

Annotated Checklist of the Lichenicolous Fungi of Hungary

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Abstract: Knowledge of lichenicolous fungi is limited at a worldwide level and needs further basic information, as in the case of Central and Southern Europe. The literature sources for “Revised checklist of the Hungarian lichen-forming and lichenicolous fungi” by Lőkös and Farkas in 2009 contained 54 lichenicolous and other microfungi species of 38 genera. Due to recent field studies and microscopic work, the number of known species has increased to 104 lichenicolous species in 64 genera during the last decade, including 53 new species for the country. Old records of five species were confirmed by new collections. Key characteristics of some of the most interesting species are illustrated by microscopic views and two distribution maps are provided. Recent biodiversity estimates suggest that the number of currently known species could be 1.5 (–2) times higher with more detailed work on field collections. Although lichenicolous fungi have been less well studied in Hungary in the past, the relative diversity of lichenicolous fungi there, as indicated by Zhurbenko’s lichenicolous index, was found to be slightly higher than the mean value calculated for the world.

Keywords: distribution; diversity; lichen-inhabiting fungi

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1. Introduction

The symbiosis of lichenized fungi in the strict sense consists of one fungal (mycobiont) and one photosynthetic (photobiont) partner [1]. However, a series of close associations are known, where further lichen associated symbionts accompany these two compulsory components [2–4]. One or two additional photosynthetic partners occur typically in cephalodia, which are morphologically more or less well-defined special region on the thallus surface or inside the thallus; the number of partners may therefore reach even four in this way. However, if the number of fungi is increased by one or more additional species, the number of partners can similarly be three (a tripartite symbiotic relationship) or more. These additional fungi are the lichen-inhabiting or lichenicolous fungi. There is also the special case of the four-membered symbiotic relations, where a lichenized fungus lives together with another lichenized fungus, forming a miniature ecosystem. Today, due to the wide range of developed systems in microscopy, microbiology, and molecular genetics, the nature of this ecosystem can be extended further when coexisting bacteria [3] and basidiomycete yeasts [4] are considered. This interpretation of mini-ecosystems was proposed by [5] and extended by others [6–9], focusing on lichen-associated animals such as mites, snails, and slugs.

Lichenicolous fungi are generally very small and inconspicuous, since their major part is often hidden inside the lichen thallus and only the appearance of their fruiting bodies indicates their presence; therefore, they often remain unnoticed by collectors [10]. Lichenicolous fungi are usually studied by lichen specialists and not by mycologists working on free-living fungi, since the former, when visiting the field, notice the unusual morphological characters or fruit-bodies produced by the additional fungus and frequently collect a specimen. In recent decades, numerous lichenologists–mycologists have

mostly concentrated on lichenicolous fungi, whilst maintaining their interest in lichenized fungi. Other groups of microfungi are studied almost exclusively by lichenologists, such as the so-called lichen-attached microfungi, namely the non-lichenized fungi living together with lichens in the same community and habitat, most often saprophytically on decaying wood or on various rocks. While this special group of fungi represents a considerable morphological and, consequently, taxonomic diversity, their molecular genetic study is still very far from complete, since a series of technical problems arises in connection with the small size, symbiotic nature, and difficulties with isolating them. Therefore, except for exceptional pioneer studies [11–15], several taxa have not been analyzed phylogenetically, and in particular, local taxonomic problems have not been solved.

In addition to the morphological and taxonomic diversity, lichenologists usually differentiate between parasitic, commensalistic, and saprophytic lifestyles among lichenicolous fungi [2,10,16–19].

Knowledge of lichenicolous fungi is limited at a worldwide level and needs further basic information, as in the case of Central and Southern Europe [20–27]. In the revised checklist of Hungary [28], the lichen-forming and lichenicolous (and other lichen-related) taxa were separated, since our knowledge on lichens was much more advanced than that of lichenicolous taxa; the latter were mainly treated by literature sources, while lichens were studied in more detail from the literature, herbarium material, and in the field. The list was based primarily on Magyarország mikroszkopikus gombáinak határozókönyve 1–3 (identification book of Hungarian microscopic fungi) by J. Bánhegyi et al. [29–31] and, further, 26 literature sources. In all, 54 lichenicolous and other lichen-related species of 38 genera were listed from Hungary in 2009.

The present aim is to update our knowledge of the lichenicolous taxa in Hungary and compile a separate list of these species, which can be regularly updated. Our extended fieldwork over the last decade has confirmed several former literature records, added new occurrences of numerous species, and provided new distributional data for various regions of Hungary. Based on these records, the diversity of these fungi is considered from various points of view (geographic distribution, host, systematics) in the checklist below.

2. Materials and Methods

New collections were identified with the help of various literature sources [10,32–34]. The morphology and anatomy were studied by means of a NIKON Eclipse/NiU (DIC, epifluorescence) compound microscope (Nikon Corporation, Tokyo, Japan), Nikon SMZ18 stereo microscope (Nikon Corporation, Tokyo, Japan), and Olympus SZX9 and Olympus BX50 (DIC) microscopes (Olympus Corporation, Tokyo, Japan). Micrographs were prepared by Olympus E450 camera (with Quick Photo Camera 2.3 software; Olympus Corporation, Tokyo, Japan) and Nikon DS-Fi1c and Fi3 camera (with NIS-Elements BR ML software; Nikon Corporation, Tokyo, Japan) with the indicated microscopes. Microscopic examinations were carried out in water, where it was necessary in 10% KOH (K) (Reanal, Budapest, Hungary), Lugol's iodine (Merck KGaA, Darmstadt, Germany), directly (I) or after 10% KOH pre-treatment (K/I).

The nomenclature mainly follows the IndexFungorum [35], similarly to the previous checklist [28], but the work by Lawrey and Diederich 2018 [36], several chapters by Paul Diederich in [33], and other literature sources by Hawksworth, Kocourková, and Santesson et al. [18,32,37,38] were also employed. The nomenclatures of old literature data were checked repeatedly and revised. Information on the host is generally based on specimens collected in Hungary. In the case of literature records, we could only rely on the original text available.

Specimens are deposited in herbaria BP, CBFS, DE, EGR, M, SZE, UPS, VBI, and W—abbreviations follow [39].

Distribution maps were constructed by the computer program for geographical information system QGIS 3.18.2 'Zürich', released in 2020, applying an adaptation of the Central European grid system [40,41]; the symbols (dots) represent units of *c.* 5 km × 6 km areas.

3. Results

The following checklist contains 104 species; a nomenclatural revision of the taxa treated by Lőkös and Farkas in 2009 [28] and identification of specimens recently collected mostly by N. Varga throughout Hungary. In total, 53 lichenicolous fungi have been confirmed as new to the country, and old records of five species have been confirmed by new collections. Host lichen species are named wherever possible, and geographical distribution is provided according to the main regions within the country. Anatomical and morphological annotations refer to the specimens collected in Hungary in some cases, especially if they differ in some respects from the known description.

3.1. List of Lichenicolous Fungi

New species for Hungary are indicated by an asterisk (*).

1. *Abrothallus bertianus* De Not., G. bot. ital. 2(1.1): 192 (1846)

Host: *Melanohalea elegantula*

Reported by P. Czarnota et al. [42] from the Bükk Mts (Cserépfalu, Bükk National Park), the only known locality in Hungary.

2. *Abrothallus caerulescens* I. Kotte, Centbl. Bakt. ParasitKde, Abt. II 24: 86 (1909) (Figure 1; 2a,b)

Hosts: *Xanthoparmelia conspersa*, *X. stenophylla*, *X. tinctina*

First recorded as *A. berterianus* and as *A. parmeliarum* by A. Kiszely-Vámosi [43] from the Mátra Mts in 1980. Not rare in Hungary, it occurs at several localities in mountainous areas, i.e., in the Northern Mountain Range (Börzsöny, Mátra and Zemplén Mts), in the Balaton Upland [44], and in the Mecsek Mts (BP 97037; BP 97038).

Note: Former specimens identified as *A. tulasnei* have also been included here.

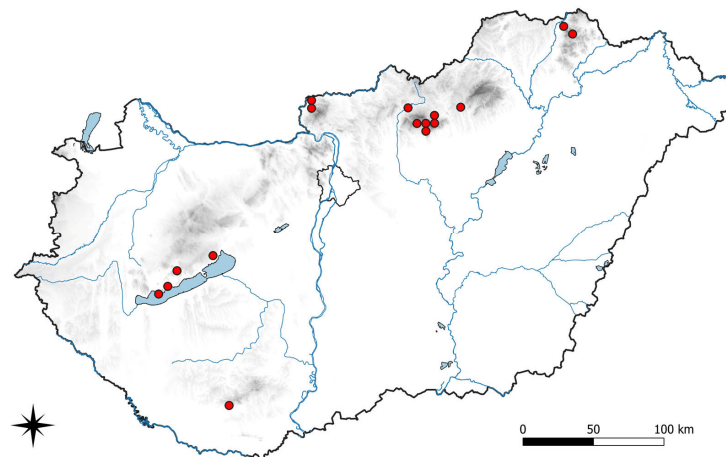


Figure 1. Distribution of *Abrothallus caerulescens* in Hungary.

3. **Abrothallus cladoniae* R. Sant. and D. Hawksw., in Hawksworth, Notes R. bot. Gdn Edinb. 46(3): 392 (1990)

Host: *Cladonia* sp.

Recorded from the Zemplén Mts at Telkibánya (BP 97001), the only known locality in Hungary.

4. **Abrothallus microspermus* Tul., Ann. Sci. Nat., Bot., sér. 3 17: 115 (1852)

Host: *Flavoparmelia caperata*

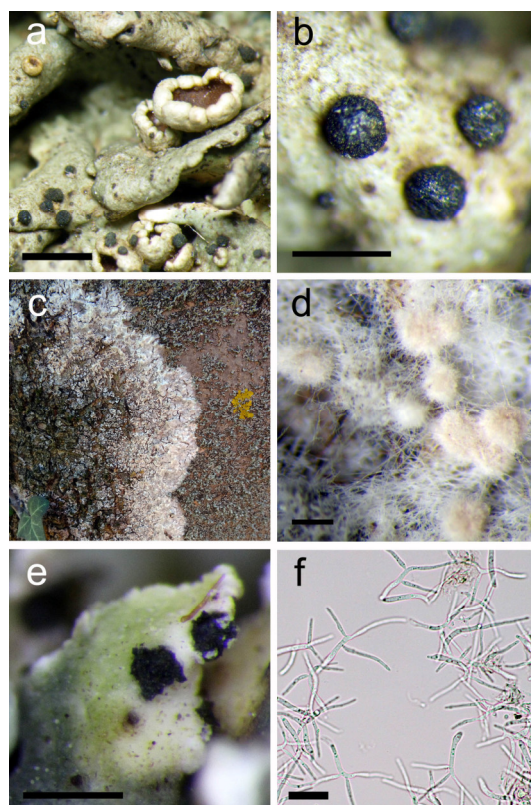


Figure 2. (a,b) *Abrothallus caerulescens*, apothecia on the thallus of *Xanthoparmelia stenophylla* (scales 1 mm; 500 μ m); (c) *Athelia arachnoidea*, mycelia on epiphytic *Phaeophyscia* and *Physcia* spp.; (d) developing young sclerotia of *Athelia arachnoidea* (scale 200 μ m); (e) *Cladoniicola staurospora*, brown conidiomata in the host thallus (scale 500 μ m); (f) H-shaped conidia with diverging arms of *Cladoniicola staurospora* (scale 200 μ m).

Observed as an anamorphic stage, *Vouauxiomyces truncatus* on the thallus of *Flavoparmelia caperata*. Recently recorded from the Zala Hills at Zalacsány and the Zemplén Mts at Telkibánya in Hungary (BP 97002; BP 97003).

5. *Abrothallus parmeliarum* (Sommerf.) Arnold, Flora, Regensburg 57: 102 (1874)

Host: *Hypogymnia physodes*

Only one old literature record as *Abrothallus smithii*, without voucher specimen, by F. Hazslinszky in 1859 [30,45] from the Zemplén Mts (near Kékedfűrdő).

6. **Abrothallus prodiens* (Harm.) Diederich and Hafellner, in Diederich, Mycotaxon 37: 300 (1990)

Host: *Hypogymnia physodes*

Recorded from only one locality in the Balaton Upland (Kóvágóörs) (BP 97004).

7. *Abrothallus suecicus* (Kirschst.) Nordin, Svensk bot. Tidskr. 58: 226 (1964)

Hosts: *Ramalina* spp.

The old literature source [30] mentions this species with possible hosts but without exact locality and voucher specimens; therefore, it must be regarded as a dubious record.

8. *Aposphaeria cladoniae* Allesch. and Schnabl, in Allescher, Ber. bayer. bot. Ges. 4: 32 (1895)

Host: *Cladonia* sp.

Reported from *Cladonia pyxidata* var. *neglecta* f. *lophyra* on a sandy grassland area near Kecskemét (Nyír) by L. Hollós in 1913 [30,46]. No recent occurrence is known.

9. *Arthonia varians* (Davies) Nyl., Lich. Scand. (Helsinki): 260 (1861)

Host: *Lecanora rupicola*

An old record as *Celidium varians* from the Visegrád Mts (near Dobogókő) was published by G. Moesz in 1942 [30,47,48], but the cited voucher specimen (together with the host *Lecanora sordida*) collected by G. Timkó is not available.

10. *Athelia arachnoidea* (Berk.) Jülich, Willdenowia, Beih. 7: 53 (1972)
(Figures 2c,d)
Hosts: various lichens (e.g., *Candelariella reflexa*, *Parmelia sulcata*, *Phaeophyscia orbicularis*, *Physcia adscendens*, *Ph. stellaris*, *Ph. tenella*, *Xanthoria parietina*), mosses, bark, and leaf litter
Widespread throughout Hungary [44,49–53]; frequent in anthropogenic environment (parks, gardens, roadside trees, agricultural areas, etc.). In most cases it is sterile; the spreading mycelia without hymenium, basidia, or basidiospores, only the creamy-to-brownish sclerotia, can be observed.
11. *Bilimbia killiasii* (Hepp) H. Olivier, Bull. Acad. Intern. Géogr. Bot. 15: 213 (1905)
Host: *Peltigera* sp.
In addition to an old, dubious literature record as *Mycobilimbia killiasii* without exact locality and voucher specimens [30], it has also been collected recently in a sandy area in the Nyírség (near Hajdúhadház) from *Peltigera* sp. (BP 97005).
12. *Bryostigma apotheciorum* (A. Massal.) S. Y. Kondr. and Hur, in Kondratyuk et al., Acta bot. hung. 62(1–2): 99 (2020)
Host: *Protoparmeliopsis muralis* s. lat.
It was reported as *Conida clemens* on *Placodium saxicolium* from the Bükk Mts (near Eger) by F. Hazslinszky in 1870 [54].
13. **Bryostigma parietinarium* (Hafellner & A. Fleischhacker) S. Y. Kondr. and Hur, in Kondratyuk et al., Acta bot. hung. 62(1–2): 100 (2020)
Host: *Xanthoria parietina*
Recorded from several localities in Hungary, mainly from lowland areas: Kiskunság, Little Hungarian Plain, Nyírség, Órség. It often grows together with other xanthoriicolous species.
14. **Bryostigma phaeophysciae* (Grube & Matzer) S. Y. Kondr. and Hur, in Kondratyuk et al., Acta bot. hung. 62(1–2): 100 (2020)
Host: *Phaeophyscia orbicularis*
Known from several localities in Hungary, abundant from lowlands to mountains, and spreading.
15. *Burgoa angulosa* Diederich, Lawrey, and Etayo, in Diederich and Lawrey, Mycol. Progr. 6(2): 66 (2007)
Host: *Bacidina* sp.
Reported from only one locality, Zemplén Mts (Füzér), by P. Diederich and J. D. Lawrey in 2007 [55].
16. **Capronia suijsae* Tsurykau and Etayo, Lichenologist 49(1): 2 (2017)
Host: *Xanthoria parietina*
This species, described in 2017, was detected soon after from the Kiskunság sandy area (Bugac) (BP 97050).
17. *Cercidospora epipolytropa* (Mudd) Arnold, Flora, Regensburg 57(10): 154 (1874)
Hosts: *Lecanora* spp.
An old record, without exact locality and voucher specimens, was recorded by J. Bánhegyi et al. in 1985 [30]. It is regarded as common species in Hungary.
18. *Cercidospora macrospora* (Uloth) Hafellner and Nav.-Ros., Lichen Flora of the Greater Sonoran Desert Region (Tempe) 2: 638 (2004)
Hosts: *Lecanora* spp., *Protoparmeliopsis muralis*
Although there is only one literature record, as *C. ulothii*, without exact locality and voucher specimens [30], it has recently been recorded from the Balaton Upland on *Protoparmeliopsis muralis* (at Tihany) (VBI 5747) and is probably a common species in Hungary.
19. *Chaenothecopsis pusilla* (Ach.) A. F. W. Schmidt, Mitt. Staatsinst. Allg. Bot. Hamburg 13: 148 (1970)
Host: –

Reported from several localities [56–59], i.e., the Bükk Mts at Miskolc-Tapolca [54,60,61], the Great Hungarian Plain at Kecskemét-Nyír [46], and the Somogy Hills at Balatonlelle [62]. Although all old specimens and additional recent collections from the Bükk Mts (near Jávorkút) and from the Somogy Hills (near Ropoly) are from decaying wood, its lichenicolous occurrence is also expected in Hungary.

20. *Chaenothecopsis pusiola* (Ach.) Vain., Acta Soc. Fauna Flora Fenn. 57 (no. 1): 70 (1927)

Host: –

Known only from decaying wood in the Visegrád Mts at Dömös, as *Calicium floerkei* f. *polycephalum* [57–59,63]; however, its lichenicolous occurrence is also expected in Hungary.

21. *Chaenothecopsis savonica* (Räsänen) Tibell, Beih. Nova Hedwigia 79: 666 (1984)

Host: –

The only Hungarian record from an *Alnus glutinosa* fen near Dabas in the Great Hungarian Plain was recorded by G. Thor in 1988 [64] (UPS, VBI). Its lichenicolous occurrence should be confirmed.

22. *Chaenothecopsis subparoica* (Nyl.) Tibell, in Tibell and Ryman, Nova Hedwigia 60(1–2): 215 (1995)

Host: *Haematomma ochroleucum*

Recorded as *Calicium subparoicum*, from only one locality in the Mátra Mts (Disznókő) by A. Kiszely-Vámosi in 1980 [43].

23. **Cladoniicola staurospora* Diederich, van den Boom, and Aptroot, Belg. J. Bot. 134(2): 128 (2001)

(Figure 2e,f)

Host: *Cladonia chlorophaea* aggr.

Recently recorded from the Zemplén Mts (near Füzérkomlós) (BP 97006); the only Hungarian record.

24. **Clypeococcum hypocenomycis* D. Hawksw., Notes R. bot. Gdn Edinb. 38(1): 167 (1980)

(Figure 3a)

Host: *Hypocenomyce scalaris*

Known from several old and recent localities (e.g., Börzsöny, Villány and Zemplén Mts); it appears to be widespread and frequent in Hungary.

25. *Corticifraga fuckelii* (Rehm) D. Hawksw. and R. Sant., Bibl. Lichenol. 38: 125 (1990)

Host: *Peltigera* sp.

Reported from Hungary by D. Hawksworth and R. Santesson in 1990 [65] without exact locality and voucher specimens.

26. **Didymocyrtis cladoniicola* (Diederich, Kocourk. and Etayo) Ertz and Diederich, in Ertz et al., Fungal Diversity 74: 67 (2015)

Hosts: *Cladonia foliacea*, *Cl. pyxidata* s. lat.

Known in the Great Hungarian Plain from several sandy grassland locations, as well as from the Zemplén Mts (BP 97008; BP 97009).

27. **Didymocyrtis epiphyscia* Ertz and Diederich, in Ertz et al., Fungal Diversity 74: 71 (2015)

Host: *Oxneria fallax*

Known only from a recent collection from the Mátra Mts (BP 97007).

28. **Didymocyrtis foliaceiphila* (Diederich, Kocourk. and Etayo) Ertz and Diederich, in Ertz et al., Fungal Diversity 74: 73 (2015)

Host: *Cladonia foliacea*

Known only from a sandy grassland area from the Kiskunság (BP 97010).

29. **Didymocyrtis slaptonensis* (D. Hawksw.) Hafellner and Ertz, in Ertz et al., Fungal Diversity 74: 80 (2015)

Host: *Xanthoria parietina*

Not rare in Hungary, being known from recent collections from the Buda and Bükk Mts, the Little Hungarian Plain, and from the Zala Hills (BP 97013; BP 97014; BP 97015; BP 97016).

30. **Epicladonia sandstedei* D. Hawksw., Bull. Br. Mus. nat. Hist., Bot. 9(1): 16 (1981)
Host: *Cladonia chlorophaea* aggr.
Recorded recently from the Zemplén Mts (Füzérkomlós) (BP 97035).
Note: It induces galls on the basal squamules as well as on the scypi of the host thalli. Most of the measured conidia are simple, not septate (cf. [66]).
31. **Epithamnolia xanthoriae* (Brackel) Diederich and Suija, Mycologia 109(6): 896 (2017)
Host: *Xanthoria parietina*
Only recorded from the Bakony Mts near Bakonybél (Bakony Natural History Museum, Zirc).
32. *Erythricium aurantiacum* (Lasch) D. Hawksw. and A. Henrici, Field Mycology 16(1): 16 (2015) (= *Marchandiomyces a.*)
Host: *Physcia adscendens*
Only recently reported [53], but it seems to be frequent in Hungary.
33. *Halospora deminuta* (Arnold) Tomas. and Cif., Archo. bot. ital. 28: 11 (1952) (= *Merismatium deminutum*)
Hosts: on various crustose lichens
Reported, as *Polyblastia deminuta*, from the Bükk Mts (Mályinka: Bartus-kő) by A. Kiszely-Vámosi et al. in 1989 [56,67], its only Hungarian locality.
34. *Hanseniaspora osmophila* (Niehaus) Phaff, M. W. Mill. and Shifrine, Antonie van Leeuwenhoek 22: 147 (1956)
Host: –
Old, dubious literature record without host, exact locality, and voucher specimens [29].
35. **Heterocephalacria bachmannii* (Diederich and M. S. Christ.) Millanes and Wedin, in Liu et al., Stud. Mycol. 81: 120 (2015)
Host: *Cladonia furcata*
Recently found in sandy areas of the Great Hungarian Plain (Kiskunság, Tatárszentgyörgy) (BP 97017). Probably more frequent in Hungary but overlooked.
36. **Heterocephalacria physciacearum* (Diederich) Millanes and Wedin, in Liu et al., Stud. Mycol. 81: 120 (2015)
Hosts: *Physcia adscendens*, *Ph. tenella*
Recently collected in the Órség National Park (Vendvidék) in the western part of Hungary (BP 97051; BP 97052).
Note: Tremelloid galls have been found on many host specimens in recent collections from Hungary. According to recent studies [11,68,69], tremelloid species can be distinguished mostly by molecular genetic methods. In the lack of basidia and/or basidiospores, the presence of these taxa could not be confirmed [70].
37. *Illosporiopsis christiansenii* (B. L. Brady and D. Hawksw.) D. Hawksw., in Sikaroodi et al., Mycol. Res. 105(4): 457 (2001) (Figure 3b)
Host: *Physcia adscendens*
Recorded from the Visegrád Mts by E. Farkas in 1990 [49] and from the Soroksár Botanical Garden (Budapest) by N. Varga et al. in 2016 [53], but it seems to be widespread and common in Hungary.

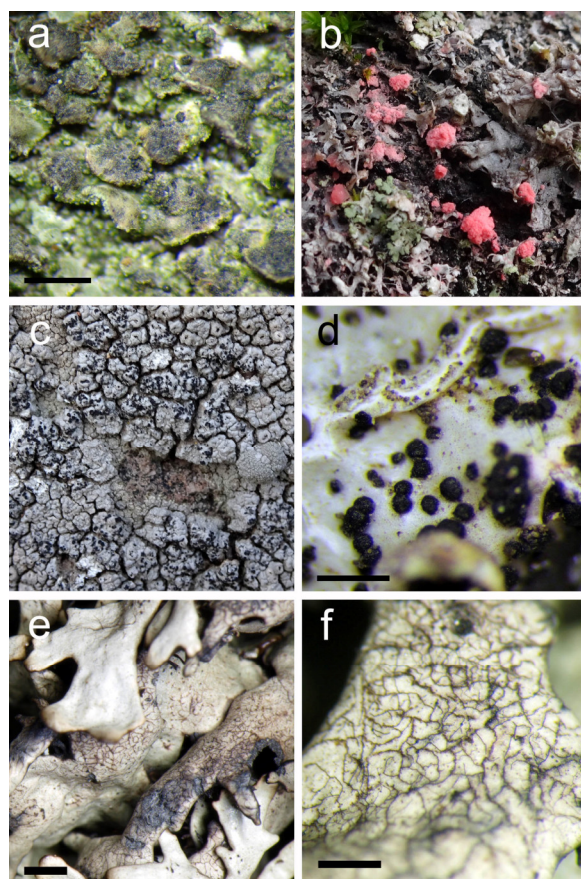


Figure 3. (a) *Clypeococcum hypocenomycis*, perithecia in the thallus of *Hypocenomyce scalaris* (scale 500 μm); (b) pink sporodochia of *Illosporopsis christiansenii* on *Physcia adscendens*; (c) *Karschia talcophila* on *Diploschistes scruposus*; (d) *Lichenopuccinia poeltii* on *Parmelia sulcata* (scale 500 μm); (e,f) *Lichenostigma cosmopolites* on *Xanthoparmelia* sp. (scales 1 mm; 500 μm).

38. **Illosporium roseum* Mart., Fl. crypt. erlang. (Nürnberg): 325 (1817)
Host: *Peltigera* sp.
Reported, as *Illosporium carneum*, from a recent collection from the Villány Mts (Csarnóta) (VBI 5746).
39. **Intralichen christiansenii* (D. Hawksw.) D. Hawksw. and M. S. Cole, Fungal Diversity 11: 90 (2002)
Host: *Xanthoria parietina*
Recognized only recently from the Great Hungarian Plain near Hajós (BP 97018) but could be widespread and overlooked.
40. **Karschia talcophila* (Ach.) Körb., Parerga lichenol. (Breslau) 5: 460 (1865)
(Figure 3c)
Host: *Diploschistes scruposus*
Recently detected in the Börzsöny and the Mátra Mts but thought to be more frequent in Hungary (BP 97019; BP 97020).
41. **Lichenochora obscuroides* (Linds.) Triebel and Rambold, Bibl. Lichenol. 48: 168 (1992)
Host: *Phaeophyscia orbicularis*
Recently found on bark of *Populus* sp. near Hajós in the Great Hungarian Plain and in the Bükk Mts (Szarvaskó) (BP 97011; BP 97012).
42. *Lichenocodium erodens* M. S. Christ. and D. Hawksw., in Hawksworth, Persoonia 9(2): 174 (1977)
Hosts: *Hypogymnia physodes*, *Lecanora conizaeoides*, *Parmelia sulcata*

It is known in Hungary from several localities, from the Northern Mountain Range and the Little Hungarian Plain, as well as the Soroksár Botanical Garden (Budapest) [53]; a frequent parasite causing bleached lesions surrounded by a black margin.

43. *Lichenocodium lecanorae* (Jaap) D. Hawksw., Bull. Br. Mus. nat. Hist., Bot. 6(3): 270 (1979)

Hosts: *Parmelia sulcata*, *Squamarina lentigera*

It occurs in the Balaton Upland region (Tihany) [66,71] and, more recently, in the Great Hungarian Plain (Tiszalúc) on *Parmelia sulcata* (BP 97021).

Note: Similar to *L. erodens* and maybe more frequent in the country.

44. **Lichenocodium pyxidatae* (Oudem.) Petr. and Syd., Feddes Repert., Beih. 42: 135 (1927)

Host: *Cladonia pyxidata* s. lat.

Found in various habitats at several localities in Hungary.

45. **Lichenocodium usneae* (Anzi) D. Hawksw., Persoonia 9(2): 185 (1977)

Hosts: *Cladonia furcata*, *Xanthoparmelia conspersa*

Recognized from recent collections from the Mecsek Mts (BP 97041) and the Mátra Mts (BP 97042); found only on the apothecia of *Xanthoparmelia conspersa*.

46. **Lichenocodium xanthoriae* M. S. Christ., Friesia 5(3–5): 212 (1956)

Host: *Xanthoria parietina*

Known from several localities mainly in the lowland areas.

47. **Lichenodiplis lecanorae* (Vouaux) Dyko and D. Hawksw., in Hawksworth and Dyko, Lichenologist 11(1): 52 (1979)

Host: *Lecanora* sp.

Known from the Great Hungarian Plain (near Hajós) (BP 97022); the only locality in Hungary.

48. *Lichenopeltella cetrariicola* (Nyl.) R. Sant., Nordic J. Bot. 9(1): 99 (1989)

Host: *Cetraria islandica*

Recorded without exact locality and voucher specimens [30]. Its host species is rare in Hungary. An old herbarium specimen infected by *Lichenopeltella cetrariicola* has been found recently (BP 83751); however, it also lacks an exact locality.

49. **Lichenopuccinia poeltii* D. Hawksw. and Hafellner, in Hawksworth, Beih. Nova Hedwigia 79: 374 (1984)

(Figure 3d)

Host: *Parmelia sulcata*

Known only from the Aggtelek Karst (BP 97024) in Hungary.

50. *Lichenostigma cosmopolites* Hafellner and Calat., Mycotaxon 72: 108 (1999)

(Figures 3e,f)

Hosts: *Xanthoparmelia conspersa*, *X. mougeotii*, *X. protomatrae*, *X. pulvinaris*, *X. stenophylla*, *X. tinctina*

Widespread and abundant throughout Hungary on various *Xanthoparmelia* species from lowlands to mountains; recently recorded from the Zemplén Mts by G. Matus et al. [72].

51. *Lichenostigma elongatum* Nav.-Ros. and Hafellner, Mycotaxon 57: 213 (1996)

Host: *Lobothallia radiosia*

Only known in Hungary from Dédesvár near Mályinka (Bükk National Park) in the Bükk Mts [73,74] (CBFS JV4377).

52. **Lichenostigma rouxii* Nav.-Ros., Calat. and Hafellner, in Calatayud et al., Mycol. Res. 106(10): 1237 (2002)

Host: *Squamarina cartilaginea*

Probably unpublished, old record from the Bükk Mts (Mályinka: Buzgó-kő) (M). Its occurrence is awaits confirmation from recent collections.

53. **Lichenothelia rugosa* (G. Thor) Ertz and Diederich, Fungal Diversity 66: 135 (2014)

Host: *Diploschistes scruposus*

Probably unpublished record from the Zemplén Mts (Füzér: Castle Hill) (M).

54. *Lichenzyma pisutiana* Černajová and Škaloud, Fungal Biology 123(9): 634 (2019)
Hosts: *Cladonia rangiformis*, *C. rei*
An endolichenic yeast, known from culture. Its Hungarian distribution is represented by two localities, one in the Balaton Upland (Tihany) and the other in the Vértes Mts (Csákberény) [75].
55. *Marchandiomyces corallinus* (Roberge) Diederich and D. Hawksw., in Diederich, Mycotaxon 37: 312 (1990)
(Figure 4a)
Host: *Parmelia saxatilis*
First published by E. Farkas et al. [44] from the Balaton Upland (Szentbékállá: Fekete-hegy) and the Zemplén Mts (BP 94422; BP 97025; VBI). It seems to be widespread in Hungary.
56. *Melaspilea leciographoides* Vouaux, Bull. Soc. mycol. Fr. 29: 472 (1913)
Hosts: *Verrucaria* spp.
An old literature record, as *Mycomelaspilea leciographoides*, mentioned without exact locality and voucher specimens but with possible hosts [30].

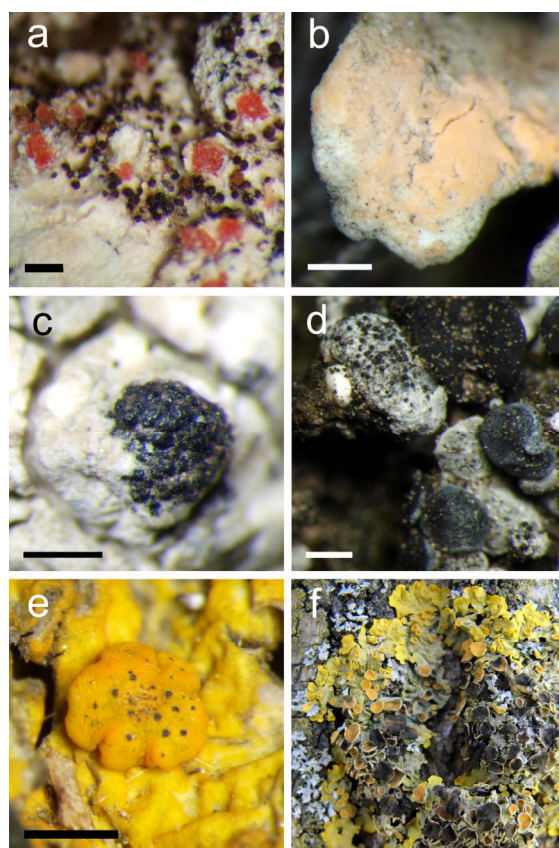


Figure 4. (a) Pinkish conidiomata of *Marchandiomyces corallinus* on *Parmelia saxatilis* (scale 500 μm); (b) *Penttilamyces lichenicola* on *Cladonia foliacea* (scale 500 μm); (c) aggregated perithecia of *Stigmidium eucline* on *Varicellaria lactea* (scale 500 μm); (d) *Stigmidium tabacinae* on *Thalloidima* sp. (scale 500 μm); (e) *Telogalla olivieri* forming galls on *Xanthoria parietina* (scale 500 μm); (f) *Xanthoria parietina* infected by *Xanthoriicola physciae*, resulting in black spots on apothecia.

57. **Microcalicium disseminatum* (Ach.) Vain., Acta Soc. Fauna Flora fenn. 57(no. 1): 77 (1927)
Host: –
Recognized from an old collection from the Bükk Mts (BP 63433, BP 85066) from decaying oak wood. Its presence on thalli of other calicioid lichen needs confirmation.
58. **Monodictys epilepraria* Kukwa and Diederich, Lichenologist 37(3): 217 (2005)

- Host: *Lepraria lobificans*
Detected recently from a few localities (e.g., BP 97046).
59. **Muellerella hospitans* Stizenb., Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 30(no. 3): 51 (1863)
Hosts: *Bacidia fraxinea*, *B. rubella*
Frequently occurs on *Bacidia* spp. (e.g., BP 97053 on mixed hosts), but no published records.
60. **Muellerella lichenicola* (Sommerf.) D. Hawksw., Bot. Notiser 132(3): 289 (1979)
Host: *Xanthoria parietina*
Recognized recently from the Kiskunság sandy area (Bugac); further occurrences have also been detected (BP 97049).
61. *Neolamyia peltigerae* (Mont.) Theiss. and Syd., Ann. Mycol. 16(1–2): 29 (1918)
Host: *Peltigera didactyla*
Known in Hungary from one locality in the Bükk Mts (Szarvaskő: Pyrker-sziklák) (BP 50825) [76].
62. *Opegrapha rupestris* Pers., Ann. Bot. (Usteri) 5: 20 (1794)
Hosts: *Bagliettoa* spp., *Verrucaria calciseda*
This parasitic *Opegrapha* species is represented by several specimens named *Opegrapha persoonii* from the Aggtelek Karst and the Bükk Mts [56].
63. **Penttilamyces lichenicola* (Thorn, Malloch and Ginns) Zmitr., Kalinovskaya et Myasnikov, Folia Cryptog. Petropol. (St.-Peterburg) 7: 8 (2019) (Figure 4b)
Host: *Cladonia foliacea*
Known only from a recent collection from the Great Hungarian Plain (Kiskunság) (BP 97036).
64. *Plectocarpon lichenum* (Sommerf.) D. Hawksw., in Hawksworth and Galloway, Lichenologist 16(1): 86 (1984) (= *Celidium lichenum*)
Host: *Lobaria pulmonaria*
Reported from one locality in the Visegrád Mts (Dömös: Keserűs-hegy) [77]. No further *Plectocarpon* specimens were found after checking all available Hungarian *Lobaria pulmonaria* specimens deposited in Hungarian collections. Since the host has become a rare lichen species in Hungary, future occurrences of this lichenicolous fungus are doubtful.
65. **Pleospora xanthoriae* Khodos. and Darmostuk, Opusc. Philolich. 15: 8 (2016)
Host: *Xanthoria parietina*
The only Hungarian locality is in the Great Hungarian Plain (Bugac) (BP 97000); however, since the host species is very frequent in Hungary, further occurrences are expected.
66. *Polycoccum marmoratum* (Kremp.) D. Hawksw., in Hawksworth et al., Lichenologist 12(1): 107 (1980) (= *Microthelia marmorata*)
Host: *Polyblastia* sp.
Known from the Aggtelek Karst and the Bükk Mts [78], as well as the Villány Mts [56].
67. *Polycoccum microsticticum* (Leight.) Arnold, Ber. bayer. bot. Ges. 1(Anhang): 132 (1891) (= *Didymosphaeria microstictica*)
Hosts: *Acarospora smaragdula*, *Acarospora* sp.
Reported from the Visegrád Mts (Dömös: Vadálló kövek) by G. Moesz in 1942 [47,48] and from a recent collection from the Zemplén Mts (BP 97048).
68. **Polycoccum pulvinatum* (Eitner) R. Sant., Lichens and Lichenicolous Fungi of Sweden and Norway (Lund): 175 (1993)
Host: *Physcia caesia*
Known only from two localities in Hungary, from the Mátra Mts (Kékes) (EGR, as *P. galligenum*), and from the Visegrád Mts (Tahi: Ábrahám-bükk) (VBI 5748, as *P. galligenum*).
69. *Pronectria robergei* (Mont. and Desm.) Lowen, Mycotaxon 39: 462 (1990)
Hosts: *Peltigera* spp.

Old, dubious literature record, as *Nectriella robergei*, without exact locality and voucher specimens but with possible hosts [29].

Note: Its anamorph is *Illosporium roseum*.

70. *Punctelia oxyspora* (Tul.) Divakar, A. Crespo and Lumbsch, in Divakar et al., Fungal Diversity 84: 114 (2017) (= *Nesolechia oxyspora*)

Host: *Parmelia* sp.

An old literature record without exact locality and voucher specimens [30].

71. *Pyrenochaeta xanthoriae* Diederich, Mycotaxon 37: 318 (1990)

Host: *Xanthoria parietina*

Only its locality from the Balaton Upland (Szigliget, Bozóti-legelő) has been recently published (BP 96097) [51], but it is not rare in Hungary, as several other localities are known.

72. *Rhagadostoma lichenicola* (De Not.) Keissl., Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 8: 320 (1930)

Host: *Solorina crocea*

An old, dubious literature record [29]. The host, an alpine species, does not occur in Hungary.

73. *Rhizocarpon advenulum* (Leight.) Hafellner and Poelt, Herzogia 4(1–2): 10 (1976)

Hosts: *Pertusaria* spp.

An old, dubious literature record, as *Karschia advenula*, without exact locality and voucher specimens, but mentioning possible hosts [30].

74. *Roselliniella cladoniae* (Anzi) Matzer and Hafellner, Bibl. Lichenol. 37: 59 (1990)

Hosts: *Cladonia furcata*, *C. pyxidata* agg.

Known only from several localities in the Kiskunság and the Balaton Upland (Mt Tamás-hegy) (e.g., BP 97026; BP 97027).

75. *Sarcopyrenia gibba* (Nyl.) Nyl., Mém. Soc. Acad. Maine Loire 4: 69 (1858)

Hosts: *Candelariella aurella*, *Lecanora dispersa*, *Rinodina bischoffii*, *Verrucaria nigrescens*, etc.

Reported from several localities from natural as well as anthropogenic habitats throughout the country [79].

76. *Sclerococcum epicladonia* Zhurb., in Zhurbenko and Pino-Bodas, Opusc. Philolich. 16: 235 (2017)

Host: *Cladonia chlorophaea*

Reported from the Zemplén Mts (Fövényes) (BP 97028).

77. *Sclerococcum lobariellum* (Nyl.) Ertz and Diederich, in Diederich et al., Bryologist 121(3): 398 (2018)

Host: *Lobaria pulmonaria*

Its only Hungarian locality in the Visegrád Mts (Pilisszentlélek: Hoffmann-kunyhó) has been recently recognized from an old collection (BP 81558).

Notes: Black apothecia with true margin grow on the host thallus; hypothecium darkens after K/I; asci contain eight ascospores; ascospores ornamented granularly, 12–14 × 4.8–6.4 µm.

78. *Sclerococcum parasiticum* (Flörke) Ertz and Diederich, in Diederich et al., Bryologist 121(3): 399 (2018)

Hosts: *Pertusaria* spp.

An old, dubious literature record, as *Leciographa inspersa*, without exact locality and voucher specimens, but mentioning possible hosts [30].

79. *Sclerococcum parellarium* (Nyl.) Ertz and Diederich, in Diederich et al., Bryologist 121(3): 399 (2018)

Hosts: *Lecidea* spp.

An old, dubious literature record, as *Leciographa parellaria*, without exact locality and voucher specimens, but mentioning possible hosts [30].

80. *Scutula epiblastematica* (Wallr.) Rehm, Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.3(lief. 32): 322 (1890) (1896)

Host: *Peltigera canina*

Known only from the Vértes Mts (near Csákvár) in Hungary from old collections, as *Hollósia vertesensis* (BP 33899) [76,80].

81. **Scutula tuberculosa* (Th. Fr.) Rehm, in Saccardo and Saccardo, Syll. fung. (Abellini) 18: 174 (1906)

Host: *Solorina saccata*

Recently recognized from a recent collection from the Vértes Mts (BP 92218).

82. **Sphinctrina leucopoda* Nyl., Flora, Regensburg 42: 44 (1859)

Host: *Diploschistes scruposus*

Recognized from a recent collection from the Zemplén Mts (Holló-kő) (BP 97034).

83. **Sphinctrina tubaeformis* A. Massal., Memor. Lich.: 155 (1853)

Host: *Lecanora* sp.

Only one old specimen has been confirmed from the Bükk Mts (Bükkszenterzsébet, Orosz-kút) (BP 63587; further recent collections are necessary).

84. *Sphinctrina turbinata* Fr., Syst. orb. veg. (Lundae) 1: 121 (1825)

Host: *Pertusaria pertusa*

Known from old collections, as *Sphinctrina gelasinata*, from several localities in the Bükk Mts and from one locality in the Somogy Hills [56–58,81]. Recent occurrences from other regions are also expected.

85. **Spirographa lichenicola* (D. Hawksw. and B. Sutton) Flakus, Etayo and Miądl., in Flakus et al., Plant and Fungal Systematics 64(2): 328 (2019)

Hosts: *Hypogymnia physodes*, *Lecanora conizaeoides*

Recently recorded from an abandoned orchard in the Northern Mountain Range (Gömörszőlős: Szőlőhegy) (BP 97029).

Notes: Asexual stage on the host thallus forms discolored areas surrounded by a distinct black margin. Pycnidia in groups, immersed in the thallus, conidia Y-shaped with cellular forks, $8.0\text{--}8.5 \times 1.6 \mu\text{m}$. Associated with *Lichenocodium erodens*.

86. *Stigidium congestum* (Körb.) Triebel, Mycotaxon 42: 290 (1991)

Host: *Lecanora campestris*

Its only Hungarian locality from the Bükk Mts (near Eger) was recorded as *Pharcidia congesta* by F. Hazslinszky in 1884 [61].

87. **Stigidium eucline* (Nyl.) Vězda, Česká Mykol. 24(4): 228 (1970)

(Figures 4c and 5)

Host: *Varicellaria lactea*

Recognized from old and recent collections (Börzsöny, Bükk, Mátra, Zemplén Mts, etc.).

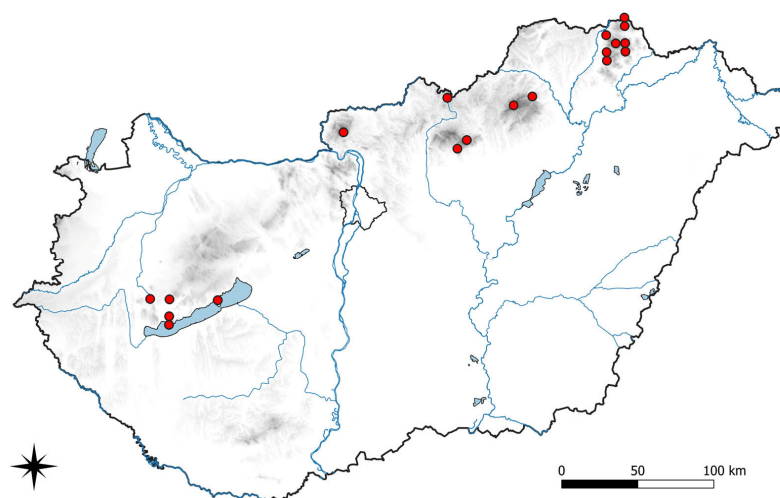


Figure 5. Distribution of *Stigidium eucline* in Hungary.

88. **Stigidium microspilum* (Körb.) D. Hawksw., Kew Bull. 30(1): 201 (1975)
Host: *Graphis scripta*
Recently found in the Somogy Hills (at Zselickisfalud) (BP 97030).
89. **Stigidium pumilum* (Lettau) Matzer and Hafellner, Bibl. Lichenol. 37: 115 (1990)
Host: *Physcia caesia*
Known from the Börzsöny Mts from a recent collection (BP 97045).
90. *Stigidium rouxianum* Calat. and Triebel, Lichenologist 35(2): 109 (2003)
Host: *Acarospora cervina*
Known only from the Bükk Mts (Dédestapolcsány: Dédes-vár) (CBFS JV4407) [74].
91. **Stigidium solorinarium* (Vain.) D. Hawksw., Lichenologist 15(1): 14 (1983)
Host: *Solorina saccata*
Several localities have been reported from the Bakony and Vértes Mts.
Notes: Ascospores 10–16 × 3.2–4.8 µm, apex pointed in overmature stage; number of septa variable, 1–3.
92. **Stigidium squamariae* (B. de Lesd.) Cl. Roux and Triebel, Bull. Soc. linn. Provence 45: 511 (1994)
Host: *Protoparmeliopsis muralis* s. lat.
Known only from several localities in the Little Hungarian Plain (e.g., BP 97043, BP 97044).
93. **Stigidium tabacinae* (Arnold) Triebel, Bibl. Lichenol. 35: 236 (1989)
(Figure 4d)
Hosts: *Thalloidima opuntioides*, *Th. sedifolium*
Widely distributed and common in Hungary in rocky grassland habitats.
94. **Stigidium xanthoparmeliarum* Hafellner, Bull. Soc. linn. Provence 44: 231 (1994)
Host: *Xanthoparmelia stenophylla*
Known only from several localities in the Balaton Upland and the Börzsöny Mts (e.g., BP 97039, BP 97040).
95. **Syspastospora cladoniae* Etayo, Cryptog. Mycol. 29(1): 88 (2008)
Host: *Cladonia pyxidata* s. lat.
Collected from only one location in the Great Hungarian Plain, in a sand dune near Fülöpháza, in the shadow of *Juniperus communis* (BP 97031).
96. **Taeniolella phaeophysciae* D. Hawksw., Bull. Br. Mus. nat. Hist., Bot. 6(3): 255 (1979)
Host: *Phaeophyscia orbicularis*
Recently found in the Great Hungarian Plain on bark of *Sambucus nigra* near Hajós (BP 97032). Probably a frequent species, similar to its host, but very few records are available to date.
97. **Talpapellis beschiana* (Diederich) Zhurb., U. Braun, Diederich and Heuchert, in Heuchert et al., Fungal Syst. Evol. 2: 231 (2018)
Host: *Cladonia chlorophaea* aggr.
Recognized from a recent collection from the Zemplén Mts (BP 97047).
98. **Telogalla olivieri* (Vouaux) Nik. Hoffm. and Hafellner, Bibl. Lichenol. 77: 109 (2000)
(Figure 4e)
Host: *Xanthoria parietina*
Regarded as a common and widely distributed species in Hungary.
99. *Tetramelas phaeophysciae* A. Nordin and Tibell, Lichenologist 37(6): 495 (2005)
Hosts: *Parmelia* spp.
An old, dubious literature record, as *Karschia pulverulenta*, without exact locality and voucher specimens, but with possible hosts [30].
100. *Tetramelas pulverulentus* (Anzi) A. Nordin and Tibell, Lichenologist 37(6): 497 (2005)
Hosts: *Parmelia* spp.
An old, dubious literature record, as *Karschia pulverulenta*, without exact locality and voucher specimens, but mentioning possible hosts [30].

101. **Thelocarpon epibolum* Nyl., Not. Sällsk. Fauna et Fl. Fenn. Förh., Ny Ser. 8: 188 (1866)
Host: *Solorina saccata*
It has been recognized from recent collections from the Vértes Mts (BP 92218).
102. **Vouauxiella lichenicola* (Linds.) Petr. and Syd., Feddes Repert., Beih. 42: 484 (1927)
Host: *Lecanora* cf. *chlarofera*
Recorded from a recent collection from the Balaton Upland (Ódörög) (BP 97033).
103. *Xanthoriicola physciae* (Kalchbr.) D. Hawksw., in Hawksworth and Punithalingam, Trans. Br. mycol. Soc. 61(1): 67 (1973) (= *Coniosporium physciae*) (Figure 4f)
Host: *Xanthoria parietina*
Widely distributed and common throughout Hungary wherever *Xanthoria parietina* is present [30,46,51–53,82,83].
104. *Zwackhiomyces immersae* (Arnold) Grube and Triebel, in Grube and Hafellner, Nova Hedwigia 51(3–4): 318 (1990)
Host: *Clauzadea monticola*
Recently published from a collection made by H. Lojka in 1880 near Lipótmézó in the Buda Mts (W0088943) [84].

4. Discussion

The 104 listed species represent a relatively good level of diversity compared to data of various European countries and the mean value of the world calculated according to the lichenicolous index (LI) [85], previously adopted for the Bulgarian lichenicolous fungi [20]; updated LI values for several other countries are provided in Table 1, the value for lichenicolous fungi in Hungary being just above the mean value for the world. There are countries or regions that reach more than twice the average value for the world (e.g., Bavaria (Germany), Great Britain, Belgium), but countries such as Fennoscandia, Ukraine, and France, which have more humid oceanic and/or Mediterranean climates or a more diverse landscape and habitats or a larger altitudinal range, and thereby would be expected to be important for lichens and lichenicolous fungi, have values not much higher than that of Hungary.

Table 1. Lichenicolous index values worldwide and in selected European countries, USA, and Canada, and the numbers of species the calculation based on.

Country or region	Lichenicolous fungi	Lichens	LI ¹ (lichenicolous index)	References
Bavaria (Germany)	399	1624	0.246	[86]
Great Britain	384	1677	0.229	[18,87]
Belgium, Luxembourg, and N France	201	930	0.216	[88]
Germany	392	1946	0.201	[89]
Italy	492	2565	0.192	[90,91]
France, 2020	592	3185	0.186	[92]
Fennoscandia	430	2387	0.180	[38]
France, 2017	546	3082	0.177	[93]
France, 2014	513	3528	0.145	[94]
USA and Canada	631	4880	0.129	[95]
Ukraine	246	1910	0.129	[96]
Hungary	104	926	0.112	present paper
World	2000	19387	0.103	[97,98]
Albania	38	398	0.095	[21,22,26,27]
Russia	276	3388	0.081	[99,100]
Greece	64	1353	0.047	[101]
Bulgaria	45	1120	0.040	[20]
Romania	40	1194	0.034	[102]
Serbia	15	668	0.022	[22,23–25]

¹ LI = species number of lichenicolous fungi/species number of lichens [85].

Since lichenicolous species belong to a large number of higher taxa (64 genera, 43 families, and 33 orders), they represent a rather high systematic diversity. The most species-rich genera are *Stigmidium* with nine, *Abrothallus* with seven, and *Didymocyrtis* with four, while 49 genera contain only one species.

Lichenicolous fungi are found on c. 80 host species in Hungary, which is a relatively low number compared to the total number of lichens (926). This suggests that lichenicolous fungi might be discovered on further host species in the future, even if not all lichen species are known as hosts of lichenicolous fungi. It is not known why some lichens are found more frequently with lichenicolous fungi, while others are usually without; the effect of lichen secondary metabolites might be a possible explanation [7]. We can also assume that the knowledge of lichenicolous fungi is far from complete globally, and a great number of new taxa are to be described. According to a recent estimate, only c. 3–8% of the world's fungi is known [103].

Additional fieldwork may result in a more detailed knowledge of the distribution of taxa with the possibility for preparing distribution maps for the known species similarly to the current examples, *Abrothallus caerulescens* (Figure 1) and *Stigmidium eucline* (Figure 5). Further floristical novelties for Hungary are expected by detailed investigations of the frequent host species in the genera *Xanthoria*, *Phaeophyscia*, *Physcia*, and *Lecanora*, as well as the understudied genera such as *Anaptychia*, *Pseudevernia*, *Ramalina* and *Usnea*.

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