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Identification of anamorphic Indian powdery mildews (*Erysiphaceae*) based on sequence analyses

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Abstract

Powdery mildews (*Erysiphaceae*) are one of the most important groups of pathogenic fungi causing detrimental diseases on wild and cultivated plants worldwide, with significant economic impacts. Most previous records of powdery mildews were based on morphological features of the anamorphs, which can be extremely difficult without sequencing in this fungal group. Hence, identifications of anamorphic powdery mildew specimens from India have been identified based on morphological and DNA analyses in the present study. The phylogenetic analyses were based on ITS and partial nuc 28S rDNA D1-D2 regions. *Aster amellus* is a new host record for *Golovinomyces ambrosiae* and the first record on a host of the genus *Aster* (s. str.). An anamorphic specimen found on *Tecoma fulva* subsp. *guarume* was identified as *Erysiphe peckii*, which is a North American powdery mildew predominately found on *Campsis radicans*. This is the first record of *E. peckii* on the host genus *Tecoma*. *Ipomoea triloba* has been verified as a new host for *E. fallax* and *Azadirachta indica* and *Nicandra physalodes* are new host records for *E. aquilegiae* s. lat. (commonly referred to as the *E. aquilegiae* complex). Furthermore, the second records (based on ITS sequences) of *E. hosagoudarii* and *E. santalicola* are included. The identifications of *E. lespedezae* (on *Bauhinia purpurea*), *E. pseudolonicerae* (on *Cocculus hirsutus*), *E. quercicola* (on *Acacia auriculiformis*) and *Leveillula clavata* on *Euphorbia leucocephala* have been confirmed. *L. taurica* on *Cyamopsis tetragonoloba* is described, illustrated and discussed. The present analysis provides new host records and reports for India and highlights the difficulty of identifying the anamorphs of powdery mildews without sequence analyses.

Keywords – *Erysiphe* – *Golovinomyces* – *Helotiales* – ITS+28S – *Leveillula* – *Maharashtra* – *Phyllactinia*

Introduction

Powdery mildews are a widespread and economically significant group of plant pathogens, affecting a vast array of crops, ornamental plants, and wild species (Bradshaw et al. 2024c). These

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fungi, belonging to the family *Erysiphaceae*, are obligate biotrophs easily recognizable by their characteristic white, powder-like appearance on the surfaces of leaves, stems, and flowers.

The Indian subcontinent, with its vast territory and rich biodiversity, provides an extensive array of potential hosts for powdery mildew fungi. This region's plant diversity has attracted attention from researchers aiming to study the distribution of these fungal pathogens. Surveys focused on the powdery mildews of India, such as those conducted by Paul & Thakur (2006) and Hosagoudar & Agarwal (2009), have revealed significant insights into the ecology and prevalence of these fungi across different regions of the subcontinent.

Except for some regions in the north, particularly those at higher elevations, the Indian climate is primarily tropical and subtropical. These warm, humid conditions are conducive to the development of powdery mildew anamorphs, which represent the asexual, conidium-producing stage of the fungus. However, this same climate tends to inhibit the formation of chasmothecia, the sexual fruiting bodies (teleomorphs).

The predominance of anamorphs, and the corresponding scarcity of teleomorphs in these environments, poses a significant challenge for accurately identifying powdery mildew species. Anamorphic stages often exhibit morphological similarities across closely related species, and environmental factors can further complicate their identification.

Given these challenges, molecular analyses have become the most reliable method for the accurate identification of anamorphic powdery mildew specimens. DNA-based techniques, such as sequencing of the ITS regions, provide a more definitive approach to species identification. These molecular methods allow for the detection of genetic differences between closely related species, even when morphological traits overlap or vary.

In regions like India, where teleomorphs are infrequent, molecular techniques not only enable accurate identification but also help to clarify the phylogenetic relationships among powdery mildew species. Understanding the genetic diversity and host specificity of these fungi is crucial for managing plant diseases caused by powdery mildews, especially in agriculturally important crops where they pose a serious threat to yield and quality.

Through continued surveys and advanced molecular techniques, researchers can deepen their understanding of powdery mildew diversity in India, potentially uncovering new species and host associations, while also developing more effective strategies for disease management.

Materials & Methods

Sample collection, morphological examination, and deposition

Fresh specimens were collected during field studies in Maharashtra, India. Herbarium specimens were prepared by pressing and drying in a common plant press. Morphological examinations of fresh samples were performed in tap water + cotton blue (aniline blue). Dried herbarium specimens were put into drops of lactic acid, gently heated, and stained with cotton blue. Microscopic examinations were carried out using an Olympus BX50 light microscope. Duplicates of the herbarium specimens are deposited at the following herbaria: Ajrekar Mycological Herbarium at Agharkar Research Institute, Pune (M.S.) India, Herbarium of Martin Luther University, Institute of Botany, Department of Geobotany and Botanical Garden, Halle (Saale), Germany (HAL), and at the Larry F. Grad Mycological Herbarium of the North Carolina State University, Raleigh, USA (NCSLG). Specimens deposited at the latter herbarium were used for sequence analyses.

DNA extraction, PCR amplification and sequencing

DNA extractions were done using the Chelex method (Hirata & Takamatsu 1996, Walsh et al. 1991). Polymerase chain reaction (PCR) was carried out for the ITS region using the primer pairs PM10/PM2 (Bradshaw & Tobin 2020). PCR specs for each reaction included 35.7 µl of molecular grade water, 5 µl of Dream Buffer, 4 µl of 2% BSA, 1 µl of each the forward and reverse primers at a 10 µm concentration, 1 µl of a 10 mM DNTP concentration, 2 µl of DNA and 0.3 µl of Dream at a 5U/µl concentration. The annealing temperature was set to 58 degrees. Crude amplicons were sent in for cleaning up and sequencing to Azenta Biotech (USA).

Table 1 Lists of taxa, hosts, vouchers, collection localities, and GenBank accession numbers of the specimens examined in the current study.

Taxa	**Host**	**Voucher** (NCSLG)	**Collection Locality**	**ITS GenBank Number**
Erysiphe aquilegia s. lat.	*Azadirachta indica*	24510	India	PP976625
E. aquilegia s. lat.	*Nicandra physaloides*	24515	India	PP976630
E. fallax	*Ipomoea triloba*	24523	India	PP992298
E. hosagoudarii	*Nycanthes arbor-tristis*	24509	India	PP976624
E. lespedezae	*Bauhinia purpurea*	24514	India	PP976629
E. peckii	*Tecoma fulva* subsp. *guarume*	24517	India	PP976632
E. pseudolonicerae	*Cocculus hirsutus*	24519	India	PP976634
E. quercicola	*Acacia auriculariformis*	24520	India	PP976635
E. quercicola	*Bixa orellana*	24518	India	PP976633
E. santalicola	*Santalum album*	24449	India	PP681085
Golovinomyces ambrosiae	*Aster amellus*	24513	India	PP976628
Leveillula clavata	*Euphorbia leucocephala*	24516	India	PP976631
L. taurica	*Cyamopsis tetragonoloba*	24511	India	PP976626
Phyllactinia moricola	*Morus alba*	24512	India	PP976627

Phylogenetic analysis

A phylogenetic tree was constructed from ITS sequences of the specimens from the present study and selected *Erysiphe* species from GenBank based on the analyses by Bradshaw et al. (2023, 2024a, 2024b). Sequences were aligned and edited using MUSCLE in MEGA11:Molecular Evolutionary Genetics Analysis Version 11 (Tamura et al. 2021). A GTR+G+I evolutionary model was used for phylogenetic analyses as it is the most inclusive model of evolution and includes all other evolutionary models (Abadi et al. 2019). A fixed parameter-rich model (such as GTR+G+I) can be used in lieu of running a test to select the most suitable evolutionary model (Abadi et al. 2019). The phylogeny was inferred using Bayesian analysis of the combined loci using a Yule tree prior (Gernhard 2008) and a strict molecular clock, in the program BEAST version 1.10.4 (Suchard et al. 2018). A single MCMC chain of 107 steps was run, with a burn-in of 10%. Posterior probabilities were calculated from the remaining 9,000 sampled trees. A maximum clade credibility tree was produced using TreeAnnotator version 1.10.4 (part of the BEAST package). Stationarity was confirmed by running the analysis multiple times, which revealed convergence between runs. The resulting tree was visualized using FigTree ver. 1.3.1 (Rambaut 2009). A maximum likelihood analysis was accomplished using raxmlGUI (Silvestro & Michalak 2012) under the default settings with a GTR+G+I evolutionary model. Bootstrap analyses were conducted using 1000 replications (Felsenstein 1985).

Results

Phylogenetic analyses

All newly generated sequences were submitted to GenBank (Table 1). The phylogenetic analyses evaluated a total of 43 powdery mildew specimens collected from throughout the world.

Of these 43 specimens, 12 were sequenced for the current study from India. A maximum clade credibility tree was constructed using Bayesian analyses from the ITS+28S region (Fig. 1). Posterior probabilities ≥ 90 are displayed followed by bootstrap values greater than 70% for the maximum likelihood (ML) analyses conducted. The representative maximum clade credibility tree is illustrated in Fig. 1.

Each taxon with sequence data from *Erysiphe* forms a monophyletic group with strong support with reliable identifications/sequences from GenBank except for specimens from the *E. alphitoides* complex which needs other loci for species confirmation (Bradshaw et al. 2023b).

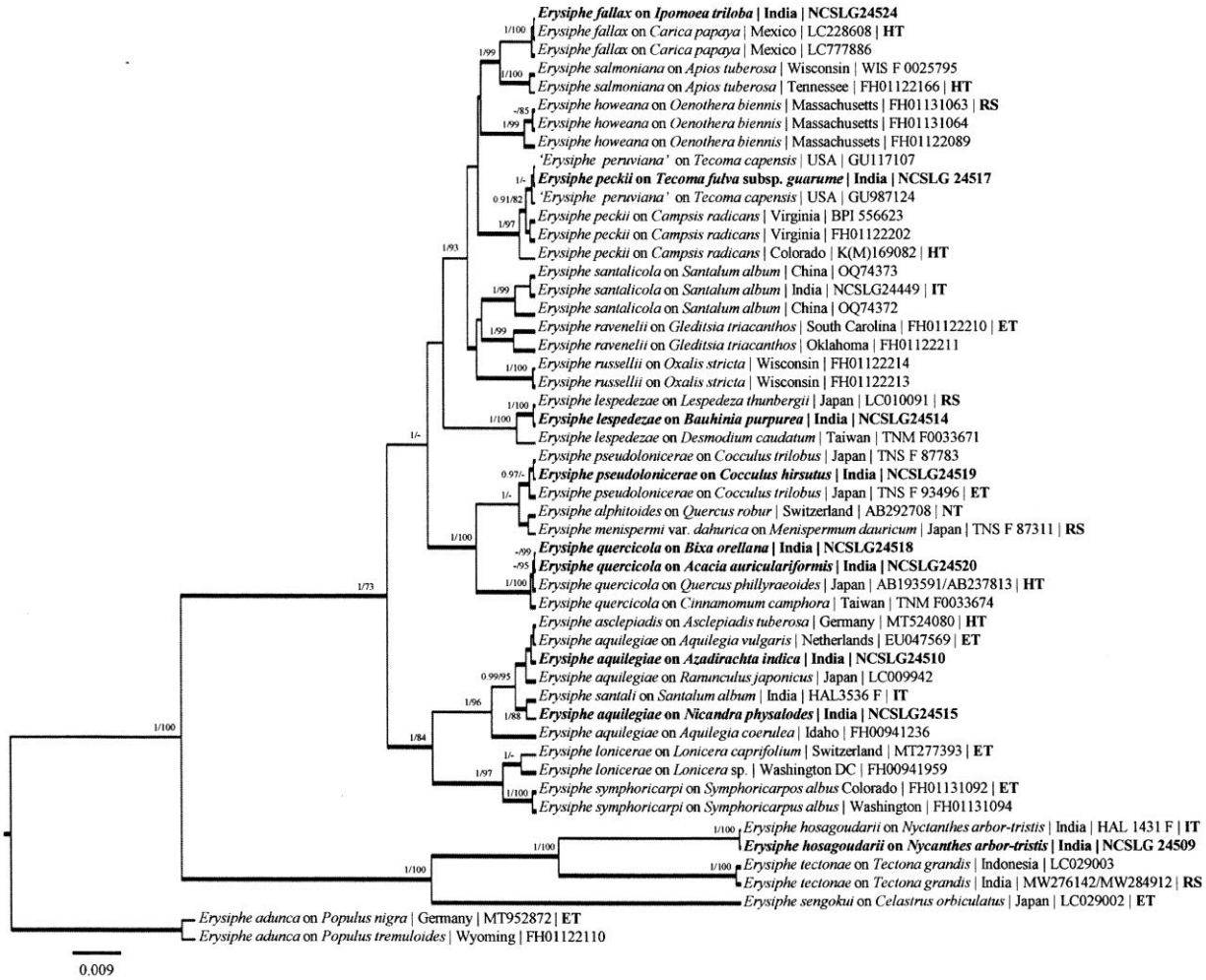

Fig. 1 – Bayesian maximum clade credibility tree of the ITS regions of select species from the genus *Erysiphe*. Posterior probabilities ≥ 90 are displayed followed by bootstrap values greater than 70% for the maximum likelihood (ML) analyses conducted. Taxa in bold were sequenced for the current study. ET=ex epitype sequence, HT=ex holotype sequence, IT=ex isotype sequence, NT=ex neotype sequence, RS=reference sequence.

Taxonomic results

Erysiphe aquilegiae DC., Fl. franç., Edn 3 (Paris) 5/6: 105 (1815), s. lat. (complex, sensu Bradshaw et al. 2024a).

Material examined – India, Maharashtra, Ambegaon, Ghodegaon, on leaves of *Azadirachta indica*, August 2020, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3496 F, NCSLG24510). Sequences – PP976625 (ITS+28S). India, Maharashtra, Ambegaon, Rajewadi, on leaves of

Nicandra physalodes, September 2021, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3498 F, NCSLG25515). Sequences – PP976630 (ITS+28S).

Notes – The *Erysiphe aquilegiae* complex (*E. aquilegiae* s. lat.) is an insufficiently resolved group of powdery mildews (in ITS analyses). The complex is composed of a wide range of powdery mildews, including many described older species. It was first detected by Takamatsu et al. (2015), followed by comprehensive discussions by Shin et al. (2019) and Bradshaw et al. (2020). Bradshaw et al (2024a) made the first attempts to get better resolutions on the species level using a multilocus approach and introduced the designation "*Erysiphe aquilegiae* complex" for this clade. *Azadirachta indica* (*Meliaceae*) and *Nicandra physalodes* (*Solanaceae*) are new host species for *E. aquilegiae* s. lat. The anamorph on *A. indica* is morphologically characterized as follows: Mycelium white, amphigenous, mainly epiphyllous, loosely effuse, forming patches to dense in severe infections, coalescent, persistent. Hyphae branched, 3–7 µm wide, thin-walled, hyaline, smooth, septate; hyphal appressoria solitary, lobed. Conidiophores arising from the upper surface of the hyphal mother cell, erect, foot cells cylindrical, straight to occasionally flexuous and 25–45 × 9–12 µm, followed by 1–2 shorter cells or occasionally cells about as long as the foot cell. Conidia formed singly, doliiform to cylindrical, 35–48 × 15–18 µm, germ tubes perihilar, 25–64 µm long, terminating in a lobed appressorium. The anamorph on *N. physalodes* shows the follows characteristics: Mycelium amphigenous, effuse or in patches, persistent. Hyphae 4–6 µm wide, thin-walled, hyaline, smooth; hyphal appressoria lobed. Conidiophores arises from upper surface of superficial hyphae, straight or sometimes erect, foot cell cylindrical, 29–34 × 8–10 µm, followed by 1–2 shorter cells, forming conidia singly. Conidia ellipsoid-doliiform, 30–40 × 20–24 µm, germ tubes perihilar, 25–77 µm long, terminating in a lobed appressorium.

Pseudoidium meliacearum (U. Braun) U. Braun & R.T. A. Cook (Braun & Cook 2012), described from Europe on *Melia azedarach* (also *Meliaceae*) belongs to the *E. aquilegiae* complex (Bradshaw et al. 2024a). Diverse hosts of the *Solanaceae* are known to be hosts to these powdery mildews (Takamatsu et al. 2015, Shin et al. 2019, Bradshaw et al. 2020, 2024a), however, *Nicandra physalodes* was not confirmed as a host by molecular means until the current work. Amano (1986) listed only *Oidium* sp. on *A. indica* from India, Niger, and Pakistan, and *Oidium* sp. on *N. physaloides* from India.

Erysiphe fallax C. Blomq., Roon.-Lath. & Fern.-Pavía, in Braun et al., Mycosphere 8(9): 1411 (2017) Fig. 2

Material examined – India, Maharashtra, Mulashi, Ambavane, on *Ipomoea triloba*, October 2021, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3503 F, NCSLG24524). Sequences – PP992298 (ITS+28S).

Known distribution – on *Carica papaya*, Mexico, USA (California); *Ipomoea triloba*, India (Maharashtra); *Macroptilium lathyroides*, USA (Florida).

Notes – Sequences retrieved from the sample on *Ipomoea triloba* coincide with ex-type sequences of *E. fallax*, and the morphology of this anamorphic powdery mildew is also in agreement with *E. fallax*, which was described from papaya in Mexico and California (Braun et al. 2017): Mycelium amphigenous, forming patches or effuse. Hyphae branched, septate, thin-walled, smooth, hyphal cells 10–50 µm long and 3–7 µm wide; hyphal appressoria rarely observed, lobate. Conidiophores arising from the upper surface of the hyphal mother cells, erect, 40–90 µm long, foot cells cylindrical, straight to usually flexuous, sinuous, 15–70 × 5–8 µm, followed by 1–2(–4) shorter cells, 12–25 µm long. Conidia formed singly, primary conidia ovoid, apex rounded, base truncate, secondary conidia broad ellipsoid, longer conidia subcylindrical to cylindrical, 25–45 × (10–)12–17(–18) µm, Ø 34 × 14 µm, length/width ratio 1.8–2.5(–3.3), Ø 2.3, ends truncate or shallowly rounded, a few conidia germinated on the leaves have been observed (germ tubes subterminal, perihilar, short to moderately long, cylindrical to subclavate, apex somewhat swollen, but not lobed.

The detection of *E. fallax* on *Ipomoea* in India is surprising. This species was described from papaya in Mexico and the USA (California). One of the common *Erysiphe* species on *Ipomoea*

would have been expected, viz., *Erysiphe convolvuli* DC. and *E. ipomoeae* (J.M. Yen & Chin C. Wang) H.Y. Hsiao & Y.M. Shen (Bradshaw et al. 2024b). However, *E. fallax* is readily distinguishable from the anamorph of *E. convolvuli* and from *E. ipomoeae*, two species with straight, cylindrical conidiophore foot cells, by having flexuous-sinuous foot cell (Braun & Cook 2012, Hsiao et al. 2022), and the three species are genetically distinct. Poudel & Zhang (2019) detected *E. fallax* on the legume *Macroptilium lathyroides* in Florida, USA.

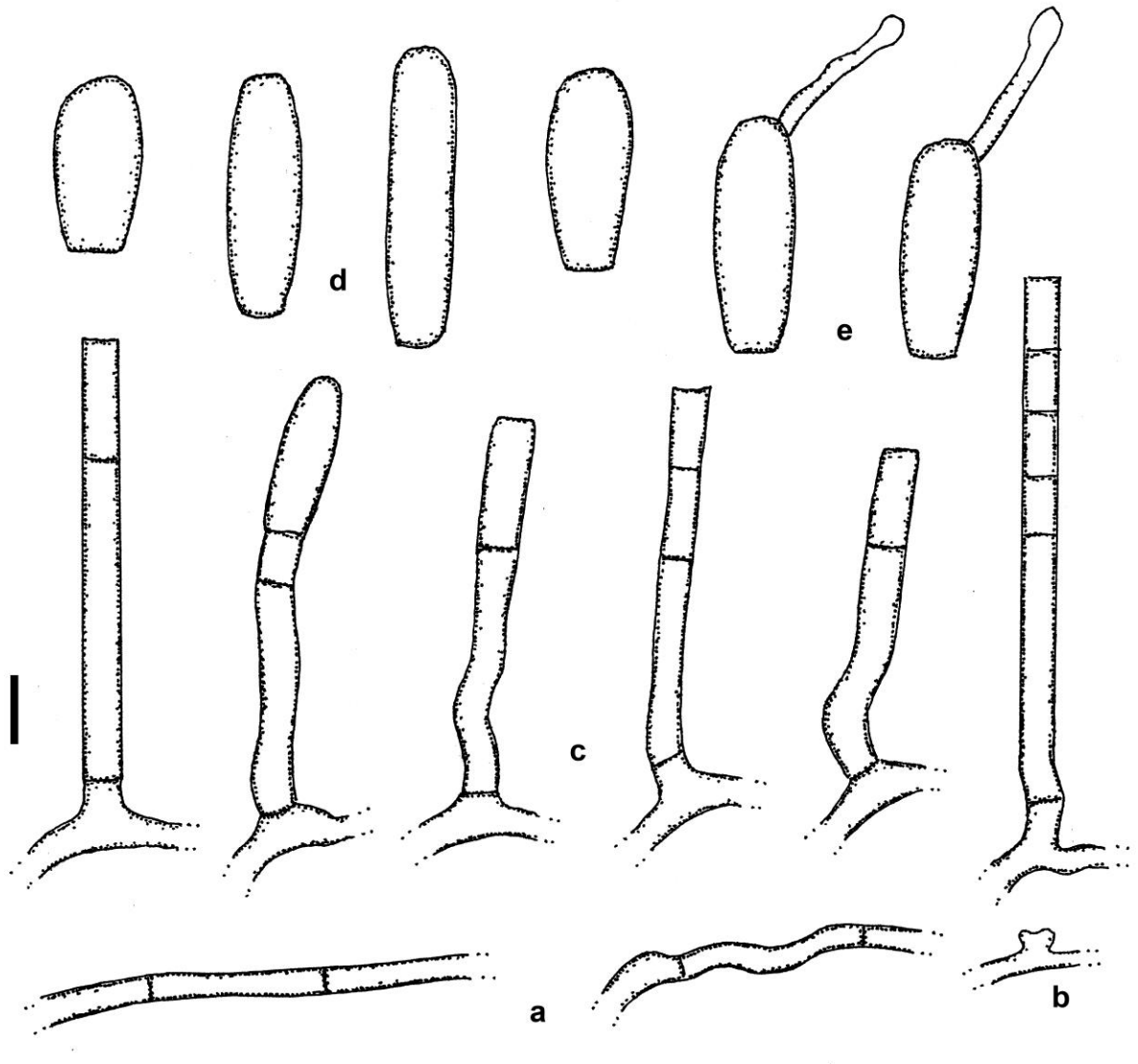

Fig. 2 – *Erysiphe fallax*, on *Ipomoea triloba* (HAL 3503 F). a hyphae. b hyphal appressorium. c conidiophores. d conidia. e conidia with germ tubes. Scale bar = 10 µm. U. Braun del.

Erysiphe hosagoudarii M. Bradshaw, U. Braun & Pfister, Mycologia 115(6): 886 (2023)

≡ *Oidium braunii* Hosag., Sydowia 37: 50 (1984), non *Erysiphe braunii* Y. Nomura, 1997.

≡ *Pseudoidium braunii* (Hosag.) U. Braun & R.T.A. Cook, Taxonomic Manual of the *Erysiphales* (Powdery Mildews): 599 (2012).

Material examined – India, Maharashtra, Baramati, Jalgaon Supe, on leaves of *Nyctanthes arbor-tristis*, February 2022, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3499 F, NCSLG24509). Sequences – PP976624 (ITS+28S).

Known distribution – on *Nyctanthes arbor-tristis*, India (Maharashtra, Tamil Nadu), Sri Lanka.

Notes – Based on multilocus sequence analyses of isotype material of *Oidium braunii* [India, Tamil Nadu, Coimbatore, on *Nyctanthes arbor-tristis*, 28 March 1984, A. Venkata Rao (HAL 1431 F)], Bradshaw et al. (2024a) revealed the phylogenetic-taxonomic position of *Oidium braunii*. The ex-type sequences formed a well-supported species clade in sister position to the Asian *Erysiphe tectonae* (E.S. Salmon) U. Braun & S. Takam. (Braun & Cook 2012: 587). *Erysiphe tectonae*, a species belonging to the *Uncinula* lineage of *Erysiphe* is known from India and Myanmar. The sequences obtained from the sample collected in Maharashtra are in agreement with the ex-type sequences. Amano (1986) listed *Oidium* sp. on *N. arbor-tristis* from Sri Lanka, which probably pertains to *E. hosagoudarii*. *E. hosagoudarii* is morphologically characterized as follows: Mycelium amphigenous, effuse or in irregular patches, finally covering the entire leaf, white, persistent. Hyphae 3–7.5 µm wide, hyaline, branched, septate; hyphal appressoria lobed, mostly solitary. Conidiophores arising from the upper surface of mother cells, erect, 80–250 µm long, foot cells cylindrical, straight, curved or somewhat flexuous at the base, about 50–95 × 6.5–11 µm, followed by 1–2 shorter cells, forming conidia singly. Conidia ellipsoid-ovoid to doliiform-cylindrical, about 23–35 × 11–18 µm, germ tubes at an end, short, conidial appressoria alobate to moderately lobed.

Erysiphe lespedezae R.Y. Zheng & U. Braun, Mycotaxon 18: 142 (1983)

≡ *Erysiphe glycines* var. *lespedezae* (R.Y. Zheng & U. Braun) U. Braun & R.Y. Zheng, Mycotaxon 22: 88 (1985).

= *Oidium caesalpiniacearum* Hosag. & U. Braun, in Braun, Mycotaxon 25: 267 (1986). [Holotype: India Karnataka, Bangalore, on *Bauhinia purpurea* (originally as *Bauhinia* sp.), 1984, V. B. Hosagoudar (HAL 1430 F).] Ex-holotype sequence: MG545902 (ITS+28S).

≡ *Pseudoidium caesalpiniacearum* (Hosag. & U. Braun) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 600 (2012).

Material examined – India, Maharashtra, Purandur, Jawalarjun, on *Bauhinia purpurea*, January 2022, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3505 F, NCSLG24514). Sequences – PP976629 (ITS+28S).

Known distribution – see Braun & Cook (2012: 390), Bradshaw et al. (2024b).

Notes – Bradshaw et al. (2024b) treated and discussed the phylogeny and taxonomy of *Erysiphe lespedezae* in detail. Xu et al. (2018) sequenced type material of *Oidium caesalpiniacearum* and reduced this name to synonymy with *E. lespedezae*. This is a further sequenced Indian collection on *Bauhinia purpurea*, confirming the synonymy of *O. caesalpiniacearum* with *E. lespedezae*. The new specimen on *B. purpurea* is morphologically characterized as follows: Mycelium amphigenous, effuse or forming patches. Hyphae 3–7 µm wide, branched, septate, thin-walled, smooth; hyphal appressoria solitary or in opposite pairs, lobed. Conidiophores arising from the upper surface of hyphal mother cells, erect, foot cells cylindrical, straight to somewhat curved-sinuous, 22–38 × 6–10 µm, followed by 1–2(–3) shorter cells. Conidia formed singly, ellipsoid-ovoid, subcylindrical, 23–38 × 12–19 µm, length/width ratio 1.6–2.2, germ tubes not observed.

Erysiphe peckii (U. Braun) U. Braun & S. Takam., Schlechtendalia 4: 12 (2000) Fig. 3

≡ *Microsphaera peckii* U. Braun, Mycotaxon 15: 125 (1982).

Material examined – India, Maharashtra, Baramati, Botanical Garden of the Tuljaram Chaturchand Colleage, on leaves of *Tecoma fulva* subsp. *guarume*, September 2021, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3491 F, NCSLG24517). Sequences – PP976632 (ITS+28S).

Known distribution – see Braun & Cook (2012: 491), present work.

Illustration (anamorph) – Glawe et al. (2010: Figs. 1–4, as *Erysiphe peruviana*).

Notes – The anamorph found on *Tecoma fulva* subsp. *guarume* is morphologically characterized as follows: Mycelium strictly epiphyllous, effuse or forming irregularly shaped thin, white patches, later confluent, covering the entire leaf blade (infections sometimes causing premature leaf fall). Hyphae superficial, branched at right angles, straight to sinuous, sometimes

strongly sinuous-geniculate, hyphal cells (15–)30–50(–55) µm long and 3–7 µm wide, thin-walled, hyaline, smooth. Hyphal appressoria solitary or two per hyphal cell, rarely more than two, nipple-shaped, slightly to moderately lobate, rarely multilobate, 2–8 µm diam. Conidiophores arising from the upper surface of hyphal mother cells, usually towards one septum, rarely in the middle between two septa, erect, rarely curved throughout, relatively short, (15–)30–60 µm long, foot cells straight cylindrical, 12–25 × 5–9(–10) µm, followed by 1–2 usually shorter cells, basal septum at the junction with the hyphal mother cell or somewhat elevated, to 5(–10) µm. Conidia formed singly, cylindrical, ovoid, ellipsoid-doliiform, 25–42.5 × (9–)12–19 µm, length/width ratio 1.8–3.5.

Glawe et al. (2010) described and illustrated an anamorphic powdery mildew, found in Arizona, USA, on *Tecomaria capensis*, assigned it to *Erysiphe peruviana* (Syd.) U. Braun & S. Takam., and provided ITS sequences (GenBank numbers = GU117107.1 and GU987124). The sequences obtained from the Indian specimen coincide with the sequences from the samples collected in the USA (100% match). The morphological characteristics of the collection from India agrees with the description given in Glawe et al. (2010). Bradshaw et al. (2024b) demonstrated that the North American sequences published by Glawe et al. (2010) form a sister subclade to an ex-type sequence of *E. peckii* (U. Braun) U. Braun & S. Takam., a widespread North American powdery mildew on *Campsis radicans* (Braun & Cook 2012: 491–492), and an additional ITS sequence (LC777874.1) retrieved from '*E. peruviana*' on the South African *Podranea ricasolina* (≡ *Tecoma ricasolina*, *Tecomaria ricasolina*), collected in Mexico. These results show that *E. peckii* is able to infect additional allied hosts of tribe *Tecomeae*, including the genera *Podranea*, *Tecoma*, and *Tecomaria*. *E. peckii* seems to comprise at least two genetically discernable biological races, which needs, however, further examinations.

In any case, it is not justified to assign the anamorphs on *Tecoma* and *Tecomaria* spp. to *E. peruviana* (the anamorph of this species is unknown, Braun & Cook 2012), which is a species of *Erysiphe* sect. *Uncinula* (Takamatsu et al. 2015, Bradshaw et al. 2023a), whereas sequences obtained from *E. peckii* cluster in the *Microsphaera* lineage (Takamatsu et al. 2015, Bradshaw et al. 2024b). So far, sequences of all species of *Erysiphe* sect. *Uncinula* with apically curved-circinate chasmothecial appendages cluster within the *Uncinula* lineage (Bradshaw et al. 2023a). Furthermore, *Tecoma* and *Tecomaria* are genera pertaining to *Bignoniaceae* tribe *Tecomeae* (Olmstead et al. 2009), whereas *E. peruviana* is known on *Handroanthus heptaphyllus* (≡ *Tecoma ipe*) and *H. ochraceus* (≡ *Tecoma ochracea*) from Brazil and Peru (Braun & Cook 2012: 577). The genus *Handroanthus* belongs to the '*Tabebuia* alliance (clade)' which is phylogenetically distant from the *Tecomeae* clade (Olmstead et al. 2009). *Uncinula peruviana* was described from Peru on *Tecoma grandiceps*, which is a synonym of *H. ochraceus*. Since the type material is not preserved, Braun (1987) designated a specimen collected on '*Tecoma* sp.' in Brazil (S-F69004) as the neotype (the identity of the neotype host is unknown, but it can be expected that it is a species of *Handroanthus*, based on the current taxonomy of genera of the *Bignoniaceae*), i.e., *E. peruviana* is probably confined to hosts of the latter genus.

Erysiphe pseudolonicerae (E.S. Salmon) U. Braun & S. Takam., Schlechtendalia 4: 12 (2000)

≡ *Microsphaera alni* var. *pseudolonicerae* E.S. Salmon, Ann. Mycol. 6: 4 (1908).

≡ *Microsphaera penicillata* var. *pseudolonicerae* (E.S. Salmon) Sacc. & Trott., Syll. fung. 22: 24 (1913).

≡ *Microsphaera pseudolonicerae* (E.S. Salmon) S. Blumer, Beitr. Krypt.-Fl. Schweiz 7(1): 351 (1933).

Material examined – India, Maharashtra, Shirur, Kokadewadi, on leaves of *Cocculus hirsutus*, November 2019, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3493 F, NCSLG24519). Sequences – PP976634 (ITS+28S).

Known distribution – see Amano (1986), Braun & Cook (2012: 496), Bradshaw et al. (2024b).

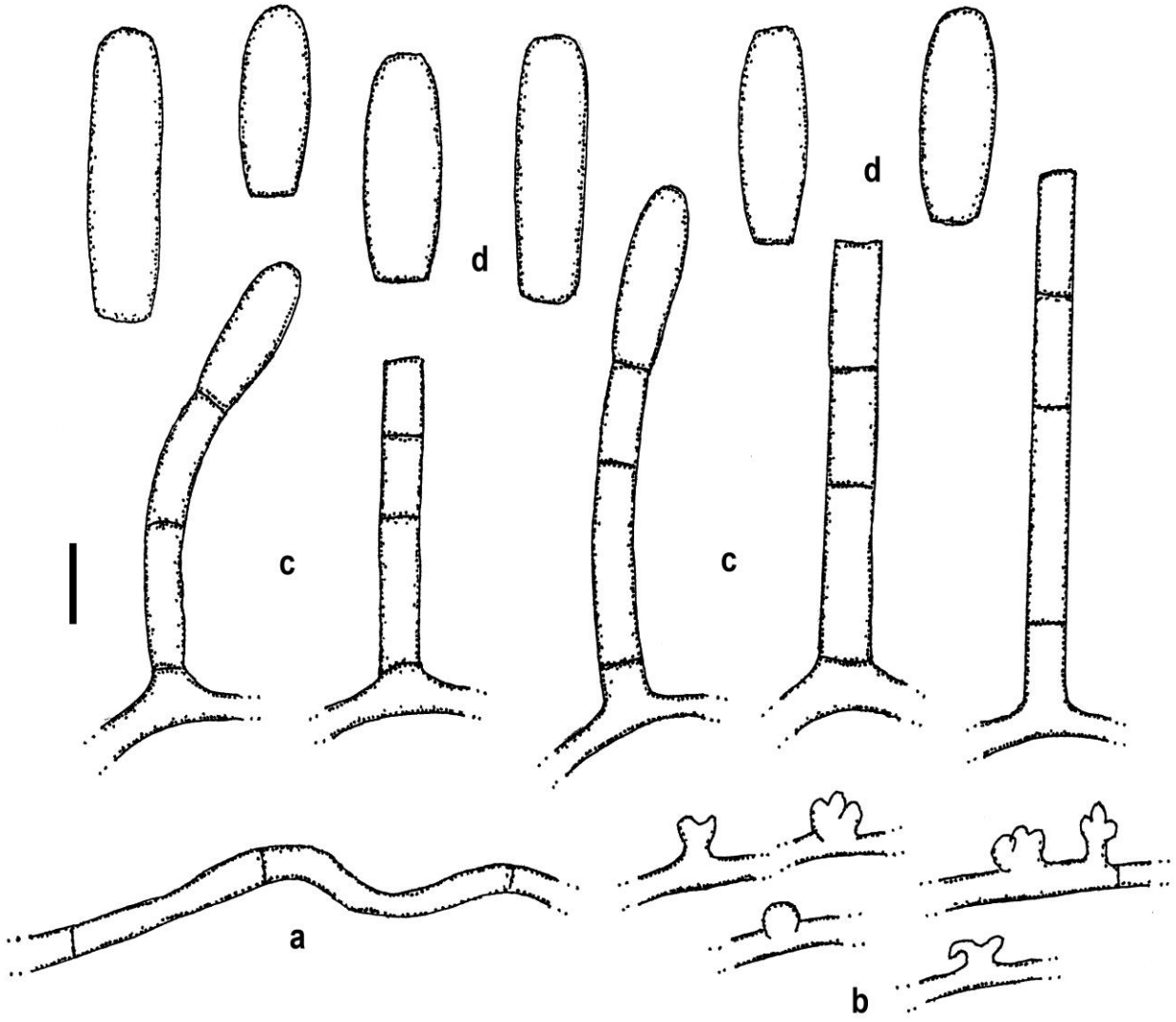

Fig. 3 – *Erysiphe peckii*, on *Tecoma fulva* subsp. *guarume* (HAL 3491 F). a hypha. b hyphal appressoria. c conidiophores. d conidia. Scale bar = 10 µm. U. Braun del.

Notes – Bradshaw et al. (2024a treated the phylogeny and taxonomy of *Erysiphe pseudolonicerae*. The sequences of the present Indian specimen collected on *Cocculus hirsutus* have a 100% agreement with other ITS sequences of *E. pseudolonicerae* in GenBank (see OR424959). The examined new specimen from India is morphologically characterized as follows: Mycelium mainly epiphyllous, occasionally amphigenous, white, in patches or finally sometimes covering entire leaf surface. Hyphae 3–7 µm wide, branched, thin-walled, hyaline, smooth; hyphal appressoria nipple shaped to slightly lobed. Conidiophore arises from the upper surface of hyphal mother cells, erect, foot cells straight, cylindrical, 48–59 × 5–7 µm, followed by 1–2 shorter cells. Conidia formed singly (occasionally adhering in false chains), doliiform to cylindrical, 29–44 × 11–15 µm, germ tubes perihilar, almost straight, 41–89 µm long, occasionally terminating in a lobed appressorium. Given the anamorph description as well as the host identification we identified this specimen as *E. pseudolonicerae*. However, the ITS region is not sufficient to confirm the identify of this species (Bradshaw et al. 2023) and additional loci will need to be sequenced in the future to get absolute confirmation. Amano (1986) listed *Oidium* sp. on *C. hirsutus* from India. Pawar & Patil (2011) recorded *C. hirsutus* from India (Maharashtra) as host of *E. pseudolonicerae*, and Hosagoudar (2013) listed *E. pseudolonicerae* on *C. hirsutus* from Tamil Nadu.

Erysiphe quercicola S. Takam. & U. Braun, in Takamatsu et al., Mycol. Res. 111(7): 819 (2007), nom. cons.

Material examined – India, Maharashtra, Velhe, Madhe-ghat, on leaves of *Acacia auriculiformis*, September 2021, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3501 F, NCSLG24520). Sequences – PP976635 (ITS+28S). India, Maharashtra, Haveli, Gorhe khurd, on leaves of *Bixa orellana*, December 2020, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3504 F, NCSLG24518). Sequences – PP976633 (ITS+28S).

Known distribution – see Limkaisang et al. (2006), Takamatsu et al. (2007), Braun & Cook 2012, Bradshaw et al. (2022a, 2024b).

Notes – *Erysiphe quercicola* is a common widespread powdery mildew with wide host range, and is commonly reported in tropical-subtropical areas (Takamatsu et al. 2007, Braun & Cook 2012, Bradshaw et al. 2022a, 2024b). *Bixa orellana* is a common host of this species. So far, there are only two records of *E. quercicola* on *Acacia auriculiformis*, one from India (Thite et al. 2017) and one from Malaysia (Limkaisang et al. 2006). The morphology of the anamorphs on the Indian specimens on *Acacia auriculiformis* and *Bixa orellana* agree well with previous descriptions, such as Braun & Cook (2012: 497): Mycelium amphigenous, effuse or forming patches, persistent. Hyphae branched, 3–6 μm wide, hyaline, smooth, thin-walled; hyphal appressoria solitary or in opposite pairs, 3–7 μm diam., lobed. Conidiophores erect, arising from the upper surface of hyphal mother cells, foot cells cylindrical, 22–38 × 6–10 μm, straight or curved at the base, followed by 1–2 cells, shorter or about as long as the foot cell. Conidia formed singly; primary conidia obovoid-ellipsoid, apex rounded, base subtruncate, secondary conidia ellipsoid-cylindrical ellipsoid-cylindrical, doliiform, 25–40 × 13–20 μm.

Erysiphe santalicola M. Bradshaw, S.H Wagh, M.B. Kanade & S.V. Thite, Mycologia (2024), Doi 10.1080/00275514.2024.2386230

Material examined – India, Maharashtra, Ambegaon, Shinoli, on leaves of *Santalum album*, December 2020, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3497 F, holotype). Isotype: NCSLG24449. Ex-holotype sequence – PP681085 (ITS).

Known distribution – on *Santalum album*, Asia (China, India).

Notes – Based on results of phylogenetic multilocus analyses and a comparison with sequences retrieved from type material of the Indian *Erysiphe santali* M. Bradshaw, U. Braun & Pfister (≡ *Oidium santalacearum* U. Braun & Hosag., non *Erysiphe santalacearum* V.P. Heluta, Tikhon., Burgyuk. & Dudka, 1987), Bradshaw et al. (2024b) showed that the specimen collected in Maharashtra represents an undescribed species. Sequences obtained from a Chinese sample on *Santalum album* (Li et al. 2023), identified as *Pseudoidium santalacearum* (U. Braun & Hosag.) U. Baun & R.T.A. Cook (Braun & Cook 2012), are identical with sequences obtained from the new species from India, suggesting that *E. santalicola* also occurs in China. *E. santalicola* is morphologically characterized as follows: Mycelium amphigenous, forming circular to irregular thin white patches or effuse. Hyphae colorless, branched, septate, thin-walled, smooth, hyphal cells 40–60 μm long and 2–8 μm wide; hyphal appressoria solitary, occasionally in opposite pairs, almost nipple-shaped, slightly to multilobate, c. 3–8 μm diam.; a single or occasionally two conidiophores arise from the upper surface of hyphal mother cells, position mostly toward one septum, i.e., not in the middle of the mother cell, erect, ca. 40–80 μm long (without conidia), foot cells straight to curved-sinous, 15–30 × 6–9 μm, followed by (1–)2(–3) cells, shorter than the foot cell, about as long as the foot cell or occasionally somewhat longer, 8–25 μm. Conidia formed singly, ellipsoid-cylindrical, (20–)25–38 × 10–15 μm, germination not observed.

E. santali clusters in a basal position to the *E. aquilegiae* DC. complex (Bradshaw et al. 2024a), whereas *E. santalicola* is phylogenetically close to *E. palczewskii* (Jacz.) U. Braun & S. Takam. and the *E. trifoliorum* (Wallr.) U. Braun complex (Bradshaw et al. 2024b).

Golovinomyces ambrosiae (Schwein.) U. Braun & R.T.A. Cook, in Cook & Braun, Mycol. Res. 113: 628 (2009), emend Qiu et al. (2020: 51, 8).

≡ *Erysiphe ambrosiae* Schwein., Trans. Amer. Philos. Soc., N.S., 4: 270 (1834).

= *Erysiphe spadicea* Berk. & M.A. Curtis, Grevillea 4: 159 (1876).

≡ *Golovinomyces spadiceus* (Berk. & M.A. Curtis) U. Braun, in Braun & Cook, CBS Biodiversity Series 11: 329 (2012).

Material examined – India, Maharashtra, Baramati, Jalgaon Supe, on leaves of *Aster amellus*, January 2021, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3502 F, NCSLG24513). Sequence – PP976628 (ITS+28S).

Known distribution – see Braun et al. (2019), Qiu et al. (2020), Bradshaw et al. (2022b).

Notes – Qiu et al. (2020) revised the *Golovinomyces ambrosiae* (= *G. spadiceus*) complex and introduced the combination *G. latisporus* (U. Braun) P.L. Qiu & S.Y. Liu for powdery mildews on *Helianthus* spp. and species of allied genera of tribe *Heliantheae*. Unequivocal identifications based on sequence analyses in this complex require a multilocus approach. However, *G. ambrosiae* and *G. latisporus* can also be differentiated by morphological differences in the anamorphs. The anamorph of *G. ambrosiae* on *Aster amellus* is morphologically characterized as follows: Mycelium amphigenous, forming white patches, sometimes confluent, persistent. Hyphae 3–8 µm wide, thin-walled, smooth, hyaline; hyphal appressoria solitary, nipple-shaped. Conidiophores erect, arising from upper surface of hyphal mother cell, foot cells cylindrical, 40–75 × 9–13 µm, followed by 1–3 shorter cells. Conidia catenescent, ellipsoid-ovoid, doliiform-subcylindrical, 25–38 × 13–20 µm, length/width ratio 1.4–2.1, conidial germination of the Euoidium type.

Aster spp. are common hosts of *Golovinomyces asterum* (Schwein.) U. Braun (Braun & Cook 2012). The present Indian collection represents the first record of *G. ambrosiae* on a species of the genus *Aster* (s. str.). So far, this species was only known from species of the allied genus *Symphyotrichum*. Braun et al. (2019) assigned sequences retrieved from *S. novi-belgii* (≡ *A. novi-belgii*) in Denmark and *S. subulatum* (≡ *A. subulatus*) in Japan to *G. ambrosiae* (as *G. spadiceus*). The sequence obtained from *S. novi-belgii* in Denmark was first published by Mork et al. (2011) as *G. cichoracearum* (DC.) Heluta (s. lat.). The morphological differentiation between *G. asterum* and *G. ambrosiae* on *Aster* spp. is difficult, above all when only anamorphs are involved, which underlines the importance of sequence analyses to confirm unequivocal identifications.

Leveillula clavata Nour, Trans. Brit. Mycol. Soc. 40(4): 477 (1957)

= *Ovulariopsis erysiphoides* Pat. & Har., J. Bot. (Morot) 14: 245 (1900).

Material examined – India, Maharashtra, Baramati, Botanical Garden of the Tuljaram Chaturchand Colleage, on leaves of *Euphorbia leucocephala*, December 2020, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3491 F, NCSLG24516). Sequence – PP976631 (ITS+28S).

Known distribution – see Braun & Cook (2012: 189).

Notes – *Leveillula clavata* was described from Kenya on *Euphorbia pulcherrima* (Nour 1957). Wagh et al. (2023) recorded *Euphorbia leucocephala* as a new host species for *Leveillula clavata* from India, confirmed by morphological examinations and analyses of ITS sequences, which had 99.79 % identity with sequences retrieved from a Chinese specimen of this species on *E. heterophylla* (MH922994, Wu et al. 2019) and a Japanese sample on *E. pulcherrima* (LC108845, Takamatsu et al. 2016). The morphology of the anamorph from India on *Euphorbia leucocephala* agrees well with the description of *L. clavata* (Braun & Cook 2012): Mycelium internal and external, superficial mycelium amphigenous, mainly hypophyllous, forming white patches or covering entire leaves. Hyphae straight to sinuous or somewhat geniculate, branched at right angles, 2–5 µm wide, colorless, septate, thin-walled, smooth; hyphal appressoria rather indistinct. Conidiophores solitary, arising from superficial hyphae, erect, colorless, long, filiform, foot cells cylindrical to somewhat flexuous, 50−160 × 5−9 µm, followed by 1–3 mostly shorter cells, basal septum at the junction with the hyphal mother cells or somewhat elevated. Conidia formed singly, clavate to spathuliform, apex obtuse, rounded, not distinctly papillate, 40–75 × 12–22 µm, conidial germination not observed.

A previous Indian record of *L. clavata* on *Euphorbia heterophylla* (as *L. clavata* on *E. geniculata*) goes back to Shahare (2016).

Leveillula taurica (Lév.) G. Arnaud, Ann. Épiphyt. 7: 92 (1921), s. lat.

Material examined – India, Maharashtra, Shirur, Karade, on *Cyamopsis tetragonoloba*, Dec. 2019, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3494 F, NCSLG24511). Sequence – PP976626 (ITS+28S).

Known distribution – see Amano (1986), Braun & Cook (2012: 203).

Notes – *Leveillula* on *Cyamopsis tetragonoloba*, usually identified as *Leveillula taurica*, is known from diverse countries, including Australia, India, Kenya, Pakistan, Sudan, and the USA (Amano 1986). In India, *L. taurica* is considered one of the main plant diseases of *C. tetragonoloba* and has a negative impact on its cultivation (Sangani et al. 2018). This powdery mildew is also known from Maharashthra on the same host species (Bankar et al. 2019). The taxonomy of this powdery mildew is still unclear. Morphologically it is characterized as follows: Superficial mycelium hypophyllous, forming dense white patches, confluent, finally covering the entire leaf surface; superficial hyphae branched, septate, hyaline, thin-walled. Hyphal appressoria solitary, nipple-shaped to strongly lobate. Conidiophores solitary, 80–180 µm long and 3–7 µm wide, a very long foot cell followed by 1–3 shorter cells. Conidia formed singly. Primary conidia lanceolate, apex usually pointed, occasionally obtuse, base obconically truncate, sometimes rounded or vase-like, 50–62 × 10–17 µm, Ø 58 × 14 µm, length/width ratio 3.3–5.0, Ø 4.1, widest diameter below the middle or more or less in the middle, rarely more or less subcylindrical in the central portion, upper part attenuated towards a pointed tip, base truncate, shallowly rounded or vase-like; secondary conidia cylindrical, ellipsoid with truncate to shallowly rounded ends, or clavate, 40–68 × 10–18 µm, Ø 56 × 13 µm, length/width ratio 2.9–6.2, Ø 4.4. Based on differences in the morphology of the primary conidia, Braun & Cook (2012) assigned *Leveillula* on legumes, previously referred to as *L. taurica* (s. lat.), to *L. papilionacearum* (Kom.) U. Braun, which is likely a morphologically and genetically heterogeneous complex. ITS sequences obtained from diverse leguminous crops cluster within the big '*L. taurica* clade' (Khodaparast et al. 2001), which also applies to the present ITS sequence retrieved from *C. tetragonoloba*. This newly achieved sequence is identical with many sequences deposited in GenBank as '*L. taurica*'. However, based on the conidial shape, size, and length/width ration of the primary conidia, *Leveillula* on *Cyamopsis tetragonoloba* (length/width ratio 3.3–5.0, Ø 4.1) cannot be assigned to *L. papilionacearum* in the sense of Braun & Cook (2012), which has a length/width ratio of (2.1–)2.5–3.3(–4.5), maximum width variable, in the middle or somewhat below or even int he upper half. The *C. tetragonoloba* powdery mildew can currently only be assigned to *L. taurica* s. lat. (complex). Final conclusions to the taxonomy of this powdery mildew are currently not possible. *Leveillula* spp. in general and the species on *C. tetragonoloba* particularly, require a phylogenetic multilocus approach to come to better resolutions at the species level.

Phyllactinia moricola (Henn.) Homma, Trans. Sapporo Nat. Hist. Soc. 11: 174 (1930)

Material examined – India, Maharashtra, Velhe, Vinzer, on leaves of *Morus alba*, September 2021, S.H. Wagh, M.B. Kanade & S.V. Thite (HAL 3491 F, NCSLG24512). Sequence – PP976627 (ITS+28S).

Known distribution – see Amano (1986), Braun & Cook (2012: 262).

Notes – *Phyllactinia moricola* is known from India (Amano 1986, Hosagoudar & Agarwal 2009, Braun & Cook 2012) and has been confirmed by diverse unpublished sequences deposited in GenBank, including MH819522, MH819522, MH819670, MH819671, MH828187, and OR039816.1–OR039828.1. Unfortunately, for these sequences the hosts are not specified, i.e., only 'mulberry' is cited. The morphology of the anamorph of the new Indian specimen of *Ph. moricola* agrees well with previous descriptions, such as Braun & Cook (2012: 262): Mycelium internal and external, superficial mycelium hypophyllous, effuse or in patches, white, evanescent to subpersistent; hyphal appressoria nipple-shaped, hooked to lobed. Conidiophores arising from external hyphae, on the upper surface of mother cells, erect, foot cells long, filiform, straight or almost so, basal septum at the junction with the mother cell, 40–120 × 5–8 µm, followed by 1–3

short cells. Conidia formed singly, clavate to obpyriform-spathulate, apex rounded to somewhat narrowed, but not papillate, 50–80 × 18–32 µm, conidial germination not observed.

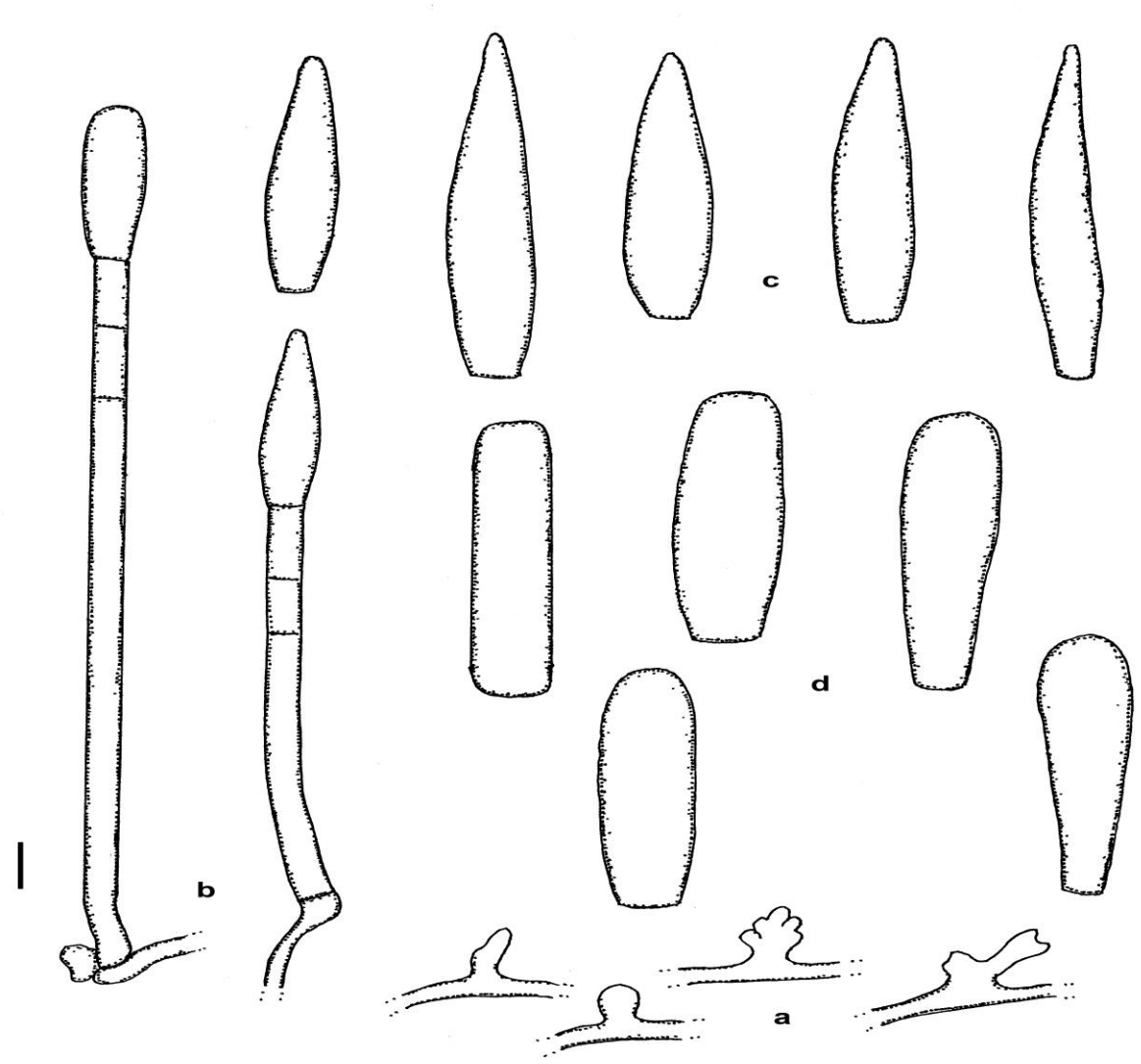

Fig. 4 – *Leveillula taurica* s. lat., on *Cyamopsis tetragonoloba* (HAL 3494 F). a hyphal appressoria. b conidiophores. c primary conidia. d secondary conidia. Scale bar = 10 µm. U. Braun del.

Discussion

Most powdery mildew records from India, a mainly tropical-subtropical country, are based on anamorphs (Paul & Thakur 2006, Hosagoudar & Agarwal 2009). Teleomorphs (fruiting bodies, chasmothecia) are rarely collected, and if collected are mostly from non-tropical regions and areas with higher elevations in the north. Identifications of anamorphic specimens are difficult and often not possible based on solely morphology. Anamorphs of unrelated species may be very similar and confusable. Sometimes nearly indistinguishable conidiophores and conidia on an individual host may pertain to different species. *Erysiphe* on *Santalum album* is an example. *Erysiphe santali* (≡ *Oidium santalacearum*, *Pseudoidium santalacearum*) from India groups in sister position to the *E. aquilegiae* complex (Bradshaw et al. 2024a), whereas new morphologically similar collections on *S. album* from India and China (Li et al. 2023), reported as *P. santalacearum*, represent a new species, described as *E. santalicola* (Bradshaw e al. 2024b), which clusters close to *E. palczewskii* and the *E. trifoliorum* complex (Bradshaw et al. 2024b). There are also many other cases of powdery mildew anamorphs found on unusual host species, such as *Erysiphe* sp. on *Ipomoea triloba*, which turned out to belong to *E. fallax*, and *Erysiphe* sp. (*Pseudoidium* sp.) on *Tecoma*

fulva subsp. *guarume* (present record). Sequence analyses revealed that the latter material pertains to *E. peckii*, a holomorphic species described from North America on *Campsis radicans* (Braun & Cook 2012). Sequences obtained from a North American sample found on *Tecomaria capensis*, assigned to *E.* '*peruviana*' (Glawe et al. 2010), proved to be identical with the Indian sequences. The identification as *E.* '*peruviana*' by Glawe et al. (2010) was due to there being no reliable sequences available for a phylogenetic comparison. Bradshaw et al. (2024b) managed to retrieve sequences from specimens of *E. peckii*, including type material, which led to the correct identification of the causative agent of this powdery mildew on *Tecoma* and *Tecomaria* spp. In conclusion, it can be emphasized that identifications of anamorphic powdery mildew specimens should, whenever possible, be performed using sequence analyses. In this sense, the present sequence analyses are meant to be a contribute to a better knowledge of powdery mildews from India, including new records for India, such as *E. fallax* and *E. peckii*, but also new host reports, e.g., *Azadirachta indica* and *Nicandra physalodes* for *E. aquilegiae* s. lat., and *Golovinomyces ambrosiae* on *Aster amellus*, as well as phylogenetic confirmations of species know from India, but previously only morphologically identified, e.g., *E. pseudolonicerae*.

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