



Powdery mildew species on papaya – a story of confusion and hidden diversity

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Abstract

Carica papaya and other species of the genus *Carica* are hosts of numerous powdery mildews belonging to various genera, including some records that are probably classifiable as accidental infections. Using morphological and phylogenetic analyses, five different *Erysiphe* species were identified on papaya, viz. *Erysiphe caricae*, *E. caricae-papayae* sp. nov., *Erysiphe diffusa* (= *Oidium caricae*), *E. fallax* sp. nov., and *E. necator*. The history of the name *Oidium caricae* and its misapplication to more than one species of powdery mildews is discussed under *Erysiphe diffusa*, to which *O. caricae* is assigned as a heterotypic synonym. *Sphaerotheca caricae-papayae* is synonymized with *Podosphaera xanthii*. *Podosphaera caricicola* comb. nov. and additional powdery mildew species occurring on papaya are also described. A key to the papaya powdery mildew species that are considered is provided.

Key words – *Carica papaya* – Erysiphales – *Erysiphe* – molecular – *Podosphaera* – phylogeny – taxonomy

Introduction

Papaya (*Carica papaya*) is an important fruit tree cultivated in most tropical countries. The native distribution of papaya ranges from southern Mexico to Costa Rica (Cavalho 2013). Powdery mildews are important fungal diseases on many different crops and several powdery mildew species have been described on papaya. *Oidium caricae*, introduced by Noack (1898), was the first name given to a powdery mildew based on material collected in Brazil. The original description of this species was brief and incomplete, which led to this name being misapplied to different species of papaya powdery mildew worldwide. Braun (1987) applied this name to a papaya powdery mildew with catenulent conidia, containing fibrosin bodies and reduced it to synonymy with *Sphaerotheca caricae-papayae*. When Liberato et al. (2004) re-examined type material of *O.*

caricae, deposited at Kew (K(M)102465), it was nearly exhausted. Fortunately, H.J. Boesewinkel, who had previously examined and annotated the specimen, described a powdery mildew with multilobed hyphal appressoria and cylindrical conidia, 37–47 × 10–15 µm, formed singly (Boesewinkel 1982b). Based on Boesewinkel's observations, *O. caricae* belongs to the genus *Erysiphe* (= *Pseudoidium*), and was accordingly epitypified by Liberato et al. (2004) with a new Brazilian collection deposited as VIC 26556.

Erysiphe caricae U. Braun & Bolay (in Bolay 2005) was described on the basis of the asexual and sexual morph (chasmothecia) found in Switzerland on *Vasconcellea ×heilbornii* (≡ *Carica ×heilbornii*, = *Carica ×pentagona*). The striking morphological similarities between the asexual morphs of *Erysiphe caricae* and *Oidium caricae*, led to the two species being synonymized by Bolay (2005). Braun & Cook (2012) reallocated *Oidium caricae* to *Pseudoidium* Y.S. Paul. Previously many papaya powdery mildews have been indiscriminately referred to as *Oidium caricae*. Most were insufficiently examined and described or were simply classified as papaya powdery mildew without any specification (Burchill 1978, Freire & Viana 2001). Preliminary unpublished studies using molecular analyses of papaya powdery mildews have shown that the European *E. caricae* and Brazilian *O. caricae* sequences are not identical, suggesting they are distinct species of *Erysiphe*. These preliminary results imply that the name *O. caricae* has been erroneously used for multiple species of papaya powdery mildew. Records of other papaya powdery mildews, including *Podosphaera* spp., are also unresolved due to insufficient herbarium material and sequence data. The purpose of this work was to provide a comprehensive taxonomic examination, including ITS sequence analyses, of powdery mildews on this important tropical fruit crop.

Materials & Methods

Morphology: Fresh powdery mildew collections were examined in distilled water using an Olympus BX50 microscope. Dried herbarium samples were put into a drop of lactic acid and gently heated before examination. Both fresh and dried samples were stained in aniline blue. Measurements of 30 conidia and other structures were made whenever possible at a magnification of ×1000 and 95% confidential intervals are given with extreme values in parentheses.

Molecular phylogeny: Whole-cell DNA was extracted from mycelia on leaves using the chelex method (Walsh et al. 1991) as described by Hirata & Takamatsu (1996). For the sample collected in Thailand (MUMH1853), separate sequences were obtained from mycelia taken from fruits and leaves. For the California and Hawaii samples, DNA was extracted from mycelium using the DNA plant mini kit (Qiagen, Carlsbad, California). The rDNA internal transcribed spacer (ITS) regions were amplified by polymerase chain reaction (PCR) using the respective primer pairs: PM5 (Takamatsu & Kano 2001)/NLP2 (Mori et al. 2000) for 3'-half of ITS and 28S rDNA, and ITS5/PM6 (Takamatsu & Kano 2001) for 5'-half of ITS. KOD FX Neo DNA polymerase (Toyobo, Japan) was used in the PCR according to the manufacturer's protocol. For California and Hawaii samples, Takara Premix Ex Taq™ DNA Polymerase (Mountain View, CA) was used. Most amplicons were sent to Solgent Co. Ltd. (Daejeon, South Korea) for direct sequencing using primers PM5 and NLP2 for the PM5/NLP2 fragment and PM6 for the ITS5/PM6 fragment. The California and Hawaii amplicons were sent to GENEWIZ in San Francisco, CA (USA). New sequences determined in this study were deposited in the DNA Data Bank of Japan (DDBJ) under the accession numbers LC228607–LC228619. These sequences were aligned with other related sequences retrieved from DNA databases using MUSCLE (Edgar 2004) implemented in MEGA6 (Tamura et al. 2013). Alignments were further manually refined using the MEGA6 program and were deposited in TreeBASE (<http://www.treebase.org/>) under the accession number S20817. Phylogenetic trees were obtained from the data using the maximum parsimony (MP) and maximum likelihood (ML) methods. MP analysis was performed in PAUP 4.0a152 (Swofford 2002) with heuristic search option using the tree bisection reconnection (TBR) algorithm with 100 random sequence additions to find the global optimum tree. All sites were treated as unordered and unweighted, with gaps treated as missing data. The strength of internal branches of the resulting

trees was tested with bootstrap (BS) analysis using 1000 replications with the step-wise addition option set as simple (Felsenstein 1985). Tree scores, including tree length, consistency index (CI), retention index (RI), and rescaled consistency index (RC), were also calculated. The ML analysis was done using raxmlGUI (Silvestro & Michalak 2012), under a GTRGAMMA model. The BS supports and trees were obtained by running rapid bootstrap analysis of 1000 pseudo-replicates followed by a search for the tree with the highest likelihood.

Results

Phylogenetic analyses

New ITS sequences were obtained for eight *Erysiphe* samples on *Carica papaya* in this study. These sequences were analyzed with three other *Erysiphe* sequences deposited in GenBank. The data set consisted of 62 sequences and 608 characters, of which 213 (35.0%) characters were variable and 130 (21.4%) characters were informative for parsimony analysis. A total of 2.4×10^4 equally parsimonious trees with 578 steps were constructed by the MP analysis. Topologies were nearly consistent among the trees except for branching orders of the terminal branches and branch length. A typical tree is shown in Fig. 1. Since the maximum likelihood analysis generated nearly the same tree topology as the MP analysis, only BS supports are shown. Eleven sequences from samples on *Carica papaya* were included in this analysis. ITS sequence GU358452, reported by Tsay et al. (2011) was identical to those of *E. diffusa* (AB078800, AB078806, AB078813) and differed only by two nucleotides (99.6% similarity) from the sequence of “*Oidium caricae*” collected in Brazil (MF616622). Two sequences from papaya collected in North America (Mexico and USA) were identical and formed a distinct clade with BS supports of 99% (MP) and 100% (ML). “*O. caricae*” and the North American samples differed by 9 nucleotides (98.5%). The ITS sequences from five samples collected in Thailand were identical and also matched *Erysiphe aquilegiae* (AB015929) and *Erysiphe euphorbiae* (LC010073). These sequences differed by only one base from GU358451 deposited as “*Oidium neolycopersici*” from Taiwan (Tsay et al. 2011) and were members of the *Erysiphe aquilegiae* clade (Takamatsu et al. 2015). A sequence named *Erysiphe caricae* that was collected in Ukraine (LC009901) was phylogenetically distant from other *Erysiphe* spp. on papaya.

A BLAST query of an ITS sequence obtained from a collection in Hawaii matched with 100% identity to a sequence of *Erysiphe necator* (AF011325), the pathogen which causes powdery mildew of grapevine. Additional sequences of *E. necator* from grapevine obtained from GenBank and an ITS sequence from a specimen on *Caryocar brasiliense* (Caryocaraceae) collected in Brazil were used to construct a phylogenetic comparison with the Hawaiian isolate. The data set consisted of 17 sequences and 568 characters, of which 91 (16%) characters were variable and 23 (4%) characters were informative for parsimony analysis. Parsimony analysis generated nearly two million equally parsimonious trees with 100 steps. All these trees were identical in topology and differed only in branch lengths. One tree is represented here (Fig. 7). The sequences from both *Carica papaya* and *Caryocar brasiliense* belonged to the same clade as *Erysiphe necator* and are undoubtedly conspecific.

Four powdery mildew specimens collected in this study were shown to be in the *Podosphaera* group, based on ITS sequence analysis. Two specimens were from the US and two were from Thailand. These ITS sequences were analyzed phylogenetically with other *Podosphaera* sequences retrieved from GenBank. *Cystotheca lanestris* and *Cy. wrightii* were used as outgroup taxa. The data set consisted of 39 sequences and 494 characters, of which 145 (29.4%) characters were variable and 110 (22.3%) characters were informative for parsimony analysis. Parsimony analysis generated two equally parsimonious trees with 290 steps. A tree with higher likelihood value is shown in Fig. 8. Sequence GU358450 from Taiwan belonged to the clade of *Podosphaera xanthii*. The four sequences from this study were identical and form a separate clade with strong BS supports (MP = 85%, ML = 97%). This clade belongs to subsect. *Sphaerotheca* in *Podosphaera* sect. *Sphaerotheca*.

Multiple taxa of *Erysiphe* hidden within “*Oidium caricae*”

Asexual morphs found on papaya forming lobed hyphal appressoria and solitary conidia had been previously referred to as *Oidium caricae*. Initial molecular analyses cast doubts upon whether these collections represent a single taxon (Tsay et al. 2011, Takamatsu et al. 2015). In addition, *Pseudoidium* asexual morphs on papaya that were sequenced did not cluster together in our phylogenetic trees, suggesting that several *Erysiphe* species cause papaya powdery mildew. These results led to a more detailed examination of this complex of species. The molecular analysis of *Oidium caricae* material from Brazil, close to the region of the location of epitype material designated by Liberato et al. (2004), was the key to distinguishing *O. caricae* from other papaya powdery mildews in the *Erysiphe* group. New samples were collected and the sequences were obtained from Robert Barreto’s working group in Viçosa, Brazil. Based on the present phylogenetic results, the following *Erysiphe* spp. have been identified on papaya.

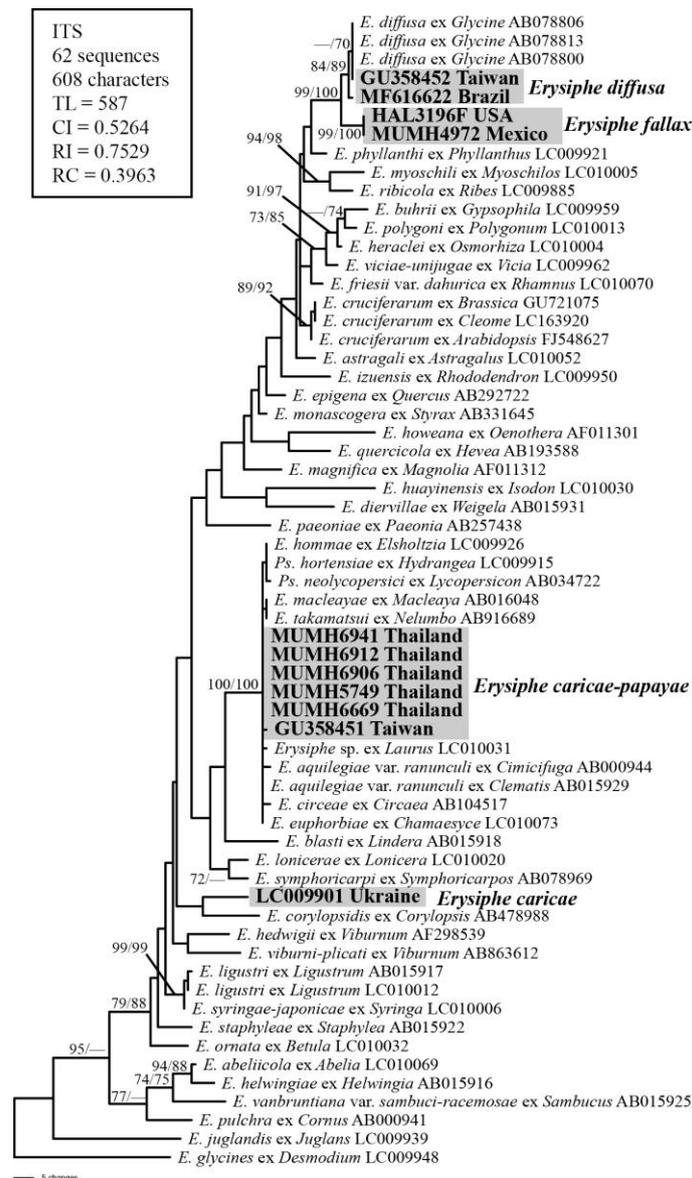


Figure 1 – Phylogenetic analysis of *Erysiphe* species on *Carica papaya* was based on combined DNA sequences of internal transcribed spacer (ITS) region. This is a representative tree of the 2.4×10^4 equally parsimonious trees with 578 steps, which were found using a heuristic search. Horizontal branch 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.

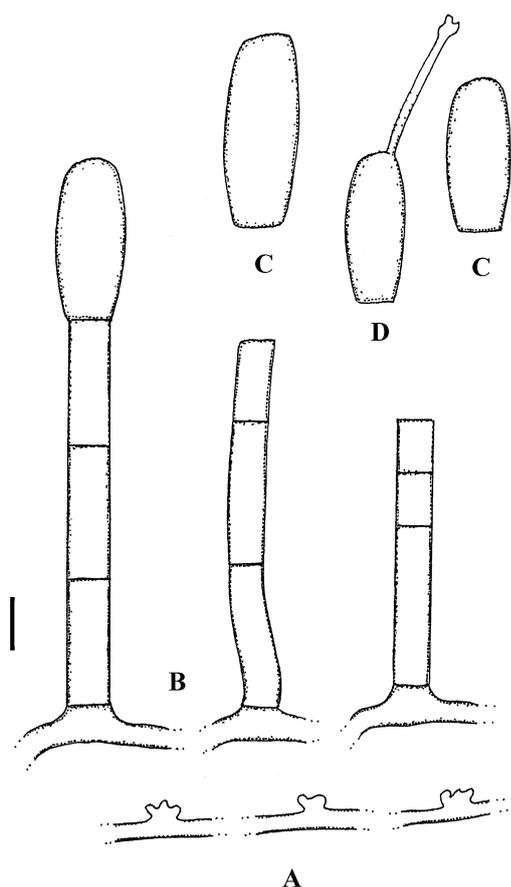


Figure 2 – *Erysiphe caricae* on *Carica papaya*. A–D HAL 1819 F. A Hyphal appressoria. B Conidiophores. C Conidia. D Conidium with germ tube. Bar = 10 μ m.

Description of the sexual morph (chasmothecia): see Bolay (2005: 46) and Braun & Cook (2012: 369).

Material examined (asexual morph and chasmothecia) – Switzerland, VS, Conthey, Les Fougères, on *Vasconcellea xheilbornii* (\equiv *Carica xheilbornii*, = *Carica xpentagona*), 28 November 1989, A. Bolay (holotype HAL 3200 F; isotype G00298363). Ukraine, Kiev, University, O.V. Fomin Botanical Garden, on *Carica papaya*, 30 March. 2004, V. Kovalchuk (HAL 1819 F).

Notes – *Erysiphe caricae* was introduced by Braun & Bolay (in Bolay 2005), based on European material collected in Switzerland. This was the first *Erysiphe* species on papaya based on holomorph material that included mature chasmothecia. Additional specimens with ascomata were collected in Ukraine and included in molecular sequence analyses in Takamatsu et al. (2015), which confirmed the status of *E. caricae* as a distinct species, clustering in a different clade that is distant from other *Erysiphe* spp. on papaya (Fig. 1). The asexual morphs of *E. caricae* and *Oidium caricae* are nearly indistinguishable by morphology, which explains the earlier treatment of *O. caricae* as a synonym of *Erysiphe caricae* in Braun & Cook (2012). However, our phylogenetic analyses clearly showed that *E. caricae*, which is, to the best of our knowledge, only known from Europe, and *O. caricae*, described from Brazil, are two unrelated species. A specimen collected in Germany (Brandenburg, Oranienburg, Oranienburger Schloßgarten, on *Carica papaya*, 26 August 2009, V. Kummer, only asexual morph, HAL 3190 F) seems to belong to *Erysiphe caricae*, but has not yet been confirmed by sequence analyses.

(2) *Erysiphe caricae-papayae* Meeboon & S. Takam., **sp. nov.**

MycoBank MB822384; Facesoffungi number: FoF 03789

Etymology – Epithet derived from the host species, *Carica papaya*.

(1) *Erysiphe caricae* U. Braun & Bolay, Cryptog. Helv. 20: 46, 2005. Fig. 2

Misapplied name: *Oidium caricae* auct. (sensu Bolay 2005, Braun & Cook 2012).

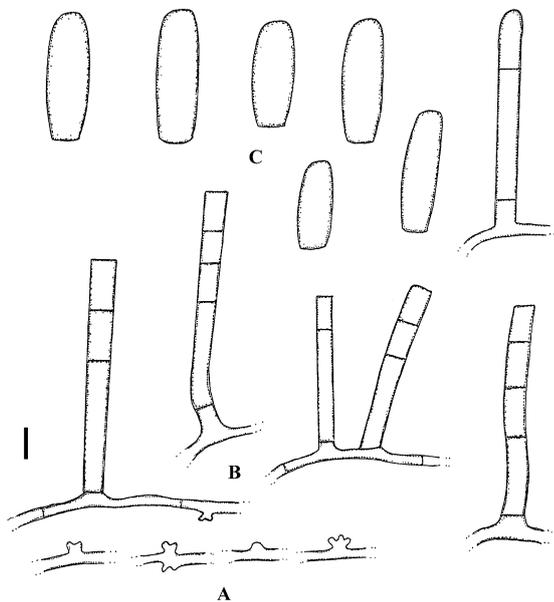
Illustrations: Bolay (2005: 46–47, figs 18–19), Braun & Cook (2012: 369, fig. 412).

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Morphology of the asexual morph of *E. caricae*: *Mycelium* on leaves, amphigenous, also on petioles, effuse or in patches, white, thin to dense and felted; *hyphae* 4–8 μ m wide, hyaline, thin-walled, smooth; *hyphal appressoria* solitary, occasionally in opposite pairs, nipple-shaped to moderately lobed, 3–7 μ m diam; *conidiophores* arising from superficial hyphae, from the upper part of the mother cell, erect, up to about 90 μ m long (without conidia), foot-cells (20–)25–55 \times 6–9 μ m, usually straight, occasionally somewhat curved or slightly sinuous, followed by 1–2 shorter cells or second cell about as long as the foot-cell or even slightly longer, 12–30 μ m long. *Conidia* solitary, ellipsoid-ovoid to cylindrical, (25–)30–50(–60) \times 12–23(–25) μ m, germ tubes perihilar, short to moderately long, with terminal lobed appressoria.

Fig. 3, 4

Mycelium on leaves, amphigenous, also on petioles, forming thin to dense white patches or effuse, evanescent to persistent; *hyphae* superficial, branched, 2–7 μm wide, septate, hyaline, thin-walled, smooth; *hyphal appressoria* solitary or in opposite pairs, nipple-shaped or slightly lobed to multilobed, 3–7 μm diam. *Conidiophores* arising from superficial hyphae, on the upper surface of the mother cell, erect, 60–150 μm long (without conidia), foot-cells 20–70 \times 5–9 μm , cylindrical, usually straight, occasionally somewhat curved to sinuous, followed by 1–3(–4) cells, 8–50 \times 8–12 μm , mostly shorter than the foot-cell, second cell occasionally about as long as the foot-cell or even longer, width of the following cells often gradually increasing towards the end of the conidiophores, somewhat wider than the foot-cells. *Conidia* solitary, ellipsoid-ovoid, subcylindrical to almost cylindrical, 25–40 \times 14–18 μm , apex rounded to subtruncate, base rounded to truncate. *Germination* not observed. *Chasmothecia* scattered to gregarious, 103–185 μm diam; *peridium cells* irregularly polygonal, 10–20 μm diam; *appendages* about 4–10(–15), arising between base and equator, horizontally spread, simple, occasionally 1–2 times irregularly branched, coarse and straight, flexuous or slightly sinuous-geniculate, 140–325 long and 6–8 μm wide, septate, brown below and paler towards the apex or brown throughout when mature, wall thickened towards the base, 2.3–3.5 μm , smooth, sometimes faintly rough; *asci* 4–9, ellipsoid-obovoid, clavate-saccate, 35–60 \times 27–36 μm , wall thick, 2.5–4 μm , sessile or short-stalked, (2–)3–5(–6)-spored; *ascospores* ellipsoid-ovoid, 11–24 \times 8–13 μm , hyaline or faintly yellowish.



Material examined – Thailand, Chiang Rai, on *Carica papaya* (*Caricaceae*), 22 November 2013, J. Meeboon (holotype TSU-MUMH5749), GenBank number (ITS): LC228610; Chiang Mai, 19 January 2016, J. Meeboon (TSU-MUMH 6669, HAL 3191 F), GenBank number (ITS): LC228611; Chiang Rai, 24 December 2000, S. Takamatsu (TSU-MUMH 3383, HAL 3192 F), mixed infection together with *Podosphaera* sp.; Chiang Rai, 29 December 2016, J. Meeboon & S. Takamatsu (TSU-MUMH 6906, HAL 3193 F), GenBank number (ITS): LC228612; Chiang Rai, 30 December 2016, J. Meeboon & S. Takamatsu (TSU-MUMH 6912, HAL 3194 F), GenBank number (ITS+28S): LC228613.

Figure 3 – *Erysiphe caricae-papayae* sp. nov. on *Carica papaya*. A–C HAL 3194 F. A Hyphal appressoria. B Conidiophores. C Conidia. Bar = 10 μm .

Notes – Tsay et al. (2011) examined asexual powdery mildews on papaya in Taiwan, including molecular sequence analyses, and identified one of them as *Oidium neolycopersici* L. Kiss. In the course of the present study, additional sequences obtained from papaya powdery mildews collected in Thailand were found to be identical with the Taiwanese sequence (see Fig. 1). The sexual morph (chasmothecia) was found in one of the collections. *Pseudoidium neolycopersici* (L. Kiss) L. Kiss phylogenetically belongs to a complex clade, classified as “*Erysiphe aquilegiae* clade” in Takamatsu et al. (2015). This clade is composed of closely allied *Erysiphe* species, including *Pseudoidium neolycopersici*, but has insufficient resolution within the ITS region. This phenomenon is not uncommon in other complexes of closely allied ascomycete species including the *Cercospora apii* Fresen. complex (Groenewald et al. 2012) and species of *Cladosporium* Link (Bensch et al. 2012). Further phylogenetic examinations using sequences from additional genes are necessary for trees with better resolutions. The identification of these powdery mildew collections on papaya as “*Oidium neolycopersici*” by Tsay et al. (2011) is not tenable. Conidiophores and conidia of the species in the *E. aquilegiae* complex are rather uniform, with few characters that can

be morphologically differentiated. However, the sexual fruiting bodies found on papaya in Thailand allow more precise comparisons and differentiations. The chasmothecia found on papaya in Thailand are much larger than *Erysiphe aquilegiae* fruiting bodies (103–185 µm diam vs. (65–)75–115(–125) µm in *E. aquilegiae*), with fewer appendages 4–10(–15) per chasmothecium (vs. numerous, (4–)10–30(–50) in *E. aquilegiae*), thicker-walled towards the base of the appendage (wall 2.3–3.5 µm wide vs. 1–2(–2.5) µm wide in *E. aquilegiae*), and contain asci that are thicker-walled, (2.5–)3.5–4 µm vs. 1–2.5(–3) in *E. aquilegiae*. Amongst other species of *Erysiphe* sect. *Erysiphe*, *E. malvae* Heluta is morphologically comparable with *E. caricae-papayae*, but this species differs in having frequently branched, only 0–1-septate chasmothecial appendages (Braun & Cook 2012). Based on the genotypic and phenotypic results, the present *Erysiphe* species on papaya in Thailand is undoubtedly a distinct species.

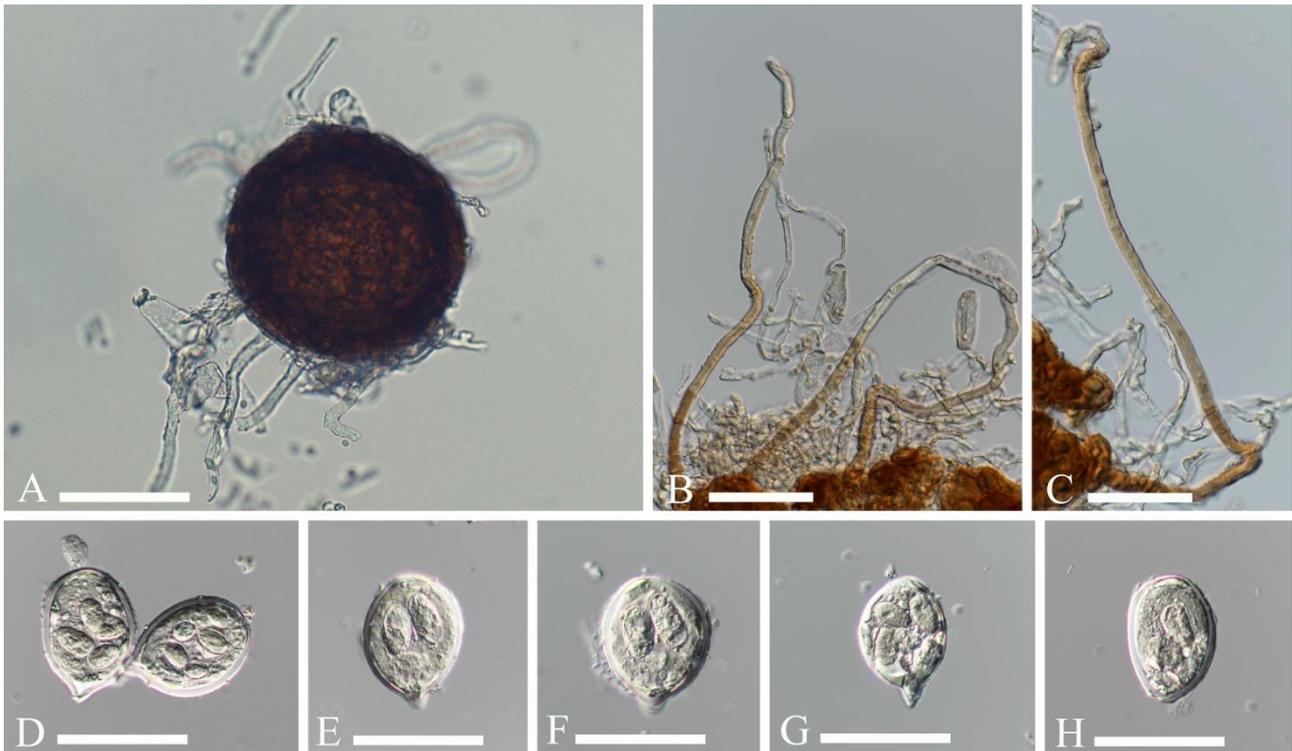


Figure 4 – *Erysiphe caricae-papayae* sp. nov. on *Carica papaya*. A–H TSU-MUMH5749. A Chasmothecium. B, C Appendages. D–H Asci. – Bars = 50 µm.

(3) *Erysiphe diffusa* (Cooke & Peck) U. Braun & S. Takam., Schlechtendalia 4: 7, 2000. Fig. 5
 ≡ *Microsphaera diffusa* Cooke & Peck, J. Bot. 10: 13, 1873.
 = *Oidium caricae* F. Noack, Bol. Inst. Agron. Estado São Paulo 9(2): 81, 1898, **syn. nov.**
 ≡ *Pseudoidium caricae* (F. Noack) U. Braun & R.T.A. Cook, CBS Biodiversity Series 11: 369, 2012.

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Morphology of the asexual morph found on papaya (based on VIC 26556, 44310): *Mycelium* amphigenous, thin, inconspicuous to conspicuous, persistent, forming dense white patches, confluent; *hyphae* branched, 4–8 µm wide, hyaline, thin-walled, smooth, septate; *hyphal appressoria* slightly lobed to multilobed, solitary or in opposite pairs; *conidiophores* arising from superficial hyphae, on the upper surface of mother cells, erect, 55–100 × 9–12.5 µm (without conidia), foot-cells straight or occasionally somewhat curved or flexuous, 20–45 µm long, followed by 1–2(–3) cells, mostly shorter or about as long as the foot-cell; *conidia* formed singly, ellipsoid-ovoid to cylindrical, 25–60 × (10–)13–20(–25) µm, both ends rounded to subtruncate, germ tubes perihilar, short to two times as long as the conidial length, simple or occasionally forked, terminal appressoria unlobed to lobed.

Material examined – Brazil, Minas Gerais, Viçosa, on *Carica papaya*, 29 May 2003, J.R. Liberato (epitype of *Oidium caricae*, designated by Liberato et al. 2004, VIC 26556); Minas Gerais, Viçosa, on *Carica papaya*, 27 July 2016, D.M. Macedo (VIC 44310), GenBank number (ITS): MF616622.

Notes – Tsay et al. (2011) reported *Erysiphe diffusa* on papaya from Taiwan and confirmed the identification by means of molecular sequence analyses. ITS sequences obtained from papaya were 100% match to sequences from *E. diffusa* on *Glycine* spp., suggesting that papaya may be another host of *E. diffusa*. This is the first report of *E. diffusa* on a host other than a legume. Since the morphology of the asexual morph found on papaya was not described in detail in Tsay et al. (2011), it is unknown if isolates from the two hosts are morphologically similar. A sequence retrieved from representative material of *Oidium caricae* from Brazil is 99.6 % identical (two bp difference) to *E. diffusa* sequences, suggesting that a single species is involved (Fig. 1). The Brazilian sequence was not retrieved from the scanty epitype material but from a sample recollected at the epitype locality in 2016 by M. de Macedo. Therefore, we consider that *O. caricae* is synonymous with *E. diffusa*. The name *Oidium caricae* has been often used incorrectly for papaya powdery mildews that were not related to *O. caricae*. Braun (1987) erroneously reduced the

name *O. caricae* to synonymy with *Sphaerotheca caricae-papayae*, which was influenced by Noack's misleading original description, primarily the given conidial size of only 23–25 × 14.5–20 µm. Yen's (1966) treatment of *O. caricae* may also be a different species (see Liberato et al. 2004). Yen (l.c.) mentioned that he had examined material deposited at PC, which was collected by Noack in Brazil, and a specimen from Kenya deposited at IMI that he referred to as *O. caricae*, but he classified the powdery mildew concerned as "Euoidium type" suggesting that the conidia were catenescant. However, *O. caricae* represents a *Pseudoidium* characterized by having lobed hyphal appressoria and long ± cylindrical conidia formed singly, which could be confirmed by the examination of type material (Brazil, Campinas, on *Carica papaya*, Nov. 1897, F. Noack, holotype K(M)102465, exhausted material; see Boesewinkel 1982b). The type material deposited at K was annotated by the latter author accordingly.

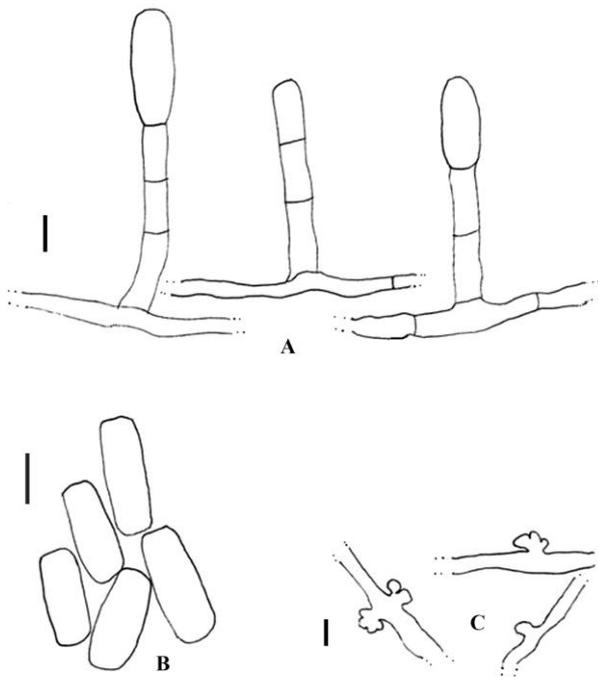


Figure 5 – *Erysiphe diffusa* (= *Oidium caricae*) on *Carica papaya*. A–C VIC 44310. A Conidiophores. B Conidia. C Hyphal appressoria. – Bars, A = 10 µm, B = 20 µm, C = 5 µm.

Unfortunately, the type material is now almost devoid of any fructification. Therefore, Liberato et al. (2004) designated an epitype collected in Brazil. Boesewinkel (1982a,b) examined papaya powdery mildew found in New Zealand and provided a detailed survey and discussion. Boesewinkel (1982b) carried out inoculation experiments and was able to inoculate *Erysiphe cruciferarum* Opiz ex L. Junell from radish to papaya. Therefore, he proposed to reduce *O. caricae* to synonymy with *E. cruciferarum*, and several authors followed Boesewinkel's (l.c.) taxonomic conclusion and used *E. cruciferarum* for *Pseudoidium* anamorphs on papaya (e.g., Gorter 1993, Crous et al. 2000, South Africa; Teixeira et al. 2007; Cunningham & Nelson 2012, Hawaii). However, this "identification" was based only on papaya powdery mildew collected in New Zealand and cannot be simply applied to *O. caricae* described from Brazil. Furthermore, there are several morphologically very similar asexual *Erysiphe* morphs on papaya worldwide. Since

detailed descriptions and sequences of the collections from Hawaii, New Zealand as well as South Africa are not available, these records cannot be properly identified currently. However, sequence analyses of material of *O. caricae*, collected in Brazil and representative for this species, showed that the Brazilian papaya powdery mildew does not cluster with *E. cruciferarum* sequences but matches *E. diffusa* (Fig. 1). The name *O. caricae* has been applied to papaya powdery mildews worldwide (Fossard 1969, Amano 1986), but due to the widespread misapplication of this name explained above and the occurrence of different *Erysiphe* species with morphologically similar asexual morphs on papaya, most of these records cannot be assigned to names with any confidence.

Erysiphe diffusa is common in North America and known from South America (Amano 1986, Braun & Cook 2012). Fu et al. (2015) recently recorded *E. diffusa* on *Wisteria sinensis* in China. A first report of *Erysiphe* on *Glycine* dates back to Wahl (1921) who listed *Erysiphe polygoni* on this host, followed by Lehman (1931) who also identified this powdery mildew as *E. polygoni*. Later, Lehman (1947) re-examined it and identified it as *Microsphaera* sp. The first

published reports of the sexual morph of the *Glycine* powdery mildew seem to refer to Paxton & Rogers (1974) and McLaughlin et al. (1977). Mignucci & Chambertain (1978) carried out detailed inoculation experiments with *E. diffusa* on *Glycine* and numerous other legumes and demonstrated the ability of this powdery mildew to infect various other hosts of the Fabaceae. *Desmodium canadense*, the type host of *E. diffusa*, was unfortunately not included in these examinations. Nevertheless, all available data suggest that the host range of *E. diffusa* includes more than *Glycine* spp., on which this species is widespread in North and South America [Brazil, Canada, USA (Basu 1980, Mendes et al. 1998, Braun & Cook 2012, Takamatsu et al. 2002)]. Outbreaks of powdery mildew infections on *Glycine* spp. by *E. diffusa*, accompanied by significant spread of this disease, have recently been reported in Asia (South Korea, northeast India, Japan, Taiwan, Vietnam) and Australia (Queensland) (Takamatsu et al. 2002, Cho & Shin 2004, McTaggart et al. 2012, Baiswar et al. 2016).

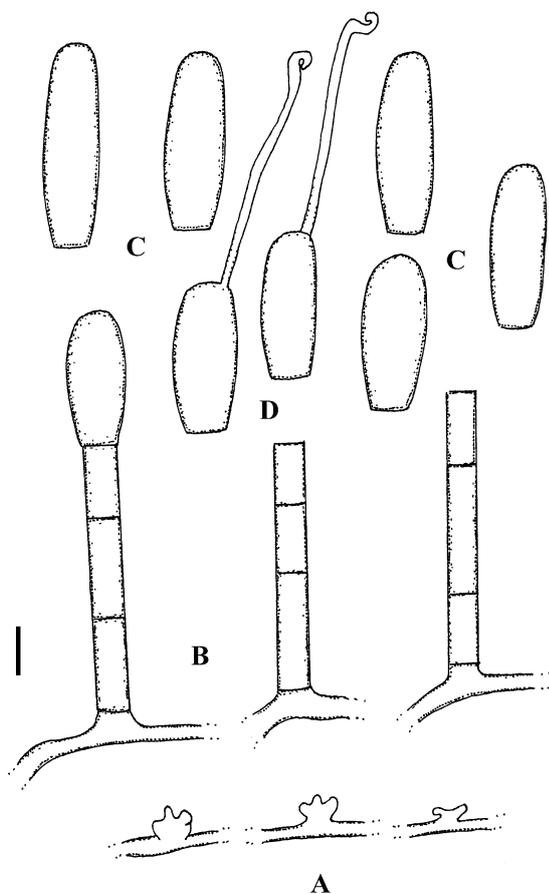


Figure 6 – *Erysiphe fallax* sp. nov. on *Carica papaya*. A–D HAL 3194 F. A Hyphal appressoria. B Conidiophores. C Conidia. D Conidia with germ tubes. Bar = 10 µm.

(4) *Erysiphe fallax* C. Blomq., S. Rooney-Latham & Fernández Pavía, **sp. nov.**

Fig. 6

MycoBank MB822385; Facesof fungi number: FoF 03791

Etymology: fallax (“deceptive”), referring to the confusion with *Oidium caricae* and other asexual *Erysiphe* morphs on papaya.

Sexual morph unknown. *Mycelium* amphigenous, thin, forming loose to dense white patches or effuse; *hyphae* branched, 3–8 µm wide, hyaline, thin-walled, smooth, septate; *hyphal appressoria* slightly to distinctly lobed, 3–8 µm diam; *conidiophores* arising from superficial hyphae, on the upper surface of mother cells, erect, 50–100 µm long (without conidia), foot-cells 25–50 × (6–)7–9(–10) µm, cylindrical or subcylindrical, straight, occasionally flexuous, somewhat sinuous, basal septum at the junction with its mother cell or slightly elevated (to 5 µm),

occasionally constricted at the basal septum (5–6 µm wide), foot-cells followed by 1–3 cells, 10–35(–40) µm long, shorter than the foot-cells or about as long as the foot-cells, occasionally even longer; *conidia* formed singly, ellipsoid, subcylindrical to cylindrical, (30–)35–50 × 13–20 µm, apex rounded to subtruncate, base truncate to subtruncate, germ tubes perihilar, short to moderately long, terminal appressoria unlobed to lobed or apex curved-sigmoid (only a few germ tubes naturally developed on leaves have been observed).

Material examined – Mexico, Huamuxtitlan, Mpio. de Huamuxtitlan, Gro., 10 January 2009, Juan Manuel Tovar Pedraza (holotype TSU-MUMH4972), GenBank number (ITS+28S): LC228608. USA, California, Santa Barbara Co., outdoor collection, on *Carica papaya*, 23 July 2014, H. Scheck (HAL 3196 F), GenBank number (ITS): LC228618; on *Carica papaya*, cultivar “Maradol”, 28 July 2014, H. Scheck (HAL 3197 F); on *Carica papaya*, cultivar “Solo”, 28 July 2014, H. Scheck (HAL 9198 F).

Notes – Amano (1986) listed “*Erysiphe communis*” on papaya from Mexico. Alvarez (1976) reported *Erysiphe polygoni* and *Oidium caricae* from Mexico, followed by Mexican reports of *Oidium caricae* in Alvarez (1981), Soldaña et al. (1985), Yáñez-Morales et al (2009), and Fernández-Pavía et al. (2015). These reports might refer to *E. fallax*, which is morphologically barely distinguishable from the asexual morph of *E. diffusa*. Sequences of this papaya powdery mildew (ITS/28S rDNA) from specimens collected in Mexico and the USA are identical and cluster close to sequences of *E. diffusa* (including *O. caricae* from Brazil). However, they cluster with a correlation rate of 98.5%, suggesting that two different species are involved (Fig. 1). Since asexual morphs of *Erysiphe* spp. on papaya are morphologically similar, reliable identification of *E. fallax* collections must be confirmed by means of molecular sequence analyses.

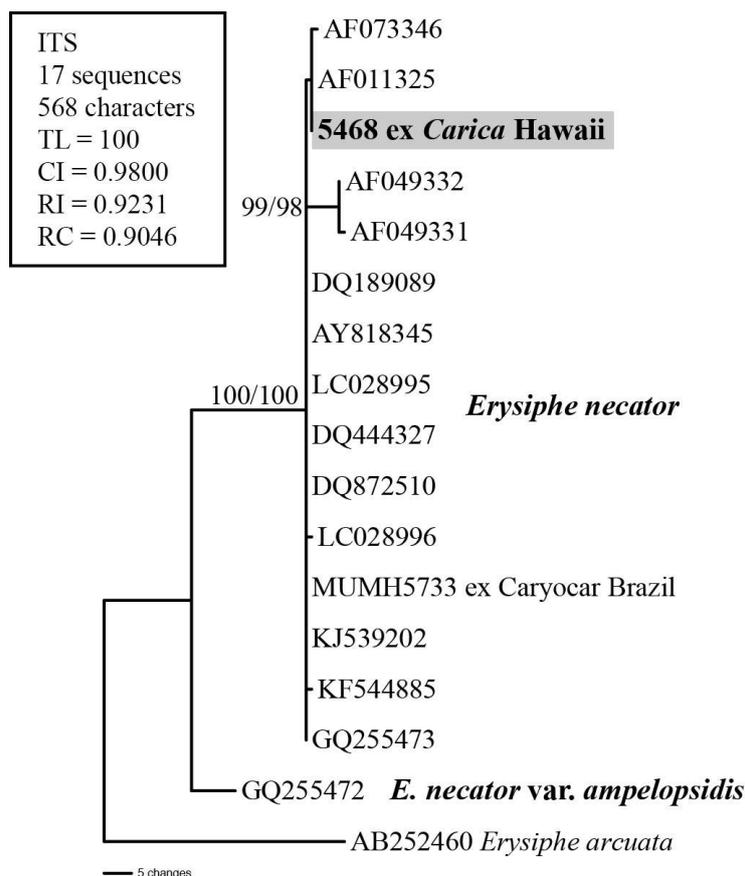


Figure 7 – Phylogenetic analysis of *Erysiphe necator* on *Carica papaya* based on combined DNA sequences of internal transcribed spacer (ITS) region. This is one of the nearly two million equally parsimonious trees with 100 steps, which were found using a heuristic search. Horizontal branch lengths 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.

(5) *Erysiphe necator* Schwein., Trans. Amer. Philos. Soc. II, 4: 270, 1834.

≡ *Uncinula necator* (Schwein.) Burrill, in Ellis & Everh., North Amer. Pyrenomyc.: 15, 1892.

Material examined – USA, Hawaii, Hilo, on *Carica papaya*, 10 Jan. 2017, Stacey Chun (HAL 3202 F), GenBank number (ITS): LC228619.

Facesoffungi number: FoF 03792

Notes – In the course of the present studies, an asexual morph (*Pseudoidium*) morphologically agreeing with *Erysiphe necator* was unexpectedly found on papaya in Hawaii. Results of sequence analyses confirmed this identification and demonstrated the potential ability of this important and widespread *Vitis* powdery mildew to cause accidental infections on an unrelated host (Fig. 7). However, an unequivocal morphological confirmation was not possible since twisted foot-cells of the conidiophores, which are characteristic for *E. necator*, were not observed on papaya. Powdery mildew of *Carycar* sp. (Caryocaraceae) by *E. necator* (material collected in Brazil in 2004 by J.C. Dianese, TSU-MUMH 5733, GenBank number (ITS): LC228609), identified by molecular sequence analyses, is an additional case of a possible cross-infection of *E. necator* on an unrelated host. However, the morphology of the *Carycar* collection could not be proven and the remaining material is insufficient for a detailed analysis. Morphologically, the powdery mildew on *Carycar* sp. could only be shown to belong to *Erysiphe* (appressoria lobed, conidia formed singly).

Additional powdery mildew species occurring on papaya

Podosphaera caricicola (J.M. Yen & Chin C. Wang) U. Braun & S. Takam., **comb. nov.** (sect. *Sphaerotheca* subsect. *Sphaerotheca*).

MycoBank MB822386

Basionym: *Oidium caricicola* J.M. Yen & Chin C. Wang, Rev. Mycol. 37(3): 133, 1973.

Illustration: Yen & Wang (1973: 130, fig 3).

Facesoffungi number: FoF 03793

Description of the asexual morph: *Mycelium* on leaves, forming thin white patches or effuse; *hyphae* 4–8 µm wide, septate, thin-walled, smooth; *hyphal appressoria* indistinct to nipple-shaped; *conidiophores* arising from superficial hyphae, on the upper surface of the mother cell, arising more or less centrally on the mother cell or mostly non-centrally, i.e. towards one end, erect, straight, about 50–100 µm long (without conidia), foot-cells cylindrical, relatively short, 30–50 × 9–13 µm, followed by 1–3 shorter cells, about 10–25 µm long, often slightly constricted at the basal septum at the junction with the supporting hypha, 7–8 µm wide; *conidia* catenulent, ellipsoid-ovoid to doliiform, 25–38 × 14–20 µm, with fibrosin bodies, apex rounded in primary conidia, subtruncate in secondary conidia, base subtruncate, germ tubes long and cylindrical-filiform, continuous to septate, without distinct terminal appressorium.

Holotype: Taiwan, Fengshan, on *Carica papaya*, 8 Jan. 1973, C.C. Wang, F.S. No. 44 (not preserved).

Lectotype (designated here, MycoBank MBT378320): J.M. Yen & Chin C. Wang, Rev. Mycol. 37(3): 130, fig. 3, 1973 (original drawing).

Material examined – Thailand, Chiang Rai, on *Carica papaya*, 20 December 2002, S. Takamatsu (epitype TSU-MUMH 1853, designated here, MycoBank MBT378321), GenBank number (ITS): AB525918, LC228607; duplicate of epitype HAL 3195 F. USA, California, Santa Barbara Co., green house collection, on *Carica papaya*, 13 May and 19 August 2014, H. Scheck (HAL 3199 F), GenBank number (ITS): LC228616; California, Orange Co., Buena Park, 26 April 2017, M. Del Toro & L. Kumagai (HAL 3213 F). THAILAND, Chiang Rai, on *C. papaya*, 24 December 2000, S. Takamatsu (TSU-MUMH 3383, HAL 3192 F).

Notes – Clare (1964) listed a powdery mildew on papaya from Australia, including ascomata, and classified it as a species of *Sphaerotheca* which is now known as *Podospaera aphanis* (Wallr.) U. Braun & S. Takam. This powdery mildew caused significant damage to papaya and could even kill the young growing tips and infect fruits (Simmonds 1965, Boesewinkle 1982b). Species of the *P. aphanis* complex (subsect. *Sphaerotheca*) are readily distinguishable from *P.*

xanthii (subsect. *Magnicellulatae*) in having chasmothecia with much smaller peridial cells and clear differences in the asexual morphs, including a quite distinct conidial germination pattern (Braun & Cook 2012). In the course of the present examinations of papaya powdery mildews, two sequences from Thailand and two from the USA, clustering near to *P. aphanis* and *P. fugax* (Penz. & Sacc.) U. Braun & S. Takam., have been obtained (Fig. 8), which may be Clare's (1964) species detected in Australia. Boesewinkel (1982b) interpreted a record of "*Oidium caricae*" from Java (van Overeem & Schwarz 1926) as "*Sphaerotheca alchemillae*" (now *Podosphaera aphanis*), which might also be the same papaya powdery mildew. The collections on papaya recently found in Thailand and in the USA have been sequenced and cluster among other species of *Podosphaera* sect. *Sphaerotheca* subsect. *Sphaerotheca*, but they are not identical to *P. aphanis*, i.e. they are genetically and morphologically distinct. The asexual morph of this taxon on papaya differs morphologically from that of *P. aphanis* and other species of subsect. *Sphaerotheca* in having much shorter cylindrical conidiophores (30–50 µm long, versus 30–160 µm long) and conidiophores that do not increase in width towards the apex, as they do in *P. aphanis*. These results suggest that this powdery mildew belongs to an unknown species distinct from *P. aphanis*. The sample from Thailand (TSU-MUMH 3383) proved to be a mixed infection of two powdery mildew species, viz. a *Podosphaera* sp., morphologically agreeing with the epitype of *P. caricicola*, and a species of *Erysiphe* with lobed hyphal appressoria and conidia formed singly which seems to belong to *Erysiphe caricae-papayae*. Attempts to locate the Australian collection with ascomata failed. We prefer to use the name *Oidium caricicola* for this species by fixing its application via lecto- and epitypification, rather than introducing a new species. Based solely on the morphology of the asexual morphs, the two species of *Podosphaera* on papaya, *P. caricicola* and *P. xanthii* (incl. *P. caricae-papayae*) are not easily distinguishable. The conidiophores of *P. caricicola* are unusually short for a species of *Podosphaera* sect. *Sphaerotheca* subsect. *Sphaerotheca* and resemble those of *P. xanthii* belonging in subsect. *Magnicellulatae*. Conidial germination, ascoma morphology, or molecular sequence analyses are necessary to distinguish these species.

Yen & Wang (1973) introduced *O. caricicola* and described nipple-shaped hyphal appressoria, long conidiophores (80–185 × 15–18 µm, including conidial chains) with relatively short cylindrical foot-cells, 30–40 × 11–12 µm, and catenescant conidia, 25–33 × 16–21 µm. The presence or absence of fibrosin bodies was not mentioned. Braun & Cook (2012) interpreted this species as a possible synonym of *Podosphaera xanthii* based on relatively small conidia formed in chains, since *Sphaerotheca caricae-papayae* was reduced to synonymy with *P. xanthii*. However, Yen & Wang (1973) illustrated simple, long germ tubes without any conspicuous terminal appressoria, which conflicts with the interpretation of this species as *P. xanthii*, a species that belongs to *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae*. Species of the latter subsection were previously referred to as *Sphaerotheca fuliginea* s. lat., a species complex characterized by having quite distinct, usually short and stout, often even forked lateral germ tubes (Braun & Cook 2012). Long cylindrical-filiform germ tubes suggest this species belongs to *Podosphaera* sect. *Sphaerotheca* subsect. *Sphaerotheca* (*P. aphanis* complex). Boesewinkel (1982b) considered *O. caricicola* a potential synonym of "*Erysiphe cichoracearum*" which is questionable, since the conidial size and the described germ tubes are not characteristic of a *Golovinomyces*. Furthermore, infections on papaya are rather to be expected by the plurivorous *G. orontii*, which is characterized by having conidiophore foot-cells that are often curved at the base. Since type material of *O. caricicola* could not be located and was likely not preserved, Liberato et al. (2004) classified this species as a doubtful, unclear taxon, either belonging to *Golovinomyces* or *Podosphaera*. A solution to this problem would be possible either by tracing and examining the holotype or by lectotypification of *O. caricicola* complemented by epitypification. Since the holotype of *O. caricicola* could not be traced and is possibly not maintained, we prefer to take the latter path. The original, detailed drawing published by Yen & Wang (1973) agrees very well with epitype material from Thailand. This illustration is the only thing remaining of the original material for this species and is therefore designated as lectotype (according to ICN, Art. 9.2, 9.3, 9.12).

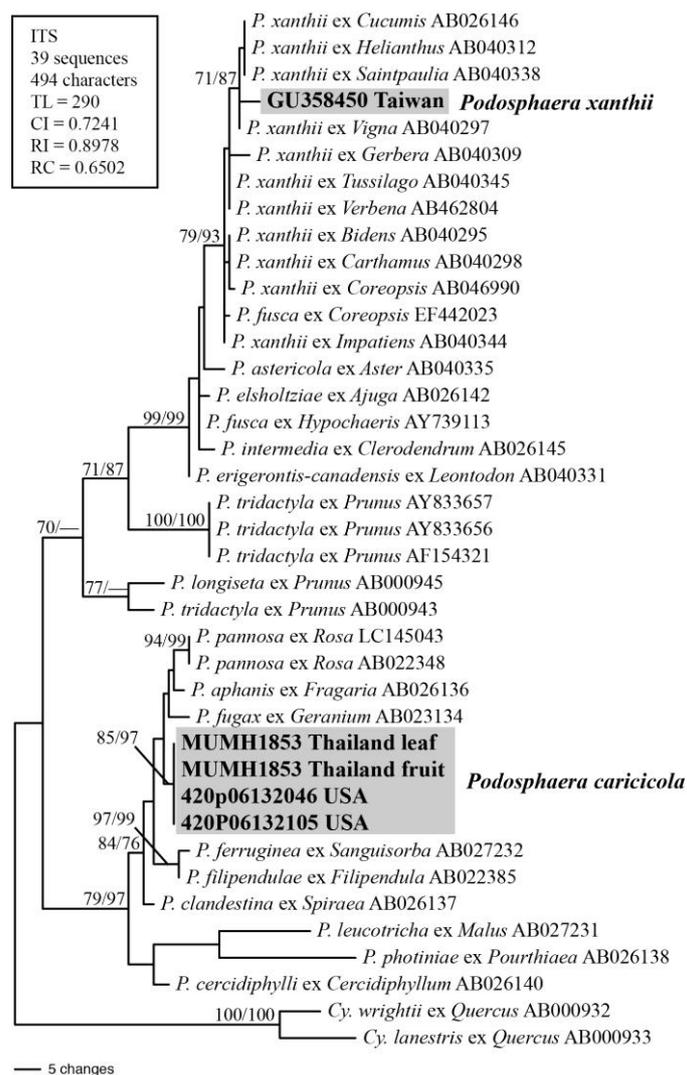


Figure 8 – Phylogenetic analysis of *Podosphaera* species on *Carica papaya* based on combined DNA sequences of internal transcribed spacer (ITS) region. This is one of the two equally parsimonious trees with 290 steps, which were found using a heuristic search. Horizontal branch lengths are proportional 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.

Podosphaera xanthii (Castagne) U. Braun & Shishkoff, Schlechtendalia 4: 31, 2000 (sect. *Sphaerotheca* subsect. *Magnicellulatae*) Fig. 9

= *Sphaerotheca caricae-papayae* Tanda & U. Braun, Trans. Mycol. Soc. Japan 26: 316, 1985.

≡ *Podosphaera caricae-papayae* (Tanda & U. Braun) U. Braun & S. Takam., Schlechtendalia 4: 27, 2000.

Misapplied name: *Oidium caricae* auct. (Braun 1987).

Description of the sexual morph on papaya (based on a re-examination of holotype material): *Chasmothecia* scattered to gregarious, 91–109 μm diam; *peridium cells* conspicuous, large, 21–72 μm diam, shape irregularly polygonal; appendages few, in the lower half, mycelioid, simple or irregularly branched, often interwoven with each other and the mycelium, 50–110 \times 5–8 μm , hyaline, later brown throughout or paler towards the tips, septate, walls thin, smooth to rough; *ascus* broad ellipsoid-ovoid to subglobose, 72–94 \times 49–64 μm , sessile or with a very short stalk, wall 3.8–5 μm thick, terminal oculus 15–20 μm diam, (6–) 8-spored; *ascospores* broad ellipsoid-ovoid to subglobose, 15–18 \times 10–12 μm , colorless.

Material examined – Japan, Tokyo, Sakuragaoka, Setagaya-ku, on *Carica papaya*, 2 Dec. 1984, S. Tanda (holotype of *Sphaerotheca caricae-papayae* TUAMH 2779, isotype HAL 1460 F).

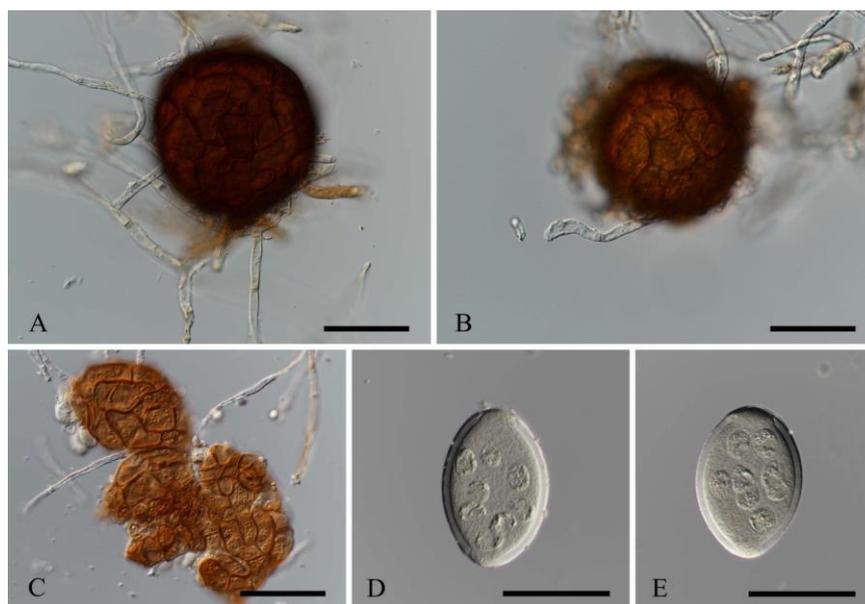


Figure 9 – *Podosphaera xanthii* on *Carica papaya*. A–E TUAMH2779 (holotype of *Sphaerotheca caricae-papayae*). A, B Chasmothecium. C Peridium cells. D, E Asci. Bars = 50 µm.

Notes – *Podosphaera xanthii* is readily distinguishable from other papaya powdery mildews by forming catenescence conidia with distinct fibrosin bodies. The hyphal appressoria are unlobed (indistinct to nipple-shaped), and the chasmothecia are characterized by having large peridial cells, about 15–55 µm diam, and asci with large terminal oculi, (10–)15–25 µm diam. The asexual morph of this powdery mildew has previously been confused with *Oidium caricae* (e.g., in Braun 1987). Verma & Sharma (1999: 483) emphasized that *Oidium caricae*, *O. indicum*, and *Sphaerotheca fuliginea* refer to a single species. Tanda & Braun (1985) found fruiting bodies of this papaya powdery mildew and described it as *Sphaerotheca caricae-papayae*. The combination *Podosphaera caricae-papayae* was later introduced by Braun & Takamatsu (2000). Braun & Cook (2012) reduced this species to synonymy with the plurivorous *P. xanthii*, mainly based on the morphological similarity between the papaya *Podosphaera* and *P. xanthii* on cucumber and other hosts, as well as the report by Miller (1938) stating that papaya was infected in a greenhouse in California by “cucurbit powdery mildew”. Chitambar (2015) emphasized that the synonymy of *P. caricae-papayae* and *P. xanthii* is unclear, unproven and in urgent need to be investigated further. Therefore, he maintained the name *P. caricae-papayae*, at least tentatively. The assignment of *Podosphaera* on papaya in Thailand to *P. xanthii* in Meeboon et al. (2016) was erroneous and refers to *P. caricicola*. However, a sequence recently retrieved from a powdery mildew collection of *Podosphaera* on papaya in Taiwan clusters within the large *P. xanthii* clade (Fig. 8) and supports the taxonomy of *P. caricae-papayae* proposed in Braun & Cook (2012), including the reduction of the latter species to synonymy with *P. xanthii*, and should be maintained. Attempts to retrieve sequence data from type material of *Sphaerotheca caricae-papayae* were not possible due to the paucity of the material concerned. Braun & Cook (2012) cited *Oidium caricicola* as synonym of *P. xanthii*, which is, however, doubtful (see notes under *O. caricicola*). The description of conidiophores and conidia of *O. caricicola* agrees well with *P. xanthii*, but the germ tubes illustrated in Yen & Wang (1973) are in conflict with an interpretation of this species as *P. xanthii* since they are close to those of *Podosphaera* species of sect. *Sphaerotheca* subsect. *Sphaerotheca*. Based on available relatively reliable data and information, the distribution of *P. xanthii* on papaya can be summarized as follows: Australia, China, Cook Islands, India, Japan, New Zealand, Thailand, USA (Miller 1938, Alcorn 1968, Munjal & Karpoor 1973, Dingley et al. 1981, Boesewinkel 1982b, Amano 1986, Braun 1987, Verma & Sharma 1999, Paul & Thakur 2006,

Braun & Cook 2012, Chitambar 2015, Meeboon et al. 2016, as “*Sphaerotheca fuliginea*”, *S. caricae-papayae*, *Podosphaera caricae-papayae* or *P. xanthii*). Additional records of *Sphaerotheca* sp. on papaya from Australia (Shivas 1989), Hawaii (Raabe et al. 1981), and Ukraine (Dudka et al. 2004) might belong to *P. xanthii* as well, but they are unproven.

***Phyllactinia* spp. on papaya**

Papaya is attacked by several species of the genus *Phyllactinia*, including *Ovulariopsis* (Braun & Cook 2012). Takamatsu et al. (2016) carried out detailed phylogenetic analyses of a basal clade of *Phyllactinia* spp. comprising American species of this genus. *Ovulariopsis caricicola* U. Braun (\equiv *Streptopodium caricae* Liberato & R.W. Barreto) on papaya proved to be one of the species of this basal clade. Based on the current Code (ICN) and the new “one fungus one name” rule, the new combination *Phyllactinia caricicola* (U. Braun) Liberato, R.W. Barreto & S. Takam. was introduced in this paper, along with formal reallocations of *Ovulariopsis caricae* Sawada and *O. papayae* Van der Byl to *Phyllactinia*, i.e. four *Phyllactinia* spp. are now known on papaya, viz. *P. caricae* (Sawada) U. Braun, *P. caricicola*, *P. papayae* (Van der Byl) U. Braun, and *P. caricifolia* Viégas. Descriptions and illustration are to be found in Braun & Cook (2012). The relation between *P. caricicola* and *P. caricifolia* is unclear. It is possible that the two taxa belong to a single species. The two species have similar dimorphic conidia, but type material of *P. caricifolia* is insufficient for a final conclusion (Liberato et al. 2004, Braun & Cook 2012).

Excluded, doubtful and insufficiently known taxa described from or reported on papaya

Erysiphe cruciferarum Opiz ex L. Junell, Sv. Bot. Tidskr. 61(1): 217, 1967.

Notes – Boesewinkel (1982b) carried out inoculation experiments with papaya powdery mildew and *E. cruciferarum* from wild radish (*Raphanus raphanistrum*) which was first transferred to *Brassica napus*. Later he managed to infect papaya in glass house experiments with *E. cruciferarum*, which led to his erroneous conclusion that *O. caricae* might be the “imperfect state” of *E. cruciferarum*. In the event that Boesewinkel (1982b) performed correct inoculation experiments, it cannot be excluded that *E. cruciferarum* was, indeed, able to cause infections on papaya in New Zealand. However, the occurrence of *E. cruciferarum* on papaya still needs to be studied using molecular methods.

Golovinomyces orontii (Castagne) Heluta, Ukrayins’k. Bot. Zhurn. 45(5): 63, 1988.

\equiv *Erysiphe orontii* Castagne, Suppl. Cat. Pl. Marseille: 52, 1851.

Misapplied name: *Erysiphe cichoracearum* (auct. p.p.).

Notes – Although unproven by means of inoculation experiments or results of molecular sequence analyses, it is possible that the plurivorous powdery mildew species *G. orontii* may infect papaya. Boesewinkel (1982b) found “*Erysiphe cichoracearum*” on papaya in New Zealand. Other records of “*Erysiphe cichoracearum*” from Mexico (Alvarez 1976, 1981) and Peru (Dongo & Rocha 1968) might refer to *G. orontii* as well. Boesewinkel’s (1982b) interpretation that the characteristics of *Oidium caricicola* are similar to “*Erysiphe cichoracearum*” is, however, doubtful since important details like the presence or absence of fibrosin bodies in the conidia are lacking in the original description. *O. caricicola* fits better to a species of *Podosphaera* sect. *Sphaerotheca* subsect. *Sphaerotheca* that also occurs on papaya (see *Podosphaera caricicola*).

Leveillula taurica s. lat.

Records of *Leveillula taurica* s. lat. on papaya are known from Australia, Malawi, Nigeria, Zambia, and Zimbabwe (Amano 1986, Peregrine & Siddiqi 1972, Simmonds 1966, Whiteside 1966). However, first attempts have been made to split *L. taurica* s. lat. into smaller “units” (species) based on results of molecular sequence analyses and morphology (Braun & Cook 2012). In the light of this new taxonomic approach, and due to lacking morphological details and sequence

data of *Leveillula* on papaya, the powdery mildew concerned can currently only be referred to as *Leveillula* sp.

Oidium caricae-papayae J.M. Yen, Rev. Mycol. 31: 316, 1966.

Material examined – Taiwan, Nantou, on *Carica papaya*, 16 Mar. 1966, S.K. Sun (holotype PC0022110).

Notes – The name *O. caricae-papayae* has often been confused with *O. caricae* and considered to be a synonym of the latter species (Bappammal et al. 1995, Hosagoudar & Agarwal 2009). Braun & Cook (2012) listed *O. caricae-papayae* under “Anamorphic powdery mildews (*Oidium*) of unclear generic affinity” and provided a description. The hyphal appressoria are lobed, conidiophores are relatively broad, to 12 µm, and the conidia are formed in chains of 3 to 9 (catenulent). The combination of lobed appressoria and catenate conidia is unusual and mainly known from species of the genus *Neoerysiphe*. In Boesewinkel (1980), *O. caricae-papayae* was also keyed out under species with conidia formed in chains, and Boesewinkel (1982b) recognized it as a species of its own. Menzies & Kempler (1991) described and illustrated “*Oidium caricae-papayae*” on papaya from a greenhouse in British Columbia, Canada, but the description seems to refer rather to the North American *Erysiphe fallax*, although conidia in short chains were mentioned. Chen & Yang (2002) reported *O. caricae-papayae* on *Eriobotrya japonica* from China (Fujian), which is, however, unconfirmed and doubtful. The taxonomic status and generic affinity of *O. caricae-papayae* are quite unclear.

However, a careful analysis of Yen’s (1966) publication and illustration suggests that his description was based on two species co-existing on papaya. A currently examined collection from Thailand (TSU-MUMH3383, HAL 3192 F) with a mixed infection of *Podosphaera caricicola* and *Erysiphe caricae-papayae* represents a similar striking case. Figs 1A (conidiophores with solitary conidia) and E (lobed appressoria) in Yen’s (1966: 313) illustration seem to represent a *Pseudoidium*, whereas Fig. B (conidiophores with catenulent conidia) might belong to another species. Based on relatively short conidiophores, 36–55.2 × 8.4–12 µm, and doliiiform conidia (Yen 1966: 313, Fig. D), the powdery mildew with catenate conidia might rather pertain to *Podosphaera*, either *P. caricicola* or *P. xanthii*. Germ tubes shown in Fig. F rather suggest *P. caricicola*. This is, of course, speculative and uncertain. Thus, it is better to treat *O. caricae-papayae* as an unclear, excluded species. If the name *O. caricae-papayae* was, indeed, based on two different elements (powdery mildew taxa), its application depends on a lectotypification. In this case, the name *O. caricae-papayae* should be confined to the *Erysiphe* element with lobed hyphal appressoria and conidia formed singly. However, since several *Erysiphe* spp. are known on papaya, the true identity of *O. caricae-papayae* remains unclear, pending results of molecular sequence analyses or epitypification.

Liberato et al. (2004) classified *O. caricae-papayae* as an invalid name due to lack of designation of type material, which is, however, not correct since Yen (1966) cited a single specimen that has to be considered holotype material according to ICN, Art. 9.1 (including Note 1). Art. 40.1 is fulfilled by the citation of a single collection examined, and Art. 40.6 cannot be applied since this article was not effective before 1 Jan 1990.

Oidium indicum Kamat, in Chiddarwar, Curr. Sci. 24(7): 240, 1955, nom. inval. (ICN, Art. 39.1).

Notes – *O. indicum* is an invalid name. The original description of this species is absolutely insufficient (hyphae 5–7.5 µm wide; conidia obovoid to barrel-shaped, 31.5–46.8 × 13.7–23.4 µm, formed in chains of 3 to 5). The conidiophores and the presence or absence of fibrosin bodies in conidia were not described. Based on the given details, it was impossible to assign this species to any of the powdery mildew genera. Yen (1966) examined type material of this species (IMI 60596) and provided a description and illustration (Yen 1966: 315, fig. 2) that clearly shows a *Pseudoidium* with lobed hyphal appressoria and conidia formed singly, 37.2–51.6 × 14.4–21.6 µm. Yen & Wang (1973) reported a powdery mildew sample collected from a papaya in Taiwan which agreed morphologically with Yen (1966) as *O. caricae*. Boesewinkel (1982b) considered *O.*

indicum to be morphologically identical with *O. caricae*, probably due to the conidial size given in the original description and Yen's (1966) publication, although the conidia were described to be catenate. Verma & Sharma (1999) regarded *O. indicum* and *O. caricae* as synonyms of *Sphaerotheca fuliginea*, and Braun & Cook (2002) reduced *O. indicum* to synonymy with *O. caricae-papayae*. All interpretations of this name are, however, doubtful and speculative. Based on Yen's (1966) examination of type material, *O. indicum* seems to be an asexual morph of *Erysiphe*, however, given the numerous *Erysiphe* species on papaya, it is impossible to assign this name to any of the recognized species. Furthermore, the name *O. indicum* is invalid and must be excluded.

Key to powdery mildew species on papaya (confirmed and unconfirmed species)

1. Mycelium internal and external; conidiophores usually emerging through stomata; conidia relatively large, usually 40–80 µm long, on an average > 50 µm, dimorphic, with morphologically differentiated primary and secondary conidia; chasmothecia large, usually more than 150 µm diam, appendages mycelioid, asci usually 2-spored *Leveillula* sp.
1. Mycelium external, conidiophores arising from superficial hyphae; conidia catenescence or solitary, smaller, on an average < 50 µm, not dimorphic; chasmothecia, when formed, smaller, < 150 µm (*Erysiphe*, *Golovinomyces*, *Podosphaera*) or mycelium internal and external, but conidiophores consistently arising from external hyphae; chasmothecia also large, but with equatorial lanceolate appendages bulbous at the base and penicillate cells in the upper half (*Phyllactinia*) 2
2. Mycelium exclusively external; conidia catenescence or solitary, on an average < 50 µm long, ellipsoid-ovoid, doliiform or ± cylindrical; chasmothecia, when formed, with mycelioid appendages (*Erysiphe*, *Golovinomyces*, *Podosphaera*) 3
2. Mycelium internal and external; conidia large, on an average > 50 µm, uniformly clavate or dimorphic, clavate and lanceolate; chasmothecia when formed with equatorial lanceolate appendages bulbous at the base and penicillate cells in the upper half (*Phyllactinia*) 9
3. Conidia formed in chains (catenescence); hyphal appressoria indistinct to nipple-shaped 4
3. Conidia formed singly; hyphal appressoria lobed (*Erysiphe*) 6
4. Conidia without fibrosin bodies (fresh collections), conidial chains with sinuate edge line; foot-cells of the conidiophores straight to often curved at the base; chasmothecia with several asci, mostly 2-spored *Golovinomyces orontii*
4. Conidia with fibrosin bodies (fresh collections), conidial chains with crenate edge line; foot-cells of the conidiophores straight at the base; chasmothecia with a single ascus, 6–8-spored 5
5. Conidiophore foot-cells 30–70(–100) µm long, cylindrical; conidia with short and stout, often even forked germ tubes, often lateral; chasmothecia with large peridial cells, 15–55 µm diam *Podosphaera xanthii* s. lat. (incl. *P. caricae-papayae*)
5. Conidiophore foot-cells 30–50 µm long, cylindrical; conidia with simple germ tubes, cylindrical to filiform, terminal to lateral; chasmothecia with smaller peridial cells, 5–25(–30) µm diam, on an average ≤ 20 µm *Podosphaera caricicola*
6. Conidiophores with sinuous to spirally twisted foot-cells *Erysiphe necator*
6. Conidiophores with straight foot-cells, at most occasionally curved or slightly sinuous 7
7. Asexual and sexual morphs formed; conidia ellipsoid-ovoid to cylindrical, 25–60 × 14–25 µm; hitherto only known from Asia and Europe 8
7. Only asexual morphs known, morphologically barely distinguishable from *E. caricae* and *E. caricae-papayae*, further identifications only possible by means of molecular sequence analyses; see also *E. cruciferarum*, *E. diffusa*, and *E. fallax*
8. Chasmothecia large, 103–185 µm diam, with 4–10(–15) appendages, and 4–9 asci; Asia (Taiwan, Thailand) *Erysiphe caricae-papayae*
8. Chasmothecia smaller, (65–)85–125 µm diam, with numerous appendages (usually > 10), and only 3–5 asci; Europe *Erysiphe caricae*

9. Conidia dimorphic, primary conidia lanceolate, apically pointed, secondary conidia clavate; South America *Phyllactinia caricicola* (and *P. caricifolia*)
9. Conidia uniformly clavate 9
10. Conidia apiculate; Asia *Phyllactinia caricae*
10. Conidia non-apiculate; Africa *Phyllactinia papayae*

Discussion

Carica papaya and other species of the genus *Carica* are hosts of numerous powdery mildews belonging to various genera, including some records that are probably classifiable as accidental infections. Some powdery mildew species described on papaya are insufficiently known and have been notoriously confused. Many of these species are reassessed in this work, while others are listed in the section of “Excluded, doubtful and insufficiently known taxa” which urgently require re-examinations of type material and molecular sequence analyses of new collections. In the interim, the names concerned should not be applied in order to avoid further confusion. *Oidium caricae*, which is probably the most misapplied name amongst powdery mildews on papaya, was especially problematic. This name has been applied to various papaya powdery mildew worldwide. The first published results of molecular sequence analyses of *O. caricae*-like powdery mildews suggested that different *Erysiphe* species were involved (Tsay et al. 2011, Takamatsu et al. 2015). Additional phylogenetic examinations of *O. caricae*-like powdery mildews, including a collection from Brazil, have been carried out to distinguish the complex of taxa involved. Results of the analyses showed that at least five different *Erysiphe* taxa are able to infect papaya, including *E. caricae* and *E. caricae-papayae*, currently the only species for which a sexual morph is known. *O. caricae*, described from Brazil, is reduced to synonymy with *Erysiphe diffusa*. Collections from Mexico and the USA proved to belong to a separate species, described as *E. fallax* sp. nov., which is possibly widespread in the native distribution area of papaya from southern Mexico to Costa Rica. This is, however, speculative and needs further studies in the natural range of papaya. Identifications of papaya infections by *Erysiphe cruciferarum* in New Zealand obtained in the course of inoculation experiment carried out by Boesewinkel (1982b) also need confirmation by means of molecular methods. Similar asexual powdery mildew morphs collected on papaya in Asia belong to different species, including *Erysiphe diffusa* and *E. caricae-papayae*. All asexual morphs on papaya belonging to *Erysiphe* spp., except for *E. necator*, are difficult to distinguish morphologically and must be confirmed by molecular sequence analyses. The present studies of *Erysiphe* spp. of papaya are preliminary. Relatively few samples have been analysed to be able to even speculate about the genuine distribution of the taxa involved. Further examinations and analyses of *Erysiphe* spp. on papaya collected from areas where papaya is native or widely grown are urgently needed. Sequences retrieved from papaya powdery mildews that pertain to *Podosphaera* are genetically not uniform and cluster in different places on the phylogenetic tree. They represent two different species, viz. *P. xanthii* (including *P. caricae-papayae*), belonging to sect. *Sphaerotheca* subsect. *Magnicellulata*, and *P. caricicola*, a species of *Sphaerotheca* subsect. *Sphaerotheca*. The currently available knowledge about the occurrence of the two *Podosphaera* spp. on papaya is still fragmentary but suggests a wide distribution.

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