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# Long-distance dispersal and speciation of Australasian and American species of *Cortinarius* sect. *Cortinarius*

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***Abstract:*** We present a multigene phylogeny (partial nuc rDNA and *RPB2*) of *Cortinarius* sect. *Cortinarius* (i.e. the *C. violaceus* group), which reveals eight species distributed in Europe, Australasia, South America, Central America and North America. Relaxed molecular clock analyses suggested that diversification began during the Miocene, thus rejecting more ancient Gondwanan origin scenarios among the taxa currently occurring in the northern and southern hemispheres. There was strong support for an Australasian origin of the *C. violaceus* group with initial dispersal to the Neotropics, followed by migration into North America and Europe. A dispersal-extinction cladogenesis model that includes a parameter for founder effects was the most highly supported biogeographic model in the program BioGeoBEARS. A maximum likelihood analysis showed the most recent common ancestor of sect. *Cortinarius* was an angiosperm ectomycorrhizal associate. Ancestral associations at the plant family level, however, were ambiguous. Of eight recovered species-level lineages, *C. violaceus* is the only one that associates with Pinaceae and the only species to associate with both Pinaceae and angiosperms. This analysis showed that long-distance dispersal and founder event speciation have been important factors during evolution of the *C. violaceus* group.

***Key words:*** *Cortinarius violaceus*, diversification, ectomycorrhizal fungi, evolution, phylogeny, phylogeography

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## Introduction

Research in genetic diversity and phylogeographic patterns of closely related macrofungal species generally has revealed higher taxonomic and genetic diversity than previously detected and highly structured biogeographic distributions (Chapela and Garbelotto 2004, Zervakis et al. 2004, Geml et al. 2008, Lumbsch et al. 2008, Ryberg et al. 2008, Dentinger et al. 2010, Morgado et al. 2013, Tamm and Põldmaa 2013). Many of these studies suggest allopatric speciation is important for establishing current species distributions. However, continental-scale disjunct distributions are often best explained by long-distance dispersal (LDD) in studies where fungal taxa are younger than ancient vicariant events (Hibbett 2001, Moncalvo and Buchanan 2008, Matheny et al. 2009, Wilson et al. 2012, Bonito et al. 2013). It is generally assumed that there is tight co-evolution of the ectomycorrhizal fungus and its plant host; so much so that it is often hypothesized that host association might affect speciation and distribution (Chapela and Garbelotto 2004, den Bakker et al. 2007, Kennedy et al. 2011, Rochet et al. 2011, Murata et al. 2013).

In addition, a growing number of macroevolutionary studies support host shifts of ectomycorrhizal (ECM) basidiomycetes from ancestral angiosperm partners (e.g. Fagaceae, Myrtaceae, Ericaceae, Betulaceae, Salicaceae) to coniferous (Pinaceae) partners during the Cenozoic (Chapela and Garbelotto 2004; Hosaka et al. 2008; Matheny et al. 2009; Ryberg and Matheny 2011, 2012k Skrede et al. 2011). Ancestral ECM associations with Pinaceae, however, have been suggested for the agaric genera *Catathelasma* Lovejoy, *Tricholoma* (Fr.) Staude, and *Hygrophorus* Fr., which might have co-diversified with Pinaceae in the northern hemisphere during the late Cretaceous (Ryberg and Matheny 2012), and in the lineage containing *Sebacina* Tul. & C. Tul., which began to diversify during the Paleogene also with conifers (Tedersoo et al. 2014).

In this study we examine *Cortinarius* sect. *Cortinarius* (Pers.) Gray, a group of ECM fungi with a known

distribution on all continents, except Africa and Antarctica, and associated with a diverse array of ECM plant partners of Fagales, Salicaceae, Myrtaceae, Fabaceae and Pinaceae (Moser 1968, Brandrud 1983). It also contains the type species for the genus *Cortinarius*: *C. violaceus* (L: Fr.) Gray. Gasparini (2001) suggested a Gondwanan origin of the *C. violaceus* group due to the greater number of species found in this clade in the southern hemisphere compared to the northern hemisphere. However, such an ancient origin is not likely in that Ryberg and Matheny (2012) calculated a more recent Miocene origin for the group ca. 12 Mya in a relaxed molecular clock analysis. Yet there is a prevailing thought that long-distance dispersal is limited among ECM fungi because soil and climate conditions present barriers to establishment over long distances and because a suitable host may not be found in the new location (Garnica et al. 2009, Peay et al. 2012). Thus we test the hypothesis that species in *Cortinarius* sect. *Cortinarius* are limited by biogeographic barriers and/or plant associates. If correct, then we would expect to see more clades in the group, each clade corresponding to a different geography and/or plant associate.

Species in sect. *Cortinarius* are characterized by a unique suite of biochemical and morphological features. The dark violet or dark purple fruit body reported for *C. violaceus* is due to a vacuolar and encrusting pigment identified as (R)-3′,4′-dihydroxy-β-phenylalanine [(R)-β-dopa] (Gill 2001) (FIG. 1). In addition, most species in the section share the presence of cheilocystidia and pleurocystidia and a trichodermial pileipellis (Moser 1983). All members have a color change reaction to KOH to red in all parts of the fruit body tissues.

*Cortinarius violaceus* is regarded as a widely distributed species, occurring in Europe, eastern Asia, southeastern Asia (Malaysia), North America, Central America, South America (Colombia), Papua New Guinea, Australia and New Zealand (Moser 1968, 1986; Bougher and Syme 1998; Watling and Lee 1999; Ridley 2006). Moser (1967, 1976) regarded *C. violaceus* and *C. hercynicus* (Pers.) M.M. Moser as two distinct species, while Brandrud (1983) treated *C. hercynicus* as a variant of *C. violaceus* and then as a subspecies (Brandrud et al. 1990), the former having ellipsoid-subglobose basidiospores and associating with coniferous trees, the latter having amygdaliform-ellipsoid basidiospores and associating with broadleaf trees.

Six additional species in sect. *Cortinarius* have been described from the Neotropics and/or southern hemisphere. *Cortinarius kerrii* Singer & I.J.A. Aguiar was described from the state of Amazonas in Brazil in campinarana-like vegetation (Singer et al. 1983). *Cortinarius subcalyptrosporus* M.M. Moser, *C. paraviolaceus* M.M. Moser and *C. atroviolaceus* M.M. Moser were described from Sabah, Malaysia (Moser 1986). *Cortinarius subcalyptrosporus* is characterized by the presence of a perisporium, a loosening of the outer spore wall (Moser 1986). *Cortinarius atrolazulinus* M.M. Moser was described from New Zealand (Moser 1986). In addition to having been found in Sabah, Malaysia, *C. atroviolaceus* and *C. atrolazulinus* also have been reported in New Zealand with *Nothofagus* (Moser 1986).

FIG. 1. *Cortinarius violaceus* auct. mult. in Mount Baker-Snoqualmie National Forest, Washington, USA. Bar = 1 cm. Photo by Noah Siegel.

*Cortinarius gayi* E. Horak was not placed within a section in the genus *Cortinarius*, but it has the same violet coloration and KOH reaction as other members of sect. *Cortinarius* according to Horak (1980a). It was described from *Nothofagus* forest in Argentina (Horak 1980a). Additional species have been placed within sect. *Cortinarius* solely due to their violet coloration by their respective authors. Moser (1986) cast some doubt about whether *C. paraviolaceus* belongs in sect.

*Cortinarius* due to the absence or rarity of cheilocystidia and pleurocystidia. *Cortinarius austroviolaceus* Gasparini was described from Tasmania by Gasparini (2001), who suggested an alliance with species of sect. *Cortinarius*. An RFLP analysis by Chambers et al. (1999) indicated that an Australian collection of *C. violaceus* was not conspecific with the northern hemisphere *C. violaceus*, but no follow-up studies have occurred. In total, eight species have been ascribed to sect. *Cortinarius* worldwide.

Here we document global genetic and taxonomic diversity of *Cortinarius* sect. *Cortinarius* guided by multigene phylogenetic analyses based on three nuclear gene regions: nuc rDNA ITS1-5.8S-ITS2 (ITS), the D1-D2 domains of the 28S region and the second largest subunit of the RNA polymerase II gene (*RPB2*). In addition, we reconstruct historical ranges and test the hypothesis that sect. *Cortinarius* has an Australasian origin because the majority of the extant species reside in this region. If so, an ancestral host association might be predicted with the southern hemisphere *Nothofagus* (southern beech) because this genus has been a dominant ECM partner at southern latitudes since its origin in the late Cretaceous (Malloch et al. 1980, Hill 1992, Bougher et al. 1994). An ancestral association with Myrtaceae is a possibility if the group originated some time after the Cretaceous.

## MATERIALS AND METHODS

*Taxon sampling, DNA extraction, amplification and sequencing* .—Collections sequenced in this study are summarized (SUPPLEMENTARY TABLE I). *Cortinarius kerrii* and *C. gayi*, both described from South America and southeastern Asian collections of *C. atroviolaceus*, *C. subcalyptrosporus* and *C. paraviolaceus*, were not included in this study because requests for loans of the types were declined. However, we were able to obtain collections identified as the Malaysian species (with the exception of *C. paraviolaceus*) from New Zealand. Multiple collections of an undescribed species from Guyana, in the Guiana Shield region of northeastern South America, also were obtained.

DNA extraction, PCR and sequencing protocols follow Matheny et al. (2010). We used an E.Z.N.A high performance (HP) fungal DNA extraction kit (Omega Bio-Tekfor, Norcross, Georgia) for specimens older than 20 y. Primers ITS1F/ITS4 (White et al. 1990) were used to amplify the ITS region, including the 5.8S rDNA region, except when DNA quality was poor, in which case primer pairs ITS1F/ITS2 and 5.8SR/ITS4 (White et al. 1990) were used. LR0R/LR5 (White et al. 1990) was used to amplify the 28S rDNA (28S) region. Primers b6F/b7.1R were used initially to amplify the most variable region of *RPB2* (Liu et al. 1999, Matheny 2005). The *C. violaceus* specific *RPB2* PCR primers CviolF (5′–GAA TCC CTG GAA GAR CAC TCC–3′) and CviolR (5′–CTT ACT TGG TTR TGG TCK GG–3′) were designed and used to obtain additional *RPB2* sequences.

*Alignment and phylogenetic analyses.*—Alignments were produced in MAFFT 7.110 using the e-INS-i algorithm (Katoh and Standley 2013) and optimized manually. All nucleotide positions were used for phylogenetic analysis. ITS, 28S and *RPB2* alignments were concatenated after individual alignment and inspection for intergenic conflict following Baroni and Matheny (2011). Two datasets were assembled. One, a supermatrix of 100 ITS, 24 28S and 29 *RPB2* sequences, was generated to assess overall genetic diversity within sect. *Cortinarius* worldwide. This dataset comprises sequences from 100 taxa. *Cortinarius vitiosus* (M. M. Moser) Niskanen, Kytöv., Liimat. & S. Laine (JN114094–JN114096), *C. walpolensis* A.A. Francis & Bougher (DQ328131), *C.* cf. *submeleagris* (AY669638), *Cortinarius* sp. (sect. *Dermocybe*) (HQ604652), and uncultured *Cortinarius* sequences (JX316449/JX316363) were used as outgroups based on nearest BLAST hits to *C. austroviolaceus* and Holarctic *C. violaceus* ITS sequences. We created a second dataset to generate a time-calibrated tree to map historical geographic ranges and reconstruct ancestral plant host associations. This dataset consisted of the eight taxa in the *C. violaceus* group and *C. vitiosus* and *C. austroviolaceus* as outgroups based on prior phylogenetic analyses. Alignments are available in TreeBASE under accession number S16049 (http://purl.org/phylo/treebase/phylows/study/TB2:S16049).

PartitionFinder 1.10 (Lanfear et al. 2012) was used to determine gene partitions and models for the 100 species dataset under the Bayesian information criterion (BIC). The alignment was partitioned into three segments: (ITS) (28S,*RPB2* sites 1+2) (*RPB2* site3). The HKY+G, HKY+I and K80+G models were used in MrBayes 3.2 (Ronquist et al. 2012) for the three partitions, respectively. Four chains were run 20 000 000 generations using two independent runs sampling trees from the posterior distribution every 5000 generations. When calculating posterior probabilities, the first 1000 trees were burned from each run. RAxML 7.2.8 (Stamatakis 2006) was used to reconstruct a maximum likelihood (ML) tree with 1000 bootstrap replicates under a GTRGAMMAI model. Mesquite 2.75 (Maddison and Maddison 2011) was used to generate pairwise distance matrices for the ITS, 28S and *RPB2* gene sequences, respectively, using the Kimura 2-parameter model, which can account for superimposed substitutions (Felsentein 2004).

*Relaxed molecular clock analysis.*—An ultrametric tree was created in BEAST 1.8.0 (Drummond et al. 2012) using an uncorrelated lognormal clock. The alignment was partitioned into ITS, 28S and *RPB2*, each with their own HKY + G substitution models. The tree was calibrated at the node encompassing sect. *Cortinarius*, which is dated at 12.1 ± 1.0 MYA following Ryberg and Matheny (2012). A uniform distribution was used as a prior for the uncorrelated lognormal clock. BEAST ran with a chain length of 10 000 000 generations, saving a tree every 1000 generations. This was repeated four times. Tracer 1.5 (Rambaut and Drummond 2009) was used to determine that sufficient ESS values (> 200) were obtained. The burn-in value was

determined to be sufficient by examining the ln L trace plot. These four runs were combined in LogCombiner 1.8.0 (Drummond et al. 2012) with a final burn-in of 10 000 trees.

Mesquite 2.75 (Maddison and Maddison 2011) was used to reconstruct ancestral plant host associations using the default maximum likelihood algorithm. BioGeoBEARS (Matzke 2012, 2014) was used to reconstruct ancestral geographic ranges under a dispersal extinction cladogenesis + jumping (DEC+J) model.

*Haplotype analysis.*—The SNAP Workbench (Price and Carbone 2005, Aylor et al. 2006) was used to determine the number of ITS haplotypes present in *C. violaceus* auct. mult.

## RESULTS

*Taxonomic and genetic diversity within sect. Cortinarius.*—Eight species-level lineages, together forming a monophyletic group, were identified from Australia, New Zealand, Guyana, Costa Rica, Colombia southeastern USA and the holarctic. These lineages were recognized as *C. violaceus* auct. mult., *Cortinarius* sp. CR1, *Cortinarius* sp. CR2, *Cortinarius* sp. NA1, *Cortinarius* sp. SA1, *C. violaceus* sensu Moser 1986, *Cortinarius* sp. AU1, and *Cortinarius* sp. AU2 (FIG. 2). Intraspecific variation was 1.0% or less across all loci examined (SUPPLEMENTARY TABLE II). Interspecific variation was 2.0% or greater at the ITS locus (SUPPLEMENTARY TABLE III). *Cortinarius austroviolaceus* was placed with the outgroup taxa outside sect. *Cortinarius*. This placement is consistent with the fact that *C. austroviolaceus* lacks pleurocystidia while members of sect. *Cortinarius* possess them. Attempts to sequence the type specimen of *C. atrolazulinus* (ZT69-276) were unsuccessful.

*Cortinarius violaceus* auct. mult. was the most widely distributed species in our dataset, occurring in eastern and western North America and Europe. However, the name has historically been broadly applied to what are now known to be different phylogenetic lineages (Bougher and Syme 1998, Halling and Mueller 2005). Minor intraspecific variation was detected within *C. violaceus* auct. mult., but most internal subgroups exhibited little genetic distance and poor branch support (FIG. 2). In addition, at least two haplotypes appear to be common and widespread, occurring both in North America and Europe (TABLE I). No support was found for genetic differences between individuals associated with coniferous hosts versus those with hardwoods (FIG. 2). Within the Americas, however, four lineages (CR1, CR2, SA1, NA1) were detected that, based on current sampling effort, have been found either in Costa Rica and Colombia, Costa Rica, Guyana or Florida, respectively. The name *C. violaceus* has been applied to some of these taxa (e.g. Halling and Mueller 2004), but these lineages represent undescribed species. Morphological data also support their separation. These new taxa will be presented in a forthcoming paper. The two sympatric species in Costa Rica (CR1 & CR2) differed in the size and shape of their basidiospores as well as the presence or absence of caulocystidia. The Guyana species (SA1) had a large stipe length to cap width ratio. The species found in Florida (NA1) did not have caulocystidia in contrast to *C. violaceus* auct. mult., which has abundant caulocystidia.

We wanted to test whether the pigment that makes the *C. violaceus* group purple is the same pigment that makes *C. austroviolaceus* purple. We were not able to extract the purple pigment ((R)-β-dopa) from any dried specimens due to the tendency of the pigment to oxidize quickly to brown. Future attempts to determine the source of the purple pigment in *C. austroviolaceus*, which falls outside the *C. violaceus* group, need to be based on freshly collected, undried specimens.

Collections of sect. *Cortinarius* from New Zealand and Australia sorted into three lineages: the first, *C. violaceus* sensu Moser 1986, best matches Moser's description of *C. violaceus* specimens collected from Sabah, Malaysia, and Papua New Guinea and include the presence of pileocystidia and pale context consistent with Moser's concept (Moser 1986). This species, however, will require a new name because it obviously is not *C. violaceus* based on our phylogenetic results (FIG. 2). The second, *Cortinarius* sp. AU1, is trans-Tasman in distribution having been recorded with the myrtaceous plant genera *Leptospermum* in New Zealand and *Eucalyptus* in southern Australia. This species is remarkably similar to *C. atroviolaceus* originally described from Borneo at high elevation (Moser 1986) but with unknown plant associates. Candidate plant associates from Borneo include members of the Ericaceae, Fagaceae and Myrtaceae based on possible ECM plant groups that occur at this elevation (Beaman et al. 2000, Beaman and Anderson 2004). *Cortinarius atroviolaceus* (from Malaysia with unknown plant associates) and *Cortinarius* sp. AU1 (from Australia and New Zealand with Myrtaceae) are likely ecologically differentiated, hence we treat them as different species. The third, *Cortinarius* sp. AU2, is unique among the *C. violaceus* group in that it has a smooth pileus instead of a squamulose surface that all other members of the group possess. *Cortinarius* sp. AU2 was interpreted as *C. violaceus* by Bougher and Syme (1998). None of the Australasian collections examined here have calyptrate spores indicative of *C. subcalyptrosporus* originally described from Malaysia. Thus we doubt that *C. subcalyptrosporus* is actually present in

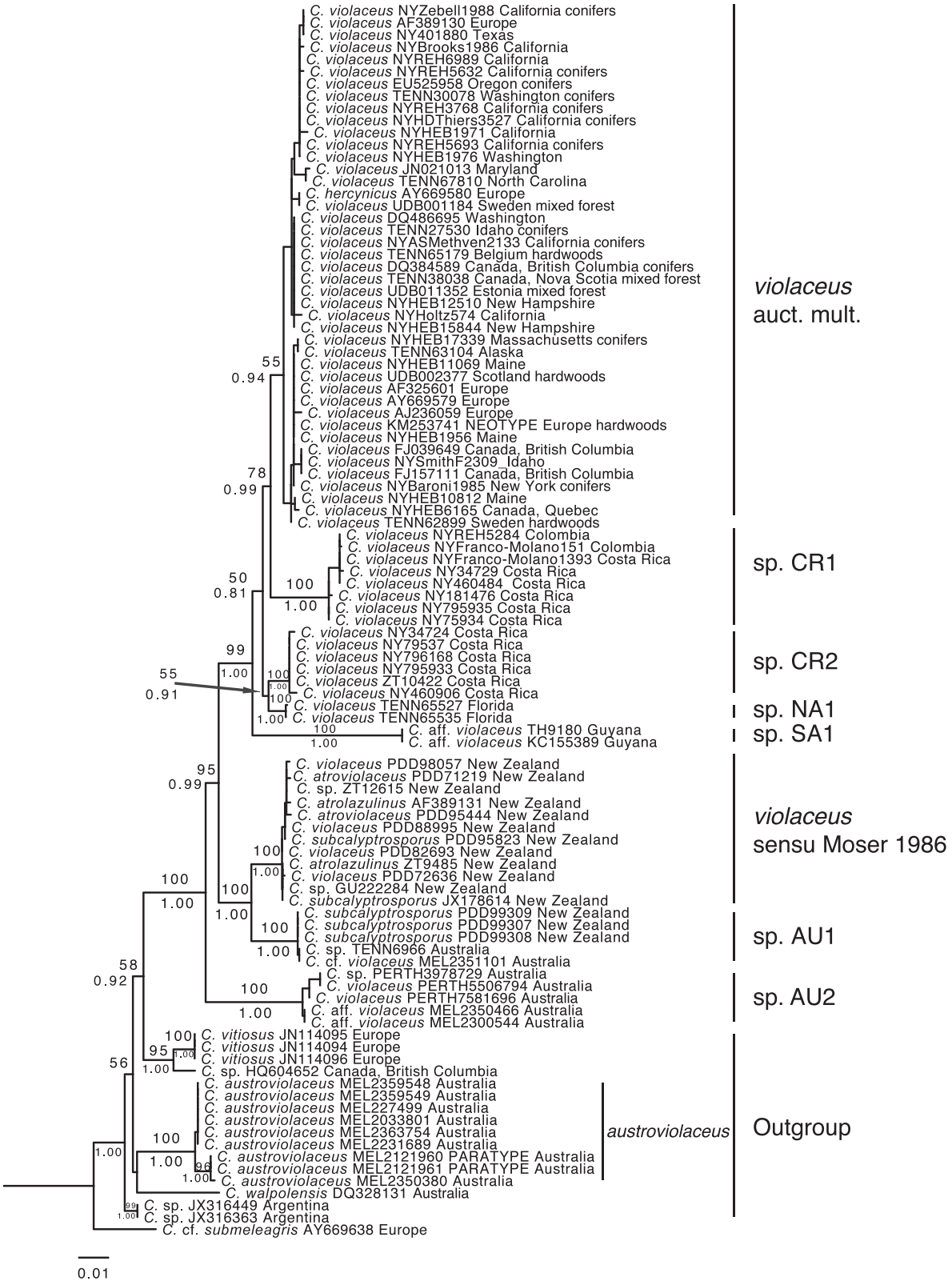


FIG. 2. Maximum likelihood (ML) phylogenetic tree of the combined nuclear ITS, 28S and *RPB2* sequences. ML Bootstrap support more than 50% is above nodes and Bayesian posterior probabilities above 0.90 indicated below nodes. Specific epithets are those designated on original collections. Following the specific epithet are collection number, GenBank accession number or UNITE number followed by the country (or state) in which the specimen was found. Forest type is indicated for *Cortinarius violaceus* auct. mult. where known.

TABLE I. Number, geography and DNA sequences of ITS haplotypes in *C. violaceus* auct. mult.

| Haplotype | No. of sequences | Geography | Sequence |
|---|---|---|---|
| H1 | 17 | EU, NA | …CCTATAAACCGGTATT… |
| H2 | 3 | NA | …TCTATAAACCGGTGTT… |
| H3 | 1 | NA | …CGTGGAAATCGGTATT… |
| H4 | 1 | NA | …CCCAGAAGCCGGAACT… |
| H5 | 8 | EU, NA | …CCTGGAAATCGGTATT… |
| H6 | 2 | EU | …CCTGTAAACCGGTATC… |
| H7 | 1 | NA | …CCTAGAAGCCGGAACT… |
| H8 | 1 | NA | …CCTATTAACCGGTATT… |
| H9 | 1 | EU | …CCTATATACCGCTATT… |
| H10 | 1 | NA | …CCTATAAACGAGTATT… |
| H11 | 1 | NA | …CCTATAAACCAGTATT… |

Australia and New Zealand based on collections examined to date.

We examined a collection (KEP S-S 1419) that was reported as *Cortinarius* cf. *violaceus* found in lowland dipterocarp forest in Semangkok Forest Reserve, Selangor, Malaysia (Watling and Lee 1999). Our examination of this specimen shows an absence of pleurocystidia and cheilocystidia and tissues fail to turn red in KOH. Thus the collection lacks the key diagnostic features of sect. *Cortinarius*. A BLAST query using the ITS region places it 93% similar to the New Zealand species *C. chalybeus* Soop, which belongs to *Cortinarius* section *Purpurascentes* (Soop 2008).

*Phylogeographic analyses.*—*Cortinarius* sect. *Cortinarius* appears to have initially diversified ca. 14–10 Mya with a mean crown group origin at ca. 12 Mya (FIG. 3). Ancestral area analysis (FIG. 4) suggested the lineage diversified initially in Australasia in association with an angiosperm host(s), but an ancestral family designation is ambiguous. Fagaceae, Fabaceae, Myrtaceae/Casuarinaceae and Nothofagaceae are equally probable hosts. Thus these data do not strongly support or reject an ancestral association with Nothofagaceae as proposed by Moser (1986). The split between Australasian and Euro-American groupings is estimated between 13–7 Mya (mean 10 Mya) and favors a long-distance dispersal into the Neotropics perhaps in association with a fagaceous host ($P = 0.52$), but this has a relatively low probability.

*Cortinarius* sp. SA1 and its host (*Dicymbe*) are restricted to the Guiana Shield. This species is sister to a clade containing species currently present in Central America, North America and Europe (*C. violaceus* auct. mult., *Cortinarius* sp. NA1, *Cortinarius* sp. CR1, *Cortinarius* sp. CR2), all of which have been recorded in association with *Quercus*. During the next 10 000 000 y, the closing of the Panamanian land bridge would have facilitated an interchange of species between North and South America. The intercontinental *C. violaceus* appears recently derived from this group of American species and today features what is likely a holarctic distribution. Either sympatric or allopatric speciation ensued in Central America on the same *Quercus* host species, while two other speciation events resulted in one southeastern North American lineage (*Cortinarius* sp. NA1 remaining on *Quercus*) and *C. violaceus* auct. mult. that is found with Fagaceae, Pinaceae and Salicaceae.

To test whether a host association with *Quercus* originated in South America or Central America, we compared the dates for speciation of the *Quercus*-associating lineages with the dates of fossilized *Quercus* pollen in Central and South America. The host switch to *Quercus* occurred 9.3–2.9 mya (FIGS. 3, 4). *Quercus* is detected in the Gatun Formation on the north side of the Isthmus of Panama 11.4–5.8 mya (Collins et al. 1996) before the land bridge connecting North and South America was formed. *Quercus* is not detected in South America until 330 000 y ago in Colombia (Graham 1999). The late arrival of *Quercus* in South America indicates that the arrival of *Cortinarius* sp. CR1 in Colombia is likely a recent range expansion. Due to the gap in the fossil record, it cannot be determined whether the association was established before or during the formation of the land bridge connecting North and South America 3.5–2.5 mya (Graham 1999).

BioGeoBEARS gave a higher log likelihood (lnL= −7.3) for the dispersal-extinction-cladogenesis (DEC) model that incorporated a parameter for founder-event speciation (DEC+J) when compared to the standard DEC model (lnL= −14.9) as implemented in LAGRANGE (Ree and Smith 2008). When the likelihood of the DEC model was compared to the DEC+J model, which incorporates founder-event speciation (j-parameter), the latter was statistically better than the DEC model ($X^2 = 15.23$, df = 1,

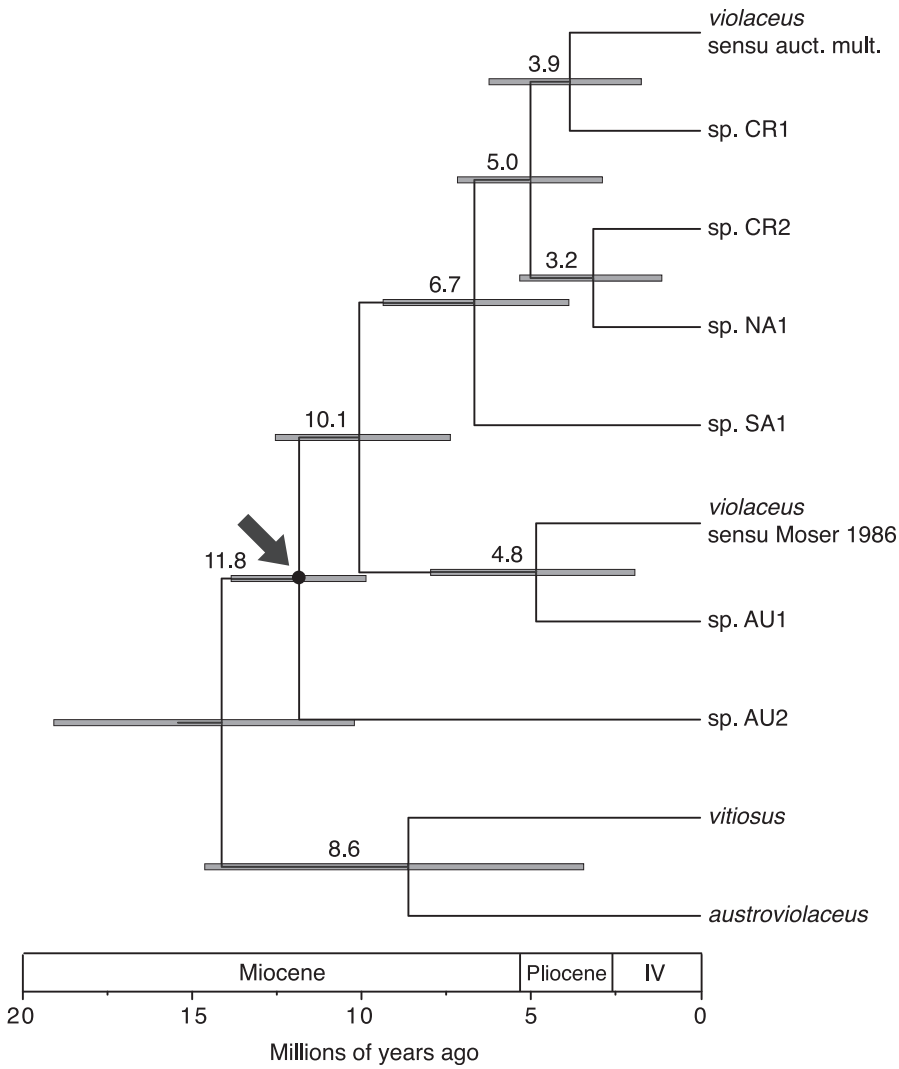


FIG. 3. Chronogram obtained with the uncorrelated log normal relaxed-clock method (implemented in BEAST) with an age constraint (12.1 ± 1.0 mya) at the node indicated by the arrow. Numbers correspond to mean age estimates (in million years), and gray bars represent 95% credibility intervals.

*P value* = 9.5 $\times 10^{-5}$; AIC weight ratio 746.2:1). Indeed founder event speciation was a dominant process at play (founder-event [j] = 0.349, dispersal [d] = 1.0 $\times$ $10^{-12}$, extinction (e) = 1.0 $\times$ $10^{-12}$).

The number and geographic distribution of ITS haplotypes in *C. violaceus* auct. mult. is provided (TABLE I). Of 43 sequences, 11 haplotypes were found. Two haplotypes were present in both Europe and North America, seven haplotypes were detected only in North American and two different haplotypes were found exclusively in Europe.

## DISCUSSION

We have uncovered hidden and novel taxonomic and genetic diversity in *Cortinarius* sect. *Cortinarius*. From the broad areas sampled across the globe, we recovered eight species-level monophyletic groups. While we used a phylogenetic species concept (Taylor et al. 2000), interspecific variation was 2% or less in the ITS region, which is in agreement with other studies that found a 2.0% dissimilarity threshold value optimal to delimit *Cortinarius* species (Stefani et al. 2014). Intraspecific variation was 1% or less. These include putative new species from Costa Rica (two), Guyana (one), Australia (two), New Zealand (two) and another from the Gulf Coast of Florida (FIG. 2). *Cortinarius austroviolaceus*, as the specific epithet suggests, originally was thought to share an alliance with sect. *Cortinarius* based on the shared violaceous basidioma colors (Gasparini 2001), but this species lies outside the sectional clade as identified here and

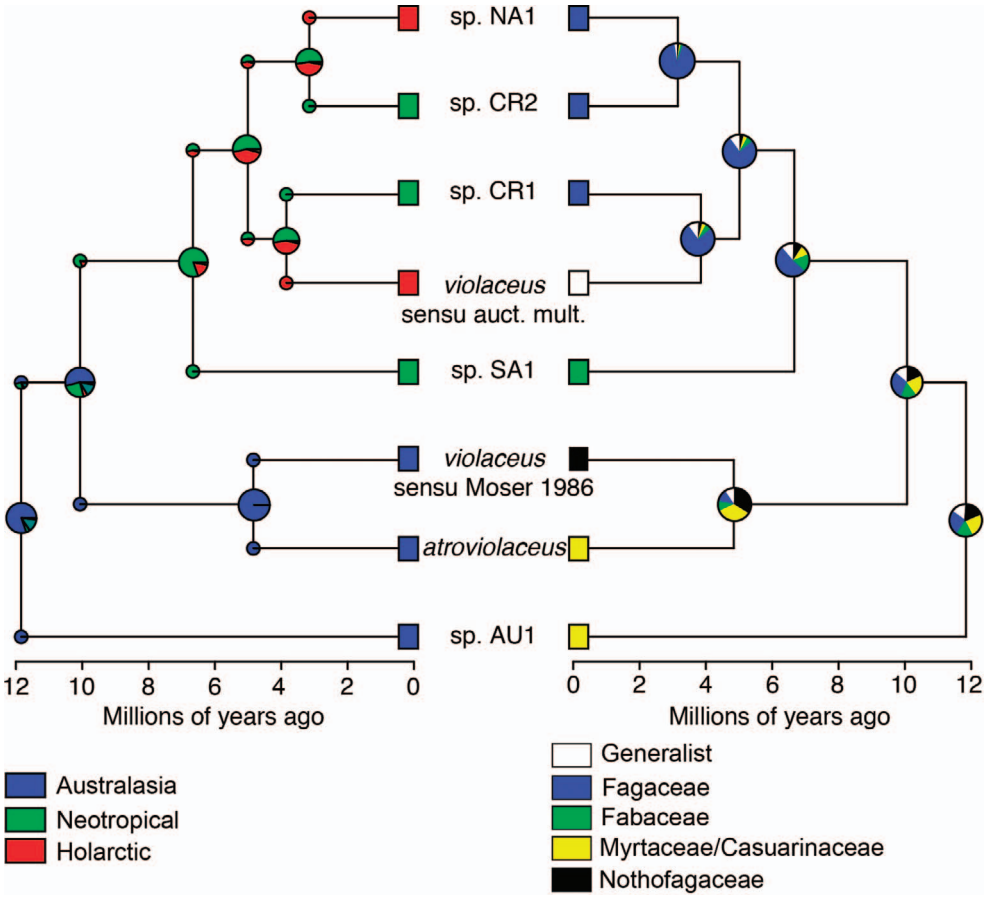


FIG. 4. Reconstruction of historical ranges produced in BioGeoBEARS is represented on the left. Occurrence in two (or more) locations is represented as a mixture of two or more colors. Ancestral state reconstruction of host association, using maximum likelihood, as implemented in Mesquite, is on the right.

also lacks the diagnostic pleurocystidia present in other members of the group. Due to limits of taxon sampling, we are unable to suggest into which *Cortinarius* section or subclade *C. austroviolaceus* should be placed. BLASTN results suggested that *C. austroviolaceus* is related to the secotioid *C. walpolensis* from Australia or a cortinarioid fungus known only as an Argentinian environmental sequence.

In light of the results reported here, the circumscription of *Cortinarius* sect. *Cortinarius* will require emendation. Moser (1983) defined *Cortinarius* sect. *Cortinarius* in part as having a trichodermial pileipellis. However, *Cortinarius* sp. AU2 was found to belong to the *C. violaceus* group but possesses a repent cutis. Thus the section should be defined more restrictively by the combination of the universal deep violet coloration and the presence of both cheilocystidia and pleurocystidia with a typical presence of a trichodermial pileipellis.

*Cortinarius violaceus* auct. mult. is found across North America and Europe with a wide variety of potential ECM host plant genera in the families Pinaceae, Fagaceae, Betulaceae and Salicaceae. While sampling of European *C. violaceus* auct. mult. was limited in this study, we detected no significant genetic difference at the species level between what would be named *C. violaceus* and *C. hercynicus* based on host association. Additional sampling of specimens identified as *C. hercynicus* are necessary to confirm the preliminary results here and the suggestion of Brandrud (1983) that *C. hercynicus* be treated as a variety of *C. violaceus*.

We found one taxon, *C. violaceus* sensu Moser 1986, that best matches the species description for *C. violaceus* described from Malaysia and Papua New Guinea by Moser (1986). It differs from *C. atroviolaceus* and *C. atrolazulinus* by the size and shape of its spores. Moser (1986) documented this taxon as having characteristically smaller basidiomata and possessing pileocystidia, which distinguish it from *C. violaceus* auct. mult. All collections examined by us belonging to *C. violaceus* sensu Moser 1986 occur in

New Zealand with *Nothofagus*. Because *C. violaceus* sensu Moser 1986 is not conspecific with *C. violaceus* auct. mult., it requires formal description.

Our phylogenetic analyses indicate that the *C. violaceus* group has its origins in Australasia. Three species-level lineages were recovered from this region. *Cortinarius* sp. AU1 is found with *Eucalyptus* and *Allocasuarina* in eastern Australia and with *Leptospermum* in New Zealand. *Cortinarius* sp. AU2 occurs in Western Australia and Tasmania with *Eucalyptus* and *Allocasuarina* in sclerophyll forest. *Cortinarius violaceus* sensu Moser 1986 occurs in New Zealand with *Nothofagus* as mentioned above. However, our sampling of the global molecular diversity of the *C. violaceus* group is incomplete. Species are known to occur in Papua New Guinea and southeastern Asia (Malaysia). Additional species in the *C. violaceus* group could be discovered in undersampled locations such as the *Nothofagus* forests of southern South America and the caesalpionioid forests of Africa.

Long-distance dispersal and founder event speciation appear to have featured prominently in the historical biogeography of the *C. violaceus* group, which was estimated to have initially diversified during the Miocene (Ryberg and Matheny 2012). Within the clade, three Australasian lineages form a paraphyletic group from which the five Euro-American lineages are derived. By the Miocene, all of the continents were more or less at their present location. Thus, long-distance dispersal is the most likely means by which the species reached the Americas from Australasia, as well as to New Zealand. Counter to previous thinking, long-distance dispersal of ECM fungi may be a relatively frequent phenomenon. Similar to the data presented here, Geml et al. (2012) found that multiple ECM species (including *Cortinarius* spp.) colonized the remote Svalbard Archipelago via long-distance dispersal as recently as 10 000 y ago post glaciation. The nearest land is more than 400 km away.

Founder event speciation was an important parameter included in our biogeographic analyses. Founder effect speciation describes a process whereby a small subset of a larger population undergoes a rare dispersal that results in instant genetic isolation (Templeton 2008). This process has been discussed extensively in island biogeography studies and is applicable to our dataset, in that continents may act as islands separating populations by oceanic barriers. Founder effect speciation explains the origin of species of the *C. violaceus* group in South America, Central America and North America, their ancestors having arrived from Australasia. However, migration from Australasia into southeastern Asia and then into the holarctic is a pattern we cannot reject.

*Cortinarius* sp. SA1 appears to have arrived in the Neotropics 13–7 Mya via long-distance dispersal from Australasia or southeastern Asia, possibly via trade winds and suggests a host shift to Fabaceae. We expect *C. kerrii* from the northern Brazilian Amazon to be closely related to *Cortinarius* sp. SA1 due to their co-occurrence in the greater Guiana Shield region in association with fabaceous hosts.

It is possible that the direct ancestor of *Cortinarius* sp. SA1 arrived in Central America and became established with *Quercus* before arriving in Guyana. Regardless, whether *Cortinarius* sp. SA1 arrived in Guyana directly from Australasia or from Central America, it would have had to arrive there via long-distance dispersal because none of the host ranges would have overlapped with that of the Guiana Shield endemic *Dicymbe*.

Our analyses are ambiguous about the phylogeographic origins of the Costa Rican species. It is not clear whether they evolved from holarctic or from Neotropical ancestors. Members of the Boletaceae appear to have originated within North America and migrated south with their plant associates (*Quercus*) as the range of these plants expanded into South America (Halling 1996, Halling et al. 2008, Kennedy et al. 2011). Evidence supporting this hypothesis comes from the observation that species found in Costa Rica and Mexico are morphologically more similar to, and in many cases considered conspecific with, North American species, relative to those of lowland tropical and temperate South America (Mueller and Halling 1995, Halling and Mueller 2002, Montoya et al. 2010). However, few phylogenetic studies involving ECM fungi, with complete sampling throughout the Americas, have been completed to corroborate these patterns. In this study the arrival of *Cortinarius* sp. CR1 in Colombia seems to agree with this pattern of southward migration with *Quercus*. Diversification occurred in the *C. violaceus* group in the Americas during the great American interchange, and it appears that dispersal could have occurred either northward or southward.

Within the genus *Cortinarius* a substantial number of species and clades are shared on different continents in the northern hemisphere (Peintner et al. 2004, Garnica et al. 2009, Harrower et al. 2011). No southern hemisphere species occur naturally in the northern hemisphere. Few clades of *Cortinarius* include both northern and southern hemisphere endemics (Stefani et al. 2014). Representatives of southern hemisphere clades include the *Splendidi*, known only from Australia, and an unnamed clade known from Australia and South America (Stephani et al. 2014). However, multiple dispersals across independent lineages between the northern and

southern hemispheres have likely taken place during diversification of *Cortinarius*.

Few studies of phylogeography among *Cortinarius* have been completed. Garnica et al. (2011) examined four species complexes in section *Calochroi* that have disjunct distributions between North America and Europe. One species complex, the *C. arcuatorum* group, was interpreted as having a widely distributed ancestral population that diverged into distinctive sympatric populations in North America, including one species in Costa Rica (*C. jardinensis* Garnica, Ammirati & Halling). The authors focused on allopatric populations between Europe and North America and favored the hypothesis that species migrated into Europe by land via the Beringian land bridge (BLB). However, long-distance dispersal could not be ruled out.

*Cortinarius violaceus* auct mult. is the only species in the *C. violaceus* group that could have migrated across the BLB because it is the only species in the group that is known to currently occur in Europe (if we assume no extinction has occurred). We do detect some population substructure within *C. violaceus* auct mult., but its full elucidation is currently limited by the low taxon sampling of Asian and European taxa. A microsatellite analysis might be a better approach for answering questions about the population genetic history in this species. Among the 43 *C. violaceus* auct. mult. ITS sequences analyzed here, we observe some identical sequences shared between North American and European samples, but nine haplotypes are seemingly rare and more geographically restricted. Nevertheless we suspect that frequent long-distance dispersal or migration (gene flow) between Europe and North America is responsible for the low genetic diversity observed in this lineage.

The ancestral plant host of the *C. violaceus* group was most likely an angiosperm associate (FIG. 4). Indeed *C. violaceus* auct. mult. was the only species to occur with three or more angiosperm hosts and the only species to occur with Pinaceae. This ability to associate with a wide range of hosts in this species may have contributed to its ability to expand its distribution throughout North America and Europe and likely into Asia.

In some cases sister species can be differentiated based on plant associations and in other cases, on ecology. Based on present data, species of the *C. violaceus* group in New Zealand appear to occupy different niches with either *Leptospermum* or *Nothofagus*. However, some species of agarics, like some *Inocybe* spp., may associate with either plant partner in New Zealand (Horak 1979, 1980b). In Australia species occupy different niches depending on the environmental characteristics (e.g. sclerophyll or rainforest). *Cortinarius* sp. SA1 from South America, however, is unique in that it apparently associates with *Dicymbe* and possibly other ECM plant genera such as *Aldina* and *Pakaraimaea*. This association may contribute to the restriction of *Cortinarius* sp. SA1 to the Guiana Shield. In Costa Rica two different species are sympatric and associate with the same *Quercus* host species. They may have speciated during or after the formation of the Talamanca Mountains 5.5–3.5 Mya (Gräfe et al. 2002). Costa Rica was an archipelago before the formation of the mountains (Coates and Obando 1996). Thus these two Costa Rican lineages could have arisen through allopatric speciation from isolation on two sides of a mountain range or from origination elsewhere with re-colonization of Costa Rica at a later date.

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