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RESEARCH ARTICLE

Which species of *Sawadaea* (*Erysiphaceae*) parasitise *Acer negundo* in Ukraine?

Vasyl P. HELUTA*, Vera P. HAYOVA
M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine,
2 Tereshchenkivska Str., Kyiv 01601, Ukraine
* Author for correspondence: *vheluta@gmail.com*

Abstract. A critical re-examination of powdery mildew collections on boxelder maple (*Acer negundo*, *Sapindaceae*) in Ukraine has demonstrated a shift in fungal pathogens of the genus *Sawadaea* affecting this common tree and introduction of two *Sawadaea* species into the country. The East Asian species *Sawadaea polyfida* was found to have spread on this host plant within the country since the early 21st century, largely displacing the previously dominant *S. bicornis*. Considering recent reports of *S. polyfida* in Western and Southern Europe on other maple species, specimens of powdery mildew collected on *A. negundo* in these regions require further critical study. In October 2025, one more species of East Asian origin, *S. negundinis*, was recorded on *A. negundo* in several locations for the first time in Ukraine. Given the potential for *S. negundinis* to spread rapidly within Europe, this fungus is likely to be expected in, or may have already invaded, other European countries.

Keywords: boxelder maple, distribution, Europe, invasion, powdery mildew

Introduction

Sawadaea Miyabe (*Erysiphaceae*, *Helotiales*, *Ascomycota*) is a relatively small genus of tree-infecting powdery mildew fungi that until recently comprised ten species (Hyde et al., 2024). The majority of them were described as parasites on various species of *Acer* L. (*Sapindaceae*). However, except for maples as principal hosts, some of these fungi are also known to occur on other host genera of *Sapindaceae*, viz. *Aesculus* L., *Alectryon* Gaertn., *Dodonaea* Mill. and *Koelreuteria* Laxm. (Braun, Cook, 2012).

A most recently published comprehensive phylogenetic and taxonomic analysis of powdery mildews on *Acer* spp. from East Asia, Europe and North America revealed three more new species of *Sawadaea* described from Asia (Feng et al., 2025). In that article, a boxelder maple (*Acer negundo* L.) is listed as a host plant for three of the 13 species of *Sawadaea* studied morphologically and genetically. For two species, *S. bicornis* (Wallr.) Homma and *S. negundinis* Homma, numerous collections ex *A. negundo* from different countries were examined, as well as newly obtained sequences and those retrieved from NCBI GenBank database were analysed. *Acer negundo* as a host is also listed for the third species, *S. polyfida* (C.T. Wei) R.Y. Zheng & G.Q. Chen (Feng et al., 2025); however, for the specimen used for DNA extraction (GenBank

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accession number MT174231), this host is apparently mentioned erroneously in the GenBank database and in the article, since Kiss et al. (2020) reported this specimen (BRIP68806) from Australia on *A. palmatum*. *Sawadaea bicornis* is a common and widely distributed species on a wide range of *Acer* spp. in Europe, Asia and North America, introduced in South America and New Zealand. *Sawadaea negundinis* based on the collections confirmed by sequence data, on the contrary, was demonstrated not to be strictly confined to *A. negundo* and known almost exclusively from Asia (Feng et al., 2025), except for a single record from the European part of RF, Rostov Region, which is an area bordering Ukraine.

With respect to the above, a relevant question can be raised: which species of *Sawadaea* occur on *A. negundo* in Ukraine? The present article provides the answer to this question.

Materials and Methods

A collection of all specimens of the leaves of *A. negundo* infected by powdery mildews (Table 1) deposited at the Mycological Herbarium (Fungarium) of the National Herbarium of Ukraine at the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine (KW-M), was critically studied. The samples prepared in distilled water following standard protocol were examined using light microscopy. Photographs of all microstructures were taken with a Canon A 300 digital camera attached to a Primo Star microscope (Carl Zeiss, Germany). All measurements were made using AxioVision 4.7 software.

Results and Discussion

Prior to this study, only two species of *Sawadaea* have been reported in Ukraine, *S. bicornis* and *S. tulasnei* (Fuckel) Homma. They both are obligate biotrophic fungi infecting various hosts, primarily *Acer* spp., although the former species was also occasionally recorded on *Aesculus hippocastanum* L. (Heluta, Marchenko, 1984; Heluta, 1989; Heluta, Anishchenko, 2021). Morphologically, these species are quite close but distinguishable by different infection appearance on host plant and morphology of chasmothecial appendages. In addition, they have rather distinct host ranges.

Sawadaea bicornis has been reported in Ukraine on a wide range of hosts including *Acer campestre* L., *A. negundo*, *A. platanoides* L., *A. pseudoplatanus* L., *A. saccharinum* L., *A. velutinum* Boiss. and *Aesculus hippocastanum*. Mycelium of this fungus, as well as conidia and chasmothecia, develop on both sides of the leaves (amphigenous), at first as irregular greyish-white patches, later confluent. Chasmothecial appendages are 1–2(3) times dichotomously branched in the upper half of the stalk, with uncinate-circinate apices.

Sawadaea tulasnei was recorded in the country only on *A. platanoides* and *A. tatarica* L. Its mycelium is mostly (on *A. tatarica* almost exclusively) epiphyllous, at first forming distinct white patches, later enlarging to cover the entire leaf surface, so that severely infected leaves appear as if they are covered with a talc-like powder. Chasmothecial appendages are of two types, simple and dichotomously branched, with those unbranched prevailing, all appendages with uncinate apices. However, appendages in *S. tulasnei* are of a peculiar branching pattern, from the middle of the stalk upwards. It is also noteworthy that the two species can simultaneously occur on the same leaves of *A. platanoides*, a host common for both species. Thus, a careful microscopic examination of the infected leaves of this host plant is required for correct identification of the species of *Sawadaea*.

As already noted, following a recent discovery of the record of *S. negundinis* on *Acer negundo* from Rostov Region, RF, confirmed by molecular analysis (Feng et al., 2025), a re-examination of all previously collected specimens of powdery mildews on this host in Ukraine has been made, including not yet identified collections deposited at the Mycological Herbarium of the M.G. Kholodny Institute of Botany, NAS of Ukraine (KW-M). The outcome of the present examination was quite unexpected. Based on morphology of the appendages on chasmothecia, all studied specimens have split into three groups. The first group consisted of the specimens with the appendages dichotomously or trichotomously branched 1–2(–3) times, mainly in the upper half of the stalk (Fig. 1). These specimens are assigned to *S. bicornis*, a common species in Europe, including Ukraine. Majority of them were collected in the second half of the 20th century (Table 1), with the exception of two specimens dated back to the early 2000s (KW-M33244 from Donetsk Region and KW-M71769 from Kyiv City).

The second group of the examined collections proved to be more interesting. It was expected that they would belong to *S. negundinis*. However, chasmothecia in these specimens have numerous

Table 1. **Specimens of the species of *Sawadaea* on *Acer negundo* collected in Ukraine (listed in chronological order)**

Specimen	Locality	Collection date	Collector	Species of *Sawadaea*
KW-M33761	Kyiv, John McCain Str.	10.10.1972	I.O. Dudka	*S. bicornis*
KW-M33766	Kyiv, National Botanical Garden	04.10.1976	Perehon, Potayenko	*S. bicornis*
KW-M33767	Kyiv, National Botanical Garden	12.10.1976	Perehon, Potayenko	*S. bicornis*
KW-M33770	Kyiv Region, Bucha	06.09.1979	V.P. Heluta	*S. bicornis*
KW-M33769	Kyiv, National Botanical Garden	10.09.1979	H.S. Morochkovska	*S. bicornis*
KW-M140	Volyn Region, Lutsk City	30.09.1981	P.D. Marchenko	*S. bicornis*
KW-M33762	Kyiv, Tereshchenkivska Str.	14.09.1987	V.P. Heluta	*S. bicornis*
KW-M33759	Kyiv, Velyka Zhytomyrska Str.	05.10.1987	V.P. Heluta	*S. bicornis*
KW-M33763	Kyiv, Tereshchenkivska Str.	13.10.1987	V.P. Heluta	*S. bicornis*
KW-M33764	Kyiv, Tereshchenkivska Str.	16.10.1987	V.P. Heluta	*S. bicornis*
KW-M31568	Kyiv, T.G. Shevchenko park	17.10.1988	V.P. Heluta	*S. bicornis*
KW-M28199	Kyiv, Feofania	27.09.1990	V.P. Heluta	*S. bicornis*
KW-M28198	Zaporizhzhya Region, Rozivka settl.	26.09.1997	V.P. Heluta	*S. bicornis*
KW-M33625	Kyiv Region, Krasne-Pershe village	02.10.2002	I.O. Dudka	*S. polyfida*
KW-M71775	Kyiv, National Botanical Garden	30.10.2002	S.O. Voityuk	*S. polyfida*
KW-M33244	Donetsk Region, Khomutovskyi Steppe Nature Reserve	20.10.2003	V.P. Heluta	*S. bicornis*
KW-M71772	Donetsk City	30.09.2005	I.V. Bondarenko-Borysova	*S. polyfida*
KW-M71776	Kyiv, National Botanical Garden	04.10.2007	V.P. Heluta, S.O. Voityuk	*S. polyfida*
KW-M71782	Kyiv, Sviatoshyn	12.10.2007	V.P. Heluta	*S. polyfida*
KW-M71773	Donetsk City	21.10.2007	K.G. Savchenko	*S. polyfida*
KW-M71769	Kyiv, Tereshchenkivska Str.	19.10.2009	V.P. Heluta	*S. bicornis*
KW-M71785	Kyiv, Hetman Pavlo Skoropadskyi Str.	12.10.2010	V.P. Heluta	*S. polyfida*
KW-M71783	Kyiv, Kyiv-Volynskyi	19.10.2010	V.P. Heluta	*S. polyfida*
KW-M71777	Kyiv, Acad. Korolyov Avenue	12.10.2011	V.P. Heluta	*S. polyfida*
KW-M71781	Kyiv, Symyrenko Str.	26.10.2011	V.P. Heluta	*S. polyfida*
KW-M71771	Kyiv, Vakhtang Kikabidze Str.	30.10.2011	V.P. Heluta	*S. bicornis* + *S. polyfida*
KW-M71774	Transcarpathian (Zakarpatska) Region, Uzhhorod City	20.09.2012	I. Akata	*S. polyfida*
KW-M71778	Kyiv, Acad. Korolyov Avenue	22.10.2012	V.P. Heluta	*S. polyfida*
KW-M71784	Kyiv, Bohdan Khmelnytskyi Str.	01.11.2012	V.P. Heluta	*S. polyfida*
KW-M71786	Lviv City	14.09.2013	O. Kryva	*S. polyfida*
KW-M71788	Khmelnytskyi Region, Kamianets-Podilskyi District, Sokil village	20.09.2013	V.P. Heluta	*S. polyfida*
KW-M71787	Khmelnytskyi Region, Kamianets-Podilskyi town	22.09.2013	V.P. Heluta	*S. polyfida*
KW-M71770	Kyiv, Acad. Korolyov Avenue	25.10.2015	V.P. Heluta	*S. bicornis* × *S. polyfida*
KW-M71779	Kyiv, Vakhtang Kikabidze Str.	24.10.2019	V.P. Heluta	*S. polyfida*
KW-M71780	Kyiv, Vakhtang Kikabidze Str.	31.10.2022	V.P. Heluta	*S. polyfida*
KW-M71790	Kyiv, Tereshchenkivska Str.	10.10.2025	V.P. Heluta	*S. negundinis*
KW-M71791	Kyiv, Svyatoshyn	15.10.2025	V.P. Hayova	*S. negundinis*
KW-M71794	Kyiv, Vakhtang Kikabidze Str.	21.10.2025	V.P. Heluta	*S. negundinis*
KW-M71795	Kyiv, Yevhen Chykalenko Str.	22.10.2025	V.P. Hayova	*S. negundinis*

appendages (over 100), mostly branched dichotomously, trichotomously to occasionally tetrachotomously from near the middle of the stalk or below, down to the bottom of the stalk, deeply cleft, rarely unbranched (Fig. 2). In *S. negundinis*, appendages are less numerous, usually up to 100 per chasmothecium, branching from almost the middle of the stalk. With regard to the observed characters, according

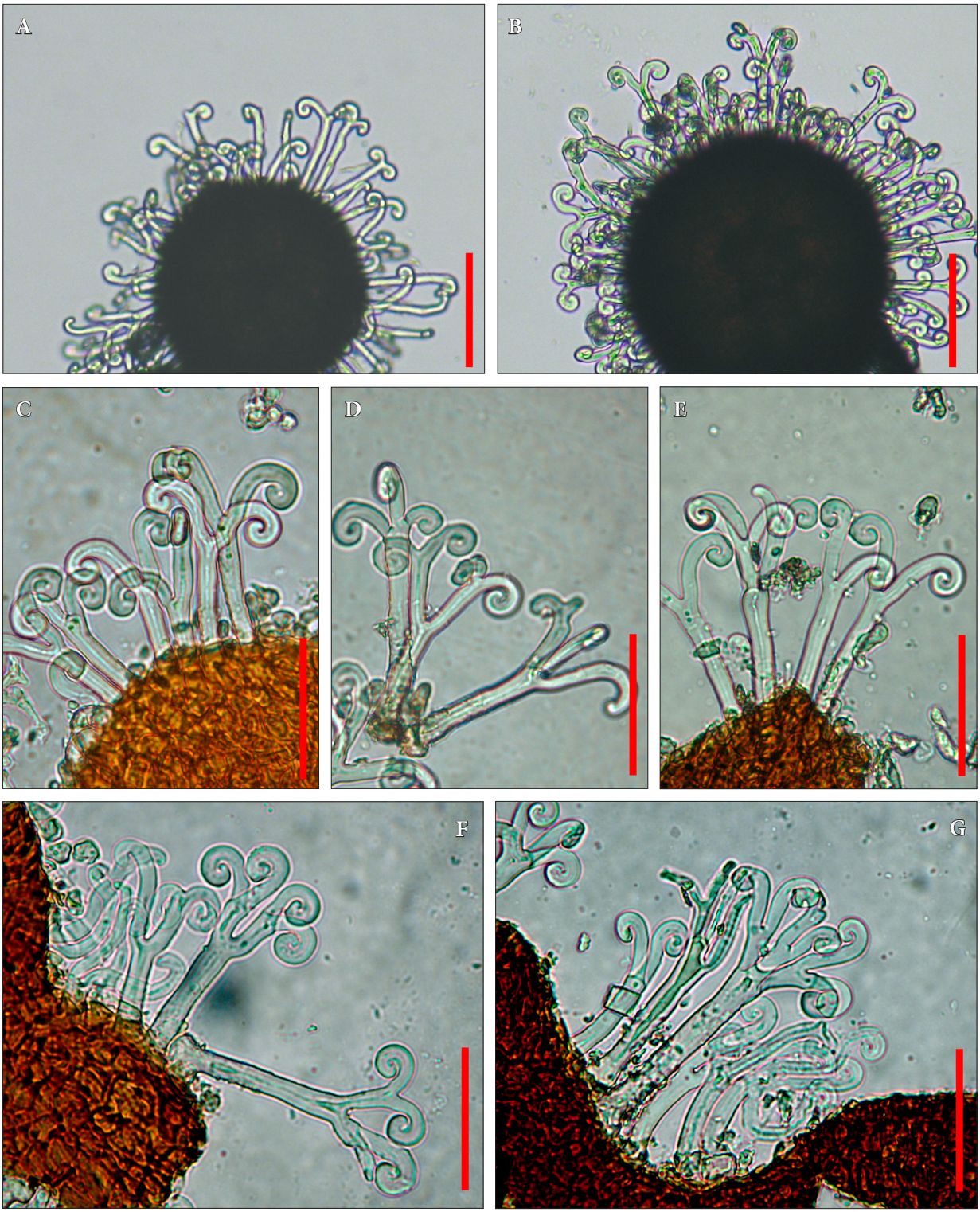

Fig. 1. *Sawadaea bicornis* ex *Acer negundo*: chasmothecia (A, B) and appendages (C–G). A–C: KW-M33763; D: KW-M53578; E–G: KW-M33770. Bars: A, B — 100 µm, C–G — 50 µm

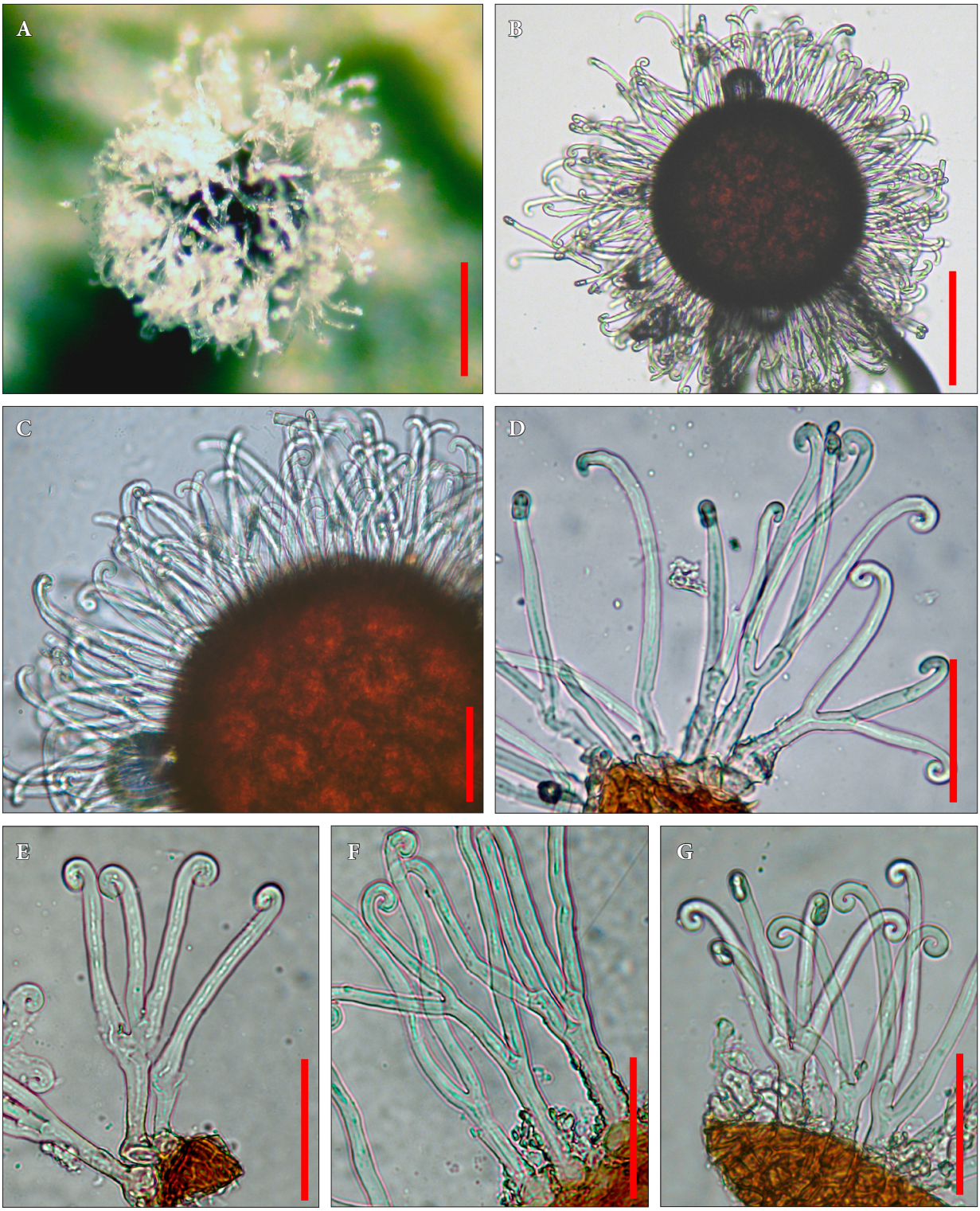

Fig. 2. *Sawadaea polyfida* ex *Acer negundo*: chasmothecia (A, B) and appendages (C–G). A–D: KW-M71786; E: KW-M59233; F: KW-M71772; G: KW-M71787. Bars: A, B — 100 μm, C–G — 50 μm

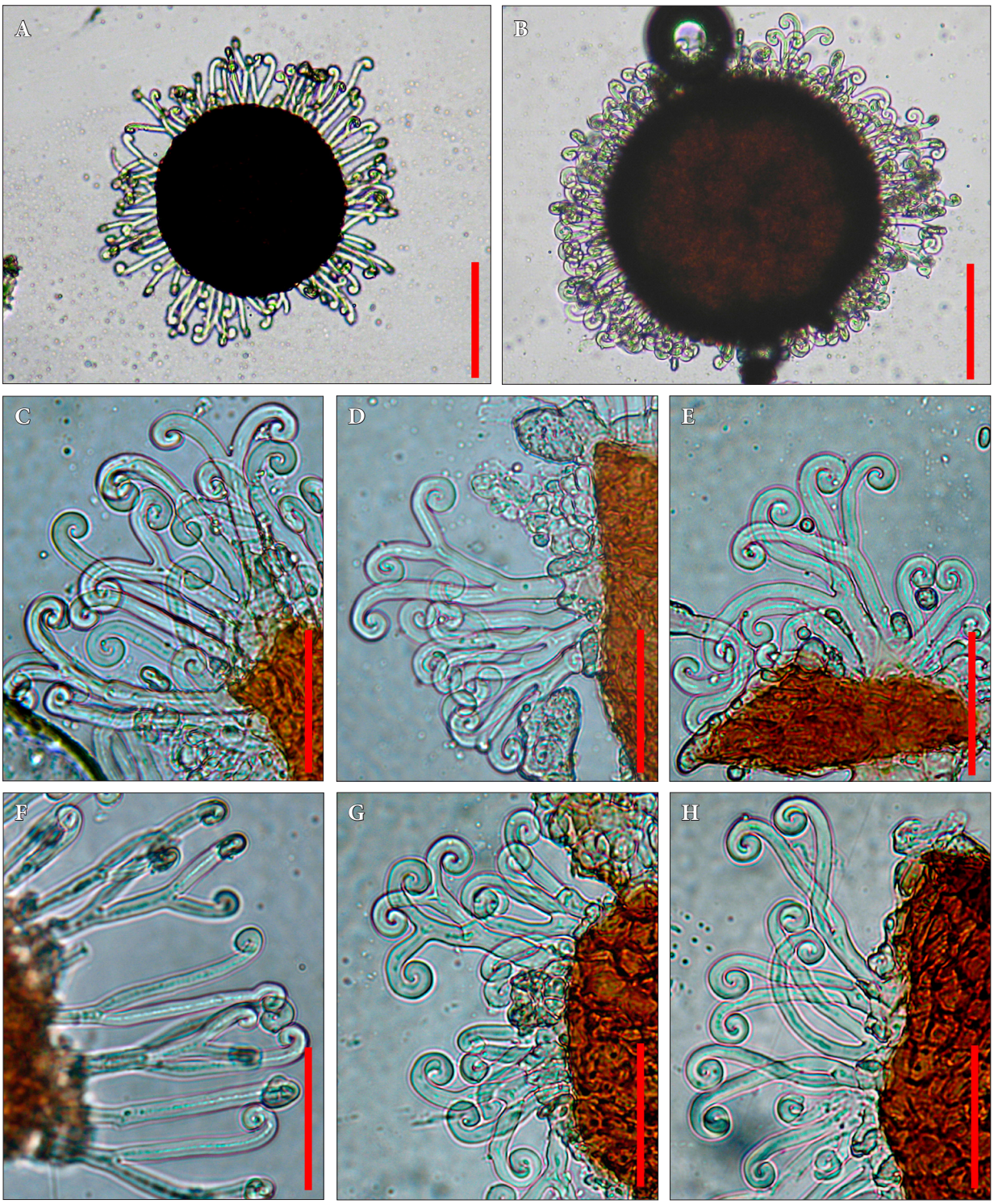

Fig. 3. Chasmothecia (A, B) and appendages (C–F) of a supposed hybrid, *Sawadaea bicornis* × *S. polyfida* ex *Acer negundo* (KW-M71770). Appendages of two different chasmothecia (KW-M71771) morphologically corresponding to *S. bicornis* (G) and *S. polyfida* (H). Bars: A, B — 100 µm, C–G — 50 µm

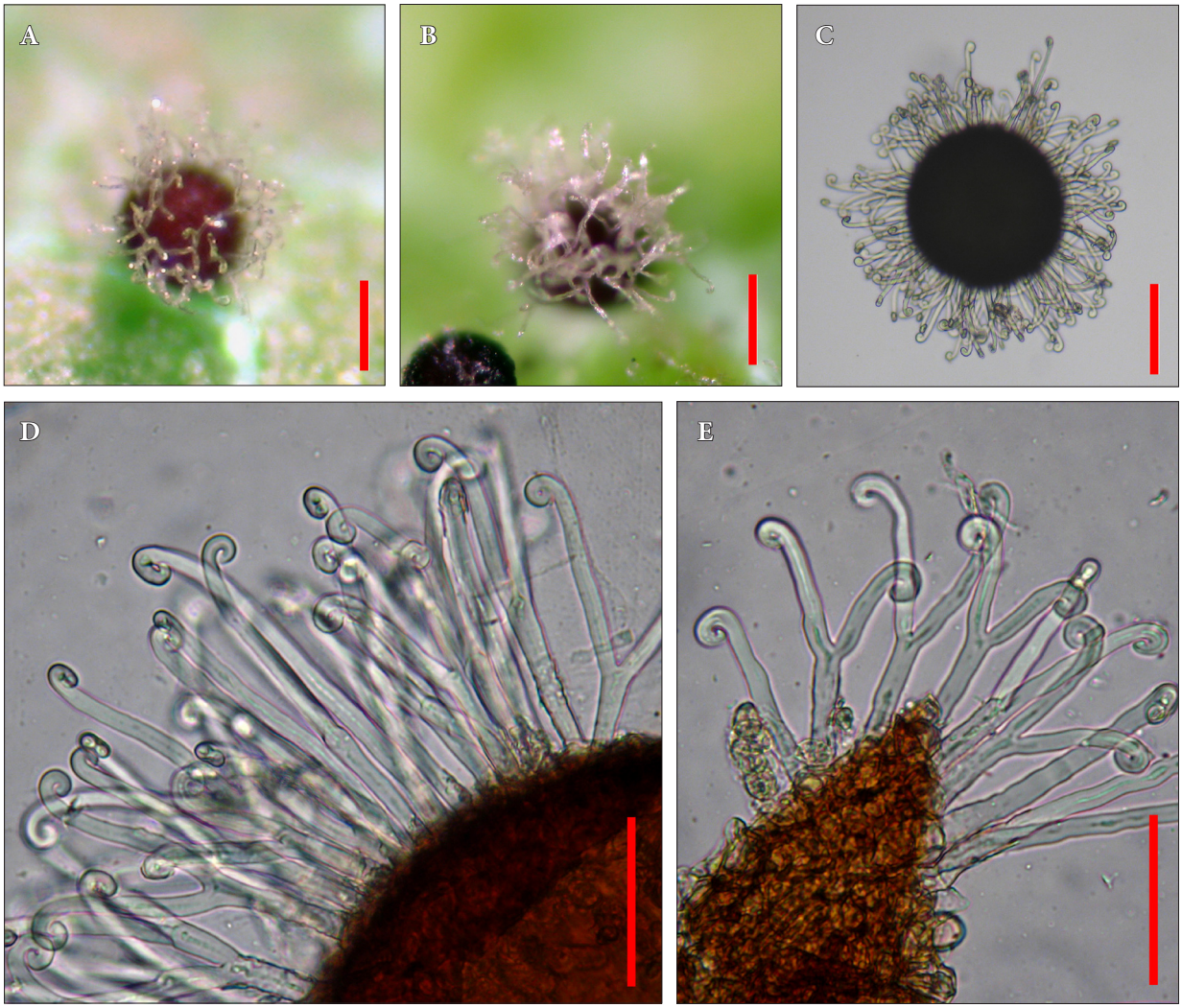

Fig. 4. *Sawadaea negundinis* ex *Acer negundo*: chasmothecia (A–C) and appendages (D, E). A: KW-M71794; B–E: KW-M71795. Bars: A, B — 100 µm, C–G — 50 µm

to the morphology-based key in Braun and Cook (2012), our specimens can be identified as *S. polyfida*. This species, originally described from Eastern Asia, has been recorded in China, Japan and South Korea on various species of *Acer*, predominantly on hosts of *Acer* sect. *Palmata* (Zheng, Chen, 1980; Shin, 2000; Hirose et al., 2005; Lee et al., 2011; Meeboon et al., 2015; Wan et al., 2022; Feng et al., 2025), and introduced to Australia and North America (USA) (Kiss et al., 2020; Feng et al., 2025). Recently, *S. polyfida* was also reported from two countries in Europe, Austria and Switzerland, on the ornamental Japanese maples, *Acer japonicum* Thunb. and *A. palmatum* Thunb. (Beenken et al., 2023; Hofbauer, Braun, 2023), and in Germany, on local maples, *A. campestre* L. and *A. platanoides* L. (Wemheuer et al., 2019).

The morphology of appendages in our samples (Fig. 2) aligns well the descriptions and illustrations of those for *S. polyfida* from Switzerland, an identification confirmed by molecular data (Beenken et al., 2023). The appendage morphology in our specimens is, however, inconsistent with the description of *S. polyfida* on *A. australe* (Momot.) Ohwi & Momot. originating from Japan (Meeboon et al., 2015). The Japanese collection is morphologically distinct, with chasmothecial appendages that branch from the approximate midpoint of the stalk. Furthermore, its nucleotide sequences in the Internal

Transcribed Spacer (ITS) region diverge from other specimens of *S. polyfida* (see Fig. 1 in Feng et al., 2025). This combination of morphological and genetic differences suggests that the Japanese collection may represent a new, yet undescribed species within the *S. polyfida* s. l. species complex.

Thus, our specimens of the second group fully correspond to *S. polyfida* reported on Japanese maples from Western Europe. In Ukraine, however, it has apparently expanded its host range to include *A. negundo*. As indicated in Table 1, the first documented occurrences of *S. polyfida* on this host plant in the country date to the start of the 21st century. It is highly probable that this fungus also occurs on *A. negundo* further west of Ukraine, in Central, South and Western Europe. Consequently, a re-examination of powdery mildew samples collected from this host plant over the past two decades is recommended.

The third group comprises two specimens, KW-M71770 and KW-M71771, which can be assigned neither to *S. bicornis* nor to *S. polyfida*. In the first collection, KW-M71770, some chasmothecia have deeply cleft appendages as in *S. polyfida*, but in lower number (below 100, see Fig. 3A), which does not fit this species. At the same time, there are chasmothecia with very numerous appendages (over 100, see Fig. 3B) typical of *S. bicornis* (Fig. 3B, C). Interestingly, appendages with the intermediate morphological characters can be also observed (Fig. 3D–F). Therefore, this material is apparently of hybrid origin. In the second specimen, KW-M71771, there are two types of chasmothecia: one with those typical of *S. bicornis* (Fig. 3G), other — characteristic of *S. polyfida*, with no intermediate forms (Fig. 3H). In this case, it is evident that both species simultaneously occur on the same leaves. Notably, these two specimens were collected in close proximity within Kyiv City, the first being collected in 2011 and the second in 2015.

Based on the data in Table 1, the first occurrence of *S. polyfida* on *A. negundo* in Ukraine can be documented from at least 2002. Since that time, this species has almost completely replaced *S. bicornis* on this host, so that the latter is now very rarely found. Both species are easily distinguishable by their micromorphological characteristics, although there is no obvious difference in the symptoms; however, *S. polyfida* is likely to cause stronger infection of the host plant than *S. bicornis*.

In mid-October 2025, when this article was undergoing final revision, the authors collected within Kyiv City several additional specimens of leaves of *Acer negundo* infected by powdery mildew (Table 1). Microscopic analysis of the specimens has demonstrated mainly fewer than 100 appendages per chasmothecium (Fig. 4A–C). The appendages were found to be 1(–2) times dichotomously branched, deeply cleft, branching from the middle of the stalk or quite often below, but very rarely above the middle of the stalk (Fig. 4D, E).Therefore, the freshly collected specimens were identified as *Sawadaea negundinis*, the expected in the country species, recently reported near Ukraine's southeastern border. Considering the potential for powdery mildews to spread rapidly, it is presumed that this fungus will soon be recorded in other European countries.

Conclusions

The present critical re-examination of all powdery mildew collections on *Acer negundo* in Ukraine has revealed that since the beginning of the 21st century *Sawadaea bicornis* on this host plant has been largely replaced by *S. polyfida*, a pathogen of maples introduced from East Asia. It is suggested that *S. polyfida* is likely spreading on boxelder maple in Europe beyond Ukraine. Another East Asian species, *S. negundinis*, has been recently recorded in the country on the same host, and its occurrence in several locations is reported in the present study. A comprehensive re-evaluation of the recent herbarium specimens of *Sawadaea* spp. on *Acer negundo* across the continent, followed by molecular confirmation, is therefore essential to understand the current distribution of these pathogens and assess its potential consequences.

ETHICS DECLARATION

The authors declare no conflict of interest.

ORCID

V.P. Heluta https://orcid.org/0000-0001-7849-2162
V.P. Hayova https://orcid.org/0000-0002-7038-1633

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Які види роду *Sawadaea* (*Erysiphaceae*) уражують *Acer negundo* в Україні?

В.П. ГЕЛЮТА, В.П. ГАЙОВА
Інститут ботаніки ім. М.Г. Холодного НАН України,
вул. Терещенківська 2, Київ 01601, Україна

Реферат. Унаслідок критичного перегляду колекції борошнисторосяних грибів доведено, що на початку XXI ст. на території України на американському клені (*Acer negundo*, *Sapindaceae*) поширився східноазійський борошнисторосяний гриб *Sawadaea polyfida*, який майже повністю замістив раніше відомий тут *S. bicornis*. Оскільки *S. polyfida* може траплятися і в Західній та Південній Європі, то зібрані там на *A. negundo* зразки борошнисторосяних грибів потребують додаткового критичного перегляду. У жовтні 2025 р. авторами статті було зібрано на території Києва кілька свіжих зразків листків *Acer negundo*, уражених ще одним грибом східноазійського походження — *Sawadaea negundinis*, якого нещодавно знаходили поблизу південно-східного кордону України. Враховуючи потенційні можливості блискавичного розповсюдження борошнисторосяних грибів, можна припустити, що цей вид найближчим часом також буде зареєстрованим і в інших європейських країнах.

Ключові слова: борошниста роса, Європа, інвазія, клен ясенелистий, поширення