

Phylogeny and taxonomy of *Acer* powdery mildews, including genera *Sawadaea* and *Takamatsuella* (Erysiphaceae, Ascomycota)

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Abstract: *Acer* (Sapindaceae) is a major genus of broadleaf trees dominating deciduous forests in the Northern Hemisphere, with Asia exhibiting the highest species diversity. Many economically important *Acer* species are cultivated for ornamental or timber purposes. *Acer* powdery mildew, caused by fungi in the tribe *Cystotheceae*, poses significant global economic and ecological threats. The pathogenicity spectrum remains unclear due to taxonomic uncertainties in its primary causal genera, *Sawadaea* and *Takamatsuella*. This study presents a comprehensive phylogenetic-taxonomic analysis of the two genera across East Asia, Europe, and North America. Using 75 ITS and 58 28S rDNA newly obtained sequences, we resolved 12 *Sawadaea* species and one *Takamatsuella* species into nine monophyletic clades, revealing marked cryptic diversity (three new species: *S. acerina*, *S. aceris-arguti*, *S. taiii*) and two paraphyletic groups (*S. bifida*/*S. negundinis*). Taxonomic revisions include: *S. bicornis* split into two *formae* (*f. bicornis* and *f. polyphaga* *f. nov.*) with distinct host preferences; *S. tulasnei* (*sensu stricto*) restricted to Europe/North America, invalidating previous Asian records; *S. nankinensis* and *S. koelreuteriae* form two basal lineages. Phylogenetic positioning confirmed *Takamatsuella* as a distinct genus sister to *Sawadaea*, supported by an ITS1 26 bp deletion. Host specificity analysis revealed narrow host ranges (primarily *Acer*) with two evolutionary host expansions to *Koelreuteria*, *Aesculus*, and *Liquidambar*. This study also newly describes the asexual morphs of four species (*S. aesculi*, *S. bifida*, *S. bomiensis* and *S. kovaliana*) and establishes a molecular framework for disease management through clarified phylogeny and taxonomy. Our findings provide critical insights into fungal evolution, host-pathogen interactions, and strategies for mitigating powdery mildew impacts in forest ecosystems.

Key words: Diversity, *Erysiphaceae*, *formae*, *Helotiales*, new species.

Taxonomic novelties: New forma: *Sawadaea bicornis* *f. polyphaga* M. Bradshaw & U. Braun. **New species:** *Sawadaea acerina* G.X. Guan & S.Y. Liu, *Sawadaea aceris-arguti* S. Takam. & U. Braun, *Sawadaea taiii* G.X. Guan & S.Y. Liu.

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INTRODUCTION

Acer (Sapindaceae, incl. Aceraceae) is an important broad leaves genus that prominent deciduous forests of the Northern Hemisphere, and comprises about 125 to 156 species based on the applied species concepts. Asia harbours the highest species diversity, where multiple species are important economically in that they are planted as ornamental trees or for timber (Gao *et al.* 2020). East Asia, especially China is considered the present centre of diversification for *Acer* (Suh *et al.* 2000). The taxonomy of *Acer* species is well documented (Li *et al.* 2006, Grimm *et al.* 2007), whereas Li *et al.* (2019) provided a modern classification of *Acer* into sections, substantiated by phylogenetic data, which

largely coincides with previous subgeneric concepts (de Jong 2002). Microfungi associated with *Acer* species have diverse host-plant interactions. Among these phytopathogenic ascomycetes, including powdery mildews is one of the important diseases on acer plants (Johnston *et al.* 2019, Haelewaters *et al.* 2021).

Powdery mildews are obligate biotrophic fungi forming characteristic, conspicuous symptoms caused by whitish superficial mycelial patches or films of the sexual morph (Braun & Cook 2012). They are cosmopolitan in distribution and occur on more than 10,000 plant species, including numerous important crops (Amano 1986, Braun & Cook 2012; Bradshaw *et al.* 2022). The currently accepted generic system of powdery mildews in the world containing five tribes, including 17 sexual morph genera and two asexual morph

Sawadaea *Takamatsuella* *lum*
 Cystothecaceae
 Acer
 Sawadaea *lum*
Uncinula aceris (Sawadaea aceris)
 Sawadaea
 Sawadaea
 Sawadaea
 U. *tulasnei* Sawadaea
 Sawadaea
 Sawadaea
 Sawadaea
 Otani 1988, Heluta 1989). Scanning electron microscopy revealed embossed strips, which significantly differs from outer conidial Erysiphe *Uncinula*
 Sawadaea
 Erysiphaceae
 Sawadaea
 Sawadaea
 Sawadaea
 Sawadaea
 Sawadaea
 Braun & Cook 2012). And five of these eight species were proposed
 S. *aesculi* S. *bomiensis*
 et al.
 Sawadaea *nankinensis* [= *Uncinula nankinensis*] *Acer buergerianum*
 Sawadaea
 S. *bicornis* *Uncinula aceris*
Acer barbinerve S. *tulasnei*
 [= *Uncinula aceris*] *tulasnei* *Acer*
 S. *koelreuteriae* [= *Erysiphe koelreuteriae*]
 Koelreuteria *paniculata* S. *polyfida* [= *Uncinula polyfida*] *Acer amplum* *platypifolium*
 et al. S. *negundinis* [= *Uncinula negundinis*] *Acer negundo*
 S. *aesculi* S. *bomiensis*
wilsonii S. *bomiensis*
 S. *Acer caudatum*
 Sawadaea
 S. *bicornis*
 S. *tulasnei* Sawadaea
 Sawadaea
 Sapindaceae
 Oceania, and South America [Argentina] (Braun & Cook 2012).

Sawadaea
lum
 Sawadaea et al. *lum*
 W. Sawadaea
 S. *bicornis*
 et al. et al. *lum*
 Sawadaea
 Takamatsuella
 superficial mycelium, composed of hyaline thin-walled, septate,
 likely not formed at all. Chasmothecium is somewhat flattened,
 aseptate, hyaline, subcylindrical-filiform, uncinuloid, apices circinate;
 a monospecific genus containing only *T. circinata*
Uncinula circinata *Acer spicatum*
 U. *bicornis*
 Erysiphe *circinata*.
 S. *circinata* S. *bicornis*
 Sawadaea
 S. *circinata*
 Cook (2012) confirmed that the appendages in this species remain
 Takamatsuella *lum*
Uncinula circinata
 Sawadaea
 S. *circinata*
 A Chines collection identified as *Uncinula circinata* *lum*
circinata
Acer wilsonii
 (HMAS 37698), identified as *U. circinata*
wilsonii
Acer griseum
lum
U. circinata,
Uncinula *Erysiphe*
griseum *Erysiphe*
circinata
lum
Ijubarskii.

Uncinula circinata *Dodonaea viscosa* *Sapindus drummondii* *S. marginatus* *Sapindus* *E. flexuosa* *Takamatsuella* *Sawadaea* *Takamatsuella* *Sawadaea* *Takamatsuella*

MATERIALS AND METHODS

Fungal materials

countries. In total, 123 specimens from five countries (China, Of these, 62 specimens of *Sawadaea* *Takamatsuella*

Morphological examination

DNA extraction, PCR amplification and sequencing

spacer (ITS) regions, including the 5.8S rDNA, were amplified *et al.*

amplified with primers pairs LSU1/LSU2 (Scholin *et al.*

components were 2 μ L of total genomic DNA, 2.5 μ L 10 \times PCR buffer (TaKaRa, Japan), 2 μ L dNTP mixture (10 mM total, 2.5 mM each), 1 μ L each primer (20 ng/ μ L), 0.1 μ L *Taq* (TaKaRa, Japan) (5 U/ μ L) and sterile ddH₂O up to a final volume of 25 μ L. The amplification reactions were conducted under the

52–56 °C for annealing, and 30 s at 72 °C for extension, and a final

gel in 0.5 \times TBE buffer. The amplicons were sent to Sangon Biotech

Phylogenetic analyses

additions to find the global optimum tree. All gaps were treated as

both analyses. For BI analysis, the best-fit substitution models

and trees were sampled every 100 generations. The first 25 %

RESULTS

The phylogeny of *Sawadaea* and *Takamatsuella*

Seventy-five ITS sequences including the ITS1-5.8S rDNA-ITS2 and 58 28S rDNA sequences including D1/D2 domains were generated in this study and were aligned with sequences retrieved from the NCBI GenBank nucleotide database. The ITS+28S rDNA sequence alignment matrix consisted of 203 sequences including 950 characters, of which 168 (17.7 %) were parsimony informative

and 18 (1.2 %) were parsimony-uninformative. *Cystotheca castanopsis* and *C. wrightii* were selected as outgroups. The maximum parsimony (MP) and maximum likelihood (ML) tree with the highest likelihood value of more than 70 % and posterior probabilities value greater than 0.90 for Bayesian Inference (BI) are shown in Fig. 1. Phylogenetic trees generated from ML and BI analyses are almost identical to the MP tree, which is, therefore, not shown.

The tree topology revealed the molecular phylogeny among species in *Sawadaea* and a much higher species diversity than



Fig. 1. Phylogenetic analysis of the ITS+28S rDNA regions. Nodes are labelled with bootstrap values from Parsimony bootstrap/Maximum likelihood/Bayesian posterior probabilities values. Posterior probabilities greater than bootstrap support values (> 70 %) by maximum parsimony (MP), maximum likelihood (ML) and 0.90 for Bayesian Inference (BI) methods are shown on the respective branches. The newly generated sequences in this study are in bold. *Cystotheca castanopsis* and *C. wrightii* are used as outgroup taxa.

previously assumed, especially in Eastern Asia. Twelve species of *Sawadaea* and one species of *Takamatsuella* formed nine monophyletic clades (clades 1–5, 7, 9–11) and two non-monophyletic clades (clade 6 and clade 8). The insertion/deletion differences between sites 60 and 107 of the ITS1 region were summarized among these clades (Fig. 2). *Takamatsuella circinata* (Clade 1; MP = 100 %, ML = 100 %, BI = 1.00) formed a sister clade to genus *Sawadaea* with high support which is mainly caused by a 26 bp deletion between sites 64 and 89 of the ITS1 region. This result supports the treatment of *Takamatsuella* as an independent genus. The differences among *Sawadaea* species were caused mainly by a 6–14 bp insertion/deletion (indel) between sites 65 and 101 of

the ITS1 region. *Sawadaea nankinensis* (Clade 2), *S. koelreuteriae* (Clade 3), *S. aesculi* (Clade 4), *S. negundinis* (Clade 6), *S. bifida* (Clade 6), *S. tulasnei* (Clade 7), *S. taii* (Clade 8) and *S. kovaliana* (Clade 8) had 10 bp deletions. *Sawadaea nankinensis* formed a separate clade (Clade 2; MP = 100 %, ML = 100 %, BI = 1.00) with the other species of *Sawadaea*, which was mainly caused by the two bases insertion at sites 65 and 66 and one base deletion at site 89 (Fig. 2), and its distinguished unbranched uncinate-circinate appendages (Fig. 3). *Sawadaea koelreuteriae* formed a separate clade with high support (MP = 100 %, ML = 100 %, BI = 1.00). *Sawadaea aceris-arguti* has a 6 bp deletion between sites 93 and 98, and *S. acerina* has a 7 bp deletion between sites 94 and 100.

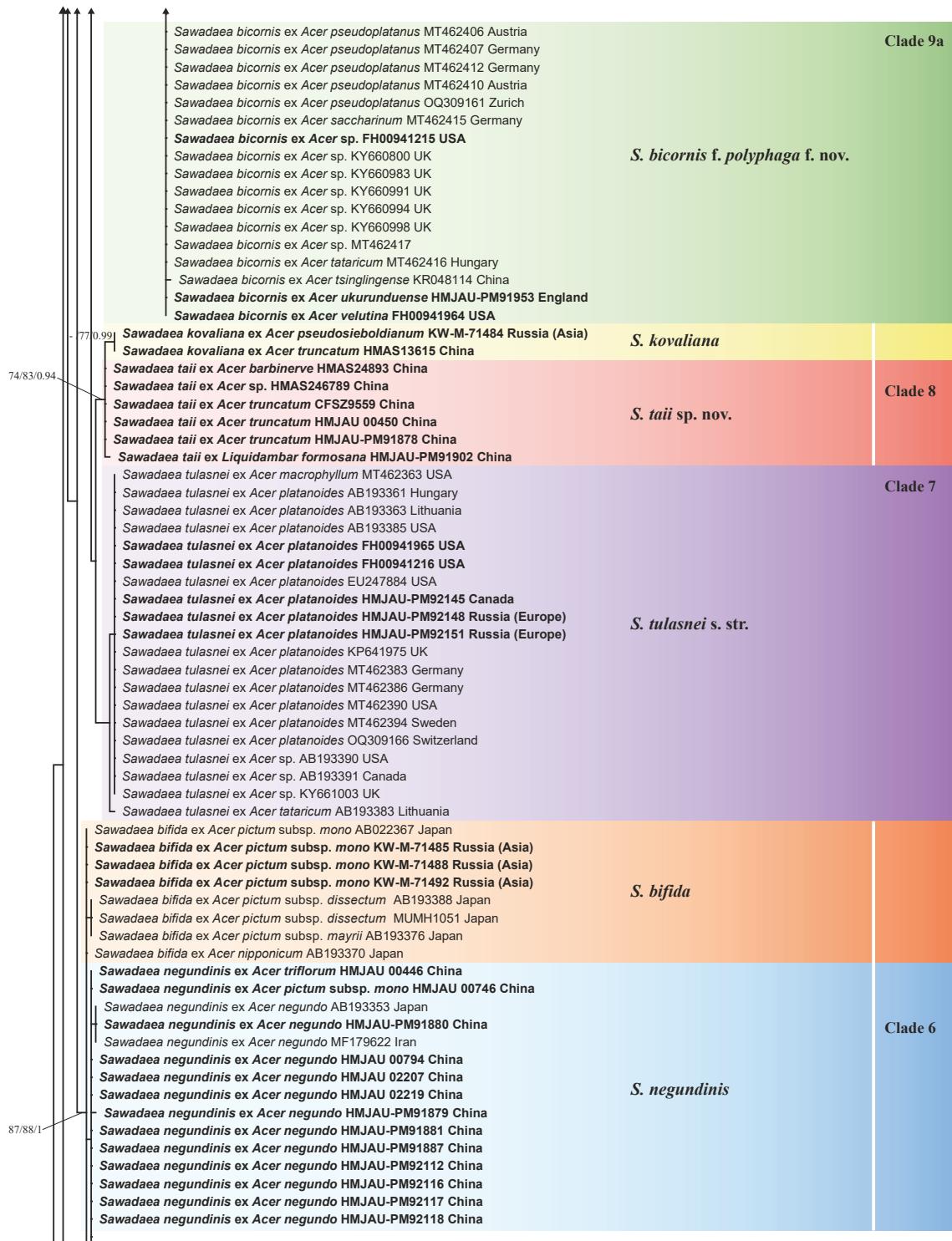


Fig. 1. (Continued)

They form two separate clades with high support in the phylogenetic tree, viz., *S. aceris-arguti* (Clade 10, MP = 100 %, ML = 100 %, BI = 1.00), and *S. acerina* (Clade 11; MP = 93 %, ML = 97 %, BI = 1.00). *Sawadaea bicornis* and *S. polyfida* had no deletion between sites 92 and 101.

Furthermore, specimens of *S. polyfida* (Clade 5) from six countries (China, Japan, Korea, Australia, USA, and Switzerland) exhibit a high degree of genetic diversity. *Sawadaea bifida* and *S. negundinis* form a non-monophyletic clade (Clade 6) including a sequence of a collection on *Acer ginnala* from Japan identified as *S. tulasnei*. Sequences of collections on *Alectryon excelsus* from

New Zealand, previously identified as *S. negundinis*, and isolates on *Acer* spp. (*A. crataegifolium*, *A. ginnala*, *A. platanoides* and *A. rufinervis*) from Japan, previously assigned to *S. tulasnei*, are nested in the *S. negundinis* clade (Clade 6), but cluster distant from the true *S. negundinis* clade as well as the *S. tulasnei* clade. *Sawadaea kovaliana* and *S. taii* form sister groups in Clade 8, which are clustered with *S. tulasnei* s. str. (Clade 7). *Sawadaea bicornis* (clade 9) is divided into two highly supported subclades that are taxonomically considered genetically established biological races, treated as *formae*, viz., *S. bicornis f. bicornis* (Clade 9b) and *S. bicornis f. polyphaga* (Clade 9a).

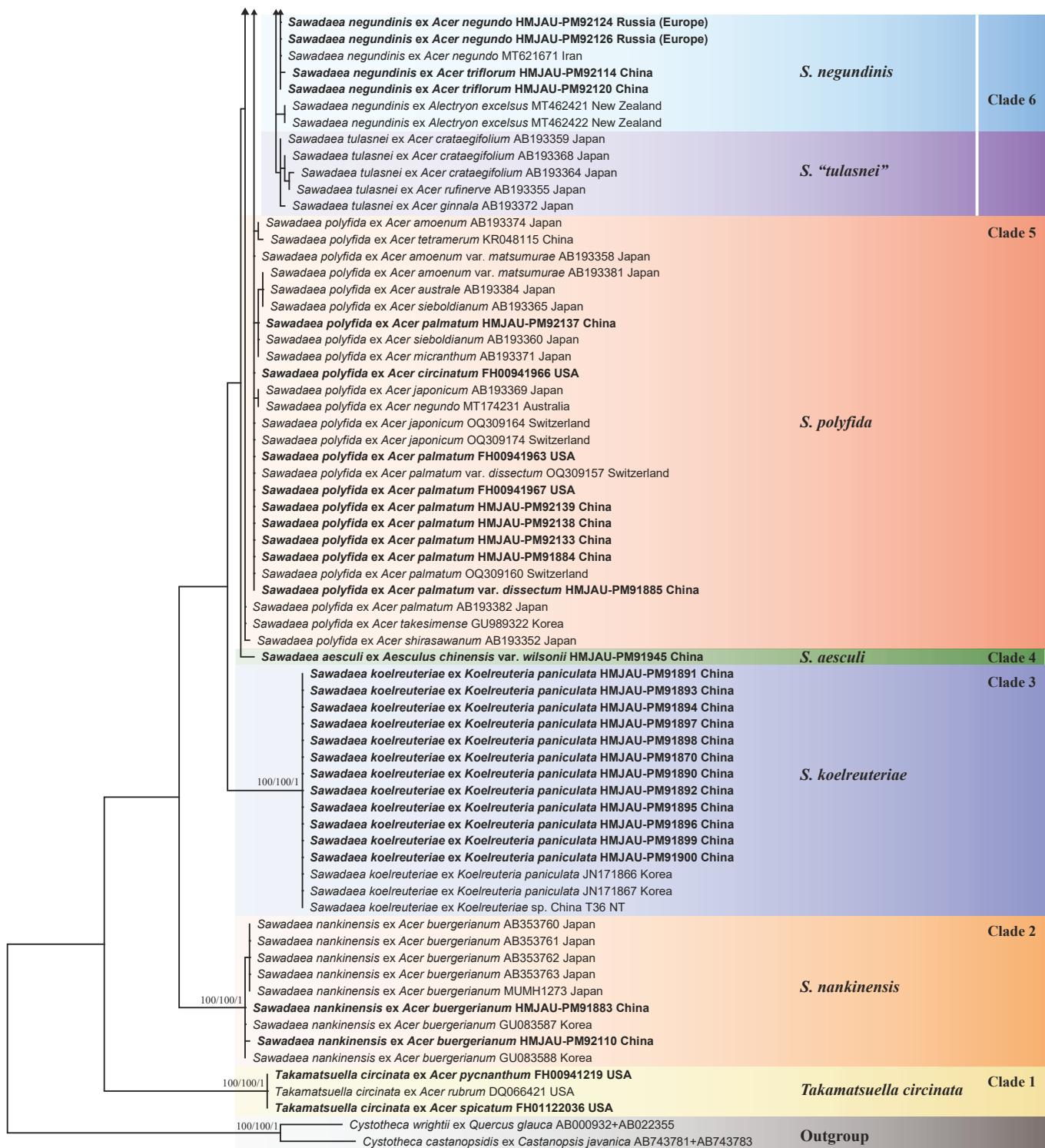


Fig. 1. (Continued)

	60	70	80	90	100
<i>Sawadaea acerina</i> (Clade 11)	TG-AT	ATATCA	GGCTGCTCTGGTGGGCCAG		CTGCCGG
<i>Sawadaea aceris-arguti</i> (Clade 10)	TG-AT	ATATCA	GGCTCCTCTGGGGGCCA		ACCTGCCGG
<i>Sawadaea kovaliana</i> (Clade 8)	TG-AT	ATATCA	GGCTGCTCTGGTGGGCC		TGCCGG
<i>Sawadaea taii</i> (Clade 8)	TG-AT	ATATCA	GGCTGCTCTGGTGGGCC		TGCCGG
<i>Sawadaea tulasnei</i> s. str. (Clade 7)	TG-AT	ATATCA	GGCTGCTCTGGCGGGCC		TGCCGG
<i>Sawadaea bifida</i> (Clade 6)	TG-AT	ATATCA	GGCTGCTCTGGCGGGCC		TGCTGG
<i>Sawadaea negundinis</i> (Clade 6)	TG-AT	ATATCA	GGCTGCTCTGGCGGGCC		TGCTGG
<i>Sawadaea aesculi</i> (Clade 4)	TG-AC	ATATCA	GGCTGCCCTGGTGGGCC		TGCCGG
<i>Sawadaea koelreuteriae</i> (Clade 3)	TG-AT	ATATATCCGGCTGCTCCGGTGGGCC			TGCCAG
<i>Sawadaea nankinensis</i> (Clade 2)	CG-ACTCATATCC		GGTTGCCCTGGCGG-CC		TGCCGG
<i>Sawadaea bicornis</i> f. <i>bicornis</i> (Clade 9b)	TG-AT	ATATCA	GGCTACTTGGCGGGCCAGGCTCGACCTACC GG		
<i>Sawadaea bicornis</i> f. <i>polyphaga</i> (Clade 9a)	TG-AT	ATTTC	GGCTACTTGGCGGGCCGGGCTCGACCTACC GG		
<i>Sawadaea polyfida</i> (Clade 5)	TG-AT	ATATCA	GGCTGCTCTGGTGGGCCAGGCTCGACCTGCCGG		
<i>Takamatsuella circinata</i> (Clade 1)	TG-A		CC		T-GGTT
<i>Cystotheca wrightii</i> (Outgroup)	TCTATCTTCTCATGTTGCTTTGGCGGGCCGGGCC		TGTGCCCTCCC GG		
<i>Cystotheca castanopsisidis</i> (Outgroup)	TCTATCTTCTCATGTTGCTTTGGCGGGCCGGGCC		TCGTGCCCTCCTGG		

Fig. 2. Insertion/deletion (indel) found between sites 60 and 107 of ITS1 regions of *Sawadaea*, *Takamatsuella* and *Cystotheca*. The insertion or deletion is related to the formation of clades in the phylogenetic tree and the presentation of phylogenetic relationships.

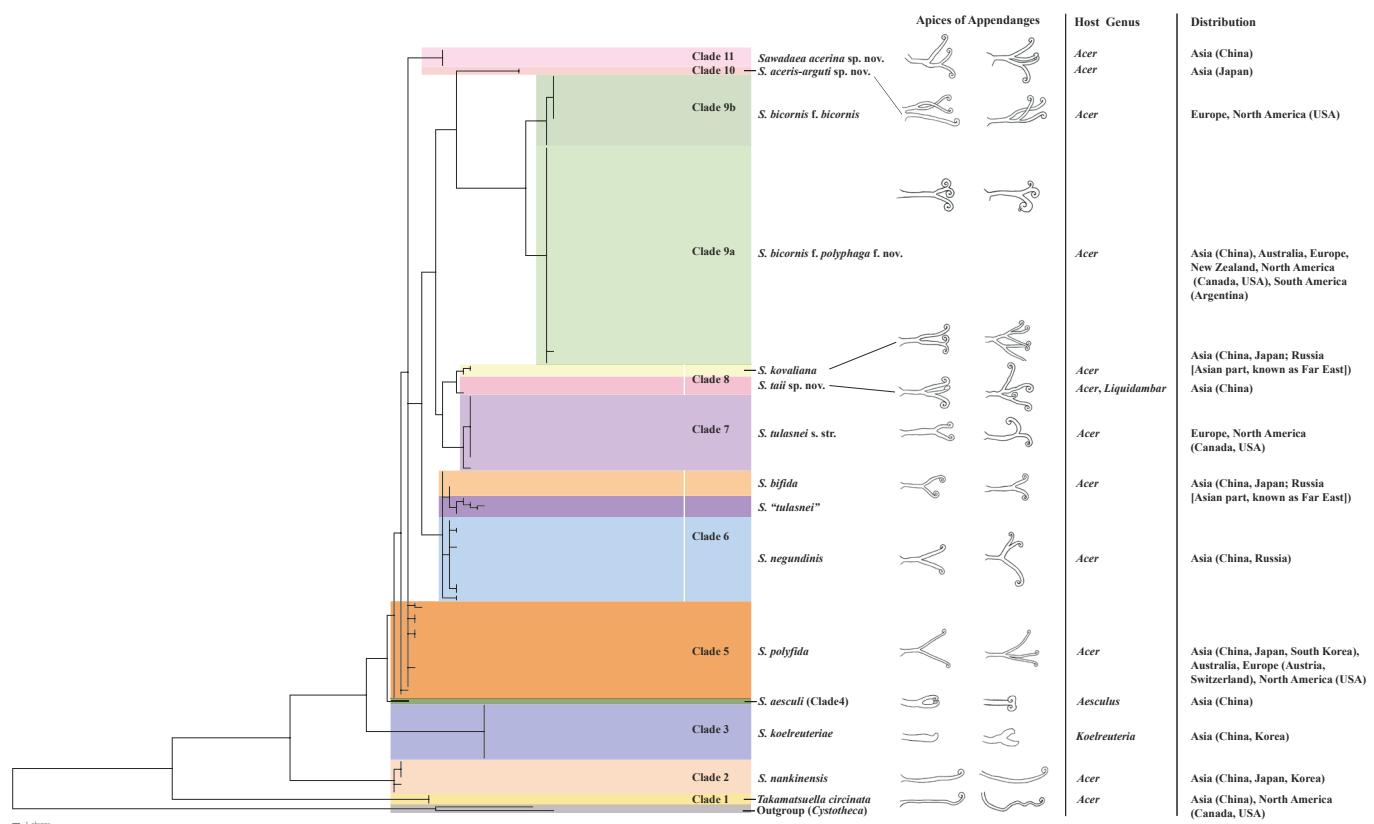


Fig. 3. Phylogenetic outline of the ITS+28S rDNA regions combining typical characteristics of appendages on chasmothecia.

Taxonomy

Twelve species of *Sawadaea* and one species of *Takamatsuella* were recognized, including three new species, namely *Sawadaea acerina* sp. nov., *Sawadaea aceris-arguti* sp. nov., and *Sawadaea taii* sp. nov. described from Asia. *Sawadaea bicornis* comprises two biological formae, *Sawadaea bicornis* f. *bicornis* and f. *polyphaga* f. nov., with different host preferences. Asexual morphs of *S. aesculi*, *S. bifida*, *S. kovaliana* and *T. circinata* have also been detected and described for the first time.

***Sawadaea* Miyake, Special Bull Agric. Exp. Stat. Formosa 9: 49. 1914.**

Synonyms: *Uncinula* sect. *Sawadaea* (Miyake) U. Braun, Feddes Repert. 88: 663. 1978.

Oidium subgen. *Octagoidium* R.T.A. Cook et al., Mycol. Res. 101: 998. 1997 [type species: *Oidium aceris* Rabenh.]

Octagoidium (R.T.A. Cook et al.) R.T.A. Cook & U. Braun, in Braun & Cook, *Taxonomic manual of the Erysiphales (powdery mildews)*: 172. 2012.

Table 1.  Fungal species^a

Fungal species ^a	Host	Specimen No. ^b	Collection locality		GenBank accession number
			ITS	28S rDNA	
<i>Sawadadea acerina</i> sp. nov.	<i>Acer tataricum</i>  <i>binnala</i>				
	<i>A. tataricum</i>  <i>binnala</i>			—	QQ866185
	<i>A. tataricum</i>  <i>binnala</i>				QQ866186
	<i>A. tataricum</i>  <i>binnala</i>			—	QQ875005
	<i>A. tataricum</i>  <i>binnala</i>			QQ866170	—
	<i>A. tataricum</i>  <i>binnala</i>			—	—
	<i>A. tataricum</i>  <i>binnala</i>				—
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	<i>A. tataricum</i> <i>binnala</i>				—
	<i>A. tataricum</i> <i>binnala</i>			<img alt="leaf icon" data-bbox="485 1745 5	

Table 1. ¶

Fungal species ^a	Host	Specimen No. ^b	Collection locality	GenBank accession number
			ITS	28S rDNA
<i>A. pictum</i> ¶ <i>mono</i>				OR166373
<i>A. pictum</i> ¶ <i>mono</i>				OR166374
<i>A. pictum</i> ¶ <i>mono</i>				—
<i>A. pictum</i> ¶ <i>mono</i>				—
<i>A. pictum</i> ¶ <i>mono</i>				—
<i>A. pictum</i> ¶ <i>mono</i>				—
<i>A. pictum</i> ¶ <i>mono</i>				—
<i>A. pictum</i> ¶ <i>mono</i>				—
<i>A. pictum</i> ¶ <i>mono</i>				—
<i>A. caudatum</i>				—
<i>Acer</i> ¶				—
<i>Koelreuteria paniculata</i>				—
<i>K. paniculata</i>				QQ866184
<i>K. paniculata</i>				QQ866179
<i>K. paniculata</i>				QQ866180
<i>K. paniculata</i>				QQ866181
<i>K. paniculata</i>				QQ866182
<i>K. paniculata</i>				QQ866187
<i>K. paniculata</i>				QQ866188
<i>K. paniculata</i>				QQ866183
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>K. paniculata</i>				—
<i>A. pseudosieboldianum</i>				QQ866167
<i>A. truncatum</i>				QQ866168
<i>A. buergerianum</i>				—
<i>A. buergerianum</i>				QQ866173
<i>S. kovaliana</i>				—
<i>S. nankinensis</i>				—

Table 1.

Table 1. 

Fungal species ^a	Host	Specimen No. ^b	Collection locality	GenBank accession number
			ITS	28S rDNA
<i>S. tali</i> sp. nov.	<i>A. palmatum</i>                          <img alt="checkmark icon" data-bbox="285 7620 300 76			

Table 1.   Fungal species^a

Fungal species ^a	Host	Specimen No. ^b	Collection locality	ITS	28S rDNA	GenBank accession number
<i>A. platanoides</i>	<i>A. platanoides</i>					
<i>A. platanoides</i>	<i>A. pycnanthum</i>					
<i>A. rubrum</i>						
<i>A. spicatum</i>						
<i>A. wilsonii</i>						
<i>Acer</i> ♀						
<i>A. platanoides</i>	<i>A. tataricum</i>					
<i>A. tataricum</i>						

Type species: *Sawadaea aceris* (DC.) Miyake (≡ *S. bicornis*) 

 *Sawadaea we* 

 *Sawadaea acerina*  sp. nov. 

Etymology *Acer*,
+ Latin adjectival suffix -ina (belonging to).

Typus: **China**,   *Abertataricum pinnala*  X. Guan
& J. Feng **holotype**  

 *Diagnosis*:  *Sawadaea polyfida*, 

Mycelium 

 *Hyphae*  thin-walled, 27.0–69.5(–83.0) × 2.5–6.5 µm; *hyphal appressoria*  *micro-conidiophores*  59.5 × 4.0–6.5 µm, arising from the mother cell centrally or towards one septum, foot-cells cylindrical, straight, 12.5–29.0 × 4.0–6.0 µm, basal septum sometimes elevated, 7.0–16.5 µm distant from

 *micro-conidia*  ovoid, 5.5–9.5(–13.5) × 5.0–7.5(–11.0) µm, length/width ratio 1.0–1.5(–2.5) (av. 1.3), with fibrosin bodies; *macro-conidiophores* 25.5–79.0 × 5.5–10.5 µm, arising from the upper surface of the mother cells, foot-cells cylindrical, straight, 13.5–36.0 × 5.5–10.5 µm, basal septum sometimes elevated, 3.5–18.5 µm distant from

 *macro-conidia* 

 *germ tubes*  doliform, fresh conidia 20.5–38.5(–54.5) × 12.5–23.0 µm, length/width ratio 1.0–4.0 (av. 1.8), with fibrosin bodies; *germ tubes* 

 *orthotubus* 

 *Fibroidium*  *Chasmothecia*  (126.5)–141.5–211.5 µm diam.; *peridium cells*  4.0–19.5 µm diam., arranged ± radially; *appendages* 

 branched, (31.5)–63.0–195.5 × 4.5–14.0 µm, 0.2–1.3 (av. 0.8) times

 *ascospores* 

 56.0–98.0 × 35.0–53.0 µm, length/width ratio 1.2–2.5 (av. 1.8), wall up to 4.7 µm, short-stalked or almost sessile, (6)–8-spored; *ascospores* ellipsoid-ovoid, 12.5–26.5 × 11.0–15.0 µm, length/width

S.R. Tang & L. Liu (HMJAU-PM91888, 28S rDNA GenBank No.: Q866186).

Host range and distribution: On *Acer (saccharinum, tataricum subsp. ginnala)*, Sapindaceae, Asia (China).

Notes: The new species can be morphologically readily distinguished from other species of *Sawadaea*: (1) from *S. koelreuteriae* and *S. nankinensis* by having branched appendages; (2) from *S. aesculi* and *S. bomiensis* by having a much larger number of chasmothelial appendages (58–142 vs < 50); (3) by having chasmothelial appendages branched in the middle or lower part (vs appendages branched in the middle or upper part of the appendages in *S. bicornis*); (4) by having larger chasmothecia (141–212 μm diam., vs 115–185 μm in *S. bifida*); (5) by having shorter macro-conidiophores (up to 79 μm vs 150 μm) and shorter foot-cells (21–31 μm vs 25–50 μm) compared with *S. negundinis*, but larger macro-conidia and micro-conidia compared with *S. negundinis* and *S. tulasnei* (macro-conidia 25–55 \times 13–21 μm vs 24–30 \times 15–19 μm and vs 16–28 \times 10–18 μm , micro-conidia 21–31 \times 13–23 μm vs 6–8 \times 5–7 μm and vs 2–11 \times 6–9 μm). The new species is morphologically similar to *S. polyfida*, but it differs in having mainly unbranched or 1–2 times branched chasmothelial appendages and it forms a separate

well-supported species clade in the molecular phylogenetic tree. In addition, we need a special explanation that there were only a few fully mature chasmothecia on the holotype specimen, due to the early collection season.

***Sawadaea aceris-arguti* S. Takam. & U. Braun, *sp. nov.* MycoBank MB 849117. Fig. 5.**

Etymology: Epithet derived from the name of the host plant, *Acer argutum*.

Typus: **Japan**, Nagano Pref., Ueda-shi, Sugadaira, Tsukuba University, Sugadaira Research Station, on *Acer argutum*, 30 Sep. 2000, S. Takamatsu [holotype TNS-F-87577, ex-holotype sequence: GenBank No. AB193367 (ITS rDNA)].

Diagnosis: Morphologically close to *Sawadaea polyfida*, but chasmothecia only with 50–100 appendages, fewer asci, 7–13, and shorter and, above all, narrower ascospores, 17–22 \times 9–11 μm (vs 100–250 appendages, 8–38 asci, 12.5–33 \times 9.5–19 μm in *S. polyfida*). Genetically different from all other species within *Sawadaea* by forming a well-supported separate species clade.

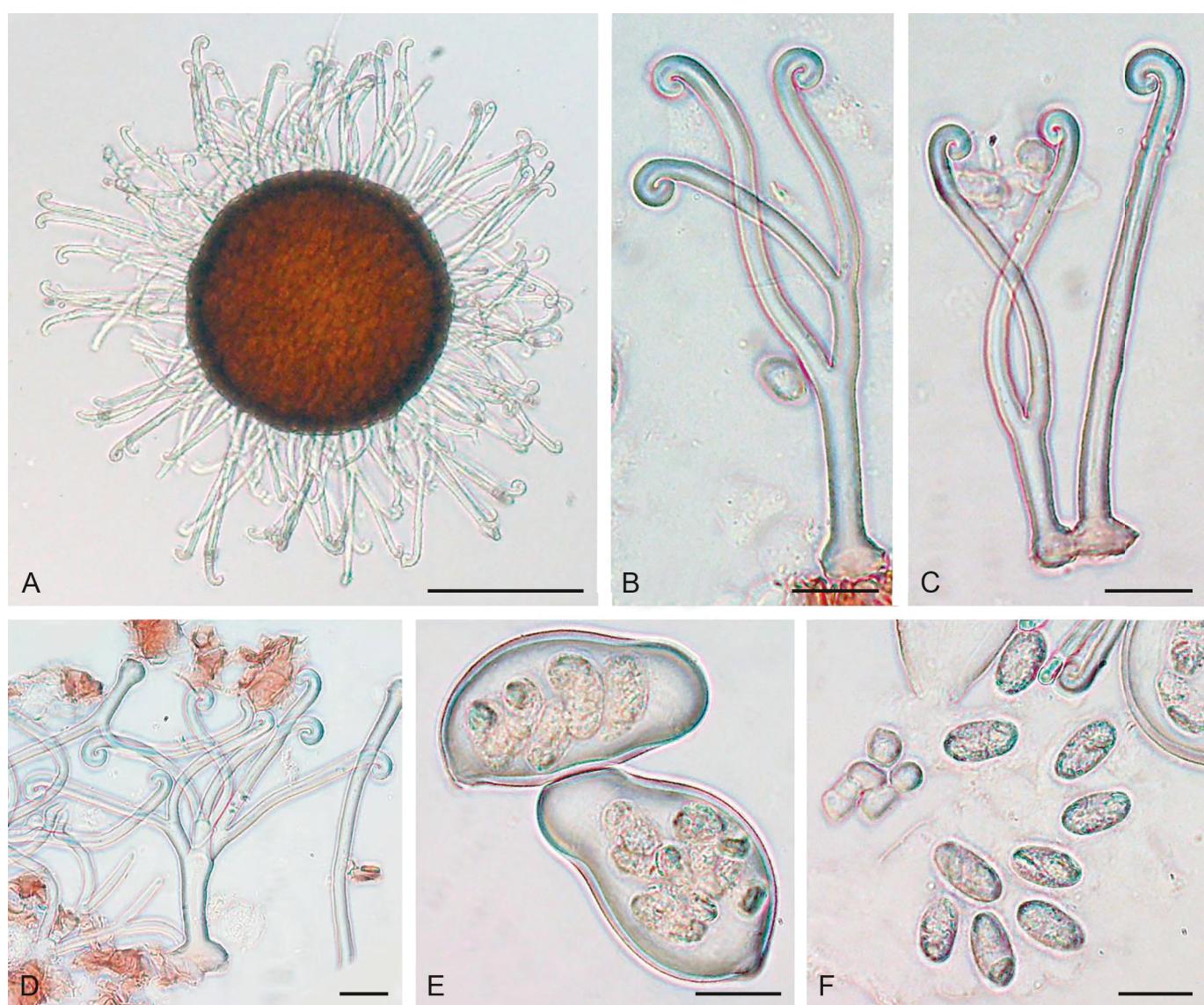


Fig. 5. *Sawadaea aceris-arguti* sp. nov. (TNS-F-87577, holotype). A. Chasmothecium. B–D. Appendages. E. Ascus. F. Ascospores. Scale bars: A = 100 μm ; B–D = 50 μm ; E, F = 20 μm .

Mycelium**hyphae**

μm wide, hyaline, septate, thin-walled, smooth. *Chasmothecia* scattered, depressed globose, (130.0–)140.0–180.0 μm diam.; *peridium cells* appendages

macro-conidiophores

macro-

conidia

apertures

macro-

conidium

apertures

macro-conidiophores

macro-conidiophores

85.5) × 4.5–8.5 μm, arising from mother cells, foot-cells cylindrical, straight, (12.0–)23.5–36.0(–56.0) × 4.5–9.0 μm, basal septum sometimes elevated, 1.5–12.5 μm from the junction with the mother

macro-

conidiophores

macro-

Micro-

conidia variable in shape, ellipsoid-ovoid, $18.0\text{--}28.0 \times 13.5\text{--}19.0 \mu\text{m}$, length/width ratio 1.0–1.7 (av. 1.5), with fibrosin bodies; macroconidiophores $52.5\text{--}88.5\text{--}112.5 \times 5.5\text{--}8.0 \mu\text{m}$, arising from mother cells, foot-cells cylindrical, straight, $18.5\text{--}54.5 \times 5.5\text{--}8.5 \mu\text{m}$, basal septum sometimes elevated, to $17.5 \mu\text{m}$ from the junction with the

macro-conidia

Chasmothecia

$4.0\text{--}65.0 \times 10.5\text{--}20.0 \mu\text{m}$, length/width ratio 1.7–4.1(–5.1) (av. 2.4), with fibrosin bodies; germ tubes terminal, short to moderately

orthotubus fibroidium

scattered to ± gregarious, $102.0\text{--}170.0 \mu\text{m}$ diam.; peridium cells irregularly polygonal, $3.0\text{--}14.0 \mu\text{m}$ diam., arranged ± radially;

appendages

bridge

foot

neck

$31.5\text{--}137.5 \times 4.5\text{--}8.5 \mu\text{m}$, 0.2–1.2 times (av. 0.8) as long as the

asci

$8\text{--}20$, ellipsoid-ovoid, saccate-clavate, $57.0\text{--}98.0\text{--}108.0 \times 40.0\text{--}65.0 \mu\text{m}$, length/width ratio 1.0–2.0 (av. 1.4), wall up to $4.6 \mu\text{m}$ thick, short-stalked or almost sessile, (6)–8-spored; ascospores ellipsoid-ovoid, $19.5\text{--}28.0 \times 11.0\text{--}21.0 \mu\text{m}$, length/width ratio 1.1–

Subspecific classification: *hirsuta*

Sawadaea bicornis *hirsuta*

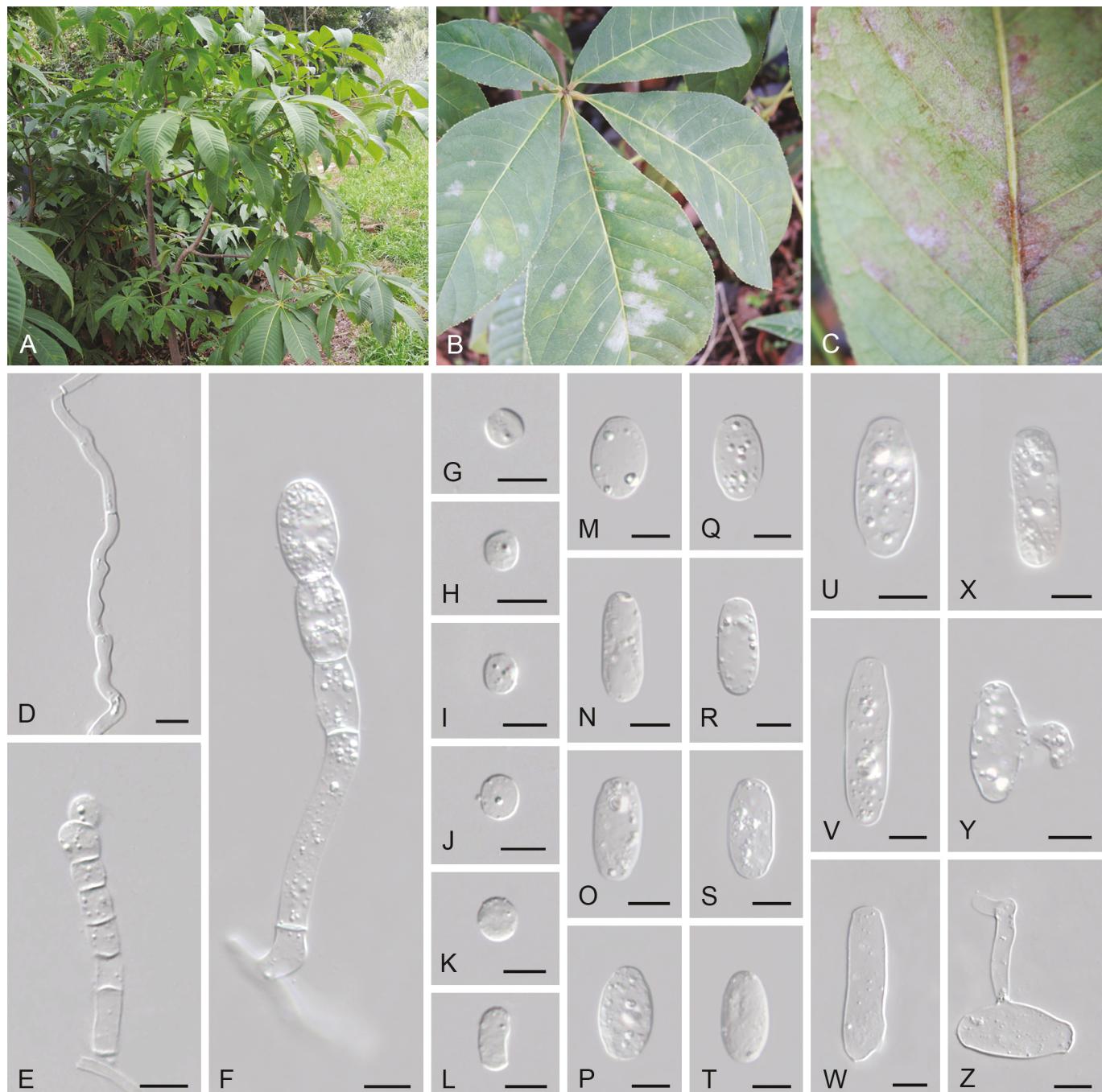


Fig. 6. *Sawadaea aesculi*
A-D. *S. aesculi*
E-F. *S. bicornis*
tubes. Scale bars = $10 \mu\text{m}$.

A. *S. aesculi*

B. *S. aesculi*

C. *S. aesculi*

D. *S. aesculi*

E. *S. aesculi*

F. *S. aesculi*

G. *S. aesculi*

H. *S. aesculi*

I. *S. aesculi*

J. *S. aesculi*

K. *S. aesculi*

L. *S. aesculi*

M. *S. aesculi*

N. *S. aesculi*

O. *S. aesculi*

P. *S. aesculi*

Q. *S. aesculi*

R. *S. aesculi*

S. *S. aesculi*

T. *S. aesculi*

U. *S. aesculi*

V. *S. aesculi*

W. *S. aesculi*

X. *S. aesculi*

Y. *S. aesculi*

Z. *S. aesculi*

M-X. *S. bicornis*

Z. *S. bicornis*

subclades that reflect two biological races with different host
genetically established and verifiable, they deserve a formal naming
formae speciales 
formae b

'ormae' is that it is an official taxonomic
~~name~~
~~name~~ *S. bicornis* *bicornis*
~~name~~ *S. bicornis* *bicornis*
subclades with specific host preferences (F)

Sawadaea bicornis f. bicornis (Acer campestre
platanoides (Acer) Platanoidea)

Additional materials examined: Russia

Acer campestre, 5
T.S. Bulgakov
OQ866171); Rostov region, Shakhty, Alexandrovsky Park, on Acer

campestre, 41 T.S. Bulgakov 
rDNA GenBank No.: OQ866172); Rostov region, Shakhty, Hospital
 *Acer campestre*, 24 Oct. 2018, T.S. Bulgakov 
PM92107, ITS+28S rDNA GenBank No.: OQ866160).

***Sawadaea bicornis* f. *polyphaga*, nov.**

Etymology

Typus: Germany

Acer pseudoplatanus, 29
holotype 29

J. Kruse

Diagnosis *Diagnosis* **bicornis** *bicornis*
Acersinella *Acersinella* **leguminosae** *leguminosae* **Palmata** *Palmata* **Platanoidea** *Platanoidea*,
Subsp. *Subsp.* **in** *in*

Additional materials examined: **Canada**, Ontario, Niagara Region, *Metasequoia* *negundo* (L.) V. Ilyukhin



Fig. 7. *Sawadaea bicornis* ■
♂ G-I.M

A, B. 
J-L.M M-O.M

C.  D. 
P, Q. Germ tubes. Scale bars = 10 μ m.

E. F. M.

contamination or host misidentifications. Future research should

Sawadaea *Acer*
et al.

A. campestre *bicornis*
A. pseudoplatanus *f. polyphaga*

Acer campestre
pseudoplatanus

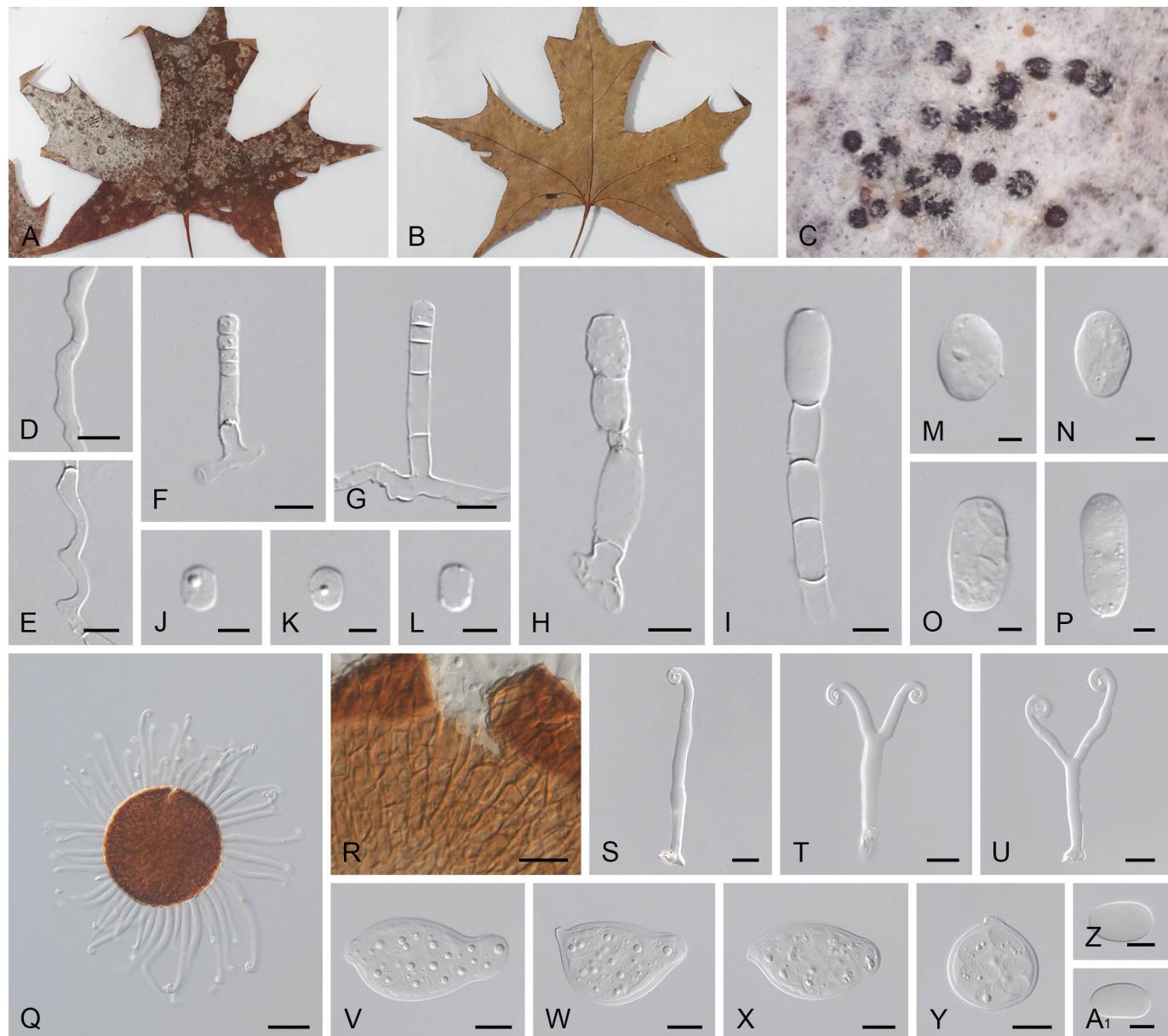


Fig. 9. *Sawadaea bifida* ■. ■
 E. G. ■
 R. ■ S-U. ■

H, I, J-L, M
V-Y A 7 A1 Ascospores. Scale bars:

B.P.

C.B

M-PBL

WESTERDIJK
FUNGALBIO
DIVERSITY

S. bicornis
Acer campestre
A. platanoides,
Erysiphaceae of Japan
holotype
Sawadaea
Trans. Mycol. Soc. Japan 2009, 50(2): 131–136
Typus: Russia
Acer pictum
mono, 1 Oct. 1989, V.P. Heluta
sequence: OR166385 (ITS+28S rDNA)].
Mycelium
branched, thin-walled, 12.0–46.5 × 2.5–6.5 µm; hyphal appressoria
micro-conidiophores
43.0 × 3.0–7.0 µm, arising from the upper surface of mother cells,
× 3.5–6.5 µm, basal septum sometimes elevated to 11.0 µm from
micro-conidia

S. bicornis
S. bicornis
negundo
A. platanoides
A. negundo
S. bicornis, and these results have been confirmed by

Sawadaea bifida Kravins'k. Bot. Zhurn. 47(1): 103, 1972
Synonyms: Sawadaea zhengii

Taxonomical study of

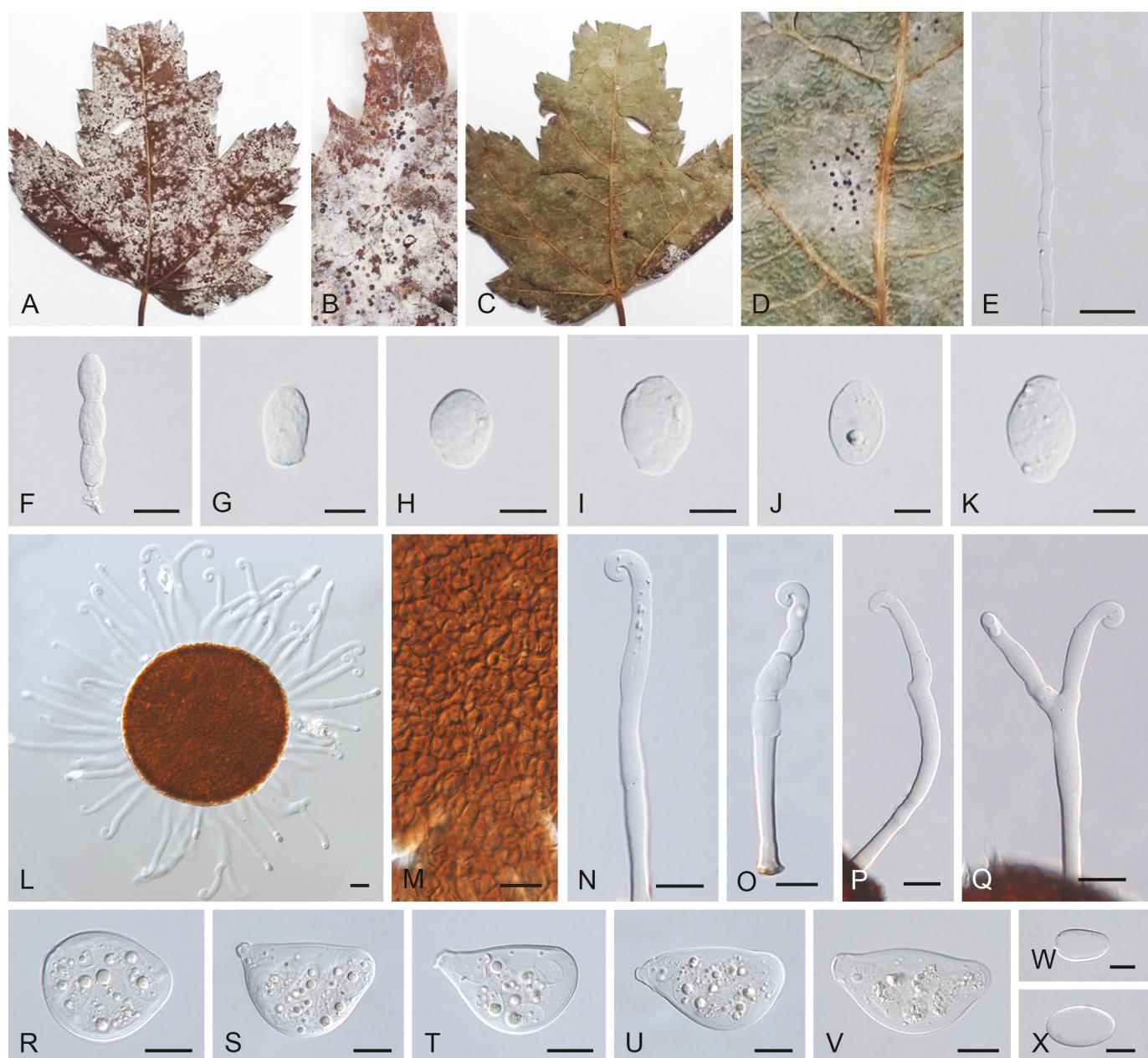


Fig. 10. *Sawadaea bomiensis*
holotype
Sawadaea
Trans. Mycol. Soc. Japan 2009, 50(2): 131–136
Typus: Russia
Acer pictum
mono, 1 Oct. 1989, V.P. Heluta
sequence: OR166385 (ITS+28S rDNA)].
Mycelium
branched, thin-walled, 12.0–46.5 × 2.5–6.5 µm; hyphal appressoria
micro-conidiophores
43.0 × 3.0–7.0 µm, arising from the upper surface of mother cells,
× 3.5–6.5 µm, basal septum sometimes elevated to 11.0 µm from
micro-conidia

R-V. W, X. Ascospores. Scale bars: E, F, L-V = 20 µm; G-K, W, X = 10 µm.

ovoid, $5.0\text{--}14.0 \times 4.5\text{--}12.5 \mu\text{m}$, length/width ratio 1.0–1.6; *macroconidiophores* $27.0\text{--}52.5 \times 7.5\text{--}10.5 \mu\text{m}$, arising from the upper surface of mother cells, foot-cells cylindrical, straight, $18.5\text{--}34.5 \times 4.0\text{--}6.5 \mu\text{m}$, followed by 1–3 shorter cells and catenescient conidia; *macro-conidia* 

17.0–29.0 × 9.5–18.5 μm , length/width ratio 1.2–1.9. *Chasmothecia*

μm diam.; *peridium cells* 
oblong, 4.5–23.0 μm diam.; *appendages*

nodulose, deeply cleft, first branching point in the lower half, often
chasmothecial diam., 34.0–187.5 × 7.0–11.5 µm, about 0.2–1.2

47.0–96.5 × 33.5–57.5 μm , length/width ratio 1.0–2.4, wall relatively thick, up to 4.5 μm , almost sessile to short-stalked, (6–)8-spored; ascospores ellipsoid, 18.5–30.0 × 10.5–15.0 μm , length/width ratio

Additional materials examined: China, ~~EX~~

Platycerium pictum (L.) C. Chr. mono, 5 Oct. 1975, Y.N. Yu & S.J. Han

Acacia pictum

mono, F.Z.

¶ *acer pictum*

Y.J. Lu

Sacer pictum

H. Huan

Acer

Fig. 11. *Sawadaea koelreuteriae* B. 
 ♀ F, G. H-J.
 D-G, O-T = 10 μ m; K-N = 5 μ m.

K-N.M

C. 
O-R.M

D, E, H
S, T. Germ tubes. Scale bars: H–J = 20 μm ;

Typus: *China Koelreuteria*S.X. Wei & L. Guo **Homotype**

Mycelium

hyphae
sinuous, 5.0–6.0 μm wide; *hyphal appressoria*
micro-conidiophores
44.0–76.0 \times 7.5–9.0 μm , foot-cells 19.5–49.5 \times 6.0–8.5 μm ; *micro-conidia* broad ellipsoid-ovoid, 18.5–28.5 \times 13.0–18.0 μm , length/
macro-conidiophores 83.0–139.5 \times 7.5–11.0
 μm , arising from the mother cell, centrally or towards one septum,
foot-cells cylindrical, straight, 43.5–97.5 \times 7.0–9.0 μm , followed
macro-conidia
limoniform, fresh conidia 34.5–49.5 \times 10.0–16.0 μm , length/width
ratio 2.5–4.1, with fibrosin bodies; *germ tubes*

Anthotubus fibroidium

Chasmothecia scattered, 135.5–209.0 μm diam.; *peridium cells*
irregularly polygonal, 8.0–18.5 μm diam.; *appendages*
to seldom forked, often curved, 26.0–54.5 μm , 0.1–0.3 times as
long as the ascus; *asci*
clavate-saccate, 56.0–89.5 \times 31.0–53.0 μm , sessile or short-
ascospores
16.5–23.0 \times 13.0–16.5 μm , length/width ratio 1.2–1.4, colourless.

Additional materials examined: *China**Koelreuteria paniculata*, Feng, L. Liu &
R.J. Jiang*Koelreuteria paniculata*, 21 Oct. 2018, S.R. Tang & L. Liu
(HMJAU-PM91891, ITS rDNA GenBank No.: OQ866179); Hubei*Koelreuteria paniculata*

S.R. Tang & L. Liu

*Koelreuteria**paniculata*, S.R. Tang & L. LiuITS rDNA GenBank No.: OQ866180; HMJAU-PM91897, ITS rDNA
GenBank No.: OQ866182, 28S rDNA GenBank No.: OQ866187;*Koelreuteria**Koelreuteria paniculata*

Oct. 2018, S.R. Tang & L. Liu

*Koelreuteria**Koelreuteria paniculata*

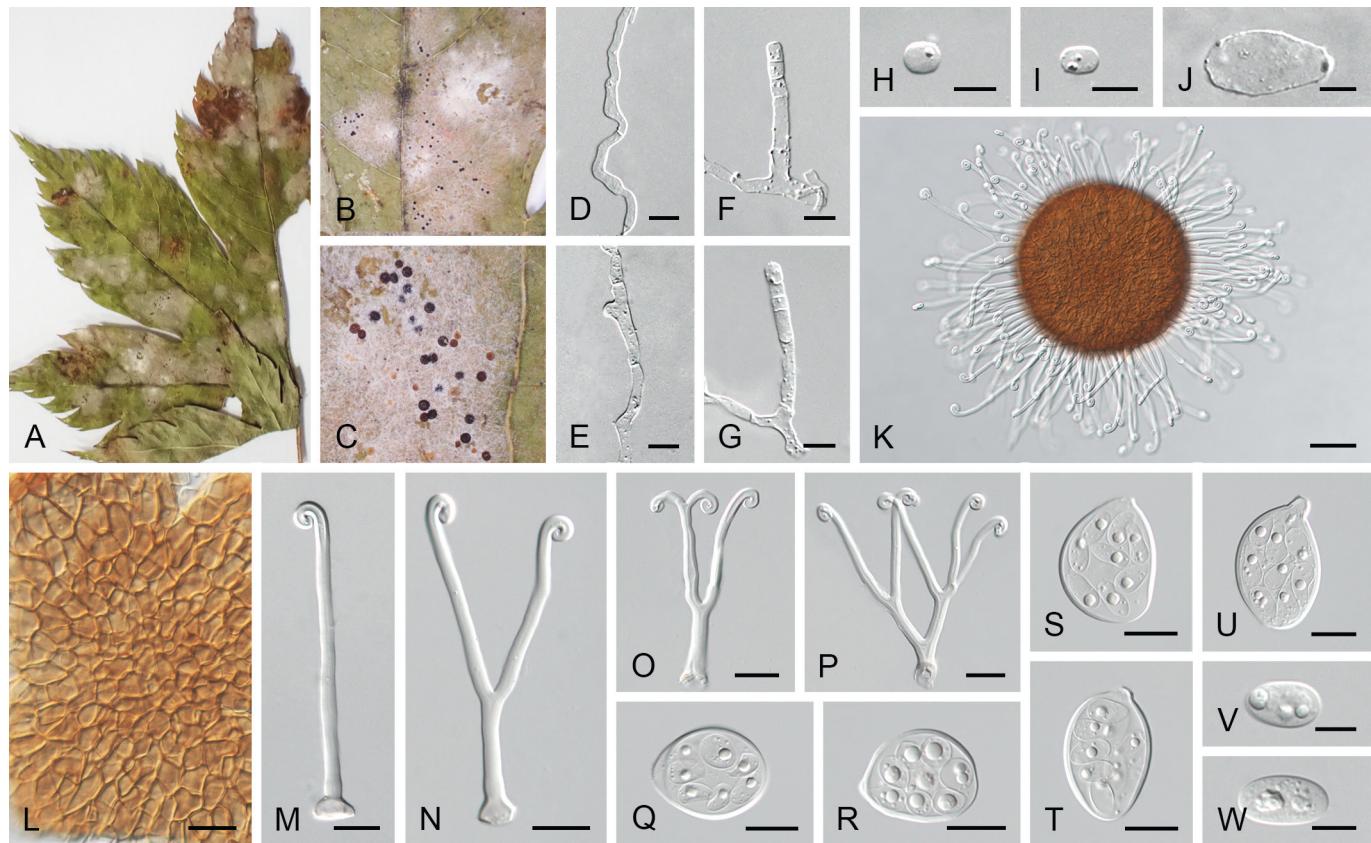
J. Feng

Koelreuteria paniculata, S.R. Tang & L. Liu*Koelreuteria**Koelreuteria paniculata*, S.R. Tang & L. Liu

S.R. Tang & L. Liu

*Koelreuteria**Koelreuteria paniculata*, S.R. Tang & L. Liu28S rDNA GenBank No.: OQ866184; HMJAU-PM91898, ITS rDNA
GenBank No.: OQ866183, 28S rDNA GenBank No.: OQ866188;*Koelreuteria paniculata*

S.R. Tang & L. Liu

Fig. 13. *Sawadaea kovaliana*

M-P, Q-U, V, W. Ascospores. Scale bars: K = 50 μm ; L–U = 20 μm ; D–J, V, W = 10 μm .

Koelreuteria paniculata R. Tang & L. Liu
PM91894, ITS rDNA GenBank No.: OQ866181); Sichuan Province,
Koelreuteria paniculata R. Tang
& L. Liu

Host range and distribution: On *Koelreuteria bipinnata*, *paniculata*,
Koelreuteria (Sapindaceae).

Notes: This species was first reported by Miyake (1913) and described
a *Uncinula koelreuteriae*

b *Phyllactinia*

Erysiphe *E. koelreuteriae*

Typhulochaeta

T. koelreuteriae

Uncinula

Typhulochaeta

Erysiphe

6 *Sawadaea*

Sawadaea which was confirmed by molecular analyses. Liu et al.

S. koelreuteriae

sequences were obtained to confirm that this powdery mildew in
Koelreuteria belongs to the genus *Sawadaea*.

Sawadaea kovaliana *Ukrayins'k. Bot. Zhurn.* 47: 13

Typus: Russia

Arpseudosieboldianum

2 Oct. 1989, V.P. Heluta **holotype**

sequence: GenBank No. OQ866167 (ITS+28S rDNA)].

Mycelium epiphyllous, forming distinct patches, confluent; *hyphae* 3.0–7.5(–9.5) μm ; *hyphal appressoria* 36.0–54.5 \times 4.5–7.0 μm , foot-cells straight, cylindrical, 14.0–27.5 \times 4.0–6.0 μm , basal septum sometimes elevated, up to 10.5 μm from the junction; *micro-conidia* ellipsoid-ovoid, 7.5–10.5 \times 5.0–8.5 μm , length/width ratio 1.1–1.9; *macro-conidiophores* *macro-conidia* ellipsoid, 26.0–36.0 \times 15.0–18.5 μm , length/width ratio 1.5–2.0. *Chasmothecia* gregarious, semiglobose, 146.0–218.0 μm diam.; *peridium cells* small, irregularly polygonal, about 4.0–27.5 μm diam.; *appendages* (45.0–)98.5–135.5(–171.5) \times 3.5–10.5 μm , 0.2–1.0 times as long

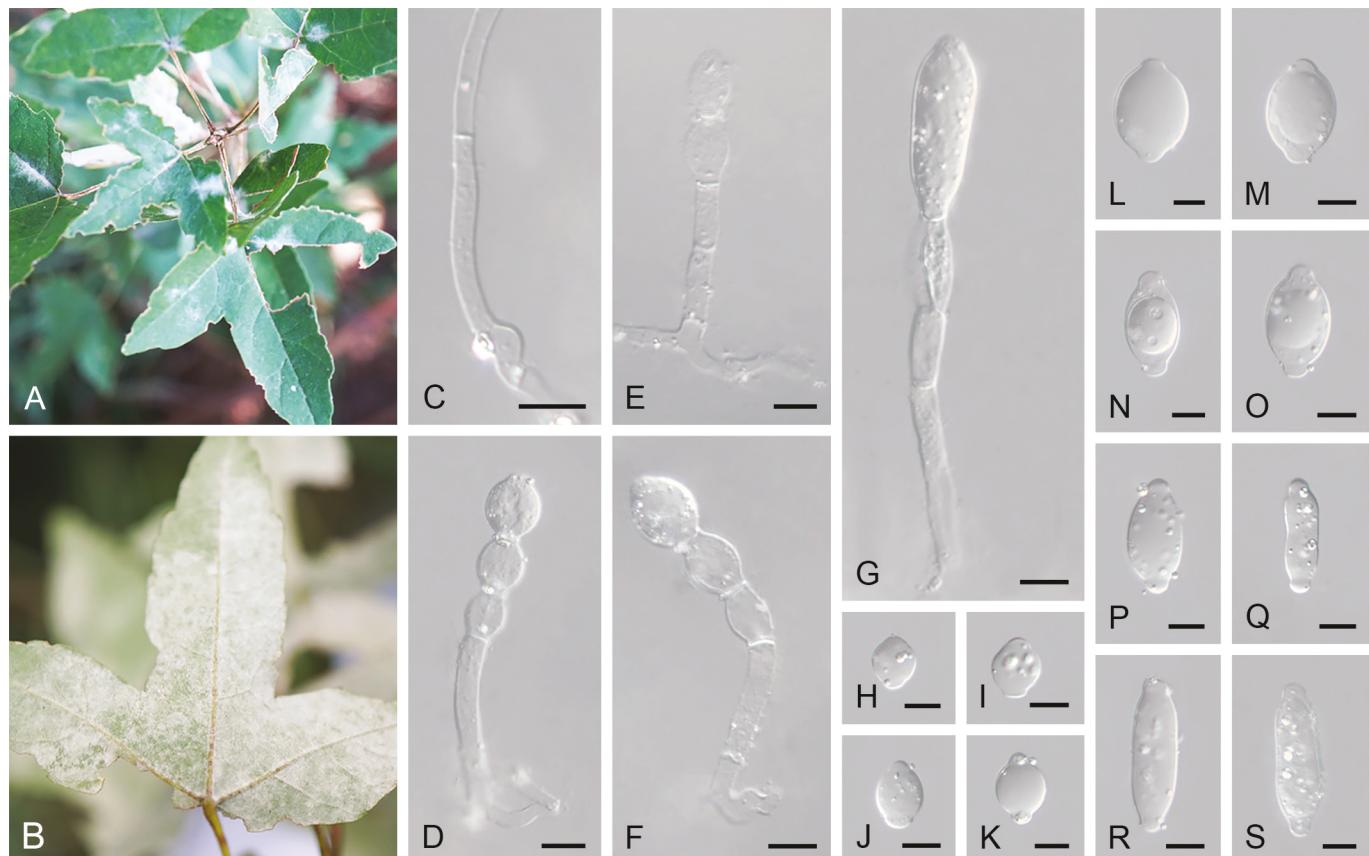


Fig. 14. *Sawadaea nankinensis*

D–F. *Macroconidia*

G–I

A. *Macroconidia*

H–K. *Chasmothecia*

B. *Macroconidia*

C. *Macroconidia*. L–S. *Macroconidia*. Scale bars = 10 μm .

hasci 2b

about $42.0\text{--}83 \times 30.0\text{--}48.5 \mu\text{m}$, length/width ratio 1.3–2.2, short-stalked, $5.0\text{--}13.5 \times 6.5\text{--}11.5 \mu\text{m}$, wall up to $3.5 \mu\text{m}$ thick, 8-spored; ascospores 11.5–24.0 \times 8.0–14.0 μm , length/width ratio (1.0–)1.7–2.5(–2.9), b

Additional material examined: China

■ *Acer truncatum* Y. Zhao

GenBank No.: OQ866168).

Host range and distribution: On *Acer pseudosieboldianum*, *truncatum* Sapindaceae

■

Notes: ■■■■■

■ *Sawadaea kovaliana* ■■■■■

■ *Sawadaea kovaliana* ■■■■■

■■■■■ *Sawadaea*

■■■■■ *S. kovaliana*

■■■■■ *Acer sieboldianum*

■■■■■ *S. kovaliana* , *Acer Palmata*

■■■■■ *Acer* ■■■■■

■■■■■ *Platanoidea*

■■■■■ *A. kovaliana*

■■■■■

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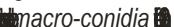
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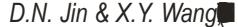
■■■■■

micro-conidiophores 27.0–59.5 × 5.0–6.5 μm , foot-cells straight, cylindrical, basal septum sometimes elevated, up to 19.5 μm from  almost globose, 12.0–21.0 × 10.0–20.0 μm , length/width ratio  90.0–140.0 × 7.0–10.0 μm , followed  47.0 × 11.0–18.5 μm , length/width ratio 1.3–3.9. *Chasmothecia* hypophyllous, scattered to ± gregarious, large, 233.5–319.5 μm diam. (av. 285.5 μm), globose-lenticular, basal part becoming finally concave; *peridium cells* 17.0(–23.5) μm diam.; *appendages* 

145.0–286.0 × 5.0–12.5 μm , appendages about 0.5–1.0(–1.2)   100.0(–116.0) × 31.0–52.0 μm , length/width ratio 1.7–3.2 (av. 2.3), mostly short-stalked, stalk about 7.5–17.5(–24.5) × 6.5–10.5(–12.0) μm , rarely sessile, (2–)5–8-spored; *ascospores*  ovoid, 18.0–27.0 × 11.0–15.5 μm , length/width ratio 1.2–2.0(–2.4) 

Additional materials examined: China, 

Acer buergerianum, 21 Oct. 2019, D.N. Jin & X.Y. Wang

Acer buergerianum, 24 Oct. 

Q0866173); Jiangsu Province, Nanjing City, on *Acer buergerianum*, 29 Oct. 1954, R.Y. Zheng 

Acer buergerianum, D.L. Liu 

Host range and distribution: On *Acer buergerianum*, Sapindaceae, 

Notes: This species was firstly reported as *Uncinula nankinensis* 

 *Sawadaea*,  not mentioned. Only the macro-conidia were described, with germ       *E. nankinensis*   sequences for the first time. Phylogenetic trees were constructed    *nankinensis*. Moreover, Zheng & Yu (1987) did not find any conidia     in size than previously reported, viz., 233.5–319.5 μm . Zheng  et al. 



Sawadaea negundinis  38

Synonyms: *Uncinula negundinis* 

Fungus diseases on cultivated plants of Jilin Province 

Sawadaea bicornis 

Typus: Japan, *Acer negundo*, 21 Oct. 1922, 

Mycelium 



3.5–5.0 μm wide; *hyphal appressoria* 

micro-conidiophores 22.5–48.5 × 4.5–7.5 μm , foot-cells 17.0–32.5 × 4.5–7.5 μm , followed by 1–3 shorter cells, basal septum elevated, 4.5–11.0 μm from the junction with the mother   ellipsoid-ovoid, 7.0–12.5(–17.5) × 5.0–10.0(–13.0) μm , length/width ratio 1.1–2.0, with fibrosin bodies; *macro-conidiophores* 30.5–86.0 × 6.0–10.5 μm , arising from the middle or 

× 6.0–10.5 μm , followed by 1–3(–4) shorter cells and catenescent 

18.5–31.0 × 11.0–23.5 μm , length/width ratio 1.1–1.8(–2.9), with  

long, about 10.0–67.5 × 2.5–6.0 μm , *orthotubus* 

Fibroidium 

247.5 μm diam.; *peridium cells* 

5.0–21.0 μm diam.; *appendages* 

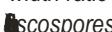


deeply cleft, first branching point near the middle of the stalk, 

60.5–114.5 × 4.0–13.0 μm , appendages about 0.4–1 times as long 



ovoid, subglobose or irregular, 66.0–82.0 × 30.5–33.0 μm , length/width ratio 2.1–2.6, sessile or short-stalked, 5.5–12.5 × 4.5–9.0 μm



almost globose, subcylindrical or irregular, 18.0–20.5 × 10.5–13.5 μm , length/width ratio 1.3–1.8, colourless.

Additional materials examined: China, 

Acer negundo, Y. Liu & F.Y. Zhao 

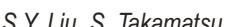
(HMJAU 02219, ITS rDNA GenBank No.: OR711904, 28S rDNA 

Acer negundo, Liu 

Acer negundo, Y. Zhao, J.N. Li & J.S. Lu 

Acer negundo, Y. Zhao, V.N. Nguyen, J.N. Li & J.S. Lu 

Acer negundo, G.X. Guan & L. Zhao 

Acer triflorum, L.L. Yang 

S.Y. Liu, S. Takamatsu,

OR708548, 28S rDNA GenBank No.: MT462443); Jilin Province, *Acer pictum*  *mono*, 24 Oct. 2010, W.T. Jiang (HMJAU 00746, ITS rDNA GenBank No.: OR711903, 28S ); *Acer negundo*, S.Y. Liu & G.X. Guan ; *Acer negundo*, G.X. Guan ; *Acer negundo*, G.X. Guan & J. Feng ; Q866174); Jilin Province, Changchun City, on *Acer negundo*, G.X. Guan & J. Feng ; rDNA GenBank No.: Q866162); Jilin Province, Changchun City, *Acer negundo*, G.X. Guan & J. Feng ; PM92117, ITS rDNA GenBank No.: Q866175); Jilin Province, *Acer negundo*, G.X. Guan & J. Feng (HMJAU-PM92118, ITS rDNA GenBank No.: Q866176); *Acer triflorum*, G.X. Guan & J. Feng ; Q866177); Jilin Province, Gongzhuling City, on *Acer negundo*, P.K. Qiu *Acer triflorum*, 4 Oct. ; S.Y. Liu, S. Takamatsu, P.L. Qiu & J. Feng 

ITS+28S rDNA GenBank No.: Q866161); Jilin Province, Yanbian *Acer negundo*, 13 Oct. 2011, W.T. Jiang ; ITS rDNA GenBank No.: OR708549, 28S rDNA GenBank No.:  Russia ; *Acer negundo*, 28 Oct. 2018, T.S. Bulgakov ; HMJAU-PM92126, ITS+28S rDNA GenBank No.: Q866163).

Host range and distribution: On *Acer negundo*, *pictum*  *mono*  *triflorum*  *Sapindaceae* 

Notes:  *Sawadaea*  *Acer negundo*

 *Sawadaea bicornis*, *S. negundinis*,  *S. tulasnei*, *Acer negundo*   *S. bicornis*, *Acer negundinis*   *S. bicornis*,  *Sawadaea negundinis*              *Acer negundo*                                                                                             

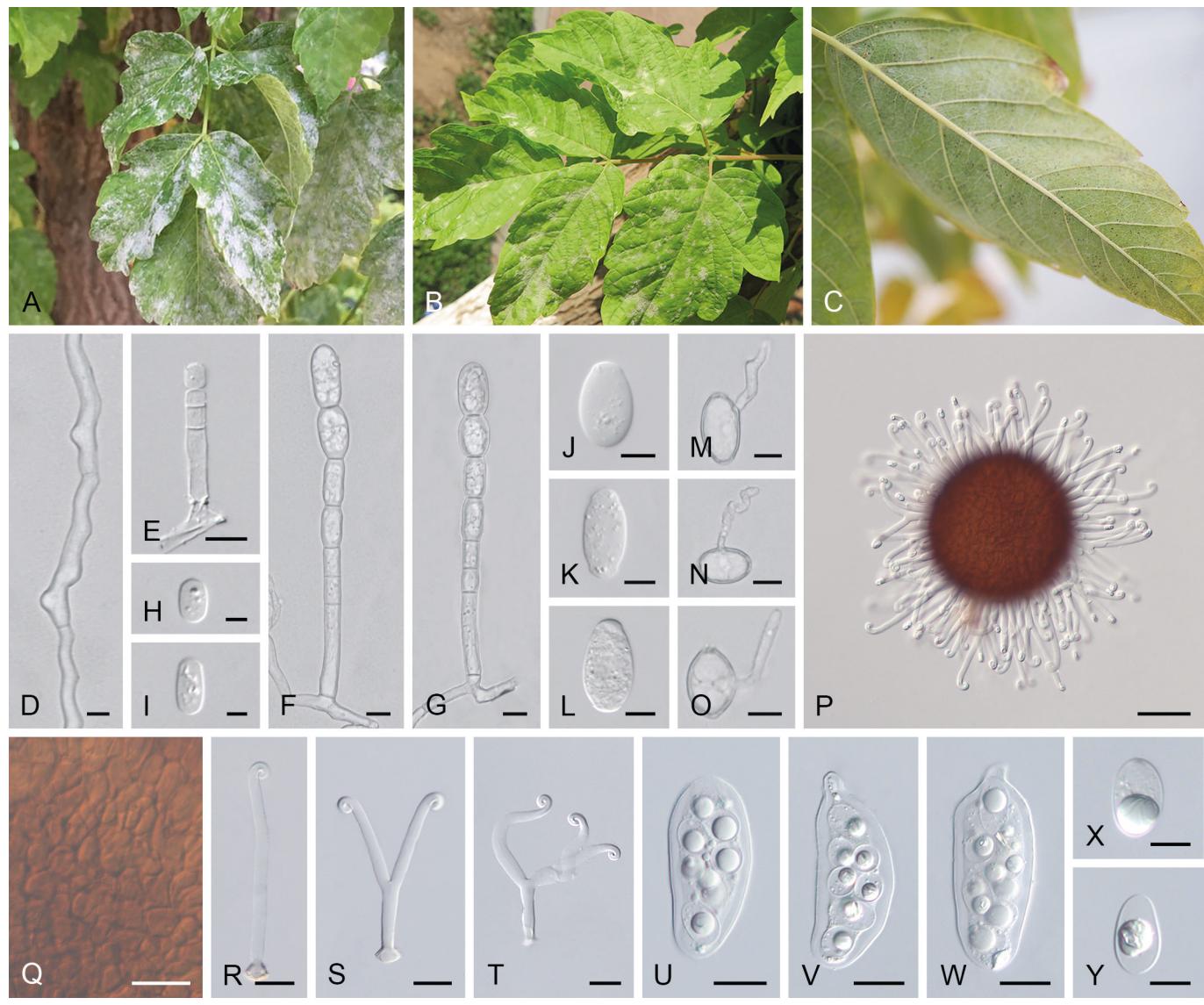


Fig. 16. *Sawadaea negundinis* 

D, E, G, H

R-T

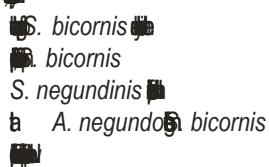
U-W

X, Y

Ascospores. Scale bars: P = 50 μ m; F, G, Q-W = 20 μ m; D, E, J-O, X, Y = 10 μ m; H, I = 5 μ m.

et al.

found significant differences between chasmothelial appendages of *S. negundinis* and *S. bicornis*. *S. negundinis*



S. bicornis
S. negundinis
A. negundinis
A. bicornis

Sawadaea polyfida 

Microbiol. Sin. 2011

Basionym *Uncinula polyfida* Wankling J.

Synonym: *Sawadaea polyfida* 

Mycotaxon 2011

polyphaga in

Typus: China

***Cercamplum catalpifolium* (≡ *A. catalpifolium*)**



Mycelium

hyphae
straight to sinuous, septate, branched, thin-walled, 3.0–5.0 μm , 

mycelial appressoria

micro-
conidiophores 26.0–39.0 \times 5.0–7.5 μm , arising from the upper 

 **micro-conidia**
x 5.0–7.0 μm , basal septum sometimes elevated, followed by 1–2 

shape, ellipsoid-ovoid, 7.5–9.5 \times 6.0–9.0 μm , length/width ratio 1.1–1.3, (av. 1.2), with fibroin bodies; **macro-conidiophores** 

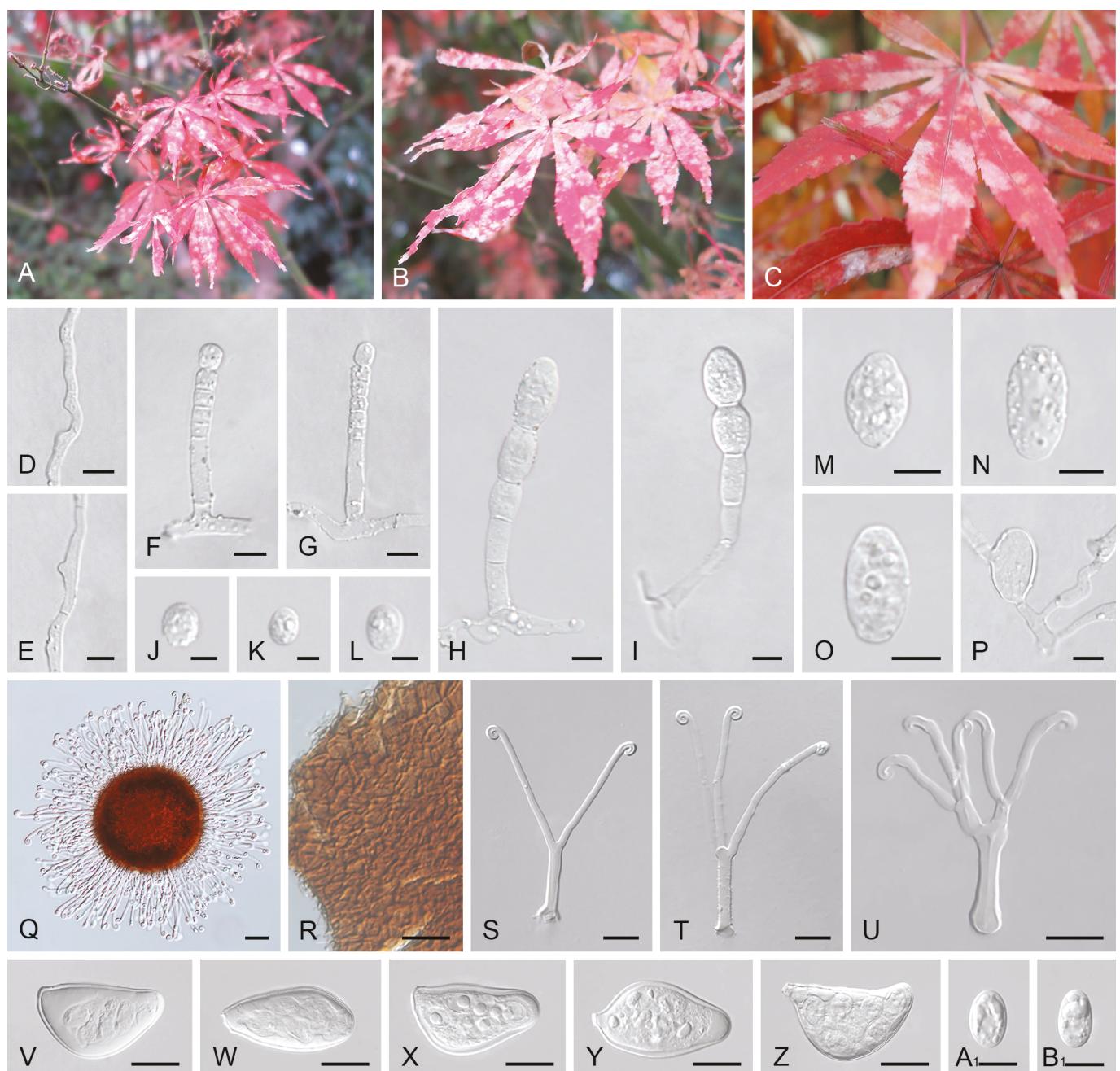


Fig. 17. *Sawadaea polyfida* 

D, E

F, G

R, S-U

H, I

J-L

M-O

P

= 5 μm .

V-Z

A1

B1

× 5.5–9.0 μm , arising from the mother cell, foot-cells cylindrical, straight, 16.0–30.5 × 5.0–8.5 μm , followed by 1–2 shorter cells and macroconidia

× 11.5–15.5 μm , length/width ratio 1.5–2.0 (av. 1.7), with fibrosin germ tubes

orthotubus *fibroidium* Chasmothecia scattered to ± gregarious, 129.5–276.5 μm diam.; peridium cells irregularly polygonal, 4.0–24.5 μm diam., arranged ± radially; appendage

apex, apices uncinate to circinate, 28.0–162.5 × 3.5–8.5(–12.5) μm , 0.2–0.9 times as long as the chasmothelial diam., thick

asci 8–38, ellipsoid-obovoid, saccate-clavate, (41.0–)70.0–110.0 × (20.0–)46.5–61.5 μm , length/width ratio 1.1–2.3 (av. 1.8), wall thick, 1.8–4.0 μm , almost sessile or with a stalk, 8.5–36.0 × 9.0–17.0 μm , ascospores ellipsoid-ovoid, 12.5–33.0 × 9.5–19.0 μm , length/width ratio 1.1–2.2 (av. 1.7), colourless.

Additional materials examined: China

Acer palmatum, S.R. Tang & L.

Liu

Acer palmatum

dissectum, S.R. Tang & L. Liu

Acer palmatum, Y.

Zhang & D.N. Jin

Acer palmatum

S.R. Tang & L. Liu

Acer palmatum, 6

Z. Y. Zhang & D.N. Jin

Acer palmatum

Z. Y. Zhang & D.N. Jin

No.: OR863613); Jilin Province, Wangqing, on *Acer*

Y.C. Yang et al.

Acer palmatum

Oct. 2020, Z. Y. Zhang & D.N. Jin

GenBank No.: OR701408); Jiangsu Province, Suzhou City, Qiantang

Acer palmatum, 9 Oct. 2020, Z. Y. Zhang & D.N. Jin (HMJAU-PM92138, ITS+28S rDNA GenBank No.: OR701409);

Acer palmatum, 7

Z. Y. Zhang & X.Y. Wang

Acer palmatum, S.R. Tang

& L. Liu

Acer amplum *catalpifolium*, F.

Tao (HMAS13624, 28S rDNA GenBank No.: OQ874975); Yunnan

Acer palmatum, Y. Zhang & D.N. Jin

palmatum, 13 Oct. 2020, Z. Y. Zhang & D.N. Jin

ITS+28S rDNA GenBank No.: OR701411). USA, *Acer*

palmatum, M. Bradshaw

rDNA GenBank No.: OR166384); Boston, on *Acer palmatum*, 2

M. Bradshaw

OR166379); Boston, on *Acer circinatum*, M. Bradshaw

(FH00941966, ITS rDNA GenBank No.: OR166376).

Host range and distribution: On *Acer* *plum* *catalpifolium* [= *catalpifolium*] *japonicum*, *micranthum*, *negundo*, *palmatum* *palmatum*, *palmatum* *samoenum* [= *amoenum*] *palmatum* *matsumurae* [= *amoenum* *matsumurae*] *pseudosieboldianum* [= *takesimense*] *shirasawanum*, *sieboldianum*, *stachyophyllum* [= *tetramerum*] *tschonoskii* *australe* [= *australe*] *tenuifolium*) *Sapindaceae*.

Notes: *Uncinula polyfida*

Acer amplum *catalpifolium* *Acer*

A. palmatum *palmatum* *matsumurae*

japonica *A. palmatum* *matsumurae* (= *A. palmatum* *matsumurae*) (100–)150–200 μm diam. However, owing to the strong variability of *S. polyfida*

the Chinese type and Japanese collections is difficult. Hence, Braun *S. polyfida*

Sawadaea polyfida

S. polyfida

Acer *Palmata* *A. circinatum*

A. palmatum *pseudosieboldianum*

shirasawanum, *A. sieboldianum*, *A. tenuifolium*

Acer *Palmata* *S. polyfida*

A. circinata

A. circinata *Palmata*

Asia. On the other hand, there are some sequences retrieved from *S. polyfida* o *Ace*

A. amplum *catalpifolium* (Platanoidea) *A. micranthum*

A. tschonoskii *australe* (*micrantha*) *A. negundo*

Negundo *stachyophyllum* (Arguta) *Sawadaea polyfida*

A. pseudosieboldianum [= *A. takesimense*]

et al. *et al.*

introduction of this species in Europe (Switzerland). Other records

S. polyfida

A. amplum *catalpifolium*

S. polyfida *et al.*

would be useful for a further clarification of the phylogeny and

platanoides

polyfida

are not enough for further attempts. So we tentatively identified it as *S. polyfida*. Further study is needed to confirm if *S. polyfida* o *A. platanoides*.

Sawadaea tali sp. nov.

Etymology:

Typus: China, *Yunnan*

Acer truncatum, S. Liu, S. Takamatsu,

G.X. Guan & L. Zhao *holotype* *sotype*

Diagnosis *S. bomiensis*

Mycelium septate, branched, thin-walled, $17.0\text{--}34.5 \times 1.5\text{--}6.5 \mu\text{m}$; **hyphal appressoria** **micro-conidiophores** $34.0\text{--}43.0 \times 4.0\text{--}5.5 \mu\text{m}$, a septum, foot-cells cylindrical, straight, $15.5\text{--}31.5 \times 4.0\text{--}5.5 \mu\text{m}$, basal septum sometimes elevated, to $9.5 \mu\text{m}$ away from the junction

Conidia **macro-conidiophores** $5.0\text{--}12.0 \times 4.0\text{--}9.0 \mu\text{m}$, length/width ratio $1.0\text{--}1.9$ (av. > 1), with fibrosin bodies; **macro-conidiophores** $38.0\text{--}50.5 \times 5.5\text{--}8.0 \mu\text{m}$, a septum, foot-cells cylindrical, straight, $21.5\text{--}39.0 \times 5.5\text{--}8.0 \mu\text{m}$, **macro-conidia** variable in shape, ellipsoid-ovoid, $15.0\text{--}28.0 \times 11.0\text{--}15.5 \mu\text{m}$, length/width ratio $1.1\text{--}1.9$ (av. > 1.5), with fibrosin bodies; **germ tubes** **orthotubus** **Fibroidium** **Chasmothecia** gregarious, $(115.0\text{--})142.5\text{--}185.0\text{--}(226.0) \mu\text{m}$ diam.; **peridium cells** irregularly polygonal, $4.5\text{--}17.5 \mu\text{m}$ diam., arranged \pm **appendages**

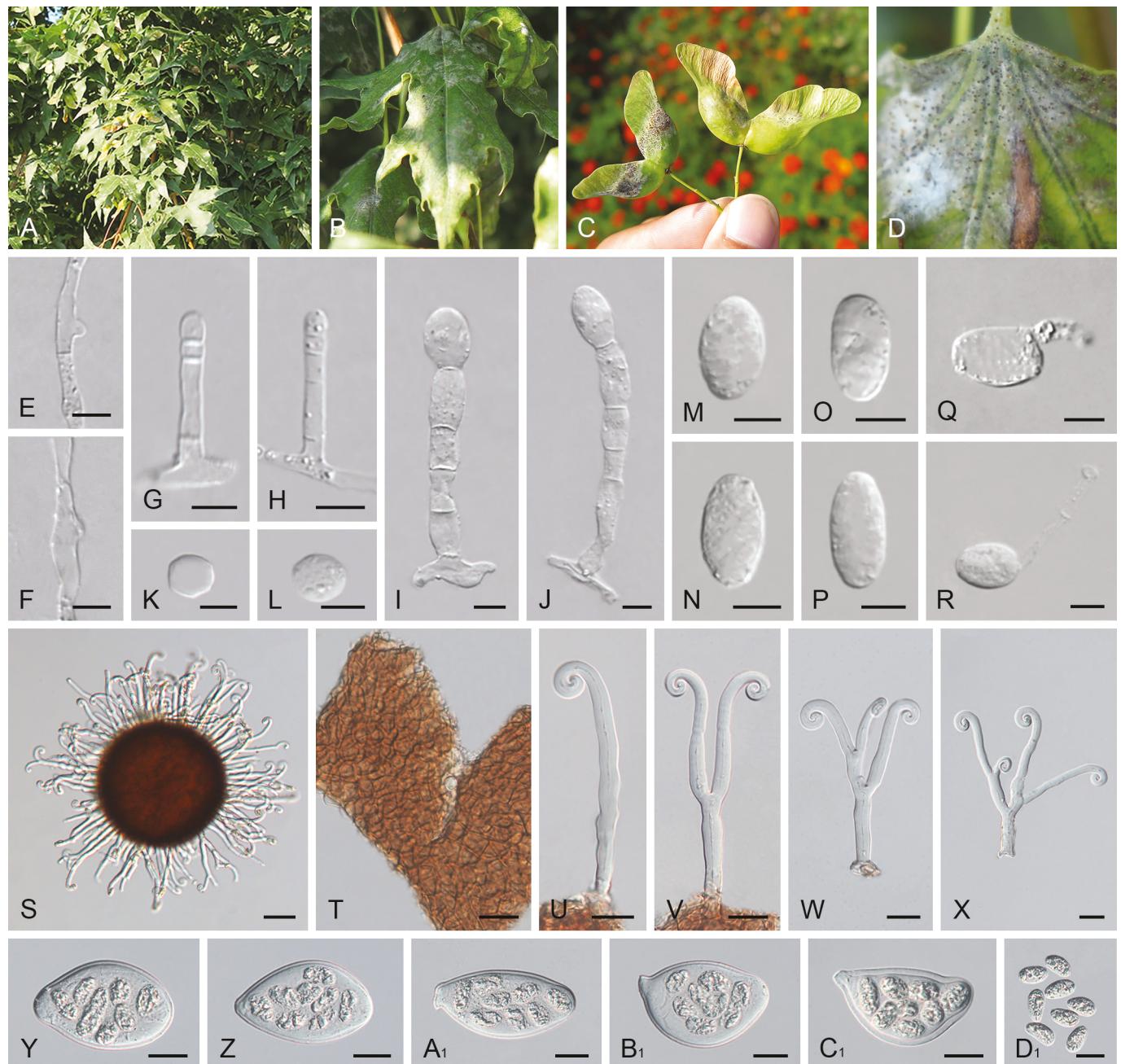


Fig. 18. *Sawadaea taii* sp. nov.

Q, R. S. $10 \mu\text{m}$; E–R, D1 = $10 \mu\text{m}$.

A, B, C, D.

E, F. T.

G, H. U–X.

Y–C1. A.

I, J.

C.

K, L.

M–P.

D1. Ascospores. Scale bars: S = $100 \mu\text{m}$; T–C1 = $20 \mu\text{m}$.

70.0–167.5(–225.0) × 4.0–14.0 μm , 0.4–1.3 times (av. 0.8) as

asci

× 47.5–68.0 μm , length/width ratio 1.2–1.7 (av. 1.4), wall thick, 1.5–7.0 μm , short-stalked or almost sessile, stalk length up to 7.0 μm ,

ascospores ellipsoid-ovoid, 16.0–23.5 × 12.5–15.5 μm , length/width ratio 1.1–1.8 (av. 1.4), colourless.

Additional materials examined: China

Japan

Liquidambar formosana, 21 Oct. 2018, S.R. Tang & L. Liu

Acer truncatum T.Z. Liu

rDNA GenBank No.: OQ866158); Jilin Province, Changchun City,

Acer truncatum L.

Yang

Acer truncatum, 2 Oct. 2018,

S.

Takamatsu, S.Y. Liu, P.L. Qiu & J. Feng

Yang

Q.M. Wang

OR841072); Yunnan Province, Weixi Lisu Autonomous County, on *Acer barbinerve* J. Han, GenBank No.: OQ866169).

Host range and distribution: On *Acer barbinerve*, *truncatum*) Sapindaceae, *Liquidambar formosana*, Hamamelidaceae,

Notes: *Sawadaea* n. sp.

Hamamelidaceae is reported in this study for the first time. *Sawadaea taiii*

S. bomiensis

S. bomiensis

S. acerina o

ginnala, *tataricum*

</

Host range and distribution (phylogenetically proven hosts): On *Acer platanoides*, *macrophyllum*, *tataricum* (Sawadaea *tulasnei*)



Notes: Sawadaea *tulasnei* is on *Acer platanoides*

tulasnei is largely confined



et al. et al.

al. et al.

S. tulasnei on *A. macrophyllum* (Acer *Macrophylla*)

A. tataricum (Ginnala)

et al. et al.

S. tulasnei is not strictly confined

b *A. platanoides* (Platanoidea)



o *Acer* (*crataegifolium*, *japonicum*, *macrophyllum*, *miyabei*, *monspessulanum* b *cinerascens* [\equiv *cinerascens*] *palmatum*,

A. pictum b *mayrii* [\equiv *mayrii*] *A. pictum* b *mono* [\equiv *mono*]

platanoides, *stevenii*, *tataricum* b *tataricum*, *tataricum* b

ginnala [\equiv *ginnala*] *truncatum*, *ukurunduense* b

et al.



A. cappadocicum d *A. monspessulanum* b *turcomanicum*

(\equiv *A. turcomanicum*) et al. b

tulasnei b



Acer (*crataegifolium* Sawadaea *bifida* b *A. pictum* b *mayrii*)

b *mono* (S. *bifida*) *A. palmata* (S. *taiii*) *A. tatarica* (S.

ginnala (S. *acerina*, S. *bifida*) *A. truncatum* (S. *kovaliana*, S. *taiii*)

Sawadaea *Acer*

A. japonicum

A. miyabei et al.

S. bicornis

d *S. tulasnei* b *A. monspessulanum*

from Turkey. The latter record is doubtful and in need of confirmation



A. truncatum b *S. tulasnei*



Sawadaea *A. truncatum* b *S. taiii*

b *S. tulasnei* b



Takamatsuella b Taxonomic

manual of the Erysiphales (powdery mildews) b

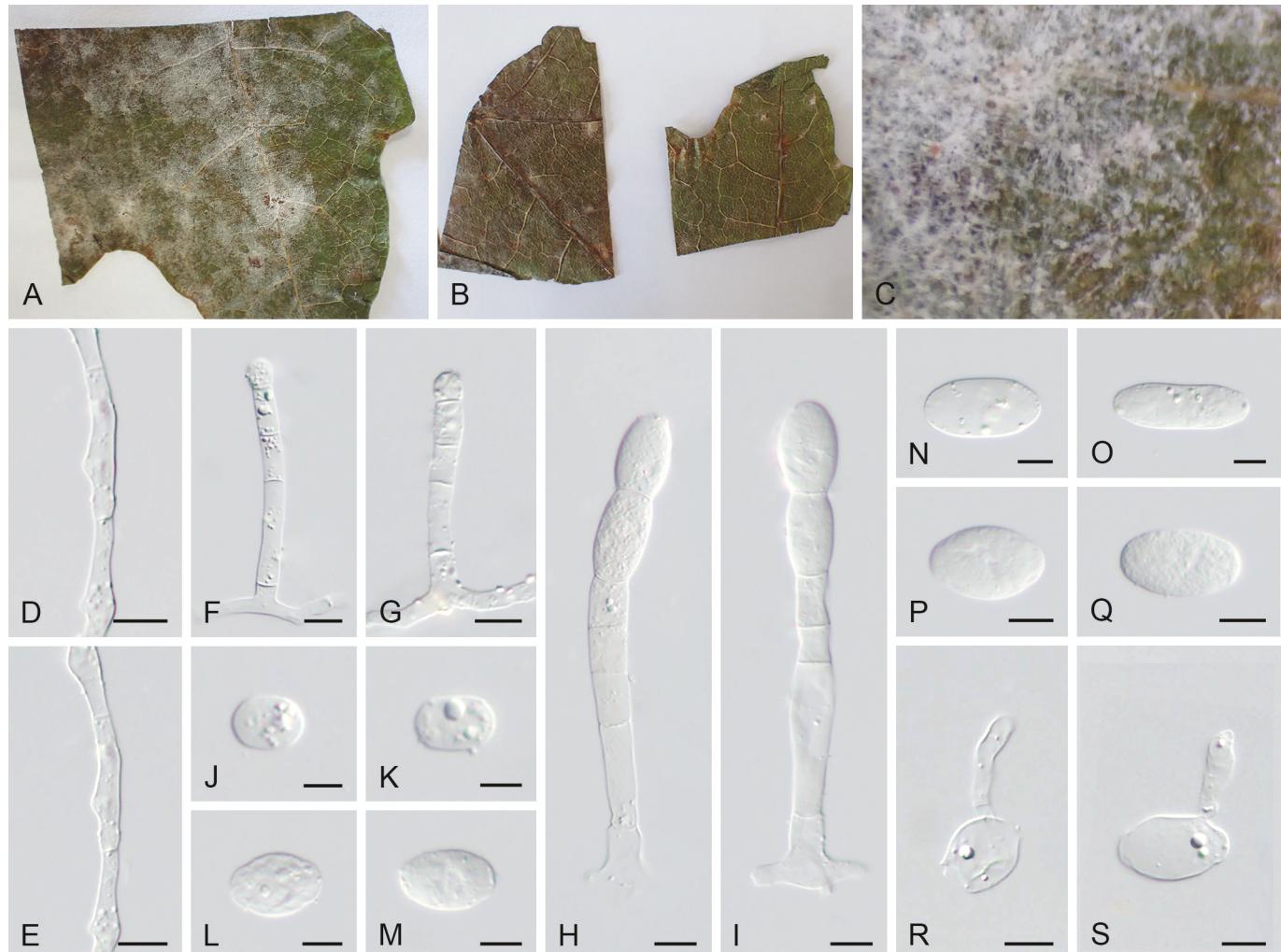


Fig. 19. *Sawadaea tulasnei* b

b D, E, G, H

bars: D–I, N–S = 10 μ m; J–M = 5 μ m.

A. b

H, I, J, K, L, M, N

B. b

N–Q. b

C. b

R, S. b

Notes 
 *Acer spicatum*
 *U. bicornis*
 *U. circinata*
 al. 

 *Sawadaeaia*





 *U. circinata*
 *U. circinata*




 *Takamatsuella* 

 *Uncinula circinata*

 *circinata* ~~sp. aff.~~
 *sp. aff. U.*
 *circinata* *(Acer wilsonii)*

 *Acer wilsonii*.


Uncinula circinata B.
, B.

B.

B.

B.

W. circinata
~~bluebird~~
~~W.~~
~~W.~~
can confirm t
The confirmat
~~W.~~
cer griseum
~~W.~~
~~W.~~
cinulata
~~W.~~
Erysiphe
~~W.~~
E. circinata
~~W.~~

the distribution of *T. circinata*.
n of molecular sequences in China requires further

DISCUSSION

Since Homma (1937) updated the classification of *Sawadaea*, **h**
g *S. bicornis*, S.
negundinis **h** *S. tulasnei* **h** *S. aesculi* **h**
g et al. **h** *S. bomiensis* , *S. polyfida*
g *S. bifida* **h** *S. kovaliana* **h**

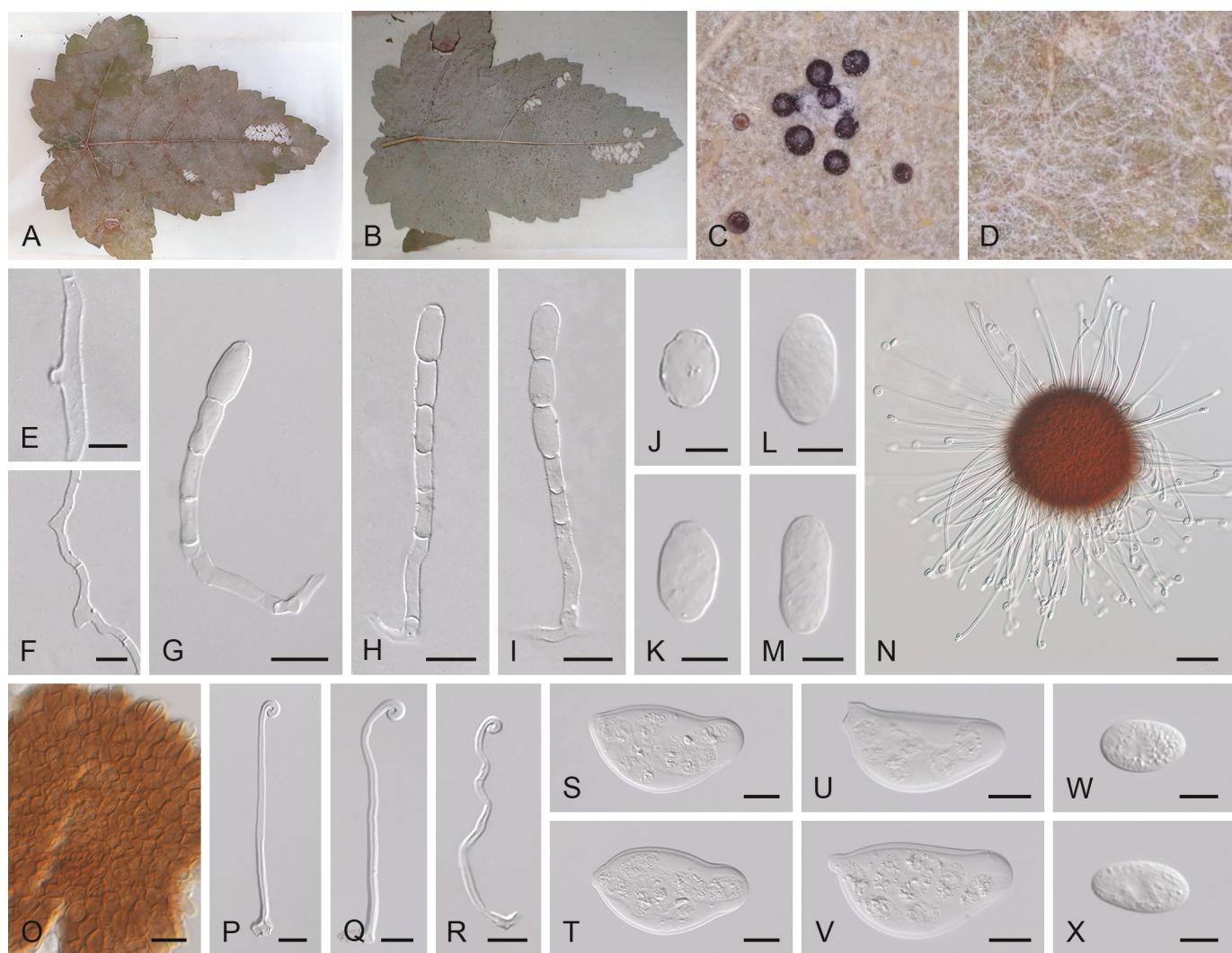


Fig. 21. *Takamatsuella circinata*

5
B. F. B.-I. S.-M. B. B.

W, X. Ascospores. Scale bars: N = 50 μm ; G–I, O–V = 20 μm ; E, F, J–M, W, X = 10 μm .

A. B. C. D.

O.B.+R.A.

S-VA

et al. *S. nankinensis*
 b Sawadaea, ~~Uncinula~~ *Uncinula*
koelreuteriae b Sawadaea
 Sawadaea
 S. bifida d S. kovaliana clarified the two names and allowed us
acerina, S. aceris-
arguti, S. *taii*.
 an important role in the reflection of the phylogenetic relationships
 Sawadaea *Takamatsuella*
 Takamatsuella
 Sawadaea. *Takamatsuella circinata* b
 only species in the genus, and confirmed from China based on
 morphological examinations, although phylogenetic confirmation is
 Sawadaea
Acer *S. koelreuteriae*
Koelreuteria *aesculi* *Aesculus*
taii *Acer* *Sapindaceae*
Liquidambar *Hamamelidaceae*)
Erysiphe *necator*,
Urticaceae, *Carica*
papaya *Caricaceae* et al.
 Sawadaea
 Acer
 Acer
 b *Koelreuteria*, *Aesculus* *Liquidambar*
Acer
Acer buergerianum
S. nankinensis)
Koelreuteria *puniculata* *S. koelreuteriae*
Aesculus
chinensis *S. aesculi*)
Acer
S. polyfida, *S. negundinis*, *S. bifida*
 Sawadaea
 b *S. bicornis*, *S. polyfida* *S. tulasnei*
 Sawadaea
S. acerina,
S. bicornis, *S. koelreuteriae* *S. nankinensis*,
 clades are not yet sufficiently supported, e.g., the two species *S. bifida* d *S. negundinis*
 et al. *S. bifida*,
pictum, *Acer* *Platanoidea*
S. bifida + *S. negundinis*
 cluster (Clade 6) that possibly reflects an additional cryptic species,

et al. *S. tulasnei* "b
Sawadaea *Acer crataegifolium* d
A. rufinerve, *Acer* Macrantha
Sawadaea
A. ginnala *Ginnala*
 cases, the identities of the host plants should be checked to confirm identifications.
Sawadaea tulasnei
 S. bifida
acerina d *S. taii*. *Sawadaea bicornis*
 et al.
 subclades, one of these is largely confined to *Acer campestre*
S. bicornis *A. platanoides*
 b *Acer* *Platanoidea*
A. negundo d *A. pseudoplatanus*
Forma speciales
forma speciales
 as such they do not have types that make such names verifiable.
Forma speciales
 difficult. As such it is not surprising that results by different authors have often been contradictory, difficult to understand, and hard to *Erysiphe* *neolycopersici*
 et al. *Pseudoidium neolycopersici*
 render these races objectively verifiable. In addition, the genetic *Formae*
 such cases warrants the application of an official rank covered by the *Formae*
Formae
Formae
Formae
Formae
 century and the first half of the 20th
Formae
Formae
Formae
 1910). Jaczewski (1927) was the first author in powdery mildews *Formae*
Formae
Formae
Formae

reflected in well-supported clades/subclades and are accompanied

Sawadaea ~~sp.~~ ¹ **Sawadaea** ~~sp.~~ ² **Alectryon**
excelsus **Sapindaceae**
S. negundinis ~~et al.~~ ³
S. bifida ~~sp.~~ ⁴ **negundinis** ~~sp.~~

come to a phylogenetic tree that reflects a more realistic evolutionary

 Sawadaea 
 S. koelreuteriae 

 Podosphaera 
 tridactyla  S. koelreuteriae 

 nankinensis 
 Blumeria  Cystotheca 
 Parauncinula 
 S. koelreuteriae  nankinensis

- Plumeria* *cystothecata*

mainly by means of molecular analyses. Our analyses

research, mainly by means of molecular analyses. Our analyses of *Sawadaea* are

Rawadaea Asia, makes identifications based on morphology more difficult and requires well-developed holomorphs. Confirmations of identifications

identification difficult in this region. Furthermore, *Acer*  *Sawadaea*  *A. pictum*  *mono*  *A. truncatum*.  *Acer negundo* 

Sawadaea
♂ *S. bicornis* f. *polyphaga*, *S. negundinis*, ♂ *S. polyfida*.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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