

## New species, phylogeny, host-associations and geographic distribution of genus *Cryptosporella* (Gnomoniaceae, Diaporthales)

Luis C. Mejía<sup>1</sup>

*Systematic Mycology & Microbiology Laboratory, USDA-ARS, Room 304, B011A, 10300 Baltimore Avenue, Beltsville, Maryland 20705, and Department of Plant Biology and Pathology, Rutgers University, New Brunswick, New Jersey 08901*

Amy Y. Rossman

Lisa A. Castlebury

*Systematic Mycology & Microbiology Laboratory, USDA-ARS, B010A, 10300 Baltimore Avenue, Beltsville, Maryland 20705*

James F. White Jr.

*Department of Plant Biology and Pathology, Rutgers University, New Brunswick, New Jersey 08901*

**Abstract:** The phylogeny of *Cryptosporella* is revised to include recently discovered species. Eight species new to science are described and two new combinations are proposed, raising the total number of species accepted in *Cryptosporella* to 19. The species delimitation and phylogeny for *Cryptosporella* are determined based on analyses of DNA sequences from three genes ( $\beta$ -tubulin, ITS and *tef1- $\alpha$* ), comparative morphology of sexual structures on their host substrate, and host associations. The inferred phylogeny suggests that *Cryptosporella* has speciated primarily on Betulaceae with 16 species occurring on hosts in that plant family. The host range of most species seems to be narrow with nine species reported from a single host species or subspecies and seven species occurring on plants within a single host genus. A key to species is provided. The known distribution of *Cryptosporella* is expanded to mountain cloud forests of the provinces of Chiriquí in Panama and Tucumán in Argentina.

**Key words:** Argentina, Ascomycetes, Betulaceae, Panama, systematics

### INTRODUCTION

Fungi in the Gnomoniaceae are an important component of the endophytic mycobiota in temperate forests. Phylogenetic studies have shown that several of the dominant endophyte species belong in genera of the Gnomoniaceae, such as *Apiognomonia* Höhn., *Cryptosporella* Sacc., *Ditopella* De Not., *Gnomonia* Ces. & De Not., *Ophiognomonia* (Sacc.) Sacc.,

and *Plagiostoma* Fuckel (synonym *Cryptodiaporthe* Petr.) (Castlebury et al. 2002, Sogonov et al. 2008). Species in the Diaporthales have been reported as frequently present or dominant endophytes in broad-leaf trees, for example Aceraceae, Betulaceae, Fagaceae, Salicaceae and Tiliaceae in temperate forests (see Sieber 2007, Stone et al. 2004). Sieber (2007) proposed that endophyte communities associated with angiosperms are dominated by species of Diaporthales and that this association might date to near the time of the origin of angiosperms. With regard to host associations, species of genera in Gnomoniaceae seem to have narrow host ranges, sometimes limited to a single host species (Barr 1978, Mejía et al. 2008, Monod 1983, Sogonov et al. 2008).

Species of *Cryptosporella* have been reported as the dominant endophyte in branches and twigs of alders and birches (Betulaceae). For example *Cryptosporella suffusa* (Fr.) L.C. Mejía & Castlb. or its anamorph *Disculina vulgaris* (Fr.) Sutton have been reported as the most frequently isolated endophyte species in the bark of *Alnus glutinosa* in Europe and *A. rubra* in North America (Fisher and Petrini 1990, Sieber et al. 1991). Similarly *C. betulae* (Tul. & C. Tul) L.C. Mejía & Castlb. is the most frequently isolated endophyte in branches of *Betula pendula* and *B. pubescens* in Europe (Barengo et al. 2000, Kowalski and Kehr 1992).

Sixty species have been described as *Cryptosporella*. However most of these have been excluded from the genus, transferred principally to *Wuestneia* Auersw. ex Fuckel, now placed outside the Gnomoniaceae (Gryzenhout et al. 2008), but also to other genera, such as *Botryosphaeria*, *Diaporthe*, *Kapooria*, *Keinstirschia*, *Kensinjia*, *Mebarria*, and *Wehmeyera* (see Reid and Booth 1989). Castlebury et al. (2002) determined that genus *Cryptosporella* belongs in the Gnomoniaceae (Diaporthales). This contrasted with classifications that placed *Cryptosporella* or its synonyms in Cryptosporellaceae (von Arx and Müller 1954), Diaporthaceae (Höhnelt 1917) or Melanconidaceae (Barr 1978).

Mejía et al. (2008) recircumscribed *Cryptosporella* (synonym *Ophiovalsa* Petr., anamorph *Disculina* Höhn.), accepting nine species in the genus. Although the type species, *C. hypodermia*, occurs on *Ulmus* spp., most species of *Cryptosporella* are associated with hosts in Betulaceae. Since then a number of new species have been encountered. In this paper

eight new species of *Cryptosporella* are distinguished based on phylogenetic analyses of three loci and described based on morphological characters and host associations. A key to the 19 species accepted in *Cryptosporella* is presented.

#### MATERIALS AND METHODS

*Collection of specimens, culture preparation and morphological observations.*—Sampling for specimens of *Cryptosporella* was focused on plants in Betulaceae, Tiliaceae and Ulmaceae because previously reported hosts belong to these families. Additionally plant species in Aceraceae, Fagaceae, Hippocastanaceae and Salicaceae that co-occur with these hosts were investigated for the presence of *Cryptosporella* and other bark-inhabiting Gnomoniaceae. Specimens consisted of dead, often still attached twigs and branches with perithecia of *Cryptosporella*. They were collected in Argentina (Tucumán), France (Deux-Sèvres), Germany (Frankfurt), Panama (Chiriquí) and the United States (Maryland, New Hampshire, New York, Oregon, Washington) in 2007 and 2008. Specimens were placed in paper bags left open overnight at room temperature to reduce moisture. For long term storage paper bags containing specimens were placed in tightly sealed plastic bags and stored in the dark at 8–10 C, remaining viable for up to 6 mo. Methods for isolation of cultures, morphological observations and digital imaging are described in Mejía et al. (2008). Specimens were deposited at the U.S. National Fungus Collections (BPI). Fungal cultures were deposited at the Centraalbureau voor Schimmelcultures (CBS, the Netherlands).

*DNA extraction and sequencing.*—DNA was extracted as specified in Mejía et al. (2008). Three genes,  $\beta$ -tubulin, ITS and *tef1- $\alpha$* , were sequenced. Conditions and primers used for amplification of the ITS and *tef1- $\alpha$*  genes were as described by Sogonov et al. (2008). When necessary the *tef1- $\alpha$*  gene was amplified as two overlapping fragments with the primer combinations EF1-728F/EF1-1199R and EF1-983F/EF1-1567R and sequenced with the PCR primers (Carbone and Kohn 1999, Castlebury unpubl data for primer 1199R 5' GGG AAG TAC CMG TGA TCA TGT 3', Rehner 2001). The  $\beta$ -tubulin gene fragment was amplified with primers T1 and T22 as described by O'Donnell and Cigelnik (1997) with primers T1, T2, T12 and T22 for sequencing. DNA sequencing methods were as described by Mejía et al. (2008).

*Phylogenetic analyses.*—Editing and alignment of sequences were described in Mejía et al. (2008). Individual alignments of the genes were concatenated into a single alignment composed of ITS (560 bp),  $\beta$ -tubulin (1645 bp) and *tef1- $\alpha$*  (1169 bp) for 50 isolates (TABLE I). The taxa included in this alignment represent 17 of the 19 species of *Cryptosporella* with *Ditopella ditopa* and *Plagiostoma petiophilum* as outgroup taxa. Outgroup taxa were selected based on the close relationships of the genera *Ditopella* and *Plagiostoma* to *Cryptosporella* (Sogonov et al. 2008). The concatenated alignment was partitioned by gene and conflict among

genes was analyzed with a reciprocal bootstrap test (Reeb et al. 2004) as described in Sogonov et al. (2008). Maximum parsimony (MP) analysis and MP bootstrap analysis were performed as described in Mejía et al. (2008). Bayesian analysis was performed as specified in Sogonov et al. (2008) with MrModeltest 2 (Nylander 2004) to determine the best model for each gene region. A consensus phylogram was constructed from 7800 trees saved after the burn-in period of 50 000 generations with the resulting Bayesian posterior probabilities (PP) noted for individual nodes. A maximum likelihood (ML) analysis was performed as detailed in Sogonov et al. (2008). The alignment was deposited in TreeBASE as10598.

In this work we used genealogical concordance phylogenetic species recognition (Taylor et al. 2000) and morphological characters for delimiting species boundaries. Additionally we used host identities and geographic distribution for characterizing the species.

#### RESULTS

Specimens of *Cryptosporella* were collected from previously reported hosts of *Cryptosporella* as well as from species of Betulaceae with no reported association with *Cryptosporella*. Examination of hosts other than Betulaceae, Tiliaceae and Ulmaceae did not yield any new specimens of *Cryptosporella*.

The likelihood parameters obtained for each gene for the reciprocal bootstrap analyses were:  $\beta$ -tubulin: Base = (0.1867 0.3358 0.2535) Nst = 2 TRatio = 1.7644 Rates = gamma Shape = 0.4684 Pinvar = 0; ITS: Nst = 6 Rmat = (1.0000 3.2902 1.0000 1.0000 7.9560) Rates = gamma Shape = 0.8158 Pinvar = 0.5986; *tef1- $\alpha$* : Base = (0.2103 0.3169 0.2435) Nst = 6 Rmat = (1.0000 1.9032 1.0000 1.0000 3.7089) Rates = gamma Shape = 0.3413 Pinvar = 0. Reciprocal bootstrap analyses indicated no conflict among the genes analyzed; no single gene resolved all the species as terminal monophyletic clades with bootstrap support > 70%. Although the ITS tree resolved most species of *Cryptosporella*, only four species were supported with bootstrap support > 70%. The  $\beta$ -tubulin and *tef1- $\alpha$*  trees resolved clades for most species analyzed with 12 species of *Cryptosporella* supported as monophyletic clades with bootstrap support > 70% in individual analyses (trees not presented). In general  $\beta$ -tubulin and *tef1- $\alpha$*  trees supported well resolved clades of closely related species, such as the subclade containing *C. pacifica*, *C. suffusa* and *C. multicontinentalis* and the subclade containing *C. betulae*, *C. tomentella*, *C. corylina* and *C. hypodermia* (FIG. 1). The gene tree topologies were similar for  $\beta$ -tubulin and *tef1- $\alpha$* ; both differed slightly from the ITS tree. The topological differences observed were not supported by bootstrapping analysis.

These models were estimated and applied to the gene partitions in the Bayesian analyses: HKY + G for  $\beta$ -tubulin, GTR + I + G for ITS, GTR + G for *tef1- $\alpha$* . The model TrN + G was estimated to be the best for the entire alignment and employed in the ML analysis. The likelihood parameters for this model were: Base = (0.2133 0.3105 0.2415) Nst = 6 Rmat = (1.0000 2.5629 1.0000 1.0000 4.0229) Rates = gamma Shape = 0.2924 Pinvar = 0. Maximum parsimony analysis of the combined data resulted in 1212 most parsimonious trees (length = 1117, CI = 0.830, RI = 0.902). The same topology resulted from Bayesian and ML analyses of the concatenated alignment. Maximum likelihood analysis of the concatenated alignment resulted in one tree  $-\ln L$  score of 9746.37704 that is presented here as the inferred phylogeny of *Cryptosporella* (FIG. 1).

The inferred phylogeny of *Cryptosporella* (FIG. 1) based on three genes supports the recognition of eight new species of *Cryptosporella*, which are described in TAXONOMY. No specimens or cultures of *C. rabenhorstii* and *C. tiliae* were available for DNA extractions, although the type specimen of *C. rabenhorstii* was examined morphologically.

Three major clades supported by Bayesian analysis and MP bootstrapping can be observed in the phylogeny (FIG. 1, marked with asterisks). One clade (100% MP, PP) contains seven species that occur exclusively on *Alnus* spp. with a subclade (100% MP, PP) of three species, *C. pacifica*, *C. suffusa* and *C. multicontinentalis*, characterized by having necks fused and forming a single ostiolar cavity at the center of the perithecial group. Each of the other four species of *Cryptosporella* included in this major clade is known to occur in one host species. These four species are split into two subclades. One (100% MP, PP) contains two species on hosts with distinct geographic distributions in North America: *C. alni-sinuatae* on *A. viridis* subsp. *sinuata* in the Pacific Northwest (USA) and *C. jaklitschii* on *A. serrulata* in eastern North America. The other (100% MP, PP) includes two species whose hosts co-occur in the Pacific Northwest (USA): *C. alni-rubrae* on *A. rubra* and *C. alni-tenuifolia* on *A. incana* subsp. *tenuifolia* (TABLE II).

A second major clade (77% MP, 56% PP) includes six species of which five (*C. wehmeyeriana*, *C. alnicola*, *C. confusa*, *C. femoralis* and *C. marylandica*) are found in eastern North America and one (*C. amistadensis*) in Central and South America. Except for *C. wehmeyeriana* on *Tilia* spp. all these species occur on hosts in Betulaceae (*Alnus*, *Betula* and *Corylus*). *Cryptosporella amistadensis* was found only on *Alnus acuminata* in the mountain cloud forests of Argentina and Panama. *Cryptosporella wehmeyeriana*, *C. alnicola*

and *C. confusa* are characterized by long cylindrical ascospores while *C. amistadensis*, *C. femoralis* and *C. marylandica* have femuroid ascospores.

A third major clade (100% MP, PP) includes four species, *C. betulae*, *C. tomentella*, *C. corylina* and *C. hypodermia*. *Cryptosporella betulae* and *C. tomentella* were considered to be the same species because of their morphological similarities and occurrence on species of *Betula* (Reid and Booth 1987, Mejía et al. 2008). The multigene phylogeny separates these two species. Observation of the type specimens of these species indicates that they have morphological differences and should be regarded as distinct species. Additionally *C. betulae* is restricted to Europe and *C. tomentella* to North America. Another species included in this major clade is *C. hypodermia*, type species of genus *Cryptosporella*, that grows on *Ulmus* spp. in Europe and North America. Immature ascospores of *C. betulae* and *C. tomentella* resemble those of *C. hypodermia*; however, mature ascospores of *C. betulae* and *C. tomentella* are cylindrical with rounded ends while those of *C. hypodermia* are ellipsoid with acute ends. *Cryptosporella corylina*, the sister species of *C. betulae* and *C. tomentella*, has long cylindrical ascospores and is associated with the host genus *Corylus*.

The geographic distribution of *Cryptosporella* is here extended to Central and South America and regionally to more localities in North America and Europe. Although *Cryptosporella* has been reported from Japan, specimens were not available for inclusion in the multigene phylogeny. Sequences deposited in GenBank of the ITS rDNA region for isolates from a survey of endophytic fungi in China were compared with sequences from this research and confirmed to be *Cryptosporella* as a potential new species on *Betula platyphila* (tree not shown). Isolates or specimens of this species are not available.

#### DISCUSSION

In this study the species diversity of genus *Cryptosporella* is expanded from Mejía et al. (2008), in which the nomenclature of the generic names *Cryptosporella* and *Ophiovalsa* was discussed and the type species, *C. hypodermia* and *C. suffusa* (as *Ophiovalsa suffusa*), were described and illustrated. At that time nine species were included in the key to species of *Cryptosporella*. Since then a number of additional species have been encountered. Nineteen species of *Cryptosporella* are now accepted in the genus, 16 of which occur on Betulaceae. Two previously described species, *Cryptosporella rabenhorstii* and *C. tiliae* (Tul. & C. Tul.) L.C. Mejía & Castl., were not available for DNA extraction. The type specimen of *C. rabenhorstii*

TABLE I. Source of isolates and specimens used in phylogenetic analyses. DNA sequences generated in this research and types or epitypes are labeled in boldface

Taxon	Specimen	Culture	Country	Host	Collector	$\beta$ -tubulin	ITS	tefl- $\alpha$
<i>Cryptosporella alnicola</i>	BPI879227	CBS121074	USA	<i>Corylus cornuta</i>	L. Vasilyeva	EU219138	EU199204	EU199160
<i>Cryptosporella alni-rubrae</i>	<b>BPI879199</b>	LCM499.01	USA	<i>Abnus rubra</i>	L.C. Mejía	<b>GU826014</b>	<b>GU826096</b>	<b>GU826055</b>
<i>Cryptosporella alni-rubrae</i>	BPI879200	LCM489.01	USA	<i>Abnus rubra</i>	L.C. Mejía	<b>GU826012</b>	<b>GU826094</b>	<b>GU826053</b>
<i>Cryptosporella alni-rubrae</i>	BPI879202	LCM498.01	USA	<i>Abnus rubra</i>	L.C. Mejía	<b>GU826009</b>	<b>GU826091</b>	<b>GU826050</b>
<i>Cryptosporella alni-rubrae</i>	BPI879203	LCM411	USA	<i>Abnus rubra</i>	L.C. Mejía	<b>GU826008</b>	<b>GU826090</b>	<b>GU826049</b>
<i>Cryptosporella alni-rubrae</i>	BPI879203	LCM411.02	USA	<i>Abnus rubra</i>	L.C. Mejía	<b>GU826011</b>	<b>GU826093</b>	<b>GU826052</b>
<i>Cryptosporella alni-rubrae</i>	BPI879204	CBS126120 (= LCM466.01)	USA	<i>Abnus rubra</i>	L.C. Mejía	<b>GU826010</b>	<b>GU826092</b>	<b>GU826051</b>
<i>Cryptosporella alni-rubrae</i>	BPI879206	LCM408b.01	USA	<i>Abnus rubra</i>	L.C. Mejía	<b>GU826013</b>	<b>GU826095</b>	<b>GU826054</b>
<i>Cryptosporella alni-sinuatae</i>	<b>BPI879210</b>	CBS125662 (= LCM412)	USA	<i>Abnus viridis</i>	L.C. Mejía	<b>GU826005</b>	<b>GU826087</b>	<b>GU826046</b>
<i>Cryptosporella alni-sinuatae</i>	BPI878446	AR4200	USA	subsp. <i>sinuata</i> <i>Abnus viridis</i>	A.Y. Rossman	<b>GU825989</b>	<b>GU826086</b>	<b>GU826045</b>
<i>Cryptosporella alni-tenuifoliae</i>	<b>BPI879211</b>	CBS125663 (= CM480.01)	USA	subsp. <i>sinuata</i> <i>Abnus incana</i>	L.C. Mejía	<b>GU826015</b>	<b>GU826097</b>	<b>GU826056</b>
<i>Cryptosporella amistadensis</i>	<b>BPI879214</b>	CBS125664 (= LCM27.03)	Panama	subsp. <i>tenuifolia</i> <i>Abnus acuminata</i>	L.C. Mejía	<b>GU826031</b>	<b>GU826108</b>	<b>GU826072</b>
<i>Cryptosporella amistadensis</i>	BPI879219	CBS126128 (= LCM618.01)	Argentina	<i>Abnus acuminata</i>	L.C. Mejía	<b>GU826032</b>	<b>GU826109</b>	<b>GU826073</b>
<i>Cryptosporella betulae</i>	BPI879251	LCM477.01	Russia	<i>Betula pendula</i>	M. V. Sogonov	<b>GU826018</b>	<b>GU826098</b>	<b>GU826059</b>
<i>Cryptosporella betulae</i>	BPI879251	CBS121078	Scotland	<i>Betula pendula</i>	S. Green	<b>GU826016</b>	EU199213	<b>GU826057</b>
<i>Cryptosporella betulae</i>	BPI748448	CBS121079	Scotland	<i>Betula pendula</i>	S. Green	<b>GU826017</b>	EU199216	<b>GU826058</b>
<i>Cryptosporella betulae</i>	BPI879222	CBS109703	Austria	<i>Betula pendula</i>	W. Jaklitsch	EU221884	EU199180	EU219105
<i>Cryptosporella corylina</i>	<b>BPI879236</b>	LCM391.04	France	<i>Corylus avellana</i>	L.C. Mejía	<b>GU826022</b>	<b>GU826100</b>	<b>GU826063</b>
<i>Cryptosporella femoralis</i>	BPI879223	CBS121076	USA	<i>Abnus incana</i>	L. Vasilyeva	EU221951	EU199220	EU219139
<i>Cryptosporella femoralis</i>	BPI879224	LCM196.04	USA	subsp. <i>rugosa</i> <i>Abnus incana</i>	L.C. Mejía	<b>GU826025</b>	<b>GU826102</b>	<b>GU826067</b>
<i>Cryptosporella femoralis</i>	BPI879225	LCM103.01	USA	subsp. <i>rugosa</i> <i>Abnus incana</i>	L.C. Mejía	<b>GU826026</b>	<b>GU826103</b>	—
<i>Cryptosporella hypodermia</i>	<b>BPI 748432</b>	LCM92.01	USA	subsp. <i>rugosa</i> <i>Ulmus americana</i>	L.C. Mejía	—	<b>GU826101</b>	<b>GU826065</b>
<i>Cryptosporella hypodermia</i>	BPI748433	CBS122593	Austria	<i>Ulmus minor</i>	W. Jaklitsch	<b>GU826024</b>	EU199181	<b>GU826066</b>
<i>Cryptosporella hypodermia</i>	BPI879231	CBS 109753	Austria	<i>Ulmus minor</i>	W. Jaklitsch	<b>GU826023</b>	EU199224	<b>GU826064</b>
<i>Cryptosporella jakitschii</i>	<b>BPI879231</b>	CBS 171.69	Netherlands	<i>Ulmus</i> sp.	H. van der Aa	EU219231	EU199225	EU221881
<i>Cryptosporella jakitschii</i>	<b>BPI879231</b>	LCM112.01	USA	<i>Abnus serrulata</i>	L.C. Mejía	<b>GU826007</b>	<b>GU826089</b>	<b>GU826048</b>
<i>Cryptosporella jakitschii</i>	<b>BPI879231</b>	CBS125665 (= LCM112.04)	USA	<i>Abnus serrulata</i>	L.C. Mejía	<b>GU826006</b>	<b>GU826088</b>	<b>GU826047</b>
<i>Cryptosporella marylandica</i>	<b>BPI879232</b>	CBS125666 (= LCM386.04)	USA	<i>Abnus maritima</i>	L.C. Mejía	<b>GU826028</b>	<b>GU826105</b>	<b>GU826069</b>
<i>Cryptosporella marylandica</i>	BPI879232	LCM386.05	USA	<i>Abnus maritima</i>	L.C. Mejía	<b>GU826029</b>	<b>GU826106</b>	<b>GU826070</b>



TABLE I. Continued

Taxon	Specimen	Culture	Country	Host	Collector	$\beta$ -tubulin	ITS	tef1- $\alpha$
<i>Cryptosporella marylandica</i>	BPI879250	LCM581.01	USA	<i>Abnus maritima</i>	L.C. Mejía	GU826030	GU826107	GU826071
<i>Cryptosporella multicontinentalis</i>	<b>BPI879226</b>	CBS125667 (= LCM401.01)	France	<i>Abnus glutinosa</i>	L.C. Mejía	GU826001	GU826083	GU826042
<i>Cryptosporella multicontinentalis</i>	BPI879227	LCM406.01	France	<i>Abnus glutinosa</i>	L.C. Mejía	GU826003	GU826084	GU826043
<i>Cryptosporella multicontinentalis</i>	BPI879228	LCM427.01	Germany	<i>Abnus glutinosa</i>	L.C. Mejía	GU826004	GU826085	GU826044
<i>Cryptosporella multicontinentalis</i>	BPI879229	CBS126119 = LCM93.01	USA	<i>Abnus incana</i> subsp. <i>rugosa</i>	L.C. Mejía	GU825999	GU826081	GU826040
<i>Cryptosporella multicontinentalis</i>	BPI879230	LCM93b.02	USA	<i>Abnus incana</i> subsp. <i>rugosa</i>	L.C. Mejía	GU826000	GU826082	GU826041
<i>Cryptosporella multicontinentalis</i>	BPI879258	CBS126118 = LCM394.01	France	<i>Abnus hirsuta</i>	L.C. Mejía	GU825998	GU826080	—
<i>Cryptosporella multicontinentalis</i>	—	CBS155.47	Netherlands	<i>Abnus glutinosa</i>	S. Truter	GU866002	EU199206	—
<i>Cryptosporella multicontinentalis</i>	<b>BPI879239</b>	CBS126117 (= LCM461.01)	USA	<i>Abnus incana</i> subsp. <i>tenuiifolia</i>	L.C. Mejía	GU825994	GU826076	GU826036
<i>Cryptosporella pacifica</i>	BPI879240	LCM453.01	USA	<i>Abnus incana</i> subsp. <i>tenuiifolia</i>	L.C. Mejía	GU825995	GU826077	GU826037
<i>Cryptosporella pacifica</i>	BPI879241	LCM420.01	USA	<i>Abnus incana</i> subsp. <i>tenuiifolia</i>	L.C. Mejía	GU825993	GU826074	—
<i>Cryptosporella pacifica</i>	—	CBS122311	USA	<i>Abnus viridis</i>	S. Lattomus & LCM	GU825991	EU199208	GU826034
<i>Cryptosporella pacifica</i>	—	CBS122312	USA	<i>Abnus viridis</i> subsp. <i>sinuata</i>	S. Lattomus & LCM	GU825992	EU199209	GU826035
<i>Cryptosporella suffusa</i>	BPI871231	CBS121077	Austria	<i>Abnus incana</i> subsp. <i>sinuata</i>	W. Jaklitsch	EU219127	EU199184	EU221891
<i>Cryptosporella suffusa</i>	<b>BPI748449</b>	CBS109750	Austria	<i>Abnus incana</i>	W. Jaklitsch	EU219106	EU199207	EU221945
<i>Cryptosporella suffusa</i>	BPI879242	LCM576.01	Germany	<i>Abnus</i> sp.	L.C. Mejía	GU825997	GU826079	GU826039
<i>Cryptosporella suffusa</i>	BPI879242	LCM576.03	Germany	<i>Abnus</i> sp.	L.C. Mejía	GU825996	GU826078	GU826038
<i>Cryptosporella tomentella</i>	BPI879243	CBS126440 (= LCM184b.01)	USA	<i>Betula</i> <i>allegghanienensis</i>	L.C. Mejía	GU826021	GU826099	GU826062
<i>Cryptosporella tomentella</i>	BPI843595	CBS121075	USA	<i>Betula</i> sp.	L. Vasilyeva	—	EU199214	—
<i>Cryptosporella tomentella</i>	BPI872328	CBS121073	USA	<i>Betula</i> sp.	L. Vasilyeva	GU826019	EU199217	GU826060
<i>Cryptosporella tomentella</i>	BPI843497	CBS121080	USA	<i>Betula</i> sp.	L. Vasilyeva	GU826020	—	GU826061
<i>Cryptosporella wehmeyeriana</i>	BPI879244	LCM85.02	USA	<i>Tilia americana</i>	L.C. Mejía	GU826027	GU826104	GU826068
<i>Cryptosporella wehmeyeriana</i>	BPI843485	CBS121085	USA	<i>Tilia</i> sp.	L. Vasilyeva	EU219110	EU199205	EU221959
<i>Ditopella ditopa</i>	BPI879247	CBS126115 (= LCM94.02)	USA	<i>Abnus incana</i> subsp. <i>rugosa</i>	L.C. Mejía	GU825990	GU826075	GU826033
<i>Plagiostoma petiophilum</i>	BPI878970	LCM181.01	USA	<i>Acer spicatum</i>	L.C. Mejía	GU367023	GU367078	GU367112

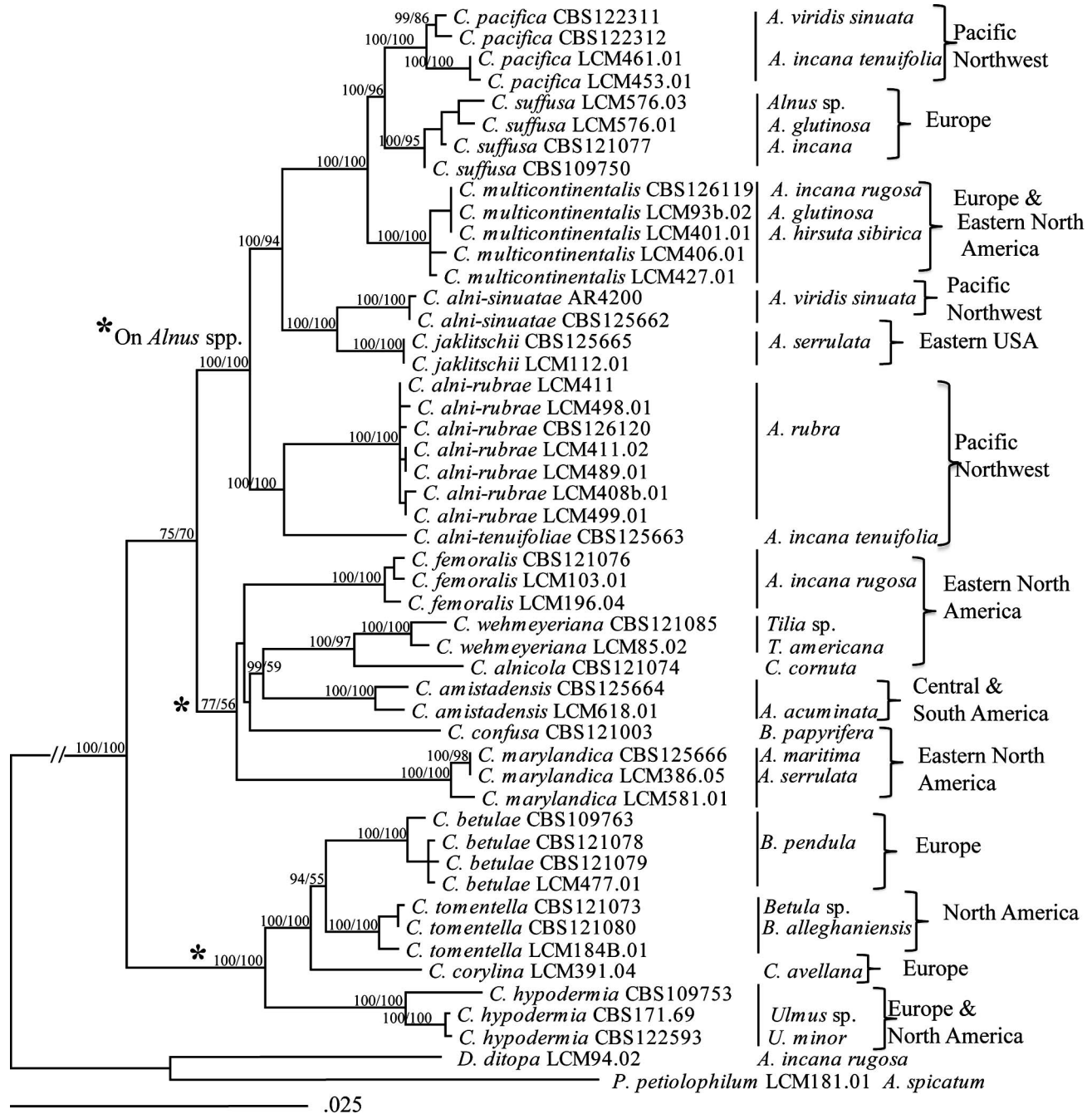


FIG. 1. ML phylogenetic analysis (ML score =  $-\ln L$  9746.38) of sequences for the ITS,  $\beta$ -tubulin and *tef1- $\alpha$*  multigene analysis of species of *Cryptosporella* with *Ditopella ditopa* and *Plagiostoma petiophilum* as outgroup taxa. Bayesian posterior probabilities and maximum parsimony bootstrap support appear on the left and right side of a dash respectively and next to branches. Asterisks denote three major clades of *Cryptosporella*.

was examined and accepted as a species of *Cryptosporella*. It was determined that reports of *C. tiliae* from North America are actually *C. wehmeyeriana* (Reid and Booth 1987). No specimens of *C. tiliae* were available for examination in spite of an attempt to collect *C. tiliae* in the type locality (Meudon, France). *Cryptosporella tiliae* is accepted here on the basis of

the morphology as described by the original authors (Tulasne and Tulasne 1863).

In this work the rationale for prospecting for new species of *Cryptosporella* was based on the apparent long evolutionary association between species of *Cryptosporella* and their hosts and the assumption that *Cryptosporella* has speciated primarily in *Betula*

TABLE II. Summary of species of *Cryptosporella* and their host associations

Species of <i>Cryptosporella</i>	Host	Distribution
<i>C. alnicola</i>	<i>Alnus</i> spp. and <i>Corylus</i> sp.	Eastern North America
<i>C. alni-rubrae</i>	<i>A. rubra</i>	Pacific Northwest (OR, WA)
<i>C. alni-sinuatae</i>	<i>A. viridis</i> subsp. <i>sinuata</i>	Pacific Northwest (WA)
<i>C. alni-tenuifoliae</i>	<i>A. incana</i> subsp. <i>tenuifolia</i>	Pacific Northwest (OR)
<i>C. amistadensis</i>	<i>A. acuminata</i>	Central and South America
<i>C. betulae</i>	<i>Betula</i> spp.	Europe
<i>C. confusa</i>	<i>B. alba</i> and <i>B. papyrifera</i>	Europe (morphology) and Eastern North America (DNA)
<i>C. corylina</i>	<i>Corylus avellana</i>	Europe
<i>C. femoralis</i>	<i>A. incana</i> subsp. <i>rugosa</i>	Eastern North America
<i>C. hypodermia</i>	<i>Ulmus</i> spp. <sup>1</sup>	Europe and North America
<i>C. jaklitschii</i>	<i>A. serrulata</i>	Eastern North America (NY)
<i>C. marylandica</i>	<i>A. maritima</i> and <i>A. serrulata</i>	Eastern USA (MA)
<i>C. multicontinentalis</i>	<i>A. incana</i> subsp. <i>rugosa</i> , <i>A. glutinosa</i> , <i>A. hirsuta</i>	Europe and North America, Japan?
<i>C. pacifica</i>	<i>A. incana</i> subsp. <i>tenuifolia</i> , <i>A. viridis</i> subsp. <i>sinuata</i>	Pacific Northwest (CA, OR, WA)
<i>C. rabenhorstii</i>	<i>Betula</i> sp.	Europe
<i>C. suffusa</i>	<i>A. incana</i> and <i>Alnus</i> spp.	Europe
<i>C. tiliae</i>	<i>Tilia cordata</i>	Europe
<i>C. tomentella</i>	<i>B. papyrifera</i> , <i>B. populifolia</i> , <i>Betula</i> sp.	Eastern North America
<i>C. wehmeyeriana</i>	<i>T. americana</i>	Eastern North America
<i>Cryptosporella</i> sp. (NCBI deposited DNA sequences FJ025237, FJ025250, FJ025265, FJ025249)	<i>B. platyphylla</i>	Beijing, China

<sup>1</sup> *Cryptosporella hypodermia* has been reported in hosts other than *Ulmus*. In three cases the original report was under other names that later were synonymized with *C. hypodermia*, specifically *Cryptospora compta-macrospora* on *Fagus sylvatica*, *C. veneta* on *Populus tremula* and *Sphaeria limminghii* on *Platanus orientalis*. All specimens of *Cryptosporella hypodermia* sequenced in this study were collected on *Ulmus*.

ceae. This approach proved valuable in discovering the eight species of *Cryptosporella* newly described in this work. Three were found on betulaceous hosts not previously reported to harbor *Cryptosporella* but congeneric with known hosts, *C. amistadensis* on *Alnus acuminata*, *C. jaklitschii* on *A. serrulata*, and *C. marylandica* on *A. maritima*. The five remaining species of *Cryptosporella* described in this study occur on hosts already known to harbor *Cryptosporella*; however the host range attributed to previously described species appears to be too broad. For example, in the past all collections of *Cryptosporella* with a fused perithecial neck forming a single ostiolar cavity were identified as *C. suffusa*, a species considered to colonize more than five species of *Alnus* (Mejía et al. 2008, Reid and Booth 1987). Specimens previously referred to as *C. suffusa* are determined here to comprise three species, each with a characteristic host association and geographic distribution. These three species are *C. pacifica* restricted to *A. viridis* subsp. *sinuata* and *A. incana* subsp. *tenuifolia* in the Pacific Northwest of North America, *C. multicontinentalis* associated with three species of *Alnus* in Europe and North America, and

*C. suffusa* on *Alnus glutinosa* and *A. incana* restricted to Europe. Another example is *Cryptosporella femoralis*, a species reported from Asia and North America with a host range on several species of *Alnus*. Three additional species, *C. alni-rubrae*, *C. amistadensis* and *C. marylandica*, are recognized that have ascospores with moderately to prominently swollen ends similar to those of *C. femoralis* and associated with *Alnus*. Nine species of *Cryptosporella* are known from only a single host species or subspecies and the remaining fungi are associated with a few congeneric hosts (TABLE II) with one exception, *C. alnicola*.

Species of *Cryptosporella* occur in America, Asia and Europe (Kobayashi et al. 1970, Mejía et al. 2008). The predominance and broad geographic distribution of *Cryptosporella* on Betulaceae and their often exclusive occurrence on one host species support the existence of an evolutionary association between *Cryptosporella* and the Betulaceae. The finding of undescribed species of *Cryptosporella* on each of three species of *Alnus* that co-occur in the Pacific Northwest suggests that diverse hosts harbor different species of *Cryptosporella*. The same is also true for species of *Cryptosporella* on co-occurring host species in eastern

North America. Geographic isolation also might play a role because species of *Cryptosporella* in western North America are not found in eastern North America. Species known from both Europe and North America are restricted to eastern North America.

The evolutionary timing of the association of *Cryptosporella* with the Betulaceae was not determined, but fossils of *Gnomonia*-like fungi co-occurring with betulaceous hosts date back to the early Miocene (Sherwood-Pike and Gray 1988). Betulaceae, a family of Laurasian origin, is well documented in the fossil record and appears to have originated during the Cretaceous and early Tertiary in China (Chen et al. 1999). Betulaceous species might have migrated between Eurasia and North America across the Bering and North Atlantic land bridges and later to South America (Chen et al. 1999). By the Oligocene 36.6–23.7 million years ago (mya) all extant genera of Betulaceae had differentiated (Chen et al. 2009). The only extant species of Betulaceae in South America is *Alnus acuminata*, which ranges from Mexico to Argentina. Based on fossil evidence *Alnus acuminata* appears to have moved north to south, passing through Panama arriving in Colombia 1 mya and later to its southernmost habitat in Argentina (Bush et al. 2007, Graham 1999). One species of *Cryptosporella*, *C. amistadensis*, was found associated with *A. acuminata* in Argentina and Panama. Populations of *A. acuminata* in Argentina and Panama are separated by extensive grasslands (Bush et al. 2007) and tropical rain forest. A connection between populations of *A. acuminata* from Panama and Argentina is unlikely; thus *C. amistadensis* might have been moved to southern South America with its host during the Pleistocene.

A few species of *Cryptosporella* have colonized hosts other than Betulaceae, that is *C. hypodermia* on *Ulmus* (Ulmaceae) and *C. tiliae* on *Tilia* (Tiliaceae). This is not surprising considering that species of *Cryptosporella* have stages in their lives where millions of ascospores and conidia are released. These spores have a high probability of landing on other hosts and occasionally infected those hosts, leading to potential host jumps or speciation. Nonetheless this would seem to be a rare occurrence because species of *Cryptosporella* seem more likely to infect closely related hosts based on results presented in this study. Further sampling for *Cryptosporella* on betulaceous hosts as well as other woody plant hosts will be necessary to further elucidate the evolutionary history of species of *Cryptosporella* and the role that host speciation or host jumps might have played.

#### TAXONOMY

Below are descriptions of eight new species as well as two new combinations and comments on two species

in *Cryptosporella* followed by a key to the 19 accepted species. For descriptions of the type species, *Cryptosporella hypodermia* and *C. suffusa*, see Mejía et al. (2008). Additional species are described in Reid and Booth (1987) as *Winterella*.

#### *Cryptosporellaalni-rubrae* L.C. Mejía, sp. nov.

FIG. 2A–J

Mycobank MB518091

*Perithecia* nigra, subglobosa, (374–)499–584(–651)  $\mu\text{m}$  alta  $\times$  (382–)466–703(–792)  $\mu\text{m}$  diametro, collis (165–)387–595(–774)  $\mu\text{m}$  longis. Asci 79.5–87.5(–92.5)  $\times$  (17.5–)21.5–27.5(–33.5)  $\mu\text{m}$ . Ascospores non-septatae, hyalinae, ossiformes, cum modice expansis vel valde inflatis extremitatibus, (39.5–)44.0–50.5(–67.0)  $\times$  (3.5–)4.0–4.5(–5.5). In *Alno rubra*, in boreo-occidentali USA habitat.

*Etymology.* The name refers to *Alnus rubra*, the only known host of this species.

*Holotypus.* UNITED STATES. WASHINGTON: Jefferson County, U.S. 101 near Queets, in *Alnus rubra*, 26 May 2008, L.C. Mejía LCM499 (BPI 879199).

Evident as scattered elevations in bark up to 0.7 mm high  $\times$  2 mm diam at base, each elevation of multiple, rounded bumps that result from perithecia pushing up host periderm. Perithecia arranged circularly in groups of up to eight, with necks parallel to host surface and oriented toward a central point, necks closely appressed but not fused, bent, projecting perpendicularly, penetrating through host periderm at center of group; often with black halo surrounding mass of protruding perithecial necks. Mature perithecia black, subglobose, (374–)499–584(–651)  $\mu\text{m}$  high  $\times$  (382–)466–703(–792)  $\mu\text{m}$  diam (mean = 528  $\times$  585  $\mu\text{m}$ , SD 96, 163, n = 6), perithecial necks (165–)387–595(–774)  $\mu\text{m}$  long (mean = 487, SD 211, n = 6), (124–)140–158(–188)  $\mu\text{m}$  diam at base (mean = 153, SD 22, n = 6), (147–)168–188(–188)  $\mu\text{m}$  diam at apex (mean = 174, SD 17, n = 5). Asci elliptical with rounded apex and acute base, with no apical ring or bodies, 79.5–87.5(–92.5)  $\times$  (17.5–)21.5–27.5(–33.5)  $\mu\text{m}$  (mean = 84.5  $\times$  25.0, SD 5.6, 5.9, n = 5), with eight ascospores parallel or interwoven. Ascospores non-septate, hyaline, femuroid, with moderately expanded to greatly swollen ends, narrow at central point, (39.5–)44.0–50.5(–67.0)  $\times$  (3.5–)4.0–4.5(–5.5)  $\mu\text{m}$  (mean = 48.5  $\times$  4.5, SD 6.6, 0.5, n = 38) l:w (8–)10–13(–16) (mean = 11.1, SD 1.9), with multiple, globular guttules varying in size.

*Host and habitat.* In the bark of dead and still attached branches of *Alnus rubra* Bong. (Betulaceae).

*Distribution.* USA: Oregon, Washington.

*Holotype.* UNITED STATES. WASHINGTON: Jefferson County, U.S. 101 near Queets, in *Alnus rubra*, 26 May 2008, L.C. Mejía LCM499 (BPI 879199, derived type culture LCM499.01).



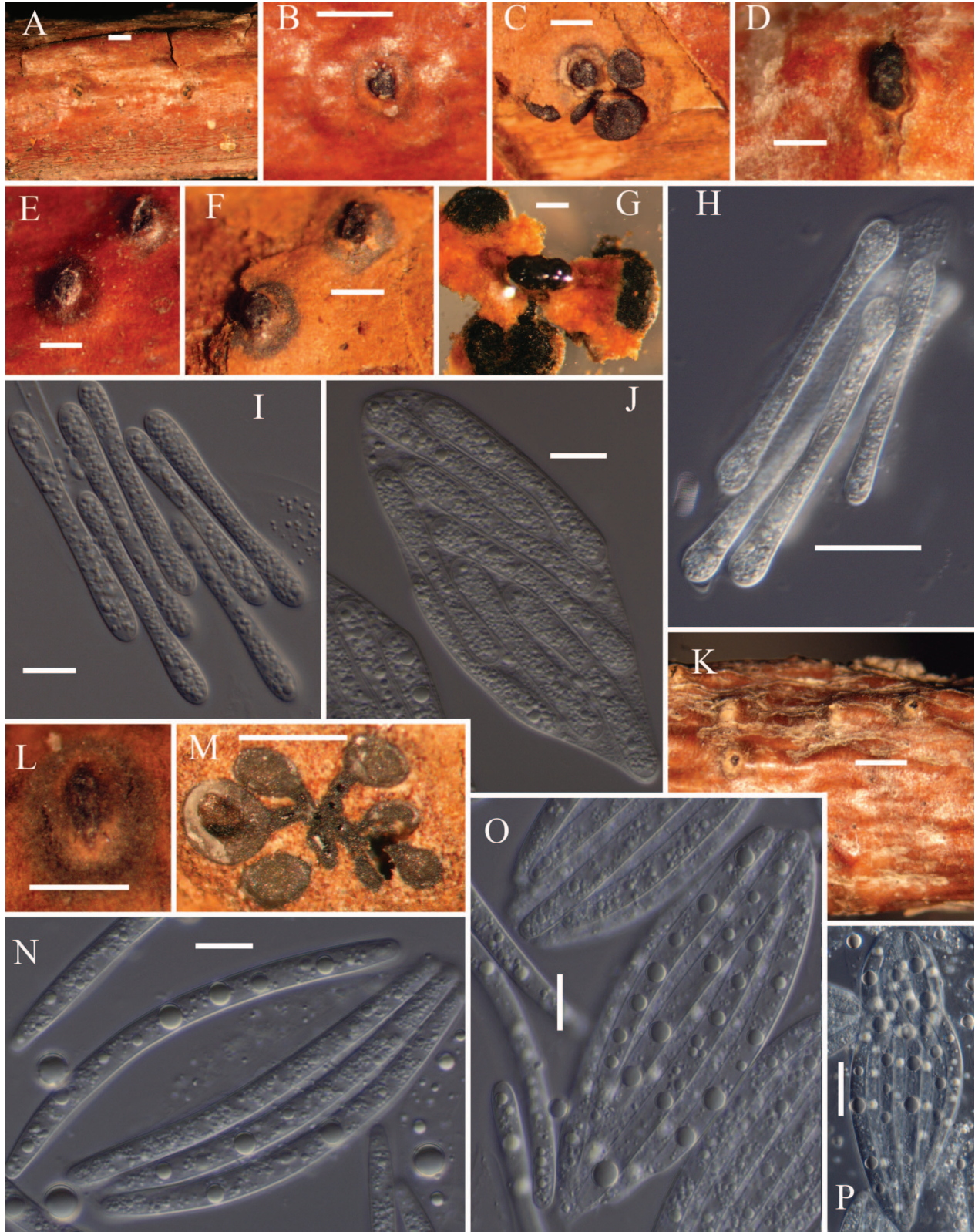


FIG. 2. A–J. *Cryptosporella abni-rubrae*. A–F. Fruiting bodies on natural substrate. G. Fruiting bodies extracted from natural substrate. H–J. Femuroid ascospores (A. BPI 879203, B–J. BPI 879199 holotype). K–P. *Cryptosporella abni-sinuatae*. K. Fruiting bodies on natural substrate. L–M. Fruiting bodies on natural substrate with apical area removed to show arrangement. N–P. Ascospores (BPI 879210 holotype). Bars: A–B, K–L = 1 mm, C–F, M = 500 μm, G = 200 μm, H, N–O = 20 μm, I–J, P = 10 μm.



*Other specimens observed.* UNITED STATES. OREGON: Lane County, Oregon 58, approx. one mile west of Salt Creek Tunnel, on *Alnus rubra*, 22 May 2008, *L.C. Mejía LCM466* (BPI 879204, derived culture CBS 126120 = LCM466.01); Lane County, Salmon Creek campground, close to Lowell, on *Alnus rubra*, 22 May 2008, *L.C. Mejía LCM407* (BPI 879205, derived culture LCM407, ITS sequence HM017895); same, *L.C. Mejía LCM408b* (BPI 879206, derived culture LCM408b.01); Alder Dune Campground, close to Florence, from *Alnus rubra*, 24 May 2008, *L.C. Mejía LCM487* (BPI 879207, derived culture LCM487.01, ITS sequence HM017897); Lincoln County, Rocky Creek scenic view point, from *Alnus rubra*, 24 May 2008, *L.C. Mejía LCM486* (BPI 879208, derived culture LCM486.01, ITS sequence HM017896); Cape Foulweather, from *Alnus rubra*, 24 May 2008, *L.C. Mejía LCM496* (BPI 879209, derived culture LCM496.01, ITS sequence HM017899); WASHINGTON: Grays Harbor County, Humptulips, in *Alnus rubra*, 25 May 2008, *L.C. Mejía LCM489* (BPI 879200, derived culture LCM489.01); same, *L.C. Mejía LCM488* (BPI 879201, derived culture LCM488.01, ITS sequence HM017898); Jefferson County, Intersection of U.S. 101 and Hoh River, close to Cottonwood, from *Alnus rubra*, 26 May 2008, *L.C. Mejía LCM498* (BPI 879202, derived culture LCM498.01); Clallam County, Olympic National Park, Heart O'Hill Campground, from *Alnus rubra*, 29 May 2008, *L.C. Mejía LCM411* (BPI 879203, derived cultures LCM411 and 411.02).

*Notes.* Among species of *Cryptosporella* on *Alnus*, *C. alni-rubrae* is similar to *C. femoralis* in having femuroid ascospores with distinctly swollen ends. The ascospores of *C. femoralis* are septate while those of *C. alni-rubrae* lack a septum.

***Cryptosporella alni-sinuatae* L.C. Mejía, sp. nov.**

FIG. 2K–P

Mycobank MB518092

Stroma cinereum perithecorum cingens. Perithecia nigra, globosa, (251–)339–389(–457)  $\mu\text{m}$  alta  $\times$  (253–)272–374(–403)  $\mu\text{m}$  lata, collis (224–)242–265(–347)  $\mu\text{m}$ . Asci (76.5–)80.0–93.5(–103.0)  $\times$  (23.0–)26.5–30.5(–31.5)  $\mu\text{m}$ . Ascospores non-septatae, hyalinae, cylindraceae sine expansis extremitatibus, (57.0–)66.5–70.5(–79.0)  $\times$  (4.5–)5.5–6.0(–6.5)  $\mu\text{m}$ . In *Alno viridi* subsp. *sinuata*, in boreali USA habitat.

*Etymology.* The name refers to *Alnus viridis* subsp. *sinuata*, the only host known for this species.

*Holotypus.* UNITED STATES. WASHINGTON: Clallam County, Olympic National Park, Hurricane Ridge, from *Alnus viridis* subsp. *sinuata*, 28 May 2008, *L.C. Mejía LCM 412* (BPI 879210).

Perithecia evident as scattered elevations in bark up to 0.4 mm high; often with an oval, dark brown spot, up to 0.7 cm diam on top of elevations. Perithecia black, in groups, up to eight, oriented parallel or in angles of 45 degrees toward bark surface, with necks

converging in center, fused to form a single, thick-walled cavity, with a semi-biconic, flat-tipped, protruding rounded cone of 175  $\mu\text{m}$  high  $\times$  340  $\mu\text{m}$  at base. Mature perithecia black, globose, (251–)339–389(–457)  $\mu\text{m}$  high  $\times$  (253–)272–374(–403)  $\mu\text{m}$  wide (mean = 360  $\times$  323, SD 69, 63, n = 6), perithecial necks (224–)242–265(–347)  $\mu\text{m}$  long (mean = 266, SD 43, n = 6), (83–)95–100(–102)  $\mu\text{m}$  diam at base (mean = 96., SD 7.2, n = 6), (72–)78–103(–108)  $\mu\text{m}$  diam at apex (mean = 92, SD 16, n = 6). Asci obovoid, without apical ring, (76.5–)80.0–93.5(–103.0)  $\times$  (23.0–)26.5–30.5(–31.5)  $\mu\text{m}$  (mean = 88.0  $\times$  28.0, SD 13.5, 4.5, n = 3), with eight ascospores parallel or interwoven. Ascospores nonseptate, hyaline, cylindrical, slightly curved, tapering toward rounded ends, with up to eight circular guttules, (57.0–)66.5–70.5(–79.0)  $\times$  (4.5–)5.5–6.0(–6.5)  $\mu\text{m}$  (mean = 69.0  $\times$  5.5, SD 5.0, 0.5, n = 36), l:w (10.7–)11.8–12.7(–15) (mean = 12.5, SD 1.1).

*Host and habitat.* In the bark of branches of *Alnus viridis* subsp. *sinuata* (Regel) A. Love & D. Love (Betulaceae).

*Distribution.* USA: Washington.

*Holotype.* UNITED STATES. WASHINGTON: Clallam County, Olympic National Park, Hurricane Ridge, from *Alnus viridis* subsp. *sinuata*, 28 May 2008, *L.C. Mejía LCM 412* (BPI 879210, derived culture CBS 125662 = LCM412).

*Other specimen examined.* UNITED STATES. WASHINGTON: Yakima County, along Rimrock Lake, from *Alnus viridis* subsp. *sinuata*, 2 Aug 2005, A.Y. Rossman (BPI 878446, derived culture AR4200).

*Notes.* A dark brown area visible on the host surface is gray stromatic tissue that develops atop the perithecia and surrounds the main perithecial neck cavity. This distinguishes *C. alni-sinuatae* from other species of *Cryptosporella* on *Alnus* in North America. *Cryptosporella suffusa* on *Alnus* in Europe also has that dark area on the host surface but the perithecial necks are fused to form a single ostiolar cavity. This is unlike *C. alni-sinuatae* in which the perithecial necks are erumpent closely appressed or as a single mass.

***Cryptosporella alni-tenuifoliae* L.C. Mejía, sp. nov.**

FIG. 3A–G

Mycobank MB518093

Perithecia nigra, subglobosa, (269–)285–308(–315)  $\mu\text{m}$  alta  $\times$  (399–)414–434(–438)  $\mu\text{m}$  lata, collis (401–)414–476(–524)  $\mu\text{m}$ . Asci (52.5–)69.0–88.5(–103.0)  $\times$  (11.5–)13.5–18.5(–25.5)  $\mu\text{m}$ . Ascospores non-septatae, hyalinae, cylindraceae vel parum in medio dilatatae, in extremitatibus decretescentes, (33.0–)45.5–52.5(–63.5)  $\times$  4.0–4.5 (–6.0)  $\mu\text{m}$ . In *Alno incana* subsp. *tenuifolia*, in Oregon (USA) habitat.

*Etymology.* The name refers to *Alnus incana* subsp. *tenuifolia*, the only known host of this species.

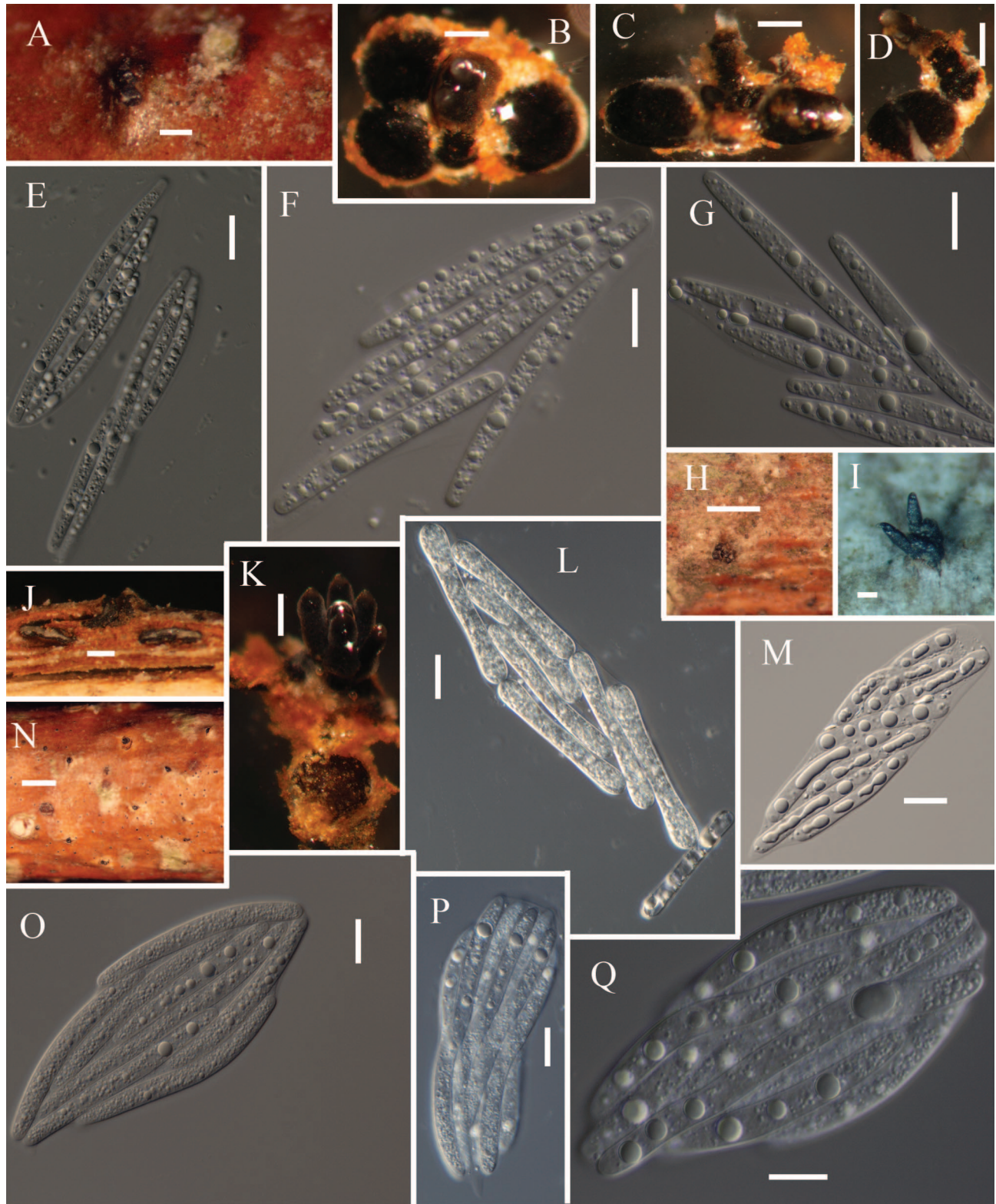


FIG. 3. A–G. *Cryptosporrella alni-tenuifoliae*. A. Fruiting bodies on natural substrate. B–D. Fruiting bodies extracted from natural substrate. E–G. Ascospores (BPI 879211 holotype). H–M. *Cryptosporrella amistadensis*. H–K. Fruiting bodies on natural substrate. L–M. Asci and ascospores (H, J, L = BPI 879218, I = BPI 879249, K, M = BPI 879214 holotype). N–Q. *Cryptosporrella multicontinentalis*. N. Fruiting bodies on natural substrate. O–Q. Asci and ascospores (BPI 879226 holotype). Bars: A–D, J–K = 200  $\mu$ m, E, L–N, O–Q = 20  $\mu$ m, F–G = 10  $\mu$ m, H, N = 1 mm, I = 300  $\mu$ m.



*Holotypus*. UNITED STATES. OREGON: Jackson County, Rogue River National Forest, Upper Rogue River Trail close to River Bridge Campground, in *Alnus incana* subsp. *tenuifolia*, 21 May 2008, L.C. Mejía LCM480 (BPI 879211).

Perithecia evident as scattered, small elevations in bark up to 0.3 mm with 2–3 hyaline ostiolar openings slightly protruding from center. Perithecia black, in groups of up to eight, arranged circularly, flattened and oriented parallel to bark surface or grouped, attached at base, with necks converging at center of group, either bending or oriented vertically toward surface or merged to form thick-walled ostioles oriented vertically toward and protruding through host surface. Mature perithecia black, subglobose, (269–)285–308(–315)  $\mu\text{m}$  high  $\times$  (399–)414–434(–438)  $\mu\text{m}$  wide (mean = 295  $\times$  422, SD 24,  $n = 3$ ), perithecial necks (401–)414–476(–524)  $\mu\text{m}$  long (mean = 451, SD 65,  $n = 3$ ), (100–)105–121(–132)  $\mu\text{m}$  diam at base (mean = 114, SD 16.1,  $n = 3$ ), (105–)106–116(–124)  $\mu\text{m}$  diam at apex (mean = 112, SD 10.3,  $n = 3$ ). Asci cylindrical to elliptical with rounded apex and acute base, without apical ring, (52.5–) 69.0–88.5(–103.0)  $\times$  (11.5–)13.5–18.5(–25.5)  $\mu\text{m}$  (mean = 80.9  $\times$  16.6, SD 14.5, 3.7,  $n = 16$ ), with eight ascospores arranged parallel or interwoven. Ascospores nonseptate, hyaline, cylindrical, slightly tapering toward rounded ends, with multiple, globose guttules that differ in size, (33.0–)45.5–52.5(–63.5)  $\times$  4.0–4.5 (–6.0)  $\mu\text{m}$  (mean = 49.3  $\times$  4.4, SD 6.9, 0.6,  $n = 41$ ), l:w (8.2–)10–12.3(–13.2) (mean = 11.2, SD 1.3,  $n = 41$ ).

*Host species and habitat*. In the bark of still attached branches of *Alnus incana* subsp. *tenuifolia* (Nutt.) Breitung (Betulaceae).

*Distribution*. USA: Oregon.

*Holotype*. UNITED STATES. OREGON: Jackson County, Rogue River National Forest, Upper Rogue River trail close to River Bridge campground, in *Alnus incana* subsp. *tenuifolia*, 21 May 2008, L.C. Mejía LCM480 (BPI 879211, derived culture CBS 125663 = LCM 480.01).

*Other specimens examined*. UNITED STATES. OREGON: Jackson County, Rogue River National Forest, Upper Rogue River trail near River Bridge campground, in *Alnus incana* subsp. *tenuifolia*, 21 May 2008, L.C. Mejía LCM475 (BPI 879212); Rogue River National Forest, Upper Rogue River Trail close to River Bridge Campground, in *Alnus incana* subsp. *tenuifolia*, 21 May 2008, L.C. Mejía LCM481 (BPI 879213).

*Notes*. *Cryptosporella alni-tenuifoliae* differs from several species of *Cryptosporella* on *Alnus* by having cylindrical ascospores. Among those species on *Alnus* having cylindrical ascospores, *C. alni-tenuifoliae* has ascospores that are wider toward the middle. In

addition this species has perithecial necks that are not fused to form a central cavity.

***Cryptosporella amistadensis*** L.C. Mejía, sp. nov.

FIG. 3H–M

MycoBank MB518094

Perithecia nigra, (291–)365–404(–465)  $\mu\text{m}$  alta  $\times$  (385–)412–466(–601) diam, collis (473–)507–570(–645)  $\mu\text{m}$  longis. Asci (71.5–)88.5–101.0(–112.0)  $\times$  (22.5–)23.5–26.0(–28.5). Ascospores non-septatae, hyalinae, guttulateae, ossiformes cum modice expansis extremitatibus, (33.5–)40.5–49.0(–57.5)  $\times$  (3.5–)4.5–5.5(–6.5)  $\mu\text{m}$ . In Alno acuminata, in Centrali et Australi America habitat.

*Etymology*. Name refers to the type locality and place where this species was first found, La Amistad International Park in Chiriquí, Panama.

*Holotypus*. PANAMA. CHIRIQUÍ: Las Nubes, Parque Internacional La Amistad, on *Alnus acuminata*, 22 Dec 2006, L.C. Mejía LCM27 (BPI 879214).

Perithecia evident as slight elevations in bark periderm usually up to 0.3 mm high, with perithecial necks of 2–3 or up to eight protruding from center ca. 0.5 mm above host epidermis. Perithecia arranged in groups of up to eight, with necks oriented at 45 degree angle toward center, closely appressed but not fused, protruding vertically or pushing each other away from central point. Mature perithecia black, shiny, flask-shaped, (291–)365–404(–465)  $\mu\text{m}$  high  $\times$  (385–)412–466(–601) diam (mean = 386  $\times$  457, SD 64, 86,  $n = 5$ ), perithecial necks (473–)507–570(–645)  $\mu\text{m}$  long (mean = 542, SD 67,  $n = 5$ ), (114–)122–155(–178)  $\mu\text{m}$  diam at base (mean = 139, SD 26,  $n = 5$ ), (110–)112–141(–174)  $\mu\text{m}$  diam at apex (mean = 134, SD 26,  $n = 5$ ). Ostiolar openings cone-shaped, hyaline. Asci (71.5–)88.5–101.0(–112.0)  $\times$  (22.5–)23.5–26.0(–28.5)  $\mu\text{m}$  (mean = 93.6  $\times$  25.5, SD 11.6, 2.0,  $n = 9$ ), cylindrical with rounded apex to slightly obovoid, apical ring not observed, eight ascospores per ascus arranged obliquely parallel or interwoven. Ascospores nonseptate, hyaline, guttulated, cylindrical, thick, slightly swollen at rounded ends, (33.5–)40.5–49.0(–57.5)  $\times$  (3.5–)4.5–5.5(–6.5)  $\mu\text{m}$  (mean = 45.3  $\times$  4.9, SD 6.1, 0.7,  $n = 45$ ), l:w (7.2–)8.6–10.3(–11.5) (mean = 9.4, SD 1.1,  $n = 45$ ).

*Host species and habitat*. In the bark of dead branches of *Alnus acuminata* Kunth (Betulaceae).

*Distribution*. Argentina (Tucumán) and Panama (province of Chiriquí).

*Holotype*. PANAMA. CHIRIQUÍ: Las Nubes, Parque Internacional La Amistad, on *Alnus acuminata*, 22 Dec 2006, L.C. Mejía LCM27 (BPI 879214, derived cultures CBS 125664 = LCM 27.03, additional derived cultures LCM27.01, LCM27.02, LCM27.04, and LCM27.05).



*Other specimens examined.* PANAMA. CHIRIQUÍ: Las Nubes, Parque Internacional La Amistad, from *Alnus acuminata*, 21 Dec 2006, L.C. Mejía LCM 25 (BPI 879215), LCM 26 (BPI 879248), LCM28 (BPI 879216); 29 Dec 2007, L.C. Mejía LCM342 (BPI 879217), LCM 357 (BPI 879249, derived culture LCM357, ITS sequence HM017907). ARGENTINA. TUCUMÁN: Villa Nougues, in *Alnus acuminata*, 16 Nov 2008, L.C. Mejía LCM 617 (BPI 879218, derived culture LCM 617.01); same, L.C. Mejía LCM 618 (BPI 879219, derived cultures CBS 126128 = LCM618.01 and LCM 618.03, ITS sequence HM017908); same, L.C. Mejía LCM 619 (BPI 879220, derived culture LCM619.01, ITS sequence HM017909); same, L.C. Mejía LCM621 (BPI 879221).

*Notes.* *Cryptosporrella amistadensis* is similar to *C. marylandica* in having slightly femuroid, nonseptate ascospores. These two species can be distinguished only by their occurrence on different host species of *Alnus* and their geographic distribution. Based on the multigene phylogeny presented here, these two species are clearly distinct.

*Cryptosporrella betulae* (Tul. & C. Tul.) L.C. Mejía & Castleb., Mycol. Res.112:32 (2008).

≡ *Cryptospora betulae* Tul. & C. Tul., Sel. Fung. Carpol. 2:149 (1863).

≡ *Winterella betulae* (Tul. & C. Tul.) Kuntze, Rev. Gen. Pl. 1:34 (1891).

*Host species and habitat.* In the bark of dead branches of *Betula alba*, *B. lenta*, *B. pendula*, *B. verrucosa* and *Betula* spp. (Betulaceae).

*Distribution.* Europe.

*Specimens examined.* AUSTRIA. NIEDEROESTERREICH: Losenheim, Laerchkogel. Mapping grid square 8261/1, on *Betula lenta*, 5 Jul 2003, W. Jaklitsch 2271 as *Winterella betulae* (BPI 843595). RUSSIA. NIZHNIY NOVGOROD: Oblast Piliha, on *Betula pendula*, 30 Jun 2008, M. V. Sogonov LCM 477 (BPI 879251, derived culture LCM477.01).

*Notes.* *Cryptosporrella betulae* is herein conceived more narrowly than by previous authors (Reid and Booth 1987 as *Winterella betulae*, Mejía et al. 2008); it is restricted to specimens without a basal tomentum occurring on *Betula* in Europe as in *C. tomentella*. Specimens on *Betula* in North America similar to *C. betulae* are now recognized as *C. tomentella*, a species previously considered a synonym of *C. betulae*. Both *C. betulae* and *C. tomentella* have ascospores that are slightly curved, fusoid, cylindrical or cylindrical fusoid with rounded ends, while the only other species on *Betula*, *C. alnicola* and *C. confusa*, have cylindrical, generally longer ascospores. Ascospores of *C. betulae* are (29–)33–38.5(–56) × 5–6 μm (mean = 38 × 5.7, SD 8.8, 0.6, n = 11), l:w (4.6–)5.4–7.6(–11) (mean = 6.8, SD 2.0, n = 11). The range of *C. betulae* is extended to Russia.

*Cryptosporrella femoralis* (Peck) L.C. Mejía & Castleb. Mycol. Res.112:33 (2008).

≡ *Valsa femoralis* Peck, New York State Mus. Rep. 28:74, 1874 (1879).

≡ *Cryptospora femoralis* (Peck) Sacc., Syll. Fung. 2:362 (1883).

≡ *Winterella femoralis* (Peck) Kuntze, Rev. Gen. Pl. 1:34 (1891).

≡ *Ophiovalsa femoralis* (Peck) Petr., Sydowia 19:273. 1965 (1966).

= *Cryptospora humeralis* Dearn. & House, Circ. New York State Mus. 24:41 (1940).

*Host species and habitat.* In the bark of dead branches of *Alnus incana* subsp. *rugosa*, *A. serrulata*, and *Alnus* spp. (Betulaceae).

*Distribution.* North America. Also reported from Asia but this has not been confirmed (Kobayashi 1970).

*Type specimens examined.* UNITED STATES. NEW YORK: West Albany, from *Alnus*, C.H. Peck (NYS-F1166, as *Valsa femoralis*, HOLOTYPE fide Reid and Booth 1987); Greenbush, from *Alnus*, C.H. Peck (NYS-F1167, as *Valsa femoralis*, PARATYPE); UNITED STATES. NEW YORK: St Lawrence County, Cranberry Lake, Adirondack Mountains, on *Alnus rugosa*, 13 Jun 2002, L. Vasilyeva as *Ophiovalsa femoralis* (BPI 872326, **epitype designated here**; derived culture CBS 121076 = AR 3868).

*Other specimens examined.* UNITED STATES. NEW YORK: Essex County, Adirondack High Peaks region, head trail, Adirondack Loj, on *Alnus incana* subsp. *rugosa*, 12 Jun 2007, L.C. Mejía LCM103 (BPI 879224, derived cultures LCM103.01 and LCM103.02); Essex County, Adirondack High Peaks region, on *Alnus incana* subsp. *rugosa*, L.C. Mejía LCM196 (BPI 879223, derived cultures LCM196.01, ITS sequence HM017900, LCM196.02 and LCM196.04). Other specimens observed are listed in Mejía et al. (2008).

*Notes.* This common North American species of *Cryptosporrella* is distinct in having femuroid ascospores that have one median septum unlike all other species of *Cryptosporrella* that have nonseptate ascospores. Perithecia (540–)552–575(–629) μm high × (536–)556–583(–614) μm diam (mean = 570 × 571, SD 39.6, 32.6, n = 4), necks (476–)486–507(–518) μm long (mean = 497, SD 29.6, n = 2), (166–)170–178(–182) μm diam at base (mean = 174, SD 11.4, n = 2), (153–)165–189(–201) μm (mean = 177, SD 34.3, n = 2). Asci (62–)74–122(–145) × (15–)18–21(–28.5) μm (mean = 102 × 20.3, SD 24.9, 3.4, n1 = 17, n = 17). Ascospores (24–)47.5–56(–74) × (3–)4(–5) μm (mean = 52.3 × 4.12, SD 8.3, 0.4, n = 36), l:w (5–)12–14(–18) (mean = 12.7, SD 2.06, n = 36).

***Cryptosporrella jaklitschii*** L.C. Mejía, sp. nov. FIG. 4A–E MycoBank MB518095

Perithecia nigra, globosa, (402–)406–419(–426) μm alta × (384–)404–417(–435) diam, collis (530–)539–584(–608) μm longis et ostioli orificio papillato. Asci (74.0–)81.0–

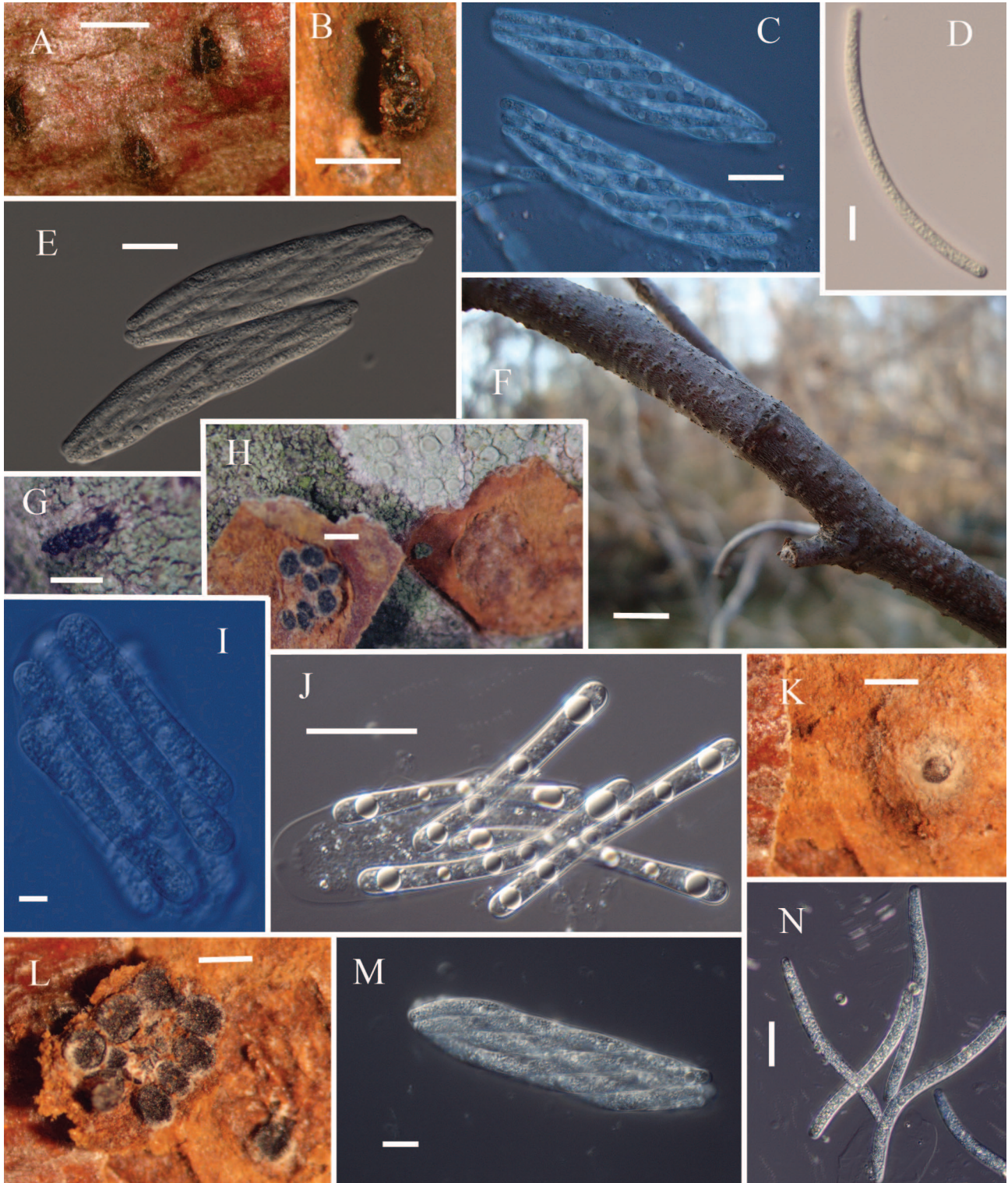


FIG. 4. A–E. *Cryptosporrella jaklitschii*. A–B. Fruiting bodies on natural substrate. C–E. Asci and ascospores. (BPI 879231 holotype). F–J. *Cryptosporrella marylandica*. F. Branch of *Alnus serrulata* with perithecia. G. Fruiting bodies on natural substrate. H. Fruiting bodies on natural substrate with substrate removed to show perithecial arrangement. I–J. Asci and ascospores (F = BPI 879485, G–I = BPI 879232 holotype, J = BPI 879236). K–N. *Cryptosporrella pacifica*. K. Fruiting bodies on natural substrate. L. Fruiting on natural substrate with substrate removed to show perithecial arrangement. M–N. Ascospores and ascospores. (K–L = BPI 879240, M = BPI 879241, N = BPI 879239 holotype). Bars: F = 5 mm, A, G–H = 1 mm, B, K–L = 500  $\mu$ m, C–E, I = 10  $\mu$ m, J, M–N = 20  $\mu$ m.



85.5(–92.0) × (13.0–)17.0–18.0(–21.5) μm. Ascospores nonseptatae, cylindratae sine expansis extremitatibus, (64.0–)74.0–79.5(–107.0) × (3.5–)4.0–5.0(–5.5) μm. In *Alnus serrulata*, in boreali USA hábitat.

*Etymology.* The species is named after Walter Jaklitsch, Austrian mycologist, in recognition of his contributions to the systematics of the Diaporthales.

*Holotypus.* UNITED STATES. NEW YORK: Essex County, Adirondack High Peaks region, Marcy Dam, on *Alnus serrulata*, 11 Jun 2007, *L.C. Mejía LCM112* (BPI 879231).

Initially perithecia evident as scattered elevations in bark up to 0.4 mm high. Erumpent perithecial necks protrude from periderm at central area of elevations either in a row or as a mass; from host surface few perithecial necks seen, when host periderm peeled off, up to 10 often visible; perithecia arranged circularly with necks projecting toward center of group. Perithecial necks closely appressed in center, appearing to fuse, protruding through periderm; only ca. 0.2 mm of distal part of perithecial necks extends beyond rupture in bark. Perithecia black at maturity, globose, shiny, (402–)406–419(–426) μm high × (384–)404–417(–435) μm diam (mean = 413 × 410, SD 20.6, 11, n = 4), perithecial necks (530–)539–584(–608) μm long (mean = 564, SD 35, n = 4), (114–)123–131(–137) μm diam at base (mean = 126, SD 9.8, n = 4), (127–)127–138(–164) μm diam at apex (mean = 137, SD 18, n = 4). Stromatic tissue scanty, gray, flat, below host epidermis, on top of perithecia and surrounding necks. Ostiolar region appearing like a dome-shaped papilla, about 50 μm high × 70 μm at base seated on top of distal part of neck with an area of 35 μm surrounding base of dome, appearing like a rounded lip. Asci oblong elliptical, with no apical ring, (74.0–)81.0–85.5(–92.0) × (13.0–)17.0–18.0(–21.5) μm (mean = 83.7 × 17.3, SD 4.7, 2.0, n = 21), with eight ascospores slightly twisted to interwoven. Ascospores cylindrical to sigmoid, nonseptate, hyaline, with multiple rounded guttules, (64.0–)74.0–79.5(–107.0) × (3.5–)4.0–5.0(–5.5) μm (mean = 78.4 × 4.6, SD 8.6, 0.5, n = 27), l:w (14.1–)14.9–18.2(–29.2) (mean = 17.3, SD 3.4, n = 27).

*Host species and habitat.* In the bark of branches of *Alnus serrulata* (Aiton) Willd. (Betulaceae).

*Distribution.* USA: New York.

*Holotype.* UNITED STATES. NEW YORK: Essex County, Adirondack High Peaks region, Marcy Dam, on *Alnus serrulata*, 11 Jun 2007, *L.C. Mejía LCM112* (BPI 879231, derived cultures CBS 125665 = LCM 112.04 and LCM112.01).

*Notes.* *Cryptospora jaklitschii* is similar to *C. alnicola* in having perithecial necks that do not fuse to form a single cavity, cylindrical ascospores, and occurring on *Alnus*. Unlike *C. alnicola*, the ostiolar opening of *C. jaklitschii* are papillated.

***Cryptospora marylandica* L.C. Mejía, sp. nov.**

FIG. 4F–J

MycoBank MB518096

*Perithecia nigra, globosa, (339–)371–422(–472) μm alta × (370–)405–467(–495) μm diam, collis (330–)350–458(–530) μm longis. Asci (68.5–)76.0–82.5(–93.5) × (22.0–)24.5–33.5(–39.5) μm. Ascospores nonseptatae, ossiformes cum modice expansis extremitatibus, (39.0–)46.0–51.0(–58.5) × (3.5–)5.0–5.5(–7.0) μm. In *Alnus maritima* vel *A. serrulata*, in USA (Maryland et cingentibus regionibus) habitat.*

*Etymology.* Name refers to the state of Maryland, USA, where this species was found.

*Holotypus.* UNITED STATES. MARYLAND: Dorchester County, Marshyhope Creek, Richard Henson Scout Reserve, on *Alnus maritima*, 11 Jun 2008, *L.C. Mejía LCM386* (BPI 879232).

On *Alnus maritima* scattered groups or rows of ostiolar openings exposed through slits in host periderm about 0.8 mm long, level with host surface. On *Alnus serrulata* forming circularly arranged swellings in host periderm around a central point about 1.5 mm diam × 0.5 mm high where distal part of perithecial neck protrudes slightly beyond host epidermis. Perithecia black, globose, with rounded ostiolar openings, in groups of up to eight, with necks oriented toward a central point, closely appressed, protruding vertically as a column or parallel in rows through host periderm, (339–)371–422(–472) μm high × (370–)405–467(–495) μm diam (mean = 394 × 438, SD 39.2, 42, n = 11), necks (330–)350–458(–530) μm long (mean = 410, SD 68.1, n = 11), (104–)112–125(–145) μm diam at base (mean = 119, SD 13.8, n = 11), (101–)116–136(–158) μm diam at apex (mean = 126, SD 17.8, n = 11). Asci obovoid with rounded apex and acute base or looking like a parallelogram when ascospores are fully develop and extend ascus wall, (68.5–)76.0–82.5(–93.5) × (22.0–)24.5–33.5(–39.5) μm (mean = 80.1 × 29.2, SD 6.7, 5.7, n = 11), without apical ring, with eight ascospores parallel or slightly interwoven. Ascospores nonseptate, hyaline, thick, short cylindrical, usually straight, with broadly rounded ends, slightly wider than center, (39.0–)46.0–51.0(–58.5) × (3.5–)5.0–5.5(–7.0) μm (mean = 48.8 × 5.1, SD 4.4, 0.6, n = 69), l:w (6.4–)8.7–10.8(–15.1) (mean = 9.8, SD 1.7, n = 69).

*Host species and habitat.* In the bark of branches of *Alnus maritima* (Marshall) Muhl. ex Nutt. and *A. serrulata* (Betulaceae).

*Distribution.* USA: Maryland.

*Holotype.* UNITED STATES. MARYLAND: Dorchester County, Marshyhope Creek, Richard Henson Scout Reserve, on *Alnus maritima*, 11 Jun 2008, *L.C. Mejía LCM386* (BPI 879232, derived cultures CBS 125666 = LCM386.04 and LCM386.05).

*Additional specimens examined.* UNITED STATES. MARYLAND: Prince George's County, Beltsville, Little Paint Branch Park, on *Alnus serrulata*, 2 Mar 2008, *L.C. Mejía LCM359* (BPI 879233, derived cultures LCM359, LCM359.01, ITS sequence HM017903, and LCM359.02); same, 28 Apr 2008, *L.C. Mejía LCM631* (BPI 879235); same, 15 Jun 2008, *L.C. Mejía LCM580* (BPI 879236, derived cultures LCM580.01 and LCM580.02); same, *L.C. Mejía LCM581* (BPI 879250, derived cultures LCM581.01 and LCM581.02); same, 29 Mar 2009, *L.C. Mejía LCM625* (BPI 879485); Dorchester County, Richard Henson Scout Reserve, on *Alnus maritima*, 11 Jun 2008, *L.C. Mejía LCM387* (BPI 879237); same, LCM388 (BPI 879238); same, *L.C. Mejía LCM587* (BPI 879492).

*Notes.* *Cryptosporella marylandica* is similar to *C. amstadensis* in having slightly femuroid, nonseptate ascospores. These species can be distinguished only by their occurrence on different host species of *Alnus* and their geographic distribution. Based on the multigene phylogeny presented here, these two species are clearly distinct. Within *C. marylandica* the arrangement of the perithecia varies with the host. In addition the ascospore length is sometimes greater on *Alnus serrulata* than on *A. maritima*. Despite these slight morphological differences, molecular data indicate that these specimens comprise a single species.

***Cryptosporella multicontinentalis* L.C. Mejía, sp. nov.**

FIG. 3N–Q

Mycobank MB518097

Perithecia nigra, (284–)346–392(–455)  $\mu\text{m}$  alta  $\times$  (318–)345–411(–557)  $\mu\text{m}$ , collis connatis unam ostioli cavitatem formantibus, (156–)247–382(–483)  $\mu\text{m}$  longis. Asci (61.5–)77.0–94.0(–98.0)  $\times$  (16.5–)19.5–25.5(–38.5)  $\mu\text{m}$ . Ascospores cylindraceae, flexuosae, versus extremitates decedentes, (46.5–)54.5–67.0(–73.5)  $\times$  4.5–5.5(–6.0)  $\mu\text{m}$ . In Alno, in Europa et boreo-orientali America.

*Etymology.* The name refers to the geographic distribution of this species on at least two continents (Europe and North America).

*Holotypus.* FRANCE. DEUX-SÈVRES: Amure, Port Le Goron, on *Alnus glutinosa*, 15 Apr 2008, *L.C. Mejía LCM401* (BPI 879226).

Perithecia in scattered groups, immersed in bark of host branches; each group containing 9–10 perithecia, evident as elevations in bark that appear as a circle of bumps with a single ostiolar cavity in center that protrudes through a central elevation of periderm; alternatively perithecia near center cause an elevation of periderm that appears cone-shaped with a flattened apex. Ostiolar opening single, wide, appearing labiated. No black spot on host surface. White mycelium may develop at base of perithecial group. Perithecia black, with thin necks oriented parallel to host surface toward center of group. Central ostioles surrounded by a whitish to cream

stromatic tissue. Perithecia (284–)346–392(–455)  $\mu\text{m}$  high  $\times$  (318–)345–411(–557)  $\mu\text{m}$  (mean = 370  $\times$  393, SD 71, 46, n = 9), perithecial necks (156–)247–382(–483)  $\mu\text{m}$  long (mean = 310, SD 111, n = 9), (67.0–)82.5–89.5(–107.0)  $\mu\text{m}$  diam at base (mean = 86.3, SD 10.9, n = 9), (69.0–)72.0–86.5(–108.0)  $\mu\text{m}$  at apex (mean = 83.3, SD 13.1, n = 9). Asci oval to obovoid narrowing to base and apex, (61.5–)77.0–94.0(–98.0)  $\times$  (16.5–)19.5–25.5(–38.5)  $\mu\text{m}$  (mean = 82.9  $\times$  24.1, SD 11.2, 6.2, n = 21), with eight ascospores. Ascospores cylindrical, flexuous commonly narrowing toward ends, (46.5–)54.5–67.0(–73.5)  $\times$  4.5–5.5(–6.0)  $\mu\text{m}$  (mean = 60.1  $\times$  5.1, SD 7, 0.6, n = 49), l:w (9.2–)10.4–12.3(–16.8) (mean = 11.8, SD 1.9, n = 49).

*Host species and habitat.* In the bark of dead, still attached branches of *Alnus* spp. (Betulaceae): *A. glutinosa* (L.) Gaertn., *A. hirsuta* (Spach) Turcz. ex Rupr. and *A. incana* subsp. *rugosa* (Du Roi) R.T. Clausen.

*Distribution.* Europe (France, Germany), North America (USA).

*Holotype.* FRANCE. DEUX-SÈVRES: Amure, Port Le Goron, on *Alnus glutinosa*, 15 Apr 2008, *L.C. Mejía LCM401* (BPI 879226, derived culture CBS 125667 = LCM 401.01).

*Other specimens examined.* FRANCE. DEUX-SÈVRES: Melle, on *A. glutinosa*, Apr 2008, *L.C. Mejía LCM 406* (BPI 879227, derived culture LCM 406.01); Melle Arboretum, on *A. hirsuta*, 15 Apr 2008, *L.C. Mejía LCM394* (BPI 879258, derived culture CBS 126118 = LCM394.01, LCM394.02, ITS sequence HM017894, LCM394.04). GERMANY. FRANKFURT: Naturschutzgebiet, on *A. glutinosa*, 20 Apr 2008, *L.C. Mejía LCM427* (BPI 879228, derived culture LCM427.01); UNITED STATES. NEW YORK: Anondaga County, Syracuse, Heiberg Memorial Forest, Kochanek pond, on *Alnus incana* subsp. *rugosa*, 6 Jun 2007, *L.C. Mejía LCM93* (BPI 879229, derived culture CBS 126119 = LCM93.01); same, *L.C. Mejía LCM93b* (BPI 879230, derived culture LCM93b.02).

*Notes.* Among the species of *Cryptosporella* having perithecial necks fused into a single cavity, *C. multicontinentalis* is similar to *C. suffusa* in having cylindrical ascospores that are less than 6  $\mu\text{m}$  wide. However, *Cryptosporella multicontinentalis* lacks a darkened area on the host surface and stromatic tissue as found in *C. suffusa*.

***Cryptosporella pacifica* L.C. Mejía, sp. nov.** FIG. 4K–N  
Mycobank MB518098

Perithecia nigra, (312–)322–351(–394)  $\mu\text{m}$  alta  $\times$  (339–)344–423(–470)  $\mu\text{m}$  diam, collis connatis unam ostioli cavitatem formantibus, (212–)287–360(–376)  $\mu\text{m}$  longis. Asci (87.0–)88.5–93.0(–104.0)  $\times$  (25.5–)26.0–28.0(–29.0)  $\mu\text{m}$ . Ascospores cylindraceae, cum rotundatis extremitatibus, (68.5–)74.5–84.0(–94.0)  $\times$  (5.5–)6.0–6.5  $\mu\text{m}$ . In Alno



incana subsp. tenuifolia and *A. viridis* subsp. sinuata, in boreo-occidentali USA habitat.

*Etymology.* Name refers to the geographic distribution of this species in the Pacific Northwest (USA).

*Holotypus.* UNITED STATES. CALIFORNIA: Lassen County, Lassen National Forest, Lassen Campground, on *Alnus incana* subsp. *tenuifolia*, 18 May 2008, L.C. Mejía LCM461 (BPI 879239).

Perithecia in groups of up to nine, scattered in bark of host branches. Groups of perithecia commonly arranged in circles, with necks oriented toward center and merging to form a single thick neck that protrudes vertically; white stromatic mycelium surrounding ostiolar opening. Perithecia (312–)322–351(–394)  $\mu\text{m}$  high  $\times$  (339–)344–423(–470)  $\mu\text{m}$  diam (mean = 342  $\times$  390, SD 36, 61, n = 4), necks (212–)287–360(–376)  $\mu\text{m}$  long (mean = 313, SD 73, n = 4), (88.0–)89.5–95.0(–105.0)  $\mu\text{m}$  diam at base (mean = 93.5, SD 8.0, n = 4), (82.0–)85.5–98.5(–108.0)  $\mu\text{m}$  diam at apex (mean = 93.0, SD 11.5, n = 4). Asci oval to obovoid with rounded apex, narrowing toward base, (87.0–)88.5–93.0(–104.0)  $\times$  (25.5–)26.0–28.0(–29.0)  $\mu\text{m}$  (mean = 92.4  $\times$  27.2, SD 8.0, 1.7, n = 4), no apical ring, with eight ascospores. Ascospores cylindrical, with rounded ends, (68.5–)74.5–84.0(–94.0)  $\times$  (5.5–)6.0–6.5  $\mu\text{m}$  (mean = 79.0  $\times$  6.0, SD 8.7, 0.3, n = 10), l:w (11.6–)12.2–14(–15) (mean = 13, SD 1.2, n = 10).

*Host species and habitat.* In still attached branches of *Alnus viridis* subsp. *sinuata* and *A. incana* subsp. *tenuifolia* (Betulaceae).

*Distribution.* UNITED STATES (California, Oregon, Washington).

*Holotype.* UNITED STATES. CALIFORNIA: Lassen County, Lassen National Forest, Lassen Campground, on *A. incana* subsp. *tenuifolia*, 18 May 2008, L.C. Mejía LCM461 (BPI 879239, derived culture CBS 126117 = LCM461.01).

*Other specimens examined.* UNITED STATES. CALIFORNIA: Plumas County, Little Last Chance campground, on *A. incana* subsp. *tenuifolia*, 17 May 2008, L.C. Mejía LCM453 (BPI 879240, derived culture LCM453.01); OREGON: Jackson County, Upper Rogue River trail near River Bridge Campground, 20 May 2008, on *A. incana* subsp. *tenuifolia*, L.C. Mejía LCM 420 (BPI 879241, derived culture LCM420.01); WASHINGTON: Yakima County, near Rimrock Lake, isolated from healthy branches of *A. viridis* subsp. *sinuata*, 2006, S. Lattomus, isol. L.C. Mejía (cultures CBS122311, CBS 122312, CBS 122313).

*Notes.* *Cryptosporella pacifica* is unique among species of *Cryptosporella* in having perithecial necks fused into a single cavity and cylindrical ascospores that are generally wider than 6  $\mu\text{m}$ .

***Cryptosporella rabenhorstii*** (Berk. & Broome) L.C. Mejía, comb. nov. FIG. 5A–C

$\equiv$  *Sphaeria rabenhorstii* Berk. & Broome, Ann. & Mag. Nat. Hist. Ser. 2, 9:324 (1852).

Mycobank MB518099.

*Host species and habitat.* On dead branch of *Betula* sp. (Betulaceae).

*Distribution.* United Kingdom.

*Type specimen examined.* ENGLAND. WILTSHIRE, Spye Park, on bark of *Betula* sp., Mar 1859 (Herb. Berkeley, K(M) 163853, Holotype of *Sphaeria rabenhorstii*).

*Notes.* This species had been considered a synonym of *C. suffusa* (Reid and Booth 1987). A characteristic feature of *C. suffusa* is the fusion of perithecial necks to form a single ostiolar cavity. Examination of the holotype of *Sphaeria rabenhorstii* (K(M) 163853) showed that the perithecial necks are not fused and the asci and ascospores differed from those of *C. suffusa*. The asci of *S. rabenhorstii* are cylindrical to clavate (74–)78–82(–82.5)  $\times$  (14–)15–16.5(–17)  $\mu\text{m}$  (mean = 79.6  $\times$  15.6, SD 4.6, 1.6, n = 3), different than those of *C. suffusa*, which are ovate to obovoid. The ascospores of *S. rabenhorstii* are cylindrical slightly tapering toward rounded ends, (35–)44–55(–81)  $\times$  (5–)5–(6)  $\mu\text{m}$  (mean = 51.5  $\times$  5.3, SD 14.4, 0.34, n = 13), l:w (6–)8–11(–15) (mean = 9.8, SD 2.8, n = 13), and appear wider at the center than those of *C. suffusa*, which are cylindrical. *Cryptosporella suffusa* is a species associated with genus *Alnus*, while the holotype of *S. rabenhorstii* was collected on *Betula*. Therefore *S. rabenhorstii* is considered a species distinct from *C. suffusa*.

***Cryptosporella suffusa*** (Fr.) L.C. Mejía & Castleb., Mycol. Res. 112:31 (2008). FIG. 5D–G

$\equiv$  *Sphaeria suffusa* Fr., Syst. Mycol. 2:399 (1823).

$\equiv$  *Valsa suffusa* (Fr.) Fr., Summ. Veg. Scand. 412 (1846).

$\equiv$  *Cryptospora suffusa* (Fr.) Tul. & C. Tul., Sel. Fung. Carpol. 2:145 (1863).

$\equiv$  *Winterella suffusa* (Fr.) O. Kuntze, Rev. Gen. Pl. 1:34 (1891).

$\equiv$  *Ophiovalsa suffusa* (Fr.) Petr., Sydowia 19: 272, 1965 (1966).

= *Sphaeria cryptosporii* Curr., Microsc. J. 3:271 (1855).

= *Valsa rhabdospora* de Not., Sfer. Ital. Cent. I: 39 (1863) fide Reid and Booth (1987).

$\equiv$  *Cryptospora rhabdospora* (de Not.) Sacc., Syll. Fung. 2:362 (1883).

Anamorph. *Disculina vulgaris* (Fr.) B. Sutton, Mycol. Pap. 141:75 (1977).

$\equiv$  *Cryptosporium vulgare* Fr., Syst. Myc. 3: 482 (1832).

*Host species and habitat.* On dead branches of *Alnus glutinosa*, *A. incana* and *Alnus* spp. (Betulaceae).

*Distribution.* Europe.

*Type specimens examined.* SWEDEN. on *Alnus*, *Fries* (Scleromycetae Sueciae 229 BPI Sbarbaro collection,

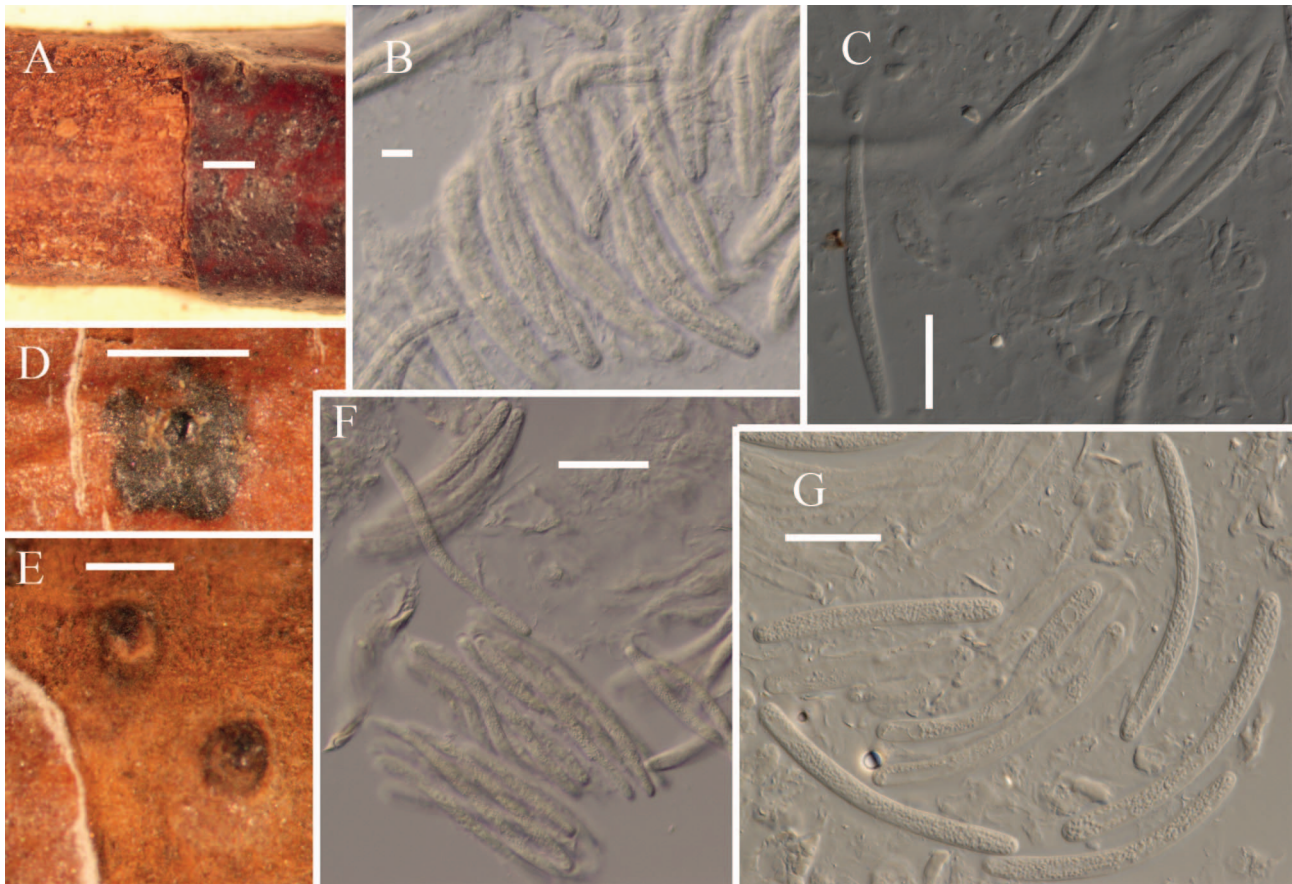


FIG. 5. A–C. *Cryptosporella rabenhorstii*. A. Fruiting bodies on natural substrate. B–C. Asci and ascospores (K(M) 163853 holotype of *Sphaeria rabenhorstii*). D–G. *Cryptosporella suffusa*. D–E. Fruiting bodies on natural substrate. F–G. Asci and ascospores (BPI-Scleromyceti Sueciae 229, type of *C. suffusa*). Bars: A, D = 1 mm, B = 10  $\mu$ m, C, F–G = 20  $\mu$ m, E = 500  $\mu$ m.

isolecotype of *Sphaeria suffusa*). The lectotype specimen of this name is housed at UPS as designated by Reid and Booth (1987). ENGLAND. WEST KENT: Eltham, on *Alnus* sp., 10 Jan 1855 (K(M) 163855, as *Cryptospora suffusa*, syntype of *Sphaeria cryptosporii*, ex. Herb. F. Currey); Chislehurst, Petts Wood, on *Alnus* sp., Sep 1855 (K(M)16385417, syntype of *Sphaeria cryptosporii*, ex. Herb. F. Currey). AUSTRIA. TIROL: Overtilliach an der Gail, grid square 924/4, on *Alnus incana*, 29 Aug 2000, W. Jaklitsch 1556 as *Ophiovalsa suffusa* (BPI 748449, **epitype designated here**, derived culture CBS 109750).

*Other specimens examined.* AUSTRIA. VIENNA: Marchfeldkanalweg 7764/2, 21st district, on *Alnus incana*, 19 May 2002, W. Jaklitsch 1892 (BPI 871231, derived culture CBS 121077 = AR 3825). GERMANY. FRANKFURT: Botanical Garden of Johann Wolfgang Goethe Universität, 22 Apr 2008, on *Alnus* sp., L.C. Mejía LCM 576 (BPI 879242, derived cultures LCM576.01, LCM576.03). HUNGARY. ALTENBURG: prope Ungarisch, in ramis aridis *Alni incanae* DC, Apr 1885, Linhart, Rabenhorst-Winter Fungi europaeie 3458 as *Cryptosporella suffusa* (BPI); an abges-

torbenen Aesten von *Alnus glutinosa* beim Kloster Zella unweit Nossen um Pfingsten 1877 mit reifen schlauchen gesammelt von W. Krieger, Rabenhorst Fungi Europaei 2322 as *Cryptospora suffusa* (BPI exsiccati).

*Notes.* *Cryptosporella suffusa* is distinct in having perithecial necks that fuse into an ostiolar cavity and a brown to black spot on the host surface resulting from stromatic tissue beneath the epidermis. The asci are oval to obovoid (52–)73–85(–100)  $\times$  (11.5–)20–25(–31)  $\mu$ m (mean = 78.4  $\times$  22.4, SD 10.6, 4.4, n = 51). Ascospores are cylindrical (34–)53.5–67(–88)  $\times$  (3–)4–5(–6)  $\mu$ m (mean = 62.6  $\times$  4.7, SD 13, 0.61, n = 97), l:w (8–)11–15.5(–20) (mean = 13.5, SD 2.9, n = 97). *Valsa commutata* Fuckel, Fungi Rhen. 620 (1863) has been considered a synonym of *Cryptosporella suffusa* (Reid and Booth 1987). Images of the exsiccati as the type specimen of *V. commutata* (Fungi Rhenani 620, Germany, on *Betula*) from the Swedish Museum of Natural History suggest that this specimen represents a species of *Melanconis*. The ascospores are unlike those of *Cryptosporella*. Therefore we do not consider *Valsa commutata* to be a synonym of *C. suffusa*.



***Cryptosporrella tomentella* (Peck) L.C. Mejía, comb. nov.**

- ≡ *Valsa tomentella* Peck, New York State Mus. Rep. 35:144, 1881 (1884).
- ≡ *Cryptospora tomentella* (Peck) Berl. & Vogl., Add. Syll. 1-4:192 (1886).
- ≡ *Cryptospora betulae* var. *tomentella* (Peck) Berl., Icones Fung. 2:157 (1889).
- ≡ *Ophiovalsa tomentella* (Peck) Petr., Sydowia 19:275. 1965 (1966).

Mycobank MB518100

Perithecia (481–)567–623(–642) µm high × (440–)455–519(–655) µm diam (mean = 584 × 503, SD 58.6, 81, n = 6), necks (716–)735–789(–970) µm long (mean = 790, SD 92.7, n = 6), (183–)186–228(–238) µm diam at base (mean = 208, SD 23.9, n = 6), (152–)156–195(–198) µm diam at apex (mean = 176, SD 21.3, n = 6). Asci (81–)84–98(–107) × (17–)20–24(–26) µm (mean = 91.8 × 21.6, SD 8.61, 2.88, n = 11). Ascospores slightly curved, fusoid, cylindrical, or cylindrical fusoid with rounded ends (37.5–)43–51(–74) × (4.6–)5–6(–9) µm (mean = 48 × 5.6, SD 7.6, 0.8, n = 33), l:w (5.6–)7–10(–13) (mean = 8.7, SD 1.7, n = 33).

*Host species and habitat.* On bark of branches of *Betula* spp. (Betulaceae).

*Distribution.* UNITED STATES (New York).

*Type specimen.* UNITED STATES. NEW YORK: West Albany, on *Betula populifolia*, May, C.H. Peck (NYS-F3197, as *Valsa (Cryptospora) tomentella*, **herein designated LECTOTYPE**); same (NYS-F3608, as *Valsa tomentella*).

*Other specimens examined.* UNITED STATES. NEW YORK: Adirondack, on *Betula* sp., 20 Jun 2002, L. Vasilyeva as *Ophiovalsa betulae* (BPI 843497, derived culture CBS121080); on *Betula* sp., 20 Jun 2002, L. Vasilyeva as *Ophiovalsa betulae* (BPI 872328, derived culture CBS 121073); Essex County, North Pole, White Face Mountain, on *Betula alleghaniensis*, 9 Jun 2007, L.C. Mejía LCM184B (BPI 879243, derived culture CBS 126440 = LCM184B.01).

*Notes.* *Cryptosporrella tomentella* had been considered a synonym of *Cryptosporrella betulae* as *Winterella betulae* (Reid and Booth 1987). *Cryptosporrella betulae* is limited in distribution to Europe. Examination of the type specimen suggests that *C. tomentella* is the correct name for the North America species. *Cryptosporrella tomentella* is distinguished by the tomentum surrounding the base of the perithecia, while *C. betulae* lacks this feature.

KEY TO SPECIES OF *CRYPTOSPORELLA*

- 1. Ascospores with one median septum at maturity, ends swollen, thus appearing like a leg bone or femur; on *Alnus* spp. in North America *C. femoralis*
- 1. Ascospores nonseptate, femuroid or otherwise; on *Alnus* and other hosts in North America and elsewhere . . . . . 2
- 2. Ascospores ellipsoidal to fusoid, acute ends; on *Ulmus* spp . . . . . *C. hypoderma*

- 2. Ascospores cylindrical to cylindrical femuroid, with or without swollen ends; on other hosts . . . . . 3
- 3. Perithecial necks fused forming a single ostiolar cavity . . . . . 4
- 3. Perithecial necks erumpent as a mass or closely appressed, but not forming a single ostiolar cavity 7
- 4. Ascospores cylindrical, generally wider than 6 µm; on *A. incana* subsp. *tenuifolia* and *A. viridis* subsp. *sinuata* in the Pacific Northwest (USA) . *C. pacifica*
- 4. Ascospores cylindrical generally less than 6 µm wide; on hosts other than *A. incana* subsp. *tenuifolia* and *A. viridis* subsp. *sinuata*, not in the Pacific Northwest (USA) . . . . . 5
- 5. Ascospores widest at center, slightly tapering toward ends . . . . . *C. rabenhorstii*
- 5. Ascospores not widest at center, not tapering toward ends . . . . . 6
- 6. Dark to black spot on host surface and on top of perithecial group, whitish to cream stromatic tissue delimited by a black halo surrounding central ostiolar cavity; on *Alnus* in Europe . . . . *C. suffusa*
- 6. Dark to black spot absent, no stromatic tissue delimited by a black halo; on *Alnus* in Europe and eastern North America . . . . . *C. multicontinentalis*
- 7. Ascospores slightly curved, fusoid, cylindrical, or cylindrical fusoid with rounded ends . . . . . 8
- 7. Ascospores femuroid or cylindrical with slightly to strongly swollen ends . . . . . 9
- 8. Perithecia with whitened tomentum at base; on *Betula* in North America . . . . . *C. tomentella*
- 8. Perithecia without tomentum; on *Betula* sp. in Europe . . . . . *C. betulae*
- 9. Ascospores cylindrical to femuroid, 27–35 × 5–6.5 µm; on *Tilia* sp. in Europe . . . . . *C. tiliae*
- 9. Ascospores cylindrical, with slightly or strongly swollen ends or femuroid, greater than 35 µm long; on *Tilia* in North America or other hosts in Europe and North America . . . . . 10
- 10. On *Tilia americana* in North America; ascospores (49.5–)74–92.5(–109) × (4–)5–6(–7) µm, l:w (9–)13.5–16(–22.5) . . . . . *C. wehmeyeriana*
- 10. On Betulaceae including *Alnus* spp., *Betula* spp. and *Corylus* spp. in Europe and the New World . 11
- 11. On *Betula* spp. and *Corylus* spp. in North America and Europe . . . . . 12
- 11. On *Alnus* spp. in the New World . . . . . 13
- 12. Ascospores (87.5–)88.5–89.5(–91.0) × 3.0–3.5 µm; on *Betula* spp. in North America and Europe . . . . . *C. confusa*
- 12. Ascospores (21.5–)26.5–75.0(–82.5) × (3.5–)4.0–4.5(–10) µm; on *Corylus* spp. in Europe . *C. corylina*
- 13. Ascospores femuroid, with swollen ends . . . . . 14
- 13. Ascospores cylindrical, without swollen ends . . . 16
- 14. Ascospores elongated with strongly swollen ends; on *A. rubra* in the Pacific Northwest (USA) . . . . . *C. alni-rubrae*
- 14. Ascospores femuroid with slightly swollen ends . 15
- 15. On *A. maritima* or *A. serrulata* in Maryland and near areas . . . . . *C. marylandica*

15. On *A. acuminata* in Central and South America . . . . . *C. amistadensis*
16. Ascospores cylindrical to slightly wider at center, narrowing at ends; on *A. incana* subsp. *tenuifolia* . . . . . *C. alni-tenuifolia*
16. Ascospores cylindrical; on other species of *Alnus* 17
17. Gray stroma surrounding perithecial necks; on *A. viridis* subsp. *sinuata* in northern USA . . . . . *C. alni-sinuatae*
17. Without gray stroma surrounding perithecial necks; on different hosts in North America . . . . . 18
18. Ostiolar region papillated; ascospores (64.0–)74.0–79.5(–107.0) × (3.5–)4.0–5.0(–5.5) μm; on *A. serrulata* in northern USA . . . . . *C. jaklitschii*
18. Ostiolar region not papillated; ascospores (53.5–)62.0–78.5(–99.0) × (3.0–)3.5–4.5 μm; on *Alnus* spp. in North America . . . . . *C. alnicola*

## ACKNOWLEDGMENTS

This work was financially supported by the National Science Foundation Partnerships for Enhancing Expertise in Taxonomy (NSF 03-28364). Additional financial support for field work by LCM was received through Rutgers University, New Brunswick, New Jersey, from the Neyra Fund, the Spencer Davis Research Award from the Department of Plant Biology and Pathology, a Special Study Support Award, and a Graduate School Travel Award as well as a Short-Term Research Fellowship from the Smithsonian Tropical Research Institute and the Myron Backus Award from the Mycological Society of America. The herbaria that loaned specimens are gratefully acknowledged, specifically the Royal Botanic Gardens at Kew (K), the New York State Museum in Albany (NYS) and the Swedish Museum of Natural History in Stockholm (S). Christian Feuillet kindly provided translations of the diagnoses into Latin. Tunesha Phipps and Sasha Allen are acknowledged for their technical expertise in the molecular laboratory. LCM sincerely appreciates the following people for hosting visits for collecting and facilitating the shipment of specimens: Michael Giraud, Adriana Hladki, Tina Hoffman, Christian Lechat, Christophe Lecuru and Ralph Mangelsdorff.

## LITERATURE CITED

- Barengo N, Sieber TN, Holdenrieder O. 2000. Diversity of endophytic mycobiota in leaves and twigs of pubescent birch (*Betula pubescens*). *Sydowia* 52:305–320.
- Barr ME. 1978. The Diaporthales in North America with emphasis on *Gnomonia* and its segregates. *Mycol Mem* 7:1–232.
- Bush MB, Hanselman JA, Hooghiemstra H. 2007. Andean montane forests and climate change. In: Bush MB, Flenley JR, eds. Tropical rainforest responses to climatic changes. Chichester, UK: Praxis Publishing Ltd. p 33–54.
- Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* 91:553–556, doi:10.2307/3761358
- Castlebury LA, Rossman AY, Jaklitsch WJ, Vasilyeva LN. 2002. A preliminary overview of the Diaporthales based on large subunit nuclear ribosomal DNA sequences. *Mycologia* 94:1017–1031, doi:10.2307/3761867
- Chen ZD, Manchester SR, Sun HY. 1999. Phylogeny and evolution of the Betulaceae as inferred from DNA sequences, morphology and paleobotany. *Am J Bot* 86:1168–1181, doi:10.2307/2656981
- Fisher PJ, Petrini O. 1990. A comparative study of fungal endophytes in xylem and bark of *Alnus* species in England and Switzerland. *Mycol Res* 94:313–319, doi:10.1016/S0953-7562(09)80356-0
- Graham A. 1999. The tertiary history of the northern temperate element in the northern Latin American biota. *Am J Bot* 86:32–38, doi:10.2307/2656952
- Gryzenhout M, Wingfield BD, Wingfield MJ. 2009. Taxonomy, phylogeny and ecology of bark-inhabiting and tree-pathogenic Fungi in the Cryphonectriaceae. St Paul, Minnesota: APS Press.
- Kobayashi T. 1970. Taxonomic studies of Japanese Diaporthaceae with special reference to their life histories. *Bull Gov Forest Exp Stn (Japan)* 226:1–242.
- Kowalski T, Kehr RD. 1992. Endophytic fungal colonization of branch bases in several forest tree species. *Sydowia* 44:137–168.
- Mejía LC, Castlebury LA, Rossman AY, Sogonov MV, White JF. 2008. Phylogenetic placement and taxonomic review of the genus *Cryptosporella* and its synonyms *Ophiovalsa* and *Winterella* (Gnomoniaceae, Diaporthales). *Mycol Res* 112:23–35, doi:10.1016/j.mycres.2007.03.021
- Monod M. 1983. Monographie taxonomique des Gnomoniaceae. *Beihefte zur Sydowia. Ann Mycol Ser* 2(9):1–315.
- Nylander JAA. 2004. MrModeltest. Version 2. Program distributed by the author. Uppsala, Sweden: Evolutionary Biology Centre, Uppsala Univ.
- O'Donnell K, Cigelnik E. 1997. Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Mol Phylogen Evol* 7:103–116, doi:10.1006/mpev.1996.0376
- Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Mol Phylogen Evol* 32:1036–1060, doi:10.1016/j.ympev.2004.04.012
- Rehner SA. 2001. EF1 alpha primers. Available online at <http://ocid.nacse.org/research/deephyphae/EF1primer.pdf>
- Reid J, Booth C. 1987. *Winterella*, the correct name for *Cryptospora* and *Ophiovalsa*. *Can J Bot* 65:1320–1342, doi:10.1139/b87-185
- , ———. 1989. On *Cryptosporella* and *Wuestneia*. *Can J Bot* 67:879–908, doi:10.1139/b89-118
- Sherwood-Pike M, Gray J. 1988. Fossil leaf-inhabiting fungi



- from northern Idaho and their ecological significance. *Mycologia* 80:14–22, doi:[10.2307/3807488](https://doi.org/10.2307/3807488)
- Sieber TN. 2007. Endophytic fungi in forest trees: Are they mutualists? *Fungal Biol Rev* 21:75–89, doi:[10.1016/j.fbr.2007.05.004](https://doi.org/10.1016/j.fbr.2007.05.004)
- , Sieber-Canavesi F, Dorworth CE. 1991. Endophytic fungi of red alder (*Alnus rubra*) leaves and twigs in British Columbia. *Can J Bot* 69:407–411, doi:[10.1139/b91-056](https://doi.org/10.1139/b91-056)
- Sogonov MV, Castlebury LA, Rossman AY, Mejía LC, White JF Jr. 2008. Leaf-inhabiting genera of the Gnomoniaceae, Diaporthales. *Stud Mycol* 62:1–77, doi:[10.3114/sim.2008.62.01](https://doi.org/10.3114/sim.2008.62.01)
- Stone JK, Polishook JD, White JF Jr. 2004. Endophytic fungi. In: Mueller GM, Bills GF, Foster MS, eds. *Biodiversity of Fungi, inventory and monitoring methods*. Burlington, Massachusetts: Elsevier Academic Press. p 241–270.
- Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC. 2000. Phylogenetic species recognition and species concepts in Fungi. *Fungal Genet Biol* 31:21–32, doi:[10.1006/fgbi.2000.1228](https://doi.org/10.1006/fgbi.2000.1228)
- Tulasne LR, Tulasne C. 1863. *Selecta Fungorum Carpologia*. Oxford, UK: Oxford Univ. Press [English translation, Grove WB, 1931].
- von Arx JA, Müller E. 1954. Die Gattungen der didymosporen Pyrenomyceten. *Beitr Kryptogamenfl Schweiz* 11:1–434.
- von Höhnelt F. 1917. System der Diaportheen. *Ber Deutschen Bot Gesellschaft* 35:631–638.