New species, new records and first sequence data of powdery mildews (*Erysiphaceae*) from Europe with special emphasis on Switzerland

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Abstract: New records of powdery mildews (*Erysiphaceae*) from Switzerland and adjacent countries are listed and annotated, including first records of multiple host plants worldwide. The collections concerned are described, illustrated, discussed, and some identifications have been confirmed by results of sequencing (ITS + 28S rDNA). The new species, *Erysiphe abeliana* (on *Abelia* \times *grandiflora*) and *Phyllactinia cruchetii* (on *Passiflora coerulea*), are described. Some previous records of powdery mildews from Switzerland based only on morphology have been confirmed by sequence data. Type specimens of *Erysiphe chifengensis* and *E. potentillae* have been sequenced, and new sequences have been generated from collections of *E. malvae* and *E. punicae*. *Microsphaera abeliae* (\equiv *Erysiphe abeliicola*) is epitypified with an ex-epitype sequence.

Zusammenfassung: Neufunde Echter Mehltaupilze (*Erysiphaceae*) aus der Schweiz und angrenzenden Ländern werden aufgelistet und kommentiert, einschließlich Erstfunde neuer Wirtpflanzenarten weltweit. Die entsprechenden Kollektionen werden beschrieben, abgebildet und diskutiert. Einige Identifizierungen wurden durch Ergebnisse von Sequenzierungen (ITS + 28S rDNA) bestätigt. Die neuen Arten

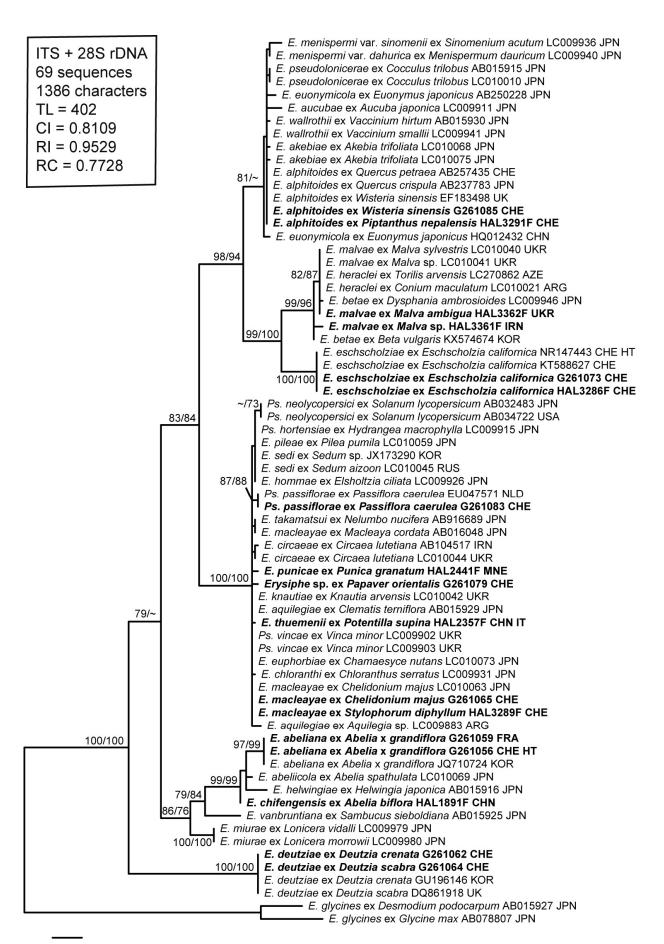
Erysiphe abeliana (auf Abelia ×grandiflora) und Phyllactinia cruchetii (auf Passiflora coerulea) werden beschrieben. Einige frühere Angaben aus der Schweiz auf Grundlage morphologischer Untersuchungen sind basierend auf Sequenzdaten bestätigt worden. Typusmaterial von Erysiphe chifengensis und E. potentillae wurde sequenziert und neue Sequenzen aus Kollektionen von E. malvae und E. punicae wurden gewonnen. Microsphaera abeliae (= Erysiphe abeliicola) wird epitypisiert mit einer aus dem Epitypus gewonnenen Sequenz.

Powdery mildew (Ascomycota, Helotiales, Erysiphaceae) is a group of fungi causing detrimental diseases on a range of plants worldwide (BRAUN & COOK 2012). Thanks to SAMUEL BLUMER (*1895, †1991), employed at the Swiss "Eidgenössische Versuchsanstalt für Ost-, Wein und Gartenbau, Wädenswil", one of the most important pioneers of the exploration of European Ervsiphaceae, the powdery mildews of Switzerland are relatively well-known. In 1933, he published the first comprehensive treatment of Central European Erysiphaceae with a special emphasis on powdery mildews of Switzerland (BLUMER 1933). In 1967, BLUMER provided a manual of European genera and species of this group of plant pathogenic fungi (BLUMER 1967). An updated comprehensive treatment of powdery mildews of Switzerland was later published by BOLAY (2005), based on new phylogenetic-taxonomic concepts introduced by BRAUN & TAKAMATSU (2000) and BRAUN & al. (2001). Meanwhile, phylogenetic methods and analyses are standard tools in mycological studies, in particular for the Erysiphaceae (e.g., BRAUN & al. 2018, 2019; BRADSHAW & al. 2020). In powdery mildews, they are helpful to resolve species complexes and cryptic speciation, and allow identifications of asexual morphs in the absence of ascomata (chasmothecia). Additional problems in the identification of powdery mildews are often caused by increasing introductions of alien powdery mildew species in Europe. Introduced powdery mildews tend to occur longer in their asexual state, which are often poor in diagnostic characteristics. Botanical gardens tend to be hot spots in this context as they tend to consist of a range of native and non-native plant hosts. The senior author (A.B.) continued to collect and identify powdery mildews up until recently in Switzerland, above all in canton of Vaud (Waadt) and in the Botanical garden of Geneva. Some of these specimens were thought to be new records or new species. Identifications required confirmation by sequence analyses. Outcomes of these examinations are accomplished and discussed in this work.

Materials and methods

Genomic DNA extraction from herbarium samples and amplification of the ITS1 (part.), 5.8S rRNA, ITS2, 28S rRNA (part.) region have been performed using a nested approach according to methods circumscribed in BRADSHAW & al. (2021a). DNA was extracted with the DNeasy plant mini kit (Qiagen, Germany) following the manufacturers protocol. For the first PCR reaction the primers PM1/TW14 (CUNNINGTON et al. 2003, MORI & al. 2000) were used followed by ITS5/PM2 (WHITE & al. 1990, CUNNINGTON & al. 2003) and PM5/NLP2 (Mori & al. 2000). Amplicons were purified (MSB Spin

Fig. 1. Phylogenetic analysis of combined data of the 5'-end of the 28S rDNA (including domains D1 and D2) and ITS region for 69 sequences from the *Microsphaera*-lineage of the genus *Erysiphe*. This is one of the 8.6×10^6 equally parsimonious trees with 402 steps, which were found using a heuristic search. 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 were shown on the respective branches. Sequences determined in this study were shown as bold faces. *E.: Erysiphe*, *Ps.: Pseudoidium*, HT: holotype, IT: isotype.



PCRapace Kit, Invitec Molecular, Germany) and sequenced in both directions (LGC Genomics GmbH, Germany). Consensus sequences were generated and edited (CLC Main Workbench 21.0.3, Qiagen Digital Insights, Germany). The sequences obtained in the present study were deposited in GenBank under the accession numbers MW600364– MW600378 and MW581143–MW581146.

These sequences were aligned with the reference sequences of *Erysiphe* species by MUSCLE implemented in MEGA 7.0 (KUMAR & al. 2016). Phylogenetic trees (Fig. 1 – *Erysiphe*, Fig. 12 – *Phyllactinia*) 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 & al. (2020). All sites were treated as unordered and unweighted, with gaps treated as missing data. Strength of the respective branches was evaluated with 1000 bootstrap (BS) values (FELSENSTEIN 1985).

Morphological examinations were carried out either in pure distilled water (ascomata) or in distilled water plus aniline blue (cotton blue) by means of standard microscopy. Asexual morphs (hyphae, hyphal appressoria, conidiophores, and conidia) from herbarium samples were put into a drop of lactic acid and gently heated before microscopical examination. Thirty ascomata, conidia and other structures were measured whenever possible at a magnification of \times 1 000, and the 95 % confidence intervals were determined (extreme values in parentheses).

Taxonomy

(1) Erysiphe on Abelia ×grandiflora (Abelia chinensis × uniflora)

Erysiphe abeliana BOLAY & U. BRAUN, spec. nova – Fig. 2 MycoBank no. MB838895, Genbank no. MW600364 (ex-holotype sequence)

Diagnosis: Phylogenetically closely allied to *Erysiphe abeliicola*, but forming a separate sister clade; morphologically distinguished by having stiff (non-flexuous), shorter chasmothecial appendages, mostly 1-1.5 times as long as the chasmothecial diam., and tips of the ultimate branchlets of the branched terminal part of the appendages remaining straight (not recurved). Morphologically very similar to *E. chifengensis* on *Zabelia biflora* (\equiv *Abelia biflora*), but phylogenetically distant. *Erysiphe chifengensis* differs in having shorter conidiophore foot-cells (20–30 µm long) and larger chasmothecia, 80–165(–200) µm diam., with numerous, (5–)10–20(–23), shorter chasmothecial appendages, (0.5–)0.7–1(–1.5) times as long as the chasmothecial diam.

Holotypus: Switzerland: Vaud, Prangins, Maison communale, 5 Oct. 2014, on *Abelia* × *grandiflora*, leg. A. Bolay (G00261056).

Etymology: composed of the name of the host genus, *Abelia*, and the Latin adjectival suffix -anus, -a, -um, = belonging to, relating to.

Description: A s e x u a l m o r p h: M y c e l i u m amphigenous, mainly epiphyllous, effuse or in thin white patches; h y p h a e branched, septate, thin-walled, 3–5 μ m wide; h y p h a l a p p r e s s o r i a solitary, rarely in opposite pairs, slightly to distinctly lobate. C o n i d i o p h o r e s (Pseudioidium type) arising from the upper surface of superficial hyphae, 60–100 μ m long, erect, foot-cells subcylindrical, straight to slightly curved or somewhat sinuous, $30-60 \times (5-)7-10(-15) \mu$ m, usually followed by 1–2 cells, shorter or about as long as the foot-cell. C o n i d i a formed singly, ellipsoid-ovoid, cylindrical, rarely doliiform, $(19-)26-35(-38) \times (9-)10.5-12.5(-17.5)$

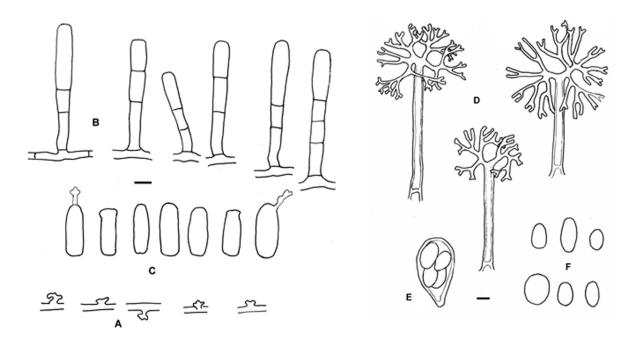


Fig. 2. *Erysiphe abeliana* sp. nov., G00261056, holotype. *A* hyphal appressoria, *B* conidiophores, *C* conidia, *D* chasmothecial appendages, *E* ascospores, *F* ascospores. – Bars: 10 μm. Drawing by A. BOLAY.

 μ m, average 31.1 \times 12.3 μ m, germ tubes subapical, short, aseptate, apex lobate (observed in vivo).

S e x u a l m o r p h : C h a s m o t h e c i a on leaves, amphigenous, subglobose, 85–130 µm diam.; p e r i d i a l c e l l s irregularly polygonal, 8–30 µm diam.; a p - p e n d a g e s more or less equatorial, 7–11, straight to curved, stiff, about 100–135 µm long (0.9–1.5 times as long as the chasmothecial diam.) [126–250 µm long, according to CHO & al. (2012)], 7–10 µm wide in the lower half, wall somewhat thickened below, thinner towards the branched terminal part, hyaline or only somewhat brown at the very base, apex 3–6 times regularly dichotomously branched, branchlets of all orders short, outline more or less rounded when mature, tips of the ultimate branchlets remaining straight; a s c i (2–)4–6, broad ovoid to saccate, sessile to short-stalked, 40–70 × 28–45 µm, 3–6(–8)-spored; a s c o s p o r e s ellipsoid-ovoid, 14–30 × 9–21 µm, hyaline.

Additional collections examined (asexual morphs): France: Corsica, Ajaccio, 10 Oct. 2015, on *Abelia* × *grandiflora*, A. Bolay (G00261059; Genbank no. MW600374); Corsica, Porto Veccio, 16 Oct. 2014, on *Abelia* × *grandiflora*, A. Bolay (G00261060); Dép. Aveyron, Espalion, Parc au bord du Lot, on *Abelia* × *grandiflora*, 3 Aug. 2018, A. Bolay (G00261061). Switzerland: Vaud, Nyon, rte de Clémenty, 1 Sep. 2014, on *Abelia* × *grandiflora*, A. Bolay (G00261053); Vaud, Nyon, Gare CFF, 20 Nov. 2014, on *Abelia* × *grandiflora*, A. Bolay (G00261052); Vaud, Nyon, ch. de Bonmont 6, 26 Aug. 2014, on *Abelia* × *grandiflora*, A. Bolay (G00261954); Vaud, Nyon, ch. du Midi, 15 Oct. 2018, on *Abelia* × *grandiflora*, A. Bolay (G00261055); Vaud, Morges, EMS Nelty de Beausobre, 22 Oct. 2015, on *Abelia* × *grandiflora*, A. Bolay (G00261057); Vaud, Prangins, parking sous l'église, 23 Oct. 2018, on *Abelia* × *grandiflora*, A. Bolay (G00261048); Genève, Jardin botanique 18 Oct. 2018, on *Abelia* × *grandiflora*, A. Bolay (G00261058).

Notes: There are currently two differing interpretations of phylogenetic examinations of tribe *Linnaeeae* (*Caprifoliaceae*). In phylogenetic multilocus analyses, it has been shown that this tribe is composed of six monophyletic clades, which conform with *Di*-

pelta, Kolkwitzia, Linnaea, Vesalea, and Abelia sect. Abelia as well as Abelia sect. Bilaciniatae ser. Serratae, which made Abelia polyphyletic (LANDREIN 2010, LANDREIN & al. 2012). LANDREIN (2010) introduced Diabelia for the latter clade reflecting Abelia sect. Bilaciniatae ser. Serratae to reach a monophyletic concept for Abelia. The underlying morphological differentiations between the recognised genera have been outlined and exhibited in a recently published monograph of Linnaea and allied genera (LANDREIN & FARJON 2019). A wider concept, only recognizing the whole Linnaeeae "clade" (lineage) as a single genus, Linnaea, including Abelia and several other previously recognised genera, was proposed by CHRISTENHUSZ (2013), but was based on a differing interpretation of previous phylogenetic results, i.e., without any further phylogenetic data and evidence. We accept and follow the convincing, morphologically and phylogenetically substantiated concept proposed by LANDREIN (2010) and LANDREIN & al. (2012), which is in addition supported by powdery mildews of the genus Erysiphe that developed in co-evolution with the genera of tribe Linnaeeae. It should be noted that obligate plant pathogenic fungi, such as powdery mildews, rusts and smuts, are often "reliable phylogenetic predictors" (TAKAMATSU & al. 2013; BRADSHAW & al. 2020, 2021b). Sequences retrieved from Erysiphe on Abelia ×grandiflora cluster together with a sequence generated from powdery mildew on this host in Korea, which was erroneously identified as Erysiphe abeliicola (CHO & al. 2012). A sequence retrieved from a collection of the type host of E. abeliicola, Diabelia spathulata (\equiv Abelia spathulata) clusters separately in sister position to the clade formed by sequences of the powdery mildew on Abelia × grandiflora. Furthermore, E. abeliicola is morphologically quite different from E. abeliana and is characterised by having flexuous, rather long chasmothecial appendages (2–4 times as long as the chasmothecial diam.) with recurved tips of the ultimate branchlets of the branched apex when mature (versus stiff and shorter appendages, about 1-1.5(-2) times as long as the chasmothecial diam., and tips of the ultimate branchlets of the branched apices remaining straight in the powdery mildew on A. ×grandiflora). Based on these characteristics, the powdery mildew on A. ×grandiflora is morphologically rather close to Erysiphe chifengensis (LIU & BRAUN 2006: 494), described from China on Zabelia biflora (= Abelia biflora), a host of the genus Zabelia, which is phylogenetically distant from Abelia s. str. (LANDREIN 2010, LANDREIN & al. 2012). However, E. chifengensis is phylogenetically distinguished from Erysiphe on A. ×grandiflora (type material sequenced, see Fig. 1) and clusters close to E. abeliicola, although the two species are morphologically quite different. Although morphologically similar, Erysiphe chifengensis differs slightly morphologically from E. abeliana in that it has shorter conidiophore foot-cells (20-30 µm long) and larger chasmothecia, 80-165(-200) µm diam., with numerous, (5-)10-20(-23) µm, shorter chasmothecial appendages, (0.5-)0.7-1(-1.5) times as long as the chasmothecial diam.

These results support the introduction of a new species for the powdery mildew on Abelia \times grandiflora. The phylogenetic analyses suggest obvious co-evolution of Erysiphe spp. along with hosts of tribe Linnaeeae within Caprifoliaceae. The three species, E. abeliana, E. abelicola and E. chifengensis, are phylogenetically closely allied. Erysiphe abelicola is confined to Diabelia serrata (\equiv Abelia serrata), D. spathulata (\equiv A. spathulata), and D. tetrasepala (\equiv A. tetrasepala). The three hosts, previously assigned to Abelia sect. Bilaciniatae subsect. Serratae, are closely related, form a monophyletic clade (LANDREIN 2010, LANDREIN & al. 2012), and hybridize easily with each

other (LANDREIN & FARJON 2019). In order to determine *E. abeliicola* genetically, we propose the following epitype:

Microsphaera abeliae HOMMA, J. Fac. Agric. Hokkaido Univ. **38**: 392, 1937, non *Erysiphe abeliae* R. Y. ZHENG & G. Q. CHEN, 1980.

≡ Erysiphe abeliicola U. BRAUN & S. TAKAM., Schlechtendalia 4: 4, 2000.

Lectotype (designated in BRAUN & COOK 2012: 430): on *Diabelia spathulata* (≡ *Abelia spathulata*), Japan: Pref. Echigo, Mt. Ijimino, 10 Oct. 1924, HOMMA (TNS-F-217379).

Epitype (**designated here**, MycoBank no. MBT10000105): on *Diabelia spathulata* (≡ *Abelia spathulata*), Japan, Okayama Pref., Hiruzen, Shimo-Nagata, 2 November 2006, S. TAKAMATSU (TNS-F-88071); ex-epitype sequence – LC010069.

Erysiphe chifengensis is confined to Zabelia biflora (\equiv Abelia biflora). The new species E. abeliana occurs on Abelia \times grandiflora, a hybrid between A. chinensis and A. uniflora; two species previously placed in Abelia sect. Abelia (now Abelia s. str.), which constitutes a monophyletic clade of closely allied species (LANDREIN 2010, LANDREIN & al. 2012). This suggests that the new species is confined to hosts belonging to this phylogenetic group. So far, powdery mildew is only known to occur on A. \times grandiflora, i.e., powdery mildew has not yet been recorded on its parent species, but it is to be expected that such infections may occur, above all in China.

Key to the species of *Erysiphe* on hosts belonging to *Caprifoliaceae*, tribe *Linnaeeae*

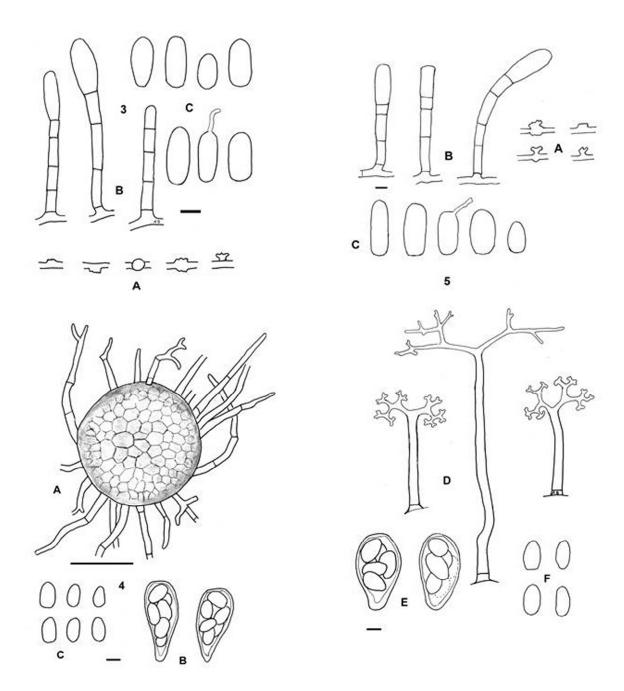
1. Chasmothecial appendages mycelium-like, apex simple, unbranched (sect. <i>Erysiphe</i>) rarely loosely uncinate-circinate; on <i>Abelia</i> sp., China
1* Chasmothecial appendages with dichotomously branched apex (sect. <i>Microsphaera</i>
2. Chasmothecia 70–110 μm diam., appendages long and flexuous, 2–4 times as long a the chasmothecial diam., apex 3–4 times dichotomously branched, loose to dense primary and secondary branchlets often elongated, tips of the ultimate branchlets recurved when fully mature; on <i>Diabelia</i> spp., Japan
2* Chasmothecial appendages stiff, not flexuous, and shorter, usually 0.5–1.5 times a long as the chasmothecial diam., on <i>Abelia</i> s. str., <i>Dipelta</i> or <i>Zabelia</i>
3. Chasmothecia small, 60–105 μm diam., appendages short, 0.6–1.6 times as long a the chasmothecial diam., apex 3–6 times dichotomously branched, tips of the ultimat branchlets recurved when mature; on <i>Dipelta floribunda</i> , China
3* Apex of the chasmothecial appendages regularly branched, dense, tips of the ultimat branchlets remaining straight, not recurved; on <i>Abelia</i> (s. str.) spp. or <i>Zabelia</i>
4. Conidiophore foot-cells short, 20–30 μm; chasmothecia large, 80–165(–200) μr diam., with numerous, (5–)10–20(–23), rather short appendages, (0.5–)0.7–1(–1.5 times as long as the chasmothecial diam.; on <i>Zabelia biflora</i> , China

(2) Erysiphe alphitoides on Cotinus, Piptanthus and Wisteria

Erysiphe alphitoides (GRIFFON & MAUBL.) U. BRAUN & S. TAKAM., Schlechtendalia 4: 5, 2000 – Figs. 3, 5.

Collections examined: Switzerland: Vaud, Nyon, ch. de Bonmont 7, on *Cotinus coggygria*, 6 Oct. 2018, A. Bolay (HAL 3363 F, asexual morph); Nyon, rte. de Signy 5, on *Wisteria sinensis*, 21 Nov. 2018, A. Bolay (G00261084, asexual morph); ibid., 3 Nov. 2018, A. Bolay (G00261085; Genbank no. MW600368, holomorph); Genève, Jardin botanique, on *Piptanthus nepalensis*, 29 Oct. 2009, A. Bolay (G00261086, asexual morph); ibid., 13 Oct. 2012, A. Bolay (G00261087); ibid., 13 Oct. 2012, A. Bolay (HAL 3291 F, holomorph; Genbank no. MW600377).

Notes: Cotinus coggygria is known to belong to the host range of Erysiphe alphitoides (BOLAY 2005, BRAUN & COOK 2012). Wisteria sinensis is also known as phylogenetically proven host of this species from the UK (HENRICOT & COOK 2008, COOK & al. 2015). This is the first record of E. alphitoides on W. sinensis from Switzerland (asexual morph and immature chasmothecia) that includes sequencing. In addition, DENTON & al. (2013) reported E. alphitoides from the UK on Wisteria brachybotrys and W. frutescens. The powdery mildew on Piptanthus nepalensis, collected in the botanical garden in Geneva, is more intricate. The asexual morph agrees well with the anamorph of E. alphitoides on oaks [hyphae 3–7 μm wide; hyphal appressoria nipple-shaped to lobate; foot-cells of the conidiophores straight, cylindrical to curved, $10-60 \times 5-7 \mu m$, followed by (0-)1-3 cells, shorter than the foot-cell or about as long, conidia formed singly, ellipsoid-ovoid, subcylindrical, doliiform, $(17-)29-34.5 \times 10-17 \mu m$ (herbarium material)]. The ITS sequence retrieved from the asexual morph on *Piptanthus* clusters within the E. alphitoides clade, which confirms that the latter species may infect the Asian Piptanthus nepalensis under the condition of a botanical garden. However, some chasmothecia (not separately sequenced) do not morphologically agree with E. alphitoides (fig. 4). They rather resemble E. trifoliorum (WALLR.) U. BRAUN [chasmothecia 85-125 μm diam., peridial cells 5-30 μm diam., with 8-35 appendages, straight to curved-sinuous, 0.7-6.3 times as long as the chasmothecial diam., colourless, thinwalled, 0-2-septate, ends simple or occasionally subdichotomously branched, asci 3-6 per chasmothecium, 50-70 × 20-30 µm, sessile or short-stalked, 3-6-spored, ascospores, ellipsoid-ovoid, colourless, 15–20 × 8–12 µm]. A mixed infection of *Piptanthus* leaves cannot be excluded, but to address this issue further research is needed. In any case, the present reports support previous records and examinations which reflect and prove the wide host range of E. alphitoides, which covers, besides Fagaceae (Castanea, Castanopsis, Fagus, Quercus spp., BRAUN & COOK 2012), species of various other plant families: Anacardiaceae (Cotinus and Mangifera spp., BRAUN & COOK 2012), Convolvulaceae (Ipomoea obscura, PAN 2020), Fabaceae (Piptanthus nepalensis, this work; Wisteria spp., HENRICOT & COOK 2008, COOK & al. 2015, DENTON & al. 2013, this work), Menispermaceae (Cocculus orbiculatus, including C. trilobus, CHEON & al.



Figs. 3–5. 3. Erysiphe alphitoides, asexual morph on Piptanthus nepalensis, HAL 3291 F. A hyphal appressoria, B conidiophores, C conidia. 4. Erysiphe sp., sexual morph on Piptanthus nepalensis, HAL 3291 F (associated with the asexual morph of E. alphitoides). A chasmothecium, B asci, C ascospores. 5. Erysiphe alphitoides, asexual and sexual morph on Wisteria sinensis, G00261084 and G00261085 (asexual and sexual morph, respectively). A. hyphal appressoria, B conidiophores, C conidia, D immature chasmothecial appendages, E asci, F ascospores. – Bars: 10 μm (all bars except for 4 A, which represents 50 μm). Drawing by A. BOLAY.

2014), Rosaceae (Exochorda racemosa, ZHANG & al. 2018; Sorbaria sorbifolia, DENTON & al. 2013), Sapindaceae (Aesculus hippocastanum, BRAUN & COOK 2012).

(3) Collections belonging to the Erysiphe aquilegiae complex (clade)

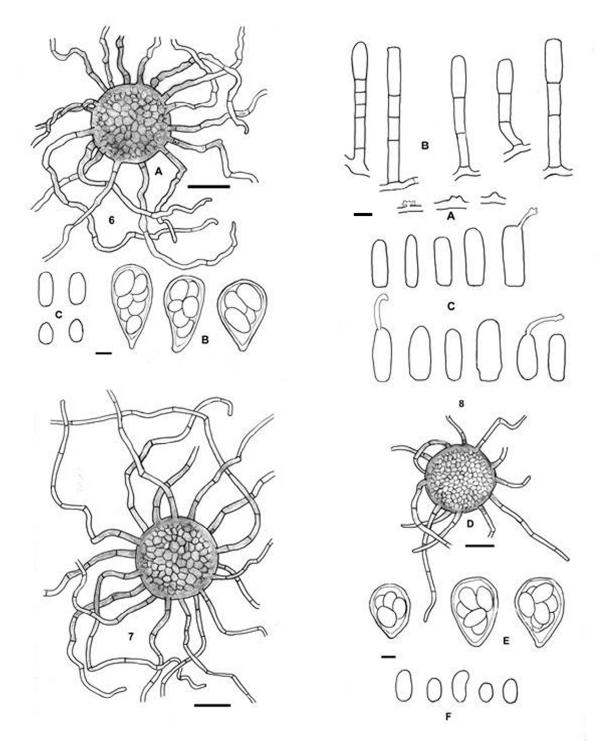
The phylogenetically circumscribed *Erysiphe aquilegiae* clade, based on nrDNA ITS + 28S rDNA sequence data, was introduced and circumscribed by TAKAMATSU & al.

(2015). This clade is composed of sequence data of numerous species of *Erysiphe* sect. Erysiphe, which are characterised by having pseudoidium-like asexual morphs, mycelium-like chasmothecial appendages, and 3-8-spored asci. The resolution on species level within this clade based solely on ITS + 28S rDNA data is insufficient. Thus, phylogenetic multi-locus approaches are necessary for better resolutions of the taxa involved in this clade. However, several additional markers have been tested for better species resolutions in powdery mildews, such as the new approaches used in ELLING-HAM & al. (2019), but so far without decisive breakthrough, i.e., an additional generally successfully applicable marker for powdery mildews has not yet been found. The Erysiphe aquilegiae clade and resulting taxonomic implications have been discussed in detail by SHIN & al. (2019) in which the name Erysiphe aguilegiae complex was proposed for this clade in taxonomic contexts and for taxonomic purposes. In a recently published treatment of this complex, BRADSHAW & al. (2021) provided a "guideline" to handle this complex taxonomically. Until multi-locus revisions of this complex will be available, the described common powdery mildew species should be maintained (based on BRAUN & COOK 2012), independent of being mono- or para- or even polyphyletic. Single new collections genetically pertaining to this complex, above all on cultivated hosts or host plants found outside of their natural ranges, should be treated as Erysiphe sp. In such cases, one should refrain from introducing new species until sufficient evidence will be available that new species are involved and occasional host switches can be precluded. This proposal seems to be a good compromise for the interim. The *E. aquilegiae* complex encompasses several described *Erysiphe* spp. that are morphologically barely distinguishable from each other, together with other morphologically clearly different species. The most striking example being Erysiphe tortilis (WALLR.) LINK on Cornus spp., which has usually been assigned to Erysiphe sect. Microsphaera based on the morphology of its sexual morph. However, BRADSHAW & al. (2021) demonstrated that ITS sequences retrieved from this powdery mildew, including ex-epitype sequences, cluster within the E. aquilegiae clade. The following additional sequences generated from powdery mildew specimens collected in Switzerland and retrieved from type material of Erysiphe thuemenii as well as reference material for E. punicae pertain to this clade as well.

(3.1.) Erysiphe macleayae and Erysiphe sp. on Papaveraceae

Erysiphe macleayae R. Y. ZHENG & G. Q. CHEN, Sydowia **34**: 290, 1981 – Figs. 6, 7.

Collections examined: Italy: Piemont, Pinerolo, 30 km south west of Torino, on *Chelidonium majus*, 17 Oct. 2012, A. BOLAY (G00261069, asexual morph). Switzerland: Genève, Jardin botanique, La Console, on *Chelidonium majus*, 18 June 2009, A. BOLAY (G00261066, asexual morph); Vaud, Morges, ch. Sorby 8, on *Chelidonium majus*, 18 Sep. 2009, A. BOLAY (G00261068, asexual morph); Vaud, Nyon pont CFF, on *Chelidonium majus*, 1 Nov. 2015 A. BOLAY (G00261065; Genbank no. MW600371, asexual morph); Ticino, Intragna, près de la gare, on *Chelinonium majus*, 1. Nov. 2013, T. BRODBECK (G00261067); Genève, quai Wilson, on *Macleaya cordata*, 27 Oct. 2015, A. BOLAY (G00261077, HAL 3285 F, holomorph); ibid., 18 Oct. 2018 (G00261078, asexual morph); Genève, Jardin botanique, on *Macleaya cordata*, 29 Oct. 2009, A. BOLAY (G00261076, asexual morph); ibid., 13 Oct. 2012, A. BOLAY (G00261096, asexual morph); Genève, Jardin botanique, on *Macleaya microcarpa*, 13 Oct. 2012, A. BOLAY (G00261096, asexual morph); Genève, Jardin botanique, on *Stylophorum diphyllum*, 22 Aug. 2006, A. BOLAY (G00261080, holomorph); ibid., 10 Sep. 2012, A. BOLAY (G00261081); ibid., 13 Oct. 2012, A. BOLAY (HAL 3289 F; Genbank no. MW600376, holomorph).



Figs. 6–8. 6. *Erysiphe macleayae*, sexual morph on *Macleaya cordata*, G00261077. *A* chasmothecium, *B* asci, *C* ascospores. 7. *E. macleayae*, sexual morph (chasmothecium) on *Stylophorum diphyllum*, HAL 3289 F. 8. *Erysiphe* sp., holomorphe on *Papaver orientalis*, G00261079. *A* hyphal appressoria, *B* conidiophores, *C* conidia, *D* chasmothecium, *E* asci, *F* ascospores. Bars: 10 μm (all bars except for 6 A, 7 and 8 D, which represents 50 μm). Drawing by A. BOLAY.

Notes: Pastirčáková & al. (2016) published a comprehensive phylogenetic treatment of *Erysiphe* spp. on *Papaveraceae*, including a single anamorphic powdery mildew collection on *Chelidonium majus* from Switzerland, which was originally identified as *E. cruciferarum*. Based on the morphology of the asexual and sexual morphs found on *Chelidonium majus* and results of sequence analyses, this powdery mildew could be identified as *E. macleayae*, which belongs to the *E. aquilegiae* complex and clade (=

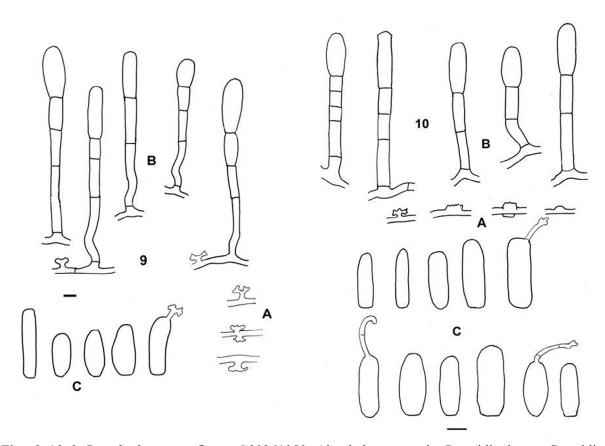
Clade 1 in PASTIRČÁKOVÁ & al. 2016). Erysiphe macleayae is a species that, although belonging to this complex, has been generally recognised as a species of its own, which is supported by its particular morphology of the conidiophores and ascomata, above all the frequently sinuous conidiophores foot-cells, the small ascomata (diameter on average < 100 μm), and the rather long chasmothecial appendages, supplemented by results of inoculation tests (PASTIRČÁKOVÁ & al. 2016). These tests confirmed that E. macleayae has a wider host range within Papaveraceae (E. macleyae from Chelidonium majus caused infections on host species of the genera Argemone, Chelidonium, Glaucium, Macleaya, Meconopsis, and Papaver), but under natural conditions, this species was only found on Chelidonium and Macleava. However, identifications of Erysiphe collections on *Papaveraceae* remain complicated and require combinations of morphological examinations of holomorphs and sequence data, at best supplemented by inoculation tests, above all since papaveraceous hosts may be infected by several Erysiphe species with similar morphology. PASTIRČÁKOVÁ & al. (2016) included a sparse anamorphic sample from Switzerland on Stylophorum diphyllum in their phylogenetic analyses. They identified it as E. cruciferarum s. lat. (Clade 1 = E. aquilegiae clade), but stressed that the taxonomic status and identity are still uncertain. Chasmothecia and abundant conidiophores and conidia have later been found on Stylophorum diphyllum and proved to be in agreement with the characteristics of E. macleayae (relatively small chasmothecia with long appendages). Based on the combination of morphology and results of sequence analyses, it is likely that powdery mildew collections on S. diphylla pertain to E. macleayae. However, it is still necessary to include this host in inoculation tests.

Erysiphe sp. (*E. aquilegiae* complex) on *Papaver orientalis* – Fig. 8.

Collection examined: Switzerland, Vaud, Begnins, ch. des Perrières, on *Papaver orientalis*, 8 Oct. 2017, A. BOLAY (G00261079; Genbank no. MW600370; asexual and sexual morph).

Notes: Pastirčáková & al. (2016) sequenced several powdery mildew collections on various Papaver spp. as well as on Stylophorum diphyllum and assigned them to Erysiphe cruciferarum (s. 1.). However, these sequences clustered in clade 1, which coincides with the E. aquilegiae clade, distant from E. cruciferarum s. str. on its type host, Alyssum alyssoides, so that the name "E. cruciferarum" should rather be avoided for such collections, i.e., they should be referred to as "Erysiphe sp. (E. aquilegiae complex)" until the identity of *Erysiphe* sp. collections on *Papaver* spp. are clarified. This is the first sequence retrieved from Erysiphe on Papaver orientalis, but it clearly agrees with other sequences obtained from *Papaver* spp. that cluster within the *E. aquilegiae* clade. The taxonomic status of such collections on papaveraceous hosts is still unclear, and a species name for such collections is not available in case that this fungus would turn out to represent a species of its own. In any case, collections on these *Papaver* spp. are not assignable to E. macleavae, although the powdery mildew of the latter species on Chelidonium was able to infect Papaver spp. in inoculation tests (PASTIRČÁKOVÁ & al. 2016). Erysiphe sp. on Papaver spp. as well as E. macleayae are part of the E. aquilegiae complex, i.e., ITS sequences cluster together within the E. aquilegiae clade. However, the powdery mildew on *Papaver* spp. differs from *E. macleayae* in having almost consistently straight conidiophore foot-cells and larger chasmothecia, 90–150 µm diam. (average $> 100 \mu m$), with shorter appendages.

Erysiphe on Papaveraceae has previously been referred to as *E. cruciferarum* (BRAUN & COOK 2012), but based on phylogenetic examinations, this treatment is not tenable any longer. Fortunately, PASTIRČÁKOVÁ & al. (2016) generated ex-type sequences from the Czech type collection of *E. cruciferarum* on Alyssum alyssoides (type host), and in doing so they defined *E. cruciferarum* s. str. phylogenetically [Erysiphe cruciferarum OPIZ ex L. JUNELL, Sv. Bot. Tidskr. 61(1): 217, 1967; holotype – Czech Republic, Praha, Libeň (Lieben), on Alyssum alyssoides, 1841, M. OPIZ (PRM 194779); ex-type sequences – KU672364 (ITS), KU672344 (28S)].



Figs. 9–10. 9. *Pseudoidium passiflorae*, G00261050. *A* hyphal appressoria, *B* conidiophores, *C* conidia. 10. *Erysiphe eschscholziae*, HAL 3286 F. *A* hyphal appressoria, *B* conidiophores, *C* conidia. Bars: 10 μm. Drawing by A. BOLAY.

(3.2.) First sequences retrieved from *Erysiphe punicae* and type material of *E. thue-menii* (*E. aquilegiae* complex)

Erysiphe punicae T. M. ACHUNDOV, Nov. Sist. Niz. Rast. 24: 95, 1987.

Sequenced collection: Montenegro, on *Punica granatum*, 1 Oct. 2010, A. BOLAY (HAL 2441 F; Genbank no. MW581143, asexual morph).

Notes: This species was described from Azerbaijan on *Punica granatum*. Isotype material (LE 34530) has been examined (see BRAUN & COOK 2012). The sequence retrieved from the sample collected in Montenegro revealed that *E. punicae* belongs to the *E. aquilegiae* complex.

Erysiphe thuemenii U. Braun, Mycotaxon 18(1): 121, 1983.

Basionym: Erysiphe communis f. potentillae JACZ., Karm. Opred. Grib., Vip. 2. Muchn.-rosj. griby: 285, 1927.

Types: Neotype (designated in BRAUN & COOK 2012: 413): China: Inner Mongolia, Hohot City, Arboretum, on *Potentilla supina*, T. Z. LIU (CFSZ 03092). Isoneotype: HAL 2357 F; Genbank no. MW600378, ex-isoneotype sequence.

Notes: BRAUN (1983) introduced the new name *Erysiphe thuemenii* for *E. communis* f. *potentillae*, non *E. potentillae* LIB. Appropriate type material of this forma is not preserved in LE and LEP (herb. JACZEWSKI). Therefore, BRAUN & COOK (2012) designated a neotype. The isoneotype material has recently been successfully sequenced and proved to be part of the *E. aquilegiae* clade and complex.

(3.3.) *Pseudoidium passiflorae* (POLITIS) U. BRAUN & R. T. A. COOK, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 613, 2012 – Fig. 9.

Basionym: Oidium passiflorae POLITIS, Prakt. Akad. Athèns 13: 608, 1938.

- = Oidium passifloracearum HOSAG., Sydowia 43: 28, 1991.
- = Oidium goosii BAPPAMM., HOSAG. & UDAIYAN, New Botanist 22: 125, 1995.

Illustrations: Bappammal & al. (1995: 126, fig. 49), Braun (1998: 38, fig. 7), Liberato (2006: 74, Fig. 2), Jankovics & al. (2008: 532, fig. 1 C, H), Hosagoudar & Agarwal (2009: 47, fig. 52), Braun & Cook (2012: 614, fig. 826).

Description: As exual morph: Mycelium amphigenous, mainly hypophyllous, effuse or in thin patches, white; hyph a e branched, septate, hyaline, thinwalled, smooth, hyphal cells about 25–70 × 2.5–8 μm; hyphal appressoria solitary or in opposite pairs, lobate to multilobate, occasionally nipple-shaped, 5–10 μm diam.; conidiophore sarising from the upper surface of mother cells, erect, variable in length, 35–120 μm long, foot-cells cylindrical or subcylindrical, straight to slightly flexuous, sinuous, 15–80 × 4–11.5 μm, followed by (0–)1–3(–4) cells, shorter than the foot-cell, about as long or second cell sometimes even longer, forming conidia singly or mature conidia adhering in short false chains; conidia cylindrical to ellipsoid-ovoid, doliiform, 25–63 × 7–19 μm, length/width ratio 1.5–3.5, germ tubes subterminal, short, 2–4 μm wide, conidial appressoria swollen, alobate or distinctly lobate.

Host range and distribution: on *Passiflora caerulea* [Germany (BRAUN 1998, BRAUN & al. 2009, HARDTKE & OTTO 1998, JAGE & al. 2010), Greece (type of *Oidium passiflorae*), the Netherlands (JANKOVICS & al. 2008), Switzerland (present work), USA, California (GARDNER & al. 1970, as *Erysiphe polygoni*], *P. calcarata* [India (type of *Oidium goosii*], *P. foetida* [Australia, Queensland (LIBERATO 2006), India (type of *Oidium passifloracearum*)], *P. loefgrenii* [Germany (JAGE & al. 2010)]. [BRAUN & COOK (2012) listed *Passiflora stipulata* (Sri Lanka, see AMANO 1986, as *Oidium* sp.) as host of *P. passiflorae*. However, this record is unproven, doubtful, and should be dropped.]

Collections examined (asexual morphs): Switzerland: Vaud, Rolle, rue du Port, on *Passiflora caerulea*, 16 Aug. 2008, A. BOLAY (HAL 2296 F); ibid., 12 Oct. 2010 (G00261050); ibid., 30 Jul. 2010 (G00261051); Vaud, Nyon, route de Signy 5, 4 Nov. 2009, A. BOLAY (G00261049); Vaud, Morges, rue des Tanneurs 1, on *Passiflora caerulea*, 31 Oct. 2008, A. BOLAY (HAL 2297 F); ibid., 16 Sep. 2017, A. BOLAY (G00261082); ibid., 22 Nov. 2017, A. BOLAY (G00261083; Genbank no. MW600369).

Notes: ITS sequences retrieved from *Pseudoidium passiflorae* on *Passiflora caerulea* from the Netherlands and Switzerland cluster within the *Erysiphe aquilegiae* clade and cannot be genetically differentiated from other taxa within this complex. For various reasons, final conclusions to the taxonomic status of this species are not yet possible. The sexual morph of this species is still unknown. Inoculation experiments showing that this powdery mildew is confined to *Passiflora* spp. are unknown, and the resolution of ITS data within the *E. aquilegiae* clade is insufficient for species level clarification. It cannot be excluded that *Passiflora* spp. might belong in the host range of a plurivorous powdery mildew species of this complex. Cross-infection tests and molecular multilocus approaches are necessary to clarify the taxonomic status of the *Passiflora* powdery mildew. Since the status of *Pseudoidium passiflorae* as an acceptable species of its own is still unclear, we refrain from transferring this name to *Erysiphe* to which it belongs and propose to maintain and use the anamorph name *Pseudoidium passiflorae* for the interim.

BRAUN & COOK (2012) treated *Oidium passifloracearum*, described from India on *Passiflora foetida*, under "Anamorphic powdery mildews (*Oidium*) of unclear generic affinity", above all because catenate conidia were mentioned in the original description. However, the characteristics of the hyphal appressoria (lobate), conidiophores and conidial shape and size agree well with *Pseudoidium passiflorae*, which is also known on *P. foetida* in Australia. Conidia in short (false) chains are common in *P. passiflorae*. Therefore, it is very likely that *O. passifloracearum* represents a synonym of *P. passiflorae*.

(4) Erysiphe eschscholziae on Eschscholzia californica

Erysiphe eschscholziae PASTIRČ. & JANKOVICS, in Pastirčáková & al., Mycol. Progr. **15**(no. 36): 11, 2016 – Fig. 10.

Collections examined (asexual morphs): Switzerland: Vaud, Nyon, on *Eschscholzia californica*, 31 Oct. 2015, A. BOLAY (HAL 3286 F; Genbank no. MW600373; Vaud, Nyon, rte de Signy, on *Eschscholzia californica*, 23 Oct. 2018, A. BOLAY (G00261073; Genbank no. MW600365); Genève, quai Wilson, on *Eschscholzia californica*, 18 Oct. 2018, A. BOLAY (G00261072).

Notes: Pastirčáková & al. (2016) described *Erysiphe eschscholziae* based on type material from Switzerland. A single nrDNA 28S sequence, two ITS sequences, and results of inoculation experiments showed that *Eschscholzia californica* is not susceptible to *Erysiphe* sp. on *Papaver* (*E. cruciferarum* s. l., sensu Pastirčáková & al. 2016) and *E. macleayae* from *Chelidonium*. *E. eschscholziae* is only known from its asexual morph (chasmothecia not yet observed), but sequences retrieved from collections of this species form a well-supported clade distant from all other clades containing sequences of *Erysiphe* spp. obtained from papaveraceous hosts and also from all other species of this genus. The two newly generated sequences of *E. eschscholziae* confirm previous results and conclusions. Shape and size of hyphal appressoria, conidiophores and conidia are

also in agreement: Hyphal appressoria lobate to multilobate, rarely nipple-shaped; conidiophores solitary, erect, straight, $85{\text -}130~\mu m$ long, foot-cells cylindrical, straight to often curved-sinuous, $25{\text -}50 \times 7{\text -}9~\mu m$, followed by $1{\text -}3$ cells, shorter than the foot-cell, about as long or second cells sometimes even longer; conidia formed singly, cylindrical, ellipsoid-doliiform, $30{\text -}52.5 \times 7{\text -}19~\mu m$, germ tubes subterminal, $0{\text -}2$ -septate, terminal appressorium unlobed to lobate.

(5) Erysiphe deutziae on Deutzia spp.

Erysiphe deutziae (BUNKINA) U. BRAUN & S. TAKAM., Schlechtendalia 4: 7, 2000.

Collections examined: Switzerland: Vaud, Nyon, Pré-Fleuri, on *Deutzia crenata*, 18 Oct. 2018, A. BOLAY (G00261062; Genbank no. MW600366, holomorph); Genève, Jardin botanique, on *Deutzia scabra*, 18 Oct. 2018, A. BOLAY (G00261064; Genbank no. MW600367, asexual morph).

Notes: BOLAY & al. (2005) described and discussed the epidemic spread of *E. deutziae* in Europe in detail, including specimens collected in Switzerland, which were also described in BOLAY (2005). In Europe, this species is known from France, Germany, Poland, Switzerland, and the UK (BOLAY & al. 2005, BRAUN & COOK 2012). Recently, it was also recorded from the Czech Republic on *Deutzia scabra* (MIESLEROVÁ & al. 2020). *Erysiphe deutziae* was also recorded from Iran on *Deutzia gracilis* (ABBASI & al. 2013). Previous records only referred to the asexual morph. The two sequences retrieved from Swiss samples of *E. deutziae* and the formation of chasmothecia in the specimen collected in 2018 on *Deutzia crenata* confirm the occurrence of this species in Europe and in particular Switzerland.

(6) New sequences retrieved from *Erysiphe malvae*

Erysiphe malvae V. P. HELUTA, Ukrayins'k. Bot. Zhurn. 47(4): 75, 1990

Sequenced collections (holomorphs): Iran: Guilan, Manjil, on *Malva* sp., 25 Jul. 2007, S. A. KHODAPARAST (HAL 3361 F, Genbank no. MW581145). Ukraine: Crimea, Yalta, *Malva ambigua*, 15 Sep. 2003, V. P. HELUTA (HAL 3362 F, Genbank no. MW581144).

Notes: Erysiphe malvae was described from Ukraine on Malva erecta. This species is known from Asia (Iran, Israel) and Europe (Ukraine). The morphology of this species is very close to Erysiphe heraclei on numerous Apiaceae (BRAUN & COOK 2012), above all with regard to the frequently irregularly branched chasmothecial appendages. The close affinity of the two species has been confirmed by results of phylogenetic analyses published by TAKAMATSU & al. (2015) as well as the present sequence analyses. Erysiphe malvae only differs from E. heraclei in having longer conidiophore foot-cells [frequently longer than 50 μm, usually shorter than 50 μm in E. heraclei (see key to the species of Erysiphe in BRAUN & COOK 2012)]. Based on host range differences (Apiaceae vs. Malvaceae), slight morphological differences and an ITS similarity of

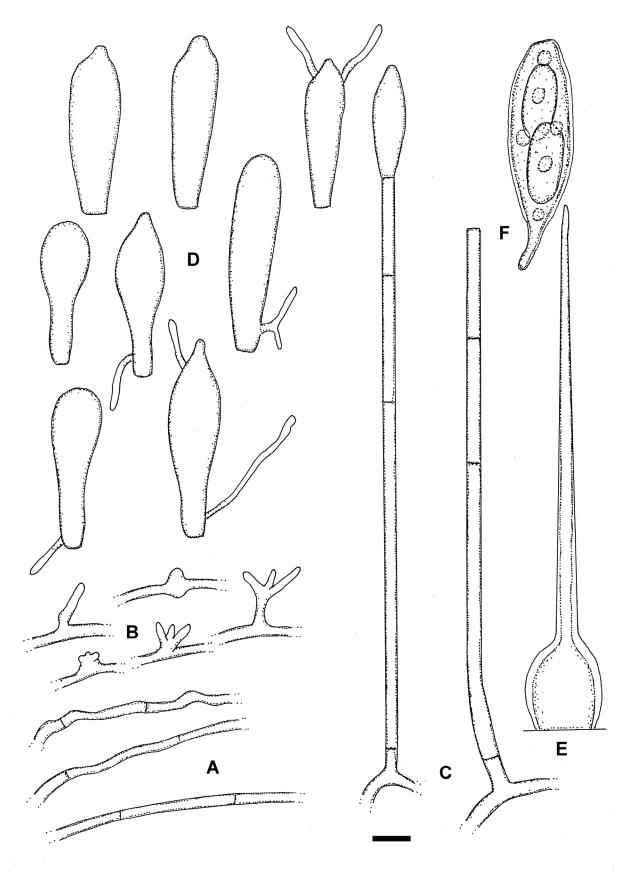


Fig. 11. *Phyllactinia cruchetii* sp. nov., HAL 3290 F, isotype. *A* hyphae, *B* hyphal appressoria, *C* conidiophores, *D* conidia (with and without germ tubes), *E* chasmothecial appendages, *F* ascus (chasmothecia agreeing with those of most other *Phyllactinia* species, see Braun & Cook 2012: 252, Fig 252). Bar: 10 μm. Drawing by U. BRAUN.

about 98 %, we prefer to keep *E. malvae* as a separate species, at least for the interim until biological examinations (inoculation tests) will be available.

(7) A new Phyllactinia species on Passiflora caerulea

Phyllactinia cruchetii BOLAY & U. BRAUN, spec. nova – Fig. 11. MycoBank no. MB838896, Genbank no. MW600375, ex-isotype sequence.

Diagnosis: Morphologically very close to the phylogenetically allied species, *Phyllactinia betulae* and *P. linderae*, but genetically clearly distinct and different in having shorter chasmothecial appendages (up to 2.5 times as long as the chasmothecial diam. in *P. betulae* and *P. linderae*).

Holotypus: Switzerland: Vaud, Morges, rue des Tanneurs 1, on *Passiflora caerulea*, *Passifloraceae*, 16 Dec. 2016, A. BOLAY (G00261095). Isotype: HAL 3290 F.

Etymology: dedicated to PAUL CRUCHET (*1875, †1964), Swiss botanist and mycologist.

Description: A s e x u a 1 m o r p h: M y c e l i u m hypophyllous, effuse, white; h y p h a e branched, septate, thin-walled, smooth, 2–7 µm wide, hyphal cells about 30– 110 µm long; h y p h a l a p p r e s s o r i a solitary, occasionally in opposite pairs, nipple-shaped, somewhat lobate to oblong or somewhat coralloid, sometimes with a short stalk, up to 20 µm long, and terminal branchlets; c o n i d i o p h o r e s arising from the upper surface of hyphal mother cells, erect, straight, filiform, mostly 120–230 µm long, foot-cells straight, cylindrical-filiform, 80–150 μm long and (4–)5–7(–9) μm wide, followed by (1-)2(-4) shorter cells, 10-65 µm long, basal septum usually elevated, (3-)8-15 µm distant from the branching point with the mother cells; c o n i d i a formed singly, clavate-spathuliform, apex rounded to apiculate (umbonate), apiculus 4–10 µm wide and up to 7 μ m high, 57.5–92.5 × 15–32.5 μ m, Q = 75.5 × 22 μ m (N = 30), length/width ratio 2.1-4.7(-5), Q = 3.6, germ tubes at both ends, subapical and subterminal, with a single germ tube below or above or with two germ tubes at both ends or both tubes subapical, filiform, straight to sinuous, to 70 µm long, aseptate, apex undifferentiated or with a swollen or slightly lobed terminal appressorium, germ tubes rarely branched near the base.

S e x u a 1 m o r p h : C h a s m o t h e c i a hypophyllous, scattered, subglobose, 185–250 μ m diam.; p e r i d i a 1 c e 11 s rounded in outline to somewhat angular-irregular, daedaleoid, 8–25 μ m diam.; p e n i c i 11 a t e c e 11 s not observed (degenerated); a p p e n d a g e s 9–13 per chasmothecium, equatorial, about as long as the chasmothecial diam. (180–280 μ m), acicular with bulbous basal swelling, 25–35(–40) μ m diam., wall to 4 μ m thick near the base; a s c i numerous, 8–18, clavate-saccate, stalked, with oil droplets, 60–75 × 25–30 μ m, thin-walled, terminal oculus 10–15 μ m diam., 2-spored; a s c o s p o r e s broad ellipsoid, hyaline, 20–32 × 12–15 μ m.

Additional collections examined (asexual morphs, sometimes with immature chasmothecia): Switzerland: Vaud, Morges, rue des Tanneurs 1, on *Passiflora caerulea*, 19 Oct. 2009, A. BOLAY (G00261088); ibid., 14 Nov. 2009 (G00261089); ibid., 23 Dec. 2009 (G00261090); ibid., 25 Oct. 2013 (G00261091);

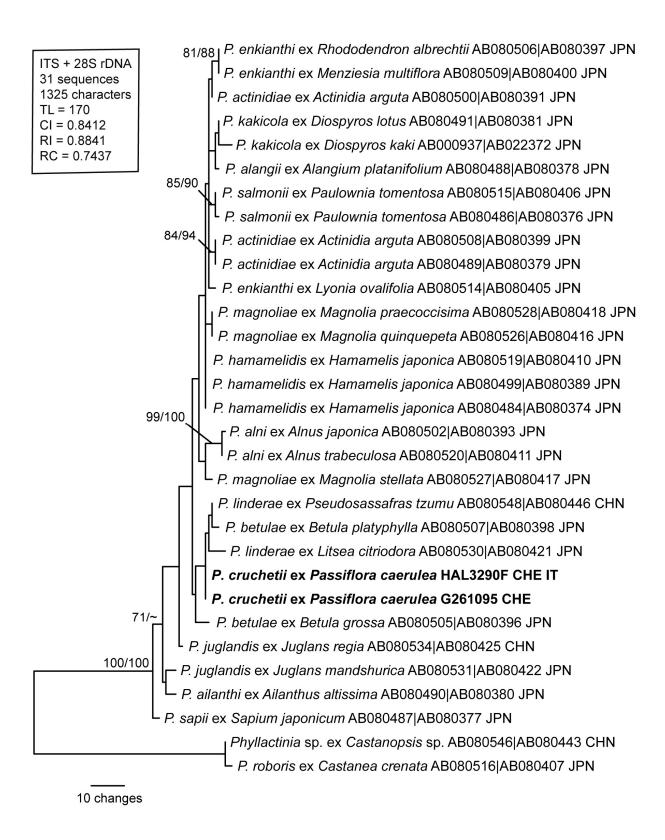


Fig. 12. Phylogenetic analysis of combined data of the 5'-end of the 28S rDNA (including domains D1 and D2) and ITS region for 31 sequences from the genus *Phyllactinia*. This is the tree with the highest likelihood value out of 12 equally parsimonious trees with 170 steps, which were found using a heuristic search. 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 were shown on the respective branches. Sequences determined in this study were shown as bold faces. *P.: Phyllactinia*, IT: isotype.

ibid., 28 Oct. 2013 (G00261092); ibid., 22 Oct. 2015 (G00261094; Genbank no. MW600372); ibid., 28 Nov. 2015 (G00261093).

Notes: BRAUN & COOK (2012: 292) discussed a sample of this fungus on *Passiflora caerulea* from Switzerland as *Phyllactinia* sp. The chasmothecia were immature and phylogenetic data were not yet available for a final conclusion in that time. *Ovulariopsis passiflorae* SYD. (= *Streptopodium passiflorae* (SYD.) LIBERATO & R. W. BARRETO), known on various *Passiflora* spp. in South Africa, Asia (India), and South America, is quite distinct from *P. cruchetii* by having sinuous conidiophore foot-cells and dimorphic, non-apiculate conidia.

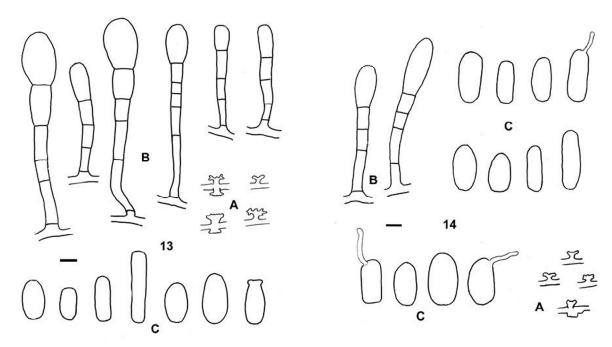
(8) Additional records of powdery mildew from Switzerland

(8.1) *Erysiphe convolvuli* DC., in LAMARCK & de CANDOLLE, Fl. franç., Edn 3, **2**: 274, 1805 – Fig. 13.

= ? Pseudoidium ipomoeae (J. M. YEN & CHIN C. WANG) U. BRAUN & R. T. A. COOK, Taxonomic Manual of the Erysiphales (Powdery Mildews): 607, 2012.

Collection examined: Switzerland: Genève, Jardin botanique, on *Ipomoea lobata*, Sep. 2011, A. Bo-LAY (G00261353, asexual morph).

Notes: This is the first record of powdery mildew on *I. lobata*. The asexual morph found on this host agrees well with the asexual morph of Erysiphe convolvuli and the description of Pseudoidium ipomoeae in BRAUN & COOK (2012), as well as the description and illustration of this species on *Ipomoea aquatica* in Thailand (MEEBOON & TAKAMATSU 2016). The conidiophores are erect, width slightly increasing from base to top, foot-cells straight to somewhat curved or sinuous throughout, 15–45 × 5–10 µm, followed by 2–4 mostly shorter cells; conidia formed singly, ellipsoid-ovoid, cylindrical, 25–50 × 12–20 μm. ABASOVA & al. (2018) added a sequence obtained from powdery mildew on I. aquatica in China (KJ885178) to a phylogenetic tree, in which this sequence clustered within the E. convolvuli clade, suggesting that Ipomoea species belong to the host range of the latter species. However, the taxonomic identity of *P. ipomoeae* is still unclear. MEEBOON & TAKAMATSU (2016) sequenced powdery mildew on Ipomoea obscura (type host of *P. ipomoeae*) from Thailand, which clustered separately from other *Erv*siphe species, including E. convolvuli. However, the described asexual morph on I. obcura in Thailand does not agree with the original description of P. ipomoeae and the circumscription published in BRAUN & COOK (2012). The foot-cells of the conidiophores in the specimen on *I. obcura* from Thailand are distinctly curved-sinuous at the base, suggesting that more than one Erysiphe species may occur on Ipomoea spp. Epitypification of P. ipomoeae with material from Taiwan on Ipomoea obscura with exepitype sequences is necessary to clarify the identity of this species. BOLAY (2005) listed Erysiphe convolvuli on Ipomoea hederacea and I. purpurea from Switzerland. Further studies, above all sequence analyses of powdery mildew collections on *Ipomoea* sp. are urgently necessary.



Figs. 13–14. 13. *Erysiphe convolvuli*, asexual morph on *Ipomoea lobata*, G00261353. *A* hyphal appressoria, *B* conidiophores, *C* conidia. 14. *Erysiphe howeana*, asexual morph on *Oenothera lindheimeri*, G00261355 and 261356 (germinated conidia). *A* hyphal appressoria, *B* conidiophores, *C* conidia. Bars: 10 µm. Drawing by A. BOLAY.

(8.2) Erysiphe guarinonii (BRIOSI & CAVARA) U. BRAUN & S. TAKAM., Schlechtendalia 4: 9, 2000.

= Erysiphe baptisiae U. BRAUN & J. KRUSE, in BRAUN & al., Mycotaxon 112: 176, 2010.

Collection examined: Switzerland: Genève, Jardin botanique, on *Baptisia australis*, Sep. 2004, A. Bo-LAY (G00261354, asexual morph).

Notes: Based on results of phylogenetic analyses, including type material of *E. baptisiae*, the latter species has been reduced to synonymy with *E. guarinonii* (BRADSHAW & al. 2021). This species is known from Switzerland on *Chamaecytisus hirsutus*, *Laburnum alpinus* and *L. anagyroides* (BOLAY 2005), but *Baptisia australis* is a new host record for this country. The asexual morph of the Swiss collection is characterised as follows: Mycelium amphigenous, forming white patches or effuse; hyphae 3–7 μ m wide, hyaline; hyphal appressoria crenulate to lobate; conidiophores cylindrical, 40–80 μ m long, foot-cells straight to curved-sinuous, 15–35 × 5–7 μ m, followed by 1–3 shorter cells; conidia solitary, ellipsoid-ovoid, cylindrical, doliiform, 22–38 × 10.5–16 μ m.

(8.3) *Erysiphe howeana* U. BRAUN, Mycotaxon **14**(1): 373, 1982 – Fig. 14.

Collections examined: France: Corse, Solenzara, café du port, on *Oenothera lindheimeri* (≡ *Gaura lindheimeri*), Oct. 2014, A. BOLAY (G00261355, asexual morph). Switzerland: Genève, Jardin botanique, Le Chêne, on *O. lindheimeri*, Oct. 2015, A. BOLAY (G00261356, asexual morph); Vaud, Morges, quai Lochmann, bord du lac, on *O lindheimeri*, Dec. 2016, A. BOLAY (G00261357, asexual morph).

Notes: Erysiphe howeana is known from Switzerland. The holomorph was described and illustrated in detail in Bolay (2005). Species of the former genus Gaura (now Oenothera sect. Gaurae) are known as hosts of E. howeana, such as Oenothera curtiflora [= Gaura parviflora] (Braun & Cook 2012), but Oenothera lindheimeri being a new host for this species. The morphology of the asexual morph on this new host agrees well with the characteristics of E. howeana (Braun & Cook 2012): Conidiophores erect, foot-cells cylindrical, $20-30 \times 5-7$ µm, followed by 1-2 shorter cells, conidia ellipsoid-ovoid, cylindrical, $25-42 \times 12-17.5$ µm. Gaura has been reduced to synonymy with Oenothera since Gaura species deeply nested within the Oenothera clade in phylogenetic analyses (Wagner & al. 2013).

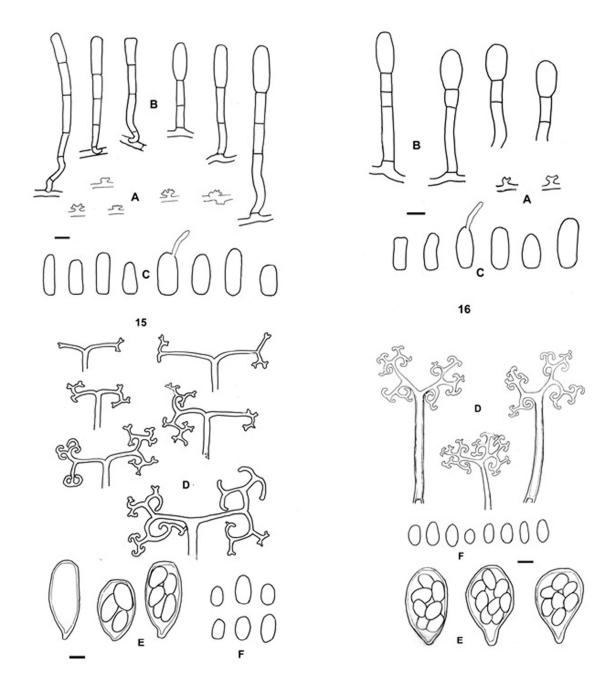
(8.4) *Erysiphe pseudoacaciae* (P. D. MARCHENKO) U. BRAUN & S. TAKAM., Schlechtendalia 4: 12, 2000 – Fig. 15.

Collections examined: Italy: Piémont, S.S. Pinerolo, 30 km south of Torino, on *Robinia pseudoacacia*, Oct. 2012, A. Bolay (G00261358, holomorph). Switzerland: Kanton Freiburg, Murten, on *Robinia pseudoacacia*, Aug. 2010, A. Bolay (G00261359, holomorph); ibid., Sep. 2011, A. Bolay (G00261360, holomorph).

Notes: Erysiphe pseudoacaciae is new for Italy, and this is the first unequivocal record of this species from Switzerland on Robinia pseudoacacia. An old record of this species on Colutea arborescens from Switzerland by BLUMER (1933: 344–345) under the name Microsphaera coluteae KOM. (see BRAUN 1987 and BRAUN & COOK 2012, under E. pseudoacaciae) is unclear and has not been confirmed since that time, i.e., it is in need of confirmation. SCHMIDT & BRAUN (2020) described in detail the asexual morph (including conidial germination) and chasmothecia of E. pseudoacacae, based on German collections. The chasmothecia found in Italy and Switzerland agree well with the morphology of this species: Chasmothecia 80–110 μ m diam., peridial cells 10–25 μ m diam., with 5–15 appendages, long and flexuous, 3–12 times as long as the chasmothecial diam., to 10 μ m wide below and 3–5 μ m wide above, aseptate or with a single basal septum, colourless or only brown at the very base, apex 1–5 times loosely but regularly dichotomously branched, primary branched mostly elongated, tips of the ultimate branchlets mostly recurved when fully mature, with 3–7 asci per chasmothecium, asci $40-60 \times 20-35 \mu$ m, 3–7-spored, ascospores $14-25 \times 8-14 \mu$ m.

(8.5) Erysiphe pulchra (COOKE & PECK) U. BRAUN & S. TAKAM., Schlechtendalia 4: 12, 2000 – Fig. 16.

Collections examined: Germany: Schleswig-Holstein, Lübeck, urban park, on *Cornus mas*, 3 Nov. 2018, A. SCHMIDT (HAL 3366 F, KR-M-0013226, holomorph, mixed infections together with *Phyllactinia corni* H.D. SHIN & U. BRAUN). Italy: Piémont, Carisio, highway Turin-Milan, restaurant Paladin, on *Cornus kousa*, Oct. 2015, A. BOLAY (G00261361, asexual morph). Switzerland: Vaud, Lutry, Petit-Bochat, on *Cornus alba*, Oct, 2011, A. BOLAY (G00261362, asexual morph); Nyon, gare CFF, on *Cornus florida*, Oct. 2012, A. BOLAY (G00261363, asexual morph); Genève, Jardin botanique, on *Cornus florida*, Oct. 2012, A. BOLAY (G00261364, asexual morph); Genève, Jardin botanique, on *Cornus kousa*, Oct. 2015, A. BOLAY (G00261365, holomorph).



Figs. 15–16. 15. Erysiphe pseudoacaciae, holomorph on Robinia pseudoacacia, G00261359. A hyphal appressoria, B conidiophores, C conidia, D chasmothecial appendages, E asci, F ascospores. 16. Erysiphe pulchra, on Cornus kousa, asexual and sexual morph, G00261362 and G00261364, respectively. A hyphal appressoria, B conidiophores, C conidia, D chasmothecial appendages, E asci, F ascospores. Bars: 10 μm. Drawing by A. BOLAY.

Notes: The phylogeny and taxonomy of *Erysiphe pulchra* has recently been clarified by MEEBOON & TAKAMATSU (2017). They reassessed *E. pulchra* s. str., excluding the Japanese *Microsphaera japonica* HENN. which has been reinstated as *Erysiphe cornicola* MEEBOON & S. TAKAM. Collections on *Cornus alba*, *C. florida* and *C. kousa* belong to *E. pulchra*, which is known from Asia, Europe and North America (BRAUN & COOK 2012, MEEBOON & TAKAMATSU 2017). This is the first report of this species from Switzerland, and the first report of *C. kousa* as a host from Italy. In Europe, *E. pulchra* has been recorded from Germany, Italy, and the UK (GARIBALDI & al. 2009, BRAUN & COOK 2012, CHATER & WOODS 2019, KRUSE & al. 2020). European infections of *E. pulchra* usually occur on exotic *Cornus* species, but a recent collection of this species

on *Cornus mas* in Germany (mixed infections with *Phyllactinia corni* H. D. SHIN & U. BRAUN, published under the latter name by SCHMIDT & BRAUN 2020) suggests that it may also infest native European *Cornus* spp. *Cornus mas* is a new host for *E. pulchra*. The asexual and sexual morphs found on these hosts in Italy and Switzerland agree perfectly with the general traits of *E. pulchra*: Hyphae 3–6 μ m wide; conidiophores 40–80 μ m long, foot-cells to 40×5 –8 μ m, flexuous, followed by (0-)1-2 shorter cells; conidia formed singly, ellipsoid-ovoid, cylindrical, $23-42 \times 6-18$ μ m. Chasmothecia (on *Cornus kousa*) 78–117 μ m diam., peridial cells 9–28 μ m diam., 5–15 appendages per chasmothecium, 0.9–2 times as long as the chasmothecial diam. (100–185 μ m), 7–10 μ m wide at the base, 3–6 μ m wide above, aseptate or with a single basal septum, hyaline or only brown at the very base, apex 4–6 times regularly dichotomously branched, tips of the ultimate branchlets recurved, 4–11 asci per chasmothecium, broad ellipsoid-ovoid, saccate, subsessile or short-stalked, $60-75 \times 35-45$ μ m, (4-)5-7(-8)-spored, ascospores $14-21 \times (7-)8-12$ μ m.

(8.6) *Erysiphe* sp. (*Pseudoidium* sp.) on *Fumaria* spp. and *Pseudofumaria lutea*.

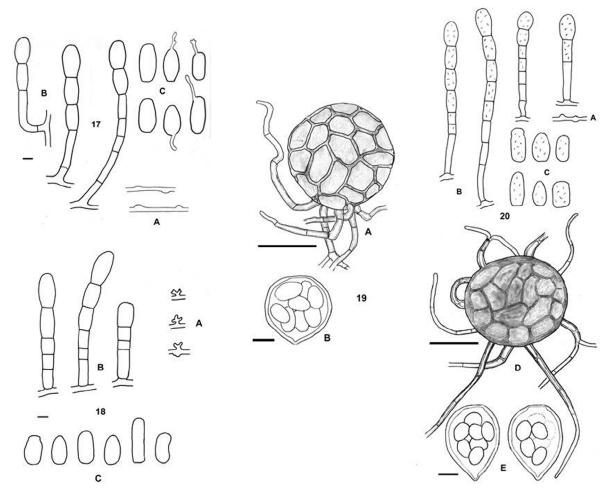
Collections examined: France: Côte d'Azur, Var, Cap Estérel, village Pierre & Vacances, Le Dramont, on *Fumaria capreolata*, 27 Sep. 2000, A. BOLAY (G00261074, asexual morph). Switzerland: Vaud, Aubonne, Arboretum, on *Fumaria officinalis*, 23 Oct. 2011, A. BOLAY (G00261075, asexual morph); Genève, Jardin botanique, on *Pseudofumaria lutea*, 24 Oct. 2000, A. BOLAY (G00261070, asexual morph); ibid., 3 Oct. 2011, A. BOLAY (G00261071, asexual morph).

Notes: Powdery mildew on *Pseudofumaria lutea* and *Fumaria* spp. is morphologically close to the asexual morph of *Erysiphe cruciferarum* and was previously assigned to this species (see BRAUN & COOK 2012), including records from Switzerland (BOLAY 2005). However, the status of the *Fumaria* powdery mildew could not be clarified by means of sequence analyses. The available collections were too sparse. Therefore, this powdery mildew should currently be referred to as *Erysiphe* sp. Conidiophores and conidia found on *Pseudofumaria lutea* agrees well with the description and illustration published by SCHMIDT & SCHOLLER (2011) as *Oidium* sp., based on material collected on this host in Germany. The asexual morph on *Fumaria* spp. is characterized as follow: Hyphal appressoria usually solitary, slightly to distinctly lobate; conidiophores arising from the upper surface of superficial hyphae, erect, 55-75 µm long (without conidia), foot-cells straight to mostly curved-sinuous, $18-55 \times 5-8$ µm, followed by 1-3 cells, 10-35 µm long, mostly shorter than the foot-cells, sometimes about as long or second cells even longer than the foot-cell; conidia formed singly, usually ellipsoid or ellipsoid-ovoid, occasionally subcylindrical, $25-40 \times 14-18$ µm.

(8.7) Golovinomyces depressus (WALLR.) V. P. HELUTA, Ukrayins'k. Bot. Zhurn. 45(5): 62, 1988.

Collection examined: Switzerland: Vaud, Cossonay-ville, rte. de Morges 9, on *Psephellus dealbatus* (≡ *Centaurea dealbata*), 25 Sep. 2018, A. BOLAY (HAL 3364 F, holomorph).

Notes: This is the first record of this species on *Psephellus dealbatus* (BRAUN & COOK 2012). The asexual morph and the chasmothecia agree well with collections on *Arctium* and *Centaurea* spp. (BRAUN & COOK 2012).



Figs. 17–20. 17. Golovinomyces monardae, on Verbena bonariensis, asexual morph, G00261366. A hyphal appressoria, B conidiophores, C conidia. 18. Neoerysiphe aloysiae, Aloysia citriodora, asexual morph, G00261369. A hyphal appressoria, B conidiophores, C conidia. 19. Podosphaera macrospora, on Heuchera parviflora, sexual morph, G00261370. A chasmothecium, B ascus. 20. Podosphaera solanacearum, on Capsicum sinensis, holomorph, G00261378. A hyphal appressoria, B conidiophores, C conidia, D chasmothecial appendages, E asci. Bars: 10 μm (except for 19 A and 20 D = 50 μm). Drawing by A. BOLAY.

(8.8) *Golovinomyces monardae* (G. S. NAGY) M. SCHOLLER, U. BRAUN & ANKE SCHMIDT, in SCHOLLER & al., Mycol. Progr. **15** (Article 56): 4, 2016 – Fig.17.

Collections examined (asexual morph): Switzerland: Vaud, Nyon, rue de la Morâche, on *Verbena bonariensis*, Oct. 2015, A. BOLAY (G00261366); ibid., Nov. 2016, A. BOLAY (G00261367); Vaud, Coinsins, auberge de la Réunion, on *Verbena bonariensis*, Oct. 2016, A. BOLAY (G00261368).

Notes: Golovinomyces monardae on Verbena bonariensis is new to Switzerland. Based on phylogenetic data, the taxonomy of Golovinomyces on Verbena (including Glandularia) species has recently been clarified by SCHOLLER & al. (2016) and BRADSHAW & al. (2021). In the latter work, G. verbenae (SCHWEIN.) V. P. HELUTA has been reassessed, described, epitypified with ex-epitype sequences. The authors reduced G. glandulariae to synonymy with G. verbenae. SCHOLLER & al. (2016) showed by means of sequencing that G. monardae, characterised by having conidiophores with usually curved foot-cells, may also occur on Verbena spp., including V. bonariensis and V. ×hybrida (a sequence retrieved from a specimen collected in Switzerland, AB769438, see

TAKAMATSU & al. 2013). The cited new Swiss anamorphic collections on V. bonariensis agree with G. monardae: Hyphae 3–5 μ m wide; hyphal appressoria nipple-shaped; conidiophores 25–90 μ m long, foot-cells usually curved-flexuous, $20–50 \times 7–12$ μ m, followed by (0–)1–2 shorter cells; conidia catenescent, outline of the chains sinuate, ellipsoid-ovoid, subcylindrical, doliiform, $25–38 \times 10–16$ μ m. The asexual morph of G. verbenae differs in having consistently straight conidiophores foot-cells (BRADSHAW & al. 2021). The occurrence of G. orontii (CASTAGNE) V. P. HELUTA (s. lat.) on Verbena is only known from artificial inoculation experiments under glass house conditions (BRAUN & al. 2019).

- **(8.9)** *Neoerysiphe aloysiae* (WOLCAN, S. TAKAM. & HAVRYL.) S. TAKAM., in WIJAYAWARDENE & al., Fungal Divers. **86**: 306, 2017 Fig.18.
- = Oidium aloysiae Wolcan, S. Takam. & Havryl., Mycol. Res. 112(6): 644, 2007.
- ≡ Striatoidium aloysiae (WOLCAN, S. TAKAM. & HAVRYL.) WOLCAN, S. TAKAM. & HAVRYL., Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 347, 2012.

Collection examined: Italy: Piemont, Pinerolo, on *Aloysia citriodora*, Oct. 2012, A. BOLAY (G00261369, asexual morph).

Notes: The specimen from Italy agrees well with type material of *N. aloysiae* (hyphal appressoria lobate; foot-cells of the conidiophores 20–35 × 8–11 μm, followed by two shorter cells; conidia catenescent, ellipsoid-ovoid, doliiform, subcylindrical, 25–40 × 12–16 μm, finely striate. This species was described from Argentina on *Aloysia citriodora* and has recently been reported on this host from Mexico (SOLANO-BÁEZ & al. 2020). This is the first European record of this species. The owner of the garden in Italy transplanted the host plant from Argentina to Pinerollo when she came back to Italy after the Second World War. TAKAMATSU & al. (2008) analysed the phylogenetic position of this species and showed that it belongs to *Neoerysiphe*, which is in full concordance with the morphology of the *Aloysiae* powdery mildew.

(8.10) *Podosphaera macrospora* (U. BRAUN) U. BRAUN & V. KUMM., Schlechtendalia 17: 48, 2008 – Fig. 20.

Collection examined: Switzerland: Nyon, ch. de Bourgogne 9, on *Heuchera parviflora*, 20 Oct. 2014, A. BOLAY (HAL 3365 F, holomorph), ibid., Dec. 2018, A. BOLAY (G00261370)

Description: A s e x u a l m o r p h: M y c e l i u m hypophyllous, effuse, white, brownish at the end of the season; h y p h a e branched, septate, thin-walled, smooth, 3–8 μ m wide; h y p h a l a p p r e s s o r i a indistinct; c o n i d i o p h o r e s arising from the upper surface of hyphal mother cells, erect, straight, 80–200 μ m long (foot-cells, following cells and conidia), foot-cells straight, subcylindrical, 40–80 μ m long and 8–15 μ m wide, followed by 1–3 shorter cells, basal septum at the junction with the mother cells or slightly elevated; c o n i d i a catenescent, ellipsoid-ovoid to doliiform, with fibrosin bodies, 25–45 \times 12–25 μ m.

S e x u a l m o r p h: C h a s m o t h e c i a amphigenous, scattered, globose, 95–115 μ m diam.; p e r i d i a l c e l l s i r r e g u l a r l y angular-irregular, 25–40 × 15–25 μ m diam.; a p p e n d a g e s few per chasmothecium or almost lacking, in the basal half, about 0.5–3 times as long as the chasmothecial diam., mycelioid, unbranched

or occasionally branched, septate, thin-walled, hyaline or brownish below; a s c u s sub-globose, broad ellipsoid, $50-65 \times 40-50$ µm, thin-walled, terminal oculus 10-20 µm diam., 8-spored; a s c o s p o r e s broad ellipsoid-ovoid, hyaline, $40-55 \times 26-33$ µm.

Notes: *Podosphaera macrospora* is known from Switzerland (BOLAY 2005, BRAUN & COOK 2012), but *Heuchera parviflora* is a new host record for this country.

(8.11) *Podosphaera pruinosa* (COOKE & PECK) U. BRAUN & S. TAKAM., Schlechtendalia 4: 31, 2000.

Collections examined (asexual morph): Switzerland: Vaud, Nyon, ch. du Midi, on *Rhus typhina*, Oct. 2011, A. BOLAY (G00261371); Vaud, Nyon, la Levratte, av. Cortot, on *Rhus typhina*, Aug. 2014, A. BOLAY (G00261372); Vaud, Lutry, on *Rhus typhina*, av. Conversion, on *Rhus typhina*, Oct. 2011, A. BOLAY (G00261373); Vaud, Prangis, cimetière, on *Rhus typhina*, Sep. 2011, A. BOLAY (G00261374); Vaud, Aubonne, ville, on *Rhus typhina*, Oct. 2011, A. BOLAY (G00261375); Vaud, Aubonne, Arboterum, on *Rhus typhina*, Sept. 2011, A. BOLAY (G00261376); Vaud, Aubonne, Arboterum, on *Rhus typhina*, Sept. 2011, A. BOLAY (G00261377).

Notes: *Podosphaera pruinosa* is a North American species, introduced in Europe (Germany, BOYLE & al. 2008; Switzerland, BRAUN & COOK 2012; Czech Republic, MIESLEROVÁ & al. 2020). BOLAY (2005) did not yet list this species from Switzerland. The sexual morph of this species has not yet been found in Europe. *Rhus* × *pulvinata* represents a new host record for this species.

(8.12) *Podosphaera solanacearum* U. BRAUN, in BRAUN & COOK, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 160, 2012 – Fig. 20.

Description: A s e x u a l morph: Mycelium amphigenous, effuse or in patches, white; primary hyphae hyaline, branched, septate, thin-walled, smooth, 3–5 μm wide, secondary hyphae developed, greyish brown, 5–8 μm diam.; hyphal appressoria rarely developed, nipple-shaped; conidiophores arising from the upper surface of hyphal mother cells, usually towards one septum of the mother cell, erect, straight, 70-150(-180) μm long (foot-cells and following cells), foot-cells straight, subcylindrical to somewhat curved-sinuous, 30-90 μm long and 7-12 μm wide, slightly increasing from base to top, followed by (0-)1-2(-4) shorter cells, 10-13 μm wide, basal septum at the junction with the mother cells or slightly elevated (-8 μm); conidia catenescent, ellipsoid-ovoid, subcylindrical, with fibrosin bodies, $24.5-38.5 \times 11.5-21$ μm, $Q = 30.0 \times 14.8$ μm (N = 20).

S e x u a l m o r p h : C h a s m o t h e c i a amphigenous, scattered to gregarious, associated with secondary hyphae, globose, 70–110 µm diam.; p e r i d i a l c e l l s irregularly shaped, 10–50 µm diam.; a p p e n d a g e s few to moderately numerous per chasmothecium, interwoven with secondary hyphae, in the basal half, $50-150 \times 5-8$ µm, mycelioid, septate, thin-walled, brownish below, pale or colourless towards the tip; a s - c u s subglobose to broad ellipsoid-ovoid, $50-80 \times 50-65$ µm, thin-walled, terminal oculus 10-18 µm diam., 6-8-spored; a s c o s p o r e s broad ellipsoid-ovoid, hyaline, $15-20 \times 10-18$ µm.

Collection examined: Switzerland, BE, Frutigen, Tropenhaus, serre chaude, on *Capsicum sinensis*, 23 Jul. 2012, A. BOLAY (G00261378, HAL 3292 F, holomorph).

Notes: *Podosphaera solanacearum* is new to Switzerland, and this is the first record of this species on *Capsicum sinensis*. Chasmothecia are present and agree well with type material of this species (BRAUN & COOK 2012). However, the taxonomic status of this species is still in need of phylogenetic confirmation.

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