Asexual morphs of powdery mildew species (*Erysiphaceae*) – new and supplementary morphological descriptions and illustrations

Anke SCHMIDT & Uwe BRAUN

Abstract: Schmidt, A. & Braun, U. 2020: Asexual morphs of powdery mildew species (*Erysiphaceae*) – new and supplementary morphological descriptions and illustrations. Schlechtendalia **37**: 30–79.

Descriptions of asexual morphs of powdery mildew species are provided, with a particular focus on characteristics of the conidiophores and conidial germination patterns. Descriptions and illustrations are based on collections made by the first author in the course of long-term examinations of species of the *Erysiphaceae*. In some cases, detailed descriptions and illustrations of conidiophores and, above all, conidial germination patterns could be obtained for the first time. The first record of *Neoerysiphe nevoi* for Germany on *Lapsana communis* is included in this work. Conidial germination patterns of *Erysiphe* spp. on legumes are compared and discussed in more detail.

Zusammenfassung: Schmidt, A. & Braun, U. 2020: Asexuelle Morphen von Mehltauarten (*Erysiphaceae*) – neue und ergänzende morphologische Beschreibungen und Abbildungen. Schlechtendalia **37**: 30–79.

Beschreibungen asexueller Morphen von Mehltau-Arten werden zur Verfügung gestellt, mit einem besonderen Schwerpunkt auf Merkmale der Konidien-Träger und Keimungsmuster der Konidien. Beschreibungen und Abbildungen basieren auf Kollektionen der Erstautorin, die sie im Rahmen langjähriger Untersuchungen von Arten der *Erysiphaceae* gefunden hat. In einigen Fällen war es möglich, erstmalig detaillierte Beschreibungen und Abbildungen von Konidien-Trägern und vor allem von Konidien-Keimungsmustern zu erstellen. Der Erstnachweis von *Neoerysiphe nevoi* für Deutschland auf *Lapsana communis* ist in dieser Arbeit enthalten. Keimungsmuster der Konidien von *Erysiphe*-Arten auf Leguminosen werden detaillierter verglichen und diskutiert.

Key words: *Helotiales* (*Erysiphales*), anamorphs, traits, conidial germination.

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Introduction

Powdery mildews (*Helotiales*, *Erysiphaceae*) are one of the most important groups of plant pathogenic ascomycetes of significant economical and phytopathological relevance. They occur on a wide range of monocots and dicots as hosts with an almost worldwide distribution. The first monographic treatment of this fungal groups was issued by Salmon (1900), followed by Braun (1987). A modern taxonomic handbook, based on first phylogenetic examinations of powdery mildews was published by Braun & Cook (2012). The history of the exploration and taxonomic application of asexual morphs of powdery mildews goes back to Salmon (1900) who totally ignored conidiophores and conidia and considered these structures meaningless. The perception of the diagnostic and taxonomic relevance of asexual structures developed gradually, starting with Neger's (1902) first conidial germination experiments, and began later to prevail. More comprehensive germination experiments with powdery mildew conidia were performed by Hirata (1942, 1955) and Zaracovitis (1966), who tried to generalize the germination patterns. Much later, Cook & Braun (2009) deepened this generalization by linking certain conidial germination patterns to the particular powdery mildew genera, based on the new phylogenetic genus concept, including formal terms that were introduced for particular patterns. The proposed new system was later accepted and applied in Braun & Cook (2012).

However, several general problems are connected with examinations of asexual morphs. In herbarium samples, they are often poorly developed and in bad condition. Better results are to be expected when examinations are based on fresh collections. Furthermore, the formation of conidial stages is often ceased with the commencing development of chasmothecia, with the consequence that well-developed asexual morphs are mostly lacking in older herbarium specimens since previous mycologists and phytopathologists, influenced by Salmon's undervaluation of asexual morphs, usually collected late stages of powdery mildews with prevailing fruiting bodies. This is a general problem that taxonomists, dealing with *Erysiphaceae*, have to face. This was also a serious problem during the course of the preparation of the powdery mildew monographs of Braun (1987) and Braun & Cook (2012). Fresh collections for all treated species were not always at hand. Furthermore, examinations aiming at obtaining the conidial germination patterns require, of course, living collections. It is, therefore, particularly important to supplement little or insufficiently known asexual morphs of powdery mildews on the basis of fresh collections and to carry out germination experiments with conidia. This was the

main objective of this publication. The presented descriptions and illustrations are the result of long-term studies of powdery mildews, particularly focusing on asexual morphs, performed from 1998 to 2020 by the first author. Descriptions and measurements were performed on the basis of fresh material, including fresh turgescent conidia, which provides additional advantages since previous data and measurements were often obtained from dried herbarium samples. Measurements based on dried herbarium samples usually differ from those obtained on the basis of fresh conidia (the length and above all width values are usually smaller). Dry conidia of herbarium samples are often gently heated in lactic acid. However, even conidia treated in this way also tend to be somewhat smaller, above all narrower than fresh, fully turgescent conidia observed in water. Blumer (1922, 1933, 1967) found fairly constant factors for converting data obtained for dried samples to equivalent data for fresh samples. Thus, it is only necessary to multiply the conidial width of dried conidia by the factor 1.2 and the conidial length by 1.15. However, only few authors have used Blumer's method, or at least its application is usually not clearly stated in the publications concerned.

Some descriptions and illustrations have already been published in previous taxonomic treatments, such as Schmidt (1999), Schmidt & Scholler (2002, 2006, 2011, 2012), and Scholler et al. (2016).

Materials and methods

The germination experiments described in the present work were performed as follows: Fresh conidia were dusted on glass slides and deposited in Petri dishes with moist cellulose tissue or kept dry and moistened after 12 hrs. The closed Petri dishes were kept at room temperature behind a north-sided window for about 24 hrs with a natural change between day light and darkness. Measurement were usually based on about 25 conidia and made in tap water. Voucher specimens were deposited in the mycological collection of the herbarium KR (Natural History Museum, Karlsruhe, Germany).

Results

Descriptions and illustrations of asexual morphs of several powdery mildew species with special emphasis on the conidial germination

[The descriptive terminology used in this work is based on Braun & Cook (2012), including special terms used for types and patterns of the conidial germination, such as "perihilar" (subapical in conidia with a terminal hilum, i.e., around the hilum rim in catenescent conidia or in secondary conidia with truncated apex when formed singly).]

Arthocladiella

Arthocladiella mougeotii (Lév.) Vassilkov Figs. 1, 2

Material examined: Germany, Schleswig-Holstein, Ostholstein, Timmendorfer Strand, OT Niendorf, near the port, on *Lycium barbarum*, 29 Jul. 2000, A. Schmidt, KM 119 (KR-M-0020806); Schleswig-Holstein, Ostholstein, Scharbeutz, Badeweg, on *Lycium barbarum*, 28 Aug. 2004, A. Schmidt, KM 198 (KR-M-0021919); Hamburg, Teufelsbrück, breakwater between Elbe and marina port, on *Lycium* cf. *chinense*, 02 Aug. 2000, A. Schmidt, KM 120 (KR-M-0020807).

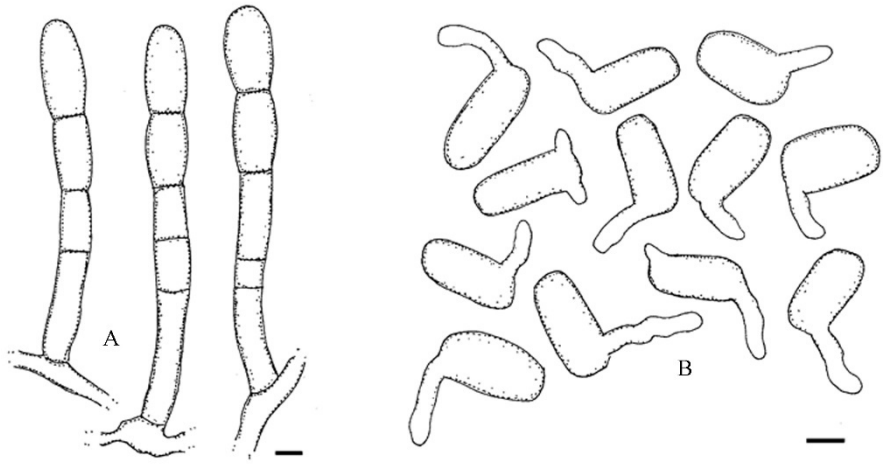


Fig. 1: *Arthrocladiella mougeotii*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

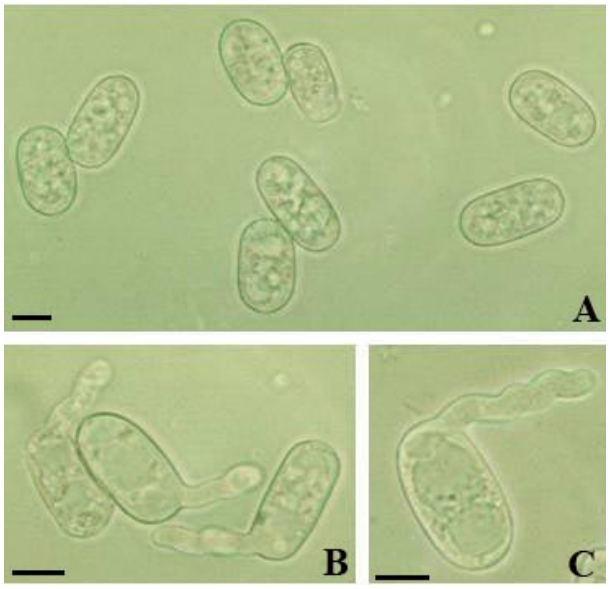


Fig. 2: *Arthrocladiella mougeotii*. A: Conidia; B, C: Conidia with germ tubes. Scale bars = 10 µm.

The conidiophores (foot-cells cylindrical, straight, 30–45 × 7–10 µm, followed by 1–3 shorter cells) and conidia (26–38 × 14–20 µm, length/width ratio 1.4–2.6, on average 2.0) correspond well with the descriptions published in Paulech (1995: 185) and Braun & Cook (2012: 350). In the latter publication, the conidial germination is only briefly described and not illustrated. Based on the experiments carried out by the first author, it can be described as follows: Germ tubes solitary, perihilar, rarely with two germ tubes, uniformly short, usually not longer than the conidial length, cylindrical to somewhat clavate, straight to curved-sinuous, consistently aseptate, apex undifferentiated to somewhat swollen. This type of germination resembles the Euoidium (Reticuloidium) type of *Golovinomyces* and was assigned to this type in Cook & Braun (2009).

Erysiphe

Erysiphe alphitoides (Griff. & Maubl.) U. Braun & S. Takam. Figs. 3, 4

Material examined: Germany, Niedersachsen, Landkreis Rotenburg (Wümme) near Sittensen, Thörenwald, on *Quercus* sp. 06 Sep. 2003, A. Schmidt, KM 180 (KR-M-0021931); Schleswig-Holstein, Lübeck, Dummersdorfer Ufer, "Höhenweg" towards Travemünde, on *Quercus robur*, 27 Jul. 2005, A. Schmidt, KM 208 (KR-M-0021944).

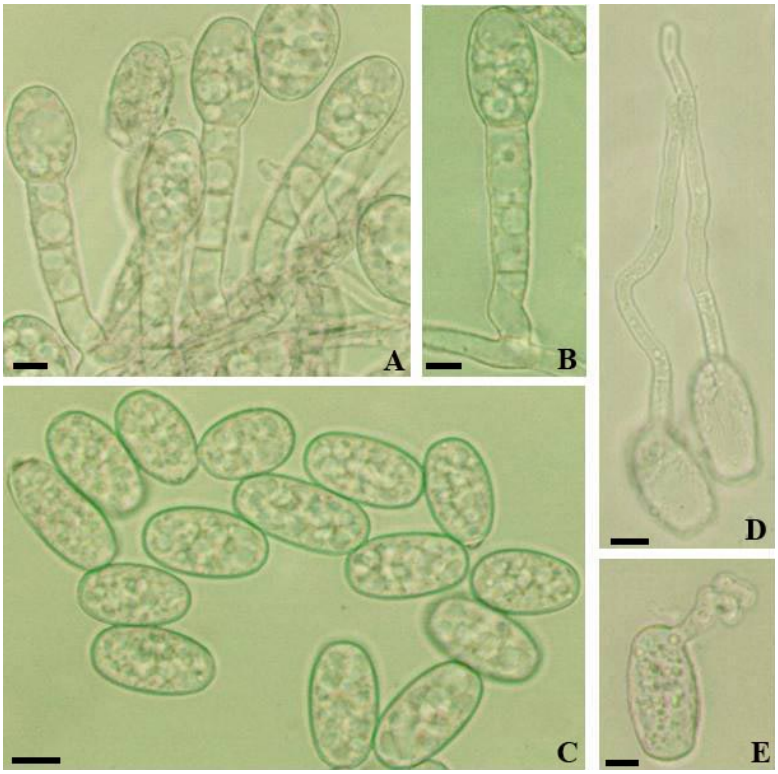


Fig. 3: *Erysiphe alphitoides*. A, B: Conidiophores; C: Conidia; D, E: Conidia with germ tubes. Scale bars = 10 µm.

The asexual morph of *Erysiphe alphitoides* has been examined in detail in several previous studies. Braun & Cook (2012) provided a detailed description, but the illustration is, in contrast to the description, meagre and only based on a few conidia with short germ tubes germinated on the natural substrate, i.e., not under moist chamber conditions. The description is more detailed, including an indication of the occurrence of up to 10% of conidia showing longitubus pattern germination. The conidiophores and conidia (26.5–42 × 16–20 µm, length/width ratio 1.4–2.4, on average 1.8) coincide

with previous reports, such as Bolay (2005: 36–37) and Braun & Cook (2012: 433). The germination experiments under moist chamber and dry conditions based on the material cited above yielded the following results: Usually with a single subapical germ tube, rarely with two, with short and long (longitubus pattern) germ tubes, up to about five times as long as the conidial length, aseptate or with a single septum at the base or somewhat distant from the point of attachment, occasionally with two septa (only in very long germ tubes), apex in short germ tubes with a swollen to lobed conidial appressorium, apex of long germ tubes undifferentiated or somewhat swollen. Hirata (1942: 45, fig. 6 J; 1955, 34, fig. 9 D, E) described and illustrated only short germ tubes with distinctly lobed terminal appressoria that agree well with the short germ tubes found in the present examination. Otherwise, the results agree well with the data specified in Braun & Cook (2012), except for a higher percentage of conidia with longitubus pattern. It seems that the degree of development of longitubus pattern germination being variable, depending on the source of conidia and the specific conditions. Pap et al. (2013) examined the conidial germination of *E. alphitoides* in detail and pointed out that the germination is significantly influenced by temperature, relative humidity and light. The maximum length of germ tubes was attained at 25°C (shorter at lower and higher temperatures). Germination happened between 10 and 100% relative air humidity (RH), with a maximum length at 90% and the best germination was found in full light, in contrast to lower values in total darkness.

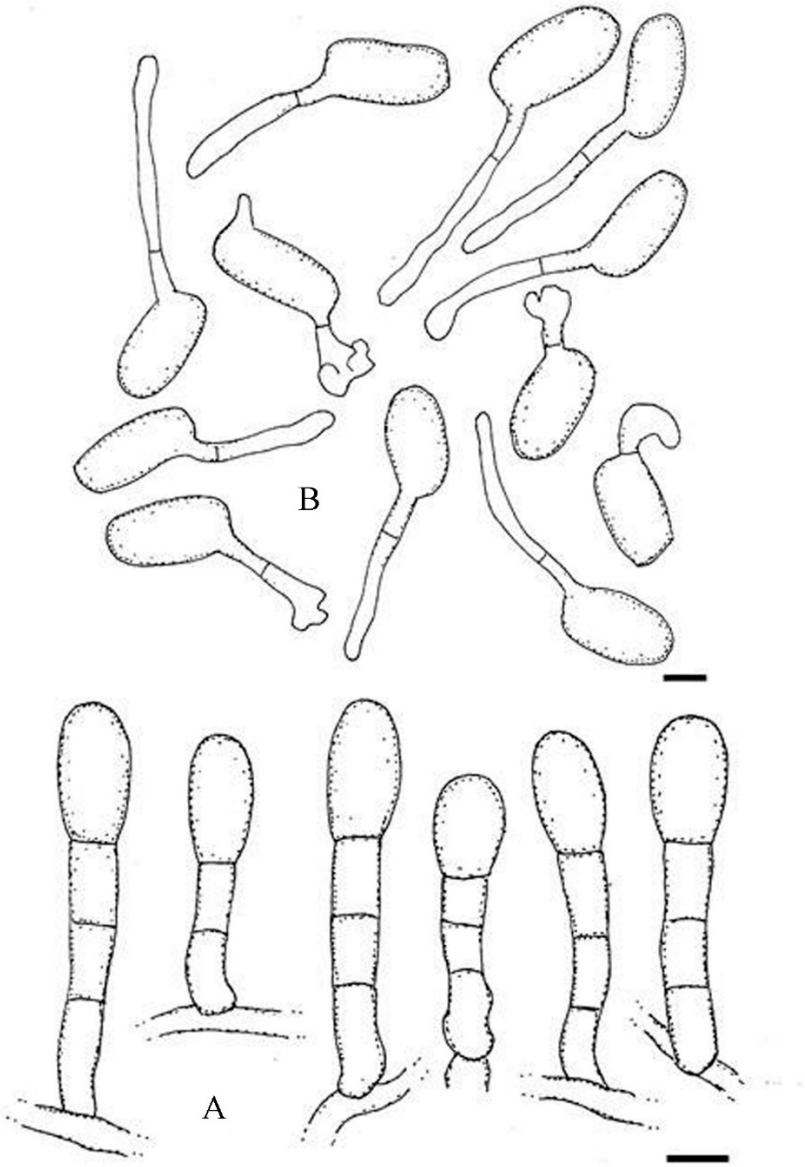


Fig. 4: *Erysiphe alphitoides*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe aquilegiae DC. var. ***aquilegiae*** Figs. 5, 6

Material examined: Germany, Hamburg, Klein Flottbek, botanical garden, on *Aquilegia caerulea*, 30 Jul. 2006, A. Schmidt, KM 223 (KR-M-0022023); Schleswig-Holstein, Lübeck, St. Gertrud, Israelsdorf, on *Aquilegia* sp. cult., 03. Sep. 2006, A. Schmidt, KM 229 (KR-M-0022012).

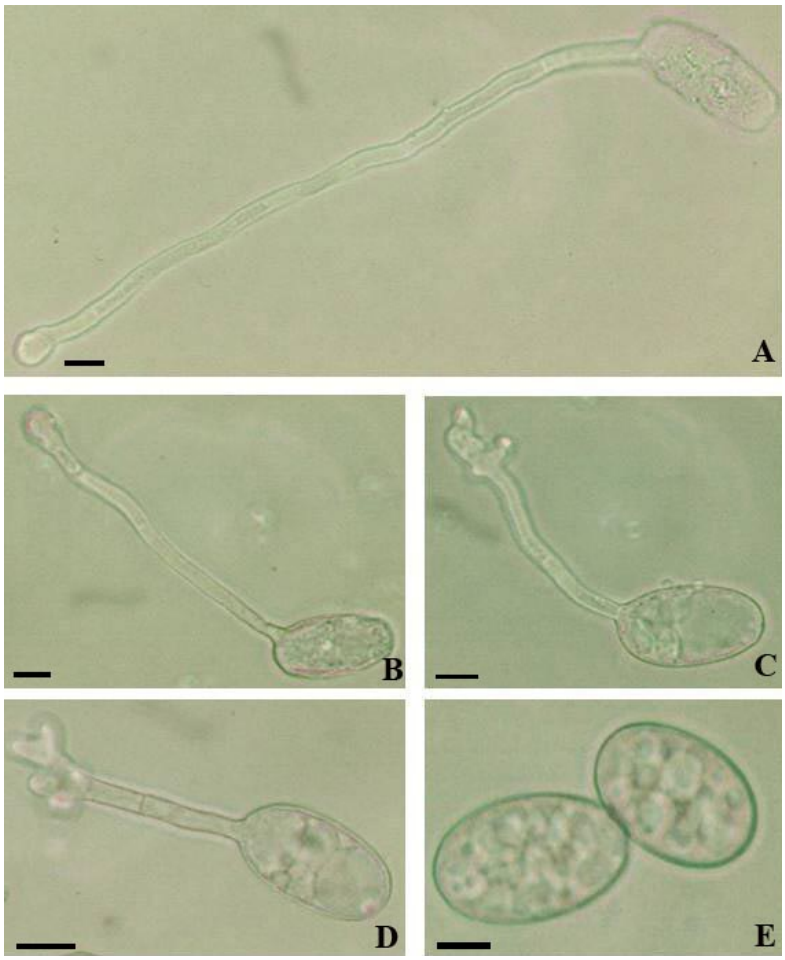


Fig. 5: *Erysiphe aquilegiae* var. *aquilegiae*. A–D: Conidia with germ tubes; E: Conidia. Scale bars = 10 µm.

The conidiophores (foot-cells cylindrical, straight to somewhat curved or sinuous, 20–60 × 8–10.5 µm, followed by 1–2 cells shorter than the foot-cell or about as long) and conidia (30–56 × 16–24 µm, length/width ratio 1.5–3.3, on average 2.1) agree well with previous descriptions, as for example in Paulech (1995: 115), Shin (2000: 33–34), and Braun & Cook (2012: 362). The latter work also contains a detailed description of the conidial germination, which largely coincides with the present results, except for the percentage of longitubus pattern germination, which seem to be influenced by the particular conditions of the germination experiments. Conidia only treated in a moist chamber show a higher percentage of longitubus pattern, whereas conidia first treated in a dry chamber and then in a moist chamber have a higher percentage of short germ tubes with multilobed terminal appressoria. The present germination experiments yielded the following results: Mostly with a single subapical germ tube, occasionally with two germ tubes, either both germ tubes terminal or one terminal and one at the base, germ tubes short, with a slightly to multilobed terminal appressorium, or long (longitubus pattern), 15–215 µm long, straight to sinuous, apex usually swollen, sometimes undifferentiated, germ tubes mostly with a single septum at the base or distant from the point of attachment, up to about the middle of the germ tube, longer germ tubes often with two septa distant from each other.

The described conidial germination on *Aquilegia* refers to *E. aquilegiae* s. str. In phylogenetic rDNA ITS trees, this species belongs genetically to the *E. aquilegiae* complex (Takamatsu et al. 2015, Shin et al. 2019), which is insufficiently resolved and in urgent need of revision based on multilocus approaches (see discussion in Shin et al. 2019). *E. aquilegiae* s. lat. is probably heterogeneous. ITS sequences retrieved from collections morphologically identified as *E. aquilegiae* var. *aquilegiae* and *E. aquilegiae* var. *ranunculi* (≡ *E. ranunculi*) are identical (see Takamatsu et al. 2015, Shin et al. 2019).

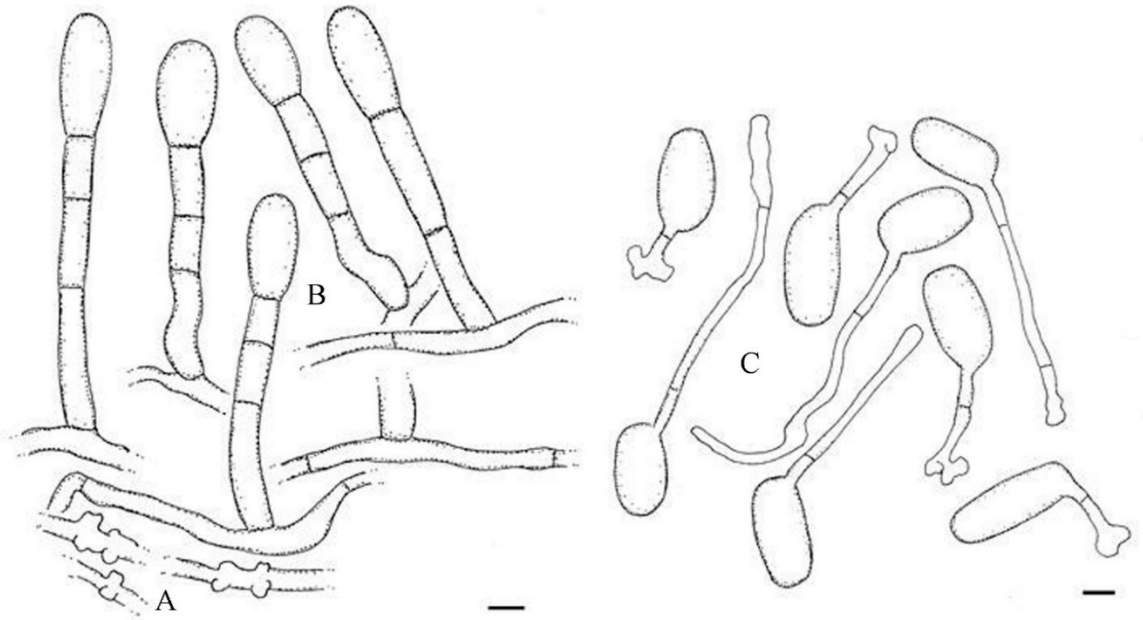


Fig. 6: *Erysiphe aquilegiae* var. *aquilegiae*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe aquilegiae var. ***ranunculi*** (Grev.) R.Y. Zheng & G.Q. Chen Figs. 7, 8

Material examined: Germany, Hamburg, Rissen, Wepenstieg, garden, on *Delphinium* sp., 17 June 2006, A. Schmidt, KM 217 (KR-M-0022018), Schleswig-Holstein, Herzogtum Lauenburg, Groß Grönau, nursery, on *Delphinium grandiflorum*, 14 Aug. 2008, A. Schmidt, KM 270 (KR-M-0002824).

Conidiophores (foot-cells 20–25 × 8–10 µm, followed by 1–2 cells, shorter than the foot-cell, about as long or even longer), conidia (30–46 × 18–22 µm, length/width ratio 1.4–2.3, on average 1.8), and the conidial germination of the powdery mildew on *Delphinium* coincide well with the characteristics described above for *E. aquilegiae* var. *aquilegiae*, except for details of the germ tube septation (on *Delphinium* septa at the base or only somewhat distant from the point of attachment). Shin (2000: 64, fig. 17) illustrated germ tubes of *Erysiphe aquilegiae* var. *ranunculi* (*E. ranunculi*), either short and aseptate or long and two-septate, with both septa distant from the point of attachment, the second septum up to the upper half. Unfortunately, the source (host) of the illustration is unclear and was not cited in this work.

Fig. 7: *Erysiphe aquilegiae* var. *ranunculi*. A: Conidiophore; B, C, E: Conidia with germ tubes; D: Conidia. Scale bars = 10 µm.

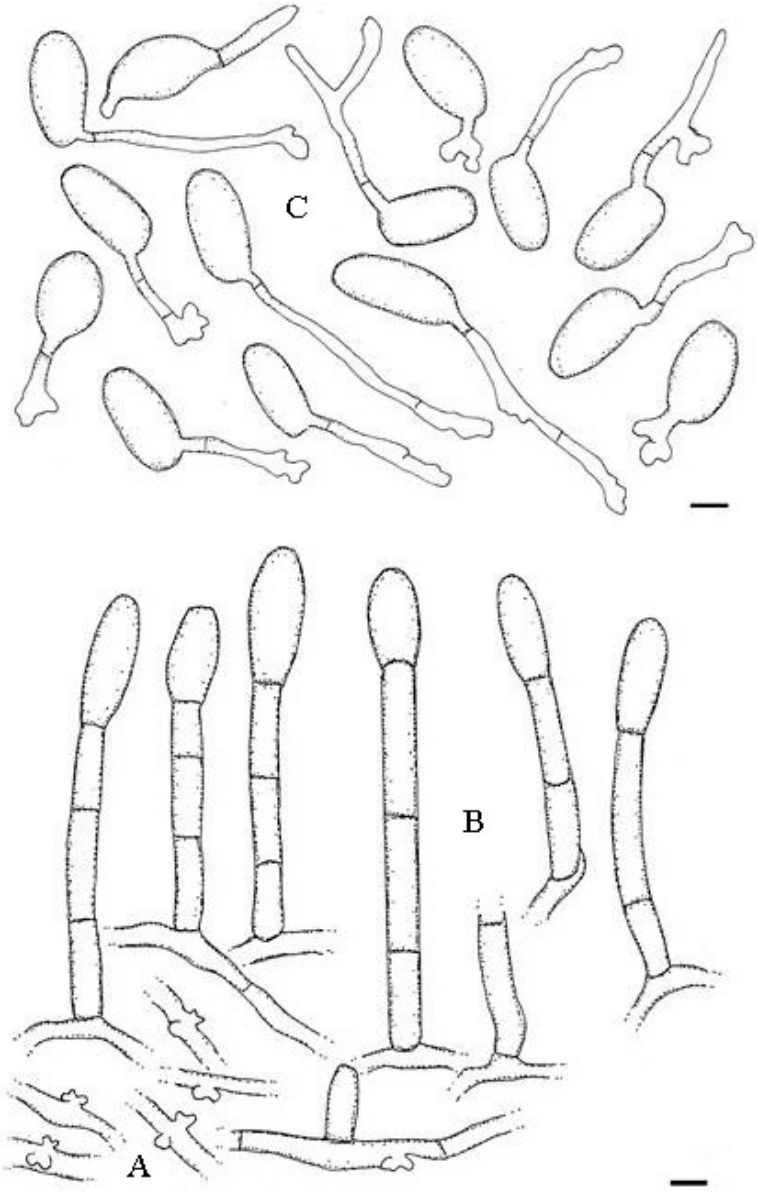


Fig. 8: *Erysiphe aquilegiae* var. *ranunculi*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe astragali DC. Figs. 9, 10

Material examined: Germany, Mecklenburg-Vorpommern, Landkreis Nordwestmecklenburg, near Lassahn, east bank of Schaalsee, on *Astragalus glycyphyllos*, 01 Jul. 1999, A. Schmidt, KM 85 (KR-M-0020840); Schleswig-Holstein, Lübeck, Dummersdorfer Ufer, shore near Stülper Huk, on *Astragalus glycyphyllos*, 12 June 2000, A. Schmidt, KM 107 (KR-M-0020846); Schleswig-Holstein, Lübeck, Dummersdorfer Ufer, on *Astragalus glycyphyllos*, 10 June 2001, A. Schmidt, KM 129 A (KR-M-0022009); Schleswig-Holstein, Lübeck, Travemünde, Priwall, right bank of river Trave, on *Astragalus glycyphyllos*, 13 Jul. 2002, A. Schmidt, KM 158 (KR-M-0021956).

The conidiophores (foot-cells more or less cylindrical, straight or occasionally only slightly curved or sinuous, 25–34 × 6.5–11 µm, followed by two somewhat shorter cells) and conidia (29–53 × 14–24 µm, length/width ratio 1.5–3.1, on average 2.1) agree well with previous descriptions, such as Paulech (1995: 191) and Braun & Cook (2012: 434). The conidial germination was not described in the latter work. The conidia form single subapical germ tubes, short to long (longitubus pattern), 15–165 µm long, straight to curved-sinuous, with a single septum at the base or somewhat distant from the point of attachment, longer germ tubes sometimes with two septa distant from each other, short germ tubes cylindrical to clavate, with swollen apex or distinctly lobed conidial appressorium [short germ tubes above all more abundant when first treated in a dry chamber (12 hrs), followed by a treatment in a moist chamber (24 hrs)], long germ tubes (longitubus pattern) with undifferentiated or swollen apex, sometimes short forked, hooked or irregular [longitubus pattern dominant when the conidia have only been treated in a moist chamber].

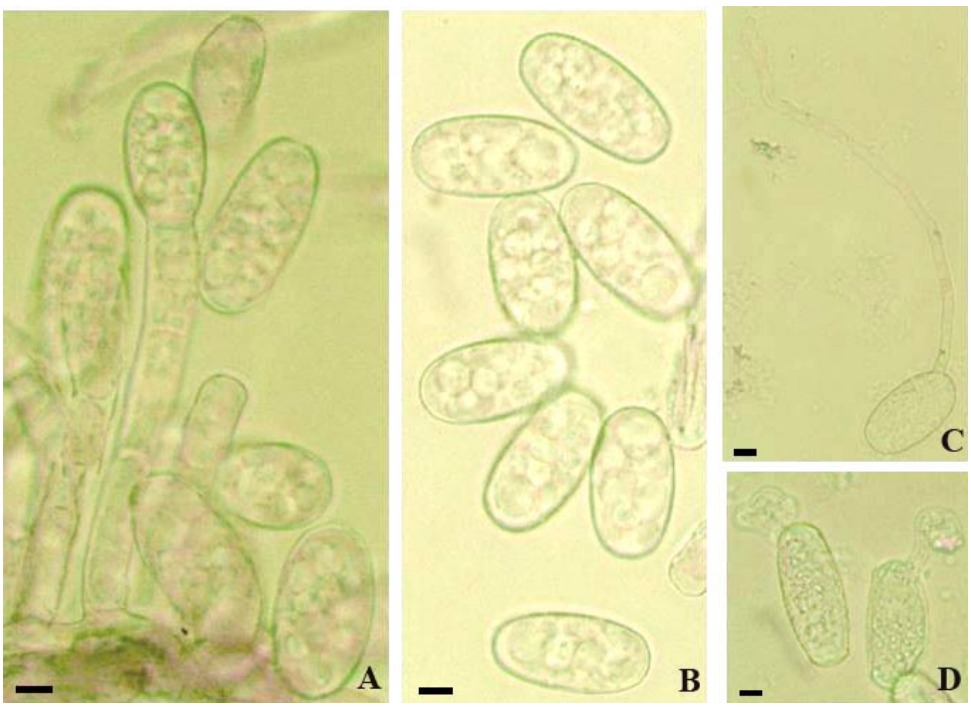


Fig. 9: *Erysiphe astragali*. A: Conidiophores and conidia; B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm.

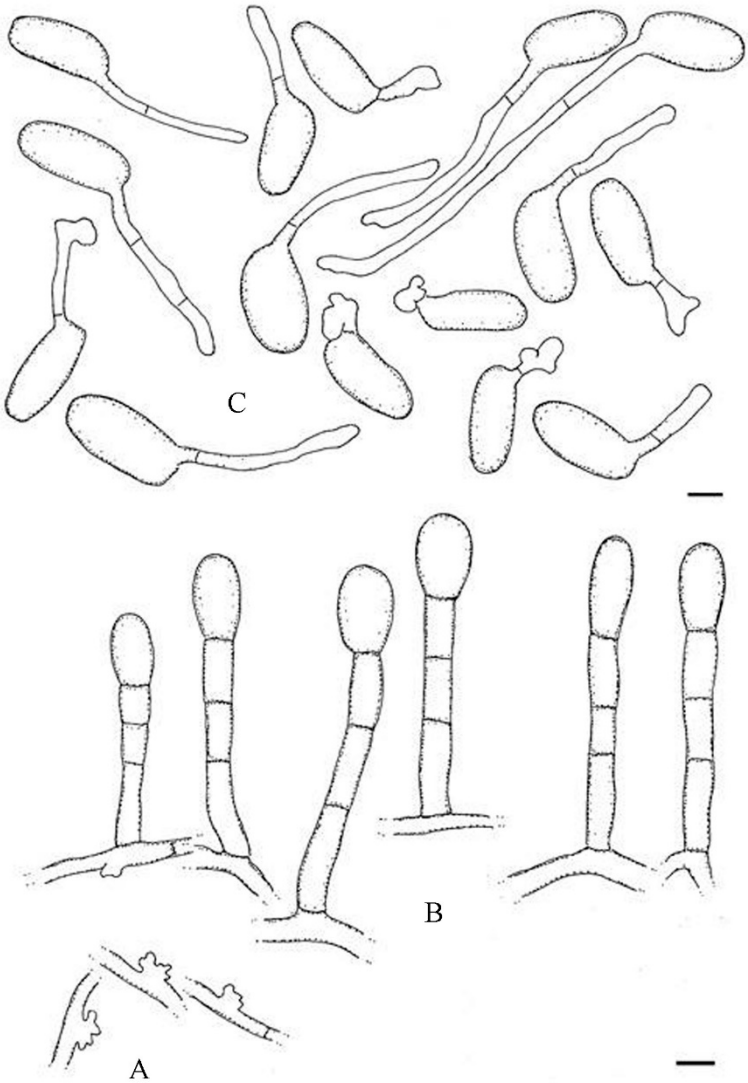


Fig. 10: *Erysiphe astragali*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bar = 10 µm.

Fig. 11: *Erysiphe azaleae*. A: Conidia; B–D: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe azaleae (U. Braun) U. Braun & S. Takam.

Figs. 11, 12

Material examined: Germany, Schleswig-Holstein, Lübeck, St. Gertrud, Stadtpark, on *Rhododendron* sp. cult., 06 Jul. 2006, A. Schmidt, KM 219 (KR-M-0022021).

The conidiophores (foot-cells straight to curved at the base, 18–30 × 8–10 µm, followed by a cell about as long as the foot-cell or two shorter cells), conidia (cylindrical or ellipsoid, 29.5–42 × 14.5–21 µm, length/width ratio 1.5–2.8, on average 2.1, with yellowish oil droplets in fresh conidia), and the conidial germination of the present collection coincide well with the description of the asexual morph published by Bolay (2005: 42) and Braun & Cook (2012: 436), except for wider conidia, which may probably be caused by differences between fresh turgescent conidia and conidia in herbarium material. The germination is characterised by a mixture of short germ tubes, usually with a slightly to multilobed terminal conidial appressorium, sometimes rather irregularly shaped, and long germ tubes (longitubus pattern), to about six times as long as the conidial length (to about 150 µm), apex undifferentiated or somewhat swollen, long germ tubes sometimes rather irregularly shaped, geniculate or with short branches (longitubus pattern not prevailing), germ tubes aseptate or with a single or with two septa, usually distant from the point of attachment (two septa also observed in short germ tubes).

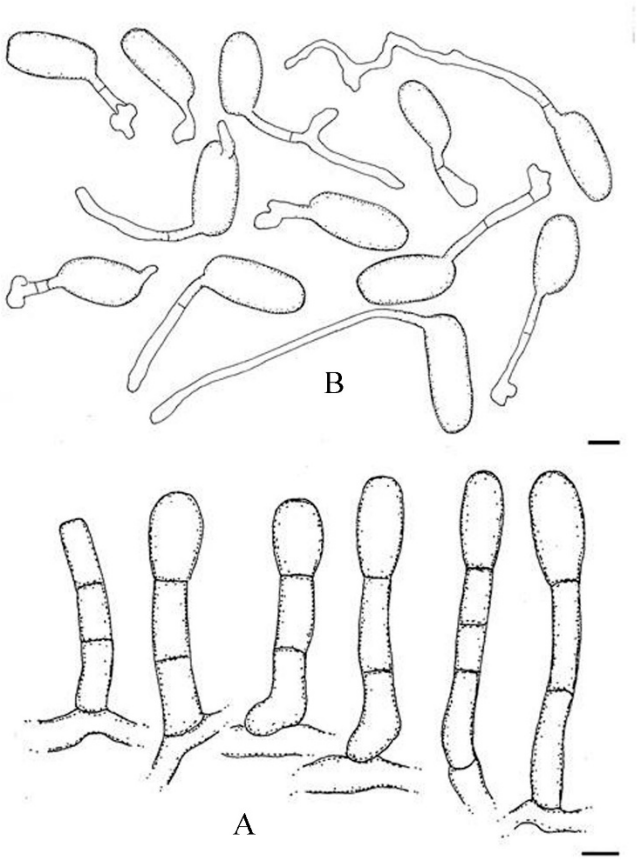


Fig. 12: *Erysiphe azaleae*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe baeumleri (Magnus) U. Braun & S. Takam. Fig. 13

Material examined: Germany, Hamburg, Nienstedten, cemetery, on *Vicia cracca*, 23 Jul. 2000, A. Schmidt, KM 115 (KR-M-0020820); Schleswig-Holstein, Lübeck, Israelsdorf, Schellbruch, Treidelsteig, on *Vicia cracca*, 29 Aug. 2002, A. Schmidt, KM 163 (KR-M-0021953); Schleswig-Holstein, Lübeck, Wallhalbinsel, near Marienbrücke, on *Vicia hirsuta*, 22 Jul. 2001, A. Schmidt, KM 137 (KR-M-0021929a); Schleswig-Holstein, Lübeck, St. Gertrud, Hafenstraße, on *Vicia hirsuta*, 22 June 2002, A. Schmidt, KM 152 (KR-M-0021937).

Vicia cracca and *V. hirsuta* are known to be hosts of *Erysiphe baeumleri* (Braun & Cook 2012). The characteristics of the conidial germination are insufficiently described in the latter work. The illustrated conidia with germ tubes were based on conidia germinated in vivo. In the main, the traits of the conidia and conidiophores in the present collections coincide well with previous descriptions, including Braun & Cook (2012). The material examined is characterised as follows: Hyphal appressoria usually solitary, slightly to multilobed; conidiophores erect, composed of a cylindrical foot-cell, straight to somewhat curved-sinuous, 19–40 × 8–11 µm, followed by 1–2 cells, shorter than the foot-cell, about as long as the foot-cell or even longer; conidia ellipsoid-cylindrical, 24.5–42 × 14.5–21 µm, length/width ratio 1.4–2.5, on overage 1.9, conidia with a single germ tube, subapical, short to long (longitubus pattern), 10–150 µm, short germ tubes cylindrical-clavate, long germ tubes filiform, straight to curved-sinuous, sometimes geniculate, aseptate or with a single septum at the base or usually somewhat distant from the point of attachment, long germ tubes occasionally with two septa distant from each other, apex undifferentiated (alobatus pattern), swollen (club-shaped) to lobed, occasionally apex short bifurcate or hooked (a treatment or pre-treatment of the conidia in a dry chamber increases the germination rate and the percentage of short germ tubes with swollen or lobed conidial appressoria).

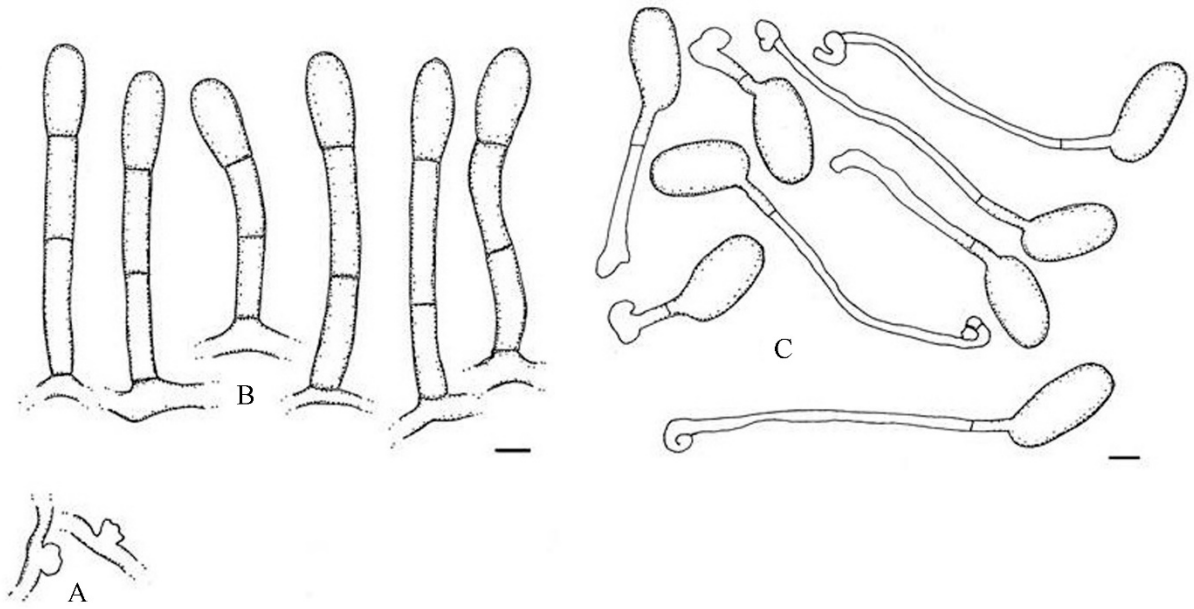


Fig. 13: *Erysiphe baeumleri*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe buhrii U. Braun Figs. 14, 15

Material examined: Germany, Schleswig-Holstein, Lübeck, St. Jürgen, Seydlitzstraße, on *Lychnis coronaria*, 01 Jul. 2007, A. Schmidt, KM 234 (KR-M-0021889).

The conidiophores (foot-cells cylindrical, 40–65 × 8–10.5 µm, followed by 1–2 shorter cells, sometimes second cells rather long) and conidia (cylindrical or ellipsoid, 32.5–47 × 16.5–22 µm, length/width ratio 1.6–2.7, on average 2.1) agree well with previous descriptions, as for example in Paulech (1995: 142) and Braun & Cook (2012: 368). An illustration of the conidial germination is not included in the latter work, only a description, which largely corresponds with the present observations: Germinated conidia with a single subapical germ tube, short and long (longitubus pattern) germ tubes developed, short germ tubes cylindrical to clavate, with a terminal conidial appressorium, swollen to moderately lobed, long germ tubes to about three times as long as the conidia length (to about 110 µm), apex undifferentiated to swollen, all germ tubes with a single septum at the base or somewhat distant from the point of attachment, sometimes aseptate.

Fig. 14: *Erysiphe buhrii*. A: Conidiophore; B: Conidia; C: Conidium with germ tube. Scale bars = 10 µm.

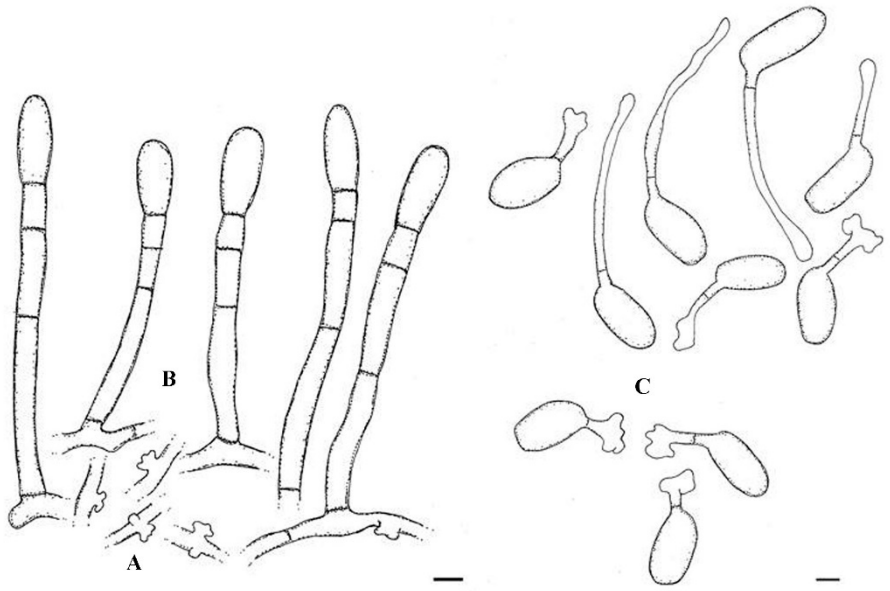


Fig. 15: *Erysiphe buhrii*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe cruchetiana S. Blumer Figs. 16, 17

≡ *Erysiphe pisi* DC. var. *cruchetiana* (S. Blumer) U. Braun

Material examined: Germany, Hamburg, Klein Flottbek, botanical garden, on *Ononis spinosa*, 10 Jul. 2004, A. Schmidt, KM 190 (KR-M-0021962); Brandenburg, Potsdam-West, former Güterbahnhof Wildpark, on *Ononis repens*, 6 Sep. 2007, V. Kummer, KM 249 (KR-M-0021903); ibid., on *Ononis repens*, 15 Jul. 2008, V. Kummer, KM 258 (KR-M-0002827).

A detailed description of the asexual morph of this variety was not provided in Braun & Cook (2012). Based on the examination of the present specimens, it can be characterised as follows: Hyphal appressoria solitary or in opposite pairs, nipple-shaped to lobed (slightly to multilobed); conidiophores

erect, straight, foot-cells cylindrical, straight, 18–43 × 6.5–11 µm, followed by one or two cells, shorter or about as long as the foot-cell or second cell sometimes longer; conidia formed singly, ellipsoid-doliiform, 28–46.5 × 18–24 µm, length/width ratio 1.4–2.5, on average 1.8; short germ tubes and longer ones (longitubus pattern) mixed, development similar when treated in dry and moist chambers or proportion of short germ tubes with lobed conidial appressorium increased by a pre-treatment in a moist chamber, subapical, short germ tubes cylindrical to clavate, apically usually with distinctly lobed conidial appressorium, longer germ tubes only moderately elongated, two to three times as long as the conidial length (about 50–100 µm long), apex unlobed or only slightly so, but usually swollen, germ tubes with a single septum at the base or only slightly or moderately elevated (up one third of the tube length).

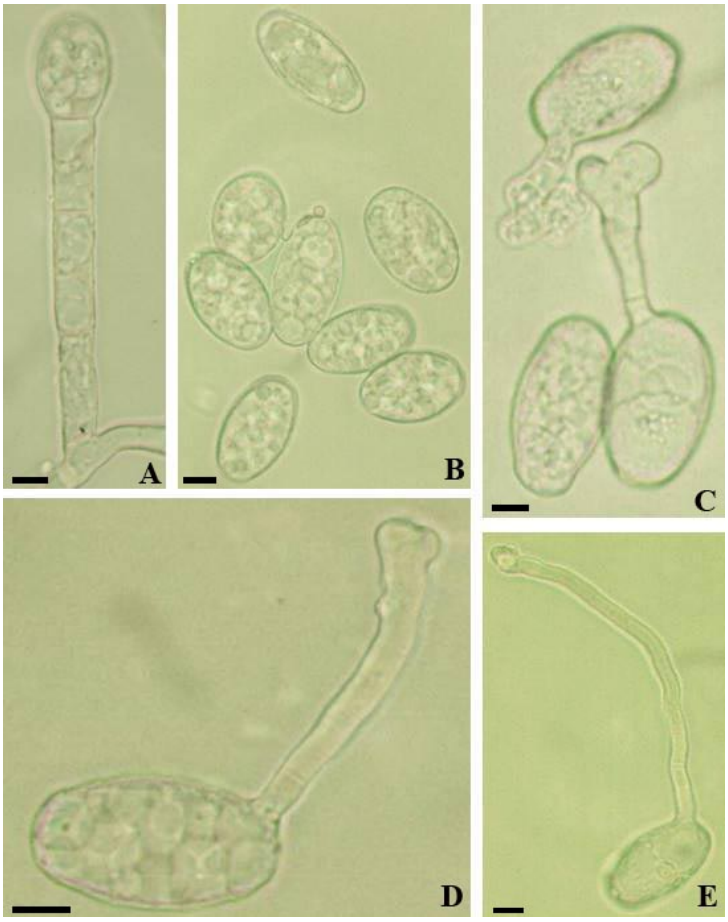


Fig. 16: *Erysiphe cruchetiana.* A: Conidiophore; B: Conidia; C–E: Conidia with germ tubes. Scale bars = 10 µm.

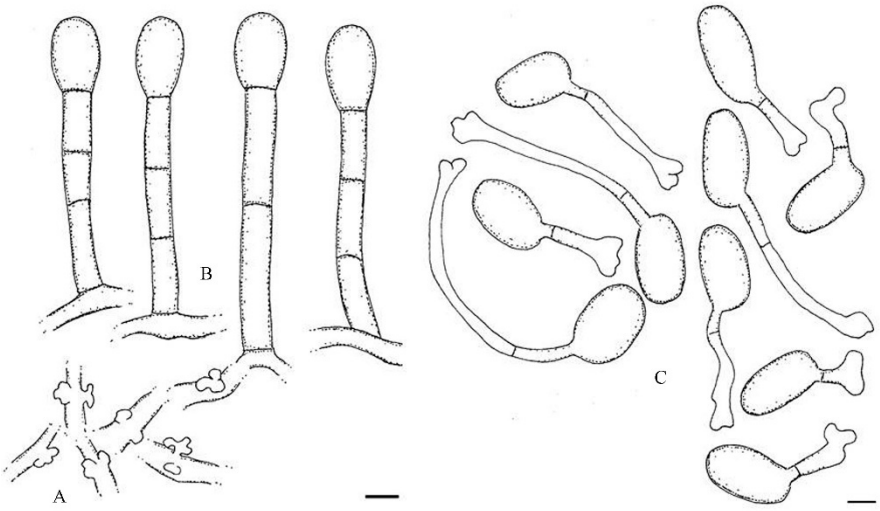


Fig. 17: *Erysiphe cruchetiana.* A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

A comparison of the conidial germination between *E. pisi* (on *Medicago lupulina*) and *E. cruchetiana* shows various significant differences in the mode of the conidial germination, formation of distinctly lobed conidial appressoria in short germ tubes, and in the share of long germ tubes and their length, which is obviously in favour of the involvement of two distinct taxa. There are numerous studies on various aspects of the conidial germination of *Erysiphe* on pea (see notes under *E. pisi*), but detailed descriptions and illustrations of the germ tubes, including septation and formation of conidial appressoria, are not yet available. The germination of *E. pisi* s. lat. on various hosts is rather variable (see Hirata 1955: 33, fig. 7 A–K), suggesting that this species might be a complex of cryptic taxa. In phylogenetic analyses carried out by Takamatsu et al. (2015) and Ellingham et al. (2019), based on rDNA ITS data, sequences retrieved from *E. pisi*, including collections on pea, turned out to form a separate clade distant from *E. trifoliorum*. However, sequence data based on a much larger number of specimens on different host, including *Ononis* spp., and from different regions are necessary for a better insight into the phylogeny and taxonomy of *E. pisi* s. lat. However, the significant differences in the structure of the chasmothecial appendages, supplemented by different patterns of the conidial germination support that the powdery mildew on *Ononis* species should rather be treated as species of its own, as originally proposed.

Erysiphe euonymi DC. Figs. 18, 19

Material examined: Germany, Schleswig-Holstein, Lübeck, Lauerholz; place for storing of trunks, near Travemünder Allee, on *Euonymus europaea*, 20 June 2007, A. Schmidt, KM 232 (KR-M-0021888).

The conidiophores (foot-cells straight, cylindrical or often curved-sinuous at the base or sometimes throughout) and conidia (ellipsoid-cylindrical, 27.5–43 × 15–18 µm, length/width ratio 1.6–2.5, on average 2.1) coincide well with previous descriptions, such as Paulech (1995: 195–196) and Braun & Cook (2012: 460). In the latter work, the conidial germination was not described. It is characterised as follows: Germ tubes solitary, subapical, short germ tubes cylindrical to clavate, with a terminal swelling or usually with a lobed hyphal appressorium, long germ tubes (longitubus pattern) usually up to three times as long as the conidial length (to about 95 µm), apex undifferentiated or swollen (a treatment in a dry chamber followed by a further germination in a moist chamber promotes the development of short germ tubes with lobed appressoria), germ tubes aseptate or with a single septum at the base or somewhat distant from the point of attachment, longer germ tubes occasionally with two septa distant from each other.

Fig. 18: *Erysiphe euonymi*. A: Conidia. B–D: Conidia with germ tubes. Scale bars = 10 µm.

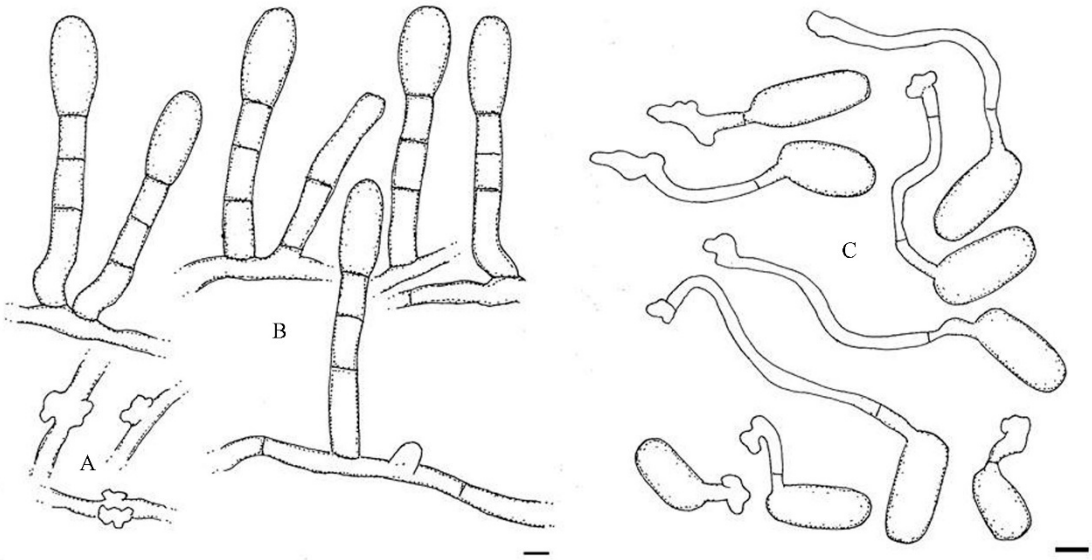


Fig. 19: *Erysiphe euonymi*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe flexuosa (Peck) U. Braun & S. Takam. Figs. 20, 21

Material examined: Germany, Hamburg, Nienstedten, Jürgensallee, on *Aesculus ×carnea*, 26 Sep. 2004, A. Schmidt, KM 191 (KR-M-0021970).

The conidiophores in the present collection (foot-cells 28–58 × 6–10 µm, curved at the base, followed by 1–3 shorter cells), are in accordance with previous descriptions and observations (Bolay 2005: 54, Braun & Cook 2012: 558), including foot-cells that are frequently curved-sinuous at the very base. The conidiophores on the lower leaf surface were usually somewhat longer than epiphyllously formed conidiophores, and fresh conidia were filled with numerous yellowish oil droplets. The conidia in the present specimen were wider, probably due to measurements based on fresh, turgescent conidia. The conidial germination was described by Braun & Cook (l.c.) in detail, but not illustrated. The conidia and the conidial germination of the material collected on *Aesculus ×carnea* were characterised as follows: Conidia cylindrical, 31–42 × 14–19 µm, length/width ration 1.8–2.5, on average 2.2, germinating conidia with 1–4 subapical (above) or perihilar (below) germ tubes, consistently short and aseptate, cylindrical, clavate, apex undifferentiated, swollen or slightly lobed to multilobed (longitubus pattern not observed). Thus, the conidial germination agrees well with the description in Braun & Cook (2012), except for the lacking formation of very long germ tubes (longitubus pattern). The germinated conidium shown in Braun & Cook (2012: 18, fig. 9 L) agrees with the described pattern based on the present examination.

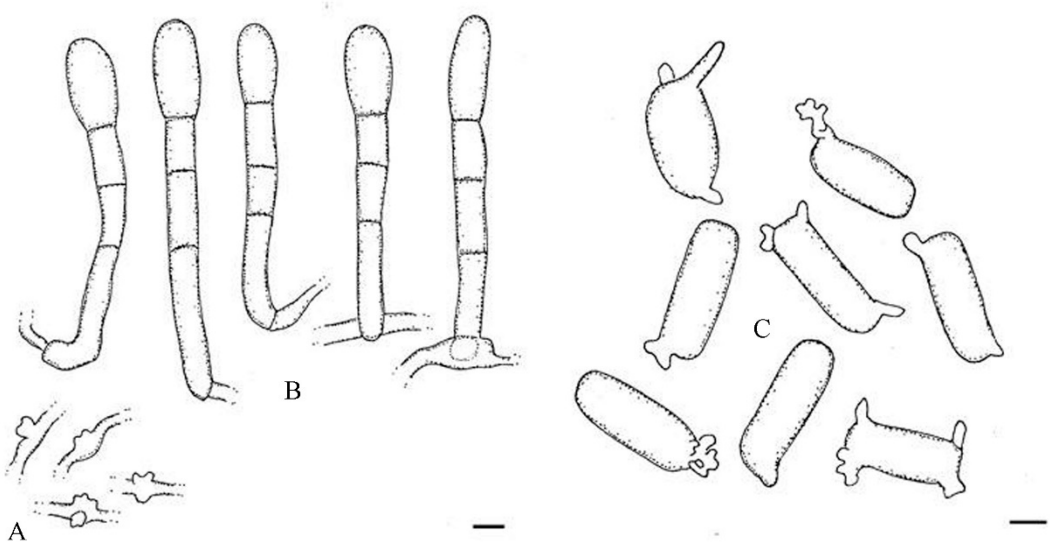


Fig. 20: *Erysiphe flexuosa*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

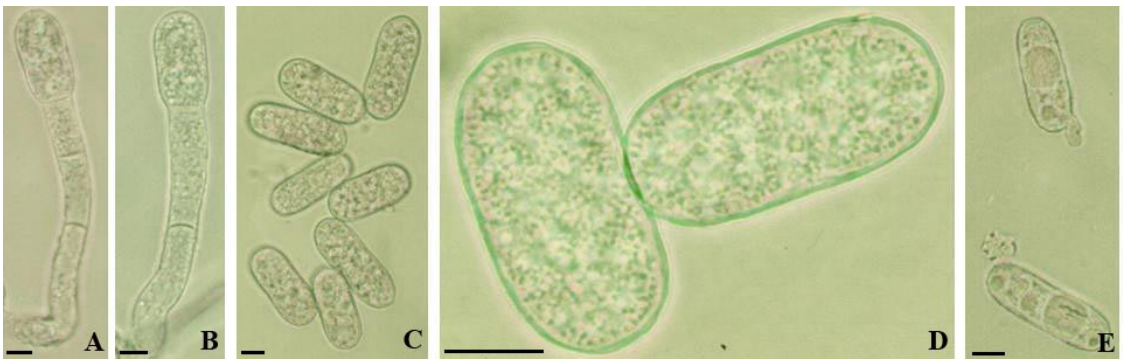


Fig. 21: *Erysiphe flexuosa*. A, B: Conidiophores; C, D: Conidia; E: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe howeana U. Braun Figs. 22, 23

Material examined: Germany, Schleswig-Holstein, Lübeck, St. Gertrud, Israelsdorf, Buchenweg, on *Oenothera glazioviana*, 23 June 2007, A. Schmidt, KM 233 (KR-M-0021887).

The conidiophores (foot-cells straight, cylindrical, 13–30 × 8.5–11 µm, followed by 1–3 cells, shorter than the foot-cell, about as long or occasionally longer) and conidia (25–37 × 18–22.5 µm, length/width ratio 1.3–1.9, on average 1.5) in the present material agree well with previous descriptions, as, for example, in Bolay (2005: 58) and Braun & Cook (2012: 387). Single subapical germ tubes are formed. They are short to long (up to about 80 µm, = longitubus pattern), cylindrical, clavate, oblong cylindrical-filiform, straight to curved-sinuous, a single septum at the base or somewhat distant from the point of attachment, long germ tubes sometimes with two septa distant from each other, apex in shorter germ tubes mostly swollen or with moderately lobed conidial appressorium, apex of long germ tubes undifferentiated or swollen. The germ tubes illustrated in Braun & Cook (2012: 387, fig. 438) were based on observations of a few conidia germinated in vivo. The germ tubes illustrated in Cook & Braun (2009: 620, fig. 3 A) refer to short germ tubes formed by *E. howeana*. Braun & Cook (2012) described the formation of up to 10% longitubus pattern in *E. howeana*. In the present germination experiments, long germ tubes (longitubus pattern) were much more abundant in moist chamber experiments as well as under dry conditions and even prevailing.

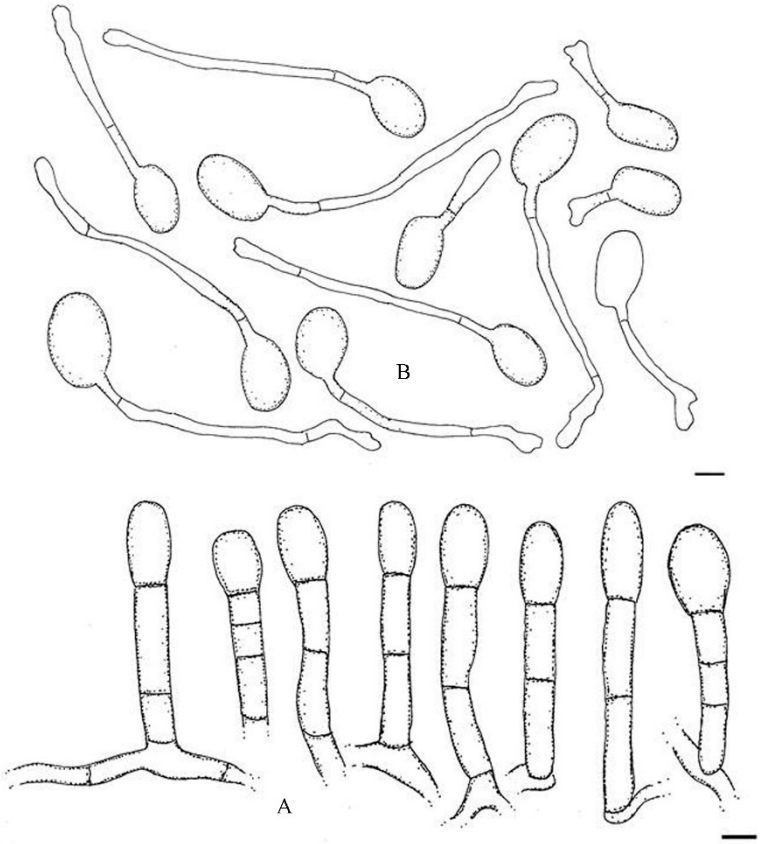


Fig. 22: *Erysiphe howeana*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Fig. 23: *Erysiphe howeana*. A: Conidiophore; B–D: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe intermedia (U. Braun) U. Braun Fig. 24

Material examined: Germany, Schleswig-Holstein, Ostholstein, between Sereetz and highway A1, near the car park, on *Lupinus polyphyllus*, 09 Jul. 2000, A. Schmidt, KM 112 (KR-M-0020803); Lübeck, Wallhalbinsel, on *Lupinus polyphyllus*, 04 Aug. 2001, A. Schmidt, KM 143 (KR-M-0021912); Mecklenburg-Vorpommern, Landkreis Nordwestmecklenburg, Grevesmühlen, east bank of the Vielbecker lake, on *Lupinus polyphyllus*, 16 Aug. 2001, A. Schmidt, KM 145 (KR-M-0021913).

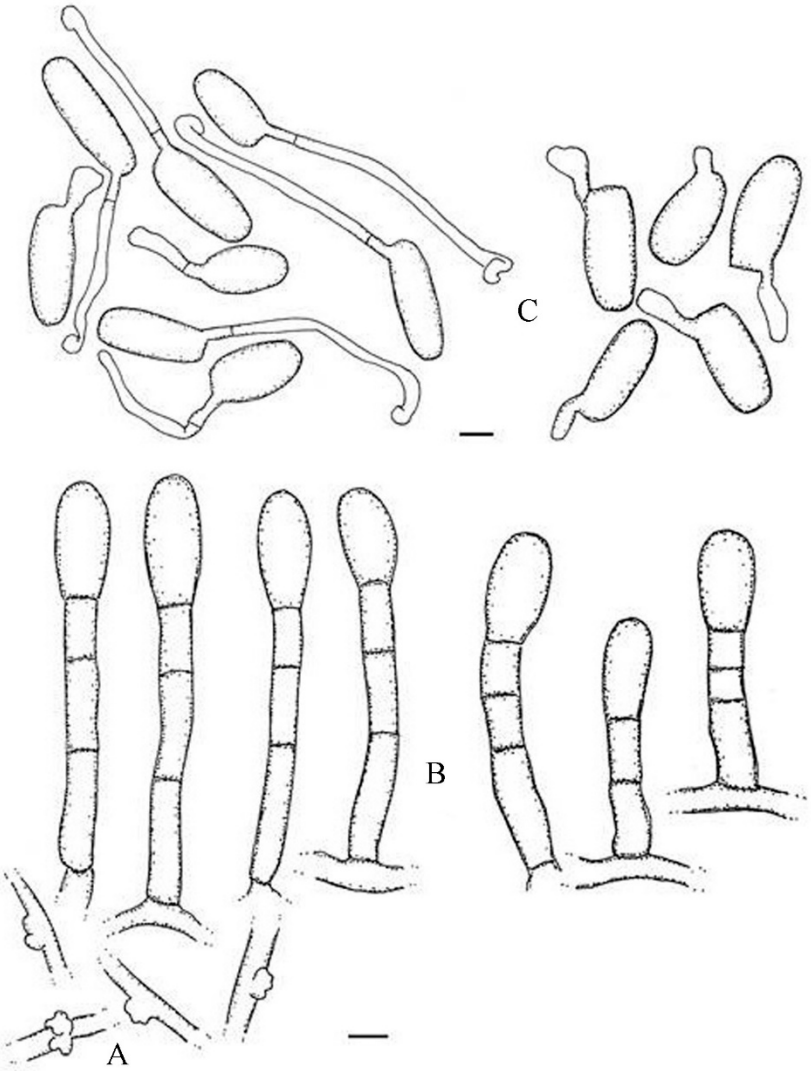


Fig. 24: *Erysiphe intermedia*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

The examined collections are characterised as follows: Conidiophores composed of a cylindrical foot-cell, straight to somewhat curved-sinuous, 17–43 × 8–11 µm, followed by 1–2 cells, shorter than the foot-cell or about as long as the foot-cell; conidia ellipsoid-cylindrical, 28–46.5 × 17.5–22.5 µm, length/width ratio 1.4–2.3, on average 1.9; germinated conidia with a single or rarely two subapical germ tubes, short to long (longitubus pattern), 10–140 µm long, short germ tubes cylindrical to clavate, long germ tubes filiform, straight to curved-sinuous, aseptate or with a single septum at the base or somewhat distant from the point of attachment, long germ tubes sometimes with two septa distant from each other, apex mostly undifferentiated or swollen (club-shaped), occasionally lobed or hooked. The description of the asexual morph of *E. intermedia* (conidiophores and conidia) in Braun & Cook (2012) agrees well with the results obtained during the course of the present examinations, except for the characteristics of the conidial germination, which is insufficiently described in the latter work.

Erysiphe lythri L. Junell Figs. 25, 26

Material examined: Germany, Schleswig-Holstein, Herzogtum Lauenburg, Groß Grönau, nursery, on *Lythrum salicaria*, 27 Aug. 2018, A. Schmidt, KM 347 (KR-M-0006468).

The conidiophores (foot-cells straight, cylindrical, 25–45 × 8–10 µm, followed by 1–2 shorter cells, second or third cell sometimes about as long as the foot-cell or even longer) and conidia (ellipsoid-subcylindrical, 30–47 × 14–23 µm, length/width ratio 1.4–2.8, on average 2.1) are in correspondence with previous descriptions, including Braun & Cook (2012: 393). A description of the conidial germination is lacking in the latter work. It is characterised as follow: Conidia with a single germ tube, subapical, short and long germ tubes mixed, short germ tubes cylindrical, aseptate (common) or with a single septum at the base or only somewhat elevated, apex mostly with a multilobed conidial appressorium, long germ tubes (longitubus pattern) only moderately elongated, about two to three times as long as the conidial length (ca. 50–85 µm), aseptate, with a single septum somewhat distant from the point of attachment, occasionally with two septa distant from each other, apex undifferentiated or swollen, at most slightly lobed.

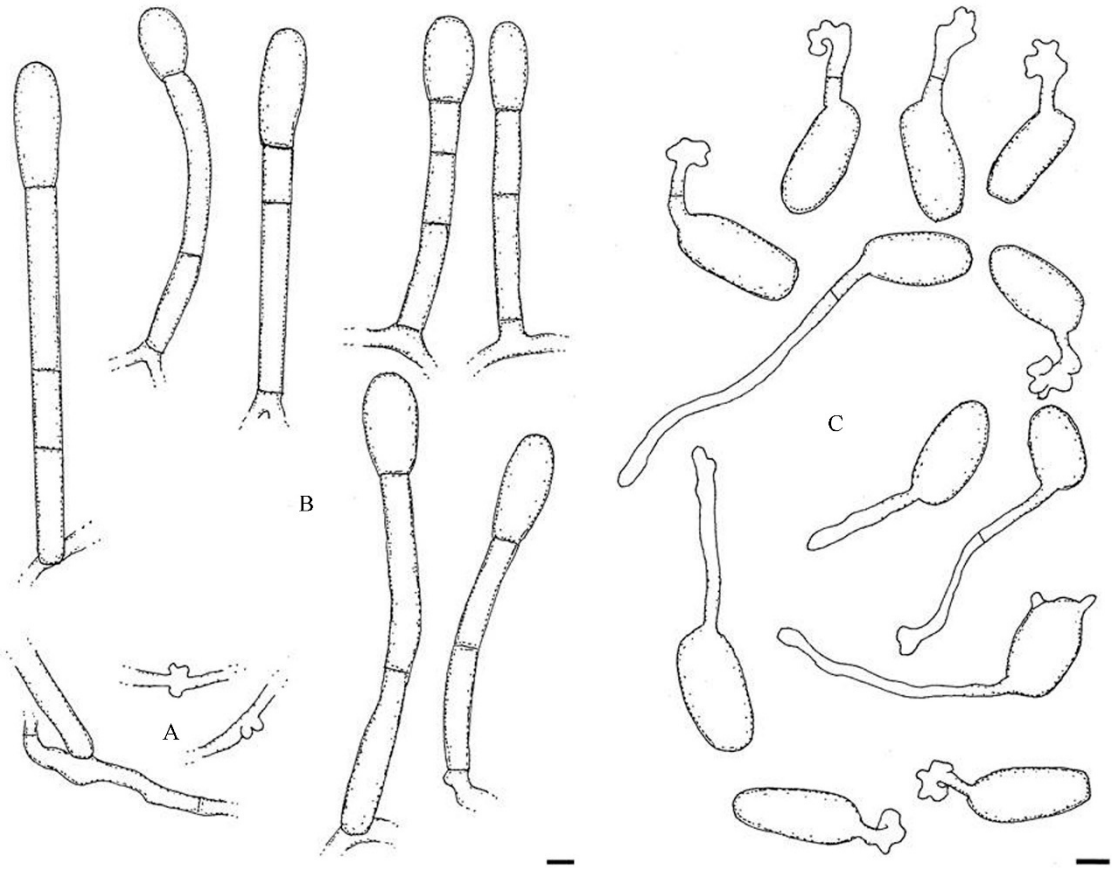


Fig. 25: *Erysiphe lythri*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

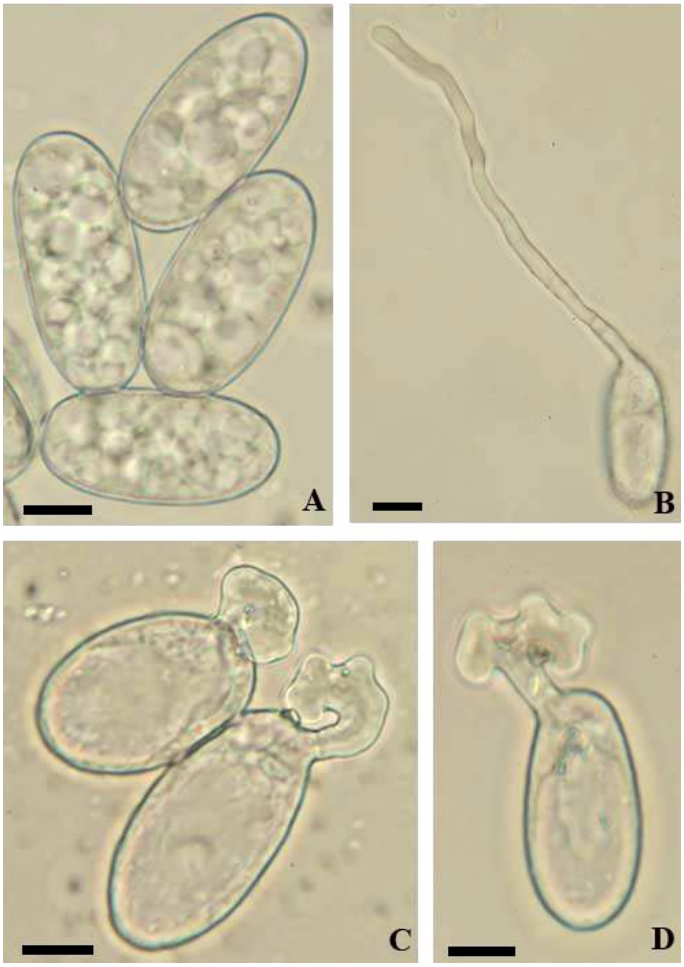


Fig. 26: *Erysiphe lythri*. A: Conidia; B–D: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe palczewskii (Jacz.) U. Braun & S. Takam. Fig. 27

Material examined: Germany, Schleswig-Holstein, Herzogtum Lauenburg, Mölln, Gartenweg, on *Caragana arborescens*, 17 June 2000, A. Schmidt, KM 108 (KR-M-0020849); Schleswig-Holstein, Ostholstein, between Sereetz and highway A1, on *Caragana arborescens*, 9 Jul. 2000, A. Schmidt, KM 111 (KR-M-0020835); Schleswig-Holstein, Lübeck, Stadtpark, on *Caragana arborescens*, 21 June 2001, A. Schmidt, KM 130 A (KR-M-0021983).

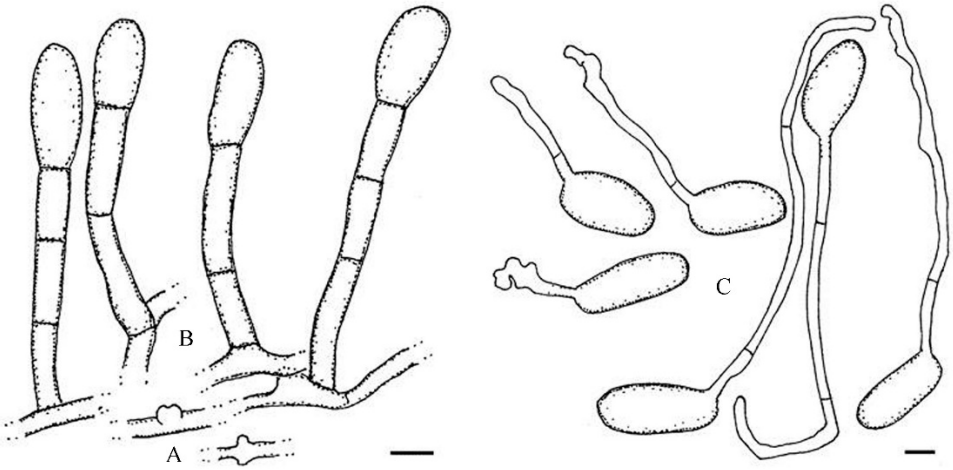


Fig. 27: *Erysiphe palczewskii*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

The present collections are characterised as follows: Hyphal appressoria lobed; conidiophores composed of a cylindrical foot-cell, straight or short curved-sinuous at the base, 20–35 × 6–8.5 µm, followed by 1–2 cells, shorter than the foot-cell, about as long or even longer, conidia ellipsoid-cylindrical, 25–42.5 × 15–20 µm, length/width ratio 1.4–2.6, on average 2.0, usually with a single subapical germ tube, with

short and long germ tubes, long germ tubes (longitubus pattern) prevalent, pre-treatments in a dry chamber increase the proportion of short germ tubes with lobed appressoria, germ tubes 9–215 µm long, aseptate, with a single septum at the base or distant from the point of attachment, long germ tubes sometimes with two septa distant from each other, short germ tubes cylindrical-clavate, apex swollen or lobed, long germ tubes filiform, straight to curved-sinuous, apex undifferentiated, swollen, sometimes lobed or hooked.

Erysiphe pisi DC. s. lat. (on *Lotus corniculatus* spp.)

Material examined: Germany, Niedersachsen, Landkreis Winsen (Luhe), near Neu Wulmstorf, former military trainings area of former "Röttiger" barracks, now Wulmstorfer Heide-Bornberg, on *Lotus corniculatus*, 25 Aug. 2007, A. Schmidt, KM 247 (KR-M-0021899).

The asexual morph on *Lotus corniculatus* is characterised as follows: Hyphal appressoria slightly to multilobed; conidiophores erect, composed of a cylindrical foot-cell, straight to somewhat curved or sinuous, 15–35 × 8–10 µm, followed by 1–2 cells, shorter than the foot-cell, about as long or followed by a single longer cell; conidia ellipsoid-cylindrical, 28–41.5 × 14–18 µm, length/width ratio 1.8–2.5, on average 2.1, usually with a single subapical germ tube, short to moderately long (longitubus pattern), 10–80 µm, short germ tubes subcylindrical to clavate, apex swollen to slightly lobed, longer germ tubes filiform, straight to curved-sinuous, apex undifferentiated, swollen, slightly lobed or hooked, germ tubes aseptate or with a single septum, usually distant from the point of attachment, up to the middle, occasionally even up to the upper half.

Note: The asexual morph on *Lotus corniculatus* (chasmothecia not formed) agrees well with *E. pisi* on *Medicago* spp. *Lotus* spp. are hosts of *E. pisi* as well as *E. trifoliorum* (Braun & Cook 2012). The length/width ratio of the conidia of *E. pisi* on *Lotus* and *Medicago* is higher, compared to collections of *E. trifoliorum* on *Trifolium* spp., and there are differences in the conidial germination (longitubus germ tubes shorter on *Lotus corniculatus*, only with a single septum, which is often elevated up to the middle or even upper half, vs. longitubus germ tubes on *Trifolium* spp. much longer, single septa closer to the base, often with two septa).

Fig. 28: *Erysiphe pisi* (on *Medicago*). A: Conidia; B–E: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe pisi DC. s. lat. (on *Medicago* spp.) Figs. 28, 29

Material examined: Germany, Schleswig-Holstein, Lübeck, Karlshof, Glashüttenweg, on *Medicago* cf. ×*varia*, 29 Jul. 2000, A. Schmidt, KM 118 (KR-M-0020813); Schleswig-Holstein, Lübeck, Wallhalbinsel, Marienbrücke, on *Medicago lupulina*, 4 Aug. 2001, A. Schmidt, KM 142 (KR-M-0021924); Schleswig-Holstein, Lübeck, Marienkirche, on *Medicago lupulina*, 23 Aug. 2001, A. Schmidt, KM 147 (KR-M-0021915); Schleswig-Holstein, Lübeck, Herreninsel, on *Medicago* cf. ×*varia*, 3 Oct. 2004, A. Schmidt, KM 196 (KR-M-0021958).

The conidiophores (foot-cells straight, cylindrical, at most slightly sinuous throughout, 15–50 × 7.5–10(–12) µm, followed by 1–2 cells, shorter than the foot-cell, about as long or somewhat longer) and conidia (ellipsoid-cylindrical, 28–44 × 14.5–23 µm, length/width ratio 1.4–2.5, on average 2.1) agree well with those described by previous authors, such as Paulech (1995: 127–128) and Braun & Cook (2012: 401). Obvious differences between conidiophores on the upper (shorter) and lower leaf surface (longer) have been observed. The conidial germination of *E. pisi* is rather diverse, depending on the particular hosts and conditions (Hirata 1955: 33, fig. 7 A–K; Braun & Cook 2012). Furthermore, it is possible that *E. pisi* constitutes a phylogenetically and taxonomically heterogeneous complex. Most

previous studies focused on *E. pisi* on pea (e.g., Aires 1983; Singh et al. 2000, 2001). Shin (2000: 54–57, including fig. 14 on page 56) described the asexual morph in detail and published detailed illustration. However, the source (host) of the illustration was not stated. The conidial germination on *Medicago* spp. is characterised as follows: Germ tubes solitary, rarely two, subapical, short, cylindrical to clavate, apex swollen, distinctly lobed appressoria usually not developed, short germ tubes more abundant when the conidia have been first treated under dry conditions and then in a moist chamber, long germ tubes (longitubus pattern) prevailing, above all under moist chamber conditions, 15–165 µm long, apex undifferentiated, swollen, somewhat irregular, slightly lobed or hooked, germ tubes aseptate or with a single septum, longer germ tubes sometimes with two, usually distant from the point of attachment, single septa often elevated up to the middle, even in short tubes.

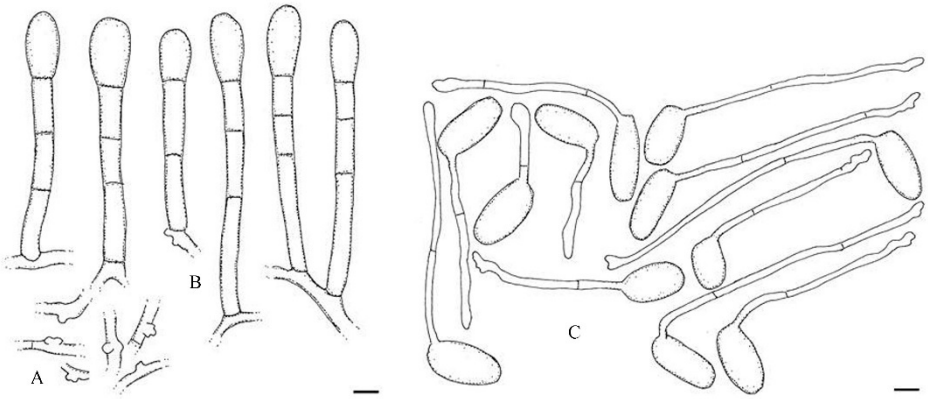


Fig. 29: *Erysiphe pisi* (on *Medicago*). A: Conidia; B–E: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe pseudoacaciae (P.D. Marchenko) U. Braun & S. Takam. Figs. 30, 31

Material examined: Germany, Hamburg, Nienstedten, Newmans Park, on *Robinia pseudoacacia*, 23 Jul. 2000, A. Schmidt, KM 116 (KR-M-0020822); Hamburg-Borgfelde, between Landwehr and Landwehr Platz, on *Robinia pseudoacacia*, 20 Jul. 2000, H. W. Hedinger, KM 117, with chasmothecia (KR-M-0020841, KR-M-0020842); Schleswig-Holstein, Kreis Pinneberg, Haseldorf, on *Robinia pseudoacacia*, 13 Jul. 2001, A. Schmidt, KM 134 (KR-M-0021928); Schleswig-Holstein, Ostholstein, Scharbeutz, Seestraße/Hamburger Ring, on *Robinia pseudoacacia*, 20 Jul. 2001, A. Schmidt, KM 136 (KR-M-0021927); Schleswig-Holstein, Lübeck, Marienkirchhof, on *Robinia pseudoacacia*, 21 Aug. 2001, A. Schmidt, KM 146 (KR-M-0021914); Schleswig-Holstein, Lübeck, St. Gertrud, Israelsdorf, on *Robinia pseudoacacia*, 20 Sep. 2002, A. Schmidt KM 165, with chasmothecia (KR-M-0021951). Note: The collections without chasmothecia are only tentatively referred to as *E. pseudoacaciae* since the differentiation of the asexual morphs of *E. pseudoacaciae* and *E. palczewskii*, which may also occur on *Robinia* spp., being difficult.

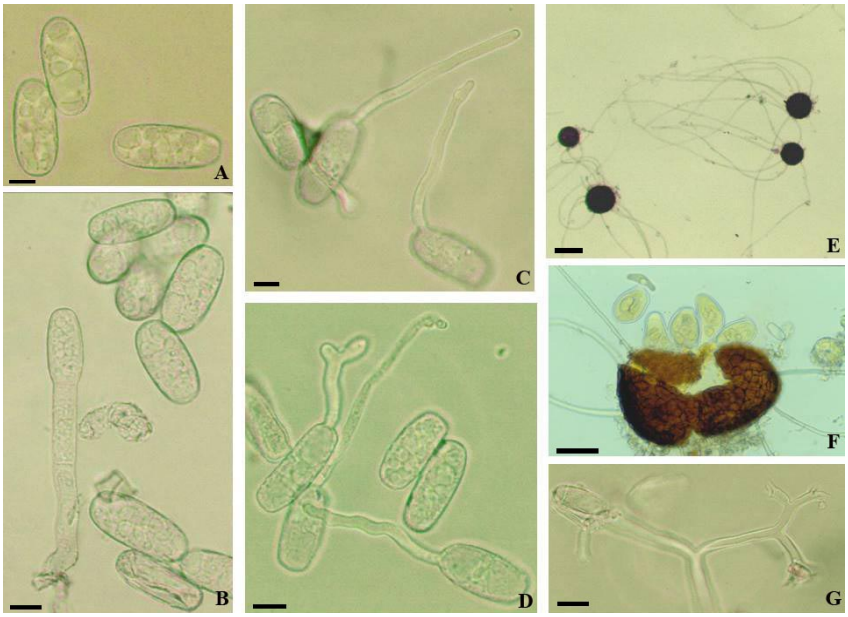


Fig. 30: *Erysiphe pseudoacaciae*. A: Conidia; B: Conidiophore and conidia; C, D: Conidia with germ tubes; E, F: Chasmothecia; G: Branched apex of an appendage. Scale bars (A–D, G) = 10 µm, E = 100 µm, F = 25 µm.

The identification of two collections could be proven on the basis of developed mature chasmothecia with well-developed appendages, asci and ascospores [chasmothecia 88–117 µm diam.; with 5–11 very long appendages, up to nine times as long as the chasmothecial diam., with an obvious tendency to point towards one direction, aseptate and completely colourless, apex simple or up to four times loosely dichotomously branched; with 3–6 asci, 4–5-spored; ascospores 20–26.5 × 13.5–17 µm]. *Erysiphe robiniae* Grev., the second, common powdery mildew on *Robinia pseudoacacia*, differs in having chasmothecia, 70–130 µm diam., with 6–25 very long appendages, but horizontally spread, 1–6-septate, hyaline or pale brown, up to the upper half [up to the uppermost septum] (Braun & Cook 2012: 500). The asexual morph of *E. pseudoacaciae* is still unknown, i.e., it has not yet been described and illustrated [the description given in Foitzik (1990: 12) under the name *Microsphaera pseudoacaciae* is doubtful and does undoubtedly not belong to *E. pseudoacaciae* (conidia usually 27–30 × 10–12.5 µm, germ tubes uniformly short)]. Based on the present collections, it is characterised as follows: Hyphal appressoria solitary or in opposite pairs, almost nipple-shaped to moderately lobed; conidiophores erect, composed of a cylindrical foot-cell, distinctly curved-sinuous at the base, 22.5–35 × 6.5–9 µm, consistently followed by two shorter cells, 10–19 µm long; conidia solitary, ellipsoid, occasionally subcylindrical, 24–43 × 12–20.5 µm, length/width ratio 1.4–2.9, on average 2.1, with a single subapical germ tube, short and cylindrical-clavate, with swollen to lobed apex, to usually rather long (longitubus pattern), 14–128 µm long, cylindrical-filiform, straight to curved-sinuous, usually with a single septum at the base or somewhat distant from the point of attachment, long germ tubes sometimes with two distant septa, apex usually undifferentiated (without distinct appressorium), sometimes swollen (in short germ tubes), occasionally hooked or forked. The asexual morphs of *E. pseudoacaciae* and *E. robiniae* are readily distinguishable from each other. The foot-cells of the conidiophores in the latter species are straight or only occasionally slightly flexuous throughout (Braun & Cook 2012: 495). The conidial germination of *E. robiniae* is not yet known. The sexual morph of *Erysiphe palczewskii* (Jacz.) U. Braun & S. Takam., which also occurs on *Robinia* spp., is quite different from chasmothecia of *E. pseudoacaciae* (Braun & Cook 2012: 490–491), but the asexual morphs of the two species, including the conidial germination patterns, are very similar and confusable (see also Shin 2000: 134–135, under "*Microsphaera robiniae*"). Hence, identifications of isolated asexual morphs on *Robinia* (without chasmothecia), just based on morphology, remain difficult or they are even impossible. Sequence data would be helpful, but they are not yet available for all species involved.

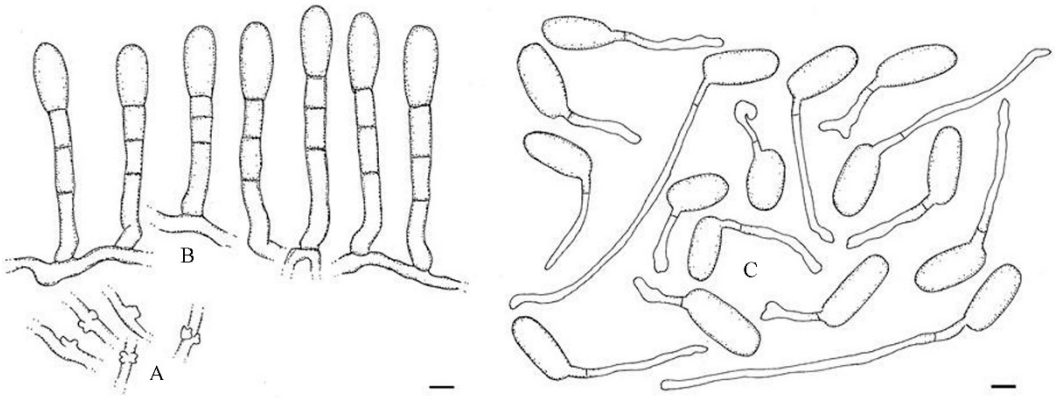


Fig. 31: *Erysiphe pseudoacaciae*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe pseudoregularis U. Braun (in Braun & Cook 2012: 581) Figs. 32, 33

Material examined: Germany, Mecklenburg-Vorpommern, Nord Vorpommern, Darß, between Prerow and Darßer Ort, on *Salix caprea*, 11 Aug. 2000, A. Schmidt, KM 123 (KR-M-0020829).

The very long conidiophores (a long foot-cell, 35–60 × 7.5–10 µm, usually followed by a second cell about as long as the foot-cell or longer, to 90 µm) and the conidia (ellipsoid, 30.5–44 × 17.5–24 µm, length/width ratio 1.4–2.1, on average 1.7, with small oil drop when fresh) agree well with the original description published in Braun & Cook (2012). Fresh conidia contained yellowish oil droplets. The conidial germination was not described in detail in the latter work and only a single conidium with a germ tube formed in vivo was depicted. The conidial germination is very peculiar and characterised as follows: Germ tubes solitary, subapical, short and cylindrical, with a terminal lobed conidial appressorium or usually long (longitubus pattern), up to four times as long as the conidial length (to about 120 µm), longitubus pattern prevailing under dry chamber as well as moist chamber conditions,

apex undifferentiated or somewhat swollen, germ tubes consistently aseptate. The conidial germination of this species is characterised by the predominance of longitubus pattern and germ tubes consistently aseptate. The asexual morph of *E. pseudoregularis* is quite distinct from conidiophores and conidia of *Erysiphe adunca* (Wallr.) Fr. and *E. capreae* DC. ex Duby, the second common *Erysiphe* species on *Salix caprea*, by its very long conidiophores with long foot-cells followed by a second cell about as long as the foot-cell or even longer (vs. much shorter conidiophores with short foot-cells followed by shorter following cells). The conidia are much larger in comparison to *E. capreae*, and the conidial germination is also distinguished from the other two *Erysiphe* species, in which the conidial germ tubes remain short with lobed terminal conidial appressoria (see Hirata 1942: 43, fig. 5 D; Braun & Cook 2012: 535).

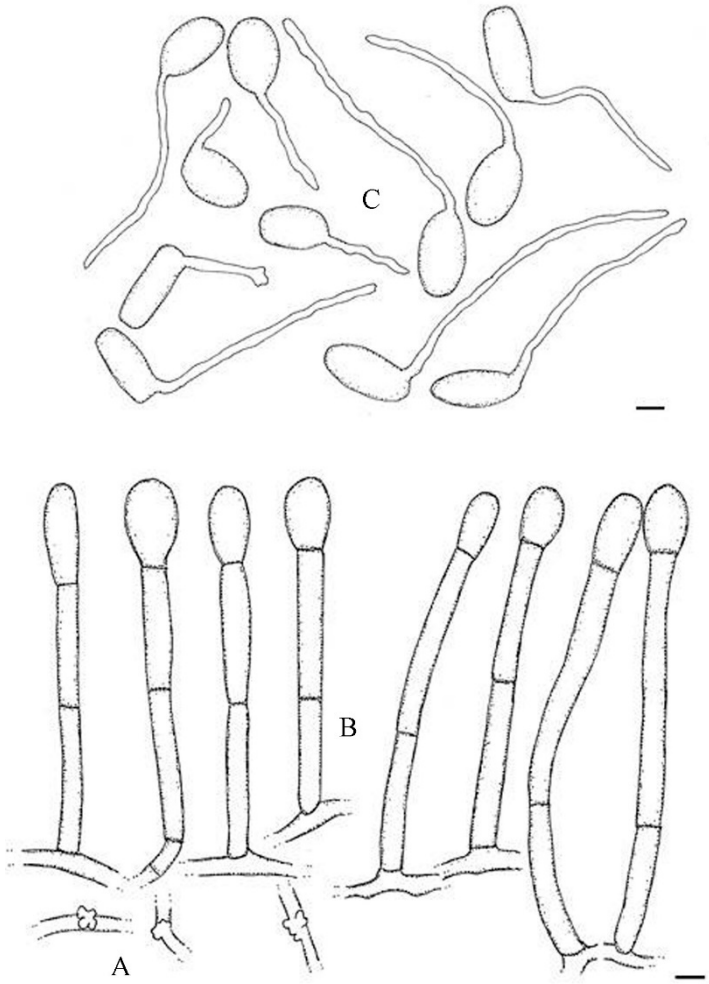


Fig. 32: *Erysiphe pseudoregularis*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm

Fig. 33: *Erysiphe pseudoregularis*. A, B: Conidia with germ tubes. Scale bars = 10 µm

Erysiphe sedi U. Braun Figs. 34, 35

= *Oidium kalanchoes* Lüstner ex U. Braun.

≡ *Pseudoidium kalanchoes* (Lüstner ex U. Braun) U. Braun & R.T.A. Cook.

Material examined: Germany, Schleswig-Holstein, Lübeck, Holunderweg, on *Kalanchoe* sp. cult., 17 June 2004, A. Schmidt, KM 186 (KR-M-0021911).

The taxonomy and phylogeny of *Oidium kalanchoes* and its synonymy with *Erysiphe sedi* have recently been clarified by Götz et al. (2019). The conidiophores (foot-cells cylindrical, 25–35 × 7.5–11 µm, followed by 1–2 cells, shorter than the foot-cell or about as long) in the present collection agree well with previous descriptions (Bolay 2005: 105, Shin 2000: 65–67, Braun & Cook 2012, Götz et al. 2019). Fresh conidia are cylindrical, ellipsoid, 32–58 × 14–20.5 µm, length/width ratio 1.8–4.1, on average 2.6. The germination (Pseudoidium type) is characterised as follows: Conidia usually with a single subapical germ tube, occasionally with two or rarely three germ tubes arising from one end or opposite, from the base and apex, short, 15–40 µm, straight to curved, sinuous or occasionally even geniculate, aseptate or with a single septum at the base or somewhat distant from the point of insertion, rarely with two septa, apex with a slightly to multilobed conidial appressorium or undifferentiated (alobatus pattern). The conidial germination of the present material on *Kalanchoe* agrees well with the description and illustration of germinated conidia of *E. sedi* on *Sedum* spp. in Korea (Shin 2000).

Fig. 34: *Erysiphe sedi*. A: Conidiophores, conidium; B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm

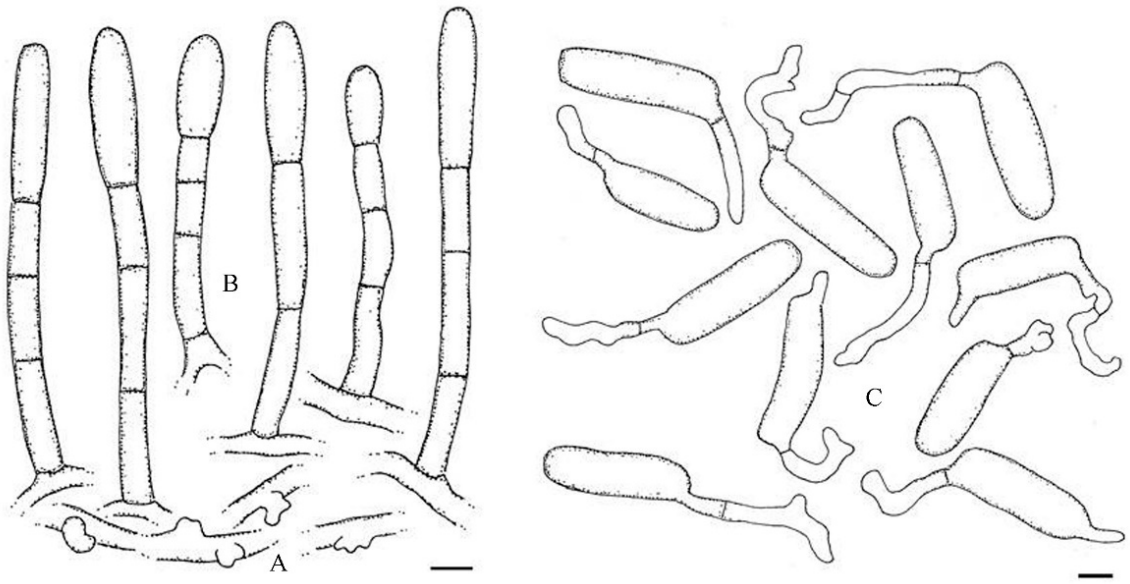


Fig. 35: *Erysiphe sedi*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

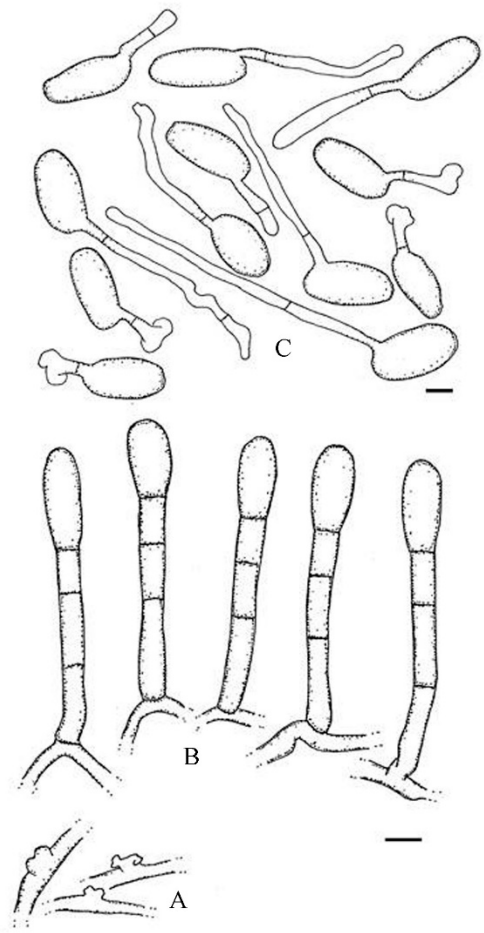


Fig. 36: *Erysiphe trifoliorum*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe trifoliorum (Wallr.) U. Braun (s. str. on *Trifolium* spp.) Fig. 36

Material examined: Germany, Mecklenburg-Vorpommern, Landkreis Nordwestmecklenburg, northwest of Dassow, OT Harkensee, on *Trifolium campestre*, 1 Jul. 2000, A. Schmidt, KM 110 (KR-M-0020848); Mecklenburg-Vorpommern, Landkreis Nordwestmecklenburg, near Utecht, northeast bank of Ratzeburger lake, on *Trifolium campestre*, 6 Jul. 2001, A. Schmidt, KM 132 (KR-M-0021930); Schleswig-Holstein, Lübeck, Travemünde, Priwall, on *Trifolium campestre*, 13 Jul. 2002, A. Schmidt, KM 160 (KR-M-0021940); Mecklenburg-Vorpommern, Landkreis Nordvor-pommern, Darß, near Darßer Ort, on *Trifolium dubium*, 11 Aug. 2000, A. Schmidt, KM 126 (KR-M-0020818); Schleswig-Holstein, Lübeck, Israelsdorf, Holunderweg, on *Trifolium dubium*, A. Schmidt, KR 131 A (KR-M-0021985); Hamburg, Klein-Flottbek, botanical garden, on *Trifolium hybridum*, 10 June 2000, A. Schmidt, KM 106, (KR-M-0020817); Mecklenburg-Vorpommern, Landkreis Nordvor-pommern, east of Wustrow, on *Trifolium pratense*, 12 Aug. 2000, A. Schmidt, KM 125 (KR-M-0020845); Hamburg, Blankenese, near marina port, on *Trifolium pratense*, 13 Jul. 2001, A. Schmidt, KM 135 (KR-M-0021926).

Braun & Cook (2012: 515) described the asexual morph of *E. trifoliorum* in detail, including the characteristics of the conidial germination. The results of the examinations of the present collections from northern Germany are essentially in agreement with the description in Braun & Cook (2012): Conidiophores composed of cylindrical, straight to curved-sinuous foot-cells, 15–40 × 7–12 µm, followed by 1–2 cells, shorter than the foot-cell, about as long or even longer; conidia 27.5–46.5 × 16–26 µm, length/width ratio 1.3–2.5, on average 1.8, usually with a single terminal or subterminal germ tube, occasionally with two or three, short to very long (longitubus pattern), 20–185 µm, straight to curved-sinuous, short germ tubes cylindrical to clavate, longer ones filiform (the treatment in a dry chamber or the pre-treatment in a dry chamber followed by a treatment in a moist chamber increase the conidial germination rate and further the development of short germ tubes with a lobed terminal appressorium), germ tubes aseptate, with a single septum at the base or somewhat distant, longer germ tubes may have two germ tubes distant from each other, second septum in the upper half, apex undifferentiated, swollen to lobed, sometimes distinctly hooked to sinuous-spirally twisted or short bifurcate or with short lateral branchlets.

Erysiphe trifoliorum (Wallr.) U. Braun (s. lat. on *Lathyrus* spp.)

Material examined: Germany, Schleswig-Holstein, Lübeck, Israelsdorf, meadow between Hasselbruchweg and Lustholz, on *Lathyrus pratensis*, 7 Aug. 2000, A. Schmidt, KM 122 (KR-M-0020843, KR-M-0020844), with chasmothecia; Mecklenburg-Vorpommern, Kreis Nordvorpommern, Darß, near Darßer Ort, on *Lathyrus pratensis*, 11 Aug. 2000, A. Schmidt, KM 127 (KR-M-0020816), with immature chasmothecia; Schleswig-Holstein, Kreis Pinneberg, Haseldorf, Deichreihe, on *Lathyrus odoratus*, 8 Sep. 2001, A. Schmidt, KM 148 (KR-M-0021916), with chasmothecia; Schleswig-Holstein, Lübeck, St. Gertrud, Roekstraße, on *Lathyrus latifolius*, 23 Aug. 2005, A. Schmidt, KM 211 (KR-M-0022007); Baden-Württemberg, Karlsruhe, Rintheim, on *Lathyrus latifolius*, 29 Jul. 2008, M. Scholler & D. Matalla, KM 266 (KR-M-0004805); Schleswig-Holstein, Nordfriesland, Insel Amrum, Norddorf, on *Lathyrus* cf. *heterophyllus*, 24 Sep. 2010, A. Schmidt, KM 289 (KR-M-0027777).

The asexual morph of collections on *Lathyrus* spp., including conidial germination pattern, is characterised as follows: Hyphal appressoria distinctly lobed; conidiophores erect, foot-cells cylindrical, straight to somewhat curved-sinuous, 25–40 × 7–12 µm, followed by 1–2 cells, shorter than the foot-cell, about as long as the foot-cell or followed by a single longer cell; conidia ellipsoid-cylindrical, 30–51.5 × 16–22 µm, length/width ratio 1.5–3, on average 2.0, usually with a single subapical germ tube, rarely two, short to long (longitubus pattern), 15–155 µm long, short germ tubes usually clavate, apex swollen to somewhat lobed, sometimes hooked, long germ tubes filiform, straight to curved-sinuous, occasionally with short branchlets, apex undifferentiated, swollen to somewhat lobed or hooked, germ

tubes aseptate or usually with a single septum at the base or usually somewhat distant from the point of attachment, but not strongly elevated, long germ tubes sometimes with two septa distant from each other. Note: The characteristics of the asexual morph, including the conidial germination pattern, of collections on *Lathyrus* spp. coincide well with those of specimens on *Trifolium* spp.

Erysiphe trifoliorum (Wallr.) U. Braun (s. lat. on *Melilotus* spp.)

Material examined: Germany, Schleswig-Holstein, Ostholstein, between Sereetz and Bad Schwartau, on *Melilotus albus*, 14 Jul. 2000, A. Schmidt, KM 113 (KR-M-0020821); Schleswig-Holstein, Lübeck, Wallhalbinsel, near Marienbrücke, on *Melilotus albus*, 22 Jul. 2001, A. Schmidt, KM 138 (KR-M-0021968); Schleswig-Holstein, Lübeck, Israelsdorf, Schellbruch, Treidelsteig, on *Melilotus altissimus*, 26 Jul. 2001, A. Schmidt, KM 140 (KR-M-0021925); Schleswig-Holstein, Lübeck, St. Gertrud, between Hafen- and Konstinstraße, on *Melilotus officinalis*, 28 Jul. 2002, A. Schmidt, KM 162 (KR-M-0021949); Schleswig-Holstein, Lübeck, Herreninsel, on *Melilotus officinalis*, 17 Jul. 2004, A. Schmidt, KM 193 (KR-M-0021904).

Collections on *Melilotus* spp. are characterised as follows: Conidiophores composed of cylindrical foot-cells, straight to somewhat curved-sinuous, 20–40 × 7–12 µm, followed by 1–2 cells, shorter than the foot-cell, about as long or even longer; conidia 21–43 × 16.5–22 µm, length/width ratio 1.3–2.5, on average 1.9, conidia with a single germ tube, rarely two, subapical, with short and long (longitubus pattern) germ tubes, 14–150 µm long, short germ tubes usually clavate, apex swollen or lobed, long germ tubes filiform, straight to curved or sinuous, aseptate or usually with a single germ tubes somewhat distant from the point of attachment, long germ tubes sometimes with two germ tubes distant from each other, apex undifferentiated, swollen, somewhat lobed, sometimes short furcate or hooked.

Note: The characteristics of the asexual morphs, including conidial germination patterns, on *Melilotus* spp. agree well with those of collections on *Trifolium* spp.

Erysiphe vanbruntiana (Gerard) U. Braun & S. Takam. Fig. 37

Material examined: Germany, Schleswig-Holstein, Lübeck, Waldhusener Forst, parking place, on *Sambucus racemosa*, 20 Jul. 1998, A. Schmidt, KM 77 (KR-M-0037706); Hamburg, Nienstedten, Quellental, on *Sambucus racemosa*, 14 Jul. 2007, A. Schmidt, KM 237 (KR-M-0021892).

The conidiophores (foot-cells straight, cylindrical, followed by 1–3 cells, shorter than the foot-cell, about as long or occasionally longer) and conidia (30–43 × 14.5–22 µm, length/width ratio 1.4–2.6, on average 2.0), including conidial germination, agree very well with the description in Paulech (1995: 216), Bolay (2005: 82), and Braun & Cook (2012: 517). The result of the germination experiment based on the present material showed a uniform pattern: Germ tubes uniformly short, solitary, subapical, cylindrical to clavate, straight to sinuous or even somewhat geniculate, sometimes almost sessile, i.e., conidial appressorium almost sessile, apex undifferentiated, swollen (club-shaped) or slightly to multilobed, aseptate or with a single septum at the base or only slightly elevated.

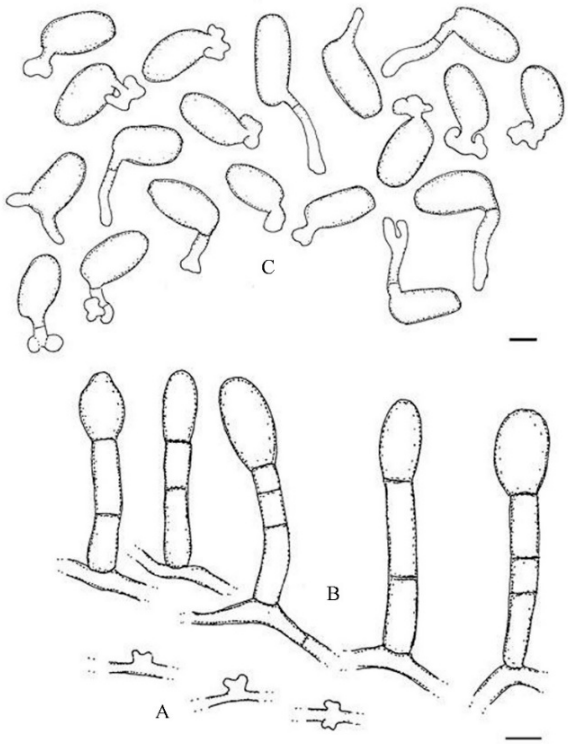


Fig. 37: *Erysiphe vanbruntiana*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Erysiphe sp. (on *Cytisus decumbens*)

Material examined: Germany, Hamburg, Alt-Osdorf, on *Cytisus decumbens*, 23 Jul. 2005, A. Schmidt, KM 205 (KR-M-0021936); Mecklenburg-Vorpommern, near Feldberg, Hauptmannsberg, on *Cytisus scoparius*. 6 Oct. 2005, A. Schmidt, KM 213 (KR-M-0022008).

This is the first record of a powdery mildew on *Cytisus decumbens*. The asexual morph on this host is characterised as follows: Mycelium amphigenous; hyphal appressoria solitary, slightly to multilobed; conidiophores composed of cylindrical foot-cells, 20–35 × 7.5–9 µm, straight to curved sinuous, followed by 1–2 cells, shorter than the foot-cell, about as long or followed by a single longer cell (length of the conidiophores formed on both leaf surfaces more or less equal); conidia ellipsoid, 29–39.5 × 16–20 µm, length/width ratio 1.6–2.4, on average 2.0, conidia with a single germ tube, subapical, rarely with two at both ends, short to long (longitubus pattern), 15–140 µm, short germ tubes cylindrical to clavate, apex swollen to lobed (pre-treatments in a dry chamber increase the share of short germ tubes with lobed conidial appressoria), long germ tubes filiform, straight to curved-sinuous, apex usually undifferentiated, occasionally swollen or hooked, germ tubes aseptate or with a single septum at the base or somewhat distant from the point of attachment, long germ tubes sometimes with two septa distant from each other, the second septum in the upper half.

The collection on *Cytisus scoparius* is characterised by having very similar ellipsoid conidia, 31.5–38.5 × 16–20 µm, length/width ratio 1.7–2.3, on average 2.0.

Note: The proper identification of these collections was not possible, above all due to lacking formation of chasmothecia. The asexual morphs might belong to *Erysiphe guarionii* (Briosi & Cavara) U. Braun & S. Takam., but there are some differences (conidiophores and conidia wider). On the other hand, the asexual morph of *E. guarinonii* is still insufficiently known. The description and illustration in Braun & Cook (2012) were just based on herbarium material. A clear identification only based on conidiophores, conidia and the conidial germination is not possible since the asexual morphs, including conidial germination patterns, of most *Erysiphe* spp. on legumes are rather similar to each other and not distinguishable with certainty.

Erysiphe sp. (on *Pachypodium lamerei*) Figs. 38, 39

Material examined: Germany, Baden-Württemberg, Karlsruhe, Albsiedlung, on *Pachypodium lamerei*, 14 Jan. 2013, M. Scholler, KM 311 (KR-M-0035017).

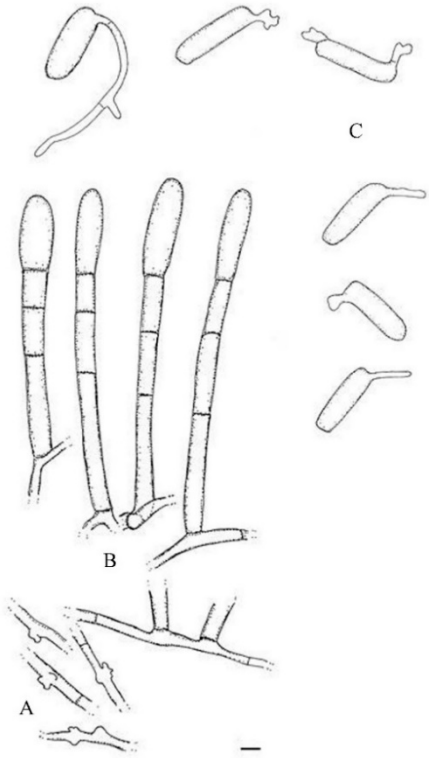


Fig. 38: *Erysiphe* sp. on *Pachypodium lamerei*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

The asexual morph of the present collection is characterised as follows: Hyphal appressoria solitary or in opposite pairs, nipple-shaped to moderately lobed; conidiophores 80–105 µm long (without conidia), foot cells usually straight, cylindrical, 40–60 × 7–9 µm, followed by two shorter cells; conidia formed singly, cylindrical (-ellipsoid), 37–50 × 13.5–18 µm, length/width ratio 2.3–3.6, on average 2.8, germination of the conidia characterised by a single subapical germ tube, sometimes two at both ends, short, cylindrical-clavate, apex swollen or with a lobed conidial appressorium, germ tubes aseptate or with a single basal septum, or germ tubes longer (longitubus pattern) and with two septa distant from each other.

This collection comprises the asexual morph and a few not quite mature chasmothecia (asci immature). *Erysiphe pachypodii* was described on *Pachypodium lamerei* in Lebeda et al. (2002). However, according to the original description, this species differs from the present collection in having much smaller chasmothecia, 70–115 µm diam. (130–135 µm diam. in the present collection) and much narrower conidia, 30–42 × 9–13.5 µm (vs. 37–50 × 13.3–18 µm), and shorter foot-cells of the conidiophores, 24.5–55 × 6–9 µm (vs. 40–60 µm long).

Erysiphe asclepiadis V. Kummer & U. Braun (see Braun & Cook 2012: 364 and Bolay 2013: 113) can also be ruled out.

This species, known to infect *Asclepis* spp., is readily distinguishable from the present collection on *Pachypodium lamerei* by its shorter conidiophores, 40–90 µm long (without conidia), shorter foot-cells, 12–40 × 5–10 µm, and broad ellipsoid (-ovoid), doliiform, conidia, (25–)28–50 × (9–)10–20(–24) µm, length/width ratio (1.4–)1.5–2(–2.2). These differences are significant and do not allow a proper identification of the present German collection.

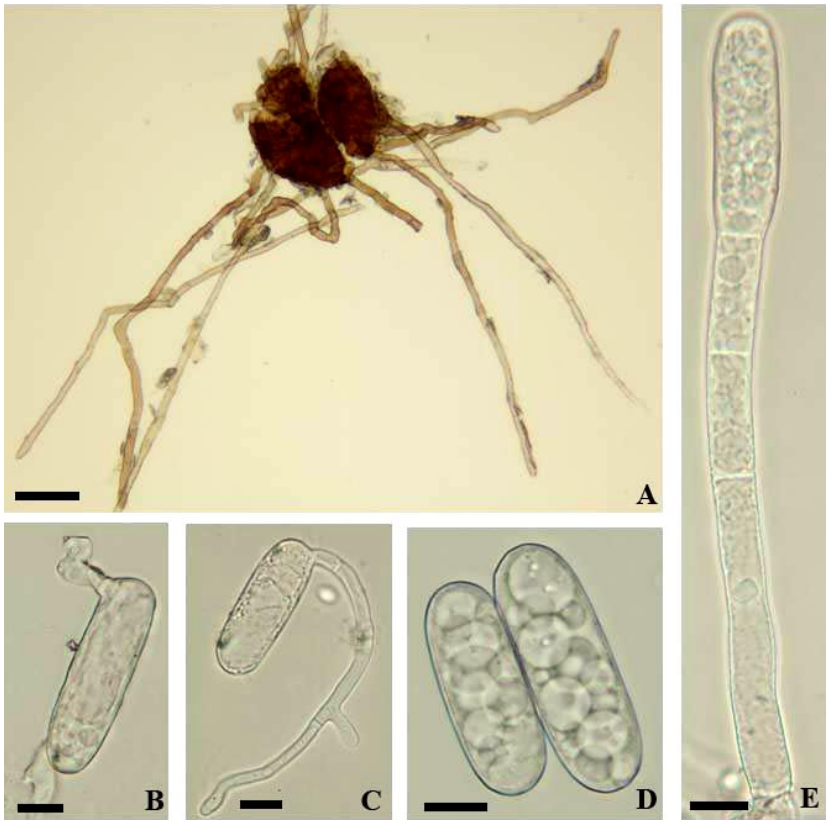


Fig. 39: *Erysiphe* sp. on *Pachypodium lamerei*. A: Chasmothecium; B, C: Conidia with germ tubes; D: Conidia; E: Conidiophore. Scale bars = 10 µm.

Golovinomyces

Golovinomyces depressus (Wallr.) Heluta Figs. 40, 41

Material examined: Germany, Schleswig-Holstein, Lübeck, Lauerholz, Lübecker Weg, on *Arctium nemorosum*, 29 Aug. 2004, A. Schmidt, KM 200 (KR-M-0021960); Schleswig-Holstein, Lübeck, St. Jürgen, Seydlitzstraße, on *Centaurea montana*, 11 June 2006, A. Schmidt, KM 216 (KR-M-0022017).

Fig. 40: *Golovinomyces depressus*. A: Conidiophore; B: Conidium with long germ tube (longitubus pattern); C: Conidia; D, E: conidia with short germ tubes. Scale bars = 10 µm.

Golovinomyces depressus is the type species of *Golovinomyces* sect. *Depressi*. The sexual and asexual morphs of the present collection on *Arctium nemorosum* coincide perfectly with previous descriptions, including Paulech (1995: 153–154), Bolay (2005: 90–91), and Braun & Cook (2012: 312). The conidia on *Arctium nemorosum* are doliiform-limoniform, 28.5–44 × 22–27 µm, length/width ratio 1.3–1.8, on average 1.4 [on *Centaurea montana* 30–42.5 × 22–29.5 µm, length width ratio 1.2–1.6, on average 1.4]. The basal septum of the conidiophores was usually distinctly elevated, i.e., not at the very base.

The conidiophores on *Centaurea montana* were longer on the lower leaf surface and shorter above. Germinating conidia were characterised by forming a single perihilar germ tube, long and filiform (longitubus pattern), longitubus pattern predominant

when first treated in a dry chamber and then in a moist chamber (when exclusively treated in a moist chamber only with very long germ tubes), short germ tubes usually clavate, with swollen (club-shaped) terminal hyphal appressorium, long germ tubes up to about eight times as long as the conidial length (to about 260 µm), apex always undifferentiated, unswollen, all germ tubes exclusively aseptate. The germ tubes of conidia from *Centaurea montana* are very similar to the germination pattern of conidia developed on *Arctium nemorosum*, except for a single basal septum occasionally formed in short germ tubes and the shape of short germ tubes that can sometimes be rather irregular. The conidial germination depicted in Braun & Cook (2012: 16, fig. 7 E) agrees well with the present observations.

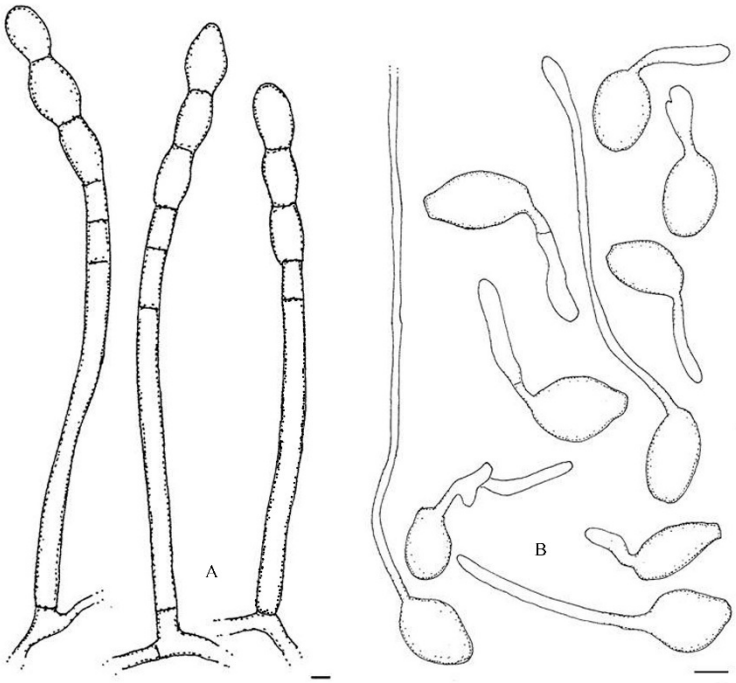
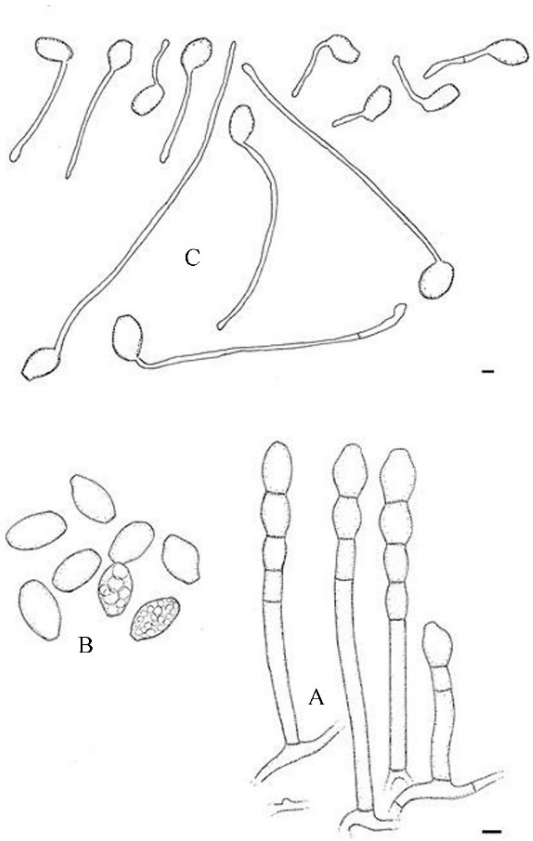


Fig. 41. *Golovinomyces depressus.* A: Conidiophores; B: Conidia with long (longitubus pattern) and short germ tubes. Scale bar = 10 µm



Golovinomyces echinopis (U. Braun) Heluta Fig. 42

Material examined: Germany, Schleswig-Holstein, Lübeck, Israelsdorf, Wilhelm-Ohnesorge-Weg, on *Echinops ritro*, 13 Jul 2008, A. Schmidt, KM 257 (KR-M-0002828).

Conidiophores and conidia of the present collection correspond with previous observations and measurements, including Paulech (1995: 158) and Braun & Cook (2012: 313). The conidial germination differs in forming a certain percentage of short germ tubes, above all when first treated in a dry chamber, followed by a treatment in a moist chamber: Conidia with a single germ tube, terminal to perihilar, short germ tubes cylindrical-clavate, usually with a swollen apex, aseptate or only rarely with a single septum, long to very long germ tubes (longitubus pattern) prevailing, up to 12 times as long as the conidial length (to about 335 µm), apex undifferentiated or swollen, always aseptate.

Fig. 42. *Golovinomyces echinopis*. A: Conidiophores; B: Conidia; C: Conidia with long (longitubus pattern) and short germ tubes. Scale bars = 10 µm.

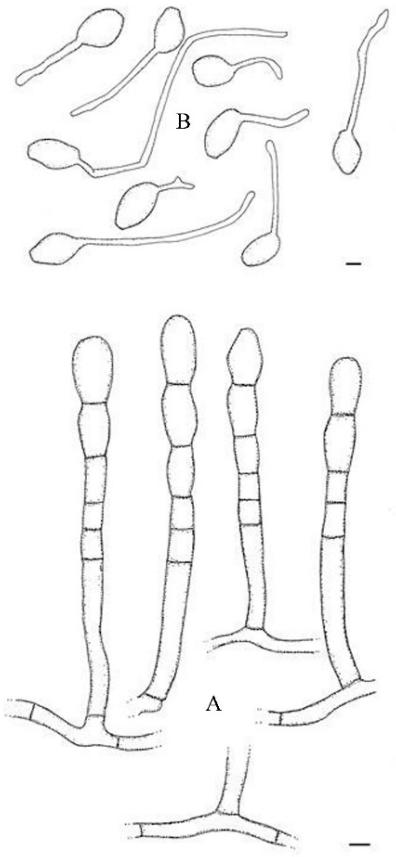


Fig. 43. *Golovinomyces inulae*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Golovinomyces inulae U. Braun & H.D. Shin Figs. 43, 44

Material examined: Germany, Niedersachsen, Kreis Lüchow-Dannenberg, Hitzacker, 0.9 km south-east of Bitter, on *Inula britannica*, 21 Oct. 2019, H. Thiel, KM 362 (KR-M-0013222).

This species was described by Braun and Shin, in Braun & Cook (2012: 317). Appressoria, conidiophores (foot-cells cylindrical, 40–70 × 10–12 µm, followed by 1–2 short cells) and conidia (doliiform-limoniform, 29–40.5 ×18.5–24.5 µm, length/width ratio 1.4–2.0, on average 1.7) agree well with the original description. The measured conidial width in the present collection is somewhat larger in comparison with the original description, which is undoubtedly resulting from measurements of fresh conidia in the present case (vs. data obtained from dried herbarium samples in the original description). The conidial germination was not described in Braun & Cook (2012). It is characterised as follows: Germinated conidia with a single perihilar germ tube, short germ tubes cylindrical-clavate, with undifferentiated or swollen (club-shaped) apex, long germ tubes (longitubus pattern) prevailing, up to about eight times as long as the conidial length (to about 170 µm), cylindrical-filiform, straight, curved or somewhat sinuous, apex undifferentiated or sometimes swollen, all germ tubes consistently aseptate. This mode of conidial germination is rather specific by having predominantly developed longitubus pattern and consistently aseptate germ tubes. In general, the characteristics of the conidial germination of *G. inulae* are in favour of placing this species in *Golovinomyces* sect. *Depressi* (see Braun & Cook 2012: 295).

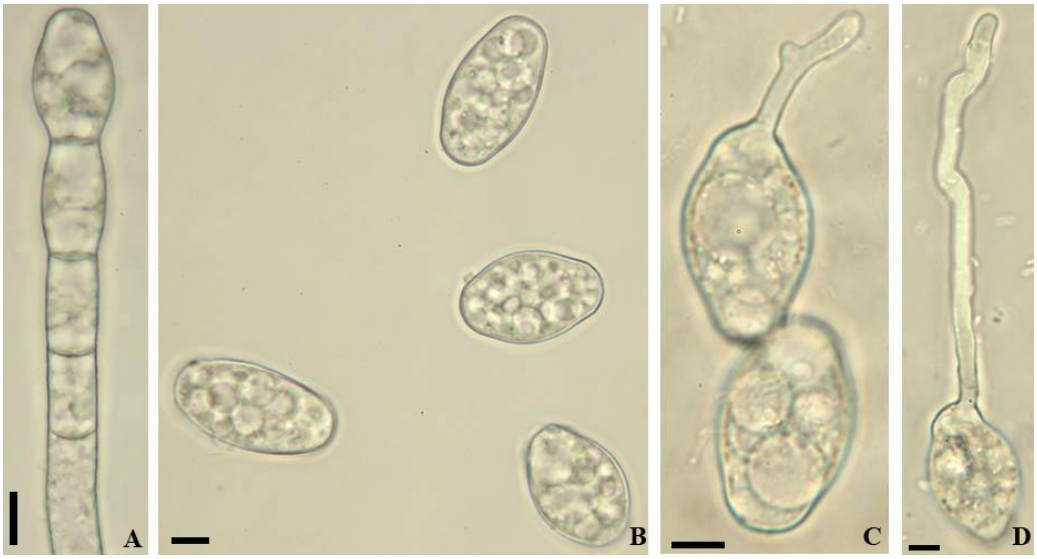


Fig. 44. *Golovinomyces inulae*. A: Conidiophore; B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm.

Golovinomyces latisporus (U. Braun) P.L Qiu & S.Y. Liu (Qui et al. 2020) Figs. 45, 46

≡ *Oidium latisporum* U. Braun.

Misapplied name: *Golovinomyces ambrosiae* (e.g., in Braun & Cook 2012: 299).

Material examined: Germany, Schleswig-Holstein, Herzogtum Lauenburg, Groß Grönau, nursery, on *Helianthus decapetalus*, 27 June 2019, A. Schmidt, KM 355 (KR-M-0013229).

The conidiophores (foot-cells cylindrical, straight to slightly curved or sinuous throughout, 40–85 × 11–14 µm, followed by 1–2 short cells) and conidia (doliiform-limoniform, 30–42.5 × 20.5–24 µm, length/width ratio 1.3–1.9, on average 1.6) agree well with previous descriptions, as for example in

Braun & Cook (2012: 299, as *Golovinoymces ambrosiae*) and Qiu et al. (2020). The conidial germination, based on the present collection, is characterised as follows: Conidia with a single perihilar or sometimes terminal germ tube, short and long (longitubus pattern) germ tubes mixed, short germ tubes cylindrical with swollen apex to clavate throughout, aseptate or occasionally with a single septum at the base or elevated, long germ tubes two to six times as long as the conidial length (to 170 µm), apex undifferentiated or swollen.

Fig. 45. *Golovinomyces latisporus*. A, B: Conidiophores; C, D: Conidia with germ tubes; E: Conidia. Scale bars = 10 µm.

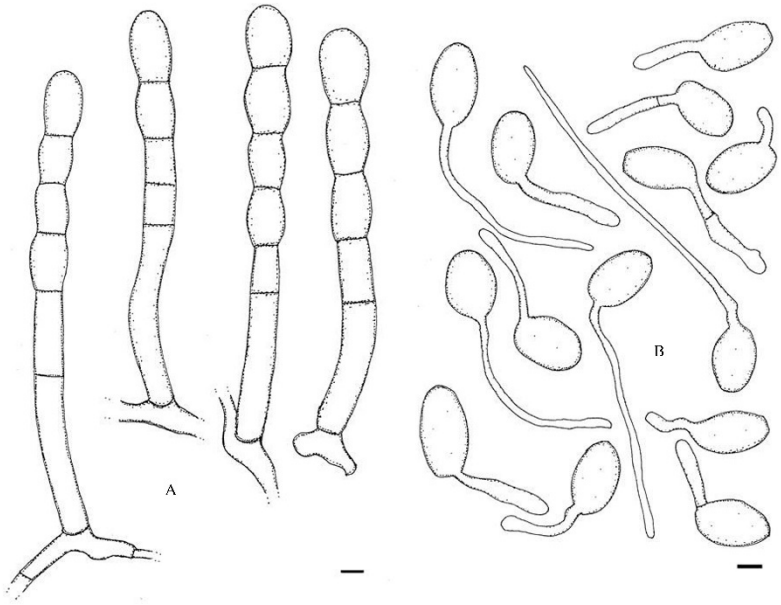


Fig. 46. *Golovinomyces latisporus*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Golovinomyces longipes (Noordel. & Loer.) L. Kiss (in Braun et al. 2019: 352) Fig. 47, 48

≡ *Oidium longipes* Noordel. & Loer.

≡ *Euoidium longipes* (Noordel. & Loer.) U. Braun & R.T.A. Cook.

Material examined: Germany, Schleswig-Holstein, Lübeck, St. Gertrud, Israelsdorf, on *Petunia* sp. cult., 27 Aug. 2003, A. Schmidt, KM 178 (KR-M-0021917); Schleswig-Holstein, Lübeck, St. Gertrud, Israelsdorf, on *Petunia* sp. cult., 29 Aug. 2014, A. Schmidt, KM 324 (KR-M-0043633).

The conidiophores of this species are rather variable. The very long conidiophores in the present collections are within the morphological range of this species (Bolay 2005: 106–107, Braun & Cook 2012: 335). A long foot-cell is followed by much shorter cells or by a second cell about as long as the foot-cell or even longer. The basal septum is mostly somewhat elevated. The catenescent conidia are ellipsoid-ovoid, doliiform or subcylindrical, 26–38 × 17–24 µm, length/width ratio 1.3–2, on average

1.7. The conidial germination (Euodium type) is characterised by forming solitary germ tubes, mostly perihilar, occasionally terminal or lateral, mostly stubby, cylindrical to clavate, some germ tubes longer and more filiform (longitubus pattern), aseptate or with a single basal septum.
Notes: The conidia fall into the variation for this species, but they are on average relatively short. The conidial germination was previously insufficiently known. The germ tubes illustrated in Braun & Cook (2012: 334, fig. 369) were only based on a few observations in vivo.

Fig. 47. *Golovinomyces longipes*. A, B: Conidiophores; C: Conidia; D, E: Conidia with germ tubes. Scale bars = 10 µm.

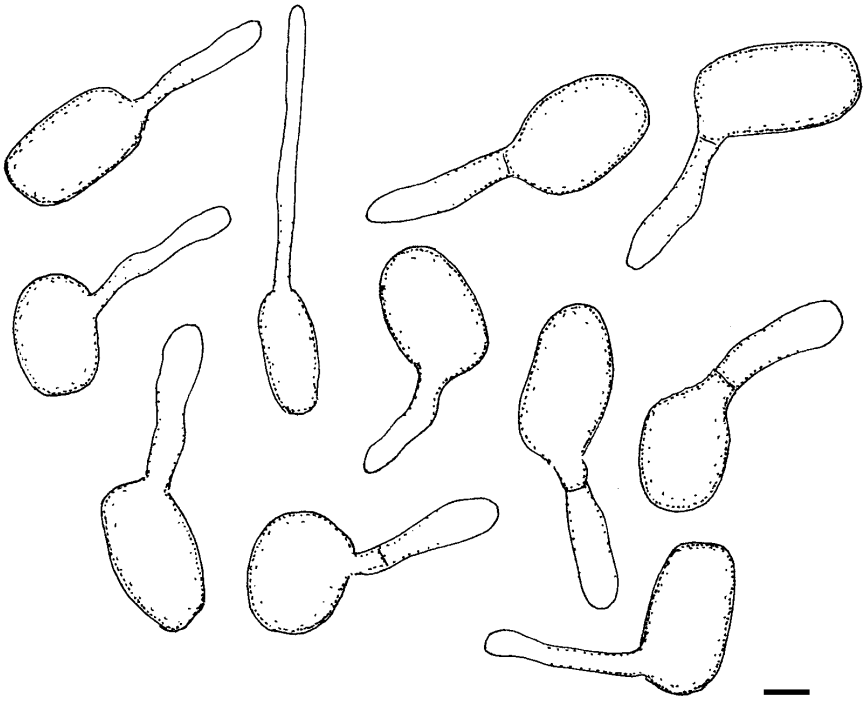


Fig. 48. *Golovinomyces longipes*. Conidia with germ tubes. Scale bars = 10 µm.

Golovinomyces verbasci (Jacz.) Heluta Figs. 49, 50

Material examined: Germany, Mecklenburg-Vorpommern, Landkreis Nordwestmecklenburg, Palingen, on *Verbascum nigrum*, 04 Aug. 1999, A. Schmidt, KM 102 (KR-M-0020854); Schleswig-Holstein, Lübeck, Dummersdorfer Ufer, slope near Stülper Huk, on *Verbascum* sp., 04 Jul. 2004, A. Schmidt, KM 189 (KR-M-0021907); Schleswig-Holstein, Ostholstein, Scharbeutz, OT Schürsdorf, nursery, on *Verbascum nigrum*, 20 June 2014, A. Schmidt, KM 322 (KR-M-0043206).

The conidiophores (foot-cells 70–170 × 10–13 µm) and conidia (mostly doliiform, 29–46 × 20–28 µm, length/width ratio 1.2–2.1, on average 1.6) agree well with previously descriptions, including Braun & Cook (2012: 332). The basal septum in the present collection was mostly somewhat raised, i.e., not at the very base. The conidial germination is characterised by forming a single perihilar germ tube, short to long, length 20–115 µm, cylindrical-filiform, aseptate, occasionally with a single septum distant from the point of attachment, apex simple, undifferentiated or usually swollen, which differs from the description published in Braun & Cook (2012), in which only long germ tubes (longitubus pattern within Euoidium type), terminal and lateral, without swollen apex, were described. It seems that the germination of conidia, on which the description in the latter work was based, was not yet completed. The germination of conidia of species belonging to *Golovinomyces* sect. *Depressi* may be influenced by external conditions, such as humidity (see discussion), which might also be responsible for the observed differences.

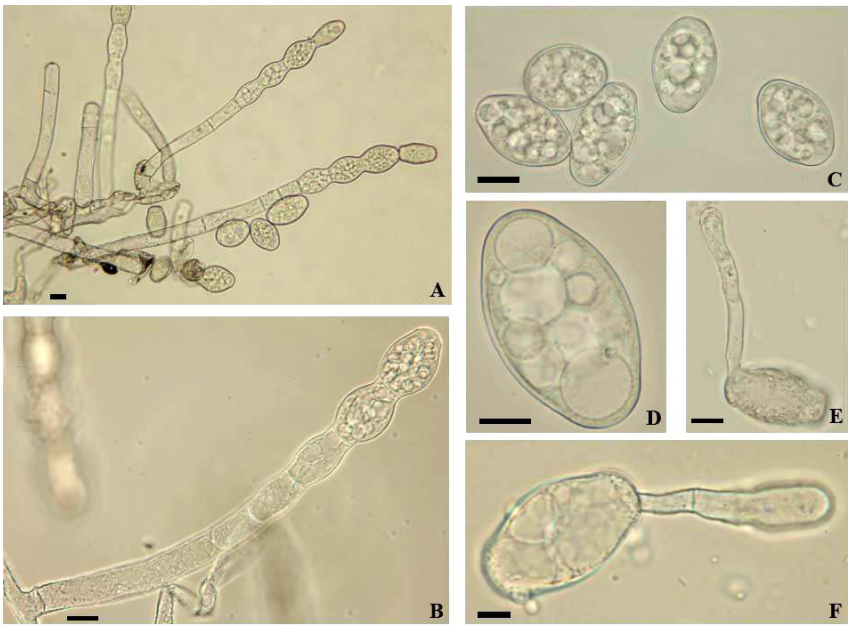


Fig. 49. *Golovinomyces verbasci*. A, B: Conidiophores; C, D: Conidia; E, F: Conidia with germ tubes. Scale bars = 10 µm.

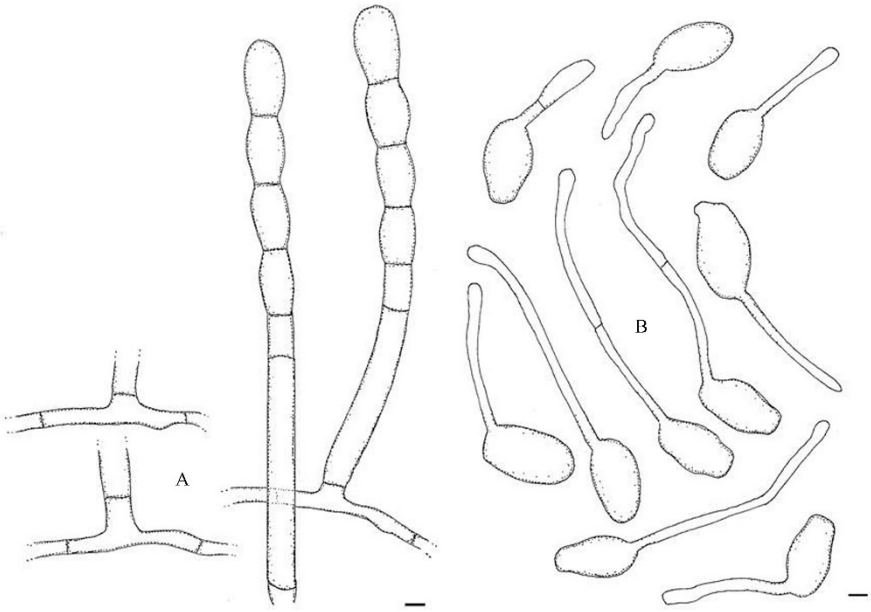


Fig. 50. *Golovinomyces verbasci*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Golovinomyces sp. Fig. 51

Material examined: Germany, Mecklenburg-Vorpommern, Landkreis Nordwestmecklenburg, Klütz, on *Bellis perennis*, 04 Aug. 2007, A. Schmidt, KM 242 (KR-M-0021896).

Mycelium amphigenous, often covering the entire surface, also caulicolous; hyphal appressoria lacking or sparingly developed; conidiophores erect, composed of a long foot-cell, 50–85 × 11.5–13.5 µm, followed by 1–2 short cells, forming catenescent conidia (2–4), foot-cells curved at the base; conidia broad ellipsoid-ovoid, doliiform, 25–36 × 17.5–21.5 µm, length/width ratio 1.3–1.9, on average 1.5, with a single perihilar germ tube, short and long germ tubes (longitubus pattern) mixed, short germ tubes cylindrical to clavate, mostly aseptate, sometimes with a single septum at the base or distant from the point of attachment (up to the middle of the germ tube), either entire germ tube club-shaped or apex swollen, long germ tubes two to five times as long as the conidial length (to about 150 µm), aseptate or with a single septum in the middle or upper half of the germ tube, apex undifferentiated or mostly swollen.

Without results of sequence analyses, this asexual morph cannot be properly identified. *Bellis* pertains to subtribe *Bellidinae* of tribe *Astereae* within the composite subfamily *Asteroideae*. *Golovinomyces asterum* (Schwein.) U. Braun is a common powdery mildew species on hosts of this tribe. *G. asterum* var. *asterum* is characterised by conidiophores with straight foot-cells, but *G. asterum* var. *moroczkovsii* (Heluta) U. Braun differs in having foot-celled curved at the basis (Braun & Cook 2012). The conidiophores and conidia are also rather similar to the present specimen on *Bellis perennis*. However, the asexual morph of *G. orontii* (s. str.) is also similar and cannot be excluded with certainty (Braun et al. 2019).

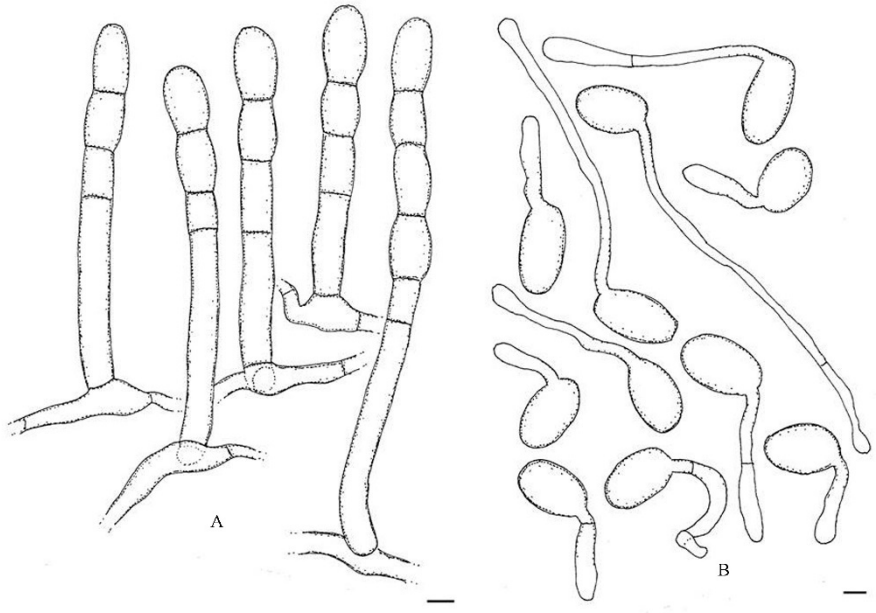


Fig. 51. *Golovinomyces* sp. (on *Bellis perennis*). A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Neoerysiphe

Neoerysiphe galii (S. Blumer) U. Braun Fig. 52

Material examined: Germany, Schleswig-Holstein, Lübeck, Schlutup, meadow near the rails, on *Galium aparine*, 14 Jul. 1998, A. Schmidt, KM 74 (KR-M-0020853); Schleswig-Holstein, Lübeck, Herreninsel, on *Galium aparine*, 27 June 2004, A. Schmidt, KM 187 (KR-M-0021906).

The conidiophores (foot-cells cylindrical, 40–70 × 9.5–13.5 µm, followed by 1–3 shorter cells) and conidia (broad ellipsoid, 25–33.5 × 14–22 µm, length/width ratio 1.3–2.3, on average 1.7) coincide with previous descriptions, including Paulech (1995: 152), Bolay (2005: 101), and Braun & Cook (2012: 343). The conidial germination (Striatoidium type), based on germination experiments carried out with the present material, is characterised as follows: Conidia with a single or sometimes two germ tubes, perihilar or somewhat lateral, uniformly short (not exceeding the conidial length, often less than half of

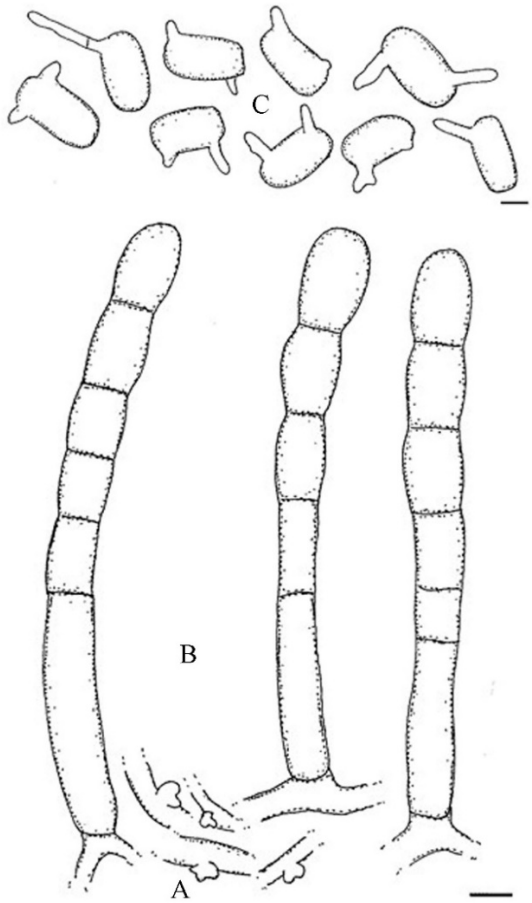


Fig. 52. *Neoerysiphe galii*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

the conidial width), cylindrical to somewhat clavate, usually aseptate, occasionally with a single basal septum, apex undifferentiated, somewhat swollen, occasionally slightly lobed or short bifurcate.

The description and illustration of an asexual morph of "*Neoerysiphe galii*" on *Galium* spp. in Korea in Shin (2000: 156 and 157, fig. 56) are not in agreement with true *N. galii* and rather refer to a species of *Golovinomyces*. Two species of this genus are common on *Galium*, viz., *G. riedlianus* (Speer) Heluta (Braun & Cook 2012: 325) and *G. tabaci* (Sawada) H.D. Shin et al. [including *G. rubiae* (H.D. Shin & Y.J. La) U. Braun] (Braun et al. 2019).

Neoerysiphe nevoi Heluta & S. Takam.

Figs. 53, 54

Material examined: Germany, Schleswig-Holstein, Lübeck, Dummersdorf, Hirtenbergweg, on *Lapsana communis*, 25 Jul. 2008, A. Schmidt, KM 259 (HAL 3333 F, KR-M-0002826); Lübeck, Lustholz, near NSG Schellbruch, 25 June 2020, A. Schmidt, KM 366 (HAL 3338 F).

The examined collection on *Lapsana communis* is characterised by forming catenescent conidia with a striate surface pattern combined with lobed hyphal appressoria and germ tubes with lobed conidial appressoria, which is characteristic for *Neoerysiphe*. Amongst species of this genus, the present specimen is in accordance with the asexual morph of *N. nevoi* (see Braun & Cook 2012: 346), which occurs on various hosts belonging to the Asteraceae tribe *Cichorieae*. The occurrence of *N. nevoi* on *Lapsana communis* is already known (see Braun & Cook 2012: 21, fig. 12 C, germinated conidium), but this species is new to Germany. The occurrence of this species on *Lapsana* is not surprising. This genus is allied to *Crepis* and pertains in subtribe *Crepidinae* of tribe *Cichorieae* (Pak & Bremer 1994). *Crepis* spp. are known to be common hosts of *N. nevoi*. So far, *Neoerysiphe cumminsiana* (on *Bidens ferulifolia*) was the only *Neoerysiphe* species recorded from Germany (Ale-Agha et al. 2008, Jage et al. 2010). The present identification is still in need to be confirmed by sequence analyses. The material on *Lapsana* is characterised as follows: Mycelium on stems, at the calyx and on leaves, amphigenous, in thin white patches or covering almost the entire surface; hyphae straight to sinuous, branched, septate, hyaline, smooth, hyphal cells 40–60 µm long and 3–9 µm wide; hyphal appressoria solitary or sometimes in opposite pairs, nipple-shaped to distinctly lobed, 3–6 µm diam.; conidiophores on the upper surface of the supporting hypha, not in the middle between two septa but usually towards one septum, erect, straight, foot-cells cylindrical, straight, at most slightly curved throughout, basal septum at the very base or slightly elevated (to 5 µm), sometimes somewhat constricted at the basal septum, 35–70 × 9–12 µm, followed by 1–3 shorter cells, about 10–20 µm long, giving rise to conidial chains with sinuate outline; conidia catenescent, broad ellipsoid-doliiform, 27.5–35.5 × 15–20 µm, length/width ratio 1.5–2.3, on average 1.7, surface of the conidia striate (under light microscopy

Fig. 53. *Neoerysiphe nevoi*. A: Conidiophore; B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm.

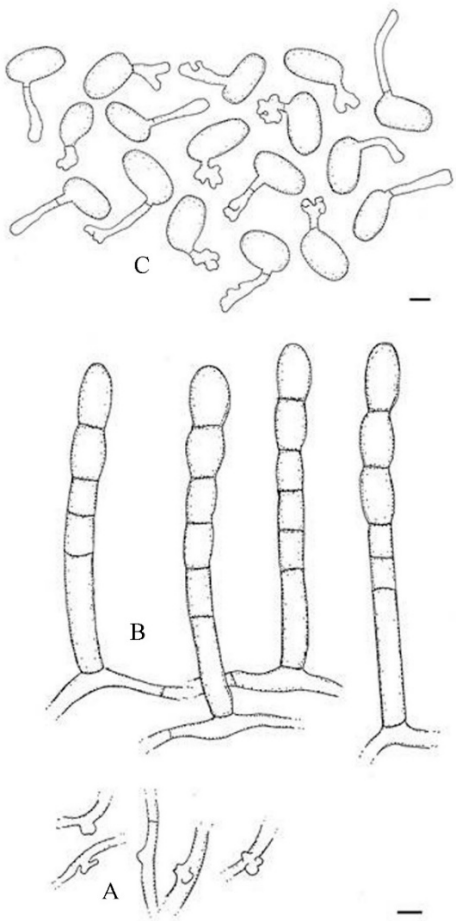


Fig. 54. *Neoerysiphe nevoi*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

readily visible, less evident in turgescent conidia), conidial germination characterised by forming a single perihilar germ tube (sometime lateral in germ tubes developed in vivo), occasionally two, uniformly short, usually not longer than the conidial length (about 10–40 µm long), sometimes almost sessile, i.e., with an almost sessile appressorium, cylindrical to clavate, straight to somewhat curved, aseptate or with a single basal septum, apex swollen, club-shaped, to distinctly lobed (germ tubes germinated in vivo have been observed that later evolve into superficial hyphae). The single germinated conidium of *N. nevoi* on *Lapsana communis* shown in Braun & Cook (2012: 21, fig. 12 C) match well with our own more comprehensive observations.

Phyllactinia

Note: Fresh conidia of all examined *Phyllactinia* ssp. contained numerous yellowish oil droplets, which later disappeared in germinated conidia.

Phyllactinia betulae (DC.) Fuss Figs. 55, 56

Material examined: Germany, Schleswig-Holstein, Lübeck, Holunderweg, on *Betula pendula*, 10 Aug. 2012, A. Schmidt, KM 305 (KR-M-0035020).

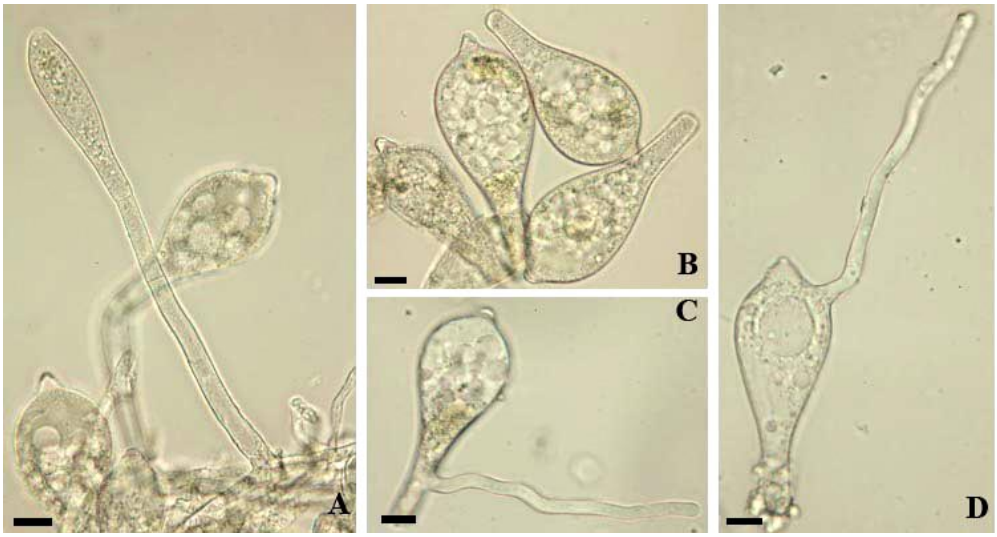


Fig. 55. *Phyllactinia betulae*. A: Conidiophores; B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm.

The characteristics of the hyphal appressoria (simple to multilobed), conidiophores (long cylindrical-filiform foot-cells, 65–120 µm long and 6.5–9 µm wide, followed by 0–4 shorter cells), and conidia (mostly spathulate, 68–89 × 24.5–34.5 µm, length/width ratio 2.2–3.3, on average 2.7) in the present collection agree well with previous descriptions and illustrations, including Braun & Cook (2012: 231). However, the conidial germination was not described in the latter work. Based on the present collection, it is characterised as follows: Usually with a single germ tube, sometimes two, subapical to somewhat lateral or somewhat lateral near the narrowed base, long and filiform, straight to sinuous, consistently aseptate, apex undifferentiated.

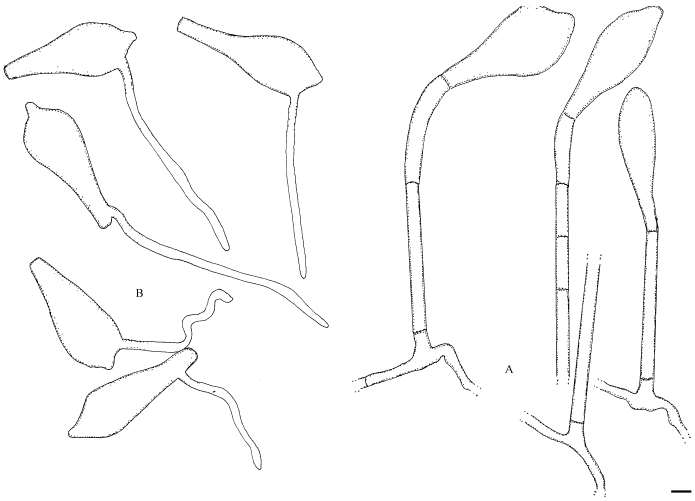


Fig. 56. *Phyllactinia betulae.* A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Phyllactinia corni H.D. Shin & M.J. Park Figs. 57, 58

Material examined: Germany, Schleswig-Holstein, Lübeck, Stadtpark, on *Cornus mas*, 13 Aug. 2019, A. Schmidt, KM 358 (KR-M-0013226).

The German collection (asexual and sexual morph) corresponds well with the original description in Braun & Cook (2012: 241). A comprehensive description and a detailed illustration of this species were also published in Shin (2000: 170–173, including figs 60-1 and 60-2). However, the conidial germination was not described in detail in the latter work. The present collection is characterised as follows: Hyphal appressoria (few) nipple-shaped to hooked; the foot-cells of the conidiophores are long and cylindrical-filiform, 35–160 × 6–8 µm, straight to somewhat flexuous at the base, followed by 1–3 shorter cells, basal septum at the base or only slightly elevated; conidia clavate to spathulate, 60–95 × 17–27 µm, length/width ratio 2.7–4.7, on average 3.5, with a single germ tube, at the apex, subapical to somewhat lateral or at the base or near the base, short to very long, 30–240 µm, straight to strongly sinuous, sometimes even spirally twisted, aseptate or with a single septum distant from the point of attachment, apex undifferentiated or slightly to distinctly lobed.

Fig. 57. *Phyllactinia corni.* A: Conidiophore; B: Base of a conidiophore; C, D, E: Conidia with germ tubes. Scale bars = 10 µm.

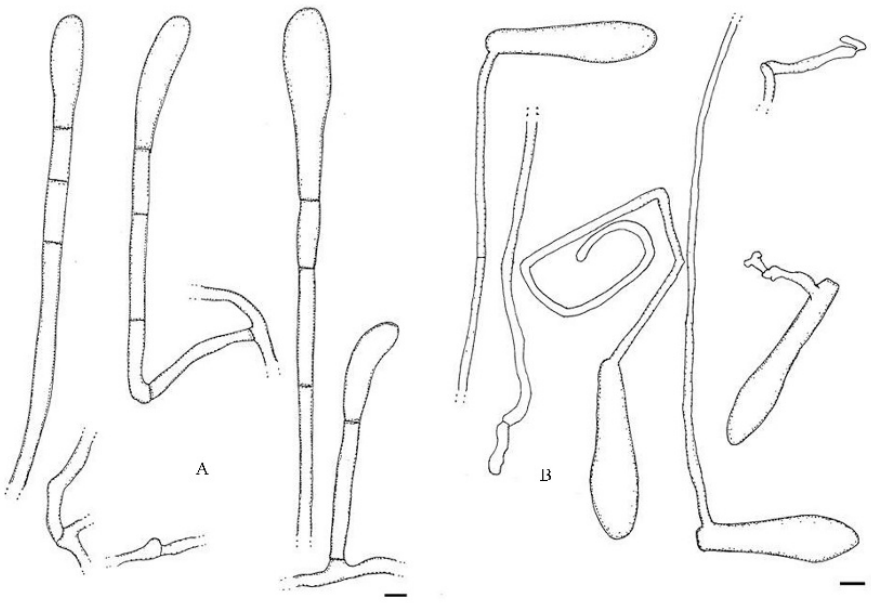


Fig. 58. *Phyllactinia corni.* A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Phyllactinia guttata (Wallr.) Lév. Figs. 59, 60

Material examined: Germany, Schleswig-Holstein, Lübeck, Dummersdorfer Ufer, Travehang, on *Corylus avellana*, A. Schmidt, 27 Aug. 2013, KM 317 b (KR-M-0038210).

The asexual morph found in the present collection agrees well with the description published in Bolay (2005: 111–112) and Braun & Cook (2012: 252), except for the conidial germination which was not illustrated in the latter work and only insufficiently described: Hyphal appressoria hooked to lobed; conidiophores very long and filiform, 5–8 µm wide; conidia clavate to somewhat spathulate, 57–88 × 16–28 µm, length/width ratio 2.5–4.1, on average 3.1, with a single or occasionally two germ tubes, usually more or less lateral, in the upper or lower half, uniformly short and aseptate, apex usually with a distinctly lobed appressorium.

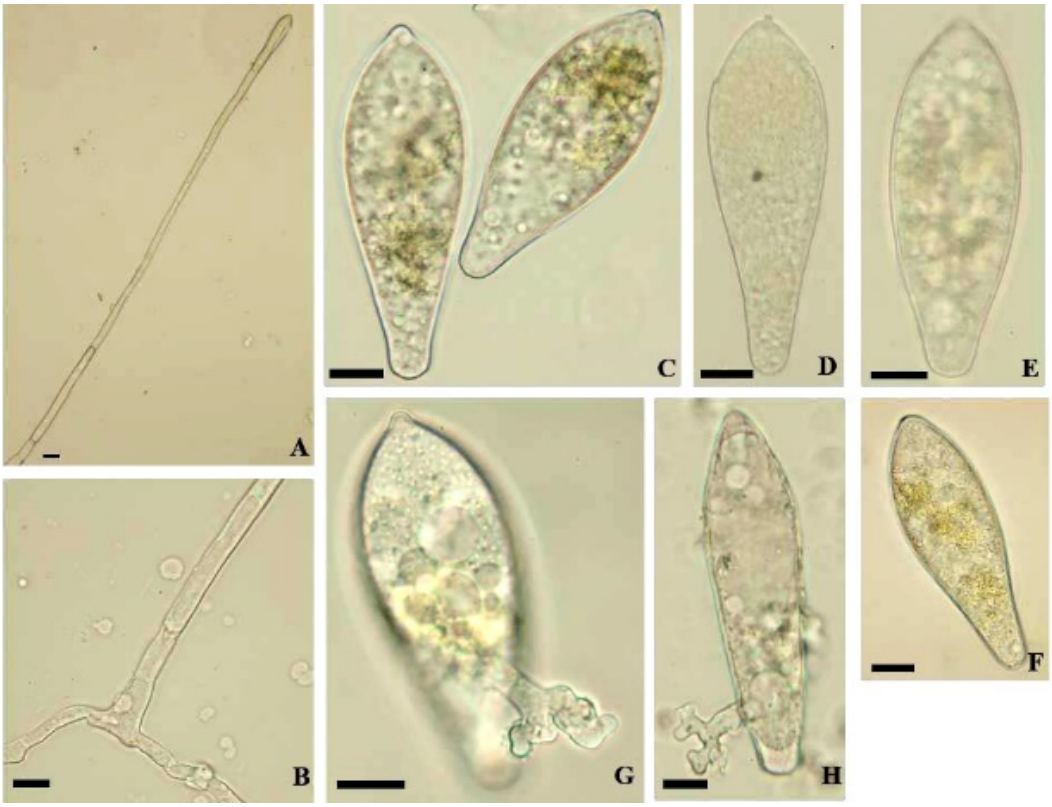


Fig. 59. *Phyllactinia guttata.* A, B: Conidiophores; C–F: Conidia; G, H: Conidia with germ tubes. Scale bars = 10 µm.

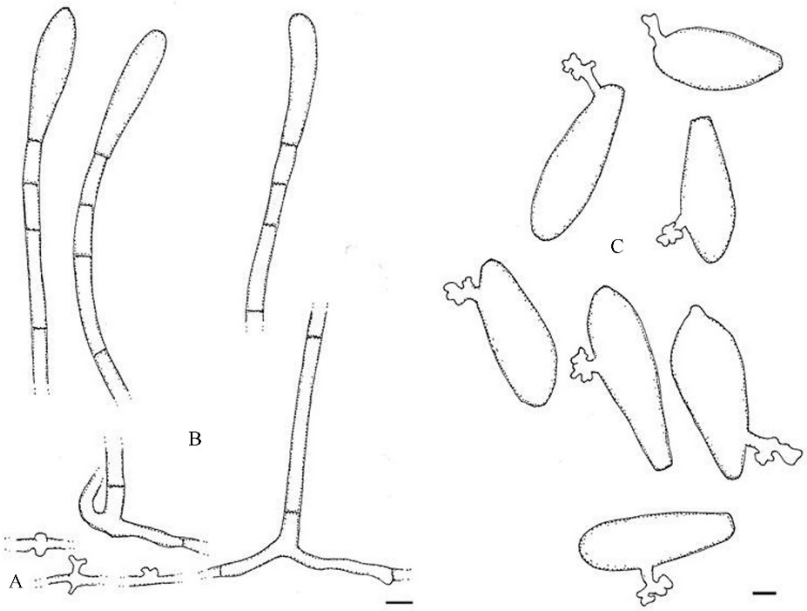


Fig. 60. *Phyllactinia guttata*. A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

Phyllactinia hippophaes Thüm. ex S. Blumer Fig. 61

Material examined: Germany, Brandenburg, Landkreis Potsdam-Mittelmark, Kloster Lehnin, OT Reckahn, on *Hippophae rhamnoides*, 30 Aug. 2014, V. Kummer and F. Tosch, KM 325 (KR-M-0043208), used for the conidial germination experiments; Sachsen-Anhalt, Landkreis Wittenberg, Kemberg, Straße der MTS, on *Hippophae rhamnoides*, 25 Aug. 2011, H. Jage, KM 299 (KR-M-0033264); Sachsen-Anhalt, Saalekreis, Braunsbedra, OT Roßbach, on *Hippophae rhamnoides*, 09 Sep. 2014, U. Richter, KM 326 (KR-M-0043205).

The characteristics of the asexual morph of *Phyllactinia hippophaes* were insufficiently described in Braun & Cook (2012), except for the conidial shape and size. The present collections are characterised as follows: Hyphal appressoria nipple-shaped; conidiophores erect, composed of straight, cylindrical-filiform foot-cells, up to 110 µm long, 6–8 µm wide, followed by 1–3 shorter cells, about 20–70 µm long, basal septum at the junction with the supporting hypha or somewhat elevated; conidia cylindrical to dumbbell-shaped (wider at both ends, between them cylindrical), 52–88.5 × 14–26 µm, length/width ratio 2.7–4.6, on average 3.5, with a single germ tube, apical to subapical, short to very long, 35–250 µm, straight to sinuous, aseptate, apex undifferentiated or only slightly swollen.

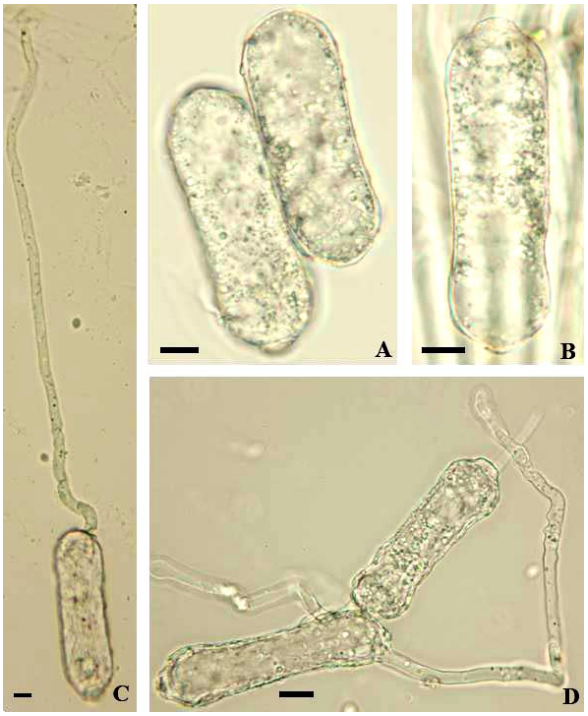


Fig. 61. *Phyllactinia hippophaes*. A, B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm.

Phyllactinia mali (Duby) U. Braun Figs. 62. 63

Material examined: Germany, Schleswig-Holstein, Lübeck, Dummersdorfer Ufer, near Stülper Huk, on *Crataegus monogyna*, 7 Aug. 2013, A. Schmidt, KM 337 B (KR-M-0006463).

The description of the asexual morph of *Phyllactinia mali* in Braun & Cook (2012: 261) is insufficient. The conidial germination was so far unknown. Bolay (2005: 114, fig. 95) provided a drawing, but did not describe the asexual morph in detail. The following details are based on the present collection: Conidiophores erect, foot-cells long and filiform, straight, 75–160 × 4.5–8 µm, followed by 1–3 shorter cells, basal septum usually somewhat elevated; conidia clavate-spathuliform, 53.5–78.5 × 14.5–22 µm, length/width ratio 3.0–4.3, on average 3.7, with a single germ tube near the base or subapical, occasionally two, straight to curved-sinuous, long, 60–130 µm, aseptate or with a single, occasionally two septa distant from the point of attachment, up to the upper half, apex usually swollen.

Fig. 62. *Phyllactinia mali*. A: Conidia; B–D: Conidia with germ tubes. Scale bars = 10 µm.

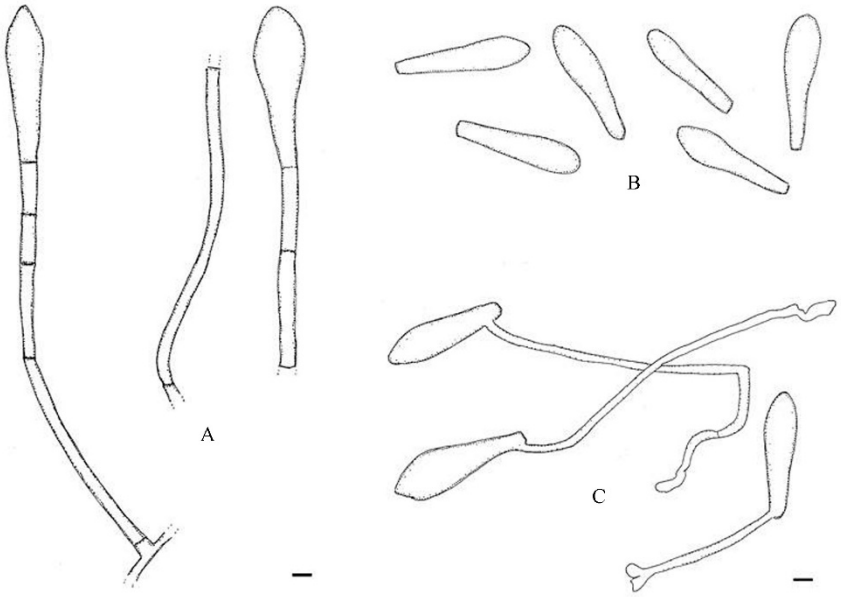


Fig. 63. *Phyllactinia mali*. A: Conidiophores; B: Conidia; C: Conidia with germ tubes. Scale bars = 10 µm.

Podosphaera

Podosphaera amelanchieris Maurizio Figs. 64, 65

Material examined: Germany, Hamburg, Nienstedten, Am Internationalen Seegerichtshof, on *Amelanchier* sp., 06 June 2004, A. Schmidt, KM 185 (KR-M-0021908).

The characteristics of the asexual morph in the present collection agree well with the description published in Braun & Cook (2012: 99), except for longer conidiophore foot-cells: Foot-cells of the conidiophores 70–130 µm long and 9–11 µm wide, followed by 1–2 shorter cells; conidia broad ellipsoid-doliiform, with fibrosin bodies, 24.5–33.5 × 14.5–20 µm, length/width ratio 1.4–2.0, on average 1.7, with a single germ tube, perihilar to lateral, short to moderately long, 7–80 µm, straight to

somewhat curved or sinuous, short germ tubes cylindrical to clavate, long germ tubes cylindrical-filiform, usually aseptate, occasionally with a single septum near the base, apex little differentiated (orthotubus subtype of Fibroidium type).

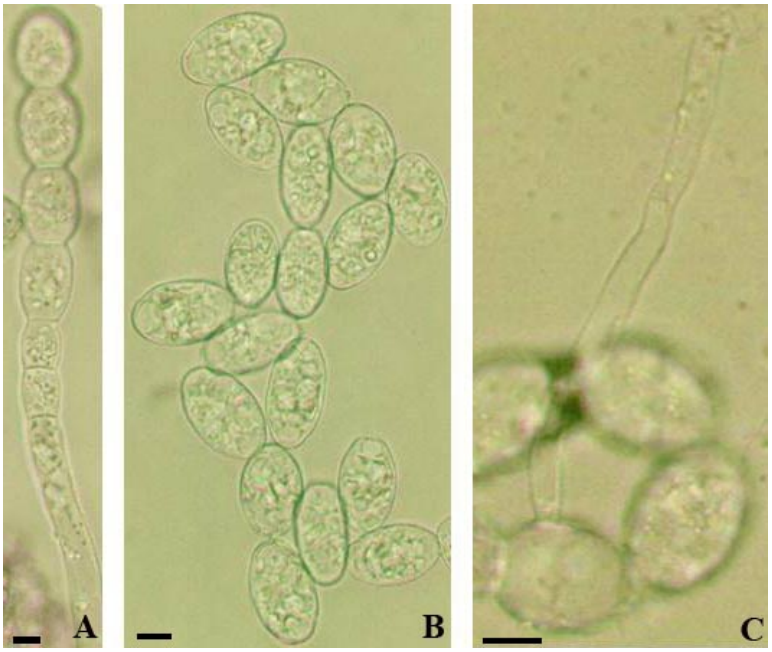


Fig. 64. *Podosphaera amelanchieris.* A: Conidiophore; B: Conidia; C: Conidium with germ tubes. Scale bars = 10 µm.

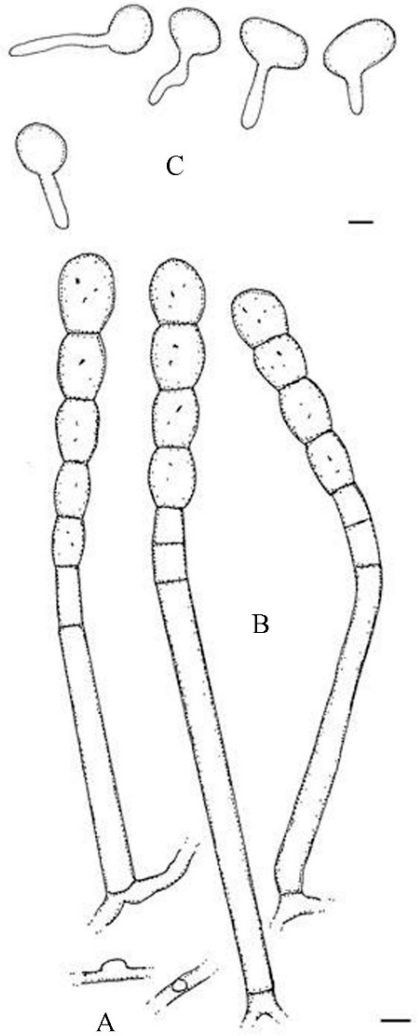


Fig. 65. *Podosphaera amelanchieris.* A: Hyphal appressoria; B: Conidiophores; C: Conidia with germ tubes. Scale bars = 10 µm.

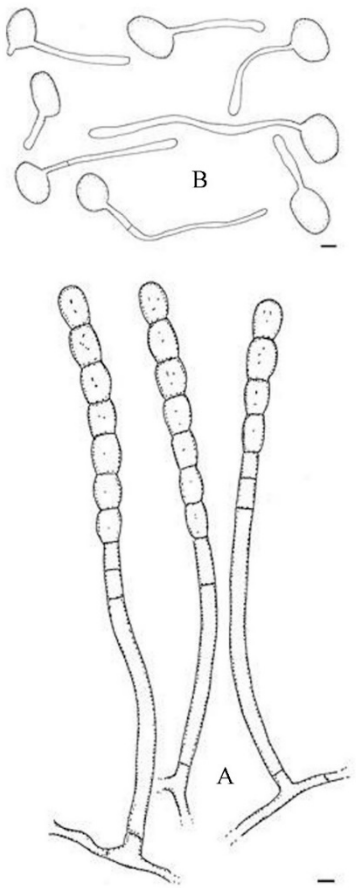


Fig. 66. *Podosphaera aphanis*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm

Podosphaera aphanis (Wallr.) U. Braun & S. Takam. Figs. 66, 67

Material examined: Germany, Schleswig-Holstein, Herzogtum Lauenburg, Groß Grönau, nursery, on *Fragaria ×ananassa*, 27 June 2012, A. Schmidt, KM 302 (KR-M-0035024).

The description of the asexual morph in Braun & Cook (2012: 122) was based on examinations of this species on various hosts, i.e., it is a cumulative description. Furthermore, *P. aphanis* is undoubtedly a genetically and morphologically heterogeneous complex probably encompassing cryptic speciation. The status of *P. aphanis* var. *hyalina* (U. Braun) U. Braun & S. Takam. is also unclear and in need of a phylogenetic reassessment. Bolay (2005: 118, fig. 97) illustrated conidiophores and conidia on *Potentilla palustris* and *Fragaria ×ananassa*. Shin (2000: 219, fig. 75-2) published an illustration of *P. aphanis* on *Fragaria ×ananassa* in Korea with very long foot-cells and strongly elevated basal septum. The examined material found on strawberry is characterised as follows: Conidiophores formed on the lower leaf surface up to 300 µm long, above shorter, up to 205 µm, foot-cells cylindrical to somewhat increasing in width from base to top, about 40–220 × 10–12 µm, followed by 1–2 shorter cells, basal septum somewhat elevated; conidia doliiform, with fibrosin bodies, 28–36 × 19–26 µm, length/width ratio 1.2–1.6, on average 1.4, with a single germ tube, perihilar to lateral, short to long, 20–130 µm, clavate or cylindrical-filiform, aseptate or occasionally with a single septum distant from the point of attachment, apex little differentiated or with swollen apex (orthotubus subtype of Fibroidium type).

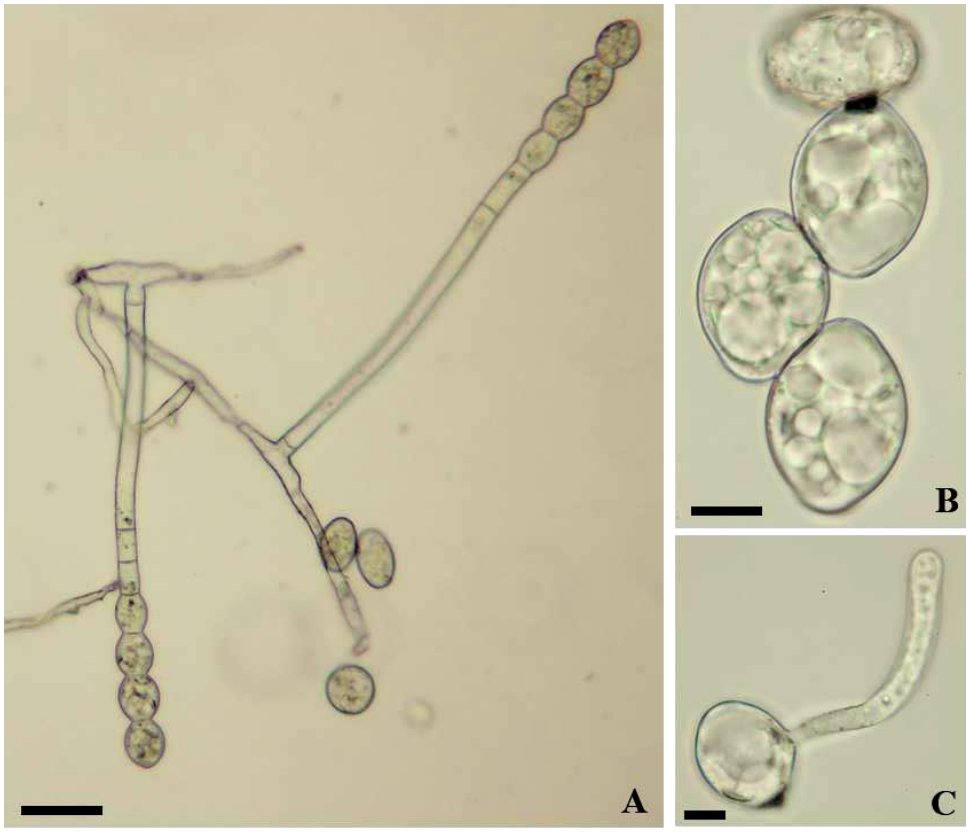


Fig. 67. *Podosphaera aphanis*. A: Conidiophores and conidia; B: Conidia; C: Conidium with germ tubes. Scale bars, A = 35 µm; B, C = 10 µm.

Podosphaera delphinii (P. Karst.) U. Braun & S. Takam. Figs. 68, 69

Material examined: Germany, Schleswig-Holstein, Herzogtum Lauenburg, Groß Grönau, nursery, on *Trollius ×cultorum* (garden hybrid), 19 Jul 2019, A. Schmidt, KM 356 (KR-M-0013228).

The descriptions of the asexual morph of *P. delphinii* in Paulech (1995: 1581–82) and Braun & Cook (2012: 131) are incomplete. The conidial size was based on herbarium material, and details of the conidial germination are lacking. The present material is characterised as follows: Conidiophores composed of a cylindrical foot-cell, straight to somewhat curved, 40–85 × 8–11 µm, followed by 0–2 short cells, basal septum at the junction with the mother cell; conidia broad ellipsoid-doliiform, with fibrosin bodies, 27–37 × 14.5–20 µm, length/width ratio 1.6–2.2, on average 1.9, with a single germ tube, apical, perihilar to lateral, uniformly stubby, 10–28 µm long, aseptate, broad cylindrical, obclavate or maximum width in the middle (brevitubus subtype of Fibroidium type).

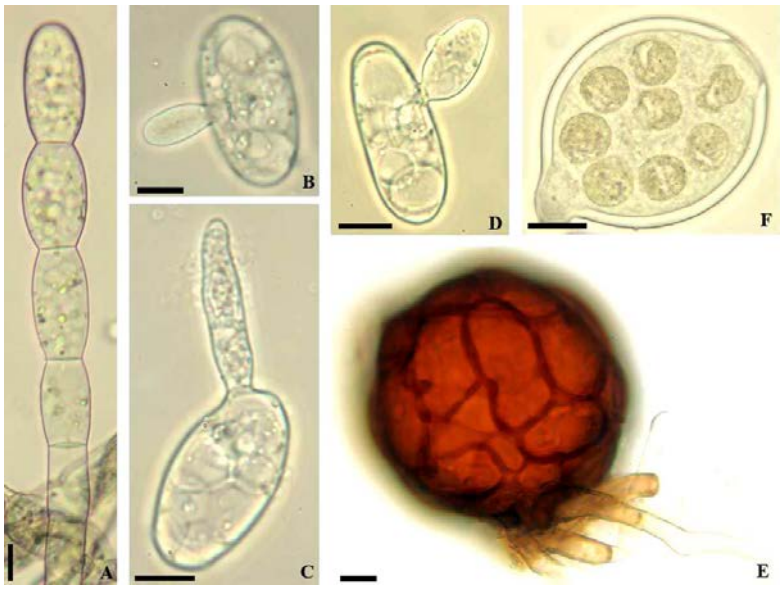


Fig. 68. *Podosphaera delphinii*. A: Conidiophore; B–D: Conidia with germ tubes; E: Chasmothecium; F: Ascus. Scale bars = 10 µm.

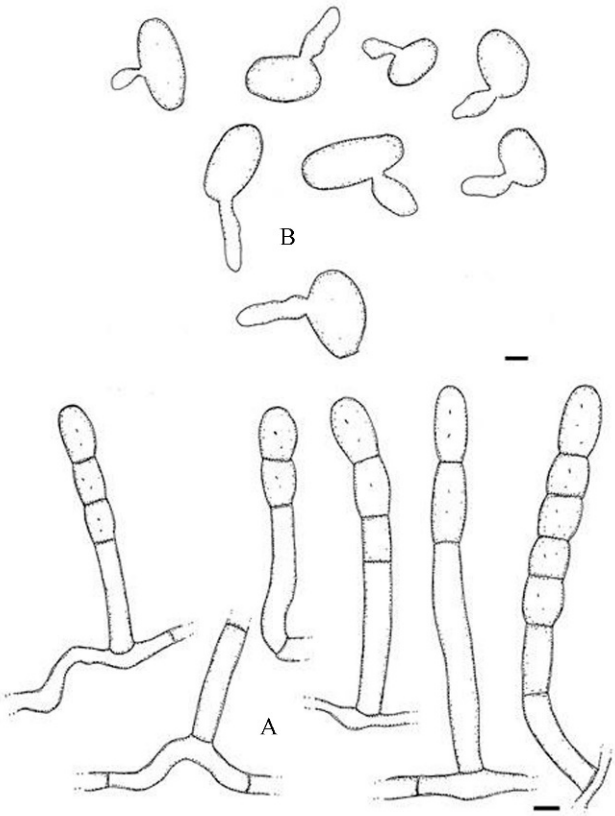


Fig. 69. *Podosphaera delphinii*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Podosphaera epilobii (Wallr.) U. Braun & S. Takam. Figs. 70, 71

Material examined: Germany, Schleswig-Holstein, Kreis Plön, Plöner See, Prinzeninsel, on *Epilobium hirsutum*, 15 Jul. 2006, A. Schmidt, KM 220 (KR-M-0022014).

The examined material on *Epilobium hirsutum* agrees well with previous descriptions, including Paulech (1995: 73–73) and Braun & Cook (2012: 134), except for longer conidiophore foot-cells and consistently formed brevitubus subtype in the present germination experiments. The characteristics of this material can be summarised as follows: Conidiophores erect, straight, composed of a long foot-cell, 55–125 × 10–12 µm, followed by 0–2 short cells, basal septum at the junction with the mother cell; conidia broad ellipsoid-ovoid, doliiform, with fibrosin bodies, 22.5–31 × 16.5–20 µm, length/width ratio 1.3–1.6, on average 1.4, with a single germ tube, perihilar to lateral, uniformly short, about 10–30 µm long, stubby, subcylindrical, clavate, maximum width in the middle or somewhat irregular, consistently aseptate (brevitubus subtype of Fibroidium type, longitubus pattern not observed).

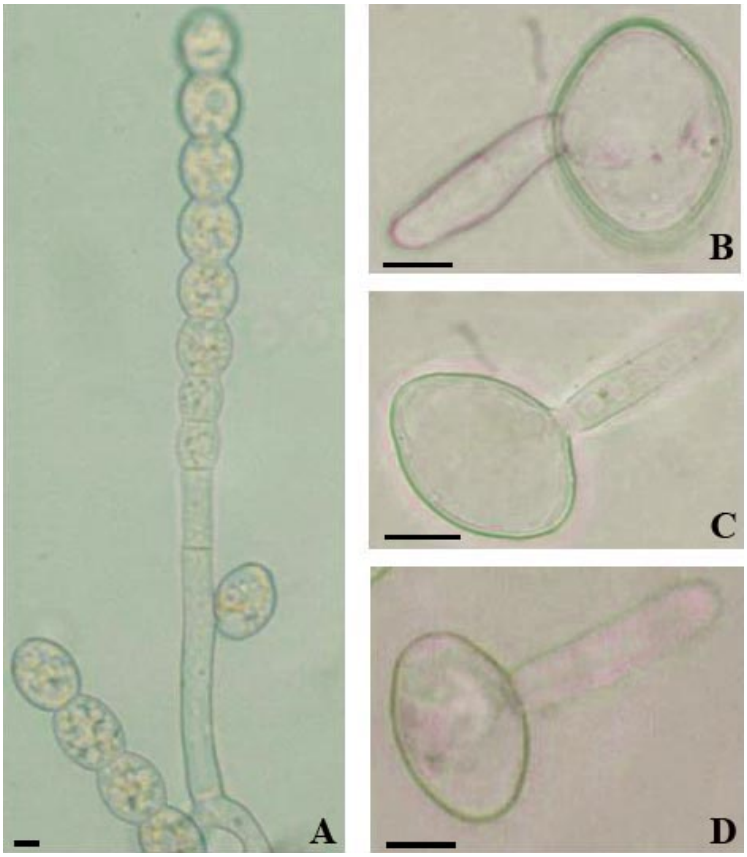


Fig. 70. *Podosphaera epilobii*. A: Conidiophore; B–D: Conidia with germ tubes. Scale bars = 10 µm.

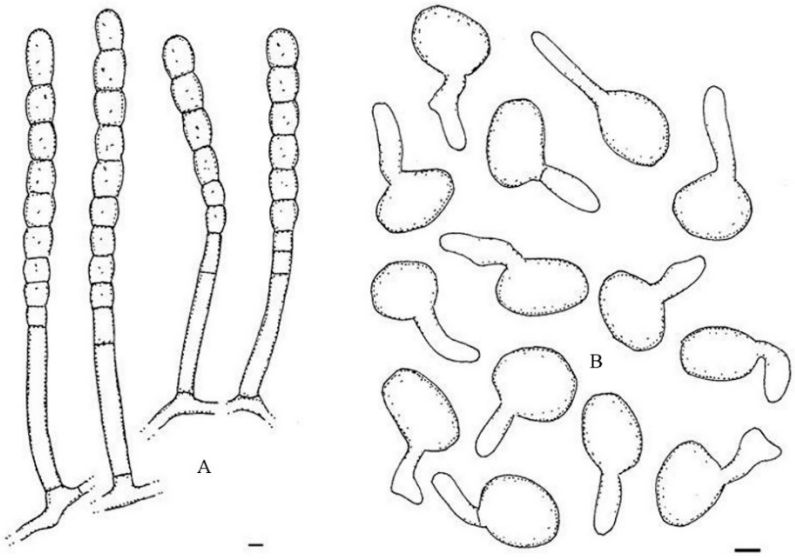


Fig. 71. *Podosphaera epilobii*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Podosphaera erigerontis-canadensis (Lév.) U. Braun & T.Z. Liu Figs. 72, 73

Material examined: Germany, Schleswig-Holstein, Lübeck, Herreninsel, on *Conyza canadensis*, 29 Aug. 2004, A. Schmidt, KM 199 (KR-M-0021966).

The conidiophores, conidia, and conidial germination of the present collection agree well with previous descriptions, including Braun & Cook (2012: 135). In the latter work, the conidial germination is described but not illustrated. The specimen cited above is characterised as follows: Conidiophores erect, composed of cylindrical foot-cells, 35–60 × 10–11 µm, followed by 1–2 shorter cells; conidia ovoid-ellipsoid, doliiform, with fibrosin bodies, 26.5–34 × 16–22 µm, length/width ratio 1.3–1.9, on average 1.6, with a single germ tube, perihilar to lateral, uniformly stubby, clavate to almost subglobose, sometimes short forked or broadened, with two short arms almost parallel to the conidial side (brevitubus subtype of Fibroidium type). The germinated conidium exhibited in Braun & Cook (2012: 21, fig. 12 F–H) matches well with our own observations.

Fig. 72. *Podosphaera erigerontis-canadensis.* A: Conidiophore; B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm.

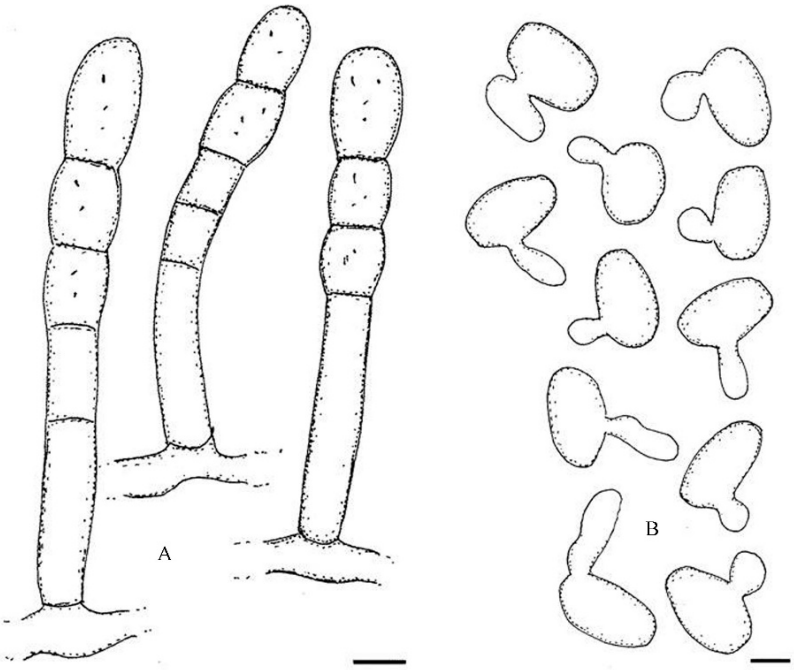


Fig. 73. *Podosphaera erigerontis-canadensis.* A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Podosphaera plantaginis (Castagne) U. Braun & S. Takam. Figs. 74, 75

Material examined: Germany, Schleswig-Holstein, Lübeck, St. Gertrud, Hafenstraße, on *Plantago lanceolata*, 01 Jul. 2006, A. Schmidt, KM 218 (KR-M-0022019).

The conidiophores and conidia in the present specimens coincide well with previous descriptions, including Paulech (1995: 87–88) and Braun & Cook (2012: 155). However, the conidial germination is not described in the latter work. The collection cited above is characterised as follows: Conidiophores erect, foot-cells cylindrical, 40–70 × 10–12 µ, followed by 0–2 shorter cells; conidia ellipsoid-doliiform, with fibrosin bodies, 28–36 × 18–21.5 µm, length/width ratio 1.5–2, on average 1.7, with a single germ tube, perihilar to lateral, stubby, 7–20(–40) µm long, subcylindrical, knob-like, hooked or with two arms almost parallel to the conidial side.

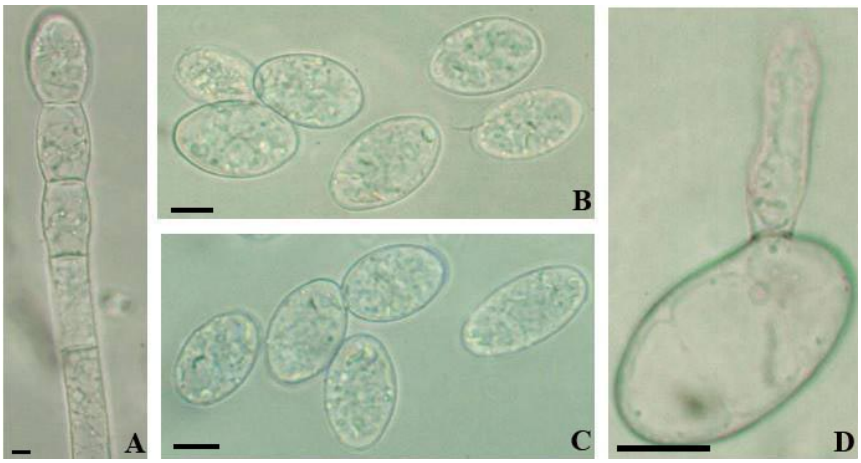


Fig. 74. *Podosphaera plantaginis*. A: Conidiophore; B, C: Conidia; D: Conidium with germ tube. Scale bars = 10 µm.

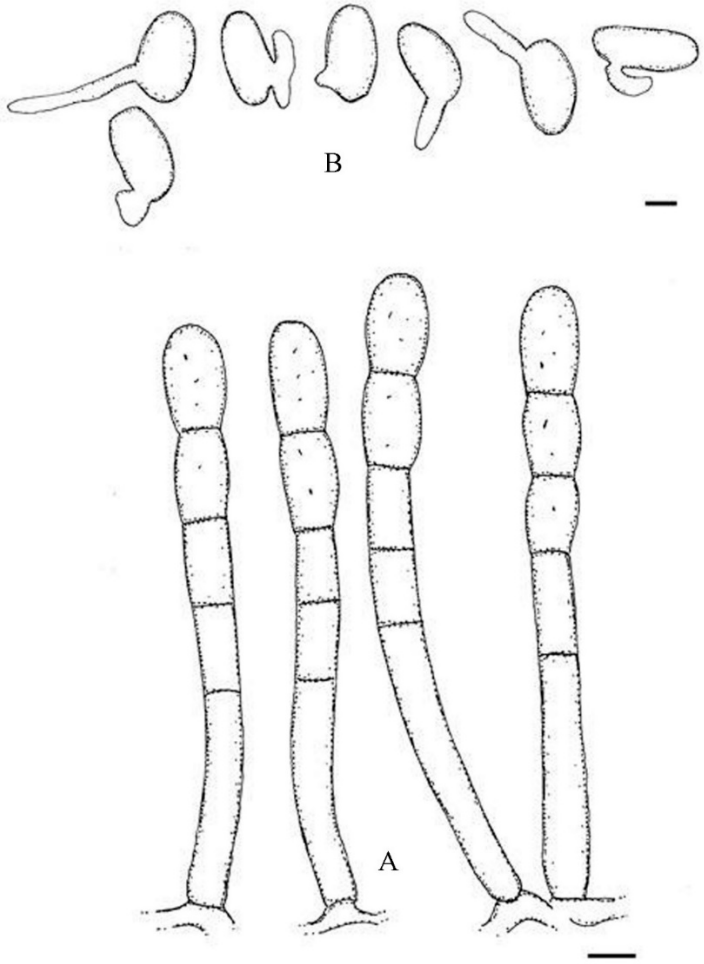


Fig. 75. *Podosphaera plantaginis*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Pseudoidium

Pseudoidium hortensiae (Jørst. ex S. Blumer) U. Braun & R.T.A. Cook Figs. 76, 77

≡ *Oidium hortensiae* Jørst., Skr. Norske Vidensk.-Akad. Oslo, I. Mat.-Naturvidensk. Kl., 1925, **10**: 106, 1926, nom. inval. (Art. 36, Ex. 1).

≡ *Oidium hortensiae* Jørst. ex S. Blumer, Z. Pflanzenkr. Pflanzenschutz **38**: 78, 1928.

Material examined: Germany, Schleswig-Holstein, Lübeck, St. Gertrud, Israelsdorf, on *Hydrangea macrophylla*, 1 Sep. 2017, A. Schmidt KM 338 (KR-M-0049599).

This species was described in detail and illustrated in Bolay (2005: 105) and Braun & Cook (2012), including peculiarities of the conidial germination pattern provided in the latter paper. A detailed description was also published in Schmidt & Scholler (2011), including a reference to the occurrence of 5–6-celled conidiophores on both leave surfaces besides "common" 2–3-celled ones. The characteristics of the present collection agree well with previous descriptions, except for uniformly multicellular conidiophores (4–8-celled). The conidia were 30.5–49 × 14–20 µm, length/width ratio 1.7–3.4, on average 2.2, germ tubes (Pseudoidium type) subapical, short, apex multilobed (lobatus pattern), some germ tubes oblong cylindrical (longitubus pattern), with unlobed apex.

The nomenclature and typification of *Oidium hortensiae* were discussed in detail in Shin et al. (2019). Phylogenetically, this species pertains into the *Erysiphe aquilegiae* complex (clade), composed of numerous at least in some cases morphologically differentiated species of *Erysiphe* sect. *Erysiphe* which are, however, not or barely distinguishable in rDNA ITS analyses. Multi-locus analyses are necessary for better resolutions within this complex of closely allied species. In Shin et al. (2019), it was emphasized that the status and identity of the hortensia powdery mildew being unresolved, but might represent a species of its own. The peculiar characteristics of the conidiophores, characterized by forming multi-celled structures, vs. consistently or usually 2–3-celled conidiophores in other species of the *E. aquilegiae* complex, are in favour of a species of its own. However, some requirements are in addition necessary for a final conclusion, viz., either sequence data retrieved from the lectotype or, when not possible, an appropriate epitype (material collected in Sweden) and an ex-epitype sequence, above all as rDNA sequences obtained from *Hydrangea* spp. in different regions of the world do not cluster together within the *E. aquilegiae* clade (Takamatsu et al. 2015, Shin et al. 2019). Therefore, we prefer for the time being to keep this species as *Pseudoidium hortensiae* and refrain from transferring it to *Erysiphe* until all necessary conditions are fulfilled.

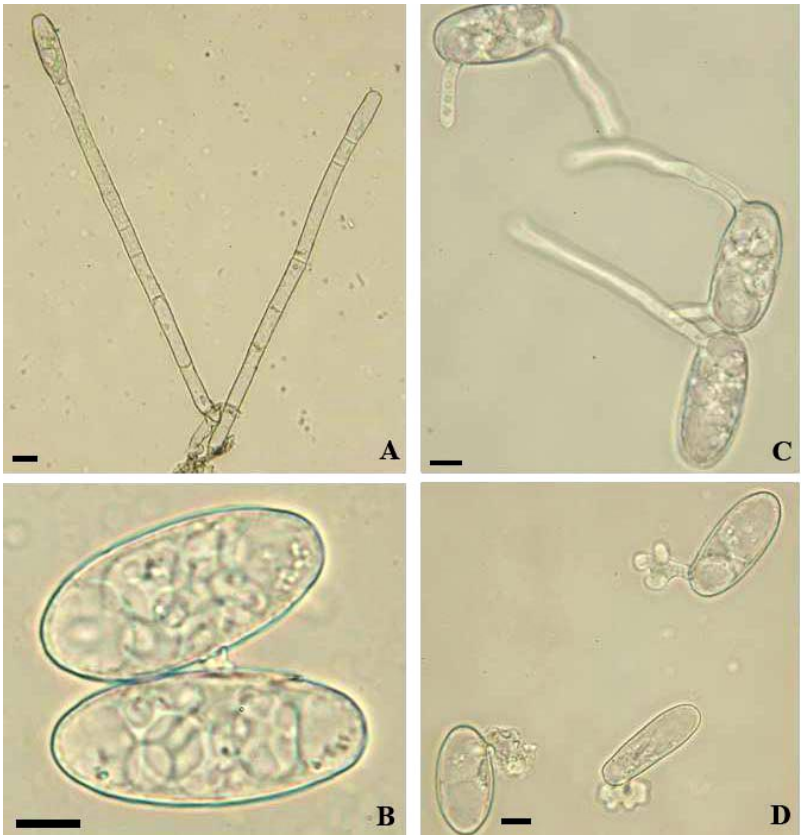


Fig. 76. *Pseudoidium hortensiae*. A: Conidiophores; B: Conidia; C, D: Conidia with germ tubes. Scale bars = 10 µm.

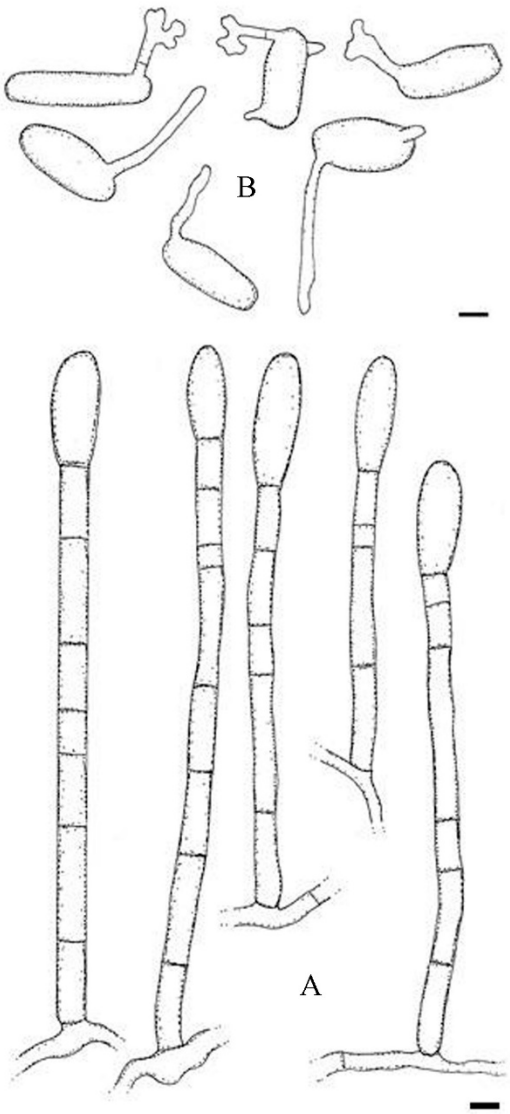


Fig. 77. *Pseudoidium hortensiae*. A: Conidiophores; B: Conidia with germ tubes. Scale bars = 10 µm.

Discussion

The taxonomic significance of the different conidial germination patterns evolved gradually, beginning with Neger's (1902) germination experiments. A first attempt to categorise the particular germination patterns and their associations to powdery mildew genera was made by Hirata (1955), who introduced four main types: *polygoni*, *cichoracearum*, *pannosa* and *fuliginea*, named after the epithets of representative species showing in each case the typical characteristics. Braun (1977) used this system, but merged the *pannosa* and *fuliginea* type and proposed the term "*Sphaerotheca* type" for the conidial germination patterns characteristic for *Podosphaera* and *Sphaerotheca* species. Zaracovitis (1965) left the common path and described three groups, A, B and C, mainly according to germination rates. Braun et al. (2002) linked the particular germination types to subgenera of the anamorph-typified genus *Oidium* (later raised to genus level) in a revised classification of the *Erysiphaceae* and renamed Hirata's germination types to reflect the relations of these types to the asexual morphs of particular genera, so that *polygoni*, *cichoracearum*, *pannosa* and *fuliginea* were called respectively *Pseudoidium*, *Reticuloidium* (later *Euoidium*), *Fibroidium* and *Magnicellulatae* types. These basic types, linked to the particular powdery mildew genera, provide important supplementary characteristics that are relevant for diagnostic, phylogenetic and taxonomic purposes, but they are not sufficient to cover the whole variation of conidial germination patterns within powdery mildews worldwide.

Therefore, Braun & Cook (2012: 15–22) proposed a comprehensive and detailed new system of conidial germination types, subtypes and patterns, reflecting basic types linked with particular powdery mildew genera and sections, but also specific variations characteristic for particular species.

The individual germination patterns may be influenced by air humidity, temperature, light, and the particular substrate (agar surface, glass, plastic, onion epidermis and other plant surfaces). Braun (1977) tested the conidial germination on onion epidermis and glass, but did not find basic differences, and he performed his experiments under day light conditions and compared the results with those of Zaracovitis (1965), who carried out his experiments in the dark, but did also not find significant differences. On the other hand, Cook (in Braun & Cook 2012) found best results, comparable to the germination on the natural host, when the conidia were germinated on plastic (plastic Petri dishes). He outlined and recommended a standard protocol in Braun & Cook (2012: 23).

The treatment of conidia in a dry chamber or at first a pre-treatment (12 hrs) in a dry chamber followed by keeping the conidia in a moist chamber for about 24 hrs led to different reactions depending on the powdery mildew species involved. In some cases, differences in the germination rates and patterns between treatments in dry and moist chambers could not be observed, as for instance in *Arthrocladiella mougeotii*, *Erysiphe aquilegiae*, *E. cruchetiana*, *E. buhrii*, *E. pseudoregularis*, *Podosphaera amelanchieris*, and *P. epilobii*. In other cases, the treatment in a dry chamber or, above all, the pre-treatment of the conidia in a dry chamber followed by a transfer into a moist chamber for the final germination yielded higher germination rates and furthered the formation of shorter germ tubes with

well-developed terminal conidial appressoria. This was particularly evident in numerous species of the genus *Erysiphe* in which the dry treatments increased the percentage of short germ tubes with distinctly lobed conidial appressoria (lobatus pattern) and reduced the percentage of germinated conidia showing longitubus pattern, when occurring in the species concerned. This phenomenon was found in *Erysiphe alphitoides*, *E. astragali*, *E. azaleae*, *E. euonymi*, *E. flexuosa*, *E. howeana*, *E. pisi*, *E. pseudoacaciae*, *E. trifoliorum*, and also in *Neoerysiphe galii*, i.e., it seems to be rather common in and characteristic for *Erysiphe* spp., although not occurring in all species of this genus. Furthermore, in species of *Golovinomyces* sect. *Depressi*, it seems that pre-treatments of conidia under dry conditions may also increase the percentage of germinated conidia with short germ tubes and swollen terminal conidial appressoria (the common pattern within the Euoidium type) in proportion to conidia showing the longitubus pattern germination. This was observed in *Golovinomyces depressus*, *G. echinopis*, and *G. verbasci*. However, it is still necessary to examine additional species belonging to sect. *Depressi*.

The diagnostic and taxonomic relevance of the particular conidial germination types, above all on generic level, is evident and well known for a long time (see above). However, there is also a hitherto little explored potential for using the individual conidial germination patterns of particular species for diagnostic and taxonomic purposes, above all due to the lack of corresponding data for numerous powdery mildew species and usually lacking examinations of conidia from wider ranges of hosts in species occurring on numerous hosts. There is only a limited number of publications with detailed descriptions and illustrations of the conidial germination of powdery mildew species. Numerous regional monographic treatments of powdery mildews have been published. Most of them, such as, for instance, Chen et al. (1987) and Fakirova (1991), do not contain any details on the germination of conidia. In several other works, only a few conidia with germ tubes are depicted (e.g., Grigaliūnaitė 1997, Voytyuk et al. 2009, Liu 2010). There are only a few monographic works on powdery mildews in which the asexual morphs have been described and illustrated in detail (Shin 2000 being an excellent example). Publications focusing on conidial germination patterns of wider ranges of powdery mildew species are also very limited (such as Neger 1902; Hirata 1942, 1955; Zaracovitis 1965, and the present work). The capacity to use germination pattern for diagnostic and taxonomic purposes on species level is varying and differs from genus to genus. The conidial patterns in species of *Golovinomyces* sect. *Golovinomyces* and *Podosphaera*, above all, sect. *Sphaerotheca* subsect. *Magnicellulatae*, are rather uniform and little diagnostic on species level in most cases. The conidial germination patterns of *Erysiphe* spp., including subtypes, length of germ tubes, septation, and type and structure of the lobed conidial appressoria, are much more verified and provide, at least in some cases, useful differences, even between allied species.

Erysiphe species on legumes provide a good example. There are, for instance, clear differences in the asexual morphs and conidial germination between *Erysiphe pisi* and *E. cruchetiana* (the latter often considered a variety of *E. pisi*), which support the reinstatement of the original treatment of *Erysiphe* on *Ononis* spp. as species of its own. The position and status of *E. palczewskii* on *Caragana arborescens* as a separate species of its own has been phylogenetically proven (Takamatsu et al. 2015). The characteristics of the conidial germination of this species are close to those found for *E. trifoliorum*, but the conidiophores are significantly narrower, 6–8.5 µm wide, and the foot-cells of the conidiophore are curved-sinuous at the very base. Germinated conidia of *E. pisi* on *Lotus corniculatus* and *Medicago* spp. can be distinguished from those of *E. trifoliorum* by forming germ tubes with a single septum further away from the point of attachment (up to the middle or even in the upper half), vs. closer to the base in *E. trifoliorum*. This difference allowed to identify an asexual morph on *Lotus corniculatus* as *E. pisi*, although *Lotus* spp. are hosts of *E. pisi* as well *E. trifoliorum* (Braun & Cook 2012). The asexual morph and conidial germination of *E. pseudoacaciae* is described for the first time in detail and turned out to be characteristic and diagnostic, differing from the anamorph of *E. trifoliorum* in having consistently straight and narrower conidiophore foot-cells, 6.5–9 µm wide. *E. astragali*, *E. baeumleri*, *E. intermedia* (≡ *Microsphaera trifolii* var. *intermedia*), and *E. trifoliorum* are usually considered a complex of closely allied, very similar species (Braun 1987, 1995; Braun & Cook 2012), which is supported by the corresponding characteristics of the conidiophores and conidia, as well as the patterns of the conidial germination of these species, which are very similar to each other and barely distinguishable. This complex urgently requires more comprehensive phylogenetic analyses based on a broader array of hosts from a wider geographical range. First phylogenetic examinations published by Takamatsu et al. (2015) and Ellingham et al. (2019) support *E. astragali* and *E. baeumleri* as separate species, clustering away from *E. trifoliorum*. Furthermore, sequences retrieved from *Erysiphe* on *Lupinus* spp. clustering close to sequences obtained from *E. trifoliorum* on *Trifolium* spp. (see Ellingham et al. 2019) confirm the

close affinity of *E. intermedia* and *E. trifoliorum*, the former previously considered a variety of the latter species.

Another striking example relates to species of the genus *Phyllactinia*. *Phyllactinia guttata*, now confined to *Corylus* spp., was previously applied in a very broad sense, covering collections on a wide range of hosts belonging to numerous plant families (Salmon 1900, Blumer 1967, Braun 1987, 1995). *Phyllactinia betulae*, *Ph. corni*, *Ph. guttata* s. str. (on *Corylus*), *Ph. hippophaes* and *Ph. mali*, examined in the present study, were previously considered to be part of a single species, referred to as *Ph. guttata* s. lat. The conidial germination patterns of these species are all different from each other. The uniformly short germ tubes with distinctly lobed terminal conidial appressorium in *Ph. guttata* s. str. are obviously different from the patterns found in the other examined *Phyllactinia* species, although all of them were previously considered a single species. The conidial germination patterns of powdery mildews are undoubted much more diverse and specific than previously expected, but much more examinations on a much broader geographical basis and on a much wider range of species and hosts are urgently necessary.

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Addresses of the authors

Anke Schmidt, Holunderweg 2 b, 23568 Lübeck, Germany.
(E-mail: apoas@web.de)

Uwe Braun, Martin-Luther-Universität, Institut für Biologie, Bereich Geobotanik und Botanischer Garten, Neuwerk 21, 06099 Halle (Saale), Germany.
(E-mail: uwe.braun@botanik.uni-halle.de)

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