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Geographic distributions in *Chromosera* species—continental and oceanic barriers, including a new species, a new variety and a new combination

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Abstract

Chromosera cyanophylla was initially described from Europe and, when it was named type of the genus, was thought to be distributed throughout Europe and North America. Molecular phylogenies revealed that *Chromosera* "*cyanophylla*" from eastern and western North America represent two separate species and that neither is conspecific with European *C. cyanophylla* nor with the more recently described *C. ambigua*. Here we describe a new species from western North America as *Chromosera loreleiae*. We resurrect the species Peck described from eastern North America as *Agaricus lilacifolius* by recombining it in *Chromosera* and describe a new lilac variety lacking yellow pigments. The range of *C. cyanophylla s.s.* across eastern Eurasia including China is confirmed. *Chromosera citrinopallida*, described from Washington state, USA, comprised one clade in Washington that we infer is *C. citrinopallida s.s.* and a separate circumarctic clade distributed in Scandinavia, Iceland and Alaska.

Key words: *Agaricales*, *Basidiomycota*, biogeography, *Clitocybe violaceifolia*, *Hygrophoraceae*, key, nomenclature, taxonomy

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Introduction

The genus *Chromosera* Redhead, Ammirati & Norvell was first described by Redhead *et al.* (1995) with *Chromosera cyanophylla* (Fr.) Redhead, Ammirati & Norvell (validated by Redhead *et al*. 2012) as the type species. Originally, *C. cyanophylla,* described from Europe, was thought to represent a single species distributed across Europe and North America. Therefore, *Agaricus lilacifolius* Peck, a species originally described as *Agaricus lilacinus* Peck (*nom. illeg.* Art. 53.1, a homonym, *non Agaricus lilacinus* Schumach.), from New York state in eastern North America, was treated as a taxonomic synonym of *C. cyanophylla*.

The description of *C. cyanophylla* for its combination in *Chromosera* was based upon both fresh and dried collections made in northwestern North America (Mt. Rainier, Washington state) by Lorelei Norvell and Scott Redhead, rather than collections from Europe. However, Lodge *et al*. (2014) suggested that western North American collections might represent an undescribed species based on molecular phylogenies, a hypothesis later supported by Holec *et al*. (2015). Moreover, it was suggested that the sequenced western North American species might differ from the eastern North American species described by Peck as *A. lilacifolius* but attempts to sequence eastern collections had previously failed.

Recent collections through the North American Mycoflora Project (NAMP, now the Fungal Diversity Survey) and contributions from other amateur and paraprofessional mycologists who posted records on Mushroom Observer (https://mushroomobserver.org/) and iNaturalist (https://www.inaturalist.org/) provided additional collections for sequencing. These efforts revealed that the eastern and western North American *Chromosera* populations are not conspecific. Based on these findings, we resurrect the name *Agaricus lilacifolius* for the eastern North American species and recombine it within *Chromosera*. We include a more comprehensive description of this species, its variation, and its confirmed distribution, ranging from eastern Canada, west to Indiana, and southwest to Texas, Arizona, and southern Colorado. Additionally, we describe a new, lilac variety lacking yellow pigments from the province of Québec in Canada.

For the western North American *Chromosera*, we propose a new species name and confirm its distinctiveness from *C. cyanophylla,* which we confirm to range across Eurasia, including China. Furthermore, Geml *et al*. (2012) identified a circumarctic clade comprised of collections from Scandinavia, Iceland and Alaska as *C. citrinopallida*. We recover this circumarctic clade, but also another clade comprised solely of western North American collections identified as *C. citrinopallida*. We infer the latter to represent the true *C. citrinopallida.*

In this study, we revise the taxonomy of species within the *Chromosera cyanophylla* complex in the northern hemisphere, with additional commentary on other north-temperate *Chromosera* species. We also provide a key for the identification of all currently known *Chromosera* species.

Materials and methods

Specimens in this study

Both the type and an authentic collection of *Agaricus lilacifolius* Peck were borrowed from NYS and compared to sequenced collections by NAMP members in New York (deposited at NY) and Ohio (deposited at MU). Additional specimens from eastern North America were obtained from Pennsylvania and Texas (deposited at NY), Indiana (deposited at PUL) and Québec (deposited at DAOM). An all-lilac variety from Sainte-Marguerite-du-lac-Masson, Québec, Canada was repeatedly collected from the same log over a number of years. The western North American specimen originally detailed under the name *C. cyanophylla* when *Chromosera* was coined (Norvell & Redhead collection LLN 93.11.11-7 from Mt. Rainier Nat. Park, Ipsut Creek, WTU-F-001648) is designated as the holotype of a new species, *Chromosera loreleiae*. Herbarium abbreviations follow Index Herbariorum (Thiers, continuously updated).

Morphological studies

Basidiome colors recorded for the western North American species are from Redhead *et al*. (1995) and capitalized names are from Ridgway (1912). Colors recorded for *C. lilacifolius* are based on Peck's (1878) description. Additional color variations recorded for both species were documented photographically. All microscopic examinations were made

on dried specimens. Hand-cut cross-sections of lamellae and scalp mounts of *C. lilacifolius* were examined using light microscopy after rehydration with ammonia and examined in ammonia with or without 1% Congo Red or Melzer's reagent (rehydration with 70% ethanol and mounting in 5% KOH gave poor results). Numbers of sterigmata on basidia were noted. Spore observations were made by DG with the 40x objective lens of an OMAX M83EZ microscope. Photos were taken with a Nikon D3100 digital camera attached to the microscope. The dimensions (length x width) of 30 spores per collection were measured using Piximetre 5.9; Piximetre was calibrated with a stage micrometer before measurements were taken. Measurements were made by DJL using a calibrated ocular micrometer and 60x or 100x objective on an Olympus BH-2 microscope. Twenty to 25 spores each were measured from Peck's type, an authentic Peck collection from N. Elba NY, and a recent, matching collection from western Pennsylvania which was sequenced to provide a reference ITS sequence; 8–20 spores were measured from each of the other collections. The following notations were used for spore measurement: x = arithmetic mean of the spore length and width; Q = quotient of length and width indicated as a range with the upper and lower quartiles in parentheses.

gDNA extraction

Fragments of specimens or mycelia were excised using a sterile, single-use razor blade; when necessary, dried specimens were washed in Tris buffer to remove debris. gDNA was extracted using a modified version of the hair, nails, and feathers protocol in the E.Z.N.A® Forensic DNA Kit (Omega Bio-tek, USA). DTT was omitted. Sterile, single-use pestles were used to grind samples, and gDNA was eluted with 30–100 µL of pre-heated (70°C) elution buffer and stored at -20°C. DNA was extracted from DAOM985251 following the method described in Swenie *et al*. (2018) for material older than 50 years.

PCR amplification, cloning, and DNA sequencing

The following regions were PCR-amplified: partial 18S-ITS1-5.8S-ITS2-partial 28S (nuc rDNA unit) with primer pairs NS1 and LR5; ITS-partial 28S with primers ITS1 and LR5; ITS with primers ITS1 and ITS4; and ITS with primers ITS1F, ITS2, 5.8SR, and ITS4 (Vilgalys & Hester 1990, White *et al*. 1990, Gardes & Bruns 1993).

The ITS region of specimens HRL0080, HRL0497, HRL2506, and MUOB360690 was amplified in a reaction mix containing (µl/reaction): 10X Titanium Buffer (Takara Bio USA Inc, USA) (5); 10 mM dNTPs (New England Biolabs, NEB, USA) (2); 10 µM each primer (Integrated DNA Technologies, USA) (2 + 2); 50x Titanium Taq polymerase (Takara Bio USA Inc) (1); molecular biology-grade water (36); and gDNA (2). The cycling parameters were: 95 °C for 2 min; 35 cycles of 95 °C for 30 sec, 52 °C for 20 sec, 68 °C for 1 min; final extension at 68 °C for 8 min; and holding at 10 °C.

The ITS region of DAOM985251 was amplified in a reaction mix containing (µl/reaction): autoclaved Milli-Q filtered water (Millipore-Sigma, USA) (10.875); 5X green GoTaq reaction buffer (Promega, USA) (5), TBT-PAR (Samarakoon *et al.* 2013) (5); 10 µM each primer (1.25 + 1.25); 10 mM dNTPs (0.5); DreamTAQ DNA polymerase (Thermo Fisher, USA) (0.125); and gDNA (1). Cycling parameters followed Swenie *et al*. (2024).

The ITS-partial 28S fragment of MUOB366870 was amplified in a reaction mix containing (µl/reaction): Taq 2X PCR MasterMix (Applied Biological Materials, Canada) (25); 10 µM each primer (2.5 + 2.5); molecular biology-grade water (19); and gDNA (1). The cycling parameters were: 94 °C for 3 min; 35 cycles of 94 °C for 30 sec, 52 °C for 30 sec, 72 °C for 2 min; final extension at 72 °C for 5 min; and holding at 10 °C. The reaction mix for specimens DAOM985108 and DAOM208603 contained (µl/reaction): 5X Q5 Reaction Buffer (NEB) (10), 10 mM dNTPs (NEB) (1), 10 µM of each primer pair (2.5 + 2.5); Q5 High-Fidelity DNA Polymerase (NEB) (0.25); molecular biology-grade water (39.75); and gDNA (2). The cycling parameters were: 95 °C for 2 min; 30–35 cycles of 95 °C for 30 sec, 52 °C for 10 sec, 72 °C for 2 min; final extension at 72 °C for 5 min; and holding at 10 °C.

The nuc rDNA unit of culture DAOMC225985 was targeted in a reaction mix containing (µl/reaction): 5X Q5 Reaction Buffer (5), 10 mM dNTPs (NEB) (0.5), 10 µM of each primer pair (NS1 + ITS4 in reaction 1/ITS1 + L5 in reaction 2)(1.25 + 1.25); Q5 High-Fidelity DNA Polymerase (0.5); molecular biology-grade water (32.5); and gDNA (1). The cycling parameters were the same as above.

The ITS of specimen HRL0497 was cloned using the TOPO TA vector (ThermoFisher Scientific USA) according to the manufacturer's protocol. For blue-white screening of clones, 75 µL of filter-sterilized ampicillin (60 mg/ml) and 40 µl of X-gal (5-Bromo-4-chloro-3-indolyl beta-D-galactopyranoside, 20 mg/ml, Bioshop Canada Inc, Canada) were spread onto pre-warmed LB plates, which were then inoculated with 100 µl of cells and incubated at 37 °C overnight. White colonies were screened for expected inserts using PCR in a reaction mix containing (µl): 10X Titanium Taq

(2.5), 10 mM dNTP (0.5), 10 µM each ITS1 and ITS4 primers (0.5 each), water (20.5). Cells were boiled at 99 °C for 10 minutes and cooled on ice before adding to each reaction tube, and 0.25 µl of Titanium Taq was then added to each tube. The cycling parameters were the same as above.

Plasmid DNA was purified using the Monarch plasmid miniprep kit (NEB) according to the manufacturer's protocol; DNA was eluted in 50 µL of elution buffer. PCR products were purified using the Monarch PCR and DNA Cleanup kit (NEB), using the enclosed protocol: DNA was eluted in 8–25 µl of elution buffer. PCR products obtained from DAOM985251 were cleaned with a QIAquick PCR Purification Kit (Qiagen, Valencia, California) following the manufacturer's standard protocol. Sequence reaction preparation followed Matheny *et al*. (2007) Sequencing products were cleaned using Sephadex G-50 spin columns (General Electric Healthcare, USA) using Princeton Separations (USA) separator strips. Cleaned sequencing products were submitted to Eurofins Genomics Engineering LLC (USA) for Sanger sequencing.

For sequencing collections other than DAOM985251, 1 µL of purified DNA was added to a reaction mix containing (µl/reaction): 1:8 BigDye v3.1 (ThermoFisher Scientific) (8), 3.2 µM primer (1). The BigDye reagent was diluted in a mix containing (µL): 5X sequencing buffer (1.75), 20 % trehalose (2.5), water (3.75), BigDye (0.5). The sequencing cycle parameters were: 95 °C for 3 min; 40 cycles of 95 °C for 30 sec, 50 °C for 10 sec, 60 °C for 2 min; and a final hold at 4 °C. Sequencing amplicons were purified and injected into an ABI 3500xL Genetic Analyzer (ThermoFisher Scientific) according to in-house sequencing protocols at Agriculture and Agri-food Canada (Molecular Technologies Laboratory, Science and Technology Branch, Ottawa). Sequences generated in this study are indicated in Table 1.

TABLE 1. Taxa, collection and/or herbarium accession numbers, location where collected, and sequence accession numbers (GenBank—NCBI prefix; BOLD—NOBAS prefix; UNITE—UDB prefix) for taxa appearing in the ITS-28S phylogenetic tree (Figure 1). Bolded GenBank numbers were generated for this study.

Taxon	Collection, accession number (herbarium)	Geographic location	Sequence accession	
			ITS	28S
Aphroditeola olida	1230, 4665 (personal herb. HRL)	Québec, Canada	KM248880	NA[1]
A. olida	226047 (DAOM)	British Columbia, Canada	KF381518	KF381541
A. olida	SCL14825	Oregon, USA	KU574728	KX670974
A. olida	388298	Montana, USA	OM987400	NA
A. olida	JK212	Washington, USA	ON478197[2]	NA
A. olida	f3427 (SYKO)	Komi republic, Russia	OP821376	NA
Chromosera ambigua	18008-1 (GE)	St. Gemme, France	MK645573	MK645587
C. ambigua	18008-2 (GE)	St. Gemme, France	MK645574[2]	MK645588
C. ambigua	18008-3 (GE)	St. Gemme, France	MK645575	MK645589
Chromosera aff. *citrinopallida*	Boertmann 2006/2, DEN-29(CFMR)	Greenland	KF291072	KF291073
C. aff. *citrinopallida*	GG312_86 arctic	Norway	GU234145	NA
C. aff. *citrinopallida*	Lutzoni 930731-1, (DUKE)	Iceland	U66435	U66435
C. aff. *citrinopallida*	252385 (O-F)	Norway	NOBAS3254-16	NA
C. aff. *citrinopallida*	244008 (O-F)	Norway	NOBAS8746-21	NA
C. aff. *citrinopallida*	SAT-22-244-06	Alaska, USA	OQ987863	NA
Chromsera citrinopallida ss	iNaturalist # 185495362	Washington, USA	**PP925619**	NA
C. citrinopallida ss	iNaturalist # 96314499	Washington, USA	**ON856377**	NA
C. citrinopallida ss	iNaturalist # 176912116	Washington, USA	**PP748837**	NA
Chromosera cyanophylla	21972 (HMJAU)	China	OR646537	OR646538
C. cyanophylla	TL-5091 (CFMR)	Ussuria, Eastern Russia	KF291043	NA
C. cyanophylla	922848 (PRM)	Czech Republic	KJ194074	NA
C. cyanophylla	139003 (TUF)	Estonia	UDB07672300[2]	NA
C. cyanophylla	28831 (WU)	Austria	KJ194075[2]	NA
Chromosera loreleiae	SAR 8038, 225985 (DAOMC) culture	British Columbia, Canada	**PP853161**	**TBA**
C. loreleiae	MUOB 317467[3]	California, USA	MH429982	NA
C. loreleiae	RHM-22-2, iNaturalist # 112874004	Washington, USA	**OP076772**	NA

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TABLE 1. (Continued)

Taxon	Collection, accession number (herbarium)	Geographic location	Sequence accession	
			ITS	28S
C. loreleiae	iNaturalist # 34380700	Washington, USA	OM522252	NA
C. loreleiae	PBM 1577, AFTOL-ID 1684 (WTU)	Wyoming, USA	DQ486688	DQ457655
Chromosera lilacifolia	2019-58, 985108 (DAOM)	Ontario, Canada	**PP853163**	NA
C. lilacifolia	0497 (HRL), 985106 (DAOM)	Québec, Canada	**PP853165**	NA
C. lilacifolia	0080 (HRL), 985104 (DAOM)	Québec, Canada	**PP853166**	NA
C. lilacifolia	MUOB 506043	Arizona, USA	OR336186	NA
C. lilacifolia	iNaturalist # 25244460	Indiana, USA	ON561439	NA
C. lilacifolia	iNaturalist # 18524774	Indiana, USA	MN173968[2]	NA
C. lilacifolia	iNaturalist # 18565341	Indiana, USA	MN173969[2]	NA
C. lilacifolia	iNaturalist # 24222314	Indiana, USA	MN173970[2]	NA
C. lilacifolia	iNaturalist # 25197305	Indiana, USA	ON561438[2]	NA
C. lilacifolia	iNaturalist # 27182368	New Jersey, USA	MN752422	NA
C. lilacifolia	iNaturalist # 27588741 (NY)	New York, USA	MN752426[2]	NA
C. lilacifolia	RP-10705, 58791 (TENN)	New York, USA	MG050103	NA
C. lilacifolia	MUOB 296364, 000292829 (MU-F)	Ohio, USA	OK376727	NA
C. lilacifolia	MUOB 366870, 985107 (DAOM)	Pennsylvania, USA	**PP853164**	NA
C. lilacifolia	MUOB 360690, 985105 (DAOM)	Texas, USA	**PP853167**	NA
C. lilacifolia var. *totililacicolor*	HRL1723, 242735 (DAOM)	Québec, Canada	**PQ182943**	NA
Chromosera lilacina	18035 (GE)	Labrador, Canada	MK645577	MK645591
C. lilacina	MQ18R213, 30729 (QFB)	Québec, Canada	**MN992121**	NA
C. lilacina	74615 (O-F)	Norway	NOBAS1711-15[2]	NA
C. lilacina	252965 (O-F)	Norway	NOBAS4312-17	NA
C. lilacina	18038 (GE)	Norway	MK645580	NA
C. lilacina	T. Borgen 86.294 (CFMR)	United Kingdom	KF291054	NA
C. lilacina	SAT-16-239-05, 073154 (WTU-F)	Alaska, USA	MZ054359	NA
C. lilacina, Uncultured fungus	OTU1072, tundra soil	Alaska, USA	MN152161	NA
Chromosera viola	RBG Kew, 20264 [K(M)]	United Kingdom	EU784352	NA
C. viola	002653S1181 (TU-E) forest soil	Germany	UDB01999109	NA
C. viola	002653S1181 (TU-E) forest soil	Germany	UDB01999117	NA
Chromosera xanthochroa (as *C. citrinopallida*)	18036 (GE)	Labrador. Canada	MK645578	MK645592
C. xanthochroa	G0152, NL-3680, 18033 (GE)	Labrador, Canada	MK645576	MK645590
C. xanthochroa	18037 (GE)	Norway	MK645579	NA
C. xanthochroa (as *C. citrinopallida*)	301181 (O-F)	Norway	NOBAS5180-18	NA
C. xanthochroa (as *C. citrinopallida*)	361167 (O-F)	Norway	NOBAS8745-21	NA
C. xanthochroa (as *C. citrinopallida*)	288409 (O-F)	Norway	NOBAS8744-21	NA
Gloioxanthomyces nitidus	DJL06NC87c4 (TENN)	North Carolina, USA	KF468706	NA
G.s nitidus	21126F (ACAD)	Nova Scotia, Canada	ON412794	NA
G. nitidus	21147F (ACAD)	Nova Scotia, Canada	ON412809	NA
G. nitidus	iNaturalist # 94853216	Michigan, USA	ON856357	NA
G. nitidus	iNaturalist # 136221390, vouch. 5542	Pennsylvania, USA	OP749159	NA
G. nitidus	iNaturalist # 137604474	Pennsylvania, USA	OP749292[2]	NA
G. nitidus	41710_1 (GDGM)	China	MG712283	MG712282
G. nitidus	41710_2 (GDGM)	China	MG712284[2]	MG712282

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TABLE 1. (Continued)

Taxon	Collection, accession number (herbarium)	Geographic location	Sequence accession	
			ITS	28S
G. nitidus	61934 (HMJAU)	China	ON045772	ON046289
G. vitellinus	1617064 (LD)	Sweden	KF468706	NA
G. vitellinus	251626 (O-F)	Norway	NOBAS3218-16	NA
Haasiella venustissima (= *C. splendidissima*)	JVG1071013-1	Spain	JN944395	JN944396
H. venustissima	A. Gminder, 971488 (STU)	Italy	KF291092	KF291093
H. venustissima	160893 [K(M)]	United Kingdom	MZ159391[2]	NA
H. venustissima	n. 3666 Herb. Roux, (MARSSJ)	France	JN944398	JN944399
H. venustissima	n. 4044 Herb. Roux, (MARSSJ)	France	JN944400	JN944401
H. venustissima	5654 (WU)	Austria	JN944397	NA
H. venustissima	KN_1173_20221105_BZ1	Switzerland	OQ991145	NA
H. venustissima	MNS-114	Switzerland	OQ280975[2]	NA
H. venustissima	U.R.050-068	Switzerland	OQ280974	NA
H. venustissima	E.C. 08191	Italy	JN944393	JN944394
Sinohygrocybe tomentosipes	43351 (GDGM)	China	MG685872	MG696901
S. tomentosipes	50075 (GDGM)	China	MG685873	MG696902
S. tomentosipes	50149 (GDGM)	China	MG685874	MG696903
Macrotyphula phacorrhiza	IO.14.200 (S)	France	MT232363	MT232314

[1] NA—sequence data not available.

[2] This ITS sequence is identical and is indicated by "=" on the phylogenetic tree in Figure 1. Identical sequences were removed prior to running phylogenetic analyses.

[3] MUOB—GenBank designated acronym for Mushroom Observer.org.

Sequence analyses

The original dataset was composed of 88 taxa selected from genera believed to be closely related to or possibly confused with *Chromosera*, including the outgroup. Selected genera were *Aphroditeola* Redhead & Manfr. Binder, *Gloioxanthomyces* Lodge, Vizzini, Ercole & Boertm., *Haasiella* Kotl. & Pouzar, and *Sinohygrocybe* C.Q. Wang, Ming Zhang & T.H. Li. We accepted the conspecificity of *Haasiella splendidissima* with *H. venustissima* proposed by Vizzini *et al*. (2012). Sequences were analyzed using tools in Geneious Prime (version 2022.2.2). Sequence reads were visualized, contigs were manually edited when necessary and assembled. For phylogenetic analyses, additional sequence data were obtained from NCBI, BOLD, and UNITE. Alignments were generated for partial 18S rDNA, ITS, partial 28S rDNA, and partial DNA-directed RNA polymerase II subunit (RPB2) sequences using Geneious alignment with default parameters. Alignments were concatenated and manually refined, and the 18S and RPB2 were excluded from the final analysis because there were few sequences available for this group. Identical ITS sequences were removed; the final dataset comprised 71 taxa. The outgroup was *Typhula phacorrhiza* IO.14.200 (S) (18S: MT232505, ITS: MT232363, 28S: MT232314, RPB2: MT242347). Taxa and accession numbers are described in Table 1.

Phylogenetic analyses were carried out using MrBayes v3.2.6 x64 (parallel version) on the biocluster at Agriculture and Agri-food Canada (Science and Technology Branch, Ottawa). The ITS-partial 28S region was analyzed using the following parameters: ITS and 28S were partitioned; Nst=6; rates=gamma; ngen=15 million; sampling frequence=1000; nchains=6; burnin=50%. All other parameters were kept constant. Phylogenetic trees were drawn using the Bayesian consensus outfile and annotations were added using Inkscape 0.92.4.

The distribution map template is a Lambert conformal conic projection (Strebe 2011) modified by cropping at the equator, Mexico in W and Korea in E, and changing from natural color to gray. The Lambert projection was used because it does not inflate distances near the pole as much as other types. The original used 15° graticule, standard parallels at 20° N and 50° N, and an imagery derivative of NASA's Blue Marble summer month Refcomposite with oceans lightened to enhance legibility and contrast (Strebe 2011). The image was created with the Geocart map projection software by Strebe. The locations of sequenced and verified photographic records (Tables 1, S1) were added by hand in PowerPoint.

Results

Phylogenetic analyses

The ITS-partial 28S rDNA region from 13 species of *Chromosera* and allied genera was examined using Bayesian analysis (Figure 1). The tree shown is the consensus tree generated by MrBayes. Sequences were obtained from GenBank, BOLD (prefix "NOBAS"), or UNITE (prefix "UBD") databases, as well as generated in-house for this study.

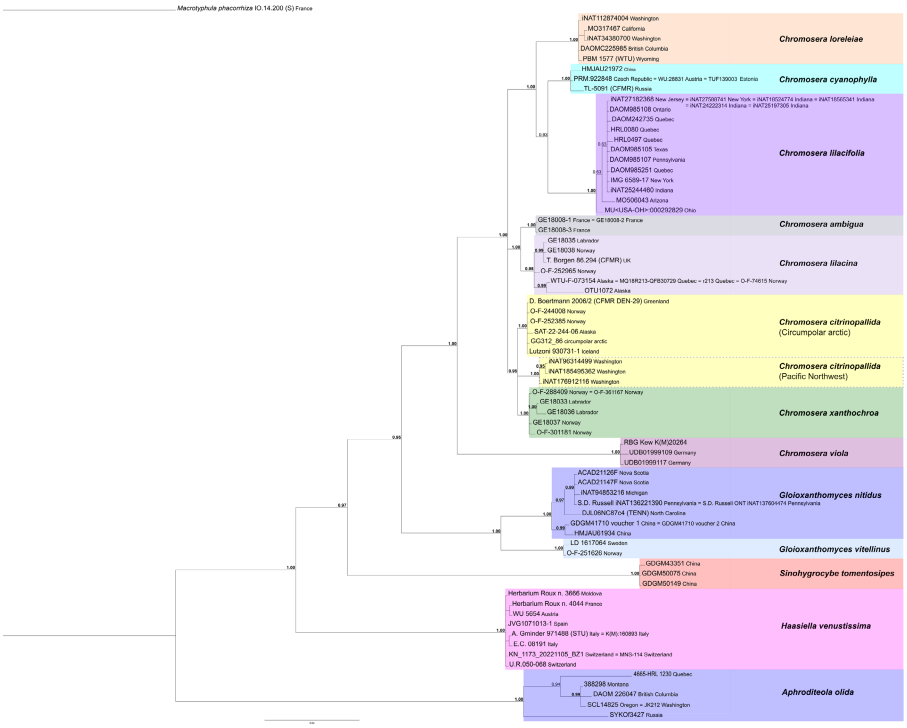

FIGURE 1. ITS-28S Phylogeny of *Chromosera* and related species. Bayesian probabilities are shown for the ITS-5.8S plus 28S region in *Chromosera* species and related taxa. The phylogeny was rooted with *Macrotyphula phacorrhiza.* Sequences that were identical to the first listed (indicated by "=") were included in the alignment but were removed prior to running phylogenetic analyses.

The genus *Chromosera* is a strongly supported clade (posterior probability value 1.00) that is clearly separate from closely related sister genera. Bayesian support for the majority of species is high, with posterior probability values ranging from 0.98 (*C. lilacina*) to 1.00. There are two notable exceptions, however. *C. citrinopallida* isolates from the Pacific Northwest from Washington state cluster in a strongly supported (1.0) clade distinct from circumarctic *"C. citrinopallida"* isolates from the North Atlantic and Alaska. The Pacific Northwest isolates are nestled between *C. xanthochroa* and circumarctic strains identified as "*C. citrinopallida"* by Geml. *et al*. (2012, found in their project database). In addition to single nucleotide polymorphisms (snp) within ITS1 and ITS2 and two single nucleotide insertions/deletions (indels), there is presence of TTGAAT in ITS1 and an absence of ACT in ITS2 of Washington isolates of *C. citrinopallida* differentiating them from the circumarctic clade. We hence refer to the circumarctic clade as *C*. aff. *citrinopallida*. The presence of TTGAAT in ITS1 of Washington sequences of *C. citrinopallida* also distinguishes them from *C. xanthochroa*.

Chromosera loreleiae, *C. cyanophylla*, and *C. lilacifolia* form a strongly supported clade, distinct from *C. ambigua*, *C. lilacina*, *C. citrinopallida*, *C.* aff. *citrinopallida,* and *C. xanthrochroa*. *Chromosera ambigua* and *C. lilacina* form a strongly supported clade, as do *C. citrinopallida, C.* aff. *citrinopallida,* and *C. xanthochroa.* These three clades are recovered in a polytomy sister to *C. viola.*

Chromosera cyanophylla and *C. lilacifolia* are distinguished by numerous snp and single nt indels in the ITS1 and ITS2 fragments. In addition, there are 2 notable motif differences: CCTCC in *C. cyanophylla* (nt positions 50–54) is CCCCT in *C. lilacifolia* (positions 50–55) and ACATTTT in the former species (position 132–138) is CTTTAAT in the latter (position 132–138). The average %GC for the *C. cyanophylla* isolates in this study is 40.5, whereas the average %GC is 42.7 for the strains of *C. lilacifolia* with complete ITS-5.8S rDNA sequences.

Geographic distributions

Isolates of *C. loreleiae* were collected primarily in the Pacific region of North America except for PBM1577 (WTU-F-001654), which was isolated from the state of Wyoming, in the Mountain West region of North America (Tables 1, S1; Figure 2C). Specimens of *C. lilacifolia* were collected predominantly in eastern North America, from Québec south to Texas, as well as in the southwestern US (Arizona and southern Colorado)(Figure 2A). The distributions of *C. loreleiae* and *C. lilacifolia* apparently do not overlap (Figures 2A, 2C). *Chromosera cyanophylla* is widespread within Eurasia (Figure 2B), being found in central Europe, the Baltics, and East Asia (Bau & Liu, 2010, Boesmiller 1996, Holec *et al*. 2015). Currently, *C. ambigua* is limited to France (Figure 2G); only three isolates of this species with sequences could be found in public databases. *Chromosera lilacina* is widely distributed throughout northern regions of Europe and North America (Québec, Labrador, Greenland, Iceland, Norway, and Alaska; Figure 2H), whereas *C. viola* is only known from the UK and from soil samples in Germany (Table 1; Figure 2I).

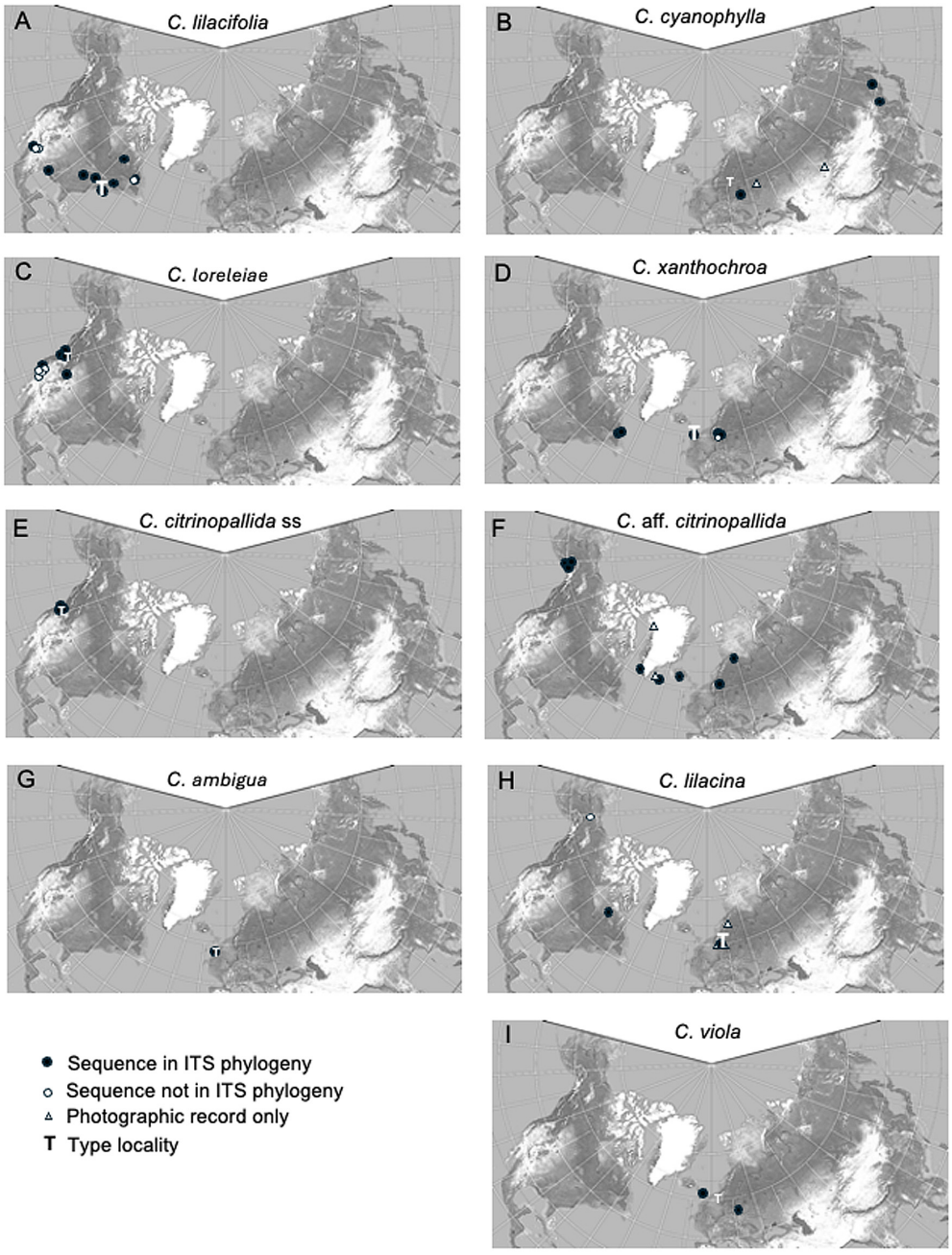

FIGURE 2. Distribution maps of *Chromosera* species, clades and type localities using a modified Lambert conformal conic projection N hemisphere map (Strebe 2011) as a template. A. *C. lilacifolia*. B. *C. cyanophylla*. C. *C. loreleiae*. D. *C. xanthochroa.* E. *C. citrinopallida s.s.* from NW of North America. F. *C.* aff. *citrinopallida*—circumarctic clade. G. *C. ambigua*. H. *C. lilacina*. I. *C. viola*.

Specimens of *C. xanthochroa* (Figure 2D) and of the circumarctic clade labelled *C.* aff. *citrinopallida* were collected from high latitudes (Alaska, Iceland, Labrador, Norway, and Greenland), whereas specimens of the Pacific Northwest clade of *C. citrinopallida* were all collected in Washington state, which is also where the type was collected (Smith & Hesler 1954) (Figure 2E). We therefore infer that the Washington state clade likely represents *C. citrinopallida sensu stricto* and that the circumarctic clade will need a new name. Studies of *Chromosera* collections identified as *C. citrinopallida* by Laursen *et al*. (1977) and by Borgen and Arnolds (2004) from Alaska and Greenland, respectively, suggest that there may be more than one un-named species in this complex.

Taxonomy

***Chromosera lilacifolia* (Peck) Grootmyers, Lodge, Redhead, Mullineux & S.D. Russell,** *comb. nov.* Figs. 3A–B, 4
MycoBank #:—MB854331

Basionym:—*Agaricus lilacifolius* Peck, Ann. Rep. New York State Mus., 24: 63 (1878)
≡ *Agaricus lilacinus* Peck (1872) [1871] (illeg., Art. 53.1, homonym, ≠ *A. lilacinus* Schumach. 1803 (*Agaricaceae*); ≠ *A. lilacinus* Lasch 1828 (*Lactarius lilacinus*), ≠ *A. lilacinus* Lasch 1828 (*Pluteus lilacinus*) (illeg. Art. 53.1).
≡ *Omphalia lilacifolia* (Peck) Peck, Ann. Rep. New York State Mus., 45: 94 (34) (1893)
≡ *Omphalina lilacifolia* (Peck) Murrill, North Am. Flora, 9: 346 (1916)
≡ *Clitocybe lilacifolia* (Peck) Singer, Lloydia, 5: 105 (1942)
≡ *Mycena lilacifolia* (Peck) A.H. Sm., North Amer. Species of *Mycena*: 414 (1947)

Type—USA. New York: Oneida Co., Trenton Falls, 230 m elev., 43.271, -75.160, September 1872, *C.H. Peck s.n.* (**NYSf1712**, holotype)

Reference specimen:—USA. Pennsylvania: Luzerne Co., Ricketts Creek State Park, lower Falls Trail on Kitchen Creek, just N of Rt. 118, 630 m elev. 41.300396, -76.274795, 18 May 2019, D. Wasilewski, MUOB366870 (DAOM985107), GenBank ITS MG050103.

Diagnosis:—Basidiospores shorter than in *C. loreleiae* (mostly ≤ 6.5 µm vs, mostly ≥ 6.5 µm), lamellae bluish instead of pinkish lilac and distributed in eastern North America.

GenBank:—MG050103 (ITS)

Description:—*Pileus* 5–10(–18) mm diam., diameter 1–2.5 x length of stipe, membranous, convex-umbilicate, margin often flared; color dull yellow with a slight greenish or lilac tint when fresh, buttons sometimes lilac with yellow tint, hygrophanous, drying bright sulfur yellow or yellow with a brown tint, surface smooth, viscid; margin translucent-striate. *Lamellae* arcuate-decurrent, subclose, pale lilac, lilac or pinkish lilac, some with a dull yellow tint near pileus or stipe. *Stipe* 12–30 x 2 mm equal or slightly expanded toward base, often with a sub-bulbous base, pale brownish yellow, rarely white, usually with a lilac mycelial pad at base, hollow; surface viscid.

Basidiospores inamyloid, 5.3–6.8(–8.4) x (2.2–)3–4(–5.1) µm, Q = 1.4–2.0(–2.44) in collections with only 4-sterigmate basidia; (4.8–)5.2–7.4(–9.2) x (2.0–)3.2–4.0(–5.5) µm, Q = 1.63–2.4 in collections with 1-, 2- and 4-sterigmate basidia; corresponding means: 5.9–6.2 x 3.2–3.6 µm, Q = 1.7–2, and 5.9–7.1 x 3.6–4.2 µm, Q = 1.7–1.9. *Basidia* all 4-sterigmate or mixed with 1- and 2-spored basidia, 15.3–26.0 x 3.3–6.5 µm, all bearing basal clamp connections. *True cystidia* absent but degenerate cystidia-like basidia present on sides and lamellae of many collections that have 1-spored basidia. *Lamellar context* subregular, with chains of short, swollen hyphae 8–48 x 4–18.5 µm. *Pileipellis* an ixocutis 20–24 µm deep with embedded hyphae 3–8 µm diam. *Hypodermium* with short, inflated hyphae 12–24 x 10.4–13.6 µm. Dextrinoid reactions present but often weak in the pileus context, weakly present in the lamellar context near the pileus and stipe or absent.

Distribution:—Eastern North America, documented so far from the province of Québec (Canada) south to Texas and west to Indiana and Arkansas. Based upon eastern North American records reported by Redhead *et al*. (1995), found in Ontario, Québec, New Brunswick and Nova Scotia (Canada), and in Michigan (USA). Also present in the Southwestern USA (Arizona).

Habitat:—Gregarious on conifer logs (*Abies*, *Pinus* and *Tsuga*).

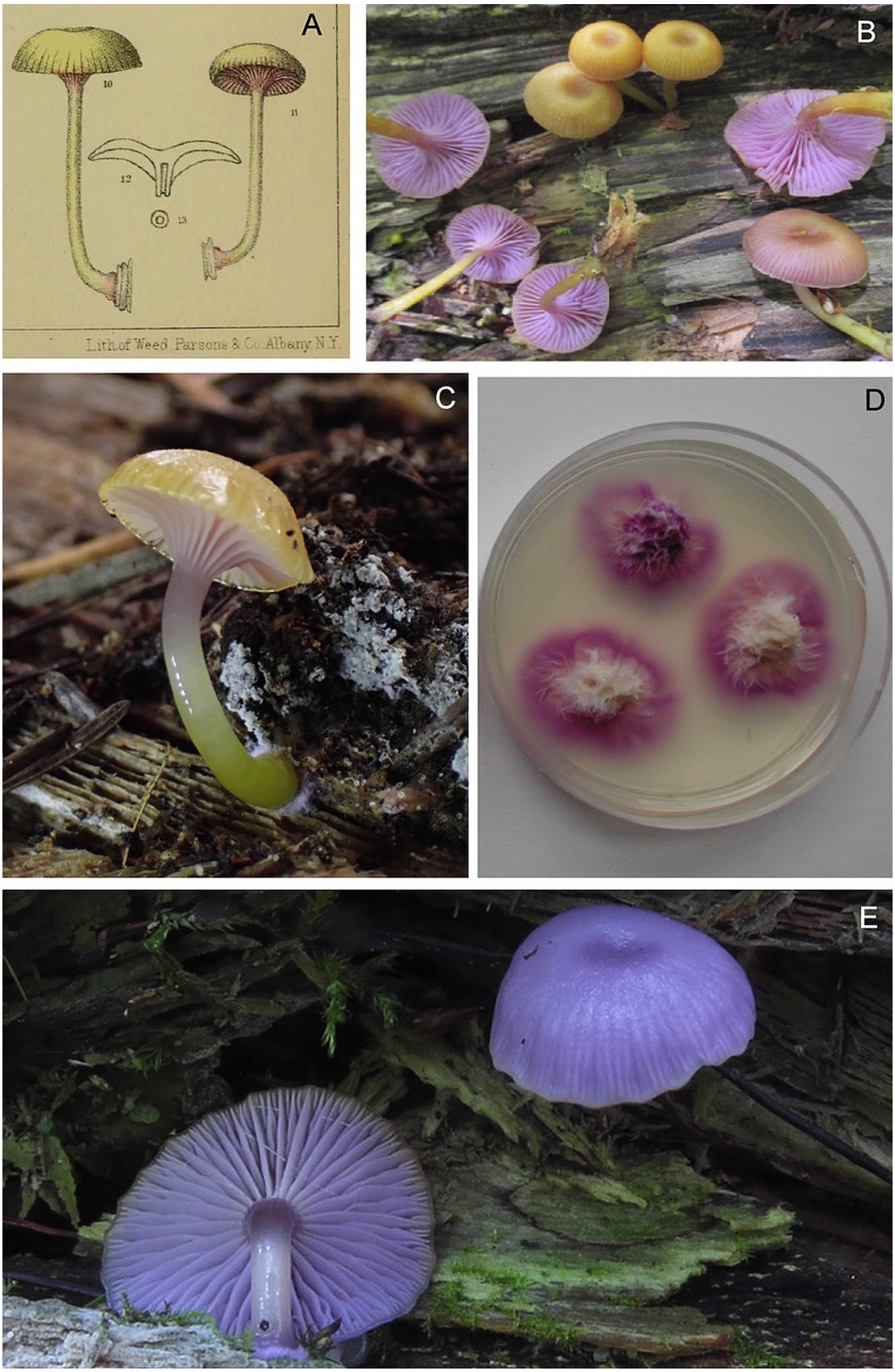

FIGURE 3. North American *Chromosera* species basidiomes. A–B. *Chromosera lilacifolia* A. Painting of the holotype (NYSf1712) of *Agaricus lilacina* Peck 1872 illeg., later renamed *A. lilacifolius* Peck 1878. B. *Chromosera lilacifolia* from Pennsylvania, USA (MUOB366870, DAOM985107; David Wasilewski). C–D. *Chromosera loreleiae*. C. *Chromosera loreleiae* from Washington, USA (iNaturalist #34380700, WTU-F078934; Sadie Hickey). D. Culture of *C. loreleiae* from British Columbia, Canada grown on PDA (DAOMC225985). E. *Chromosera lilacifolia* var. *totililacicolor* from Québec, Canada (HRL1723, DAOM242735; Gwenaël Cartier).

Additional specimens examined:—**CANADA:** Québec Prov., La Plaine, R. Lebeuf, 16 August 2010, HRL0497, DAOM985106, GenBank PP853165; ibid., Mascouche, R. Lebeuf, 24 June 2008, HRL0080, DAOM985104, GenBank PP853166. **USA:** Indiana, Brown Co., Nashville, Yellowwood State Forest, 39.141876, -86.295479, 17 November 2018, iNat18524774, S. Russell 66878, PUL F28069, GenBank MN173968. Monroe Co., Bloomington, 39.191881, -86.512986, 30 April 2019, iNat24222314, R. Kerner 66477, PUL F25616, GenBank MN173970; ibid, Griffy Lake, 39.201995, -86520496, 3 November 2017, R. Kerner, iNat18565341, PUL F25616, GenBank MN173969. New York: Essex Co., N. Elba, Oneida Co., date not recorded, C.H. Peck, NYSf1712.2; ibid, Trenton Falls, September 1872, C.H. Peck, s.n., **TYPE** NYSf1712, duplicate NY774801; ibid, Nassau Co., Long Island, Oyster Bay, 40.859376, -73.556688, on downed *Pinus* log, P. Tomko, 21 April 2017, det. J. Horman, NY03818151, GenBank MG050103. Ohio, Hocking Co., Logan, Hocking State Forest, rock climbing and rappelling area, 39.4565, -82.5588, 200 m elev., 21 October 2017, D. Grootmyers 296364, MUOB296364, MU 000292829, GenBank PP853168. Pennsylvania, Luzerne Co., Ricketts Creek State Park, Hunlock Creek, 41.3778, -76.3256, 18 May 2019, D. Wasilewski, MUOB366870, DAOM985107, GenBank MG050103. Texas: Montgomery Co., Caney Creek at Lone Star Hiking Trail, 30.4868, -95.6795, 2 March 2019, A. Sergeev, MUOB360690, DAOM985105, GenBank PP853167.

Comments:—This species differs from C. *loreleiae* in having shorter spores (mostly ≤ 6.5 µm vs mostly ≥ 6.5 µm), and often more intensely pigmented lamellae. In addition, collections with 1- and 2-sterigmate basidia usually have aberrant basidia that appear as cystidia-like structures on the sides of the lamellae, but the ITS sequences are the same or nearly identical to collections with 4-sterigmate basidia including the selected reference specimen. This species differs from *C. cyanophylla* in ITS sequences and slight pigment differences. The lamellae are tinted pinkish lilac and rarely have a blue tint whereas *C. cyanophylla* usually has blue-tinted lamellae.

Chromosera lilacifolia* var. *totililacicolor* Lebeuf, G. Cartier, Grootmyers & Lodge, *var. nov. Fig. 3E
MycoBank #:—MB 855448

Etymology:—Toto- entirely, lilacicolor—lilac colored.

Type—Canada. Québec Province : Sainte-Marguerite-du-lac-Masson, rue du Lac-Clair, 46.09239, -74.05392, on *Pinus strobus* log, Gwenaël Cartier S.N., 25 July 2014, HRL1723 (**DAOM985251**, holotype)

Diagnosis:—Entirely lilac-colored. Differs from the type variety in lacking yellow pigments in the pileus and stipe.

GenBank:—PQ182943

Distribution:—Only known from three collections at the type locality, Lac-Charlebois, Québec, Canada.

Habitat:—Growing on *Pinus strobus* logs.

Additional specimens examined:—CANADA, Québec Prov., Sainte-Marguerite-du-lac-Masson, rue du Lac-Clair, on *Pinus strobus* log, Gwenaël Cartier S.N., 6 July 2013, photo record only (https://www.flickr.com/photos/14486802@N02/9234939698); ibid, 12 July 2015, photo record only (https://www.flickr.com/photos/14486802@N02/19480004699).

Comments:—Except for the absence of yellow pigments, the macroscopic and microscopic features of this variety are the same as those in the type variety of *C. lilacifolia*. The molecular phylogeny also indicates that they represent the same species, with *C. lilacifolia* var. *totililacicolor* DAOM985251 differing from other *C. lilacifolia* isolates only by an additional C in ITS2.

Chromosera loreleiae* Lodge, Redhead, & Mullineux *sp. nov. Fig. 3C–D, Figs. 2–5 in Redhead, Ammirati & Norvell. 1995. Sydowia X: 162–164
MycoBank # MB854280

Etymology:—Named in honor of Dr. Lorelei L. Norvell who co-described the genus *Chromosera*.

Type:—USA, Washington, Pierce County, Mt. Rainier Nat. Park, Ipsut Creek, 46.97056, -121.83195, 245 m elev., 11 November 1993, Scott Redhead and Lorelei Norvell LLN 93.11.11-7, (**WTU-F-001648**, holotype).

Reference specimen:—Canada, British Columbia, Vancouver, University of British Columbia Lands, 12 October 1998, S.A. Redhead (8038) and K. Seifert DAOM 985252; cultured as DAOMC225985, GenBank PP853161

Diagnosis:—Occurring in northwestern North America, usually differing from Eurasian *C. cyanophylla* in having paler lamellae that are rosy lilac versus bluish lilac, and in ITS sequences. Differing from *C. lilacifolia* in eastern North America by longer spores (≥ 6.5 µm) and ITS sequences.

Description:—Adapted from Redhead, Ammirati & Norvell. 1995. Sydowia X: 162–164. *Pileus* 3–25 mm diam., convex with a flattened to depressed center, glabrous, translucent-striate, darkest in center, pale luteous to amber, honey color, olivaceous-buff, to Cream color to Naples yellow with faint rosy vinaceous, pale rosy vinaceous, rosy vinaceous or Pale Lilac, fading with age (or losing lilac pigments with sunlight and drying). *Lamellae* arcuate-decurrent, pale vinaceous, rosy vinaceous, or Pale Lilac, fading with age, edges concolorous, moderately spaced, 1–2 lengths of lamellulae inserted. *Stipe* 10–30(–45) x 1–2.5 mm, equal above a slightly swollen base, cartilaginous, hollow, viscid, amber with a grayish rose to vinaceous tinted apex, frequently with vinaceous to lilac tints at base. Odor not significant.

Basidiospores 6.5–9(–11) x 3.5–4.5 µm, amygdaliform to ellipsoid, with prominent tapered apiculus, thin-walled, smooth, hyaline, inamyloid, not cyanophilous. Basidia 20–25(–29) x 4–5(–6.5) µm, clavate, 4-sterigmate, lacking siderophilous granules. *Pleurocystidia* and cheilocystidia absent. *Pileipellis* a thin collapsed ixotrichoderm, hyphae 3–5 µm diam., hyaline, inamyloid, smooth, thin-walled, clamped, embedded in a thin slime which easily disperses, sparsely covered with small, yellowish, refractive pigment globules 1.5–2 µm diam. *Subpellis* poorly differentiated from the trama except for increased concentrations of extracellular and possibly intracellular pigment corpuscles 6–7 µm diam. consisting of radially arranged globules around a colorless core. *Pigment bodies* present in only relatively recent collections—noted up to 1 year after drying but apparently volatilizing or degrading in herbarium specimens hence lacking in older material—subhyaline to faintly yellow in water, becoming bright yellow in dilute NH_4OH sol. or Melzer's reagent. *Pilear trama* hyphae mostly 5–15 µm diam., thin-walled and loosely packed, hence many collapsed in rehydrated material, hyaline except for scattered pigment globules and corpuscles, walls weakly to moderately dextrinoid**.** *Lamellar trama* more or less regular but becoming slightly disorganized with age, hyphae mostly 5–10 µm diam., similar to those of the pilear trama, mixed with fewer pigment corpuscles, moderately dextrinoid.

Distribution:—Western North America.

Habitat:—Growing on conifer wood.

Additional specimens examined*:*—USA: Washington, Kittitis County, Cle Elum Pine Flats, 47.201463, -120.956758, 3000 m elev., 26 March 1962, IS1725 (WTU-F-001646); ibid., T20N R18E S8, 47.2426, -120.61, 27 May 2000, M.W. Beug, 1cMWB52700 (WTU-F-001655); Skamania Co., 14 October 2019, 46.106937, -121.548056, iNat34380700, S. Hickey, L. Ré & S. Ness, 62201, iNat34380700, GenBank OM522252, (WTU-F078934); ibid., San Juan Co., San Juan Island, 18 March 2022, R.H. Morrison, RHM-22-2, iNat 112874004, (WTU-F-07714).

Additional sequenced collections:—USA: California, Calaveras County, Camp Connell, Black Spring OHV Campground between Ganns and Cottage Springs, 4 June 2023, D. Tighe, iNat166099724, GenBank OR750619, (HAY-F-005387); ibid., El Dorado County, El Dorado National Forest, Crystal Basin, near Icehouse Reservoir, 9 June, 2019, 38.8292, -120.3697, 1697 m elev., D. Klein, MUOB 368868, Rockefeller-2554; ibid., 26 May 2018, MUOB 317467, GenBank MH429982; ibid., Humbolt County, near Eureka, 40.77495, -124.14897, 5 April 2023, M. Hackney, iNat153604651, GenBank OR886743, (HAY-F-000710); ibid., San Bernadino County, San Bernadino Mts., 34.25295, -116.91354, September 2023, A. Tupac, iNat184200790, GenBank PP791242, (HAY-F-001368); Siskiyou County, Etna, 29 May 2023, D. Lyons, iNat164655333, GenBank OR771793 (HAY-F-004994); ibid., about 1 mi. S of Jot Dean Ice Cave, E side of Rt. 49, 41.48107, -121.63107, D. Tighe, iNat165851695, GenBank OR656490, (HAY-F-003041); Tehama County, 40.36595, -121.5642, 15 May 2023, W. Cardimonas, iNat167244818, GenBank PP849881, (HAY-F-004955). Washington: King County, Asahel Curtis Nature Trail, Mount Baker-Snoqualmie National Forest, 47.57861, -122.28833, 1000 m elev., 6 May 2007, S. Trudell SAT 07-126-02, (WTU-F- 000132); Kittitas County, Cle Elum Pine Flats about 1 mi from Cle Elum. 47.201463, -120.956758, 26 March 1962, unk. IS1725, (WTU-F-001646); ibid., Okanogan-Wenatche National Forest Rd. 3507, 47.2426, -120.61, 27 May 2000, M.W. Beug, 1cMWB52700, (WTU-F-001655).

Comments:—The rosy lilac pigment typically found in the mycelium at the base of the stipe is also produced in multispore derived agar culture, where both pigments—yellow and rosy lilac—are expressed in different parts of the mycelium (Fig. 3D). This species is difficult to distinguish macroscopically from the Eurasian *C. cyanophylla* and the eastern North American *C. lilacifolia*. However, its lamellae are usually paler, with a rosy hue rather than the bluish lilac of the former, and it usually exhibits paler lamellae and a smaller pileus diameter to stipe length ratio than the latter.

The spores of *C. loreleiae* are longer than those of *C. lilacifolia* in eastern North America (≥ 6.5 µm) but spore dimensions are similar to those of Eurasian *C. cyanophylla*. Besides the differences in geographic ranges, divergence in ITS sequences is useful for separating C. *loreleiae and C. cyanophlla.* For example, in ITS1 beginning ca. 58 bp

before the 5.8S region, the sequence in C. *loreleiae* is aaaaa-atCyTgaatgt-Gatt compared to aaaaaCatTtTgaatgtAAatt in *C. cyanophlla*. *Chromosera lilacifolia* has a different ITS1 motif, AAAA-CTTTAATGAATGT-GATT, as does the European *C. ambigua*, AAAA- -TTT-TTGAATGT-CATT. The provisional species names *Chromosera* "cyanophylla-CA01" and *Chromosera "*CA-01" have previously been used for this species in GenBank and iNaturalist.

Singer (1942) suggested that the species Murrill (1913) described from Oregon as *Clitocybe violaceifolia* was related to *A. lilacifolius*, raising the possibility of a prior name for *Chr. loreleiae*. However, the first author studied the holotype of *Cl. violaceifolia* (NY 657675**)** and excluded it from *Chromosera* based on the more robust basidiomes lacking yellow pigments. ITS sequence data generated from the type (GenBank OR886357) also supports Murrill's placement of this species in *Clitocybe sensu stricto* distant from *Chromosera*. Additionally, the holotype of *Cl. violaceifolia* was reported as growing on *Quercus* wood while *Chr. cyanophylla*, *Chr. loreleiae*, and *Chr. lilacifolia* are all found growing exclusively on the wood of conifers.

The gross morphology and microscopic features of the holotype of *C. loreleiae* (WTU-F-001648) are illustrated (as *Chromosera cyanophylla*) in Redhead *et al*. (1995).

Additional type examined:—*Clitocybe violaceifolia* Murrill. USA. Oregon: Marion Co., near Salem, on decaying *Quercus* wood, 7 June 1911, Morton E. Peck *s.n*. (**NY 657675**, holotype).

Discussion

The ITS-28S phylogenetic tree reaffirms the phylogenies presented by Holec *et al*. (2015) and by Tanchaud *et al*. in Crous *et al*. (2019), which showed that what was previously called *Chromosera cyanophylla* from western North America is a separate species. We have, therefore, described the western North American *Chromosera* as a new species in section *Chromosera* and named it in honor of Dr. Lorelei Norvell, co-author of the genus *Chromosera*. In addition, we demonstrate for the first time that collections of *Chromosera* from eastern North America (previously synonymized under *C. cyanophylla*) represent a species distinct from the Eurasian *C. cyanophylla,* the European *C. ambigua,* as well as the new Western North American *Chromosera* species. *Chromosera ambigua* Tanchaud, Jargeat & Eyssart described from France is sister to *C. lilacina* and falls in a separate subgenus, *Oreocybe*.

Singer (1942), in his type studies of *Clitocybe*, suggested that *Clitocybe violaceifolia* Murrill (1913) described from Oregon might be related to *Chromosera lilacifolia* (as *Clitocybe lilacifolia* (Peck) Singer). However, the first author examined the type of *C. lilacifolia* (NY 657675) and excluded it from *Chromosera* based on the more robust basidiomes lacking yellow pigments. ITS sequence data generated from the type (GenBank OR886357) also support Murrill's placement of this species in *Clitocybe sensu stricto* distant from *Chromosera.*

Previous phylogenies published by Vizzini & Ercole (2011), Holec *et al*. (2015) and Tanchaud *et al*. in Crous *et al*. (2019) did not include sequences from eastern North America as none were available. Based on our comparisons of Peck's type with a matching recent collection from Pennsylvania that we sequenced to serve as a reference (deposited at NY), we resurrect Peck's (1878) name for the species described from New York as *Agaricus lilacifolius* and recombine it in *Chromosera*. This species of *Chromosera* has previously been controversially placed in various genera including *Omphalina, Clitocybe* and *Mycena* (Aurora 1986, Redhead *et al*. 1995, Singer 1942, Smith 1947).

The molecular analysis confirms the range expansion of the Eurasian *C. cyanophylla* into far-east Asia to include China (Figure 2B) as reported by Bau & Liu (2010). The species distributions in this clade comprise *Chromosera* subgenus *Chromosera* which shows both a continental (eastern to southwestern vs northwestern North America) and two intercontinental oceanic barriers (Atlantic and Pacific) among the related species. However, there are two amphi-Atlantic species lacking an oceanic barrier (*C. lilacina* and *C. xanthochroa*, Figures 2D, H) and one taxon (labeled *Chromosera* aff. *citrinopallida,* Figure 2F) with a circumarctic distribution as found in the database of Geml *et al*. (2012).

Chromosera citrinopallida (A.H. Smith & Hesler) Vizzini & Ercole presents a notable biogeographic conundrum that is yet to be resolved. No sequence data are available for the type of *C. citrinopallida,* from Mt. Rainier in Washington state, USA (Smith & Hesler 1954). However, sequences from three collections made in northwestern Washington state and matching the type description (labeled Pacific Northwest in the ITS tree in Figure 1, *C. citrinopallida s.s.* in Figure 2E) form a clade that is distinct from the clade comprised of isolates from the circumpolar arctic and Scandinavia (labeled Circumpolar arctic in Figure 1, *C*. aff. *citrinopallida* in Figure 2F). Strains in the Washington state group contain several SNPs and indels in the ITS region, suggesting that isolates from the Pacific coast may be evolving independently of those found in the North Atlantic and arctic Alaska. It remains ambiguous whether the newly sequenced

collections from Washington or the circumpolar taxon represent the true *C. citrinopallida*, or an undescribed taxon, but we infer that the former is more likely to represent *C. citrinopallida sensu stricto*.

Borgen & Arnolds (2004) reported *C. citrinopallida* from Greenland and noted that a portion of their collections had both normal spores and abnormally long and narrow spores. A more recent collection from Greenland identified by Borgen as *C. citrinopallida* (CFMR DEN-29) falls within our circumpolar *C.* aff. *citrinopallida* clade. Sequence data are lacking for other *C. citrinopallida*-like collections from Greenland, leaving it unclear whether they represent one or multiple species. Similarly, Laursen *et al*. (1987) reported *C. citrinopallida* from arctic Alaska, as well as a similar species, "*Chromosera* aff. *citrinopallida*", differing in having olive or gray pigmentation on the pileus and stipe. Our analyses support the presence of the circumpolar taxon in arctic Alaska but sampling from the region is limited. It remains to be determined whether these olive and gray collections represent the circumpolar taxon or a different *Chromosera* species, as none of the collections studied by Laursen *et al.* have sequence data available.

Sequencing of additional collections and sequence data from protein-coding regions and mitochondrial genes may help clarify identities in the *C. citrinopallida* complex. It should be noted that mitochondrial genomes tend to be intron-rich, and these introns are not stable markers for species identification.

Reflecting upon previous classifications, we note that *Chromosera* continues to be supported as a distinct genus in the *Hygrophoraceae* Lotsy, and is type of Tribe *Chromosereae* Vizzini, Lodge, Norvell & Redhead, which now includes *Gloioxanthomyces* and *Sinohygrocybe* (C. Q. Wang *et al.* 2018). Kühner (1980: 876) was prescient in suggesting that "*Hygrocybe cyanophylla*" (invalid comb.) belonged in "*Hygrocybe* subg. *Gloiophorus*" when others classified it as a *Mycena* (Pers.) Roussel (*Mycenaceae* Overeem) or *Omphalina* Quél. (*Omphalinaceae* Vizzini, Consiglio & M. Marchetti). Subgenus *Chromosera* now includes *C. cyanophylla*, *C. lilacifolia* and *C. loreleiae*. Subgenus *Oreocybe* (Boertm.) Vizzini & Lodge is supported and includes *C. citrinopallida* and *C. xanthochroa*. Subgenus *Subomphalia* Vizzini, Lodge & Padamsee, containing *C. viola,* remains monotypic, leaving *C. ambigua and C. lilacina* together and without a subgenus.

Vizzini *et al*. (2024) recently split *Hygrophoraceae* into five families: *Cantharellulaceae* (Lodge, Redhead, Norvell & Desjardin) Vizzini, Consiglio & P. Alvarado, *Cuphophyllaceae* (Z.M. He & Zhu L. Yang) Vizzini, Consiglio & P. Alvarado, *Hygrophoraceae, Hygrocybaceae* (Padamsee & Lodge) Vizzini, Consiglio & P. Alvarado (≡*Hygrocybaceae* Locq. *nom. inval.*), and *Lichenomphaliaceae* (Lücking & Redhead) Vizzini, Consiglio & P. Alvarado. Under this system, *Chromosera* is a member of the family *Hygrocybaceae.*

However, we (primarily the first author) favor treating *Chromosera* as part of a larger *Hygrophoraceae* corresponding to *Hygrophorineae* Aime, Dentinger & Gaya *sensu* Vizzini *et al*. and to *Hygrophoraceae sensu* Lodge *et al.* (2013). Our decision is based on the principle that more inclusive clades tend to be more taxonomically stable over time than less inclusive clades (de Hoog *et al*. 2023, Nicolle *et al*. 2024). A larger family is more resistant to further splitting as taxon sampling improves. For example, many species likely belonging to this clade remain unsequenced. Should any of these species fall within the broader *Hygrophoraceae sensu* Lodge *et al.* but outside of one of Vizzini *et al*.'s five families, the "smaller family" system would compel authors to describe additional new families where authors following the "larger family" system would treat them under *Hygrophoraceae*. This broader classification would enhance taxonomic stability in the long term and may be more practical for non-taxonomists. We argue that treating these smaller families as subfamilies or tribes, as Lodge *et al*. did, may be equally useful and less disruptive.

Vizzini *et al*. failed to recover *Hygrophorineae sensu* Dentinger *et al*. (2016) as monophyletic in their analyses (Vizzini *et al.* 2024, supplemental Fig. S1). Specifically, *Hygrophoraceae* and *Clavariaceae* were not recovered as sister families. Support values for all backbone nodes between the node uniting *Clavariaceae* with the remainder of *Agaricales* (excluding *Typhulaceae*) and the node uniting *Pluteineae, Pleurotineae*, and *Agaricineae* fell below their significance thresholds. Notably, *Clavariaceae* and *Cyphellopsidaceae* were pruned *a priori* for the analyses shown in their figures 1-3, which artificially increased backbone support values. Under these conditions, *Hygrophorineae* becomes monotypic and effectively equivalent to *Hygrophoraceae.* While a monotypic *Hygrophorineae* is not unprecedented (*e.g.,* Olariaga *et al*. 2020, G. S. Wang *et al*. 2023), Vizzini *et al.* argued that if *Hygrophorineae* is a suborder, then it should contain multiple families, but did not apply this logic to *Clavarineae* or *Typhulineae*, which were also recovered as monotypic. We prioritize increasing taxonomic stability over reducing the number of monotypic taxa.

It is also worth noting that *Lichenomphaliaceae* (Lücking & Redhead) Vizzini, Consiglio & P. Alvarado is incorrect but not illegitimate under Art. 52.4, as it explicitly includes the types of both *Coraceae* Tomas. *ex* Tomas. and *Dictyonemataceae* Tomas. *ex* Tomas. Both names were published and validated in the same publication and have equal priority (Art. 11.5) so authors following the "smaller family" system would need to select which name to adopt (Tomaselli 1949, Tomaselli 1950). *Arrheniaceae* Locq. *nom. inval.* would also be a synonym. We propose treating all

of these families as junior synonyms of *Hygrophoraceae.* The following invalid names from Locquin (1984) are also synonymous with *Hygrophoraceae*: *Camarophyllaceae* Locq. and *Hygroasteraceae* Locq.

Notably, unlike most genera of the *Hygrophoraceae*, *Chromosera*, represented by *C. loreleiae* (DAOMC225985), is culturable. This helps clarify the ambiguity in nutritional strategies mentioned by Halbwachs *et al*. (2018). Additionally, *C. loreleiae* expresses both yellow and lilac pigments in culture (Fig. 3D). All species of *Chromosera* produce either yellow or lilac/bluish pigments or both. Presumably all species are saprophytic rather than mycorrhizal or otherwise biotrophic. In at least the case of *Chromosera lilacifolia* var. *totililacicolor*, a mutant suppressing the development of one pigment has occurred. In other cases, such as in *C. lilacina*, the lilac pigment normally present can be obscured by fading or poor production (Voitk & Voitk 2020).

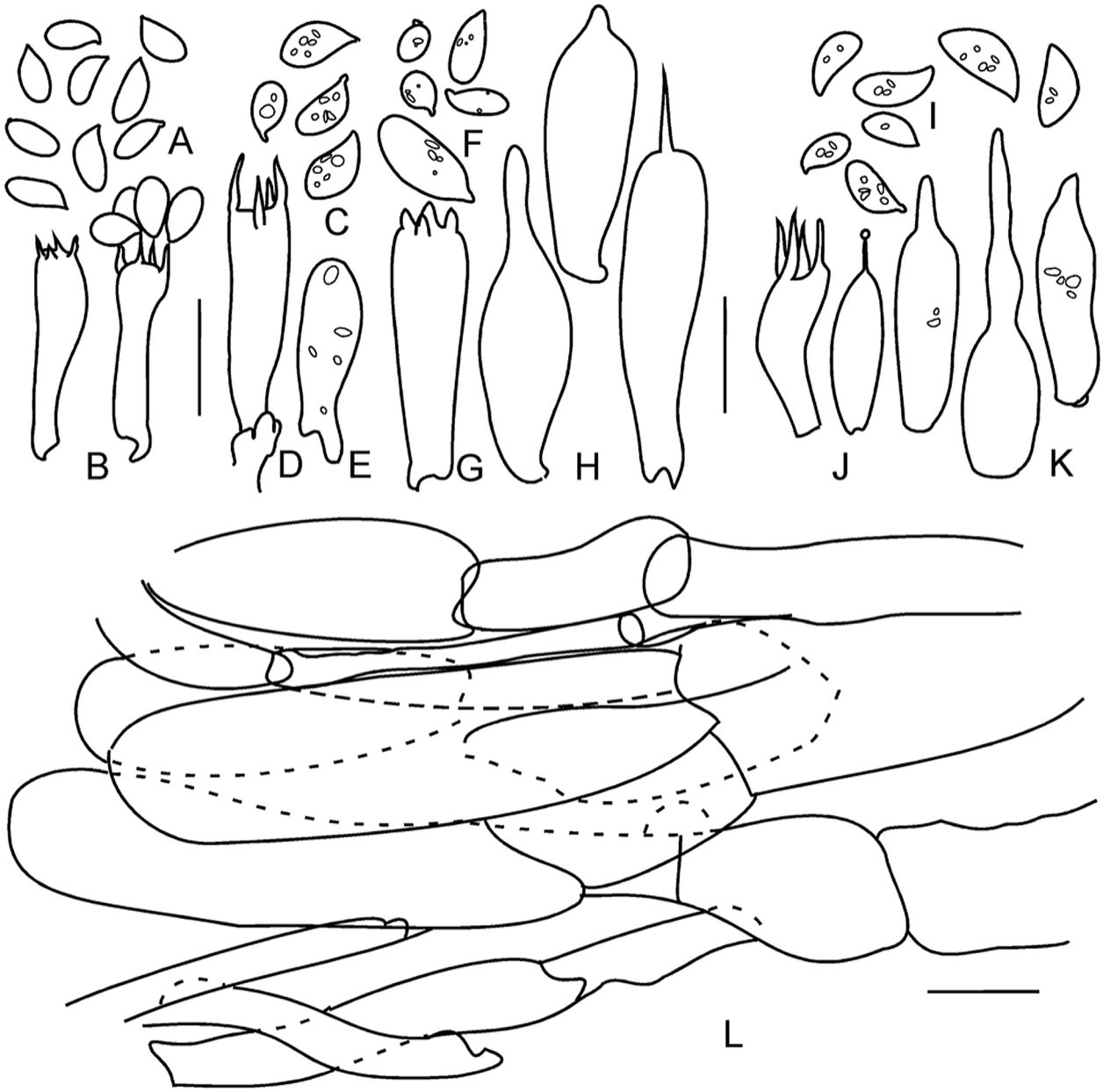

FIGURE 4. Microscopic characters of *Chromosera lilacifolia*. A–B. Holotype of *Agaricus lilacifolius* Peck (as *A. lilacina* illeg.) from New York, USA (NYSf1712). A. Basidiospores. B. Basidia. C–E. *Chromosera lilacifolia* from Pennsylvania, USA (MUOB366870, DAOM985107). C. Basidiospores. D. Basidium. E. Basidiole. F–H. *Chromosera lilacifolia* from Ohio, USA (MUOB296364, MU 000292829). F. Basidiospores from 1- and 4-sterigmate basidia. G. 4-sterigmate basidium. H. 1-sterigmate basidia and degenerate cystidia-like basidia. I-L. *Chromosera lilacifolia* from Pennsylvania, USA (MUOB366870, DAOM985107). I. Basidiospores from 1- and 4-sterigmate basidia. J. 1- and 4-sterigmate basidia. K. degenerate cystidia-like basidia. L. Lamellar trama. Scale bars = 10 µm.

Conclusions

Continents separated by oceans and large continents lacking contiguous habitat can provide dispersal barriers leading to allopatric speciation, which is consistent with present distributions of several species in *Chromosera* subg. *Chromosera*. In contrast to the presence of an eastern and a western species of *Chromosera* in North America, the Eurasian *C. cyanophylla* has a continent-wide distribution from Europe through eastern Russia and China, and both *C. lilacina* and *C. xanthochroa* have amphi-Atlantic distributions.

Using morphological and molecular data, a new species from western North American is described as *Chromosera loreleiae*. Additionally, molecular and morphological analyses were used to resurrect the species Peck described from eastern North America as *Agaricus lilacifolius* by recombining it in *Chromosera.* New data from a collection from China confirm the range expansion of *C. cyanophylla ss*. across eastern Eurasia. We observed a circumarctic distribution among collections recorded in the database of Geml *et al*. (2012) which they identified as '*C. citrinopallida'*—a common pattern Geml *et al*. noted in their text regarding *Lichenomphalia*. Those North Atlantic circumarctic "*C. citrinopallida*" sequences fell within a clade distinct from a clade containing three isolates from Washington state. We infer that the Washington state collections likely represent *C. citrinopallida sensu stricto*, as the species was described from that state, so that the circumarctic taxon will likely need a new name.

Key to species of *Chromosera*

1	Basidiomes terrestrial, on mossy to lichen colonized peaty to sandy soil or heath	2
1'	Basidiomes lignicolous, on decaying coarse conifer wood (stumps, logs, branches)	7
2	Basidiomes entirely light to dark violet to pale lilac	3
2'	Basidiomes overall bright yellow, olivaceous, or orangish yellow to orangish or yellow mixed with lilac on the stipe (base or top), and/or lamellae, and/or pileus	4
3	Basidiomes violet to dark lilac (lacking yellow); spores broadly ellipsoid to globose, 5–6 µm diameter; pileus and stipe not viscid	*C. viola*
3'	Basidiomes lilac; basidiospores ellipsoid, never subglobose, 4–8 µm wide; pileus and stipe slightly viscid	*C. lilacina*
4	Basidiomes chrome yellow, sometimes olivaceous, lacking lilac or orange tints	*C. citrinopallida* complex (see discussion)
4'	Basidiomes with some lilac or orange tints	5
5	Basidiospores 5–8 x 3.5–5.5 µm, pileus usually orange-yellow	*C. xanthochroa*
5'	Basidiospores longer, mostly 7–12 µm, basidiomes usually with some lilac tints	6
6	Basidiospores 4–8 µm wide; from transatlantic arctic and alpine zones	*C. lilacina*
6'	Basidiospores mostly 4.5–5.5 µm broad, known from heaths in western Europe (France)	*C. ambigua*
7	Totally lilac	*C. lilacifolia* var. *totililacicolor*
7'	Pileus with yellow coloration	8
8	Mean spore length 5.9–7.1 µm, majority ≤ 6.5 µm long, eastern to southwestern North America	*C. lilacifolia*
8'	Mean spore length longer, 7.7 µm, all > 6.5 µm long	9
9	Lamellae usually pale rosy lilac, found in northwestern North America	*C. loreleiae*
9'	Lamellae often bluish lilac, pale or strongly colored, Eurasian species	*C. cyanophylla*

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Supplementary material

Supplementary materials for this study, including Table S1, the DNA alignment in .nex format, and the treefile in both .tre and .pdf formats, are available at https://github.com/heelsplitter/Geographic_distributions_in_Chromosera_species_SUPPLEMENTAL and have also been archived at https://web.archive.org/web/20250120011556/https://github.com/heelsplitter/Geographic_distributions_in_Chromosera_species_SUPPLEMENTAL

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