FULL PAPER

Susumu Takamatsu · Yukio Sato · Genki Mimuro · Sawwanee Kom-un

Erysiphe wadae : a new species of *Erysiphe* sect. *Uncinula* on Japanese beech

S. Takamatsu · S. Kom-un
Faculty of Bioresources, Mie University, Tsu, Japan

Y. Sato · G. Mimuro
College of Agriculture, Toyama Prefectural University, Toyama, Japan

Corresponding Author:
Susumu Takamatsu
Faculty of Bioresources, Mie University, 1515 Kamihama, Tsu 514-8507, Japan
Tel. +81-59-231-9497; Fax +81-59-231-9637
e-mail: takamatu@bio.mie-u.ac.jp

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Abstract A new species of *Erysiphe* sect. *Uncinula* is described and illustrated from Japan. *Erysiphe wadae* sp. nov., found on Japanese beech (*Fagus crenata*, Fagaceae), is characterized by having two types of appendages, i.e., long (true) appendage arising from the equatorial zone of ascomata, and short appendage arising from the upper part of ascomata. This characteristic is shared by *E. simulans*, *E. australiana*, *E. flexuosa*, *E. liquidambaris*, *E. prunastri*, and *E. togashiana*. *Erysiphe wadae* differs from the latter five species in its brown-colored appendage. *Erysiphe simulans* is most similar to *E. wadae*, but differs in its loosely uncinate appendage and smaller number of ascospores. Identity of the nucleotide sequences of rDNA ITS region is 92.3% between the two species. Significance of two types of appendage in taxonomy and phylogeny of powdery mildews was discussed based on molecular phylogenetic analysis.

Key words Secondary appendage・ Erysiphaceae・ Fagaceae・ *Fagus crenata*・ Powdery mildew

Introduction

Only one species of *Erysiphe* sect. *Uncinula* (formerly the genus *Uncinula*), *Erysiphe curvispora* (Hara) U. Braun & S. Takamatsu [≡ *Uncinula curvispora* (Hara) Hara], has been reported on *Fagus crenata* Blume (Hara 1915). This fungus is unique among the Erysiphales in its septate and numerous appendages arising from the upper half of the ascomata, and curved ascospores. Although specimen of this species is not available now, molecular phylogenetic analysis revealed that the allied species, *E. septata* (E. S. Salmon) U. Braun & S. Takam. (≡ *Uncinula septata* E. S. Salmon), is placed at the primitive base of the Erysiphales (Mori et al. 2000). We found occurrence of a powdery mildew belonging to *Erysiphe* sect. *Uncinula* on *F. crenata* at Aomori, Akita, and Toyama in 2001, and at Fukushima and Shiga in 2002. The present fungus distinctly differs from *E. curvispora* in its fewer numbers of appendages arising from the equatorial zone of ascomata, and smaller ascomata. The most conspicuous characteristic of this fungus is having two types of appendages, i.e., long (true) appendage arising from the equatorial zone of ascomata, and short appendage arising from the upper part of ascomata. Here, we describe and illustrate the newly found fungus as a new

species *Erysiphe wadae*. We also discuss about significance of two types of appendages in taxonomy and phylogeny of the Erysiphales based on the nucleotide sequences of the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA (rDNA).

Materials and methods

Morphological observation

Anamorph

Fresh hyphae, conidiophores and conidia were stripped off from the leaf surfaces with clear adhesive tape, mounted on a microscope slide with the fungal materials uppermost and examined in water under a light microscope. The following information was noted during the examination: size and shape of conidia; presence or absence of fibrosin bodies; nature of conidiogenesis; characteristics of the conidiophore, e.g. size and shape of foot cell, position of the basal septum; shape and position of hyphal appressoria; position of germ tubes of conidia and shape of appressoria on germ tubes of conidia.

Teleomorph

Ascomata were transferred onto a microscope slide with a needle under a dissecting microscope, and observed in 3% NaOH under a light microscope. The following information was noted during the examination: size and shape of ascomata, asci, and ascospores; characteristics of appendages, e.g. number, length, color, shape of the apex; number of asci and ascospores.

DNA extraction, PCR, and sequencing

Whole-cell DNA was isolated from mycelia by the chelex method (Walsh et al. 1991; Hirata and Takamatsu 1996). The nuclear rDNA region, including the ITS regions (ITS 1 and ITS 2), and the 5.8S rRNA gene were amplified by the polymerase chain reaction (PCR) using the primers ITS5 (White et al. 1990) and P3 (Kusaba and Tsuge 1995). PCR reactions were done in 50 µl volumes as previously described (Hirata and Takamatsu 1996). A negative control lacking template DNA was included for each set of reactions. One microliter of the first

reaction mixture was used for the second amplification with the partial nested primer set ITS1 (White et al. 1990) and P3. The PCR product was subjected to preparative electrophoresis in 1.5% agarose gel in TAE buffer. The DNA product of each amplification was then excised from the ethidium-stained gel and purified using the JETSORB kit (GENOMED, Germany) following the manufacturer's protocol. Nucleotide sequences of the PCR products were obtained for both strands using direct sequencing in an Applied Biosystems 373A sequencer (Applied Biosystems). The sequence reactions were conducted using the PRISM Dye Terminator Cycle Sequencing kit (Applied Biosystems) following the manufacturer's instructions.

Molecular phylogenetic analysis

The sequences were initially aligned using the Clustal V package (Higgins et al. 1992). The alignment was then visually refined with a word processing program, using color-coded nucleotides, and ambiguously aligned sites were removed from the data set in the following analyses. The alignment is available upon request to the corresponding author. Phylogenetic trees were obtained from the data using maximum-likelihood (ML) and parsimony methods. For ML analysis, the most appropriate evolution model was determined for a given data set using PAUP* 4.0b4 (Swofford 1999) and Modeltest 3.06 (Posada and Crandall 1998). A starting tree was obtained with neighbor-joining method. With this tree, likelihood scores were calculated for 56 alternative models of evolution by PAUP*. The output file was then imported to Modeltest to compare the models by likelihood ratio test. Once a model of evolution was chosen, it was used to construct phylogenetic trees with ML method by a heuristic search option of PAUP*.

For the parsimony analysis, we used the maximum-parsimony (MP) method with a heuristic search using PAUP*. This search was repeated 100 times with different random starting points, using the stepwise addition option to increase the likelihood of finding the most parsimonious tree. All sites were treated as unordered and unweighted, with gaps treated as missing data. The branch-swapping algorithm was TBR, the MULPARS option was in effect, and zero-length branches were collapsed. The strength of the internal branches from the resulting trees was tested by bootstrap analysis using 100 (ML) or 1000 (MP) replications (Felsenstein 1985).

Kishino-Hasegawa (KH; Kishino and Hasegawa 1989) test was conducted to evaluate a taxonomic and phylogenetic significance of two types of appendages. A

constrainted tree was constructed using Tree Window option of MacClade 3.08 (Maddison and Maddison 1992), and was imported into PAUP* to find a ML tree consistent with a specific constraint hypothesis. The log likelihoods of the constrained tree and unconstrained ML tree were calculated using PAUP*. Evolution model appropriate for the data set was determined by PAUP* and Modeltest as described above to calculate log-likelihoods in KH test.

Results

Taxonomy

Erysiphe wadae S. Takamatsu & Y. Sato, sp. nov. Figs. 1–8

Mycelium hypophyllum, raro amphigenum in foliis, evanescens, tenue; hyphae hyalinae. Appressoria lobulata. Conidiophora erecta, cellulis basalibus cylindraceis, 2–3 cellulis sequentibus longitudine aequalibus. Conidia solitaria, ellipsoidea, 19.8–23.8 × 7.9–11.9 µm. Ascomata sparsa, globosa, (74–)84–105(–125) µm diam, in maturitate fusco-brunea. Appendices biformis. Appendices longiores (12–)18–32, aequatoriales, rectae vel curvatae, in latitudine aequales, uniseptatae vel aseptatae, apice circinatae vel uncinatae, attenuatae, basim brunneae et sursum pallide brunneae, (129–)153–215(–225) µm longae, diametro ascomatis 1.5–2.5plo longiores). Appendices breviores (3–)4–10(–13), hyalinae, rectae vel facatae, (10–)13–23(–30) µm longae. Asci (3–)4–6, ovatae, hyalinae, (40–)43–53(–55) × (30–)33–37.5(–43) µm. Ascosporae (4–)6–8, ovatae vel ellipsoideae, hyalinae, (13–)15–18(–20) × (8–)10–13 µm.

Holotypus: in foliis vivis *Fagi crenatae* Blume (buna), Iwakisan, Iwaki-machi, Aomori, Japonica, 10 Sep. 2001, leg. S. Takamatsu & Y. Sato, in Herbario Musei Scientiae nationalis, Tsukuba, Japonia (TNS-F-5685) conservatus.

Etymology: The new species is named in honor of the late Ms. Kumiko Wada who worked on the Erysiphales at Niigata University, Japan.

Colonies: Mycelia on leaves hypophyllous, rare amphigenous, hyaline, very thin, evanescent. Appressoria simply lobed, single or opposite in pairs (Fig. 8).

Anamorph: *Oidium* subgen. *Pseudoidium* Jacz. Conidiophores somewhat rare, arising from the upper part or the side of mother cells, 75.2–104.9 × 7.9–11.9 µm (Fig. 2). Foot cells straight or curved at the base, relatively long, up to 89.1 µm, followed by 2–3 cells. Conidia

produced solitary, unicellular, hyaline, ellipsoid, 19.8–23.8 × 7.9–11.9 µm, without conspicuous fibrosin bodies, usually containing large oil drops, producing germ tubes on the shoulder (Fig. 3). Germ tubes having two appressoria: multilobed appressorium at the base and simply lobed appressorium at the end of germ tube (Polygoni-type; Braun 1987) (Fig. 4).

Teleomorph: Ascomata scattered, blackish brown, globose, (74–)84–105(–125) µm in diameter, having two types of appendages (Figs. 1a, 5). Long appendages (12–)18–32 in number, equatorial, simple, straight to mildly curved, width subequal throughout, apex closely circinate, sometimes loosely circinate or subhelicoid, tapering towards the tip, 4–8 µm wide, (129–)153–215(–225) µm in length (1.5–2.5 times as long as the ascomatal diameter), dark brown at the base and gradually paler upwards, thick-walled at the base, gradually thinner upwards, aseptate or uniseptate at the base (Figs. 1b, 6). Short appendages (3–)4–10(–13) in number, substraight to sickle-shaped, (10–)13–23(–30) µm long, 5–7 µm wide, hyaline (Figs. 1c, 8). Asci (3–)4–6 in an ascoma, (40–)43–53(–55) × (30–)33–37.5(–43) µm, shortly stalked, ovoid, hyaline, thick-walled (Figs. 1d, 7). Ascospores (4–)6–8 in an ascus, unicellular, hyaline, ovoid, ellipsoid to oblong, (13–)15–18(–20) × (8–)10–13 µm.

Materials studied: Sukayu Onsen, Hakkoda Mountain, Aomori-shi, Aomori, Japan, 8 Sep. 2001, Leg. S. Takamatsu, MUMH1534; Iwaki Muntain, Iwaki-machi, Aomori, Japan, 10 Sep. 2001, leg. S. Takamatsu & Y. Sato, TNS-F-5685 (holotype), MUMH1660 (isotype); Oirase, Towadako-machi, Aomori, Japan, 12 Sep. 2001, leg. S. Takamatsu & Y. Sato, MUMH1550; Tamagawa Onsen, Tazawako-machi, Akita, Japan, 14 Sep. 2001, leg. S. Takamatsu & Y. Sato, MUMH1632; Shirakimine, Toyama, Japan, 8 Oct. 2001, leg. Y. Sato & G. Mimuro, TPU-3830; Buna-ga-take, Shiga, Japan, 19 Sep. 2002, leg. S. Takamatsu, MUMH1728; Tochiore-toge, Yatsuo-machi, Toyama, Japan, 14 Oct. 2002, leg. Y. Sato, TPU-3963; Hibarako lake, Kita-shiobara village, Fukushima, Japan, 14 Oct. 2002, leg. S. Takamatsu & Y. Nomura, MUMH1729.

Phylogenetic analysis

In order to evaluate the significance of two types of appendages as a phylogenetic character, we determined the ribosomal DNA ITS sequences for three species of *Erysiphe* sect. *Uncinula* having two types of appendages. These three sequences were deposited at DDBJ under the accession numbers AB091774 to AB091776 (Table 1). These sequences were aligned with a total of 15 sequences of *Erysiphe* spp., *Typhulochaeta japonica* S. Ito & Hara,

and *Brasiliomyces trina* (Harkn.) R. Y. Zheng obtained from DNA databases (Table 1). The alignment data matrix consists of 18 taxa and 636 characters, of which 146 sites were removed because of ambiguous alignment. Of the 496 remaining characters, 208 sites were variable and 123 sites were phylogenetically informative for parsimony analysis. *Erysiphe australiana* (McAlpine) U. Braun & S. Takam. (≡ *Uncinula australiana* McAlpine) was used as an outgroup taxon based on Mori et al. (2000). Using Modeltest (Posada and Crandall 1998) under the likelihood ratio test criterion, we concluded that the Tamura-Nei model (Tamura and Nei 1993), with equal base frequencies, a gamma-distributed rate heterogeneity model (Yang 1994; four rate categories, G = 0.3318) and an estimated proportion of invariant sites (0) was the most appropriate model of evolution for this data set. A heuristic search with this model produced a single ML tree with -ln likelihood score of 2950.75606 (Fig. 9 left). MP analysis found six equally parsimonious trees of 494 steps (CI = 0.632, RI = 0.572, RC = 0.361) (Fig. 9 right). There is no conflict between the two trees. *Erysiphe wadae* was included in a large clade composed of fungi parasitic to Fagaceae (*Typhulochaeta japonica*, *Brasiliomyces trina*, and *E. gracilis* R. Y. Zheng & G. Q. Chen), Rosaceae [*E. simulans* (E. S. Salmon) U. Braun & S. Takam. (≡ *Uncinula simulans* E. S. Salmon) and *E. prunastri* DC. (≡ *U. prunastri* (DC.) Sacc.)], Hippocastanaceae [*E. flexuosa* (Peck) U. Braun & S. Takam. (≡ *U. flexuosa* Peck)], and Moraceae [*E. mori* (I. Miyake) U. Braun & S. Takam. (≡ *U. mori* I. Miyake)] with high bootstrap support (87–89%). In the clade, *E. wadae* grouped with *E. simulans* with low bootstrap support (51–53%). Nucleotide sequence identity was 92.3% between *E. wadae* and *E. simulans*.

Of the 18 taxa used in this analysis, six taxa [*E. australiana*, *E. flexuosa*, *E. prunastri*, *E. simulans*, *E. togashiana* (U. Braun) U. Braun & S. Takam. (≡ *U. togashiana* U. Braun), and *E. wadae*] have two types of appendages. These six species did not group into a clade. Instead, they mixed with taxa having a single type of appendages in the phylogenetic trees. A constrainted tree assuming these six taxa to be monophyletic was significantly worse than the best tree (Fig. 9 left). The differences of ln *L* values (–in *L*), the standard deviation of the difference (SD), and the *P* value for significance between the best and constraint tree were as follows: –ln *L* = 44.90252, SD = 13.30935, $P < 0.001$.

Discussion

According to Viennot-Bourgin (1966), 15 powdery mildew species covering six genera

have been recorded on *Quercus* L. (Fagaceae). Because there are no other plant genera recorded such many kinds of powdery mildews, close evolutionary relationship between *Quercus* and powdery mildews has been suggested in several reports (Viennot-Bourgin 1966; Hirata 1968; Gardner et al. 1972; Amano 1986; Mori et al. 2000). Whereas, five species, *E. erineophila* (Peck) U. Braun & S. Takam. (≡ *Microsphaera erineophila* Peck), *E. alphitoides* (Griffon & Maubl.) U. Braun & S. Takam. (≡ *M. alphitoides* Griffon & Maubl.), *E. curvispora*, *Phyllactinia guttata* (Wallr.:Fr.) Lév., and *P. angulata* (E. S. Salmon) S. Blumer are so far recorded on *Fagus* spp. (Braun 1987). Although the present fungus clearly belongs to *Erysiphe* sect. *Uncinula* based on its appendages with circinate tips, it distinctly differs from *E. curvispora* in its fewer number of appendages arising from the equatorial zone of ascomata, short secondary appendages arising from the upper part of ascomata, and smaller ascomata.

The most conspicuous character of the present fungus is having two types of appendages. Among species of *Erysiphe* sect. *Uncinula*, this characteristic is shared by *E. simulans*, *E. australiana*, *E. flexuosa*, *E. liquidambaris* (R. Y. Zheng & G. Q. Chen) U. Braun & S. Takam., *E. prunastri*, and *E. togashiana*. *Erysiphe wadae* differs from the latter five species in its brown-colored appendages. *Erysiphe simulans* is most similar to *E. wadae*, but differs in its loosely uncinate appendage and smaller number of ascospores. The moderately high identity (92.3%) of rDNA ITS sequences between *E. simulans* and *E. wadae* supports their morphological similarity, and also confirms that *E. wadae* is an independent species.

Zheng and Chen (1979) reported the existence of two types of appendages, i.e., "normal" appendages, and bristle-like secondary appendages arising from the upper part of ascomata, in *Uncinula simulans* (≡ *E. simulans*) on *Rosa* spp., and transferred the fungus to their newly raised genus *Uncinuliella*. Since then, several *Uncinula* species have been transferrred into the genus *Uncinuliella* based on the characteristic. However, Braun (1995) regarded the bristle-like secondary appendages as immature "normal" appendages, and reduced the genus *Uncinuliella* into a subgenus of *Uncinula*. Scanning electron microscopic examinations of the ontogeny of these appendages showed that the secondary appendages arise at the early stage of ascomatal formation together with hyphal-like appendages arising from the lower part of ascomata (Takamatsu et al. 1979). The "normal" appendages begin elongating at the later stage when ascomata grow into almost the full size of matured one. Therefore, the bristle-like secondary appendages have an origin quite different from the "normal" appendages.

Molecular phylogenetic analysis based on the nucleotide sequences of rDNA indicated that the taxa having two types of appendages do not group into a clade, which supported the taxonomic treatment of Braun (1995) (Mori et al. 2000). In the present study, we newly determined the nucleotide sequences of the rDNA ITS region for three species including *E. wadae* having two types of appendages, and used them for the phylogenetic analysis with other taxa of the genus *Erysiphe*. Again, the result indicates that the taxa do not group into a clade. Instead, they are mixed with taxa having a single type of appendages. Kishino-Hasegawa test significantly rejected the monophyly of the taxa having two types of appendages. Therefore, the existence of bristle-like secondary appendages is a criterion of species level, but not of generic level.

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Legends of Figures

Fig. 1. *Erysiphe wadae*. **a** Ascoma. **b** Long (true) appendages with circinate tip. **c** Short appendages. **d** Ascus and ascospores. *Bars* **a** 100 µm; **b**, **d** 50 µm; **c** 10 µm

Figs. 2-4. Anamorph of *Erysiphe wadae.* **2** Conidiophore. **3** Conidia containing large oil drops. **4** Germ tube having two appressoria. White arrowhead: multilobed appressorium at the base. Black arrowhead: simply lobed appressorium at the end of germ tube. *Bars* 20 µm

Figs. 5-8. Teleomorph (ascoma) of *Erysiphe wadae.* **5** Ascoma, **6** Appendages with circinate tip. **7** Asci and ascospores; 8 Young, immatured ascoma. Note secondary appendages (black arrowhead) arising at the early stage of ascomatal formation. White arrowhead: Appressoria on hyphae produced singly or in opposite pairs. *Bars* 100 µm

Fig. 9. Phylogeny of *Erysiphe wadae* inferred from ITS data for a total of 18 isolates of *Erysiphe* spp., *Brasiliomyces trina*, and *Typhulochaeta japonica*. Solid circle indicates species having two types of appendages. Left: A maximum-likelihood (ML) tree. Model parameters: equal base frequencies with rate heterogeneity; gamma shape parameter = 0.3318; proportion of invariable sites = 0; six rate categories; Tamura-Nei model (Tamura and Nei 1993) with transformation parameters [A-C] = 1.0000, [A-G] = 2.7829, [A-T] = 1.0000, [C-G] = 1.0000, [C-T] = 4.0387, [G-T] = 1.0000. Percent bootstrap support (100 replications) is indicated above nodes. Right: Strict consensus of 6 equally parsimonious trees of 484 steps. Percent bootstrap supports (1000 replications) are shown above nodes. The consistency index (CI) is 0.632; the retention index (RI) is 0.572; and the rescaled consistency index (RC) is 0.361.

[論文] *Erysiphe wadae*: ブナで発見された *Erysiphe* 属 *Uncinula* 節の新種

高松　進[1)]・佐藤幸生[2)]・三室元気[2)]・Sawwanee Kom-un[1)]

[1)] 三重大学生物資源学部、514-8507、津市上浜町 1515

[2)] 富山県立大学短期大学部、939-0311、富山県射水郡小杉町黒河 5180

ブナ上で発見された *Erysiphe* 属 *Uncinula* 節の新種 *Erysiphe wadae* を記載した。本菌は閉子のう殻の赤道部から伸長する長い付属糸と閉子のう殻上部から伸長する短い付属糸の 2 種類の付属糸を持つ。この特徴は *E. simulans, E. australiana, E. flexuosa, E. liquidambaris, E. prunastri* および *E. togashiana* にもみられるが、本菌の付属糸が褐色に着色する点で後 5 者の菌とは区別される。形態上本菌に最も近い *E. simulans* は付属糸先端の巻き方がルーズな点や子のうあたりの子のう胞子数が少ないことで本菌と区別される。*E. wadae* と *E. simulans* 間のリボソーム DNA ITS 領域の塩基配列の相同性は 92.3%であった。二つのタイプの付属糸を有することのうどんこ病菌における分類学的、系統学的意義について分子系統解析に基づいて考察した。

Table 1. Fungal materials and sequence database accession numbers used for phylogenetic analysis

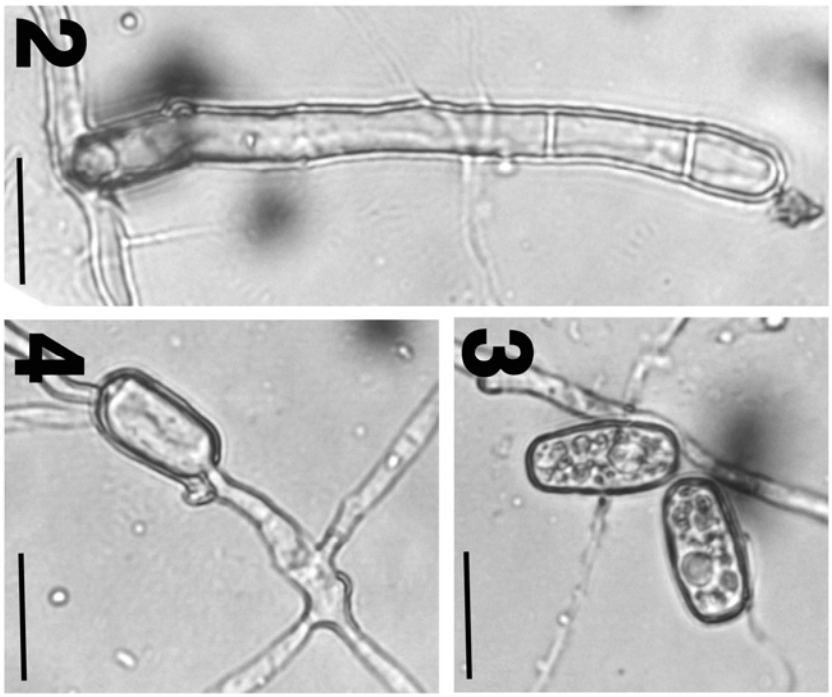
Fungus	Host plant	Isolate[a]	Country of origin	Database accession no.[b]
Erysiphe adunca	*Populus* sp.	UC1512287	USA	AF011324
E. adunca	*Salix vulpina*	MUMH39	Japan	D84383
E. aquilegiae var. *ranunculi*	*Cimicifuga simplex*	TPU-495	Japan	AB000944
E. australiana	*Lagerstroemia indica*	DNA	Japan	AB022408
E. flexuosa	*Aesculus hippocastanum*	MUMH1429	Germany	AB091774[c]
E. friesii var. *dahurica*	*Rhamnus japonica* var. *decipiens*	MUMH6	Japan	AB000939
E. glycines	*Desmodium podocarpum* subsp. *oxyphyllum*	MUMH52	Japan	AB015927
E. gracilis	*Quercus glauca*	MUMH122	Japan	AB022358
E. heraclei	*Daucus carota*	MUMH73	Japan	AB000942
E. japonica	*Swida controversa*	MUMH90	Japan	AB000941
E. mori	*Morus australis*	MUMHs77	Japan	AB000946
E. necator	*Vitis vinifera*	VPRI19719	Australia	AF073346
E. prunastri	*Prunus spinosa*	MUMH652	Switzerland	AB046983
E. simulans	*Rosa miltiflora*	TPU-439	Japan	AB015926
E. togashiana	*Styrax japonica*	MUMH84	Japan	AB091775[c]
E. wadae	*Fagus crenata*	MUMH1534	Japan	AB091776[c]
Brasiliomyces trina	*Quercus agrifolia*	MUMH114	USA	AB022351
Typhulochaeta japonica	*Quercus cuspidata*	MUMHs75	Japan	AB022416

[a] MUMH = Mie University Mycological Herbarium; TPU = Herbarium of Toyama Prefectural University; VPRI = Plant Disease Herbarium, Institute for Horticultural Development, Victoria, Australia; UC = University of California Herbarium; DNA = Preserved by DNA, herbarium specimen not available

[b] DDBJ, EMBL, and GenBank database accession number of the nucleotide sequence data

[c] DNA sequence determined in this study

a
c
b
d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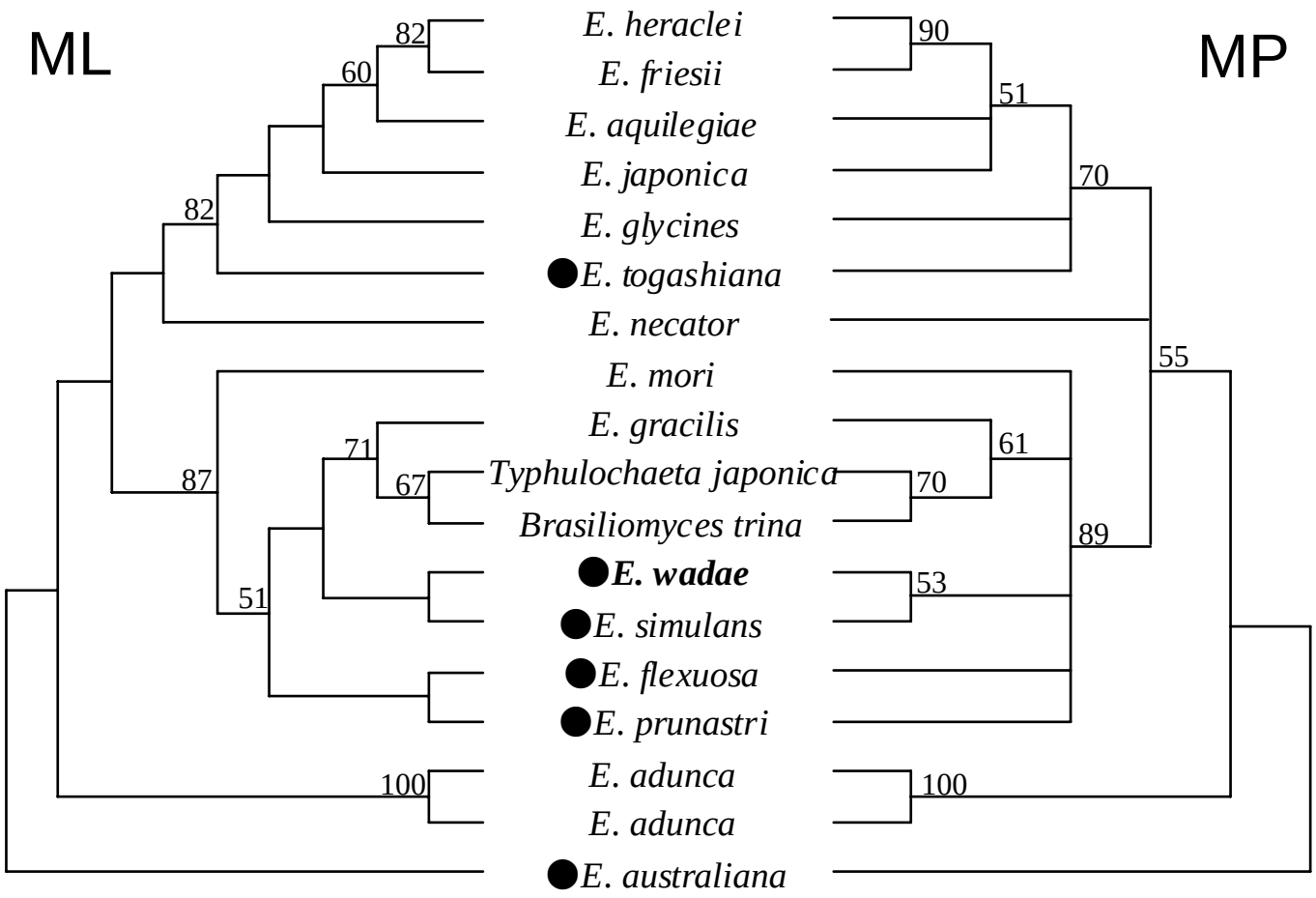
7

8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E. friesii
E. aquilegiae
E. japonica
E. glycines
E. togashiana
E. necator
E. mori
E. gracilis
Typhulochaeta japonica
Brasiliomyces trina
E. wadae
E. simulans
E. flexuosa
E. prunastri
E. adunca
E. adunca
E. australiana