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Finding the needle in the haystack: a revision of *Crittendenia*, a surprisingly diverse lichenicolous genus of *Agaricostilbomycetes*, *Pucciniomycotina*

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ABSTRACT. While most lichenicolous fungi belong to the Ascomycota, c. 5% of them are members of the Basidiomycota. Among these, the poorly known genus *Crittendenia* in the Pucciniomycotina has recently been described for lichenicolous fungi with minuscule needle-like synnematos basidiomata. Although only two species were hitherto known, the wide observed host-spectrum suggested a larger number of mainly host-specific species. A classical revision using morphological characters alone proved to be virtually impossible, because of the large variability of the material from each host genus, and the scant morphological differences between hypothetically distinct species from different hosts. We studied over sixty specimens and made a large number of measurements of the available morphological characters. We additionally generated 18 ITS and 21 nuLSU rDNA sequences and conducted maximum likelihood and Bayesian analyses. We also performed one species delimitation analysis (bPTP-ML). By combining sometimes subtle morphological differences, host choice and phylogenetic results, we were able to accept eighteen morphologically and/or genetically distinct species, all confined to a single host genus or to several closely related host genera. Two further putative species are left unnamed, as richer material is needed and molecular data are missing. Sixteen new species are described: *Crittendenia absistentis* (on *Bacidia absistens*), *C. bacidinae* (on *Bacidina apiahica*), *C. bryostigmatis* (on *Bryostigma muscigenum*), *C. byssolomatis* (on *Byssoloma maderense*), *C. crassitunicata* (on *Melanohalea ushuaiensis*), *C. heterodermiae* (on *Heterodermia comosa*), *C. hypotrachynae* (on *Hypotrachyna*), *C. kakouettae* (on '*Byssoloma kakouettae*'), *C. lecanorae* (on *Lecanora*), *C. lecidellae* (on *Lecidella elaeochroma*), *C. lopadii* (on *Lopadium disciforme*), *C. parvispora* (on *Bacidia*), *C. physciiphila* (on *Phaeophyscia*, *Physcia* and *Physciella*), *C. physconiae* (on *Physconia distorta*), *C. stictae* (on *Sticta fuliginosa*) and *C. teloschistis* (on *Teloschistes*). Further, a ML analysis of the Agaricostilbomycetes using ITS and nuLSU sequences suggested that *Crittendenia* cannot be included in any known family, and the new family Crittendeniaceae is therefore described for the genus.

KEYWORDS. Basidiomycetes, *Chionosphaera*, Crittendeniaceae, heterobasidiomycetes, lichenicolous fungi, phylogeny, taxonomy.



Lichenicolous fungi are a very successful biological group specialized in having symbiotic or parasitic

relationships with lichenized fungi. Diederich et al. (2018) presented a catalogue of the 2000 species known at that time, and new species are regularly being added. While most of them belong to the ascomycetes, c. 100 basidiomycetous species are

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known, most belonging to the Tremellomycetes. Just two genera with four species were reported from the Pucciniomycotina, one of them being the genus *Chionosphaera* D.E.Cox, of which the lichenicolous species have recently been transferred to the new genus *Crittendenia* Diederich et al., based on molecular phylogenetic evidence (Millanes et al. 2021).

From a historical point of view, Cox (1976) was the first to study “a new homobasidiomycete with anomalous basidia,” with tiny, synnemata-like basidiocarps, aseptate 7-spored apobasidia lacking basal clamps, developing over dead branches of trees, that he described as the new genus and species *Chionosphaera apobasidialis* Cox. Oberwinkler & Bandoni (1982) later introduced the new family Chionosphaeraceae Oberw. & Bandoni that also included the genus *Stilbum* Tode ex Mérat, within the new order Atractiellales Oberw. & Bandoni, described for “heterobasidiomycetous species with gasteroid meiosporangia of the auricularioid or holobasidiate types.” A first lichenicolous species, *Chionosphaera lichenicola* Alstrup, Sutton & Tønsberg, collected by T. Tønsberg on corticolous *Micarea prasina*, was described from Norway (Alstrup 1993). In his revision of lichenicolous heterobasidiomycetes, Diederich (1996) studied three similar specimens collected by J. Etayo on the thallus of *Lecidella elaeochroma*, *Parmelina quercina* and *Teloschistes flavicans*; despite some morphological variability in this material, he did not find any convincing arguments to distinguish these specimens as distinct species and called them provisionally *Chionosphaera* cf. *apobasidialis*, awaiting the discovery of more and richer specimens on these and other host lichens. Roberts (1997) studied a rich Scottish specimen on *Melanelixia glabrata*, differing from *C. apobasidialis* and *C. lichenicola* by the 4-spored basidia with basal clamps, that he described as the new *Chionosphaera coppinsii* P.Roberts; a further Scottish specimen on *Lecidella elaeochroma* studied by him had shorter, 4–6-spored basidia and was provisionally included in *C. coppinsii*. Kirschner et al. (2001) described the new *Chionosphaera cuniculicola* R.Kirschner, D.Begerow & Oberw. growing in galleries of bark beetles on conifers in Central Europe, presented a first phylogenetic analysis including *C. apobasidialis* and *C. cuniculicola*, combined *Fibulostilbum phylai-cicola* Seifert & Bandoni in *Chionosphaera*, restud-

ied the type of *C. lichenicola* and found that basidia possess basal clamps, and concluded that Roberts’ specimen on *Lecidella* belongs to *C. lichenicola*. Kirschner & Chen (2008) further combined the poorly known *Stilbum erythrinae* Hansf. in *Chionosphaera*.

Millanes et al. (2021) obtained ITS and nuLSU sequences from *Chionosphaera coppinsii* and seven unidentified lichenicolous *Chionosphaera* specimens from diverse hosts. Their phylogenetic results suggested that all lichenicolous species formed a clade that was only distantly related to the type of *Chionosphaera*, and they consequently described the new genus *Crittendenia* for the lichenicolous taxa. They also obtained *Crittendenia coppinsii* sequences from host thalli devoid of basidiomata, but growing together with infected thalli, showing that the fungus may be present asymptotically within the host thallus.

Most *Crittendenia* species are extraordinarily rare or overlooked, and many lichenologists interested in lichenicolous fungi had never collected them. Further, basidiomata in many species are so small that they are difficult to detect, even under a binocular microscope with a high magnification. On some well-known and common hosts, their rarity is striking. For example, from *Physcia adscendens*, with almost 44,000 results in the GBIF database (www.gbif.org; 23 Nov. 2021), only two infected specimens are known, collected by the same person (P. Pinault) in two neighboring localities. Hunting in the field for *Crittendenia* species is therefore much like searching for the proverbial needle in the haystack, the slender, synnemata-like basidiomata with an enlarged capitulum strongly resembling a pinhead needle.

The aim of this paper was to prepare a taxonomic revision of the species of *Crittendenia*, using molecular phylogenies and morphological characters. Preliminary studies have shown that *Crittendenia* specimens from the same host may be morphologically particularly variable. On the other hand, specimens from different host species or genera may be extremely similar, the small differences observed possibly just resulting from the limited sampling. To revise these species with classical morphological methods therefore rapidly proved to be virtually impossible. By combining molecular phylogenetic results, morphological data combined with statistical analyses, and the host

choice, we have succeeded in proposing a taxonomic treatment and a key that should allow the identification of most specimens, even when sequences are not available, and at the same time allow collectors to recognize which specimens are likely to represent undescribed species, and those for which DNA data should be obtained.

MATERIAL AND METHODS

Morphological studies. The material examined is deposited in BG, BR, C, E, G, K (incl. former IMI), LI, LPB, MAF, NY, PO, PRA, TRH, UBC and WIS, and in the private collections of W. von Brackel, M. Eichler & R. Cezanne, J. Etayo, P. van den Boom and E. Zimmermann. Dry herbarium specimens were examined and measured under a binocular microscope Leica MZ 7.5. Macroscopic photographs were done using a Canon 6D camera with Nikon BD Plan 10× or Nikon BD Plan 60× ELWD microscope objectives, StackShot (Cognisys) and Helicon Focus (HeliconSoft) for increasing the depth of field. For microscopical examination, squash preparations and rarely vertical sections of all specimens were examined in 5% KOH + phloxine B, of some specimens also in water, 5% KOH, ammoniacal Congo red and Melzer's reagent. Microscopic photographs were prepared using a Leica DMLB microscope with DIC optics and a Leica EC3 camera, and Helicon Focus for increasing the depth of field. Measurements of microscopical characters were done in 5% KOH + phloxine B.

Measurements from a specimen are given as $(min)x-sd - x+sd(max)$, where x represents the mean, sd the standard deviation, min the smallest value and max the largest value observed, followed by the number of measurements n . This represents the 69% probability interval, thus excluding the smallest and the largest 15.5%. Measurements from a species are given as $(min)[min x-sd]x-sd - x+sd[max x+sd](max)$, where 'min $x-sd$ ' represents the smallest ' $x-sd$ ' value obtained within the specimens examined and 'max $x+sd$ ' the largest ' $x+sd$ ' value obtained within these specimens. For example, if the basidial length from three specimens is (27)30–60(68) μm , (23)40–50(62) μm and (34)40–70(91) μm , and that of the species (including the three specimens) is (23)35–60(91) μm , then the resulting measurements will be given as (23)[30]35–60[70](91) μm . Values between square

brackets will be omitted when a species is known from a single specimen. In the identification key, extreme values between parentheses are omitted. The following abbreviations are used: StH (stipe height, including capitulum), StD (stipe diameter), CaD (capitulum diameter), these three measured under a binocular microscope, BaL (basidial length), BaD (basidial diameter, at the middle of the basidium), BaApD (broadest basidial diameter, close to the apex), SpL (spore length) and SpB (spore breadth).

DNA extraction, amplification and sequencing.

DNA was extracted from either recently collected or dried herbarium material (Table 1). From each specimen, between three and ten fruiting bodies were carefully separated from the lichen thallus with a scalpel and tweezers to minimize the lichen material in the DNA extraction. Total DNA was extracted using the Qiagen DNeasy Plant Mini Kit (Qiagen, Venlo, the Netherlands), according to the manufacturer's instructions. We amplified two molecular markers: the internal transcribed spacer (ITS) and the large subunit (nuLSU) of the nuclear ribosomal DNA.

We used the specific primers Cc-F1, Cc-R1 and ChioLSU 3-3, designed to selectively amplify the DNA of *Crittendenia*, avoiding that of other basidiomycetes and of the lichenized host (Millanes et al. 2021). These, in combination with general fungal primers, viz. ITS1F (Gardes & Bruns 1993), ITS4 (White et al. 1990), LR0R (Rehner & Samuels 1994), LR3 (Vilgalys & Hester 1990), were combined to amplify the ITS and a fragment of c. 600 bp of the nuLSU in the nuclear ribosomal DNA. Amplification reactions were performed using Illustra™ Hot Start PCR beads (GE Healthcare Life Sciences, Pittsburg, California, U.S.A.), according to the manufacturer's instructions, for a 25 μL final volume. PCR amplifications followed protocols described in Millanes et al. (2021). Nested PCR was used when samples did not amplify at a first instance—or when very faint bands were obtained—by direct PCR. For the nested protocol we ran an initial PCR using the general primer combinations ITS1F/LR3. One mL of the amplicons obtained in that first PCR was used as DNA template for the second PCR. Settings for the second (nested) PCR are the same as the ones previously described in Millanes et al. (2021) for direct PCR. We often obtained multiple amplicons—both using direct or

Table 1. Sequences of taxa in the Agaricostilbomycetes included in this study, either newly produced (all from *Crittendenia*, in bold font) or retrieved from GenBank. Host, specimen data and DNA extraction code are given for *Crittendenia* samples. A (T) next to the species name indicates a type specimen. A hash symbol indicates a sequence of *Crittendenia coppinsii* obtained from an asymptomatic lichen specimen. An asterisk next to an nuLSU GenBank accession number indicates a short sequence obtained using the reverse primer ChioLSU3-3.

Species name	Host	Specimen data	ITS	nuLSU
<i>Ballistosporomyces sasicola</i>			AF444548	AF177412
<i>Ballistosporomyces taupoensis</i>			AF444592	AF177413
<i>Bensingtonia ciliata</i>			AF444563	AF189887
<i>Bensingtonia naganoensis</i>			AF444558	AF189893
<i>Chionosphaera apobasidialis</i>			AF444599	AF177407
<i>Chionosphaera cuciculicola</i>			KJ778640	KJ708465
<i>Crittendenia absistentis</i> (T)	<i>Bacidia absistens</i>	U.K., Scotland, <i>Coppins 25367</i> (E 01002244), DNA: DI034	OM521987	OM521967
<i>Crittendenia absistentis</i>	<i>Bacidia absistens</i>	U.K., 2018, <i>Palice 25624</i> (PRA), DNA: DI035	OM521988	OM521968
<i>Crittendenia bacidinae</i> (T)	<i>Bacidina apiahica</i>	Azores, 2017, <i>van den Boom 56783</i> (BR), DNA: AM1073	MT520701	MT482333
<i>Crittendenia byssolomatis</i> (T)	<i>Byssoloma maderense</i>	Azores, 2021, <i>van den Boom 60700</i> (BR), DNA: DI069	OM521989	OM521969 *
<i>Crittendenia coppinsii</i> (T)	<i>Melanelixia glabrata</i>	U.K., Scotland, <i>Coppins 16400</i> (K(M)-39188), DNA: AM267	MT520689	MT482329
<i>Crittendenia coppinsii</i>	<i>Melanelixia glabrata</i>	Norway, 2017, <i>Westberg & Olsson</i> (UPS), DNA: AM1045	MT520690	—
<i>Crittendenia coppinsii</i>	<i>Melanelixia subaurifera</i>	France, 2020, <i>Pinault</i> (BR), DNA: DI007	OM521990	OM521970
<i>Crittendenia coppinsii</i>	<i>Melanohalea exasperatula</i>	Sweden, <i>Westberg, Ekman & von Hirschheydt</i> (UPS F-796396), DNA: SAR380	MT520691	MT482330
<i>Crittendenia coppinsii</i>	<i>Melanohalea exasperatula</i>	Belgium, 2016, <i>van den Boom 54983</i> (herb. van den Boom), DNA: AM696	MT520692	MT482331
<i>Crittendenia coppinsii</i>	<i>Melanohalea exasperatula</i>	Sweden, <i>Westberg</i> (S, UPS F-805352), DNA: AM850	MT520693	—
<i>Crittendenia coppinsii</i>	<i>Melanohalea exasperatula</i>	Sweden, <i>Westberg</i> (S, UPS F-805353), DNA: AM852	MT520694	—
<i>Crittendenia coppinsii</i> #	<i>Melanohalea exasperatula</i>	Sweden, <i>Odelvik 11471</i> (S F-206720), DNA: AM819	MT520696	—
<i>Crittendenia heterodermiae</i> (T)	<i>Heterodermia comosa</i>	Bolivia, 2015, <i>Etayo 32711</i> (LPB), DNA: DI041	OM521991	OM521971
<i>Crittendenia hypotrachynae</i> (T)	<i>Hypotrachyna endochlora</i>	Azores, 2017, <i>Etayo 31093</i> (PO), DNA: AM1130	MT520702	MT482334
<i>Crittendenia hypotrachynae</i>	<i>Hypotrachyna</i> sp.	Azores, 2017, <i>Etayo 30945</i> (herb. Etayo), DNA: AM1131	MT520703	MT482335
<i>Crittendenia kakouettae</i>	<i>Byssoloma kakouettae</i>	Canary Islands, 2007, <i>Diederich 16490</i> (BR), DNA: AM113	MT520700	MT482332
<i>Crittendenia kakouettae</i>	<i>Byssoloma kakouettae</i>	Azores, 2019, <i>van den Boom 58880</i> (herb. van den Boom), DNA: DI021	OM521992	OM521972
<i>Crittendenia kakouettae</i> (T)	<i>Byssoloma kakouettae</i>	Azores, 2019, <i>van den Boom 58956</i> (BR), DNA: DI022	OM521993	OM521973
<i>Crittendenia lecidellae</i>	<i>Lecidella elaeochroma</i>	Spain, 2011, <i>Zamora</i> (G), DNA: AM1132	MT520704	MT482336
<i>Crittendenia lecidellae</i> (T)	<i>Lecidella elaeochroma</i>	Canada, 2009, <i>Björk 17999</i> (UBC), DNA: AM530	MT520705	MT482337
<i>Crittendenia lichenicola</i>	<i>Micarea micrococca</i>	U.K., 2005, <i>Coppins 21517</i> (E), DNA: DI036	OM521994	OM521974
<i>Crittendenia lichenicola</i> (T)	<i>Micarea prasina</i>	Norway, <i>Tønsberg 12000</i> (BG L-73887), DNA: DI025	—	OM521985
<i>Crittendenia parvispora</i> (T)	<i>Bacidia laurocerasi</i>	France, 2021, <i>Quelen</i> (BR), DNA: DI047	OM521995	OM521975 *
<i>Crittendenia parvispora</i>	<i>Bacidia polychroa</i>	Cape Verde, 2006, <i>van den Boom 36943</i> (herb. van den Boom), DNA: DI008	OM521996	OM521976
<i>Crittendenia physciiphila</i>	<i>Phaeophyscia orbicularis</i>	France, 2020, <i>Pinault</i> (BR), DNA: DI009	OM521997	OM521977
<i>Crittendenia physciiphila</i>	<i>Phaeophyscia orbicularis</i>	Spain, 2009, <i>Etayo 25106</i> (herb. Etayo), DNA: DI017	OM521998	OM521978
<i>Crittendenia physciiphila</i>	<i>Phaeophyscia rubropulchra</i>	U.S.A., 1995, <i>Buck 27763</i> (NY), DNA: DI010	OM521999	OM521979 *
<i>Crittendenia physciiphila</i> (T)	<i>Physcia adscendens</i>	France, 2020, <i>Pinault</i> (BR), DNA: DI011	—	OM521986
<i>Crittendenia physciiphila</i>	<i>Physcia adscendens</i>	France, 2020, <i>Pinault</i> (BR), DNA; DI012	OM522000	OM521980
<i>Crittendenia physciiphila</i>	<i>Physciella chloantha</i>	Spain, 2001, <i>Etayo 18287</i> (herb. Etayo), DNA: DI023	OM522001	OM521981
<i>Crittendenia physcomiae</i> (T)	<i>Physconia distorta</i>	Spain, 2010, <i>Zamora</i> (G), DNA: AM1133	MT520706	MT482338
<i>Crittendenia stictae</i> (T)	<i>Sticta fuliginosa</i> s. lat.	Bolivia, 2011, <i>Etayo 26611 et al.</i> (LPB), DNA: DI003	OM522002	OM521982
<i>Crittendenia teloschistis</i>	<i>Teloschistes exilis</i>	Bolivia, 2015, <i>Etayo 32788</i> (LPB), DNA: DI024	OM522003	OM521983
<i>Crittendenia teloschistis</i> (T)	<i>Teloschistes flavicans</i>	Canary Islands, 2012, <i>Koller</i> (BR [ex herb. Berger 26836]), DNA: DI042	OM522004	OM521984
<i>Cystobasidiopsis lactophilus</i>			AF444545	AF177411
<i>Cystobasidiopsis lophateri</i>			AB126046	AB124561
<i>Jianyunia sakaguchii</i>			AF444626	AF363646

Table 1. Continued.

Species name	Host	Specimen data	ITS	nuLSU
<i>Kondoa miscanthi</i>			AF444516	AF189891
<i>Kondoa subrosea</i>			AF444565	AF189895
<i>Kurtmanomyces nectairei</i>			AF444494	AF177409
<i>Kurtmanomyces tardus</i>			AF444566	AF177410
<i>Mycogloea nipponica</i>			KJ778629	KJ708456
<i>Pseudobensingtonia ingoldii</i>			AF444519	AF189888
<i>Pseudobensingtonia musae</i>			AF444569	AF189892
<i>Ruinenia rubra</i>			AF444550	AF189992
<i>Ruinenia clavata</i>			AY364839	AY364839
<i>Sterigmatomyces elviae</i>			AF444551	AF177415
<i>Sterigmatomyces halophilus</i>			AF444556	AF177416
<i>Phyllozoma dimenmae</i> (outgroup)			AB038046	AB644404

nested PCR—and in those cases bands of the appropriate size were selected, and gel extracted using the Qiagen MinElute Gel Extraction kit. Gel extraction was tested in a new gel before sequencing. Single PCR products not gel extracted were purified with Exo-sap-ITTM (USB Corporation, Cleveland, Ohio, U.S.A.). The purified samples were sequenced by Macrogen Inc. (in Amsterdam, the Netherlands, or in Madrid, Spain).

Multiple sequence alignment, and phylogenetic and species delimitation analyses. Newly produced sequences were assembled and edited using Geneious Prime[®] 2021.0.3. (<https://www.geneious.com>). We produced two data matrices for subsequent phylogenetic analyses, using two loci (ITS and nuLSU). The first (dataset 1) included all sequenced *Crittendenia* specimens, and a sequence of *Ruinenia rubra* (Ruineniaceae, Agaricostilbales) was used as outgroup, based on previous phylogenies (Millanes et al. 2021). The second (dataset 2) included only one *Crittendenia* representative per species, representatives of the five accepted families in the Agaricostilbomycetes (i.e., Agaricostilbaceae, Chionosphaeraceae, Jianyuniaceae, Kondoaceae and Ruineniaceae: Li et al. 2020; Wang et al. 2016). *Phyllozoma dimmenae* was used as outgroup, based on Wang et al. (2016). We assembled this second dataset to 1) further test the monophyly of *Crittendenia*—including all newly described species in an expanded sampling in the Agaricostilbomycetes, and 2) to test the possible family assignment of the genus. In dataset 2, large parts of the ITS were unable to align and were therefore excluded from the matrix. Species names, voucher information,

and GenBank Accession numbers are given in **Table 1**.

For phylogenetic analyses, sequences were aligned using MAFFT version 7 (Katoh et al. 2019) with the Q-INS-i algorithm. The alignments were trimmed to exclude ambiguously aligned regions using GBlocks (Castresana 2000), following the relaxed conditions described by Talavera & Castresana (2007), and manually checked, before and after trimming, using Mesquite 3.7 (Maddison & Maddison 2021). We considered four independent partitions, ITS1, 5.8S, ITS2 and nuLSU, in analyses. Each partition was analysed individually by maximum likelihood ultrafast bootstrap in IQTree (Hoang et al. 2018) to assess for conflicts. Phylogenetic relationships were reconstructed using maximum likelihood (ML) and Bayesian approaches. Maximum likelihood analyses were carried out in IQTree (Nguyen et al. 2015). Model selection for each partition was achieved using ModelFinder in IQTree (Kalyaanamoorthy et al. 2017), with the corrected Akaike information criterion (AICc). For dataset 1, the TIM3 + F + Γ 4 was selected for the ITS1, the KP2 + I for the 5.8S, the GTR + F + Γ 4 for the ITS2, and the TN+F+I + G for the nuclear LSU. For dataset 2, the GTR + F + I + Γ 4 was selected for the ITS1, the KP2 + Γ for the 5.8S, the TVMe + Γ 4 for the ITS2, and the TIM+F+I + Γ 4 for the nuclear LSU. We assessed node support by standard bootstrap using 1000 bootstrap pseudoreplicates. Bayesian analyses were performed by Markov chain Monte Carlo (MCMC) sampling as implemented in the software MrBayes 3.2.7a (Ronquist et al. 2012) on the CIPRES Web Portal (Miller et al. 2015). As not all models tested by ModelFinder in IQTree can

be directly implemented in MrBayes, for the Bayesian analyses we selected among a subsample of substitution models using the corrected Akaike information criterion (AICc) as implemented in jModelTest 2 (Darriba et al. 2012), allowing only 3 substitution schemes, using full likelihood optimization and four discrete gamma categories. For dataset 1, the GTR + Γ was selected for the ITS1, the JC for the 5.8S, the GTR + Γ for the ITS2, and the HKY + Γ for the nuclear LSU rDNA. For dataset 2, the JC + Γ model was selected for the ITS1, the JC for the 5.8S, the K80 + Γ for the ITS2, and the GTR + I + Γ for the nuclear LSU rDNA. The combined analyses treated the different regions as separate partitions with topology linked across partitions but separate model parameter values and proportional rates across partitions. For each combined dataset, two parallel runs were performed, each with four chains, three of which were incrementally heated with a temperature of 0.15. The analyses were diagnosed for convergence every 100,000 generations and were set to halt automatically when the average standard deviation of splits across runs in the last half of the analysis descended below 0.01. Every 100th tree was saved. The first 50% of each run was discarded as burn-in. The alignments for this study have been submitted to TreeBASE with accession numbers 29494 and 29495.

To test our species delimitation hypotheses, we used the Poisson tree process model (PTP) (Zhang et al. 2013), which considers the number of substitutions between sequences. PTP detects the transition points between inter- and intraspecific branching events, considering that the number of substitutions between species is significantly higher than that within species. PTP neither requires an ultrametric tree nor a sequence similarity threshold as input. The best ML tree from the phylogenetic IQTree analysis of dataset 1, excluding the outgroup, was used as input for the bPTP-ML analysis as implemented at <https://species.h-its.org/>.

RESULTS AND DISCUSSION

Phylogeny and species delimitation. We generated 39 new sequences (18 ITS and 21 nuLSU rDNA) that were aligned together with sequences already available in GenBank (**Table 1**). No incongruence was detected among partitions in any of the datasets. The combined matrix corre-

sponding to dataset 1 contained 1264 aligned characters (ITS1, 1–393; 5.8S, 394–511; ITS2, 512–731; nuLSU, 732–1264). The combined matrix corresponding to dataset 2 contained 1000 aligned characters (ITS1, 1–93; 5.8S, 94–195; ITS2, 196–350; nuLSU, 351–1000).

The best trees obtained from the ML analyses had lnLikelihood values of –6039.788 for dataset 1 and –8753.626 for dataset 2. The Bayesian analyses halted after 500,000 generations both in analyses of dataset 1, and in analyses of dataset 2, when the average standard deviation of split frequencies across runs was <0.01, indicating that the three runs had converged (<0.01). In all analyses, Potential Scale Reduction Factor (PSRF) values for all model parameters as well as all branch lengths were close to 1. A majority-rule consensus tree was constructed from the 5,000 trees of the stationary tree sample in each case. There was no incongruence between the ML and Bayesian trees in any of the two analysed datasets. Therefore, only the ML trees corresponding to datasets 1 and 2 are shown in **Figs. 1 and 2**, respectively, with information on Bayesian posterior probability values added. Nodes with values for maximum likelihood bootstrap support (ML-BS) ≥ 70 and Bayesian posterior probability (BPP) values ≥ 0.95 were considered to be phylogenetically supported. Phylogenetic trees were visualized using FigTree v.1.4.4 (Rambaut 2019).

Our analyses revealed 14–15 independently evolving lineages—putative species—within *Crittendenia* (**Fig. 1**), understood either as monophyletic supported groups, or as putative species or operational taxonomical units (OTUs) by bPTP-ML. There are only two cases in which Bayesian and ML phylogenetic analyses and bPTP-ML analysis were not consistent: 1) *C. physciiphila* forms a group with ML-BS <70 and BPP <0.95 but is conservatively considered a single species based on bPTP-ML results; 2) *C. lichenicola* forms a monophyletic supported group, but it is split in two OTUs by bPTP-ML. We nevertheless tentatively consider it as a single species until more samples can be included in phylogenetic studies. Both *C. physciiphila* and *C. lichenicola* could, however, represent species complexes, according to our molecular results.

The genus *Crittendenia* is monophyletic, and it is not included in any of the existing families in the Agaricostilbomycetes (**Fig. 2**). At an early stage of the study, we considered that proposing a new

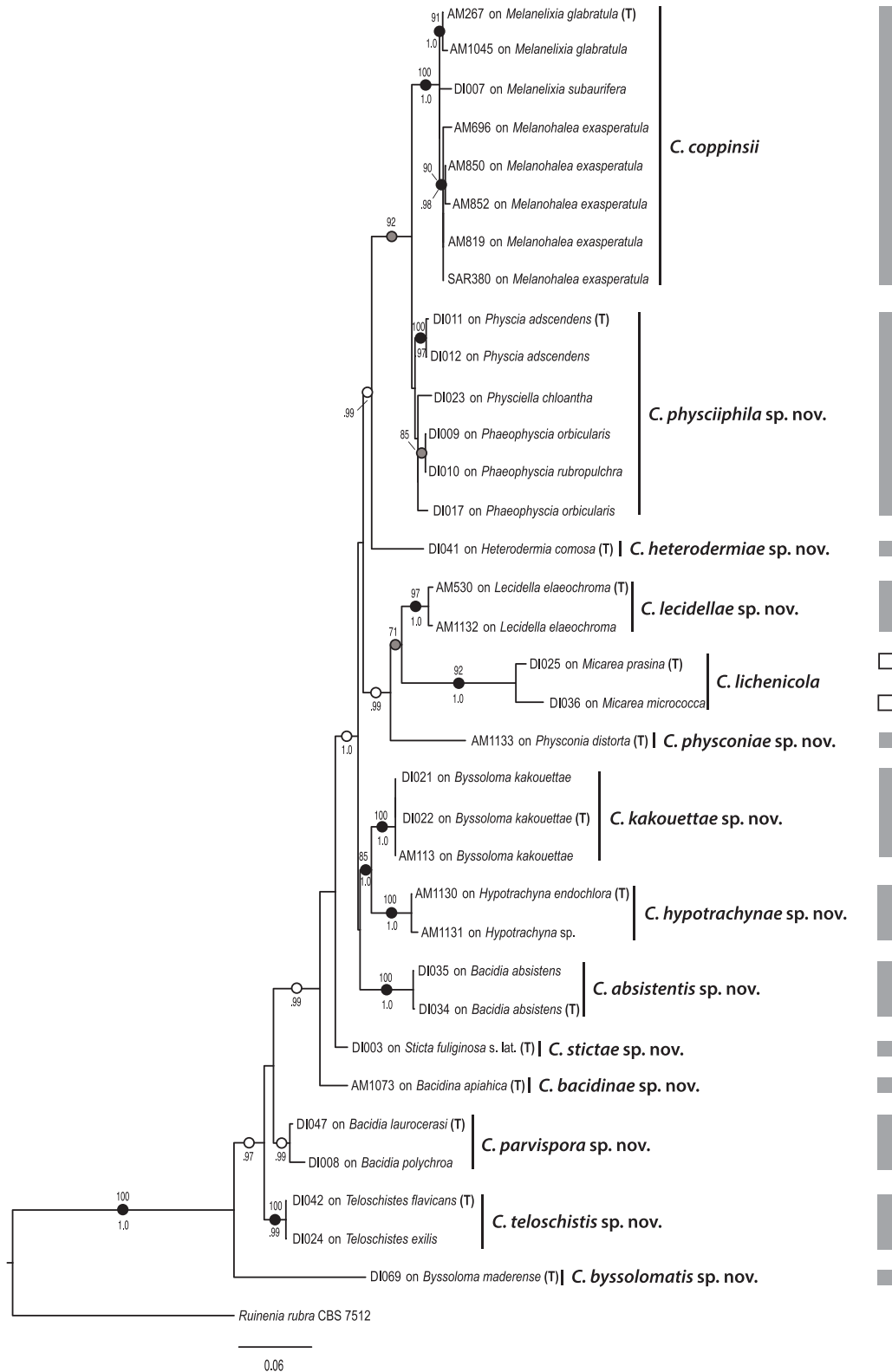


Figure 1. Maximum likelihood best tree from the combined analysis including ITS and nuLSU and representing *Crittendenia*. Black dots indicate branches supported by both ML and Bayesian analyses. Grey and white dots indicate branches supported only by ML or Bayesian analyses, respectively. ML-BS values ≥ 70 and BPP values ≥ 0.95 are indicated above and below branches, respectively. Type specimens are indicated with '(T)'. Species within *Crittendenia* are indicated to the right. Species delimitation obtained in the bPTP-ML analysis is indicated in the right margin as grey rectangles. Two white squares indicate two putative species within *Crittendenia lichenicola*, inferred by bPTP-ML. Branch lengths are scaled to the expected number of substitutions per site.

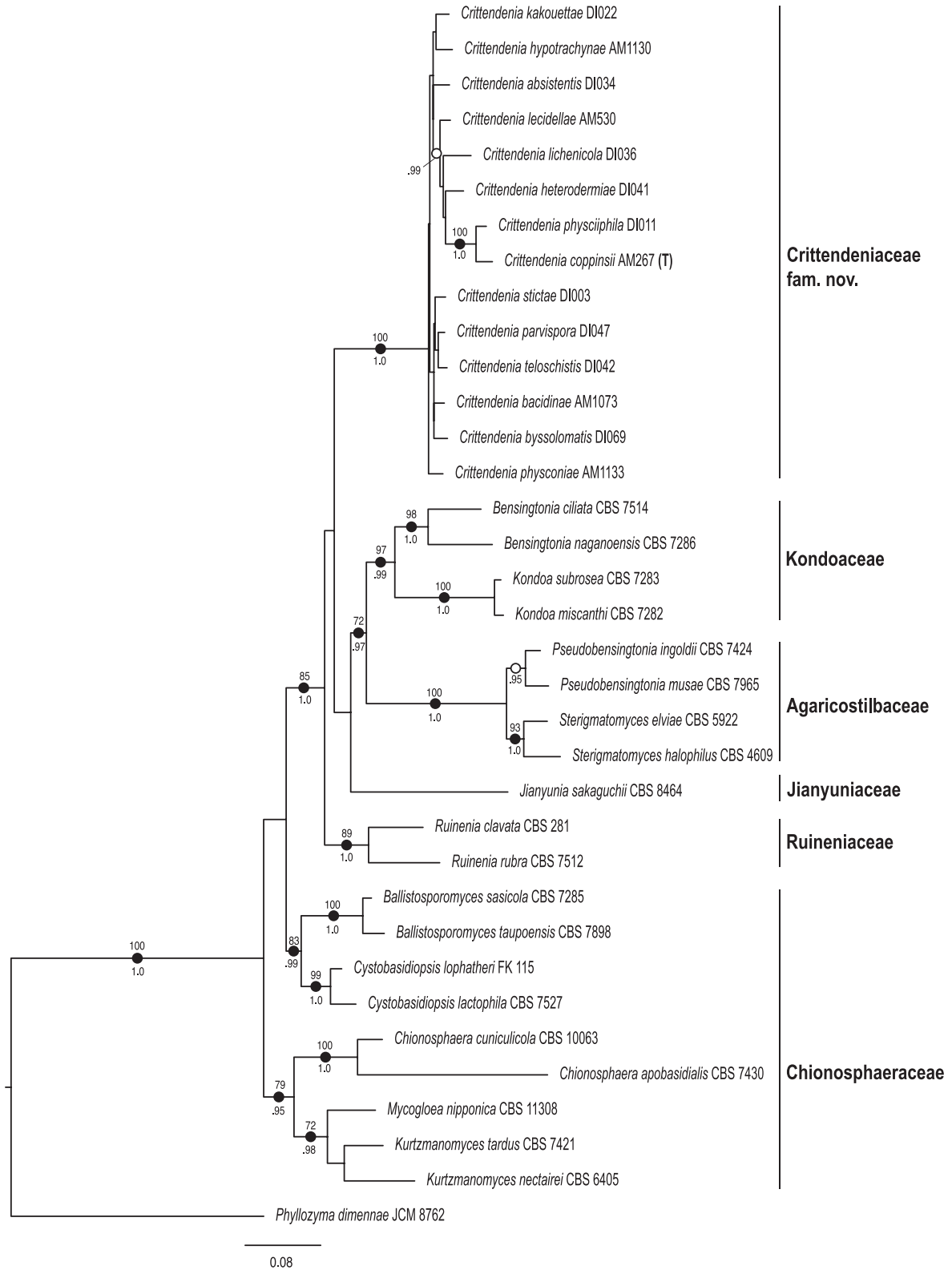


Figure 2. Maximum likelihood best tree from the combined analysis including ITS and nuLSU and representing the Agaricostilbomycetes. Black dots indicate branches supported by both ML and Bayesian analyses. White dots indicate branches supported only by Bayesian analyses. ML-BS values ≥ 70 and BPP values ≥ 0.95 are indicated above and below branches, respectively. Family assignments are indicated in the right margin. Branch lengths are scaled to the expected number of substitutions per site.

family for *Crittendenia* based on an ITS and nuLSU phylogeny could be premature. We unfortunately could not obtain sequences of other genes (nuSSU, RPB1, RPB2, TEF1-alpha, and CYTb) that would have allowed us to include *Crittendenia* in previously existing multigene phylogenies to further test the family assignment of the genus (Wang et al. 2016). However, even if the relationships between the different families are not supported by ITS and LSU, all families in Agaricostilbomycetes (depicted in Fig. 2) have already been confirmed by multigene phylogenies (Wang et al. 2016). Our results show that *Crittendenia* does not belong to any of these families in the Agaricostilbales, and we could only include the genus *Crittendenia* in a family if we considered Agaricostilbales as a single family (which is not acceptable in the light of the most recent taxonomic treatment of the group; see Wang et al. 2016). We therefore propose the new family Crittendeniaceae to accommodate the genus *Crittendenia*.

Morphology, biology and diversity. *Basidioma development.*—Basidiomatal initials are formed inside the lichen thallus and are made of the same elongated, cylindrical cells that later form the stipe of mature basidiomata (Fig. 3A). When emerging from the thallus, they are entirely surrounded by a transparent, gelatinous layer that eventually disappears while the basidiomatal stipe elongates (Fig. 3B). The stipe is entirely composed of hyaline, cylindrical, subparallel, elongated cells, without any specialized external layer (Fig. 3C). Primary septa are relatively thick and have clamp connections, while thin secondary septa may be devoid of clamps (Fig. 3D–E). Apical, almost identical cells later function as basidia (Fig. 3F). These typically have a basal clamp, able to proliferate to produce further basidia (Fig. 3G). In some species, multiple proliferations result in fascicles composed of a large number of basidia, all originating from the same hypha of the stipe (Fig. 3H), and this explains why the capitulum is generally much broader than the stipe.

Crittendenia basidiomata are extremely tiny. The smallest measured by us was observed in the holotype of *C. bacidinae* and was just 35 μm tall, with a stipe of 17 μm and a capitulum of 20 μm in diameter, which may represent the smallest basidioma ever observed. If we exclude the stipe, the fertile part of this basidioma (i.e., the capitulum),

considered as subspherical, would then have a volume of c. 4000 μm^3 .

Sporogenesis.—Mature basidia bear at their apex a crown of minuscule sterigmata that are clearly visible in some specimens, but obscure in most others, probably depending on the degree of maturity (Figs. 7D, 12D, 22E). Basidia in some species almost constantly produce (5–)7–8 sterigmata, while in others basidia with (3–)4 sterigmata dominate (Fig. 10E). In the case of eight basidiospores, the basidial crown is too small to accommodate them all, and then one of them moves to the center and is surrounded by the seven other spores. All together, they resemble, when viewed from above, a daisy flower with seven petals (or less, when some spores do not reach maturity) (Figs. 7E, 13I, 16H–I, 17D, 18G). Independent of being produced in groups of four or eight, basidiospores often detach together as a cluster of more or less equally sized spores. Basidiospores are not apiculate (although often basally slightly truncate), not borne obliquely on the sterigmata and not forcibly discharged, and represent therefore apobasidia, as defined by Rogers (1947). Mature basidiospores often remain deposited over older basidiomata (Figs. 6D, 8B, 16D, 22C), and are probably dispersed by wind or arthropods.

In some specimens, morphologically different cells are intermixed with mature basidia. They are often rather thick-walled and may be apically attenuated, sometimes resembling a kind of paraphyses or cystidia. They were already reported as ‘cystidium-like structure of unknown function’ and illustrated by Millanes et al. (2021, Fig. 3J). Sometimes, the attenuated end of these structures becomes swollen, then produces holoblastically a kind of ellipsoid spore or conidium with a similarly thickened cell wall (Figs. 9E,G, 15G, 20B). In some specimens, most mature basidia are thick-walled and produce in such a holoblastic way 1–4 spores through thick-walled sterigmata-like structures, in the absence of the typical crown made of minuscule and almost indistinct sterigmata. These kinds of spores are always thick-walled when young, but otherwise resemble in form and size the basidiospores produced on a crown. When maturing, their perispore becomes slightly rough or wrinkled, distinctly larger, then detaches from the rest of the spore, forming an envelope loosely surrounding the spore (Figs. 12E, 17D [upper photo], 20D–E), and

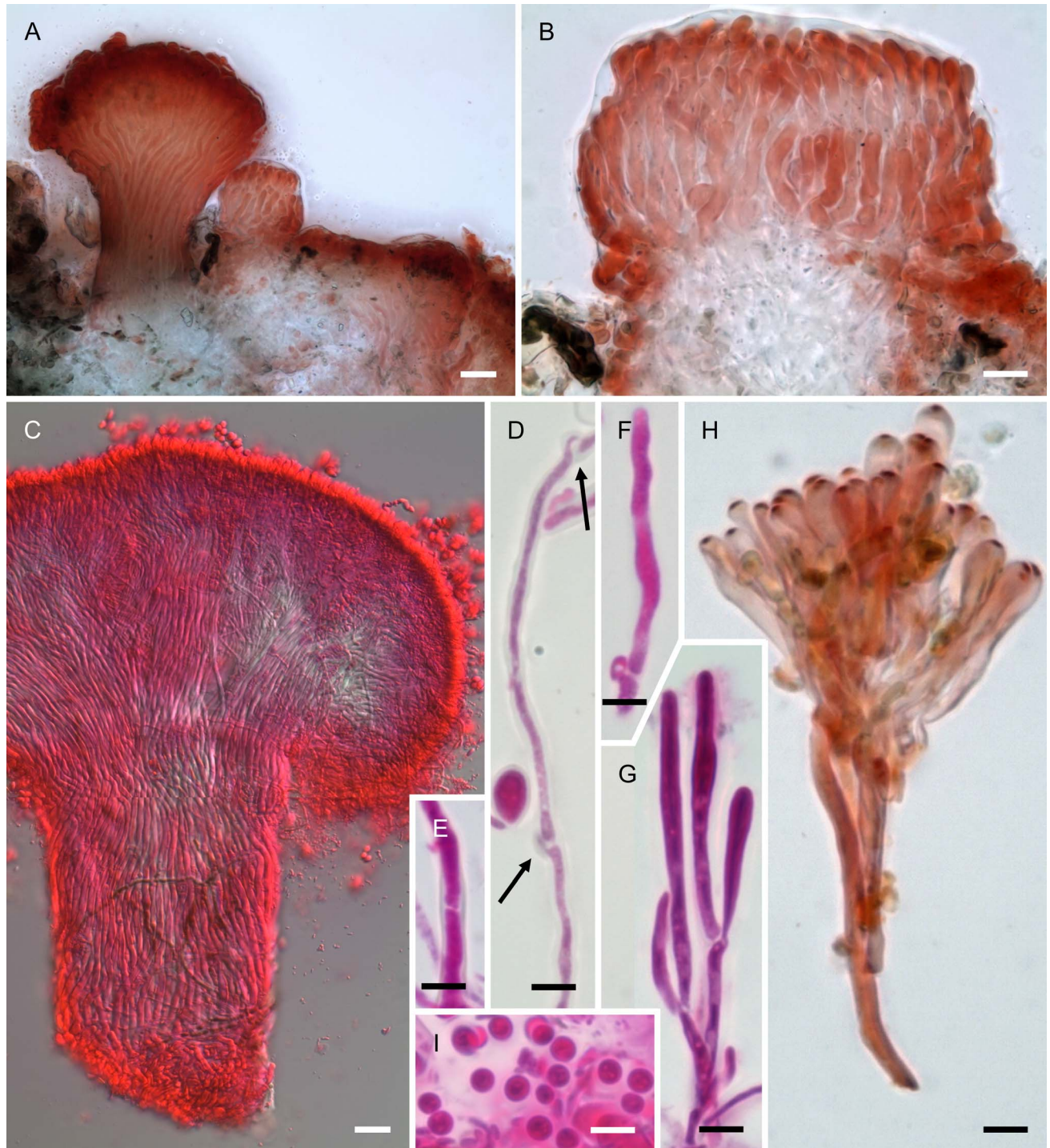


Figure 3. Basidioma and basidium development in *Crittendenia* species, and yeast cells. A–B. Section through a thallus of *Lopadium disciforme*, showing two young basidiomata; the own thalli of *Crittendenia* in A are immersed and not yet stained; the young basidioma in B is surrounded by a hyaline gelatinous layer. C. Squash preparation of a mature basidioma, showing the subparallel, cylindrical hyphae of the stipe, the hymenium and a few basidiospores. D. Thick-walled stipe hypha with clamped septa (arrows); presence of a basidiospore. E. Stipe hypha with a thin, non-clamped secondary septum. F. Young basidium with basal clamp, arising from stipe hypha. G. Proliferating basidia arising from one hypha. H. Fascicle of numerous basidia originating from one hypha. I. Putative *Crittendenia* yeast cells observed near the base of a stipe. A–B: *Crittendenia lopadii*, Tønsberg 15250, C: *C. lopadii*, Hilmo, D: *C. physciiphila*, Pinault, Cournols, on *Physcia adscendens*, E: *C. coppinsii*, Coppins 22784, F: *C. physciiphila*, Pinault, on *Phaeophyscia orbicularis*, G: *C. crassitunicatum*, holotype, H: *C. lichenicola*, holotype, I: *C. coppinsii*, Westberg (UPS F-805352). A–B, H, in ammoniacal Congo Red. C–G, I in KOH + phloxine. Scale bars: A, C = 20 μ m, B = 10 μ m, D–I = 5 μ m.

finally breaks down and disappears (Figs. 12F, 20D). The resulting spores devoid of a perispore are smooth- and thin-walled and cannot be distinguished from other basidiospores. In some specimens we have even observed spores still attached to their basidium, with the outer layer, not only of the spore (perispore), but also of the upper part of the basidium and the sterigma-like structure becoming enlarged and wrinkled, opening irregularly above and detaching gradually.

From a practical point of view, studying and measuring spores is difficult, first as the two kinds of spores can hardly be distinguished in many specimens (and we do not even know whether they are ontogenetically and functionally distinct), and second as the holoblastically produced spores initially have a tight perispore that is poorly visible (as this layer is never pigmented or stained), then becomes larger and eventually disappears, the spores thus becoming again smaller. Measurements of numerous spores for statistical purposes therefore inevitably include both types of spores at different degrees of maturity. For that reason also, we are not using a different terminology for each type of spore and always using the term ‘basidiospores’ for all the spores observed.

The outer layer of these ‘unusual’ spores may be comparable to the ‘perispore sac’, described and discussed in *Coprinus* by van Waveren (1968) as “a strongly developed perispore, surrounding the entire spore ... has the shape of a strongly wrinkled sac.” Kühner & Romagnesi (1953: 385) insisted on the fact that the perispore sac in some *Coprinus* species is well visible when young, but becomes detached and disappears when mature, exactly what we have observed in *Crittendenia*. Similarly, basidiospores of *Leucogaster* “are enclosed in a separable perispore sac” (Miller et al. 2006). Spirin et al. (2005) studied the ultrastructure of the basidiospores in *Perenniporia* and found that the perispore is a continuation of the outer layer of the sterigmata, thus recalling our observations of a perispore detaching from the spore + sterigma + upper part of basidium in some specimens.

Morphological intraspecific variability.—Species of *Crittendenia* are not only morphologically poor in taxonomically useful characters—most species differ from genetically distinct species by only a few minor characters—but further, the intraspecific variability in some species is considerable, making the use of

morphological characters for species delimitation sometimes next to impossible. As an example, the basidiomatal height in the holotype of *Crittendenia coppinsii* is 88–144 μm (the 69% probability interval) (Fig. 9B), in specimen *Zimmermann 1946* just 79–97 μm (Fig. 9C), but in *van den Boom 54983*, 148–233 μm ; the three specimens have been included in our phylogeny and are obviously conspecific. The capitulum diameter in the holotype of *C. lecidellae* is 43–78 μm (Fig. 15A), contrasting with 103–201 μm in specimen *Brackel 6418* (Fig. 15C). The basidiospores in the holotype of *C. absistentis* are 6.4–8.5 \times 2.4–3.2 μm , SpL/SpB 2.2–3.3 (Fig. 5C), while in specimen *Coppins 19800*, they are 4.1–6.5 \times 2.9–3.9 μm , SpL/SpB 1.2–2.0 (Fig. 5E).

Do Crittendenia species produce yeasts?—The vast majority of ‘heterobasidiomycete’ taxa in the Agaricomycotina and Pucciniomycotina are dimorphic, i.e., they alternate a haploid unicellular yeast phase and a dikaryotic filamentous phase during their life cycle (Bandoni 1995; Boekhout et al. 2011; Oberwinkler 1987, 2017). It has therefore generally been assumed that lichenicolous heterobasidiomycetes also have a yeast stage and, although less frequently detected by light microscopy than the filamentous phase, basidiospores germinating by budding (i.e., yeasts) have been observed and documented (Diederich 1996; Zamora et al. 2011, 2016). Recent studies have shown that lichenicolous species belonging to *Cyphobasidiales* and *Tremellales* frequently produce yeast cells within the host thallus, and that these yeasts are much more common than the sexual stage (Spribille et al. 2016; Tuovinen et al. 2019, 2021). The same could be true for species of *Crittendenia*. Roberts (1997) illustrated a specimen of *C. lecidellae* (as *Chionosphaera* aff. *coppinsii*) with yeast-like germination of basidiospores. He further wrote about *C. coppinsii* “germination probably by yeast-like conidia, but not clearly seen.” We have examined over sixty *Crittendenia* specimens microscopically and measured over 3800 spores, and none of these showed any kind of germination. Many of our microscopical preparations showed numerous yeast-like cells (Fig. 3I), but none of them was budding, and for none of these cells was it possible to demonstrate that they originate from *Crittendenia* basidiospores, or even if they belong to *Crittendenia*. Frequently, such cells are adhering to each other or to basidiospores within the mounting medium, and this might

erroneously be interpreted as budding cells. Yeast-like cells were observed on basidiomata, either on the stipe or in the basidial layer, or immersed in the host thallus close to the basidiomata, but have also been observed in host areas devoid of basidiomata. It would certainly be useful to obtain pure cultures of *Crittendenia* species and to study their life cycle, and this would also answer the question about yeast formation.

Crittendenia species are genetically very diverse but extremely rare, or at least are rarely collected, most species being known from just one or a few specimens, sometimes from different continents. One of the critical questions is thus to know where they are hiding, and how they reproduce, when basidiomata are more or less never seen. The most plausible answer may be that they are frequently present asymptotically within lichen thalli, that they spread with their hosts within vegetative diaspores, and that they only occasionally produce fruiting bodies. They may be present within the host thalli in the form of hyphae or of yeast cells. The latter hypothesis is probably more likely, as this way of life is known and obviously common in lichenicolous *Cyphobasidiales* and *Tremellales*, and because of our frequent observations of yeast-like cells close to *Crittendenia* basidiomata.

Do some Crittendenia species form simple lichenized thalli?—One of our most surprising observations was that some *Crittendenia* specimens may possess their own gelatinous, translucent lichenized thallus. At a first glance, basidiomata usually appear as growing directly on the host thallus or apothecial margin, without causing any visible symptoms. In reality, they always emerge from portions of the host thallus that are covered by a thin, usually brownish, gelatinous, translucent film that in some specimens may eventually become thicker and occasionally resemble gall-like outgrowths of the host thallus. This brownish, translucent structure is mainly made of hyphae of *Crittendenia* and should best be regarded as a non-lichenized thallus of this fungus. These minuscule thalli frequently contain, in addition to the hyaline, tubular *Crittendenia* hyphae, also large numbers of bacteria, some cyanobacteria (especially near the surface), yeast-like cells, and hyaline or brown hyphae from other fungi. In some specimens, mainly of *Crittendenia lecidellae*, these brownish gelatinous thalli may become olivaceous, due to a large number of algal cells located inside

them, and these could represent simple lichenized thalli (Fig. 4A, C). On pale-colored host thalli, the darker *Crittendenia* ‘thalli’ (lichenized or not) often strongly contrast with the host, and sterile *Crittendenia* thalli, without basidiomata, can then easily be seen (Fig. 4B). In some specimens, basidiomata are very rare, minuscule and difficult to detect, and they then need to be searched for on the darker *Crittendenia* thalli. On hosts with a thallus made of minuscule granules or goniospores, such as *Bacidina* or *Micarea* gr. *prasina*, *Crittendenia* thalli may be very reduced, hardly pigmented, and difficult to observe (Fig. 6B). Thalli of *Crittendenia coppinsi* are very similar in color to their hosts (*Melanelixia* or *Melanohalea* species), but they can be recognized by their gelatinous and shinier surface (Fig. 9B). In one specimen (*Holien* 8105, cf. Millanes et al. 2021), *C. coppinsi* basidiomata are growing in fairy rings at the edge of roundish *Crittendenia* thalli (Fig. 9A). In the type of *Crittendenia stictae*, basidiomata develop exclusively over conspicuous, pale to medium brown galls of the host thallus; some of these galls are sterile (Fig. 21A), while others are abundantly covered by basidiomata that arise from their own non-lichenized gelatinous thallus covering these galls (Fig. 21B–D). It was not possible for us to determine whether these galls were caused by the presence of *Crittendenia*, or if they were induced by another sterile fungal species.

Host specificity, semi-cryptic species and number of species.—As *Crittendenia* populations on most hosts are morphologically quite similar, one could have expected a small number of species that are not host-specific. Our phylogenetic results have shown, however, that populations from the same or closely related hosts often group together, but clearly differ from those from other hosts, suggesting a large number of mainly host-specific species. The best studied species, *C. coppinsi*, is known to be confined to hosts belonging to the two closely related genera *Melanelixia* and *Melanohalea*, and field studies have shown that it does not invade neighboring thalli of other Parmeliaceae genera. *Crittendenia lichenicola* is currently known from two specimens on members of the *Micarea prasina* group. Populations on Physciaceae belong to three morphologically and genetically distinct species, one on *Heterodermia*, one on *Physconia*, and another one on *Phaeophyscia*, *Physcia* and *Physciella*. Although some species can easily be distinguished based on morphological characters,

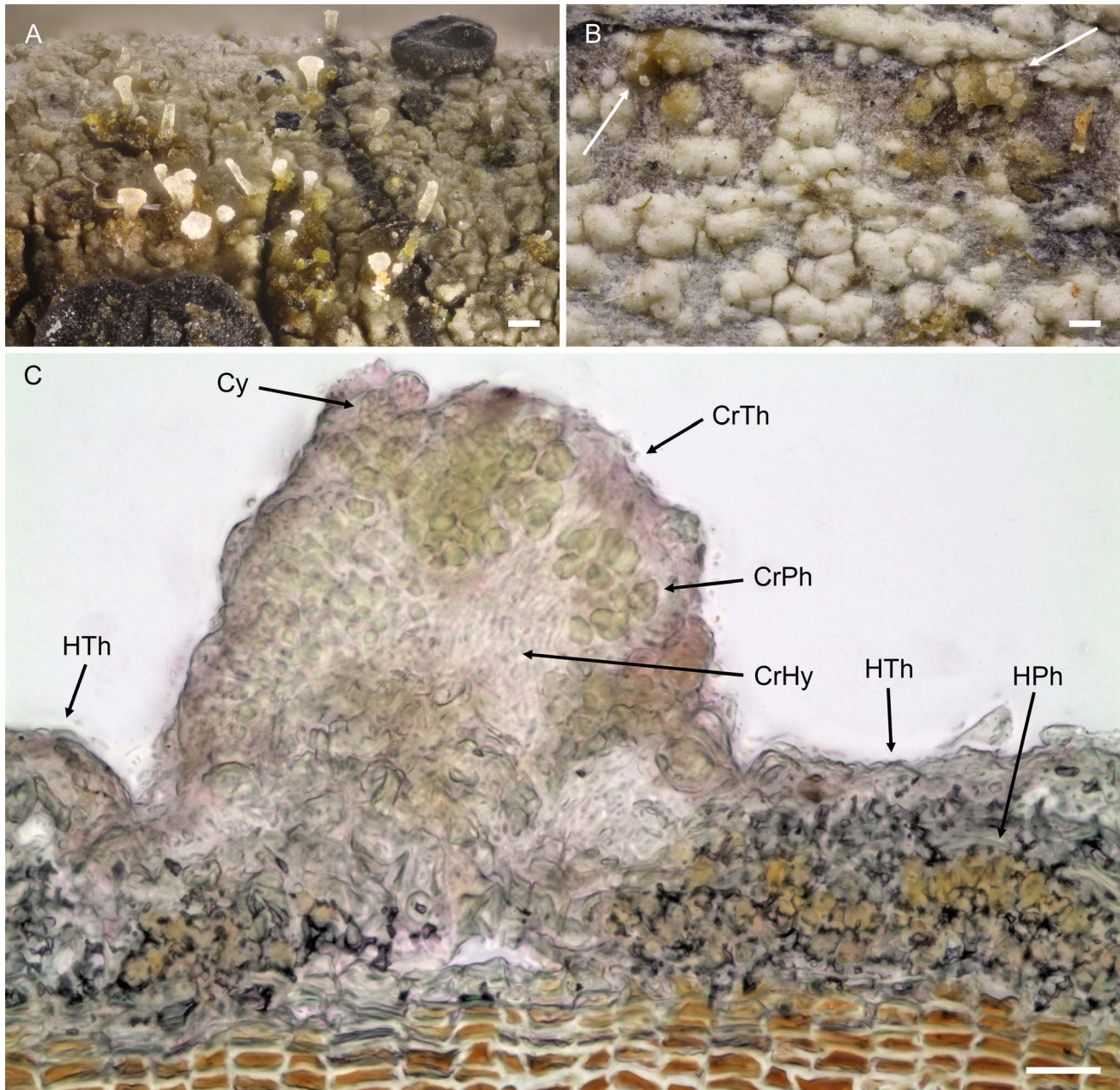


Figure 4. Putative lichenization of *Crittendenia* species. **A.** *Crittendenia lecidellae*, with olivaceous own thalli containing algae. **B.** *C. lecanorae*, with brownish own thalli devoid of algae; arrows point at groups of basidiomata. **C.** Section through presumed lichenized own thallus of *C. lecidellae*; CrTh = *Crittendenia* thallus, CrHy = *Crittendenia* hyphae, CrPh = *Crittendenia* photobiont, Cy = cyanobacteria, HTh = host thallus, HPh = host photobiont; the black parts in the host thallus originate from air inclusions in the preparation. A, C: *Coppins 22371*, B: *C. lecanorae*, holotype. C in water with traces of phloxine. Scale bars: A–B = 200 μ m, C = 20 μ m.

most species are so similar to others that only minor, often subtle differences are currently known. These apparent differences might just reflect our poor knowledge of the real morphological variability of each and may vanish when the species are better known. We anticipate therefore that the genus *Crittendenia* includes a large number of genetically

distinct species, most being strictly host-specific, and that many of these will best be qualified as semi-cryptic. The identification of such specimens will then either need molecular data or can tentatively be obtained through a combination of morphological characters and the host choice. If our hypothesis is confirmed that *Crittendenia* species mostly live

asymptomatically in lichen thalli, probably in the yeast stage, and only rarely produce basidiomata, then we can even expect the existence of a much larger number of species, some never occurring in the fertile stage, similarly to the observations of Spribille et al. (2016) in the *Cyphobasidiales*.

TAXONOMY

Crittendeniaceae Millanes, Diederich & Wedin,
fam. nov. **Fig. 2**

MYCOBANK MB 842928

A member of Agaricostilbales (Agaricostilbomycetes), distinguished from Chionosphaeraceae by basidia with a basal clamp and by the lichenicolous habitat.

TYPE GENUS: *Crittendenia* Diederich, Millanes, M. Westb., Etayo, J.C. Zamora & Wedin

Crittendenia Diederich, Millanes, M. Westb., Etayo, J.C. Zamora & Wedin, Millanes et al., *Lichenologist* 53: 111 (2021). TYPE: *Crittendenia coppinsii* (P. Roberts) Diederich, M. Westb., Millanes & Wedin.

Description. Own thallus usually present, in some species reduced, in others spreading over the host thallus, flat or swollen to subspherical, hyaline to more often brownish, often darker than the host thallus, strongly gelatinous, translucent, often containing bacteria, cyanobacteria, yeast-like cells, hyphae of other fungi, in some specimens also algal cells and then may be interpreted as representing a simple, olivaceous brown, lichenized thallus, in one species developing over galls, otherwise never visibly parasitic. Basidiomata developing on lichens, stipitate-capitate, synnemata-like, fleshy waxy, whitish, pale brownish, pinkish, or orangish, slightly translucent; capitulum slightly to strongly differentiated and enlarged. Stipe composed of subparallel, rarely branched hyphae with few septa; primary septa thick, with clamps, secondary septa thin, without clamps; these hyphae apically giving rise to one or several basidia; haustorial branches unknown. Hymenium amphigenous, entirely composed of basidia, without sterile elements or rarely with abnormal basidia-like elements of unknown function, not surrounded by an excipular layer. Basidia apical, tubular, with the largest diameter close to the apex,

aseptate, thin- or rarely thick-walled, usually with basal clamps that may proliferate to produce further basidia, when immature apically rounded, when mature with (1–)4–8 apical, short, inconspicuous, sterigmata, collapsing after spore detachment. Basidiospores hyaline, aseptate, shortly to elongate ellipsoid or fusiform, without a distinct basal apiculus (but basally often slightly truncate), not forcibly discharged, often liberating together as a cluster of 3–8 spores, wall usually smooth and relatively thin, sometimes becoming thicker and rough, developing into a loose perispore sac that eventually detaches, leaving a smaller, smooth-walled spore; germination by budding not observed. Asexual conidial stage unknown. Subspherical yeast-like cells, much smaller than basidiospores, are frequently present and abundant in the hymenium, on the basidiomatal stipe, or in the host thallus surrounding basidiomata, but their connection to *Crittendenia* is not established.

Ecology. Lichenicolous, associated with a large variety of lichens belonging to different phylogenetic lineages.

KEY TO THE SPECIES OF *CRITTENDENIA*

1. The key includes not only characters that allow distinguishing between two alternatives, but also additional characters that may help identifying atypical specimens.
2. The number of basidiospores per basidium is best determined using a microscopic preparation of a mature basidioma, without pressure on the cover glass, allowing the observation of free-swimming groups of spores originating from one basidium. Subsequent pressure on the cover glass and removal of excessive liquid with tissue paper will allow the measurement of a larger number of spores. Additional pressure on the cover glass with lateral movement will separate basidia and allow, in mature specimens, to observe and measure entire basidia. Staining of microscopical preparations is recommended, e.g., in a mixture of phloxine B and 5% KOH.
3. Measurements refer to the 69% probability intervals. Values without brackets refer to the global interval of a species (all specimens considered together), while values within square brackets refer to intervals of individual specimens (see further explanations in Material and Methods).
4. Phylogenetic results suggest that most species are host specific, and also that some species are morphologically rather variable. As most species are known from only one or few specimens, their variability is poorly known. The identification of morphologically atypical specimens may therefore be difficult, and then the host choice will be a useful help.
5. Abbreviations are those explained in Material and Methods.

- 1 Basidia (5)7–8-sterigmate; basidiospores, when liberated from the basidia, typically remaining together and arranged in form of a hexagon or heptagon with an additional central spore, recalling a daisy flower when observed from above, relatively small, <6.8[8.5] μm long; basidiomata slender, StD <49[80] μm , StH/StD >3.1[2.3]..... 2
- 1' Basidia (1)3–4-sterigmate (on *Lecidella* up to 6-sterigmate); basidiospores often larger, never arranged in form of a daisy flower with a central spore; basidiomatal stipe in most species thicker 8
- 2(1) Basidia [16]16–23[25] μm long; basidiospores [3.5]4.1–5.5[5.7] \times [2.2]2.3–3.3[3.6] μm ; basidiomata [127]140–244[296] μm tall; stipe [17]17–35[36] μm diam.; capitulum [31]33–76[97] μm diam.; on '*Byssoloma*' *kakouettae* *C. kakouettae* [if on *Fellhanera* species..... *C. aff. kakouettae*
- 2' Basidia longer, BaL >21 μm ; stipe and capitulum often wider 3
- 3(2) Basidiomata slender, StD [15]16–27[27] μm , StH/StD [4.5]4.6–8.2[8.4]; basidiospores [4.9]5.0–6.9[7.0] \times [2.7]2.7–3.7[3.8] μm ; on *Micarea* gr. *prasina*..... *C. lichenicola*
- 3' Basidiomata more robust, StD frequently >27 μm , StH/StD in some species smaller; basidiospores in some species shorter ... 4
- 4(3) Basidiospores [4.1]4.9–8.0[8.5] \times [2.4]2.6–3.9[4.2] μm , SpL/SpB [1.2]1.4–2.8[3.3]; on *Bacidia absistens*..... *C. absistentis*
- 4' Basidiospores smaller, SpL mostly <6.3 μm , SpL/SpB usually <1.7..... 5
- 5(4) Basidiospores relatively narrow, [3.7]3.7–5.2[5.9] \times [2.1]2.3–3.2[3.4] μm ; SpL/SpB [1.3]1.3–2.0[2.3]; on corticolous *Bacidia* *C. parvispora*
- 5' Basidiospores broadly ellipsoid, SpB mostly >3.0 μm ; SpL/SpB <1.8..... 6
- 6(5) Basidiospores subspherical to broadly ellipsoid, SpL [3.5]3.6–4.8[5.1] μm , SpL/SpB [1.0]1.1–1.4[1.4]; capitulum relatively broad, compared to stipe height, CaD/StH [0.4]0.4–1.1[1.3]; basidia 31–42 μm long; on *Teloschistes*..... *C. teloschistes*
- 6' Basidiospores broadly ellipsoid, SpL/SpB frequently >1.3; capitulum relatively narrow, compared to stipe height, CaD/StH <0.8..... 7
- 7(6) Basidiospores relatively short, 4.0–5.1 \times 3.0–3.9 μm ; basidia relatively short, 24–39 μm long; on *Bryostigma muscigenum* *C. bryostigmatidis*
- 7' Basidiospores frequently over 5 μm in length, [4.1]4.2–6.3[7.2] \times [3.0]3.1–4.2[4.2] μm ; basidia frequently longer, [29]30–50[59] μm long; on *Lopadium disciforme*..... *C. lopadii*
- 8(1) Basidia 19–31 μm long..... 9
- 8' Basidia >29 μm long..... 10
- 9(8) Basidiomata very small and slender, StH 69–116 μm , StD 16–27 μm , CaD 24–54 μm ; basidia very short; basidiospores 4.0–6.3 \times 2.2–2.9 μm , SpL/SpB [1.2]1.4–2.8[3.3]; on *Bacidina apialhica* *C. bacidiniae*
- 9' Basidiomata taller and more robust, with a broader capitulum, StH 112–165 μm , StD 23–43 μm , CaD 59–96 μm ; basidiospores shorter, 3.8–5.0 \times 2.4–3.0 μm , SpL/SpB [1.2]1.3–1.9[2.4]; on *Byssoloma maderense* *C. byssolomatidis*
- 10(8) Basidiospores relatively long and narrow, SpL/SpB >1.6; on Parmeliaceae..... 11
- 10' Basidiospores ratio SpL/SpB mostly <1.8 (on *Lecidella* exceptionally longer); on other hosts..... 14
- 11(10) Basidiomata very short and broad, StH c. 70–200 μm , StD c. 50–200 μm ; basidiospores 8.4–9.7 \times 4.0–5.4 μm , SpL/SpB (1.5)1.7–2.3(2.4); on *Parmelina quercina*..... *C. sp.*
- 11' Basidiomata more slender, StH/StD >1.3 12
- 12(11) Basidia very long, BaL [47]66–99[109] μm ; basidiomatal stipe relatively thick, StH/StD [0.7]1.3–3.2[4.4]; capitulum only slightly wider than the stipe, CaD/StD [0.8]1.0–1.6[2.0]; StH [79]85–163[233] μm , StD [36]37–87[139] μm , CaD [42]48–105[146] μm ; basidiospores mostly with an evenly thickened wall, [6.2]7.0–9.5[10.5] \times [3.1]3.3–4.3[4.7] μm , SpL/SpB [1.7]1.9–2.5[2.7]; on *Melanelixia* and *Melanohalea* ... *C. coppinsii*
- 12' Basidia shorter, BaL <53 μm ; basidiomata more slender, StH/StD >3.2; capitulum at maturity often much wider than the stipe, CaD/StD >1.5; basidiospores often with an unevenly thickened wall and an almost rectangular lumen..... 13
- 13(12) Basidiospores very large, 8.6–13.1 \times 3.5–4.7 μm , SpL/SpB 2.1–3.3; basidiomata very large, StH 218–353 μm , StD 37–63 μm , CaD 69–157 μm ; basidia 39–53 μm long; on *Melanohalea ushuaiensis* *C. crassitunicata*
- 13' Basidiospores smaller, [5.5]5.7–9.4[9.8] \times [2.9]3.0–4.3[4.5] μm , SpL/SpB [1.5]1.6–2.7[2.8]; basidiomata smaller, StH [110]116–232[237] μm , StD [17]24–55[68] μm , CaD [52]58–127[137] μm ; basidia shorter, [26]29–43[46] μm long; on *Hypotrachyna*..... *C. hypotrachynae*
- 14(10) Basidiomata reduced to a very large capitulum, 147–390 μm diam.; stipe reduced, not visible macroscopically; basidiospores 5.8–8.0 \times 4.7–6.1 μm ; on *Physconia*..... *C. physconiae*
- 14' Stipe present, but sometimes short, always visible; capitulum rarely >180 μm diam. 15
- 15(14) Basidiomata arising singly, rarely agglomerated, not over galls or conspicuous differently coloured own thalli; on Physciaceae 16
- 15' Basidiomata often grouped, over galls or brownish to olivaceous own thalli; on other hosts..... 17
- 16(15) Basidiomata short and broad, StH [47]75–157[198] μm , StD [33]51–153[191] μm , StH/StD [0.5]0.7–2.0[3.4]; capitulum often poorly developed, CaD/StD [0.6]0.9–1.4[1.7]; basidiospores [4.8]5.2–7.0[7.6] \times [3.0]3.5–4.9[5.6] μm ; on *Phaeophyscia*, *Physcia* and *Physciella* *C. physciiphila*
- 16' Basidiomata long and slender, StH 171–280 μm , StD 21–43 μm , StH/StD 5.1–10.1; capitulum well developed, often very broad, CaD/StD 2.0–3.6; basidiospores narrower, 4.7–6.5 \times 3.0–4.1 μm ; on *Heterodermia comosa*..... *C. heterodermiae*
- 17(15) Basidiomata developing over strongly convex galls that are often paler than the host thallus; basidiomata with a relatively large capitulum, CaD 61–172 μm , CaD/StH 0.4–1.1; basidiospores relatively broad, 4.7–7.1 \times 3.8–5.4 μm ; on *Sticta*..... *C. stictae*
- 17' Basidiomata not over galls, frequently over slightly convex, gelatinous and translucent, brownish to olivaceous thalli that may contain algal cells; capitulum often smaller; basidiospores often narrower..... 18
- 18(17) Basidiomatal stipe becoming relatively thick when mature, StD [26]22–102[175] μm , StH/StD [0.6]1.2–5.3[7.8]; capitulum relatively large, CaD [26]39–125[201] μm , CaD/StH [0.1]0.2–1.2[1.9]; basidiospores [3.4]4.2–6.8[8.0] \times [2.5]3.1 \times 4.9[5.7] μm , SpL/SpB [0.9]1.1–1.7[2.6]; on *Lecidella elaeochroma*... *C. lecidellae*
- 18' Basidiomata more slender, StD [21]22–43[44] μm , StH/StD [3.0]2.8–7.5[10.9]; capitulum smaller, CaD [32]32–79[108] μm , CaD/StH [0.2]0.3–0.5[0.5]; basidiospores [5.1]5.4–6.9[6.9] \times [3.0]3.3–4.5[4.6] μm , SpL/SpB [1.4]1.4–1.8[2.1]; on *Lecanora* *C. lecanorae*

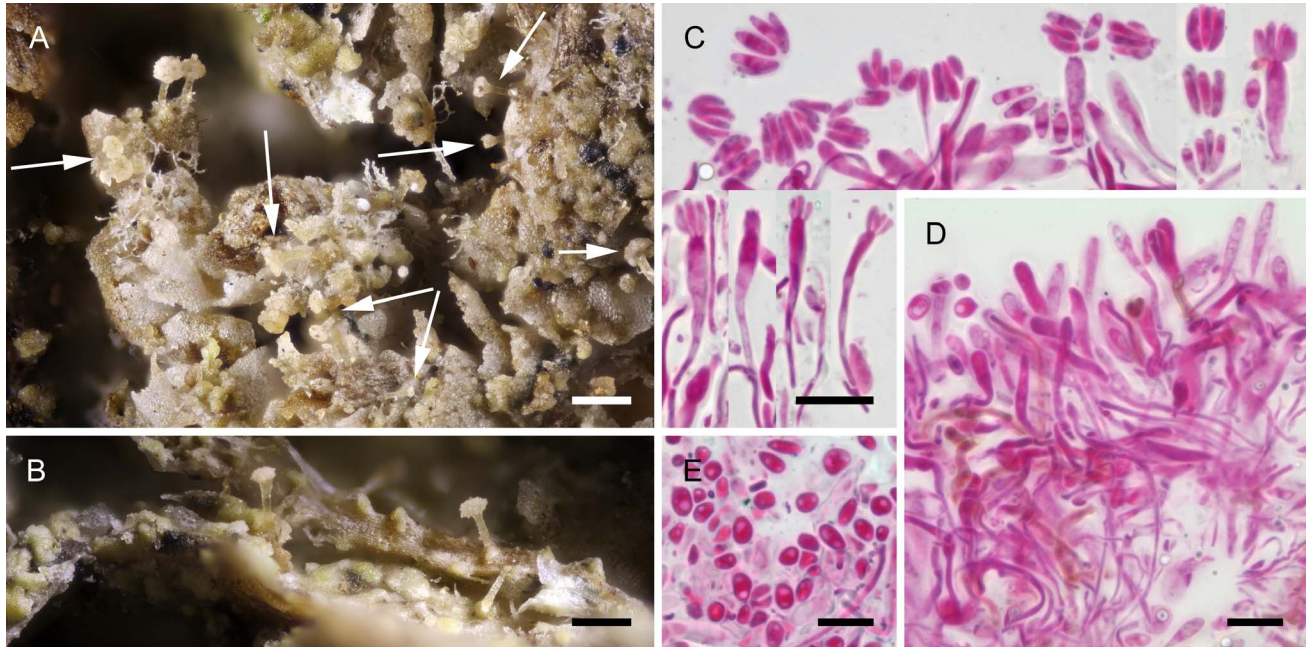


Figure 5. *Crittendenia absistentis*. A–B. Basidiomata (arrows) on the thallus of *Bacidia absistens*. C. Mature basidia with basidiospores. D. Hymenium with mainly immature basidia. E. Mature basidiospores. A, C–D: holotype, B: *Acton*, E: *Coppins 19800*. C–E in KOH + phloxine. Scale bars: A–B = 200 μm , C–E = 10 μm .

Crittendenia absistentis Diederich, Coppins & Millanes, *sp. nov.* **Fig. 5**

MYCOBANK MB 842905

Characterized by 5–8-sterigmate basidia, mainly 30–44 μm long, basidiospores mainly 4.9–8.0 \times 2.6–3.9 μm , a stipe 121–209 μm long and 21–35 μm diam., and the host choice, *Bacidia absistens*.

TYPE: UK. SCOTLAND: VC 103, Mid Ebudes, Ulva, 0.5 km S of Aird Glass, 60 m, on *Corylus*, on *Bacidia absistens*, 10 May 2017, B.J. Coppins 25367 (holotype, E 01002244!).

Description. Basidiomata dispersed over the thallus of *Bacidia absistens*, stipe relatively long and slender, pale brown, translucent, capitulum whitish, StH (80)[108]121–209[234](260) μm , StD (20)[21]21–35[40](50) μm , CaD (30)[41]49–90[98](110) μm , StH/StD (2.8)[3.7]4.1–8.1[9.2](10.5), CaD/StD (1.0)[1.5]1.8–3.3[3.4](4.4), CaD/StH (0.2)[0.3]0.3–0.6[0.7](0.9) (n = 53). Own thallus reduced, whitish. Stipe hyphae thick-walled, 2.5–3.5 μm thick, septa with clamps. Basidia subcylindrical to elongate clavate, upper third distinctly wider, with a basal clamp, 5–8-sterigmate, wall c. 0.5 μm thick before and during spore production, 0.5–1.5 μm after spore production, BaL

(25)[28]30–44[49](56) μm , BaD (1.7)[1.7]1.8–2.8[3.1](3.9) μm , BaApD (2.8)[3.0]3.2–4.5[4.6](5.2) μm (n = 29). Basidiospores often elongate ellipsoid, occasionally mixed with broadly ellipsoid basidiospores within the same basidioma, thin- to irregularly thick-walled, smooth, SpL (3.1)[4.1]4.9–8.0[8.5](10.0) μm , SpB (1.8)[2.4]2.6–3.9[4.2](5.5) μm , SpL/SpB (1.0)[1.2]1.4–2.8[3.3](4.3) (n = 225).

Etymology. From *Bacidia absistens*, the host lichen genus.

Distribution and host. Known from three localities in Scotland, always on the thallus of *Bacidia absistens*.

Notes. We have obtained sequences from the two recent specimens, including the type, both unfortunately rather reduced, while specimen *Coppins 19800* is richer. Within the species with up to 8-sterigmate basidia, the new species differs from *C. kakouettae* by the longer basidia, from *C. lichenicola* by the slightly more robust basidiomata with an often broader stipe, and from *C. bryostigmatis*, *C. lopadii*, *C. parvispora* and *C. teloschistis* by the longer basidiospores.

Additional specimens examined (both on *Bacidia absistens*). UK. SCOTLAND: VC 105, West

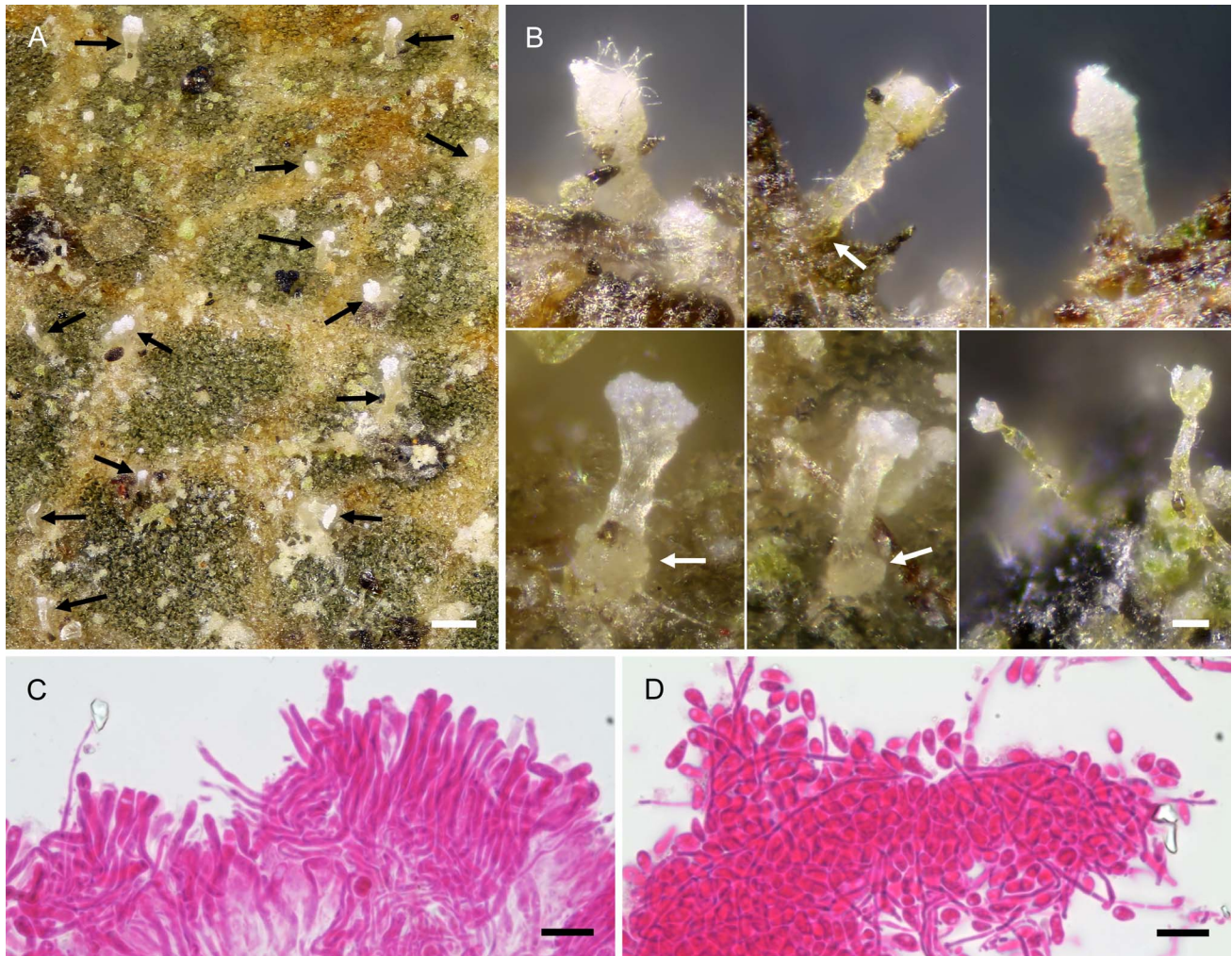


Figure 6. *Crittendenia bacidinae*, holotype. **A.** Basidiomata (arrows) on the thallus of foliicolous *Bacidina apiahica*. **B.** Idem, at a higher magnification; arrows indicate own *Crittendenia* thalli. **C.** Basidia, one mature with four basidiospores. **D.** Basidiospores. C–D, in KOH + phloxine. Scale bars: A = 100 μm , B = 20 μm , C–D = 10 μm .

Ross, Kinlochewe, Beinn Eighe NNR, Coille na Glasleitir, plantation by Allt Dorchaig, Enclosure 9, 20 m, on *Salix* by stream, 2001, *B.J. Coppins 19800* (E); Argyll, Appin, Glen Creran, oak-dominated old-growth forest at E-SE-facing slope, 56°35'48"N, 5°11'23"W, 60 m, on bark of *Sorbus aucuparia*, 2018, *A. Acton s.n.* (PRA [ex herb. Palice 25624]).

Crittendenia bacidinae Diederich, van den Boom & Millanes, *sp. nov.* **Fig. 6**

MYCOBANK MB 842906

Characterized by the particularly short, 3–4-sterigmate basidia, mainly 19–25 μm long, basidiospores mainly 4.0–6.3 \times 2.2–2.9 μm , a relatively short and slender stipe 69–116 μm long and 16–27

*μm diam., with an often much broader capitulum, 24–54 μm diam., and the host choice and habitat, foliicolous *Bacidina apiahica*.*

TYPE: PORTUGAL. AZORES: Pico, S of São Roque, secondary road on mountain range, from E (500 m) of main road ER-2 to direction of Arrife, 38°26.95'N, 28°18.36'W, 555 m, on leaf of *Laurus*, on *Bacidina apiahica*, 31 Aug. 2017, *P. van den Boom 56783* & *B. van den Boom* (holotype, BR!).

Description. Basidiomata dispersed over the host thallus or in small groups, stipe relatively short and very slender, pale brown, translucent, capitulum whitish, StH (35)69–116(160) μm , StD (10)16–27(40) μm , CaD (13)24–54(90) μm , StH/StD

(2.1)3.0–6.1(12.0), CaD/StD (1.2)1.3–2.4(4.3), CaD/StH (0.2)0.3–0.6(1.0) (n = 62). Own thallus reduced, hyaline to brownish, gelatinous, translucent, subspherical. Stipe hyphae thick-walled, 2–3 μm thick, septa with clamps. Basidia subcylindrical to clavate, apically wider, with a basal clamp, 3–4-sterigmate, thin-walled, BaL (17)19–25(25) μm (n = 6), BaD (1.8)1.9–2.3(2.4) μm (n = 9), BaApD (2.3)2.5–3.2(3.4) μm (n = 11). Basidiospores ellipsoid, relatively small, wall thin and smooth, c. 0.5 μm thick, SpL (2.7)4.0–6.3(9.5) μm , SpB (1.7)2.2–2.9(3.9) μm , SpL/SpB (1.0)1.5–2.6(4.2) (n = 117).

Etymology. From *Bacidina*, the host lichen genus.

Distribution and host. Known only from the type locality in the Azores (Pico), on foliicolous *Bacidina apiahica*.

Notes. This is a remarkable species, distinguished from all other *Crittendenia* species by the particularly small basidiomata. Indeed, it may be the basidiomycete with the smallest basidiomata known worldwide, the smallest fruiting body measured by us having just 35 μm in height, 17 μm in stipe diameter and 20 μm in capitulum diameter. Basidiomata are so small that even under a binocular microscope ($\times 50$) they are difficult to detect, and macrophotography of them was particularly challenging.

As the species grows in a similar habitat as *Crittendenia kakouettae* (confined to foliicolous ‘*Byssoloma*’ *kakouettae* and possibly *Fellhanera* species in Macaronesia) and shares with that species the shortest basidia within the genus, we expected a similar morphology and a closer phylogenetic relationship. In addition to the smaller basidiomata, *C. bacidinae* further appears to differ by the 3–4-sterigmate vs. 7–8-sterigmate basidia. However, this character is yet uncertain, as we did not clearly see free-swimming groups of basidiospores, while mature basidia observed by us mainly had 3 spores attached.

Crittendenia bryostigmatis Diederich & Tønsberg,
sp. nov. **Fig. 7**

MYCOBANK MB 842907

Characterized by 7-sterigmate basidia, mainly 24–39 μm long, basidiospores mainly 4.0–5.1 \times 3.0–3.9

*μm , a stipe 106–228 μm long and 24–47 μm diam., and the host choice, *Bryostigma muscigenum*.*

TYPE: CANADA. BRITISH COLUMBIA: Haida Gwaii (Queen Charlotte Islands), Graham Island, Queen Charlotte, 53°15.09'N, 132°07.24'W, 0–5 m, corticolous on twigs of *Salix* cf. *scouleriana* overhanging upper part of beach, on *Bryostigma muscigenum*, 22 Jul. 2003, T. Tønsberg 32070 (holotype, BG!).

Description. Basidiomata dispersed over the thallus of *Bryostigma muscigenum*, stipe relatively robust, pale brown, translucent, capitulum much broader, whitish to pale brownish, StH (65)106–228(400) μm , StD (20)24–47(80) μm , CaD (35)49–101(140) μm , StH/StD (2.2)3.1–6.8(10.4), CaD/StD (1.3)1.7–2.6(3.2), CaD/StH (0.2)0.3–0.6(0.9) (n = 48). Own thallus poorly visible over the brownish host thallus. Stipe hyphae thick-walled, 1.5–2.5 μm thick, septa with clamps. Basidia subcylindrical, relatively short, apically wider, with a basal clamp, 7-sterigmate, thin-walled, BaL (23)24–39(42) μm , BaD (1.6)1.7–2.1(2.2) μm , BaApD (2.2)2.4–3.1(3.2) μm (n = 8). Basidiospores broadly ellipsoid, wall c. 0.3 μm thick, smooth, SpL (3.3)4.0–5.1(6.5) μm , SpB (2.3)3.0–3.9(4.9) μm , SpL/SpB (1.0)1.1–1.6(2.2) (n = 220).

Etymology. From *Bryostigma*, the host lichen genus.

Distribution and host. Known only from the type locality on Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada, on the thallus of corticolous *Bryostigma muscigenum* (identification confirmed by D. Ertz, based on photos and description).

Notes. Although the type specimen is very rich, we did not obtain any sequences. Among the species with up to 8-sterigmate basidia, the new species differs from *Crittendenia kakouettae* by the longer basidia, from *C. lichenicola* by the more robust basidiomata with an often broader stipe, from *C. absistentis* by the smaller basidiospores, from *C. teloschistis* by the ellipsoid, not subspherical basidiospores and the narrower capitulum, and from *C. parvispora* by the broader basidiospores. For the characteristics that differentiate *Crittendenia bryostigmatis* from *C. lopadii*, see the discussion under *C. lopadii*.

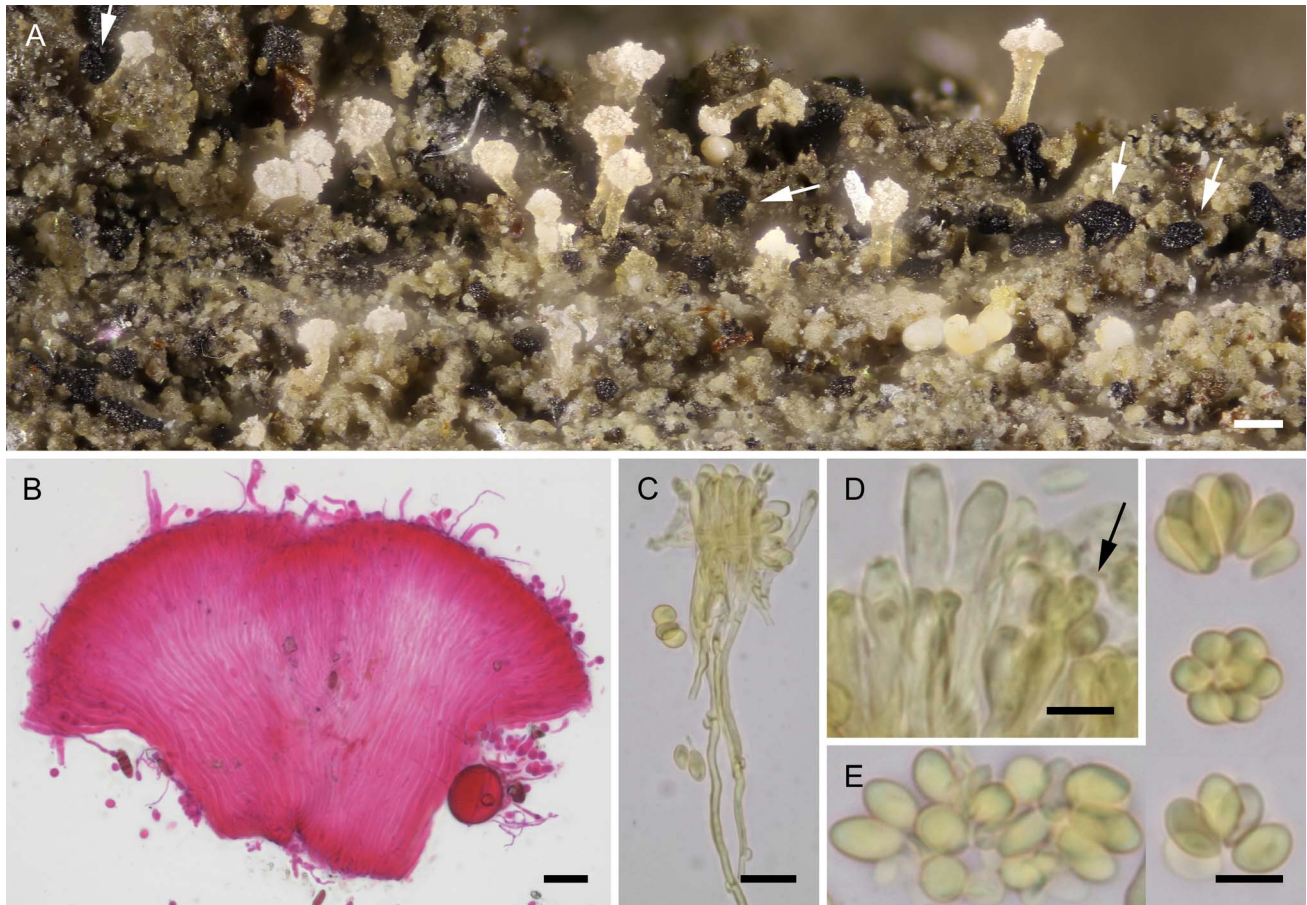


Figure 7. *Crittendenia bryostigmatis*, holotype. **A.** Basidiomata on the thallus of *Bryostigma muscigenum* (arrows point at host ascomata). **B.** Squash preparation of basidioma. **C.** Stipe hyphae with clamps and basidia. **D.** Mature basidia having produced basidiospores, one (arrow) with basidiospores still attached. **E.** Groups of basidiospores, each from one basidium. B, in KOH + phloxine, C–E, in Melzer's reagent. Scale bars: A = 100 μ m, B = 20 μ m, C = 10 μ m, D–E = 5 μ m.

Crittendenia byssolomatis Diederich, van den Boom & Millanes, *sp. nov.* **Fig. 8**

MYCOBANK MB 842909

*Characterized by short, 4-sterigmate basidia, mainly 19–31 μ m long, basidiospores mainly 3.8–5.0 \times 2.4–3.0 μ m, a medium-sized stipe 112–165 μ m long and 23–43 μ m diam., with a much broader capitulum, 59–96 μ m diam., and the host choice, *Byssoloma maderense*.*

TYPE: PORTUGAL. AZORES: Graciosa, S of Ribeirinha, along road R1-2, W of Serra Branca, 39°01.92'N, 28°02.22'W, 285 m, on twigs of *Erica azorica*, on *Byssoloma maderense*, 15 Sep. 2021, P. van den Boom 60700 & B. van den Boom (holotype, BR!).

Description. Basidiomata dispersed over the host thallus or in small groups, stipe pale brown, translucent, capitulum whitish, StH (90)112–165(200) μ m, StD (20)23–43(70) μ m, CaD (40)59–96(120) μ m, StH/StD (2.3)3.2–5.6(7.2), CaD/StD (1.3)1.8–3.1(4.1), CaD/StH (0.3)0.4–0.7(1.0) (n = 19). Own thallus reduced, hyaline to brownish, gelatinous, translucent. Stipe hyphae thick-walled, 2–2.5 μ m thick, septa with clamps. Basidia subcylindrical to clavate, apically wider, with a basal clamp, 4-sterigmate, thin/walled, BaL (19)19–31(35) μ m, BaD (1.4)1.6–2.0(2.3) μ m, BaApD (1.8)2.0–2.5(2.8) μ m (n = 17). Basidiospores ellipsoid, relatively small, wall thin and smooth, SpL (3.3)3.8–5.0(5.7) μ m, SpB (2.1)2.4–3.0(3.6) μ m, SpL/SpB (1.2)1.3–1.9(2.4) (n = 69).

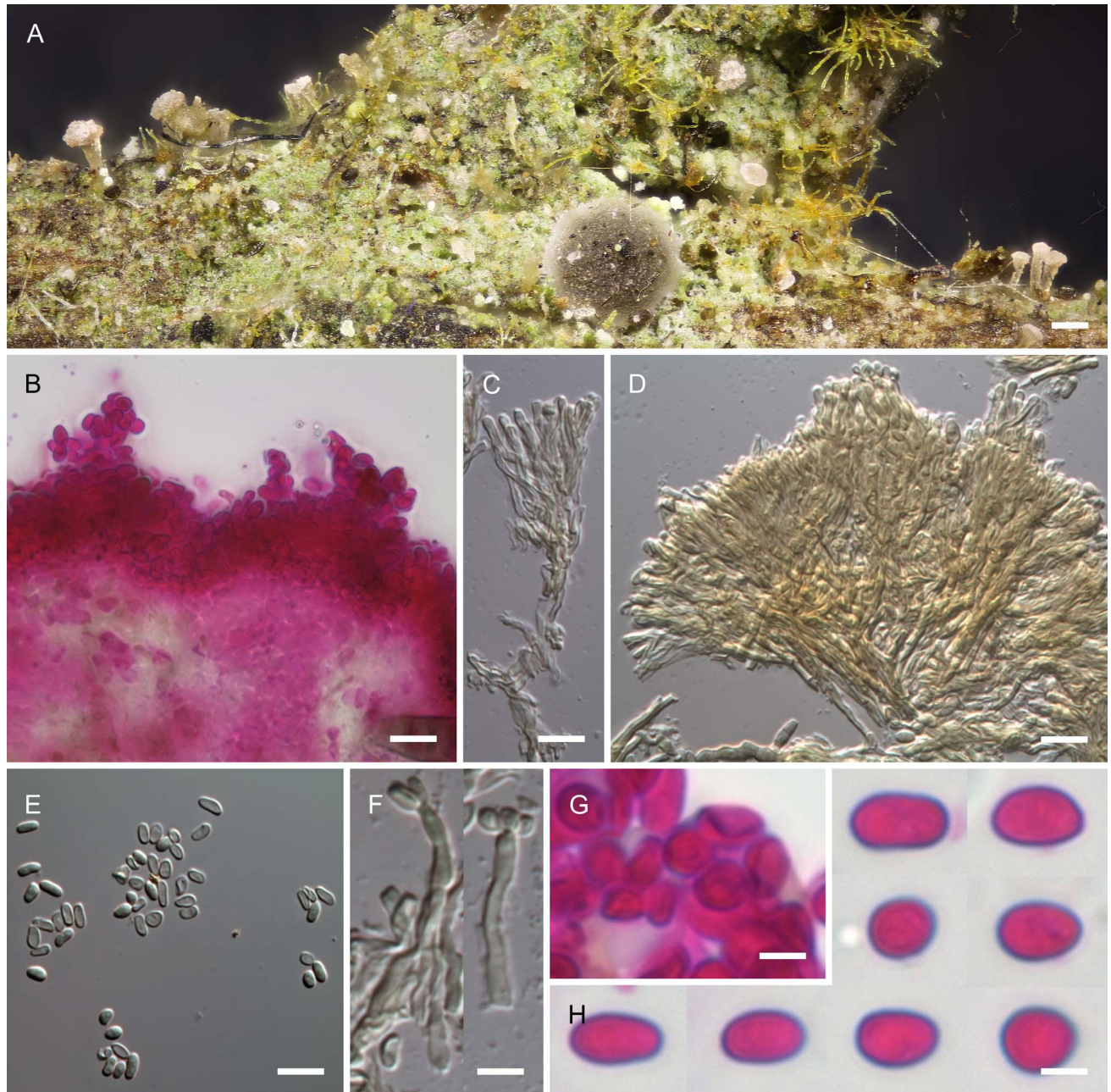


Figure 8. *Crittendenia byssolomatis*, holotype. **A.** Basidiomata on the thallus of *Byssoloma maderense*. **B.** Squash preparation of capitulum. **C.** Basidia originating from one stipe hypha. **D.** Squash preparation of hymenium. **E.** Basidiospores. **F.** Mature basidia with basidiospores. **G.** Basidia seen from top, each with four mature basidiospores. **H.** Basidiospores. B, G–H, in KOH + phloxine, C–F, in Melzer's reagent. Scale bars: A = 100 μm , B–E = 10 μm , F = 5 μm , G–H = 2.5 μm .

Etymology. From *Byssoloma*, the host lichen genus.

Distribution and host. Known only from the type locality in the Azores (Graciosa), on *Byssoloma maderense* on twigs of *Erica azorica*.

Notes. When we recently collected this species on *Byssoloma maderense* in the Azores, we were

convinced that it would be conspecific with other populations collected on foliicolous *Byssoloma kakouettae* in Macaronesia. However, the basidiomata on *B. maderense* are more robust (StH/StD 3.2–5.6) than those on *B. kakouettae* (StH/StD 5.5–9.6), the basidia 4-sterigmate and slightly longer, 19–31 μm , vs 7–8-sterigmate, 16–23 μm , and the

basidiospores slightly shorter, $3.8\text{--}5.0 \times 2.4\text{--}3.0 \mu\text{m}$ vs $4.1\text{--}5.5 \times 2.3\text{--}3.3 \mu\text{m}$. To our surprise, populations on both host species are phylogenetically only distantly related (Fig. 1). Further, the hosts might be only distantly related. While *Byssoloma maderense* is very similar and probably closely related to *B. leucoblepharum*, a species belonging to *Byssoloma* s.str. (Lücking 2008), *B. kakouettae* has only provisionally been included in *Byssoloma* and is likely to belong to another, possibly yet undescribed, genus (Sérusiaux et al. 2002). Consequently, *Crittendenia byssolomatis* on *Byssoloma* s.str. needs to be accepted as a new species distinct from the new *C. kakouettae*.

Crittendenia coppinsii (P.Roberts) Diederich, M.Westb., Millanes & Wedin **Fig. 9**

In Millanes et al., *Lichenologist* 53: 113 (2021); *Chionosphaera coppinsii* P.Roberts, *Mycotaxon* 63: 195 (1997). TYPE: UK. SCOTLAND: Wester Ross, Torridon, Inveralligan, wood & gorge of Abhainn Alligin, on *Melanelixia glabratula*, 21 Jun. 1994, B.J. Coppins 16400 & A.M. O'Dare (holotype, E!; isotype, K 39188!).

Description. Basidiomata initially aggregated in small groups, later invading the entire thallus of *Melanelixia* and *Melanohalea*, stipe relatively robust, pale to medium brown, translucent, capitulum whitish to pale brown or slightly pinkish, StH (60)[79]85–163[233](300) μm , StD (30)[36]37–87[139](200) μm , CaD (30)[42]48–105[146](200) μm , StH/StD (0.5)[0.7]1.3–3.2[4.4](6.0), CaD/StD (0.7)[0.8]1.0–1.6[2.0](2.8), CaD/StH (0.2)[0.3]0.4–1.0[1.6](2.0) ($n = 191$). Own thallus brownish, gelatinous, translucent, forming delimited patches or spreading over large areas of the host thallus. Stipe hyphae thick-walled, 1.5–2.5 μm thick, septa with clamps. Basidia subcylindrical, apically distinctly wider, very long, with a basal clamp, (1)4-sterigmate, wall c. 0.5 μm thick before and during spore production, 1–1.5 μm after spore production, BaL (46)[47]66–99[109](136) ($n = 58$), BaD (1.6)[1.8]2.0–3.2[4.0](4.7) μm ($n = 77$), BaApD (2.2)[2.5]2.9–4.0[4.6](4.9) μm ($n = 77$). Basidiospores ellipsoid to elongate ellipsoid, wall c. 0.5 μm thick, smooth, SpL (4.7)[6.2]7.0–9.5[10.5](12.4) μm , SpB (2.6)[3.1]3.3–4.3[4.7](6.2) μm , SpL/SpB (1.3)[1.7]1.9–2.5[2.7](3.1) ($n = 426$).

Distribution and hosts. The species was known from Belgium, Norway, Russia, Sweden, Switzerland and the UK (Scotland) (Millanes et al. 2021) and is here newly reported from Austria, France and Spain. The known hosts are *Melanelixia glabratula* (type specimen), *M. subaurifera*, *Melanohalea exasperata*, *M. exasperatula* and *M. olivacea*.

Notes. *Crittendenia coppinsii*, the generic type, is the most common species of the genus in Europe and is currently known from nine countries. Nevertheless, it is extremely rare and we believe its rarity is real and not a consequence of being overlooked. Infected thalli are usually abundantly covered by numerous basidiomata and thus eye-catching, and epiphytic macrolichens are usually well studied by lichenologists. It is also the only species of the genus from which many sequences are available, including from asymptomatic thalli adjacent to infected thalli, revealing a cryptic presence in healthy host thalli (Millanes et al. 2021). It is confined to the two very closely related host genera *Melanelixia* and *Melanohalea*. Among the *Crittendenia* species with 3–4-sterigmate basidia and long and narrow basidiospores, this species is distinguished by the particularly long basidia.

Additional specimens. AUSTRIA. SALZBURG: Radstädter Tauern, Lungau, NE of Tamsweg, E of Überlinger Hütte, 1720 m, on branch of *Picea* in coniferous forest, on *Melanohalea exasperatula*, 2019, R. Cezanne & M. Eichler s.n. (herb. Eichler-Cezanne [photographs seen!]). FRANCE. PUY-DE-DÔME: Châteaugay, c. 1 km au NE des Caves, 45.8614°N, 3.1082°E, 520 m, on *Quercus*, on *Melanelixia subaurifera*, 2020, P. Pinault s.n. (BR). PYRÉNÉES-ATLANTIQUES: Irati, near Chalet Pedro, near the torrent, on *Fagus*, on *Melanelixia glabratula* 1995, J. Etayo 16930 (herb. Etayo). SPAIN. GALICIA: Lugo, Faial de Liñares, Liñares LU-623, cerca del alto de San Roque, 42°41'58"N, 7°04'51"W, 1100–1200 m, on *Corylus*, on *M. glabratula*, 2021, J. Etayo 33361 & E. López de Silanes (herb. Etayo); Lugo, Courel, Devesa da Rogueira, 42°36'30"N, 7°06'21"W, 1200–1300 m, bosque mixto, on *Fagus*, on *M. glabratula*, 2021, J. Etayo 33615 & E. López de Silanes (herb. Etayo). NAVARRA: valle de Basaburúa Mayor, entre Aizároz y Arrarás, pista cementada camino de Bergañe, hayedo, on *Fagus*, on *M. glabratula*, 1994, J. Etayo 14415 (herb. Etayo). UK. SCOTLAND: VC97, Westernness, Ardnamurchan, Kil-

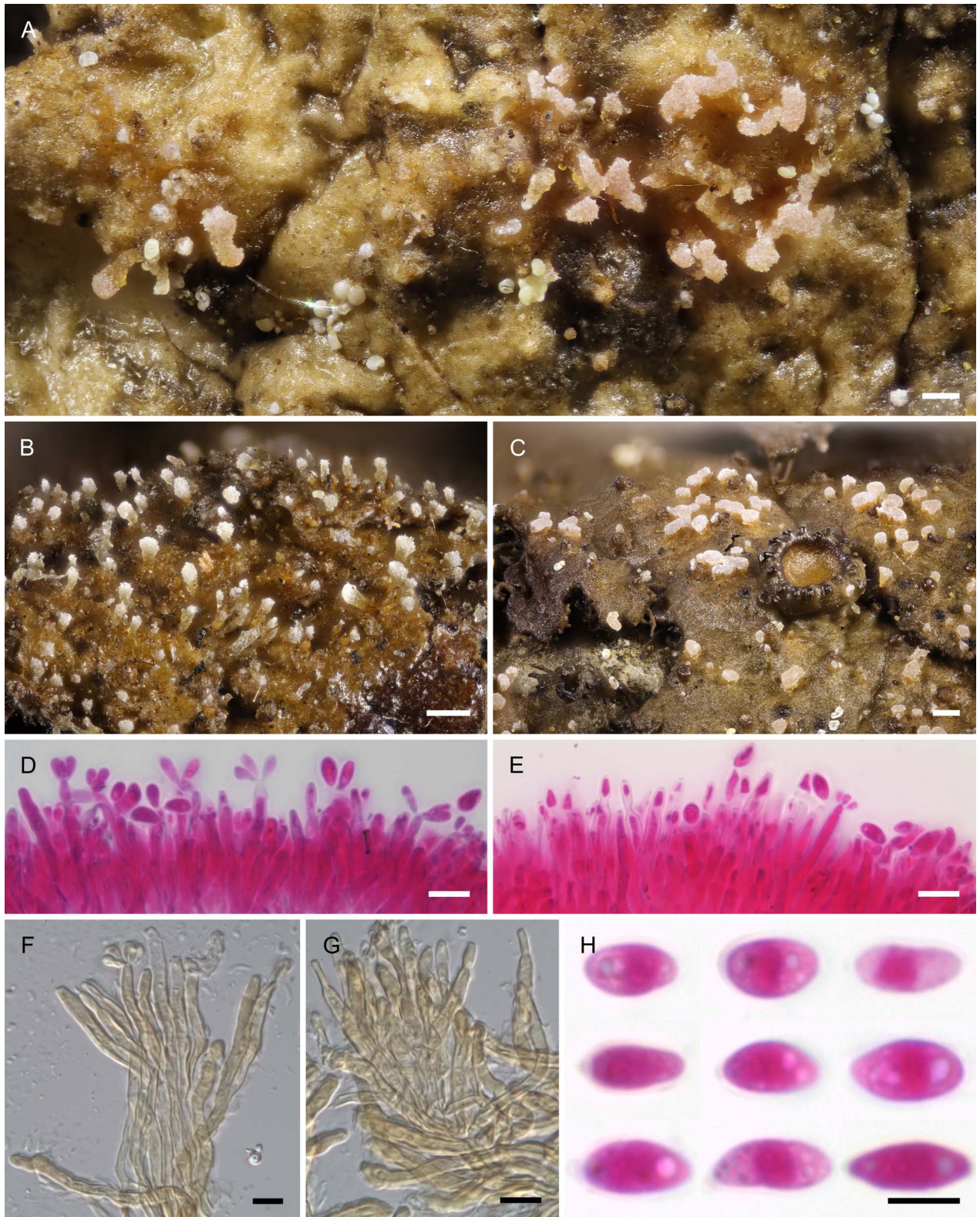


Figure 9. *Crittendenia coppinsii*. **A.** Basidiomata on the thallus of *Melanohalea exasperatula*; note the two more orange brown own thalli of *Crittendenia*, with basidiomata mainly developing at the margin of these thalli. **B.** Relatively narrow and tall basidiomata on the thallus of *Melanelixia glabrata*, the own *Crittendenia* thallus covering the entire host thallus. **C.** Broad and short basidiomata on the thallus of *Melanohalea exasperata*. **D.** Hymenium with many mature basidia carrying the basidiospores. **E.** Hymenium with mainly abnormal basidia with an apical swelling; one typical, basidiospores-carrying basidium in the right third. **F.** Overmature basidia, one still carrying the basidiospores. **G.** Abnormal basidia, some with an attenuated apex (left and right). **H.** Basidiospores. **A:** *Holien* 8105, **B, E, H:** holotype, **C:** *Zimmermann* 1946, **D:** *Westberg & Olsson* (AM1045), **F–G:** *Groner* 714. **D–E, H,** in KOH + phloxine; **F–G,** in Melzer's reagent. Scale bars: **A** = 100 μm, **B–C** = 200 μm, **D–G** = 10 μm, **H** = 5 μm.



Figure 10. *Crittendenia crassitunicata*, holotype. A–B. Basidiomata on the thallus of *Melanohalea ushuaiensis*. C. Squash preparation of basidiomata. D–E. Mature basidia, some with attached basidiospores. F. Thick-walled basidiospores. C–E, in KOH + phloxine, F, in ammoniacal Congo Red. Scale bars: A–B = 200 μ m, C = 50 μ m, D–E = 10 μ m, F = 5 μ m.

mory, Bealach Gaoith, 50–65 m, hazel-birch woodland, on *Betula*, on *M. subaurifera*, 2009, B.J. Coppins 22784 (E).

Crittendenia crassitunicata Diederich & Etayo, *sp. nov.* **Fig. 10**

MYCOBANK MB 842910

Characterized by the very large basidiomata, mainly 218–353 μ m tall, stipe 37–63 μ m diam., very large basidiospores, 8.6–13.1 \times 3.5–4.7 μ m, with a thick wall and an often almost rectangular lumen, the relatively short, (3)4-sterigmate basidia, 39–

53 μ m long, and the host choice, Melanohalea ushuaiensis.

TYPE: ARGENTINA. CHUBUT PROV.: Parque Nacional Los Alerces, on *Nothofagus*, on *Melanohalea ushuaiensis*, 4 Nov. 2006, J. Etayo 23715 (holotype, MAF-Lich!).

Description. Basidiomata in rather dense groups on the thallus of *Melanohalea ushuaiensis*, stipe very long and robust, brown, translucent, capitulum whitish, StH (160)218–353(450) μ m, StD (30)37–63(80) μ m, CaD (40)69–157(200) μ m, StH/StD (4.0)4.3–7.5(11.3), CaD/StD (1.0)1.5–3.0(4.7), CaD/

StH (0.2)0.3–0.5(0.6) (n = 34). Own thallus brownish, gelatinous, translucent, spreading over large areas of the host thallus. Stipe hyphae thin- to thick-walled, 2.5–4.5 μm thick, clamps not observed, often branched below basidia. Basidia subcylindrical, wider in the upper half, with a basal clamp, (3)4-sterigmate, wall c. 0.5 μm thick before and during spore production, c. 1 μm after spore production, BaL (32)39–53(54) μm , BaD (2.0)2.1–2.4(2.6) μm , BaApD (2.9)3.0–3.7(3.9) μm (n = 18). Basidiospores elongate ellipsoid, very large, often with a thick wall, especially at the apices, lumen ellipsoid to almost rectangular, initially smooth, later with a rough, enlarging and eventually separating perispore sac, SpL (6.8)8.6–13.1(16.5) μm , SpB (2.9)3.5–4.7(5.2) μm , SpL/SpB (1.6)2.1–3.3(4.3) (n = 84).

Etymology. From *crassus*, thick, and *tunica*, membrane, in reference to the thick-walled basidiospores.

Distribution and host. Known only from the type locality in southern Argentina, on the thallus of *Melanohalea ushuaiensis*.

Notes. No sequences have been obtained from the type. As this species grows on *Melanohalea*, a genus that also hosts *Crittendenia coppinsii*, we hesitated whether this should be included in an enlarged concept of that species or distinguished as a different taxon. Macroscopically, basidiomata of the new species are distinctly larger, and especially taller than those of *C. coppinsii* (218–353 μm vs. [79]85–163[233] μm). Similarly, basidiospores are distinctly longer (8.6–13.1 μm vs. [6.2]7.0–9.5[10.5] μm). But as we know that basidiomata and basidiospores in *Crittendenia* are rather variable, the type of *C. crassitunicata* could be interpreted as an extremely large and well developed *C. coppinsii*. The main difference between both, however, lies in the basidia that are distinctly shorter in *C. crassitunicata* (39–53 μm vs. [47]66–99[109] μm).

Crittendenia heterodermiae Diederich, Etayo & Millanes, *sp. nov.* **Fig. 11**

MYCOBANK MB 842911

Characterized by the large basidiomata, mainly 171–280 μm tall, the narrow stipe, 21–43 μm diam., medium-sized ellipsoid basidiospores, 4.7–6.5 \times 3.0–4.1 μm , the relatively long, 4-sterigmate

*basidia, 57–74 μm long, and the host choice, *Heterodermia comosa*.*

TYPE: BOLIVIA. DEPT. CHUQUISACA: Prov. Luis Calvo, Parque nacional y área natural de manejo integrado Iñaño, Serranía de Iñaño, close to Ticucha, Monteagudo, 19°39'50"S, 63°49'14"W, 1022 m, on thin branches, on *Heterodermia comosa*, 15 Jul. 2015, J. Etayo 32711 (holotype, LPB!).

Description. Basidiomata dispersed over the thallus of *Heterodermia comosa*, stipe relatively robust, whitish to pale brown, capitulum much broader, whitish to pale brown, StH (150)171–280(320) μm , StD (18)21–43(60) μm , CaD (50)59–114(160) μm , StH/StD (3.3)5.1–10.1(13.0), CaD/StD (1.7)2.0–3.6(4.0), CaD/StH (0.3)0.3–0.5(0.7) (n = 20). Own thallus hyaline to brownish, gelatinous, translucent, spreading over small areas of the host thallus. Stipe hyphae thick-walled, 2–3 μm thick, septa with clamps. Basidia subcylindrical, relatively long, apically wider, with a basal clamp, 4-sterigmate, thin-walled, BaL (52)57–74(75) μm , BaD (1.9)2.0–2.8(3.0) μm , BaApD (3.1)3.3–4.4(4.7) μm (n = 10). Basidiospores ellipsoid, wall c. 0.3 μm thick, smooth, SpL (3.9)4.7–6.5(8.0) μm , SpB (2.6)3.0–4.1(5.7) μm , SpL/SpB (1.0)1.4–1.8(2.3) (n = 80).

Etymology. From *Heterodermia*, the host lichen genus.

Distribution and host. Known only from the type locality in Bolivia, on the thallus of *Heterodermia comosa*.

Notes. The only known specimen of this species is growing on a rather small host thallus, but with plenty of well developed basidiomata. Among the species with mainly 4-sterigmate basidia, this species is distinguished from the parmeliicolous species by the shorter and often broader basidiospores, from *Crittendenia physciiphila* by the much longer and more slender basidiomata, from *C. lecanorae* and *C. lecidellae* by the dispersed, not grouped basidiomata, and from *C. stictae* by the absence of gall-like structures on the host thallus. In our phylogeny, sequences from this species are sister to a clade comprising *C. coppinsii* and *C. physciiphila*, although this relationship is only supported by the Bayesian analysis (**Fig. 1**).

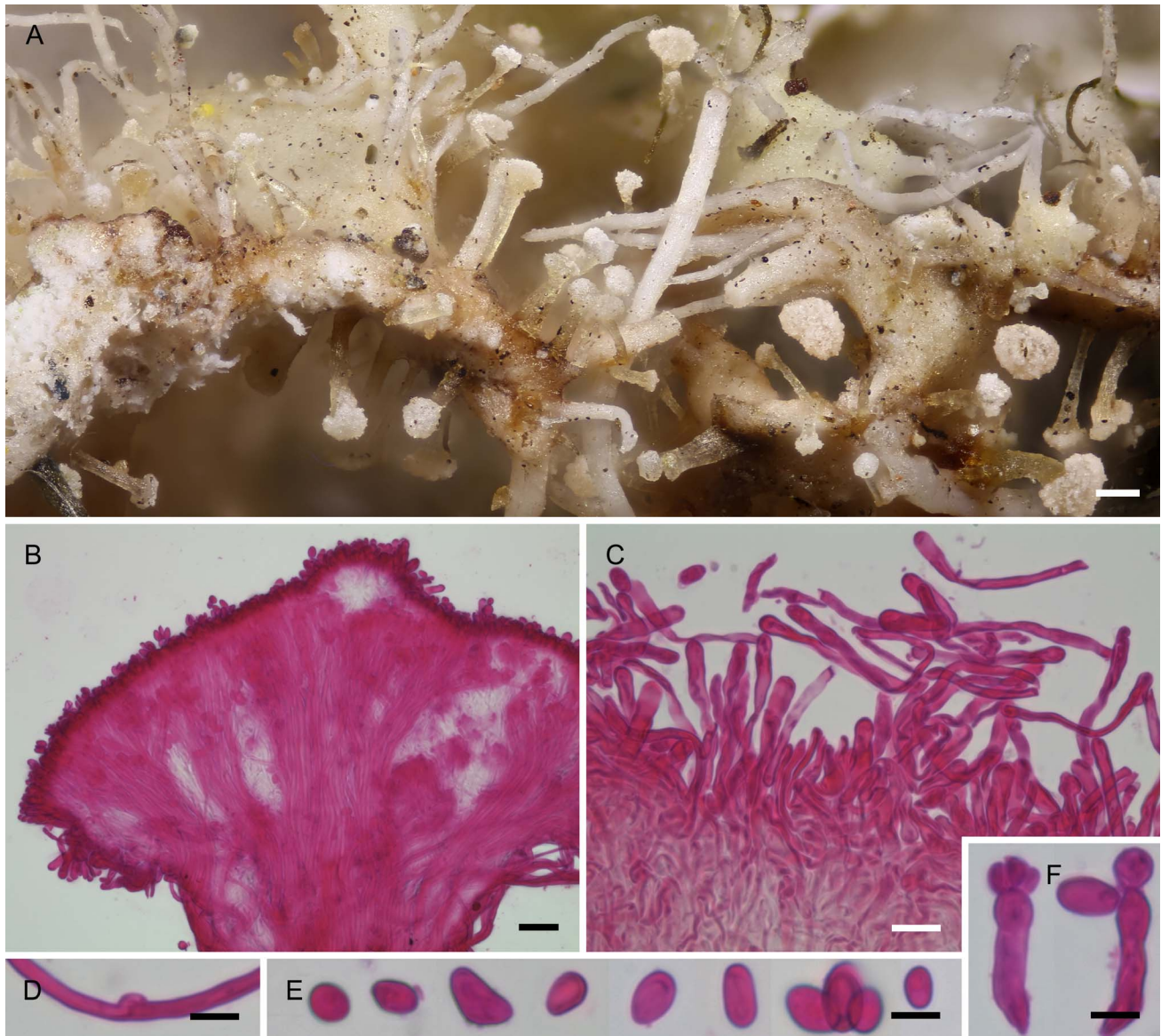


Figure 11. *Crittendenia heterodermae*, holotype. A. Basidiomata on the thallus of *Heterodermia comosa*. B. Squash preparation of basidioma. C. Mature basidia. D. Stipe hypha with septum and clamp connection. E. Basidiospores. F. Mature basidia with attached basidiospores (lower part broken). B–F, in KOH + phloxine. Scale bars: A = 100 μ m, B = 20 μ m, C = 10 μ m, D–F = 5 μ m.

Crittendenia hypotrachynae Diederich, Etayo, van den Boom & Millanes, *sp. nov.* **Fig. 12**

MYCOBANK MB 842912

*Characterized by the medium-sized basidiomata, mainly 116–232 μ m tall, and stipe, 24–55 μ m diam., the long, but relatively narrow basidiospores, 5.7–9.4 \times 3.0–4.3 μ m, the relatively short, 3–4-sterigmate basidia, 29–43 μ m long, and the host choice, *Hypotrachyna* species.*

TYPE: PORTUGAL. AZORES: Terceira, Camino de Algar do Carvão a Agualva, 38°44'01"N, 27°12'35"W, 630 m, in laurisilva, on *Hypotrachyna endochlora*, 26 Jul. 2017, J. Etayo 31093 (holotype, PO!).

Description. Basidiomata either dispersed over the thallus of *Hypotrachyna* species or limited to the host soralia, stipe relatively robust, pale brown to orange brown, translucent, capitulum whitish, frequently much wider than the stipe, StH

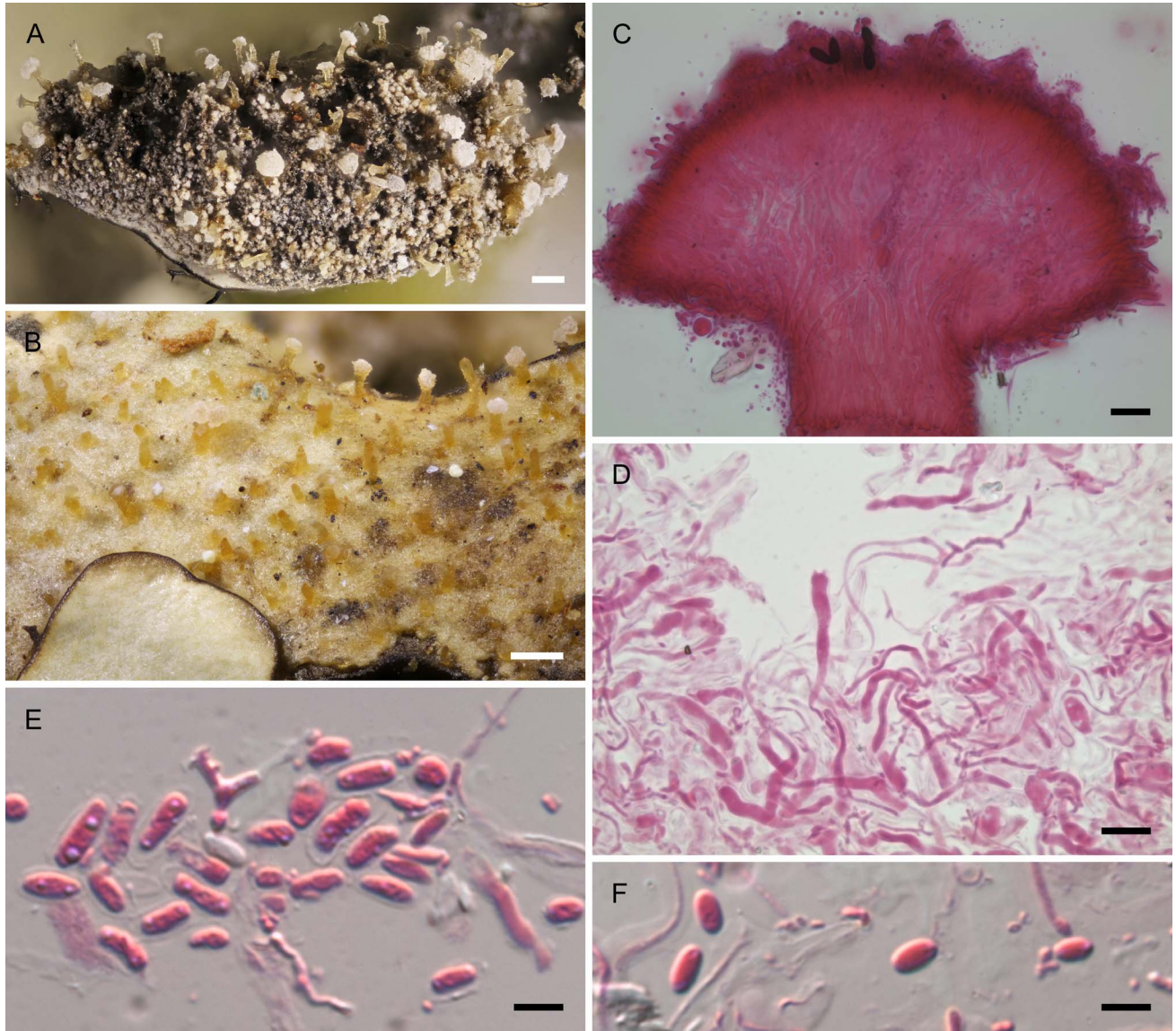


Figure 12. *Crittendenia hypotrachynae*. **A.** Basidiomata on the soredia of *Hypotrachyna endochlora*. **B.** Basidiomata on the thallus of *H. laevigata*. **C.** Squash preparation of basidioma. **D.** Mature basidia. **E.** Basidiospores with a perispore sac. **F.** Basidiospores without a perispore sac. **A, C–F:** holotype, **B:** *Diederich 4913*. **C–F** in KOH + phloxine. Scale bars: **A–B** = 200 μm , **C** = 20 μm , **D** = 10 μm , **E–F** = 5 μm .

(90)[110]116–232[237](350) μm , StD (20)[17]24–55[68](120) μm , CaD (30)[52]58–127[137](190) μm , StH/StD (2.5)[2.9]3.2–6.1[6.9](9.0), CaD/StD (1.3)[1.6]1.7–3.1[3.3](4.0), CaD/StH (0.2)[0.3]0.4–0.7[0.8](0.9) ($n = 76$). Own thallus brownish, gelatinous, translucent, present around basidiomata or spreading over large areas of the host thallus. Stipe hyphae 2.5–3.5 μm thick, septa with clamps. Basidia subcylindrical, apically slightly wider, with a basal clamp, 3–4-sterigmate, wall c. 0.5 μm thick before and during spore production, c. 1 μm after spore production, BaL (27)[26]29–43[46](52) μm

($n = 45$), BaD (1.3)[1.5]1.6–2.3[2.5](2.8) μm ($n = 46$), BaApD (1.9)[2.2]2.4–3.4[3.6](3.8) μm ($n = 47$). Basidiospores elongate ellipsoid, relatively long, wall often unevenly thickened, often with a perispore sac that may eventually detach, SpL (4.0)[5.5]5.7–9.4[9.8](13.4) μm , SpB (2.4)[2.9]3.0–4.3[4.5](6.2) μm , SpL/SpB (1.1)[1.5]1.6–2.7[2.8](4.0) ($n = 267$).

Etymology. From *Hypotrachyna*, the host lichen genus.

Distribution and hosts. Known from the Azores (Terceira) and Madeira, always on the thallus of *Hypotrachyna* species, including *H. endochlora* and

H. laevigata, sometimes in necrosed areas of the host thallus or in soralia.

Notes. Among the *Crittendenia* species with 3–4-sterigmate basidia and rather long basidiospores, this species is distinguished from *C. coppinsii*, a taxon also confined to parmelioid hosts, by the more slender basidiomatal stipe, with a StD of mainly 24–55 μm vs. 38–91 μm , a ratio StH/StD of 3.2–6.1 vs 1.2–3.4, and a ratio CaD/StD of 1.7–3.1 vs 1.0–1.5, and the much shorter basidia, mainly 27–44 μm vs 58–99 μm . *Crittendenia crassitunicata* is distinguished by the much larger basidiospores and basidiomata. In our phylogeny, the species is sister to *C. kakouettae*, a taxon with 7–8-sterigmate basidia. The two Azores specimens had already been published by Etayo (2018) as *Chionosphaera apobasidialis*.

Additional specimens examined. PORTUGAL. AZORES: Terceira, reserva nacional Serra de Santa Bárbara, domos volcánicos de Mistérios Negros, Lagoa do Negro, 38°44'01"N, 27°17'05"W, 600 m, on *Juniperus brevifolia*, on *Hypotrachyna*, 2017, J. Etayo 30945 (herb. Etayo). MADEIRA: road between Ribeira Brava and S. Vicente, 2 km N of Encumeada, 800 m, on *H. laevigata*, 1992, P. Diederich 4913 (BR); road between Ribeira Brava and S. Vicente, W of Boca da Encumeada, levada trail, W from tunnel to waterfall, 32°45.14'N, 17°02.41'W, 1010 m, on *Hypotrachyna*, 2019, P. van den Boom 58213 (BR).

Crittendenia kakouettae Diederich, van den Boom & Millanes, *sp. nov.* **Fig. 13**

MYCOBANK MB 842913

Characterized by particularly short, 7–8-sterigmate basidia, mainly 16–23 μm long, basidiospores mainly 4.1–5.5 \times 2.3–3.3 μm , a slender stipe 140–244 μm long and 20–33 μm diam., with a much broader capitulum, 33–76 μm diam., and the habitat, on the thallus of 'Byssoloma' kakouettae.

TYPE: PORTUGAL. AZORES: Santa Maria, E of Almagreira, along road ER-1-2 to Santo Espírito, Reserva Florestal das Fontinhas, picnic area, 36°57.61'N, 25°04.40'W, 335 m, on needles of *Cryptomeria*, on 'Byssoloma' kakouettae, 16 Sep. 2019, P. & B. van den Boom 58956 (holotype, BR).

Description. Basidiomata dispersed over the host thallus or in small groups, stipe very long and

slender, pale brown, translucent, capitulum whitish, relatively broad, StH (80)[127]140–244[296](320) μm , StD (15)[18]20–33[42](45) μm , CaD (20)[31]33–76[97](120) μm , StH/StD (4.0)[4.9]5.5–9.6[10.7](12.0), CaD/StD (1.0)[1.3]1.4–2.7[3.1](4.5), CaD/StH (0.1)[0.2]0.2–0.4[0.5](0.6) (n = 78). Own thallus reduced, hyaline to brownish, gelatinous, translucent. Stipe hyphae thick-walled, 2–3.5 μm thick, septa with clamps. Basidia subcylindrical to clavate, apically wider, with a basal clamp, 7–8-sterigmate, wall c. 0.5 μm thick before and during spore production, 0.5–0.8 μm after spore production, BaL (14)[16]16–23[25](27) μm , BaD (1.2)[1.6]1.9–3.0[3.2](4.2) μm , BaApD (2.4)[2.6]3.1–4.2[4.3](5.3) μm (n = 67). Basidiospores ellipsoid, relatively small, wall thin and smooth, c. 0.5 μm thick, eventually occasionally thicker, SpL (2.9)[3.5]4.1–5.5[5.7](7.0) μm , SpB (1.8)[2.2]2.3–3.3[3.6](4.7) μm , SpL/SpB (1.2)[1.3]1.4–2.1[2.2](2.7) (n = 241).

Etymology. From *Byssoloma kakouettae*, the host lichen.

Distribution and host. Known only from Macaronesia in the Azores (Santa Maria), the Canary Islands (Tenerife) and Madeira, on the thallus of foliicolous 'Byssoloma' kakouettae (a species that does probably not belong to *Byssoloma* s.str., see discussion under *Crittendenia byssolomatidis*).

Notes. The new species is distinguished from most members of the genus by the particularly short basidia (mainly 16–23 μm long), a character shared with *Crittendenia bacidinae* (19–25 μm) and *C. byssolomatidis* (19–31 μm). *Crittendenia bacidinae* differs by the much smaller basidiomata, 3–4-sterigmate basidia and a different host, *Bacidina apiahica*, and *C. byssolomatidis* by the more robust basidiomata, 3–4-sterigmate basidia and also a different host, *Byssoloma maderense*. The three species are phylogenetically distinct (**Fig. 1**).

Crittendenia kakouettae is surprisingly common, if we consider that the host, 'Byssoloma' kakouettae, is a rarely collected species that has a relatively narrow geographical range, being known from Macaronesia and a few localities in the French Pyrénées-Atlantiques, and that further in several infected specimens the host is so much reduced and almost sterile that it would be overlooked by most collectors. Unfortunately, all known specimens,

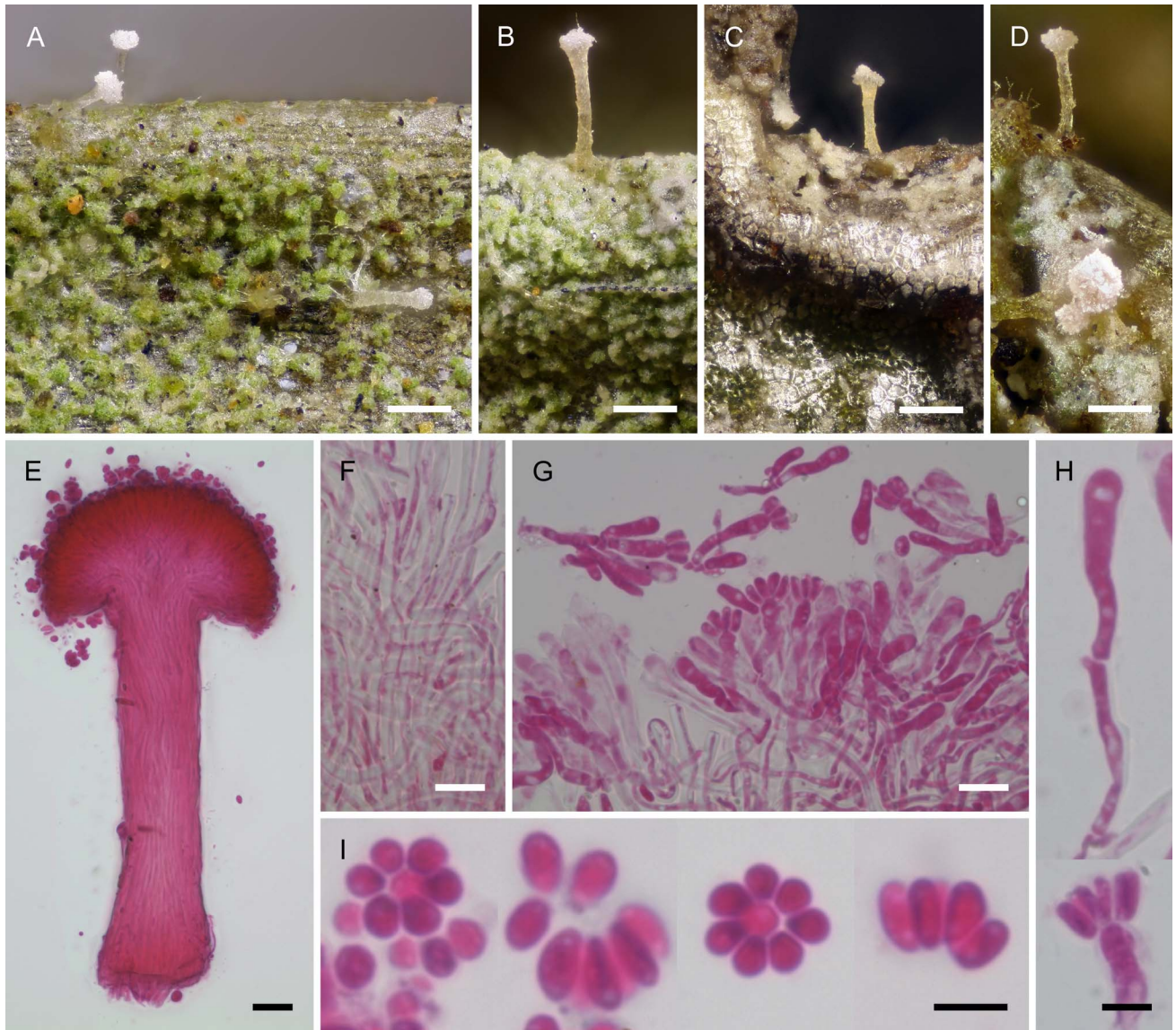


Figure 13. *Crittendenia kakouettae*. A–C. Basidiomata on the thallus of ‘*Byssoloma*’ *kakouettae*. D. Basidiomata of *C. aff. kakouettae* on the thallus of *Fellhanera bouteillei*. E. Squash preparation of basidioma. F. Thick-walled stipe hyphae. G. Mature basidia. H. Young basidium with basal clamp, and apex of mature basidium with basidiospores. I. Basidiospores. A, E–H: holotype, B, I: *van den Boom* 58880, C, *Diederich* 16490, D, *van den Boom* 56901. E–I in KOH + phloxine. Scale bars: A–D = 200 µm, E = 20 µm, F–G = 10 µm, H–I = 5 µm.

including the type, are extremely reduced. We have nevertheless decided to formally describe the new species, as three specimens, including the type, have been sequenced, and as the species is well characterized by morphology, distinct in our phylogeny, and appears to be confined to a single host species.

Additional specimens examined (all on ‘*Byssoloma*’ *kakouettae*). PORTUGAL. AZORES: Santa Maria: SE of the island, along road ER-1, between Florestal das Fontinhas and Santo Espírito, just W before Santo Espírito, 36°57.46’N, 25°03.97’W, 400

m, forest with *Cryptomeria*, on needles of *Cryptomeria*, 2019, *P. van den Boom* 58880 (BR); E of Almagreira, along road ER-1-2 to Santo Espírito, Reserva Florestal das Fontinhas, picnic area, 36°57.61’N, 25°04.40’W, 335 m, on leaf of *Camellia*, 2019, *P. van den Boom* 58949 (BR). MADEIRA: NW of Funchal, road (ER228) from Ribeira Brava to São Vicente, c. 1.5 km N of Boca da Encumeada, large picnic area with open laurisilva, including very small young trees of 2 cm diam., 32°45.64’N, 17°01.08’W, 820 m, on leaf of *Laurus*, 2012, *P. van den Boom*

47972 (BR). SPAIN. CANARY ISLANDS: Tenerife: Montañas de Anaga, Monte de las Mercedes, laurisilva along road and ridge W of Cruz del Carmen, 28°32'N, 16°17'W, 910 m, on leaves of a tree, 2007, *P. Diederich 16490* (BR); Montañas de Anaga, Monte de las Mercedes, 3.5 km on road S of Chamorga, 28.5592°N, 16.1639°W, 700 m, on leaves of a tree, 2007, *P. Diederich 19604* (BR).

Crittendenia aff. kakouettae on *Fellhanera* spp.

Fig. 13

Description. Basidiomata dispersed over the host thallus or in small groups, stipe very long and slender, pale brown, translucent, capitulum whitish, relatively broad, StH (80)[98]131–238[242](300) μm , StD (10)[17]17–35[36](50) μm , CaD (25)[34]38–76[81](100) μm , StH/StD (3.4)[4.8]5.2–9.7[10.4](14.0), CaD/StD (1.3)[1.5]1.5–3.1[3.4](5.0), CaD/StH (0.1)[0.2]0.2–0.4[0.4](0.5) (n = 42). Own thallus reduced, hyaline to brownish, gelatinous, translucent. Stipe hyphae thick-walled, 2–3.5 μm thick, septa with clamps. Basidia subcylindrical to clavate, apically wider, with a basal clamp, 7-sterigmate, wall c. 0.5 μm thick, BaL (12)[14]15–20[20](22) μm , BaD (1.7)[1.8]1.9–2.5[2.6](2.9) μm , BaApD (1.8)[2.0]2.3–3.6[3.9](4.3) μm (n = 34). Basidiospores ellipsoid, relatively small, wall thin and smooth, c. 0.5 μm thick, SpL (3.5)[4.1]4.1–5.5[5.7](7.3) μm , SpB (2.0)[2.3]2.3–3.0[3.0](3.5) μm , SpL/SpB (1.3)[1.5]1.5–2.2[2.3](2.9) (n = 144).

Distribution and hosts. Known only from the Azores (Pico, Santa Maria), on the thallus of foliicolous *Fellhanera azorica* and *F. bouteillei*.

Notes. As the Macaronesian *Crittendenia* populations growing on foliicolous lichens or on related lichens over tiny twigs are diverse, and based on our knowledge all are confined to a single host species or genus (*C. bacidinae* on *Bacidina apiahica*, *C. byssolomatis* on *Byssoloma maderense*, and *C. kakouettae* on '*Byssoloma*' *kakouettae*), the two specimens on *Fellhanera* studied by us most likely represent a distinct species. Unfortunately, both specimens are rather reduced, no sequences could be obtained, and no morphological differences to *Crittendenia kakouettae* could be observed. Further material allowing DNA sequencing must therefore be awaited before taking a decision on their taxonomic status.

Specimens examined. PORTUGAL. AZORES: Pico: ESE of Madalena, NNW slope of volcano Pico, SSW of Santa Luzia, N of main road ER-3, along small road from Redondo to Lourenço Nunes, 38°30.12'N, 28°25.18'W, 770 m, on a needle of *Cryptomeria*, on *Fellhanera bouteillei*, 2017, *P. van den Boom 56901* (BR). Santa Maria: SE of the island, along road ER-1 between Santo Espirito and Castelo, Calheta, 36°56.72'N, 25°01.96'W, 255 m, on leaf of *Buxus* in a garden, on *F. azorica*, 2019, *P. van den Boom 58920* (BR).

Crittendenia lecanorae Diederich & Etayo, *sp. nov.*

Fig. 14

MYCOBANK MB 842914

*Characterized by the medium-sized basidiomata, mainly 92–219 μm tall, the slender stipe, 22–43 μm diam., medium-sized ellipsoid basidiospores, 5.4–6.9 \times 3.3–4.5 μm , the relatively long, mainly 3–4-sterigmate basidia, 45–65 μm long, and the host choice, corticolous *Lecanora* species.*

TYPE: BRAZIL. ALAGOAS: c. 35 km N of Maceió, 9°30'S, 35°32'W, 1 m, in a mangrove with *Rhizophora mangle* and *Avicennia*, on *Lecanora*, 1 Aug. 1993, *K. Kalb 27958* & *A. Kalb* (holotype, wis!).

Description. Basidiomata aggregated on the thallus of *Lecanora* species, stipe relatively slender, pale brown, capitulum whitish to brownish, StH (80)[104]92–219[308](320) μm , StD (10)[21]22–43[44](60) μm , CaD (20)[32]32–79[108](120) μm , StH/StD (2.3)[3.0]2.8–7.5[10.9](12.4), CaD/StD (0.7)[1.0]1.2–2.3[3.1](4.0), CaD/StH (0.1)[0.2]0.3–0.5[0.5](0.7) (n = 46). Own thallus brownish, gelatinous, translucent, spreading over small areas of the host thallus. Stipe hyphae thick-walled, 2.0–3.5 μm thick, septa with clamps. Basidia subcylindrical, relatively long, apically wider, with a basal clamp, 3–4-sterigmate, thin-walled, BaL (43)45–65(67) μm (n = 4), BaD (1.6)1.7–2.4(2.6) μm (n = 9), BaApD (2.3)2.5–3.7(3.9) μm (n = 9). Basidiospores ellipsoid to broadly ellipsoid, wall c. 0.5 μm thick, smooth, SpL (4.5)[5.1]5.4–6.9[6.9](8.9) μm , SpB (2.6)[3.0]3.3–4.5[4.6](5.5) μm , SpL/SpB (1.2)[1.4]1.4–1.8[2.1](2.3) (n = 56).

Etymology. From *Lecanora*, the host lichen genus.

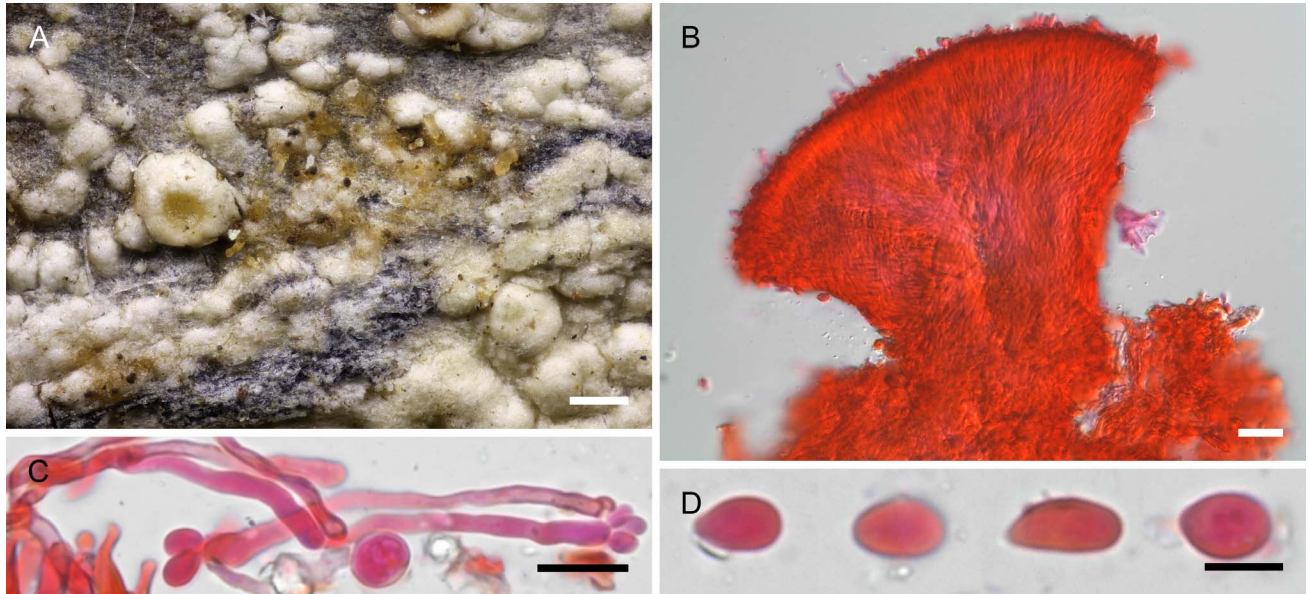


Figure 14. *Crittendenia lecanorae*, holotype. **A.** Brownish own thallus on the thallus of *Lecanora* sp., with several basidiomata. **B.** Squash preparation of basidioma. **C.** Mature basidia, some with attached basidiospores. **D.** Basidiospores. B–D in KOH + phloxine. Scale bars: A = 200 µm, B = 20 µm, C = 10 µm, D = 5 µm.

Distribution and hosts. Known from Argentina and Brazil, on unidentified corticolous *Lecanora* species.

Notes. Among the *Crittendenia* species with 4-sterigmate basidia, and basidiospores with a length/breadth ratio below 1.8, this species is distinguished by the basidiomata frequently arising in groups over olivaceous to brownish own thalli. It differs from the similar *C. lecidellae* by basidiomata with a constantly slender stipe and a smaller capitulum. Unfortunately, none of the two known specimens could be successfully sequenced. It is interesting to note that the specimens show clearly delimited, brownish thalli, from which the basidiomata arise. These are flattened in the Brazilian specimen and elevated to subspherical in the Argentinian specimen. Sterile *Crittendenia* thalli, devoid of basidiomata, are frequently present. The Argentinian specimen had already been published by Etayo & Breuss (1998) as *Chionosphaera* cf. *apobasidialis*.

Additional specimen examined. ARGENTINA. PROV. TUCUMÁN: Dept. Famailla/Monteros, c. 7 km S of El Mollar along road from Tafi del Valle to Famailla, 1600 m, epiphytic on bark of fresh stems of pasture fence, on *Lecanora*, 1993, W. Till 10242 (LI 321179, herb. Etayo 18145).

Crittendenia lecidellae Diederich, Etayo & Millanes, sp. nov. **Fig. 15**

MYCOBANK MB 842915

Characterized by the medium-sized basidiomata, mainly 88–212 µm tall, the variable, narrow to broad stipe, 22–102 µm diam., medium-sized ellipsoid basidiospores, 4.2–6.8 × 3.1–4.9 µm, the relatively long, mainly 4-sterigmate basidia, 40–71 µm long, and the host choice, Lecidella elaeochroma.

TYPE: CANADA. BRITISH COLUMBIA: bridge at Boston Bar, on *Acer macrophyllum*, on *Lecidella elaeochroma*, 7 May 2009, C. Björk 17999 (holotype, UBC!).

Description. Basidiomata dispersed over the thallus of *Lecidella elaeochroma*, often aggregated in small groups, stipe extremely variable, from relatively slender to short and broad, pale brown, capitulum whitish to pinkish, StH (50)[67]88–212[295](400) µm, StD (20)[26]22–102[175](250) µm, CaD (15)[26]39–125[201](270) µm, StH/StD (0.3)[0.6]1.2–5.3[7.8](10.4), CaD/StD (0.7)[0.8]1.0–1.9[2.5](3.2), CaD/StH (0.1)[0.1]0.2–1.2[1.9](3.3) (n = 178). Own thallus brownish to olivaceous, gelatinous, translucent, spreading over

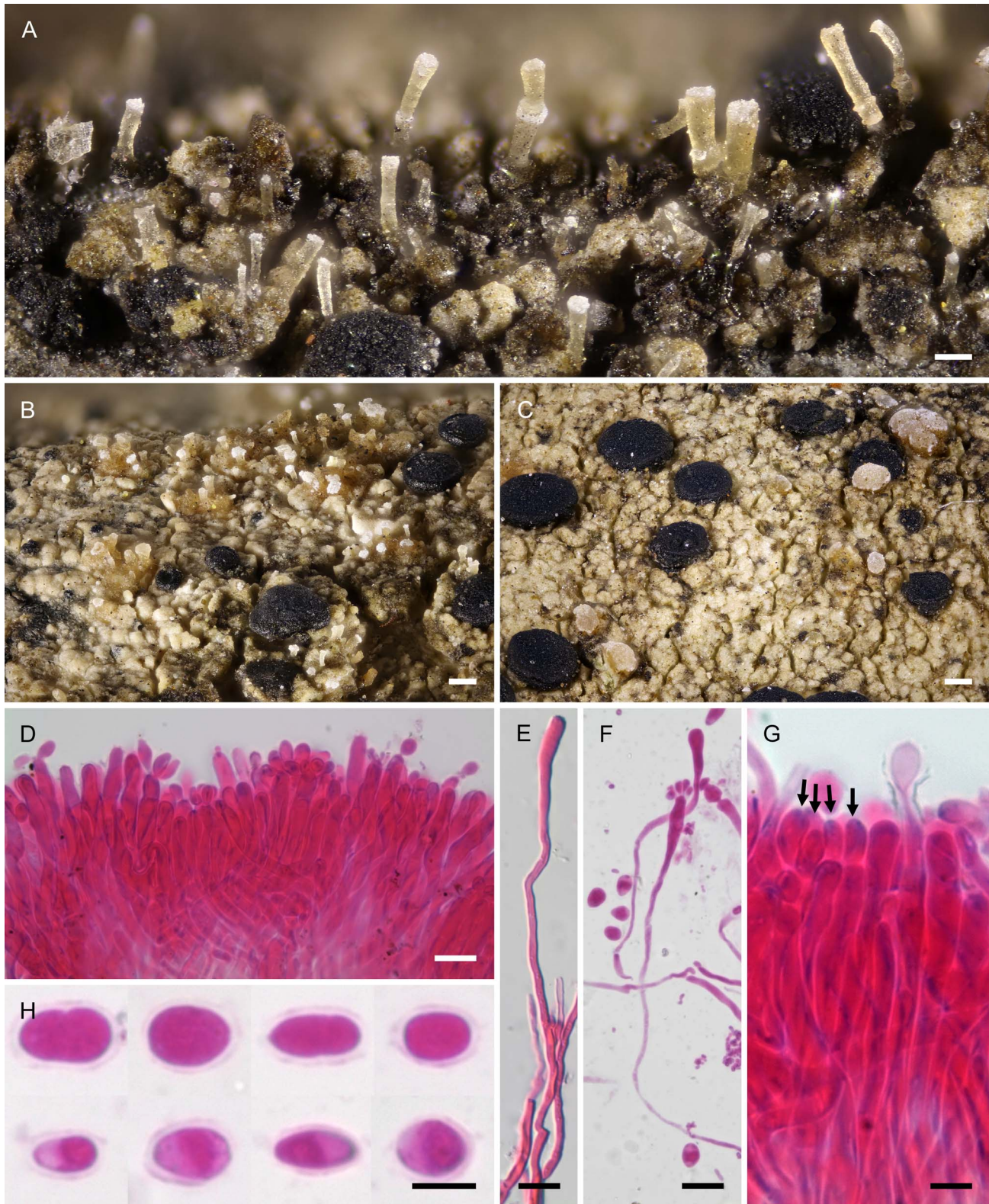


Figure 15. *Crittendenia lecidellae*. A–C. Basidiomata on the thallus of *Lecidella elaeochroma*; in A tall and narrow, in C broad and short, in B grouped over brown own thalli. D. Mature basidia. E. Immature basidium with basal clamp. F. Mature basidia with basidiospores. G. Abnormal basidium-like ‘sporophore’ producing one spore, both elements surrounded by a perispore sac; arrows point to real basidiospores. H. Thick-walled basidiospores. A, D–E, G: holotype, B, F, H: *Zamora* (c), C: *Brackel 6418*. D–G in KOH + phloxine. Scale bars: A = 100 μ m, B–C = 200 μ m, D–F = 10 μ m, G–H = 5 μ m.

small or larger areas of the host thallus, frequently including algal cells and then representing simple lichen thalli. Stipe hyphae thick-walled, 2.0–3.7 μm thick, septa with clamps. Basidia subcylindrical, relatively long, apically slightly to distinctly wider, with a basal clamp, (1?)4(6)-sterigmate, thin- to thick-walled, BaL (28)[31]40–71[88](96) μm (n = 60), BaD (1.6)[1.7]1.8–2.5[3.3](3.9) μm (n = 66), BaApD (2.2)[2.5]2.8–3.9[4.3](4.4) μm (n = 64). Basidiospores ellipsoid to broadly ellipsoid, wall 0.5–1 μm thick, SpL (2.9)[3.4]4.2–6.8[8.0](9.0) μm , SpB (2.1)[2.5]3.1–4.9[5.7](7.7) μm , SpL/SpB (1.0)[0.9]1.1–1.7[2.6](2.8) (n = 373).

Etymology. From *Lecidella*, the host lichen genus.

Distribution and host. Known from Europe (France, Italy, Norway, Spain, Switzerland and the UK), the Canary Islands (La Gomera), North America (Canada: British Columbia) and New Zealand, always on the thallus of *Lecidella elaeochroma*.

Notes. This species is similar to *Crittendenia lecanorae*, from which it differs by basidiomata with a frequently much more robust stipe and a larger capitulum. Two specimens, including the holotype, have been sequenced. In our phylogeny, they group together, and the clade formed by both is sister to *C. lichenicola*, but with relatively low support (Fig. 1). Basidiomata usually grow over brownish to olivaceous swellings that sometimes contain an own algal photobiont and thus represent simple lichenized thalli (Fig. 4). Sterile thalli, without basidiomata, are often present. Specimen *Coppins 10202* had already been studied by Roberts (1997) who provisionally referred it to *C. coppinsii*. The specimen from La Gomera had already been published and illustrated as *Chionosphaera* cf. *apobasidialis* by Diederich (1996) and Etayo (1996), and the Italian specimen by Brackel (2015) as *C. cf. apobasidialis*.

Additional specimens examined (all on *Lecidella elaeochroma*). FRANCE. ORNE: Giel-Courteilles, La Rançonnière, 2017, *D. Vaudoré s.n.* (completely consumed by analysis; photos and measurements seen by us). ITALY. MARCHE: Ascoli-Piceno, Parco Nazionale dei Monti Sibillini, Val Tenna W Montefortino, Gola dell'Infernaccio, 42°55'07"N, 13°16'26"E, 905 m, on *Acer campestre*, 2011, *W. v. Brackel 6418* (herb. von Brackel). NEW ZEALAND. SOUTH ISLAND: Southland, Fiordland

National Park, Lake Monowai, 45°51'S, 167°29'E, 200 m, 1981, *H. Mayrhofer* (wis [ex herb. Kalb 27184]). NORWAY. HORDALAND: Voss, W of Strondaelva, along road E16, 0.5 km N of jct (bridge) road to Gjøastein, 60°44'N 6°30'E, 120 m, on *Sorbus aucuparia*, 1992, *T. Tønsberg 17533* (BG L-71712). SPAIN. CANARY ISLANDS: La Gomera, Hermigua, mirador de El Bailadero, 1010 m, on *Myrica faya*, 1994, *J. Etayo 13304* (herb. Etayo, [!P. Diederich in 1994, specimen lost at return of loan]). NAVARRA: Unzué, Peña Unzué, subida desde el pueblo, carrascal en ladera, 42°39'23"N, 1°36'54"W, 900 m, on *Quercus rotundifolia*, 2012, *J. Etayo 27839* (herb. Etayo). MADRID: Horcajo de la Sierra, 41°03'34"N, 3°35'17"W, 1620 m, on *Fraxinus angustifolia*, 2011, *J.C. Zamora* (G). SWITZERLAND. BERN: Oberwil, Rossberg, Heideweideni, 46°38'36.2"N, 7°27'25.9"E, 1090 m, on branches of *Fraxinus*, 2012, *E. Zimmermann 815* (herb. Zimmermann [photos seen]). UK. SCOTLAND: VC 101, Kintyre, Knapdale, Taynish NNR, Cmpt 5, avenue N of Taynish House, 10 m, on *Ulmus* branch, 2007, *B.J. Coppins 22371* (E); VC 105, West Ross, Dundonnell, S of Dundonnell House, E side of river, 50 m, on *Fraxinus* branches, 2007, *B.J. Coppins 22464* (E); VC 108, Sutherland, Bettyhill, Invernaver NNR, on *Corylus*, 1983, *B.J. Coppins 10202* (E).

Crittendenia lichenicola (Alstrup, B.Sutton & Tønsberg) Diederich, Millanes & Wedin
In Millanes et al., *Lichenologist* 53: 113 (2021); *Chionosphaera lichenicola* Alstrup, B.Sutton & Tønsberg, *Graphis Scripta* 5: 97 (1993). TYPE: NORWAY. HORDALAND: Fjell, Lokøy, the peninsula S of Storafjellet, alt. 10 m, on *Sorbus aucuparia*, on *Micarea prasina* s.l., 27 Aug. 1989, *T. Tønsberg 12000* (holotype, BG L-73887!; isotypes, c!, κ[former IMI!]). **Fig. 16**

Description. Basidiomata dispersed over the thallus and apothecia of *Micarea* species, stipe long and slender, pale brown, translucent, capitulum whitish, StH (65)[93]96–165[166](230) μm , StD (10)[15]16–27[27](40) μm , CaD (20)[30]32–65[72](105) μm , StH/StD (3.3)[4.5]4.6–8.2[8.4](12.0), CaD/StD (1.3)[1.5]1.6–3.1[3.3](4.2), CaD/StH (0.2)[0.2]0.3–0.5[0.6](0.9) (n = 58). Own thallus rather indistinct, hyaline to brownish. Stipe hyphae relatively thick-walled, 2–3.5 μm thick. Basidia subcylindrical to clavate, rather short,

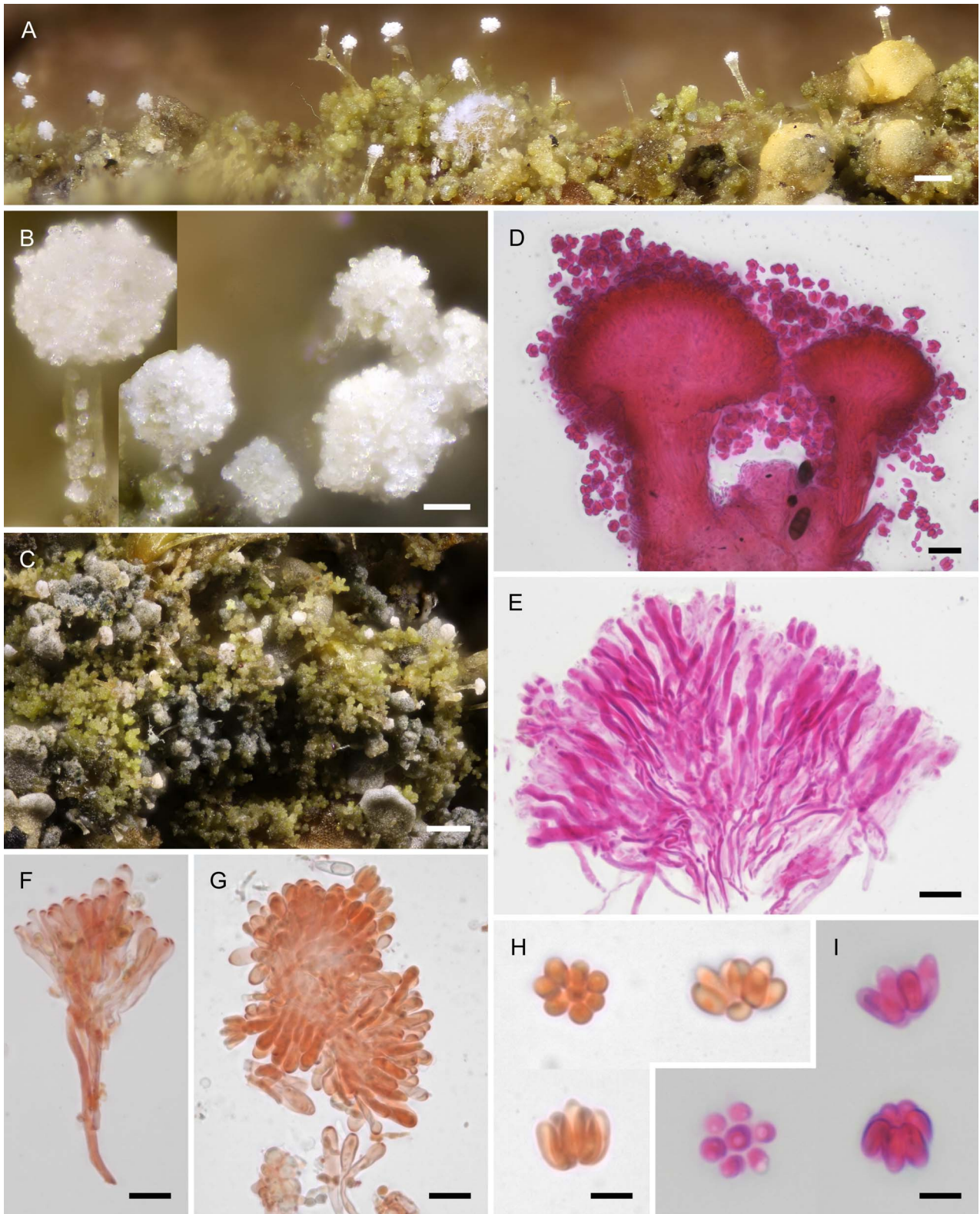


Figure 16. *Crittendenia lichenicola*. **A.** Basidiomata on the thallus of *Micarea prasina* s.l. **B.** Idem, at a higher magnification, showing groups of basidiospores produced each from one basidium, covering the capitulum, with some attached to the stipe. **C.** Basidiomata on the thallus of *M. micrococca*. **D.** Squash preparation of basidiomata covered by groups of basidiospores. **E.** Mature basidia. **F.** Basidia originating from a single stipe hypha, proliferating at the original basal clamp. **G.** Mature basidia with basidiospores. **H–I.** Groups of 7–8 basidiospores originating from individual basidia, each group with one spore moved to the centre. **A–B, D–I:** holotype, **C:** *Coppins 21517*. **D–E, I** in KOH + phloxine, **F–H** in ammoniacal Congo Red. Scale bars: **A** = 100 μ m, **B** = 20 μ m, **C** = 200 μ m, **D** = 20 μ m, **E–G** = 10 μ m, **H–I** = 5 μ m.

apically wider, with a basal clamp, 5–8-sterigmate, wall c. 0.5 μm thick before and during spore production, 0.5–1 μm after spore production, BaL (19)[23]21–39[55](54) μm , BaD (1.8)[2.0]2.0–2.6[2.6](3.0) μm , BaApD (2.0)[2.5]2.5–3.8[4.0](4.5) μm (n = 29). Basidiospores elongate ellipsoid, rather long, thin-walled, smooth, SpL (3.9)[4.9]5.0–6.9[7.0](8.1) μm , SpB (2.4)[2.7]2.7–3.7[3.8](5.4) μm , SpL/SpB (1.2)[1.4]1.5–2.4[2.4](2.8) (n = 128).

Distribution and hosts. Known from Norway and Scotland, both on the thallus of *Micarea* gr. *prasina* (incl. *M. micrococca*).

Notes. Although the type specimen on *Micarea prasina* s.l. is extremely rich, the identity and delimitation of this species was poorly understood. Fortunately, we were able to obtain sequences from the over 30-yr-old type, and these group together with those of a Scottish specimen on *M. micrococca*, thus suggesting a fungus confined to *Micarea* hosts. The many other *Crittendenia* specimens examined with 7–8-sterigmate basidia all differ by minor morphological differences, and those sequenced appear in different places in our phylogenetic tree (Fig. 1). *Crittendenia lichenicola* differs from the new *C. kakouettae* by the longer basidia, and from the other species with 7–8-sterigmate basidia by the particularly slender basidiomata. The type specimen had been re-studied by Kirschner et al. (2001) who observed basidia $20\text{--}46 \times 3\text{--}5 \mu\text{m}$ and basidiospores $5\text{--}7 \times 2\text{--}3 \mu\text{m}$. The Scottish specimen had already been published by Aguirre-Hudson & Spooner (2005).

Additional specimen examined. UK. SCOTLAND: Isle of Skye, VC 104, North Ebudes, access road to Kinloch Lodge Hotel, Kinloch & Kyleakin Hills SSSI, 10 m, in wet *Betula-Salix* woodland, on *Betula*, on *Micarea micrococca*, 2005, B.J. Coppins 21517 (E).

Crittendenia lopadii Diederich, Holien & Tønsberg, *sp. nov.* **Fig. 17**

MYCOBANK MB 842916

*Characterized by 7-sterigmate basidia, mainly 30–50 μm long, basidiospores mainly $4.2\text{--}6.3 \times 3.1\text{--}4.2 \mu\text{m}$, a stipe 104–205 μm long and 24–58 μm diam., and the host choice, *Lopadium disciforme*.*

TYPE: U.S.A. ALASKA: Kodiak Island Borough, Kodiak Island E, along road to Anton Larsen Bay, bank

of Red Cloud River, $57^{\circ}49.0'N$, $152^{\circ}37.6'W$, 20 m, on trunk of *Alnus*, on *Lopadium disciforme*, 15 May 1991, T. Tønsberg 15250 (holotype, BG L-69060!).

Description. Basidiomata dispersed over the thallus of *Lopadium disciforme*, stipe relatively slender, pale brown, capitulum whitish to brownish, StH (60)[95]104–205[213](280) μm , StD (15)[20]24–58[80](135) μm , CaD (25)[40]55–115[120](150) μm , StH/StD (1.2)[2.3]2.8–5.3[5.6](7.7), CaD/StD (0.6)[1.2]1.6–2.7[2.8](3.5), CaD/StH (0.3)[0.3]0.4–0.8[0.9](1.1) (n = 59). Own thallus brownish, gelatinous, translucent, spreading over small areas around basidiomata, often swollen. Stipe hyphae thick-walled, 2.5–4 μm thick, clamps not observed. Basidia subcylindrical, apically wider, with a basal clamp, 7-sterigmate, thin-walled, BaL (18)[29]30–50[59](65) μm , BaD (1.5)[1.6]1.6–2.5[2.8](3.2) μm , BaApD (1.6)[2.1]2.2–3.8[4.4](5.2) μm (n = 21). Basidiospores ellipsoid to broadly ellipsoid, wall thin to thick, some with a distinct perispore sac, SpL (3.2)[4.1]4.2–6.3[7.2](8.4) μm , SpB (2.7)[3.0]3.1–4.2[4.2](6.2) μm , SpL/SpB (1.0)[1.1]1.1–1.8[2.1](2.4) (n = 186).

Etymology. From *Lopadium*, the host lichen genus.

Distribution and host. Known from North America (Alaska: Kodiak Island) and Norway, always on the thallus of *Lopadium disciforme*, frequently on twigs of *Picea abies*.

Notes. The new species resembles *Crittendenia bryostigmatis*, but is distinguished by longer basidiospores, frequently over 5 μm in length, and longer basidia, frequently over 39 μm . It appears to be confined to thalli of *Lopadium disciforme*. The host thalli are often sterile and tiny, commonly intermixed with other crustose lichen thalli, and therefore may easily be overlooked or mistaken for thalli of other lichens. Unfortunately, no sequences could be obtained, as all specimens examined were too old.

Additional specimens examined (all on *Lopadium disciforme*, on twigs of *Picea abies*). NORWAY. TRØNDELAG: Sør-Trøndelag, Melhus, S of Korsvegen, N-facing slope E of river Gresja, 190 m, 1998, O. Hilmo (TRH); Sør-Trøndelag, Agdenes, E of Ingdalsætra by river Sæterelva, 120 m, 1995, H. Holien 6546b (TRH); Sør-Trøndelag, Agdenes, NW-

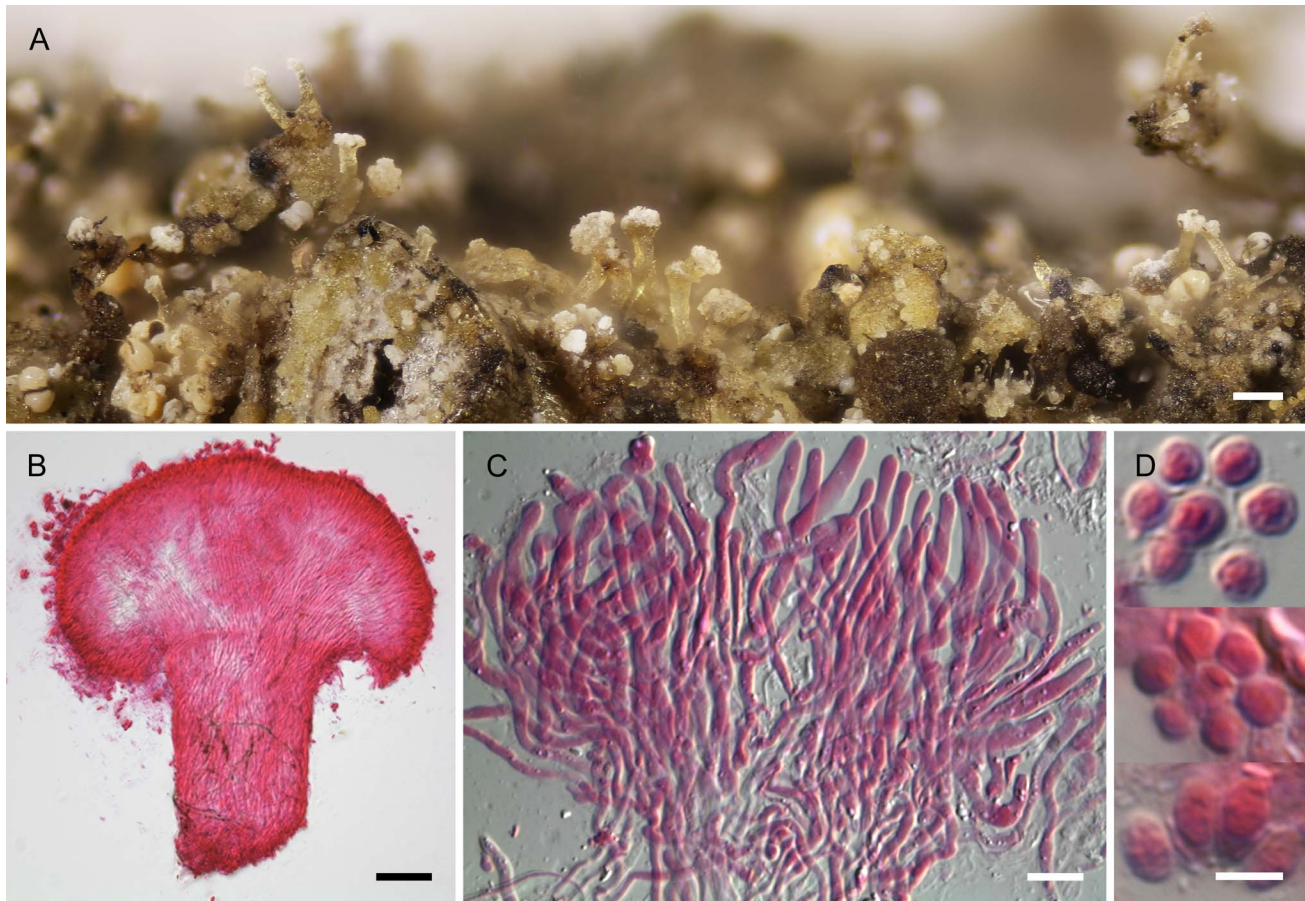


Figure 17. *Crittendenia lopadii*. A. Basidiomata on the thallus of *Lopadium disciforme*. B. Squash preparation of a basidioma. C. Mature basidia. D. Groups of 7 thick-walled basidiospores, some with a perisporeal sac. A–B, D: *Hilmo*, C: holotype. B–D in KOH + phloxine. Scale bars: A = 100 μ m, B = 50 μ m, C = 10 μ m, D = 5 μ m.

facing slope by river Ingdalselva, 120 m, 1995, *H. Holien* 6562d (κ); Nord-Trøndelag, Overhalla, W of Foss in a ravine, 80 m, 1997, *H. Holien* 7090 (TRH).

Crittendenia parvispora Diederich, van den Boom & Millanes, *sp. nov.* **Fig. 18**

MYCOBANK MB 842917

*Characterized by 7–8-sterigmate basidia, mainly 22–36 μ m long, small and particularly narrow basidiospores, 3.7–5.2 \times 2.3–3.2 μ m, a stipe 120–193 μ m long and 23–46 μ m diam., and the host choice, corticolous *Bacidia* species.*

Type: FRANCE. FINISTÈRE: Quimperlé, forêt de Toulfoën (= forêt de Carnoët), in a mixed forest with mainly *Fagus* and *Quercus*, on a thin branch of *Abies grandis*, on *Bacidia laurocerasi*, 13 Apr. 2021, Y. Quelen (holotype, BR!).

Description. Basidiomata aggregated in small or

larger groups on the thallus of *Bacidia* species, stipe slender to sometimes relatively robust, pale brown, slightly translucent, capitulum pinkish white, much broader than the stipe, StH (80)[108]120–193[198](230) μ m, StD (20)[22]23–46[52](80) μ m, CaD (30)[31]38–116[150](200) μ m, StH/StD (2.0)[3.1]3.5–6.1[6.9](7.6), CaD/StD (1.0)[1.3]1.5–3.0[3.4](4.5), CaD/StH (0.2)[0.3]0.3–0.7[0.9](1.3) (n = 46). Own thallus brownish, gelatinous, translucent, developed around basidiomata. Stipe hyphae thick-walled, 1.5–3.5 μ m thick, septa with clamps. Basidia subcylindrical to clavate, apically wider, with a basal clamp, 7–8-sterigmate, wall c. 0.5 μ m thick before and during spore production, BaL (17)[19]22–36[39](45) μ m (n = 52), BaD (1.4)[1.7]1.8–2.8[3.3](4.3) μ m (n = 59), BaApD (1.7)[2.3]2.5–3.7[4.1](4.5) μ m (n = 58). Basidiospores small, subspherical to broadly ellipsoid, wall usually thin and smooth, SpL (2.9)[3.7]3.7–

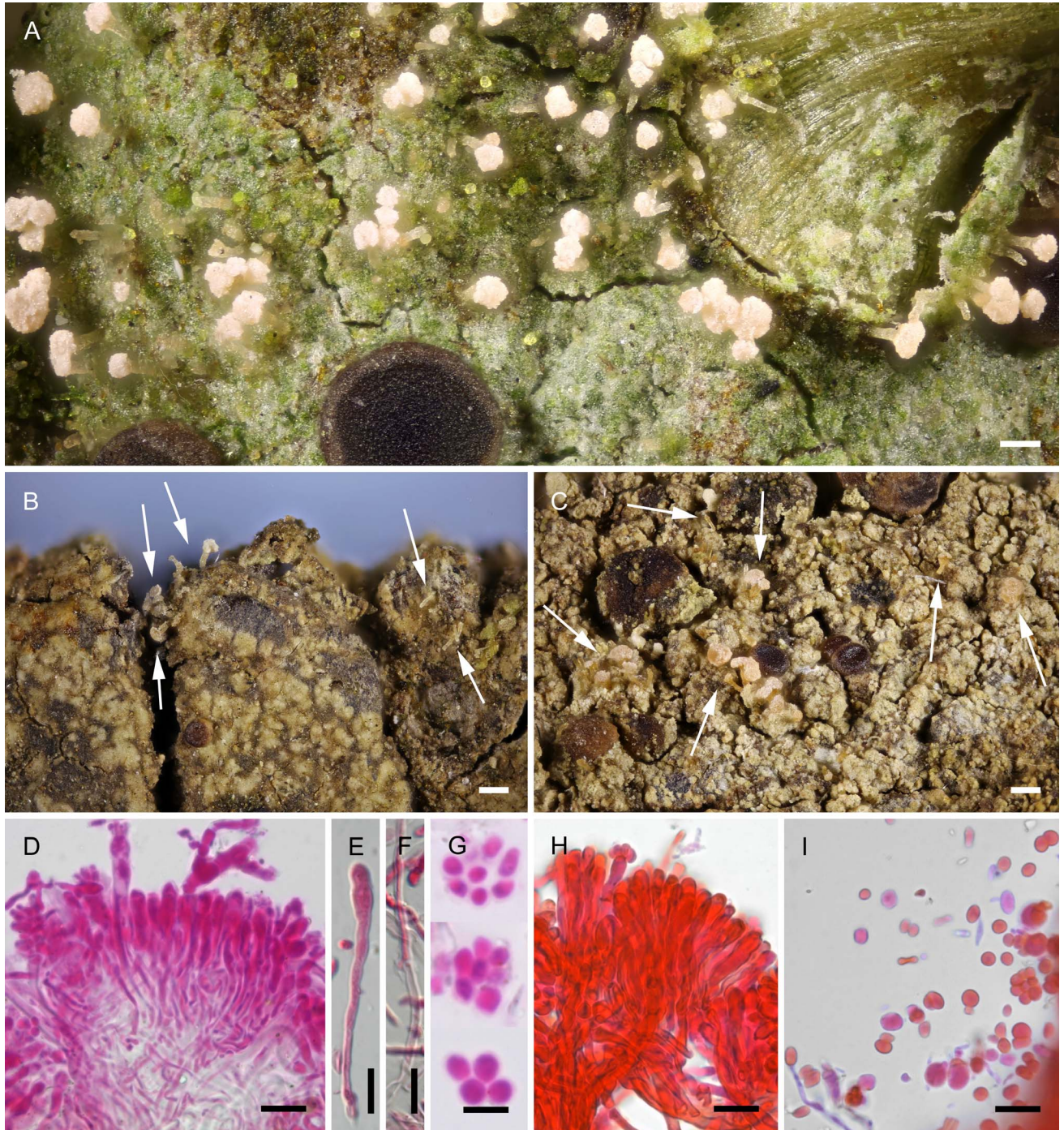


Figure 18. *Crittendenia parvispora*. **A.** Basidiomata on the thallus of *Bacidia laurocerasi*. **B.** Basidiomata on the thallus of *B. polychroa*. **C.** Basidiomata on the thallus of *Bacidia* sp. Arrows in B and C point to basidiomata. **D.** Mature basidia. **E.** Mature basidium with basal clamp. **F.** Stipe hypha with septum and clamp connection. **G.** Groups of basidiospores. **H.** Mature basidia with basidiospores. **I.** Thin-walled basidiospores. A: holotype, B, D–G: *van den Boom* 36943, C, H–I: *Kalb* 26946. D–G in KOH + phloxine, H–I in KOH + phloxine + Congo Red. Scale bars: A = 100 μ m, B–C = 200 μ m, D–F, H–I = 10 μ m, G = 5 μ m.

5.2[5.9](7.0) μm , SpB (1.9)[2.1]2.3–3.2[3.4](4.1) μm , SpL/SpB (1.0)[1.3]1.3–2.0[2.3](3.0) ($n = 226$).

Etymology. From *parvus*, small, and *spora*, designating the particularly small basidiospores.

Distribution and hosts. Known from France (Brittany), Cape Verde and Venezuela, all on corticolous *Bacidia* s.str. species, including *B. laurocerasi* and *B. polychroa*.

Notes. This species is distinguished from all other known *Crittendenia* species by the particularly narrow basidiospores, less than 3.2 μm broad. It has a remarkably wide geographical distribution, being known from Europe, Africa and South America. The hosts are *Bacidia* s.str. species, although the Venezuelan host could not be identified to species level. Two sequences have been obtained, including from the type specimen. The Cape Verde specimen had already been published as *Chionosphaera* cf. *apobasidialis* by van den Boom (2012).

Additional specimens examined. CAPE VERDE. SÃO VICENTE: Monte Verde, just below top of the mountain, 16°52.2'N, 24°56.0'W, 700 m, NW slope with acidic outcrops, shrubs and scattered small trees, on a shrub, on *Bacidia polychroa*, 2006, *P. van den Boom* 36943 (BR). VENEZUELA. MERIDA: Distr. Rivas Dávila, Páramo la Negra, c. 20 km W of Bailadores, 8°15'N, 71°50'W, 2750 m, on *Bacidia*, 1989, *K. Kalb* 26946 (WIS).

Crittendenia physciophila Diederich, Pinault, Etayo & Millanes, *sp. nov.* **Fig. 19**

MYCOBANK MB 842918

*Characterized by the medium-sized robust basidiomata, mainly 75–157 μm tall, the broad stipe, 51–153 μm diam., the frequently poorly developed capitulum, medium-sized ellipsoid basidiospores, 5.2–7.0 \times 3.5–4.9 μm , the relatively long, 3–4-sterigmate basidia, 42–72 μm long, and the host choice, *Phaeophyscia*, *Physcia* and *Physciella* species.*

TYPE: FRANCE. PUY-DE-DÔME: Châteaugay, 45.8504°N, 3.0855°E, 500 m, on *Physcia adscendens*, 26 Mar. 2020, *P. Pinault* s.n. (holotype BR!; isotype BR!).

Description. Basidiomata dispersed or aggregated in small groups on the thallus of *Phaeophyscia*, *Physcia* or *Physciella* species, stipe rarely slender to

most often rather robust, relatively short, often irregular in form, pale to orange brown, often with a rough or irregular surface, slightly translucent, capitulum whitish to pinkish or orange brown, often not well developed and then narrower than the stipe, StH (35)[47]75–157[198](240) μm , StD (30)[33]51–153[191](300) μm , CaD (30)[31]54–185[243](350) μm , StH/StD (0.3)[0.5]0.7–2.0[3.4](4.0), CaD/StD (0.7)[0.6]0.9–1.4[1.7](2.3), CaD/StH (0.2)[0.3]0.5–1.7[2.9](3.6) ($n = 107$). Own thallus brownish, gelatinous, translucent, sometimes reduced or immersed in the thallus of the host lichen, occasionally well developed and swollen. Stipe hyphae thick-walled, 2–3.5 μm thick, septa with clamps. Basidia subcylindrical to clavate, apically wider, with a basal clamp, 3–4-sterigmate, wall c. 0.5 μm thick before and during spore production, 0.5–1 μm after spore production, BaL (37)[38]42–72[93](98) μm ($n = 54$), BaD (1.5)[1.6]2.0–3.2[3.8](4.0) μm ($n = 75$), BaApD (1.8)[2.1]2.5–3.8[4.6](4.8) μm ($n = 78$). Basidiospores ellipsoid, wall usually thin or slightly thickened and smooth, SpL (3.7)[4.8]5.2–7.0[7.6](9.4) μm , SpB (2.5)[3.0]3.5–4.9[5.6](7.3) μm , SpL/SpB (1.1)[1.1]1.2–1.7[1.9](2.5) ($n = 483$).

Etymology. From *Physcia*, one of the host lichen genera, and *-philus*, *-loving*, designating the predilection for inhabiting *Physcia* species.

Distribution and hosts. Known from France, Italy, Luxembourg, Spain and the U.S.A. (Massachusetts), on the thalli of *Phaeophyscia orbicularis*, *P. rubropulchra*, *Physcia adscendens*, *P. leptalea*, *P. tenella* and *Physciella chloantha*.

Notes. Among the *Crittendenia* species with 3–4-sterigmate basidia and ellipsoid basidiospores with a length/breadth ratio < 1.7 , the new species is distinguished by the short and broad basidiomata mostly arising singly, and the relatively small, often reduced capitulum. We were surprised that specimens on the three host genera *Phaeophyscia*, *Physcia* and *Physciella* were genetically and morphologically so similar that they need to be regarded as a single species. Nevertheless, the small number of available specimens, especially on *Phaeophyscia*, and the poor condition of some, does not exclude the possibility of a complex of several morphologically similar species, each confined to a single host genus.

Specimens of this species had already been published as *Chionosphaera apobasidialis* by Etayo

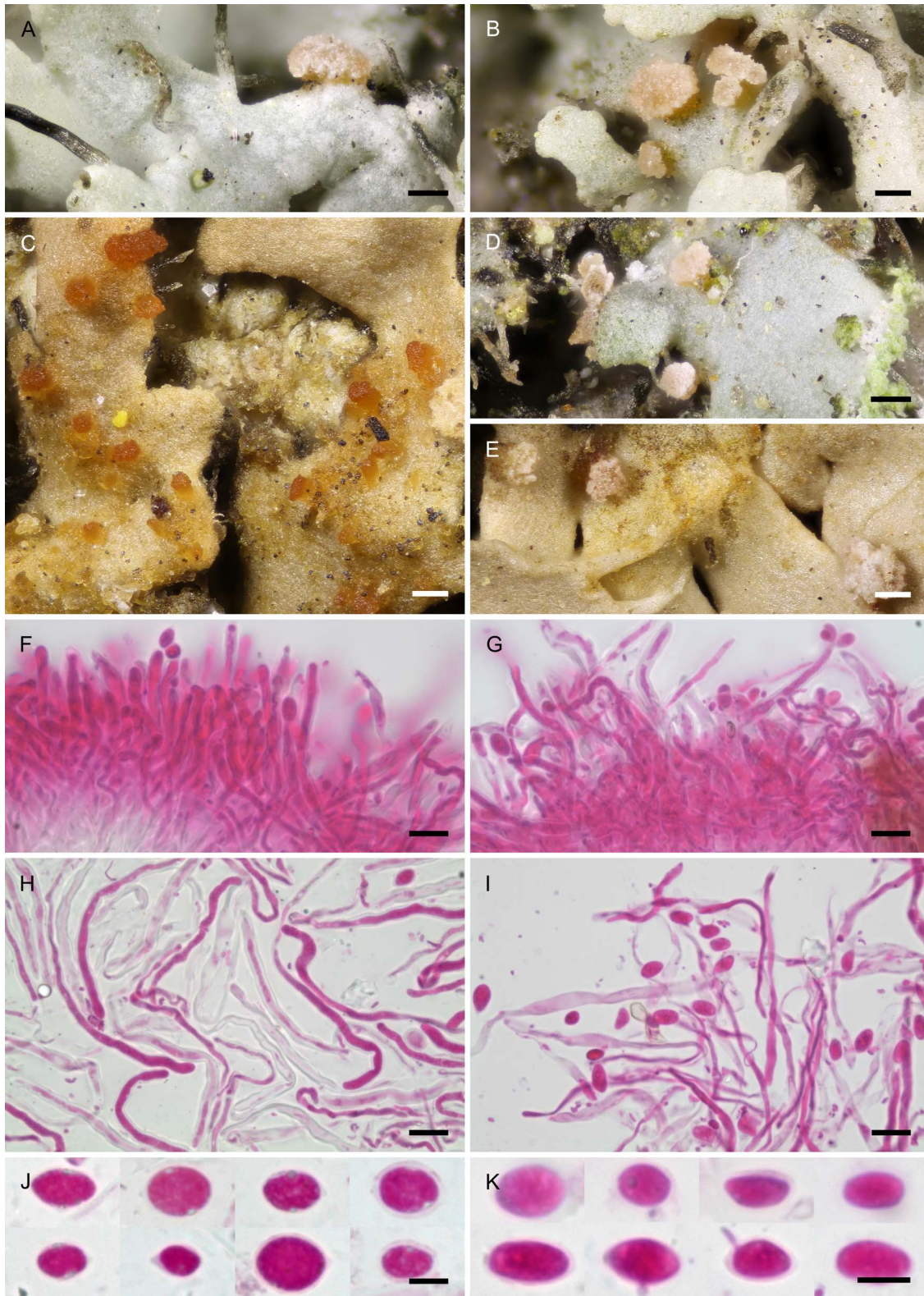


Figure 19. *Crittendenia physciiphila*. A–B. Basidiomata on the thallus of *Physcia adscendens*. C. Basidiomata on the thallus of *Phaeophyscia rubropulchra*. D. Basidiomata on the thallus of *Phaeophyscia orbicularis*. E. Basidiomata on the thallus of *Physciella chloantha*. F–I. Mature basidia and basidiospores. J–K. Basidiospores. A–B, J: holotype, C: Buck 27763, D: Pinault (Châteaugay, on *P. orbicularis*), E: Etayo 18287, F–I: Pinault (Cournols), J: van den Boom 53507. F–K in KOH + phloxine + Congo Red. Scale bars: A–E = 100 μ m, F–I = 10 μ m, J–K = 5 μ m.

(2004, 2009), Brackel (2015) and van den Boom (2021). Bricaud et al. (2009) mentioned *C. apobasidialis* as diagnostic for foliicolous *Fellhanera bouteillei* communities in southern France; this information is, however, misleading, as the authors never saw this fungus, but instead copied the information from Llop & Gómez-Bolea (2006) (Bricaud, pers. comm., 12/05/2020). The latter authors reported the species as foliicolous on *Buxus* leaves in Spain, Barcelona, Osona, El Brull, stream of Picamena, and Girona, Garrotxa, Montagut, Cal Quic (Oix); all our efforts to locate the corresponding specimens were unsuccessful (Dr. Antoni Sánchez i Cuxart, curator of BCN, and Dr. A. Gómez-Bolea and Dr. E. Llop, collectors, pers. comm., 05/10/2020); these authors did not reveal the identify of the hosts, but as we have examined another specimen from Oix on foliicolous *Physciella chloantha*, we assume that both specimens may belong to *Crittendenia physciiphila*.

Additional specimens examined. FRANCE. PUY-DE-DÔME: Cournols, 45.6474°N, 3.0355°E, 800 m, on *Physcia adscendens*, 2020, *P. Pinault s.n.* (BR); Châteaugay, c. 1 km NE des Caves, 45.8602°N, 3.0995°E, 500 m, on *Phaeophyscia orbicularis*, 2020, *P. Pinault s.n.* (BR). ITALY. LAZIO: Prov. di Roma, Monti Simbruini, between Livata and Campaegli, below Passo delle Pecore, 41°56'47"N, 13°08'27"E, 1350 m, on *Acer pseudoplatanus*, on *Physcia leptalea*, 2013, *W. v. Brackel 6731* (herb. von Brackel). LUXEMBOURG. Lamadelaine, Fuussbësch, 49.5408°N, 5.8696°E, 345 m, on *Salix*, on *Physcia tenella*, 2008, *P. Diederich 16746* (BR). SPAIN. CATALONIA: W of Oix, Cal Quic, along unpaved road near brooklet, 42°16.48'N, 2°29.87'E, 470 m, on foliicolous *Physciella chloantha*, 2015, *P. van den Boom 53507* (BR). NAVARRA: Oronoz-Mugaire, valle de Bertizarana, Señorío de Bértiz, 200 m, on *P. chloantha*, 2000, *J. Etayo 17385* (herb. Etayo); Urdax, cercanías de la cueva, 50 m, on *Salix*, on *P. chloantha*, 2001, *J. Etayo 18287* (herb. Etayo). PAÍS VASCO: Álava, Puerto de Herrera, subida hacia San León, hayedo y crestas calcáreas hacia el repetidor, 42°35'46"N, 2°41'03"W, 1100–1200 m, on *Fagus sylvatica*, on *P. orbicularis*, 2009, *J. Etayo 25106* (herb. Etayo). U.S.A. MASSACHUSETTS: Berkshire Co., Town of Adams, Mount Greylock State Reservation, W slope of Mt. Fitch along Notch Road, 42°39'N, 73°10'W, 825 m, on *Phaeophyscia rubropulchra*, 1995, *W.R. Buck 27763* (NY).

Crittendenia physconiae Diederich, J.C.Zamora & Millanes, *sp. nov.* **Fig. 20**

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Characterized by basidiomata with an extremely reduced or missing stipe and a very large capitulum, 147–390 µm diam., subspherical to broadly ellipsoid basidiospores, 5.8–8.0 × 4.7–6.1 µm, and the host choice, Physconia distorta.

TYPE: SPAIN. MADRID: San Lorenzo de El Escorial, alrededores de la Silla de Felipe II, on *Crataegus monogyna*, on *Physconia distorta*, 3 Jun. 2010, *J.C. Zamora* (holotype, g!).

Description. Basidiomata dispersed over the host thallus or apothecial margin of *Physconia*, stipe reduced, immersed, macroscopically not visible, capitulum pale pinkish brown, StH (40)57–187(300) µm, StD (120)146–387(650) µm, CaD (120)147–390(650) µm, StH/StD (0.2)0.3–0.7(0.8), CaD/StD (1.0)1.0–1.0(1.1), CaD/StH (1.3)1.4–3.6(5.8) (n = 27). Own thallus usually indistinct. Stipe hyphae thick-walled, 1.5–2.5 µm thick. Basidia subcylindrical, apically distinctly wider, basal clamp not observed, 1–3-sterigmate, basidia and sterigmata thick-walled, BaL 47–56 µm (n = 3), BaD (2.1)2.3–2.8(2.9) µm (n = 12), BaApD (2.8)3.2–4.5(5.4) µm (n = 15). Basidiospores ellipsoid, at the beginning surrounded by a thick perispore that becomes more and more loose and wrinkled, and eventually separates as a perispore sac, leaving a smooth- and thin-walled spore, SpL (5.3)5.8–8.0(10.1) µm, SpB (4.0)4.7–6.1(7.4) µm, SpL/SpB (1.0)1.1–1.5(1.9) (n = 71).

Etymology. From *Physconia*, the host lichen genus.

Distribution and host. Known only from the type locality in Spain, on the thallus of *Physconia distorta*.

Notes. This species is remarkable by the particularly short basidiomatal stipes that are visible only in microscopic section, and the exceptionally large capituli. The type specimen has been sequenced and is sister to a clade comprising *Crittendenia lecidellae* and *C. lichenicola*, although this relationship is only supported by the Bayesian analysis (Fig. 1). We have observed typical basidia producing up to 3 three basidiospores, but also unusual basidia producing only one spore. The

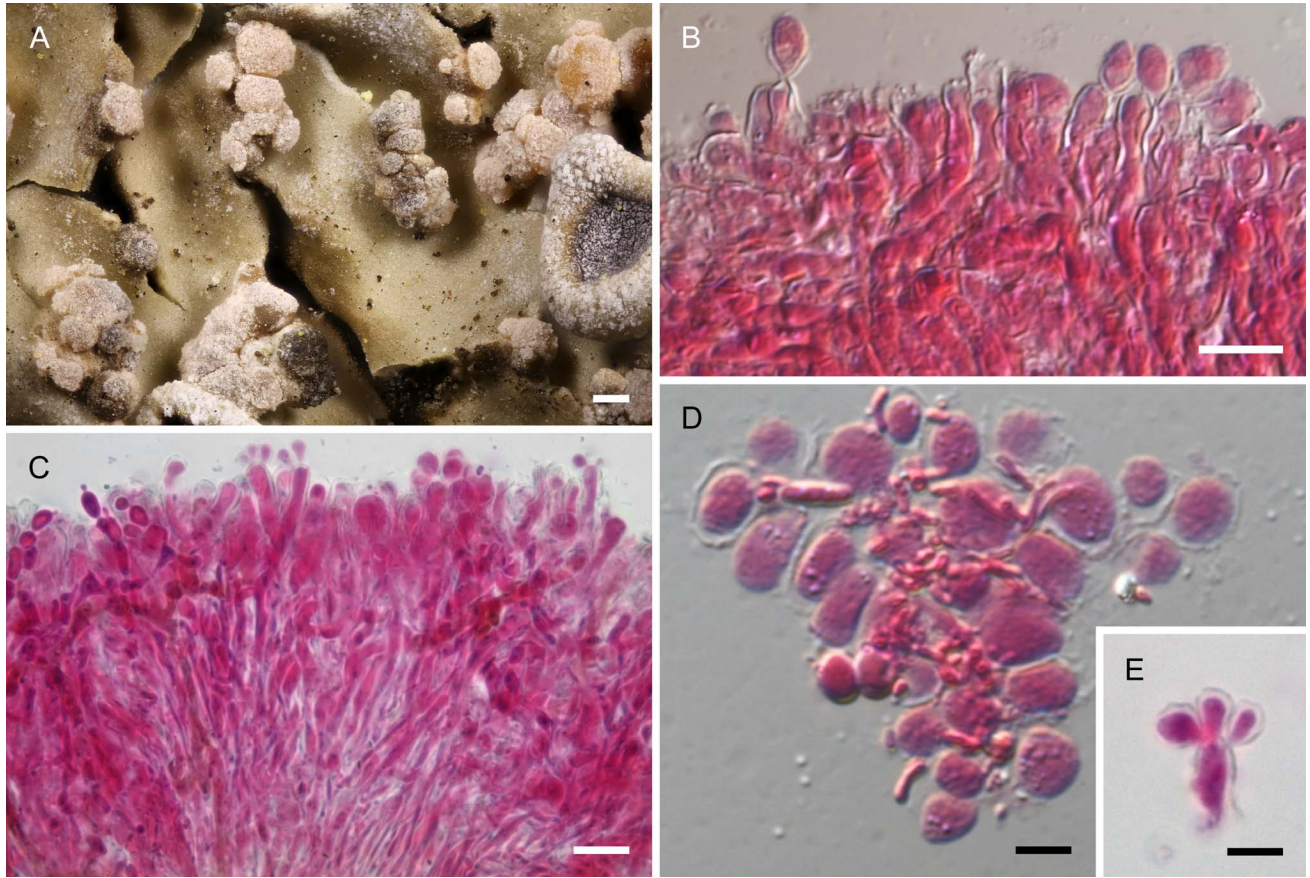


Figure 20. *Crittendenia physconiae*, holotype. **A.** Basidiomata on the thallus of *Physconia distorta*. **B.** Mature basidia, most producing a single basidiospore. **C.** Mature basidia producing up to three basidiospores. **D.** Basidiospores, most with a loose perisporeal sac. **E.** Basidium with three basidiospores and a thick wall around both basidium and basidiospores. B–E, in KOH + phloxine. Scale bars: A = 200 μm , B–C = 10 μm , D–E = 5 μm .

basidial wall is very thick and is continuous with that of the sterigmata and basidiospores, eventually separating as a perisporeal sac surrounding the spores and sometimes also the upper part of the basidia. We do not know whether the development of this perisporeal sac is due to the age of possibly postmature basidiomata, or if this character is constant within the species, and this can only be understood when more specimens become available.

Crittendenia stictae Diederich, Etayo & Millanes,
sp. nov. **Fig. 21**

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Characterized by the large and robust basidiomata, mainly 118–191 μm tall, the relatively thick stipe, 39–74 μm diam., medium-sized, broadly ellipsoid basidiospores, 4.7–7.1 \times 3.8–5.4 μm , the medium sized, mainly 3–4-sterigmate basidia, and the

*growth on large, conspicuous galls on the thallus of the host, *Sticta fuliginosa* s.l.*

TYPE: BOLIVIA. Laguna Vizcachani, camino de La Paz a Zongo, 16°11'45"S, 68°07'33"W, 3675–3860 m, on *Sticta fuliginosa* s.l. on bushes, 30 May 2011, J. Etayo et al. 26611 (holotype, LPB!; isotype, herb. Etayo!).

Description. Basidiomata densely covering galls on the thallus of *Sticta fuliginosa* s.l., relatively robust, pale brown, translucent, capitulum whitish to brownish, StH (100)118–191(260) μm , StD (35)39–74(100) μm , CaD (50)61–172(240) μm , StH/StD (1.5)1.9–3.9(4.9), CaD/StD (1.2)1.5–2.5(2.9), CaD/StH (0.3)0.4–1.1(1.4) (n = 22). Own thallus brownish, gelatinous, translucent, abundantly developed and often thick around basidiomata, developing over large, superficial, subspherical, pale to medium brown, smooth galls, 0.2–1 mm diam. Stipe hyphae thick-walled, 2–3.5 μm thick, clamps

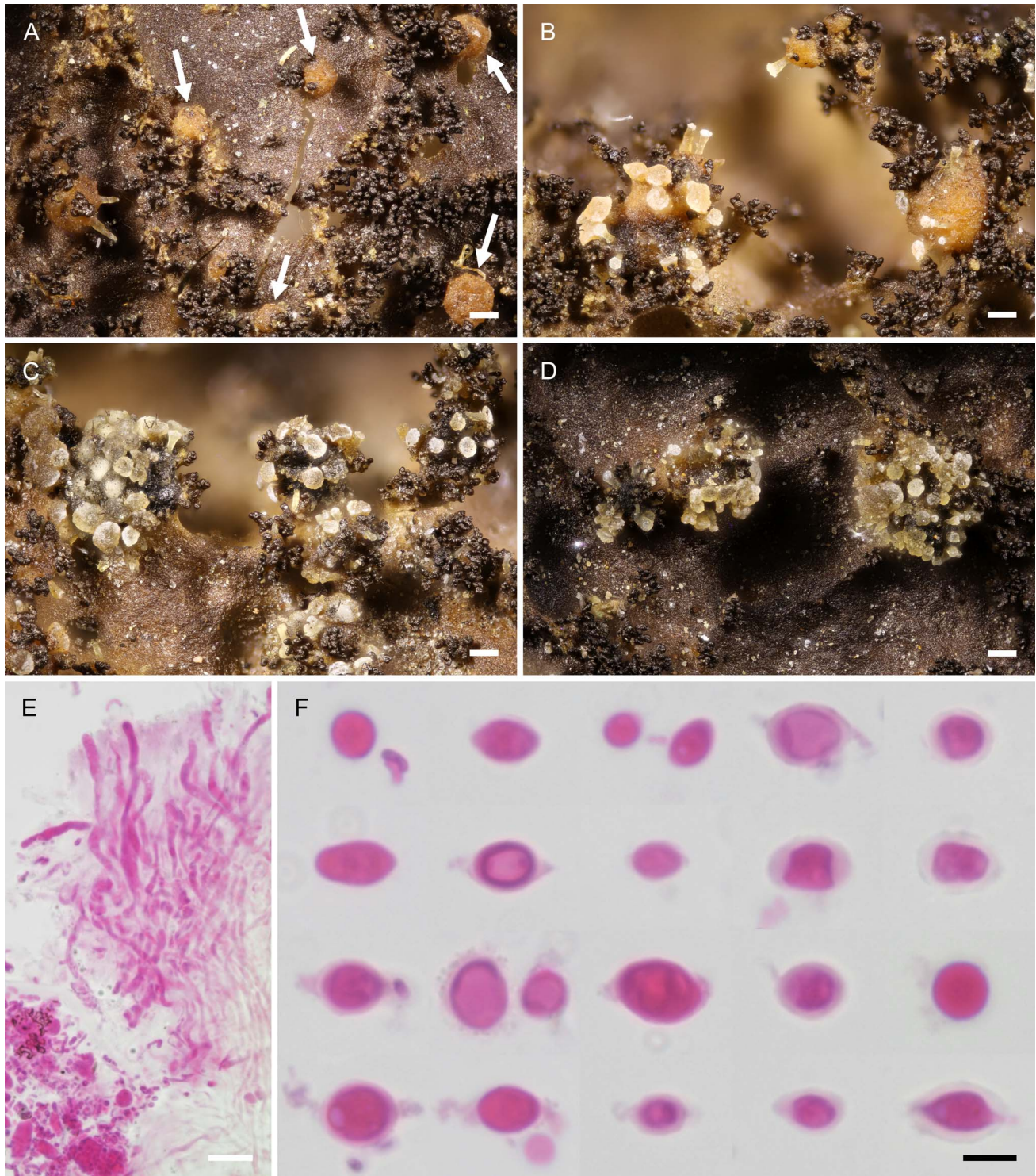


Figure 21. *Crittendenia stictae*, holotype. **A–D.** Thallus of *Sticta fuliginosa* s.l. with conspicuous galls overgrown by numerous basidiomata; arrows point to sterile galls, devoid of basidiomata. **E.** Basidia before spore-production. **F.** Basidiospores, some with a distinct thick wall, eventually loosening as a perispore sac, some with apical appendages. E–F, in KOH + phloxine. Scale bars: A–D = 200 μm, E = 10 μm, F = 5 μm.

not observed. Basidia subcylindrical, apically slightly wider, basal clamp not distinctly seen, 3–4-sterigmate, BaL c. 44–49 μm ($n = 2$), BaD c. 1.6–2.6 μm , BaApD c. 1.9–2.9 μm ($n = 5$) (most basidiomata postmature). Basidiospores broadly ellipsoid, more rarely elongate ellipsoid, thick-walled, some with indistinct apical appendages, eventually with a perispore sac, SpL (3.6)4.7–7.1(9.3) μm , SpB (2.8)3.8–5.4(6.8) μm , SpL/SpB (1.0)1.1–1.5(2.0) ($n = 72$).

Etymology. From *Sticta*, the host lichen genus.

Distribution and host. Known with certainty only from the type locality in Bolivia, on the thallus of *Sticta fuliginosa* s.l.

Notes. The type specimen is very rich. The host thallus is covered by numerous large, convex galls, some without basidiomata, but most covered by numerous basidiomata. This would be the only known species of *Crittendenia* to induce galls on the host thallus. However, it is not possible to identify whether the galls are induced by *Crittendenia* or perhaps by another lichenicolous fungus devoid of fructifications. Unfortunately, most basidiomata are postmature, and therefore only a small number of entire basidia could be observed and measured. We nevertheless decided to formally describe it as a new species, as sequence data exist, thus allowing further specimens to be easily identified when sequences are available. Among the *Crittendenia* species with 3–4-sterigmate basidia and broad basidiospores (SpL/SpB <1.5), the new species is remarkable by the relatively large and robust basidiomata developing over conspicuous galls.

We have seen another specimen on *Sticta* (ECUADOR. IMBABURA: Reserva Ecológica Regional Cotacachi-Cayapas, desde Irunguicho a Lagunas de Piñan, 2700–3100 m, on saxicolous *S. weigeli* s.l., 2003, *J. Etayo 25434*). It is very reduced and differs considerably from the type of *Crittendenia stictae*, so that we decided not to include it in that species, pending the discovery and study of further specimens on *Sticta*. Basidiomata are very slender and do not grow over galls, StH (120)123–210(230) μm , StD (15)19–36(35) μm , CaD (20)25–52(55) μm , StH/StD (3.4)4.6–8.2(8.7), CaD/StD (0.9)0.9–2.0(2.3), CaD/StH (0.1)0.2–0.3(0.3) ($n = 6$), basidia 4-sterigmate, and basidiospores very narrow, SpL (5.4)6.0–7.0(7.8) μm , SpB (2.7)2.9–3.6(4.1) μm , SpL/SpB (1.3)1.8–2.2(2.4) ($n = 44$). This specimen

had already been published as *Chionosphaera apobasidialis* by Etayo (2017). A further specimen grows on an old *Sticta* thallus overgrown by a sterile *Coenogonium*, thus simulating a growth on *Coenogonium* (BOLIVIA. DEPT. SANTA CRUZ: Prov. Caballero, camino de las orquídeas, zona baja, 17°49'20"S, 64°42'31"W, 2340 m, Yungas cloud forest, 2012, *J. Etayo 28835*). It also does not grow over galls, and some morphological characters are intermediate between the type specimen and *Etayo 25434*, hence we also provisionally exclude it from *Crittendenia stictae*: StH (100)98–178(180) μm , StD (25)26–42(45) μm , CaD (30)30–90(110) μm , StH/StD (2.2)2.5–6.2(7.2), CaD/StD (1.0)1.0–2.5(2.8), CaD/StH (0.3)0.3–0.6(0.6) ($n = 5$), basidia 2–4(?)-sterigmate, SpL (5.4)6.0–7.0(7.8) μm , SpB (2.7)2.9–3.6(4.1) μm , SpL/SpB (1.3)1.8–2.2(2.4) ($n = 44$).

Crittendenia teloschistis Diederich, Etayo, F. Berger & Millanes, *sp. nov.* **Fig. 22**

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*Characterized by 6–8-sterigmate basidia, mainly 31–42 μm long, relatively small basidiospores, 3.6–4.8 \times 3.0–4.0 μm , a stipe 116–198 μm long and 31–70 μm diam., and the host choice, *Teloschistes* species.*

TYPE: SPAIN. CANARY ISLANDS: La Gomera, NP Garajonay, on *Teloschistes flavicans*, Jul. 2012, *M. Koller s.n.* (holotype, BR [ex herb. Berger 26836]!).

Description. Basidiomata dispersed over the thallus of *Teloschistes* species, stipe relatively narrow to robust, pale brown, capitulum much broader, whitish to pale brownish, StH (65)[98]116–198[212](250) μm , StD (20)[26]31–70[81](100) μm , CaD (35)[62]62–153[180](240) μm , StH/StD (1.0)[1.6]2.1–5.0[5.7](7.0), CaD/StD (1.3)[1.5]1.6–2.8[2.9](3.6), CaD/StH (0.3)[0.4]0.4–1.1[1.3](1.7) ($n = 45$). Own thallus hyaline to brownish, gelatinous, translucent, developed around basidiomata, in the type specimen strongly swollen. Stipe hyphae thick-walled, 2–3 μm thick, septa with clamps. Basidia subcylindrical, relatively long, apically wider, with a basal clamp, 6–8-sterigmate, thin-walled, BaL (28)31–42(46) μm , BaD (1.5)1.6–2.6(3.1) μm , BaApD (2.3)2.7–3.7(4.0) μm ($n = 20$). Basidiospores subspherical to shortly ellipsoid,

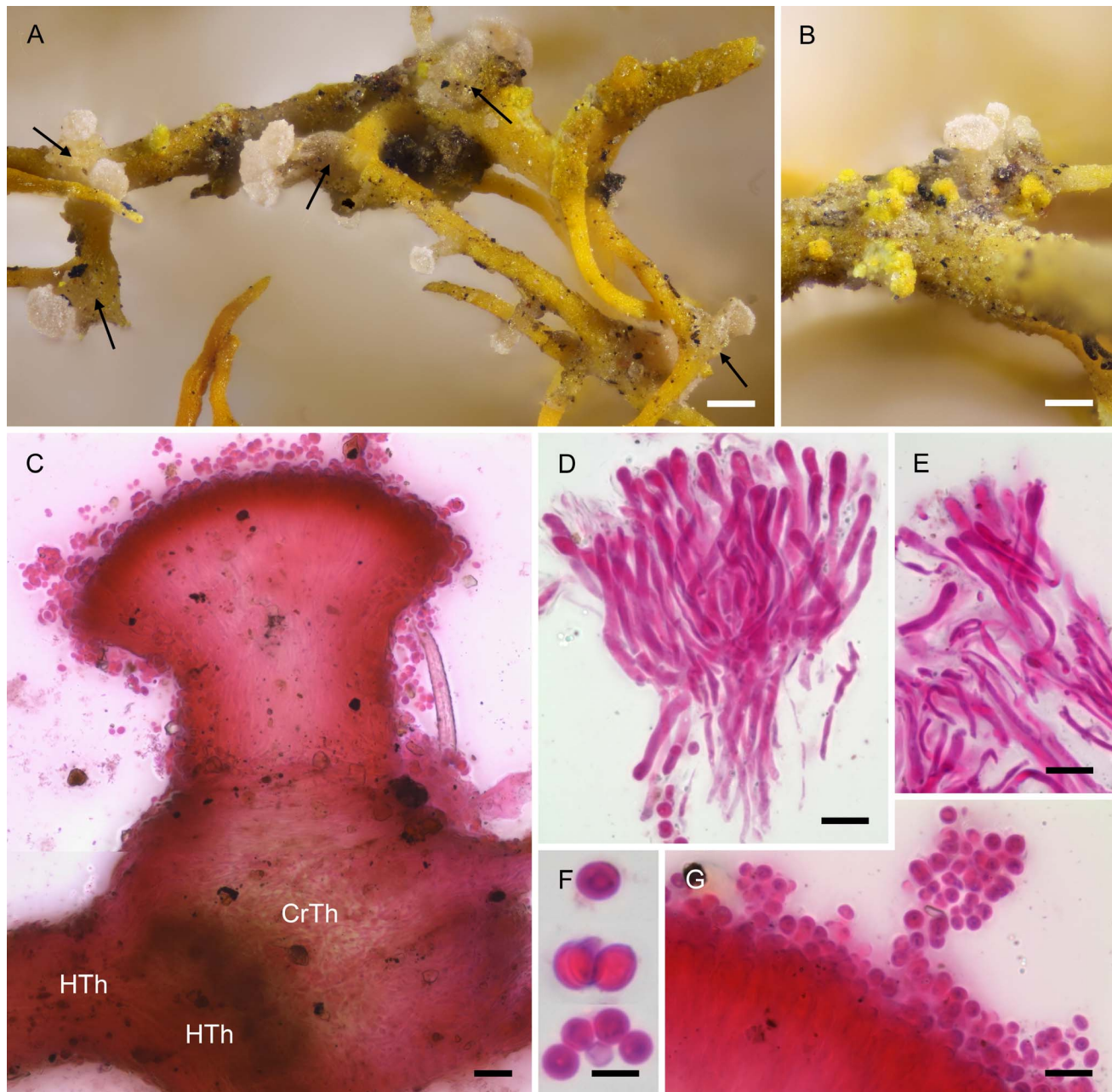


Figure 22. *Crittendenia teloschistis*, holotype. **A–B.** Basidiomata on the thallus of *Teloschistes flavicans*; arrows point to gall-like, swollen own thalli of *Crittendenia*. **C.** Squash preparation of basidioma, showing an own, non-lichenized thallus of *Crittendenia* (CrTh), developing over the host thallus (HTh). **D–E.** Immature and mature basidia. **F.** Basidiospores, the lower ones representing a partial group arising from one basidium (some spores are missing in a squash preparation). **G.** Numerous basidiospores deposited over basidia. **C–G,** in KOH + phloxine. Scale bars: **A–B** = 100 μm , **C** = 20 μm , **D–E, G** = 10 μm , **F** = 5 μm .

wall c. 0.3 μm thick, smooth, SpL (2.7)[3.5]3.6–4.8[5.1](5.6) μm , SpB (2.3)[2.9]3.0–4.0[4.2](4.8) μm , SpL/SpB (1.0)[1.0]1.1–1.4[1.4](1.8) ($n = 105$).

Etymology. From *Teloschistes*, the host lichen genus.

Distribution and hosts. Known from the Canary Islands (La Gomera) and South America (Bolivia), on the thallus of *Teloschistes exilis* and *T. flavicans*.

Notes. Among the *Crittendenia* species with mainly 7–8-sterigmate basidia, this species is

distinguished by a combination of subtle differences, mainly the particularly short, often subspherical basidiospores, and the relatively large capituli. Specimens on both host species differ considerably, the one on *Teloschistes flavicans* having relatively robust basidiomata, StH 98–170 µm, StD 42–81 µm, StH/StD 1.6–2.9, and often develop over a small swollen own thallus, while the type on *T. exilis* has slenderer basidiomata, StH 148–212 µm, StD 26–53 µm, StH/StD 3.8–5.7, without a swollen own thallus. In our phylogeny, both specimens form a clade that is sister to a clade comprising almost all other *Crittendenia* species, although this relationship is only supported by the Bayesian analysis (Fig. 1). Specimen *Etayo 13215* had already been published and illustrated by Diederich (1996) and Etayo (1996) as *Chionosphaera* cf. *apobasidialis*.

Additional specimens examined. BOLIVIA. DEPT. TARIJA: Prov. Burnet O'Connor, close to Los Pinos, old road between Entre Ríos and Tarija, 21°24'50"S, 64°18'33"W, 2150 m, Boliviano-Tucumano forest, on *Teloschistes exilis*, 2015, *J. Etayo 32788* (LPB). SPAIN. CANARY ISLANDS: La Gomera, Hermigua, Contadero, pista hacia la Ermita, 1000 m, on *Teline stenopetala*, on *T. flavicans*, 1994, *J. Etayo 13215* (herb. Etayo [!P. Diederich 1994, specimen lost at return of loan]).

Crittendenia sp. on *Parmelina quercina*

Description. Basidiomata developing on old thallus lobes of *Parmelina quercina*, pinkish brown, stipe short, StH c. 70–200 µm, StD c. 50–200 µm, CaD c. 50–400 µm. Basidia subcylindrical to elongate clavate, 4-sterigmate, c. 38–63 µm long and 2.5–3 µm thick. Basidiospores ellipsoid, wall thin to thick, some with a distinct perispore sac, SpL (7.7)8.4–9.7(10.0), SpB (3.7)4.0–5.4(6–7) µm, SpL/SpB (1.5)1.7–2.3(2.4) (n = 27). [Description obtained from notes dating 1994 and from an old microscopical slide.]

Distribution and host. Known from Spain (Mallorca and Tarragona), on the thallus of *Parmelina quercina*.

Notes. A specimen of '*Chionosphaera* cf. *apobasidialis*' had been studied and published by Diederich (1996), illustrated by a macroscopical photograph and line drawings. Unfortunately, the specimen was lost during the return of a loan, but a microscopical slide exists. A second specimen is

so poor that no basidioma could be found. Following our observations, this represents a distinct species of *Crittendenia*, but additional specimens are needed for a formal description. It differs from the other parmeliicolous *Crittendenia* species by the very short and broad basidiomatal stipe, and from the other species with 4-sterigmate basidia by the spores with a length/breadth ratio above 1.7.

Specimens examined (both on *Parmelina quercina*). SPAIN. MALLORCA: carr. Soller-Lluc, km 40, entrada a la propiedad Monnaber, carrascal con foliáceos en ramas, 670 m, 1994, *J. Etayo 12503* (herb. Etayo, [!P. Diederich 1994, specimen lost at return of loan; microscopical slide extant]). TARRAGONA: Baix Ebre, Roquetes, camino ports de Beceite, a 2 km cruce con carretera a monte Caro, 1115 m, encinar aclarado, 1995, *J. Etayo 17192* (herb. Etayo [no basidioma left]).

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LITERATURE CITED

- Aguirre-Hudson, M. B. & B. M. Spooner. 2005. New, rare and interesting lichens. *British Lichen Society Bulletin* 97: 69–79.
- Alstrup, V. 1993. News on lichens and lichenicolous fungi from the Nordic countries. *Graphis Scripta* 5: 96–104.
- Bandoni, R. J. 1995. Dimorphic heterobasidiomycetes, taxonomy and parasitism. *Studies in Mycology* 38: 13–27.
- Boekhout, T., A. Fonseca, J. P. Sampaio, R. J. Bandoni & K. J. Kwon-Chung. 2011. Discussion of teleomorphic and anamorphic basidiomycetous yeasts. Pages 1339–1372. In: C. P. Kurtzman, J. W. Fell & T. Boekhout (eds.), *The Yeasts: A Taxonomic Study*. Elsevier, London.

- Brackel, W. v. 2015. Lichenicolous fungi from Central Italy with notes on some remarkable hepaticolous, algicolous and lichenized fungi. *Herzogia* 28: 212–281.
- Bricaud, O., C. Roux & H. Bültmann. 2009. Syntaxonomie des associations de lichens foliicoles de la France méridionale. *Bulletin de la Société Linnéenne de Provence* 60: 143–150.
- Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540–552.
- Darriba, D., G. L. Taboada, R. Doallo & D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
- Diederich, P. 1996. The lichenicolous heterobasidiomycetes. *Bibliotheca Lichenologica* 61: 198 pp.
- Diederich, P., J. D. Lawrey & D. Ertz. 2018. The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. *The Bryologist* 121: 340–425.
- Etao, J. 1996. Aportación a la flora líquénica de las Islas Canarias. I. Hongos liquenícolas de Gomera. *Bulletin de la Société Linnéenne de Provence* 47: 93–110.
- Etao, J. 2004. Líquenes y hongos liquenícolas de los Pirineos occidentales y norte de la Península Ibérica. *Naturzale* 18: 143–167.
- Etao, J. 2009. Líquenes y hongos liquenícolas del País Vasco. Catálogo del año 2009. Ihobe, Sociedad Pública del Departamento de Medio Ambiente, Planificación Territorial, Agricultura y Pesca del Gobierno Vasco, Bilbao.
- Etao, J. 2017. Hongos liquenícolas de Ecuador. *Opera Lilloana* 50: 1–535.
- Etao, J. 2018. Hongos liquenícolas de las islas Azores. I. Terceira. *Ascomycete.org*. 10: 107–116.
- Etao, J. & O. Breuss. 1998. New species and interesting records of lichenicolous fungi. *Österreichische Zeitschrift für Pilzkunde* 7: 203–213.
- Gardes, M. & T. D. Bruns. 1993. ITS primers with enhanced specificity for basidiomycetes: application to the identification of mycorrhizae and rusts. *Molecular Ecology Resources* 2: 113–118.
- Hoang, D. T., O. Chernomor, A. von Haeseler, B. Q. Minh & L. S. Vinh. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522.
- Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. von Haeseler & L. S. Jermiin. 2017. ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates. *Nature Methods* 14: 587–589.
- Katoh, K., J. Rozewicki & K. D. Yamada. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 2: 1160–1166.
- Kirschner, R., D. Begerow & F. Oberwinkler. 2001. A new *Chionosphaera* species associated with conifer inhabiting bark beetles. *Mycological Research* 105: 1403–1408.
- Kirschner, R. & C.-J. Chen. 2008. *Physalacria corticola*, *P. stilboidea*, and *Stilbum vulgare*, three sphaeropedunculate Basidiomycota new to Taiwan, with notes on *Stilbum erythrinae*. *Fungal Science* 23: 43–53.
- Kühner, R. & H. Romagnesi. 1953. Flore analytique des Champignons supérieurs. Paris, 385 pp.
- Li, A.-H., F.-X. Yuan, M. Groenewald, K. Bensch, A. M. Yurkov, K. Li, P.-J. Han, L.-D. Guo, M. C. Aime, J. P. Sampaio, S. Jindamorakot, B. Turchetti, J. Inacio, B. Fungsin, Q. M. Wang & F.-Y. Bai. 2020. Diversity and phylogeny of basidiomycetous yeasts from plant leaves and soil: proposal of two new orders, three new families, eight new genera and one hundred and seven new species. *Studies in Mycology* 96: 17–140.
- Llop, E. & A. Gómez-Bolea. 2006. Foliicolous lichens and associated lichenicolous fungi in the north-eastern Iberian Peninsula: the effect of environmental factors on distribution. *Lichenologist* 38: 55–65.
- Lücking, R. 2008. Foliicolous lichenized fungi. *Flora Neotropica Monograph* 103. Organization for Flora Neotropica and The New York Botanical Garden Press, Bronx, New York, 866 pp.
- Maddison, W. P. & D. R. Maddison. 2021. Mesquite: a modular system for evolutionary analysis. Version 3.70, <http://www.mesquiteproject.org>
- Millanes, A. M., P. Diederich, M. Westberg & M. Wedin. 2021. *Crittendenia* gen. nov., a new lichenicolous lineage in the Agaricostilbomycetes (Pucciniomycotina), and a review of the biology, phylogeny and classification of lichenicolous heterobasidiomycetes. *Lichenologist* 53: 103–116.
- Millanes Romero, A. M., V. Tuovinen, J. Perriáñez, S. Freire-Rallo, P. Diederich, M. Westberg, H. Johannesson & M. Wedin. 2021. Insights in the biology and life cycle of the lichen-inhabiting fungus *Tremella hypogymniae* (Tremellales, Basidiomycota, Fungi). IAL9 Program & Abstract Book, International Association for Lichenology 9th Symposium: 220.
- Miller, S. L., E. Larsson, K.-H. Larsson, A. Verbeken & J. Nuytinck. 2006. Perspectives in the new Russulales. *Mycologia* 98: 960–970.
- Miller, M. A., T. Schwartz, B. E. Pickett, S. He, E. B. Klem, R. H. Scheuermann, M. Passarotti, S. Kaufman & M. A. O’Leary. 2015. A RESTful API for Access to Phylogenetic Tools via the CIPRES Science Gateway. *Evolutionary Bioinformatics* 11: 43–48.
- Nguyen, L.-T., H. A. Schmidt, A. von Haeseler & B. Q. Minh. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274.
- Oberwinkler, F. 1987. Heterobasidiomycetes with ontogenic yeast stages—systematic and phylogenetic aspects. *Studies in Mycology* 30: 61–74.
- Oberwinkler, F. 2017. Yeasts in Pucciniomycotina. *Mycological Progress* 16: 831–856.
- Oberwinkler, F. & R. J. Bandoni. 1982. A taxonomic survey of the gasteroid, auricularioid Heterobasidiomycetes. *Canadian Journal of Botany* 60: 1726–1750.
- Rambaut, A. 2019. Figtree v1.4.4. URL: <http://tree.bio.ed.ac.uk/software/figtree> [Accessed 1 Dec. 2021.]
- Rehner, S. A. & G. J. Samuels. 1994. Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. *Mycological Research* 98: 625–634.
- Roberts, P. 1997. New heterobasidiomycetes from Great Britain. *Mycotaxon* 63: 195–216.
- Rogers, D. P. 1947. A new gymnocarpous heterobasidiomycete with gasteromycetous basidia. *Mycologia* 39: 556–564.
- Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard & J. P. Huelsenbeck. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 1–4.
- Sérusiaux, E., A. Gómez-Bolea, A. Longán & R. Lücking. 2002. *Byssoloma llimonae* sp. nov., from continental Spain, Madeira and the Canary Islands. *Lichenologist* 34: 183–188.
- Spirin, W. A., I. V. Zmitrovich & V. F. Malysheva. 2005. Notes on Perenniporiaceae. *Folia Cryptogamica Petropolitana* (St Petersburg) 3: 1–67.

- Spribile, T., V. Tuovinen, P. Resl, D. Vanderpool, H. Wolinski, M. C. Aime, K. Schneider, E. Stabentheiner, M. Toome-Heller, G. Thor, H. Mayrhofer, H. Johannesson & J. P. McCutcheon. 2016. Basidiomycete yeasts in the cortex of ascomycete macrolichens. *Science* 353: 488–492.
- Talavera, G. & J. Castresana. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 56: 564–577.
- Tuovinen, V., S. Ekman, G. Thor, D. Vanderpool, T. Spribile & H. Johannesson. 2019. Two basidiomycete fungi in the cortex of wolf lichens. *Current Biology* 29: 476–483.e5.
- Tuovinen, V., A. M. Millanes, S. Freire-Rallo, A. Rosling & M. Wedin. 2021. *Tremella macrobasidiata* and *Tremella varia* have abundant and widespread yeast stages in *Lecanora* lichens. *Environmental Microbiology* 23: 2484–2498.
- van den Boom, P. P. G. 2012. Additions and notes to the checklist of lichens and lichenicolous fungi of Cape Verde. *Österreichische Zeitschrift für Pilzkunde* 21: 5–16.
- van den Boom, P. P. G. 2021. Foliicolous lichens and their lichenicolous fungi in Macaronesia and atlantic Europe. *Bibliotheca Lichenologica*: 1–197.
- van Waveren, E. K. 1968. The ‘stercorarius group’ of the genus *Coprinus*. *Persoonia* 5: 131–176.
- Vilgalys, R. & M. Hester. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238–4246.
- Wang, Q.-M., A. M. Yurkov, M. Göker, H. T. Lumbsch, S. D. Leavitt, M. Groenewald, B. Theelen, X.-Z. Liu, T. Boekhout & F.-Y. Bai. 2016[2015]. Phylogenetic classification of yeasts and related taxa within Pucciniomycotina. *Studies in Mycology* 81: 149–189.
- White, T. J., T. Bruns, S. Lee & J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pages 315–322. In: M. A. Innis, D. H. Gelfand, J. J. Sninsky & T. J. White (eds.), *PCR Protocols: a guide to methods and applications*. Academic Press, San Diego.
- Zamora, J. C., A. M. Millanes, M. Wedin, V. J. Rico & S. Pérez-Ortega. 2016. Understanding lichenicolous heterobasidiomycetes: new taxa and reproductive innovations in *Tremella* s.l. *Mycologia* 108: 381–396.
- Zamora, J. C., S. Pérez-Ortega & V. J. Rico. 2011. *Tremella macrobasidiata* (Basidiomycota, Tremellales), a new lichenicolous fungus from the Iberian Peninsula. *Lichenologist* 43: 407–415.
- Zhang, J., P. Kapli, P. Pavlidis & A. Stamatakis. 2013. A general species delimitation method with applications to phylogenetic placements. *Bioinformatics* 29: 2869–2876.

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