

FULL PAPER

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## *Sawadaea nankinensis* comb. nov.: a powdery mildew fungus of *Acer buergerianum*

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**Abstract** The anamorphic state of a powdery mildew on trident maple (*Acer buergerianum*, Aceraceae), belonging to *Sawadaea*, has been observed since 1980 in Tokyo and other areas of Japan. Since the autumn of 2003, this fungus has begun to produce chasmothecia in various areas of Japan, which were consistent with *Erysiphe nankinensis* (= *Uncinula nankinensis*), but apparently contradictory to the characteristics of the anamorph. Based on a molecular phylogenetic analysis using DNA separately extracted from the anamorph and teleomorph of the fungus on *A. buergerianum*, it could be demonstrated that sequences of this fungus are sister to *Sawadaea*. As the anamorph belongs to *Oidium* subgen. *Octagoidium* and because of the phylogenetic position within the *Sawadaea* clade, the new combination *Sawadaea nankinensis* is proposed for this species. The genus *Sawadaea* is emended to comprise species with consistently unbranched appendages.

**Key words** Aceraceae · Erysiphaceae · Erysiphales · *Erysiphe nankinensis* · Molecular phylogeny

### Introduction

Trident maple (*Acer buergerianum* Miq., Aceraceae), a deciduous tree with China as the geographic origin, is commonly cultivated in Japan as street, garden, or hedge trees. Two *Erysiphe* DC. species, i.e., *Erysiphe ljubarskii* var. *aduncooides* (R.Y. Zheng & G.Q. Chen) U. Braun & S.

Takam. [= *Uncinula ljubarskii* var. *aduncooides* (R.Y. Zheng & G.Q. Chen) R.Y. Zheng & G.Q. Chen], and *E. nankinensis* (F.L. Tai) U. Braun & S. Takam. (= *U. nankinensis* F.L. Tai), have been reported on *A. buergerianum* in China (Braun 1987; Chen et al. 1987). *Erysiphe ljubarskii* var. *aduncooides* was first found in Japan in 2001 (Sugahara et al. 2005). Another powdery mildew has been reported on this plant since 1980 in Tokyo and other areas of Japan (Horie and Sugata 1985). Based on the morphological characteristics, this fungus has been considered an anamorph of the genus *Sawadaea* Miyabe. However, because this fungus did not produce any teleomorph, its accurate taxonomic position has been obscure for a long time. Since the autumn of 2003, this fungus has begun to produce chasmothecia in various areas of Japan. Morphological characteristics of the teleomorph were consistent with *E. nankinensis*, which was apparently contradictory to the characteristics of the anamorph. In this study, we conducted a molecular phylogenetic analysis using DNA separately extracted from anamorph and teleomorph of the fungus on *A. buergerianum* to elucidate its taxonomic position.

### Materials and methods

Field observation, morphological studies, and samples examined

Occurrence of powdery mildew of *A. buergerianum* was periodically observed from April to November 2006 at the campus of Mie University, Tsu, Japan (34°74.472' N, 136°52.428' E). Fresh collections of the powdery mildew fungus on *A. buergerianum* were examined by standard light microscopy (Axio Imager; Carl Zeiss, Göttingen, Germany) and differential-interference-contrast optical instruments and devices. The specimens examined are deposited at MUMH (Herbarium, Faculty of Bioresources, Mie University, Tsu, Japan), and HAL [Martin-Luther-University, Institute of Biology, Geobotany and Botanical Garden, Herbarium, Halle (Saale), Germany]. Samples

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examined in this study and their DNA sequence accession numbers at DDBJ (DNA Data Bank of Japan) are as follows. MUMH 1273, HAL 2063 F: anamorph, Japan, Aichi Prefecture, Nagoya-shi, Higashiyama Botanical Garden, 8 Jul 2001, leg. S. Takamatsu, AB193389 (ITS), AB193395 (28S); MUMH 3691, HAL 2064 F: anamorph, Japan, Mie Prefecture, Tsu-shi, Prefectural Art Museum, 16 Jun 2005, leg. S. Takamatsu, AB353759 (ITS + 28S); MUMH 3799, HAL 2065 F: teleomorph, Japan, Okayama Prefecture, Okayama-shi, Ifuku-cho, 17 Nov 2005, leg. H. Yamamoto, AB353760 (ITS + 28S); MUMH 3801, HAL 2066 F: teleomorph, Japan, Mie Prefecture, Tsu-shi, Prefectural Art Museum, 8 Dec 2005, leg. S. Takamatsu, AB353761 (ITS + 28S); MUMH 4232, HAL 2067 F: anamorph, Japan, Mie Prefecture, Tsu-shi, Mie University, 17 Oct 2006, leg. S. Takamatsu, AB353762 (ITS + 28S); MUMH 4233, HAL 2068 F: teleomorph, Japan, Mie Prefecture, Tsu-shi, Mie University, 9 Nov 2006, leg. S. Takamatsu, AB353763 (ITS + 28S). We did not use the type specimen of *E. nankinensis* in this analysis because this specimen was not available to us.

#### Molecular phylogenetic study

Extraction of whole-cell DNA was performed using the chelex method (Walsh et al. 1991) as described in Hirata and Takamatsu (1996). The 5'-end of the 28S rDNA, including the domains D1 and D2, and the internal transcribed spacer (ITS) region, including the 5.8S rDNA, were amplified by polymerase chain reaction (PCR) and then sequenced using direct sequencing as described in Takamatsu et al. (2006).

The sequences were initially aligned using the Clustal X package (Thompson et al. 1997). The alignment was then visually refined with a word processing program, using color-coded nucleotides. The alignments were deposited in TreeBASE (<http://www.treebase.org/>) under the accession number S1920. Phylogenetic trees were obtained from the data using the maximum-parsimony (MP) method in PAUP\* 4.0 (Swofford 2001) and Bayesian analysis in MRBAYES 3.1.1 (Huelsenbeck and Ronquist 2001). MP analyses were performed with the heuristic search option using the tree-bisection-reconstruction (TBR) algorithm with 100 random sequence additions to find the global optimum tree. All sites were treated as unordered and unweighted, with gaps treated as missing data. The strength of the internal branches of the resulting trees was tested with bootstrap (BS) analyses using 1000 replications with the stepwise addition option set as simple (Felsenstein 1985). BS values higher than 70% are provided.

For Bayesian phylogenetic analyses, the best-fit evolutionary model was determined for each data set by comparing different evolutionary models via the Akaike information criterion (AIC) using PAUP\* and MrModeltest 2.2 (Nylander 2004). MRBAYES was launched with random starting trees for  $10^6$  generations and the Markov chains were sampled every 100 generations, which resulted in  $10^4$  sampled trees. To ensure that the Markov chain did not

become trapped in local optima, we used the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) algorithm, performing the estimation with four incrementally heated Markov chains. Of the resulting  $10^4$  trees, the first 2000 (burn-in) were discarded. The remaining 8000 trees were summarized in a majority-rule consensus tree, yielding the probabilities of each clade being monophyletic. Bayesian posterior probability (PP) values higher than 0.95 are provided.

## Results

### Field observation and morphological study

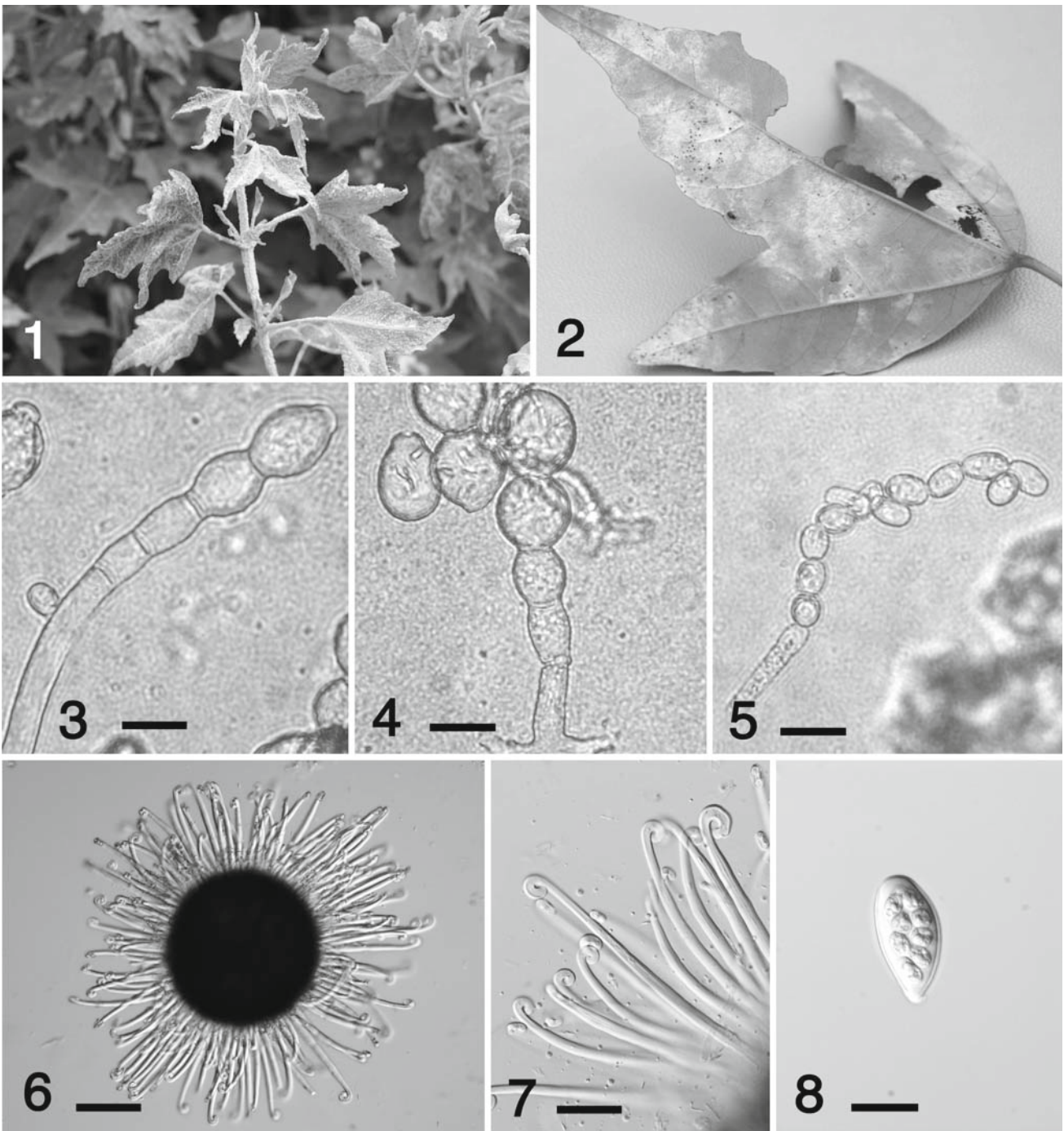
From the middle to the end of May, colonies first appear on young leaves and shoots of *A. buergerianum* to produce typical flag shoots (Fig. 1). The shoots are covered by dense white mycelial mats producing abundant conidia. In summer, the flag shoots turn gray to purple-gray and are eventually withered. In autumn, dense white colonies are found on the abaxial surface of adult leaves (Fig. 2).

Both macroconidia and microconidia are produced. Macroconidia, produced in chains, are barrel shaped with distinct fibrosin bodies,  $25\text{--}40 \times 15\text{--}22.5 \mu\text{m}$ . Macroconidiphores,  $90\text{--}145 \times 15\text{--}20 \mu\text{m}$ , arise from the upper part of hyphae and have conidial chains with sinuate edges (Figs. 3, 4). Microconidia, also produced in chains, are broadly ellipsoidal to subglobose with distinct fibrosin bodies,  $9\text{--}11.5 \times 6\text{--}7 \mu\text{m}$  (Fig. 5). These anamorphic characteristics indicate that this fungus belongs to *Oidium* subgenus *Octagonium* (Cook et al. 1997).

Chasmothecia, produced in autumn, are  $196\text{--}276 \mu\text{m}$  in diameter, blackish-brown, and depressed-globose (Fig. 6). Appendages are more than 100 in number, arising from the upper half of the chasmothecium,  $85\text{--}135 \mu\text{m}$  in length, width subequal throughout or somewhat narrowed upward, smooth, aseptate, thick-walled, hyaline, unbranched, and uncinately to circinate at the apex (Fig. 7). Asci are  $17\text{--}41$  per chasmothecium, ellipsoid to ovoid with stalk,  $60\text{--}92.5 \times 35\text{--}40 \mu\text{m}$ , and 8-spored (Fig. 8). Ascospores  $20\text{--}22.5 \times 10\text{--}12.5 \mu\text{m}$ . These teleomorphic characteristics are consistent with *Erysiphe nankinensis* (section *Uncinula*) known on *Acer buergerianum* in China (Tai 1930; Tai and Wei 1932; Braun 1987).

### Phylogenetic placement of the powdery mildew on *Acer buergerianum* in the Erysiphaceae: 28S analysis

A total of 46 sequences of 28S rDNA retrieved from the DDBJ database, including six sequences from the powdery mildew on *Acer buergerianum*, were used to construct the phylogenetic tree of the Erysiphaceae. *Byssosascus striatissporus* (G.L. Barron & C. Booth) Arx (Myxotrichaceae) was used as an outgroup taxon, based on Mori et al. (2000). The data set consisted of 968 characters, of which 209 characters were variable and 148 characters were phylogenetically informative for parsimony analysis. A total of 36

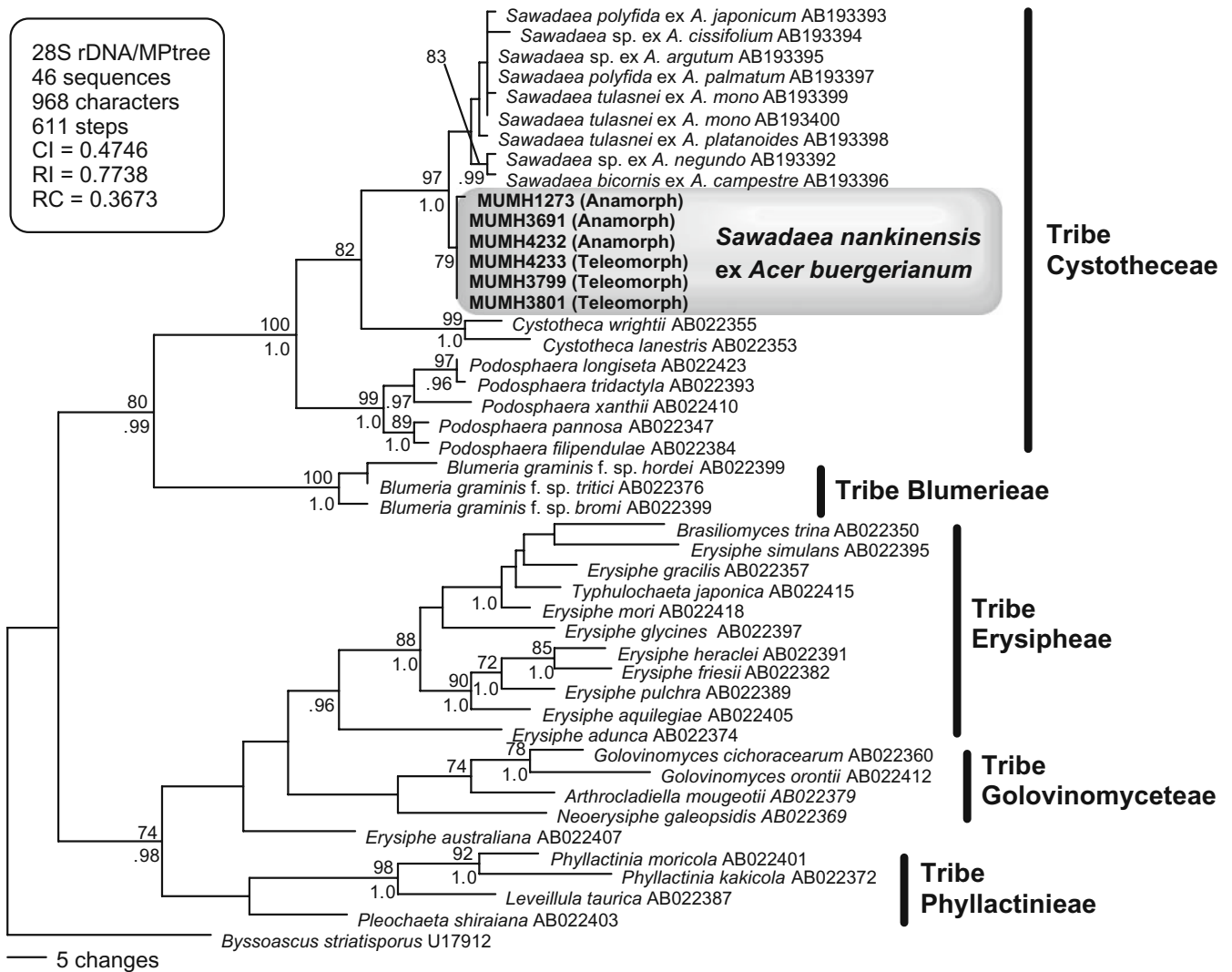


**Figs. 1–8.** *Sawadaea nankinensis*. **1** Flag shoot symptoms on *Acer buergerianum* occurring in spring season. **2** Colonies on *Acer buergerianum* in autumn season with chasmothecia (small black points). **3** Catenate conidiophore with sinuate edge. **4** Catenate conidiophore with distinct

fibrosin bodies. **5** Microconidia. **6** Chasmothecium. **7** Unbranched appendages with uncinately-circinate tips. **8** Ascus and ascospores. Bars **3, 4, 7** 20  $\mu\text{m}$ ; **5** 10  $\mu\text{m}$ ; **6** 100  $\mu\text{m}$ ; **8** 50  $\mu\text{m}$

equally MP trees with 611 steps (CI = 0.4746, RI = 0.7738, RC = 0.3673) were constructed by the MP analysis. A tree with the highest likelihood score ( $-\ln L = 5063.69$ ) among the 36 MP trees is shown in Fig. 9. Most internal branches are supported in the strict consensus of the 36 trees. Bayesian analysis generated similar tree topology. The six 28S

rDNA sequences from powdery mildew specimens on *A. buergerianum* are identical to each other, except for the sequence of MUMH1273, in which only one base differs from the other specimens. These sequences are sister to the clade of *Sawadaea* with strong statistical support (BS = 97%; PP = 1.0).



**Fig. 9.** Phylogenetic analysis of the divergent domains D1 and D2 sequences of the 28S rDNA for 46 sequences from the Erysiphaceae covering all known tribes and one outgroup taxon. The tree is a phylogram of the maximum-likelihood tree among the 36 most parsimonious trees with 611 steps, which was obtained by a heuristic search employing the random stepwise addition option of PAUP\*. Gaps were treated

as missing data. Horizontal branch lengths are proportional to the number of nucleotide substitutions that were inferred to have occurred along a particular branch of the tree. Percentage bootstrap support (1000 replications;  $\geq 70\%$ ) and posterior probability ( $\geq 0.95$ ) are shown on and under branches, respectively

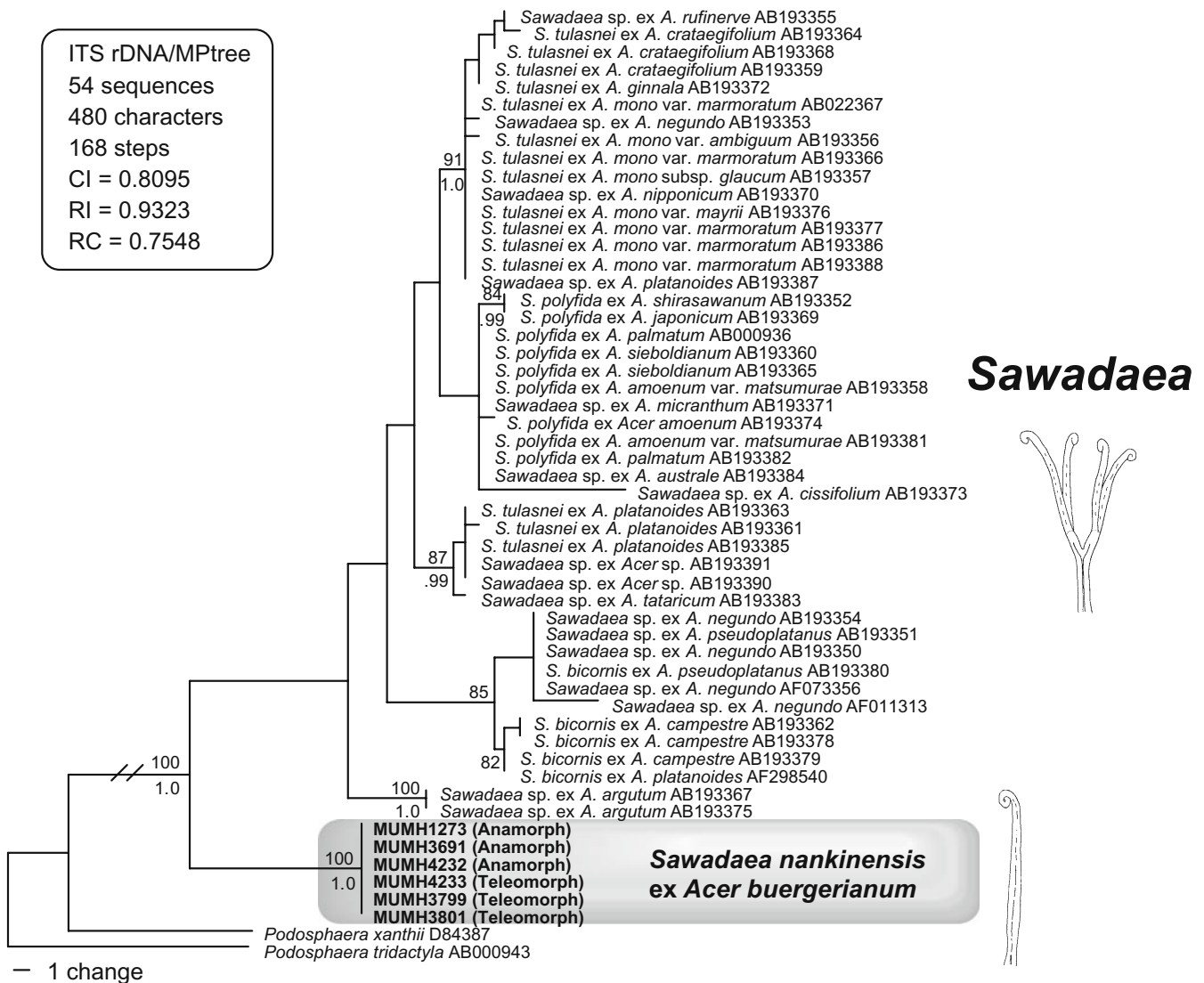
**Phylogeny within *Sawadaea*: ITS analysis**

A total of 46 ITS sequences of *Sawadaea* retrieved from DDBJ database were aligned with six sequences of the fungus on *A. buergerianum* and two outgroup sequences. The data set consisted of 54 sequences and 481 characters, of which the 11th character from the 5'-end of the ITS1 region was removed from the analysis because both G and T signals were frequently observed at the single site. Of the remaining 480 characters, 114 characters were variable and 84 characters were phylogenetically informative for parsimony analysis. A total of 29 equally MP trees with 168 steps (CI = 0.8095, RI = 0.9323, RC = 0.7548) were constructed by the MP analysis. A tree with the highest likelihood score among the 29 MP trees is shown in Fig. 10. Most internal branches are supported in the strict consensus of the 29

trees. Bayes analysis generated similar tree topology. The six ITS sequences from the fungus on *A. buergerianum* are identical to each other and sister to the clade of *Sawadaea* with strong statistical support (BS = 100%; PP = 1.0).

**Discussion**

Morphological examination of the anamorph reveals that the fungus on *A. buergerianum* belongs to *Oidium* subgenus *Octagonium* (anamorphic state of *Sawadaea*), whereas the teleomorphic characters agree with *Erysiphe nankinensis* (= *Uncinula nankinensis*, the postulated anamorph: *Oidium* subgenus *Pseudoidium*), known on this host plant in China. Therefore, there is an apparent conflict between the postu-



**Fig. 10.** Phylogenetic analysis of the nucleotide sequences of the ITS region including 5.8S rDNA for 54 sequences from *Sawadaea*, the powdery mildew on *Acer buergerianum*, and two outgroup taxa. The tree is a phylogram of the maximum-likelihood tree among the 29 most parsimonious trees with 168 steps, which was obtained by a heuristic search employing the random stepwise addition option of PAUP\*. Gaps were treated as missing data. Horizontal branch lengths are proportional to the number of nucleotide substitutions that were inferred to have occurred along a particular branch of the tree. Percentage bootstrap support (1000 replications;  $\geq 70\%$ ) and posterior probability ( $\geq 0.95$ ) are shown on and under branches, respectively

lated anamorph and the teleomorph of this fungus. The conidia of species of the genus *Erysiphe* sensu Braun and Takamatsu (2000) (*Oidium* subgenus *Pseudoidium*) are formed singly (solitary-type conidiophore: noncatenate), whereas in the genus *Sawadaea* (*Oidium* subgenus *Octagonium*) the conidia are produced in chains (chain-type conidiophore: catenate). Thus, *Erysiphe* can be easily distinguished from *Sawadaea* by the conidiogenesis. On the other hand, the teleomorphs of *Erysiphe* section *Uncinula* and *Sawadaea* are rather similar, sharing appendages with uncinately-circinate tips. The most typical difference between the two genera is that *Sawadaea* has appendages dichotomously or trichotomously branched, usually deeply cleft, down to the middle of the appendage, whereas the appendages of *Erysiphe* (section *Uncinula*) are usually unbranched. Based on the nonbranching appendages, the teleomorphic state on

*A. buergerianum* was classified as a species of the genus *Uncinula* (now it is *Erysiphe* section *Uncinula*; Braun and Takamatsu 2000).

*Uncinula nankinensis*, a powdery mildew fungus on *A. buergerianum*, was first described by Tai in 1930 based on a specimen collected in China (Tai 1930). The drawings by Tai and Wei (1932) clearly show that this fungus has catenate conidia, which is consistent with our observation, but at that time the authors did not take *Sawadaea* into consideration and they did not see any conflict in the position of this fungus in *Uncinula* because of conidial catenation. The genus *Sawadaea* was proposed by K. Miyabe, and its first description occurred in the report of Sawada (1914). However, *Sawadaea* was not recognized by taxonomists of powdery mildews for a long time because the description was written in Japanese. Homma (1937) first provided a

description of *Sawadaea* in English. However, even after Homma's description, *Sawadaea* species had long been retained in the genus *Uncinula* (Yarwood 1957, 1978; Blumer 1967; Parmelee 1977). *Sawadaea* was recognized as a valid genus only after 1980 (Braun 1987; Chen et al. 1987; Heluta 1989). Therefore, the description of the fungus on *A. buergerianum* in 1930 as an *Uncinula* species may be an understandable consequence. However, the fungus was still kept in *Uncinula* by Braun (1987) and Chen et al. (1987), although *Sawadaea* is described in these monographs. Braun (1987) argued as follows: "Tai & Wei (I.c.) depicted and described an anamorphic state from the type host (conidia in chains, pyriform, with fibrosin bodies). It is rather doubtful that this conidial state in fact belonged to *U. nankinensis*. Maybe, it was an *Oidium* state of a *Sawadaea* species simultaneously infecting the type host." The doubted, unproven context of the anamorph with catenate conidia and the uncinula-like chasmothecia was obviously the reason for the taxonomic decisions by Braun (1987) and Chen et al. (1987) to retain this species in *Uncinula*.

Therefore, we have used molecular methods to investigate whether two different powdery mildew species simultaneously infect *A. buergerianum* or whether a single species is involved. Specimens of anamorphic and teleomorphic states were collected from individuals of *A. buergerianum* at different times. DNAs were separately extracted from mycelia of anamorphic samples and from chasmothecia of teleomorphic samples and were used for sequencing. The results revealed that the sequences from anamorphs and teleomorphs were identical to each other, indicating that both morphs pertain to a single fungal species, but not to different species that simultaneously infect the host plant. Both 28S rDNA and ITS sequences show that the fungus on *A. buergerianum* is sister to *Sawadaea* with strong statistical support. Two taxonomic solutions may be possible to solve this problem. The first choice might be the introduction of a new genus to accommodate the fungus on *A. buergerianum*. The second choice would be to place this species in *Sawadaea*. Because the anamorph of the *A. buergerianum* powdery mildew coincides with the anamorphic state of *Sawadaea* and the fungus clusters together with *Sawadaea* to form one bigger clade, we prefer to follow the second solution.

Hirose et al. (2005) performed a molecular phylogenetic analysis of *Sawadaea* using nucleotide sequences of rDNA ITS regions. They used a sequence from "*Sawadaea* sp." on *A. buergerianum* in their study. In their tree, this fungus was placed within the *Sawadaea* clade, i.e., not as sister to *Sawadaea*. The fungus on *A. buergerianum* has an 11-base deletion in the ITS1 region. A similar 10-base deletion is known from *S. tulasnei* (Fuckel) Homma. Hirose et al. (2005) regarded these deletions as a synapomorphy of *S. tulasnei* and the fungus on *A. buergerianum*, and constructed a constrained tree regarding *S. tulasnei* and the fungus on *A. buergerianum* to be monophyletic. However, considering the unique morphological characteristics of this fungus, having unbranched appendages, the present tree topology placing the fungus on *A. buergerianum* at the base of *Sawadaea* may be more likely than the tree of Hirose et al.

(2005). The unique appendages of *Sawadaea*, which are dichotomously or trichotomously branched and deeply cleft, down to the middle, may be an apomorphic characteristic that evolved within this genus.

*Erysiphe circinata* (Cooke & Peck) U. Braun & S. Takam. (= *Uncinula circinata* Cooke & Peck), reported on *Acer* spp. in North America, has teleomorphic characteristics similar to *E. nankinensis* in having a number of unbranched appendages with uncinata-circinate tips and arising from the upper part of the chasmothecia. This finding suggests that *E. circinata* also should be revised as a *Sawadaea* species. However, there is no description of an anamorph of this fungus. Molecular analyses, as well as morphological observation of a potential anamorph, are required to prove the taxonomic position of this fungus.

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### Taxonomic conclusion

Because of the molecularly proven connection between the anamorph of the powdery mildew fungus on *Acer buergerianum*, belonging to *Oidium* subgen. *Octagoidium* (*Sawadaea* anamorphs), and the teleomorph agreeing with *Erysiphe nankinensis*, as well as the placement of the latter species as sister at the base of the *Sawadaea* clade, a close affinity to *Sawadaea* is evident, although the appendages are consistently unbranched. However, a certain amount of simple appendages are also formed in various *Sawadaea* species, above all in *S. tulasnei*. Furthermore, *E. nankinensis* and *Sawadaea* spp. are characterized and connected by very thick walled appendages arising from the upper half of the fruit body. Hence, we propose to reallocate *E. nankinensis* to *Sawadaea*.

***Sawadaea nankinensis*** (F.L. Tai) S. Takam. & U. Braun, comb. nov.

Basionym: *Uncinula nankinensis* F.L. Tai, Contr. Biol. Lab. Sci. Soc. China, Bot. Ser., 6(1): 2, 1930.

= *Erysiphe nankinensis* (F.L. Tai) U. Braun & S. Takam., Schlechtendalia 4: 21, 2000.

Descriptions and illustrations: Tai and Wei (1932: 108, Fig. 15), Braun (1987: 522–523, pl. 268), Chen et al. (1987: 406–408, fig. 234)

According to Braun (1987), the holotype of *U. nankinensis* is devoid of any ascomata.

The inclusion of *S. nankinensis* requires an emendation of the circumscription of *Sawadaea* to include species with consistently unbranched appendages.

***Sawadaea*** Miyabe *emend.* S. Takam. & U. Braun

Anamorph: *Oidium* subgen. *Octagoidium* (mycelium internal; conidiophores and conidia dimorphic, i.e., with large macroconidiophores and macroconidia and small microconidiophores and microconidia, conidia in chains, with fibrosin bodies). Teleomorph: Chasmothecia relatively large, ranging from about 100 to 300 µm diameter, slightly

dorsiventral, peridium multilayered, appendages numerous, arising from the equatorial zone to the upper half, thick-walled, consistently unbranched, unbranched and branched appendages mixed or appendages almost completely branched, dichotomously to trichotomously branched, usually deeply cleft, down to the middle, tips of the ultimate branchlets uncinately-circinate, asci numerous, (6–)8-spored.

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