and 6–14 (often complicated) longitudinal septa, olive brown to brown, with smooth to minutely verrucose surface. Filamentous beaks almost straight, unbranched, pale brown, conspicuously distinguishable and border the conidial body, 33–213 × 1–3 µm.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 60.4 ± 5.6 mm diam, variable among strains; aerial hypha cottony, white to pale gray, with white margins; reverse center dark green to black; diffusible pigment yellow to pale orange.

Sexual morph: Not observed.

Natural hosts: Usually *Zinnia* and the other *Asteraceae* plants (*Ageratum*, *Bidens*, *Blumea*, *Calendula*, *Callistephus*, *Carthamus*, *Coreopsis*, *Cosmos*, *Dahlia*, *Echinops*, *Eclipta*, *Eupatorium*, *Gaillardia*, *Galinsoga*, *Gerbera*, *Glebionis*, *Helianthus*, *Kleinia*, *Parthenium*, *Rudbeckia*, *Sphaeranthus*, *Spilanthes*, *Tagetes*, *Tithonia*, *Volutaria*, and *Xanthium*) (Neergaard 1945, Rao 1969, Ellis 1976, Richardson 1990, Farr & Rossman 2018). Records suggest that it may also infect *Impatiens* (*Balsaminaceae*), *Nicotiana* (*Solanaceae*), and *Papaver* (*Papaveraceae*) (Neergaard 1945, Richardson 1990).

Symptoms: Leaf spots on seedlings of *Zinnia* are brown, circular to irregular, measuring 5–10 mm diam, becoming enlarged and confluent.

Distribution: Worldwide, including Asia (China, Brunei, India, Indonesia, Japan, Korea, Malaysia, Myanmar, Nepal, and Pakistan), Europe (Armenia, Austria, Cyprus, Denmark, France, Germany, Hungary, Italy, Latvia, Netherlands, Norway, Poland, Portugal, Romania, and UK), North and Latin America (Brazil, Canada, Guyana, Jamaica, and USA), Africa (Egypt, Ethiopia, Ghana, Guinea, Kenya, Libya, Malawi, Mauritius, Rhodesia, Sierra Leone, South Africa, Sudan, Tanzania, Uganda, Zambia,

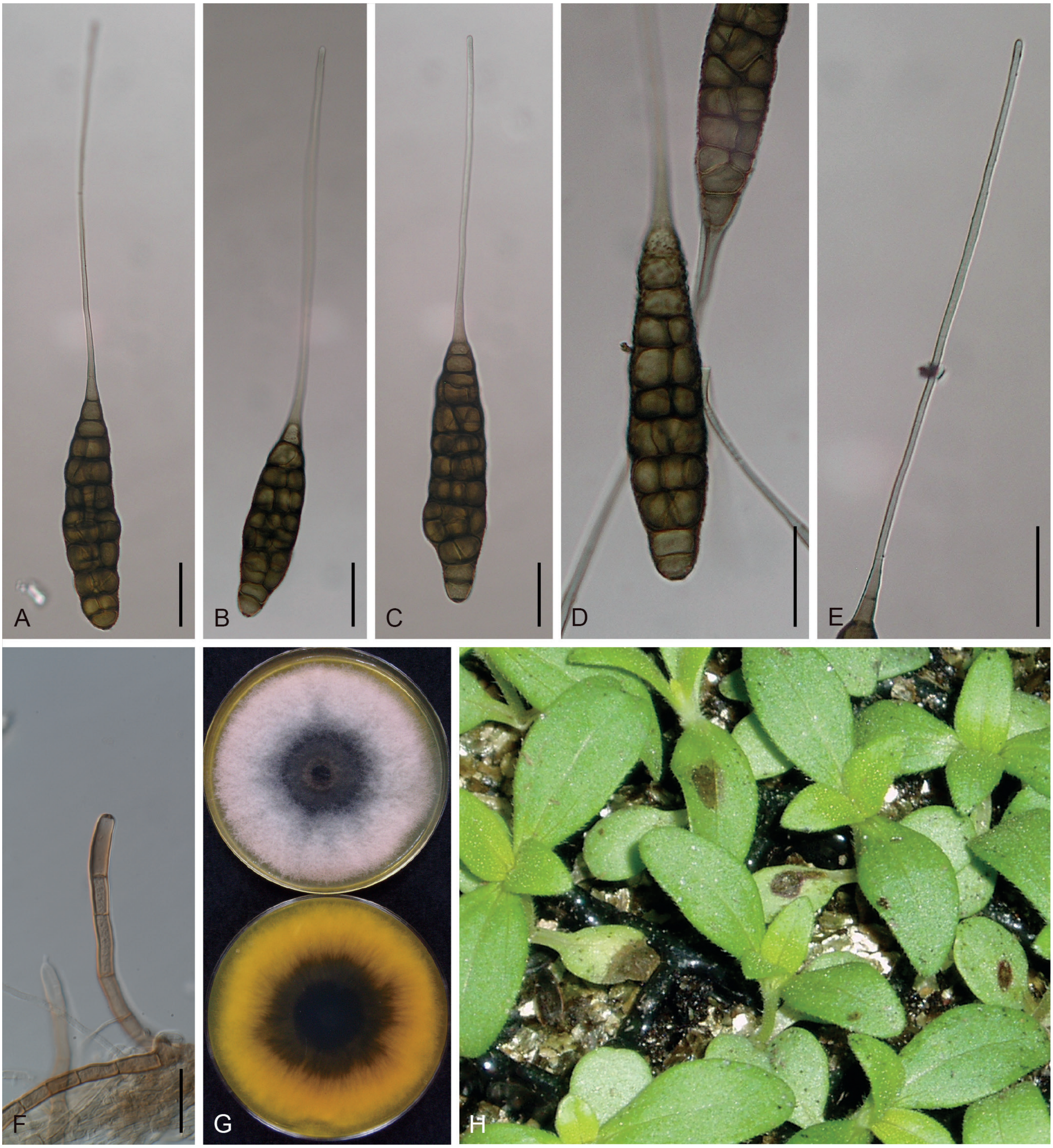

Fig. 38. Morphological features of Japanese isolates of *Alternaria zinniae* (MUCC 1704) on potato-carrot agar medium. **A–E.** Conidia. **F.** Conidiophores. **G.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **H.** Natural symptoms on seedlings of *Zinnia*. Scale bars (A–F) = 25 µm.

and Zimbabwe), and the Pacific (Australia, New Caledonia, New Zealand, and Tonga) (Kranz 1963, Rao 1969, Ellis 1976, Richardson 1990, Simmons 1997, Crous *et al.* 2000, Yu 2001, Zhang 2003, Woudenberg *et al.* 2014, Farr & Rossman 2018).

Distinctive features: Large-spored species with filamentous colored beaks as with those of *A. cucumerina*. Conidial bodies are oblong, often with complicated longitudinal septa. Colonies grown on PDA medium sometimes release yellow to pale orange pigment into the medium. This species is generally characterized by selective pathogenicity to *Zinnia* and some other *Asteraceae* plants (Neergaard 1945, Zhang 2003), and is phylogenetically recognizable via *gapdh*, *rpb2*, *tef1* (Fig. 1), *Alt a 1*, and *act* sequences (data not shown).

Note: Since there are a wide range of records listing *Asteraceae* as a host, further pathological studies within *Asteraceae*, besides *Zinnia*, are needed to characterize this species.

Section *Pseudoulocladium* Woudenb. & Crous, *Stud. Mycol.* **75**: 201. 2013.

The four species assigned to this section are characterized by simple or branched, short, and geniculate conidiophores, and catenation of mostly 3-septate conidia (Runa *et al*. 2009, Woudenberg *et al.* 2013). Gannibal & Lawrence (2018b) listed additional species in this section, *A. lanuginosa* and *A. sylvestris*, afterward.

Alternaria chartarum **Preuss, *Bot. Zeitung* 6: 412. 1848. Fig. 39.**
Basionym: *Sporidesmium polymorphum* var. *chartarum* (Preuss) Cooke, *Fungi Brit. Exs., ser. 2*: 329. 1875.
Synonyms: *Ulocladium chartarum* (Preuss) E.G. Simmons, *Mycologia* **59**: 88. 1967.
Alternaria stemphylioides Bliss, *Mycologia* **36**: 538. 1944.
Alternaria chartarum f. *stemphylioides* (Bliss) P. Joly, *Encycl. Mycol.* (*Paris*) **33**: 161. 1964.

Typus: **Germany**, Hoyerswerda, **holotype** in B, on paper, *Preuss*, Klotzsch's Herb. vivum mycol. no. 1284. **Epitype**, **Canada**, Saskatchewan, from *Populus* plywood, Jul. 1957, *S.J. Hughes*, CBS H-19059 (designated in de Hoog & Horré 2002), culture ex-epitype CBS 200.67 = ATCC 18044 = DAOM 59616b = IMI 124943 = MUCL 18564 = QM 8328.

Additional material examined: **Japan**, Tokyo, Setagaya, from seeds of *Capsicum annuum*, 8 Dec. 2000, *J. Nishikawa*, living culture MAFF 246888.

Morphological characters on PCA medium: *Conidiophores* solitary and relatively short, 18–95 × 3–5 µm, pale brown to brown, with polytretic pores at the apex, 2–4 geniculate bends, frequently proliferating at the upper nodes. *Conidia* in short chains of 3–8, frequently with lateral branches, brown to dark brown, ellipsoid to obclavate, smooth to roughened, 13–29 × 8–15 µm, with 1–4 (mostly 3) transverse and 0–4 longitudinal septa. Secondary conidiophores (false beaks) at the apical end

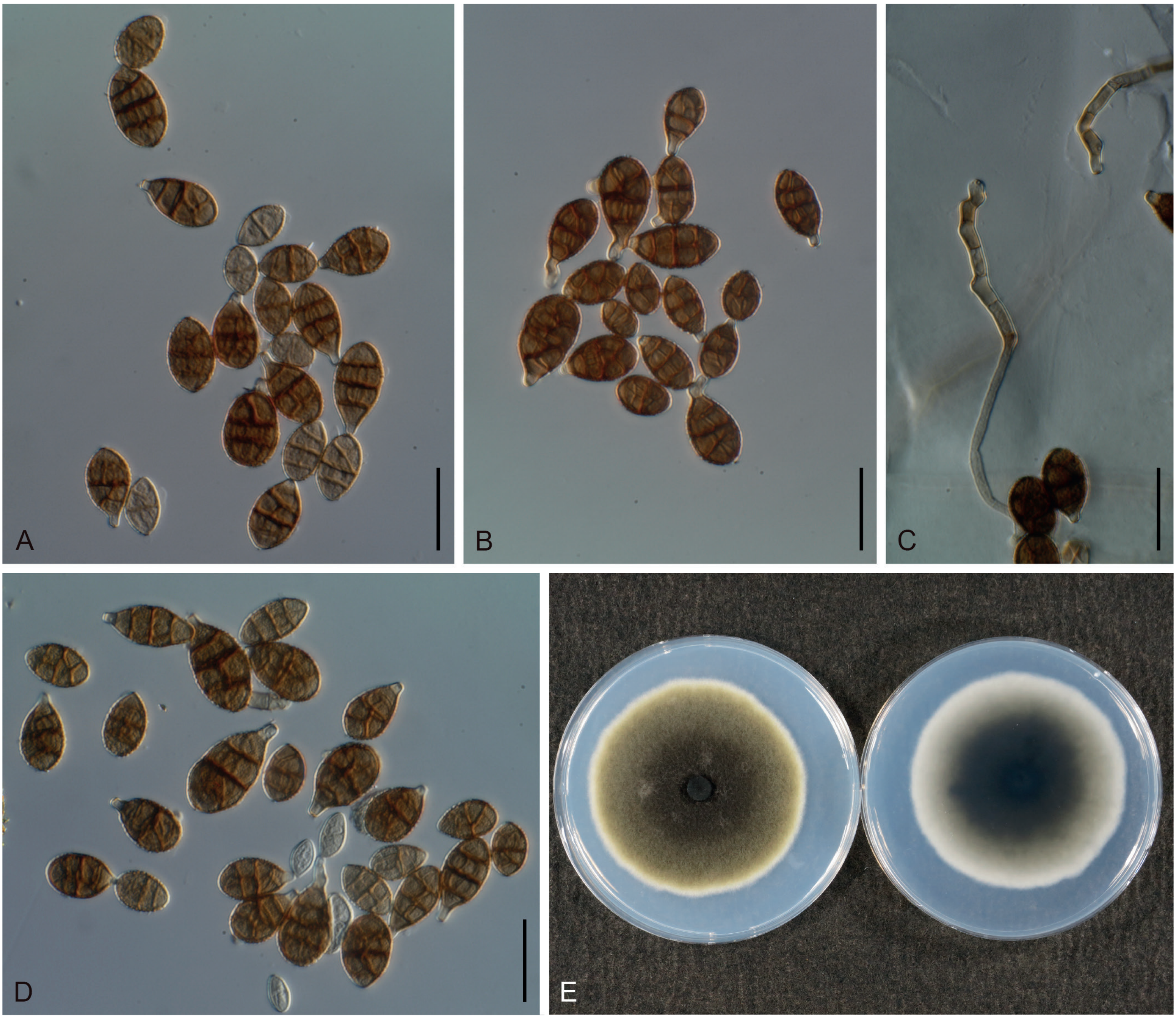

Fig. 39. Morphological features of Japanese isolates of *Alternaria chartarum* (MAFF 246888). **A–D.** Conidia and conidiophores on potato-carrot agar medium. **E.** Culture on potato-dextrose agar medium (left = surface, right = reverse). Scale bars (A–D) = 25 µm.

and median of conidium, short, mostly single-celled, sometimes proliferate and branched.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching 60.8 ± 3.1 mm diam; aerial hypha cottony to sparse, dark green to greenish brown, with white margins; reverse center dark green to pale gray; sporulation abundant; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: Saprophytic, but there are records of pathogenicity to *Quercus*, *Vaccinium*, and *Lippia* (Vannini & Vettraino 2000, Starast *et al.* 2009, Zarandi & Sharzei 2015).

Distribution: Worldwide, including Asia (China, India, Iran, Iraq, Israel, Japan, Kuwait, Pakistan, and Saudi Arabia), Europe (Lithuania, Poland, Russia, and UK), North and Latin America (Canada, Nicaragua, Uruguay, and USA), South Africa, and Australia (Rao 1969, Ellis 1976, Phillips *et al.* 1979, Rossman & Lu 1980, Watanabe *et al.* 1986, Bettucci *et al.* 1997, Chen *et al.* 2002, Nishikawa *et al.* 2006, Delgado 2011, Kowalski & Andruch 2012, Woudenberg *et al.* 2013, Zarandi & Sharzei 2015, Barkat *et al.* 2016, Farr & Rossman 2018).

Distinctive features: Short conidiophores are geniculate and proliferate frequently; obclavate conidia commonly appear in chains, with three transverse septa. This species may be phylogenetically recognizable via ITS (Fig. 2), *gapdh*, *tef1*, *Alt a 1*, and *act* sequences (data not shown).

Notes: The results of the *gapdh* and *tef1* phylogeny also suggested that isolates of *A. aspera*, *A. chartarum*, *A. concatenata*, and *A. septospora* must be conspecific (data not shown), and morphological differences between these species were unclear based on their original descriptions (Simmons 1967, 2004, Xue & Zhang 2007). This species has often been misidentified as *A. alternata* owing to its conidial catenation (Simmons 1967, de Hoog & Horré 2002, Runa *et al*. 2009).

Section *Radicina* D.P. Lawr. *et al.*, *Mycologia* **105**: 541. 2013.

Five species were recognized in this section (Lawrence *et al.* 2013, Woudenberg *et al.* 2013), which is morphologically characterized by medium-sized, beakless conidia. All recognized species in this section were sourced from *Apiaceae*. Two species, *A. petroselini* and *A. radicina*, are distributed in Japan (Yoshii 1929b, Nishikawa & Nakashima 2013), and the former was examined in the present study.

***Alternaria petroselini* (Neerg.) E.G. Simmons, in Ellis, *More dematiaceous Hyphomycetes* (*Kew*): 417. 1976. Fig. 40.**
Basionym: *Stemphylium petroselini* Neerg., *Zentralbl. Bakteriol., 2. Abt.* **104**: 411. 1942.
Synonyms: *Stemphylium radicinum* var. *petroselini* (Neerg.) Neerg., *Danish species of* Alternaria *and* Stemphylium: 357. 1945.
Alternaria radicina var. *petroselini* (Neerg.) Neerg., *Encycl. Mycol.* **33**: 123. 1964.
Macrosporium cheiranthi f. petroselini Sacc., *Rev. Mycol.* (*Toulouse*) **19**: 54. 1897.
Alternaria selini E.G. Simmons, *Mycotaxon* **55**: 109. 1995.

Typus: **Denmark**, from seeds of *Petroselinum crispum*, 4 Apr. 1941, *P. Neergaard*, **holotype** EGS 11.062 in CP, culture presumably ex-holotype CBS 112.41 = EGS 06.196.

Additional material examined: **Japan**, Shizuoka Prefecture, Kakegawa, on leaves of *P. crispum*, 27 Apr. 2007, *J. Nishikawa*, MUMH 11679, living culture MAFF 243057.

Morphological characters on PCA medium: Previously reported in Nishikawa & Nakashima (2013).

Colony characteristics on PDA after 7 d at 25 °C: Fast-growing, reaching 82.1 ± 1.8 mm diam; characteristics previously reported in Nishikawa & Nakashima 2013.

Sexual morph: Not observed.

Natural hosts: Typically, *Petroselinum*, *Coriandrum*, and *Foeniculum* (*Apiaceae*), but may also occasionally infect *Carya* (*Juglandaceae*) (Liu *et al.* 2013).

Symptoms: Leaf spots on *Petroselinum* indistinct, sooty brown, water-soaked, and expand to leaf blight (Nishikawa & Nakashima 2013).

Experimental host range: Widely pathogenic within *Apiaceae* plants, including *Ammi*, *Anethum*, *Angelica*, *Anthriscus*, *Apium*, *Bupleurum*, *Coriandrum*, *Cuminum*, *Foeniculum*, and *Petroselinum* (Nishikawa & Nakashima 2013).

Distribution: Australia, China, Italy, Japan, Netherlands, Saudi Arabia, Spain, UK, and USA (Ellis 1976, Farrar *et al.* 2004, Cunnington *et al.* 2007, Pryor & Asma 2007, Park *et al.* 2008, Infantino *et al.* 2009, Bassimba *et al.* 2012, Liu *et al.* 2013, Nishikawa & Nakashima 2013, Farr & Rossman 2018).

Distinctive features: Conidia are solitary or appear in short chains and are mostly beakless, and broad-ovoid to long-ellipsoid (but variable in shape and size). This species was widely pathogenic to *Apiaceae*, but not to *Daucus*, and is phylogenetically recognizable via its ITS (Fig. 2), *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: All the sequences of the examined Japanese isolate MAFF 243057 were identical with those of the ex-type isolates, *A. petroselini* (CBS 112.41) and *A. selini* (CBS 109382). Based on both phylogenetic analysis and morphological observations, *A. selini* was never distinguishable from *A. petroselini* (Fig. 1), and, thus, they are synonymized in the present study.

Section *Sonchi* D.P. Lawr. *et al.*, *Mycologia* **105**: 542. 2013.

This section is morphologically characterized by large conidia, which are solitary or may appear in short chains with a blunt-tapered false beak. There are only two species assigned to this section (Woudenberg *et al.* 2013), although Lawrence *et al.* (2013) included *A. brassicae* within this section.

***Alternaria cinerariae* Hori & Enjoji, *J. Pl. Protect.* (*Tokyo*) 18(8): 432. 1931. Fig. 41.**
Synonym: *Alternaria senecionis* Neerg., *Danish species of* Alternaria *and* Stemphylium: 201. 1945.

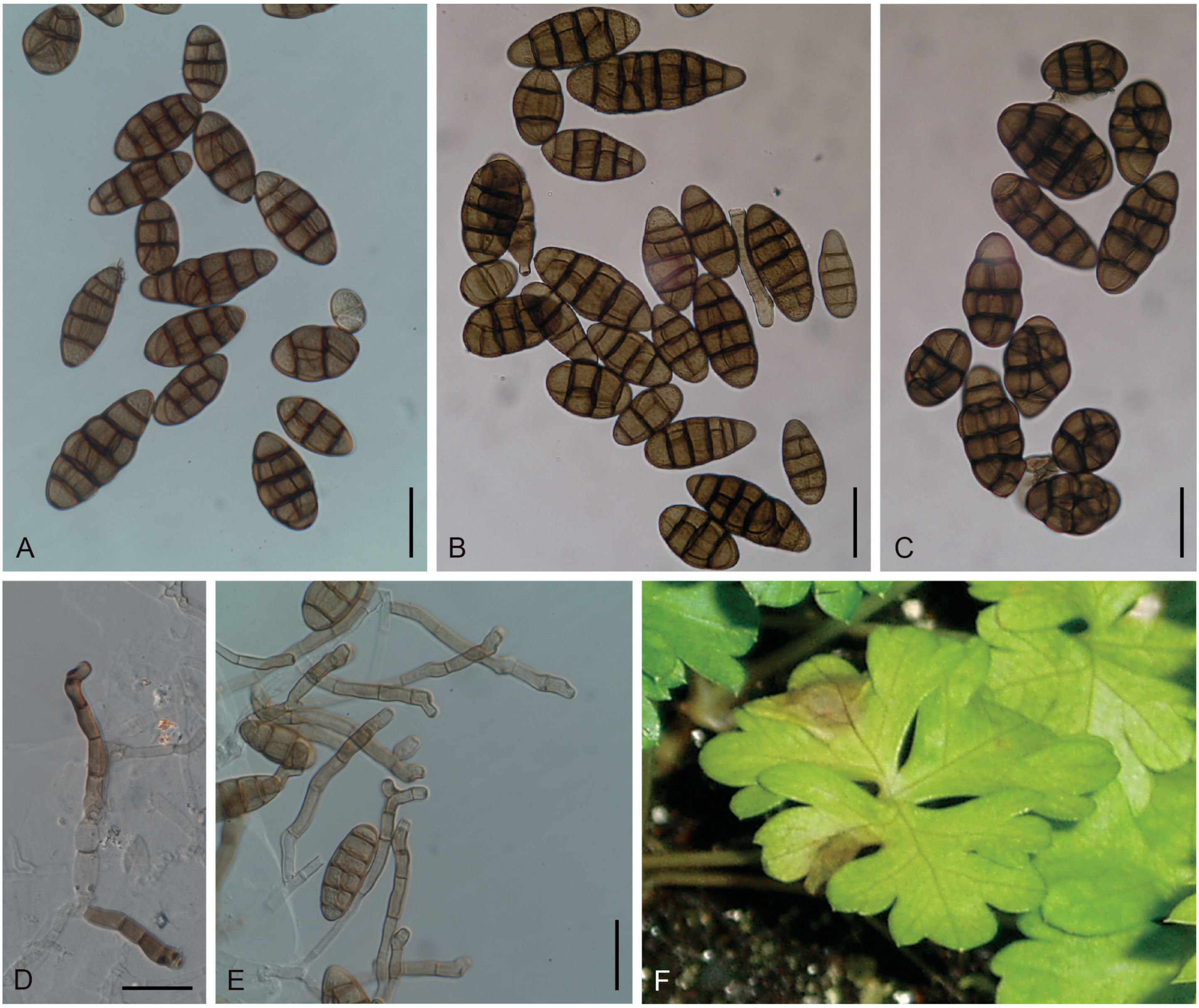

Fig. 40. Morphological features of Japanese isolates of *Alternaria petroselini* (MAFF 243057). **A–C.** Conidia on potato-carrot agar (PCA) medium. **D, E.** Conidiophores on PCA medium. **F.** Natural symptoms on *Petroselinum*. Scale bars (A–E) = 25 µm.

Typus: **Japan**, Chiba Prefecture, Chiba, Chiba Prefect. Agric. Exp. Station, on leaves of *Pericallis cruenta*, 30 Mar. 1931, and in Apr. to May 1931, *S. Enjoji* (holotype not specified; not preserved). **Lectotype**, **Japan**, Chiba Prefect. Agric. Exp. Station, on *Senecio cineraria*, 28 Apr. 1931, *S. Enjoji*, in FU (designated in Simmons 1997). **Epitype designated here**, **Japan**, Chiba Prefecture, Narita, on leaves of *P. cruenta*, 25 Oct. 2002, *J. Nishikawa*, TNS-F-85448 (dried culture specimen ex MAFF 243059) [MBT 385024], isoepitype MUMH 11691, culture ex-epitype MAFF 243059 = MUCC 1701.

Additional materials examined: **Japan**, Ibaraki Prefecture, Tsukuba, Kannondai, on leaves of *Farfugium japonicum*, Nov. 2008, *Y. Otani*, MUMH 11694, living culture MAFF 241266 = MUCC 1613; *ibid*., on leaves of *Gynura bicolor*, Nov. 2008, *Y. Otani*, MUMH 11695, living culture MAFF 241267 = MUCC 1614; Kanagawa Prefecture, Atsugi, on leaves of *Jacobaea maritima*, 23 Aug. 2017, *Y. Makizumi*, living culture MUCC 2504.

Morphological characters on V8 medium: *Conidiophores* broad, 25–196 × 6–11 µm, often branched but sometimes unbranched. *Conidia* solitary to in chains of 2–5(–9), rarely with lateral branches, faintly yellowish-tan to pale brown, smooth, long ellipsoid to obclavate, with a blunt tapered false beak, mostly straight and laterally symmetrical, 18–319 µm in total length, constricted at each transverse septum. Conidial bodies sometimes excessively swollen, 18–295 × 8–63 µm, with 1–14 transverse septa and up to 10 longitudinal septa; false beaks unbranched, up to 80–159 × 5–9 µm, concolorous with body, inconspicuous border with the conidial body. Conidia of ex-epitype culture MAFF 243059 on V8 medium solitary to in chains of 2–3 conidia; conidial bodies 30–138 × 9–46 µm, with 2–12 transverse and up to 10 longitudinal septa; secondary conidiophores up to 123 × 5–9 µm.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 62.9 ± 3.6 mm diam, variable among strains; aerial hypha cottony, grayish green to dark green, with white margins; reverse center black to dark green; sporulation sparse; diffusible pigment absent.

Sexual morph: Not observed.

Fig. 41. Morphological features of Japanese isolates of *Alternaria cinerariae* (MAFF 243059) on V8 juice agar medium. **A–H.** Conidia. **I.** Conidiophores. **J.** Dried culture specimen ex MAFF 243059 (epitype: TNS-F-85448). **K.** Natural symptoms on *Pericallis*. Scale bars (A–I) = 25 µm.

Natural hosts: *Farfugium*, *Gynura*, *Jacobaea*, *Ligularia*, *Pericallis*, and *Senecio* (*Asteraceae*) (Nishikawa & Nakashima 2015).

Symptoms: Leaf spots on *Pericallis* black, circular to irregular, and 3–10 mm diam, often with a necrotic eye at the center. They appear water-soaked, enlarge, and become confluent.

Experimental host range: Selectively pathogenic to tribe *Senecioneae*, and experiments suggest weak pathogenicity to *Cosmos bipinnatus* and *Centaurea* (Nishikawa & Nakashima 2015).

Distribution: Worldwide, but few records exist; Denmark, Germany, Japan, Korea, New Zealand, South Africa, UK, and USA (Enjoji 1931, Neergaard 1945, Ellis 1976, Richardson 1990, Yu 2001, Simmons 2007, Woudenberg *et al.* 2013, Nishikawa & Nakashima 2015, Farr & Rossman 2018).

Distinctive features: Conidia are large, solitary or in short chains with a blunt-tapered false beak. Conidiophores are long, broad, and sometimes branching. This species is selectively pathogenic to tribe *Senecioneae*, which includes genera *Senecio*, *Farfugium* and *Gynura*, and is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: Morphological variations are present between strains, including the appearance of excessively swollen bodies and chlamydospore (microsclerotia) formation (Nishikawa & Nakashima 2015). There is no ex-type culture and few reference isolates, and the epitype originated near the original type locality; therefore, an ex-epitype isolate was designated and deposited for future studies.

Section *Ulocladioides* Woudenb. & Crous, *Stud. Mycol.* **75**: 204. 2013.

There are ten species and a representative strain of *A. botrytis* assigned to this section (Woudenberg *et al.* 2013), which is typified by *A. cucurbitae*, and consists of a majority of the former *Ulocladium* spp. Recently, Gannibal & Lawrence (2018b) additionally listed ten species citing Geng *et al*. (2014). Conidial morphology resembles those of species in sect. *Ulocladium* (Woudenberg *et al.* 2013).

Alternaria atra **(Preuss) Woudenb. & Crous, *Stud. Mycol.* 75: 204. 2013. Fig. 42.**
Basionym: *Ulocladium atrum* Preuss, *Linnaea* **25**: 75. 1852.
Synonyms: *Stemphylium atrum* (Preuss) Sacc., *Syll. Fung.* **4**: 520. 1886.
Alternaria abietis Tengwall, *Meded. Phytopath. Lab.* '*WCS*' **6**: 50. 1924.

Typus: **Germany**, Hoyerswerda, on *Betula pubescens* (as *Betula alba*), *Preuss*, in B. **Epitype**, **USA**, California, from soil, Nov. 1962, *P.M.D. Martin*, BPI 444871 (designated in de Hoog & Horré 2002), culture ex-epitype CBS 195.67 = ATCC 18040 = IMI 124944 = QM 8408.

Additional materials examined: **Japan**, Tokyo, Setagaya, from seeds of *Raphanus sativus*, Jul. 2000, *J. Nishikawa*, living culture AC86; *ibid*., from seeds of *Brassica oleracea* var. *capitata*, 4 Feb. 2001, *J. Nishikawa*, living culture AC87; *ibid*., from seeds of *Brassica rapa* subsp. *pekinensis*, 18 Mar. 2001, *J. Nishikawa*, living culture AC88; *ibid*., from seeds of *A. fistulosum*, 7 Jul. 2001, *J. Nishikawa*, living culture MAFF 246889.

Morphological characters on PCA medium: *Conidiophores* solitary, usually unbranched and geniculate, frequently proliferating sympodially, pale brown to brown, 23–73 × 3–5 µm, with pores for polytretic sporulation. *Conidia* commonly solitary, varied from subsphaeroid, obovoid, obclavate to ellipsoid, brown to dark brown, roughened to conspicuously verrucose, 10–33 × 6–17 µm, with (0–)1(–3) transverse and 0–2 longitudinal septa, usually beakless, but sometimes with a secondary conidiophore at the apex. Secondary conidiophores geniculate, 3–38 × 3–5 µm.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching an average of 65.3 ± 3.1 mm diam, variable among strains; aerial hyphae cottony to sparse, grayish green to dark green or black, with white margins; reverse center pale gray to dark green or black; sporulation commonly abundant; diffusible pigment absent.

Sexual morph: Not observed.

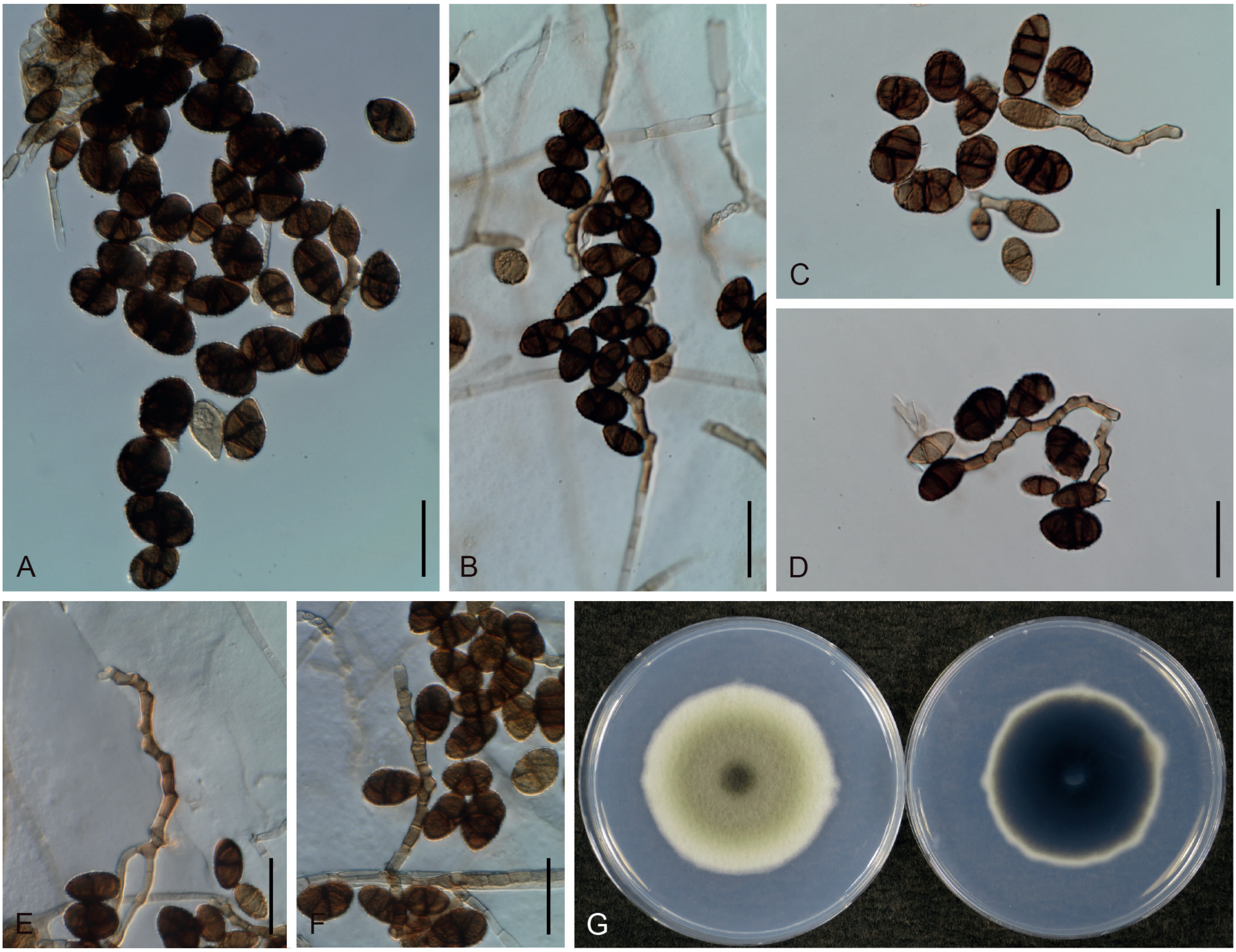

Fig. 42. Morphological features of Japanese isolates of *Alternaria atra* (MAFF 246889). **A–D.** Conidia on potato-carrot agar medium. **E, F.** Conidiophores. **G.** Culture on potato-dextrose agar medium (left = surface, right = reverse). Scale bars (A–F) = 25 µm.

Natural hosts: Saprophytic, but a few records suggest pathogenicity to *Helianthus* and *Solanum* (Shtienberg 1994, Esfahani 2018).

Distribution: Worldwide, including Asia (China, India, Iran, Israel, Japan, Korea, Kuwait, Pakistan, and Saudi Arabia), Europe (Cyprus, Denmark, Germany, Italy, Netherlands, Poland, Spain, and UK), North and Latin America (Argentina, Canada, Mexico, and USA), Africa (Egypt, Libya, and Sierra Leone), and the Pacific (Australia and New Zealand) (Ellis 1976, Abdel-Hafez 1984, Shtienberg 1994, Heredia *et al.* 1995, Chen *et al.* 2002, Lunghini *et al.* 2013, Esfahani 2018, Farr & Rossman 2018).

Distinctive features: Short conidiophores are geniculate and frequently proliferate; conidia are commonly solitary, but often appear in chains with secondary conidiophores, generally with one transverse septum in a body. This species may be phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, and *Alt a 1* sequences (data not shown).

Notes: The multi-locus phylogeny shown in this study (Fig. 1) as well as previous studies (Runa *et al*. 2009, Woudenberg *et al*. 2013, Geng *et al*. 2014) suggested that this section consists of three or more strongly supported subclades, with overlapping conidial morphology. These species were commonly regarded as saprophytes (Rena *et al*. 2009), and consequently could not be examined under the concept of integrated species recognition in this study. Therefore, we provisionally identified Japanese isolates as *A. atra* based on their conidial morphology and ITS phylogeny, which may determine species boundaries in other former *Ulocladium* spp. in sect. *Pseudoulocladium* and *Ulocladium* (Fig. 2).

Section *Ulocladium* (Preuss) Woudenb. & Crous, *Stud. Mycol.* **75**: 206. 2013.

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

Four species typified by *A. botrytis* were assigned to this section by Woudenberg *et al*. (2013), and former *Sinomyces* spp., which is *S. alternariae*, *S. fusoideus* and *S. obovoideus*, may also be included in this section. Gannibal & Lawrence (2018b) additionally listed *A. manihoticola* in this section. Two species, *A. botrytis* and *A. oudemansii*, are found in Japan (Katumoto 2010), though there are a few morphological differences between the species in this section (Simmons 1967, Runa *et al.* 2009).

***Alternaria botrytis* (Preuss) Woudenb. & Crous, *Stud. Mycol.* 75: 206. 2013. Fig. 43.**
Basionym: *Ulocladium botrytis* Preuss, *Linnaea* **24**: 111. 1851.
Synonyms: *Stemphylium botryosum* Wallr. var. *ulocladium* Sacc., *Syll. Fung*. **4**: 522. 1886.
Stemphylium botryosum Wallr. var. *botrytis* (Preuss) Lindau, *Rabenh*. *Krypt*.-*Fl*., Edn 2 **1**(9): 219. 1908.
Alternaria oudemansii (E.G. Simmons) Woudenb. & Crous, *Stud*. *Mycol*. **75**: 206. 2013.
Ulocladium oudemansii E.G. Simmons, *Mycologia* **59**: 86. 1967.

Typus: **Germany**, Hoyerswerda, on wood sliver of *Quercus*, **holotype** in B. **Epitype**, **USA**, Cambridge, Massachusetts, contaminant (air), CBS H-19057 (designated in de Hoog & Horré 2002), culture ex-epitype CBS 197.67 = ATCC 18042 = IMI 124942 = MUCL 18556 = QM 7878.

Additional material examined: **Japan**, Shizuoka Prefecture, Kakegawa, from rhizomes of *Asparagus officinalis*, 8 Apr. 2008, *J. Nishikawa*, living culture MAFF 246887.

Morphological characters on PCA medium: *Conidiophores* solitary, often branched, geniculate, frequently proliferate sympodially, pale brown to brown, 48–145 × 2–4 µm, with pores for polytretic sporulation. *Conidia* commonly solitary, brown to dark brown, roughened to conspicuously verrucose, obovoid to ellipsoid, beakless, 13–30 × 8–17 µm, with (1–)3 transverse and 0–3 longitudinal septa.

Colony characteristics on PDA after 7 d at 25 °C: Moderate-growing, reaching 68.1 ± 0.9 mm diam; aerial hypha commonly sparse, green to greenish brown, with white margins; reverse center black to dark green; sporulation abundant; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: Saprophytic (recorded on *Pinus*, *Alnus, Betula*, etc., but no records exist suggesting pathogenicity) (Wicker & Yokota 1982, Farr & Rossman 2018).

Distribution: China, Egypt, Germany, India, Japan, Kuwait, Pakistan, Poland, Russia, Thailand, UK, Uruguay, and USA (Ellis 1971, Tokumasu *et al.* 1994, Alonso *et al.* 2011, Farr & Rossman 2018).

Distinctive features: Long conidiophores are geniculate and proliferate. Conidia are solitary and typically obovoid, usually with three transverse septa. This species is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Notes: Phylogenetic analysis conducted during the present study, as well as morphological similarity, suggest that this species is conspecific with *A. alternariae* and *A. oudemansii* (Runa *et al.* 2009, Woudenberg *et al.* 2013) (Fig. 1). However, the examined isolate of *A. alternariae* (CBS 126989 = EGS 46.004) is not an authentic isolate of the species (Wang *et al.* 2011), and therefore, just *A. oudemansii* is synonymized herein. This species has already been observed (as *A. botrytis* or *A. oudemansii*) on pine and Japanese cedar seeds (Wicker & Yokota 1982, Watanabe *et al.* 1986, Watanabe & Sato 1988).

Monotypic lineages

Woudenberg *et al.* (2013) recognized six species as single species not assigned to hitherto known sections, namely *A. argyranthemi*, *A. brassicae*, *A. dennisii*, *A. helianthiinficiens*, *A. soliaridae*, and *A. thalictrigena*. Lawrence *et al.* (2016) recognized an additional two monotypic lineages, *A. peucedani* and *A. thlaspis*. Among these, *A. brassicae* is already known in Japan, and a novel species isolated from *Bupleurum* is also newly described here as a ninth monotypic lineage.

***Alternaria brassicae* (Berk.) Sacc., *Michelia* 2: 172. 1880. Figs 44, 45.**
Basionym: *Macrosporium brassicae* Berk., in Smith, *Engl. Fl., Fungi* **5**(2): 339. 1836.
Additional synonyms in Simmons (2007).

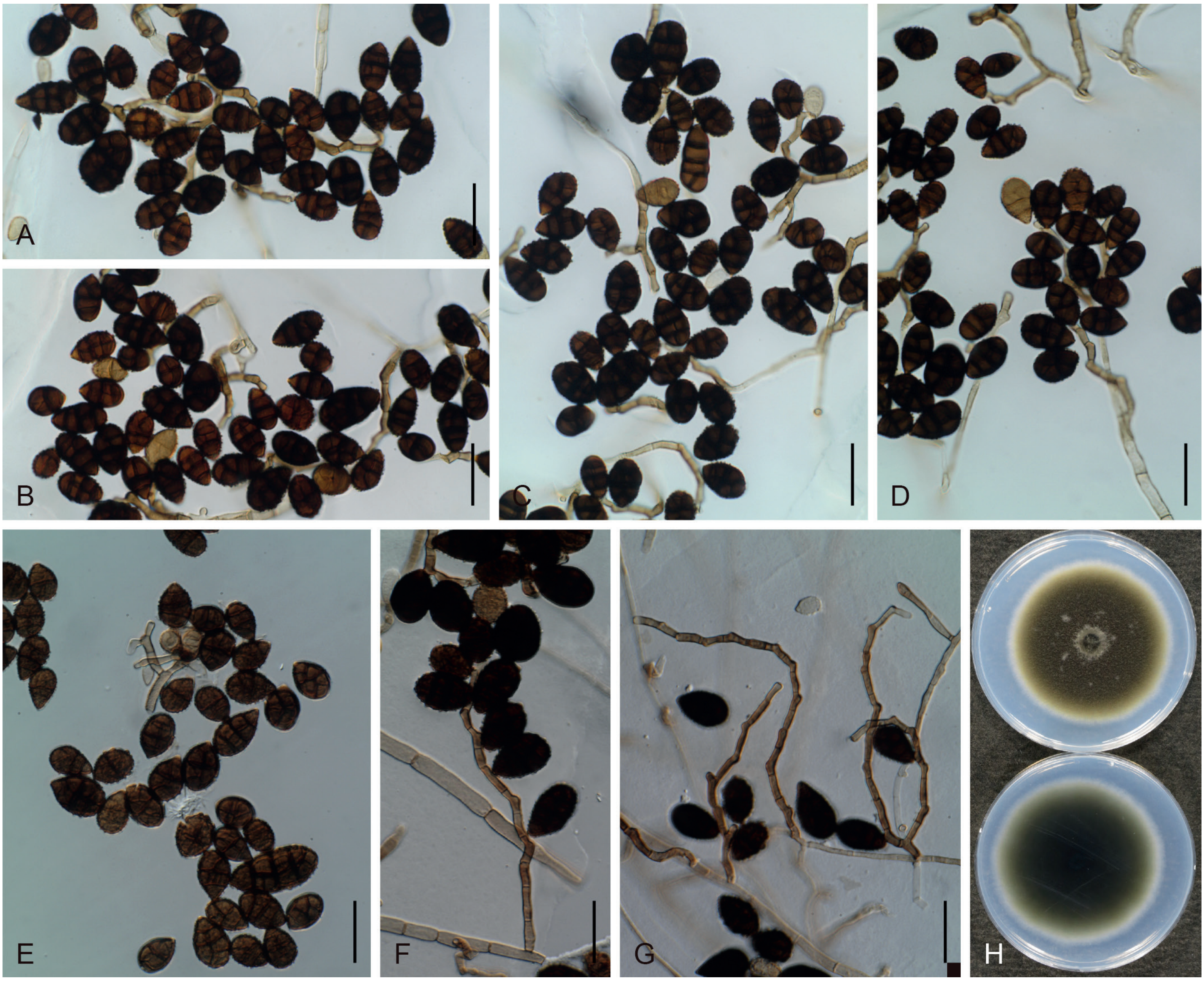

Fig. 43. Morphological features of Japanese isolates of *Alternaria botrytis* (MAFF 246887). **A–E.** Conidia on potato-carrot agar medium. **F, G.** Conidiophores producing conidia. **H.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). Scale bars (A–G) = 25 µm.

Typus: **UK**, Northamptonshire, Kings Cliffe, on decaying leaves of *Brassica oleracea* var. *capitata*, *M.J. Berkeley* (**holotype** specimen unknown according to Simmons 1995a). **Neotype**, **UK**, Essex, on leaves of *B. oleracea* var. *capitata*, 16 Oct. 1966, *E.G. Simmons*, IMI 369156 (designated in Simmons 1995a).

Ex-type culture: Unknown.

Additional materials examined: **Japan**, Shizuoka Prefecture, Kakegawa, from seeds of *Brassica rapa*, 15 Aug. 2006, *J. Nishikawa*, living culture AC29; Ibaraki Prefecture, Tsukuba, on leaves of *Raphanus sativus*, Jul. 2007, *T. Sato*, living culture MAFF 240791; Chiba Prefecture, Narita, Minami-misatozuka, on leaves of *R. sativus*, 13 Nov. 2009, *J. Nishikawa*, MUMH 11684, living culture MUCC 1615.

Morphological characters on V8 medium: *Conidiophores* pale brown to brown, broad, 38–183 × 6–11 µm. *Conidia* solitary to in short chains of 1–2, pale brown to brown, subcylindrical to oblong, with blunt-tapered beaks, 40–237 µm in total length. Conidial bodies 33–160 × 8–33 µm, with 1–10 transverse and 0–9 longitudinal septa, commonly smooth. Beaks straight, not filamentous, unbranched, concolorous with the bodies, 6–121 × 3–10 µm.

Colony characteristics on PDA after 7 d at 25 °C: Slow-growing, reaching an average of 37.6 ± 1.6 mm diam; aerial hypha cottony, white to pale gray; reverse center black to dark green; sporulation sparse; diffusible pigment absent.

Sexual morph: Not observed.

Natural hosts: *Brassicaceae* (*Arabis*, *Armoracia*, *Brassica*, *Bunias*, *Camelina*, *Cochlearia*, *Crambe*, *Descurainia*, *Eruca*, *Eutrema*, *Iberis*, *Lepidium*, *Lunaria*, *Neslia*, *Radicula*, *Raphanus*, *Rorippa, Sinapis*, *Sisymbrium*, and *Sisymbrium*), *Cucumis sativa* and *Cucurbita pepo* (*Cucurbitaceae*), and *Beta* (*Amaranthaceae*) are correct source plants according to Simmons (2007). All other recorded hosts reported by Farr & Rossman (2018) may be listed under the names of each *formae* and variety of *A. brassicae*.

Symptoms: Small, black spots appear on the leaves and petioles of *Raphanus*. They are 5 mm diam, circular to zonate, with a necrotic eye at the center, becoming enlarged and confluent.

Experimental host range: Strongly pathogenic to *Brassicaceae*, including *Diplotaxis*, *Iberis*, and *Nasturtium*; weakly pathogenic

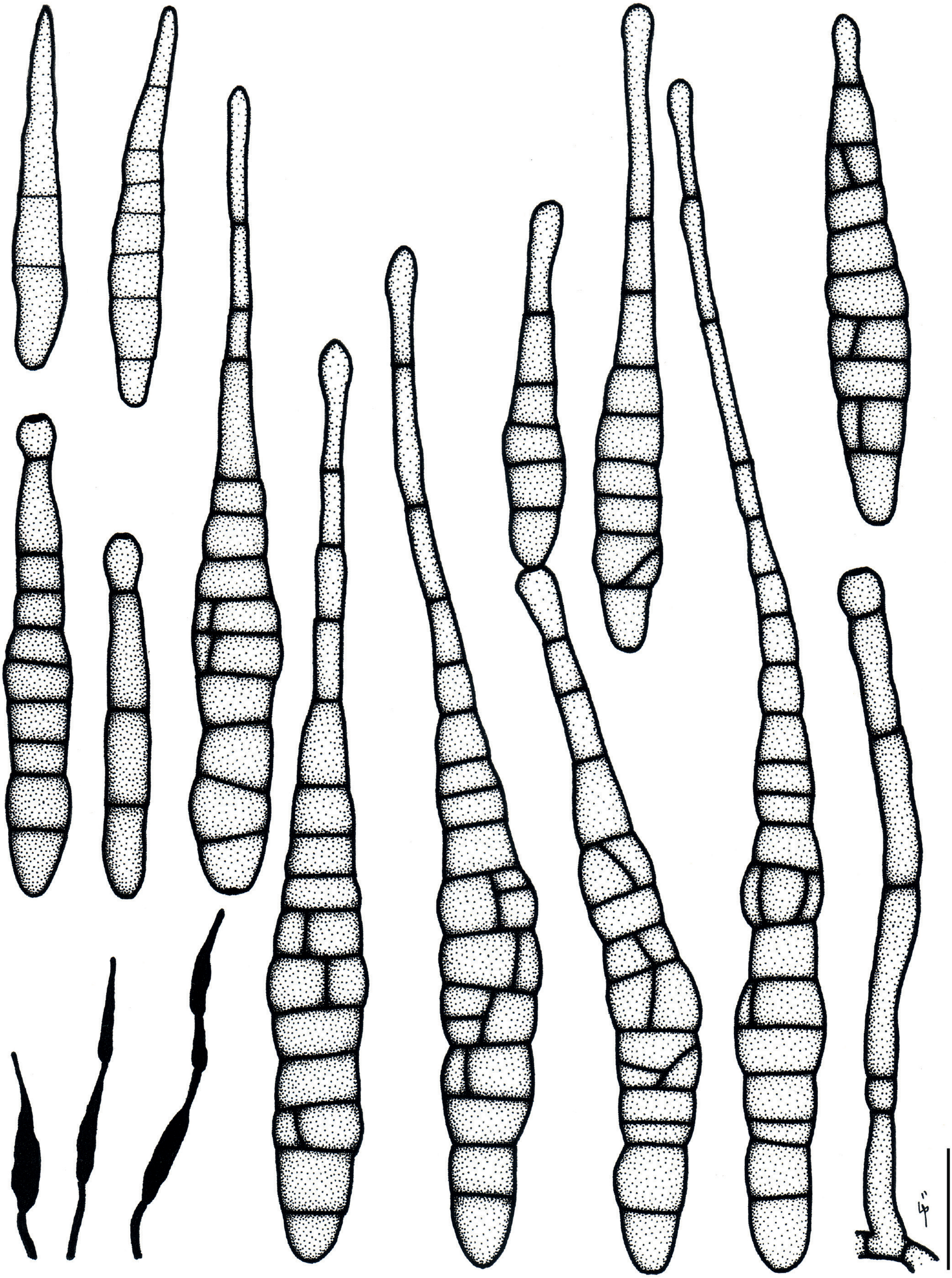

Fig. 44. Illustrations of *Alternaria brassicae* (MAFF 240791). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on V8 juice agar medium. Scale bar = 25 µm.

Fig. 45. Morphological features of Japanese isolates of *Alternaria brassicae* (MAFF 240791). **A–H.** Conidia and conidiophores on V8 juice agar medium. **I.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). Scale bars (A–H) = 25 µm.

to *Eutrema*, *Lobularia*, and *Matthiola*; almost non-pathogenic to *Aubrieta*, *Capsella*, and non-*Brassicaceae* plants (Table 5).

Distribution: Worldwide, including Asia (Bangladesh, Cambodia, China, India, Indonesia, Iraq, Japan, Korea, Kyrgyzstan, Malaysia, Myanmar, Nepal, Oman, Pakistan, Philippines, Singapore, Taiwan, Thailand, and Turkmenistan), Europe (Armenia, Austria, Azerbaijan, Bulgaria, Cyprus, Czech, Denmark, France, Germany, Greece, Italy, Latvia, Macedonia, Netherlands, Poland, Romania, Russia, Serbia, Slovenia, Spain, Turkey, and UK), North and Latin America (Argentina, Bolivia, Brazil, Canada, Chile, Colombia, Costa Rica, Cuba, Dominican Republic, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Peru, Puerto Rico, Trinidad and Tobago, Uruguay, Venezuela, Virgin Islands, and USA), Africa (Egypt, Ethiopia, Kenya, Malawi, Mauritius, Morocco, Nigeria, South Africa, Sudan, Tanzania, Zambia, and Zimbabwe), and the Pacific (Australia, New Zealand, and Papua New Guinea) (Farr & Stevenson 1963, Benjamin & Slot 1969, Rao 1969, Richardson 1990, Jasalavich *et al.* 1995, Koike 1996, Koike & Molinar 1997, Crous *et al.* 2000, Cho *et al.* 2001, Yu 2001, Zhang 2003, Gaetan & Madia 2005, You *et al.* 2005, Simmons 2007, Caesar & Lartey 2009, Gannibal & Gasich 2009, Woudenberg *et al.* 2013, Blagojević *et al.* 2015, van de Wouw *et al.* 2016, Farr & Rossman 2018).

Distinctive features: Large spores with blunt-tapered false beaks, and slow-growing on PDA medium. This species is widely pathogenic to *Brassicaceae*, including *Eutrema*, but not to *Aubrieta* and *Capsella*. It is phylogenetically recognizable via its ITS (Fig. 2), *gapdh*, *tef1*, *rpb2*, *Alt a 1*, and *act* sequences (data not shown).

Alternaria triangularis **Jun. Nishikawa & C. Nakash., *sp. nov.* MycoBank MB829137. Figs 46, 47.**

Etymology: Named after Latin "*triangularis*", referring to the triangular shape of the conidia.

Diagnosis: The morphology of this species includes isosceles triangle-shaped conidia, comprising multi-celled bodies and elongated secondary conidiophores, and is quite unique among *Apiaceae*-pathogenic species. Phylogenetic analysis suggested

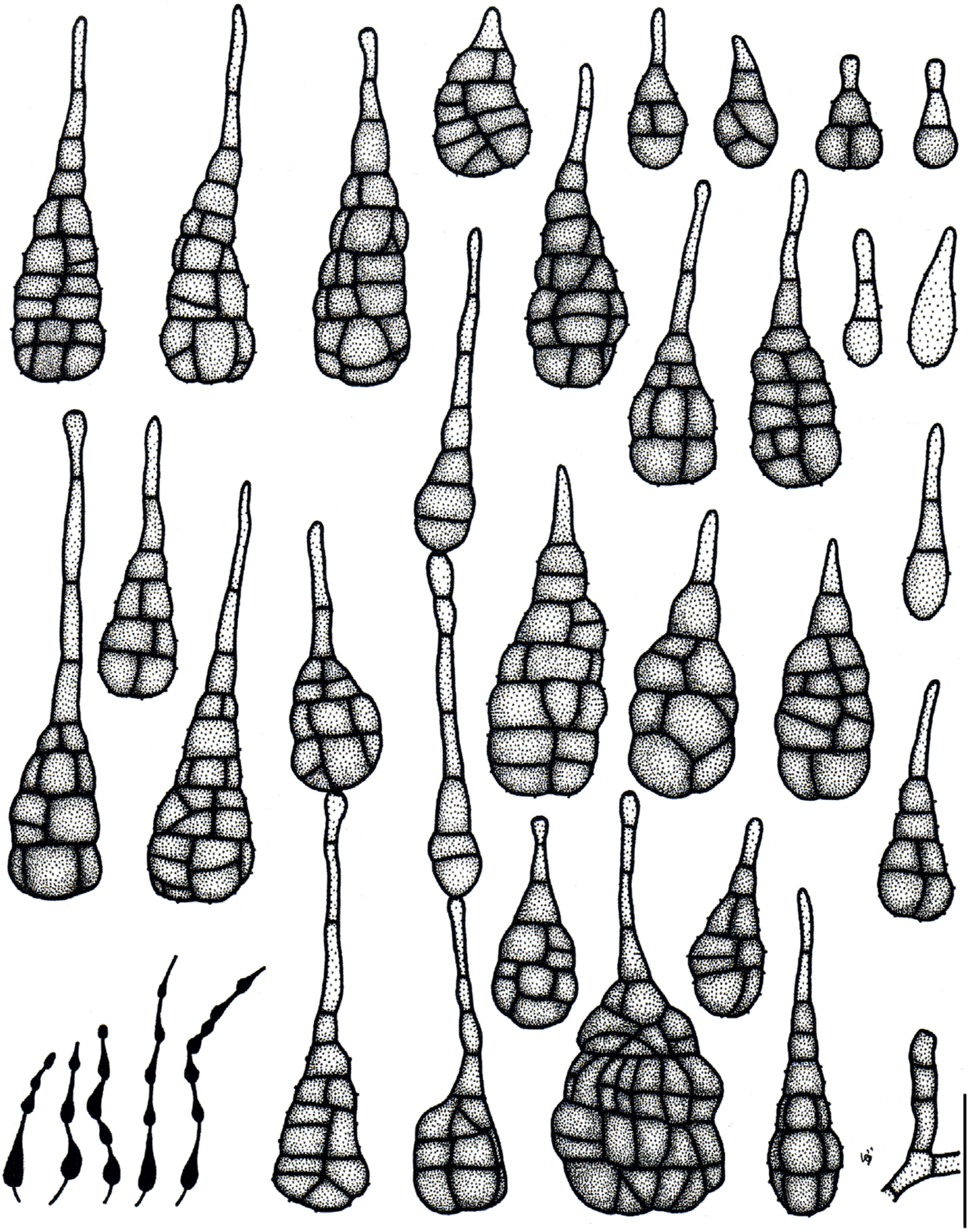

Fig. 46. Illustrations of *Alternaria triangularis* (ex-holotype culture MAFF 246776). Morphology of conidia and conidiophores, and sporulation patterns (opaque) on V8 juice agar medium. Scale bar = 25 µm.

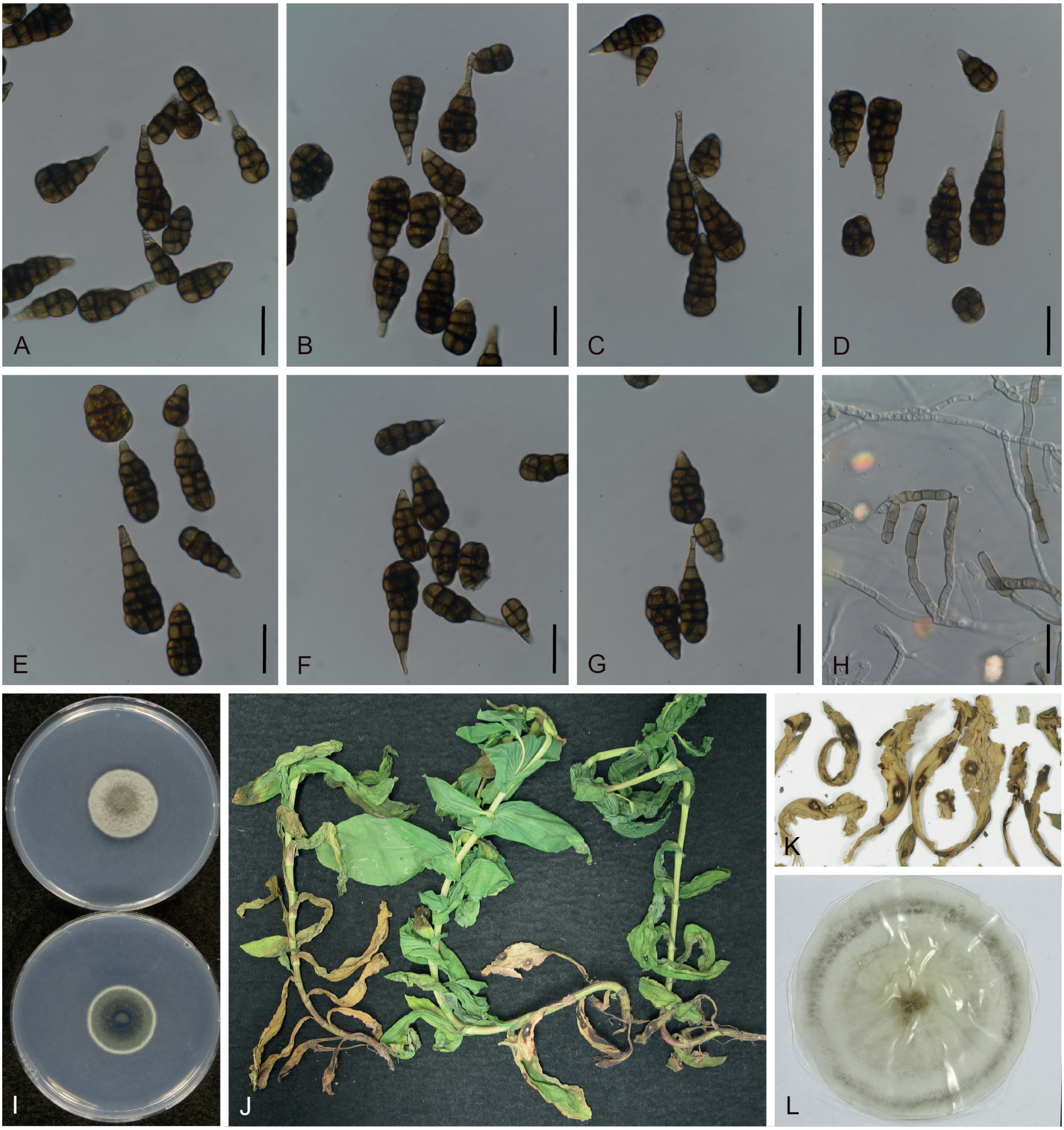

Fig. 47. Morphological features of Japanese isolates of *Alternaria triangularis* (ex-holotype culture MAFF 246776). **A–G.** Conidia on V8 juice agar (V8) medium. **H.** Conidiophores on V8 medium. **I.** Culture on potato-dextrose agar medium (upper = surface, lower = reverse). **J–K.** Natural symptoms on *Bupleurum*. **L.** Dried culture specimen ex MAFF 246776 (holotype: TSN-F-85454). Scale bars (A–H) = 25 µm.

that this species is a monotypic lineage sister to the sect. *Sonchi* and monotypic lineage *A. brassicae*. The species is also characterized by its host range, which is restricted to *Bupleurum*.

Leaf spots are circular, 4–10 mm diam, dark brown to black with a grayish eye at center, and are distinct at the border; leaf defoliation follows. On V8 medium, *conidiophores* short to moderately long, narrow, 16–59 × 4–6 µm. *Conidia* primarily in chains of 3–5, up to 8–9 (short to moderately long chains), lateral branches uncommon 5–7 d after incubation, pale brown to brown, long ovoid to obclavate, triangular to campanuloid in maturity, 15–93 µm in total length. Conidial bodies 14–53 × 6–33 µm, with 1–9 transverse septa and 0–11 (commonly in each unit, and sometimes complexed) longitudinal septa. The basal 1–2 units broadest, almost flattened bottoms, smooth to faintly rough. False beaks (secondary conidiophores) often elongated in 2–3 cells, up to 47 × 6 µm. On lesions, conidiophores 19–67 × 3–6 µm. Conidia 10–76 µm in total length; conidial bodies 10–

45 × 5–23 µm, with 0–9 transverse septa and 0–9 longitudinal septa. False beaks up to 41 × 6 µm.

Typus: **Japan**, Kochi Prefecture, Konan, on leaves of *Bupleurum rotundifolium*, 9 Jan. 2004, *J. Nishikawa* (**holotype** TNS-F-85454) (a dried culture specimen ex MAFF 246776), **isotypes** MUMH 11669 and 11700, culture ex-holotype MAFF 246776, GenBank accession number ITS: LC440629, *gapdh*: LC482050, *rpb2*: LC476837, *tef1*: LC480255, *Alt a 1*: LC481641, *act*: LC481891.

Additional material examined: **Japan**, Shizuoka Prefecture, Kakegawa, on *B. rotundifolium*, 7 Jun. 2004, *Y. Makizumi*, living culture AC95.

Experimental host range: Selectively pathogenic to *Bupleurum* among members of the *Apiaceae* family, but weakly pathogenic or opportunistic to *Angelica* (Table 6).

Distribution: Only known from Japan.

Colony characteristics on PDA after 7 d at 25 °C: Slow-growing, reaching an average of 23.9 ± 0.9 mm diam; aerial hypha cottony, dense, grayish green to dark green, with white margins; reverse center dark green to black; sporulation sparse; diffusible pigment absent.

Sexual morph: Not observed.

DISCUSSION

During our survey of *Alternaria* species in Japan, we obtained and examined 85 isolates. Based on morphological observations, molecular phylogeny, and phenotyping with an experimental host range, 23 known species (including four species newly recorded from Japan) and three novel species were found. Moreover, phenotyping with an experimental host range not only helped determine each species boundary, but also revealed closely related and indistinguishable taxa of the examined Japanese species.

In the present study, five Japanese species with two *formae speciales* were clearly recognized in sect. *Alternaria*. Based on the conidial morphology of *A. iridicola* on holotype material, Simmons (2007) determined the taxonomic affinity of the species with small-spored species, namely within sect. *Alternaria*. Although Gannibal & Lawrence (2018a) suggested that Russian isolates had intermediate characteristics in both sect. *Panax* and *Porri*, conidial morphology of the examined Japanese isolates were identical to ex-type descriptions (Ellis & Everhart 1894, Simmons 2007), especially large conidia with long false beaks and catenate conidia were particularly diagnostic for a species in sect. *Alternaria* (Figs 22, 23). As the result of the multi-locus phylogeny, it was also revealed that this species clearly belongs to sect. *Alternaria* (Fig. 1). Since there are no living ex-type isolates, a dried-culture specimen (TNS-F-85452) was deposited as an epitype of *A. iridicola*. There are two related taxa, *A. iridiaustralis* and *A. iridis*, infecting *Iris* within the section. The results of the inoculation test with *A. iridicola* demonstrated that this species is not pathogenic to *I. ensata* (Table 8), which is a natural host of *A. iridiaustralis* (Luo *et al.* 2018). Therefore, these related species were distinguishable from *A. iridicola* based on host selectivity, as well as morphology and phylogeny. In addition, a novel species, *A. cylindrica* having selective pathogenicity to *Petunia*, was described, and some of the other species in this section (*e.g.*, *A. alstroemeriae* and *A. gaisen* in the present study) also have selectivity within a host genus, species, or variety. Species in this section generally have distinct host specificity, and it is possible that potential host-selective toxin producers may be present.

In sect. *Alternantherae*, *A. paragomphrenae* was newly described in the present study. It was suggested that species in sect. *Alternantherae* were clearly differentiated in their pathogenicity to *Amaranthaceae* plants, reflecting their morphological and phylogenetic differences (Tables 3, 4; Fig. 1). Two species infecting *Gomphrena*, *A. gomphrenae* and *A. paragomphrenae*, were non-pathogenic to *Amaranthoideae* plants, including *Amaranthus* and *Celosia*, and were distinguishable from each other in pathogenicity to *Alternanthera* (Table 4). The remaining species had wide host ranges across the subfamilies in *Amaranthaceae*, and *A. celosiicola* was pathogenic to *Amaranthoideae* and *Gomphrenoideae*. In addition, it was considered that *A. alternantherae* and *A. perpunctulata* were conspecific, as they share a common original host (*Alternanthera*), are morphologically similar, and show high phylogenetic affinity (Zhao & Zhang 2005).

In sect. *Brassicicola*, Japanese isolates of *A. brassicicola* including the non-*Brassica* isolate MAFF 246773 were equally aggressive to a wide range of *Brassicaceae* hosts (Table 5). However, these isolates clustered in a well-supported single lineage together with ex-type isolates of *A. mimicula*, *A. septorioides*, and *A. solidaccana*, which were isolated from non-*Brassica* hosts – *Solanum*, *Reseda*, and soil, respectively (Fig. 1). Based on their host ranges within *Brassicaceae*, morphological similarity, and ubiquitousness of *A. brassicicola* (Simmons 2007, Farr & Rossman 2018), these three names were synonymized. Although multi-locus phylogeny resolved two subclades in this section with high BS and PP support values (Fig. 1), it was concluded that this section is a possible monotypic lineage recognized by the ITS phylogeny rather than the multi-locus phylogeny (Fig. 2).

Likewise, in sect. *Japonicae*, Japanese isolates of *A. japonica* were restricted within *Brassicaceae* (Table 5), and their conspecificity to *A. nepalensis*, the ex-type of which was isolated from *Brassica* sp., were supported by phylogenetic analyses conducted during the present study (Fig. 1). Because of its morphological similarity to the original description of *A. nepalensis* (Simmons 2007), this species was synonymized with *A. japonica*, and this section was typified as a monotypic lineage. It is interesting that during the evolution and differentiation of the genus *Alternaria*, three common pathogens that infect *Brassicaceae* (*A. brassicae*, *A. brassicicola*, and *A. japonica*) had almost no differences in their host ranges; nevertheless, they were distinctive in their conidial morphology and phylogenetic relationship to each other.

Alternaria cumini (sect. *Eureka*) and *A. triangularis*, which both infect *Apiaceae*, were morphologically and phylogenetically distinguishable from other species, including *A. dauci* (sect. *Porri*), and selectively pathogenic to each original host genus (Table 6). In sect. *Radicina*, the morphology and pathogenicity of *A. petroselini* were also easily distinguishable from those of related species, except *A. selini* (Nishikawa & Nakashima 2013). It was appropriate to synonymize *A. selini* with *A. petroselini* based on multi-locus phylogenic similarities. According to Park *et al.* (2008), two species pathogenic to *Daucus*, *A. radicina* and *A. carotiincultae*, were phylogenetically recognized as a distinct species based on their *Alt a 1*, *tef1*, and β-tubulin gene sequences, but not on their *gapdh* and *rpb2* sequences (Woudenberg *et al.* 2013). Further studies will be required to resolve these species boundaries.

In sect. *Gypsophilae*, Japanese isolates and a representative isolate of *A*. *nobilis* clustered into a single lineage together with ex-type isolates of *A*. *ellipsoidea* and *A*. *saponariae* based on the ITS phylogeny (Fig. 2). However, the multi-locus phylogeny conducted in this and previous studies delimited a distinct subclade consisting of only Japanese isolates from some subclades of existing taxa (Fig. 1; Woudenberg *et al*. 2013, Gannibal 2019). Conidial morphology of Japanese isolates was identical with those of *A. nobilis*, but not clearly distinguishable from closely related species. This study could not examine pathological phenotyping with host range evaluations under the concept of integrated species recognition. Further studies are needed to resolve this contradiction and define the species boundaries of *Dianthus* pathogens in this section.

In sect. *Panax*, Japanese isolates and three representative isolates of *A*. *panax* clustered into a single lineage together with *A*. *dendropanacis* with strong BS and PP support. However, this clade was divided into three subclades with lower BS (ML and MP) support (Fig. 1), which were assigned to *A*. *panax*, *A*. *araliae*, and *A*. *dendropanacis* by Deng *et al.* (2015). Based on its conidial morphology, culture characteristics, and original host plants of Japanese isolates, all of these features overlapped with one another and were not identical to the definition presented by Deng *et al.* (2015). Although it needs to be verified by further studies such as cross-inoculation tests, it was appropriate that these taxa should be regarded as one species, *A*. *panax*, as suggested by the ITS phylogeny (Fig. 2).

In the present study five Japanese species were clearly recognized in sect. *Porri*. Morphological distinctions based on the color of their beaks was an especially effective diagnostic feature. Among these, colored beak species (*A*. *cucumerina* and *A*. *zinniae*) were not resolved in the ITS phylogeny (Fig. 2). However, host range has been generally applied as species criteria in this section (Neergaard 1945, Ellis 1971, Zhang 2003, Simmons 2007), and these two species were also well correlated with their hosts (*Cucurbitaceae* and *Zinnia*, respectively). As the result of the multi-locus phylogeny, the species boundary between these species was strongly supported, reflecting their host range (Fig. 1). In contrast, Woudenberg *et al.* (2014) phylogenetically differentiated *A*. *porri* from *A*. *allii*, and Japanese isolates clustered across the two species with lower BS and PP support (Fig. 1). However, it was affected only by the *rpb2* phylogeny, and was not supported by other genes (ITS, *gapdh*, *tef1*, *Alt a 1*, and *act*) (data not shown). Based on the similarity of their conidial morphology and host range between both species, *A*. *allii* was rejected as a distinct species. It was also suggested that a multi-locus phylogeny was not always appropriate to resolve species boundaries in this section. This section is the largest, containing 63 species (Woudenberg *et al.* 2014), wherein phenotyping with both detailed morphological examinations and experimental host range are not sufficient. The ubiquitousness of *A*. *porri*, which was also shown in the present study, also demonstrated that integrated species recognition is strongly recommended to define the species boundaries of this section.

Thus far, we have discussed the utility of phenotyping based on experimental host ranges to distinguish closely related species. However, since the former *Ulocladium* species (especially for *A. atra* and *A. chartarum*) and one of the most frequent contaminants, *A. alternata*, were commonly established as saprophytic isolates, it is difficult to examine their taxonomy under the concept of integrated species recognition. Further approaches, such as secondary metabolite assays and inoculation tests to a few recorded susceptible hosts, are required to determine species boundaries among saprophytic species.

As a result of comprehensive inoculation tests, distinctive host selectivity was found along with the systematic ranks of each host plant, not only with genus but also subfamily, tribe, species, and variety, for most plant-pathogenic species of *Alternaria*. Moreover, phenotyping with experimental host ranges contributed to define species boundaries in *Alternaria,* supporting morphology and molecular phylogenetic data. This study also suggested that the ITS region is generally still effective with regard to DNA barcoding for the genus *Alternaria*, except for sect. *Alternaria,* and colored beak species in sect. *Porri*. It was concluded that integrated species recognition based on morphology, phylogeny, and pathogenicity helps elucidate species boundaries in the genus *Alternaria*, and will provide a practical, re-defined species concept for the genus.

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