Mycological Progress (2024) 23:76
https://doi.org/10.1007/s11557-024-02003-w

ORIGINAL ARTICLE

Luteodiscus gen. nov. (*Hyphodiscaceae*, *Helotiales*), with *L. epibryus* comb. nov. and *L. hemiamyloideus* sp. nov., two overlooked bryophilous ascomycetes with a wide host range

Hans-Otto Baral[1] · Lothar G. Krieglsteiner[2] · Zuzana Sochorová[3] · Peter Döbbeler[4] · Jean-Paul Priou[5] · Elisabeth Stöckli[6] · Enrique Rubio[7] · François Valade[8] · Günter Bauer[9] · Michel Hairaud[10] · Robin Isaksson[11] · George Greiff[12] · Katharina Krieglsteiner[2] · Michal Sochor[13] · James C. Lendemer[14]

Received: 27 June 2024 / Revised: 11 September 2024 / Accepted: 13 September 2024

Abstract

The new genus *Luteodiscus* is established to accommodate two species of bryoparasitic, helotialean discomycetes which are characterized by small, yellow, subsessile or short-stipitate, smooth to finely fimbriate apothecia that turn irreversibly bright rose-pink to wine-red in KOH. One of them, *L. epibryus*, was previously placed in *Phialea* and later *Hymenoscyphus* and has euamyloid ascus apical rings (IKI blue, type BB), comparatively long ascospores with a low lipid content, and apothecia which turn yellow-orange when dry. The much rarer *L. hemiamyloideus* is newly described and has hemiamyloid apical rings (IKI red, type RR), smaller ascospores with a higher lipid content, and smaller apothecia which turn blood-red when dry. Although previously known only from two collections on *Hypnum*, *L. epibryus* was found to have one of the most extensive and heterogeneous host ranges of all currently known bryophilous ascomycetes, comprising 14 genera in 6 orders of mosses and 14 genera in 2 orders of liverworts, with a maximum occurrence on *Hypnum*, whereas *L. hemiamyloideus* occurred on 6 genera in 2 orders of liverworts, with a preference for *Nowellia*, but never on mosses. Both species are necrotrophic parasites, forming apothecia within often conspicuous necrotic zones among healthy shoots of the host populations. The host bryophytes have been noted to grow on woody substrates (dead stumps, logs, branches, sometimes living trunks) or on mineral matter (soil and rock). *Luteodiscus epibryus* was mainly found in areas with acidic bedrock, whereas *L. hemiamyloideus* occurs at equal frequency over alkaline and acidic soil types. Both species were found in semi-shaded to shaded forests but also in open wood- and shrublands, composed of various angiosperms and/or gymnosperms. While *L. epibryus* is here reported from Europe, Macaronesia, and North America, *L. hemiamyloideus* has so far solely been recorded in Europe. Although *L. epibryus* was found to be frequent in many regions, with so far 114 collections made mainly in the period of 1989–2024, only two collections with published descriptions came to our notice: the holotype from Czechia collected in 1906 and a much younger undated collection from dépt. Orne, France. In comparison, *L. hemiamyloideus* was recorded only 15 times during 2011–2024. Sequences of rDNA obtained from six collections of *L. epibryus* and two of *L. hemiamyloideus* revealed a strong difference between the two species, ranging at p-distances of 8.4–8.9% in the ITS region and 2.7–2.9% in the LSU D1–D2 domain. Two genotypes with a 0.8% p-distance in ITS and 0.2% in LSU were observed within *L. epibryus*, but without any expression in the phenotype. Combined phylogenetic analysis of ITS + LSU D1–D4 suggests that *Luteodiscus* belongs in *Hyphodiscaceae*.

Keywords Bryophytes as host · Colour change · Discomycete · Hemiamyloidity · Hepaticolous · Muscicolous · Necrotrophic parasitism · NuITS-LSU rDNA · Vital taxonomy

Introduction

The family *Hyphodiscaceae* Ekanayaka & K.D. Hyde was recently established by Ekanayaka et al. (2019) for a group of discomycete genera with small, subsessile apothecia with warted excipular hairs, which were previously included in

---

Section Editor: Marco Thines

Extended author information available on the last page of the article

Hyaloscyphaceae Nannf. The circumscription of the new family, which was reinvestigated and discussed in more depth by Quijada et al. (2022), was mainly based on molecular data and now also includes genera with smooth hairs or a mixture of smooth and warted hairs. Quijada et al. accepted nine genera: *Fuscolachnum* J.H. Haines, *Gamarada* D.J. Midgley & Tran-Dinh, *Glutinomyces* Nor. Nakam., *Hyphodiscus* Kirschst., *Hyphopeziza* J.G. Han, Hosoya & H.D. Shin, *Microscypha* Syd. & P. Syd., *Scolecolachnum* Guatim., R.W. Barreto & Crous, *Soosiella* Hujslová & M. Kolařík, and *Venturiocistella* Raitv. A further genus, *Venturioscypha* Baral, T. Kosonen & Polhorský, was added by Baral et al. (2023a). Seven of these ten genera are known from their teleomorphic life stages, with one of them (*Hyphodiscus*) known from its anamorph as well (previously referred to *Catenulifera* Hosoya). Members of these seven genera appear to be mainly saprotrophs on dead, hygric or xeric substrates (wood and bark of spermatophytes, herbaceous angiosperms, and ferns), but possibly include also parasites (on corticioid basidiomycetes). The remaining three genera are only known from their sterile mycelia: *Gamarada* forms an ericoid mycorrhiza with various *Ericaceae*, *Glutinomyces* was isolated from *Quercus* and *Castanopsis* roots, and *Soosiella* from extremely acidic soil (see Quijada et al. 2022). Members of *Hyphodiscaceae* inhabit a high diversity of usually dead parts of higher plants and also fungi, while only two species were previously known to grow on bryophytes, viz. *Fuscolachnum necator* Huhtinen & Döbbeler and *Hyphodiscus delitescens* Huhtinen & Döbbeler (Huhtinen et al. 2010).

The first two collections of a yellow bryophilous discomycete, which came to our notice when still in the fresh, living state, were made in April 2011 by L.G. Krieglsteiner, who detected apothecia in abundance on dead leaves of *Nowellia curvifolia* (≡ *Cephalozia curvifolia*) which grew in turn on logs of *Abies alba* in a beech-fir forest around Plitvička Jezera in Croatia. The unknown fungus showed a striking colour change from yellow to pinkish- or blood-red when coming in contact with alkali (e.g., KOH) or when dried for the herbarium and had asci with hemiamyloid apical rings. Similar collections were made from 2009 onwards by G. Bauer mainly on *Barbilophozia* and *Hypnum* on granite rocks in conifer forests in the Bayerischer Wald in Germany and in 2010 by P. Ribollet on *Hypnum* sp. in an oak-chestnut forest in dépt. Loire-Atlantique in France. In contrast to the Croatian specimens, these collections tended to have larger apothecia which likewise turned pinkish with alkali but not blood-red on drying, longer ascospores with a lower lipid content, and euamyloid ascus apical rings, suggesting a different species. In short intervals, numerous further collections were made by different collectors on various other bryophytes, but these mostly represented the species with euamyloid apical rings. Several of these collections were presented on the forum www.ascofrance.com (posts 22752, 56368, 72724 & 74337), but no identification was made. Despite a broad range of hosts on which apothecia with euamyloid ascus apical rings were observed, it ultimately appeared that all of them belong to a single species. During his work on bryophyte-inhabiting ascomycetes, P. Döbbeler noticed this plurivorous species in 2017–2019 on both mosses and liverworts when studying herbarium specimens collected in Macaronesia in 1989, in Europe during 1992–1993, and in North America during 2013–2018.

Screening of literature and databases for bryophilous discomycetes revealed a few old, insufficiently described taxa with features often more or less deviating from the two *Luteodiscus* spp. One of them, *Peziza hypnorum* Fr., was only briefly described by Fries (1822) and lacks any microscopic data, and also no type specimen exists. The protologue of *Phialea epibrya* Höhnel sounded promising to us but, although detailed, did not provide enough characteristics in order to decide if it represented one of our two species or instead the similar *Bryoscyphus turbinatus* (Fuckel) Spooner. Because no redescription of the type specimen could be found in the literature, it was necessary to reexamine the type in order to settle its taxonomic identity.

Materials and methods

Observation

Macro- and microscopic characters were studied from fresh apothecia, predominantly from living (*) elements following the standards of vital taxonomy (Baral 1992), in comparison also with samples from dead (†) elements. Apothecia were rehydrated after some time for testing the drought tolerance of the excipular and hymenial elements including the spores. Tap water (H_2O) was used as a mounting medium. Colour reactions were tested with IKI, MLZ, and KOH. The latter was also applied for testing the resistance of oil drops (LBs) and optionally before iodine application. Various microscopes were used due to the numerous workers documenting their collections. Measurements were conducted in tap water, either directly or on photographs. Parentheses in measurements refer to estimated frequencies, while statistical data have been evaluated in a few collections only.

The terminology of the morphological types of ascus apical rings follows Baral (1987a) and Triebel and Baral (1996), who emphasized sharp differences between the *Hymenoscyphus*- and *Bulgaria*-type, the latter type later called *Calycina*-type in Triebel and Baral (1996).

Herbaria

Collections were deposited in the herbaria of: BP (Budapest, C. Németh), GZU (Graz, P. Döbbeler), LEB (León, E. Rubio), M (Munich, P. Döbbeler), NMW (Cardiff, G. Greiff), NY (New York, P. Döbbeler), PRM (Prague, Z. Sochorová), KR (Karlsruhe, L.G. Krieglsteiner), and UPS (Uppsala, R. Isaksson), and in the private herbaria of H.O. Baral (H.B.), G. Bauer (G.B.), Bernd Fellmann (B.F.), Gernot Friebes (G.F.), Josef Hafellner (J.H.), M. Hairaud (M.H.), Ingo Ibelshäuser (I.I.), R. Isaksson (R.I.), Edvin Johannesen (E.J.), L.G. Krieglsteiner (L.K.), Csaba Németh (C.N.), J.P. Priou (J.P.P.), Pascal Ribollet (P.R.), E. Stöckli (E.S.), Z. Sochorová (Z.S.) and others. The holotype of *Phialea epibrya* was borrowed from FH (Harvard University Herbaria, Cambridge, USA). The nomenclature of the hosts follows Hodgetts et al. (2020).

Geographic data

For the climatic regions the online map about thermoclimatic belts was used (http://www.globalbioclimatics.org). The distribution map was generated as described in Baral et al. (2020: 6).

DNA extraction, PCR amplification and sequencing

Sequences obtained from apothecia of *L. epibryus* from the Czech Republic and *L. hemiamyloideus* from Germany were generated by Michal Sochor according to the methods described in Baral et al. (2023b), those of *L. epibryus* from Spain, France, and Scotland by Pablo Alvarado (ALVALAB), Jean-Michel Bellanger, and G. Greiff, respectively. G. Greiff followed the Phire Plant Direct protocol (Fisher; F160S) with slight adjustments as follows. Two small ascomata were removed from hydrated material and transferred to 14 µl dilution buffer. 0.5 µl was used as a template for direct PCR (20 µl volume) following some crushing of the apothecia with a pipette tip. The PCR reagents were set up according to the manufacturer's instructions. ITS1, 5.8S and ITS2 were amplified using ITS1F and ITS4 primers (White et al. 1990; Gardes & Bruns 1993), LSU sequences using LR0R and LR5 or LR6 (Vilgalys & Hester 1990), and *TEF1* using EF1-983F and EF1-1567R (Rehner & Buckley 2005), with annealing temperatures of 54 °C or 56 °C for all three sets of reactions.

PCR products were checked using agarose gels and purified using the Wizard SV Gel and PCR Clean-up System (Promega; A9282). Nucleic acids were quantified on a nanophotometer before being sequenced externally (by Eurofins Genomics) according to the supplier's instructions, using both the forward and reverse primers. Sequences were assembled using SnapGene software (https://www.snapgene.com/).

Phylogenetic analysis

Sequences from data repositories used in the phylogenetic analysis are mainly those of Quijada et al. (2022). In addition, the Basic Local Alignment Search Tool (BLAST, https://blast.ncbi.nlm.nih.gov) was used for searching similar sequences in GenBank (for the dataset see Table 1). Chromatograms of the newly generated sequences were checked using the software MEGA (ver. 6.06, Tamura et al. 2013). Alignment was achieved with MAFFT ver. 7 (https://mafft.cbrc.jp/alignment/server/index.html). Phylogenetic analysis was reconstructed in MEGA (ver. 6.06) based on concatenated ITS and LSU D1−D4 rDNA, using the Maximum Likelihood (ML) method with the best substitution model (GTR + G + I) evaluated in MEGA, tested by bootstrapping, with 500 pseudoreplicates. Bayesian phylogeny inference (BI) was computed in MrBayes (ver. 3.2.7) under the same model (GTR + G + I) for 7.5 million generations by sampling every 1000th generation (Ronquist et al. 2012). Individual analyses of ITS and LSU were generated for comparison, but only the ITS analysis is shown.

Abbreviations

* = living state, † = dead state, → = from immature to mature; CR = Congo Red (aqueous), CRB = Cresyl blue (aqueous), H_2O = tap water, IKI = Lugol's solution (high-concentrated): ~ 1% I_2 and 2% KI (potassium iodide) in H_2O (type BB = euamyloid, type RR = hemiamyloid, type rB = slightly hemiamyloid, dirty red at high iodine concentration only); KOH = potassium hydroxide (~ 5%), MLZ = Melzer's reagent; IVV = https://in-vivo-veritas.de (Ascomycetes illustrations), ø = unpreserved; idem = the same, ibid. = from the same geographical region; LB = lipid body (oil drop); nt = nucleotide; OCI = oil content index (lipid content, 0 = no LBs, 5 = maximum possible content, excluding nuclear region); sq. = DNA sequence; VB = refractive vacuolar body, vid. = specimen examined also by a person other than the finder. The numbers in curled parentheses {} indicate the number of collections (numbers after the slash refer to uncertain hosts).

Taxonomic part

Luteodiscus Baral, L.G. Krieglst. & Sochorová, **gen. nov.**

MycoBank: MB 854452.

Type: *Luteodiscus epibryus* (Höhn.) Baral, Sochorová & Halasů

Etymology: named after the yellow colour of the disciform apothecia.

Generic diagnosis: **Apothecia** (0.1−)0.15−1(−1.35) mm diam., light to bright yellow when fresh, exceptionally white, hardly translucent, non-gelatinous, scattered to subgregarious; disc round, slightly concave to flat, margin not or only indistinctly protruding; exterior concolorous,

Table 1 Strains in GenBank used in the phylogenetic analyses (sequences generated during this study are highlighted in bold)

Species	Original name in GenBank	Herbarium/identification code	GenBank accession number		Reference
			ITS	LSU	
Amicodisca virella		S.B.R.H. 828	MH221521	MH485388	S. Helleman unpubl.
Arachnopeziza aurata		TNS-F11212	JN033436	AB546936	Han et al. 2014, Hosoya et al. 2011
Belonioscyphella hypnorum		Bel2	KU900903	KU900906	Egertová et al. 2016
Belonium coroniforme		ZT-Myc 64689	MW718703	MW718696	Döbbeler et al. 2021
Brunnipila fuscescens		KUS-F52031	JN033392	JN086695	Han et al. 2014
Bryoglossum gracile		MBH52481	AY789421	AY789420	Wang et al. 2005
Bryorutstroemia fulva		Z.S. 19/2021	OP035828	OP035828	Baral et al. 2023b
Bryoscyphus rhytidiadelphi		H.B. 7214	OM808923	OM720019	H.O. Baral unpubl.
“*Bryoscyphus*” *turbinatus*		E.R.D. 6964	MT370346	MT370360	E. Rubio unpubl.
“Bryoscyphus” turbinatus		**J.P.P. 19140**	**PP848980**	**PP848980**	**This study**
Calycina citrina		G.M. 2014-12-14.4	KY462815	KY462815	H.O. Baral & G. Marson unpubl.
Calycina herbarum		KUS-F51458	JN033390	JN086693	Han et al. 2014
Chalara aurea		CBS 633.75	MH860959	MH872728	Vu et al. 2019
Cistella acuum		CCF 3970	FR667211	FR667860	Koukol 2011, Žifčáková et al. 2011
Cistella albidolutea		KUS-F52678	JN033429	JN086732	Han et al. 2014
Cistella sp.		KUS-F52527	JN033419	JN086722	Han et al. 2014
Cistella spicicola		CBS 731.97	GU727553	GU727553	Bogale et al. 2010
Cyathicula microspora		M267	EU940165	EU940088	Baral et al. 2009
Dematioscypha castaneae	*Amicodisca* sp.	KUS-F51917	JN033411	JN086714	Han et al. 2014
Dematioscypha delicata	*Haplographium delicatum*	TNS-F17834	JN033438	JN086739	Han et al. 2014
Eriopezia caesia		S.B.R.H. 843	KX501126	KX501130	S. Helleman unpubl.
Eupezizella aureliella	*Hyaloscypha aureliella*	M235	EU940229	EU940153	Baral et al. 2009
Fuscolachnum misellum		S.B.R.H. 799b	KX501124	KX501129	S. Helleman unpubl.
Fuscolachnum pteridis	*Scolecolachnum nigricans*	MFLU 18-1817	MK584975	MK591973	Ekanayaka et al. 2019
Gamarada debralockiae		T6G9	PRJNA407395	NXFV01000000	Midgley et al. 2018
Gemmina gemmarum		S.B.R.H. 862	KX501127	OM218628	S. Helleman unpubl.
Gemmina juniperi	*Gemmina* sp.	H.B. 6910	OM456210	OM456211	H.O. Baral unpubl.
Glutinomyces inflatus		TNS-F80763	LC218289	LC315170	Nakamura et al. 2018
Hamatocanthoscypha laricionis		TNS-F13530	JN033441	JN086742	Han et al. 2014
Hyalodendriella betulae		CBS 261.82	EU040232	EU040232	Crous et al. 2007
Hyalopeziza nectrioidea		CBS 597.77	JN033381	JN086684	Han et al. 2014
Hyalopeziza nectrioidea		H.B. 9906	KT876982	KT876982	H.O. Baral & G. Marson unpubl.
Hyaloscypha albohyalina		TNS-F17137	JN033431	JN086734	Han et al. 2014
Hyaloscypha monodictys		TNS-F5013	JN033456	JN086756	Han et al. 2014
Hyaloscypha vitreola		M236	EU940232	EU940156	Baral et al. 2009
Hyphodiscus hyaloscyphoides	*Hyphodiscus* sp.	TNS-F13588	AB546944	AB546945	Hosoya et al. 2011
Hyphodiscus hymeniophilus		CBS 602.77	DQ227264	DQ227264	Untereiner et al. 2006
Hyphodiscus luxurians		CBS 647.75	GU727560	GU727560	Bogale et al. 2010

Table 1 (continued)

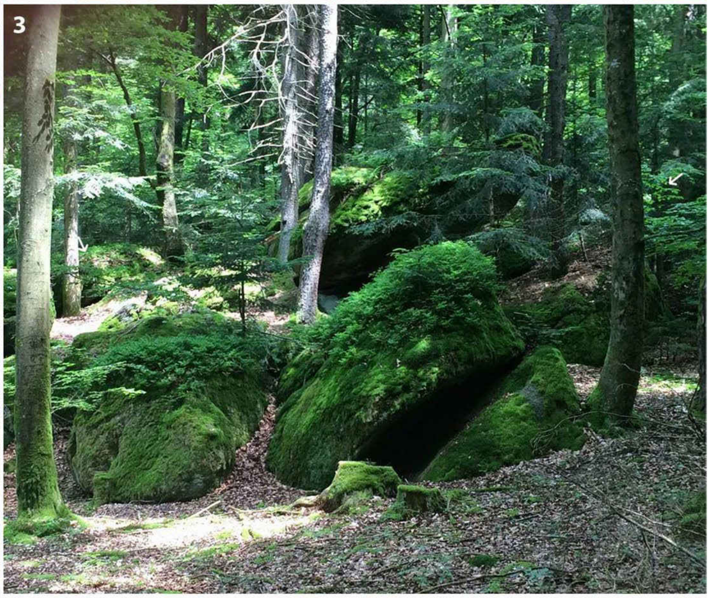
Species	Original name in GenBank	Herbarium/identification code	GenBank accession number		Reference
			ITS	LSU	
Hyphodiscus otanii		TNS-F7099	AB546949	AB546947	Hosoya et al. 2011
Hyphodiscus theiodeus		TNS-F32000	AB546953	AB546952	Hosoya et al. 2011
Hyphopeziza pygmaea	*Hyalopeziza pygmaea*	TNS-F17940	JN033448	JN086748	Han et al. 2014
Leptodontidium boreale		CBS 682.76	AY129284	NG067409	Sogonov et al. 2005, Vu et al. 2019
Leptodontidium irregulare		CBS 152.60	MH857936	MH869480	Vu et al. 2019
Leptodontidium trabinellum	*Leptodontidium elatius*	CBS 624.69	MH859388	MH871159	Vu et al. 2019
Luteodiscus epibryus	***Helotiales* sp.**	**E.R.D. 6988**	**MT370342**	**MT370357**	**This study**
Luteodiscus epibryus	*Phialea epibrya*	**J.P.P. 202038**	**PP848981**	**PP848981**	**This study**
Luteodiscus epibryus	*Phialea epibrya*	**M.H. 100216**	**PP820658**	**–**	**This study**
Luteodiscus epibryus	*Hyphodiscaceae* sp.	**Z.S. 4/2021**	**OR589464**	**–**	**This study**
Luteodiscus epibryus	*Hyphodiscaceae* sp.	**F.V. 2013021901**	**OR198862**	**–**	**This study**
Luteodiscus epibryus	*Phialea epibrya*	**G.G. 523**	**PP820661**	**PP820661**	**This study**
Luteodiscus hemiamyloideus	*Helotiales* sp.	**L.K. 3430**	**PP820660**	**PP820660**	**This study**
Luteodiscus hemiamyloideus	*Helotiales* sp.	**L.K. 3429**	**PP820659**	**PP820659**	**This study**
Psilachnum ellisii	*Microscypha ellisii*	KUS-F52489	JN033418	JN086721	Han et al. 2014
Proliferodiscus pulveraceus		G.M. 2017-03-21.3	MN066320	MN066320	G. Marson unpubl.
Psilachnum chrysostigma	*Pezizella chrysostigma*	**I.W. 109, STMA21042**	**PP835314**	**PP835314**	**This study**
Psilachnum lateritioalbum		S.B.R.H. 962	OP626155	OP626156	S. Helleman unpubl.
Psilachnum* aff. *rubrotinctum		**M.H. 50815**	**PP835535**	**PP835672**	**This study**
Psilocistella conincola	*Hamatocanthoscypha laricionis*	S.B.R.H. 938	OL752701	OM218635	S. Helleman unpubl.
Psilocistella quercina		TFCMic 24122	UDB0754107	–	Quijada et al. 2014
Roseodiscus formosus		S.B.R.H. 686	KT972711	KT972712	Baral and Haelewaters 2015
Roseodiscus rhodoleucus		H.B. 8448a	KT972704	KT972705	Baral and Haelewaters 2015
Roseodiscus subcarneus		D.H. 314A	KT972714	KT972715	Baral and Haelewaters 2015
Scolecolachnum pteridii	*Psilachnum* sp. "*pteridii*"	CPC 24666	KU597797	KU597764	Guatimosim et al. 2016
Soosiella minima		CBS 136257	JX124327	JX124327	Hujslová et al. 2014
uncultured fungus		H26 L3569	FN298703	FN298703	Tedersoo et al. 2009
uncultured fungus		H026x L3123	FN298704	FN298704	Tedersoo et al. 2009
uncultured fungus		H28 L3508	FN298706	FN298706	Tedersoo et al. 2009
uncultured fungus		H25 L3532	FN298702	FN298702	Tedersoo et al. 2009
Urceolella aspera		S.B.R.H. 827	MH221523	MH485387	Helleman 2020
Venturiocistella sp.		KUS-F52028	JN033391	JN086694	Han et al. 2014
Venturioscypha nigropila		TUR 215407	ON241823	ON241823	Baral et al. 2023a

smooth to finely fimbriate; subsessile or usually with short and stout stipe being never clearly longer than wide, hyaline to pale yellow, more translucent, superficial. **Asci** *50−95 × 7.2−11.5 µm, 8-spored, spores *obliquely biseriate; apex conical, †with pronounced apical dome, amyloid ring of *Calycina*-type; base with short to medium long stalk arising from croziers. **Ascospores** *(6.3−)7−18 (−21) × (2.4−)2.8−4(−4.5) µm, cylindric(-ellipsoid) to


1a


1b


2


3


4


5

◀**Fig. 1** Collection sites of *Luteodiscus epibryus*. **1** 16.V.2020, old conifer log with *Cardamine pentaphyllos*, on *Hypnum cupressiforme* & *Dicranum scoparium* (Swiss Jura, Source de la Dou), **2** E.S. 2020.41, old conifer stump with *C. pentaphyllos* etc., on *Tetraphis pellucida* (ibid., Lajoux, 2.V.2020), **3** H.B. 10213, spruce-beech forest, granite rocks, on *Hypnum cupressiforme* (Bayerischer Wald, Rettenbach, 12.VI.2021), **4** H.B. 10257, granite rock, on *Barbilophozia sudetica* (ibid., Altfaltern, 23.XI.2011), **5** F.V. 2013021901, sandstone rock, on *Pleurozium schreberi* (Seine-et-Marne, Fontainebleau, 19.II.2013). – Phot. **1**–**2** E. Stöckli, **3**–**4** G. Bauer, **5** M. Tanaskovic

fusoid-clavate, homo- to heteropolar, with rounded to obtuse ends, straight to slightly curved, hyaline, smooth, non-septate; containing a few small to medium-sized LBs, without sheath, wall surface not stained in CRB; turning 1-septate when overmature. **Paraphyses** ± cylindrical, straight to slightly flexuous or irregularly bent, apically not inflated, rarely apically furcate, branched only in lower part; terminal cell usually distinctly longer than lower cells, guttulate by containing slightly to strongly refractive, large, globose, rarely elongated, hyaline to pale yellowish VBs. **Medullary excipulum** hyaline to pale yellowish or rosaceous, of ± loose textura intricata. **Ectal excipulum** concolorous, of thin-walled, at lower flanks of irregularly vertically or horizontally, at upper flanks horizontally oriented textura prismatica, marginal cells guttulate, sometimes freely projecting like hairs. **Anchoring hyphae** abundant, thin-walled, hyaline. **KOH-reaction**: yellow pigment of entire apothecium turning bright pinkish to reddish, colour change also observed after bruising or cutting, after prolonged storage in water, or after drying (particularly in *L. hemiamyloideus*). **Crystals** absent. **Anamorph**: unknown.

Habitat: growing necrotrophically on mosses and foliose, rarely thallose liverworts, causing discoloration of patches within populations of the host species by penetrating and killing the host cells.

Key to species of *Luteodiscus*

1. Ascus apical ring euamyloid (blue in IKI, type BB) to slightly hemiamyloid (blue to dirty red, type rB), †0.8–1.3 → 0.7–1 µm high; ascospores *(10–)11–16(–18) × (2.5–)3–3.5(–4) µm, Q = *(3–)3.3–4.6(–5), homo- to medium heteropolar, OCI (0–)1–1.5(–2); VBs in paraphyses occupying upper 15–40 µm; apothecia fresh (0.2–)0.3–0.8(–1) mm diam., sulphur- to egg-yellow, turning light yellow(-orange) or sometimes pinkish when dry; on various mosses and foliose liverworts ....***L. epibryus***

1. Ascus apical ring hemiamyloid (pure red in IKI, type RR), †(2–)2.5–3.5(–4.5) → (0.7–)1–2.5(–3) µm high; ascospores *(7–)8–11(–12) × (2.4–)2.8–3.5(–4) µm, Q = *(2.3–)2.5–3.7(–4.3), mostly slightly to strongly heteropolar, OCI (2–)3(–4); VBs in paraphyses occupying upper 10–20 µm; apothecia fresh (0.1–)0.15–0.45(–0.55) mm diam., sulphur- to egg-yellow, turning light to deep orange or pinkish- to blood-red when dry; on foliose, rarely thallose liverworts ....***L. hemiamyloideus***

Luteodiscus epibryus (Höhn.) Baral, Sochorová & Halasů, **comb. nov.** – Figs. 1, 2, 3, 4, 5, 6, 7

MycoBank: MB 854456.

Basionym: *Phialea epibrya* Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 116: 136 (1907).

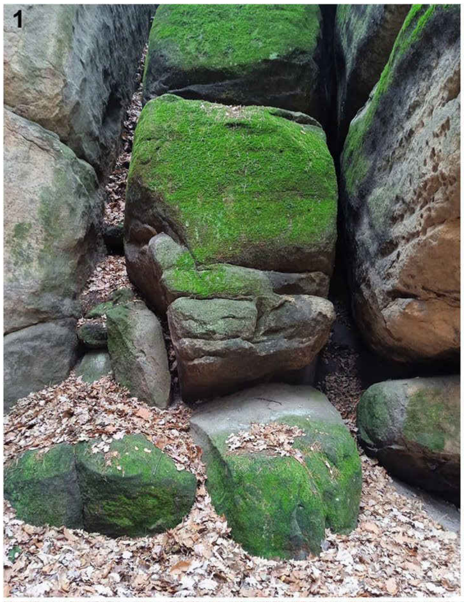
≡ *Hymenoscyphus epibryus* (Höhn.) Haluwyn, Bull. Sem. Soc. Mycol. Nord 45–46: 83 (1990) [1989].

Holotype: Czechia, Vysočina, Žďár nad Sázavou ("Saar"), ~ 49°34′N, 15°56′E, on leaves of *Hypnum* [*cupressiforme*], 1906, F. Kovář (ex herb. Höhnel A.5325, FH).

Reference specimen (designated here): Czech Republic, Liberec Region, Česká Lípa District, Svojkov, Modlivý důl, 50°43′36.5″N, 14°36′16.5″E, on *Lepidozia reptans*, *Neoorthocaulis attenuatus*, *Paraleucobryum longifolium*, *Sphenolobus minutus* & *Tetraphis pellucida* growing over quartz sandstone rock, 1.I.2021, Z. Sochorová (PRM 959992).

Etymology: named after the growth on a moss.

Apothecia fresh ((0.1–))(0.2–)0.3–0.8(–1)((–1.35)) mm diam. {32}, 0.2–0.45 mm tall, receptacle 0.1–0.22 mm thick {5}; disc light to bright sulphur- to egg-yellow, exceptionally white {1}, flat, finally slightly convex, margin smooth to finely fimbriate, not protruding; stipe ± absent or distinct, obconical to cylindric, 0.05–0.23 × 0.1–0.25 mm {6}; dry pale to light ochraceous-yellow, yellowish-cream, orange-yellow, or orange {9}. **Asci** *((39–))(50–)60–75(–85) × (7.5–)8–10.5(–11.5)((–12.5)) µm {24}, †(40–)50–70(–78) × (6–)6.5–9(–9.5)((–10)) µm {20}, 8-spored, spores */†obliquely biseriate, pars sporifera *22–35 µm long {6}, †(22–)30–40(–45) µm {4}, living mature asci protruding by ~ 5–15 µm beyond paraphyses, dead asci ± equalling them; **apex** slightly to strongly conical, apical ring in IKI pale to light blue (BB = euamyloid) {69}, sometimes very dirty red-brown seen at high concentration (rB) {3}, in MLZ pale blue (without KOH-pretreatment) {1}, apically distinctly extending (obconical), *0.6–0.8 × 1.5–2 µm {5}, †0.8–1.3 → 0.7–1 × 1.4–2 µm {7}; **base** subsessile or usually gradually narrowed in a short to medium long stalk, arising from croziers {42}. **Ascospores** *((8.5–))(10–)11–16(–18)((–21)) × (2.5–)3–3.5(–4)((–4.5)) µm {41}, Q = *((2.5))(3–)3.3–4.6(–5)((–6.6)) {5, $n = 280$}; †(8–)10–15(–16.2) × (2–)2.2–3(–3.5) µm {18}, Q = †(3–)3.8–5(–6) {3, $n = 55$}; cylindric(-ellipsoid) to fusoid-clavate, not or slightly to sometimes medium heteropolar; containing (0–)2–12 LBs of 0.4–1.4 µm diam. irregularly scattered through the whole ascospore, OCI (0–)1–1.5(–2) {25}, sometimes associated with globose low-refractive VBs of (0.7–)1–2(–2.3) µm diam. {10}


1


2


3


4


5


6

◀**Fig. 2** Collection sites of *Luteodiscus epibryus*. **1** Z.S. 154/2021, oak-pine forest, sandstone rocks, on *Sphenolobus minutus* & *Tetraphis pellucida* (Česká Lípa, Peklo NNM, 16.XI.2021), **2** UPS F-1046735, cut *Alnus glutinosa* forest with spruce etc., siliceous rocks, on *Trilophozia quinquedentata* (Jönköpings län, Sävsjö, 23.III.2022), **3** H.B. 10262, beech-spruce-fir forest with pine & birch, granite rocks, on *Hypnum cupressiforme* & *Pogonatum urnigerum* (Bayerischer Wald, Altfaltern, 10.VI.2021), **4** beech-spruce-fir forest with birch, granite rocks, on *H. cupressiforme* (ibid., Schlinding, 2.XI.2014), **5–6** E.R.D. 6988, oak-beech-chestnut forest with ash and hazel, quartzite rocks, on *Frullania tamarisci* & indet. *Hypnales* (Asturias, Oviedo, ~ 27.VIII.2023 [coll. 4.III.2017]). − Phot. **1** Z. Sochorová, **2** R. Isaksson, **3−4** G. Bauer, **5–6** M. González

that stain violet in CRB, with two large glycogen regions near the ends {4}; overmature spores often 1-septate {9}. **Paraphyses** cylindrical, rarely slightly inflated below apex, straight, sometimes slightly flexuous or bent, terminal cell *20–34 × 1.8–2.5(–2.8) µm {6}, lower cells *(6–)10–20(–23) × (1.5–)1.8–2.5(–3.5) µm {6}; VBs slightly to strongly refractive, hyaline to pale yellowish, globose, rarely elongated, (0.3–)0.5–1.5(–2) µm diam., occupying upper 15–40 µm {11}, in IKI strongly refractive, light yellow to reddish-brownish, in CRB (turquoise-)blue. **Medullary excipulum** hyaline to pale rose, 60–100 µm thick in centre, of dense to medium loose textura intricata, cells *9–18 × 2–3(–4) µm {2}, †1.5–3.3 µm wide, non-gelatinised, indistinctly to medium sharply delimited from ectal excipulum. **Ectal excipulum** hyaline to pale rosaceous, of textura (porrecta-)prismatica(-angularis), at base oriented irregularly vertically, at flanks under a 0–45° angle, 40–70 µm thick at lower flanks, cells *(5.5–)8–18(–25) × (3.5–)4.5–7.5(–9)((–12)) µm {6}, †(5–)7–17 × 3.5–7(–8) µm {3}, thin- to firm-walled (†0.2–0.4 µm), at base with distinct intercellular gel (common walls †1–3 µm thick); at upper flanks of horizontally oriented t. prismatica, 25 µm thick near margin, marginal cortical cells */†(5.5–)8–11 × 2–4.5 µm {2}; at margin and flanks with straight to flexuous, cylindrical or slightly tapering, smooth, **hair-like elements** of *9–30 × (1.7–)2–2.5(–2.8) µm {5}, 0(–1)-septate, at margin containing VB-guttules. **Anchoring hyphae** *(1.2–)1.8–2.5(–3) µm wide {2}, †1.5–2(–3) µm, thin-walled (0.2 µm), hyaline, projecting, straight to irregularly flexuous, sparse to abundant, forming an up to 40–70 µm thick layer at base, growing over and into the host cells (in host cells 1.5–4 µm wide). **KOH-reaction**: macroscopic: yellow pigment turning light to bright rose-pink to purplish or wine- to brownish- or brick-red {64}; microscopic: yellow excipulum changing to purplish-rose {4} but sometimes negative, extruding a transient yellowish stain to the medium {1}.

Habitat: growing on ± decolorised, dead stems and mainly leaves of various bryophytes (see Table 5): mosses: *Tetraphidales* {4}, *Polytrichales* {7}, *Dicranales* {29}, *Grimmiales* {1}, *Bryales* {2}, *Hypnales* {83}, indet. mosses {2}; foliose liverworts: *Jungermanniales* {35}, *Porellales* {4}, indet. foliose liverwort {1}; bryophytes growing on rock {min. 37} or soil {19}, on wood and bark of cut stumps {52} or fallen logs {31}, rarely branches {1}, sometimes on bark of living trunks {6}, of *Abies* sp. {1}, *A. alba* {1}, *Alnus glutinosa* {1}, *Betula* sp. {1}, *Castanea sativa* {6}, *Corylus avellana* {1}, *Picea abies* {1}, *Pinus* sp. {9}, *P. canariensis* {1}, *P. sylvestris* {1}, *Quercus* sp. {1}, *Ulex* {1}, indet. gymnosperm {5}, indet. angiosperm {3}, indet. trees {27}. **Associated organisms**: *Epibryon bryophilum* agg. {1}, *Lepraria* sp. {1}, *Pseudomicrodochium bryophilum* {1}. **Drought tolerance**: ectal and medullary excipulum, paraphyses and ascogenous hyphae still alive 16 h after drying {H.B. 10261}, only a few ascospores alive after 3 days in the herbarium {Z.S. 163/2021}. **Altitude**: Scandinavia and Scotland: 27–322 m, central, western and eastern Europe: 20–1000 m, Macaronesia: ~ 1250 m, USA: 65–1950 m. **Climate**: Europe: hemiboreal to orotemperate, temperate, and mesosubmediterranean humid; Macaronesia: mesomediterranean (sub)humid; USA: cold-temperate to mild-maritime humid. **Geology**: acidic (granite, quartzite, quartz and arkose sandstone, Ordovician schist etc.), sometimes alkaline (Jurassic limestone). **Phenology**: (IX–)III–VI(–VII) (see Table 2).

Variation. The diameters of the apothecia varied among the collections between 0.15–0.25 and 0.5–1, exceptionally 0.1 and 1.35 mm, with a predominance of 0.3–0.8 mm. The stipe was sometimes almost absent but mostly distinct. Apothecial colour was consistently light to bright yellow, with one exception with completely lacking pigmentation (J.P.P. 19083, Fig. 4(13)), in which also the pink reaction in KOH was absent. Microscopically, this deviating apothecia had the typical characters (see IVV). The asci varied among the collections in length between *(39–)50–65 and 65–85 µm [†40–55 and 60–78 µm] and in width between *7.5–9.5 and 10–12.5 µm [†6–7 and 8–10 µm], and the ascospore in length between *(8.5–)10–13.5 and 15–18(–21) µm [†8–12 and 11.5–16.2 µm] and in width between *2.5–3.5 and 3.5–4.5 µm [†2–3 and 3–3.5 µm]. Little variation was observed in the key character, the euamyloid reaction of the apical rings, which was mostly invariably blue at any IKI concentration, rarely dirty red at high concentration. The presence of glycogen in the ascospores was nicely seen in a collection on *Barbilophozia* (Fig. 6(11)) and in the holotype (Fig. 7o), but only indistinctly so in another specimen on *H. cupressiforme* (24.II.2015, from Belgium), whereas in some other collections tested with IKI, there was no trace of glycogen. The presence of low-refractive VBs in the ascospores was seen in several collections (Fig. 6(1d, 2c, 8a, 9)), but was only once tested by vital staining with CRB (Fig. 6(8a)). Whether the spores may contain both glycogen and VBs is unclear, since both structures look very similar when studying living spores in a water mount without staining.

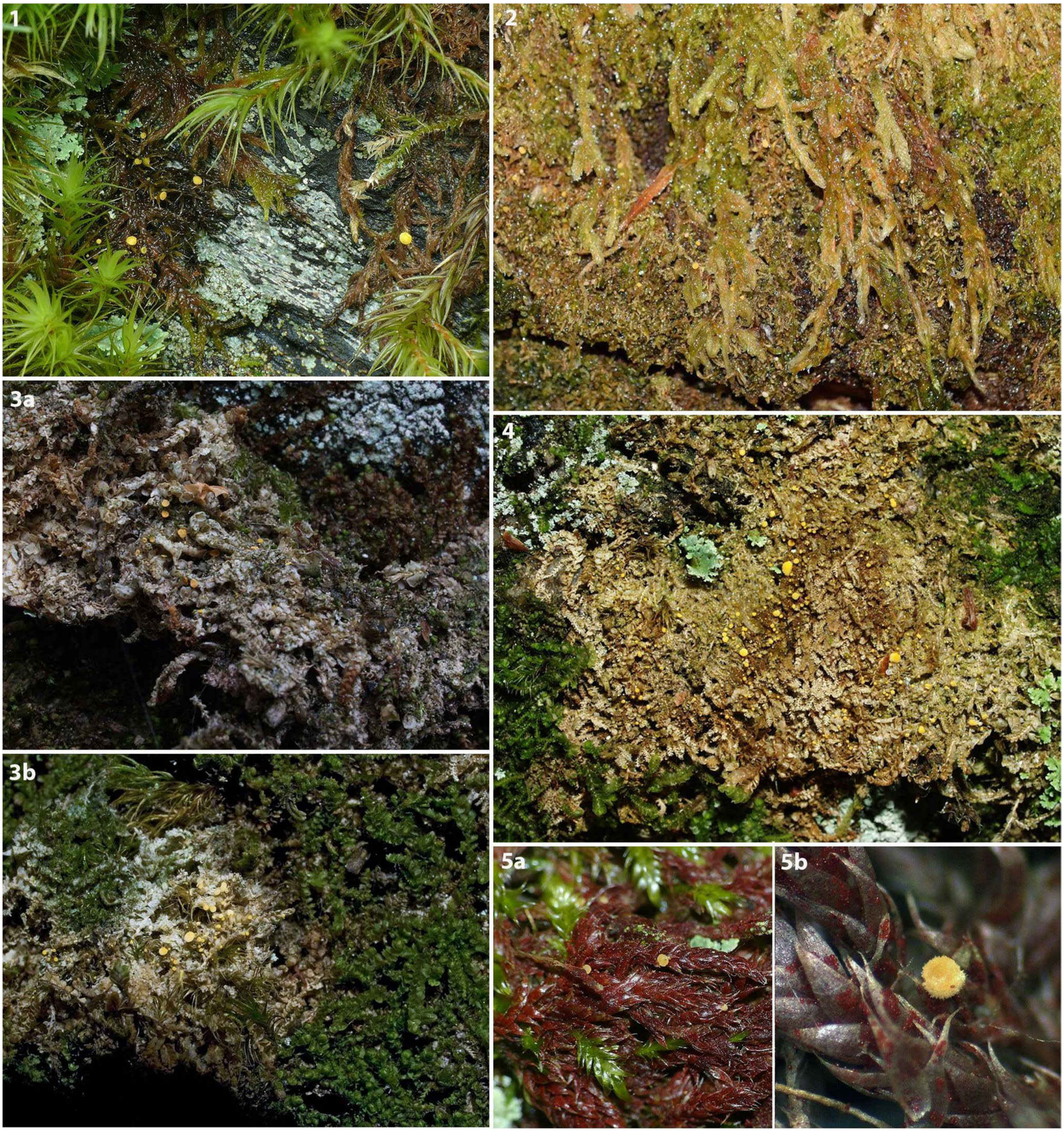


Fig. 3 *Luteodiscus epibryus* in situ. **1** B.C. 20140203A, on *Grimmia trichophylla* and *Hypnum* on acidic rock (Ardennes, Semoy, 3.II.2014), **2** E.S. 2020.02, on *Hypnum cupressiforme* on old conifer log (Bern, Cormoret, 4.I.2020), **3** H.B. 10216a/b, on *Barbilophozia sudetica* & *Isopaches bicrenatus* on granite (Bayerischer Wald, Altfaltern, 18.V.2009), **4** H.B. 10257, on *B. sudetica* (idem, 23.XI.2011), **5** 24.II.2015, on *H. cupressiforme* on acidic rock, moss invaded by an unidentified species of *Chlorophyta* with red pigment (Namur, Vierves). – Phot. **1**, **5** B. Clesse, **2** E. Stöckli, **3**–**4** G. Bauer

Remarks on the holotype of *Phialea epibrya*. Höhnel (1907) described the species on leaves of *Hypnum* sp. (substrate of moss not stated) from Saar (today Žďár nad Sázavou), Moravia, Czechia, leg. Filip Kovář, 1906 (year according to label of holotype in FH, Fig. 7a; see also notebook of Höhnel's "Herbar Index" p. 233). At Saccardo & Trotter's (1913: 657) time the town belonged to the Austria-Hungary Empire, whereas Carpenter (1981:

211) and Haluwyn (1990) erroneously referred it to Germany. The protologue includes apothecia 0.42−0.45 mm diam. with reddish egg-yellow disc and smooth exterior, a stipe of 0.1 × 0.1 mm, and a mostly rose-coloured flesh under the microscope despite its yellow external colour both when fresh and dry. The paraphyses were described as filiform, 1.5−2 µm wide, apically not inflated. Höhnel's measurements of asci (50−60 × 8−9 µm) and ascospores (12−18 × 3−4 µm, with a finely granular content) would more or less fit both *L. epibryus* and "*B.*" *turbinatus*, because data on crystals and ascus croziers are lacking. Höhnel's handwritten diagnosis on the label largely concurs with these data, except that the asci are given in the range of 52−60 × 8−9 µm and the spores in the range of 12−17 × 2.75−4 µm (Fig. 7a).

Höhnel (1902: 1007) used the generic name *Phialea* (Pers.) Gillet (non *Phialea* Quél.) after the advice of Rehm (1892: 708), who treated it as "*Phialea* Fries" in a large sense for members with a mostly short stipe, edentate margin, aseptate ascospores, and a light-coloured prosenchymatic ectal excipulum. The tough excipulum by which *Phialea* has later been characterised was not stated by Rehm in his generic circumscription as being crucial.

When Carpenter (1981) resurrected the genus *Crocicreas* Fr. in his monograph to replace the younger *Cyathicula* De Not. (= *Phialea* (Pers.) Gillet), he examined the holotype of *P. epibrya* in FH by placing his slide in herb. NYBG (NY01168070) (see https://sweetgum.nybg.org/science/vh/specimen-list/?SummaryData=Phialea%20epibrya). Carpenter found an ectal excipulum of prismatic cells and no stroma at the stipe base by concluding that it is a member of *Hymenoscyphus* Gray. Yet, he hesitated to propose the combination because he thought that other, possibly synonymous bryophilous taxa could compete with *P. epibrya*. Carpenter did not mention a copy of a detailed microscopic drawing of the holotype, which was found in the present study inside the envelope (see below).

Haluwyn (1990), on the other hand, did not mention Carpenter at all when transferring *Phialea epibrya* to *Hymenoscyphus*. Besides the type in FH, she studied a collection from Forêt domaniale du Perche (dépt. Orne, France) on *Hypnum cupressiforme* var. *filiforme* growing on *Quercus robur* made by her during winter (undated). According to Haluwyn, M. Bon and J. Hafellner confirmed her identification as *Phialea epibrya*. Haluwyn's measurements of asci (45−55 × 8−10 µm) and spores [(11−)12−16 × 3−3.5 µm, content multiguttulate] based on this collection indeed resemble Höhnel's data. Haluwyn's schematic drawing, however, is uncertain regarding the ascus base, possibly she was unaware of the importance of the feature and also might have neglected the occurrence of crystals which would characterize the similar "*B.*" *turbinatus*. Haluwyn stated that the holotype contained "drawings and microscopic preparations". It appears that she preferred not to search for apothecia on the moss but to study and rely on these drawings and preparations, which she both incorrectly attributed to Höhnel. Haluwyn emphasized that some of the drawn features are not treated in the protologue, viz. paraphyses apparently projecting beyond the asci, and asci having prominent croziers at their base and a distinct amyloid apical pore.

In her generic concept Haluwyn relied on Dennis (1975) who widened the concept of *Cyathicula* to include members with edentate margin. Because of two characteristics she argued that *P. epibrya* does not belong in *Cyathicula* but in *Hymenoscyphus*. One characteristic was the thick and glassy walls of the ectal excipulum in *Cyathicula* in contrast to thin-walled, non-gelatinised excipulum in *Hymenoscyphus*. The other characteristic, large lanceolate paraphyses projecting beyond the asci in *Cyathicula* vs. filiform paraphyses in *Hymenoscyphus*, is an unexplainable mistake, since Dennis did not speak at all of lanceolate paraphyses. The only species included by him in *Cyathicula* having lanceolate paraphyses, *C. incertella* (Rehm) Dennis, is today accepted in *Crocicreas* in a narrow sense, while most other species placed in *Crocicreas* by Carpenter now remained in *Cyathicula* or have been transferred to *Allophylaria* (P. Karst.) P. Karst.

When ordering the holotype of *P. epibrya* in April 2024, a photocopy of a drawing was found inside (see Fig. 7b). The drawing was signed by W.L. White with the date 15th March 1941 but was apparently never published by him. No doubt, this is the document to which Haluwyn referred by overlooking White as its author. Based on the magnification of 1835 × given by White, the shown mature ascus measures †68 × 6.8 µm, the ascospores †9.8−15 × 2.5−3.5 µm, Q = (3.5−)3.8−4.2(−4.6) {$n = 9$}, and the paraphyses at the apex †2−2.5 µm. The spores finally turn 1-septate and germinate. White further noted a uniform red stain to the spores (presumably in MLZ) and the absence of oil drops in them. Possibly Haluwyn examined a microscopic preparation of either White or Carpenter. In any case, no such slide was now found inside the holotype in FH.

The holotype envelope bears Höhnel's notes (Fig. 7a) which largely concur with the protologue, but include also a spore size of 12 × 2.75 µm and a positive iodine reaction of the ascus pore. The moss with its strongly falcate leaves appears to be *Hypnum cupressiforme*. Despite a thorough search, no more than three mature apothecia of 0.25−0.3 mm diam. (apothecia 1−3), besides two immature ones (apothecia 4−5), could be detected, though only after rehydration. The moss plants, on which these apothecia occurred, were darker due to the occurrence of algae and black-brown fungal cells, and carried small patches of whitish-greyish *Lepraria* thalli.

More than half of apothecium 1 was already consumed prior to this study. In order to verify its relationship with

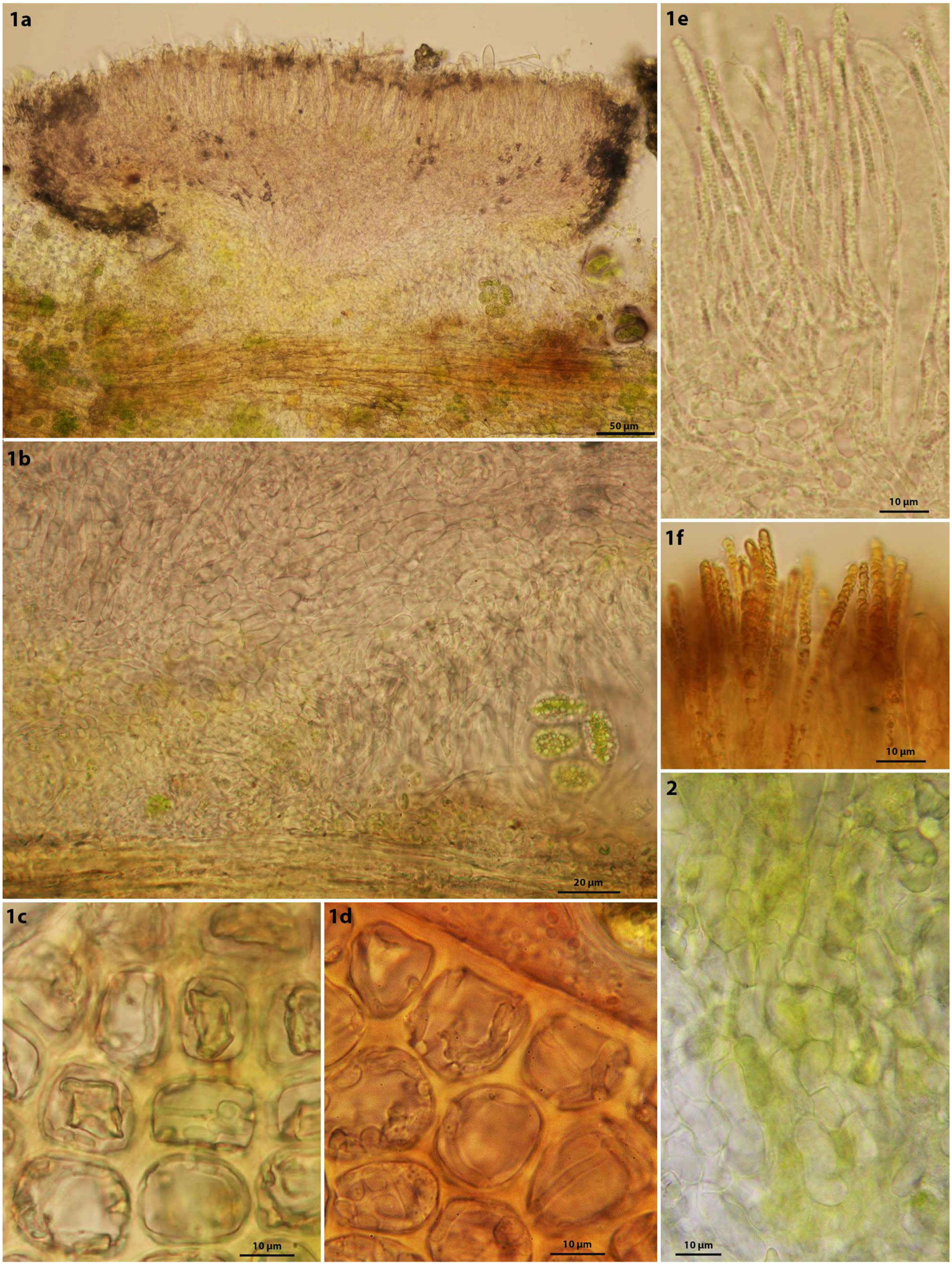

1
~1 mm
2
~2 mm
3
dry
0.5 mm
4a
~1 mm
5a
~1 mm
6
~0.5 mm
7
0.5 mm
8
~0.5 mm
9a
~0.5 mm
9b
10
~1 mm
11
KOH
~1 mm
12
KOH
1 mm
5b
0.5 mm
4b
KOH
~0.5 mm
13
~0.5 mm
14a
~1 mm
14b
~1 mm
15a
~0.5 mm
14c
~1 mm
14d
KOH
~1 mm
15b
~1 mm

◂**Fig. 4** *Luteodiscus epibryus*. Fresh apothecia (some treated by KOH, **13**: albinotic form), except for 3 (dry, after 9.5 months). **1** Z.S. 41/2021, on *Odontoschisma denudatum* & *Sphenolobus minutus* (Svojkov, Modlivý důl). **2** H.B. 10257, on *Barbilophozia sudetica* (Bayerischer Wald, Altfaltern). **3** H.B. 10216a/b, idem. **4** E.S. 2019.03, on *Hypnum cupressiforme* (Swiss Jura, Les Breuleux). **5** E.R.D. 8246, on *Hypnum* (Galicia, Oza dos Ríos). **6** B.C. 20140203A, on *Grimmia trichophylla* (Ardennes, Nohan-sur-Semoy). **7** B.C. 20181220A, on indet. pleurocarpous moss (Ardennes, La Neuville aux Haies). **8** F.V. 2013021901, on *Pleurozium schreberi* (Seine-et-Marne, Fontainebleau). **9** E.R.D. 6988, (**a**) on *Frullania tamarisci*, (**b**) on indet. *Hypnales* (Asturias, Oviedo). **10** J.P.P. 16060, on *Dicranum scoparium* & *H. cupressiforme* (Bretagne, La Gacilly). **11** J.P.P. 19079d, on *Kindbergia praelonga* (ibid.). **12** J.P.P. 16014, on *H. cupressiforme* (ibid.). **13** J.P.P. 19083, idem (ibid.). **14** Z.S. 103/2020, on *Sphenolobus minutus* (Svojkov, Modlivý důl). **15** J.P.P. 11044, *Pleurozium schreberi* (Bourgogne, Vernot). – Phot. **1, 14** Z. Sochorová, **2** B. Fellmann, **3** G. Bauer, **4** E. Stöckli, **5, 9** E. Rubio, **6–7** B. Clesse, **8** F. Valade, **10–13, 15** J.P. Priou. − In composed figures the scale bar is valid for all partial figures

Luteodiscus, apothecium 2 was treated in situ with a small drop of 10% KOH by which it immediately became deeper (rose-)red (Fig. 7h−i). The microscopic study of a part of apothecium 3 revealed asci †50−55 × 7.5−8.5 µm, with 8 spores in regular obliquely biseriate arrangement (pars sporifera 29−33 µm), a deep blue IKI reaction (euamyloid), and eguttulate ascospores of †(9.7−)10.5−14(−16.5) × 2.5−3.5 µm, Q = †3.9−4.5(−5.5) {*n* = 7}. White's statement of the spores "staining uniformly red" (presumably in MLZ) might refer to glycogen. This red reaction was twice noted in the present study (in IKI or KOH + IKI), including the type (Figs. 6: 11, 7o). The ectal excipulum is composed of thin-walled, prismatic cells of †7.5−12 × 4.5−8 µm. Contrary to Höhnel's observation of a rose tissue colour, this was yellowish in water (Fig. 7e) and hyaline in KOH. Nevertheless, it appears possible that Höhnel used KOH and therefore saw a "beautifully rose" tissue.

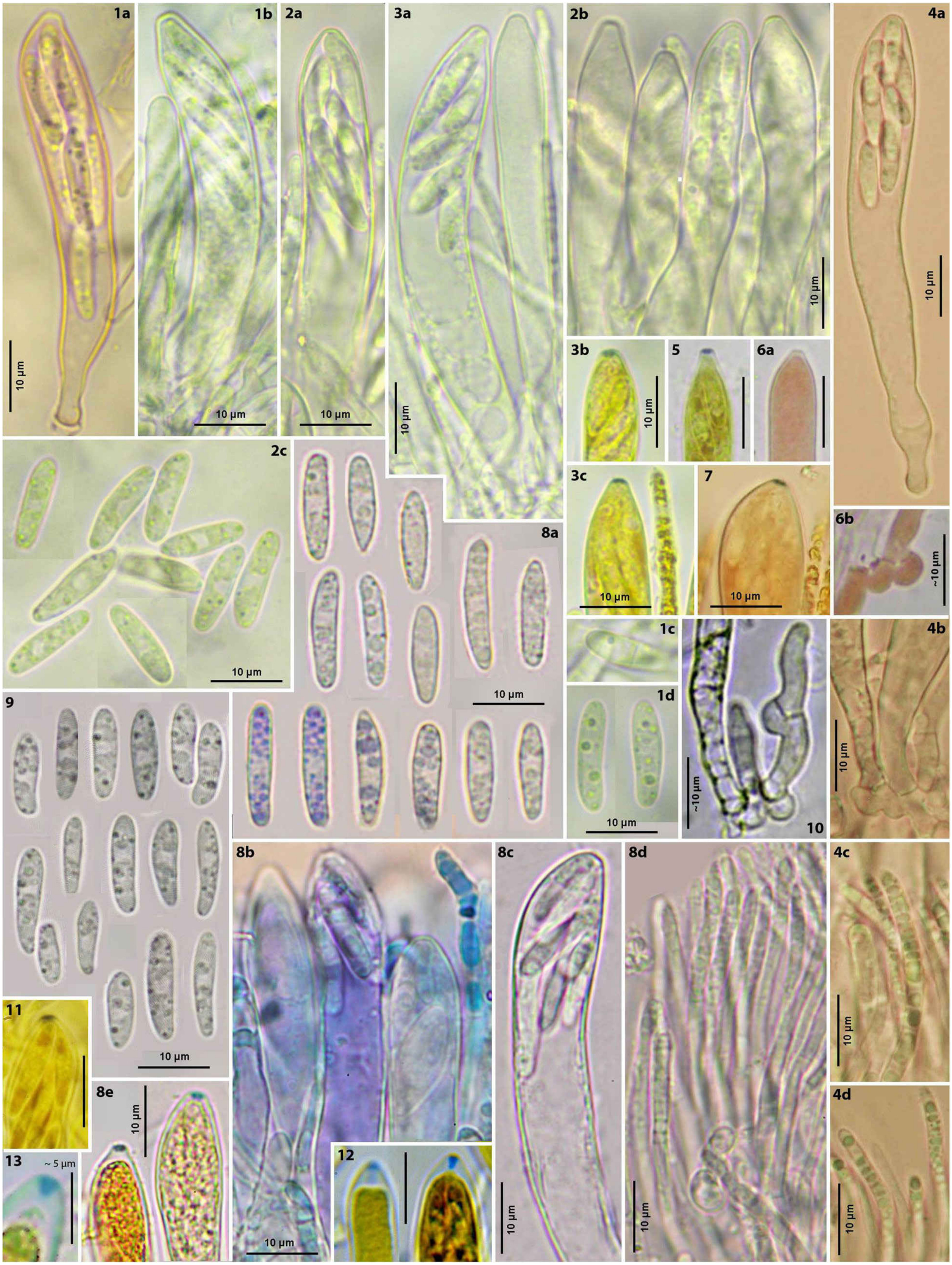
Other literature reports. Jaap (1910: 119) believed to have found *Phialea epibrya* on *Hypnum schreberi* (≡ *Pleurozium schreberi*) on 28.XII.1909 near Triglitz (Prignitz, Brandenburg, Germany), but whether a herbarium specimen exists is unclear. On the other hand, there exist some exsiccatae under the name *Phialea epibrya* in GBIF which we could not locate in the literature. One was Sydow, Mycotheca Germanica 1942 (Germany, Sachsen, SE of Dresden, Sächsische Schweiz, Königstein, Bielatal, XI.1913, W. Krieger, on *Mnium hornum*, more rarely *Dicranella* and *Polytrichum*), which bears the synonym "*Ciboria hypogena* Rehm in herb." on its label. Duplicates of this and further collections by W. Krieger, though partly from different years, exist in F, NEB, NY, PDD, and USDA. Reexamination of PDD 42645 (on *Mnium hornum*, XI.1913) by P.R. Johnston (pers. comm.) revealed it to be "*B.*" *turbinatus* (medullary excipulum with crystals, ascospores †15−23.5 × 3.5−4.5 µm). In Sydow (1923: 166), this specimen is listed as "1942. *Phialea epibrya* Hoehn." without any further comments. A collection from South Africa on *Mnium hornum* by E.M. Doidge, 13.V.1023, is deposited in PREM and one without data from Gremmen's herbarium, apparently on *Sphagnum*, in CUP. These latter specimens need reexamination for whether they have been correctly identified.

Collections included: **Norway**: **Hordaland**, ~ 22 km NNW of Knarvik, Lindås, Vatre, ~ 0–100 m, on *Hypnum cupressiforme*, 14.VII.1984, T. Tønsberg & D.O. Øvstedal, vid. P. Döbbeler (M). – **Vestland**, **Sunnhordland**, 12 km ESE of Bømlo, Spyssøya, 27 m, *Alnus glutinosa* trunk base, on *Frullania dilatata*, 28.IV.2022, L. Dalen & P. G. Larsen, vid. E. Johannesen (E.J.). — **Sweden**: **Jönköpings län**, 6.8 km WNW of Bodafors, Vikskvarn Nature Reserve, 2 km NE of Ulvahult, 310 m, *Picea abies* log, on *Dicranella* sp., 21.III.2020, R. Isaksson (ø). – ibid., 1.8 km NE of Ulvahult, 322 m, siliceous rock, on *H. cupressiforme*, 4.IV.2021, R. Isaksson (R.I.). – 3.2 km WNW of Sävsjö, 0.7 km NNE of Komstad, 235 m, siliceous rock, on *Trilophozia quinquedentata*, 23.III.2022, R. Isaksson (UPS F-1046735). – 4 km SE of Korsberga, 0.4 km WNW of Skäftesfall, 262 m, siliceous rock, on *Dicranum scoparium* & indet. moss, 2.I.2022, R. Isaksson (UPS F-1046728). − 5.2 km W of Vakås, Hattens Nature Reserve, 292 m, acidic rock, on *Hypnum cupressiforme*, 28.III.2024, R. Isaksson (ø). − **Västra Götalands län**, 1.2 km SSE of Boråsgården, 58 m, trunk base of *Corylus avellana*, on *Frullania tamarisci*, 19.IV.2024, R. Isaksson (ø). — **Great Britain**: **Scotland**, **Northwest Highlands**, N side of Loch Sunart, Resipole, ravine of Allt Mhic Chiarain, 50–150 m, on *Hypnum* sp., 19.VI.1992, B. Coppins, P.W. James & J. Poelt, vid. P. Döbbeler (GZU). – 10.3 km NNW of Fort William, Glen Loy, Puiteachan, 131 m, indet. angiosperm log, on *Cephalozia* sp., 7.VI.2018, leg. Z. Palice, vid. Z. Sochorová (Z.P. 25588). – **Moray**, 9.5 km SSW of Forres, 1.5 km NW of Dunphail, near bridge of Logie over Findhorn river, 103 m, conifer wood, on *Lepidozia reptans*, 17.IX.2023, G. Greiff (ex G.G. 523; NMW, sq.: rDNA PP820661). — **Belgium**: **Wallonie**, **Namur**, 1.2 km ESE of Vierves-sur-Viroin, vallée du Ri de Wel, 167 m, siliceous shale, on *H. cupressiforme*, 24.II.2015, B. Clesse (B.C. 20150224A ø). — **France**: **Bretagne**, **Côtes-d'Armor**, 4.2 km W of Gouarec, 2.5 km S of Laniscat, St.-Gelven, Bothoa Bihan, 149 m, indet. stump, on *D. scoparium* & *Pleurozium schreberi*, 25.III.2016, J.P. Priou (J.P.P. 16039). – idem, on *H. cupressiforme* (J.P.P. 16040). – 8 km SW of St.-Aignan, 5 km SE of Gouarec, Plelauff, 141 m, indet. log & stump, on *H. cupressiforme*, 25.III.2016, J.P. Priou (J.P.P. 16045). – 3.1 km WSW of St.-Guen, 1.3 km NE of Mur-de-Bretagne, Pont du Gléron, 134 m, indet. log & stump, on *H. jutlandicum* & *Polytrichum formosum*, 25.III.2016, J.P. Priou (J.P.P. 16038). – **Morbihan,** 3.5 km S of Caurel, 1.7 km WNW of Saint-Aignan, forest house,


1a
50 µm
1b
20 µm
1c
10 µm
1d
10 µm
1e
10 µm
1f
10 µm
2
10 µm

◂**Fig. 5** *Luteodiscus epibryus*. **1a** median section of apothecium; **1b** idem, basal part with ectal excipulum, abundant anchoring hyphae, and some algae; **1c–d** intracellular hyphae, presumably belonging to *L. epibryus*, observed in dead leaves colonised by apothecia; **1e–f** paraphyses (**e**: multiguttulate, **f**: contents distorted); **2** ectal excipulum in squash mount. – Living state (in H_2O, except for **1f**: in IKI). – **1** Z.S. 4/2021, on *Lepidozia* etc. (Svojkov, Modlivý důl). **2** J.P.P. 16055, on *Hypnum jutlandicum* (Bretagne, La Gacilly). – Phot. **1** Z. Sochorová, **2** H.O. Baral

160 m, indet. log & stump, on *Hypnum* sp., 25.III.2016, J.P. Priou (J.P.P. 16046). – 4 km NW of Carentoir, 3.2 km SSE of Tréal, Forêt de la Bourdonnais, 71 m, indet. log & stump, on *H. jutlandicum,* 8.III.2019, J.P. Priou (J.P.P. 19086). – 0.6 km WSW of La Gacilly, Naveterie, 29 m, acidic soil, on *Diplophyllum albicans*, 9.IV.2016, J.P. Priou (J.P.P. 16076). – 2.5 km SW of La Gacilly, 3 km NW of Glénac, La Forêt Neuve, 96 m, *H. cupressiforme* on *Castanea sativa* stump*,* 20.III.2019, J.P. Priou (J.P.P. 19110). – 4.2 km NE of Lanouée, 3 km SW of Mohon, Forêt de Lanouée, 91 m, indet. log & stump, on *H. cupressiforme* & *Pleurozium schreberi*, 25.III.2016, J.P. Priou (J.P.P. 16037). – 6.5 km SSW of Carentoir, 0.2 km S of St.-Nicolas-du-Tertre, Etang de la Jette, 56 m, *Castanea sativa* stump, on *H. cupressiforme*, 8.III.2019, J.P. Priou (ø). – 0.3 km SSE of St.-Nicolas-du-Tertre, 50 m, indet. stump, idem (ø). – 2 km SW of St.-Nicolas-du-Tertre, Bois de Grisan, 75 m, acidic soil, *H. cupressiforme,* 21.III.2016, J.P. Priou (J.P.P. 16031). – 4 km WNW of La Gacilly, 4.5 km NNE of Les-Fougerets, St.-Jugon, 90 m, indet. log, on *D. scoparium*, 8.III.2019, J.P. Priou (J.P.P. 19085). – idem, indet. stump, on *Polytrichum formosum* (J.P.P. 19095). – 4.7 km W of Bohal, 1 km E of St.-Guyomard, 196 m, acidic soil, on *H. cupressiforme*, 29.III.2019, J.P. Priou (J.P.P. 19125). – idem, on *Diplophyllum albicans* (J.P.P. 19124). – 2 km NE of St.-Gravé, 1 km SW of St.-Martin-sur-Oust, Chemin vers Bréhon, 43 m, indet. log, on *H. cupressiforme*, 11.III.2019, J.P. Priou (J.P.P. 19090). – 3.2 km SW of Tréal, 1.7 km NE of Ruffiac, La Boulardaie, 86 m, *Castanea sativa* stump, on *H. cupressiforme*, 8.III.2019, J.P. Priou (J.P.P. 19088). – 7.4 km NE of St.-Martin-sur-Oust, 2.6 km NW of La Gacilly, la-Haute-Bardaie, 79 m, indet. log & stump, on *Hypnum* sp. & *Dicranum* sp., 20.III.2019, J.P. Priou (J.P.P. 19111). – 1.3 km W of La Gacilly, Croix de Jacquary, 73 m, *Ulex* branch and soil, on *H. cupressiforme*, 13.III.2016, J.P. Priou (J.P.P. 16014). – ibid., path to the pond, 92 m, acidic soil, on *Diplophyllum albicans*, indet. stump, on *Dicranella heteromalla* & *H. cupressiforme*, 22.III.2016, J.P. Priou (J.P.P. 16034). – ibid., acidic soil, on *H. jutlandicum*, 28.III.2016 (J.P.P. 16055). – idem, on *H. cupressiforme*, 13.III.2016 (J.P.P. 16016). – 2.7 km SSW of La Gacilly, 4 km ENE of Les Fougerets, Chemin de Mabio, Forêt Neuve, 70 m, indet. log & stump, on *D. scoparium* & *H. cupressiforme*, 30.III.2016, J.P. Priou (J.P.P. 16060). – ibid., *Pinus* stump, on *Dicranella heteromalla*, *Dicranum scoparium*, *H. cupressiforme*, *Kindbergia praelonga* & *Pleurozium schreberi*, 7.III.2019, J.P. Priou (J.P.P. 19079). – ibid., indet. log, on *Hypnum jutlandicum*, 2.V.2019 (J.P.P. 19182). – ibid., stump of *Castanea sativa*, on *Dicranum scoparium*, 7.III.2019, J.P. Priou (J.P.P. 19084). – ibid., *Pinus* stump, on *H. cupressiforme*, 7.III.2019, J.P. Priou (J.P.P. 19083). – ibid., *Castanea sativa* log, on *H. cupressiforme*, 14.III.2020, J.P. Priou (J.P.P. 202038 ø, sq.: rDNA PP848981). – ibid., *Pinus* stump, *H. cupressiforme*, 17.V.2020, J.P. Priou (J.P.P. 202081). – 0.4 km SW of La Gacilly, Chemin de la Bergerie, 60 m, acidic soil, on *H. cupressiforme* & *Polytrichum formosum*, 22.III.2016, J.P. Priou (J.P.P. 16035). – 1.3 km SE of La Gacilly, 1.6 km NNW of Cournon, Bois du Broussay, 81 m, indet. stump, on *H. cupressiforme*, *H. jutlandicum* & *P. formosum*; *Pinus* stump, on *Dicranella heteromalla* & *Dicranum scoparium,* 6.III.2019, J.P. Priou (J.P.P. 19087). – ibid., *Pinus* stump, on *H. jutlandicum*, 21.V.2020 (J.P.P. 202085). – 2.1 NE of St.-Gravé, 1 km SW of St.-Martin-sur-Oust, Peillac, Ecluse de l'Anée, 50 m, indet. wood, on *H. cupressiforme*, 11.III.2019, J.P. Priou (J.P.P. 19089). – 4.6 km ENE of Carentoir, 0.6 NW of Quelneuc, 47 m, *Castanea sativa* stump, on *H. cupressiforme*, 12.III.2019, J.P. Priou (J.P.P. 19091). – **Ille-et-Vilaine**, 1.9 km NE of Campel, 1 km SW of Bovel, Les Forges, 115 m, acidic soil, on *H. cupressiforme,* 19.III.2021, J.P. Priou (J.P.P. 2021052). – 1.4 km E of La Gacilly, 2.6 km WSW of Sixt-sur-Aff, Trégaret, 48 m, acidic soil, on *H. cupressiforme*, 20.III.2016, J.P. Priou (J.P.P. 16028). – 3 km SE of Cournon, 2.4 km NNE of Bains-sur-Oust, La Giraudais, 151 m, *Pinus* log, on *H. cupressiforme*, 24.III.2016, J.P. Priou (J.P.P. 16036). – idem, acidic soil, on *D. scoparium*, 13.III.2019 (J.P.P. 19092a). – idem, indet. stump, on *Leucobryum juniperoideum* (J.P.P. 19092b). – 3.8 km NE of Châteaubourg, 2.6 km SSW of Marbiré, Forêt de Corbière, 98 m, acidic soil, on *H. cupressiforme*, 19.III.2016, J.P. Priou (J.P.P. 16025). – 4.4 km NE of Carentoir, 3.4 km SSW of Comblessac, Trégonan, 42 m, indet. log & stump, on *H. jutlandicum*, 27.III.2016, J.P. Priou (J.P.P. 16053). – 4 km, NW of Plélan-le-Grand, 2.2 km SE of Paimpont, Carrefour de Trecelien, 172 m, acidic soil, on *H. cupressiforme*, 5.V.2019, J.P. Priou (ø). – 4 km W of Plélan-le-Grand, 3 km SE of Paimpont, Les Forges, 140 m, acidic soil, on *Calypogeia* sp. & *Dicranella* sp.*,* 8.IV.2015, J.P. Priou (J.P.P. 15080) – 1.1 km SE of Tréhorenteuc, 5 km NNE of Campénéac, Val sans retour, 121 m, acidic soil, *H. jutlandicum*, 15.IV.2016, J.P. Priou (J.P.P. 16092). – **Pays-de-la-Loire, Loire-Atlantique**, 3.4 km S of Ste.-Marie, 1.2 km NW of Avessac, Four à chaux, 20 m, *Pinus* stump, on *H. jutlandicum*, 31.III.2016, J.P. Priou (J.P.P. 16070). – 5.5 km S of St.-Dolay, 1.5 km NNE of Missillac, D 402, acidic soil, on *D. scoparium*, 15.III.2019, J.P. Priou (J.P.P. 19102a). – idem, indet. stump, on *Leucobryum juniperoideum* & *H. cupressiforme* (J.P.P.


1a
10 µm
1b
10 µm
2a
10 µm
3a
10 µm
2b
10 µm
4a
10 µm
3b
10 µm
5
6a
2c
10 µm
8a
10 µm
3c
10 µm
7
10 µm
6b
~10 µm
1c
1d
10 µm
10
~10 µm
4b
10 µm
9
10 µm
8b
10 µm
8c
10 µm
8d
10 µm
4c
10 µm
4d
10 µm
11
8e
10 µm
12
13
~ 5 µm

◂**Fig. 6** *Luteodiscus epibryus*. **1a–b**, **2a–b**, **3a**, **4a**, **8b–c** asci at different development stages; **3b–c, 5, 7, 8e, 11–13** ascus apices with euamyloid apical rings stained by iodine; **6a** ascus apex stained by Congo Red; **4b, 6b, 10** croziers at ascus base; **1c–d, 2c, 8a, 9** ascospores containing small LBs and larger, less refractive VBs; **4c–d, 8b, d** paraphyses containing VBs. – Living state (in H_2O, **7** in IKI, **8a** pro parte & **8b** in CRB), except for **1a** (ascus, in CR), **3b–c, 5, 8e, 13** (in IKI), **11–12** (in KOH + IKI), **6a–b** (KOH + CR). – **1** 16.V.2020, on *Hypnum* (Swiss Jura); **2** E.S. 2019.03, idem; **3** E.S. 2020.41, on *Tetraphis* (ibid.); **4** Z.S. 155/2021, on *Bazzania*, *Neoorthocaulis* & *Sphenolobus* (Česká Lípa, Peklo NNM); **5** J.P.P. 16014, on *Hypnum* (Bretagne, La Gacilly); **6** J.P.P. 16060, on *Dicranum* & *Hypnum* (ibid.); **7** Z.S. 4/2021, on *Lepidozia* etc. (Svojkov, Modlivý důl); **8** E.R.D. 6988, on *Frullania* & indet. *Hypnales* (Asturias, Oviedo); **9** E.R.D. 8246, on *Hypnum* (Galicia, La Coruña); **10** B.C. 20181220A, on indet. pleurocarpous moss (Ardennes, La Neuville aux Haies); **11** H.B. 10258, on *Barbilophozia* (Bayerischer Wald, Altfaltern); **12** 2.XI.2014, on *Hypnum* & *Dicranum* (ibid., Schlinding); **13** F.V. 2013021901, on *Pleurozium* (Seine-et-Marne, Fontainebleau). – Phot. **1–3** E. Stöckli, **4, 7** Z. Sochorová, **5–6** J.P. Priou, **8–9** E. Rubio, **10** B. Clesse, **11–12** G. Bauer, **13** F. Valade. – Scale bars in **5**, **6a, 11, 12** same as in **3b**

19102b). – 10 km NW of Nantes, 2 km N of Orvault, NE of Château de La Tour, 60 m, trunk base of *Quercus*, on *Hypnum* sp., 3.IV.2010, P. Ribollet (P.R. 1005). – **Poitou–Charentes**, **Deux-Sèvres**, 25 km W of Parthenay, 1.5 km N of l'Absie, Bois de l'Absie, 212 m, angiosperm log, on *D. scoparium* & *H. cupressiforme*, 15.II.2016, M. Hairaud (M.H. 100216, sq.: rDNA PP820658). – **Île-de-France**, **Seine-et-Marne**, 19 km SSW of Melun, 2 km N of Achères-la-Forêt, Forêt de Fontainebleau, 127 m, sandstone rock, on *Pleurozium schreberi*, 19.II.2013, M. Tanaskovic, vid. F. Valade (F.V. 2013021901, sq.: rDNA OR198862). – **Champagne-Ardenne**, **Ardennes**, 20 km NNE of Charleville-Mézières, 1.1 km NE of La Neuville aux Haies, Ruisseau du Corbeau, 390 m, indet. pleurocarpous moss, 20.XII.2018, J.P. Duvivier, B. Mora & B. Clesse (B.C. 20181220A ø). – 15.5 km NE of Charleville-Mézières, 0.6 km SE of Nohan-sur-Semoy, Château de Linchamps, 224 m, acidic rock, on *Grimmia trichophylla* and *Hypnum*, 3.II.2014, B. Clesse (B.C. 20140203A ø). – **Bourgogne, Côtes-d'Or**, plateau de Langres, 18 km NNW of Dijon, 1.7 km SE of Vernot, Combe Milvy, 540 m, calcareous rock, on *Barbilophozia lycopodioides, H. cupressiforme* & *Pleurozium schreberi*, 3.III.2011, A. Gardiennet, vid. J.P. Priou (J.P.P. 11044). – **Limousin**, **Haute Vienne**, 24 km NNE of Limoges, 1.3 km SW of St.-Léger-la-Montagne, Tourbière des Dauges, 540 m, *Betula* trunk base, on *H. cupressiforme*, 22.IX.2023, M. Hairaud (M.H. 250923). – **Franche-Comté, Territoire de Belfort**, 7 km N of Belfort, E of Etang Neuf, 425 m, log of *Pinus sylvestris*, on ?*Dicranum* sp., 23.II.2024, L. Deny. – ibid, trunk base of *P. sylvestris*, on *H.* cf. *andoi*, 27.II.2024, L. Deny. — **Germany**: **Bayern**, **Oberfranken**, 3.5 km SSW of Wunsiedel, Tröstauer Forst, 762 m, granite rock, on *Dicranella* sp., *Dicranum scoparium*, *H. cupressiforme* & *Polytrichum formosum*, 10.IV.2023, I. Ibelshäuser (I.I. 2303, H.B. 10286). – **Niederbayern**, Bayerischer Wald, 3.2 km NNW of Thurmansbang, 0.7 km E of Rettenbach, W of Obernberg, 512 m, granite rock, on *H. cupressiforme*, 12.VI.2021, G. Bauer (H.B. 10214). – NE of Obernberg, WSW of Wackelstein, 550 m, idem (H.B. 10213). – 4 km NE of Thurmansbang, 1.7 km NNE of Saldenburg, N of Ödhäusl, 480 m, idem, 11.VI.2021 (H.B. 10215). – 3.7 km WSW of Thurmansbang, 1.1 km NW of Schlinding, Kotgrubenholz, 470 m, granite rock, on *H. cupressiforme*, 13.VI.2021 (ø). – idem, on *H. cupressiforme* & *Dicranum* sp., 2.XI.2014, G. Bauer, vid. B. Fellmann (B.F.). – idem, *Dicranum* sp., 20.XI.2014, G. Bauer (H.B. 10260). – idem, on *H. cupressiforme*, 2.IV.2016, G. Bauer (H.B. 10259). – 9 km E of Schöllnach, 2.5 km SSW of Thurmansbang, 0.8 km ENE of Altfaltern, NE of Stierberg, 460 m, granite rock, on *Barbilophozia sudetica* & *Isopaches bicrenatus*, 18.V.2009, G. Bauer, vid. G. Friebes (H.B. 10216a/b). – idem, on *B. sudetica*, 11.VI.2009, G. Bauer (ø). – idem, 18.X.2010 (ø). – idem, 23.XI.2011, vid. B. Fellmann (B.F., H.B. 10257). – idem, 4.VI.2012, vid. G. Friebes (G.F. 20120051). – idem, 20.VI.2012, G. Bauer (ø). – idem, 22.IV.2013 (H.B. 10258). – idem, 31.X.2014 (ø). – idem, on *H. cupressiforme* & *Pogonatum urnigerum*, 10.VI.2021, G. & Gertrud Bauer, vid. H.O. Baral (H.B. 10262). – idem, on *B. sudetica*, 7.IX.2023, vid. H.O. Baral (H.B. 10261). – idem, on *H. cupressiforme* & *B. sudetica*, 13.II.2024, G. Bauer (G.B.). – 3 km S of Thurmansbang, 4.2 km NE of Eging am See, 0.8 km NW of Kollnberg, Schadham, 518 m, granite rock, on *H. cupressiforme*, 16.XI.2021, G. Bauer (ø). — **Switzerland**: **Jura**, 6 km WNW of Les Breuleux, 2 km W of Le Noirmont, 700 m, *Abies alba* log, on *H. cupressiforme*, 17.II.2019, E. Stöckli (E.S. 2019.03). – 7 km NNE of Tramelan, 1.6 km WNW of Lajoux, Envers des Combes, 987 m, conifer log, on *Tetraphis pellucida*, 2.V.2020, E. Stöckli (E.S. 2020.41). – **Bern**, 3 km ENE of St.-Imier, 1.4 km WSW of Cormoret, Source de la Dou, 777 m, conifer log, on *H. cupressiforme*, 4.I.2020, E. Stöckli (E.S. 2020.02). – idem, on *D. scoparium* & *H. cupressiforme*, 16.V.2020, E. Stöckli (ø). – ibid., 1.3 km WSW of Cormoret, 760 m, indet. log, on *H. cupressiforme*, 30.III.2019, E. Stöckli (ø). — **Austria, Oberösterreich**: Mühlviertel, ~ 2 km NW of Niederranna, Rannatal, 320 m, on *H. cupressiforme* & *Scapania* sp., 7.III.2001, F. Berger, vid. P. Döbbeler (F.B. 15305, M). – **Steiermark**, Fischbacher Alpen, ~ 2 km NE of Pöllau, W of Pöllauberg, 500–700 m, on *H. cupressiforme*, 4.V.1978, J. Poelt, vid. P. Döbbeler (GZU). — **Czech Republic**: **Liberec Region**, **Česká Lípa District**, Lindava, 9 km NE of Česká Lípa, 300 m, sandstone rock, on *Bryum* sp., *Dicranum montanum*, *H. cupressiforme*, *Paraleucobryum longifolium*, *Pohlia nutans* & *Tetraphis pellucida*, 5.VII.2021, Z. Sochorová (Z.S. 63/2021, PRM 959995). – 7 km NE of Česká Lípa, 0.9 km NNE of Svojkov, Modlivý důl, 470 m, sandstone rock, on *Sphenolobus minutus*, 25.XII.2020, Z.


a
a. 5325
Herbarium
Prof. Dr. Fr. v. Höhnel
Phialea epibrya v. H. n. sp.
420–450 μ
Stiel 100/100
NEW YORK BOTANICAL GARDEN
A Hymenoscyphus
Annotated by S.E.Carpenter(408), 8-XII 1978
Auf Hypnum sp.
Mähren bei Saar
leg. Kovářš
1906.
v Höhnel
b
TYPE
von Hohnel Herbarium
Phialea epibrya v. H. n. sp.
Collected 1906
FARLOW HERBARIUM HARVARD UNIVERSITY
20 μm
c
apo 2
apo 4
apo 3
apo 1
dry
10 mm
d
1 mm
e
H2O
50 μm
f
0.5 mm
h
KOH
0.5 mm
j
0.5 mm
k
0.5 mm
g
0.25 mm
i
KOH
0.25 mm
l
IKI
10 μm
m
IKI
10 μm
n
IKI
10 μm
o
IKI
p
KOH+CR
10 μm
q
KOH+CR
10 μm

◂**Fig. 7** *Luteodiscus epibryus* (holotype). **a** Label with Höhnel's handwriting; **b** White's microscopic study of the type; **c** dry *Hypnum* (probably *H. cupressiforme*) with sparsely occurring apothecia in lower right area; **d** rehydrated substrate with one mature (apothecium 2) and one immature apothecium (the whitish spots belong to the thallus of a *Lepraria*); **e** piece of apothecium 3 cut with a razor blade mounted in water; **f, g** rehydrated apothecium (apothecium 2); **h, i** idem, after adding a small drop of KOH; **j, k** rehydrated apothecia (apothecia 3 & 1, respectively); **l−o** upper part of mature asci showing euamyloid apical ring (in **m** with septate spores, in **o** with glycogen in spores staining red); **p** mature ascus in KOH + CR; **q** free mature ascospores in KOH + CR. − Phot. H.O. Baral. − Scale bar in **o** same as in **n**

Sochorová (Z.S. 103/2020, PRM 959991). – idem, on *Lepidozia reptans*, *Neoorthocaulis attenuatus*, *Paraleucobryum longifolium*, *Sphenolobus minutus* & *Tetraphis pellucida*, 1.I.2021 (Z.S. 4/2021, PRM 959992, **reference specimen**, sq.: rDNA OR589464). – idem, on *Odontoschisma denudatum* & *Sphenolobus minutus*, 8.V.2021 (Z.S. 41/2021, PRM 959993). – idem, on *Paraleucobryum longifolium*, 456 m, 29.XII.2021 (Z.S. 163/2021, PRM 959994). – 3 km SW of Česká Lípa, 1.7 km NW of Nový Dvůr, Peklo National Nature Monument, 280 m, sandstone rock, on *Bazzania trilobata*, *Neoorthocaulis attenuatus* & *Sphenolobus minutus*, 16.XI.2021, Z. Sochorová (Z.S. 155/2021, PRM 959997). – 0.7 km SW of Nový Dvůr, 268 m, sandstone rock, on *Sphenolobus minutus* & *Tetraphis pellucida*, 16.XI.2021, Z. Sochorová (Z.S. 154/2021, PRM 959996). – **Hradec Králové Region, Náchod District**, Broumovské stěny National Nature Reserve, 6 km SSW of Broumov, 1 km E of Slavný, 600 m, sandstone rock, on *Paraleucobryum longifolium*, *Tritomaria exsecta* & *Scapania nemorea*, 18.IV.2022, Z. Sochorová (Z.S. 3/2022, PRM 959998). − **Vysočina Region**, **Žďár nad Sázavou District**, Žďár nad Sázavou ("Saar"), ~ 590 m, on *Hypnum* (?)*cupressiforme*, 1906, F. Kovář, vid. W.L. White (FH, **holotype**, H.B. 10279 ø). — **Slovakia**: **Prešov Region**, **Poprad District**, Vysoké Tatry, Bielovodská dolina, 900–1300 m, granite rock, on *Lophozia*-like liverwort, 4.VII.1993, I. Pišút & J. Poelt, vid. P. Döbbeler (GZU). — **Hungary**: **Borsod-Abaúj-Zemplén**, 2 km NNE of Cserépváralja, 290 m, on *Polytrichum formosum*, *D. scoparium* & *H. cupressiforme* on soil, 15.III.2024, C. Németh (ex C.N. 12214, BP 112995). — **Ukraine**: **Zakarpatska Oblast**, Eastern Carpathians, 30 km ENE of Khust, 3.5 km NE of Velyka Uhol'ka, valley of Velyka Uhol'ka, *Carpinus betulus* trunk, on pleurocarpous moss, 420 m, 12.V.2015, Z. Palice, vid. Z. Sochorová (ex Z.P. 19526, Z.S. 21/2024). — **Italy**: **Trentino-Alto Adige**, NW of Brixen, W of Vahrn, Schalderer Tal, ~ 700–1000 m, on *H. cupressiforme* & indet. *Lophoziaceae* on rock, 19.VII.1962, V.J. Grummann, vid. P. Döbbeler (ex V.J.G. 5577, M). — **Spain**: **Galicia**, **La Coruña**, 10 km SE of Betanzos, 5.2 km E of Oza dos Ríos, Monte do Gato, 393 m, indet. angiosperm log, on *Hypnum* sp., 16.II.2020, A. Couceiro, vid. E. Rubio (E.R.D. 8246). – **Asturias**, **Quirós**, 25 km SSW of Oviedo, 1.3 km S of Fresnedo, Los Chamargones, 753 m, quartzite rock, on *Frullania tamarisci* & indet. *Hypnales*, 4.III.2017, M. González, vid. E. Rubio (ex E.R.D. 6988, LEB: FUNGI-4969, sq.: rDNA MT370342, MT370357). — **Macaronesia**: **Canary Islands**, **Tenerife**, 4 km E of Las Lagunetas, Bosque de la Esperanza, ~ 1250 m, *Pinus canariensis* ?trunk, on hypnoid moss, 19.II.1989, J. & H. Hafellner, vid. P. Döbbeler (ex J.H. 30898, GZU). — **USA**: **Maine**, **Washington County**, 6 km SSE of Steuben, E of Eagle Hill Institute, trail to ocean, 65 m, on indet. *Hypnaceae*, 7. & 8.VII.2013, P. Döbbeler (P.D. 9461 & 9483, M). – ibid., acidic boulders, on *Callicladium imponens*, 26.VI.2017, W.R. Buck, vid. P. Döbbeler (ex W.R.B. 64621, NY). – **Pennsylvania**, **Somerset County**, Forbes State Forest, Baugham Rocks, 965 m, sandstone, on *C. imponens*, 27.IV.2018, W.R. Buck, vid. P. Döbbeler (ex W.R.B. 65234, NY). – **Tennessee**, **Sevier County/North Carolina**, **Swain County**, Great Smoky Mountains National Park, Mt. Love, Appalachian Trail 0.7−1.2 km E of Clingmans Dome, 1950 m, trunk of *Abies*, on indet. foliose liverwort, 18.VI.2015, J.C. Lendemer, vid. P. Döbbeler (ex J.C.L. 45712, NY). – **North Carolina**, **Swain County**, eastern Great Smoky Mts., upper NW facing slopes and summit of Mt. Hardison, 0.4 km S of Balsam Mountain Trail, 1850 m, trunk of *Prunus*, on *Frullania asagrayana*, 29.V.2014, J.C. Lendemer, vid. P. Döbbeler (ex J.C.L. 43283, M & NY).

Luteodiscus hemiamyloideus Baral, L.G. Krieglst., Stöckli, Sochorová & Priou, **sp. nov.** – Figs. 8, 9, 10, 11, 12

MycoBank: MB 854454.

Holotype: Germany, Baden-Württemberg, Welzheim, 48°52′18.4’’N, 9°36′52’’E, on *Nowellia curvifolia* growing over *Abies alba* log, 10.IV.2021, K. & L.G. Krieglsteiner (KR-M-0053729).

Etymology: named after the purely red (hemiamyloid) iodine reaction of the ascus apical ring.

Apothecia fresh (0.1–)0.15–0.45(–0.55) mm diam. {11}, 0.18–0.35(–0.45) mm tall, receptacle 0.08–0.22 mm thick {3}; disc light to bright sulphur-yellow, more egg-yellow when half-dry, flat, margin smooth to very finely pubescent, not protruding; stipe 0.05–0.15 × 0.09–0.2 mm {6}; dry turning light to deep orange, pinkish-red, or brick- to

Table 2 Phenology of *Luteodiscus epibryus* based on listed collections

Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
3	9	48	12	12	11	5	0	3	2	6	3


1
2
3
4
5
6

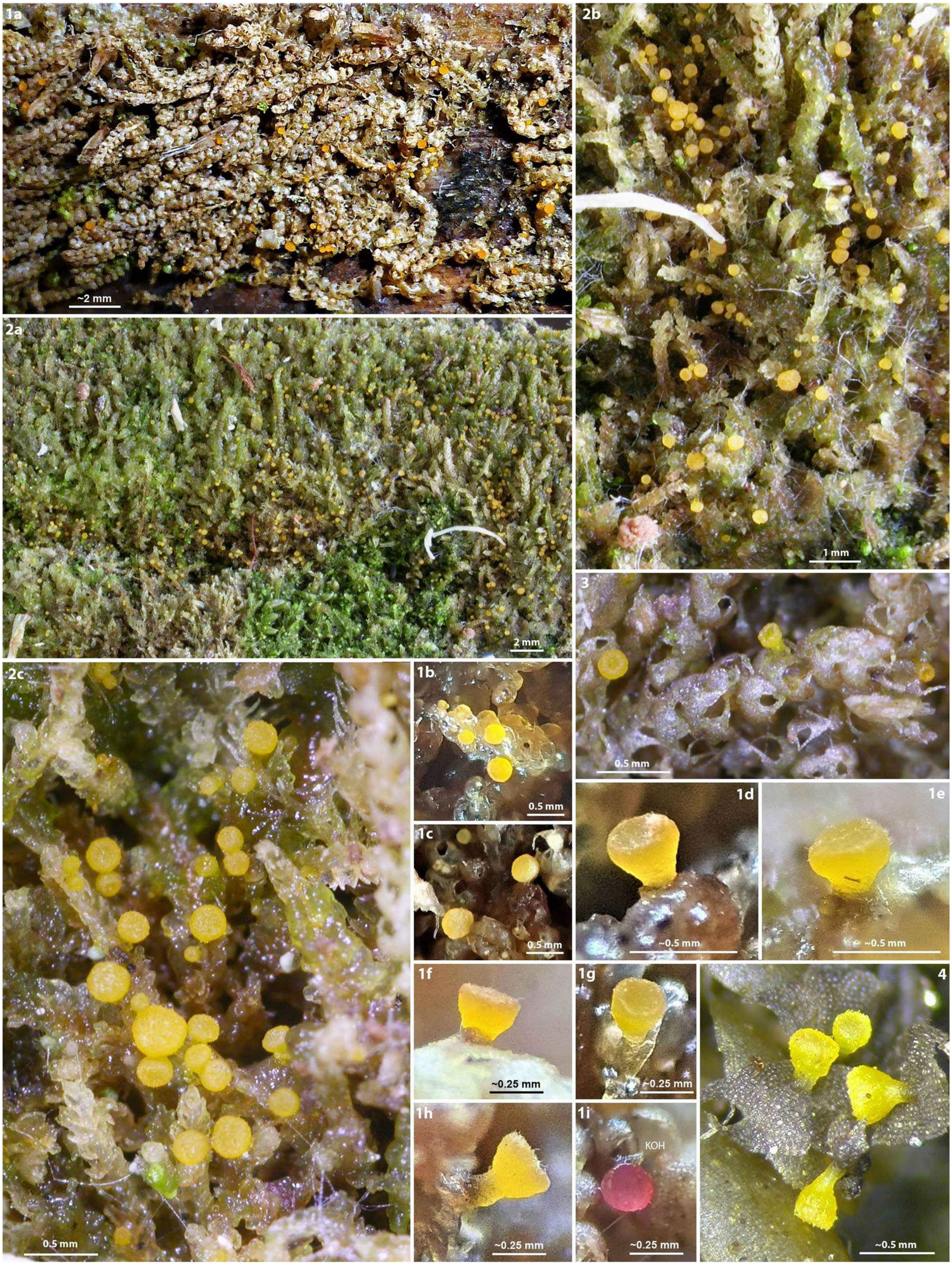
◂**Fig. 8** Collection sites of *Luteodiscus hemiamyloideus*. **1** *Picea abies* ravine forest with *Corylus avellana* at rivulet Moreravinen (Fågelfors, Kalmar län, Småland, Sweden), *Picea* log, on *Nowellia*, *Cephalozia* & *Lepidozia*; **2–6** *Picea-Abies-Fagus* forests, *Abies* logs, on *Nowellia*: **2** at rivulet Edenbach (Welzheim, Germany), **3** at rivulet Seebach (Gschwend, Germany), **4–6** Plitvička Jezera National Park (Croatia), **4–5** Čorkova Uvala virgin forest, **6** source of Crna Rijeka. – Phot. **1** R. Isaksson (22.IV.2023), **2–6** L.G. Krieglsteiner: **2** 2.II.2014 [coll. 10.IV.2021], **3** 11.II.2002 [coll. 30.III.2021], **4–5** 1.IV.2011, **6** 4.IV.2011

blood-red or red-brown {6}, changing back to yellow or pale orange when rehydrated. **Asci** *(60−)63–85(−95) {6} × (7.2–)7.7−9.5(−11) µm {7}, †65–85(−90) {4} × (6–)6.5–7.5(−8.8) µm {5}, 8-spored, spores */†obliquely biseriate, pars sporifera *(22–)24–30(−32) µm long {5}, †40–47 µm {1}, living mature asci protruding ~ 5–15 µm beyond paraphyses; **apex** slightly to strongly conical, apical ring in IKI pale to light red(-brown) (RR) {14}, after KOH-treatment light to bright blue in IKI or MLZ, cylindrical or apically distinctly extending (obconical), †(2–)2.5–3.5(–4.5) → (0.7–)1–2.5(–3) × (0.8–)1–1.8(–2.2) µm {7}; **base** gradually narrowed in a short to medium long stalk, arising from croziers {7}. **Ascospores** *((6.3−))(7–)8–11(–12)((–13)) × (2.4–)2.8–3.5(−4) µm {7}, Q = *(2.3–)2.5–3.7(−4.3) {2, $n = 45$}; †(6.4–)7.3–10.2(–10.6) × (2.3–)2.6–3.3(–3.6) µm {1}, Q = †(2−)2.4−3.3(−4.1) {1, $n = 40$}; cylindric-ellipsoid-clavate to fusoid-clavate or clavate, slightly to strongly heteropolar (rarely homopolar); containing (2–)4–8(–14) LBs of (0.3–)0.5–1.7(–2.3) µm diam. irregularly scattered through the whole ascospore, OCI (2–)3(–4) {5}, VBs not observed, glycogen absent {2} or sometimes present {1}; overmature spores 1-septate {1}. **Paraphyses** cylindrical or slightly moniliform, straight to often slightly to strongly flexuous, terminal cell *14–22(–25) {2} × (1.5–)1.8–2.5(–3) µm {4}, lower cells * ~ 9–11 × (1–)1.5–2.2 µm, branched only below or sometimes also near apex; VBs very slightly to medium or strongly refractive, hyaline to pale yellowish, globose or sometimes elongated, 0.3–1.3 µm diam. {5}, partially absent {3}, occupying upper 10–20 µm, VBs in IKI increasing in refractivity, light yellow. **Medullary excipulum** subhyaline to pale yellow, 35–40 µm thick, of dense textura intricata, cells †4–8 × 2–3(–4) µm {1}, unsharply delimited from ectal excipulum. **Ectal excipulum** subhyaline to bright yellow, turning pinkish with age, of horizontally oriented but ± undulating textura prismatica from stipe to margin, 20–25 µm thick at lower flanks, cells *(7–)10–20(–28) × 3–8(–12) µm {4}; †8–16 × (3–)4–5.3(–6) µm {2}; 10–15 µm thick near margin, marginal cortical cells *(5.5–)7–12(−16.5) × 2–4(–5.5) µm {4}, †4–7.5 × 1.4–2.7 µm {2}, containing VBs in upper 25–30 µm (guttulate), not or only slightly projecting as minute hairs. **Anchoring hyphae** *1.5–2.7 µm wide, walls 0.2 µm thick {1}, hyaline, invading dead host cells beneath apothecial stipe. **KOH-reaction**: macroscopic: yellow pigment of entire apothecium turning bright pink to purplish-to blood-red {7}; microscopic: yellow excipulum changing to purplish-rose {2}.

Habitat: growing on decolorised, dead leaves of foliose (*Jungermanniales* {18}) or sometimes thallose liverworts (*Metzgeriales* {3}) (see Tab. 5); bryophytes growing on soil {2} or on fallen logs of *Abies alba* {5}, *Picea abies* {7}, indet. conifer {2}. **Associated organisms**: "*Bryoscyphus*" *turbinatus* {1}, *Pseudomicrodochium bryophilum* {1}. **Drought tolerance**: dead in all parts after ~ 1 week in the herbarium (Z.S. 144/2021). **Altitude**: 29–1060 m. **Climate**: hemiboreal to orotemperate and temperate humid. **Geology**: acidic Ordovician schist and ?porphyry, acidic to alkaline middle Keuper (coloured marl), acidic Proterozoic-Paleozoic sandstone (meta-arkose), alkaline Jurassic limestone and dolomite. **Phenology**: (XI–)II–IV (see Table 3).

Variation. The diameters of the apothecia varied among the collections between 0.1–0.2 and 0.3–0.55 mm, with a predominance of 0.15–0.45 mm. The stipe was always ± distinct. Apothecial colour was consistently light to bright sulphur-yellow. Ascus size varied among the collections in length between *60–70 and *70–95 µm and in width between *7.2–8 and *8–11 µm, and ascospore size in length between *6.3–8.5 and *9–12(−13) µm and in width between *2.5–3 and *3–4 µm. No variation was observed in the key character, the hemiamyloid reaction of the apical rings, which was invariably red at any IKI concentration. The presence of glycogen in the ascospores was distinctly seen only in one spore of collection L.K. 3429 (IVV), whereas in the remaining spores and in two other collections tested with IKI there was no trace of glycogen.

Collections included: **Sweden**: **Småland**, **Kalmar län**, 5 km NW of Fågelfors, W of More kastell, Moreravinen, 140 m, *Picea abies* log, on *Nowellia curvifolia*, *Cephalozia* (?)*bicuspidata* & *Lepidozia reptans*, 22.IV.2023, R. Isaksson & O. Persson (UPS F-1086747). — **France**: **Bretagne**, **Morbihan**, 0.6 km WSW of La Gacilly, Naveterie, 29 m, acidic soil, on *Cephalozia bicuspidata* & *Scapania nemorea*, 31.III.2016, J.P. Priou (J.P.P. 16062). – idem, on *Calypogeia* sp., 21.III.2021, J.P. Priou (J.P.P. 2021053 ø). — **Germany**: **Baden-Württemberg**, **Ostalbkreis**, 2.5 km NNE of Gschwend, 0.4 km NNE of the lake Bergsee, Seebachtal, 425 m, *Abies alba* log, on *Nowellia curvifolia*, 30.III.2021, K. & L.G. Krieglsteiner (L.K. 3429, sq.: rDNA PP820659, *TEF1* PP869706). – **Rems-Murr-Kreis**, 1.4 km W of Welzheim, 1.8 km NNW of Breitenfürst, Edenbachtal, 451 m, *Abies alba* log, on *N. curvifolia*, 10.IV.2021, K. & L.G. Krieglsteiner (ex L.K. 3430, KR-M-0053729, **holotype**, sq.: rDNA PP820660, *TEF1* PP869707). — **Switzerland**: **Jura**, 6 km WNW of Les Breuleux, 2 km W of Le Noirmont, 700 m, *Picea* log, on


1a
~2 mm
2a
2 mm
2b
1 mm
3
0.5 mm
2c
0.5 mm
1b
0.5 mm
1c
0.5 mm
1d
~0.5 mm
1e
~0.5 mm
1f
~0.25 mm
1g
~0.25 mm
1h
~0.25 mm
1i
KOH
~0.25 mm
4
~0.5 mm

◂**Fig. 9** *Luteodiscus hemiamyloideus*. **1–3** Fresh apothecia on *Nowellia curvifolia* on conifer log (**1i**: after applying KOH); **4** idem, on *Cephalozia bicuspidata* (with *Scapania nemorea* behind) on soil. – **1a–i** L.K. 3429 (Ostalbkreis, Gschwend), **2a–c** H.B. 9478 (Dinaric Mountains, Plitvička Jezera), **3** H.B. 9477 (ibid.), **4** J.P.P. 16062 (Bretagne, La Gacilly). – Phot. **1** K. Krieglsteiner, **2–3** H.O. Baral, **4** J.P. Priou

Riccardia sp., 17.II.2019, E. Stöckli (E.S. 2019.02). − 1.7 km W of Le Noirmont, La Grosse Côte, 750 m, conifer log, on *N. curvifolia*, 12.II.2024, E. Stöckli (E.S. 2024.10). − 1.2 km NW of Les Genevez, 1025 m, conifer log, on *N. curvifolia*, 18.II.2024, E. Stöckli (E.S. 2024.11). − 1.4 km NW of Lajoux, Envers des Combes, 960 m, *Picea abies* log, on *N. curvifolia*, 19.II.2024, E. Stöckli (E.S. 2024.12). − 2.6 km NNE of Les Breuleux, Le Crât de l'Envers, 1060 m, *Picea abies* log, on *N. curvifolia* & *Riccardia* sp., 21.II.2024, E. Stöckli (E.S. 2024.13). − **Bern**, 2.6 km NW of Tavannes, 2.5 km WSW of Saicourt, Forêt d'Enfer, 800 m, *Picea abies* log, on *N. curvifolia*, 24.II.2024, E. Stöckli (E.S. 2024.14). — **Czech Republic**: **Moravian-Silesian Region**, **Bruntál District**, Jeseníky protected landscape area, 5.5 km NW of Karlova Studánka, 1.7 km WSW of Vidly, 927 m, *Picea abies* log, on *Cephalozia bicuspidata*, 6.XI.2021, Z. Sochorová (Z.S. 144/2021, PRM 959999). — **Croatia**: **Lika-Senj County**, Dinaric Mountains, Mala kapela, 9 km NW of Plitvička Jezera, 3.8 km WSW of Sertić Poljana, virgin forest Čorkova Uvala, 850 m, *Abies alba* logs, on *Nowellia curvifolia*, 1.IV.2011, L.G. Krieglsteiner, vid. H.O. Baral (H.B. 9478, L.K. HR-258). – 5.8 km S of Plitvička Jezera, 1.9 km SE of Plitvici Ljeskovac, source of Crna Rijeka, 700 m, *Abies alba* log, on *N. curvifolia*, 4.IV.2011, L.G. Krieglsteiner & H. Lotz-Winter, vid. H.O. Baral (H.B. 9477, L.K. HR-259). – ibid., 1.3 km W of Plitvici Ljeskovac, between Bijela Rijeka and Crni vrh, 750 m, *Abies alba* log, on *Nowellia curvifolia*, *Riccardia palmata* & *Lepidozia reptans,* 5.IV.2011, L.G. Krieglsteiner (L.K. HR-260).

Molecular results

Sequence similarity

Sequences of rDNA were obtained from six collections of *L. epibryus* (from with certainty at least four different host genera, viz. *Frullania*, *Hypnum*, *Lepidozia* and *Pleurozium*) and from two collections of *L. hemiamyloideus* (both on *Nowellia*). All comprise the ITS region and very short parts of SSU, those on *Frullania*, *Hypnum*, *Lepidozia* and *Nowellia* also LSU D1–D4, some of them also partial D5 or D5–D6. From the two *L. hemiamyloideus* specimens also *TEF1* was generated, but this gene region was not included in our analysis.

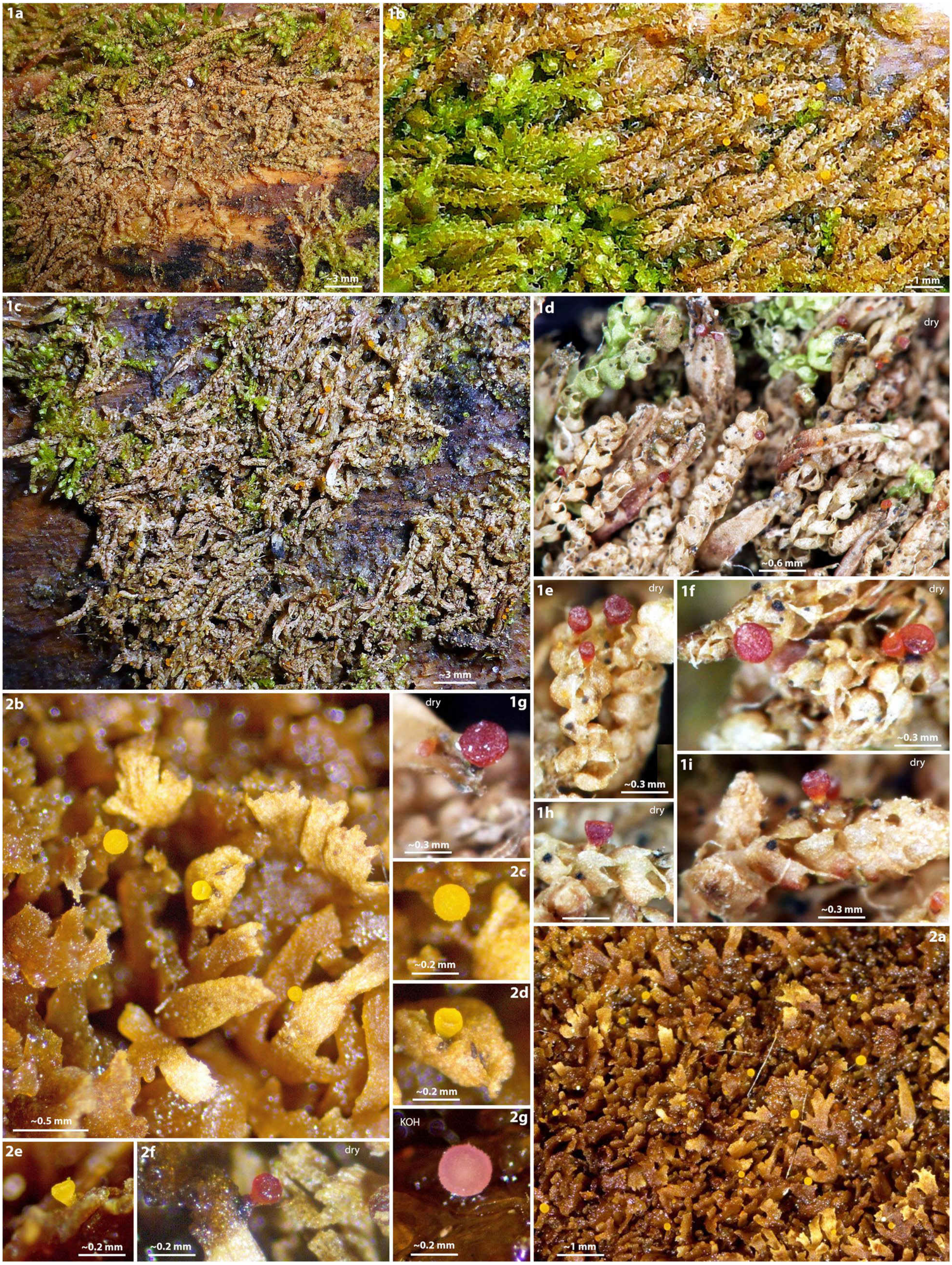
In the ITS region, four sequences of *L. epibryus* (here called genotype I) are fully identical, except for three ambiguities in the 5.8S: two in that from Seine-et-Marne (pos. 70 and 90) and one in that from Svojkov (pos. 57). The two ITS sequences of *L. hemiamyloideus* are also fully identical. In contrast to this high infraspecific conformity, the two remaining sequences of *L. epibryus* (here called genotype II), which fully concur in the ITS region except for 1 gap at the 3'-end of ITS2, deviate from genotype I by 1 nt in ITS1 and 3 nt in ITS2 (substitutions, p-distance for entire ITS 0.8%), and by 1 inserted nt close to the 3'-end of ITS1 in genotype II. All these deviations have been ascertained from the mostly very clean chromatograms, except for the ITS2 and a majority of 5.8S in the sequence from Seine-et-Marne in which the two chromatograms are very dirty and needed reconstruction by comparison with other sequences of *L. epibryus*. Morphologically, the two genotypes did not show any significant differences (Table 4).

P-distances between the two species range over the entire ITS at 8.4–8.9% (besides three consistent gaps in *L. epibryus*), the higher value applying to genotype II. Three of the numerous nucleotide positions that differ between the two species are in the 5.8S region (pos. 31, 70, 90): here *L. hemiamyloideus* concurs with all other species of our two datasets, except for *Gemmina* spp., *Roseodiscus formosus* and *Bryoglossum gracile*, which concur at pos. 70 and 90 with *L. epibryus*.

The S1506 intron at the 3-end of SSU is absent in the two sequences of *L. hemiamyloideus* and in those four of *L. epibryus* which belong to genotype I, but it is surprisingly present in the two *L. epibryus* sequences of genotype II. The intron has a length of 436 nt and shows only 1 nt deviation between the two sequences. It best matches in GenBank with various environmental sequences with a similarity around 80–83%.

In the LSU D1–D4 domain, two of the three *L. epibryus* sequences are identical and belong to genotype I, while genotype II differs from them by 1 nt (C/T) in D2. Likewise, the two LSU D1–D5 sequences of *L. hemiamyloideus* are identical. The distance between the two species lies in the D1–D2 at 2.7−2.9% (~590 nt, 4 nt in D1, 11−12 nt in D2) and in the D3–D4 at 0.9% (~330 nt, 2 nt in D3, 0 nt in D4). Towards the 3'-end of D3, *L. hemiamyloideus* has an intron of 54 nt which *L. epibryus* and apparently most other species of *Helotiales* in GenBank do not have. The intron is located 5−7 nt upstream of the L683 intron and exists in some sequences of very different relationships, e.g., in *Remleria rhododendricola* (*Pezizellaceae*, KT876986) and many lichens (e.g., *Flavoparmelia baltimorensis*, KU306736).

The two *TEF1* sequences of *L. hemiamyloideus* are identical over the 473 overlapping nucleotides. Their closest matches in GenBank are with 94.7% *Hyalopeziza alni*


1a
~3 mm
1b
~1 mm
1c
~3 mm
1d
dry
~0.6 mm
1e
dry
~0.3 mm
1f
dry
~0.3 mm
2b
~0.5 mm
1g
dry
~0.3 mm
1h
dry
1i
dry
~0.3 mm
2c
~0.2 mm
2d
~0.2 mm
2a
~1 mm
2e
~0.2 mm
2f
dry
~0.2 mm
2g
KOH
~0.2 mm

◂**Fig. 10** *Luteodiscus hemiamyloideus*. **1a–c, 2a–e** fresh apothecia; **1d–i, 2f** dry apothecia (colour change caused by drying); **2 g** apothecium treated by KOH; **1d–i** leaves with black dots of *Pseudomicrodochium bryophilum*. – **1** L.K. 3429, on *Nowellia curvifolia* (Ostalbkreis, Gschwend), **2** E.S. 2019.02, on *Riccardia* (Swiss Jura, Les Breuleux). – Phot. **1a–c** L.G. Krieglsteiner, **1d–i** Z. Sochorová, **2** E. Stöckli

and with 94.5% *Dematioscypha delicata* and *Hyaloscypha intacta*.

Phylogenetic analysis

Our Bayesian analysis of concatenated ITS + LSU revealed a strongly supported genus-level clade for the two *Luteodiscus* species and a strong support for the family *Hyphodiscaceae*, in which *Luteodiscus* clustered in an unresolved position (Fig. 13).

Other families included in our combined dataset received strong support, viz. *Arachnopezizaceae*, *Bryoglossaceae*, *Hamatocanthoscyphaceae*, *Helotiaceae*, *Lachnaceae*, and *Leptodontidiaceae*, but all these families clustered unresolved to each other, without hints on the evolutionary lines. Moreover, *Hyaloscyphaceae* and *Pezizellaceae* each appear in four different clades with sometimes low or lacking support (the paraphyletic *Pezizellaceae* s.str. was monophyletic in an earlier analysis). The strongly supported clade of *Belonioscyphella hypnorum* (Syd. & P. Syd.) Höhn. and *Roseodiscus subcarneus* (Sacc.) Baral could not be assigned to an existing family, while *R. rhodoleucus* (Fr.) Baral and *Belonium coroniforme* Rehm remained unassociated with any other taxon of the dataset. The also unassociated *Urceolella aspera* (Moug. ex Fr.) Boud. is morphologically a *Hyaloscyphaceae* in the wide sense.

Because two very closely related genotypes (I and II) were observed within *L. epibryus*, a separate Bayesian analysis of the ITS1-58S-ITS2 region was made in order to better resolve the ITS distances among the three clades within *Luteodiscus*. In this analysis, a reduced overall dataset was used but under the inclusion of four additional sequences which lack LSU (Fig. 14). Contrary to the combined analysis, the clade of *Hyphodiscaceae* received only moderate support. In this analysis, we did not include any members of *Helotiaceae*, such as *Cyathicula* (= *Phialea*) or *Hymenoscyphus*, in which *L. epibryus* earlier has been placed, because of their high distance to members of *Hyphodiscaceae*, including *Luteodiscus*. In a maximum likelihood analysis of LSU D1−D4 based on the dataset of the combined tree, *Luteodiscus* likewise nested in the *Hyphodiscaceae* clade, but without any support. Whether the two European genotypes of *L. epibryus* show a different geographic distribution as the present data suggest (see Table 4), and how the situation might be on the North American continent remains to be investigated in the future.

Morphological remarks

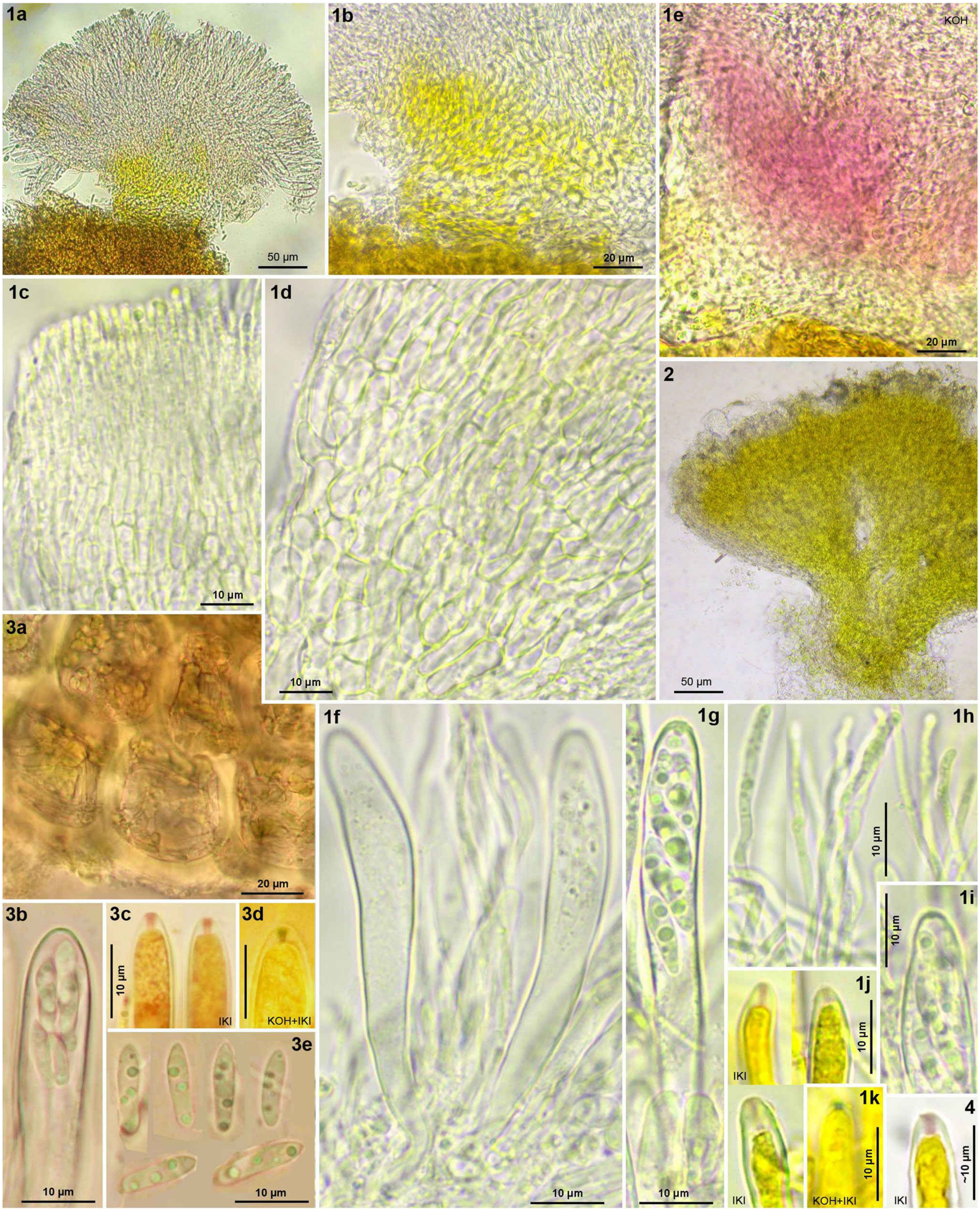
Apothecial colour and colour change

L. hemiamyloideus tends to have a more shiny yellow colour, according to observations by E.S., whereas the yellow colour of *L. epibryus* is more matt. This difference can, however, hardly be recognized in photos. The macroscopic colour of *L. hemiamyloideus* soon changed to orange or pinkish- to blood-red when air-dried, whereas that of *L. epibryus* changed only to pale orange or sometimes pinkish. After rehydration, the yellow pigment reappears but fades somewhat with the age of the herbarium specimen. Cutting or bruising a fresh apothecium may also induce reddening of its entire tissue.

The characteristic rose-red reaction of the yellow pigment in KOH in both species, which appears to be unique within the *Helotiales*, is best obtained in fresh specimens by transferring a small amount of KOH with a needle to an apothecium under the dissecting microscope. The reaction comes up less spectacular when applied to herbarium specimens, but even in the 118-year-old holotype of *L. epibryus* the reaction was still distinct (Fig. 7h−i). It is best induced by KOH but may also appear in other alkali, such as NH_4OH. Adding an acid to a KOH-treated apothecium did not change the colour; therefore, the colour change is not pH-dependent but corresponds to the reddish change obtained by mechanical influence or during drying. Superficially, the reaction resembles the purple-red colour change of the perithecia of *Nectriaceae* (*Hypocreales*) in KOH, but in that family, the reaction is only induced by alkali, whereas lactic acid provokes a yellow colour (Rossman et al. 1999). A strong colour change to blood-red during drying or ageing was often seen in *L. hemiamyloideus* but never in *L. epibryus*.

Asci and ascospores

Ascospore length overlaps in the two species when including exceptionally long or short spores, but also other characteristics, such as apothecial size and lipid content in the spores, more or less overlap. Surprisingly, ascus length is very similar in the two species, and ascus width is only slightly lower in *L. hemiamyloideus*. Curiously, the apical rings of dead asci are distinctly longer in *L. hemiamyloideus* compared to *L. epibryus* (each measured in 7 collections), although *L. epibryus* has longer ascospores. This feature and the sharp difference between the eu- (types BB and rB) vs. hemiamyloid


1a
50 µm
1b
20 µm
1e
KOH
20 µm
1c
10 µm
1d
10 µm
2
50 µm
3a
20 µm
1f
10 µm
1g
10 µm
1h
10 µm
1i
10 µm
3b
10 µm
3c
10 µm
IKI
3d
KOH+IKI
3e
10 µm
1j
IKI
10 µm
1k
IKI
10 µm
KOH+IKI
4
~10 µm
IKI

◂**Fig. 11** *Luteodiscus hemiamyloideus*. **1a, 2** Squash mount of apothecia, with yellow exudate near base or overall; **1b** closeup of **1a**; **1e** idem, in KOH; **1c** surface view on ectal excipulum at margin; **1d** idem, at flanks; **3a** intracellular hyphae, presumably belonging to *L. hemiamyloideus*, observed in dead leaves colonised by apothecia; **1f** immature asci, paraphyses; **1 g, i, 3b** mature asci; **1 h** paraphyses containing VBs; **1j, 3c, 4** apices of immature asci stained red with IKI, **1 k, 3d** idem, stained blue in iodine after KOH-treatment, **3e** ascospores. – Living state (in H_2O), except for **1j–k, 3c–d, 4** (in IKI [or KOH + IKI]). – **1** E.S. 2019.02, on *Riccardia* (Swiss Jura, Les Breuleux), **2** H.B. 9478, on *Nowellia* (Dinaric Mountains, Plitvička Jezera), **3** Z.S. 144/2021, on *Cephalozia* (Jeseníky Mts., Karlova Studánka), **4** UPS F-1086747, on *Nowellia*, *Cephalozia* & *Lepidozia* (Småland, Fågelfors). − Phot. **1** E. Stöckli, **2** H.O. Baral, **3** Z. Sochorová, **4** R. Isaksson. − Scale bar in **3d** same as in **3c**

(type RR) iodine reaction of the apical rings remain the only clear-cut morphological characteristics at the species level. Important for obtaining the red reaction of *L. hemiamyloideus* is to use Lugol's solution. Melzer's reagent (MLZ) also permits distinction between eu- and hemiamyloid by obtaining a blue vs. negative reaction, respectively. KOH-pretreated asci do not show the difference any longer by reacting blue in either reagent (Baral 1987b, 2009).

Ecological remarks

Host specificity

As far as we know at present, the two bryoparasitic species of *Luteodiscus* are generalists on a wide diversity of bryophytes, rather than specialists. They were recorded on totally 6 orders of mosses and 3 orders of liverworts (Table 5). *L. epibryus* occurred on 6 orders of mosses with 14 genera (*Bryum*, *Callicladium*, *Dicranella*, *Dicranum*, *Grimmia*, *Hypnum*, *Kindbergia*, *Leucobryum*, *Paraleucobryum*, *Pleurozium*, *Pogonatum*, *Pohlia*, *Polytrichum*, *Tetraphis*), and on 2 orders of liverworts with 14 genera (*Barbilophozia*, *Bazzania*, *Calypogeia*, *Cephalozia*, *Diplophyllum*, *Frullania*, *Isopaches*, *Lepidozia*, *Neoorthocaulis*, *Odontoschisma*, *Scapania*, *Sphenolobus*, *Trilophozia*, *Tritomaria*), with *Hypnum* being by far the most often recorded host genus. *L. hemiamyloideus* was recorded on 2 orders of liverworts with 6 genera (*Calypogeia*, *Cephalozia*, *Lepidozia*, *Nowellia*, *Riccardia*, *Scapania*), predominantly on *Nowellia curvifolia*, but never on mosses. Most of the liverworts reported in this study as hosts of *Luteodiscus* spp. are foliose, with *Riccardia* being the only thallose liverwort.

Other ecological preferences

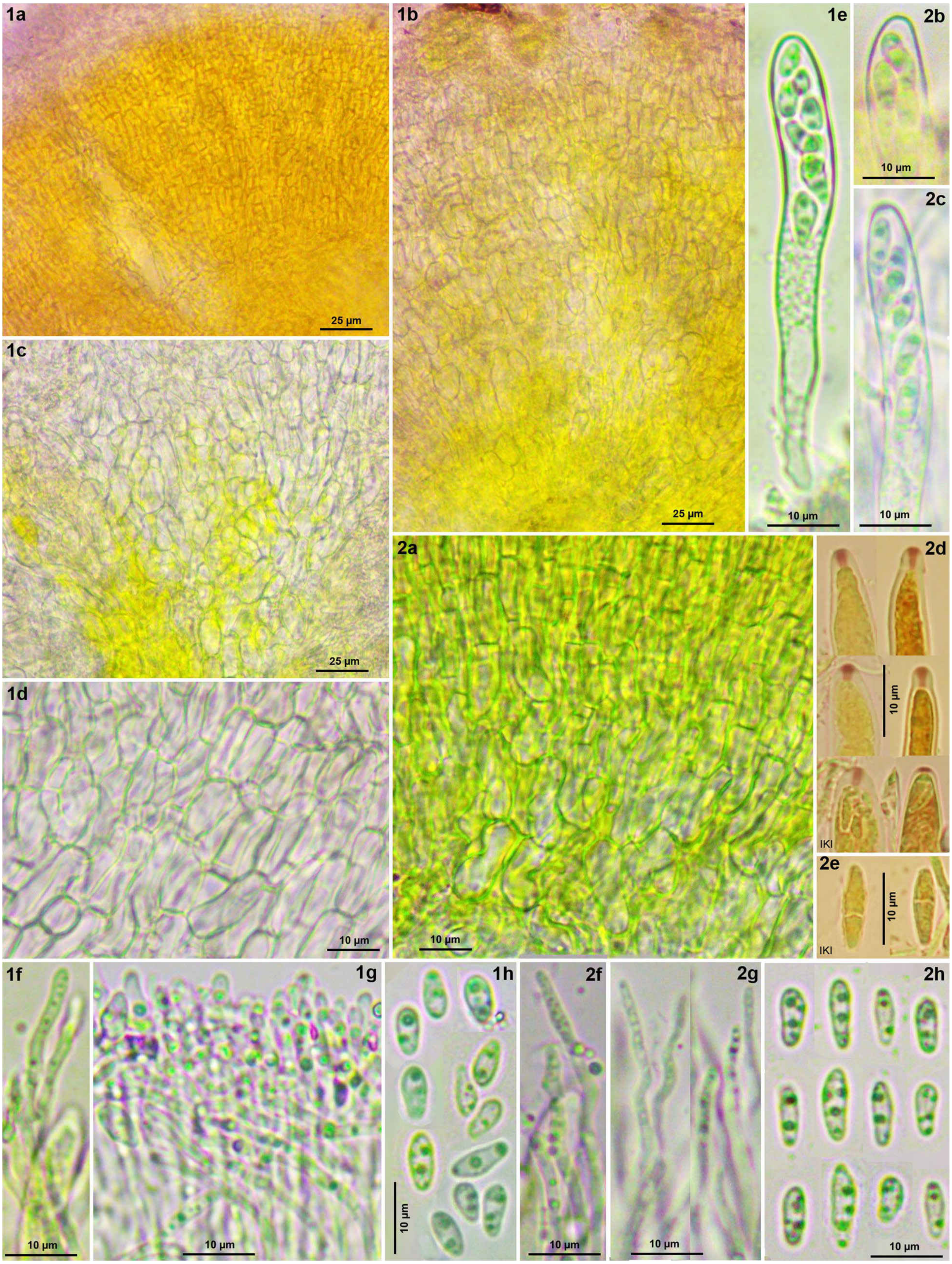
The habitats supporting occurrences of *L. epibryus* comprise different forest types in humid, (oro)temperate to hemiboreal and mesosubmediterranean regions, mostly over acidic bedrock. The bryophytes grew either on woody substrates or on rock and soil. Woody substrates included bark and wood of fallen branches and logs but also standing trunks and cut stumps, usually in an advanced stage of decay, but also on basal parts of living trees. Gymnosperms as substrate have been noted 19 × , and when identified, they originated as follows: *Picea* (Sweden), *Abies* (Switzerland, USA), *Pinus* (France, Tenerife). Angiosperms as substrate have been noted 14 × : in Scandinavia *Alnus* and *Corylus*, in France *Betula*, *Castanea*, *Quercus*, and *Ulex*, in N-America *Prunus*. The substrate of the bryophytes was remarkably uniform in some of the investigated regions, possibly influenced by the collector's habits. The pH of the soil at the collection sites was mostly acidic, but in two regions (Côtes-d'Or and Swiss Jura), it was calcareous (Jurassic).

Collection sites were partly close to water courses but also remote from them. The sites varied between shady or semi-shady (Fig. 1(3)) to strongly exposed, e.g., when occurring on rocks along a forest track, at which adjacent trees have been removed (Fig. 2(2, 5)). Places with a completely closed canopy that prevents rain from reaching the forest floor might be unsuitable. Exposed sites receive higher amounts of precipitation and dew but imply that the fungus should be drought-tolerant to some extent. Yet, this could so far not be verified in the few realised vitality tests.

Similar habitats supported the occurrence of *L. hemiamyloideus*, except that the soil was mostly alkaline. The bryophytes grew on gymnosperm wood of fallen logs in a progressed stage of decay. When the substrate was identified, it was *Picea* (Sweden, Czechia, Switzerland) or *Abies* (Croatia, Germany). Rarely the bryophytes (*Calypogeia*, *Cephalozia*, *Scapania*) grew on soil (Bretagne). The geology was calcareous in the Dinaric mountains and Swiss Jura, moderately to strongly basiphilous at the sites in Sweden and Germany, but definitely acidic at the place in Bretagne and in the Czech Republic. The sites were often shady slope forests in valleys, but also primeval forests on more shallow karstic soil, close to rivulets or far from them, but then preferably in shadowy sinkholes or under an otherwise shady microclimate.

Distribution and cooccurrence

According to the present knowledge, *L. epibryus* and *L. hemiamyloideus* inhabit different geographic regions within Europe (see Fig. 15). For instance, the two occurrences of *L. hemiamyloideus* in the Ostalbkreis and Rems-Murr-Kreis of Baden-Württemberg and the Lika-Senj County of Croatia are so far very isolated and distant from *L. epibryus*, as are most records of the much more often collected *L. epibryus*. This suggests specific requirements of each species. Yet, in three regions (South Sweden, Bretagne, Swiss Jura), both species occurred at distances of 0.5−10 km from each other, in one


1a
25 µm
1b
25 µm
1e
10 µm
2b
10 µm
2c
10 µm
1c
25 µm
1d
10 µm
2a
10 µm
2d
10 µm
IKI
2e
10 µm
IKI
1f
10 µm
1g
10 µm
1h
10 µm
2f
10 µm
2g
10 µm
2h
10 µm

◂**Fig. 12** *Luteodiscus hemiamyloideus* (on *Nowellia* from Germany). **1a–d, 2a** Surface view on ectal excipulum at margin and flanks; **1e, 2b–c** mature asci; **2d** ascus apices with hemiamyloid apical rings; **1f–g, 2f–g** upper part of paraphyses (in **1g** at margin); **1h, 2h** mature ascospores; **2e** overmature ascospores. – Living state (in H_2O), except for **2d–e** (in IKI), some paraphyses in **2g**. – **1 L.K.** 3430 (Welzheim, holotype), **2 L.K.** 3429 (Gschwend). – Phot. **1a–h, 2a–c, f–h** L.G. Krieglsteiner, **2d–e** Z. Sochorová

place of Swiss Jura even at about 20 m distance, with *L. epibryus* growing on *Hypnum cupressiforme* on an *Abies* log and simultaneously *L. hemiamyloideus* on *Riccardia* on an unidentified conifer log, and in Bretagne even at a 3 m distance, with *L. epibryus* growing on *Diplophyllum* and *L. hemiamyloideus* on *Calypogeia*, *Cephalozia*, and *Scapania*, all of which occurring on the flanks of a ditch where also *Mniaecia* aff. *nivea* occurs on *Diplophyllum albicans*.

Phenology

At first glance, *L. epibryus* appears to occur throughout the year, based on a total of ~ 115 collections at present. However, the majority of collections were made in spring, especially in March, and a minority during summer, autumn, and winter, with so far none in August (Table 2). The gap in late summer is perhaps because of frequent dryness in that month, or because the focus of collectors is more on larger mushrooms. The 15 records of *L. hemiamyloideus* were all made during spring, except for one in late autumn (Table 3).

Geographical regions

In the regions of Bretagne and adjacent Pays-de-la-Loire (northwestern France), numerous collections of *L. epibryus* were made by J.P.P. in woodlands of *Castanea sativa*, partly in mixture with *Pinus sylvestris* and *P. pinaster*, also *Abies*, mainly in 2016 and 2019. The species grew on different bryophytes, mostly *Hypnum*, but also other genera of mosses (*Dicranella*, *Dicranum*, *Kindbergia*, *Leucobryum*, *Pleurozium*, *Polytrichum*), more rarely liverworts (*Calypogeia*, *Diplophyllum*), which in turn grew on fallen logs and dead stumps, more rarely on soil, never on rock. The geology of all these sites was a markedly acidic soil covering Cambrian (Brioverian) and Ordovician shist (and greywacke), or granite. The two records of *L. hemiamyloideus* were from a single site near La Gacilly on acidic Ordovician siltstone (adjacent to Brioverian siltstone), where it grew together with *L. epibryus* at short spatial distance though on different bryophytes. At the site in Deux-Sèvres (western France, M.H.) where *L. epibryus* occurred, the forest was dominated by *Castanea sativa* and *Quercus petraea*, mixed with *Ilex aquifolium*, and the geology was granite and shale (Massif Armoricain) producing sandy-loamy soils.

Apothecia of *L. epibryus* were discovered in almost all such woodlands which have been investigated. A special microecology when occurring on the woody substrate was patches of moss ensheathed by green algae. Under high humidity conditions, the apothecia occurred in great number on a given patch and were easier to detect by their abundance. A look to the ground from a standing position, at a distance of 1.75 m, already enabled to detect the presence of apothecia.

Table 3 Phenology of *Luteodiscus hemiamyloideus* based on listed collections

Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
0	6	3	5	0	0	0	0	0	0	1	0

Table 4 Comparison of selected features obtained from five collections of *L. epibryus* with a sequence (Z.S. 103/2020 is without a sequence but from the same place as Z.S. 4/2021, while J.P.P. 202038 from Bretagne on *Hypnum cupressiforme* [genotype I] is without documentation and therefore absent from the table). The sequence from E.R.D. 6988 was obtained from apothecia on *Frullania*, but it cannot be excluded that apothecia from the other host (indet. *Hypnales*) were included. Likewise, the sequence from M.H. 100216 could either derive from apothecia on *Hypnum* and/or *Dicranum*, and that of Z.S. 4/2021 from apothecia on *Tetraphis pellucida* but probably also from other of the 5 bryophytes mentioned. #genotype in correlation with presence of S1506 intron (light blue = genotype I, grey = genotype II)

	Z.S. 4/2021 [Z.S. 103/2020]	F.V. 2013021901	E.R.D. 6988	M.H. 100216	G.G. 523
rDNA#	intron absent	intron absent	intron absent	intron present	intron present
ascospores [µm]	*(9–)10–14(–15.5) × (2.5–)3–3.5(–4)	*12.3–14.8 × 2.8–3.8	*11–18.5 × 3–4	*12–14 × 3–4	*12–14.5 × 3.5–4.2
VBs in ascospores	faintly to medium refractive	not seen	faintly to medium refractive	faintly to medium refractive	not seen
asci [µm]	[*70–84 × 10.2–11]	*60–70 × 10	*85 × 11.5	*52–63 × 8–10	?
ascus apex in IKI	blue (BB)	blue (BB)	blue (BB)	blue (BB)	?
apothecial disc [mm]	[~0.2–1]	~0.5–1.35	~0.25–1	~0.25–1	~ 0.25
apothecial stipe [mm]	[~0.1–0.15 × 0.2–0.25]	~0.17–0.23 × 0.2–0.25	~0.1 × 0.1–0.12	?	indistinct
VBs in paraphyses	medium refractive	faintly refractive	faintly refractive	medium refractive	medium refractive
host	*Lepidozia reptans, Neoorthocaulis attenuatus, Paraleucobryum longifolium, Sphenolobus minutus & Tetraphis pellucida*	*Pleurozium schreberi*	*Frullania tamarisci* (& indet. *Hypnales)*	*Hypnum cupressiforme* (& *Dicranum scoparium*)	*Lepidozia reptans*
Geography	Czech Republic	Île-de-France	Asturias	Poitou-Charentes	Scotland

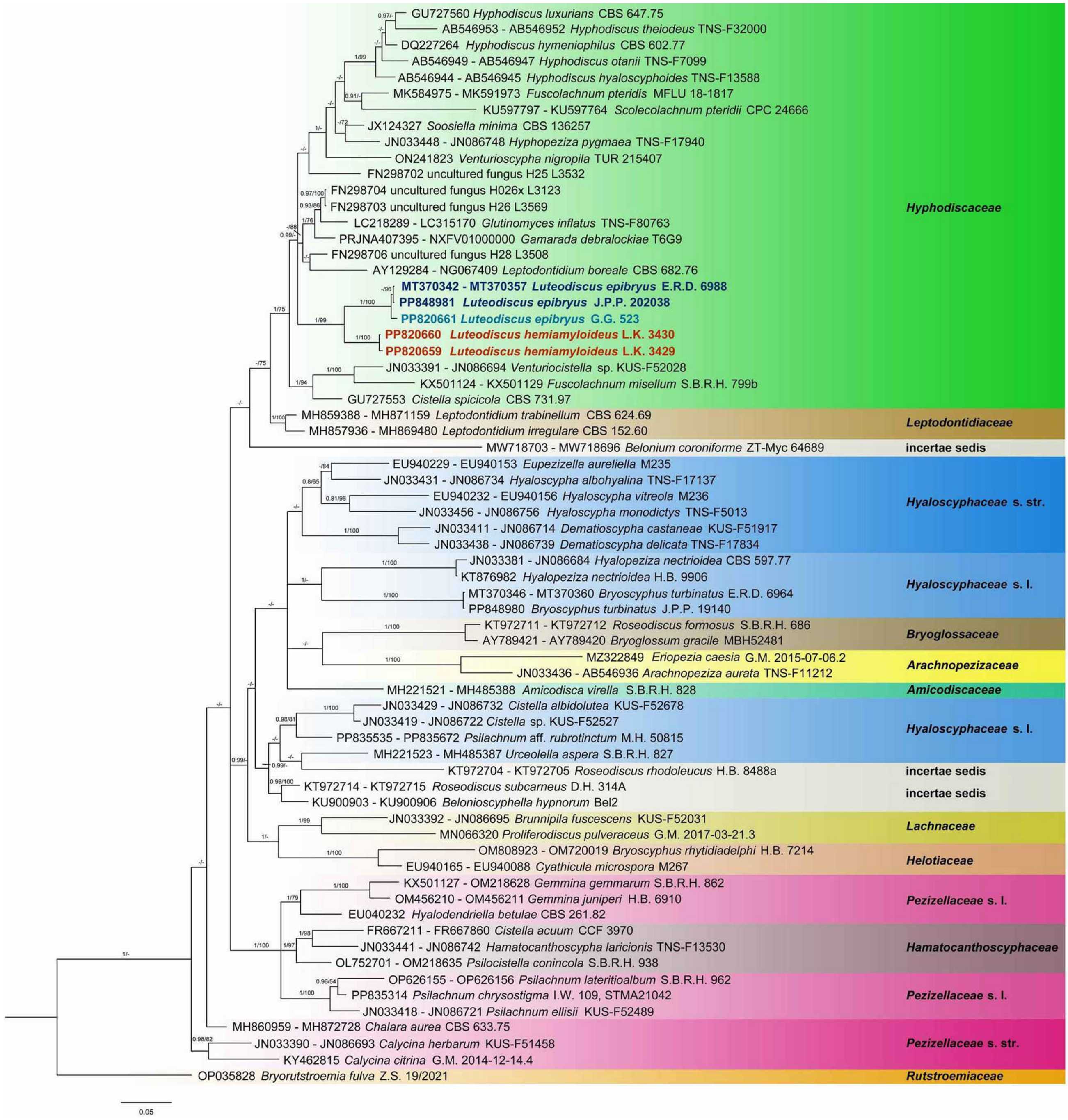


Fig. 13 Bayesian inference analysis of ITS + LSU (D1–D4) rDNA (with 7.500.000 generations; bootstrap values after the slash refer to maximum likelihood analysis generated with MEGA6, model GTR + G + I, using all sites, 500 replicates; bootstrap values below 0.8/70 omitted). The dataset comprises different families of members of *Helotiales*, mainly those with a *Calycina*-type of apical ring, with a focus on bryophilous taxa. Placement of *Luteodiscus* in *Hyphodiscaceae* received strong support. *Bryorutstroemia fulva* was used as outgroup

Searching was mainly done during March, with some more fortuitous finds in April and May, while in the remaining months, the focus was on other ascomycetes. After a targeted search at two different sites on 17.V.2020 (J.P.P. 202081) and 21.V.2020 (J.P.P. 202085), and despite a week of very strong northeast wind, many plants of *Hypnum* carried apothecia of *L. epibryus* but, for the most part, these were stuck in algae and got senescent, showing badly developed asci and spores.

It is surprising that Crouan and Crouan (1867), who have intensely herborized in western Brittany, apparently did not notice this genus in their "Florule du Finistère". The number

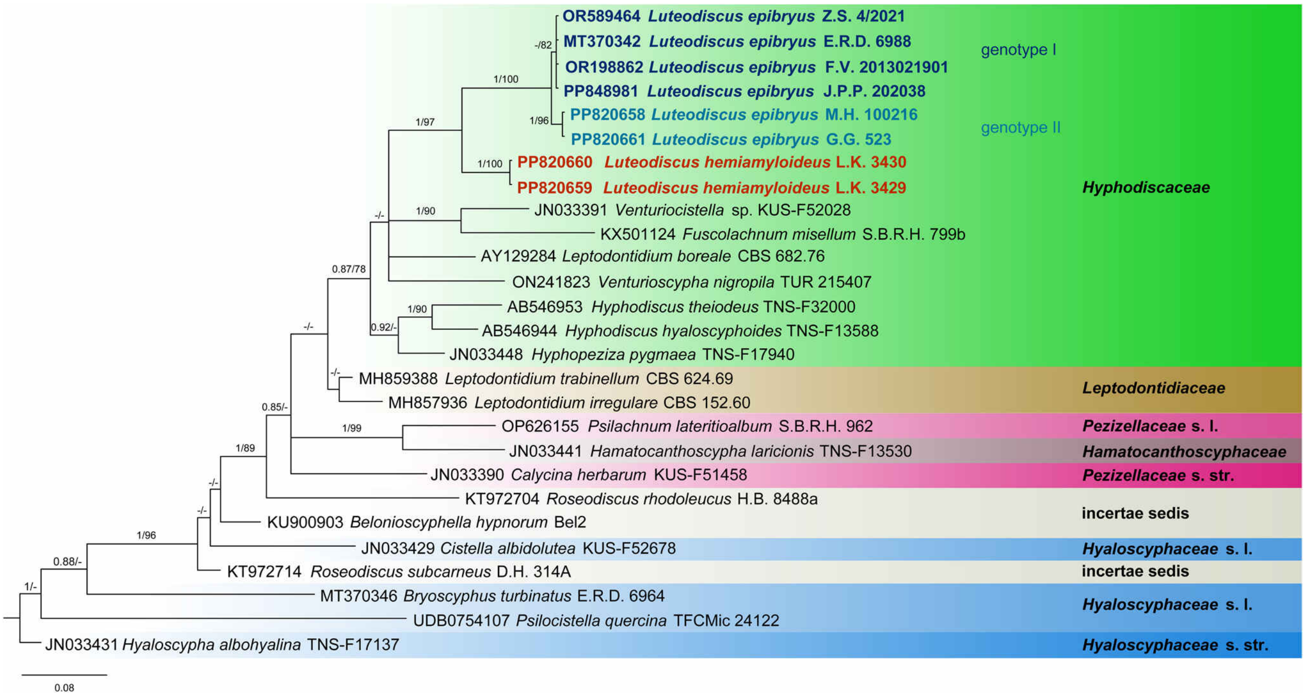


Fig. 14 Bayesian inference analysis of ITS rDNA on a reduced dataset of the combined analysis (with 10.000.000 generations; bootstrap values after the slash refer to maximum likelihood analysis generated with MEGA6, model K2+G, using all sites, 500 replicates; bootstrap values below 0.8/70 omitted). In addition, four sequences which lack LSU were included: three of *Luteodiscus epibryus* and one of *Psilocistella quercina*. Placement of *Luteodiscus* in *Hyphodiscaceae* received moderate support. "*Bryoscyphus*" *turbinatus*, *Hyaloscypha albohyalina*, and *P. quercina* were used as outgroup

of bryophilous ascomycetes described by these authors nevertheless shows their interest for this particular substrate. It appears that they and their usual suppliers have not herborized in this type of ecology conducive to the occurrence of *Luteodiscus*.

The collection sites of *L. epibryus* in Scandinavia were on siliceous soil, in Norway (Vestland, Bømlo, E.J.) a living *Alnus glutinosa* trunk in a rich deciduous forest, and in Sweden (R.I.) on a spruce log and on siliceous rocks (Jönköpings län) in pure spruce forests or mixed with *Alnus glutinosa* etc. (Fig. 2(2)), or on trunk base of *Corylus avellana* (Västra Götalands län). The single occurrence of *L. hemiamyloideus* in Småland (Fig. 8(1)) was on a spruce log over "greenstone" (alkaline igneous rock, ?porphyry) in a spruce forest mixed with *Corylus avellana*, *Betula*, and *Quercus robur*, with *Geranium sanguineum*, *Hepatica nobilis*, *Geastrum quadrifidum*, and *Exsertotheca* (*Neckera*) *crispa*.

The site of *L. epibryus* in Asturias (northern Spain, E.R.D.) is a montane rocky ravine with a mixed forest composed of *Quercus petraea*, *Fagus sylvatica*, *Castanea sativa*, *Fraxinus excelsior*, and *Corylus avellana* (Fig. 2(5−6)). The quartzite rocks on which the bryophytes grew were fully exposed and strongly insolated due to the forest track and adjacent low shrubland with *Rubus*, *Pteridium*, *Ulex* etc. which probably originates from some forestry activities or fires in the past.

In the Bayerischer Wald (southeast Germany), G.B. collected *L. epibryus* almost every year from 2009 onwards at numerous places in conifer forests with *Pinus*, *Picea*, or *Abies*, sometimes mixed with *Fagus* and *Quercus* or *Betula* (Figs. 1(3), 2(3)). The different mosses and liverworts always grew on rock of granite. No doubt, the species is frequent in these colline to submontane, acidic forests. In similar forests, Z.S. observed *L. epibryus* at many sites in the mountain range of northern Czechia, but here always on rock of acidic quartz and arkose sandstone. Despite repeated search for bryophytes on woody substrates by G.B. and Z.S., no collections of *L. epibryus* succeeded.

The locations of *L. epibryus* and *L. hemiamyloideus* in Swiss Jura (E.S.) were on northern slopes with adjacent wet- and moorland as well as in cut ravines with a watercourse. The vegetation consisted of *Fagus sylvatica*, *Corylus avellana*, and *Sorbus aucuparia* mixed with *Abies alba* and/or *Picea abies*, but it differed between the two species: for *L. epibryus*, it was twice a *Lonicera-Fagenion* with *Cardamine pentaphyllos* (Fig. 1(1−2)) and once an *Abieti-Fagenion*, and for *L. hemiamyloideus* six times an *Abieti-Fagenion*, once in transition to a high moor. Apothecia were exclusively collected on long-lying, heavily decomposed logs and stumps of conifers overgrown with moss. Because these areas are difficult to access, these logs, which have been felled by storms or forestry work, remain in the forest. The geology was always calcareous (different layers of Upper Jurassic), which is also true for the site of *L. epibryus* in the French Jura (Côtes-d'Or), which was a plateau at the top of a calcareous cave made up of oolitic limestone (Middle Jurassic).

The two sites in the Schwäbisch-Fränkischer Wald (southern Germany, L.K. & K.K.), where *L. hemiamyloideus* was recorded, are both in timbered stream gorges with potential vegetation of beech-fir forests mixed with spruce trees. The Seebach Gorge near the lake Bergsee (Gschwend, Fig. 8(3)) is a deeply cut gorge and cold-air sink, on whose slopes and low-lying areas deciduous trees (*Fraxinus excelsior*, *Acer pseudoplatanus*, *Alnus glutinosa*) are added, while on the upper slopes spruce and fir (and beech) dominate. At the bottom of the gorge and vertically up the gorge lie fallen trunks, including those populated by *Nowellia curvifolia* with the fungus on it. The Edenbach Gorge near Welzheim (Fig. 8(2)) is cut flatter and has a reasonably pure spruce-fir-beech forest at the place where the apothecia were found.

The geology at the Seebach site is middle Keuper (coloured marl), namely the lower stratum (today's Steigerwald Formation) and middle stratum (also siliceous sandstone, today's Hassberge Formation — see map viewer lgrb-bw.de). A likewise base-rich soil is formed at the upper edge of the gorge with the upper stratum (today's Mainhardt Formation), with which the entire habitat can be described as strongly calcareous-base-rich, a statement that is also supported by the observed plant vegetation, including bryophyte occurrences (e.g. *Ctenidium molluscum*, *Metzgeria pubescens*, *Thamnobryum alopecurum* and others). The Edenbach site is geologically a somewhat younger Keuper layer: down to the brook dominates Stubensandstein (today's Löwenstein Formation), while at the brook a Holocene floodplain sediment is indicated (lgrb-bw.de). However, personal observations clearly indicate that coloured marl is also present at the Edenbach, i.e., there is a mixture of acidic and more alkaline layers.

The three sites in the Plitvička Jezera National Park, a part of the Dinaric Mountains (Croatia, L.K.), where *L. hemiamyloideus* was recorded, all represent liverwort lawns on fallen *Abies* trunks in partly primeval-forest-like stands of montane, precipitation-rich spruce-fir-beech forests growing over karst limestone (Fig. 8(4–6)). These forests were humid during collection and mostly far from water courses, but moist due to recent melting of ample snow. The area of Čorkova Uvala is located in a mountainous highland with many sinkholes that can be seen as smaller, air-cold slopes in an otherwise plainer area. The site at the source of the small river Crna Rijeka consists of a limestone block field on which individual older tree trunks had fallen, without direct accompanying spermatophyte vegetation. When the apothecia were detected in spring 2011, there was still snow in many places, and the infested liverwort lawns had only recently thawed.

Only *L. epibryus* has been detected so far in Macaronesia (Tenerife) and eastern parts of North America. Climatically extraordinary is the collection from Tenerife (J.H., P.D.), which was made in a mesomediterranean (sub) humid *Pinus canariensis* forest close to the humid slopes covered by laurel forest. In North America (J.C.L. etc., P.D.), the species appears to have a classic northern temperate Appalachian-Great Lakes distribution (see Brodo et al. 2001; Tripp and Lendemer 2019). Despite ample suitable habitat, there are few collections from eastern North America relative to Europe. Apothecia of *L. epibryus* have been seen only at four places, two at the highest elevations (around 1900 m) of the Great Smoky Mountains National Park in the Southern Appalachian Mountains along the border between Tennessee and North Carolina, one at less high altitude (around 950 m) in the Central Appalachian Mountains of Pennsylvania, and one at a low elevation (65 m) in coastal New England in Maine. All of the locations have a surficial geology that consists of non-calcareous, acidic rocks: the Southern Appalachian sites have the metal-rich Anakeesta Formation which hosts several narrowly endemic lichens (Lendemer & Tripp 2015), the Central Appalachian site has massive sandstone outcrops and boulders, and the site in Maine is dominated by schists and granite (J.C. Lendemer, unpublished observations). All of the collection sites are characterized by environmental conditions typical of oceanic regions and host forests that are dominated by conifers (Tripp and Lendemer 2020). The collections from Great Smoky Mountains at high altitudes were in *Abies* dominated *Abies-Picea* forest with *Betula alleghaniensis*, *Prunus*, *Acer spicatum*, and *Rubus*, on liverworts growing on living trunks about 1.5–2.5 m up the tree, whereas those from lower altitudes were on mosses growing on rocks. The forest in Pennsylvania consisted of a *Rhododendron* thicket and hardwood, and that in Maine of *Picea* and *Betula*.

Discussion

Phylogeny

Our phylogenetic analysis provided support that *Luteodiscus* belongs to the *Hyphodiscaceae*. From a morphological point of view, this relationship is surprising, since this family was initially proposed by Ekanayaka et al. (2019) for species with granulated hairs. Quijada et al. (2022), however, showed by phylogenetic analysis of a larger dataset that it encompasses

Table 5 Overview of the orders and species of bryophytes on which *Luteodiscus* has been recorded, indicating the number of collections (uncertain hosts after the slash)

Group	Order	Species	*L. epibryus*	*L. hemiamyloideus*
Mosses	***Tetraphidales***	*Tetraphis pellucida*	4	
	Polytrichales	*Pogonatum urnigerum*	1	
		Polytrichum formosum	6	
	Dicranales	*Dicranella heteromalla*	4	
		Dicranella sp.	2	
		Dicranum montanum	1	
		Dicranum scoparium	13	
		Dicranum sp.	3/1	
		Leucobryum juniperoideum	2	
		Paraleucobryum longifolium	4	
	Grimmiales	*Grimmia trichophylla*	1	
	Bryales	*Bryum* sp.	1	
		Pohlia nutans	1	
	Hypnales	*Callicladium* (*Hypnum*) *imponens*	2	
		Hypnum cf. *andoi*	1	
		Hypnum cupressiforme	54	
		Hypnum jutlandicum	10	
		Hypnum sp.	6	
		Kindbergia (*Eurhynchium*) *praelonga*	1	
		Pleurozium schreberi	6	
		indet. *Hypnales*/*Hypnaceae*	3	
	indet. mosses		2	
Liverworts	***Jungermanniales***	*Barbilophozia lycopodioides*	1	
		Barbilophozia (*Lophozia*) *sudetica*	8	
		Bazzania trilobata	1	
		Calypogeia sp.	1	1
		Cephalozia bicuspidata		2/1
		Cephalozia sp.	1	
		Diplophyllum albicans	3	
		Isopaches (*Lophozia*) *bicrenatus*	1	
		Lepidozia reptans	2	2
		Neoorthocaulis (*Barbilophozia*) *attenuatus*	2	
		Nowellia curvifolia		11
		Odontoschisma denudatum	2	
		Scapania nemorea	1	1
		Scapania sp.	1	
		Sphenolobus minutus	5	
		Trilophozia (*Tritomaria*) *quinquedentata*	1	
		Tritomaria exsecta	1	
		indet. *Lophoziaceae*	1	
	Porellales	*Frullania asagrayana*	1	
		Frullania dilatata	1	
		Frullania tamarisci	2	
	Metzgeriales	*Riccardia palmata*		1
		Riccardia sp.		2
	indet. foliose liverworts		2	

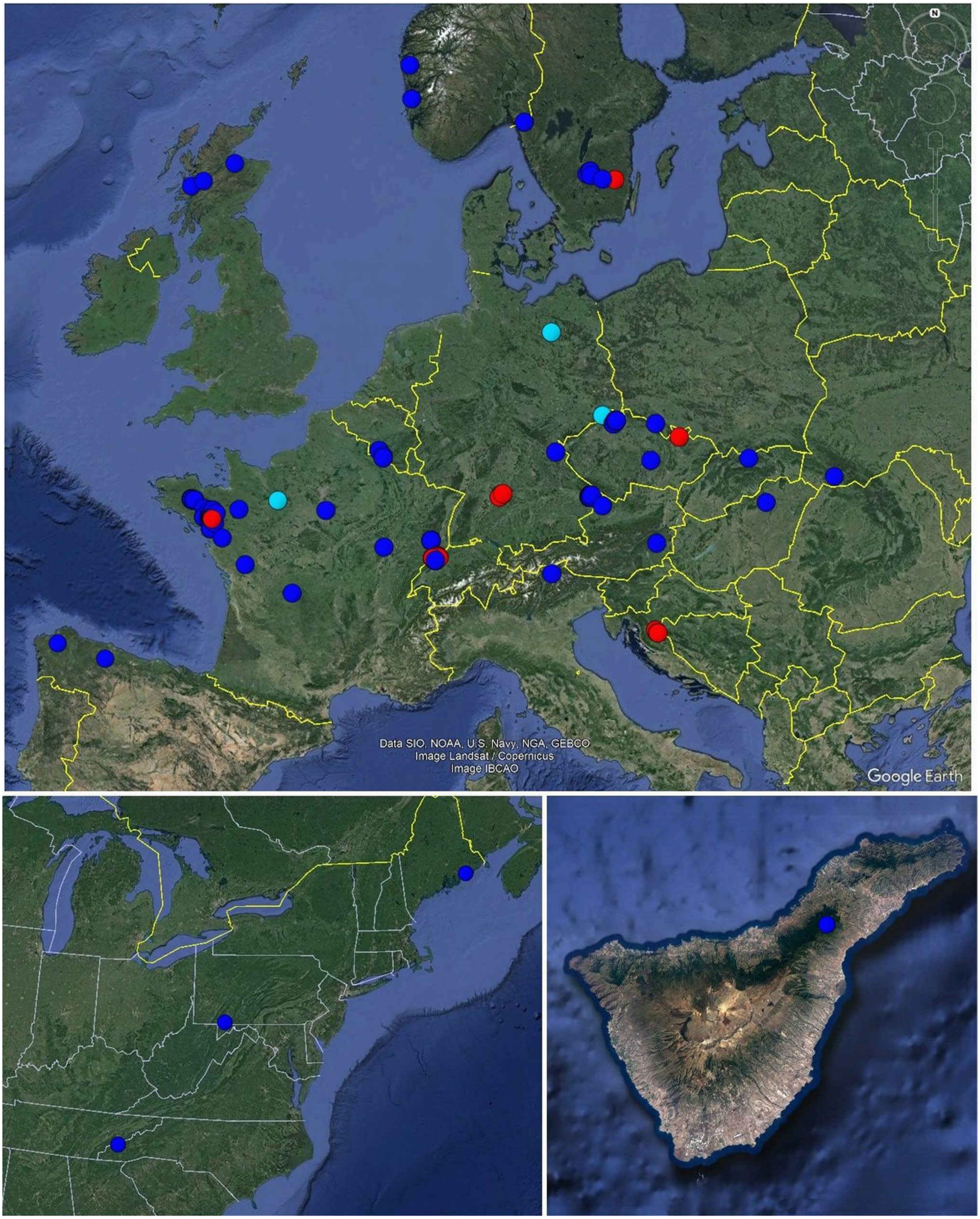


Fig. 15 Known distribution of *Luteodiscus* spp. in Europe, North America, and Tenerife (Canary Islands). Blue = *L. epibryus*, turquoise = unverified (probably *L. epibryus*), red = *L. hemiamyloideus*

a high diversity in hair morphology, including smooth hairs as in the type species of *Microscypha* Syd. & P. Syd. Whilst the hairs are usually hyaline or pale brown in this family, some genera have dark brown hairs: a remarkable combination of smooth, dark brown, spiky, thick-walled hairs and warted, light brown, blunt, thin-walled hairs is characteristic of *Venturiocistella* Raitv., whereas *Fuscolachnum* J.H. Haines possesses only the latter hair type and *Venturioscypha* (Baral et al. 2023a) only the former hair type (but with blunt tips). This assemblage of morphologically very diverse genera results from the primary attention to monophyly in phylogenetic analyses by disregarding the morphological traits of the included taxa. The question of which point of divergence should be regarded as representing the family level usually remains a matter of taste. In the present case, members of *Leptodontidiaceae* clustered as a sister group of *Hyphodiscaceae*, though with a low support. Therefore, but also for morphological reasons, they should not be included in that family. Teleomorphs of *Leptodontidiaceae* consistently lack hairs, possess strongly refractive, elongate VBs in the living paraphyses, and the ascospores form germ tubes producing small holoblastic conidia. Their hyphomycetous anamorphs are characterised by brown *Leptodontidium*-like conidiophores with holoblastic conidiogenesis. In all these features, they differ from *Hyphodiscaceae*, where a hyphomycetous anamorph is so far only known in *Hyphodiscus*, having hyaline enteroblastic *Catenulifera*-like phialides with prominent collarettes.

Morphology

Our research on the genus *Luteodiscus* suggests that two species are involved, which can easily be distinguished by the iodine reaction of the non-pretreated ascus apical ring, which was tested in 69 collections of *L. epibryus* and 14 of *L. hemiamyloideus*, also by the height of the apical ring, length and lipid content of the ascospores, and a few less clear features. Although *L. epibryus* was represented by two closely related genotypes, no morphological differences could be detected between them.

A hemiamyloid reaction of the apical ring as observed in *Luteodiscus hemiamyloideus* is known in some species of *Hyphodiscus*, but this character is widespread across the *Helotiales* and often not consistent among closely related species; therefore, it is of limited phylogenetic importance. Ecologically, members of *Hyphodiscaceae* inhabit a broad range of hosts, including pteridophytes [*Scolecolachnum pteridii* Guatim. et al., *Fuscolachnum pteridis* (Alb. & Schwein.) J.H. Haines] and bryophytes (*F. necator*, *Hyphodiscus delitescens*). Quijada et al.'s emended characterization of *Hyphodiscaceae* includes the morphology of *Luteodiscus*, e.g., regarding subsessile to short-stipitate, small apothecia with a downy to hairy receptacle, the hairs being sometimes very short and macroscopically more or less unobservable. Only the medullary excipulum of textura intricata in *Luteodiscus* vs. t. angularis to t. porrecta in Quijada et al.'s family concept appears as an albeit doubtful difference. The presence of VBs in the paraphyses of *Luteodiscus* would be exceptional within *Hyphodiscaceae*, but was once observed in *F. pteridis* (Quijada et al. 2022: 69, fig. 5D).

Distribution in Europe

Although our results suggest a wide distribution of both species within Europe (Fig. 15), various large gaps remain, especially regarding well-sampled regions. So it is surprising that no records from southwestern or middle parts of Germany came to or notice, none from England or Netherlands, and only two from Spain and two from the Alps (northern Italy and eastern Austria). It could be that *Luteodiscus* is only locally frequent, but we can be sure that much more such areas exist within Europe, which wait to be detected. On the other hand, it could be that various areas are unsuitable for this genus, at least for producing apothecia.

Is *L. epibryus* rare in North America?

The disproportion in collection numbers between North America and Europe (see Fig. 15) could reflect real differences in frequency and abundance, as has been noted for lichen species with the same disjunct geographic distributions (Howland and Lendemer 2023). It could also reflect a combination of sparse sampling and strong collector bias against small discoid microfungi in North America (see e.g., Lendemer 2020). Given the similar macroscopic appearance of *Luteodiscus* and *Coenogonium* Ehrenb. in the field (see also below), confusion is plausible with, e.g., *C. luteum* (Dicks.) Kalb & Lücking or *C. pineti* (Ach.) Lücking & Lumbsch, two lichens that cooccur in the same vegetation types and habitats as *L. epibryus*. However, these two lichens typically grow on rotten wood and bark, but they grow facultatively also on bryophytes (Tripp and Lendemer 2020). Nonetheless, revision of numerous crustose lichen herbarium specimens from eastern North America has not resulted in additional records of *L. epibryus* apothecia which could have been confused by the collector with a member of *Coenogonium* (J.C. Lendemer, unpublished data).

While the small number of records of *L. epibryus* could be due to the above factors, extensive fieldwork throughout temperate eastern North America suggests that in the region it is rare, albeit bleached bryophyte populations are locally abundant in certain habitats, and that even in those habitats where these were abundant, apothecia rarely have been observed. When apothecia are present, they are conspicuous and easily detected. Highly noticeable necrotic patches on epiphytic bryophytes have been frequently observed in the high-elevation spruce-fir habitats where *L. epibryus* occurs in the southern Appalachian Mountains. Despite being abundant and well-developed, repeated collection of these necrotic patches by J.C. Lendemer for nearly a decade failed to reveal the presence of any obvious fungal reproductive structures. One fertile collection was made in 2014 and another in 2015, but after that, no additional material was found despite intensive sampling across the region (see Boggess et al. 2024). The phenological data reported in this paper and based on collection frequency from across the distribution of the species suggest a peak of early to mid-spring fruiting for *L. epibryus* in North America. This coincides with typical lichenological and botanical fieldwork seasons in the Appalachian Mountains when spring wildflowers are at their peak and cold winter temperates have abated at high elevations. Hence if *L. epibryus* were more commonly fertile in the region it would almost certainly have been detected at a higher rate than it has been to date. However, we should be aware that the observed necrosis of bryophytes might not only be provoked by *Luteodiscus*. A molecular study could through a light on the true distribution of *L. epibryus* in North America.

Bryoparasitism and host specificity

The wide host range observed in *Luteodiscus* was very unexpected, because most bryophilous ascomycetes are specific to one bryophyte species or genus or a group of taxonomically related genera. As biotrophic parasites, these specific fungi live in an equilibrium with their hosts and do not or just slightly damage them, a phenomenon which is well known in obligate parasites, e.g., in lichenicolous species (Lawrey and Diederich 2003), in mildews, and in rust- and smut-fungi. A few examples of biotrophic ascomycetes are mentioned in the following: *Bryocentria brongniartii* (P. Crouan & H. Crouan) Döbbeler (*Hypocreales*) was found within Europe to infect only *Frullania dilatata* (Döbbeler and Hertel 2013) and in America *F. brittoniae* and *F. eboracensis* (Döbbeler and Davison 2017). *Epibryon plagiochilae* (Gonz. Frag.) Döbbeler (*Chaetothyriales*) is a common parasite on *Plagiochila asplenioides* s.l. in Europe (Döbbeler 1978) and is further reported on *P. britannica* from Wales (Bosanquet 2007) and on *P. asplenioides* s. lat. in Canada (Döbbeler 1985). In Finland, it strongly prefers *P. asplenioides* but also grows on *P. porelloides* (Marsh et al. 2010). All three liverworts belong to *Plagiochila* sect. *Plagiochila*. Among the *Helotiales*, *Pithyella chalaudii* J.P. Priou (= *P. frullaniae* Chalaud ex Döbbeler) is not rare in Europe and North America on *Frullania* spp., with only one record on *Cheilolejeunea clypeata* (Döbbeler and Davison 2021), and *Belonium coroniforme* has only been recorded on *Orthotrichales* (*Lewinskya*, *Orthotrichum*, *Pulvigera*, *Ulota*) and rarely *Hypnales* (*Leucodon*) (Döbbeler et al. 2021; Isaksson 2023). A high host specificity is also known in bryophilous *Pezizales*, with the central genus *Octospora* Hedw. and a few additional genera (Eckstein 2023). In recent years host specificity in these parasites was convincingly documented by field and morphological studies and also by molecular methods (Sochorová et al. 2020; Németh et al. 2022).

In contrast to the above, relatively few bryoparasitic species exist which are necrotrophic, causing distinct decoloration of the leaves and stems and tend to have a wider host spectrum. Besides *Luteodiscus*, the following examples belong in this group: The hypocrealean *Bryocentria metzgeriae* (Ade & Höhn.) Döbbeler occurs on liverworts of the genera *Frullania, Lejeunea, Metzgeria, Porella*, and *Radula* (Döbbeler 2004, 2010). *Belonioscyphella hypnorum* (*Helotiales*) colonises mosses of the *Dicranales* and *Hypnales*, and sporadically liverworts of the *Jungermanniales* and *Porellales* (Döbbeler 1986; Egertová et al. 2016). *Bryorutstroemia fulva* (Boud.) Sochorová, Baral & Priou has been recorded mostly on *Dicranella heteromalla*, but twice on *Dicranum scoparium* and once on *Racomitrium heterostichum* (Baral et al. 2023b, as *Bucklandiella heterosticha*). The common *Acrospermum adeanum* Höhn. (*Acrospermales*) infects and finally kills many genera of mostly pleurocarpous mosses (Racovitza 1959; Döbbeler and Hertel 2013). Likewise, *Roseodiscus subcarneus* is a necrotrophic parasite, according to various collections on different bryophytes (unpublished data).

Other bryophilous species that may be confused with *Luteodiscus*

Several taxa described in the older literature resemble to some rate one of the two species of *Luteodiscus* described here, but their brief and insufficient descriptions are difficult to interpret. Some of them can more or less safely be excluded because of their deviating characteristics, especially when they have been redescribed by later workers from the types. Others still require reexamination of the type material, if extant, to clarify their identity.

Among these taxa, four species and one variety are more or less certain synonyms, the oldest of them now recognized as "*Bryoscyphus*" *turbinatus*. This species resembles *L. epibryus* in many respects, including apothecial size and shape, ascus size, apical ring of *Calycina*-type, spore size, shape and contents, and paraphysis width, shape and contents. However, recent collections referable to *B. turbinatus* show that this species sharply differs from *Luteodiscus* spp. (see IVV): the species has a consistently simple-septate ascus base and possesses abundant crystals in the medullary excipulum; moreover, it shows a tendency of the apical rings to react hemiamyloid (type rB or RB) and it generally has a whitish-cream disc that turns red-brown with age (a KOH-induced colour change is absent). Ecologically, *B. turbinatus* has a similarly wide host range as *L. epibryus*, but its range so far includes exclusively mosses. As in *Luteodiscus*, *B. turbinatus* provokes necrobiosis to the leaves on which its apothecia are formed.

ITS and LSU rDNA data in GenBank obtained from three of these recent collections (MT370346/MT370360 = E.R.D. 6964, MW677583 = E.S. 2018.97, PP848980 = J.P.P. 19140) suggest that *B. turbinatus* is distantly related to the type species of *Bryoscyphus* Spooner (*Helotiaceae*) but clustered in an unpublished preliminary analysis of ITS + LSU with medium support unresolved in *Hyaloscyphaceae* s.str. as circumscribed by Kosonen et al. (2021, fig. 2). *B. turbinatus* differs from *Hyaloscypha* Boud. in having crystals and lacking hairs, which appears to support a genus of its own.

Fuckel (1870) described ***Leucoloma turbinatum*** Fuckel (type: Fungi rhenani 1177, as *Peziza muscorum* Fr.), which he collected in autumn on living mosses such as *Polytrichum juniperinum*, *Hypnum* etc. near Heidelberg (Germany), with turbinate, very short-stalked apothecia 2 mm tall and broad, perfectly round, pale grey outside, smooth, margin inflexed, disc pale yellow, asci 8-spored, 94 × 8 μm, spores 12 × 4 μm, oblong-ellipsoid, paraphyses filiform, brownish. Rehm (1896: 1009) reexamined the type and confirmed the apothecial size as up to 2 mm, asci up to †100 × 8—9 μm, pore blue in IKI, spores †12—15 × 3.5—4.5 μm, straight, fusoid, unicellular often with 2 large oil drops, paraphyses filiform, brownish, 1.5 μm wide, excipulum prosenchymatic. Surprisingly, Rehm placed the species in *Plicaria* (today *Pezizaceae*). When White (1942: 168) studied the type of *L. turbinatum*, besides several other specimens from Germany, he gave only a joint description which included the type of *Helotium bryogenum* Peck. His description gives apothecia up to 1 mm diam. when moistened, asci †70—90 × 8—11 μm, not arising from croziers, and spores †16–23 × 3–4 μm. Although White provided solely for the type of *H. bryogenum* an illustration, in which the absence of croziers is depicted, it can be assumed that he noticed a simple-septate ascus base also in the other specimens he had examined, including the type of *L. turbinatum*.

The brief original description of ***Helotium bryogenum*** Peck (in Peck 1878: 61), collected in September on *Hypnum delicatulum* in Maryland (New York, USA), refers to minute, substipitate, pallid or yellowish-white apothecia changing to livid-red or subviolaceous when dry, and subfusiform, sometimes curved ascospores with a length of 0.0006–0.0007', which refers to about 15–18 μm. The violaceous-red colour change would be reminiscent of *Luteodiscus*, but White's (1942: 168, fig. 5: 10) illustration of the type shows asci arising from simple septa and spores with some small drops in each half. Both Peck and White made no mention of crystals in the excipulum or the iodine reaction of the asci. The apical ring illustrated by White (possibly in KOH) resembles the *Hymenoscyphus*-type, but White in general appears not to have carefully studied ring shapes in iodine reagents.

One of the specimens studied by White (Rehm Ascom. 1279, on *Hypnum cupressiforme* [fide Spooner 1984], from Dahren, Sachsen) was described by Rehm (1899: 244) under the name *Belonium bryogenum* (Peck) Rehm, with subsessile, yellow-brownish apothecia of 0.4–0.5 mm diam, asci of 60–70 × 8 μm with amyloid apical ring, and fusiform, finally 2-septate ascospores of 15—17 × 3 μm with two small guttules. Following Rehm's description, Höhnel (1918: 594) considered this as indistinguishable from *Helotium turbinatum*, and White's reexamination of the duplicate in FH confirmed this view.

Spooner (1984: 563, figs. 7B, 8) studied and illustrated Fungi rhenani 1177 (on *Dicranum scoparium*) and Rehm Ascom. 1279 by proposing the combination *Bryoscyphus turbinatus* and listing *H. bryogenum* as a synonym. Spooner's description includes apothecia ~ 0.5 mm diam., minutely downy, asci †95—102 × 11—12 μm (1177), †78—84 × 9—10(—11) μm (1279) and spores †16—22 × (3.2—)3.5—4(—4.5) μm (1177 & 1279) (data obtained from sketches in brackets). In both specimens, he illustrated apical rings of the *Calycina*-type. The absence of croziers was not verified, but Spooner observed "pockets of crystalline matter" in the medullary excipulum, and an ectal excipulum of pale brown angular cells of 5—8 μm diam. (more elongated towards margin), covered by a thin superficial layer of interwoven, 1.5—2 μm wide hyphae.

Racovitza (1942a) described ***Phialea epibrya* var. *subclaviformis*** Racov., collected on *Hypnum cupressiforme* from Hunedoara (Romania) in Nov. 1940, as different from *P. epibrya* in larger apothecia (0.5—1.5 mm) with a wider stipe (0.25—0.5 mm) and ascospores with 2—4 guttules besides a granular content, but particularly emphasized the slightly wider (2—2.5 μm), apically subclaviform paraphyses. Ascus (50—80 × 8—9 μm) and spore size (14.5—19 × 3 μm) were similar to the type. Racovitza observed numerous crystals of calcium oxalate (15—30 μm) in the "hypothecium", which clearly excludes a species of *Luteodiscus*. Although his drawing does not permit any conclusion about the ascus base, the observed crystals suggest synonymy with "*Bryoscyphus*" *turbinatus*. Racovitza (1942b) treated in a separate article the occurrence of crystals in the medullary excipulum of *P. epibrya* var. *subclaviformis* as peculiar in comparison to different species of *Helotiales* in which the crystals were formed on the outside of the apothecia. Whether or not the type of *P. epibrya* possesses these crystals was not taken into consideration by Racovitza. Dennis (1956: 112) studied Racovitza's specimen but only briefly repeated his and also Höhnel's measurements.

Helotium polytrichicola P. & H. Crouan was described by Crouan & Crouan (1867, as "*H. polytricola*") on living leaves of *Polytrichum commune*, with substipitate, rose apothecia 1 mm diam., oblong, biguttulate ascospores (size not stated), and an ectal excipulum of globose cells surrounded by granules. According to a visit of the herbarium in Concarneau (CO) by J.P.P., there exists no herbarium specimen of this species, but an unpublished water colour sketch made by H. Crouan (labeled as "*Peziza polytricola*"), which gives a good impression of the fungus and its host. *H. polytrichicola* hereafter resembles *B. turbinatus* and *L. epibryus* in spore shape, but it differs from both species in growing on green, living leaves, obviously as a biotrophic parasite, in the pinkish-rose, possibly primary apothecial colour, in the deviating ectal excipular structure, and in the ascospores with two relatively large LBs. Spooner (1984: 565) stated that this taxon "seems likely to prove an operculate species, referable to *Octospora* Hedw. or *Inermisia* Rifai". In Wieschollek et al. (2011), *H. polytrichicola* was compared with *Roseodiscus formosus* Wiesch. et al.

Fries (1822: 149) described ***Peziza hypnorum*** Fr. as a rare species collected by him in December on *Hypnum cupressiforme* growing over large, moist rocks in forests in Sweden, with sparse, sessile, smooth apothecia 1/3 (Paris) line diam. (= 0.75 mm), cupulate, finally convex, dry yellow (as "dry, yellow"), with subflexuous margin. No microscopical features were given. Fries stated that the species resembles a *Biatora* Fr. and should also not be confused with *P. muscorum* Holmsk., for which Fries (1822: 69) gave a size of 2 line diam. No authentic specimen of *P. hypnorum* exists in Fries' herbarium at UPS (Åsa Kruys pers. comm., https://databas.evolutionsmuseet.uu.se/botanik/recordlist.php).

Saccardo (1889: 289) repeated Fries' diagnosis by interpreting the apothecial diameter as 1 mm and transferred it with hesitation to *Pezizella* (as "*Pezizella*? *hypnorum* (Fr.) Sacc.") by adding a German collection (Wallroth Crypt. n. 9489). Rehm (1891: 547) transferred *P. hypnorum* to *Mollisia* (as "*M. hypnorum* Fr.") by citing Saccardo's combination as "*Pezizella* ? *hypnorum* Sacc." and including *Pezizella bryophila* Rehm as a synonym (see below). Shortly later, Rehm (1894: 940) proposed another combination, *Humaria hypnorum* (Fr.) Rehm, by repeating Fries' diagnosis and giving an apothecial size of "ca. 1 mm". Here he stated that Fries' taxon might be a lichen and that Rabenhorst (1844: 345) did not specify the region where Wallroth's collection in Germany was made. Wallroth (1833) himself also did not specify this when saying that he found it on moist decayed mosses.

When Rehm (1891) transferred Fries' *P. hypnorum* to *Mollisia*, he included collections on *Cephalozia bicuspidata* (as *Jungermannia bicuspidata*) from Grunewald near Berlin (Sydow, Mycoth. March. 585) and on *Hypnum cupressiforme* from Thüringen (Wallroth) and listed ***Pezizella bryophila*** Rehm as a synonym (this latter name Rehm had already issued on the label of Sydow's collection). Three specimens collected by P. Sydow in Grunewald exist in S (Herbarium Catalogue, https://herbarium.nrm.se/search/specimens/?query), which now run under the name *Pithyella hypnorum* (Fr.) Boud., but simultaneously bear the name *Pezizella bryophila*: two from VI.1884, on *Cephalozia bicuspidata*, Mycoth. March. 585 (S-F8977, ex Herb. Sydow; S-F9752, ex Herb. Rehm) and one from VII.1884, between *Jungermannia* sp.? (S-F9751, ex Herb. Rehm). S-F9752 can thus be considered the holotype of *P. bryophila*. Photos of the labels were not officially available for those but were so for a duplicate of Mycoth. March. 585 in NY. Accordingly, this exsiccatum, which was issued by handwritten labels, carries merely the data *Cephalozia bicuspidata*, VI.1884, Grunewald near Berlin, leg. P. Sydow, but no diagnosis. In summary, *P. bryophila* is an invalid name because Rehm (1891) placed it in synonymy of *Mollisia hypnorum* (Fr.) Rehm when providing the diagnosis (Art. 36.1 ICN). Index Fungorum and MycoBank wrongly list *P. bryophila* as being effectively and validly published in 1891 and thus legitimate (accessed 3.V.2024).

Rehm's (1891) description of *M. hypnorum* was probably based solely on Sydow's collection on *C. bicuspidata*. It includes gregarious, sessile, smooth apothecia of 0.2–0.5 mm diam., orange, dry reddish-yellowish, asci 60–65 × 5 µm, apex rounded, pore blue in IKI, ascospores 6–8 × 3–3.5 µm, ellipsoid, uniseriate, paraphyses filiform, 1.5 µm wide, excipulum yellowish, parenchymatic. Rehm compared the species with the lichen *Biatorina pineti* (Ach.) A. Massal. (today treated in *Coenogonium*), from which he distinguished it by non-septate ascospores. Here he considered his *P. bryophila* as a doubtless synonym of *M. hypnorum*, based on the comparison with Fries' description, whereas shortly later (Rehm 1894: 940) he appears to have revised his opinion, as he stated that *P. hypnorum* might be in fact a lichen, and did not mention *P. bryophila* at all. *P. bryophila* appears to have some similarity with *Luteodiscus*, but the spores are too short in order to fit *L. epibryus* and the asci are too narrow and with the spores in a uniseriate arrangement to fit both species.

Based on Karsten's (1871) description, ***Helotium procerum*** P. Karst. (collected in June on mosses in a cave close to running water in Merimasku, Finland) resembles *L. epibryus* in apothecial diameter (~ 1 mm) and ascus (60−70 × 7 µm) and spore size (8−16 × 2−3 µm) but differs in yellowish-white to white apothecia with 4–5 mm long stipes. Dennis (1964: 76) transferred the species to *Hymenoscyphus* but did not give a redescription.

Peziza hypnicola Ellis (1877: 134) was reported as growing on *Hypnum sylvaticum* in Bethlehem, Pennsylvania (undated, leg. R. Rau). It was described with small, gregarious, sessile, obconical, pale orange apothecia with concave disc and smooth exterior, subyclindrical asci ~ 100 µm long (0.004'), apically inflated paraphyses, and uniseriate ascospores of ~ 9–10 × 2.5 µm (0.00035–0.0004 × 0.0001'). Except for the paraphyses and long asci, these data could fit *L. epibryus*. Soon after publication, however, Ellis (1878: 232) presented a short note that his *P. hypnicola* "turns out to be a Lichen – *Gyalecta*".

The rarely recorded bryophilous lichen ***Gyalidea cylindrica*** Etayo & Vězda (*Gomphillaceae*, *Ostropales*) may be confused at first glance with *Luteodiscus* (Z. Palice pers. comm.). The species has an indistinct crustose thallus and very similar yellow apothecia of 0.1–0.25 mm diam., though more translucent and very gelatinous when hydrated, growing abundantly on dead parts of mosses. It sharply differs in its large, 5–7-septate ascospores, inamyloid asci (in KOH + IKI) with thick apical tholus, and an orange KOH + IKI-reaction of the ascoplasma, also excipulum and hymenium reacting orange in IKI (Etayo and Vězda 1994). The KOH-reaction was probably negative, as Etayo & Vězda stated to have employed KOH but did not mention any reaction.

Members of the corticolous to lignicolous lichen genus ***Coenogonium*** (*Coenogoniaceae*, *Gyalectales*) may facultatively grow on mosses and liverworts. Due to their already mentioned macroscopic similarity and indistinct crustose thallus, they may be confused at first glance with members of *Luteodiscus* or other bryophilous *Helotiales*, as already stated by Rehm (l.c.) for *Peziza hypnorum*. They differ from *Luteodiscus* in hemiamyloid ascus walls, apically densely septate, swollen, capitate to moniliform paraphyses, 1-septate ascospores with a high lipid content, and a parenchymatic ectal excipulum.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11557-024-02003-w.

Acknowledgements Various collectors are thanked for sending their collections, collection data or documentation: William R. Buck, Bernard Clesse, Bernd Fellmann, Alain Gardiennet, Marta González, Ingo Ibelshäuser, Edvin Johannesen, Csaba Németh, Zdeněk Palice, Pascal Ribollet, Mila Tanaskovic and others. Markéta Šandová is thanked for sending a list of Velenovský's new taxa with their hosts, and Viktorie Halasů for generating a list of bryophilous species from Velenovský's (1934) monograph and for drawing our attention to Höhnel's *Phialea epibrya* as a possible candidate for our genus *Luteodiscus*, also for revising the manuscript. P.R. Johnston is thanked for examining Krieger's specimen in herb. Sydow under the name *Phialea epibrya*. The curators of FH (Genevieve E. Tocci) and TUB (Uta Grünert) are thanked for organizing the loan of the holotype of *P. epibrya*, and Christiane Karasch-Wittmann for technical help to study the specimen at the University of Tübingen. The bryologists Jean-Pierre Duvivier, José Durfort, Pierre Fesolowicz, David Happe, Zbyněk Hradílek, Ulrich Teuber, and Henrik Weibull have helped in the identification of many of the host plants. Molecular work was done at four institutes: Crop Research Institute, Centre of the Region Haná for Biotechnological and Agricultural Research in Olomouc (M. Sochor); ALVALAB in Oviedo (http://www.alvalab.es/pedidos.html, P. Alvarado); Centre d'écologie fonctionnelle et évolutive in Montpellier (CEFE, https://www.cefe.cnrs.fr/fr/, J.-M. Bellanger) in frame of the Mycoseq project (Société mycologique de France, Paris); University of Bristol (G. Greiff).

Author contribution HOB wrote the text including descriptions and tables, arranged the plates, reexamined the holotype of *Phialea epibrya* and made the phylogenetic analyses with MEGA. LGK, ZS, JPP, ES, ER, FV, GB, MH, RI, GG, KK, and JCL performed the field work and prepared photographic documentation of their collections of *Luteodiscus*. ZS prepared Table 1 and the layout of Figs. 13 and 14. MS and GG obtained sequences of *Luteodiscus* and MS did the Bayesian analysis. PD examined various specimens in GZU, NY, and M. All authors contributed to the manuscript and approved the final version.

Funding The authors declare that they received no funds, grants, or other support, except for M. Sochor who was supported by the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0423, and G. Greiff who has received a small grant from the British Mycological Society for fungal sequencing.

Data availability The sequences generated in this study are available in the NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) under the accession numbers given in Tab. 1.

Declarations

Conflict of interest The authors declare no competing interests.

References

Baral HO (1987a) Der Apikalapparat der *Helotiales*. Eine lichtmikroskopische Studie über Arten mit Amyloidring. Z Mykol 53(1):119–136

Baral HO (1987b) Lugol's solution/IKI versus Melzer's reagent: hemiamyloidity, a universal feature of the ascus wall. Mycotaxon 29:399–450

Baral HO (1992) Vital versus herbarium taxonomy: morphological differences between living and dead cells of Ascomycetes, and their taxonomic implications. Mycotaxon 44:333–390

Baral HO (2009) Iodine reaction in Ascomycetes: why is Lugol's solution superior to Melzer's reagent? https://in-vivo-veritas.de/articles/iodine-reaction-in-ascomycetes-why-is-lugols-solution-superior-to-melzers-reagent/

Baral HO, De Sloover JR, Huhtinen S, Laukka T, Stenroos S (2009) An emendation of the genus *Hyaloscypha* to include *Fuscoscypha* (*Hyaloscyphaceae*, *Helotiales*, *Ascomycotina*). Karstenia 49:1–17. https://doi.org/10.29203/ka.2009.430

Baral HO, Haelewaters D (2015) *Rommelaarsia flavovirens* gen. et sp. nov. (*Helotiales*), a new discomycete on *Equisetum* with a peculiar asexual state. Ascomycete.org 7(6): 321–330. https://doi.org/10.25664/art-0155

Baral HO, Weber E, Marson G (2020) Monograph of *Orbiliomycetes* (*Ascomycota*) based on vital taxonomy. Part I + II. National Museum of Natural History Luxembourg, 1752 pp. https://www.mnhn.lu/pub/mono_orb

Baral HO, Kosonen T, Polhorský A, Stöckli E, Huhtinen S, Hansen K (2023a) *Venturioscypha nigropila* (*Hyphodiscaceae*, *Helotiales*) – a new genus and species from xeric *Pinus* bark. Karstenia 60(1–2):28–48. https://doi.org/10.29203/ka.2022.516

Baral HO, Sochorová Z, Sochor M (2023b) *Bryorutstroemia* (*Rutstroemiaceae*, *Helotiales*), a new genus to accommodate the neglected sclerotiniaceous bryoparasitic discomycete *Helotium fulvum*. Life 13(4):1041. https://doi.org/10.3390/life13041041

Bogale M, Orr MJ, O'Hara MJ, Untereiner WA (2010) Systematics of *Catenulifera* (anamorphic *Hyaloscyphaceae*) with an assessment of the phylogenetic position of *Phialophora hyalina*. Fungal Biol 114(5–6):396–409. https://doi.org/10.1016/j.funbio.2010.02.006

Boggess LM, McCain CM, Manzitto-Tripp EA, Pearson SM, Lendemer JC (2024) Disturbance and diversity: Lichen species richness decreases with increasing anthropogenic disturbance. Biol Conservation 293:110598. https://doi.org/10.1016/j.biocon.2024.110598

Bosanquet SDS (2007) *Epibryon plagiochilae* in south Wales: an overlooked British bryophilous fungus. Field Bryol 91:24–25

Brodo IM, Duran Sharnoff S, Sharnoff S (2001) Lichens of North America. Yale University Press, New Haven & London

Carpenter SE (1981) Monograph of *Crocicreas* (*Ascomycetes*, *Helotiales*, *Leotiaceae*). Mem N Y Bot Gard 33:1–290

Crouan PL, Crouan HM (1867) Florule du Finistère, 262 pp. F. Klincksieck, Paris.

Crous PW, Braun U, Schubert K, Groenewald JZ (2007) Delimiting *Cladosporium* from morphologically similar genera. Stud Mycol 58:33–56. https://doi.org/10.3114/sim.2007.58.02

Dennis RWG (1956) A revision of the British *Helotiaceae*. Mycol Papers 62:1–216

Dennis RWG (1964) Remarks on the genus *Hymenoscyphus* S.F. Gray, with observations on sundry species referred by Saccardo and others to the genera *Helotium*, *Pezizella* or *Phialea*. Persoonia 3(1):29–80.

Dennis RWG (1975) New or interesting British microfungi. III Kew Bull 30(2):345–365

Döbbeler P (1978) Moosbewohnende Ascomyceten I. Die pyrenocarpen, den Gametophyten besiedelnden Arten. Mitt Bot Staatssamml München 14:1–360

Döbbeler P (1985) Moosbewohnende Ascomyceten VII. Neufunde einiger Arten der Gattung *Epibryon*. Mitt Bot Staatssamml München 21:757–773

Döbbeler P (1986) *Belonioscyphella hypnorum* (*Helotiales*, *Ascomycetes*), ein nekrotropher Parasit auf Laubmoosen. Ber Bayer Bot Ges 57:153–158

Döbbeler P (2004) *Bryocentria* (*Hypocreales*), a new genus of bryophilous ascomycetes. Mycol Progr 3(3):247–256. https://doi.org/10.1007/s11557-006-0095-7

Döbbeler P (2010) New species and records of *Bryocentria* — a hypocrealean genus of bryophilous ascomycetes. Karstenia 50:11–23. https://doi.org/10.29203/ka.2010.437

Döbbeler P, Büschlen A, Eckstein J, Gross A (2021) *Belonium coroniforme* Rehm (*Helotiales*), a highly specialized muscicolous ascomycete on *Orthotrichaceae* and *Leucodon*. Sydowia 74:163–174. https://doi.org/10.12905/0380.sydowia74-2021-0163

Döbbeler P, Davison PG (2017) *Frullania* as a hotspot for hypocrealean ascomycetes: ten new species from Southeastern North America. Nova Hedwigia 106(1–2):209–256. https://doi.org/10.1127/nova_hedwigia/2017/0428

Döbbeler P, Davison PG (2021) Non-hypocrealean ascomycetes on *Frullania* mainly from Southeastern North America. Nova Hedwigia 113(3–4):361–401. https://doi.org/10.1127/nova_hedwigia/2021/0663

Döbbeler P, Hertel H (2013) Bryophilous ascomycetes everywhere: distribution maps of selected species on liverworts, mosses and *Polytrichaceae*. Herzogia 26(2):361–404. https://doi.org/10.13158/heia.26.2.2013.361

Eckstein J (2023) Bryoparasitic *Pezizales* (continuously updated). http://www.octospora.de/species_info.htm (accessed 24 July 2023)

Egertová Z, Hairaud M, Sochor M (2016) *Belonioscyphella hypnorum* (*Helotiales*), a rarely reported bryoparasitic ascomycete new for the Czech Republic. Ascomycete.org 8(3):91–95. https://doi.org/10.25664/art-0176

Ekanayaka AH, Hyde KD, Gentekaki E, McKenzie EHC, Zhao Q, Bulgakov TS, Camporesi E (2019) Preliminary classification of *Leotiomycetes*. Mycosphere 10(1):310–489. https://doi.org/10.5943/mycosphere/10/1/7

Ellis JB (1877) South Jersey fungi. Bull Torrey Bot Club 6(26):133–135. https://doi.org/10.2307/2477388

Ellis JB (1878) Rediscovery of a lost *Sphaeria*. Bull Torrey Bot Club 6(41):231–232. https://www.jstor.org/stable/2477107

Etayo J, Vězda A (1994) Two new species of *Gyalidea* from Europe. Lichenologist 26(4):333–335. https://doi.org/10.1006/lich.1994.1027

Fries EM (1822) Systema mycologicum. Vol. 2(1), 275 pp. Lund, Sweden.

Fuckel L (1870) [1869-1870]) Symbolae mycologicae. Beiträge zur Kenntnis der rheinischen Pilze. Jahrb Nassauischen Ver Naturk 23–24:1–346

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. Mol Ecol 2(2):113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

GBIF: https://www.gbif.org/search?q=phialea%20epibrya (accessed 20.V.2024)

Guatimosim E, Schwartsburd PB, Crous PW, Barreto RW (2016) Novel fungi from an ancient niche: lachnoid and chalara-like fungi on ferns. Mycol Progr 15:1239–1267. https://doi.org/10.1007/s11557-016-1232-6

Han JG, Hosoya T, Sung GH, Shin HD (2014) Phylogenetic reassessment of *Hyaloscyphaceae* sensu lato (*Helotiales*, *Leotiomycetes*) based on multigene analyses. Fungal Biol 118(2):150–167. https://doi.org/10.1016/j.funbio.2013.11.004

Helleman S (2020) Resurrection of Boudier's generic name *Urceolella* for *Excipula aspera* Moug. ex Fr. (*Helotiales*). Ascomycete.org 12(1):29—33. https://doi.org/10.25664/ART-0293

Hodgetts NG, Söderström L, Blockeel TL, Caspari S, Ignatov MS, Konstantinova NA, Lockhart N, Papp B, Schröck C, Sim-Sim M, Bell D, Bell NE, Blom HH, Bruggeman-Nannenga MA, Brugués M, Enroth J, Flatberg KI, Garilleti R, Hedenäs L, Holyoak DT, Hugonnot V, Kariyawasam IU, Köckinger H, Kučera J, Lara F, Porley RD (2020) An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. J Bryol 42:1–116. https://doi.org/10.1080/03736687.2019.1694329

Hosoya T, Han JG, Sung GH, Hirayama Y, Tanaka K, Hosaka K, Tanaka I, Shin HD (2011) Molecular phylogenetic assessment of the genus *Hyphodiscus* with description of *Hyphodiscus hyaloscyphoides* sp. nov. Mycol Progr 10:239–248. https://doi.org/10.1007/s11557-010-0693-2

Howland JW, Lendemer JC (2023) Molecular and phenotypic study put eastern North American *Cetrelia* in a global context of biogeography and phylogeny. Bryologist 126(4):461–472. https://doi.org/10.1639/0007-2745-126.4.461

Huhtinen S, Laukka T, Döbbeler P, Stenroos S (2010) Six novelties to European bryosymbiotic discomycetes. Nova Hedwigia 90(3–4):413–431. https://doi.org/10.1127/0029-5035/2010/0090-0413

Hujslová M, Kubátová A, Kostovčík M, Blanchette RA, de Beer ZW, Chudíčková M, Kolařík M (2014) Three new genera of fungi from extremely acidic soils. Mycol Progr 13(3):819–831. https://doi.org/10.1007/s11557-014-0965-3

Isaksson R (2023) *Belonium coroniforme* (*Helotiales*) - en ascomycet ny för Sverige. Sven Mykol Tidskr 44(3):29–31

Jaap O (1910) Verzeichnis der bei Triglitz in der Prignitz beobachteten Ascomyceten. Verh Bot Ver Prov Brandenburg 52:109–150

Karsten PA (1871) Mycologia fennica I, discomycetes. Bidrag till Kännedom Af Finlands Natur Och Folk 19:1–263

Kosonen T, Huhtinen S, Hansen K (2021) Taxonomy and systematics of *Hyaloscyphaceae* and *Arachnopezizaceae*. Persoonia 46:26–62. https://doi.org/10.3767/persoonia.2021.46.02

Koukol O (2011) New species of *Chalara* occupying coniferous needles. Fungal Diver 49:75–91. https://doi.org/10.1007/s13225-011-0092-2

Lawrey JD, Diederich P (2003) Lichenicolous fungi: interactions, evolution, and biodiversity. Bryologist 106(1):80–120. https://doi.org/10.1639/0007-2745(2003)106[0080:LFIEAB]2.0.CO,2

Lendemer JC (2020) *Leprocaulon beechingii* (*Leprocaulaceae*), a new species from the southern Appalachian Mountains of eastern North America. Bryologist 123(1):1–10. https://doi.org/10.1639/0007-2745-123.1.001

Lendemer JC, Tripp EA (2015) *Lecanora anakeestiicola* (*Lecanorales*): an unusual new fruticose species from Great Smoky Mountains National Park in eastern North America. Bryologist 118(1):1–10. https://doi.org/10.1639/0007-2745-118.1.001

Marsh T, Döbbeler P, Huhtinen S, Stenroos S (2010) Ascomycetes and anamorphic fungi growing on *Plagiochila* (*Hepaticae*) in Finland. Karstenia 50(2):59–72. https://doi.org/10.29203/ka.2010.442

Midgley DJ, Sutcliffe B, Greenfield P, Tran-Dinh N (2018) *Gamarada debralockiae* gen. nov. sp. nov.—the genome of the most widespread Australian ericoid mycorrhizal fungus. Mycorrhiza 28(4):379–389. https://doi.org/10.1007/s00572-018-0835-y

Nakamura N, Hosoya T, Tanaka C, Takeuchi-Kaneko Y (2018) Detection of a root-associated group of *Hyaloscyphaceae* (*Helotiales*) species that commonly colonizes *Fagaceae* roots and description of three new species in genus *Glutinomyces*. Mycoscience 59(5):397–408. https://doi.org/10.1016/j.myc.2018.02.010

Németh C, Eckstein J, Sochor M (2022) Disentangling the taxonomy of *Octospora meslinii* (*Pezizales*), a bryophilous ascomycete on *Grimmia pulvinata*. Czech Mycol 74(1):1–24. https://doi.org/10.33585/cmy.74101

Peck CH (1878) Report of the Botanist. Annu Rep N Y State Mus Nat Hist 30:23–78

Quijada L, Huhtinen S, Hairaud M, Beltrán-Tejera E (2014) Is *Psilocistella quercina* (Velen.) Svrček a good taxon? Ascomycete.org 6(5):143−146. https://doi.org/10.25664/art-0117

Quijada L, Baral HO, Johnston PR, Pärtel K, Mitchell JK, Hosoya T, Madrid H, Kosonen T, Helleman S, Rubio E, Stöckli E, Huhtinen S, Pfister DH (2022) A review of *Hyphodiscaceae*. Stud Mycol 103(1):59–85. https://doi.org/10.3114/sim.2022.103.03

Rabenhorst L (1844) Deutschlands Kryptogamen-Flora, vol. 1: Pilze. Leipzig: Kummer.

Racovitza A (1942a) Trois champignons muscicoles. Bull Sect Sci Acad Roumaine 23: 572−577, pl. 1.

Racovitza A (1942b) Sur une intéressante localisation de cristaux d'oxalate de calcium chez un discomycète. Bull Sect Sci Acad Roumaine 23:570−571, pl. 1.

Racovitza A. (1959) Étude systématique et biologique des champignons bryophiles. Mémoires Mus Natl Hist Nat. Série B, Botanique 10:1–288, pls. 1–84.

Rehm H (1891, 1892, 1894, 1896 [1887–1896]) Ascomyceten: Hysteriaceen und Discomyceten. In: L. Rabenhorst, Kryptogamenflora von Deutschland, Österreich und der Schweiz, Leipzig.

Rehm H (1899) Ascomycetes exs. fasc. 26. Hedwigia, Beiblatt 38(1):242–246.

Rehner SA, Buckley E (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1-α sequences: Evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia 97:84–98

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61(3):539–542. https://doi.org/10.1093/sysbio/sys029

Rossman AY, Samuels GJ, Rogerson CT, Lowen R (1999) Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*, *Ascomycetes*). Stud Mycol 42:1–248

Saccardo PA (1889) Sylloge Fungorum omnium hucusque cognitorum 8. Patavia

Saccardo PA, Trotter A (1913) Sylloge fungorum omnium hucusque cognitorum 22. Patavia

Sochorová Z, Matočec N, Kušan I, Janošík L, Eckstein J, Vega M, Mešic A, Sedlářová M, Martínez-Gil R, Sochor M (2020) Amended description of the rarely reported bryophilous ascomycete *Octospora svrcekii* (*Pyronemataceae*) with notes on the phylogeny of the section *Wrightoideae*. Phytotaxa 475(1):1–17. https://doi.org/10.11646/phytotaxa.475.1.1

Sogonov MV, Schroers HJ, Gams W, Dijksterhuis J, Summerbell RC (2005) The hyphomycete *Teberdinia hygrophila* gen. nov., sp. nov. and related anamorphs of *Pseudeurotium* species. Mycologia 97(3):695–709. 11–23. https://doi.org/10.3852/mycologia.97.3.695

Spooner BM (1984) Ascomycetes. In: Kirk PM, Spooner BM. An account of the fungi of Arran, Gigha and Kintyre. Kew Bull 38(4):503–597. https://doi.org/10.2307/4108573

Sydow H (1923) Sydow, Mycotheca Germanica Fasc. XXXVII−XLI (no. 1801−2050). Ann Myc 21(3−4):165−181.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. Mol Biol Evol 30(12): 2725–2729. https://doi.org/10.1093/molbev/mst197

Tedersoo L, Pärtel K, Jairus T, Gates G, Põldmaa K, Tamm H (2009) Ascomycetes associated with ectomycorrhizas: molecular diversity and ecology with particular reference to the *Helotiales*. Environ Microbiol 11(12):3166–3178. https://doi.org/10.1111/j.1462-2920.2009.02020.x

Triebel D, Baral HO (1996) Notes on the ascus types in *Crocicreas* (*Leotiales*, *Ascomycetes*) with a characterization of selected taxa. Sendtnera 3:199–218

Tripp EA, Lendemer JC (2019) Highlights from 10+ years of lichenological research in Great Smoky Mountains National Park: celebrating the United States National Park Service Centennial. Syst Bot 44:943–980. https://doi.org/10.1600/036364419X15710776741332

Tripp EA, Lendemer JC (2020) Field guide to the lichens of Great Smoky Mountains National Park. University of Tennessee Press, Knoxville

Untereiner WA, Naveau FA, Bachewich J, Angus A (2006) Evolutionary relationships of *Hyphodiscus hymeniophilus* (anamorph *Catenulifera rhodogena*) inferred from β-tubulin and nuclear ribosomal DNA sequences. Can J Bot 84(2):243–253. https://doi.org/10.1139/b05-165

van Haluwyn C (1990) "1989") Découverte en France du *Hymenoscyphus epibryus* (von Höhnel) comb. nov. (*Ascomycetes - Helotiaceae*). Bull Semestr Soc Mycol Nord 45–46:79–84

Velenovský J (1934) Monographia Discomycetum Bohemiae, Pragae

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172(8):4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

von Höhnel F (undated) Herbar Index. 448 pp. Wien. https://www.biodiversitylibrary.org/item/241475#page/506/mode/1up

von Höhnel F (1902) Fragmente zur Mykologie (1. Mittheilung Nr. 1–63). Sitzungsber K Akad Wiss Wien, Math-Nat Kl. Abt I 111:987–1056

von Höhnel F (1907) Fragmente zur Mykologie (III. Mitteilung Nr. 92–155). Sitzungsber K Akad Wiss Wien, Math.-Nat. Kl. Abt I 116:83–162

von Höhnel F (1918) Fragmente zur Mykologie (XII. Mitteilung, Nr. 1092–1153). Sitzungsber K Akad Wiss Wien, Math.-Nat. Kl. Abt I 127:549–634

Vu D, Groenewald M, de Vries M, Gehrmann T, Stielow B, Eberhardt U, Al-Hatmi A, Groenewald JZ, Cardinali G, Houbraken J, Boekhout T, Crous PW, Robert V, Verkley GJM (2019) Large-scale generation and analysis of filamentous fungal

DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. Stud Mycol 92:135–154. https://doi.org/10.1016/j.simyco.2018.05.001

Wallroth KFW (1833) Flora Cryptogamica Germanica 2. Norimbergae.

Wang Z, Binder M, Hibbett DS (2005) Life history and systematics of the aquatic discomycete *Mitrula* (*Helotiales*, *Ascomycota*) based on cultural, morphological, and molecular studies. Am J Bot 92(9):1565–1574. https://doi.org/10.3732/ajb.92.9.1565

White TJ, Bruns T, Lee SJWT, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: M.A. Innis, D.H. Gelfand, J.J. Sninsky & T.J. White (eds.), PCR protocols: 315–322. Academic Press, San Diego, USA.

White WL (1942) Studies in the genus *Helotium*. I. A review of the species described by Peck. Mycologia 34(2):154–179. https://doi.org/10.1080/00275514.1942.12020886

Wieschollek D, Helleman S, Baral HO, Richter T (2011) *Roseodiscus formosus* spec. nov. – ein bryophiler Pionier mit falschem Namen. Z Mykol 77(2):161–174.

Žifčáková L, Dobiášová P, Kolářová Z, Koukol O, Baldrian P (2011) Enzyme activities of fungi associated with *Picea abies* needles. Fungal Ecol 4(6):427–436. https://doi.org/10.1016/j.funeco.2011.04.002

Authors and Affiliations

Hans-Otto Baral[1] · Lothar G. Krieglsteiner[2] · Zuzana Sochorová[3] · Peter Döbbeler[4] · Jean-Paul Priou[5] · Elisabeth Stöckli[6] · Enrique Rubio[7] · François Valade[8] · Günter Bauer[9] · Michel Hairaud[10] · Robin Isaksson[11] · George Greiff[12] · Katharina Krieglsteiner[2] · Michal Sochor[13] · James C. Lendemer[14]

✉ Hans-Otto Baral
zotto@arcor.de

[1] Blaihofstr. 42, 72074 Tübingen, Germany

[2] Brunnenweg 32, 73565 Spraitbach, Germany

[3] Jungmannova 911/9, 77900 Olomouc, Czech Republic

[4] Botanische Staatssammlung München, Menzinger Str. 67, 80638 Munich, Germany

[5] 7 Rue de Picardie, 56200 La Gacilly, France

[6] Haut du Village 4, CH-2345 La Chaux-Des-Breuleux, Switzerland

[7] José Cueto, 3 5ºB, 33401 Avilés, Spain

[8] Résidence du Boqueteau – Les Melezes, 91240 Saint-Michel-Sur-Orge, France

[9] Stiftsbogen 29, 81375 Munich, Germany

[10] 2 Impasse Des Marronniers, Poivendre, F 79360 Marigny, France

[11] Parallellgatan 1D, SWE-57633 Sävsjö, Sweden

[12] School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

[13] Centre of the Region Haná for Biotechnological and Agricultural Research, Crop Research Institute, Šlechtitelů 29, 77900 Olomouc, Czech Republic

[14] Research & Collections, The New York State Museum, CEC 3140222 Madison Ave, Albany, NY 12230, USA