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Taxonomy and phylogeny of the *Erysiphe lonicerae* complex (*Helotiales*, *Erysiphaceae*) on *Lonicera* spp.

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Abstract: The phylogeny and taxonomy of powdery mildews, belonging to the genus *Erysiphe*, on *Lonicera* species throughout the world are examined and discussed. Phylogenetic analyses revealed that sequences retrieved from *Erysiphe lonicerae*, a widespread powdery mildew species distributed in the Northern Hemisphere on a wide range of *Lonicera* spp., constitutes a complex of two separate species, viz., *E. lonicerae* (s. str.) and *Erysiphe ehrenbergii* comb. nov. *Erysiphe lonicerae* occurs on *Lonicera* spp. belonging to *Lonicera* subgen. *Lonicera* (= subgen. *Caprifolium* and subgen. *Periclymenum*), as well as *L. japonica*. *Erysiphe ehrenbergii* comb. nov. occurs on *Lonicera* spp. of *Lonicera* subgen. *Chamaecerasus*. Phylogenetic and morphological analyses have also revealed that *Microsphaera caprifoliacearum* (= *Erysiphe caprifoliacearum*) should be reduced to synonymy with *E. lonicerae* (s. str.). Additionally, *Erysiphe lonicerina* sp. nov. on *Lonicera japonica* in Japan is described and the new name *Erysiphe flexibilis*, based on *Microsphaera lonicerae* var. *flexuosa*, is introduced. The phylogeny of *Erysiphe ehrenbergii* and *E. lonicerae* as well as other *Erysiphe* species on honeysuckle is discussed, and a survey of all species, including a key to the species concerned, is provided.

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INTRODUCTION

Lonicera, the largest genus in the family *Caprifoliaceae*, comprises around 180 species of deciduous or evergreen shrubs as well as woody climbers that are largely distributed in temperate to subtropical regions of the Northern Hemisphere (Mabberley 2008). Various species of this genus are cultivated shrubs that are popular in gardens and parks. For example, *Lonicera japonica* and *L. tatarica* are commonly found throughout Europe (Roloff & Bärtels 2008). *Lonicera* is usually divided into two subgenera, one for species with 3-flowered cymes and perfoliate leaves that usually comprise twining shrubs (subgen. *Lonicera*), and one for species with 2-flowered cymes and free leaves (subgen. *Chamaecerasus*). The division of *Lonicera* into two subgenera has recently been confirmed by molecular methods (Theis *et al.* 2008, Nakaji *et al.* 2015). The formal naming of the two subgenera has been controversially discussed and depends on the lectotypification of this genus. The first valid lectotypification of *Lonicera* was accomplished by Hitchcock & Green (1929) who designated *Lonicera caprifolium* as lectotype. However, more recently, Hara (1983) proposed *L. xylosteum* as lectotype. Although the original lectotypification is valid, some authors, such as Nakaji *et al.* (2015), did not

accept *L. caprifolium* as lectotype and preferred to follow Hara (1983). As long as there is no accepted proposal to change the lectotypification of this genus, the first lectotypification should be followed (Art. 9.19).

Powdery mildew, caused by *Erysiphe* spp., is a common, widespread, detrimental fungal disease of plants within the *Lonicera* genus (Braun & Cook 2012). Salmon (1900: 142) noted that the European powdery mildew on *Lonicera* spp. was a variety of *Microsphaera alni* (*sensu latissimo*), which, at the time, encompassed all *Microsphaera* species that are morphologically similar to *M. penicillata* (= *M. alni*). *Microsphaera ehrenbergii*, introduced for a powdery mildew on *Lonicera tatarica*, was reduced to synonymy with *M. alni* var. *lonicerae*. The current taxonomy of *Erysiphe lonicerae* was first established by Jaczewski (1927). Following Jackzewski (1927), Blumer (1933, 1967) recognized the European *Lonicera* powdery mildew as a species of its own (including *M. ehrenbergii* on *L. tatarica* as synonym). Braun (1982b) treated the later taxon as a morphologically distinguished variety of *M. lonicerae* and introduced the combination *M. lonicerae* var. *ehrenbergii*. Braun & Takamatsu (2000) later introduced the new nomenclature *Erysiphe lonicerae* var. *ehrenbergii*. Braun & Cook (2012) recognised six *Erysiphe* species, all belonging in sect. *Microsphaera*, viz., *Erysiphe*

caprifoliacearum var. *caprifoliacearum* and var. *flexuosa*, *E. erlangshanensis*, *E. loniceræ* var. *loniceræ* and var. *ehrenbergii*, *E. loniceræ-ramosissimæ*, *E. magnusii*, and *E. miuræ*. However, this treatment was just based on morphology.

The application of molecular methods for powdery mildews is commonly used to clarify unresolved taxonomic problems. In the current study, we conducted phylogenetic analyses of the *E. loniceræ* complex to determine whether the *L. tatarica* powdery mildew should be treated as a variety of *E. loniceræ* or if it should be separated into a species of its own. We included epitypifications of *Erysiphe loniceræ* and *Microsphaera ehrenbergii* with ex-epitype reference sequences, as well as a survey of *Erysiphe* species on *Lonicera* spp. and a key to the various species concerned. The phylogenetic analysis conducted is the basis for a revised taxonomic treatment of *E. loniceræ s. lat.*

MATERIALS AND METHODS

Collections examined

Morphological examinations and phylogenetic analyses were based on herbarium specimens deposited in BPI, GLM, HAL, TNS, TSU-MUMH, and WTU. The collections used for the present examinations are cited under the particular species in the taxonomic chapter.

DNA extraction, amplification (PCR), and phylogeny

Sequences were obtained in the USA as described by Bradshaw & Tobin (2020). DNA extractions were accomplished by the Chelex method (Walsh *et al.* 1991, Hirata & Takamatsu 1996). PCR was accomplished using the primer pairs PM10 (5'-GGCCGGAAAGTTGTCCAAC-3') / PM28R (5'-ACGTTCACTTTCATTCCGCG-3') (Bradshaw & Tobin 2020). If PCR was unsuccessful a nested approach was accomplished using the Primers AITS (5'-CGATTGAATGGCTAAGTGAGG-3') (Bradshaw & Tobin 2020) / TW14 (5'-GCTATCCTGAGGGAAACTTC-3') (Mori *et al.* 2000) followed by PM10 / PM28R or PM10 / PM11 (for the ITS) and PM28F / PM28R (for the 28S) (Bradshaw & Tobin 2020). DNA was purified by isopropanol precipitation. Purified amplicons were sent to Eurofins (Luxembourg) to be directly sequenced in both the forward and reverse direction using the primer pairs above. In Germany, sequences were obtained as described by Bradshaw *et al.* (2017). Whole-cell DNA was extracted from infected leaves with the DNeasy plant mini kit (Qiagen, Germany), following the manufacturers protocol. For the first PCR reaction the primers PM1 (5'-TCGGACTGGCCYAGGGAGA-3') (Cunnington *et al.* 2003) / TW14 were used followed by ITS5 (5'-GGAAGTAAAAGTCGTAACAAGG-3') (White *et al.* 1990) / PM2 (5'-TCACTCGCCGTTACTGAGGT-3') (Cunnington *et al.* 2003) and PM5 (5'-TTGCTTTGGCGGGCCGGG-3') / NLP2 (5'-GGTCCCAACAGCTATGCTCT-3') (Mori *et al.* 2000) Amplicons were purified (MSB Spin PCRapace Kit; Stratec Biomedical AG, Germany) and sequenced in both directions (LGC Genomics GmbH, Germany) using the primers mentioned before. Consensus sequences were generated and edited (CLC Main Workbench 20.0, Qiagen Digital Insights, Germany). The sequences obtained in the present study were deposited in GenBank under the accession numbers MN211362–MN211363, MN277391–MN277395, MW045561–45570, and MW045571–MW045573 (Table 1).

These sequences were aligned with the reference sequences of *Erysiphe* species shown in Table 1 by MUSCLE implemented in MEGA 7.0 (Kumar *et al.* 2016). Phylogenetic trees were constructed by maximum parsimony (MP) and maximum likelihood (ML) methods in PAUP* v. 4.0 (Swofford 2003) and raxmlGUI v. 1.3 (Silvestro & Michalak 2012), respectively, according to the procedures of Meeboon *et al.* (2020). All sites were treated as unordered and unweighted, with gaps treated as missing data. Strength of the respective branches was evaluated with 1 000 bootstrap (BS) values (Felsenstein 1985).

Morphology

All fungal structures were examined by light microscopy, using an Olympus BX50 or Zeiss Axio imager A1 microscope. Distilled water and lactic acid were used as mounting media, and aniline blue (cotton blue) was used to stain colourless structures. If possible, measurements of 30 conidia and other structures were made at a magnification of $\times 1\ 000$, and the 95 % confidence intervals were determined (extreme values in parentheses).

RESULTS

Phylogeny of *Erysiphe loniceræ s. lat.*

Fourty nuc-rDNA sequences including ITS regions, 5.8S rDNA and 5'-end of 28 rDNA from *Erysiphe* spp. on *Lonicera* species were aligned with the sequences of closely related *Erysiphe* species retrieved from DNA databases. The alignment matrix consisted of 92 sequences and 1 384 characters, of which 284 (20.5 %) characters were variable and 216 (15.6 %) were informative for parsimony analysis (TreeBASE ID: S27001). Two sequences of *E. coryloposidis* were used as outgroup in accordance with Takamatsu *et al.* (2015). About 7×10^5 equally most parsimonious trees with 671 steps were constructed by the MP analysis. Tree topologies were almost consistent among the trees, except for branching orders of the terminal branches and branch length. One of the trees is shown in Fig. 1. A phylogenetic tree generated from ML analysis was almost identical to the MP tree, and thus only BS values were shown on the MP tree. The 40 sequences from *Erysiphe* on *Lonicera* spp. were divided into six distinct clades strongly supported by high BS values. These six clades were not monophyletic and roughly separated in two groups: one group consisting of *E. loniceræ s. str.*, *E. flexibilis*, and *E. erlangshanensis*, and another group of *E. ehrenbergii*, *E. lonicerina*, and *E. miuræ*.

Taxonomy

Taxonomic revision of *Erysiphe loniceræ s. lat.*

On account of the present phylogenetic revision, *Erysiphe loniceræ s. lat.* has to be divided into two separate species. The two species are phylogenetically and morphologically different and will be referred to as *E. loniceræ s. str.* and *Erysiphe ehrenbergii*. *E. ehrenbergii* is based on *Microsphaera ehrenbergii*, but it is now not applied as it was in previous applications, in which it was confined only to powdery mildew on *Lonicera tatarica*, either as a species of its own – as it was originally introduced – or as a variety of *Erysiphe/Microsphaera loniceræ*, as the phylogenetic analyses revealed a co-evolution

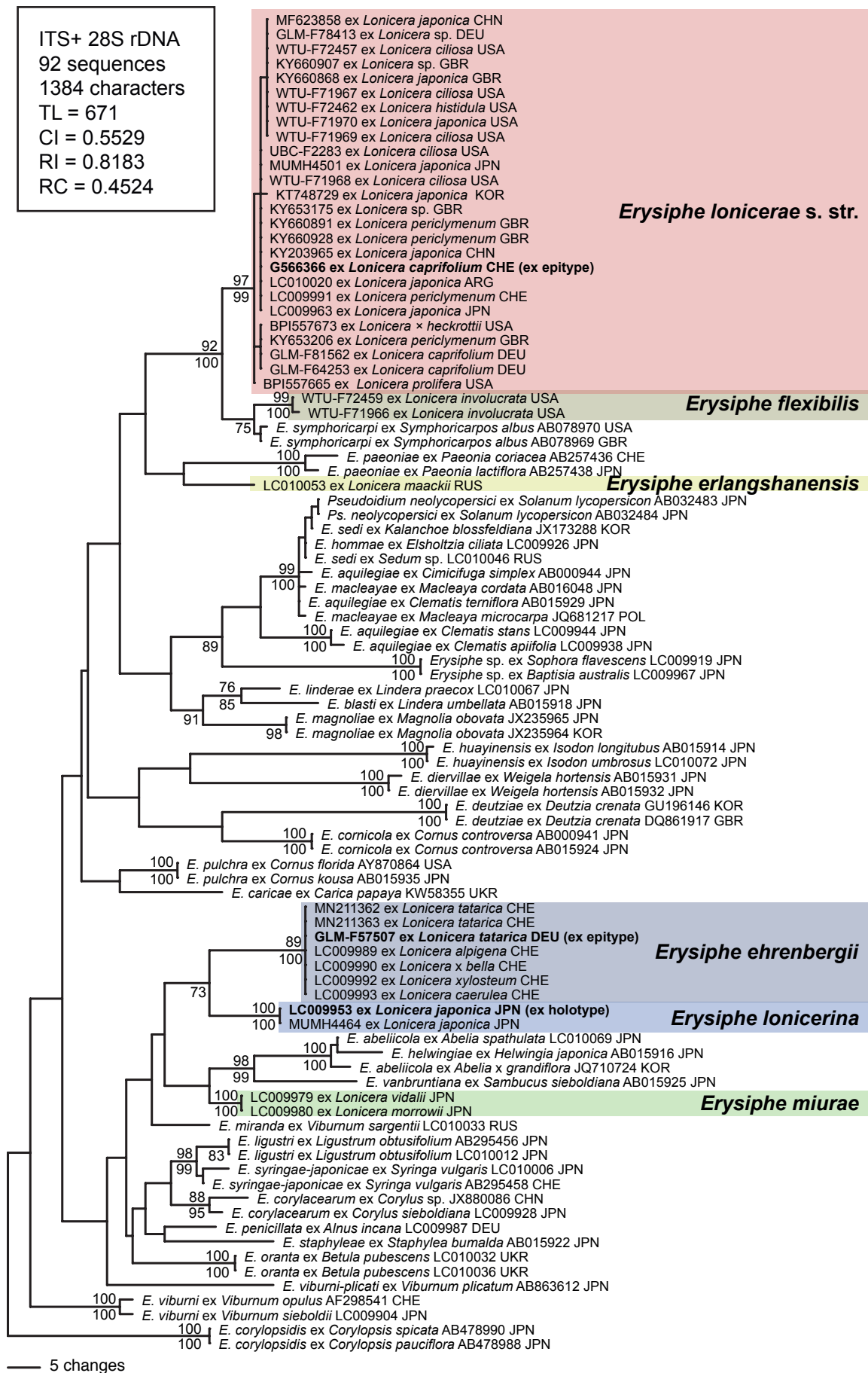


Fig. 1. Phylogenetic tree of *Erysiphe* species on *Lonicera* spp. based on combined DNA sequences of internal transcribed spacer (ITS) region and the 5'-end of the 28S rDNA (including domains D1 and D2). Horizontal branch lengths are proportional to the number of substitutions that were inferred to have occurred along a particular branch of the tree. BS ($\geq 70\%$) values by the maximum parsimony (MP) and maximum likelihood (ML) methods are shown above and below the branches, respectively.

Table 1. List of fungi, hosts, vouchers, and NCBI accession numbers of the sequences used in this study. ‘na’ indicates information not available. ‘**’ indicates ITS and 28S rDNA sequences were deposited separately. ID in parenthesis shows 28S rDNA sequence.

Fungal name	Host	Voucher	NCBI ID (ITS+28S rDNA)	References
<i>Erysiphe abeliicola</i>	<i>Abelia spathulata</i>	MUMH4472	LC010069	Takamatsu <i>et al.</i> (2015)
	<i>Abelia ×grandiflora</i>	KUS-F25628	JQ710724	Cho <i>et al.</i> (2012b)
<i>E. aquilegiae</i>	<i>Cimicifuga simplex</i>	TPU-495	AB000944 (AB022405)*	Takamatsu <i>et al.</i> (1998)
	<i>Clematis apiifolia</i>	MUMH277	LC009938	Takamatsu <i>et al.</i> (2015)
	<i>Clematis stans</i>	MUMH293	LC009944	Takamatsu <i>et al.</i> (2015)
	<i>Clematis terniflora</i>	MUMH98	AB015929 (LC009920)*	Takamatsu <i>et al.</i> (1999)
<i>E. blasti</i>	<i>Lindera umbellata</i>	MUMH2	AB015918 (LC009905)*	Takamatsu <i>et al.</i> (1999)
<i>E. caricae</i>	<i>Carica papaya</i>	KW58355	LC009901	Takamatsu <i>et al.</i> (2015)
<i>E. cornicola</i>	<i>Cornus controversa</i>	MUMH90	AB000941 (AB022389)*	Takamatsu <i>et al.</i> (1998)
	<i>Cornus controversa</i>	YNMH12992	AB015924	Takamatsu <i>et al.</i> (1999)
<i>E. corylacearum</i>	<i>Corylus sieboldiana</i>	MUMH199	LC009928	Takamatsu <i>et al.</i> (2015)
	<i>Corylus</i> sp.	Dai13042	JX880086	Liu <i>et al.</i> (2013)
<i>E. corylopsidis</i>	<i>Corylopsis pauciflora</i>	MUMH4174	AB478988 (AB478984)*	Shiroya & Takamatsu (2009)
	<i>Corylopsis spicata</i>	MUMH4104	AB478990 (AB478986)*	Shiroya & Takamatsu (2009)
<i>E. deutziae</i>	<i>Deutzia crenata</i>	KUS-F24694	GU196146	Park <i>et al.</i> (2012)
	<i>Deutzia crenata</i>	K(M)140025	DQ861917	Denton & Henricot (2007)
<i>E. diervillae</i>	<i>Weigela hortensis</i>	TPU-1669	AB015931 (LC010087)*	Takamatsu <i>et al.</i> (1999)
	<i>Weigela hortensis</i>	MUMH28	AB015932	Takamatsu <i>et al.</i> (1999)
<i>E. ehrenbergii</i>	<i>Lonicera alpigena</i>	MUMH1434	LC009989	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera caerulea</i>	MUMH1440	LC009993	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera xylosteum</i>	MUMH1438	LC009992	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera ×bella</i>	MUMH1435	LC009990	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera tatarica</i>	G566307	MN211362	This study
	<i>Lonicera tatarica</i>	G566299	MN211363	This study
<i>E. erlangshanensis</i>	<i>Lonicera maackii</i>	MUMH2586	LC010053	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera involucrata</i>	WTU-F072459	MW045572	This study
<i>E. flexibilis</i>	<i>Lonicera involucrata</i>	WTU-F071966	MW045573	This study
	<i>Helwingia japonica</i>	MUMH110	AB015916	Takamatsu <i>et al.</i> (1999)
<i>E. hommae</i>	<i>Elsholtzia ciliata</i>	MUMH167	LC009926	Takamatsu <i>et al.</i> (2015)
<i>E. huayinensis</i>	<i>Isodon longitubus</i>	MUMH30	AB015914	Takamatsu <i>et al.</i> (1999)
	<i>Isodon umbrosus</i>	MUMH4644	LC010072	Takamatsu <i>et al.</i> (2015)
<i>E. ligustri</i>	<i>Ligustrum obtusifolium</i>	MUMH264	AB295456	Seko <i>et al.</i> (2011)
	<i>Ligustrum obtusifolium</i>	MUMH2244	LC010012 (AB571057)*	Seko <i>et al.</i> (2011)
<i>E. loniceræ</i>	<i>Lonicera caprifolium</i>	G566366	MN277393	This study
	<i>Lonicera caprifolium</i>	GLM-F81562	MN277394	This study
	<i>Lonicera caprifolium</i>	GLM-F64253	MN277395	This study
	<i>Lonicera ciliosa</i>	UBC-F2283	MW045561	This study
	<i>Lonicera ciliosa</i>	WTU-F072457	MW045562	This study
	<i>Lonicera ciliosa</i>	WTU-F071967	MW045563	This study
	<i>Lonicera ciliosa</i>	WTU-F071969	MW045564	This study
	<i>Lonicera ciliosa</i>	WTU-F071968	MW045565	This study
	<i>Lonicera ×heckrottii</i>	BPI557673	MW045566	This study
	<i>Lonicera hispidula</i>	WTU-F072462	MW045567	This study
	<i>Lonicera japonica</i>	MUMH2481	LC010020	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera japonica</i>	MUMH835	LC009963	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera japonica</i>	JGSJYH002	MF623858	na

Table 1. (Continued).

Fungal name	Host	Voucher	NCBI ID (ITS+28S rDNA)	References
	<i>Lonicera japonica</i>	OE2015PMCS202	KY660868	na
	<i>Lonicera japonica</i>	KUS-F27344	KT748729	Lee <i>et al.</i> (2016)
	<i>Lonicera japonica</i>	Jinyinhua	KY203965	na
	<i>Lonicera japonica</i>	WTU-F071970	MW045568	This study
	<i>Lonicera japonica</i>	MUMH4501	MW045569	This study
	<i>Lonicera periclymenum</i>	MUMH1436	LC009991	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera periclymenum</i>	OE2015PM30CS	KY660891	na
	<i>Lonicera periclymenum</i>	OE2015PM36CS	KY660928	na
	<i>Lonicera periclymenum</i>	OE2014PM24CS	KY653206	na
	<i>Lonicera prolifera</i>	BPI557665	MW045570	This study
	<i>Lonicera</i> sp.	OE2015PM51CS	KY660907	na
	<i>Lonicera</i> sp.	OE2015PM141CS	KY653175	na
	<i>Lonicera</i> sp.	GLM-F78413	MT277391	This study
<i>E. lonicerina</i>	<i>Lonicera japonica</i>	MUMH601	LC009953	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera japonica</i>	MUMH4464	MW045571	This study
<i>E. linderae</i>	<i>Lindera praecox</i>	MUMH4379	LC010067	Takamatsu <i>et al.</i> (2015)
<i>E. macleayae</i>	<i>Macleaya cordata</i>	TPU-1873	AB016048 (LC010092)*	Takamatsu <i>et al.</i> (1999)
	<i>Macleaya microcarpa</i>	KUS-F24459	JQ681217	Park <i>et al.</i> (2012)
<i>E. magnoliae</i>	<i>Magnolia obovata</i>	MUMH5227	JX235965	Takamatsu <i>et al.</i> (2013)
	<i>Magnolia obovata</i>	KUS-F26388	JX235964	Takamatsu <i>et al.</i> (2013)
<i>E. miranda</i>	<i>Viburnum sargentii</i>	MUMH2561	LC010033	Takamatsu <i>et al.</i> (2015)
<i>E. miurae</i>	<i>Lonicera morrowii</i>	MUMH1216	LC009980	Takamatsu <i>et al.</i> (2015)
	<i>Lonicera vidalii</i>	MUMH1209	LC009979	Takamatsu <i>et al.</i> (2015)
<i>E. ornata</i>	<i>Betula pubescens</i>	MUMH2560/DB53529	LC010032	Takamatsu <i>et al.</i> (2015)
	<i>Betula pubescens</i>	MUMH2565/DB53525	LC010036	Takamatsu <i>et al.</i> (2015)
<i>E. paeoniae</i>	<i>Paeonia coriacea</i>	MUMH1449	AB257436	Takamatsu <i>et al.</i> (2006)
	<i>Paeonia lactiflora</i>	MUMH146	AB257438	Takamatsu <i>et al.</i> (2006)
<i>E. penicillata</i>	<i>Alnus incana</i>	MUMH1432	LC009987	Takamatsu <i>et al.</i> (2015)
<i>E. pulchra</i>	<i>Cornus florida</i>	na	AY870864	Shi <i>et al.</i> (2009)
	<i>Cornus kousa</i>	TPU-1731	AB015935 (LC010089)*	Takamatsu <i>et al.</i> (1999)
<i>E. sedi</i>	<i>Kalanchoe blossfeldiana</i>	KUS-F24911	JX173288	Cho <i>et al.</i> (2012a)
	<i>Sedum</i> sp.	MUMH2576	LC010046	Takamatsu <i>et al.</i> (2015)
<i>E. staphyleae</i>	<i>Staphylea bumalda</i>	MUMH16	AB015922 (LC009908)*	Takamatsu <i>et al.</i> (1999)
<i>E. symphoricarpi</i>	<i>Symphoricarpos albus</i>	MUMH1428	AB078970	Kiss <i>et al.</i> (2002)
	<i>Symphoricarpos albus</i>	MUMH974	AB078969 (LC009970)*	Kiss <i>et al.</i> (2002)
<i>E. syringae-japonicae</i>	<i>Syringa vulgaris</i>	MUMH1916	LC010006 (AB571060)*	Seko <i>et al.</i> (2011)
	<i>Syringa vulgaris</i>	MUMH1736	AB295458	Seko <i>et al.</i> (2011)
<i>E. vanbruntiana</i>	<i>Sambucus sieboldiana</i>	MUMH17	AB015925 (LC009909)*	Takamatsu <i>et al.</i> (1999)
<i>E. viburni</i>	<i>Viburnum opulus</i>	VPRI22168	AF298541	Cunnington <i>et al.</i> (2003)
	<i>Viburnum sieboldii</i>	MUMH1	LC009904	Takamatsu <i>et al.</i> (2015)
<i>E. viburni-plicati</i>	<i>Viburnum plicatum</i>	MUMH794	AB863612	Meeboon & Takamatsu (2015)
<i>Erysiphe</i> sp.	<i>Baptisia australis</i>	MUMH897	LC009967 (LC009966)*	Takamatsu <i>et al.</i> (2015)
	<i>Sophora flavescens</i>	MUMH89	LC009919	Takamatsu <i>et al.</i> (2015)
<i>Pseudoidium neolycopersici</i>	<i>Solanum lycopersicon</i>	MUMH66	AB032483 (LC009912)*	Kiss <i>et al.</i> (2005)
	<i>Solanum lycopersicon</i>	DNA231	AB032484	Kiss <i>et al.</i> (2005)

between the powdery mildews concerned along with the subgenera of *Lonicera*.

Erysiphe ehrenbergii (Lév.) U. Braun, M. Bradshaw & S. Takam., **comb. nov.** MycoBank MB837569.

Basionym: *Microsphaera ehrenbergii* Lév., *Ann. Sci. Nat., Bot.*, Sér. 3, **15**: 381. 1851.

Synonyms: *Microsphaera loniceræ* var. *ehrenbergii* (Lév.) U. Braun, *Mycotaxon* **15**: 127. 1982.

Erysiphe loniceræ var. *ehrenbergii* (Lév.) U. Braun & S. Takam., *Schlechtendalia* **4**: 10. 2000.

Illustrations: Magnus (1898: pl. II, figs 13–15), Blumer (1933: 298, fig. 108 A–C), Braun (1982a: 128, fig. 12b; 1984: 234, fig. 29, pl. 5; 1987: 329, pl. 104; 1995: 278, pl. 55, fig. B), Salata (1985: 168, fig. 67), Chen *et al.* (1987: 203, fig. 104), Simonyan (1994: 161, fig. 35), Liu (2010: 106, fig. 49), Braun & Cook (2012: 478, fig. 551).

Exsiccatae [on *Lonicera coeruleum* (L.co.), *L. tatarica* (L.t.), *L. xylosteum* (L.x.)]: Allescher & Schnabl, *Fungi Bav.* 530 (L.t.). Erikss., *Fungi Paras. Scand.* 144 (L.t.). Fuckel, *Fungi Rhen.* Exs. 696 (L.t.). Kochm., *Mycoth. Polon.* 132 (L.t.). Krieger, *Fungi Saxon.* Exs. 1224 (L.t.). Krypt. Exs. 2619 (L.t.). Lepik, *Fungi Estonici* Exs. 256–258 (L.t.). Linh., *Fungi Hung.* Exs. 357 (L.x.). Lundell & Nannf., *Fungi Exs. Suec.* 1483 (L.t.). Neger, *Forstschäd. Pilze* 155 (L.co.). Rabenh., *Fungi Eur.* Exs. 556, 2651 (L.t.). Rabenh., *Klotzschii Herb. Viv. Mycol.* 473 (L.t.). Rehm, *Ascomyc.* 847 (L.x.). Syd., *Mycoth. Germ.* 2521 (L.t.). Thüm., *Mycoth. Univ.* 450 (L.t.). Weese, *Eumyc. Sel. Exs.* 630 (L.t.).

Description: Mycelium on leaves, amphigenous, effuse or in thin white patches, persistent or almost so on the upper leaf surface, less developed and evanescent below; hyphae branched, septate, hyaline, thin-walled, smooth, 2–7 µm wide; hyphal appressoria slightly to distinctly lobed, occasionally almost nipple-shaped, 3–7 µm diam, solitary or occasionally in opposite pairs. *Conidiophores* arising from superficial hyphae, erect, terminal on mother cells, basal septum at the junction with the mother cell or slightly elevated (up to 8 µm), 45–90 µm long; foot-cells straight to moderately curved or sinuous (conidiophores with straight and curved-sinuous foot-cells mixed in all collections), 15–40 × 5–9 µm, width uniform throughout, followed by 1–3(–4) cells mostly shorter than the foot-cell, sometimes about as long as the foot-cell or only slightly longer (above all the secondary cell), 8–30 µm long, forming solitary conidia. *Conidia* cylindrical, subcylindrical to ellipsoid-ovoid, 23–39 × 10–17 µm, length/width ratio 1.9–3.2 (on average 2.4, N = 30), ends more or less truncated, apex rounded in primary conidia, conidial germination not observed. *Chasmothecia* amphigenous, on the upper leaf surface gregarious to scattered, below scattered, subglobose, 60–120 µm diam; peridial cells polygonal, rounded to irregularly shaped, 8–30 µm diam. *Appendages* 5–22, number of appendages correlated with the size of the chasmothecia, more or less equatorial, radiating, stiff, straight to curved, 1–2.5 times as long as the chasmothecial diam (60–255 µm), 6–10 µm wide below, aseptate or with a single basal septum, sometimes with a second or even third elevated septum, up to 70 µm from the base, colourless or brown below the septa, *i.e.*, when two or three septa are formed pigmented part up to 70 µm long, wall thickened, 1.5–3 µm wide below, thinner towards the tip, smooth to verruculose, apex 3–5(–6) times regularly to

somewhat irregularly dichotomously branched, loose to dense, primary branches short or oblong, 15–55 µm in length, tips of the ultimate branchlets straight or mixed with a few curved ones for a long time or up to the end of the season, a higher percentage recurved when fully mature, but straight and curved ones always mixed. *Asci* 2–6, broad ellipsoid, obovoid to saccate, sessile to short-stalked, 35–60 × 20–40 µm, hyaline, wall 1–3 µm thick, terminal oculus indistinct, 5–15 µm diam, 3–5-spored. *Ascospores* broad ellipsoid-ovoid, 14–26 × 9–14 µm, at first pale yellowish or olivaceous, later colourless.

Type: Léveillé (1851: pl. 8, fig. 22 – **lectotype**, designated by Braun 1987: 329). **Epitype:** **Germany**, Sachsen-Anhalt, Salzlandkreis, Calbe (Saale), Wartenberg, on *Lonicera tatarica*, 27 Sep. 2002, *H. Jage* (GLM-F57507; designated here, MycoBank MBT394140); ex-epitype sequence – MN277392.

Additional materials examined: **Armenia**, Gyumri (previously Leninakan), park, on *Lonicera tatarica*, 7 Sep. 1969, *S. Simonyan* (HAL 155 F). **Germany**, Sachsen, Landkreis Zwickau, Limbach-Oberfrohna, on *Lonicera coerulea*, 15 Jul. 2006, *F. Dämmrich* (GLM-F89964); Hessen, Vogelsbergkreis, east north east of Schlitz, on *Lonicera tatarica*, 22 Jul. 2000, *H. Jage* (GLM-F48342); Sachsen, Leipzig-Neustadt, on *Lonicera tatarica*, 22 Sep. 1994, *H. Jage* (GLM-F48823); Sachsen, Landkreis Zwickau, Reinsdorf, on *Lonicera tatarica*, 25 Sep. 1994, *H. Jage* (GLM-F48831); Sachsen, Görlitz-Rauschwalde, on *Lonicera tatarica*, 18 Aug. 2004, *H. Boyle* (GLM-F53683); Sachsen, Zwickau, on *Lonicera tatarica*, 20 Sep. 2006, *H. Boyle & S. Hoeflich* (GLM-F78413); Sachsen, Freiberg, on *Lonicera tatarica*, 1 Aug. 2007, *F. Klenke* (GLM-F104594); Sachsen-Anhalt, Halle (Saale), centre, green belt, on *Lonicera tatarica*, 18 Sep. 1977, *U. Braun* (HAL 152 F); Sachsen-Anhalt, Köthen, centre, college garden, on *Lonicera tatarica*, Sep. 1983, *U. Braun* (HAL 666 F); Sachsen-Anhalt, Gräfenhainichen, Hohenlubast, on *Lonicera tatarica*, 3 Oct. 1987, *H. Jage* (GLM-F50556); Sachsen-Anhalt, Landkreis Wittenberg, Kemberg, on *Lonicera tatarica*, 4 Oct. 1999, *H. Jage* (GLM-F50068); Sachsen-Anhalt, Landkreis Wittenberg, south of Kemberg, *Pinus sylvestris* forest, on *Lonicera tatarica*, 17 Oct. 1999, *H. Jage* (GLM-F477578); Sachsen-Anhalt, Wittenberg, on *Lonicera tatarica*, 15 Oct. 1999, *H. Jage* (GLM-F47531); Sachsen-Anhalt, Landkreis Wittenberg, Oranienbaum-Wörlitz, OT Wörlitz, park, on *Lonicera tatarica*, *H. Jage* (GLM-F47553); Sachsen-Anhalt, Magdeburg, centre, on *Lonicera tatarica*, 15 Nov. 2000, *H. Jage et al.* (GLM-F47206); Sachsen-Anhalt, Landkreis Wittenberg, Kemberg, on *Lonicera tatarica*, 9 Sep. 2000, *H. Jage* (GLM-F49074); Sachsen-Anhalt, Wittenberg, on *Lonicera tatarica*, 27 Sep. 2000, *H. Jage* (GLM-F49161); Sachsen-Anhalt, Landkreis Bitterfeld, Muldestausee, Pouch, Schloßpark, on *Lonicera tatarica*, 9 Oct. 2000, *H. Jage* (GLM-F49382); Thüringen, Landkreis Gotha, Friedrichroda, on *Lonicera tatarica*, 25 Sep. 2004, *H. Jage* (GLM-F65111); Hessen, Schwalm-Eder-Kreis, Bad Zwesten, OT Oberurff-Schiffelborn, on *Lonicera xylosteum*, 14 Jul. 2007, *C. Klenke* (GLM-F104900); Sachsen, Vogtlandkreis, Pöhl, OT Jocketa, on *Lonicera xylosteum*, 4 Sep. 1999, *H. Jage & F. Klenke* (GLM-F103509); Sachsen, Landkreis Görlitz, Beiersdorf, on *Lonicera xylosteum*, 2 Sep. 2004, *H. Boyle* (GLM-F53837); Sachsen, Landkreis Sächsische Schweiz-Osterzgebirge, Bad Schandau, Waltersdorf-Sellnitz, on *Lonicera xylosteum*, 9 Sep. 2009, *F. Klenke* (GLM-F102908). **Finland**, Nylandia, Helsinki, Engel Park, on *Lonicera tatarica*, 12 Jul. 1976, *P. Alanko* (HAL 150 F). **Russia**, Moscou, Lomonosov University campus, on *Lonicera tatarica*, 20 Jul. 1977, *U. Braun* (HAL 151 F). **Switzerland**, Genève, Jardin botanique, on *Lonicera alpigena*, 4 Sep. 1995, *A. Boley* (HAL 602 F); Genève, Jardin botanique, on *Lonicera xbella*, 27 Oct. 1997, *A. Boley* (G 566324); Bern, Jardin botanique, on *Lonicera coerulea*, 25 Oct. 1995, *A. Boley* (G 566363); Genève, Jardin botanique, on *Lonicera coerulea*, 26 June 2001, *A. Boley* (G 566364); *ibid.*, 9 Jul. 2002, *A. Boley*

(G 566365); *ibid.*, 18 Oct. 2006, A. Bolay (G 566326); Genève, Jardin botanique, on *Lonicera pyrenaica*, 20 Jun. 1995, A. Boley (G 566358); *ibid.*, 28 Aug. 1995, A. Boley (G 566346, HAL 600 F); *ibid.*, 4 Oct. 2000, A. Bolay (G 566345); *ibid.*, 5 Oct. 2010, A. Bolay (G 566347); Genève, Jardin botanique, on *Lonicera tatarica*, 29 Sep. 1997, A. Bolay (G 566348); NE, Neuchâtel, on *Lonicera tatarica*, 11 Oct. 2002, A. Bolay (G 566349); Genève, Jardin botanique, on *Lonicera xylosteum*, 8 Sep. 1999, A. Bolay (G 566350, G 566351); *ibid.*, on *Lonicera xylosteum*, 19 Aug. 2002, A. Bolay (G 566352).

Host range and distribution: on species of *Lonicera* subgen. *Chamaecerasus*; *Lonicera alpigena* (Europe: Austria, France, Germany, Switzerland, former Yugoslavia), *L. ×bella* (Europe: Estonia, Romania, Russia, Switzerland), *L. coerulea* (Europe: Germany, Switzerland), *L. microphylla* (Asia: China), *L. fragrantissima* (Europe: Russia, Slovakia, Ukraine), *L. nigra* (Europe: France, Germany, Romania, Russia, Slovakia, Spain, Switzerland, Ukraine, former Yugoslavia), *L. pyrenaica* (Europe: Romania, Switzerland), *L. tatarica* (Asia: China, Japan, Kazakhstan, Kyrgyzstan, Russia, Far East; Caucasus: Armenia; Europe: Austria, Belarus, Czech Republic, Estonia, Finland, Germany, Hungary; Europe: Latvia, Lithuania, Netherlands, Norway, Poland, Romania, Serbia, Slovakia, Sweden, Switzerland, UK, Ukraine; North America: Canada, USA: Kentucky, Maine, Minnesota, North Dakota, Iowa, New York, Pennsylvania, Wisconsin), *L. xylosteum* (Caucasus: Armenia; Europe: Bulgaria, Czech Republic, Finland, France, Germany, Hungary, Lithuania, the Netherlands, Norway, Poland, Romania, Russia, Slovakia, Sweden, Switzerland, former Yugoslavia) [Amano 1986; Braun (1987, 1995) Heluta (1989), Paulech (1995), Grigaliūnaitė (1997), Girilovich *et al.* (2005), Braun & Cook (2012)]; <https://nt.ars-grin.gov/fungalbases/fungushost/fungushost.cfm>].

Notes: The asexual morph of *E. ehrenbergii* develops in early summer to early autumn (in Central Europe in June to September), either together with the sexual morph or it ceases with the chasmothecial formation (in Europe it is initiated in early summer, usually July, but lasting into November). In collections from October to November, infections are usually inconspicuous, mostly hypophyllous, without any trace of mycelium or the asexual morph. In *Erysiphe ehrenbergii*, the tips of the ultimate branchlets, of the terminal branched part of the chasmothecial appendages, are straight, with a few somewhat recurved tips (in most collections, especially in mature chasmothecia collected from September to November). A higher percentage of recurved tips have been observed, but only in a few specimens, collected in autumn. This characteristic is in contrast to *Erysiphe lonicerae* s. str., which is characterised by having frequently recurved tips in fully mature collections collected later in the season. Additionally, the asexual morph differs slightly in that the conidia in *E. lonicerae* tend to be longer (25–55 × 11–24 µm vs. 23–39 × 10–17 µm in *E. ehrenbergii*).

Erysiphe flexibilis M. Bradshaw, U. Braun & S. Takam., *stat. et nom. nov.* MycoBank MB837570. Fig. 2.

Basionym: *Microsphaera lonicerae* var. *flexuosa* U. Braun, *Mycotaxon* **15**: 129. 1982 [non *Erysiphe flexuosa* (Peck) U. Braun & S. Takam., 2000].

Synonyms: *Microsphaera caprifoliacearum* var. *flexuosa* (U. Braun) U. Braun, *Nova Hedwigia* **39**: 229. 1984.

Erysiphe caprifoliacearum var. *flexuosa* (U. Braun) U. Braun & S. Takam., *Schlechtendalia* **4**: 6. 2000.

Etymology: *Flexibilis* – referring to the flexuous chasmothecial appendages.

Illustrations: Braun (1982a: 128, fig. 12c; 1984: 232, pl. 4, fig. 23b; 1987: 432, pl. 197), Braun & Cook (2012: 444, fig. 518).

Exsiccatae: Solh., Mycolf. Saximon. Exs. 1321.

Description: Mycelium amphigenous, white, effuse or in thin patches; hyphae straight to somewhat sinuous, branched at right angles, thin-walled, hyaline, smooth, septate, hyphal cells 35–70 µm long and 3–6 µm wide; hyphal appressoria solitary or occasionally in opposite pairs, nipple-shaped to slightly lobed, 3–6 µm diam. *Conidiophores* arising from the upper surface of hyphal mother cells, in the middle of the mother cell or somewhat towards one septum, erect, straight or occasionally somewhat flexuous, 60–100 µm long, width of the conidiophores mostly somewhat increasing from base to top, foot-cells cylindrical or subcylindrical, straight or somewhat curved to slightly sinuous at the very base, basal septum at the junction with the mother cells or slightly elevated (to 5 µm), foot-cells 30–58 µm long and 5–7 µm wide, followed by 1–2 shorter cells, 12–40 µm long and 6–9 µm wide, conidia formed singly, occasionally adhering in short “false chains” (but not catenescence). *Conidia* ellipsoid-ovoid to subcylindrical, ends truncated to rounded, 24–43 × 11–19 µm, length/width ratio 1.7–3.2 (on average 2.6, N = 30). *Chasmothecia* amphigenous, scattered to gregarious, 65–120 µm diam; peridium cells irregularly polygonal, 10–25 µm diam. *Appendages* more or less equatorial, 4–15, 1.5–3.5(–4) times as long as the chasmothecial diam, 6–10 µm wide below, flexuous, septate or with a single basal septum, hyaline, wall thickened below, thinner towards the tip, smooth to rough, apex 3–6 times tightly and relatively regularly branched, branches of all orders usually short, not elongated, tips of the ultimate branchlets straight. *Asci* 3–10, broad obovoid-saccate, 40–60 × 25–40 µm, subsessile or short-stalked, 4–5-spored. *Ascospores* ellipsoid-ovoid(-subglobose), 15–24 × 8–14 µm, colourless.

Type: USA, Wyoming, Centennial, on *Lonicera involucrata*, 22 Aug. 1911, *E. Bartholomew* [Barthol., Fungi Columb. 3720] (K, s.n. – **holotype**). **Isotypes:** Barthol., Fungi Columb. 3720 (e.g. BPI 556098, 556100, 556101; FLAS-F-01605; MSC0250454; NEB59550, 59595; PUL 21000; WIS-F24361; WSP 3918). Reference sequence (retrieved from WTU-F-072459, on *L. involucrata*, USA, Washington): MW045572.

Host range and distribution: on host species of *Lonicera* subgen. *Chamaecerasus*; *Lonicera canadensis* (North America: Canada; USA: New York, Ohio, Wisconsin), *L. involucrata* (North America: Canada; USA, Washington, Wyoming).

Notes: Braun (1982a) described *Microsphaera lonicerae* var. *flexuosa* with *Lonicera involucrata* as type host [the citation of a collection on *L. ciliosa* as type of this variety in Braun & Cook (2012) is incorrect]. Sequences obtained from powdery mildew on *Lonicera involucrata* form a separate clade in a sister position to the *Erysiphe symphoricarpi* clade, supporting the status that this powdery mildew is a distinct species. The name *Microsphaera lonicerae* var. *flexuosa* is available for the taxon involved, which is morphologically very close to *E. symphoricarpi* (except for more compact and more regularly branched

terminal parts of the chasmothecial appendages, in contrast to apically more loosely and irregularly branched appendages in *E. symphoricarpi*, and nipple-shaped or only slightly lobed hyphal appressoria and wider conidiophores, 5–7 μm wide below and 7–9 μm wide above, in contrast to distinctly lobed hyphal appressoria and narrower conidiophores, 4–6 μm wide below and 5–7 μm wide above, in *E. symphoricarpi*). The allocation

of var. *flexuosa* to *E. caprifoliacearum*, now a synonym of *E. loniceræ* s. str., was undoubtedly wrong.

Braun (1984) and Braun & Cook (2012) listed *Lonicera canadensis*, *L. ciliosa*, and *L. involucrata* as host species for this North American variety. *Lonicera involucrata* as well as *L. canadensis* are species of *Lonicera* subgen. *Chamaecerasus*. The powdery mildew on *L. canadensis* coincides morphologically

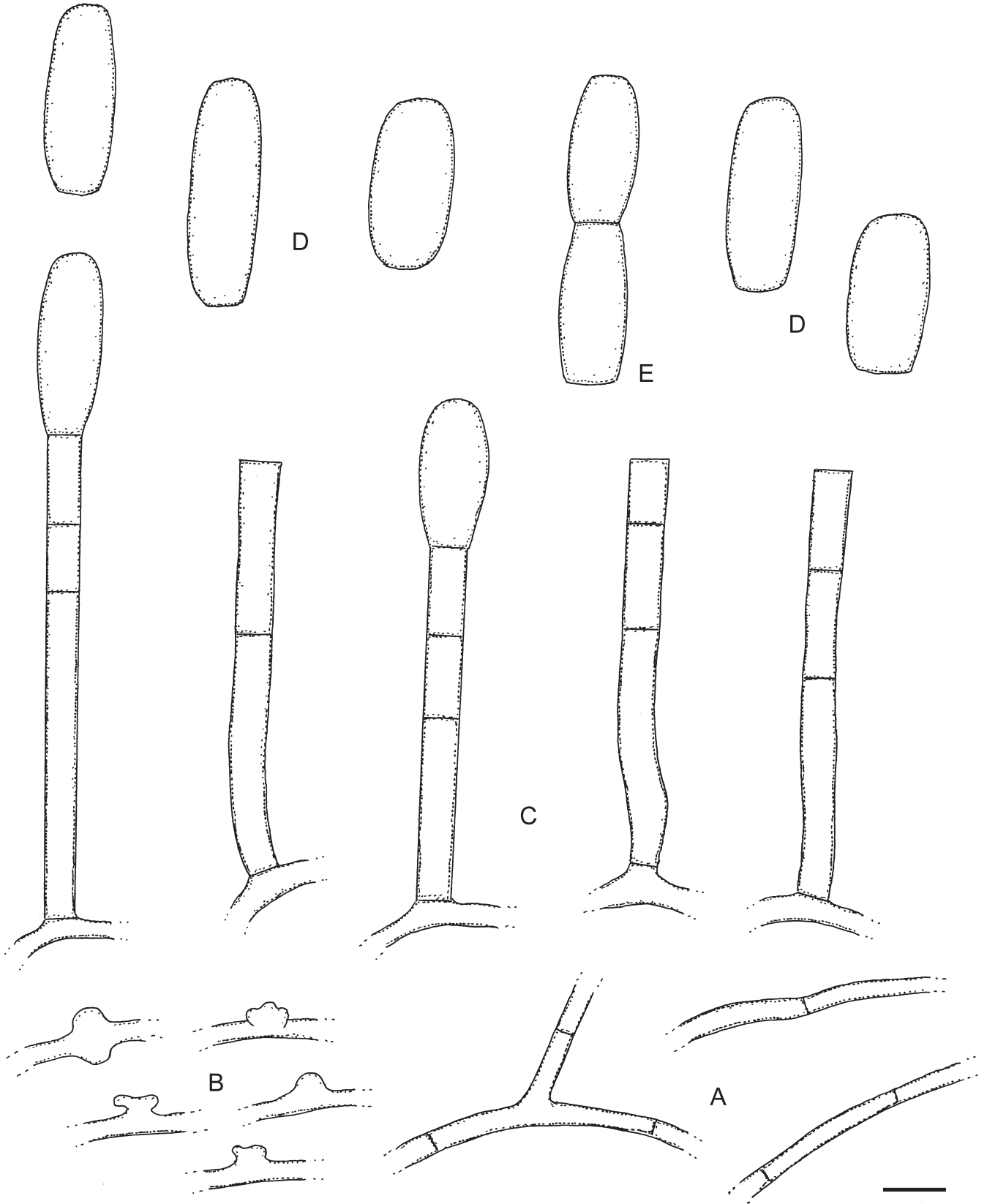


Fig. 2. *Erysiphe flexilis* (HAL 3348 F). **A.** Hyphae. **B.** Hyphal appressoria. **C.** Conidiophores. **D.** Conidia. **E.** Conidia in a short “false chain”. Scale bar = 10 μm . U. Braun del.

with collections on *L. involucreta*, but the identification as *E. flexibilis* is still in need of phylogenetic confirmation. Powdery mildew on *L. ciliosa* (*Lonicera* subgen. *Lonicera*) has to be excluded from *Erysiphe flexibilis* and pertains to *E. lonicerae* s. str. (see Fig. 1). A German collection of *Erysiphe* on *L. involucreta* has been examined (Sachsen, Görlitz-Rauschwalde, on *Lonicera involucreta*, 28 Sep. 2008, S. Hoeflich, GLM-F91168, only asexual morph), however, it is unclear if it constitutes an introduction of *E. flexibilis* or if the host was infected by *E. ehrenbergii*.

Erysiphe lonicerae DC., *Fl. franç.* 6: 107. 1815 (s. str.)

Synonyms: *Alphitomorpha divaricata* var. *lonicerae* (DC.) Schltdl., *Verh. Ges. Naturf. Freunde Berlin* 1: 49. 1819.

Erysiphe divaricata var. *lonicerae* (DC.) Link, *Sp. pl.* 4, 6(1): 113. 1824.

Erysiphe penicillata var. *lonicerae* (DC.) Fr., *Syst. mycol.* 3: 244. 1829.

Microsphaera lonicerae (DC.) G. Winter, in *Rabenhorst's Krypt.-Fl., Pilze*, 1(2): 36. 1884.

Microsphaera penicillata var. *lonicerae* (DC.) W.B. Cooke, *Mycologia* 44: 572. 1952.

Microsphaera caprifoliacearum U. Braun, *Mycotaxon* 14: 369. 1982, **syn nov.** [type: **Canada**, London, on *Lonicera* sp., Sep. 1896, J. Dearness [Ellis & Everh., *Fungi Columb.* 1032] (PH 41544 – **holotype**); **isotypes**: Ellis & Everh., *Fungi Columb.* 1032 (e.g., BPI 557667, C0285718F, CBRU1231, CLEM-F2589, FLAS-F01592, ISC-F-0087668, MSC0219819, NEB 59557, PUL 18885)]. Reference sequence (retrieved from BPI557673, USA, on *Lonicera x heckrottii*): MW045566.

Erysiphe caprifoliacearum (U. Braun) U. Braun & S. Takam., *Schlechtendalia* 4: 6. 2000.

Illustrations: Léveillé (1851: pl. 9, fig. 26), Salmon (1900: pl. 1, figs 19–20), Jaczewski (1927: 323, fig. 83), Blumer (1933: 299, fig. 109; 1967: 257, fig. 89), Golovin (1956: 337, fig. 12), Sandu-Ville (1967: 268, fig. 47), Braun (1982a: 128, fig. 12a; 1982b: 371, fig. 1; 1982c: 322, fig. 7; 1984: 232, pl. 4, Fig. 23a; 1987: 328, pl. 103, 432, pl. 196; 1995: 278, pl. 55, fig. A), Gorlenko (1983: 45, fig. 12), Eliade (1990: 445, pl. 12, fig. 52), Fakirova (1991: 82, pl. 28, fig. 2), Nomura (1992: 266, fig. 174; 1997: 143, fig. 176), Simonyan (1994: 160, figs 33–34), Paulech (1995: 218, fig. 105), Grigaliūnaitė (1997: 125, fig. 75), Kim *et al.* (2007: 6, figs 1–2), Braun & Cook (2012: 442, fig. 518 A, 477, fig. 550).

Exsiccatae [on *Lonicera caprifolium* (L. ca.), *L. periclymenum* (L. p.)]: Kari, *Fungi Exs. Fenn.* 264 (L. ca.) Kochm. & Salata, *Mycoth. Polon.* 654 (L. p.). *Krypt. Exs.* 124 (L. ca.). Kunze, *Fungi Sel. Exs.* 319 (L. p.). Lundell & Nannf., *Fungi Exs. Suec.* 1482 (L. ca.). Thüm., *Mycoth. Univ.* 1056 (L. ca.).

Description: *Mycelium* on leaves, amphigenous, effuse or in thin white patches, subcircular to irregular, sometimes covering the entire leaf surface, persistent or evanescent (persistent on the upper leaf surface, evanescent below); hyphae branched, branching at right angle, septate, hyaline, thin-walled, smooth, (1.5–)2–6(–7) μm wide; hyphal appressoria solitary, usually with a single appressorium per cells, occasionally with up to four per cell, nipple-shaped to lobed, 2–8 μm diam. *Conidiophores* arising from superficial hyphae, erect, terminal on mother cells, in the middle of the mother cell or towards one septum, 50–120 μm long (without conidia); foot-cells (12–)18–55(–75) \times 4–10 μm , straight, cylindrical or subcylindrical to moderately curved

at the base or sinuous, in most cases majority of foot-cells curved-sinuous, followed by 1–3 cells, 8–40 μm long, shorter than the foot cell or about as long, second cell sometimes somewhat longer, basal septum at the junction with the supporting hypha or only slightly elevated (up to 5 μm), conidia formed singly. *Conidia* narrowly cylindrical, subcylindrical or somewhat ellipsoid-cylindrical, 25–45(–55) \times 11–24 μm , length/width ratio 1.7–4.5 (on average 2.8, N = 30), apex rounded to almost truncated, base truncated or almost so, germ tubes perihilar, short to moderately long, terminally unlobed to lobed (*in vivo*). *Chasmothecia* amphigenous, scattered to gregarious, subglobose, 70–120 μm diam, peridial cells polygonal, rounded to irregularly shaped, 8–28 μm diam. *Appendages* (3–)5–16(–20), more or less equatorial, radiating, stiff, straight to curved or longer ones somewhat flexuous, 1–3 times as long as the chasmothecial diam (90–290 μm), stalk simple or occasionally forked in the lower half, 7–12 μm wide below, 6–10 μm wide above, aseptate or with a single basal septum, colourless or pigmented at the base, wall thickened, to 4 μm wide below, thinner towards the tip, smooth to verruculose, apex 3–6 times regularly to irregularly dichotomously branched (branched part 25–85 μm diam), primary and secondary branches short or oblong, 10–30 μm , tips of the ultimate branchlets at first straight, at most mixed with a few recurved ones, but the majority distinctly recurved when fully mature and in specimens collected late in the season. *Asci* 3–12, broad ellipsoid, obovoid to saccate, sessile to short-stalked, 40–70 \times 25–50 μm , hyaline, wall 1–2 μm thick, terminal oculus indistinct, 8–15 μm diam, (2–)3–5-spored. *Ascospores* broad ellipsoid-ovoid, rarely subglobose, 15–24 \times 8–15 μm , colourless or sometimes yellowish.

Type: **France**, on *Lonicera caprifolium*, 1813, J.F. de Chaillet (as "*Erysiphe lonicerae*, No. 503"), in herb. de Candolle (G 00122106 – **holotype**). *Epitype*: **Switzerland**, Genève, Jardin botanique, on *Lonicera caprifolium*, 16 Jul. 1997, A. Bolay (G 566366; designated here, MycoBank MBT394141); ex-epitype sequence – MN277393.

Additional materials examined: **Germany**, Bayern, Lindau, on *Lonicera caprifolium*, 29 Jun. 2008, H. Boyle & S. Hoeflich (GLM-F81552); Sachsen, Landkreis Görlitz, Herrnhut, OT Oberrennersdorf, on *Lonicera x heckrottii*, 6 Sep. 2003, collector unknown (GLM-F51351); Sachsen, Görlitz, centre, on *Lonicera periclymenum*, 14 Sep. 2005, H. Boyle (GLM-F70452); Sachsen, Landkreis Görlitz, Johnsorf, Kurpark, on *Lonicera periclymenum*, 12 Aug. 2007, H. Boyle & S. Hoeflich (GLM-F78479); Sachsen, Landkreis Bauzen, Bischofswerda, on *Lonicera periclymenum*, 12 Aug. 2007, H. Boyle & S. Hoeflich (GLM-F81067); Sachsen-Anhalt, Salzlandkreis, Calbe (Saale), on *Lonicera caprifolium*, 6 Sep. 1998, H. Jage (GLM-F49931); Sachsen-Anhalt, Saalekreis, Mücheln, OT Branderoda, on *Lonicera caprifolium*, 2 Aug. 1999, H. Jage (GLM-F46805); Sachsen-Anhalt, Burgenlandkreis, Freyburg, on *Lonicera caprifolium*, 27 Jun. 1999, U. Richter (GLM-F49112); Sachsen-Anhalt, Zeitz, Moritzburg, medical plant garden, on *Lonicera japonica*, 21 Oct. 2004, H. Jage (GLM-F66310); Sachsen-Anhalt, Landkreis Börde, Wolmirstedt, west of OT Mose, *Pinus sylvestris* forest, on *Lonicera periclymenum*, 25 Jul. 2001, H. Jage (GLM-F56796, GLM-F58634); Sachsen-Anhalt, Altmarkkreis Salzwedel, Arendsee, east of OT Schrampe, on *Lonicera periclymenum*, 26 Sep. 2001, H. Jage (GLM-F56815); Sachsen-Anhalt, Burgenlandkreis, Weißenfels, on *Lonicera periclymenum*, 8 Sep. 2002, H. Jage (GLM-F57487); Sachsen-Anhalt, Landkreis Harz, Quedlinburg, on *Lonicera periclymenum*, 16

Sep. 2003, *H. Boyle* (GLM-F51395); Sachsen-Anhalt, Altmarkkreis Salzwedel, Beetzendorf-Diesdorf, southwest of Beetzendorf, on *Lonicera periclymenum*, 14 Aug. 2004, *H. Jage* (GLM-F62570); Thüringen, Landkreis Nordhausen, about 1.5 km east of Bleicherode, “Eckstein”, on *Lonicera caprifolium*, 19 Aug. 2004, *W. Schulz* (GLM-F64253). **New Zealand**, Auckland, Waikumete cemetery, on *Lonicera japonica*, 22 Jul. 2001, *C.F. Hill* (HAL 1658 F). **Switzerland**, GE, Lullier, Centre horticole, on *L. japonica*, 28 Oct. 1996, *A. Bolay* (G 566367, 566368); *ibid.*, 4 Nov. 1996, *A. Bolay* (G 566369).

Host range and distribution: on host species of *Lonicera* subgen. *Lonicera* and *Lonicera japonica*; *Lonicera caprifolium* (Europe: Austria, Belgium, Estonia, Finland, France, Germany, Greece, Hungary, Italy, the Netherlands, Norway, Poland, Serbia, Sweden, Switzerland, Turkey, Russia, UK), *L. dioica* (North America: Canada; USA: Connecticut, Illinois, Iowa, Michigan, Minnesota, New York, Pennsylvania, Vermont, Wisconsin), *L. etrusca* (Europe: France, Russia, Spain, Switzerland, UK), *L. flava* (North America: USA: Illinois, Indiana, Iowa, Ohio), *L. glaucescens* (North America: Canada; USA: Nebraska, Wisconsin, Wyoming, Virginia), *L. ×heckrottii* (Europe: Germany; North America: Oklahoma), *L. hirsuta* (North America: Canada; USA: New York, Michigan, Minnesota, Wisconsin), *L. japonica* (Asia: China, Japan; Europe: Germany, Switzerland, UK; North America: USA: Florida; South America, Argentina), *L. parviflora* (North America: USA: Connecticut, Vermont, Wisconsin), *L. periclymenum* (Europe: France, Germany, Lithuania, the Netherlands, Norway, Poland, Romania, Sweden, Switzerland, UK; North America: Canada), *L. prolifera* [= *L. sullivantii*] (North America: USA: Colombia, Iowa, Michigan, Wisconsin), *L. sempervirens* (Asia: Korea; Europe: Estonia; North America: USA: Florida, Michigan, Minnesota, Pennsylvania, Wisconsin) [Amano (1986), Braun (1987, 1995), Grigaliūnaitė (1997), Rusanov & Bulgakov (2008), <https://nt.ars-grin.gov/fungaldatabases/fungushost/fungushost.cfm>].

Notes: The development of mycelium and the asexual morph of *Erysiphe loniceræ s. str.* is comparable with *E. ehrenbergii*: it commences in early summer (in Europe in June), with a chasmothecial formation from June to November. The conidial formation also ceases with the start of the formation of the sexual morph.

Sequences retrieved from North American *Erysiphe* samples on *Lonicera ciliosa*, belonging to *Lonicera* subgen. *Lonicera*, are identical with European sequences obtained from *L. caprifolium* (type host of *E. loniceræ*) and *L. periclymenum* and fall into the *Erysiphe loniceræ s. str.* clade. Powdery mildew on *Lonicera ciliosa* has previously been referred to as *Erysiphe caprifoliacearum* var. *flexuosa* (= *Microsphaera loniceræ* var. *flexuosa*), described from North America with a collection on *Lonicera involucrata* (*Lonicera* subgen. *Chamaecerasus*) as type material (Braun 1982a). However, *M. loniceræ* var. *flexuosa* constitutes a separate species. Sequences retrieved from *Erysiphe* on *L. involucrata* in North America form a sister clade to *E. symphoricarpi* distant from the *E. loniceræ s. str.* clade. Chasmothecia on *L. ciliosa* in North America are barely distinguishable from European collections of *E. loniceræ*. The only difference being that the chasmothecial appendages are somewhat longer and more flexuous in the North American collections compared to the European collections in which the appendages are somewhat shorter and more stiff. The more flexuous nature of the appendages in “var. *flexuosa*” on *L. ciliosa* is correlated with the appendage length and might

be a modification. Long, flexuous appendages have also been observed in some European specimens. The structure of the branched apices of the appendages in “var. *flexuosa*” on *L. ciliosa* and in European collections of *E. loniceræ s. str.* is not different, *i.e.*, in all collections the tips of the ultimate branchlets are at first (and for a longer time) straight, but tend to become recurved in fully mature specimens later in the season.

Erysiphe caprifoliacearum was described by Braun (1982b), based on differences between North American collections on *Lonicera* spp., with more regularly branched chasmothecial appendages with recurved tips, and European collections of *E. loniceræ s. str.*, characterised by having usually straight ultimate tips. However, recent comprehensive examinations of a wide range of European specimens collected from late spring to late autumn have shown that *E. loniceræ s. str.* on hosts of *Lonicera* subgen. *Lonicera* and *Lonicera japonica* is characterised by having branched chasmothecial appendages with ultimate tips that become recurved when fully mature later in the season. Since other traits of the chasmothecia are similar between *E. loniceræ s. str.* and *E. caprifoliacearum*, it is justified to reduce the latter species to synonymy with *E. loniceræ s. str.* The reduction of *E. loniceræ s. str.* and *E. caprifoliacearum* to synonymy is also supported by the present phylogenetic analyses and the host range of *E. caprifoliacearum*. Braun & Cook (2012) listed the following host species for *E. caprifoliacearum*: *Lonicera dioica* (= *L. glauca* auct.), *L. flava*, *L. glaucescens*, *L. ×heckrottii*, *L. hirsuta*, *L. oblongifolia*, *L. parviflora*, and *L. prolifera* (= *L. sullivantii*). The citation of “*L. semenovii* [= *L. glauca*]” in Braun & Cook (2012) was based on a confusion of the name *L. glauca*. North American records of powdery mildew on *Lonicera glauca* refer to *L. glauca* Hill, [which is a synonym of *L. dioica* (Rehder 1903)] and not *L. glauca* Hook. f. & Thomson, described from the Himalayas (which is a synonym of *L. semenovii*). All North American host species of *E. caprifoliacearum*, except for *L. oblongifolia*, pertain to *Lonicera* subgen. *Lonicera*, which is in agreement with the host range of *E. loniceræ s. str.* and supports the synonymy of the two species. The record of *E. caprifoliacearum* on *L. oblongifolia* (*Lonicera* subgen. *Chamaecerasus*) remains unclear and requires re-examinations of the host identity and morphology of the powdery mildew involved.

Lee et al. (2016) published a record of *Erysiphe loniceræ* on *Lonicera japonica* from Korea with a sequence that clusters in the *E. loniceræ s. str.* clade described with relatively large chasmothecia, 100–140 µm diam. The record of *Erysiphe loniceræ* on *Lonicera sempervirens* from Korea (Kim et al. 2007) seems to belong to *E. loniceræ s. str.* but should be confirmed by sequence data. Powdery mildew on *Lonicera japonica* in Florida (Alfieri et al. 1984) most likely belongs to *Erysiphe loniceræ s. str.*, but due to the occurrence of a second powdery mildew, *E. lonicerina*, on this host, morphological and phylogenetical confirmations are necessary.

Erysiphe lonicerina S. Takam., *sp. nov.* MycoBank MB837571. Fig. 3.

Etymology: Epithet composed of *Lonicera*, the name of the host genus, and the Latin suffix -ina (= belonging to).

Diagnosis: Phylogenetically distinct from *Erysiphe ehrenbergii* and *E. loniceræ s. str.*; the asexual morph differs from the latter two species in having conidiophores with almost exclusively straight foot-cells and longer conidia, 40–65 µm.

Description: Mycelium amphigenous, white, persistent; hyphae almost straight to somewhat sinuous, 4–7 µm wide, branching at right angles; hyphal appressoria well-developed, simply lobed, rarely nipple shaped, in opposite pairs or single. *Conidiophores* arising from hyphal cells, terminal on mother cells, erect, 70–128 × 9–15 µm, foot-cells usually straight, sometimes slightly curved or curved-sinuous at the very base, 34–68 × 7–12 µm, followed by 2–4 shorter cells, forming conidia singly. *Conidia* almost cylindrical to ellipsoid-ovoid, 40–65 × 15–20 µm, length/width ratio 2.2–4 (on average 3.0, N = 30), germ tubes perihilar, *Pseudoidium*-type. *Sexual morph* unknown.

Type: Japan, Chiba Prefecture, Chiba-shi, Chiba University, Nishi-Chiba Campus, on *Lonicera japonica*, 27 Nov. 1998, S. Takamatsu (TNS-F-87428 – **holotype**); ex-holotype sequence – LC009953 (ITS).

Additional material examined: Japan, Nara Prefecture, Sakurai-shi, Mt. Ryumon, on *Lonicera japonica*, 28 Oct. 2006, S. Takamatsu (TSU-MUMH 4464).

Host range and distribution: On *Lonicera japonica*, Asia (Japan).

Notes: Sequences belonging to *Erysiphe lonicerina* form a sister clade to the *E. ehrenbergii* clade. *Erysiphe lonicerina* differs from *E. ehrenbergii* and *E. lonicerae* s. str. in that it has almost exclusively straight conidiophore foot-cells and longer conidia (40–65 × 15–20 µm vs. 25–45(–55) × 11–24 µm in *E. lonicerae* and 23–39 × 10–17 µm in *E. ehrenbergii*).

Notes on additional *Erysiphe* spp. on *Lonicera* spp.

Erysiphe erlangshanensis (Y.N. Yu) U. Braun & S. Takam., *Schlechtendalia* 4: 8. 2000.

Basionym: *Microsphaera erlangshanensis* Y.N. Yu, in Yu & Lai, *Acta Mycol. Sin.* 2(2): 91. 1983.

Illustrations: Vasyagina *et al.* (1961: 300, fig. 97), Tanda *et al.* (1977: 29, pl. VIII, 30, pl. IX), Yu & Lai (1983: 92, fig. 2), Braun (1987: 424, pl. 189), Chen *et al.* (1987: 191, fig. 97), Shin (1988: 108, fig. 24; 2000: 102, fig. 30), Nomura (1992: 236, fig. 154; 1997: 127, fig. 155), Braun & Cook (2012: 459, fig. 550).



Fig. 3. *Erysiphe lonicerina* (TNS-F-87428 – holotype). **A.** Unlobed hyphal appressorium. **B.** Conidia. **C.** Conidium with *Pseudoidium*-type germ tube. **D.** Conidiophores with straight foot-cell. **E.** Conidiophore with slightly curved-sinuous foot-cell. Scale bars = 10 µm.

Descriptions: Tanda et al. (1977: 21), Braun (1987: 424), Chen et al. (1987: 190), Otani (1988: 218), Shin (1988: 106; 2000: 103), Nomura (1992: 235; 1997: 126), Braun & Cook (2012: 459).

Type: **China**, Prov. Sichuan, Erlangshan, on *Lonicera hispida*, 15 Sep. 1958, Liu & Song (HMAS 37844 – **holotype**).

Notes: Braun & Cook (2012) circumscribed the host range and distribution of *E. erlangshanensis* as follows: *Lonicera chrysantha*, *L. gracilipes*, *L. hispida*, *L. karelinii*, *L. maackii*, *L. nummulariifolia*, *L. rubrechtiana*, *L. subsessilis*, *L. tatarica*, and *L. vidalii* in Asia (Central Asia, China, Iran, Japan, Korea, Nepal, Russian Far East). All host species pertain to *Lonicera* subgen. *Chamaecerasus*. Khodaparast et al. (2000) recorded *E. erlangshanensis* on *L. nummulariifolia* from Iran, and Heluta (2004) confirmed *L. maackii* and *L. rubrechtiana* as hosts in the Far East of Russia. This species is characterised and distinguished from all other *Erysiphe* species on *Lonicera* by its very short chasmothecial appendages. The asexual morph of this species, characterised by having straight conidiophore foot-cells, was described and illustrated in detail in Shin (2000). A sequence retrieved from *E. erlangshanensis* on *L. maackii* from the Russian Far East clusters separately from *E. loniceræ* and all other sequenced *Erysiphe* spp. on *Lonicera*, supporting its status as a species of its own. However, because this species is widespread in Asia on a wide range of host species, more sequence data from different regions and hosts are necessary for proving the genetic uniformity of this species.

Erysiphe loniceræ-ramosissima (Tanda) U. Braun & S. Takam., *Schlechtendalia* **8**: 33. 2002.

Basionym: *Microsphaera loniceræ-ramosissima* Tanda, *Mycoscience* **41**: 158. 2000.

Illustrations: Tanda (2000: 158, fig. 3), Braun & Cook (2012: 479, fig. 582).

Description: Braun & Cook (2012: 478).

Type: **Japan**, Kanagawa Pref., Yokohama, Aoba-ku, Kodomonokuni children's park, on *Lonicera ramosissima*, 2 Nov. 1980, S. Tanda (TUAMH 1462 – **holotype**).

Notes: This species is morphologically barely distinguishable from *E. ehrenbergii*. *Lonicera ramosissima* is a species of *Lonicera* subgen. *Chamaecerasus*, supporting the assumption that *E. loniceræ-ramosissima* might be a synonym of *E. ehrenbergii*. The final clarification of the synonymy requires sequence data retrieved from powdery mildew on *L. ramosissima*.

Erysiphe magnusii (S. Blumer) U. Braun & S. Takam., *Schlechtendalia* **4**: 10. 2000.

Basionym: *Microsphaera magnusii* S. Blumer, *Beitr. Krypt.-Fl. Schweiz* **7**(1): 299. 1933.

Illustrations: Blumer (1933: 300, fig. 110, 301, fig. 111), Golovin (1956: 339, fig. 13), Vasyagina et al. (1961: 301, fig. 98), Braun (1987: 355, pl. 127; 1995: 283, pl. 65), Eliade (1990: 445, pl. 12, fig. 53), Fakirova (1991: 82, pl. 28, fig. 1), Simonyan (1994: 162, fig. 36), Paulech (1995: 212, fig. 100), Braun & Cook (2012: 481, fig. 586).

Descriptions: Golovin (1956: 338, 359; 1960: 148), Vasyagina et al. (1961: 299), Blumer (1967: 260), Junell (1967: 59), Eliade (1973: 203; 1990: 442), Bunkina (1979: 91), Safata (1985: 169), Braun (1987: 356; 1995: 172), Bunkina (1991: 109), Fakirova (1991: 89), Simonyan (1994: 161), Paulech (1995: 211), Bolay (2005: 63), Braun & Cook (2012: 481).

Type: **Switzerland**, Bern, Bremgartenwald, on *Lonicera nigra*, Aug. 1894, F. v. Tavel [ex herb. Volkart] (ZT – **lectotype**, designated by Braun 1987).

Notes: The host range and distribution of *E. magnusii* can be summarised as follows (Braun 1995, Braun & Cook 2012): *Lonicera alpigena*, *L. coerulea*, *L. chamissoi*, *L. nigra*, *L. orientalis* [= *L. caucasica*], *L. pallasii* [= *L. coerulea* subsp. *pallasii*], *L. stenantha*, *L. xylosteum*, *Lonicera* sp., Asia (Central Asia, Russia, Far East), Caucasus (Armenia), Europe (Austria, Bulgaria, Czech Republic, Finland, France, Germany, Hungary, Italy, the Netherlands, Norway, Poland, Romania, Russia, Slovakia, Spain, Sweden, Switzerland, Ukraine, former Yugoslavia). The record of this species from Ukraine on *Lonicera nigra* was published by Heluta et al. (2018). *Erysiphe magnusii* has not been phylogenetically confirmed, but is readily distinguishable from all other species of *Erysiphe* on *Lonicera* spp. by its very long flexuous chasmothecial appendages. The tips of the ultimate branchlets of the terminal branched part of chasmothecial appendages are distinctly recurved when mature, but in a few collections (e.g., Switzerland, VD, Le Sentier, Tête du Lac, on *Lonicera nigra*, 4 Aug. 2005, A. Bolay, G 5666325) the tips remained straight for a longer time and only became recurved relatively late in the season. Past collections might have been confused with and misidentified as *E. loniceræ*.

Erysiphe miurae (U. Braun) U. Braun & S. Takam., *Schlechtendalia* **4**: 11. 2000.

Basionym: *Microsphaera miurae* U. Braun, *Mycotaxon* **16**: 420. 1983.

Illustrations: Braun (1983: 423, fig. 5; 1987: 437, pl. 201), Nomura (1992: 212, fig. 136; 1997: 114, fig. 137), Liu (2010: 108, fig. 50), Braun & Cook (2012: 484, fig. 592 A).

Descriptions: Braun (1987: 436), Otani (1988: 224), Nomura (1992: 211; 1997: 114), Braun & Cook (2012: 483–484).

Type: **Japan**, Pref. Uzen, Omagari, on *Lonicera morrowii*, 3 Nov. 1908, Miura (TNS-F-214110 – **holotype**).

Notes: Two sequences retrieved from Japanese *Erysiphe* collections on *Lonicera morrowii* (type host of *Microsphaera miurae*) and *L. vidalii* cluster together in a clade distant from all other clades (Fig. 1), supporting *Erysiphe miurae* as a species of its own. The morphology of the powdery mildew on *L. morrowii* sequenced corresponds well with *E. miurae*, in that it includes chasmothecia with appendages about 1–1.5 times as long as the chasmothecial diam.

All host species of *Erysiphe miurae* belong to *Lonicera* subgen. *Chamaecerasus*. Braun & Cook (2012) recorded *E. miurae* from Asia (China, Japan) on *Lonicera chamissoi*, *L. ciliata*, *L. japonica*, *L. morrowii*, and *L. orientalis*. Braun (2002) recorded *E. miurae* on *Lonicera glehnii* from the Russian Far East, and Liu (2010) published a detailed description and illustration of this species

on *Lonicera tatarinovii* from China (Inner Mongolia). The identity of *Lonicera "ciliata"* is unclear (confused doubtful name). Braun & Cook (2012: 484, fig. 592 B) assigned an examined Chinese specimen on *L. japonica* to *E. miurae* (China, Prov. Liaoning, Sep. 1974, Zhang, HMAS 37845). However, this record is unclear and doubtful. The *E. miurae* on *L. japonica* is a fully developed mature sample that most likely pertains to *Erysiphe lonicerae* s. str., which is known to occur on *L. japonica* in China. Fully mature specimens of *E. lonicerae* s. str. on *L. japonica* with recurved tips of the ultimate branchlets of the branched apex of the chasmothecial appendages are easily confusable with the sexual morph of *E. miurae*.

Besides the host plants of *E. miurae* included in Braun & Cook (2012), Kobayashi (2007) listed *Lonicera korolkovii*, *L. maackii*, *L. orientalis*, *L. sempervirens* (subgen. *Chamaecerasus*), *L. strophiphora*, *L. tatarica*, and *L. vidalii* as host plants in Japan. *Lonicera vidalii* is a confirmed host species of *E. miurae* (see Fig. 1). *Lonicera maackii*, *L. tatarica*, and *L. vidalii* have been recorded from Korea as hosts of *E. erlangshanensis* (Shin 2000). It is possible that the host ranges of *E. erlangshanensis* and *E. miurae* may overlap. Future research should confirm the host ranges by further examinations that include sequences. Until future host range analyses are confirmed, the confusion of the two Asian *Erysiphe* species by Kobayashi (2007) cannot be excluded. Additionally, a more in depth phylogenetic analysis from Asian collections on *Lonicera* spp., identified as *E. erlangshanensis* and *E. miurae*, are urgently needed to confirm the identity of collections on particular host species in Asia.

Unclear, not yet assignable records of *Erysiphe lonicerae* s. lat. [= *Microsphaera lonicerae*] and *Microsphaera penicillata* [= *M. alni*] s. lat.

There are numerous records of *Erysiphe lonicerae* s. lat. on a wide range of additional host species that are still unconfirmed. These records are often referring to collections made in botanical gardens and parks, i.e., the *Lonicera* spp. concerned grew outside their natural ranges as ornamental shrubs or cultivated for scientific purposes.

All of the listed host records referred to as *Erysiphe lonicerae* (s. lat.) relate to species belonging to *Lonicera* subgen. *Chamaecerasus* (Bunkina 1979, 1991; Amano 1986; Karis 1987; Braun 1987, 1995): *Lonicera altmannii* [= *L. humilis*] (Russia), *L. xamoena* (Estonia, Russia), *L. caucasica* (Russia), *L. chamissoi* (Japan, Russia), *L. chrysantha* (Russia), *L. edulis* (Estonia, Russia), *L. glehnii* (Russia), *L. gracilipes* (Japan), *L. hispida* (China), *L. iberica* (Armenia, Russia), *L. karelinii* [= *L. heterophylla*] (Russia), *L. korolkowii* (Finland, Russia, UK), *L. maackii* (Japan, Russia), *L. maximowiczii* [= *L. sachalinensis*] (Russia), *L. microphylla* (Russia), *L. myrtillus* [= *L. angustifolia* var. *myrtillus*] (Russia), *L. numullariifolia* [= *L. arborea*] (Russia), *L. orientalis* (Japan, Romania, Russia), *L. praeflorens* (Russia), *L. prostrata* (China, Russia), *L. ruprechtiana* (Estonia, Russia), *L. stenantha* (China), *L. syringantha* [= *L. rupicola* var. *syringantha*] (Romania), *L. utahensis* (USA: Wyoming, Solheim, Mycofl. Saximont Exs. 609).

Some of these plant species are known to be host species of *Erysiphe erlangshanensis* (*L. gracilipes*, *L. hispida*, *L. maackii*, *L. ruprechtiana*) as well as *E. miurae* (*L. chamissoi*, *L. glehnii*, *L. maackii*).

The following records published from North America under *Microsphaera alni* and *M. penicilla* on *Lonicera* spp. pertaining to *Lonicera* subgen. *Chamaecerasus* are also unclear and in need of re-examination: *L. hispidula* (USA: Florida, Alfieri *et al.* 1984), *L. oblongifolia* (Canada; USA: Michigan, Ohio, Wisconsin; Anonymous 1960, Amano 1986).

Key to species of *Erysiphe* on *Lonicera*

1. Foot-cells of the conidiophores almost exclusively straight; conidia very long, 40–65 × 15–20 µm; on *Lonicera japonica*, Japan *Erysiphe lonicerina*
- 1* Foot-cells of the conidiophores either straight to curved-sinuous and conidia shorter, on average < 40 µm, or only conidia shorter 2
2. Chasmothecial appendages long and flexuous, 1.5–10 times as long as the chasmothecial diam 3
- 2* Chasmothecial appendages shorter, usually 0.8–2.5 times as long as the chasmothecial diam, and stiff, straight to curved 4
3. Chasmothecial appendages 1.5–3.5(–4) times as long as the chasmothecial diam, apex tightly and rather regularly brached, tips straight and remaining so; on *Lonicera involucreta* (and probably *L. canadensis*), North America *Erysiphe flexibilis*
- 3* Chasmothecial appendages very long, 2–10 times the chasmothecial diam, apex 2–5 times branched, tips of the ultimate branchlets recurved when mature; on *Lonicera* spp., Asia, Europe *Erysiphe magnusii*
- 4(2*) Tips of the ultimate branchlets of the branched apex of the chasmothecial appendages always straight, only with a few somewhat recurved tips, also in fully mature samples, or straight for a longer time, even when asci and ascospores are already developed, but numerous tips becoming recurved when fully mature, i.e., in older samples and above all late in the season (*Erysiphe lonicerae* s. lat. complex) 5
- 4* All or almost all tips of the ultimate branchlets recurved from the very beginning of maturity when asci and ascospores commence to develop; Asian and North American species 7
5. Chasmothecia 70–85 µm diam; appendages with a septum near the middle; asci usually 3; on *Lonicera ramosissima*, Japan *Erysiphe lonicerae-ramosissimae*
- 5* Appendages aseptate or with 1–3 septa in the lower half; asci 2–8; on other host species 6

6. Conidia 25–45(–55) × 11–24 μm, length/width ratio 1.7–4.5 (on average 2.8, N = 30); ultimate tips of the branched part of the chasmothecial appendages straight for a longer time, only with a few recurved tips, but numerous tips becoming recurved in fully mature samples, above all late in the season, appendages aseptate or with a single basal septum; on host species of *Lonicera* subgen. *Lonicera* and *L. japonica* *Erysiphe loniceræ* s. str.
- 6* Conidia 23–39 × 10–17 μm, length/width ratio 1.9–3.2 (on average 2.4, N = 30); ultimate tips of the branched part of the chasmothecial appendages straight, only with a few recurved ones throughout the season, appendages not infrequently with 1–2 or even 3 elevated septa and then pigmented below the septa; on host species of *Lonicera* subgen. *Chamaecerasus* *Erysiphe ehrenbergii*
- 7(4*) Appendages 1–2 times as long as the chasmothecial diam *Erysiphe miurae*
- 7* Appendages shorter, 0.5–1.25 times the chasmothecial diam, usually somewhat shorter than the diam *Erysiphe erlangshanensis*

DISCUSSION

The clarification of the phylogeny and taxonomy of *Erysiphe loniceræ*, including its variety *ehrenergii* on *Lonicera tatarica*, was the initial objective of the present examinations with the main goal to ascertain whether the powdery mildew on *L. tatarica* (*L. loniceræ* var. *ehrenbergii*) represented a species of its own or a synonym of *L. loniceræ*. Sequences (rDNA: ITS and 28S, the standard markers for powdery mildews) were retrieved from a wide range of collections originally identified as *E. loniceræ* and used for the construction of a phylogenetic tree, supplemented by corresponding sequences available in GenBank. The results of the current study revealed that the new sequences retrieved from powdery mildew on *L. tatarica*, and all other available sequences obtained from *E. loniceræ* s. lat. on various other *Lonicera* spp., formed six distinct, distant clades, representing six clearly separated species.

One clade, including sequences from *Erysiphe loniceræ* on *Lonicera caprifolium*, the type host of this species, has to be referred to as *E. loniceræ* s. str. It encompasses sequences retrieved from *E. loniceræ* on *L. caprifolium* and *L. periclymenum* from Europe as well as on *L. ciliosa*, *L. xheckrotii* and *L. prolifera* from North America. All host species pertain to *Lonicera* subgen. *Lonicera* (= subgen. *Caprifolium*), suggesting that *E. loniceræ* s. str. co-evolved with host species of this subgenus of *Lonicera*. However, sequences of powdery mildew on *L. japonica* also cluster within the *E. loniceræ* s. str. clade. *Lonicera japonica* currently tends to be assigned to subgen. *Chamaecerasus* sect. *Nintooa*, which is, however, polyphyletic (Nakaji et al. 2015). Previously, sect. *Nintooa* and *L. japonica* have been assumed to be a link between the two subgenera of *Lonicera* because its members have hollow branches and a climbing habit (traits that are also to be found in subgenus *Lonicerae*) yet the leaves subtending the inflorescence are not fused (Rehder 1903, Theis et al. 2008).

Lonicera japonica is a popular cultivated shrub native to Asia (Japan, Korea and East China), and is currently established in several parts of Europe, on the Azores and Madeira, South Africa, Australia, New Zealand, North and South America and Hawaii (Roloff & Bärtels 2008, Wu et al. 2011). *Erysiphe loniceræ* s. str. on *L. japonica* is also known from China and Japan, i.e., from the natural range of this host species. *Lonicera caprifolium* and *L. periclymenum* are European species, and *L. ciliosa*, *L. xheckrotii* and *L. prolifera* are native to North America. Thus, *E. loniceræ* is a powdery mildew species that is widely distributed in the Northern Hemisphere. Phylogenetic analyses revealed that *E. caprifoliacearum*, of which *L. xheckrotii* and *L.*

prolifera are common hosts, should be reduced to synonymy with *E. loniceræ* (s. str.). The inclusion of *Lonicera ciliosa* in the host range of *Erysiphe loniceræ* has been confirmed by results of the present phylogenetic and morphological analyses and is supported by the placement of this host in *Lonicera* subgen. *Lonicera*.

Powdery mildew on *L. ciliosa* was originally assigned to *Microsphaera loniceræ* var. *flexuosa* by Braun (1982a). Braun (1984) went on to treat this powdery mildew as variety of *M. caprifoliacearum*. Most recently powdery mildew on *L. ciliosa* has been assigned to *Erysiphe caprifoliacearum* var. *flexuosa* (Braun & Takamatsu 2000, Braun & Cook 2012). It should be noted that *L. ciliosa* was not the type host of *E. caprifoliacearum* var. *flexuosa*. Phylogenetic analyses of North American *Erysiphe* collections on *Lonicera involucrata*, the type host of var. *flexuosa*, have shown that another species, that is phylogenetically allied to and morphologically close to *Erysiphe symphoricarpi*, is involved. The new name *Erysiphe flexibilis*, based on *Microsphaera loniceræ* var. *flexuosa*, is introduced for this North American powdery mildew on *L. involucrata*.

The second, larger clade, is composed of sequences retrieved from powdery mildew that was previously referred to as *Erysiphe loniceræ* (s. lat.) on various *Lonicera* spp., including the type host of *E. loniceræ* var. *ehrenbergii*, *L. tatarica*. This clade is distant from the *E. loniceræ* clade. The sequences in this clade have been retrieved from powdery mildew on various *Lonicera* spp. belonging to *Lonicera* subgen. *Chamaecerasus* (the largest subgenus of this genus). The involvement of the two clades of *E. loniceræ* s. lat. as well as the two subgenera of *Lonicera* suggests a high degree of co-evolution between these powdery mildews and their host species. Because the *Lonicera tatarica* powdery mildew is included in this clade and represents a species of its own, the name *Microsphaera ehrenbergii* is available for the species involved, and thus the new combination *Erysiphe ehrenbergii* is introduced. There also exists a few morphological characteristics that differentiate *E. ehrenbergii* and *E. loniceræ*. The conidia in *E. loniceræ* tend to be longer, 25–55 × 11–24 μm, with a length/width ratio of 1.7–4.5 (on average 2.8), and the ultimate tips of the branched part of chasmothecial appendages become frequently recurved when fully mature (vs., conidia 23–39 × 10–17 μm, length/width ratio 1.9–3.2, on average 2.4 in *E. ehrenbergii*, ultimate tips of the branched part of chasmothecial appendages remaining straight, also in mature and late collections, only with a few recurved ones).

There is an additional *Erysiphe* species on *Lonicera japonica* in Japan, yet it is only known in its asexual morph, i.e.,

chasmothecia have not yet been found. Sequences belonging to this species on *L. japonica* form a sister clade to the *E. ehrenbergii* clade. This species, described as *E. lonicerina*, differs from *E. ehrenbergii* and *E. lonicerae* s. str. in having almost exclusively straight conidiophore foot-cells and longer conidia, 40–65 × 15–20 µm, vs. 25–45(–55) × 11–24 µm in *E. lonicerae* and 23–39 × 10–17 µm in *E. ehrenbergii*.

There are several other species of *Erysiphe* sect. *Microsphaera* on *Lonicera*, viz., *E. magnusii* in Europe, and the Asian species *E. erlangshanensis* and *E. miurae*. These three species are morphologically easily distinguishable from *E. lonicerae* s. lat. (see Braun & Cook 2012). A few sequences retrieved from *E. erlangshanensis* and *E. miurae* suggest that these taxa represents separate species. Future research should obtain sequences from samples of *E. magnusii* and additional ones from *E. erlangshanensis* and *E. miurae* to confirm these taxa as separate species in phylogenetic analyses (see Fig. 1).

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