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Powdery mildews (Erysiphales) species spectrum on plants of family Lamiaceae in the Czech Republic

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Abstract: This article focuses on the occurrence of powdery mildews in the Lamiaceae family in the Czech Republic. A comprehensive analysis of morphological characteristics supported by molecular analysis of partial ITS sequences and analysis of host species gained important insights regarding the occurrence and diversity of powdery mildews. Thirty-four plant samples of the Lamiaceae family infected by powdery mildew collected in the Czech Republic between 2015–2022 were analysed. In these samples, the occurrence of all newly described species within the former *Golovinomyces biocellatus* complex was confirmed (*G. biocellatus, G. salviae, G. neosalviae* and *G. monardae*), and *Neoërysiphe galeopsidis* was also verified. Moreover, our study expands the already reported host species list of *G. biocellatus* complex within the Lamiaceae family.

Keywords: Erysiphaceae; anamorph state; host specificity; internal transcribed spacer region

Family Lamiaceae is one of the largest plant families with a cosmopolitan distribution comprising more than 6 000 species in 236 genera described worldwide (Carović-Stanko et al. 2016). Representatives of this family are annual, biennial and perennial typical herbs (Carović-Stanko et al. 2016). However, some species are shrubs, trees, or vines, but in the Czech Republic, they are occurring as herbs or semi-shrubs (Slavík 2000). Many family members are widely cultivated for their aromatic qualities (Capecka et al. 2005) and ease of cultivation and use in decoration (Uritu et al. 2018).

Powdery mildews (Erysiphales, Ascomycota) are obligate biotrophic parasites of vascular plants, appearing as a white layer on the green parts of the plant and acting as a debilitating agent on the host (Braun & Cook 2012). Worldwide, up to 11 powdery mildew species in five genera have been described in the family Lamiaceae, namely *Erysiphe, Golovinomyces, Leveillula, Neoërysiphe* and *Podosphaera.* However, only three powdery mildew species have been confirmed in the Czech Republic: *Golovinomyce orontii*, *G. biocellatus* and *Neoërysiphe galeopsidis* (Braun & Cook 2012).

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In the case of *N. galeopsidis* (DC.) U. Braun is a relatively well-defined species, the taxonomy of the genus being dealt with by Takamatsu et al. (2008), who also specified the species *N. galeopsidis* on members of the Lamiaceae family. *N. galeopsidis* is distributed worldwide, mainly in Europe and Central or West Asia. This powdery mildew was confirmed in the Czech Republic, e.g., on the genus *Stachys* (Pastirčáková et al. 2008).

Much more attention is paid to *G. biocellatus* (Ehrenb.) V. P. Heluta, Braun and Cook (2012) considered it (according to its heterogeneity) a species complex and recommended a comprehensive biological and molecular re-examination of *G. biocellatus* complex before it can be split into smaller units. A comprehensive study focused on this issue was published by Scholler et al. (2016), and it dealt with the differences in asexual states, mainly conidiophores, conidia, and conidial germination types. Based on their research, the *G. biocellatus* complex was divided into four species: *G. biocellatus*, *G. salviae* (Jacz.) M. Scholler, U. Braun & Anke Schmidt, *G. neosalviae* M. Scholler, U. Braun & Anke Schmidt and *G. monardae* (G. S. Nagy) M. Scholler, U. Braun & Anke Schmidt. The taxonomic distinction of the individual species is based mainly on the differences in the asexual state (Scholler et al. 2016).

Braun and Cook (2012) reported that members of the Lamiaceae family are also parasitised by *G. orontii* (Castagne) V.P. Heluta. The study published by Takamatsu et al. (2017) deals with comprehensive molecular genetic analysis focused on individual species of *Golovinomyces* and found that *G. orontii* forms a heterogeneous polyphyletic complex. This study also reported that *G. biocellatus* occurs on members of the Lamiaceae family. Later, by detailed analyses of rDNA, *G. orontii* was split into three species, namely *G. tabaci* (Sawada) H.D. Shin, S. Takam. & L. Kiss, *G. bolayi* S. Takam., Lebeda & M. Götz and *G. orontii* s. str. (Braun et al. 2019), in this study, *G. bolayi* was determined on the species *Lamium amplexicaule* in Japan, and the host range of *G. bolayi* was described as including representatives of the Lamiaceae family.

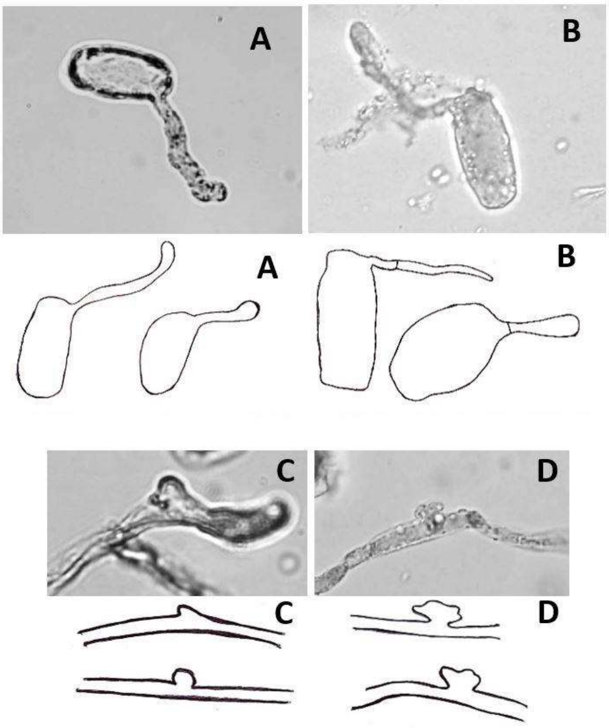

Figure 1. A–B – Euoidium-type of germination
A – Non-septate conidial germ tubes of *Golovinomyces monardae* on *Mentha aquatica*, B – One-septate conidial germ tubes of *G. biocellatus* on *Agastache rugosa*, C – nipple shape appressorium typical for *G. biocellatus* complex on *Nepeta* × *faassenii*, D – lobed appressorium typical for *Neoërysiphe galeopsidis* on *Leonurus turkestanica*. Photo and drawings: M. Michutová

The primary distinguishing morphological feature between *N. galeopsidis* and the *G. biocellatus* complex is the shape of the appressoria. *N. galeopsidis* forms lobed appressoria, and *G. biocellatus* forms nipple-shaped appressoria (Braun & Cook 2012) (Figure 1C and 1D). Although representatives of *G. biocellatus* complex species are very similar, Scholler et al. (2016) described that they can be distinguished based on the size, shape and germination type of the conidia (Figures 1A and 1B) and on the length of the conidiophores and shape of the foot-cell (Scholler et al. 2016).

This study describes the spectrum of powdery mildews found on the Lamiaceae family in the Czech Republic and the species variability of known powdery mildews in the Lamiaceae.

MATERIAL AND METHODS

Field survey. Between 2015–2022 a survey of the occurrence of powdery mildews was done on wild, medicinal, and ornamental plants in botanical gardens in the region of Central and South Moravia in the Czech Republic, namely Botanical Garden and Arboretum of Mendel University, the Academic Garden and Labyrinth of nature and garden paradise of Faculty of Horticulture Mendel University in Lednice, Medicinal Herbs Centre of Faculty of Medicine of Masaryk University in Brno, Petr Albrecht Botanical Garden in Prostějov, Botanical Garden of Palacký University Olomouc, Rosarium Olomouc. The scientific names of plants were unified according to Plants of the World Online (https://powo.science.kew.org).

Microscopic analysis of morphological characteristics. Pieces (ca 20 × 20 mm) of severely infected leaves were used for evaluation by light microscopy (Olympus BX60, Japan). The pathogen was not separated from the host tissue, and microscopy was done on leaf segments fixed in glacial acetic acid (acetic acid 99%; Lach-Ner, Czech Republic) for 48 h and stored in glycerol (Glycerolum 85%; Tamda, Czech Republic). Conidia and conidiophores, mainly on upper leaf surfaces, were examined microscopically after staining with cotton blue (methyl blue, aniline blue; Sigma-Aldrich, USA) (Lebeda & Reinink 1994). In cases where dry leaf samples were analysed, a modified method of Shin (2000) was used, i.e., the heating of herbarium sample tissues in fuchsine (Sigma-Aldrich, USA) in lactic acid (80%; Lach-Ner, Czech Republic). For statistical analyses (means, standard deviations, and range), 30 measurements (when possible) of each characteristic of conidiophore length, foot cell length, number of distal cells, and conidia length and width were calculated using MS Excel.

DNA isolation and sequencing. Anamorph mycelium and conidiophores with conidia from the herbarium samples were scraped from the leaf surfaces of *Agastachae rugosa, Glechoma hederacea, Galeopsis pubescens*, *Lycopus exaltatus, Nepeta nervosa*. Powdery mildew on these Lamiaceae species could not be reliably identified based on their morphological characteristics. Powdery mildew's DNA was isolated according to the standard protocol using DNeasy Plant Mini Kit (Qiagen, Germany).

PCR amplification of a single fragment of a partial sequence of the 18S DNA gene, the complete sequence of ITS1, 5.8S DNA, ITS2, and a partial sequence of the 28S DNA gene was conducted using PMITS1/PMITS2 Cunnington et al. (2003) primers and for same samples PM5G/ITS4 (Scholler et al. 2016).

VWR XT96 XTender96 Thermocycler (VWR, Germany) was used for PCR under the following conditions for PMITS1/PMITS2: 3 min at 94 °C; 35 cycles of 1 min at 94 °C, 1 min at 65 °C, 2 min at 72 °C; followed by a final extension step for 10 min at 72 °C. For PM5G/ITS4, the conditions were set up as follows: 3 min at 95 °C; 35 cycles of 15 s at 95 °C, 15 s at 54 °C, 50 s at 72 °C, followed by a final extension step for 10 min at 72 °C. The reaction conditions were adjusted according to the Taq PCR Master Mix Kit (Qiagen, Germany).

The obtained amplified DNAs were cleaned using the QIAquick PCR purification kit (Qiagen, Germany) following the standard protocol. Subsequently, the purified DNAs were used for pathogen identification through sequencing analysis. The sequencing reactions were performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific Inc., USA) and followed the standard protocol for fluorescence-based cycle sequencing of ITS fragments. The sequencing reaction mixtures were then purified using the BigDye XTerminator Purification Kit (Thermo Fisher Scientific Inc., USA). Finally, the samples were analysed using a 3 500 Series Genetic Analyzer (Thermo Fisher Scientific Inc., USA).

To identify the pathogens, the acquired sequences were submitted and compared with registered ITS sequences available at GenBank using NCBI BLASTN, an online database provided by the National Center for Biotechnology Information, U.S. National Library of Medicine, USA. The resulting nucleotide sequences have been deposited to GenBank and assigned accession numbers OR717594, OR752627–OR752630.

RESULTS

The measured morphological characteristics of individual powdery mildew species on representatives of the Lamiaceae family are shown in Table 1, the macroscopic symptoms of the infection are recorded in Figure 2, and the microscopic structures of conidiophores in Figure 3, the structure of appressoria and germination of conidia in Figure 1. Patches of white powdery mildew mycelium, which later coalesce to cover the whole leaf, were present on the plants. Only the anamorphic states of Striatoidium-type (*Neoërysiphe*) or Euoidium-type (*Golovinomyces*) of conidiophore were found, chasmothecia were not recorded. Based on the shape of the appressoria, the powdery mildew samples were described as *Neoërysiphe galeopsidis* with the lobed shape of appressoria and *Golovinomyces biocellatus* complex with the nipple shape appressoria.

Table 1. Morphological characteristics of asexual state powdery mildews samples collected on hosts of the Lamiaceae family [mean ± SD (min–max)]

Host species	Collection place, date	Leg.	Conidia length (µm)	Conidia width (µm)	L/W ratio	Foot-cell length (µm)	Conidiophore length (µm)	No. of distal cells
Agastache rugosa (Fisch. & C. A. Mey.) Kuntze	Olomouc, 10/2022	BM	24.7 ± 2.4 (20.0–30.0)	14.4 ± 1.09 (12.0–16.0)	1.7 ± 0.22 (1.4–2.3)	37.4 ± 6.8 (26.0–52.0)	104.7 ± 20.4 (73.0–165.0)	2.2 ± 0.4 (2.0–3.0)
Betonica officinalis L.	Huslenky, 9/2020	EH	29.5 ± 2.12 (26.8–34.2)	14.5 ± 1.5 (12.2–17.1)	2.1 ± 0.3 (1.7–2.8)	37.8 ± 10.2 (24.4–61.0)	120.9 ± 18.3 (95.2–158.6)	2.2 ± 0.4 (2.0–3.0)
Galeopsis pubescens Besser	Malá Morávka, 9/2020	EH	28.8 ± 2.39 (24.4–31.7)	16.5 ± 1.5 (12.2–17.1)	2.2 ± 0.3 (1.7–2.6)	39.5 ± 9.9 (26.8–68.3)	136.1 ± 43.7 (82.9–234.2)	2.6 ± 0.5 (2.0–3.0)
Glechoma hederacea L.	Praha, 7/2017	AV	20.4 ± 3.6 (11.5–29.5)	13.4 ± 3.5 (9.8–27.9)	1.6 ± 0.4 (0.4–2.5)	33.7 ± 8.0 (13.1–57.4)	102.9 ± 18.4 (59.0–141.0)	2.2 ± 0.8 (1.0–3.0)
	Huslenky, 8/2020	EH	28.7 ± 4.2 (21.9–36.6)	14.7 ± 1.6 (12.2–17.1)	1.9 ± 0.3 (1.4–2.8)	37.1 ± 9.7 (24.4–58.6)	108.5 ± 25.9 (56.1–158.6)	1.9 ± 0.5 (1.0–3.0)
Hyssopus officinalis L.	Prostějov, 9/2020	EH	30.8 ± 2.3 (26.8–34.2)	14.9 ± 1.2 (12.2–17.1)	2.1 ± 0.3 (1.7–2.8)	69.5 ± 22.8 (39.0–131.7)	151.9 ± 38.1 (85.4–236.7)	2.2 ± 0.4 (2.0–3.0)
Lamium album L.	Olomouc, 8/2020	EH	28.3 ± 3.6 (21.9–36.6)	15.7 ± 1.5 (12.2–19.5)	1.8 ± 0.2 (1.3–2.3)	27.4 ± 6.8 (26.8–36.6)	101.3 ± 24.7 (70.8–183.0)	2.2 ± 0.5 (2.0–4.0)
Leonurus turkestanicus V.I.Krecz. & Kuprian.	Brno, 9/2020	EH	28.5 ± 1.8 (31.7–24.4)	13.2 ± 1.3 (12.2–17.1)	2.2 ± 0.2 (1.8–2.6)	30.9 ± 7.6 (14.6–51.2)	100.9 ± 17.0 (78.1–163.5)	2.1 ± 0.3 (2.0–3.0)
Lycopus exaltatus L. f.	Brno, 7/2021	MM	25.9 ± 5.4 (19.0–39.0)	15.1 ± 1.3 (13.0–17.0)	1.7 ± 0.3 (1.3–2.4)	52.7 ± 7.9 (41.0–70.0)	129.8 ± 25.5 (90.0–175.0)	2.9 ± 0.8 (1.0–4.0)
Melissa officinalis L.	Brno, 9/2019	AV	28.6 ± 3.5 (22.5–37.5)	15.1 ± 1.9 (12.5–20.0)	1.9 ± 0.3 (1.3–2.4)	59.4 ± 10.1 (42.5–80.0)	139.5 ± 16.1 (110.0–162.5)	1.9 ± 0.5 (1.0–3.0)
Mentha aquatica var. crispa (L.) Benth.	Brno, 9/2019	AV	22.3 ± 1.9 (19.5–24.4)	15.3 ± 1.9 (12.2–19.5)	1.4 ± 0.2 (1.1–2.0)	50.9 ± 18.8 (22.0–97.6)	124.2 ± 16.6 (97.7–153.72)	1.6 ± 0.6 (1.0–3.0)
Mentha aquatica L.	Brno, 7/2021	MM	25.5 ± 2.2 (23.0–32.0)	14.4 ± 0.9 (13.0–16.0)	1.8 ± 0.2 (1.5–2.1)	41.6 ± 9.8 (21.0–57.0)	106.6 ± 19.9 (83.0–153.0)	2.1± 1.0 (0.0–4.0)
Mentha × piperita L.	Jeseník, 10/2019	AV	24.1 ± 3.9 (16.4–29.5)	14.7 ± 1.2 (11.5–14.4)	1.7 ± 0.3 (1.0–2.3)	41.5 ± 8.8 (24.6–60.7)	117.6 ± 44.1 (24.6–185.3)	1.5 ± 0.3 (1.0–2.2)
Mentha × piperita L.	Opava, 8/2020	EH	24.9 ± 3.0 (17.1–29.2)	16.2 ±1.6 (12.2–17.1)	1.6 ±0.3 (1.0–2.4)	57.7 ± 5.2 (29.3–78.1)	126.2 ± 25.7 (73.2–165.9)	2.0 ± 0.2 (2.0–3.0)
Mentha spicata L.	Olomouc, 9/2019	AV	28.2 ± 4.7 (20.5–38.4)	16.1 ± 2.2 (12.8–20.5)	1.8 ± 0.3 (1.3–2.5)	62.4 ± 19.6 (35.8–102.4)	167.4 ± 14.3 (89.6–204.8)	1.7 ± 0.5 (1.0–2.0)
Monarda didyma L.	Prostějov, 7/2021	MM	20.4 ± 2.2 (17.0–24.0)	13.6 ± 1.7 (10.0–16.0)	1.5 ± 0.2 (1.0–3.0)	39.8 ± 10.3 (29.0–74.0)	91.6 ± 15.0 (61.0–117.0)	2.0 ± 0.8 (1.0–3.0)
Monarda bradburiana Beck	Olomouc, 9/2020	EH	28.3 ± 1.8 (24.4–31.7)	15.5 ± 2.3 (14.6–26.8)	1.8 ± 0.2 (0.9–2.2)	49.8 ± 10.4 (26.6–78.1)	119.6 ± 16.8 (97.6–173.2)	2.1 ± 0.3 (2.0–3.0)
Monarda citriodora Cerv. ex Lag.	Brno, 9/2015	EH	28.7 ± 3.2 (24.4–39.0)	15.5 ± 1.8 (12.2–21.9)	1.9 ± 0.3 (1.2–2.8)	42.1 ± 6.1 (24.4–80.5)	95.9 ± 56.1 (85.4–165.9)	2.3 ± 0.5 (1.0–3.0)
Nepeta cataria L.	Olomouc, 7/2021	MM	22.9 ± 2.2 (19.0–26.0)	12.5 ± 1.8 (10.0–16.0)	1.8 ± 0.3 (1.5–2.4)	90.0 ± 16.2 (67.0–124.0)	150.8 ± 23.9 (135.0–203.0)	2.2 ± 0.3 (1.5–2.4)
	Jeseník, 10/2017	EH	31.9 ± 3.5 (26.8–43.9)	17.9 ± 1.7 (14.6–21.9)	1.8 ± 0.3 (1.2–2,3)	49.3 ± 10.8 (29,3–63.4)	129.2 ± 32.7 (85.4–195.2)	1.9 ± 0.5 (1.0–3.0)
Nepeta × faassenii Bergmans ex Stearn	Brno, 7/2021	MM	26.1 ± 3.7 (19.7–31.2)	15.4 ± 1.8 (13.1–21.3)	1.7 ± 0.3 (1.2–2.4)	53.9 ± 9.7 (34.4–75.4)	134.3 ± 22.4 (85.3–173.8)	2.6 ± 0.7 (2.0–4.0)
Nepeta nervosa Royle ex Benth.	Lednice, 7/2021	MM	25.3 ± 1.3 (24.0–27.0)	14.3 ± 0.9 (13.0–15.0)	1.8 ± 0.2 (1.6–2.1)	57.0 ± 8.8 (45.0–66.0)	136.7 ± 33.6 (92.0–173.0)	1.7 ± 0.2 (1.6–2.1)
Prunella grandiflora (L.) Turra	Prostějov, 9/2020	EH	31.6 ± 2.6 (26.8–41.5)	16.1 ± 1.5 (14.6–19.5)	2.0 ± 0.2 (1.5–2.4)	42.6 ± 10.9 (24.4–68.3)	121.4 ± 24.7 (85.4–180.6)	1.9 ± 0.2 (1.0–2.0)
Salvia farinacea Benth. 'Fairy Queen'	Lednice, 10/ 2021	MM	23.4 ± 3.2 (20.0–28.0)	13.8 ± 2.9 (10.0–18).0	1.5 ± 0.2 (1.3–1.8)	32.0 ± 2.6 (28.0–35.0)	89.9 ± 14.2 (72.0–107.0)	2.3 ± 0.4 (2.0–3.0)
Salvia napifolia Jacq.	Praha, 9/2019	AV	23.9 ± 2.0 (23.3–28.8)	15.1 ± 2.0 (12.9–20)	1.5 ± 0.2 (1.1–2.2)	56.1 ± 10.1 (43.5–81.9)	145.9 ± 25.5 (117.0–204.8)	1.8 ± 0.4 (1.0–2.0)
Salvia nemorosa L. 'Ostfriesland'	Lednice, 7/2021	MM	23.0 ± 2.0 (21.0–25.0)	14.5 ± 0.5 (14.0–15.0)	1.6 ± 0.1 (1.5–1.7)	65.0 ± 6.0 (59.0–71.0)	140.0 ± 8.0 (132.0–148.0)	2.0 ± 0.0 (2.0–2.0)

Table 1 to be continued

Host species	Collection place, date	Leg.	Conidia length (μm)	Conidia width (μm)	L/W ratio	Foot-cell length (μm)	Conidiophore length (μm)	No. of distal cells
Salvia nemorosa L. 'Pink Beauty'	Brno, 10/2021	MM	23.3 ± 16.0 (18.0–30.0)	14.9 ± 1.7 (13.0–17.0)	1.6 ± 0.3 (1.3–2.3)	47.6 ± 9.4 (38.0–61.0)	108.3 ± 6.6 (97.0–116.0)	2.1 ± 0.6 (3.0–1.0)
Salvia officinalis L.	Kroměříž, 9/2019	AV	29.1 ± 5.7 (22.0–41.5)	17.2 ± 4.3 (12.2–26.9)	1.7 ± 0.3 (1.4–2.2)	73.8 ± 36.4 (38.6–102.4)	172.3 ± 31.4 (140.8–217.4)	1.3 ± 0.5 (1.0–2.0)
	Brno, 9/2020	EH	28.6 ± 2.6 (24.4–34.2)	15.1 ± 1.8 (12.2–17.1)	1.9 ± 0.2 (1.6–2.4)	32.9 ± 18.3 (17.1–80.5)	110.6 ± 25.7 (78.1–170.8)	2.0 ± 0.0 (2.0–2.0)
Salvia pratensis L.	Olomouc, 9/2017	AV	25.1 ± 3.2 (19.7–32.8)	15.1 ± 0.9 (13.1–16.4)	1.7 ± 0.2 (1.3–2.2)	46.3 ± 9.2 (32.8–60.7)	161.5 ± 26.9 (116.4–236.2)	1.5 ± 0.5 (1.0–2.0)
Salvia sclarea L.	Brno, 9/2019	AV	25.2 ± 2.5 (22.0–29.3)	14.6 ± 1.9 (12.2–17.1)	1.7 ± 0.2 (1.3–2.4)	85.2 ± 27.2 (43.9–134.2)	192.7 ± 30.3 (131.8–239.1)	1.6 ± 0.8 (1.0–3.0)
Salvia transsylvanica (Schur ex Griseb. & Schenk) Schur 'Blue Spires'	Olomouc, 10/2021	MM	23.4 ± 2.4 (20.0–28.0)	14.4 ± 1.5 (12.0–18.0)	1.6 ± 0.2 (1.2–2.2)	52.2 ± 12.4 (32.0–85.0)	104.4 ± 17.9 (74.0–139.0)	1.6 ± 0.2 (1.2–2.2)
Salvia verticillata L.	Olomouc, 9/2019	AV	25.4 ± 4.3 (16.1–31.2)	16.2 ± 1.8 (12.2–17.1)	1.5 ± 0.2 (1.1–1.8)	47.1 ± 8.4 (33.7–35.9)	119.4 ± 22.9 (94.5–171.6)	167 ± 0.4 (1.0–2.0)
Stachys byzantina K. Koch	Brno, 8/2021	MM	24.5 ± 2.6 (21.0–30.0)	13.2 ± 1.3 (11.0–16.0)	1.89 ± 0.2 (1.6–2.3)	51.4 ± 15.7 (28.0–90.0)	128.1 ± 18.9 (104.0–156.0)	2.9 ± 0.7 (2.0–4.0)

For abbreviations explanation see Figure 2

N. galeopsidis was morphologically confirmed on *Glechoma hederacea* (Praha/2017), *Lamium album*, *Leonurus turkestanica* and *Stachys byzantina.* Moreover, on *Galeopsis pubescens* (OR717594) and *Glechoma hederacea* (Huslenky/2020) (OR752628), *N. galeopsidis* was confirmed by molecular analysis.

Representatives of *Golovinomyces biocellatus* complex are very similar in morphological characteristics. Based on these characteristics – the mostly ellipsoid, partly doliiform conidia and non-septate conidial germ tubes – *Golovinomyces monardae* was confirmed on *Betonica officinalis*, *Melissa officinalis*, *Mentha aquatica*, *Mentha aquatica* var. *crispa*, *Mentha* × *piperita*, *Mentha spicata*, *Monarda didyma*, *Monarda bradburiana* and *Monarda citriodora*.

The identification of *Golovinomyces biocellatus* was also confirmed based on a molecular analysis of *Agastache rugosa* (OR752627) and *Lycopus exaltatus* (OR752629) because the determination based on morphology was not sufficiently accurate.

Golovinomyces salviae was confirmed based on significant differences in the length of conidiophores between *G. salviae* and *G. neosalviae.* The *G. salviae* has shorter conidiophores than 140 μm. It was confirmed on *Nepeta cataria* (Jeseník/2017), *Prunella grandiflora*, *Salvia farinacea* 'Fairy Queen', *S. nemorosa* 'Pink Beauty', *S. officinalis* (Brno/2020), *S. transsylvanica* 'Blue Spires', *S. verticillata.* Based on molecular analysis, it was positively detected in *Nepeta nervosa* (OR752630). This determination method was necessary due to the excessive morphological similarity with the species *Golovinomyces biocellatus.*

The identification of *Golovinomyces neosalviae* was confirmed mainly due to the length of the conidiophores over 140 μm and the shape of foot–cell of the conidiophores on *Hyssopus officinalis, Nepeta cataria* (Olomouc/2021)*, Salvia napifolia*, *S. nemorosa* 'Ostfriesland', *S. officinalis* (Kroměříž/2018), *S. pratensis* and *S. sclarea* (Figures 3AB and 3AE).

Specific primer sets were used for molecular identification of the five samples that the usual morphological methods could not identify with confidence.

On host *Galeopsis pubescens* (OR717594), *Neoërysiphe galeopsidis* was confirmed with the primer set PMITS1, PMITS2; the product was assembled to 616 bp long contig consisting of 54 bp 18S rRNA, 185 bp ITS1, 154 bp 5.8 S rRNA, ITS2 165 bp and 28S rRNA 58 bp long.

For the remaining samples, the combination of primers PM5G and ITS4 was used with the following results *Golovinomyces biocellatus* (host *Agastache rugosa*, OR752627) 524 bp long contig, 139 bp ITS1, 153 bp 5.8 S rRNA, 173 bp ITS2 and 28S rRNA 58 bp long; *Neoërysiphe galeopsidis* (host *Glechoma hederacea*, OR752628) 481 bp long contig, 142 bp ITS1, 154 bp 5. 8 S rRNA, 165 bp ITS2 and 28S rRNA 20 bp long; *Golovinomyces biocel-*

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Figure 2. Symptoms of powdery mildew infection on Lamiaceae species cross-referenced to lists of hosts and powdery mildews in Table 2

A – *Agastache rugosa* (BM), B – *Betonica officinalis* (EH), C – *Galeopsis pubescens* (EH), E – *Glechoma hederacea* (AV), F – *Hyssopus officinalis* (EH), G – *Lamium album* (EH), H – *Leonurus turkestanica* (EH), I – *Lycopus exaltatus* (MM), J – *Melissa officinalis* (AV), K – *Mentha aquatica* var. *crispa* (AV), L – *Mentha* × *piperita* (AV), M – *Mentha aquatica* (MM), N – *Mentha* × *piperita* (EH), O – *Mentha spicata* (AV), P – *Monarda didyma* (MM), Q – *M. bradburiana* (EH), R – *M. citriodora* (EH), S – *Nepeta cataria* (MM), T – *Nepeta cataria* (EH), U – *Nepeta* × *faassenii* (MM), V – *Nepeta nervosa* (MM), W – *Prunella grandiflora* (EH), X – *Salvia farinacea* 'Fairy Queen' (MM), Y – *S. napifolia* (AV), Z – *S. nemorosa* 'Ostfriesland' (MM), AA – *S. nemorosa* 'Pink Beauty' (MM), AB – *S. officinalis* (AV), AC – *S. officinalis* (EH), AD – *S. pratensis* (AV), AE – *S. sclarea* (AV), AF – *S. transsylvanica* 'Blue Spires' (MM), AG – *S. verticillata* (AV), AH – *Stachys byzantina* (MM). Photo: AV– A. Vrbovská, BM – B. Mieslerová, EH – E. Handlová, MM – M. Michutová

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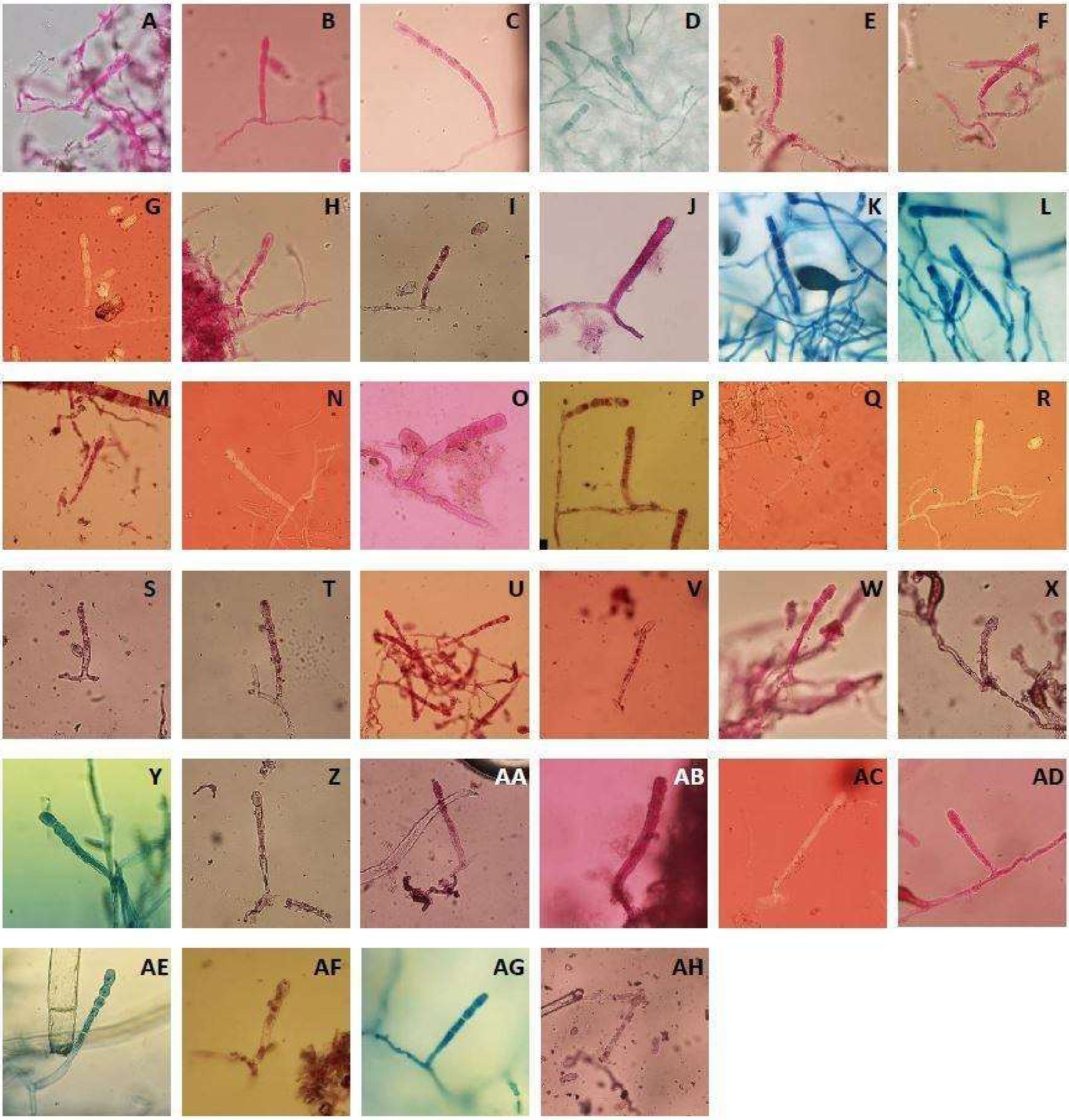

Figure 3. Conidiophores of powdery mildews occurring on the Lamiaceae species cross-referenced to lists of hosts and powdery mildews in Table 2

A – *Agastache rugosa* (MM), B – *Betonica officinalis* (EH), C – *Galeopsis pubescens* (MM), D – *Glechoma hederacea* (EH), E – *Glechoma hederacea* (AV), F – *Hyssopus officinalis* (EH), G – *Lamium album* (EH), H – *Leonurus turkestanica* (EH), I – *Lycopus exaltatus* (MM), J – *Melissa officinalis* (AV), K – *Mentha aquatica* var. *crispa* (AV), L – *Mentha* × *piperita* (AV), M – *Mentha aquatica* (MM), N – *Mentha* × *piperita* (EH), O – *Mentha spicata* (AV), P – *Monarda didyma* (MM), Q – *M. bradburiana* (EH), R – *M. citriodora* (EH), S – *Nepeta cataria* (MM), T – *Nepeta cataria* (EH), U – *Nepeta* × *faassenii* (MM), V – *Nepeta nervosa* (MM), W – *Prunella grandiflora* (MM), X – *Salvia farinacea* 'Fairy Queen' (MM), Y – *S. napifolia* (AV), Z – *S. nemorosa* 'Ostfriesland' (MM), AA – *S. nemorosa* 'Pink Beauty' (MM), AB – *S. officinalis* (AV), AC – *S. officinalis* (EH), AD – *S. pratensis* (AV), AE – *S. sclarea* (AV), AF – *S. transsylvanica* 'Blue Spires' (MM), AG – *S. verticillata* (AV), AH – *Stachys byzantina* (MM). Photo: AV – A. Vrbovská, EH – E. Handlová, MM – M. Michutová *latus* (host *Lycopus exaltatus*, OR752629) 535 bp long contig, 150 bp ITS1, 154 bp 5. 8 S rRNA, 173 bp ITS2 and 28S rRNA 58 bp long; *Golovinomyces salviae* (host *Nepeta nervosa*, OR752630) 491 bp long contig, 150 bp ITS1, 154 bp 5.8 S rRNA, 168 bp ITS2 and 28S rRNA 19 bp long.

These sequences OR717594, OR752627, OR752628 and OR752629 were identical to representatives of the species retrieved from GenBank, except OR752630, which corresponded to *Golovinomyces salviae* with 99.8% identity reported by Scholler et al. (2016) (GenBank: LC076803.1) and nucleotide variation at positions 467, 468, 470, 472 with transversion and at position 473 with deletion.

DISCUSSION

Since the rapid involvement of molecular methods, the taxonomic systems of organisms have undergone significant changes in recent years. The changes concerning powdery mildew species have been reflected by Braun and Cook (2012) in their monograph; however, later attention was paid to some problematic species, e.g. *Golovinomyces orontii* (Braun et al. 2019) and *G. biocellatus* (Scholler et al. 2016).

As mentioned above, at least five species of powdery mildews are currently known to infect the Lamiaceae family in the Czech Republic and Central Europe (Braun & Cook 2012; Scholler et al. 2016). Our study confirmed them all, namely *N. galeopsidis*, *Golovinomyces biocellatus*, *G. neosalviae*, *G. salviae* and *G. monardae* (Table 2). The determination of these species was based predominantly on morphological characteristics described in Braun and Cook (2012) and the study of Scholler et al. (2016), where representatives of *Golovinomyces biocellatus* complex were specified. In some cases, morphological methods appeared insufficient, and these data had to be supported by molecular analyses.

N. galeopsidis is a powdery mildew species infecting the Lamiaceae family in the Czech Republic and throughout Europe (Braun & Cook 2012). Lobed appressoria are formed on the mycelium (Braun & Cook 2012); therefore, they are easily distinguishable from representatives of the *Golovinomyces* genus (which bear simple to nipple-shaped appressoria). *N. galeopsidis* was first described in 1815 by de Candolle as *Erysiphe galeopsidis*. Based on the study of Takamatsu et al. (2008), *Neoërysiphe* was divided into three groups according to host families. The first group includes *N. galii* occurring in the Rubiaceae; the second group, *N. galeopsidis* occurring in the Lamiaceae; and the third group *N. cumminsina* in the Asteraceae.

Klika (1923) summarised the occurrence of powdery mildew in the Czech Republic and described the powdery mildew in the genus *Stachys* as *Erysiphe galeopsidis*. He mentioned that this powdery mildew typically has lobate appressoria; therefore, it was *Neoërysiphe galeopsidis*. A detailed study focusing on the occurrence of *N. galeopsidis* in the Czech Republic was conducted by Pastirčáková et al. (2008). This study described the distribution of that pathogen in the Czech Republic and Slovakia on the genus *Stachys*. During their research, they were able to detect the presence of the *N. galeopsidis* on herbarium items of *Stachys* sp. dating back to 1904 and on herbarium items of *Stachys byzantina* and *S. palustris*, collected between 1850 and 1859 in the Czech Republic.

In recent years several studies have reported the first occurrence of *N. galeopsidis* on members of Lamiaceae like on *Lamium purpureum* (Hong et al. 2019) and *Stachys affinis* in Korea (Choi et al. 2016) and on *S. japonica* in China (Zhang et al. 2018). In the Southern USA, *N. galeopsidis* was identified on *Lamium amplexicaule* and *L. purpureum* (Trigiano et al. 2016).

In our study, based on the morphological characteristics and molecular analysis, the occurrence of *Neoërysiphe galeopsidis* was confirmed on *Galeopsis pubescens*, *Glechoma hederacea* (Praha/2017), *Glechoma hederacea* (Huslenky/2020), *Lamium album*, *Leonurus turkestanica* and *Stachys byzantina* (Table 2).

The remaining samples were identified as species belonging to the *Golovinomyces biocellatus* complex (Scholler et al. 2016). Even though it has been split into four separate species, many reports still use the name *Golovinomyces biocellatus* complex, such as Han et al. (2011) in the case of *Monarda didyma* in Korea.

A great deal of work to reclassify the taxonomy of the *G. biocellatus* complex was done by Scholler et al. (2016). This study focused on molecular phylogenetic data and morphological characteristics of anamorphs of powdery mildews from this complex and demonstrated the existence of two clades, I and II. Clade I involved the species *G. monardae,* which occurs on several genera belonging to the Nepetoideae and can also infect *Verbe-*

Table 2. List of representatives of the Lamiaceae family infected by powdery mildews collected in the Czech Republic during 2015–2021

Host Species	Cross-referenced with photos of symptoms (Figure 2) and conidiophores (Figure 3)	Taxonomic name of powdery mildew species according to Braun and Cook (2012) unless otherwise indicated in Scholler et al. (2016)	Critical morphological and/or molecular data identifying each species*
Agastache rugosa	A, 2A	*Golovinomyces biocellatus*	A
Betonica officinalis	1B, 2B	*G. monardae*	B
Galeopsis pubescens	1C, 2C	*Neoërysiphe galeopsidis*	A
Glechoma hederacea	2D 1E, 2E	*N. galeopsidis* *N. galeopsidis*	A C
Hyssopus officinalis	1F, 2F	*G. neosalviae*	D
Lamium album	1G, 2G	*N. galeopsidis*	C
Leonurus turkestanicus	1H, 2H	*N. galeopsidis*	C
Lycopus exaltatus	1I, 2I	*G. biocellatus*	A
Melissa officinalis	1J, 2J	*G. monardae*	B
Mentha aquatica var. crispa	1K, 2K	*G. monardae*	B
Mentha aquatica	1M, 2M	*G. monardae*	B
Mentha × piperita	1L, 2L	*G. monardae*	B
Mentha × piperita	1N, 2N	*G. monardae*	B
Mentha spicata	1O, 2O	*G. monardae*	B
Monarda didyma	1P, 2P	*G. monardae*	B
Monarda bradburiana	1Q, 2Q	*G. monardae*	B
Monarda citriodora	1R, 2R	*G. monardae*	B
Nepeta cataria	1S, 2S 1T, 2T	*G. neosalviae* *G. salviae*	D E
Nepeta × faassenii	1U, 2U	*G. neosalviae*	D
Nepeta nervosa	1V, 2V	*G. salviae*	A
Prunella grandiflora	1W, 2W	*G. salviae*	E
Salvia farinacea 'Fairy Queen'	1X, 2X	*G. salviae*	E
Salvia napifolia	1Y, 2Y	*G. neosalviae*	D
Salvia nemorosa 'Ostfriesland'	1Z, 2Z	*G. neosalviae*	D
Salvia nemorosa 'Pink Beauty'	1AA, 2AA	*G. salviae*	E
Salvia officinalis	1AB, 2AB 1AC, 2AC	*G. neosalviae* *G. salviae*	D E
Salvia pratensis	1AD, 2AD	*G. neosalviae*	D
Salvia sclarea	1AE, 2AE	*G. neosalviae*	D
Salvia transsylvanica 'Blue Spires'	1AF, 2AF	*G. salviae*	E
Salvia verticillata	1AG, 2AG	*G. salviae*	E
Stachys byzantina	1AH, 2AH	*N. galeopsidis*	C

*A – molecular analysis; B – shape of conidia and conidial germ tubes; C – lobed shape of appressoria; D – conidiophores longer than 140 μm and shape of foot-cell; E – conidiophores shorter than 140 μm

na spp. (family Verbenaceae). This species differs from *G. biocellatus* primarily in the morphological features of the asexual state. *G. monardae* usually has mostly ellipsoid conidia, and conidial germ tubes are non-septate or rarely one-septate. On the contrary, *G. biocellatus* has mostly doliiform to limoniform conidia, and conidial germ tubes are often one-septate (Scholler et al. 2016).

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Several reports of the first occurrence dealing with *Golovinomyces monardae* have been published in recent years. Rajmohan et al. (2019) confirmed *G. monardae* on *Mentha spicata* in New Jersey (USA), in Italy *G. monardae* was confirmed on *Mentha piperita* (Garibaldi et al. 2018), in Mexico on *Agastache mexicana* (Leyva-Mir et al. 2019), in Turkey on *Thymbra spicata* var. *spicata* (Soylu et al. 2019a) and in China on *Monarda didyma* (Xu et al. 2022). In our study, *G. monardae* (Table 2) was primarily confirmed on representatives of the genera *Monarda*, *Betonica*, *Mentha*, and *Melissa*.

Clade II identified by Scholler et al. (2016), contains two sister subgroups. Within Subgroup IIa, focused on *Salvia* spp., they named two species based on morphological and host range data. *G. salviae*, with short conidiophores, is associated with *S. pratensis*, and *G. neosalviae*, with long conidiophores, is linked to *S. officinalis* (Scholler et al. 2016).

The situation concerning the species *G. salviae* is rather complicated. It was first described by Blumer (1933), who distinguished it as a separate species from *G. cichoracearum* (prev. *Erysiphe cichoracearum*) and named it *E. salviae*. However, it was later considered the same species as *E. biocellata* (Jaczewski 1927; Braun 1987), and the recognition of *G. salviae* as a distinct species was abandoned. Braun and Cook (2012) kept this species within the *G. biocellatus* complex, noting that further comprehensive biological and molecular analysis was needed. Only with the study conducted by Scholler et al. (2016) was this species independently described as a unique species that differed significantly from another described species, *G. neosalviae*, by having much shorter conidiophores.

The work of Götz (2018) is worth mentioning, where the author explores the possibility of two different types of *G. neosalviae*. The observed conidiophores varied greatly in length, reaching up to 800 μm and often displaying swollen sections. However, such conidiophore characteristics were not observed in our study. First reports of *G. neosalviae* have been documented in Mexico on *Salvia officinalis* (Venegas-Portilla et al. 2020), Italy on *Lavandula stoechas* (Garibaldi et al. 2020), and Turkey on *S. fruticosa* (Soylu et al. 2019b). In our study *G. neosalviae* was identified on the species *Nepeta cataria* (Jeseník/2017), *Nepeta nervosa, Prunella grandiflora, Salvia farinacea* 'Fairy Queen', *S. nemorosa* 'Pink Beauty', *S. officinalis* (Brno/2020), *S. transsylvanica* 'Blue Spires', *S. verticillata*. *G. neosalviae* was also identified on the host plant *Nepeta* × *faassenii* despite overlapping mean values of conidiophores (Figure 3U); their shape corresponded more to *G. neosalviae* due to a frequently significantly longer cell after the foot cell. *G. salviae* was identified as the remaining species of the genus *Salvia*.

Although *Salvia officinalis* is considered the type host for *G. neosalviae*, our data for powdery mildew on *Salvia officinalis* (Brno/2020) closely corresponded to those of *G. salviae*. Therefore, we were able to form the conclusion that this species is *G. salviae*.

Due to comprehensive phylogenetic analysis (Scholler et al. 2016), *G. biocellatus*, the species under which the entire complex was classified in the past, was separated into Clade II, specifically Subgroup IIb, forming a distinct clade consisting of specimens on *Lycopus* and *Glechoma*. This corresponds to this study, in which *G. biocellatus* was confirmed on *Glechoma hederacea* (Huslenky/2020) and *Lycopus exaltatus*. Apart from these species, *G. biocellatus* has been confirmed on other species, such as *Mentha piperita* in Spain (Martínez-Cruz et al. 2019).

It is also necessary to consider the importance of morphological characters for the determination of powdery mildew; some of them were mentioned in the text, e.g. shape of appressoria, length of conidiophores, shape of foot-cells and conidia germination type. Length/width (L/W) ratio is also a morphological characteristic commonly used to identify and classify powdery mildew species (Braun & Cook 2012). In our study, the L/W ratio was between 1.4–2.2; however, on the basis of this characteristic, it was not possible to clearly determine the powdery mildew species. Scholler et al. (2016) described that the L/W values for *G. salviae* were shorter than for other species (*G. neosalviae* and *G. monardae*); however, the variability of this feature is high.

This study has contributed to a more precise mapping of the powdery mildew species variability in the family Lamiaceae in the Czech Republic. Our study not only confirmed the conclusions of Scholler et al. (2016) but also expanded the list of host species from the Lamiaceae family for individual powdery mildew species. The study of morphological variability and pathogenicity of species within the former *Golovinomyces biocellatus* complex still requires a great deal of work. Especially in countries outside of Europe, this topic still inspires further research, as shown by the many new first reports in the context of the former fungal complex.

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