

PHYLOGENETIC ANALYSIS PLACES THE PHIALOPHORA-LIKE ANAMORPH GENUS CADOPHORA IN THE HELOTIALES

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ABSTRACT

Using ITS and 28S (LSU) rDNA sequences, members of the genus *Cadophora* are shown to be anamorphs of the Helotiales (discomycetes) and distinct from the morphologically similar anamorph genus *Phialophora*. The rDNA sequences of *Cadophora* spp. were similar to those of the teleomorph genera *Mollisia*, *Pyrenopeziza*, and *Tapesia* (which have anamorphs in *Ramulispora*) and to the anamorph genera *Phialocephala* and *Rhynchosporium*. The type species of *Cadophora* is *C. fastigiata*, and *C. malorum* is another common species in the genus. Also included are *C. finlandia* comb. nov., the soybean pathogen *C. gregata* comb. nov., *C. lagerbergii*, *C. luteo-olivacea* comb. nov., and *C. melinii*. *Phialophora atra* and *C. heteroderae* are synonymized with *C. malorum*. *Phialophora goidanichii* is synonymized with *C. luteo-olivacea*.

KEY WORDS: *Phialocephala*, *Ramulispora*, *Rhynchosporium*, *Pyrenopeziza*, *Tapesia*

INTRODUCTION

The anamorph genus *Phialophora* Medlar has been used for a wide range of species with simple, little-differentiated conidiophores, flask-shaped to straight phialides, and hyaline to pigmented conidia. Many of these species have not been connected to teleomorphs, but the genus is clearly polyphyletic (Gams 2000). *Phialophora* is typified by *P. verrucosa* Medlar and connected to the genus *Capronia* Sacc. (Chaetothyriales, Herpotrichiellaceae) (Haase et al., 1999, de Hoog et al., 2000), but phialophora-like anamorphs are known in at least three orders of ascomycetes.

As reviewed by Gams (2000), teleomorphs with connections to phialophora-like anamorphs are common in the Helotiales. Species of *Ascocoryne* J.W. Groves & D.E. Wilson have anamorphs in *Coryne* Nees, which is similar to *Phialophora*, as are the *Myrioconium* Syd. anamorphs of some Sclerotiniaceae. The anamorph of *Hyphodiscus hymeniophilus* (P. Karsten) Baral (= *Cistella hymeniophila* (P. Karst.) Korf) is *P. rhodogena* (Mangenot) W. Gams (= *Catenulifera rhodogena* (F. Mangenot) Hosoya) (Hosoya 2002). Using 18s and 28s rDNA sequences, Paulin and Harrington (2000) showed that the soybean pathogen *P. gregata* (Allington & Chamberlain) W. Gams has affinities with the Helotiales. The Dermateaceae, in particular, commonly have phialophora-like anamorphs, such as the *Cystodendron* Bubák anamorphs of species of *Tapesia* (Pers.) Fuckel (Aebi 1972). *Phialophora tracheiphila* (Sacc. & D. Sacc.) Korf is

associated with the teleomorph *Pseudopezizula tracheiphila* (Müll.-Thurg.) Korf & Zhuan (Korf et al., 1986).

Gams (2000) proposed that the phialophora-like anamorphs of the Dermateaceae, such as *Mollisia* (Fr.) P. Karst. and *Pyrenopeziza* Fuckel (Le Gal & Mangenot 1960, 1961), might be accommodated in *Cadophora* Lagerberg & Melin, species of which have pale to hyaline collarettes on top of their phialides. *Cadophora* was synonymized with *Phialophora* by Conant (1937), but the genus name *Cadophora* has often been used for some common bluestain fungi such as *C. fastigiata* Lagerberg & Melin, the type species of *Cadophora*. Greenleaf and Korf (1980) isolated a fungus similar to *C. fastigiata* from *Mollisia dextrinophila* Korf.

We used morphology and rDNA sequences to determine which phialophora-like species might have affinities to the Helotiales and to confirm the connection of *Cadophora* to the Dermateaceae. New combinations in *Cadophora* are proposed, and the taxonomy of the recognized species is reviewed.

MATERIALS AND METHODS

Many of the isolates used for DNA sequencing were purchased from the Centraalbureau voor Schimmelcultures (CBS). Phialophora-like species such as *C. malorum*, morphologically similar species, and their suspected synonyms were emphasized, particularly those thought to have affinities to the Helotiales. Cultures of other Phialophora species that would be representative of other orders of ascomycetes were also purchased from CBS and sequenced.

Two regions of nuclear rDNA were used: a portion (5' end) of the large subunit (LSU or 28S) and the internal transcribed spacer regions (ITS1 and ITS2), along with the highly conserved 5.8S gene. The procedures for DNA extraction, the PCR and sequencing primers, cycling conditions for PCR, and automatic sequencing were as described by Paulin et al. (2002). Complementary sequences were obtained and compared to assure fidelity.

BLAST searches were conducted with sequences of the phialophora-like species to find similar sequences. Corresponding sequences of representative species were included in the datasets for phylogenetic analyses. For analysis of the LSU dataset, sequences of representatives of the Helotiales, Sordariales and Chaetothyriales were included, and we used the sequences of *Saccharomyces* and *Bulleromyces* (Basidiomycota) as the outgroup taxa.

For each dataset, sequences were aligned manually and analyzed using PAUP 4.0b10a (Swofford 2002). A total of 566 unordered characters, including gaps, were utilized in the LSU dataset of 53 taxa, but 11 characters were eliminated because of ambiguous alignment. Of the 555 analyzed characters, 241 were constant and 73 were parsimony-uninformative. The tree was rooted to *Bulleromyces* at an internal node with basal polytomy. For the ITS dataset, the manual alignment resulted in 596 characters, including gaps. Of these, 119 were eliminated because of ambiguous alignment, 268 characters were constant, and 81 characters were parsimony uninformative. The ITS tree was rooted to *Pyrenopeziza revincta*.

Heuristic searches used stepwise (simple) addition and tree-bisection-reconnection. For both datasets, gaps were considered a "fifth base," all characters had equal weight, starting trees were obtained via stepwise addition, and tree-bisection-recombination was used. Bootstrap analyses utilized 1000 replications of heuristic searches (Felsenstein 1985).

Table 1. Isolate numbers of species and GenBank accession numbers of the ITS and LSU rDNA sequences generated in this study.

Species	Isolate Numbers ^a	ITS rDNA	LSU rDNA
<i>Cadophora fastigiata</i>	A168, CBS 307.49	AY249073	AY249084
<i>C. finlandia</i>	P60, CBS 444.86, ex-type of <i>Phialophora finlandia</i>	AY249074	
<i>C. gregata</i>	P19	AY249070	
	P21	AY249071	
<i>C. luteo-olivacea</i>	A171, CBS 352.87	AY249069	
	A174, CBS 357.51, ex-type of <i>Phialophora goidanichii</i>	AY249068	AY249082
	A175, CBS 141.41, ex-type A208	AY249066 AY249067	AY249081 AY249087
<i>C. malorum</i>	A163, CBS 266.31, ex-type of <i>Sporotrichum carpogenum</i>	AY249057	AY249080
	A165, CBS 257.89	AY249058	
	A166, CBS 377.77	AY249064	
	A167, CBS 165.42, ex-type of <i>Phialophora atra</i>	AY249059	AY249086
	A169, CBS 259.32, ex-type of <i>Cadophora heteroderae</i>	AY249060	AY249083
	A170, CBS 260.32	AY249061	
	A172, CBS 100591	AY249063	
	A173, CBS 100584	AY249062	
<i>C. melinii</i>	A164, CBS 268.33, ex-type	AY249072	AY249085
<i>Graphium rubrum</i>	C1223, CBS 210.34, ex-type	AF198245	AY266313
<i>G. silanum</i>	C1221, CBS 206.37	AY249065	
<i>Leptographium abietinum</i>	C1883		AY249091
<i>Phaeoacremonium aleophilum</i>	A207		AY249088
<i>Phialocephala dimorphospora</i>	P59, CBS 300.62	AY249075	
<i>Phialocephala fortinii</i>	P58, CBS 443.86, ex-type	AY249076	
<i>Phialophora brunnescens</i>	A178, CBS 295.39, ex-type	AY249079	
<i>Phialophora calyciformis</i>	A177, CBS 302.62, ex-type	AY249077	AY249090
<i>Phialophora richardsiae</i>	A176, CBS 270.33, ex-type	AY249078	AY249089

^a CBS = Centraalbureau voor Schimmelcultures, Netherlands; A, C and P = Culture collection of T. C. Harrington, Iowa State University.

RESULTS

LSU Sequence Analysis

Partial sequences of the LSU gene were obtained for 10 isolates of what were thought to be species of *Cadophora*. The BLAST searches for similar LSU sequences indicated that nine of the ten *Cadophora* species grouped together and suggested that they were most closely related to taxa in the Helotiales.

The LSU dataset included 53 taxa. Eight most parsimonious trees of 1434 steps were found, and a representative of those eight trees is shown in Figure 1. The consistency (CI), homoplasy (HI), retention (RI) and rescaled consistency (RC) indices were 0.3926, 0.6074, 0.6826 and 0.2680, respectively. The *Cadophora* species were grouped in a well-supported clade (96% bootstrap support), and this clade was sister to *Hymenoscyphus ericae* (D.J. Read) Korf & Kernan (64% bootstrap support). The *Cadophora/Hymenoscyphus* clade was in each of the eight most-parsimonious trees, as was the Helotiales branch, though there was no bootstrap support for the latter.

In contrast, the Sordariomycetes and Chaetothyriales clades were strongly-supported, and each contained phialophora-like or true *Phialophora* species, respectively (Fig. 1). *Phialophora richardsiae* (Nannf.) Conant and *P. calyciformis* G. Sm. were similar to each other and more closely matched members of the Sordariomycetes than the Helotiales. The LSU sequences of these *Phialophora* species were most similar to *Diaporthe medusaea* Nitschke and *Cryphonectria parasitica* (Murrill) M. E. Barr, but there was no bootstrap support for the branch connecting the *Phialophora* species to these members of the Diaporthales (Fig. 1). *Phialophora americana* (Nannf.) S. Hughes had a LSU sequence very near that of *Capronia* in the Chaetothyriales. *Phaeoacremonium aleophilum* W. Gams et al. was placed in the Sordariomycetes clade.

ITS Sequence Analysis

There was one most parsimonious tree of 454 steps in the analysis of the ITS dataset (Fig. 2). The CI, HI, RI and RC were 0.6542, 0.3458, 0.7929 and 0.5187, respectively. Most of the *Cadophora* isolates had ITS sequences identical to *C. malorum* or *C. luteo-olivacea*. These species and *C. gregata*, *C. melinii* and *C. fastigiata* were in a well-supported clade with species of *Ramulispora Miura* (anamorphs of *Tapesia* (Pers.) Fuckel species), *Rhynchosporium* Heinsen ex A.B Frank, and *Rhexocercosporidium* U. Braun. The teleomorph *Pyrenopeziza brassicae* B. Sutton & Rawl. was also found in this clade of otherwise anamorphic species. Sister to this clade was *C. finlandia* and the teleomorphic species *Hymenoscyphus ericae*.

The ITS sequences of a number of other Dermateaceae and phialophora-like anamorphs were similar to those of the above *Cadophora* clade, but there was little or no bootstrap support for grouping them with the main group of *Cadophora* species. However, *C. lagerbergii* grouped with the anamorphic species *Phialocephala dimorphospora* Kendr. and *P. fortinii* Wang & Wilcox. *Tapesia cinerella* Rehm and *Phialocephala scopiformis* Kowalski & Kehr had similar ITS sequences, as did the anamorphic species *Dactylella lobata* Dudd. and the teleomorphic species *Mollisia cinerea* (Batsch) P. Karst. The ITS sequence of *Pyrenopeziza revincta* (P. Karst.) Gremmen was the most distinct from the other Dermateaceae and their anamorphic relatives.

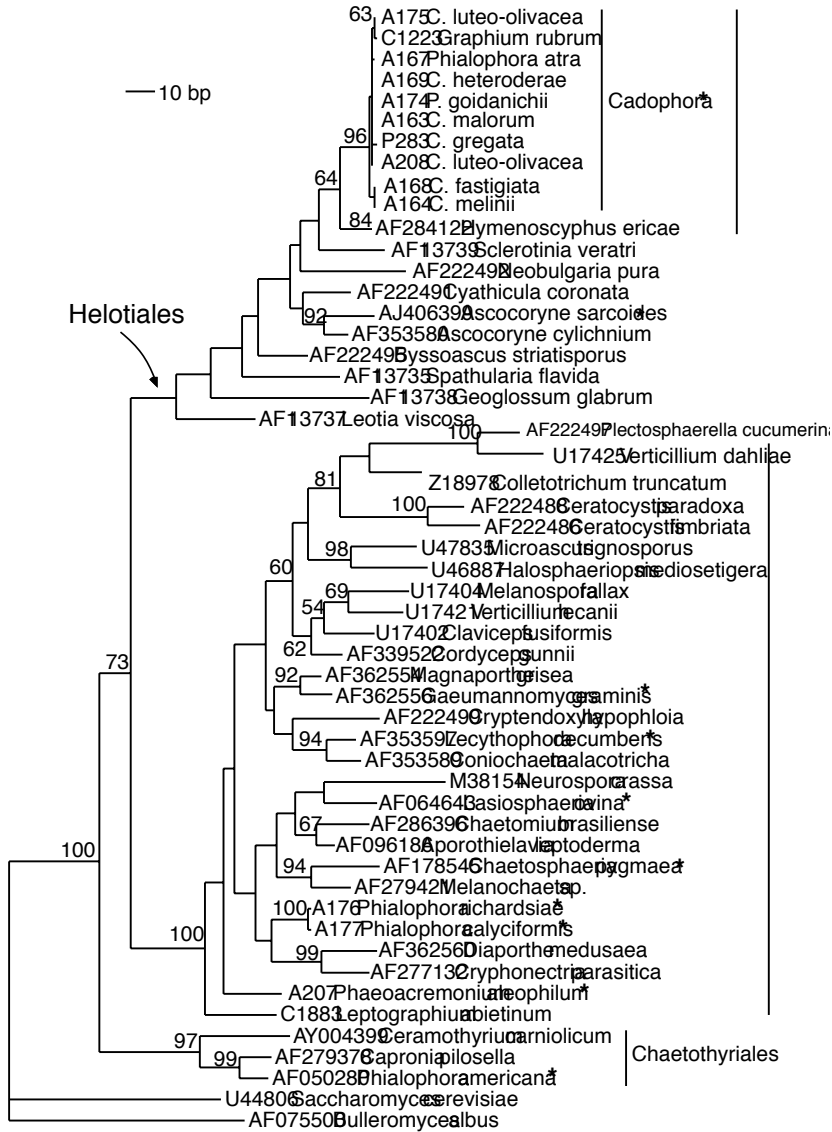


Fig. 1. One of eight most parsimonious trees based on sequences of part of the large subunit of the rDNA of phialophora-like species and other ascomycetes. Bootstrap values greater than 50% are indicated above the branches. An asterisk after the taxon indicates that there is a phialophora-like anamorph. The tree is rooted to the basidiomycete Bulleromyces albus. Isolate numbers (Table 1) or accession numbers for DNA sequences are given for each taxon.

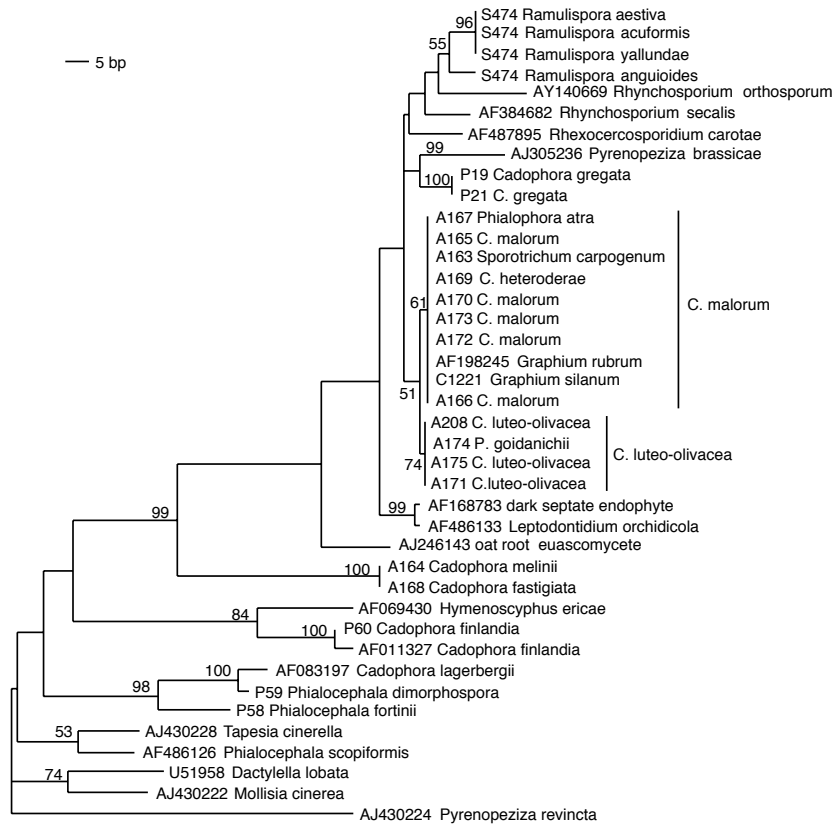


Fig. 2. The most parsimonious tree based on the sequence of ITS1, ITS2 and the 5.8s gene of the rDNA of *Cadophora* and related Helotiales. Bootstrap values greater than 50% are indicated above the branches. The tree is rooted to *Pyrenopeziza revincta*. Isolate numbers (Table 1) or accession numbers for DNA sequences are given for each taxon. Sequences for *Ramulispora* spp. are from TreeBASE.

The ITS sequences of three other *Phialophora* species (*P. calyciformis*, *P. richardsiae* and *P. brunnescens*) were similar to each other, but these sequences could not be reasonably aligned with those of the *Cadophora* species. A BLAST search with the ITS sequence of *P. brunnescens* showed that the nearest sequences were those of *P. mustea* Neerg. (AF083194), *P. richardsiae* (PRU31844), and *P. repens* (David.) Conant (AF083195). No ITS sequence of a teleomorph matched closely with those of the *Phialophora* species.

TAXONOMY

Cadophora Lagerb. & Melin, Svenska Skogsvårdsfören. Tidskrift. 25:263. 1927.

Cadophora fastigiata Lagerb. & Melin, Svenska Skogsvårdsfören. Tidskrift. 25:263. 1927.

= *Phialophora fastigiata* (Lagerb. & Melin) Conant, Mycologia 29:598. 1937.

Cadophora fastigiata was described from Sweden on blue-stained pine wood (Lagerberg & Melin 1927), but no living culture of their material is available. Isolate CBS 307.49 from bluestained wood in Sweden is thought to be representative of the species, and Schol-Schwartz (1970) noted no morphological differences between this culture and the type specimen for *C. fastigiata*. The ITS sequence of CBS 307.49 was identical to that of the isolate from the holotype of *C. melinii*, although in gross morphology the cultures look different.

Cadophora finlandia Wang & Wilcox) Harrington & McNew, comb. nov.

= *Phialophora finlandia* Wang & Wilcox, Mycologia 77:953. 1985 (basionym).

The ITS sequences of two isolates of *C. finlandia* were similar to each other and near that of *Hymenoscyphus ericae*. Both species are associated with plant roots.

Cadophora gregata (Allington & Chamberlain) Harrington & McNew, comb. nov.

= *Cephalosporium gregata* Allington & Chamberlain, Phytopathology 38:797. 1948 (basionym).

= *Phialophora gregata* (Allington & Chamberlain) W. Gams, Cephalosporium-Schimmelpilze (Hyphomycetes) p.199. 1971.

This species causes brown stem rot of soybean (*C. gregata* f. sp. *sojae*) and adzuki bean (*C. gregata* f. sp. *adzukicola*). No teleomorph has been discovered, but LSU rDNA analysis had previously placed the fungus in the Helotiales (Paulin and Harrington 2000).

Cadophora lagerbergii Melin & Nannf., Svenska Skogsvårdsfören. Tidskrift. 32:415. 1934.

= *Phialophora lagerbergii* (Melin & Nannf.) Conant, Mycologia 29:598. 1937.

The ITS sequence of this species places it close to two species of *Phialocephala*, which have phialides on top of metulae at the top of a stalked conidiophore (Crane 1971). No such metulae or stalk has been noted with *C. lagerbergii*. The culture (CBS 266.33) from which the ITS sequence (AF083197) was derived was from the holotype of *C. lagerbergii*, which was associated with bluestained wood.

Cadophora luteo-olivacea (vanBeyma) Harrington & McNew, comb. nov.

= *Phialophora luteo-olivacea* van Beyma, Antonie van Leeuwenhoek 6:280. 1940 (basionym).

= *Phialophora goidanichii* Delitala, Ann. Sperim. Agric. Roma, N. S. 6:254. 1952

In morphology, biology and ITS sequence this species is close to *C. malorum*. Schol-Schwartz (1970) considered *P. luteo-olivacea* and *P. goidanichii* synonyms for *P. malorum*, but the ITS sequence data separates the first two from *C. malorum*. The culture of *P. goidanichii* used for ITS sequencing is from the holotype.

Cadophora malorum (Kidd & Beaum) W. Gams, *Stud. Mycol.* 45:188. 2000.
= *Sporotrichum malorum* Kidd & Beaum., *Trans. Brit. Mycol. Soc.* 10:111. 1924.
= *Phialophora malorum* (Kidd & Beaum.) McColloch, *Phytopathology* 32:1094. 1942.
= *Phialophora atra* van Beyma, *Antonie van Leeuwenhoek* 8:114. 1942.
= *Sporotrichum carpogenum* Ruehle, *Phytopathology* 21:1144. 1931.
= *Cadophora heteroderæ* van Beyma, *Zentbl. Bakt. Parasitkde. (Abt. II)*, 96:430. 1937.

Numerous synonyms were proposed for *C. malorum* by Schol-Schwarz (1970), a soilborne or wood-associated species that may also rot apple fruit. We were able to generate ITS sequences for cultures authentic for the type or from the holotype of each the proposed synonyms. With the exception of *C. luteo-olivacea* and *P. goidanichii*, ITS sequence analysis confirmed the synonyms proposed by Schol-Schwarz (1970), and those synonyms are reiterated above.

The ITS sequences of *Graphium rubrum* and *G. silanum* are also identical to that of *C. malorum*. Although the culture of *G. rubrum* is reported to be from the holotype, there is some doubt if the culture does indeed represent the species (Harrington et al., 2001). A similar problem seems to exist for the culture of *G. silanum* (Harrington et al., 2001).

Cadophora melinii Nannf., *Svenska Skogsvårdsfören. Tidskrift.* 32:417. 1934.
= *Phialophora melinii* (Nannf.) Conant, *Mycologia* 29:598. 1937.

The possibility that *C. melinii* is a synonym of *C. fastigiata* was discussed above. The sequenced *C. melinii* culture was from the holotype.

DOUBTFUL OR EXCLUDED SPECIES:

Phialophora americana (Nannf.) S. Hughes, *Can. J. Bot.* 36:795. 1958.
= *Cadophora americana* Nannf., *Svenska Skogsvårdsfören. Tidskrift.* 32:412. 1934.

The LSU analysis using the sequence of a culture of *P. americana* placed this species near *Capronia pilosella* in the Chaetothyriales, and *P. americana* has been connected to *C. semiimmersa* (Candoussau & Sulmont) Untereiner & Naveau (Untereiner & Naveau 1999). *Phialophora americana* is morphologically similar to *P. verrucosa*, the type species of *Phialophora*.

Phialophora brunnescens (David.) Conant, *Mycologia* 29:598. 1937.
= *Cadophora brunnescens* Davidson, *Jn. Ag. Res.* 50:803. 1935.

The ITS sequence (AY249079) of the culture from the holotype showed this species to be closely related to *P. calyciformis* and *P. richardsiae*, which were shown to have affinities to the Sordariomycetes based on LSU analysis (Fig. 1).

Phialophora obscura (Nannf.) Conant, *Mycologia* 29:598. 1937.
= *Cadophora obscura* Nannf., *Svenska Skogsvårdsfören. Tidskrift.* 32:419. 1934.

We did not study a culture of *P. obscura*, but Schol-Schwartz (1970) examined the culture from the holotype and synonymized this species with *Phialophora bubakii* (Laxa) Schol-Schwartz (= *Margarinomyces bubaki* Laxa). It is unclear if these species have Helotialian affinities or not. Gams (2000) considered *Margarinomyces* among the "unclassified" phialophora-like genera.

Phialophora repens (David.) Conant, *Mycologia* 29:598. 1937.
= *Cadophora repens* Davidson, *J. Ag. Res.* 50:803. 1935.

An ITS sequence (AF083195) from isolate CBS 294.39 (an isolate from the holotype) shows it to be most similar to *P. mustea*, and the ITS sequences of *P. brunnescens*, *P. calyciformis* and *P. richardsiae* are also similar to that of CBS 294.39. As discussed above, these *Phialophora* species appear to have affinities to the Sordariomycetes.

Phialophora richardsiae (Nannf.) Conant, *Mycologia* 29:598. 1937.
= *Cadophora richardsiae* Nannf., *Svenska Skogsvårdsfören. Tidskrift.* 32:421, 1934.

The LSU sequence of a culture from the holotype showed its affinities to *P. calyciformis* and the Sordariomycetes, perhaps near the Diaporthales.

DISCUSSION

We are following Gams' suggestion for the use of the generic name *Cadophora* for phialophora-like species with affinities to the Dermateaceae in the Helotiales. A morphological definition of the genus will be difficult, however. Gams stated that ". . . while the vegetative hyphae in these species are more or less pigmented, the phialides are pale to hyaline, particularly the collarettes." However, pigmentation in these species is often quite variable, and diagnostic characters for *Cadophora*, other than molecular, are unclear at this time. The known *Cadophora* species and their relatives appear to be plant pathogens, root associates, or colonizers of wood.

The rDNA sequence analyses support Gams' (2000) grouping of *Cadophora fastigiata*, *C. melinii* and *C. malorum* with the Dermateaceae of the Helotiales and distinct from true *Phialophora* species, which are anamorphs of the Chaetothyriales. However, his inclusion of *P. repens* Davidson in the *Cadophora* group was not supported by ITS sequence analysis. This and some other species named in *Cadophora* were shown to have affinities to the Sordariomycetes or the Chaetothyriales.

Even among the Dermateaceae and among the other families of the Helotiales, there are several anamorphic genera of similar morphology, and a natural system of classification of these anamorphs may be impossible. *Cadophora lagerbergii* had an ITS sequence very similar to *Phialocephala fortinii* and *P. dimorphospora*, which have stalked conidiophores. The other *Cadophora* species tended to group closely to each other, but the anamorphic genera *Ramulispora*, *Rhynchosporium* and *Rhexocercosporidium* also are found among *Cadophora* species based on our ITS analysis. These anamorphic genera have sporodochia or stromatic tissue from which septate conidia are produced. *Tapesia acufomis* and *T. yallundae* have *Ramulispora* anamorphs (Stewart et al., 1999), and earlier analyses of rDNA sequences (Goodwin 2002) found that *Ramulispora* and *Rhynchosporium* are related to the teleomorphic *Tapesia* and *Pyrenopeziza brassicae*.

The anamorphic genera *Dactylella* and *Leptodontium* are morphologically distinct from *Cadophora*, but ITS sequences suggest some relationship. The recently described genus *Cantenulifera* Hosoya (Hosoya 2002) for anamorphs of *Hyphodiscus* Kirschst. (Dermateaceae) appears to be synonymous with *Cadophora*.

As recently reviewed by Goodwin (2002), the family status of many genera within the Helotiales is not clear, particularly those genera placed in the Demateaceae. In our ITS tree *Tapesia* and *Pyrenopeziza* species are found among the *Cadophora* species. *Mollisia* may be a synonym of *Tapesia* (Goodwin 2002), but the ITS sequences of *M. cinerea* and *T. cinerella* were more distant from the sequences of the *Cadophora* species than were the sequences of *T. yallundae* and *T. acuformis*. *Pyrenopeziza brassicae* had an ITS sequence similar to that of the *Cadophora* species, but the ITS sequence of *P. revincta* was distinct. Although *Hymenoscyphus* is classified by some as a member of the Helotiaceae, the LSU and ITS sequences of *H. ericae* place it among the *Cadophora* species, *Tapesia*, and *Pyrenopeziza brassicae*.

Caution must be exercised in the interpretation of our ITS tree because much of the ITS1 and ITS2 regions contains numerous insertions and deletions, and the sequences are very difficult to align without ambiguity. Also, many of these sequences were from other sources, and it is difficult to know if the isolates from which these sequences were derived were correctly identified. However, most of the *Cadophora* species were represented by isolates from the respective holotypes, and both the LSU and ITS sequences of these isolates clearly place the *Cadophora* species in the Helotiales, particularly close to the teleomorphic genera *Tapesia*, *Pyrenopeziza* and *Hymenoscyphus*.

ACKNOWLEDGEMENTS

This work was partially supported by the Iowa Soybean Promotion Board. Robert Blanchette kindly provided many of the cultures for study. Helpful reviews of the manuscript were provided by Keith Seifert and Walter Gams.

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