

RESEARCH ARTICLE

Global phylogeny and taxonomic reassessment of the lichen genus *Dendriscosticta* (Ascomycota: Peltigerales)

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Abstract The genus *Dendriscosticta* (Ascomycota: Peltigerales) encompasses several distinctive lichen-forming fungal species restricted to the Northern Hemisphere. Most are flagship species of old-growth forests with good air quality. A global phylogeny of the genus based on multilocus sequence data (ITS, *RPB1*, *EF-1α*, *MCM7*), model-based phylogenetic methods, and morphological and chemical assessments, reveals a high level of cryptic speciation often associated with restricted geographical distribution and/or chemical characters. Using sequence-based species delimitation approaches, we circumscribe two main clades referred to as the *D. wrightii* clade, with five unequivocal species, including *D. gelida* sp. nov., and the *D. praetextata* clade, with eight putative species, including *D. phyllidiata* sp. nov. The absence of recently collected material of *D. hookeri* comb. nov. from the type locality unfortunately prevents assignment of this epithet to one of the five supported lineages sharing this morphotype. Three new combinations are proposed: *D. hookeri*, *D. insinuans* comb. nov. and *D. yatabeana* comb. nov. Epitypes are designated for *D. wrightii* and *D. yatabeana*. Species diversity within the genus increased from four to nine. Our morphological assessment confirmed that *Sticta* and *Dendriscosticta* can be readily distinguished by the presence of excipular algae whereas the structure of the lower surface pores is not a reliable diagnostic feature.

Keywords *Dendriscocaulon*; epitypification; lichenized fungi; Lobariaceae; Lobarioideae; Peltigeraceae; *Sticta*

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Lichens comprise approximately one-fifth of known fungal diversity, with almost 20,000 species of lichen-forming fungi currently recognized (Lücking & al., 2017a). With more than 400 accepted species, the former Lobariaceae compose one of the largest families of lichenized fungi (Peltigerales, Ascomycota; Kirk & al., 2008; Lücking & al., 2017a). However, recent phylogenetic analyses resulted in a reclassification of the Lobariaceae as Lobarioideae within the Peltigeraceae (Kraichak & al., 2018; Lücking, 2019). Furthermore, its three

long-established genera (i.e., *Lobaria*, *Pseudocyphellaria* and *Sticta*) were split in 13 genera based on a correlation between the phylogeny and phenotypes (Galloway & Elix, 2013; Moncada & al., 2013b; Cornejo & Scheidegger, 2015; Galloway, 2015; Widholm & al., 2019; Simon & al., 2020). In addition, multiple instances of semi-cryptic speciation were uncovered in many genera (Moncada & al., 2014; Magain & Sérusiaux, 2015; Lücking & al., 2017b). Indeed, taxon concepts within Lobarioideae have changed dramatically with advances in molecular phylogenetics, matching similar instances of taxonomic overhaul across in a wide range of microlichens, such as the

Graphidaceae (Rivas Plata & al., 2013) and Trypetheliaceae (Lücking & al., 2016), or numerous genera of macrolichens, such as *Peltigera* (Magain & al., 2017, 2018) and *Cora* (Lücking & al., 2014).

The genus *Sticta* (Schreb.) Ach. has historically been diagnosed by the presence of rimmed crater-like cavities (named cypellae) on the lower surface (e.g., Yoshimura & Hurutani, 1987). This trait is now considered homoplasious, defining a polyphyletic grouping, with the *S. wrightii* group composing a distinct clade, for which the genus *Dendriscosticta* Moncada & Lücking was introduced (Moncada & al., 2013b). The placement of *Dendriscosticta* in the *Lobaria* s.l. clade, separate from *Sticta* s.str., was confirmed by phylogenomic inferences (Widholm & al., 2019), based on 400 single-copy nuclear genes. While *Sticta* and *Dendriscosticta* both develop well-delimited pores on the lower surface, the genuine cypellae in *Sticta* generally have noticeable overarching margins, whereas the cypelloid pores in *Dendriscosticta* tend to have less pronounced borders (Moncada & al., 2013b). These two genera further differ in the absence of excipular algae in *Sticta* versus their presence in *Dendriscosticta* (Takahashi & al., 2006).

Some species of both genera have the capacity to associate with either a green alga or a cyanobacterium as their main photosynthetic partner, and the resulting photomorphs can either grow independently or form composite thalli (e.g., Armaeo & Clerc, 1991; Tønsberg & Goward, 2001; Magain & al., 2012; Moncada & al., 2013a). Within *Dendriscosticta*, photomorphs are always dimorphic: the chloromorph (mycobiont primarily associated with a green alga) is green and foliose, whereas the cyanomorph (mycobiont primarily associated with a cyanobacterium) forms a dark bluish, fruticose thallus. This morphology is also found in early diverging clades in *Sticta* s.str., including species such as *S. filix* and *S. latifrons* (Ranft & al., 2018). Historically, the fruticose cyanomorphs, which also occur in other lobarioid genera such as *Ricasolia* (e.g., Jørgensen, 1996), were accommodated in the genus *Dendriscocaulon* (Nylander, 1885; Galloway, 1983; Jørgensen, 1998; Galloway, 2001). However, the advent of DNA sequencing revealed that this taxon was polyphyletic and composed of species also lichenized with green algae, and accommodated in other genera (Högnabba & al., 2009; Magain & al., 2012; Moncada & al., 2013b).

Dendriscosticta is a characteristic and conspicuous component of old-growth rainforests with good air quality in the Northern Hemisphere and is often considered a flagship group of high conservation priority in montane subtropical and temperate/boreal biomes (e.g., Goward, 1994; Goward & Arsenault, 2000; Karasev & Selivanov, 2014; Devkota & al., 2017). Ongoing rapid loss of these rainforests at a global scale (Xu & Liu, 1996; DellaSala, 2011) is an important contributor to the Holocene extinction (Kolbert, 2014; Pimm & al., 2014; Ceballos & al., 2015; Ceballos & Ehrlich, 2018; Shrimpton, 2019), threatening the survival of many taxa before they can be adequately studied or even named, and hence precluding efficient conservation efforts (Thomson & al., 2018). Despite their high conservation relevance and documented ethnobotanical uses (Ding, 2010; Wang & Qian, 2013), species

of *Dendriscosticta* are in need of taxonomic revision, given the studies by Takahashi (2006) and Moncada & al. (2013b), which suggested that presumably widespread taxa such as *D. wrightii* likely represent multiple species.

Here, we undertake a thorough taxonomic revision of the genus *Dendriscosticta* across its entire global range, encompassing three main objectives: (1) assess its evolutionary history and diversity; (2) define species boundaries using an integrative taxonomic framework, including sequence-based species delimitation approaches; and (3) evaluate and stabilize the nomenclature of its species.

■ MATERIALS AND METHODS

Taxon sampling. — Fresh material of *Dendriscosticta* was collected in Canada (British Columbia), China (Sichuan, Xizang, Yunnan), India, Japan (Hokkaido, Honshu), Russia (Komi Republic, Krasnoyarsk Krai), Taiwan, and the U.S.A. (Alaska, Minnesota). Based on earlier phylogenetic studies by Moncada & al. (2013b) and Widholm & al. (2019), we chose as outgroups *Ricasolia quercizans* (Michx.) Stizenb. and *R. virens* (With.) H.H.Bloem & Tønsberg, and gathered sequence data for a total of 234 specimens of *Dendriscosticta* (including “*Dendriscocaulon*”; Appendix 1). Type specimens were provided by FH (Farlow Herbarium, Harvard University, U.S.A.), G (Geneva Herbarium, Conservatoire et Jardin botaniques de la Ville de Genève, Switzerland), H (Finnish Museum of Natural History, University of Helsinki, Finland) and US (Smithsonian Institution, Washington, D.C., U.S.A.). Newly collected specimens were deposited at ALTA (University of Alberta, Canada), CONN (University of Connecticut, U.S.A.), KoLRI (Korean Lichen Research Institute, South Korea), KUN (Kunming Institute of Botany), LG (University of Liège, Belgium), TNS (National Museum of Nature and Science, Japan), and UBC (University of British Columbia, Canada).

Morphological, anatomical and chemical characters. — Specimens were studied at the University of Liège (Belgium), the University of Connecticut (Storrs, Connecticut, U.S.A.), and the Kunming Institute of Botany (China), using standard microscopic techniques. Morphological descriptions are based on observations using an Olympus (Olympus, Tokyo, Japan) SZ60 dissecting microscope, and an Olympus BX53 compound microscope. Anatomical sections through cypellae and cypelloid pores in *Dendriscosticta* and *Sticta* were examined in lactophenol cotton blue (LPCB). In addition, scanning electron microscopy (SEM) was carried out on selected specimens in order to highlight lobe ultrastructure (namely cortex and pores). Dry thalli were gold sputter-coated with approximately 10 nm of gold and affixed to aluminum plates using an FEI XL-30 scanning electron microscope (Field Electron and Ion Company, Hillsboro, Oregon, U.S.A.). Descriptive terminology followed the standardized approach used by Moncada & al. (2014) for the genus *Sticta*. Thin-layer chromatography (TLC) was carried out for selected specimens following Orange & al. (2001). Detailed descriptions are provided for the newly

described species (*D. gelida*, *D. phyllidiata*), the epitypified species (*D. wrightii*, *D. yatabeana* comb. nov.) and one new combination (*D. insinuans*). For all other species, we provide short descriptions. For the comparison of cyphelloid pores in *Dendriscosticta* and genuine cyphellae in *Sticta*, we chose two representatives of *Dendriscosticta* and seven species of *Sticta* that were included in Widholm & al. (2018).

DNA extraction, PCR amplification and sequencing. —

Genomic DNA was isolated from well-preserved specimens following the protocol by Cubero & al. (1999) or using Nucleospin Plant II Midi kits (Macherey-Nagel, Bethlehem, Pennsylvania, U.S.A.) following the manufacturer's guidelines. The nuclear internal transcribed spacer (ITS) region was amplified via polymerase chain reaction (PCR) for 218 specimens, using the primers ITS1F (Gardes & Bruns, 1993) and ITS4 (White & al., 1990). From these we selected 82 specimens that represented a distinct ITS haplotype from the main geographical areas from which fresh material was obtained. Three additional, nuclear fungal markers were amplified for most specimens in this subset: (1) a portion of the RNA polymerase II largest subunit (*RPB1*), (2) a portion of the translation elongation factor-1 alpha gene (*EF-1 α*), (3) and a portion of the DNA replication licensing factor (*MCM7*). The PCR conditions were as follows: denaturation at 94°C for 3 min; followed by 40 cycles with denaturation at 94°C for 1 min, annealing at 51°C–55°C for 1 min, and extension at 70°C for 1 min; followed by a final extension at 70°C for 10 min. PCR annealing temperatures and primers are detailed in Table 1. The quality and size of the amplicons were checked by visual inspection on a 1% w/v agarose gel stained by SYBR Safe DNA Gel Stain (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.). PCR products that yielded high-quality bands in agarose gel electrophoresis were purified using Exo-SAP (Affymetrix, Santa Clara, California, U.S.A.). Amplicons were sequenced by Macrogen (Seoul, South Korea) using amplification primers. Sequences were edited using Sequencher v.4.9 (Gene Codes, Ann Arbor, Michigan, U.S.A.) or Geneious v.10.0.7 (Biomatters, Auckland, New Zealand) and subjected to BLAST searches (Altschul & al., 1990) in GenBank to detect potential contaminations. All newly generated sequences were deposited in GenBank (Appendix 1).

Molecular phylogenetic analyses. — Three datasets were analyzed for this study: (1) a single-locus ITS dataset for the *Dendriscosticta wrightii* clade comprising a selection of 126 specimens, including 11 sequences retrieved from GenBank; (2) a single-locus ITS dataset for the *D. praetextata* clade comprising a selection of 108 specimens, including 6 sequences retrieved from GenBank; and (3) a 4-locus dataset comprising a selection of 82 specimens, representing the genetic and geographical diversity of the entire genus, with *Ricasolia quercizans* and *R. virens* selected as composing a monophyletic outgroup.

Alignments for each gene and dataset were assembled in Geneious v.10.0.7 (Biomatters, Auckland, New Zealand) using the MAFFT plugin v.1.4.0 run in auto mode (Katoh, 2002; Katoh & al., 2009), and the ends of each alignment were trimmed. The ITS matrix of the 4-locus dataset was realigned using default MAFFT v.6.861b settings, with two alignment iterations, as implemented in GUIDANCE v.2.01 (Penn & al., 2010). Sites with low-quality scores (i.e., with confidence scores below 0.93) were excluded from the matrix, which resulted in an alignment of 480 bp (initially 638 bp). The three protein-coding genes were analyzed with all sites included. Since the single-locus ITS matrices contained relatively few ambiguous portions, the two matrices were analyzed with all sites included (*Dendriscosticta praetextata* clade: 612 bp; *D. wrightii* clade: 617 bp).

We performed a maximum likelihood (ML) analysis on the two single-locus ITS datasets using RAxML-HPC2 v.8.2.3 (Stamatakis, 2014) on the CIPRES portal (Miller & al., 2010; <https://www.phylo.org>), using the rapid hill-climbing algorithm and bootstrapping with 1000 pseudoreplicates under a GTR+ Γ model of evolution. As for the 4-locus dataset, prior to concatenation, single-locus phylogenetic trees were produced for each marker via RAxML-HPC2 v.8.2.3 on the CIPRES portal with the same parameters as described above. Compatibility between trees was checked by testing for conflicts among well-supported clades using the program compat.py v.3.0 (Kauff & Lutzoni, 2002, 2003) and an 80% bootstrap cut-off value for supported incompatibilities. We detected no significant conflict with support values $\geq 80\%$ among putative species. Therefore,

Table 1. Polymerase chain reaction primers and annealing temperatures used for the amplification of the nuclear internal transcribed spacer region ITS, the RNA polymerase II largest subunit (*RPB1*), the translation elongation factor-1 alpha gene (*EF1- α*), and the DNA replication licensing factor (*MCM7*).

Locus	Primer name	Primer sequence (5' → 3')	Annealing temperature (°C)	Reference
ITS	ITS1F	CTTGGTCATTTAGAGGAAGTAA	51–52	Gardes & Bruns, 1993
	ITS4	TCCTCCGCTTATTGATATGC		White & al., 1990
<i>RPB1</i>	RPB1_LobF2	CATATGGYTTGGCTGATC	54	This study
	RPB1_LobR2	CCWGACTTCTGCAARGCTT		This study
<i>EF-1α</i>	EF_LobF	TCTTCAAATAYGCMTGGGT	54	This study
	EF_LobR	TCCTGGAGRGGRAGACGSA		This study
<i>MCM7</i>	MCM7_DendriF	AAGCCATCGGTGCAGGTAAA	55	This study
	MCM7_DendriR	CGATTAGGCCACACCAGGGT		This study

the sequences of the four loci were concatenated in a single dataset for subsequent analyses.

The concatenated alignment consisted of 2521 positions (ITS: 480 bp; *RPB1*: 779 bp; *EF-1 α* : 598 bp; *MCM7*: 664 bp). PartitionFinder v.2 (Lanfear & al., 2016) was used to choose the best partitioning schemes and nucleotide substitution models for the subsequent maximum likelihood (ML) analysis. Ten initial subsets were considered (ITS, *RPB1* 1st, 2nd, 3rd codon positions, *EF-1 α* 1st, 2nd, 3rd codon positions, *Mcm7* 1st, 2nd, 3rd codon positions), and the default configuration settings were used (branchlengths = linked, models = all, model_selection = BIC) with the greedy algorithm (Lanfear & al., 2012). The GTR+ Γ model was the only one allowed. An ML analysis was performed on the 4-locus matrix dataset using RAxML v.8.2.3 on the CIPRES portal using the rapid hill-climbing algorithm and bootstrapping with 1000 pseudoreplicates under a GTR+ Γ model of substitutions for each matrix or each partitioned subset (subset 1: ITS; subset 2: *RPB1* 1st, 2nd codon positions, *EF-1 α* 1st, 2nd codon positions, *MCM7* 1st, 2nd codon positions; subset 3: *RPB1* 3rd codon positions, *EF-1 α* 3rd codon positions, *MCM7* 3rd codon positions). The resulting ML trees were visualized with the R package ggtree (Yu & al., 2017). Alignments and resulting trees are available in TreeBASE (<http://purl.org/phylo/treebase/phylows/study/TB2:S26492>).

Species delimitation and species-tree inference. — Species delimitation was inferred from a combination of morphological, chemical and molecular data. Three sequence-based species delimitation methods were used and are detailed hereafter.

First, we used the species delimitation method Automatic Barcode Gap Discover (ABGD; Puillandre & al., 2012), which splits sequences into groups reflecting candidate species based on gaps between intra- and interspecific diversity of genetic barcodes. The analysis was carried out on the ITS matrix for the 82 samples included in the 4-gene dataset using the online server <https://bioinfo.mnhn.fr/abi/public/abgd/> (last accessed Nov 2020). Genetic distances between samples were estimated using the JC69 nucleotide substitution model (Jukes & Cantor, 1969), and considering a relative gap width value of 0.5. The ABGD analyses were carried out on the *Dendriscosticta praetextata* and *D. wrightii* clades separately. Ultimately, the following partitions were selected: 13 groups within the *D. praetextata* clade ($P = 4.64\text{e-}03$) and eight groups within the *D. wrightii* clade ($P = 3.73\text{e-}03$).

Second, we used the general mixed Yule coalescent (GMYC) model (Pons & al., 2006; Fujisawa & Barraclough, 2013) for delimiting species based on a single locus. As this method requires an ultrametric single-locus gene tree as input, we analyzed the ITS region marker extracted from the 4-gene dataset using BEAST v.2.4.8 (Bouckaert & al., 2014). We ran the analysis using a TrNef+I substitution model (see below), with a strict clock model and a Yule model (Yule, 1924), for 20 million generations, sampling parameters every 500th generation. We used the topology of the 4-locus tree generated in the above-mentioned ML analysis as input tree and held this topology constant. The analysis was performed on the CIPRES Science

Gateway. Convergence of parameters was assessed using Tracer v.1.6 (Rambaut & Drummond, 2013; Rambaut & al., 2018). A burn-in of 20% was removed, and a maximum credibility tree with a cut-off of 0.5 of posterior probabilities was generated in TreeAnnotator v.2.4.8 (BEAST package). The GMYC analysis was carried out on the resulting tree using the web server of the Exelixis Lab (<https://species.h-its.org/gmyc/>; last accessed Nov 2020) and the single threshold method.

Third, species delimitation was further assessed using the Bayesian phylogenetics and phylogeography method (BP&P v.3.3; Rannala & Yang, 2003; Yang & Rannala, 2010). As the number of species estimated by ABGD appeared relatively high, compared to morphological and chemical variation, we decided to use these entities as the input candidate species for the BP&P analysis. In a few cases, the ABGD delimitation was incongruent with the tree topology derived from the concatenated loci. Several input groups were therefore further divided since the program is only able to regroup several predefined candidate species into more inclusive species but cannot divide these input species (suppl. Table S1). The multi-locus coalescent-based BP&P analyses were performed using the abovementioned 4-gene ML tree as guide tree. The divergence time parameter tau (τ) was set to G(2, 38), corresponding to distribution means of 0.053. The population size parameter theta (θ) prior was tested for different values: G(4, 1000), G(8, 1000), and G(12, 1000). The matrix was analyzed without the outgroup (i.e., *R. quercizans* and *R. virens*), using the reversible-jump Markov chain Monte Carlo (rjMCMC) algorithms implemented in the program BP&P, sampling every generation for a total 5 million generations, with a burn-in period of 500,000. A posterior mean of 0.5 was used as the probability cut-off, above which input groups are considered heterospecific.

We also inferred a species tree using the coalescent-based Bayesian model *BEAST (Heled & Drummond, 2010), as implemented in BEAST v.2.4.8 (Bouckaert & al., 2014). The inference of a species tree ideally requires the inclusion of several samples per delimited species (Camargo & al., 2012). For this reason, we selected 74 individuals included in the 4-locus dataset, which were assigned to 12 candidate species groups (with at least two representatives per species) in agreement with the results of the BP&P delimitation analysis (suppl. Table S1). The 4-gene dataset was prepared in BEAUTi v.2.4.8 (BEAST package) and partitioned by locus. Substitution, clock and tree models were unlinked and the model of nucleotide substitution was selected based on the Bayesian information criterion (Schwarz, 1978) in jModelTest v.2.1.6 (Darriba & al., 2012) on the CIPRES Science Gateway (ITS: TrNef+I; *RPB1*: K80+ Γ ; *EF-1 α* : K80+ Γ ; *MCM7*: K80+ Γ). We first carried out a preliminary analysis using a relaxed, lognormal, uncorrelated clock: this run supported a clock-like rate of evolution, as the standard deviation estimate of the clock was close to zero. For this reason, we used a strict clock model in the final analysis. We also employed a Yule model (Yule, 1924) and the substitution rate for *RPB1* ($1.73 \times 10^{-3} \text{ s}^{-1} \text{ myr}^{-1}$) as secondary calibration (derived from the substitution rates within *Melanelia*; Leavitt

& al., 2012). The *BEAST analysis was run for 100 million generations, sampling parameters every 5000th generation, and performed on the CIPRES Science Gateway. Convergence, mixing, and effective sample sizes (ESS) of parameters were checked in Tracer v.1.6 (Rambaut & al., 2013). All the ESS values were larger than 200. A burn-in of 20% was removed, and a maximum credibility tree with a cut-off of 0.5 of posterior probabilities was generated with the remaining 16,000 trees in TreeAnnotator v.2.4.8 (BEAST package) and visualized with the R package ggtree (Yu & al., 2017). In addition, the 16,000 sampled posterior trees were visualized using DensiTree v.2.2.6 (Bouckaert & Heled, 2014).

Molecular barcoding approach. — Short ITS2 barcode sequences (ranging from 29 to 33 bp) were designed for most species of *Dendriscosticta* here recognized, given the lack of phenotypic characters diagnosing several taxa (see key, below). The reliability of DNA barcodes was evaluated using the query sequences in GenBank for the species encompassed in the *D. wrightii* clade. For this approach, we used the BLASTn algorithm (Altschul & al., 1990, 1997) and the default settings optimized for a short input sequence (word size = 7; match/mismatch scores = 1/-3; gap costs = existence: 5, extension:

2). In order to assess the efficiency of the designed barcodes, BLASTn top-scoring hits were ranked by E-value and compared to the species identities inferred from the formerly mentioned phylogenetic inferences. This evaluation was made possible by the inclusion of most GenBank accessions falling in the genus *Dendriscosticta* (suppl. Table S1). Ultimately, corrected reference sequence identifications were proposed for previous GenBank accessions following the strategy used by Lücking & al. (2020b).

■ RESULTS

Morphological and chemotypic diversity. — Four typical and well-delimited morphotypes were detected within *Dendriscosticta*, and their main features are as follows (Fig. 1):

- (1) Foliose thalli primarily associated with a green alga (chloromorph), with lobe apices usually curled upwards (involute) and upper surface having a pruinose appearance (Figs. 1A, 2B);
- (2) Foliose thalli primarily associated with a green alga (chloromorph) with lobe apices usually curled

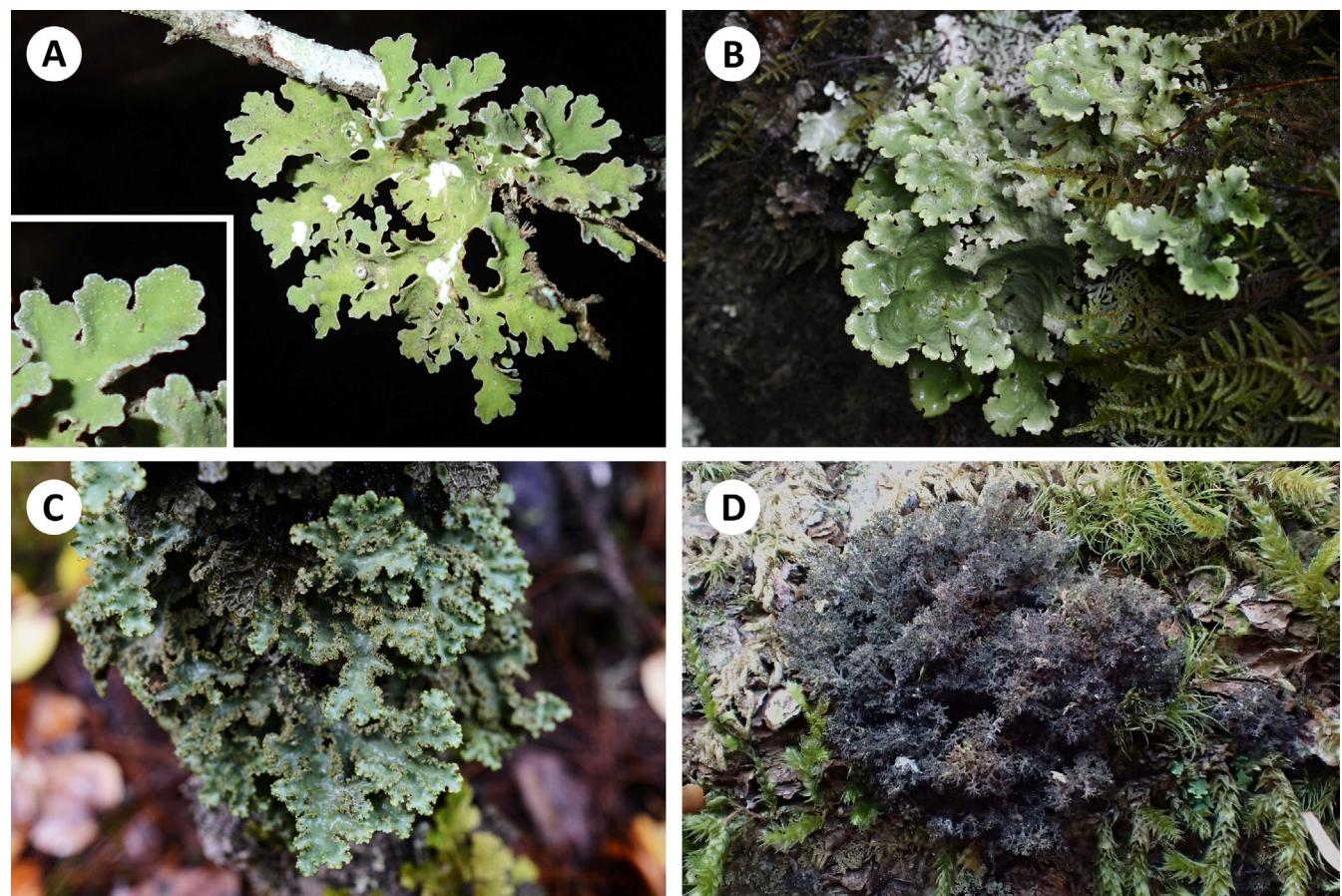


Fig. 1. The four easily distinguishable morphotypes in *Dendriscosticta*. **A**, *D. gelida* (field image from British Columbia), showing a foliose thallus with involute, seemingly pruinose lobes due to hyphae protruding from the cortex; **B**, *D. aff. hookeri* 2 (Wang 16-52068, KUN), showing a foliose thallus with revolute, smooth lobes; **C**, *D. praetextata* (Wang 16-52037, KUN), showing a foliose thallus with numerous phyllidia; **D**, Cyanomorph of *D. gelida* (Simon 458, LG), showing a dark, fruticose thallus. Photographs by A. Simon (A, D) and L.S. Wang (B, C).

- downwards (revolute) and upper surface smooth or glossy (Figs. 1B, 2C);
- (3) Foliose thalli primarily associated with a green alga (chloromorph), with lobes bearing numerous phyllidia and upper surface smooth (Fig. 1C);
 - (4) Fruticose thalli (dendriscocauloid) primarily associated with a cyanobacterium (cyanomorph), forming arbusculoid, bush-like structures with terete or slightly flattened branches, with convoluted or irregular surface (Figs. 1D, 2A).

Thin-layer chromatography was carried out on all specimens included in the 4-locus dataset (suppl. Table S1; Fig. 3). Three

major compounds were distinguished in the material studied: the depside pseudocyphellarin A (Elix & Lajide, 1984), and two well-known depsides that are commonly detected in lichenized fungi, gyrophoric and congyrophoric acids (Elix, 2014).

A comparison of the anatomy of the cyphelloid pores assumed to be diagnostic for *Dendriscosticta* (Moncada & al., 2013b) and of genuine cyphellae in *Sticta* revealed that the crater-like subcircular depressions on the lower surface vary in abundance, size, and the shape of the rim (varying from low rims with gentle slope to abrupt rims bending towards the center of the cyphellae), and that the variation of these traits is much greater within *Sticta* (Fig. 4). A focused

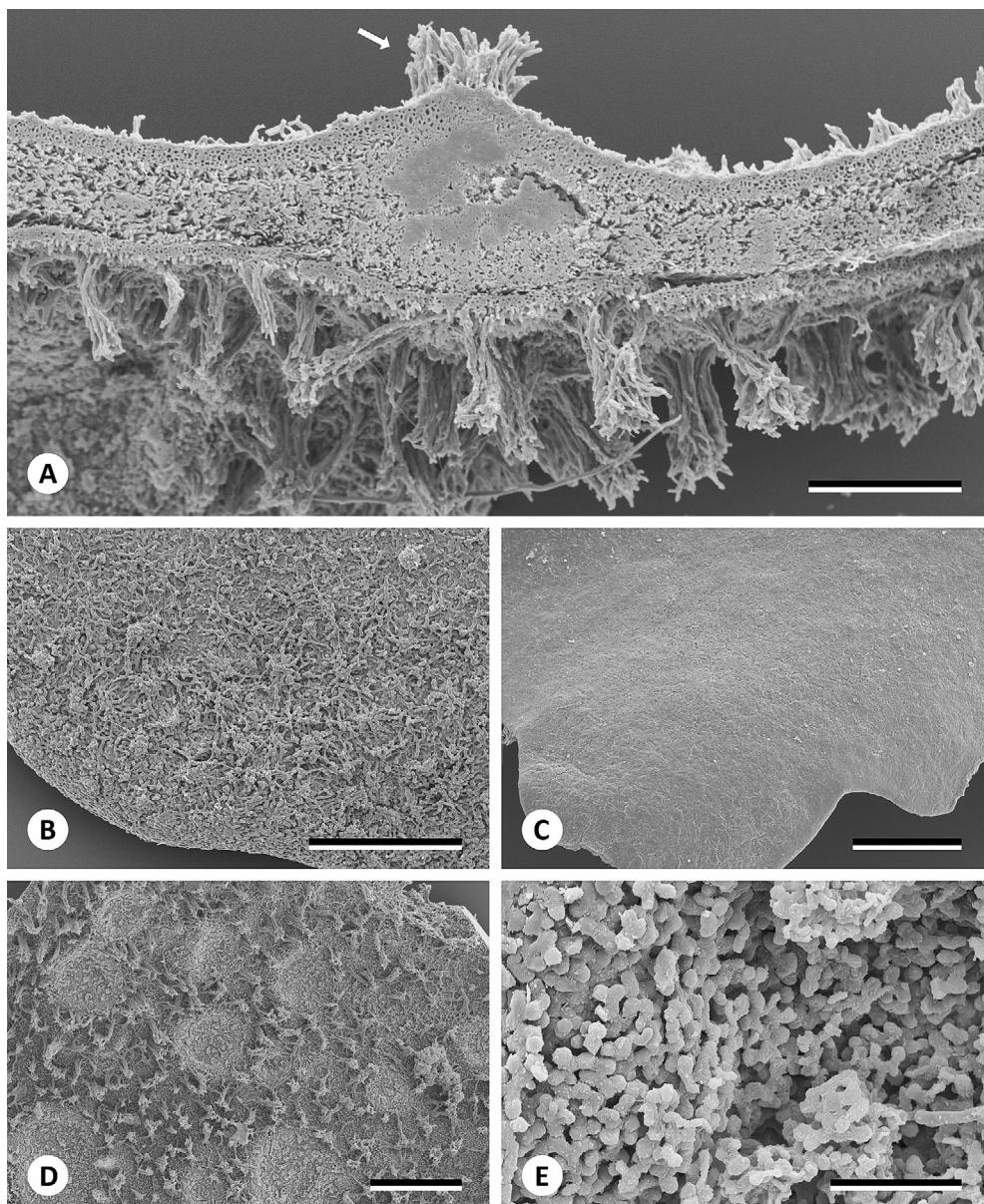


Fig. 2. Scanning electron microscopy pictures of *Dendriscosticta* species. **A**, Transversal section through *D. oroborealis* (Goffinet 10010, CONN), showing an early dendriscocauloid thallus (arrow) emerging from an internal cephalodium in a foliose, chloromorphic thallus; **B**, *D. oroborealis* (*Spribile* s.n.), showing the upper surface of a seemingly pruinose lobe with hyphae protruding from the cortex; **C**, *D. aff. hookeri* (*Spribile* 23667), showing the upper surface of a smooth lobe; **D**, *D. oroborealis* (Goffinet 10010, CONN), showing lower surface with cyphelloid pores; **E**, *D. oroborealis* (*Spribile* s.n.) showing a close-up of a cyphelloid pore with angular, dumbbell-like cells. — Scales: A = 200 µm, B–D = 500 µm, E = 50 µm.

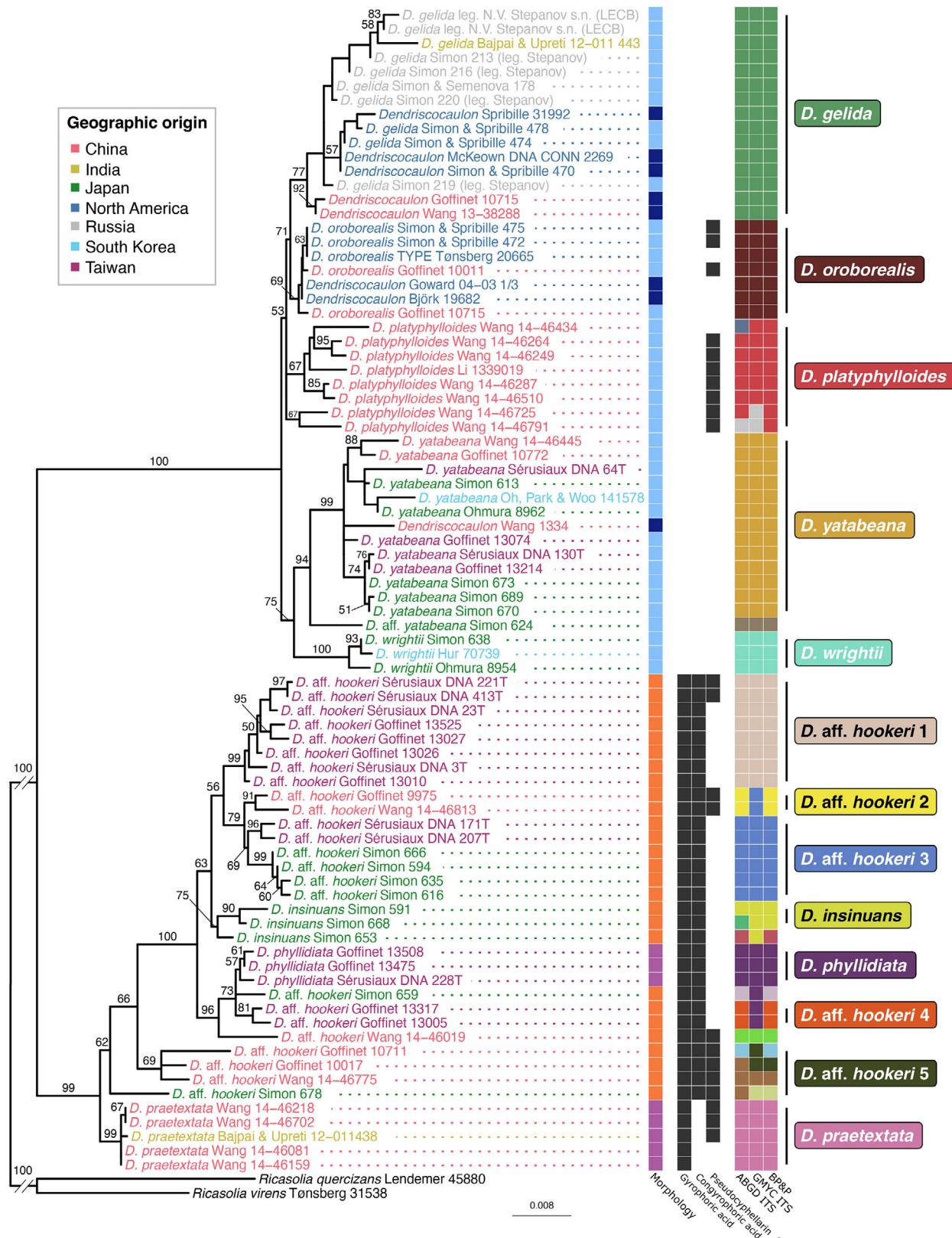


Fig. 3. Single most likely phylogenetic tree of the genus *Dendriscosticta* obtained from inferences of four-locus molecular data (ITS, *RPB1*, *EF1- α* , *MCM7*), with morphotypes (column 1: dark blue, dendriscauloid; light blue, foliose and seemingly pruinose; orange, foliose and smooth; purple, phyllidiate), chemical assessments (columns 2–4), sequence-based species delimitation (columns 5–7: ABGD, GMYC, BP&P with $\theta = G$ [4, 1000]). Values above branches represent ML bootstrap values (indicated when ≥ 50). Colors in the taxa names refer to the origin of the samples. Original identifications found in GenBank were retained. The cross-hatched branches have been shortened to one tenth.

screening of the basal membrane of the cyphelloid pores and cyphellae, revealed further variation and differences between taxa. In *Dendriscosticta*, the membrane is a c. 20 µm thick layer of intermingled, irregularly branched but with almost perpendicular branching usually dominant, and slightly but distinctly inflated hyphae (Figs. 2D,E, 4A,B). The membrane of the cyphellae of *Sticta stipitata* C.Knight and *S. cyphellulata* (Müll.Arg.) Hue is also about 20 µm thick, but the cells are more globose (Fig. 4C,D). In *S. canariensis* (Bory) Delise, the layer is slightly thicker, i.e., 25–30 µm, and all cells forming the cyphellae membrane are globose (Fig. 4E). In *S. ciliata* Tayl. and *S. fuliginoides* Magain & Sérus., two cell layers can be distinguished: a lower one, with one or two typically ovoid cells with irregular shape (5–10 µm in diameter) and an upper one

composed of smaller papillose cells (5–8 µm in diameter; Fig. 4F,G). In *S. fuliginosa* (Dicks.) Ach., the floor is composed of two or three layers of irregularly ovoid to typically globose cells (Fig. 4H). In *S. sylvatica* (Huds.) Ach., a basal layer of large globose cells (8–15 µm in diameter) is easily distinguished from the upper layer of smaller (5–8 µm) globose cells (Fig. 4I). In summary, the membrane seems to be mainly hyphal (with densely arranged hyphae leaving some interspaces) in *Dendriscosticta*, whereas in *Sticta* it appears to be more compact and a paraplectenchymatous membrane floor is clearly perceptible in most cases. While the assumed way of separating *Dendriscosticta* from *Sticta* based on lower surface pores (Moncada & al., 2013b) did not hold in every case, we conversely confirmed that the presence of algae in the excipular tissue of

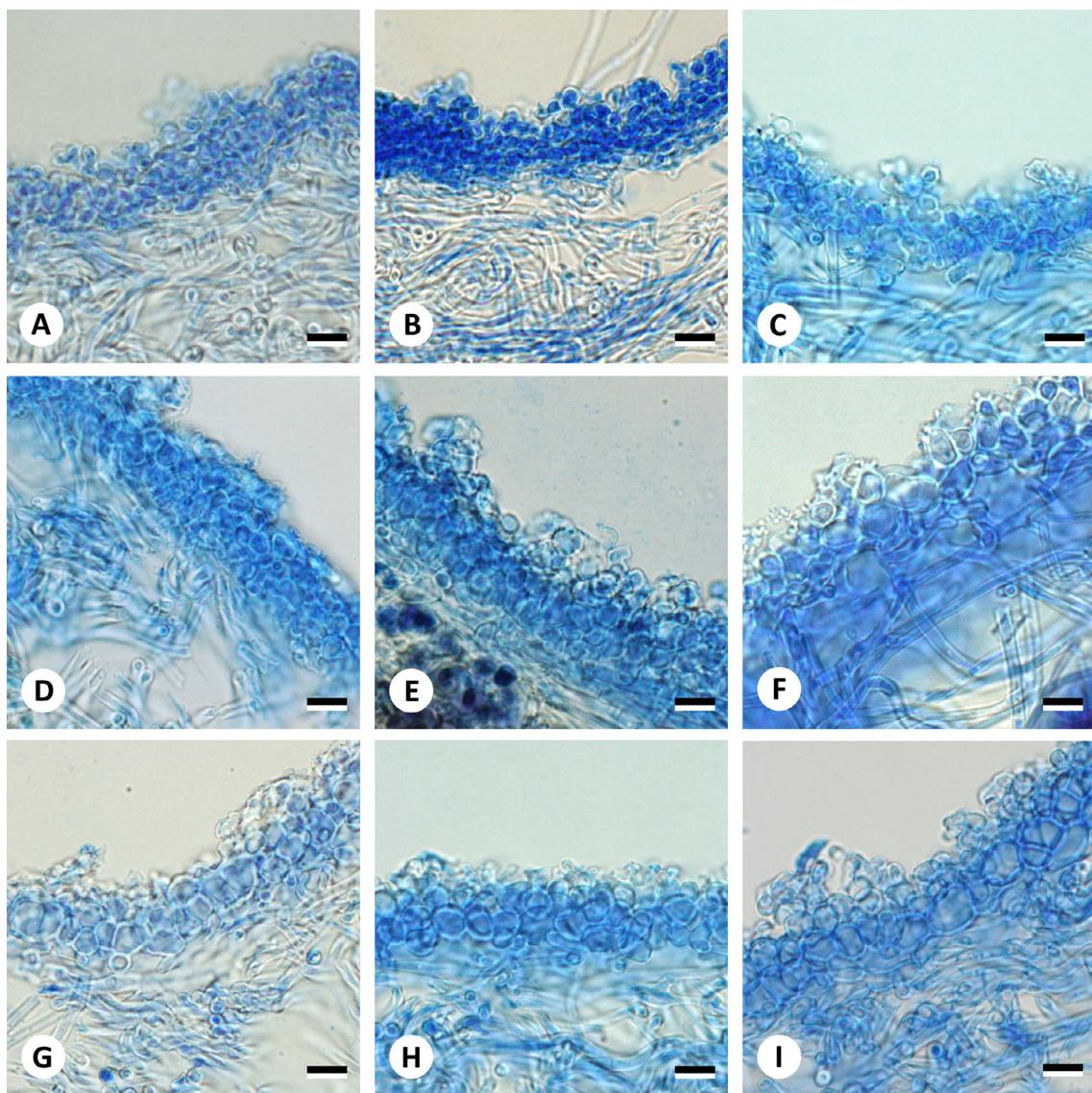


Fig. 4. Transversal sections of cyphellae and cyphelloid pores, stained with lactophenol cotton blue, in various species of *Dendriscosticta*. **A**, *D. gelida* (Simon 463, LG); **B**, *D. aff. hookeri* (Simon 653, LG); **C**, *Sticta stipitata* (Kantvilas 73/10, DNA LG 1253); **D**, *S. cyphellulata* (Sérusiaux s.n., DNA LG 1023); **E**, *S. canariensis* (Sérusiaux s.n., DNA LG 1333); **F**, *S. ciliata* (Sérusiaux s.n., DNA LG 3540); **G**, *S. fuliginoides* (Sérusiaux s.n., DNA LG 3391); **H**, *S. fuliginosa* (Sérusiaux s.n., DNA LG 901); **I**, *S. sylvatica* (Sérusiaux 7699, LG). — Scales = 10 µm.

Dendriscosticta represents a reliable, diagnostic feature to distinguish the two genera.

Phylogenetic relationships. — Phylogenetic analysis of the 4-locus dataset resulted in two main clades within *Dendriscosticta* hereafter referred to as the *D. praetextata* and *D. wrightii* clades, both with high support values (Fig. 3; bootstrap support [BS]: 99 and 100, respectively). The *D. wrightii* clade can be tentatively divided in five main subclades (Figs. 3, 5): (1) a lineage (BS: ITS, 37; 4-locus, 77) with representatives occupying a wide range in the Holarctic realm, across boreal and temperate areas, seemingly lacking lichen substances, and including the morphotypes A and D (here accommodated in *D. gelida* sp. nov.); (2) a fairly well-supported lineage (BS: ITS, 83; 4-locus, 69) comprising the holotype of *D. oroborealis* and samples from western Canada (British Columbia) and southern China (Sichuan, Xinzang, Yunnan), with pseudocyphellarin A in some instances and including the morphotypes A and D (hereafter referred to as *D. oroborealis*); (3) a lineage (BS: ITS, 99; 4-locus, 38) with representatives restricted to the Chinese provinces of Xinzang and Yunnan, with pseudocyphellarin A in all but one specimen, and including the morphotypes A and D (hereafter referred to as *D. platyphylloides*); (4) a strongly supported lineage (BS: ITS, 93; 4-locus, 99) with representatives widely distributed in East Asia (China, Japan, South Korea, Taiwan), including the morphotypes A and B (hereafter referred to as *D. yatabeana*); (5) a small, strongly supported lineage (BS: ITS, 100; 4-locus, 100) with representatives restricted to Japan and South Korea, exhibiting the morphotype A (hereafter referred to as *D. wrightii*).

A sixth subclade, only comprising two specimens from Japan (BS: ITS, 100), is strongly resolved as sister to the *Dendriscosticta yatabeana* lineage in the 4-locus analysis (BS: 94) and was provisionally assigned to “*D. aff. yatabeana*” as it might represent one additional taxon owing to the long branch holding these specimens. All specimens within the *D. wrightii* clade share the presence of hyphal outgrowths on the lobe apices in chloromorphic individuals (morphotype A). The protruding hyphae account for the scabrose or pruinose appearance (Fig. 1A). The *D. wrightii* clade is also characterized by the absence of gyrophoric and congyrophoric acids. Cyanomorphic individuals (morphotype D) always lacked secondary metabolites. All taxa assigned to a supported species can be identified by a discrete diagnostic nucleotide sequence within ITS2 (Figs. 5, 6).

The *Dendriscosticta praetextata* clade can be tentatively divided in numerous subclades (Figs. 3, 7), most notably: (1) a lineage (BS: 4-locus, 99) with representatives restricted to Taiwan and exhibiting the morphotype B (hereafter referred to as *D. aff. hookeri* 1); (2) a lineage (BS: ITS, 36; 4-locus, 75) with representatives restricted to Japan and exhibiting the morphotype B (hereafter referred to as *D. insinuans*); (3) a weakly supported lineage (BS: 4-locus, 57) but with representatives having a well-defined distribution (Taiwan) and the unusual morphotype C (hereafter referred to as *D. phyllidiata* sp. nov.); (4) a poorly resolved assemblage (BS: ITS, 29) with representatives exhibiting morphotype B from Japan and southern China,

with pseudocyphellarin A always detected (hereafter referred to as *D. aff. hookeri* 5); (5) a strongly supported lineage (BS: ITS, 96; 4-locus, 99) with representatives from southern China, always lacking congyrophoric acid, and exhibiting the morphotype C (identified as *D. praetextata*). Also, worth mentioning are the clades referred to as *D. aff. hookeri* 2–4, which received fairly strong support in the 4-locus analysis, further exemplifying the phylogenetic complexity of the *D. praetextata* clade. All specimens within the *D. praetextata* clade share a smooth upper surface (morphotypes B or C; Fig. 1B, C) and the presence of gyrophoric acid. Except for specimens of *D. praetextata*, congyrophoric acid is also always present. Cyanomorphic individuals (morphotype D) were not observed.

Molecular species delimitation. — The results of the different species delimitation analyses were projected onto the ML 4-locus phylogenetic tree (Fig. 3; suppl. Table S1). Species identifiers were assigned to the lineages delimited by the BP&P approach (with $\theta = G[4, 1000]$), which included at least two representatives of each putative species. The identifier *Dendriscosticta* aff. *hookeri* 5, although not supported by the species delimitation methods, was also assigned to the set of mostly Chinese samples recovered as a monophyletic group in the ITS tree of the *D. praetextata* clade (Fig. 7).

The three analyses (ABGD, BP&P, GMYC) yielded mostly consistent results, especially within the *Dendriscosticta wrightii* clade. In this clade, the different methods supported the recognition of five species (*D. gelida*, *D. oroborealis*, *D. platyphylloides*, *D. wrightii*, *D. yatabeana*) and potentially one more for a small clade (*D. aff. yatabeana*). The ABGD and GMYC analyses further divided *D. platyphylloides* in three and two entities, respectively. Within the *D. praetextata* clade, the three methods yielded consistent results for two cases (*D. aff. hookeri* 1, *D. praetextata*) and contrasting delimitations for others. For example, *D. aff. hookeri* 2 and 3 were lumped in the GMYC analysis but distinguished in the ABGD and BP&P analyses. Similarly, recognition of *D. phyllidiata* is supported and consistent among most analyses, with the exception of GMYC (merging this species and *D. aff. hookeri* 4 into a single entity). A few lineages were delimited differently depending on the prior used. For instance, the delimitation of *D. insinuans* was identical in the GMYC and BP&P methods when a prior θ of $G(8, 1000)$ or $G(12, 1000)$ was applied to the latter (suppl. Table S1).

Coalescent-based species tree. — The *BEAST species tree (Fig. 8) is congruent with the ML topology estimated from the concatenated 4-locus alignment, except for *Dendriscosticta insinuans*, which is sister to the clade composed of *D. aff. hookeri* 4 and *D. phyllidiata* in the first analysis (posterior probability [PP]: 0.59), but sister to the group *D. aff. hookeri* 1–3 in the ML tree (BS: 63). The clouddogram (Fig. 8) highlights the uncertainty in some species relationships across the posterior distribution of species trees, especially within the *D. praetextata* clade. Divergence estimates from the coalescent-based species tree analysis suggest that the split between the two main clades, i.e., the *D. praetextata* and *D. wrightii* clades, occurred in the Miocene, approximately

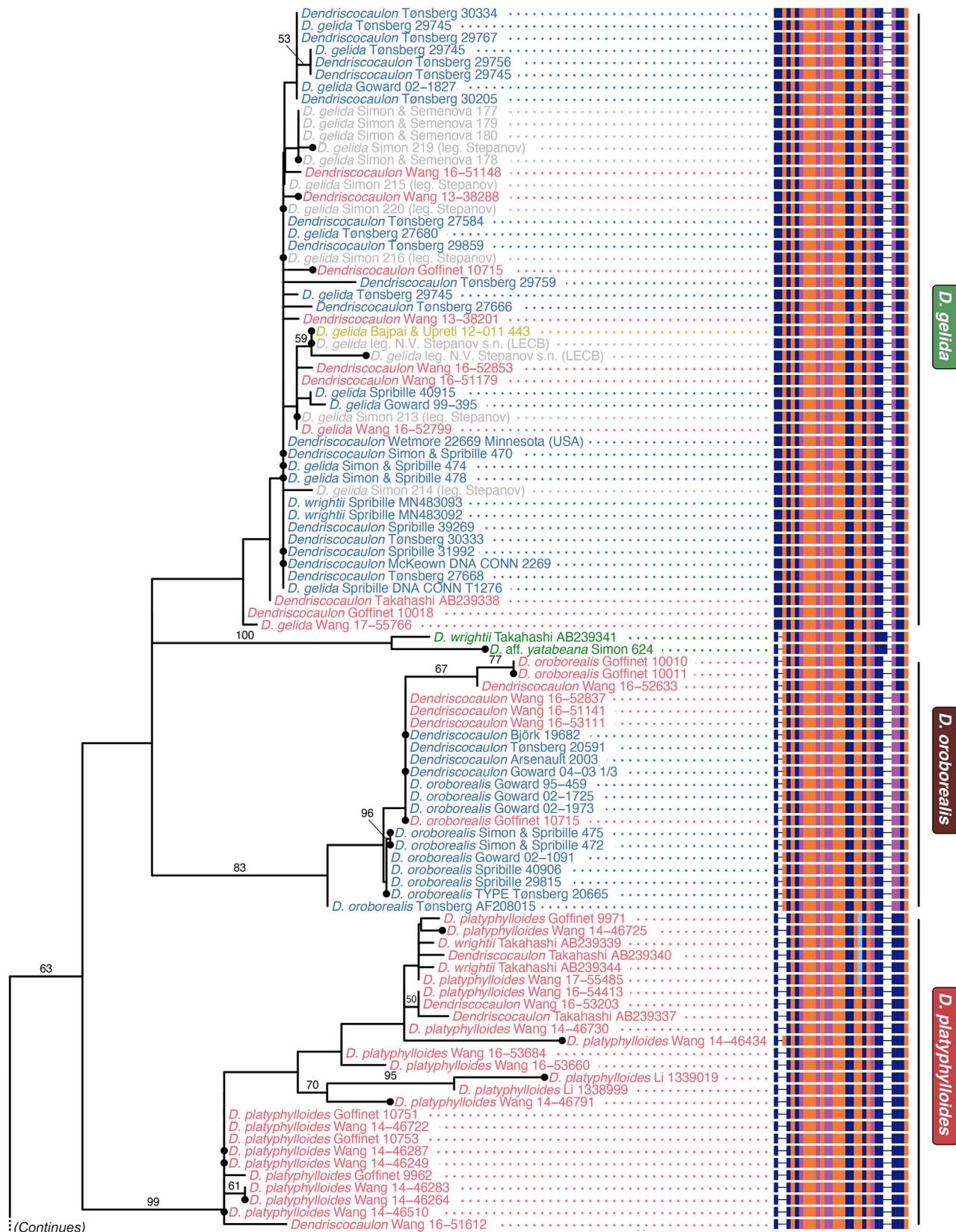


Fig. 5. Left: Single most likely phylogenetic tree of the *Dendriscosticta wrightii* clade obtained from inference of ITS. Values above branches represent ML bootstrap values (indicated when ≥ 50). Colors in the taxa names refer to the origin of the samples (see legend in Fig. 3). Black dots indicate specimens present in the 4-locus dataset. **Right:** Portion of ITS2 allowing discrimination of the species (position 18–49). For accessions retrieved from GenBank, terminal labels indicate the original sequence labels.

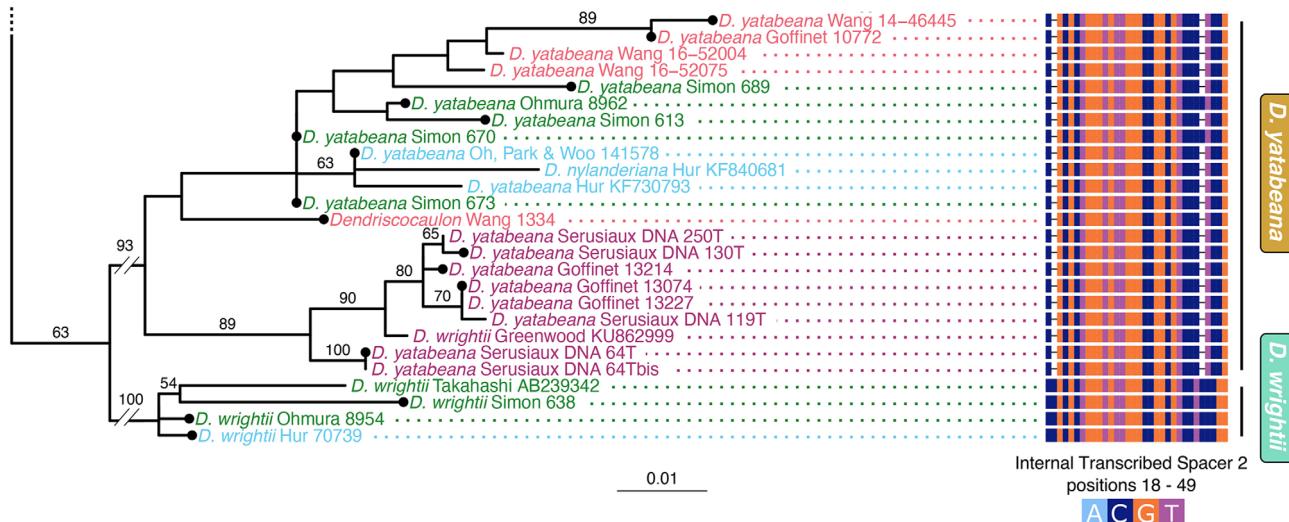


Fig. 5. Continued.

9.36 Mya (95% highest posterior density [HPD]: 6.36–12.54 Mya) with subsequent diversification in each of these during the Pliocene, that is approximately 3.85 Mya (95% HPD: 2.35–5 for the *D. praetextata* clade and approximately 3.24 Mya (95% HPD: 2.21–4.28 Mya) for the *D. wrightii* clade.

Assessment of short-sequence barcodes. — For all ITS2 barcode sequences designed to identify species within the *Dendriscosticta wrightii* clade, BLASTn top-scoring hits matched the species identity inferred from our phylogenetic inferences (suppl. Fig. S1), demonstrating the reliability of the short barcodes. However, due to the cryptic nature of this set of species, original identifications of sequences previously submitted to GenBank often differed from our revised taxonomic assessment. For this reason, we proposed a list of GenBank sequence accession numbers with corrected identifications in the context of the present study, including MycoBank registration numbers of the applicable names (suppl. Table S2). The best matches included the illegitimate genus *Dendriscocaulon* (under the unresolved sequence label “*Dendriscocaulon* sp.”), the accepted species *Dendriscosticta wrightii*, and four species previously treated in *Sticta* but now transferred to the genus *Dendriscosticta*, viz. *S. oroborealis* (\equiv *D. oroborealis*), *S. nylanderiana* nom. illeg. (\equiv *D. hookeri* comb. nov.), *S. wrightii* (\equiv *D. wrightii*), and *S. yatabeana* (\equiv *D. yatabeana* comb. nov.).

Fig. 6. Alignment of nucleotide sequences within a portion of ITS2 (position 15–49) allowing identification of the five recognized species in the *Dendriscosticta wrightii* clade. Deviations are underlined, and lowercase letters represent nucleotides that can be present or not. IUPAC ambiguity codes were used.

D. gelida
D. oroborealis
D. platyphylloides
D. wrightii
D. yatabeana

GCCCCGCGCTGGGTGTTGGGYCGGCGTCY--TCCG
GCCC-GCGCTGGGTGTTGGGCCGGCGTCC--TYCG
C-gCGCTGGGTGTTGGGCCRGCGTCC--CCCG
CCCGCGCTGGGTGTTGGGCCGGCGTCCTCCCGG
C-GCGCTGGGTGTTGGGCCGGCGTCCcTCCG

were able to confirm several diagnostic characters within the genus (see key below), at least two characters previously used in the delimitation of *Dendriscosticta* species appear homoplasious across species: (1) the presence of irregular cypheellae in *D. yatabeana* versus rounded cypheellae in *D. wrightii* (Yoshimura, 1974; Jayalal & al., 2014); and (2) the spot test reaction K+ yellow in the *D. wrightii* clade, contrary to Yoshimura (1974) and Goward & al. (1994), but consistent with Asahina (1961).

Although some species of *Dendriscosticta* could be readily distinguished by a combination of thallus morphology, distribution (suppl. Fig. S2) and to some extent chemistry (see key, below), several taxa nonetheless require molecular barcoding for reliable identification and hence qualify as cryptic species (Crespo & Lumbsch, 2010). BLASTn results using our short barcoding sequences were in agreement with the phylogenetic-driven species hypotheses presented here, although the correct species was not obvious from simple inspection in most cases, given that identifications of previously submitted GenBank sequences were not necessarily in line with our revised taxonomy (suppl. Fig. S2). Given the phenotypic plasticity and complex taxonomy in these lichens, sequence identifications in GenBank often correspond to misidentifications or outdated taxonomic concepts (see suppl. Table S2 for proposed corrections). This underlines the notion that DNA barcoding may often be misleading not because of the underlying similarity-based algorithm or problems with

the applied marker, but because the returned matches are not correctly identified (e.g., Hofstetter & al., 2019; Lücking & al., 2020a). Indeed, our results demonstrate that accurate DNA sequence-based identification of *Dendriscosticta* species can be achieved using even very short portions of the ITS2 spacer region, thus providing support for metabarcoding approaches of short reads.

The limited phenotypic variation within *Dendriscosticta* might be indicative of recent speciation within this group, as suggested by our dating analysis, which suggests that most diversification events occurred primarily during the Pliocene (Fig. 8). Our decision to assign species status to cryptic taxa follows taxonomic treatments in other lichenized groups (e.g., Altermann & al., 2016), and is consistent with direction given by the International Mycological Association regarding cryptic speciation in lichenized fungi, namely, to formally recognize morphologically cryptic species whose separation is supported by unambiguous phylogenetic signal and other evidence (Crespo & Lumbsch, 2010), such as ecology or distribution, fixed nucleotide substitutions, and ultramicroscopic feature (Lumbsch & Leavitt, 2011; Leavitt & al., 2015). We believe that the proposed taxa represent independent metapopulation lineages worthy of specific recognition (De Queiroz, 2007), as the individual single-locus analyses produced congruent, monophyletic lineages in most cases (Taylor & al., 2000; Dettman & al., 2003). From this perspective, our phylogenetic analyses would indicate that the species recognized

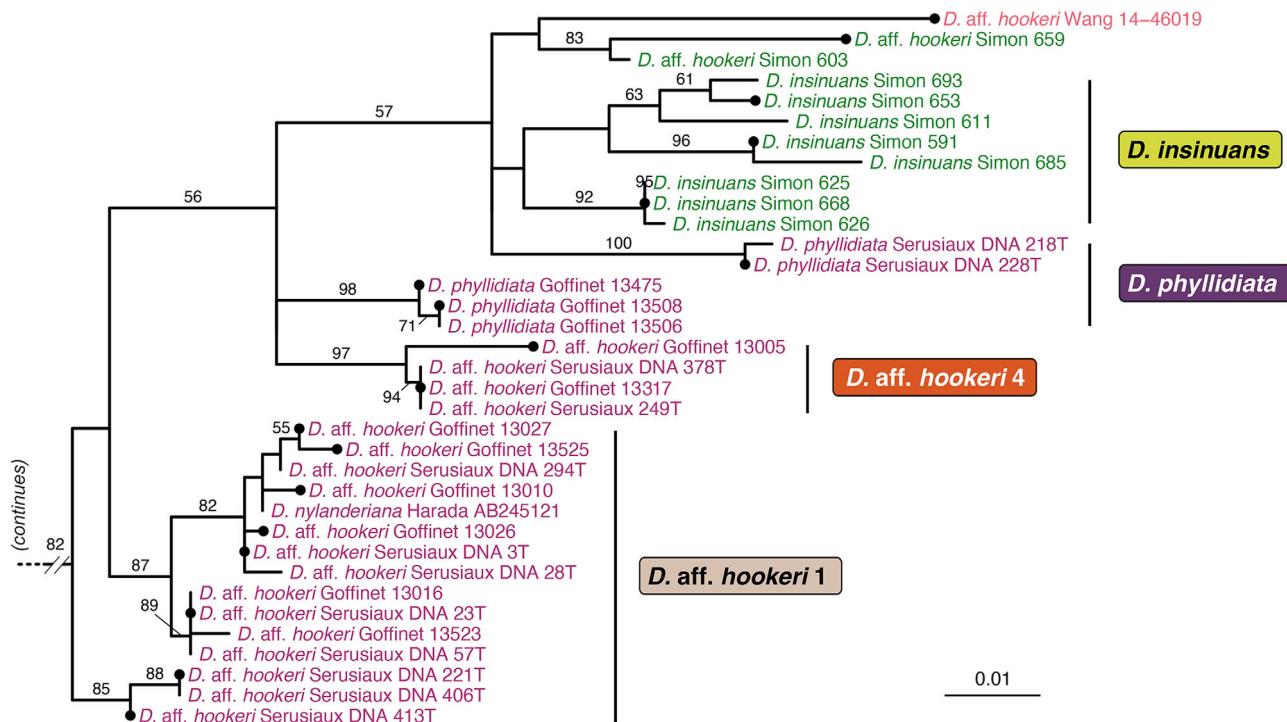


Fig. 7. Single most likely phylogenetic tree of the *Dendriscosticta praetextata* clade obtained from inference of ITS. Values above branches represent ML bootstrap values (indicated when ≥50). Colors in the taxa names refer to the origin of the samples (see legend in Fig. 3). Black dots indicate specimens present in the 4-locus dataset. For accessions retrieved from GenBank, terminal labels indicate the original sequence labels. The cross-hatched branch has been shortened to one tenth.

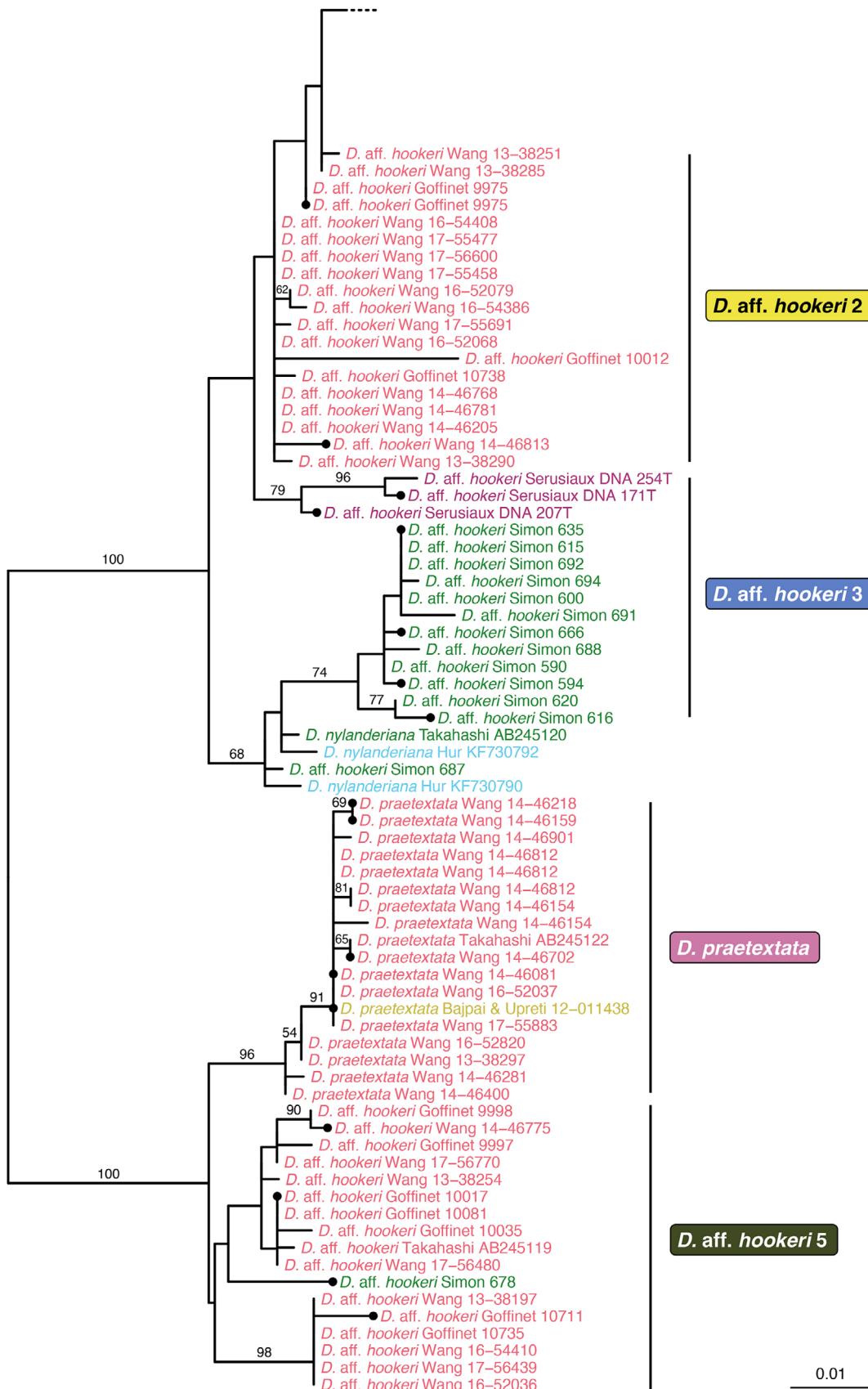


Fig. 7. Continued.

within *Dendriscosticta* represent evolutionarily significant entities sensu Moritz (1994), worthy of specific conservation efforts.

Newly described species. — Within the *Dendriscosticta wrightii* clade, the newly described species *D. gelida* appears to be the most widespread, as it occurs throughout the Holarctic realm. Reports of *D. wrightii* from North America (e.g., Krog, 1968; Goward & al., 1996; Stehn & al., 2013; Esslinger, 2019) belong to this new taxon, and likely so do those from Europe (e.g., Krempelhuber, 1861, 1862; Türk & Wunder, 2000; Fadeeva, 2005, 2009). *Dendriscosticta gelida* is clearly

distinguishable morphologically from its strongly supported sister species *D. oroborealis*, which is sympatric in British Columbia (Tønsberg & Goward, 2001). This was taken as evidence that the two clades are reproductively isolated lineages, and we therefore considered *D. gelida* and *D. oroborealis* two closely related but distinct species. The relatively young age of these sister species also weighs in favor of recognizing older, yet semi-cryptic, lineages within the *D. wrightii* clade as separate species despite the lack of unambiguous phenotypic discrimination.

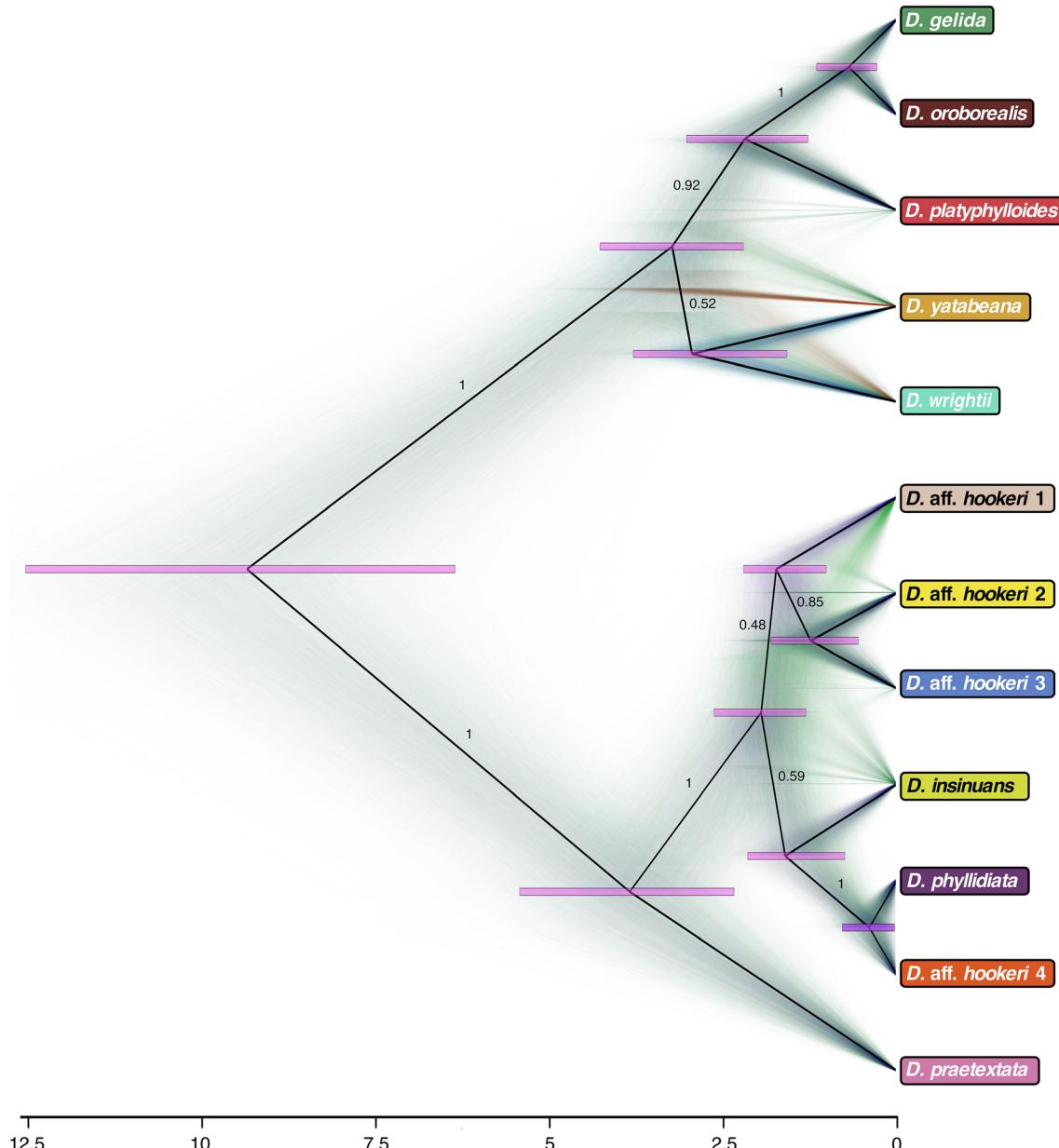


Fig. 8. Black lines: *Dendriscosticta* species tree obtained from a *BEAST analysis and estimated from a partitioned dataset consisting of four loci (ITS, RPB1, EF1- α , MCM7) under a strict molecular clock. Values above branches represent posterior probabilities. The node bars indicate the 95% posterior density intervals. Colored lines: clodogram of the posterior distributions of species trees from the *BEAST analysis. Areas where the majority of trees agree in topology and branch lengths are shown as darker, plain areas (well-supported clades), whereas areas with little agreement are shown as webs. The most popular tree is blue, the second most popular red, and the third most popular light green; the rest is dark green. Scale: millions of years before present.

Within the *Dendriscosticta praetextata* clade, the newly described species *D. phyllidiata* can be easily set apart by its chemistry from the morphologically similar, and thus also phyllidiate *D. praetextata*, by the presence of congyrophoric acid. Furthermore, *D. phyllidiata*, whose recognition is supported by DNA-based species delimitation methods, appears to be restricted to Taiwan, whereas *D. praetextata* is mostly found in the eastern Himalayan range (northern India and southern China).

Taxonomic reassessment and epitypification. — Our detailed study of species delimitation within the genus demonstrates a notable array of cryptic species, challenging the assignment of historical type collections to a given lineage. Epitypification based on recently collected material from the type locality was considered necessary to apply available epithets based on old type specimens for which DNA data could not be acquired and whose taxonomic interpretation is thus ambiguous. To ensure nomenclature stability of *Dendriscosticta wrightii* and *D. yatabeana*, two species well-supported by DNA-based species delimitation methods, we followed the guidelines provided by Lendemer (2020) and epitypified these species using sequenced specimens from the type (or nearby) localities. In these two cases, we recently collected material from the geographic area from where the original type collection was gathered, to acquire exploitable DNA and sequences of the ITS barcode. Two epithets (*S. henryana* Müll. Arg., *S. hookeri* (Trevis.) Nyl.) could not be evaluated as their geographical origin (Chinese province of Hubei and Nepal, respectively) was not explored as part of this study.

Using evidence from chemical and morphological data, we also propose new combinations for three species previously accommodated in *Sticta*: *Dendriscosticta hookeri*, *D. insinuans*, and *D. yatabeana*. While *S. henryana* unambiguously belongs to *Dendriscosticta* owing to its morphological features, we refrained from proposing a formal new combination for this species since the type locality was not sampled and we could not rule out that this species may be synonymous with another species within *Dendriscosticta*. The status of *D. hookeri* requires further investigation as the *D. hookeri* morpho- and chemotype is shared by an unresolved complex of several putative species.

■ TAXONOMIC TREATMENT

Key to recognized species of *Dendriscosticta*

- 1 Chloromorph: thallus foliose; lobe tips scabrous and matt (appearing pruinose), usually upturned toward the tips; medulla KC– (gyrophoric acid absent). Cyanomorph: thallus dendriscocauloid (with *Nostoc*).....2
- 1 Chloromorph: thallus foliose; lobe tips smooth and glossy, and usually downturned toward the tips; medulla KC+ red (gyrophoric acid present). Cyanomorph: not observed....5
- 2 Chloromorph: lobes pale green when wet, broadly rounded, not much longer than wide, without scalloped or lacerate margins; thallus becoming pinkish in the herbarium;

cortex usually K+ yellow (pseudocyphellarin A usually present). Cyanomorph: usually rhizinate. Distribution: western Canada and southern China. ITS2 barcode: CGCGCTGGGTGTTGGGCCGGCGTCCTYCG

..... ***D. oroborealis***

- 2 Chloromorph: lobes dark green when wet, typically longer than wide, sometimes with scalloped or lacerate margins; thallus color unchanged in the herbarium; cortex K+ yellow or K– (pseudocyphellarin A present or absent). Cyanomorph: without rhizines. Distribution: various. ITS2 barcode: not as above 3
- 3 Chloromorph: lobe underside usually whitish to beige, covered by a pale brown tomentum; cortex K+ yellow (pseudocyphellarin A almost always present). Distribution: southern China. ITS2 barcode: C(G)CGCTGGGTGTTGGGCCGRG GTCCCCCG ***D. platyphylloides***
- 3 Chloromorph: lobe underside usually beige to brown, covered by a dark brown to black tomentum; cortex generally K– (pseudocyphellarin A usually absent). ITS2 barcode: not as above 4
- 4 Distribution: East Asia, Russia, northwestern North America, northern India. ITS2 barcode: CCGCGCTGGGTGTT GGGYCGGCCTCYTCCG ***D. gelida***
- 4 Distribution: Japan, South Korea. ITS2 barcode: CCGCGC TGGGTGTTGGGCCGGCGTCCTCCGG ***D. wrightii***
- 4 Distribution: East Asia. ITS2 barcode: CGCGCTGGG TGTTGGGCCGGCGTCCC(C)TCCG ***D. yatabeana***
- 5 Thallus with phyllidia
- 5 Thallus without phyllidia
- 6 Congyrophoric acid present. Distribution: Taiwan. ITS2 barcode: CAACGCCATGTCGCTCGC ***D. phyllidiata***
- 6 Congyrophoric acid absent. Distribution: southern China to northern India. ITS2 barcode: GGCGACGTYCCG TTC
- 6 Congyrophoric acid absent. Distribution: southern China to northern India. ITS2 barcode: GGCGACGTYCCG TTC
- 7 Distribution: Japan. ITS2 barcode: CAYGCCATGTCG CTCGGCRG
- 7 Distribution: East Asia (southern China, Japan, South Korea, Taiwan). ITS2 barcode: not as above
- ***D. hookeri* aggregate**

Notes: Barcodes represent homologous positions within each clade. The sequence corresponds to a portion of ITS2 of the nuclear ribosomal DNA repeat in position 15–49 and 104–122 for the *Dendriscosticta wrightii* clade and the *D. praetextata* clade, respectively. Letters placed in parentheses represent nucleotides that can be present or not.

Dendriscosticta gelida Ant.Simon, Goward & T.Sprib., sp. nov.

[MB 835910] – Holotype: Russia. Komi Republic: Priluzsky District, approximately 4 km W of the ghost village of Pentjura (Пентюра) and 11 km NW of Lojma (Лойма), 60°35'16"N, 48°37'37"E, on *Sorbus* trunk, in old mixedwood forest of *Picea-Sorbus*, 24 Aug 2017, A. Simon 177 & N. Semenova (LE barcode LE L-16211; isotypes: LG, UBC).

Fig. 9A–D

Exsiccata. — RUSSIA, Rossia septentrionalis, regio et distr. Vologdaensis, praedium sylvaticum Jaroslavskaja in silva ad ramos Picea excelsae, 1928, leg. Am. Leontjev (V.P. Savicz, *Lichenotheca Rossica* No. 107, TU!).

Etymology. — The epithet is based on the Latin word *gelidus*, meaning cold, frosty, icy, referring to the characteristic “frosted” appearance of the lobe tips.

Diagnosis. — Thallus dimorphic. Chloromorphic thallus macrofoliose, similar to *Dendriscosticta oroborealis* but differing by the longer, often more or less dissected lobes.

Cyanomorphic thallus fruticose (dendriscocauloid), differing from *D. oroborealis* in the absence of rhizines.

Description. — Chloromorph: photobiont green (presumably *Dictyochloropsis* s.l.). Stipe absent. Thallus foliose, epiphytic, radially plicate-rugose, orbicular in outline, up to 15 cm in diam., coriaceous and resistant, rather thick, branching anisotomous or pleurotomous. Lobes somewhat involute, ligulate, imbricate, longer than wide, more or less ascending; margins sinuose to rather lacerate, slightly thickened; lobe internodes 4–20 mm long. Upper surface smooth or weakly

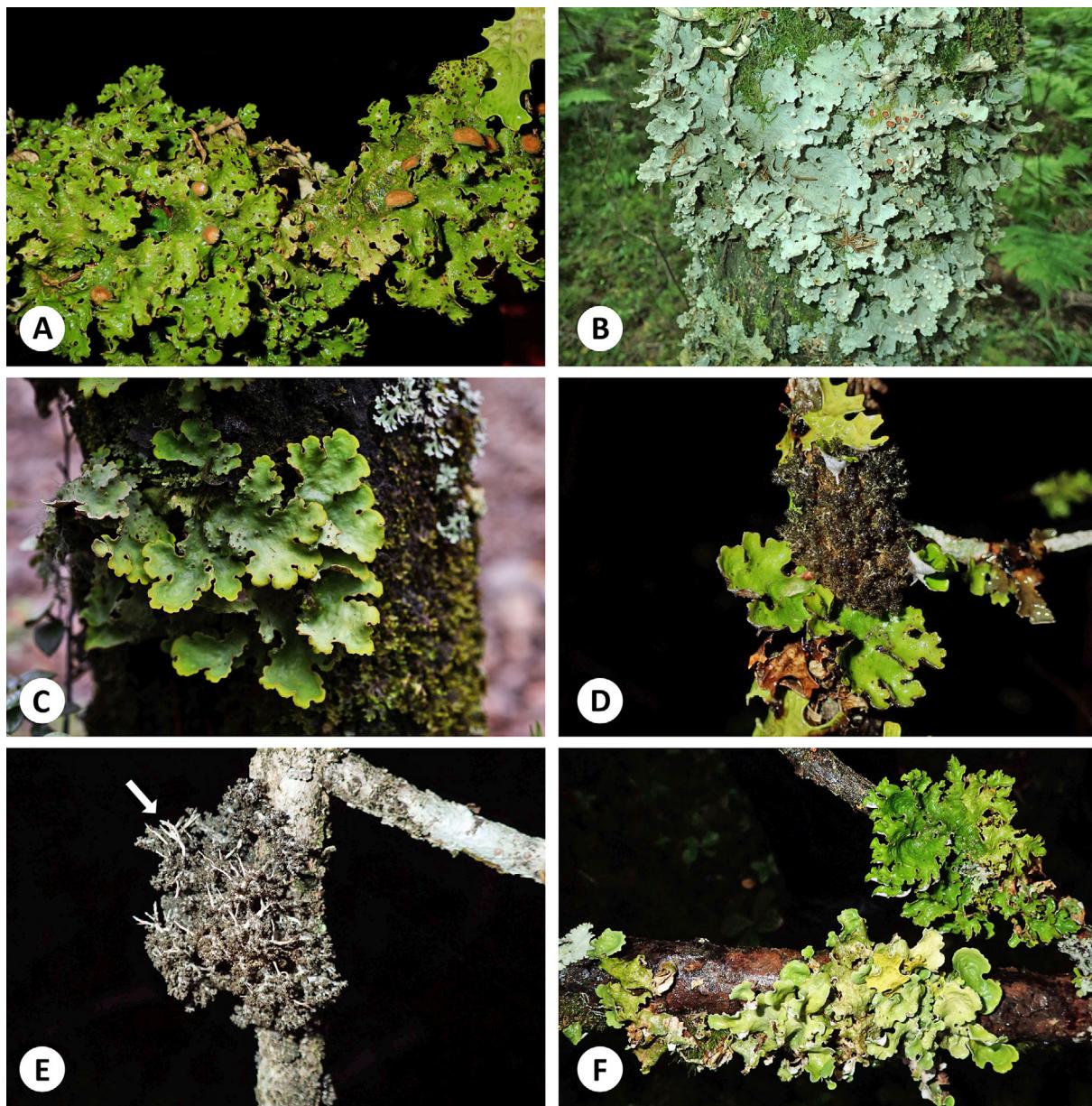


Fig. 9. Habit of *Dendriscosticta* species. **A–C**, *D. gelida* (A, field image from British Columbia; B, Simon 178, LG: topotype; C, Wang 17-55766, KUN), showing upper surface with numerous apothecia (A, B) and pycnidia (C); **D**, Photomorphs pair of *D. gelida* (Simon 441, LG), showing foliose chloromorph (bottom) and fruticose, dendriscocauloid cyanomorph (top); **E**, Free-living cyanomorph of *D. oroborealis* (Simon 446, LG), showing characteristic rhizines (arrow); **F**, *D. oroborealis* (bottom, Simon 472, LG) and *D. gelida* (top right, Simon 449, LG). — Photographs by A. Simon (A, B, D–F) and L.S. Wang (C).

rugose, dark green when fresh, paler toward margins, turning pale brown in herbarium, opaque, with margin concolorous; surface scabrose, or seemingly pruinose, due to the presence of cortical hairs, especially along margin. *Cilia* absent. *Apothecia* either absent, or if present, then usually abundant, cup-shaped, up to 7 mm diam., laminal, dispersed, pedicellate, with pronounced basal invagination, with glossy orange disk. *Medulla* compact, white, K– (cortex rarely K+ yellow), C–, KC–, P–. *Lower surface* smooth, cream to brown-colored. *Lower tomentum* dense throughout, patchily thick and thin, spongy, soft or rough, concolorous with lower surface. *Rhizines* sparse, dispersed, fasciculate, cream to brown-colored, up to 5 mm long. *Cyphelloid pores* abundant, 21–40 per cm² (central) to 41–60 per cm² (marginal), dispersed, rounded to irregular, urceolate with wide pore, immersed, below level of tomentum, with cream to brown-colored etomentose margins; pore to 3 mm in diam.; basal membrane pruinose, white. *Pycnidia* occasionally present, immersed, with black ostiole.

Upper cortex paraplectenchymatous, 35–65 µm thick, homogeneous, consisting of 6–8 cell layers with cells 6–10 µm diam., their lumina round-isodiametric. *Photobiont* layer 20–35 µm thick, cells 4.5–7.5 µm diam. *Medulla* 260–430 µm thick, hyphae c. 5 µm broad, without crystals. *Lower cortex* paraplectenchymatous, 20–40 µm thick, with 3–5 cell layers; cells 5–11 µm diam. *Hairs* of lower tomentum in fascicles of 6–12 hyphae with intertwined apices. *Cephalodia* usually present (internal). *Cyphelloid pores* with cells of basal membrane polygonal and entangled, 3–5 µm wide, without papillae.

Apothecia occasionally present, excipulum containing algae and with lateral verrucose protuberances. *Hymenium* 120–220 µm high. *Ascospores* 1–3-septate, acicular, 40–50 × 3–4 µm, hyaline.

Cyanomorph: thallus fruticose (dendriscocauloid); *photobiont* blue-green (*Nostoc*).

ITS2 barcode. – GCCCCGCGCTGGGTGTTGGGYC
GGCGTCYTCCG.

Chemistry. – No substances detected by TLC.

Distribution. – In North America, the species is present in Canada (British Columbia) and the United States (Alaska, Michigan, Minnesota), where it was previously treated under the name *Sticta wrightii* (Krog, 1968; Goward & al., 1996; Tønsberg & Goward, 2001; Stehn & al., 2013). Confirmed from northern India (Uttarakhand) and southern China (Xin-zang, Sichuan, Yunnan). In Russia, confirmed from the Komi Republic and Krasnoyarsk Krai; the specimens reported as *Dendriscosticta wrightii* (or *S. wrightii*) from Karelia, Kostroma Oblast and Perm Krai (Fadeeva, 2005, 2009; Kuznetsova & Skazina, 2010; Karasev & Selivanov, 2014) most likely belong to this species as well since *D. wrightii* was not detected in Russia in our dataset. However, these records need confirmation.

Comments. – *Dendriscosticta gelida* is the most widespread species of the genus, ranging from China to Eurasian Russia and northwest North America. Earlier reports of *D. (Sticta) wrightii* from North America and Russia (e.g., Krog, 1968; Makryi, 2008; Esslinger, 2019; Spribble & al., 2020) belong to this species. *Sticta wrightii* has also been

reported from Germany (Krempehuber, 1862; Türk & Wunder, 2000), but all records are historical and the taxon is likely extinct in this region. Although these old European records probably belong to *D. gelida*, the material from Germany has scattered marginal lobules, and hence its identity remains uncertain (H. Lojka: Lichenotheca Universalis. Fasc. II (1885) N. 67. *Ricasolia Wrightii* (Tuck.) Nyl., “in cortice Aceris prope Berchtesgaden in Bavaria. Leg. Rauchenberger – Perpauca specimina accepi e reliquiis beati von Krempehuber”; observed in G).

Additional specimens examined. – Refer to Appendix 2.

***Dendriscosticta hookeri* (Trevis.) Moncada & Lücking, comb. nov.** [MB 835912] = *Lobaria hookeri* Trevis. in Lichenoth. Veneta 1–2: no. 77. 1869 = [nom. nov. pro] *Sticta platyphylla* Nyl., Syn. Meth. Lich. 1: 357. 1860, nom. illeg., non *S. platyphylla* A. Massal., Mem. Lichenogr: 32. 1853, = *Sticta nylanderiana* Zahlbr., Cat. Lich. Univ. 3: 356. 1925 = *Stictina nylanderiana* (Zahlbr.) C.W. Dodge, Beih. Nova Hedwigia 12: 193. 1964 – Lectotype (designated by Joshi & Awasthi in Biol. Mem. 7: 183. 1982): Nepal. *J.D. Hooker & T. Thomson* 1963 (H-NYL No. 33652 [H barcode H9505981]!).

Fig. 10A,B

Description (type). – *Thallus* macrofoliose, subcoriaceous, rather thin, branching anisotomous, primarily associated with a green alga; other features, such as presence of stipe or diameter, not discernable as only a small portion is preserved. *Lobes* more or less plane, flabellate, adjacent, approximately as long as wide, adnate, with relatively plane apices; margins plane; lobe internodes 3–5 mm long. *Upper surface* smooth, brownish in herbarium, slightly glossy, with margin concolorous; surface smooth (without tomentum), without papillae, pruina and cortical hairs. *Cilia* absent. *Apothecia* abundant, cup-shaped, up to 2.5 mm in diam., laminal, dispersed but dense, shortly pedicellate, without basal invagination (or weak), with slightly glossy, dark brown disk. *Cortex* K+ yellow. *Medulla* white, KC+ pink to red. *Lower surface* not discernable (as the small piece is glued to cardboard). *Lower tomentum* visible along the margins, rather thin, dark brown. *Rhizines* and *cyphelloid pores* not discernable. *Pycnidia* not observed.

Apothecia with laterally more or less smooth margins. *Ascospores* 1–3-septate, fusiform, 30.7–40.9 × 4.6–5.1 µm (annotated by K. Takahashi, March 2003).

Chemistry. – Gyrophoric acid, congyrophoric acid and pseudocyphellarin A (annotated by K. Takahashi, March 2003).

Distribution. – Reported (generally as *Sticta platyphylla* or *S. nylanderiana*) from Bhutan (Upreti & Ranjan, 1988), China (Wei, 1991; Chen & al., 1994), India (Joshi & al., 2016), Japan (Yoshimura, 1974; Ohmura & Kashiwadani, 2018), Mongolia (Biazrov, 2013), Nepal (Devkota & al., 2017), Russia (Budaeva, 2014; Makryi, 2008), South Korea (Jayalal & al., 2014) and Thailand (Wolseley & al., 2002; Buaruang & al., 2017). In light of our results, these records likely represent several cryptic species, and further molecular studies are needed to clarify the taxonomy of this species-complex.

Comments. – The publication of the homonymic names *Sticta platyphylla* A.Massal. (Massalongo, 1853) and *S. platyphylla* Nyl. (Nylander, 1860) has led to much taxonomic confusion. The first (Massalongo, 1853) is based on a collection from Martinique and appears to belong to *Sticta* s.str., i.e., unrelated to *Dendriscosticta*. The second (Nylander, 1860) is based on a collection by J.D. Hooker and T. Thomson from Nepal that unambiguously belongs to *Dendriscosticta*, but the name unfortunately represents an illegitimate later homonym. Trevisan (1869) published in his exsiccata *Lichenotheca Veneta* a specimen that he believed was conspecific with *S. platyphylla* A.Massal., and combined it into *Lobaria platyphylla* (A.Massal.) Trevis. In the same publication, he also realized

that *S. platyphylla* Nyl. was a later homonym and gave it a replacement name, *L. hookeri* Trevis. He did not mention a specimen along with that replacement name, so it is automatically typified by the type of Nylander's name. Subsequent confusion originated from Zahlbrückner (1925), who made no distinction between the two taxa originally described by Massalongo (1853) and Nylander (1860), despite their unrelatedness, placing *L. platyphylla* (A.Massal.) Trevis. in synonymy of *S. platyphylla* Nyl. He then introduced a superfluous replacement name for the latter, *S. nylanderiana* Zahlbr., when under his concept, the name *Sticta platyphylla* A.Massal. would have been available. He also associated Trevisan's combination with nos. 75 and 76 in Trevisan's *Lichenotheca Veneta*, when in fact



Fig. 10. Habit of *Dendriscosticta* species. **A & B**, *D. aff. hookeri* 2 (A, Wang 17-55477, KUN; B, Wang 16-52079, KUN), showing upper surface with numerous apothecia; **C & D**, *D. platyphylloides* (C, Wang 16-53660, KUN; D, Wang 16-53684, KUN), showing upper surface (C) and close-up of lobe tips with cypellae (D); **E**, *D. praetextata* (Wang 16-52037, KUN), showing upper surface with phyllidia. — Photographs by L.S. Wang.

the correct number would have been 77 (<http://dryades.units.it/lichenothecaveneta/index.php?procedure=taxonpage&taxon=77>). Number 76 refers to *L. macrophylla* (Bory) Trevis. and no. 75 to *L. pulmonaria* (L.) Hoffm.; however, as part of the label of the latter, Trevisan (1869) gave a summary outline of his concept of *Sticta* and related genera, where all names treated by him are listed, including the replacement name *Lobaria hookeri* Trevis. for *Sticta platyphylla* Nyl. (<http://dryades.units.it/lichenothecaveneta/index.php?procedure=taxonpage&taxon=75>).

Moncada & al. (2013b) were unaware of Zahlbrückner's misinterpretation and followed *Index Fungorum* in considering *Lobaria platyphylla* sensu Trevis. as replacement name for *Sticta platyphylla* Nyl. However, *L. platyphylla* sensu Trevis. must be considered a legitimate combination of the legitimate basionym *Sticta platyphylla* A. Massal., as *L. platyphylla* (A. Massal.) Trevis., referring to a green-algal species of *Sticta* s.str. Therefore, the combination *Dendriscosticta platyphylla* sensu Moncada & al. is invalid, as by extension, and unintentionally, it refers to *S. platyphylla* A. Massal., not *S. platyphylla* Nyl., and no valid basionym was cited; it also has to be considered a homotypic synonym of *S. platyphylla* A. Massal. The correct replacement name for *S. platyphylla* A. Massal. is *Lobaria hookeri* Trevis., which is therefore the epithet to be adopted in *Dendriscosticta*.

Our sampling and DNA-based species delimitation highlighted several supported lineages with the morphochemistry of *Dendriscosticta hookeri*. Unfortunately, the lectotype is minuscule and does not show unique features linking it unambiguously to a particular clade. As the type region could not be assessed from the original label and no fresh material suitable for DNA extraction and sequencing was available from the type region, it is currently not possible to assign the epithet *hookeri* with certainty to one of these lineages. However, based on the geographic origin of the type and the annotated chemistry (containing pseudocyphellarin A), currently only "D. aff. *hookeri* 2" or "D. aff. *hookeri* 5" would be conceivable matches, both of which are known from China and produce pseudocyphellarin A.

Dendriscosticta insinuans (Nyl.) Ant. Simon, Magain & Sérus., comb. nov. [MB 835913] = *Sticta insinuans* Nyl., Lich. Jap.: 30. 1890 – Syntypes: Japan. Itchigomé, 1879, E. Almquist s.n. (S No. F158658 n.v.); Fusijama Itjigome, E. Almquist s.n. (S No. F158659 n.v.).

Fig. 11F

Description. – *Photobiont* green (presumably *Dictyochloropsis* s.l.). *Stipe* absent. *Thallus* foliose, epiphytic, orbicular in outline, up to 10 cm in diam., subcoriaceous, rather thin, branching anisotomous or pleurotomous. *Lobes* somewhat revolute or undulate, flabellate or ligulate, imbricate, approximately as long as wide, adnate, with relatively plane apices; margins plane to undulate; lobe internodes 3–20 mm long. *Upper surface* smooth, green when fresh, turning brown in herbarium, glossy, with margin concolorous; surface smooth (without tomentum), without papillae,

pruina and cortical hairs. *Cilia* absent. *Apothecia* either absent, or if present usually abundant, cup-shaped, up to 4 mm in diam., laminal, dispersed, pedicellate, without basal invagination (or weak), with glossy, orange to brown disk. *Cortex* K+ yellow or K-. *Medulla* compact, white, K-, C+ salmon pink, KC+ salmon pink, P-. *Lower surface* smooth, cream to brown-colored. *Lower tomentum* dense, absent towards margin, rather thin, concolorous with lower surface. *Rhizines* sparse, dispersed, fasciculate or tomentose, cream to brown-colored, up to 2 mm long. *Cyphelloid pores* abundant, 41–60 per cm² (central) to 21–40 per cm² (marginal), dispersed, rounded to irregular, urceolate with wide pore, immersed, below level of tomentum, with cream to brown-colored margins; pore to 1.5(–3) mm in diam.; basal membrane pruinose, white. *Pycnidia* immersed, with blackish ostiole.

Upper cortex paraplectenchymatous, c. 40 µm thick, homogeneous, consisting of 4–5 cell layers with cells 5–9 µm diam., their lumina round-isodiametric. *Photobiont* layer c. 30 µm thick, its cells 5–7 µm diam. *Medulla* 200–260 µm thick, its hyphae c. 5 µm broad, with gyrophoric acid crystals. *Lower cortex* paraplectenchymatous, 30–35 µm thick, with 2–3 cell layers; cells 5–9 µm diam. *Hairs* of lower tomentum in fascicles of 6–12 hyphae with intertwined apices. *Cephalodia* usually present (internal). *Cyphelloid pores* with cells of basal membrane polygonal and entangled, 3–5 µm wide, without papillae.

Apothecia with excipulum containing algae, with lateral verrucose protuberances. *Hymenium* 150–250 µm high. *Ascospores* 1–3-septate, fusiform, 35–55 × 5–6.5 µm, hyaline.

ITS2 barcode. – CAYGCCATGTCGCTCGGCRG.

Chemistry. – Gyrophoric acid and congyrophoric acids.

Distribution. – Reported from Japan (Yoshimura, 1974) and Russia (Blum & al., 1975; Makryi, 2008). In his protologue, Nylander (1890) mentioned similar material collected by H. Cuming from the Philippines. Confirmed only from Japan based on the results presented here.

Comments. – In the protologue, Nylander (1890) cites original material, presumably collected by E. Almquist from Itchigomé, which refers to Mount Fuji, Shizuoka Prefecture, Honshu, Japan. Two specimens collected by E. Almquist in this region (F158658, F158659) are in S under the basionym in the general collection (i.e., not recognized as type material). While at least one of these samples could undoubtedly serve as a reference for the original description and would be appropriate for lectotypification, we refrained from designating a lectotype as the general collection at S was inaccessible at the time of this study. Once a lectotype is formally selected for this species, the designation of an interpretative type (epitype) may be needed to clarify the application of this species name.

Specimens examined. – Refer to Appendix 2.

Dendriscosticta oroborealis (Goward & Tønsberg) Moncada & Lücking in Lichenologist 45: 223. 2013 ≡ *Sticta oroborealis* Goward & Tønsberg in Bryologist 104: 19. 2001

— Holotype: Canada. British Columbia: N of Hazelton, E of Kispiox Range, N of Date Creek 17 km NW of Kispiox, along and W of a gravel road near a small unnamed creek, $55^{\circ}24.7'N$, $127^{\circ}48.2'W$, 510 m, on twig of *Tsuga heterophylla* in shaded ravine, 3 Oct 1994 T. Tønsberg 20665 & T. Goward (BG!; isotype: CANL n.v.).

Fig. 9E,F

Short description. — Thallus dimorphic. Chloromorphic thallus macrofoliose, similar to *Dendriscosticta gelida*, but with lobes shorter than wide and entire, not at all lacerate. Cyanomorphic thallus fruticose (dendriscocauloid), differing

from *D. gelida* by the presence of rhizines. For a detailed description, see Tønsberg & Goward (2001).

ITS2 barcode. — GCCCGCGCTGGGTGTTGGGCCGG CGTCCTYCG.

Chemistry. — Pseudocyphellarin A usually present.

Distribution. — Known from British Columbia (Canada; Tønsberg & Goward, 2001) and newly reported from southern China. A new collection from the Incomappleux drainage (British Columbia) represents a significant range extension compared to its previously known distribution in Canada.



Fig. 11. Habit of *Dendriscosticta* species. **A**, *D. wrightii* (Simon 638: epitype, FH); **B–D**, *D. yatabeana* (B, Simon 613, LG; C, Wang 14-46445, KUN; D, Wang 16-52075, KUN), showing upper surface with numerous apothecia (B), close-up of seemingly pruinose lobes with hyphae protruding from the cortex (C), and upper surface with pycnidia (C & D); **E**, *D. phyllidiata* (field image from Taiwan), showing upper surface with phyllidia; **F**, *D. insinuans* (Simon 668, TNS), showing upper surface with apothecia. — Photographs by A. Simon (A, B, F), L.S. Wang (C, D) and B. Goffinet (E).

Comments. – Assignment of this taxon is unambiguous as the holotype is included in our phylogenetic analyses.

Additional specimens examined. – Refer to Appendix 2.

Dendriscosticta phyllidiata Ant.Simon, Goffinet & Sérus., sp. nov. [MB 835911] – Holotype: Taiwan. Chiayi County: Alishan Township, Alishan Range, Alishan National Forest Recreation Area, Alpine Botanical Garden, below alpine garden, 23°30'149"N, 120°49'367"E, ±2480–2500 m, on large *Acer*, 25 Oct 2016, B. Goffinet 13475 & E. Sérusiaux (TAIE barcode TAIE046233!; isotype: CONN!).

Fig. 11E

Etymology. – This taxon is named after its most characteristic feature, the production of abundant phyllidia, mostly at lobe margins.

Diagnosis. – Thallus macrofoliose with abundant, marginal phyllidia; differing from *Dendriscosticta praetextata* in the presence of congyrophoric acid.

Description. – *Photobiont* green (presumably *Dictyochloropsis* s.l.). *Stipe* absent. *Thallus* foliose, epiphytic, orbicular in outline, up to 15 cm in diam., papyraceous and fragile, usually rather thick when dry, branching pleurotomous or polytomous. *Lobes* somewhat involute or undulate, ligulate, imbricate, adnate, with plane apices; margins lacerate or crisp, not thickened; lobe internodes 3–15 mm long. *Upper surface* smooth, green when fresh, turning light brown in herbarium, moderately glossy, with margin concolorous; surface smooth (without tomentum), without papillae, pruina and cortical hairs. *Cilia* absent. *Apothecia* either absent, or if present, sparse, cup-shaped, up to 2 mm in diam., laminal, dispersed, pedicellate, without basal invagination (or weak), with glossy, orange disk. *Phyllidia* abundant, marginal (rarely laminal), dispersed, unbranched, palmate, up to 2 mm long and 0.6 mm wide, glossy, dorsiventral, lobuliform. *Medulla* compact, white, K– (cortex occasionally K+ yellow), C+ salmon pink, KC+ salmon pink, P–. *Lower surface* smooth, cream to brown-colored. *Lower tomentum* dense, absent towards margin, rather thick, fasciculate or spongy, soft or rough, concolorous with lower surface. *Rhizines* sparse, centrally aggregate, fasciculate or penicillate, cream to brown-colored, up to 5 mm long. *Cyphellae* abundant, 41–60 per cm² (central) to 21–40 per cm² (marginal), dispersed, rounded to irregular, urceolate with wide pore, immersed, below level of tomentum, with cream to brown-colored margins lacking tomentum; pore to 1.5 mm in diam.; basal membrane pruinose, white, K–, C+ salmon pink, KC+ salmon pink, P–. *Pycnidia* immersed, with blackish ostiole.

Upper cortex paraplectenchymatous, c. 25–45 µm thick, homogeneous, consisting of 4–6 cell layers with cells 5–8 µm diam, their lumina round-isodiametric. *Photobiont* layer 30–40 µm thick, its cells c. 5 µm diam. *Medulla* 120–180 µm thick, its hyphae c. 5 µm broad, with gyrophoric acid crystals. *Lower cortex* paraplectenchymatous, 15–35 µm thick, with 2–3 cell layers; cells 6–8 µm diam. *Hairs* of lower tomentum in fascicles of 6–12 hyphae with intertwined apices. *Cephalodia* not observed. *Cyphelloid pores* with cells of basal membrane polygonal and entangled, 3–5 µm wide, without papillae.

Apothecia with excipulum containing algae, with lateral verrucose protuberances. *Hymenium* 100–130 µm high. *Ascospores* not observed (immature apothecia).

ITS2 barcode. – AACGCCATGTCGCTCGCGGG.

Chemistry. – Gyrophoric acid, congyrophoric acid, and occasionally pseudocypellarin A.

Distribution. – So far only known from Taiwan.

Additional specimens examined. – Refer to Appendix 2.

Dendriscosticta platyphylloides (Nyl.) Moncada & Lücking in Lichenologist 45: 223. 2013 ≡ *Sticta platyphylloides* Nyl. in Bull. Soc. Bot. France 34: 22. 1887 – Type: China. Yunnan: “ad Quercus in fauibus Hoang-se-ia-keou, prope Tapin-tze”, alt. 1800 m, 11 May 1885, P.J.M. Delavay 1607 (H-NYL No. 33655 [H barcode H9505982!]).

?= *Sticta henryana* Müll.Arg. in Flora 74: 374. 1891 – Type: China. Hubei Province, A. Henry 6932 (G barcode G00295320!).

Fig. 10C,D

Short description. – *Thallus* macrofoliose, primarily associated with a green alga. *Upper surface* apparently scabrous or pruinose, without phyllidia. *Lower surface* cream to beige-colored, paler towards margins. *Medulla* KC–.

ITS2 barcode. – C(G)CGCTGGGTGTTGGGCCGRCG TCCCCCG.

Chemistry. – Pseudocypellarin A usually present.

Distribution. – Reported from Bhutan (Søchting, 1999), China (Chen & al., 1994; Li & al., 2013), India (Joshi & al., 2016), Nepal (Devkota & al., 2017), Sri Lanka (Weerakoon, 2015; Weerakoon & Aptroot, 2014), Thailand (Wolseley & al., 2002; Buaruang & al., 2017) and Vietnam (Nguyen & al., 2019). These records need to be confirmed by DNA sequencing owing to the paucity of unambiguous morphological characters in the genus. Based on the results presented here, this species is confirmed from southern China (Sichuan, Xinzang, Yunnan).

Comments. – A single collection is mentioned in the original description of this species (Nylander in Hue, 1887) and can thus be considered as the holotype collection. *Dendriscosticta platyphylloides* can be distinguished from closely related species (i.e., *D. gelida*, *D. oroborealis*, *D. wrightii* and *D. yatabeana*) by its paler lower surface, usually ranging from whitish to beige.

Sticta henryana is a likely synonymous species reported from India (Kumar, 2000) and Nepal (Devkota & al., 2017). The type collection of *S. henryana* comes from Hubei Province in central China, from which no other specimen is available. The type material was examined in G and it undoubtedly belongs to *Dendriscosticta* and, as it lacks gyrophoric acid, to the *D. wrightii* clade. While the specimen could not morphologically be linked to any particular accepted species, this taxon might be synonymous with another species within this clade owing to the paucity of unambiguous morphological characters available to distinguish these closely related species. TLC yielded pseudocypellarin A, a chemical feature most often encountered in the species *D. platyphylloides*. For this reason, we believe that *S. henryana* is most likely a synonym of *D. platyphylloides*.

Additional specimens examined. – Refer to Appendix 2.

Dendriscosticta praetextata (Räsänen) Moncada & Lücking in Lichenologist 45: 223. 2013 ≡ *Sticta platyphylla* var. *praetextata* Räsänen in Suom. Elain-ja Kasvit. Seuran Van. Tiedon. 6: 84. 1952 ≡ *Sticta praetextata* (Räsänen) D.D. Awasthi in Biol. Mem. 7: 185. 1982 – Holotype: India. Uttarakhand: NW Himalaya, Almora, Dhakuri Ridges en route to Pindari Glacier, 9500 ft., corticolous, May 1950, *D.D. Awasthi 109 & A.M. Awasthi* (H!; isotype: LWG n.v.). Fig. 10E

Short description. – Thallus macrofoliose with abundant marginal phyllidia, similar to *Dendriscosticta phyllidiata*, differing in the absence of congyrophoric acid.

ITS2 barcode. – GGCCGACGTYCCGTTTC.

Chemistry. – Gyrophoric acid and occasionally pseudocypellarin A.

Distribution. – Reported from Bhutan (Søchting, 1999), China (Chen & al., 1994), India (Kumar, 2000; Joshi & al., 2016), Japan (Takahashi & al., 2012; Ohmura & Kashiwadani, 2018) and Nepal (Devkota & al., 2017). Based on the results presented here, this species is confirmed from northern India (Uttarakhand) and southern China (Xinzang, Yunnan).

Comments. – A recent collection from near the type locality (*Bajpai & Upreti 12-011438*, LG) has been successfully sequenced.

Additional specimens examined. – Refer to Appendix 2.

Dendriscosticta wrightii (Tuck.) Moncada & Lücking in Lichenologist 45: 224. 2013 ≡ *Sticta wrightii* Tuck. in Amer. J. Sci. Arts 28: 204. 1859 ≡ *Ricasolia wrightii* (Tuck.) Nyl., Syn. Meth. Lich. 1: 366. 1860 – Lectotype (designated by Asahina in J. Jap. Bot. 36: 225. 1961): Japan. Hokkaido: Hakodadi, mountain sides, on beech trunks, *C. Wright s.n.* (FH barcode 00213370 a & a'!); islectotype: US barcode 00432750! – **Epitype designated here [MBT10000071]:** Japan. Hokkaido: Kameda District, Nanae, along the road towards Mt. Yokotsu, 41.917848N, 140.764491E, 883 m, in deciduous forest including *Acer*, *Quercus*, and *Sorbus*, with dense bamboo undergrowth, on *Fagus*, 16 Aug. 2019, *A. Simon & al.* 638 (TNS barcode TNS-L-130566!).

?= *Sticta miyoshiana* Müll.Arg. in Flora 74: 111. 1891 – Type: Japan. Uzen, corticolous, *M. Miyoshi s.n.* (G barcode G00052580 n.v.).

?= *Sticta yasudae* Vain. in Bot. Mag. (Tokyo) 35: 64. 1921 – Type: Japan. Inaba Province, Mount Nagi, corticolous on tree, 31 Oct 1914, *M. Nakaji s.n.*, hb. A. Yasuda (holotype: unlocated; isotype: TNS n.v.).

Fig. 11A

Description. – *Photobiont* green (presumably *Dictyochloropsis* s.l.). *Stipe* absent. *Thallus* foliose, epiphytic, radially plicate-rugose, orbicular in outline, up to 15 cm in diam., coriaceous and tough, rather thick, branching anisotomous or pleurotomous. *Lobes* somewhat plane or undulate, flabellate or ligulate, imbricate, longer than wide, adnate, with plane or involute apices; margins sinuose; lobe internodes to 20 mm

long. *Upper surface* smooth or weakly rugose, dark green when fresh, turning pale brown in herbarium, opaque, with margin concolorous; surface scabrose, or seemingly pruinose, due to the presence of cortical hairs, especially along margins. *Cilia* absent. *Apothecia* either absent, or if present usually abundant, cup-shaped, up to 5 mm in diam., laminal, dispersed, pedicellate, with pronounced basal invagination, with glossy, orange to brown disk. *Apothecia* absent. *Medulla* compact, white, K- (cortex occasionally K+ yellow), C-, KC-, P-. *Lower surface* smooth, brown-colored. *Lower tomentum* dense throughout, patchily thick and thin, spongy, soft or rough, concolorous with lower surface. *Rhizines* sparse, dispersed, fasciculate or squarrose, cream to brown-colored, up to 2 mm long. *Cyphelloid pores* abundant, 21–40 per cm² (central) to 41–60 per cm² (marginal), dispersed, rounded to irregular, urceolate with wide pore, immersed, below level of tomentum, with cream to brown-colored margins; pore to 2 mm in diam.; basal membrane pruinose, white. *Pycnidia* not observed.

Upper cortex paraplectenchymatous, 50–75 µm thick, homogeneous, consisting of 7–8 cell layers with cells 6–12 µm diam., their lumina round-isodiametric. *Photobiont* layer 35–65 µm thick, its cells 5–8 µm diam. *Medulla* 250–450 µm thick, its hyphae 3.5–4.5 µm broad, without crystals. *Lower cortex* paraplectenchymatous, 20–40 µm thick, with 4 or 5 cell layers; cells 3.5–5.0 µm diam. *Hairs* of lower tomentum in fascicles of 6–12 hyphae with intertwined apices. *Cephalodia* usually present (internal). *Cyphelloid pores* with cells of basal membrane polygonal and entangled, 3–5 µm wide, without papillae.

Apothecia with excipulum containing algae, with lateral verrucose protuberances. *Hymenium* 120–200 µm high. *Ascospores* 1–3-septate, acicular, 40–65 × 3–5 µm, hyaline.

ITS2 barcode. – CCGCGCTGGGTGTTGGGCC GGCGTCCTCCCGG.

Chemistry. – No chemistry detected by TLC, but occasionally K+ yellow (traces of pseudocypellarin A).

Distribution. – *Dendriscosticta wrightii* is an epiphytic lichen of humid temperate and subtropical regions. As diagnosed here, it is so far restricted to Hokkaido (Japan; e.g., Ohmura & Kashiwadani, 2018) and South Korea (e.g., Kashiwadani & al., 2002; Hur & al., 2004). Earlier reports from Mongolia (Biazrov, 2013), Russia (Fadeeva, 2005, 2009; Makryi, 2008; Karasev & Selivanov, 2014; Kuznetsova & Skazina, 2010), and Thailand (Wolseley & al., 2002; Buaruang & al., 2017) likely represent another species. The records from northwestern North America refer to *Dendriscosticta gelida* or *D. oroborealis*; those from continental Europe (e.g., Karelia and Germany) probably belong to *D. gelida*, and those from India and China either to *D. platyphyloides* or *D. yatabeanus*.

Comments. – *Dendriscosticta wrightii* had also been mentioned from Cameroon (Orock & al., 2012) and the corresponding material was examined, but no exploitable DNA could be obtained. However, it is unlikely that the material belongs to *Dendriscosticta* as it consists of a foliose cyanolichen.

Dendriscosticta wrightii has been used in traditional medicine in China, such as for treating kidney inflammation or for

its spleen-tonifying action (Ding, 2010; Wang & Qian, 2013). However, this species may have been easily confused with *D. platyphylloides*, which appears to be the most common species in southern China.

Nomenclatural notes. – To clarify the application of the widely used name *Dendriscosticta wrightii*, we propose a sequenced epitype that is morphologically and geographically consistent with the lectotype (FH). As already noted by Asahina (1961) the original material was collected on Hokkaido, Japan and consists of four thalli representing two species: the largest thallus and one of the smaller ones belong to *D. wrightii* s.str. (accordingly, with the characters mentioned in the original protologue), whereas the two remaining smaller thalli belong to another species in the *D. praetextata* clade (referred to as “*Sticta insinuans* Nyl.” by Asahina). Thus, as the original type consisted of heterogeneous elements Asahina (1961) recognized two thallus fragments in this collection as the lectotype (labelled a and a' in the publication). The type specimen is, however, ambiguous, in terms of its interpretative value as *D. wrightii* is phenotypically indistinguishable from *D. yatabeana* with which it is sympatric in Japan and South Korea. The two species are confidently distinguished by their ITS2 barcode. Since sequences could not be obtained for the lectotype, which is therefore demonstrably ambiguous, an epitype (associated with sequence data for ITS2) is herein designated to serve an interpretative type. The epitype was collected in Kameda Peninsula, Hokkaido, Japan, a region that includes the type locality, “Hakodadi, Japan”. This interpretative type represents the traditional concept of *D. wrightii* and fits the original type.

The type locality, Hakodadi (= Hakodate; Tuckerman, 1859), is a major city in southern Hokkaido, Japan. We explored the wooded hill behind the city that forms a prominent part of the Kameda Peninsula (“Mount Hakodate”). This locality is now highly disturbed, and extensively planted with *Cryptomeria japonica*. No lobarioid lichens were observed. We therefore explored other localities in the Kameda Peninsula and located a healthy population of *Dendriscosticta* that fits the original description and material collected by Wright.

Sticta miyoshiana Müll.Arg. and *S. yasudae* Vain. have been reduced to synonymy with *S. wrightii* by Asahina (1961) and we propose not to resurrect these two epithets. Indeed, epitypification with fresh and sequenced material would be needed to do so. *Sticta miyoshiana* was collected in the “Uzen province” in the Yamagata Prefecture (northern part of Honshu), whereas *S. yasudae* was collected in the Tottori Prefecture (central part of Honshu, West of Kyoto). The synonymy of the two species with *D. wrightii* (or *D. yatabeana*) is thus not currently confirmed and could be challenged by collections with exploitable DNA from these two localities.

Additional specimens examined. – Refer to Appendix 2.

***Dendriscosticta yatabeana* (Müll.Arg.) Ant.Simon, Goffinet & Sérus., comb. nov.** [MB 835914] ≡ *Sticta yatabeana* Müll.Arg. in Flora 74: 111. 1891 ≡ *Ricasolia yatabeana* (Müll.Arg.) Stizenb. in Flora 81: 112. 1895 ≡ *Lobaria*

yatabeana (Müll.Arg.) Zahlbr., Cat. Lich. Univ. 3: 320. 1925 – Type: Japan. Honshu: Mount Ontake, 1890, *F. Miyoshi* 118 (G barcode G00052578!; isotype: TNS n.v.) – **Epitype designated here** [MBT10000072]: Japan. Honshu: Nagano Prefecture, Kiso-gun, Otaki, Hakkaisan, vicinity of Mount Ontake, along Road 256 and Omata River, 35.858436N, 137.532966E, 1042 m, in mixedwood forest with dense bamboo undergrowth, on *Ulmus*, 21 Aug 2019, A. Simon 670 & E. Sérusiaux (TNS barcode TNS-L-130567!).

Fig. 11B–D

Description. – Chloromorph: photobiont green (presumably *Dictyochloropsis* s.l.). Stipe absent. Thallus foliose, epiphytic, rarely saxicolous, radially plicate-rugose, orbicular in outline, up to 15 cm in diam., coriaceous and resistant, rather thick, branching anisotomous or pleurotomous. Lobes somewhat involute, flabellate or ligulate, imbricate, approximately as long as wide, adnate or ascending, with plane or involute apices; margins sinuose, slightly thickened; lobe internodes 3–20 mm long. Upper surface smooth or weakly rugose, dark green when fresh, turning brown in herbarium, opaque, with margin concolorous; surface scabrose, or seemingly pruinose, due to the presence of cortical hairs, especially in marginal areas of lobes. Cilia absent. Apothecia either absent, or if present usually abundant, cup-shaped, up to 5 mm in diam., dispersed, pedicellate, with pronounced basal invagination, with glossy, orange to brown disk. Apothecia absent. Medulla compact, white, K– (cortex occasionally K+ yellow), C–, KC–, P–. Lower surface smooth, cream to brown-colored, clearer towards margins. Lower tomentum irregular, patchily absent, spongy, soft or rough, concolorous with lower surface. Rhizines sparse, dispersed, fasciculate or tomentose, cream to brown-colored, up to 6 mm long. Cyphelloid pores abundant, 21–40 per cm² (central) to 41–60 per cm² (marginal), dispersed, rounded to irregular, urceolate with wide pore, immersed, below level of tomentum, with cream to brown-colored margins; pore to 1(–2) mm in diam.; basal membrane pruinose, white. Pycnidia occasionally present, immersed, with black ostiole.

Upper cortex paraplectenchymatous, 40–60 µm thick, homogeneous, consisting of 7 or 8 cell layers with cells 5–8 µm diam., their lumina round-isodiametric. Photobiont layer 35–45 µm thick, its cells 4.5–7.5 µm diam. Medulla 250–500 µm thick, its hyphae 3.5–4.5 µm broad, without crystals. Lower cortex paraplectenchymatous, 25–35 µm thick, with 4 or 5 cell layers; cells 3.5–6.5 µm diam. Hairs of lower tomentum in fascicles of 6–12 hyphae with intertwined apices. Cephalodia usually present (internal). Cyphelloid pores with cells of basal membrane polygonal and entangled, 3–5 µm wide, without papillae.

Apothecia with excipulum containing algae, with lateral verrucose protuberances. Hymenium 130–190 µm high. Ascospores 1–3-septate, acicular, 50–80 × 3.5–5 µm, hyaline.

Cyanomorph: photobiont blue-green (*Nostoc*). Thallus dendriscocauloid (fruticose).

ITS2 barcode. – CGCGCTGGGTGTTGGGCCGGCGT CCC(C)TCCG.

Chemistry. – No substances detected by TLC.

Distribution. – Reported from Japan (Yoshimura, 1974), Russia (Makryi, 2008) and South Korea (Jayalal & al., 2014). Based on the results presented here, this species is confirmed from southern China (Sichuan, Xizang, Yunnan), Japan, South Korea, and Taiwan.

Nomenclatural notes. – A single collection is mentioned in the original description of this species and can thus be considered as the holotype collection. The epitype selected for this epithet comes from the type locality on Mount Ontake (Japan, Honshu); it morphologically fits the original type and description, and was successfully sequenced. The decision to epitomify *Dendriscosticta yatabeana* followed the same rationale as detailed for *D. wrightii* hereabove. These two partially sympatric species cannot be distinguished phenotypically, that is based on morphological or chemical traits, and identification currently relies on the ITS2 barcode. Since no molecular data could be obtained for the type specimen of this taxon and that the type specimen is thus demonstrably ambiguous, an epitype (associated with sequence data for the internal transcribed spacer 2) is herein designated to serve as an interpretative type. The epitype's geographical provenance (Japan, Honshu, Mount Ontake) is in full agreement with the locality cited in Johannes Müller Argoviensis's protologue.

Additional specimens examined. – Refer to Appendix 2.

■ AUTHOR CONTRIBUTIONS

AS designed the study, carried out fieldwork, generated the molecular data, performed the phylogenetic analyses, prepared the taxonomic treatment, and drafted the study. BG, NM, and ES carried out fieldwork, assisted in taxonomic treatment, and advised on all aspects of the research. LSW and NVS carried out fieldwork and provided voucher specimens. TS carried out fieldwork, contributed to the taxonomic treatment and conducted scanning electron microscopy. TG provided voucher specimens and critically contributed to the discussion. TP and NS coordinated field research. BM and RL contributed to the interpretation of the results and the nomenclature to be adopted. The submitted draft has been reviewed and accepted by all the authors. — AS, <https://orcid.org/0000-0002-7766-5751>; BG, <https://orcid.org/0000-0002-2754-3895>; TS, <https://orcid.org/0000-0002-9855-4591>; TP, <https://orcid.org/0000-0003-2215-4724>; NVS, <https://orcid.org/0000-0002-0692-8796>; BM, <https://orcid.org/0000-0001-9984-2918>; RL, <https://orcid.org/0000-0002-3431-4636>; NM, <https://orcid.org/0000-0001-5409-9518>; ES, <https://orcid.org/0000-0002-0456-0131>

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Appendix 1. Voucher information and GenBank accession numbers for specimens used in the phylogenetic analyses.

Species name, authority, country, region, collector, collector number, herbarium code, and GenBank accession numbers for the nuclear ribosomal internal transcribed spacer region (ITS), the RNA polymerase II largest subunit (*RPB1*), the translation elongation factor-1 alpha gene (*EF1- α*), and the DNA replication licensing factor (*MCM7*). Newly generated sequences are highlighted in bold. Missing sequences are indicated by a dash (–). The bold numbers in parentheses indicate the different lineages with the morpho-chemotype of *D. hookeri*. For species producing photomorphs, chloromorphs and cyanomorphs are indicated using the suffix method proposed by Heidmarsson & al. (1997); when unspecified, the fungus is primarily associated to a green alga. For accessions retrieved from GenBank, names denote the original sequence labels.

Dendriscosticta gelida Ant.Simon, Goward & T.Srib./chlor.: Russia, Komi Republic, *A. Simon & N. Semenova* 177 (LG), **MT590974**, –, –, –; Russia, Komi Republic, *A. Simon & N. Semenova* 178 (LG), **MT590975**, **MT612486**, **MT612645**, **MT612566**; Russia, Komi Republic, *A. Simon & N. Semenova* 179 (LG), **MT590976**, –, –, –; Russia, Komi Republic, *A. Simon & N. Semenova* 180 (LG), **MT590977**, –, –, –; Russia, Krasnoyarsk Krai, *A. Simon* (leg. N.V. Stepanov) 213 (LG), **MT590983**, **MT612489**, **MT612646**, **MT612570**; Russia, Krasnoyarsk Krai, *A. Simon* (leg. N.V. Stepanov) 216 (LG), **MT590986**, **MT612480**, **MT612639**, **MT612560**; Russia, Krasnoyarsk Krai, *A. Simon* (leg. N.V. Stepanov) 219 (LG), **MT590987**, **MT612481**, **MT612640**, **MT612561**; Russia, Krasnoyarsk Krai, *A. Simon* (leg. N.V. Stepanov) 220 (LG), **MT590988**, **MT612485**, **MT612644**, **MT612565**; Canada, British Columbia, *A. Simon & T. Spribile* 474 (LG), **MT590969**, **MT612483**, **MT612642**, **MT612563**; Canada, British Columbia, *A. Simon & T. Spribile* 478 (LG), **MT590971**, **MT612484**, **MT612643**, **MT612564**; Canada, British Columbia, *K. McKeown* 2269 (CONN), **MT590848**, **MT612478**, **MT612637**, **MT612558**; U.S.A., Alaska, *T. Tønsberg* 27680 (BG), **MT590826**, –, –, –; U.S.A., Alaska, *T. Tønsberg* 29745 (BG), **MT590834**, –, –, –; U.S.A., Alaska, *T. Tønsberg* 29745 (BG), **MT590835**, –, –, –; U.S.A., Alaska, *T. Tønsberg* 29745 (BG), **MT590836**, –, –, –; Canada, British Columbia, *T. Goward* 02-1827 (UBC), **MT590841**, –, –, –; India, Uttarakhand, *R. Bajpai & D.K. Upreti* 12-011 443 (LG), **MT590982**, –, –, –; China, *L.S. Wang* 16-52799 (KUN), **MT590785**, –, –, –; China, *L.S. Wang* 17-55766 (KUN), **MT590797**, –, –, –; Russia, Krasnoyarsk Krai, *A. Simon* (leg. N.V. Stepanov) 214 (LG), **MT590984**, –, –, –; Russia, Krasnoyarsk Krai, *A. Simon* (leg. N.V. Stepanov) 215 (LG), **MT590985**, –, –, –; Canada, British Columbia, *T. Goward* 99-395 (UBC), **MT590838**, –, –, –; U.S.A., Alaska, *T. Spribile* 26302 (KLGO), **MT590991**, –, –, –; U.S.A., Alaska, *T. Spribile* 36122 (MSC), *MN483092*, –, –, –; U.S.A., Alaska, *T. Spribile* 39269 (MSC), *MN483093*, –, –, –;

Appendix 1. Continued.

- Canada, British Columbia, *T. Spribile* 40915 (hb. Spribile), **MT590996**, –, –, –; Canada, British Columbia, *T. Spribile* 31992 (CONN), **MT590849**, **MT612490**, **MT612647**, **MT612571**; Russia, Krasnoyarsk Krai, N.V. Stepanov s.n. DNA AS6197 (LE), **MT590978**, **MT612487**, –, **MT612568**; Russia, Krasnoyarsk Krai, N.V. Stepanov s.n. DNA AS6197 (LE), **MT590979**, **MT612488**, –, **MT612569**; *Dendriscosticta gelida* Ant.Simon, Goward & T.Sprib./cyan.: Canada, British Columbia, A. Simon & T. Spribile 470 (LG), **MT590967**, **MT612482**, **MT612641**, **MT612562**; China, B. Goffinet 10018 (CONN), **MT590856**, –, –, –; U.S.A., Minnesota, C. Wetmore 22669 (MIN), **MT590912**, –, –, –; Canada, British Columbia, *T. Tønsberg* 27584 (UBC), **MT590823**, –, –, –; Canada, British Columbia, *T. Tønsberg* 27666 (UBC), **MT590824**, –, –, –; Canada, British Columbia, *T. Tønsberg* 27668 (UBC), **MT590825**, –, –, –; U.S.A., Alaska, *T. Tønsberg* 29745 (BG), **MT590837**, –, –, –; Canada, British Columbia, *T. Tønsberg* 29756 (UBC), **MT590828**, –, –, –; Canada, British Columbia, *T. Tønsberg* 29759 (UBC), **MT590844**, –, –, –; Canada, British Columbia, *T. Tønsberg* 29767 (UBC), **MT590829**, –, –, –; Canada, British Columbia, *T. Tønsberg* 29859 (UBC), **MT590830**, –, –, –; Canada, British Columbia, *T. Tønsberg* 30205 (UBC), **MT590831**, –, –, –; Canada, British Columbia, *T. Tønsberg* 30333 (UBC), **MT590832**, –, –, –; Canada, British Columbia, *T. Tønsberg* 30334 (UBC), **MT590833**, –, –, –; China, B. Goffinet 10715c (CONN), **MT590864**, **MT612479**, **MT612638**, **MT612559**; China, L.S. Wang 13-38201 (KUN), **MT590870**, –, –, –; China, L.S. Wang 13-38288 (KUN), **MT590876**, **MT612491**, **MT612648**, **MT612572**; China, L.S. Wang 16-51148 (KUN), **MT590959**, –, –, –; China, L.S. Wang 16-51179 (KUN), **MT590960**, –, –, –; China, L.S. Wang 16-52853 (KUN), **MT590964**, –, –, –; U.S.A., Alaska, *T. Spribile* DNA CONN T1285b (MSC), **MT590994**, –, –, –; *Dendriscosticta* aff. *hookeri* (Trevis) Moncada & Lücking; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 603 (LG), **MT590932**, –, –, –; Japan, Honshu, A. Simon & E. Sérusiaux 659 (LG), **MT590945**, **MT612539**, **MT612696**, **MT612618**; China, B. Goffinet 9997 (CONN), **MT590851**, –, –, –; China, L.S. Wang 14-46019 (KUN), **MT590900**, **MT612540**, **MT612697**, **MT612619**; *Dendriscosticta* aff. *hookeri* (Trevis) Moncada & Lücking (1); Taiwan, B. Goffinet & E. Sérusiaux 13010 (CONN), **MT590915**, **MT612530**, **MT612687**, **MT612610**; Taiwan, B. Goffinet & E. Sérusiaux 13016 (CONN), **MT590916**, –, –, –; Taiwan, B. Goffinet & E. Sérusiaux 13026 (CONN), **MT590917**, **MT612531**, **MT612688**, **MT612611**; Taiwan, B. Goffinet & E. Sérusiaux 13027 (CONN), **MT590918**, **MT612532**, **MT612689**, **MT612612**; Taiwan, B. Goffinet & E. Sérusiaux 13523 (CONN), **MT590926**, –, –, –; Taiwan, B. Goffinet & E. Sérusiaux 13525 (CONN), **MT590927**, **MT612533**, **MT612690**, **MT612613**; Taiwan, E. Sérusiaux & B. Goffinet 221T (LG), **MT590813**, **MT612535**, **MT612692**, **MT612615**; Taiwan, E. Sérusiaux & B. Goffinet 23T (LG), **MT590803**, **MT612534**, **MT612691**, **MT612614**; Taiwan, E. Sérusiaux & B. Goffinet 28T (LG), **MT590804**, –, –, –; Taiwan, E. Sérusiaux & B. Goffinet 294T (LG), **MT590818**, –, –, –; Taiwan, E. Sérusiaux & B. Goffinet 3T (LG), **MT590778**, **MT612537**, **MT612694**, **MT612617**; Taiwan, E. Sérusiaux & B. Goffinet 406T (LG), **MT590820**, –, –, –; Taiwan, E. Sérusiaux & B. Goffinet 413T (LG), **MT590821**, **MT612536**, **MT612693**, **MT612616**; Taiwan, E. Sérusiaux & B. Goffinet 57T (LG), **MT590805**, –, –, –; *Dendriscosticta* aff. *hookeri* (Trevis) Moncada & Lücking (2); China, B. Goffinet 9975 (CONN), **MT590853**, **MT612515**, **MT612672**, **MT612597**; China, B. Goffinet 9975b (CONN), **MT590861**, –, –, –; China, B. Goffinet 10012 (CONN), **MT590908**, –, –, –; China, B. Goffinet 10738 (CONN), **MT590866**, –, –, –; China, L.S. Wang 13-38251 (KUN), **MT590877**, –, –, –; China, L.S. Wang 13-38285 (KUN), **MT590872**, –, –, –; China, L.S. Wang 13-38290 (KUN), **MT590871**, –, –, –; China, L.S. Wang 14-46205 (KUN), **MT590890**, –, –, –; China, L.S. Wang 14-46768 (KUN), **MT590904**, –, –, –; China, L.S. Wang 14-46781 (KUN), **MT590906**, –, –, –; China, L.S. Wang 14-46813 (KUN), **MT590883**, **MT612516**, **MT612673**, **MT612598**; China, L.S. Wang 16-52068 (KUN), **MT590782**, –, –, –; China, L.S. Wang 16-52079 (KUN), **MT590784**, –, –, –; China, L.S. Wang 16-54386 (KUN), **MT590789**, –, –, –; China, L.S. Wang 16-54408 (KUN), **MT590790**, –, –, –; China, L.S. Wang 17-55458 (KUN), **MT590793**, –, –, –; China, L.S. Wang 17-55477 (KUN), **MT590794**, –, –, –; China, L.S. Wang 17-55691 (KUN), **MT590796**, –, –, –; China, L.S. Wang 17-56600 (KUN), **MT590801**, –, –, –; *Dendriscosticta* aff. *hookeri* (Trevis) Moncada & Lücking (3); Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 590 (LG), **MT590928**, –, –, –; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 594 (LG), **MT590930**, **MT612517**, **MT612674**, **MT612599**; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 600 (LG), **MT590931**, –, –, –; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 615 (LG), **MT590935**, –, –, –; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 616 (LG), **MT590936**, **MT612518**, **MT612675**, **MT612600**; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 620 (LG), **MT590937**, –, –, –; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 635 (LG), **MT590941**, **MT612519**, **MT612676**, **MT612601**; Japan, Honshu, A. Simon & E. Sérusiaux 666 (LG), **MT590944**, **MT612520**, **MT612677**, –; Taiwan, E. Sérusiaux & B. Goffinet 171T (LG), **MT590810**, **MT612521**, **MT612678**, **MT612602**; Taiwan, E. Sérusiaux & B. Goffinet 207T (LG), **MT590811**, **MT612522**, **MT612679**, **MT612603**; Taiwan, E. Sérusiaux & B. Goffinet 254T (LG), **MT590817**, –, –, –; Japan, Hokkaido, A. Simon (leg. N. Magain) 687 (LG), **MT590951**, –, –, –; Japan, Hokkaido, A. Simon (leg. N. Magain) 688 (LG), **MT590952**, –, –, –; Japan, Hokkaido, A. Simon (leg. N. Magain) 691 (LG), **MT590954**, –, –, –; Japan, Hokkaido, A. Simon (leg. N. Magain) 692 (LG), **MT590955**, –, –, –; Japan, Hokkaido, A. Simon (leg. N. Magain) 694 (LG), **MT590957**, –, –, –; *Dendriscosticta* aff. *hookeri* (Trevis) Moncada & Lücking (4); Taiwan, B. Goffinet & E. Sérusiaux 13005 (CONN), MT110111, **MT612523**, **MT612680**, **MT612604**; Taiwan, B. Goffinet & E. Sérusiaux 13317 (CONN), **MT590922**, **MT612524**, **MT612681**, **MT612605**; Taiwan, E. Sérusiaux & B. Goffinet 249T (LG), **MT590815**, –, –, –; Taiwan, E. Sérusiaux & B. Goffinet 378T (LG), **MT590819**, –, –, –; *Dendriscosticta* aff. *hookeri* (Trevis) Moncada & Lücking (5); Japan, Honshu, A. Simon & E. Sérusiaux 678 (LG), **MT590949**, **MT612547**, **MT612705**, **MT612626**; China, B. Goffinet 9998 (CONN), **MT590862**, –, –, –; China, B. Goffinet 10017 (CONN), **MT590859**, **MT612541**, **MT612698**, **MT612620**; China, B. Goffinet 10035 (CONN), **MT590860**, –, –, –; China, B. Goffinet 10081 (CONN), **MT590855**, –, –, –; China, B. Goffinet 10711 (CONN), **MT590910**, **MT612548**, **MT612706**, **MT612627**; China, B. Goffinet 10735 (CONN), **MT590865**, –, –, –; China, L.S. Wang 13-38197 (KUN), **MT590868**, –, –, –; China, L.S. Wang 13-38254 (KUN), **MT590869**, –, –, –; China, L.S. Wang 14-46775 (KUN), **MT590878**, –, **MT612699**, **MT612621**; China, L.S. Wang 16-52036 (KUN), **MT590780**, –, –, –; China, L.S. Wang 16-54410 (KUN), **MT590791**, –, –, –; China, L.S. Wang 17-56439 (KUN), **MT590799**, –, –, –; China, L.S. Wang 17-56480 (KUN), **MT590800**, –, –, –; China, L.S. Wang 17-56770 (KUN), **MT590802**, –, –, –; *Dendriscosticta insinuans* (Nyl.) Ant.Simon, Magain & Sérus.: Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 591 (LG), **MT590929**, **MT612528**, **MT612685**, –; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 611 (LG), **MT590933**, –, –, –; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 625 (LG), **MT590939**, –, –, –; Japan, Hokkaido, A. Simon, N. Magain & E. Sérusiaux 626 (LG), **MT590940**, –, –, –; Japan, Honshu, A. Simon & E. Sérusiaux 653 (LG), **MT590943**, **MT612538**, **MT612695**, –; Japan, Honshu, A. Simon & E. Sérusiaux 668 (TNS), **MT590946**, **MT612529**, **MT612686**, **MT612609**; Japan, Hokkaido, A. Simon (leg. N. Magain) 685 (LG), **MT590950**, –, –, –; Japan, Hokkaido, A. Simon (leg. N. Magain) 693 (LG), **MT590956**, –, –, –; *Sticta nylanderiana* Zahlbr.: China, K. Takahashi (KUN), AB245119, –, –, –; South Korea, J.S. Hur (KoLRI [000468]), KF730792, –, –, –; Japan, Hokkaido, K. Takahashi 2975 (HIRO), AB245120, –, –, –; South Korea, J.S. Hur (KoLRI [000321]), KF730790, –, –, –; Taiwan, H. Harada 21782 (CBM-FL), AB245121, –, –, –; South Korea, J.S. Hur (KoLRI [000460]), KF840681, –, –, –; *Dendriscosticta oroborealis* (Goward & Tønsberg) Moncada & Lücking/ chlor.: Canada, British Columbia, A. Simon & T. Spribile 472 (LG), **MT590968**, **MT612475**, **MT612634**, **MT612555**; Canada, British Columbia, A. Simon & T. Spribile 475 (LG), **MT590970**, **MT612476**, **MT612635**, **MT612556**; China, B. Goffinet 10010 (CONN), **MT590858**, –, –, –; China, B. Goffinet 10011 (CONN), **MT590854**, **MT612477**, **MT612636**, **MT612557**; Canada, British Columbia, T. Goward 02-1725 (UBC), **MT590842**, –, –, –; China, B. Goffinet 10715ch (CONN), **MT590863**, **MT612473**, **MT612632**, **MT612553**; Canada, British Columbia, T. Goward 92-1973 (UBC), **MT590840**, –, –, –; Canada, British Columbia, T. Goward 95-459 (UBC), **MT590827**, –, –, –; Canada, British Columbia, T. Spribile 29815 (hb. Spribile), **MT590990**, –, –, –; Canada, British Columbia, T. Tønsberg 20664, AF208015, –, –, –; Canada, British Columbia, T. Tønsberg 20665 (UBC), **MT590843**, **MT612471**, **MT612630**, **MT612551**; Canada, British Columbia, A. Arsenault 2003 (UBC), **MT590846**, –, –, –; *Dendriscosticta oroborealis* (Goward & Tønsberg) Moncada & Lücking/cyan.: Canada, British Columbia, C.R. Bjork 19682 (UBC), **MT590850**, **MT612474**, **MT612633**, **MT612554**; Canada, British Columbia, T. Tønsberg 20591 (UBC), **MT590822**, –, –, –; Canada, British Columbia, T. Goward 04-03 1/3 (UBC), **MT590847**, **MT612472**, **MT612631**, **MT612552**; Canada, British Columbia, T. Spribile 40906 (hb. Spribile), **MT590995**, –, –, –; China, L.S. Wang 16-51141 (KUN), **MT590958**, –, –, –; China, L.S. Wang 16-52633 (KUN), **MT590962**, –, –, –; China, L.S. Wang 16-52837 (KUN), **MT590963**, –, –, –; China, L.S. Wang 16-53111 (KUN), **MT590965**, –, –, –; *Dendriscosticta phyllidiata* Ant.Simon, Goffinet & Sérus.: Taiwan, B. Goffinet & E. Sérusiaux 13475 (CONN), **MT590923**, **MT612525**, **MT612682**, **MT612606**; Taiwan, B. Goffinet & E. Sérusiaux 13506 (CONN), **MT590924**, –, –, –; Taiwan,

Appendix 1. Continued.

B. Goffinet & E. Sérusiaux 13508 (CONN), MT590925, MT612526, MT612683, MT612607; Taiwan, *E. Sérusiaux & B. Goffinet* 2187 (LG), MT590812, –, –; Taiwan, *E. Sérusiaux & B. Goffinet* 2287 (LG), MT590814, MT612527, MT612684, MT612608; *Dendriscosticta platyphylloides* (Nyl.) Moncada & Lücking; **chlor:** China, *B. Goffinet* 9962 (CONN), MT590852, –, –; China, *B. Goffinet* 9971 (CONN), MT590857, –, –; China, *B. Goffinet* 10751 (CONN), MT590907, –, –; China, *B. Goffinet* 10753 (CONN), MT590909, –, –; China, *J. Li* 1338999 (KUN), MT590875, –, –; China, *J. Li* 1339019 (KUN), MT590874, MT612494, MT612650, MT612576; China, *L.S. Wang* 14-46249 (KUN), MT590898, MT612497, MT612653, MT612579; China, *L.S. Wang* 14-46264 (KUN), MT590899, MT612498, MT612654, MT612580; China, *L.S. Wang* 14-46283 (KUN), MT590896, –, –; China, *L.S. Wang* 14-46287 (KUN), MT590895, MT612496, MT612652, MT612578; China, *L.S. Wang* 14-46434 (KUN), MT590881, MT612501, MT612657, MT612583; China, *L.S. Wang* 14-46510 (KUN), MT590879, MT612495, MT612651, MT612577; China, *L.S. Wang* 14-46722 (KUN), MT590901, –, –; China, *L.S. Wang* 14-46725 (KUN), MT590902, MT612499, MT612655, MT612581; China, *L.S. Wang* 14-46730 (KUN), MT590880, –, –; China, *L.S. Wang* 14-46791 (KUN), MT590893, MT612500, MT612656, MT612582; China, *L.S. Wang* 16-53660 (KUN), MT590787, –, –; China, *L.S. Wang* 16-53684 (KUN), MT590788, –, –; China, *L.S. Wang* 16-54413 (KUN), MT590792, –, –; China, *L.S. Wang* 17-55485 (KUN), MT590795, –, –; *Dendriscosticta platyphylloides* (Nyl.) Moncada & Lücking; **cyan:** China, *L.S. Wang* 16-51612 (KUN), MT590961, –, –; China, *L.S. Wang* 16-53203 (KUN), MT590966, –, –; *Dendriscosticta praetextata* (Räsänen) Moncada & Lücking; India, Uttarakhand, *R. Bajpai & D.K. Upreti* 12-011438 (LG), MT590989, MT612546, MT612704, –; China, *L.S. Wang* 13-38297 (KUN), MT590873, –, –; China, *L.S. Wang* 14-46081 (KUN), MT590892, MT612543, MT612701, MT612623; China, *L.S. Wang* 14-46154 (KUN), MT590884, –, –; China, *L.S. Wang* 14-46159 (KUN), MT590903, MT612545, MT612703, MT612625; China, *L.S. Wang* 14-46218 (KUN), MT590886, MT612542, MT612700, MT612622; China, *L.S. Wang* 14-46246 (KUN), MT110112, –, –; China, *L.S. Wang* 14-46281 (KUN), MT590891, –, –; China, *L.S. Wang* 14-46400 (KUN), MT590887, –, –; China, *L.S. Wang* 14-46496 (KUN), MT590888, –, –; China, *L.S. Wang* 14-46702 (KUN), MT590897, MT612544, MT612702, MT612624; China, *L.S. Wang* 14-46806 (KUN), MT590889, –, –; China, *L.S. Wang* 14-46812 (KUN), MT590894, –, –; China, *L.S. Wang* 14-46901 (KUN), MT590905, –, –; China, *L.S. Wang* 16-52037 (KUN), MT590781, –, –; China, *L.S. Wang* 16-52820 (KUN), MT590786, –, –; China, *L.S. Wang* 17-55883 (KUN), MT590798, –, –; China, *K. Takahashi* 2493 (HIRO), AB245122, –, –; *Dendriscosticta wrightii* (Tuck.) Moncada & Lücking; Japan, Hokkaido, *A. Simon, N. Magain & E. Sérusiaux* 638 (FH), MT590942, MT612492, –, MT612573; Japan, *Y. Ohmura* 8954 (TNS), MT590980, MT612493, MT612649, MT612575; South Korea, *J.S. Hur* 70739 (KoLRI), MT590972, –, –, MT612574; Taiwan, *S. Greenwood* D3_31_SPL2 (E), KU862999, –, –; Japan, Honshu, *K. Takahashi* 2016 (HIRO), AB239342, –, –; China, *K. Takahashi* 2349 (HIRO), AB239339, –, –; China, *K. Takahashi* 2346 (HIRO), AB239344, –, –; Japan, Honshu, *K. Takahashi* 1815 (HIRO), AB239341, –, –; *Dendriscosticta yatabeana* (Müll.Arg.) Ant.Simon, Goffinet & Sérus./chlor: Japan, Hokkaido, *A. Simon, N. Magain & E. Sérusiaux* 613 (LG), MT590934, MT612504, MT612660, MT612586; Japan, Honshu, *A. Simon & E. Sérusiaux* 670 (G), MT590947, MT612507, MT612664, MT612589; Japan, Honshu, *A. Simon & E. Sérusiaux* 673 (LG), MT590948, MT612506, MT612662, MT612588; Japan, Hokkaido, *A. Simon, N. Magain & E. Sérusiaux* 689 (LG), MT590953, MT612505, MT612661, MT612587; Japan, *Y. Ohmura* 8962 (TNS), MT590981, MT612511, MT612668, MT612593; China, *B. Goffinet* 10772 (CONN), MT590911, MT612512, MT612669, MT612594; Taiwan, *B. Goffinet & E. Sérusiaux* 13074 (CONN), MT110113, MT612508, MT612665, MT612590; Taiwan, *B. Goffinet & E. Sérusiaux* 13214 (CONN), MT590920, MT612509, MT612666, MT612591; Taiwan, *B. Goffinet & E. Sérusiaux* 13227 (CONN), MT590921, –, –; South Korea, *S.O. Oh, J.S. Park & J.J. Woo* 141578 (KoLRI), MT590973, –, –; MT612663, –; Taiwan, *E. Sérusiaux & B. Goffinet* 119T (LG), MT590808, –, –; Taiwan, *E. Sérusiaux & B. Goffinet* 130T (LG), MT590809, MT612510, MT612667, MT612592; China, *L.S. Wang* 14-46445 (KUN), MT590882, MT612503, MT612659, MT612585; China, *L.S. Wang* 16-52004 (KUN), MT590779, –, –; China, *L.S. Wang* 16-52075 (KUN), MT590783, –, –; Taiwan, *E. Sérusiaux & B. Goffinet* 250T (LG), MT590816, –, –; Taiwan, *E. Sérusiaux & B. Goffinet* 64T (LG), MT590806, MT612513, MT612670, MT612595; Taiwan, *E. Sérusiaux & B. Goffinet* 64Tbis (LG), MT590807, –, –; South Korea, *J.S. Hur* (KoLRI [008817]), KF730793, –, –; *Dendriscosticta yatabeana* (Müll.Arg.) Ant.Simon, Goffinet & Sérus./cyan: China, *L.S. Wang* 1334 (KUN), MT590867, MT612502, MT612658, MT612584; *Dendriscosticta* aff. *yatabeana* (Müll.Arg.) Ant.Simon, Goffinet & Sérus./chlor: Japan, Hokkaido, *A. Simon, N. Magain & E. Sérusiaux* 624 (LG), MT590938, MT612514, MT612671, MT612596; *Dendrocaulon* sp. Nyl.: China, *K. Takahashi* 2401 (HIRO), AB239338, –, –; China, *K. Takahashi* 2349 (HIRO), AB239340, –, –; China, *K. Takahashi* 2350 (HIRO), AB239337, –, –; *Ricasolia quercizans* (Michx.) Stibenz., U.S.A., Arkansas, *J. Lendemer* 45880 (NY), MT590913, MT612550, MT612708, MT612629; *R. virens* (With.) H.H.Bloom & Tønsberg, Norway, *T. Tønsberg* 31538 (BG), MT590845, MT612549, MT612707, MT612628.

Appendix 2. Additional specimens of *Dendriscosticta* examined.

Taxon, country and/or locality, GPS coordinates, substrate and/or habitat, collector(s), date, collection number and/or DNA number, herbarium.

Dendriscosticta gelida Ant.Simon, Goward & T.Sprib.

Additional specimens examined: CANADA, British Columbia, Kispiox Valley, N of Hazelton, north central BC, Muldoe Forest Service Road at km 13.3, N55°32'52.78" W127°43'45.22", on *Tsuga heterophylla*, mostly on suppressed trees in a 250–300-year-old forest, *K. McKeown, A. Banner & E. Hall*, Jul 2009, *McKeown KM09001-4* (CONN), DNA-UConn 2269; British Columbia, Kitimat-Stikine, in the vicinity of Mt Thominson, approximately 20 km N of Kispiox, along Skeena River, N55°23'23" W127°45'04", on *Tsuga heterophylla*, in old-growth temperate rainforest including *Thuja plicata*, *A. Simon & T. Spribille*, 27 Oct 2016, *Simon 456* (LG); *Simon 470* (LG); Kitimat-Stikine, in the vicinity of Kispiox Mountain, approximately 5 km NW of Kispiox, along Muldoe Service Road, N55°33'31" W127°44'39", on *Tsuga heterophylla*, in old-growth temperate rainforest including *Thuja plicata*, *A. Simon & T. Spribille*, 27 Oct 2016, *Simon 471* (LG); *Simon 473* (LG); *Simon 474* (LG); in the vicinity of Kispiox Mountain, approximately 20 km NW of Kispiox, N55°28'42.612" W127°53'22.242", epiphytic, in old-growth forest including *Thuja plicata* and *Tsuga heterophylla*, *A. Simon, P. Bartemucci & Irina Stepanchikova*, 22 Sep 2018, *Simon 373* (ALTA-CP); Kitimat-Stikine, approximately 3 km N of Stewart, along Glacier Hwy (37A), N55°58'27" W129°57'41", on *Alnus rubra*, in moist alder forest, *A. Simon & T. Spribille*, 29 Oct 2016, *Simon 477* (LG); *Simon 478* (LG); Kitimat-Stikine, about 6 km W of Bear Glacier Provincial Park, along Glacier Hwy, Argyle Creek Culvert, N56°06'59" W129°48'26", on *Alnus rubra*, under *Populus* ("drip zone effect"), at the edge of an old-growth forest, *A. Simon & T. Spribille*, 29 Oct 2016, *Simon 479* (LG); British Columbia, Fraser-Fort George, northernmost part of the Robson Valley, along Bowron Forest Service Road, N54°00'21" W121°48'52", *A. Simon & T. Spribille*, 30 Oct 2016, *Simon 489* (LG); Fraser-Fort George, Robson Valley, approximately 2 km S of Uring, N53°39'04.64" W120°51'59.394", on *Alnus*, on a damp valley floor, *A. Simon, S. Goyette & G. Tagirdzhanova*, 28 Oct 2018, *Simon 355* (ALTA-CP); British Columbia, Robson Valley, Viking Ridge trail, 53°51'N 120°28'W, 890 m, on *Tsuga* branch, *T. Spribille & D. Radies*, 4 Oct 2002, *Goward 02-1827* (leg. Spribille, UBC); British Columbia, Quesnel Lake, 52°40'N 120°52'W, 750 m, on *Tsuga* branch in spray zone of Roaring Creek Falls, *T. Goward & A. Roberts*, 2 Aug 1999, *Goward 99-345* (UBC); British Columbia, Selkirk Mountains, Incomappleux River, 2.08 km NE of Beaton, steep NW-facing slope above mouth of river on Arrow Lake, N50°74'40" W117°70'893", 13 Sep 2014, *Spribille 40915* (hb. Spribille), DNA extract T1377; Incomappleux River, about 780 m S of confluence with Battle Brook, N50°59'54.0" W117°35.002", 16 Oct 2009, *Spribille 31992* (CONN), DNA extract UConn 2271. CHINA, Sichuan Province, Daofu Co., Yala Snow Mt., nature reserve, N30°31'13.30" E101°37'25.15", alt. 3280 m, on *Rhododendron* bark, *L.S. Wang, X.Y. Wang, H.X. Shi, M.X. Yang* 16-52799 (KUN-L); Sichuan Province, Daofu Co., Yala Snow Mt., nature reserve, N30°31'13.30" E101°37'25.15", 3280 m, cyanomorph, on *Rhododendron* bark, *L.S. Wang, X.Y. Wang, H.X. Shi, M.X. Yang* 16-51590 (KUN-L 55010); Sichuan Province, Daocheng Co., Yading village, N28°26'78.5" E100°20'836", 3900 m, cyanomorph, on *Picea*, 16 Sep 2002, *Wang 02-21537* (KUN-L 18928); on Rhododendron, 4300 m, 15 Sep 2002, *Wang 02-21502* (KUN-L 18929); Yunnan Province, Lijiang County, S of Lijiang, Jiuhue village, Laojunshan Mountain, at the border with Jianchuan, along trail from parking lot to peak, N26°38'53.8" E99°

Appendix 2. Continued.

43.509–45.992°, 3510–3900 m, montane forest dominated by *Abies* and further up by *Rhododendron*, B. Goffinet, L.S. Wang, S.L. Guo & S.Y. Huang, 16 Jul 2010, *Goffinet 10018* (CONN), DNA-UConn 2938; Yunnan Province, Shangri-la County, N of Shangri-la Xiao Xueshan Mountain, along road from Shangri-la to Sichuan, Geza village, 28°17'08.35"N 99°45'58.20"E, 3461 m, along stream bed, with steep densely vegetated slope with *Rhododendron*, L.S. Wang, X.Y. Wang, D. Liu & S.Y. Huang, 5 Jul 2012, *Goffinet 10735* (CONN), DNA extracts: UConn 3062 (cyanomorph) & 3063 (cyanomorph); Yunnan Province, Weixi County, on the way from Weixi to Zhongdian, 2950 m, N27°19'37.82"E 99°16'38.56", on hemlock, L.S. Wang & X.Y. Wang, 16 Jun 2013, *Wang 13-38288* (KUN-L), DNA-UConn 3869; Yunnan, Zhongdian Co., Geza village, Daxueshan Mt., N28°34'E 99°51', 3600–4200 m, cyanomorph, on *Salix*, 15 Jun 2004, *Wang 04-23253* (KUN-L); on *Picea*, 11 Oct 2001, *Wang 01-20803* (KUN-L); Yunnan, Deqin Co., Baimaxueshan Mt., N28°22'E 98°59', 4320 m, *Wang 04-23253*, cyanomorph, on *Sorbus*, 11 Nov 2003, 4000 m, 22 Jun 2013, L.S. Wang & X.Y. Wang *13-38550* (KUN-L); Yunnan, Simao Co., Caiyanghe, N22°35'E 101°04', 1570 m, cyanomorph, on bark, 7 Feb 2009, *Wang 09-30144* (KUN-L); Yunnan, Nanjian Co., Fenghuangshan Mt., N24°54'19.20"E 100°18'44.48", 2240 m, cyanomorph, on *Ternstroemia* bark, 14 Jun 2012, L.S. Wang & al. *12-34338* (KUN-L); Yunnan, Jingdong Co., Wuliangshan Mt., N24°17'E 100°47", 2000 m, cyanomorph, on stump, 20 Jun 2005, *Wang 05-23776* (KUN-L); Yunnan, Jingdong Co., Jinguo Village, N24°48'E 100°24', 2230 m, cyanomorph, on *Alnus*, 25 May 2012, L.S. Wang & al. *12-33699* (KUN-L); Yunnan, Tengchong Co., Houqiao village, N25°11'E 98°19', 2910 m, cyanomorph, on branch, 28 May 2012, L.S. Wang & al. *12-33368* (KUN-L). **INDIA**, Uttarakhand, Uttarkashi District, Harkidun forest guest house, N31°08'22.17"E 78°24'30.56", 3205 m, D.K. Upadhyay & R. Bajpai, 11 Jun 2012, *Upadhyay 12-011443* (LG), DNA-Lg AS6213. **RUSSIA**, Krasnoyarsk Krai, Ermakovskiy District, Western Sayan, Kulumys Ridge, north facing slope, 25 km South from the Tanzibey village, Maraliy Klyuch river, N53°01'57.7"E 93°10'07.6", 440 m above sea level, mixed dark coniferous forest with *Betula platyphylla* and *Sorbus sibirica*, on bark of *Salix rorida*, 15 Jul 2005, leg. N.V. Stepanov s.n. (LE), DNA-Lg AS6194; Krasnoyarsk region, Kuraginsky District, Eastern Sayan, near Mozharskiye Ozera wildlife sanctuary (Tiberkul lake), N53°50'21.6"E 93°59'55.1", 450 m above sea level, taiga (*Abies sibirica* + *Pinus sibirica*), on bark of *Sorbus sibirica*, N.V. Stepanov, 28 Jul 2011, *Simon 220* (leg. Stepanov, LG), DNA-Lg AS6221; Krasnoyarsk region, Novoselovsky District, border of the Minusinsk Valley, Anashenskiy Bor wildlife sanctuary, N54°55'47.0"E 91°11'42.9", *Pinus sylvestris* + *Betula pendula* forest with grass and *Pteridium pinetorum*, N.V. Stepanov, 10 Jul 2017, *Simon 219* (leg. Stepanov, LG), DNA-Lg AS6220; Kulumys ridge, near Aleev Kluch river, N53°04'39.0"E 93°07'07.6", 400 m above sea level, taiga (*Abies sibirica* + *Pinus sibirica*), on bark of *Sorbus sibirica*, N.V. Stepanov, 3 Jun 2017, *Simon 215* (leg. Stepanov, LG), DNA-Lg AS6216; Kulumys ridge, near Chebizhek river, Pervaya Petlyya locality, N52°55'40.1"E 93°14'46.6", 1020 m above sea level, taiga (*Abies sibirica* + *Pinus sibirica*), on bark of *Sorbus sibirica*, N.V. Stepanov, 3 Jun 2017, *Simon 215* (leg. Stepanov, LG), DNA-Lg AS6217; Western Sayan, Kurtushibinsky ridge, near the mouth of the Oresh River, N52°28'01.2"E 93°29'44.7", 1000 m above sea level, N.V. Stepanov, 11 Jul 2017, *Simon 213* (leg. Stepanov, LG), DNA-Lg AS6214; Western Sayan, Ergaki ridge, basin of Nizhnyaya Buyba River, Tarmazakovskiy, N52°48'42.3"E 93°17'01.9", 1350 m above sea level, *Pinus sibirica* taiga with moss and *Vaccinium myrtillus*, on bark of *Sorbus sibirica*, N.V. Stepanov, 20 Aug 2017, *Simon 214* (leg. Stepanov, LG), DNA-Lg AS6215; Komi Republic, Priluzsky District, approximately 4 km W of the ghost village of Pentjura (Пентюра) and 11 km NW of Lojma (Лойма), N60°35'17.58"E 48°37'39.21", on *Sorbus* trunk, in old mixedwood forest of *Picea-Sorbus*, A. Simon & N. Semenova, 24 Aug 2017, *Simon 178* (LG), DNA-Lg AS6191. **U.S.A.**, Alaska, Chilkoot Trail, 59°34.608'N 135°19.880'W, on *Betula* bark, 26 Jul 2008, *Spribile 26302* with S. Pérez-Ortega (KLGO), DNA extract T1276; Alaska, Glacier Bay National Park, Bartlett Cove, ca. 340 m NE of NPS docks, 58°27.463'N 135°51.858'W, on bark of *Picea sitchensis* twig at beach fringe, 4 Sep 2011, *Spribile 36122* (MSC), DNA extract T1284; Glacier Bay National Park, East Arm of Glacier Bay, mouth of unnamed creek E of Muir Point, 58.83594°N 136.05309°W, on *Alnus* bark, 30 Jul 2012, *Spribile 39269* with A. Fryday & M. Svensson (MSC), DNA extract T1285; Alaska, Tongass National Forest, small islet, S of Browning Island, Ernst Sound, 55°55.330'N 132°10.271'W, alt. <3 m, beachfringe forest, S aspect, bole of *Alnus rubra*, 3 Aug 2003, *Dillman 2003-582* (CONN); Tongass National Forest, Mitof Island, S of Petersburg, beachfringe forest across form the Stikine river delta, S aspect, 56°35.764'N 132°32.569'W, alt. <3 m, on bole of *Picea sitchensis*, 29 Aug 2003, *Dillman 2003-1139* (CONN); *Dillman 2003-1142* (CONN); *Dillman 2003-1152* (CONN); *Dillman 2003-1163* (CONN); Michigan, Keweenaw, Isle Royale National Park, Between Tonkin Bay and Conglomerate Bay, 3 Jul 1959, C.M. Wetmore 4239 (MSC 0142801); Minnesota, Cook, Seagull Creek, Gunflint Trail, Superior National Forest, 48°07'34"N, 90°51'51"W, 2 Jul 1974, C.M. Wetmore 22669 (MIN).

***Dendriscosticta insinuans* (Nyl.) Ant. Simon, Magain & Sérus.**

Additional specimens examined: **JAPAN**, Hokkaido Prefecture, Kawakami District, Shibecha experimental forest, old forest with a lot of dead wood, N43.35°E 144.66°, c. 100 m, on a wood along the river, in undergrowth with bracken fern, N. Magain with A. Saito & S. Mori, 20 Aug 2019, *Simon 693* (LG, leg. Magain), DNA-LG 6430; Nakagawa-gun, Nakagawa, near Penkenai River, N44.835566°E 142.137846°, 248 m, on *Tilia*, A. Simon, N. Magain & E. Sérusiaux, 6 Aug 2019, *Simon 626* (LG), DNA-LG 6430; Nakagawa-gun, Otoineppu-mura, Kamiotoineppu, along Tenkita River and Road 275, N44.798973°E 142.25779°, 143 m, on bark, A. Simon, N. Magain & E. Sérusiaux, 5 Aug 2019, *Simon 591* (LG), DNA-LG 6418; *Simon 625* (LG), DNA-LG 6429; Shari-gun, Shari-cho, Shiretoko National Park, along the trail from Iwabetsu Onsen, N44.11°E 145.09°, c. 215–500 m, old-growth montane forest, N. Magain with A. Saito & S. Mori, 18 Aug 2019, *Simon 685* (LG, leg. Magain), DNA-LG 6441; Urakawa-gun, Urakawa, Nobuka, on the trail towards Mt. Petekari starting from Petekari Sanso (ペテカリ山荘), N42.484997°E 142.821997°, 883 m, on *Betula*, A. Simon, N. Magain & E. Sérusiaux, 12 Aug 2019, *Simon 611* (LG), DNA-LG 6422; Honshu, Nagano Prefecture, Kiso-gun, Otaki, Hakkaisan, in the immediate vicinity of the ski resort Ontake 2240, on the south-eastern slopes of Mt Ontake, N35.861459°E 137.531333°, 1665 m, on *Quercus*, A. Simon & E. Sérusiaux, 20 Aug 2019, *Simon 611* (LG), DNA-LG 6422; *Simon 668* (TNS), DNA-LG 6437.

***Dendriscosticta oroborealis* (Goward & Tønsberg) Moncada & Lücking**

Additional specimens examined: **CANADA**, British Columbia, Kitimat-Stikine, Aiyansh, along Nisga'a Hwy, near Dragon Lake, N55°19'33" W128°57'08", on *Tsuga heterophylla*, A. Simon & T. Spribile, 28 Oct 2016, *Simon 476* (LG); Kitimat-Stikine, in the vicinity of Kispiox Mountain, approximately 5 km NW of Kispiox, along Muldoe Service Road, N55°32'40" W127°43'42", on *Tsuga heterophylla*, in old-growth temperate rainforest including *Thuja plicata*, A. Simon & T. Spribile, 27 Oct 2016, *Simon 472* (LG) & *Simon 475* (LG); Kitimat-Stikine, near Kispiox, N55°32.933' W127°43.625', on fallen small *Tsuga heterophylla*, 14 Sep 2008, *Spribile 29815* (hb. Spribile), DNA T1269; Incomappleux River, 2.08 km NE of Beaton, steep NW-facing slope above mouth of river on Arrow Lake, N50.74829°W 117.70948°, 13 Sep 2014, *Spribile 40906* (hb. Spribile), DNA extract T1374; British Columbia, Robson Valley, Hungary Creek near highway, 53°52'N 121°32'W, 770 m, on *Tsuga* branch, T. Spribile & D. Radies, 5 Oct 2002, *Goward 92-1973* (UBC, leg. Spribile), DNA extract UConn 1513; Robson Valley, slopes and gullies above Fraser River, 53°25'N 120°31'W, 885 m, on *Tsuga* branch, T. Spribile & D. Radies, 3 Oct 2002, *Goward 02-1725* (UBC, leg. Spribile), DNA extract UConn 1515; British Columbia, Columbia-Shuswap, Wood River, 34 km up logging road, 52°18'N 118°05'W, open old-growth forest, on *Tsuga* branch, T. Goward & M. Zhurbenko, 24 Jul 2002, *Goward 02-1091* (UBC), DNA extract UConn 1508. **CHINA**, Xizang, Milin Co., Lilong village, N29°11'17.31"E 94°02'19.44", 3044 m, L.S. Wang & al. 19-66239 (KUN-L 70647), cyanomorph, on *Quercus* sp., 31 Jul 2019; Xizang, Chayu Co., Hydropower station in Guyu Town, N28°47'E 97°28', 2465 m, cyanomorph, on rock, 24 Sep 2014, L.S. Wang & al. 14-46421 (KUN-L 48369); Xizang, Basu Co., along the road from Ranwu to Chayu, N29°19'E 96°57', 4563 m, cyanomorph, on *Populus* sp., 23 Sep 2014, L.S. Wang & al. 14-46568 (KUN-L 48516); Yunnan, Tengchong Co., Houqiao village, N25°11'E 98°19', 1910 m, L.S. Wang & al. 12-33402, cyanomorph, on bark, 28 Mar 2012; *Wang 12-33394* (KUN-L), *Wang 12-33380* (KUN-L); Yunnan, Jingdong Co., Wuliangshan Mt., N24°19'E 100°47', 2420 m, cyanomorph, on bark, 20 Jun 2005, *Wang 05-23533* (KUN-L); Yunnan, Lijiang Co., Laojunshan Mt., N26°39'E 99°46', 3690 m, cyanomorph, on bark of *Abies*, 28 Aug 2005, L.S. Wang & al. 05-25299 (KUN-L); Yunnan, Deqin Co., Baimaxueshan Mt., N28°19'E 99°05', 4350 m, cyanomorph, on rock, 2 Nov 2015, L.S. Wang & al. 15-49652 (KUN-L); Yunnan, Zhongdian Co., Geza village, Xiaoxueshan Mt., N28°17'08.35"E 99°45'58.20", 3461 m, cyanomorph, on *Salix*, 5 Jul 2012, L.S. Wang & al. 12-34903 (KUN-L). ***Dendriscosticta phyllidiata* Ant. Simon, Goffinet & Sérus.**

Additional specimens examined: **TAIWAN**, Chiayi County, Alishan Township, Alishan range, Alishan National Forest area, Alpine botanic garden, N23°30.149'E 120°49.367', 2480–2500 m, on large maple, below alpine garden, B. Goffinet & E. Sérusiaux, 25 Oct 2016, *Goffinet 13506* (topotype, CONN),

Appendix 2. Continued.

DNA-UConn 4748; *Goffinet 13508* (topotype, CONN), DNA-UConn 4749; Taroko National Park, Hualien County, Xiulin Township, Fushi village, off Hwy 8, N of intersection with Hwy 14a, trail to Mount Pilu, starting immediately N of tunnel, N24°10.949' E121°18.490', trail through mixedwood montane forest and *Pinus* forests, E. Sérusiaux & B. Goffinet, 20 Oct 2016, *Sérusiaux s.n.* (LG), DNA-218T; DNA-228T.

Dendriscosticta platyphyloides (Nyl.) Moncada & Lücking

Additional specimens examined: CHINA, Sichuan, Kangding Co., Mugecuo nature reserve, *Rhododendron* valley, N30°08'35.93" E101°51'35.27", 2790 m, on *Abies* bark, L.S. Wang, X.Y. Wang, H.X. Shi, M.X. Yang 16-52649 (KUN-L 56069); Xizang, Bomi Co., along the road from Bomi to Ranwu, N29°48.412' E95°49.114', 2811 m, on deadwood, 2 Sep 2014, Wang 14-46264 (KUN-L 48212); Wang 14-46249 (KUN-L 48197); Xizang, Chayu Co., Hydropower station in Guyu Town, N28°54.729' E97°28.293', 2904 m, on rock, L.S. Wang, J. Wang, H.X. Shi, 24 Sep 2014, Wang 14-46434 (KUN-L 48382); Xizang, Chayu Co., Sangjiu village, N28°47.631' E97°29.905', 2709 m, on bark, 25 Sep 2014, Wang 14-46791 (KUN-L 48739); Xizang, Chayu Co., Muruo village, N28°35.267" E98°01.503', 3912 m, on *Sorbus*, 26 Sep 2014, Wang 14-46730 (KUN-L 48678); Xizang, Bomi Co., Dongqu village, N29°43.891' E96°02.069', 3052 m, on *Quercus*, 21 Sep 2014, Wang 14-46283 (KUN-L 48231); Xizang, Chayu Co., Hydropower station in Guyu Town, N28°54.729' E97°28.293', 2904 m, on stump, 24 Sep 2014, Wang 14-46510 (KUN-L 48458); Xizang, Chayu Co., Muruo village, N28°35.267' E98°01.503', 3912 m, on bark, 26 Sep 2014, Wang 14-46725 (KUN-L 48673); Xizang, Bomi Co., Dongqu village, N29°43.891' E96°02.069', 3052 m, on *Quercus*, 21 Sep 2014, Wang 14-46287 (KUN-L 48235); Xizang, Bomi Co., Guxiang village, N29°53'58.02" E95°30.27.65", 2680 m, on *Quercus*, 24 Sep 2016, L.S. Wang, X.Y. Wang, H.X. Shi, M.X. Yang 16-54413 (KUN-L 57833); Xizang, Linzhi Co., on the way from Bomi to Linzhi, near G318 road, N29°52'18.20" E94°46'31.81", 2860 m, on *Sorbus* bark, 24 Sep 2016, Wang 16-53660 (KUN-L 57080); Xizang, Linzhi Co., on the way from Bomi to Linzhi, beside G318 road, N29°52'18.20" E94°46'31.81", 2860 m, on *Lonicera* bark, 24 Sep 2016, L.S. Wang (KUN-L 57104); Yunnan, Lijiang Prefecture, Lijiang Co., S of Lijiang, Juhue village, along trail from parking lot to peak, N26°39.218' E99°46.585', ±3451 m, montane forest dominated by *Abies* and further up by *Rhododendron*, B. Goffinet, LS. Wang, S.L. Guo & S.Y. Huang, 16 Jul 2010, *Goffinet 9971* (CONN), DNA extract UConn 2939.

Dendriscosticta praetextata (Räsänen) Moncada & Lücking

Additional specimens examined: CHINA, Xizang, Chayu Co., Sangjiu village, N28°47.631' E97°29.905', 2709 m, on rock, 25 Sep 2014, Wang 14-46806 (KUN-L 48754); Xizang, Bomi Co., Gang village, N29°52.983' E95°33.593', 2688 m, on rock, 20 Sep 2014, Wang 14-46154 (KUN-L 48102); Xizang, Chayu Co., Sangjiu village, N28°47.631' E97°29.905', 2709 m, on rock, 25 Sep 2014, Wang 14-46812 (KUN-L 48760); Xizang, Chayu Co., along the road from Muruo village to Bingzhongluo, N28°35.781' E98°06.404', 3833 m, on stump, 26 Sep 2014, Wang 14-46774 (KUN-L 48722); Xizang, Bomi Co., Gang village, N29°52.983' E95°33.593', 2688 m, on *Pinus yunnanensis*, 20 Sep 2014, Wang 14-46218 (KUN-L 48166); Xizang, Chayu Co., along the road from Muruo village to Bingzhongluo, N23°35.781', E98°06.404', 3833 m, on bark, 26 Sep 2014, Wang 14-46779 (KUN-L 48727); Xizang, Bomi Co., Gang village, N29°52.983' E95°33.593', 2688 m, on bushes, 20 Sep 2014, Wang 14-46159 (KUN-L 48107); Xizang, Bomi Co., Gawalon, N29°49.838' E95°43.009', 3211 m, on stump, 20 Sep 2014, Wang 14-46081 (KUN-L 48029); Xizang, Chayu Co., Luoma village, N29°01.571' E97°22.795', 2930 m, on *Salix*, 23 Sep 2014, Wang 14-46702 (KUN-L 48650); Xizang, Bomi Co., along the road from Bomi to Ranwu, N29°48.412' E95°49.114', 2811 m, on *Quercus*, 21 Sep 2014, Wang 14-46246 (KUN-L 48194); Xizang, Bomi Co., Dongqu village, N29°43.891' E96°02.069', 3052 m, on *Quercus*, 21 Sep 2014, Wang 14-46281 (KUN-L 48229); Xizang, Chayu Co., Hydropower station in Guyu Town, N28°54.729' E97°28.293', 2904 m, on rock, 24 Sep 2014, Wang 14-46496 (KUN-L 48444); Xizang Chayu Co., Hydropower station in Guyu Town, N28°47.363' E97°28.983', 2465 m, on rock, 24 Sep 2014, Wang 14-46400 (KUN-L 48348); Yunnan Province, Weixi Co., on the way of Weixi to Zhongdian, on the way of Weixi to Zhongdian, N27°19'37.82" E99°16'38.56", 2950 m, on hemlock, 16 Jun 2013, L.S. Wang, X.Y. Wang 13-38297 (KUN-L 24008). INDIA, Uttarakhand, Uttarkashi District, Harkidun forest guest house, N31°08'22.17" E78°24'30.56", 3205 m, on *Abies*, D.K. Upadhyay & R. Bajpai, 11 Jun 2012, *Upreti 12-011438* (LG), DNA-Lg 3168.

Dendriscosticta wrightii (Tuck.) Moncada & Lücking

Additional specimens examined: JAPAN, Honshu, Yamanashi Prefecture, en route from Kitazawa Pass to Sensui Pass, Minami-Alps-city, N35°44'24.0" E138°13'05.2", 2010 m, on bark of *Salix* sp., Y. Ohmura & A. Frisch, 28 Jun 2012, Y. Ohmura 8954 (TNS), DNA-LG AS6209. SOUTH KOREA, Mt. Hamback, N37°10'09.8" E128°54'55.0", 1438 m, on bark, 19 Jun 2007, Jae-Seoun Hur 070739 (KoLRI007591), DNA-LG 6185.

Dendriscosticta yatabeana (Müll.Arg.) Ant.Simon, Goffinet & Sérusiaux

Additional specimens examined: CHINA, Xizang, Bomi Co., Guxiang village, forest near G 318 road, N29°53'58.02" E95°30'27.65", 2680 m, on *Pinus* bark, L.S. Wang, X.Y. Wang, H.X. Shi, M.X. Yang 16-52075 (KUN-L); 16-52004 (KUN-L); Xizang, Chayu Co., Hydropower station in Guyu Town, N28°54.729' E97°28.293', 2904 m, on rock, L.S. Wang, J. Wang & H.X. Shi, 24 Sep 2014, Wang 14-46445 (KUN-L 48393), DNA extract UConn 3944; Shangri-la Co. N of Shangri-la, Xiao Xueshan Mountain, along road from Shangri-la to Sichuan, Geza village, N28°16'49.90" E99°45'35.52", 3289 m, along stream in secondary woodland and in *Abies* woodland, *Goffinet 10772* (CONN), DNA extract UConn 4170. JAPAN, Hokkaido Prefecture, Kawakami District, Shibecha experimental forest, old forest with a lot of dead wood, N43.35° E144.66°, c. 100 m, epiphytic, N. Magain with A. Saito & S. Mori, 20 Aug 2019, Simon 689 (LG, leg. Magain), DNA-LG 6444; Urakawa-gun, Urakawa, Nobuka, on the trail between Petekari Sanso (ペテカリ山荘) and Kamui Sanso (神威山荘), N42.452584° E142.846037°, 547 m, on *Fraxinus* in a young conifer plantation, A. Simon, N. Magain & E. Sérusiaux, 12 Aug 2019, Simon 613 (LG), DNA-LG 6423; Honshu, Fukushima Prefecture, Yama District, Kitashiobara, Hibara, on the ski slope at Grandeco Snow Resort, N37.717553° E140.129157°, 1384 m, on *Fagus*, A. Simon & E. Sérusiaux, 24 Aug 2019, Simon 673 (LG), DNA-LG 6439; Yamanashi Prefecture, en route from Kitazawa Pass to Sensui Pass, Minami-Alps-city, N35°44'24.0" E138°13'05.2", 2010 m, on trunk of *Populus suaveolens*, Y. Ohmura & A. Frisch, 28 Jun 2012, Ohmura 8962 (TNS), DNA-LG AS6209. SOUTH KOREA, Sodo-dong, Taebaek-si, Gangwon-do, N37°05'46.5" E128°57'04.4", 1415 m, 23 Dec 2014, S.O. Oh, J.S. Park, J.J. Woo 141578 (KoLRI032251), DNA-LG AS6189. TAIWAN, Hualien County, Xiulin Township, Fushi village, Taroko National Park, about 2.7 km on Hwy 14a past the high elevation endemic research institute, N24°10.717', E121°18.264', 2750 m, trail through deciduous upper montane forest with dense bamboo undergrowth, grading into *Pinus* forest with willows along the trail, B. Goffinet & E. Sérusiaux, 19 Oct 2016, *Goffinet 13214*, DNA extract UConn 4737; *Goffinet 13227* (CONN), DNA extract UConn 4738.