A REVIEW OF *Ceratocystis sensu stricto* WITH SPECIAL REFERENCE TO THE SPECIES COMPLEXES *C. coerulescens* AND *C. fimbriata*

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ABSTRACT

*The genus **Ceratocystis sensu stricto** Ellis & Halst. includes many economically important plant pathogens of both angiosperms and gymnosperms, worldwide. Diseases caused by these fungi include vascular wilts, sap stains on logs and lumber, stem cankers and rots of roots, stems and fruits. Most Ceratocystis species are well adapted to dispersal by insects. Many species produce volatile metabolites with fruity odors that attract a wide range of insects to infected tissues. However, the degree of this association between insects and **Ceratocystis** species is highly variable, ranging from a mutualistic relationship such as that between **C. polonica**, **C. laricicola** and **C. rufipennis** and their specific bark beetle vectors, to non-specific associations, as are found in the case of **C. paradoxa**, **C. fagacearum** and **C. fimbriata,** with nitidulid beetles, flies and ambrosia beetles. The high degree of morphological similarity found amongst these fungi probably results from convergent evolution driven by selection for insect dispersal, and has made it difficult to clearly define the boundaries between species of **Ceratocystis**. During the course of the last decade, the use of phylogenetic studies based on comparisons of DNA sequence data has contributed substantially to clarify the taxonomy of this group of fungi. These studies have led to the conclusion that some **Ceratocystis** species thought to be single entities in the past actually represent complexes of cryptic species. This review is primarily intended to provide an introduction to experimental studies presented on species of **Ceratocystis sensu stricto**. However, in order to provide a firm background to this fungal genus, a brief outline is presented on related fungi that can broadly be referred to as the ophiostomatoid fungi.*

Key words: Ophiostomatoid fungi, phylogenetic analysis, cryptic species, forest pathology.

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RESUMEN

REVISIÓN DE *Ceratocystis sensu stricto* CON ESPECIAL REFERENCIA A LOS COMPLEJOS DE LAS ESPECIES *C. coerulescens Y C. fimbriata*

El género Ceratocystis sensu stricto incluye un alto número de hongos fitopatógenos de plantas angiospermas y gimnospermas en diversas regiones del mundo. Entre las principales enfermedades causadas por estos hongos se destacan los marchitamientos vasculares, manchado de maderas, chancros y pudriciones radiculares, de tallos y frutos. Muchas especies producen metabolitos volátiles con olores que atraen una amplia variedad de insectos a los tejidos vegetales infectados, sin embargo, el grado de asociación entre los insectos y las diferentes especies de ***Ceratocystis*** *es altamente variable, presentandose asociaciones mutualistas tales como aquellas entre* ***C. polonica, C. laricicola*** *y* ***C. rufipenni*** *e insectos escolítidos, así como también relaciones no específicas como en los casos de* ***C. paradoxa***, ***C. fagacearum*** *y* ***C. fimbriata*** *con nitidúlidos, moscas y diversos coleópteros. El alto grado de similitud morfológica encontrada entre estos hongos hace difícil la definición de los límites entre las especies de* ***Ceratocystis****. Durante la pasada década, la utilización de estudios filogenéticos basados en comparaciones de DNA ha contribuido sustancialmente a clarificar la taxonomía de este grupo de hongos, así por ejemplo, dichos estudios han permitido concluir que algunas especies de* ***Ceratocystis*** *realmente representan complejos de especies crípticas. Esta revisión tiene como objetivo principal proveer una introducción a los estudios experimentales desarrollados para las especies de* ***Ceratocystis*** *sensu stricto y brevemente discutir aspectos relacionados con los denominados hongos ophiostomatoides.*

Palabras claves: Hongos ophiostomatoides, análisis filogenético, especies cripticas, patología forestal.

The ophiostomatoid fungi include more than 100 species of ascomycetes that share morphological characteristics and adaptation to dispersal by insects and other arthropods (Wingfield *et al.* 1993, Harrington 1993a, Kile 1993). These fungi are found on a wide variety of substrates in tropical, subtropical and temperate regions of the world. Ecologically, they occupy a wide range of niches, ranging from saprotrophs to primary pathogens of both angiosperm and gymnosperm plants. Some species are agents of sap stain on conifers and hardwood trees, while others are aggressive pathogens of economically important agronomic crops (e.g. sweet potato, tobacco, coffee, citrus, cacao, pineapple, sugarcane, rubber) or forest trees (e.g. oak, elm, eucalyptus and plane trees) (Upadhyay 1981 1993, Wingfield *et al*. 1993). In addition, several ophiostomatoid fungi cause virulent systemic diseases in humans and animals (Summerbell *et al*. 1993).

Morphologically, the ophiostomatoid fungi are characterised by spherical ascomatal bases with elongated necks, deliquescent asci borne irregularly throughout the centrum of the ascocarps, and single-celled ascospores that lack germ-pores, often have ornamented sheaths and are produced in a mucilagenous matrix that exudes in sticky droplets through ostioles at the apices of the necks. The many different anamorph states found among the ophiostomatoid fungi all have holoblastic conidium development, but display a variety of conidiophore and conidial forms (Hunt 1956, Upadhyay 1981 1993, Spatafora and Blackwell 1994). The sticky spore masses (including the conidial masses produced by some species) facilitate insect dispersal, as they easily adhere to the insect bodies (Malloch and Blackwell 1993). The high degree of morphological similarity found amongst these fungi is probably a result of convergent evolution, driven by selection for insect dispersal (Spatafora and Blackwell 1994).

The morphological similarity among the ophiostomatoid fungi made it difficult to establish valuable taxonomic characters to delimitate them at both lower (species, genera) and higher (families, orders) taxonomic levels (Spatafora and Blackwell 1994). Consequently, controversial and often confusing taxonomic debates have surrounded their classification. This confusion stems back to even 1891, when Halsted and Fairchild misinterpreted the ascocarps of the first described species, *Ceratocystis fimbriata* Ellis & Halst. as pycnidia (Nannfeldt 1932, Hunt 1956, Griffin 1968, De Hoog 1974, Benny and Kimbrough 1980, Upadhyay 1981, De Hoog and Scheffer 1984, Von Arx and Van Der Walt 1988). Indeed the term "ophiostomatoid fungi" to some extent illustrates this confusion and emerged from a meeting of scientists in 1990 who recognised that genera such as *Ophiostoma* and *Ceratocystis* were phyologenetically unrelated but morphologically and ecologically similar (Wingfield *et al*. 1993).

Fifteen genera have historically been grouped within what are considered to be ophiostomatoid fungi. Some of these genera such as *Ceratocystis* Ellis & Halstead and *Ophiostoma* H. & P. Sydow, have been widely accepted, whereas others have had limited recognition and have later been considered as synonyms or invalid genera (e.g. *Ceratocystiopsis* pad. & Kendrick, *Endoconidiophora* Münch, *Europhium* Parker) (Wingfield, Seifert and Webber 1993). To complicate matters further, more than 15 hyphomycete genera with a wide range of conidiophores, co-nidium ontogeny, and conidial forms, have been linked to the ophiosto-matoid fungi (Upadhyay and Kendrick 1975, Upadhyay 1981,1993).

A major theme of the taxonomic debates surrounding the ophiosto-

matoid fungi has been whether they represent one or several genera, and more specifically whether *Ceratocystis* and *Ophiostoma* should be treated as congeneric (Hunt 1956, Griffin 1968, Olchowecki and Reid 1974, Upadhyay 1981 1993) or as distinct genera (De Hoog 1974, De Hoog and Scheffer 1984, Wingfield, Van Wyk y Marasas 1988). However, more recent phylogenetic analyses based on DNA sequence comparisons have demonstrated unequivocally that despite their morphologically similar teleomorphs, these genera are phylogenetically unrelated even at the ordinal level, with *Ceratocystis* residing in the Microascales and *Ophiostoma* being more closely related to species in the Diaporthales (Hausner *et al*. 1993a, b, Spatafora and Blackwell 1994, Wingfield, Viljoen, y Wingfield 1999). Currently, five genera are accepted to belong to the wider group referred to as ophiostomatoid fungi. These include *Ceratocystis*, *Ophiostoma*, *Ceratocystiopsis*, *Gondwanamyces* Marais & Wingfield and *Cornuvesica* Viljoen & Winfield (Wingfield, Seifert and Webber 1993, Upadhyay 1993, Marais *et al*. 1998, Viljoen, Wingfield and Wingfield 2000). This is despite the fact that they represent polyphyletic lineages.

Ceratocystis. The name *Ceratocystis sensu lato* has been used collectively for all the ophiostomatoid fungi, while *Ceratocystis sensu stricto* is used exclusively for species with anamorphs in the form-genus *Thielaviopsis* Went emend. Paulin, Harrington et, McNew (Wingfield *et al*. 1993, Paulin-Mahady, Harrington, y McNew 2002). These anamorphs are distinguished by conidium development of ring wall building (enteroblastic conidiogenesis) (Minter, Kirk y Sutton 1983, Minter 1987), and were recently transferred from the genus *Chalara* (Corda) Rabenh. to *Thielaviopsis* based on analysis of sequence data from the ribosomal RNA (rRNA) operon (Paulin-Mahady, Harrington y McNew 2002). Species of *Ceratocystis sensu stricto* can also be distinguished from other ophiostomatoid fungi by the lack of cellulose and rhamnose in their cell walls (Spencer and Gorin 1971, Jewell 1974, Weijman and De Hoog 1975) and their sensitivity to the antibiotic cycloheximide (Harrington 1981).

Ophiostoma. Fungi residing in the genus *Ophiostoma* are characterised by having cellulose and rhamnose in their cell walls and being tolerant to cycloheximide in culture (Harrington 1981, De Hoog and Scheffer 1984). The anamorphs of these species are accommodated in several hyphomycete genera, such as *Leptographium* Lagerberg & Melin, *Pesotum* Crane & Schocknecht, *Sporothrix* Hektoen & Perkins: Nicot & Mariat, *Knoxdaviesia* Wingfield, van Wyk & Marasas and *Hyalorhinocladiella* Upadhyay & Kendrick (Wingfield *et al*. 1993, Okada *et al*. 1998, Hausner, Reid y Klassen 2000, Jacobs and Wingfield 2001). In all these genera conidium develop-

ment occurs exogenically through apical wall building (holoblastic conidiogenesis) (Minter, Kirk y Sutton 1982).

Ceratocystiopsis. The genus *Ceratocystiopsis* was established to accommodate ophiostomatoid fungi with elongate or falcate ascospores surrounded by a falcate sheath with attenuated ends (Upadhyay and Kendrick 1975, Upadhyay 1981, Wingfield 1993). Anamorphs of these species are formed by both enteroblastic and holoblastic conidiogenesis and have included *Sporothrix, Hyalorhinocladiella, Chalara* and *Knoxdaviesia* states. However, the validity of this genus remains uncertain, as morphological and molecular data have shown that most species should be included within *Ophiostoma* (Wingfield 1993, Hausner, Reid y Klassen 1993a 1993 b) but that others with *Knoxdaviesia* and *Chalara* anamorphs reside in genera such as *Gondwanamyces* and *Cornuvesica*, respectively (Marais *et al.* 1998, Viljoen *et al*. 2000) that are unrelated to *Ophiostoma*.

Gondwanamyces and Cornuvesica. The genus *Gondwanamyces* was recently established to accommodate two ophiostomatoid species with *Knoxdaviesa* anamorphs (*Ceratocystiopsis proteae* Wingfield, Van Wyk & Marasas and *Ophiostoma capense* Wingfield & Van Wyk) (Marais *et al*. 1998). *Cornuvesica* was erected to include the former species *Ceratocystiopsis falcata* (Wright & Cain) Upadhyay, which has a *Chalara*-like anamorph but is phylogenetically unrelated to *Ceratocystis sensu stricto* (Hausner, Reid y Klassen 1993-b , Viljoen, Wingfield y Wingfield 2000).

Ceratocystis sensu stricto. The genus *Ceratocystis sensu stricto* includes many economically important plant pathogens that especially occur in tropical and sub-tropical regions of the world. Most species require wounds in order to infect their hosts, and their pathogenicity varies widely from weakly virulent fungi to very aggressive pathogens. Some species have even a saprotrophic life style (*Ceratocystis moniliformis* (Hedgc.) C. Moreau). Diseases caused by these fungi include vascular wilts, sap and lumber stains, stem cankers and rots of roots, stems and fruits (Kile 1993, Harrington, Wingfield and Kile 1996).

The most virulent *Ceratocystis* species generally cause vascular wilts and stem cankers of trees and other woody plants. For example, *Ceratocystis fagacearum* (Bretz) Hunt causes the disease known as oak wilt of *Quercus* spp. in North America (Henry *et al*. 1944), *Ceratocystis fimbriata* causes wilt and cankerstain diseases on a wide range of hosts including cocoa (*Theobroma cacao* L.) (Schieber 1969), coffee (*Coffea arabica* L.) (Pontis 1951) and plane trees (*Platanus* spp.) (Walter 1946, Panconesi 1981), *Chalara autralis*

Walker & Kile cause a serious wilt disease of *Nothofagus cunninghamii* (Hook.) Oerst (Kile and Walker 1987) and *Ceratocystis polonica* (Siemaszko) Moreau displays relatively high levels of virulence to Norway spruce (*Picea abies* L. Karst.) and other spruce species in Eurasia (Siemaszko 1939, Solheim 1986 1988, Krokene and Solheim 1998, Kirisits 2001).

Weaker pathogens include agents of sap stain of lumber such as *Ceratocystis coerulescens* (Münch) Bakshi on conifers and *Ceratocystis douglasii* (Davidson) Wingfield & Harrington on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Münch 1907, Harrington, Wingfield and Kile 1996, Wingfield, Harrington and Solheim 1997, Harrington and Wingfield 1998). Other weak pathogens include species producing lumber stain in hardwoods such as *Ceratocystis virescens* (Davidson) C. Moreau on maple (*Acer saccharum* Marsh.) (Davidson 1944) and *Ceratocystis eucalypti* Yuan & Kile on *Eucalyptus* spp. (Kile *et al*. 1996).

Likewise, various annual crop plants are also seriously affected by *Ceratocystis* species. *Ceratocystis paradoxa* (Dade) Moreau causes tissue rot on sugar cane (*Saccharum officinarum* L.), *Musa* spp. and *Cocus nucifera* L. (Kile 1993). Similarly, *Ceratocystis adiposa* (Hedgcock) Moreau incites tissue rot on sugar cane (Butler 1906) and *Ceratocystis radicicola* (Bliss) Moreau causes a root rot on date palms (*Phoenix dactylifera* L.) (Bliss 1941).

Members of the genus *Ceratocystis* have several means of transmission and dispersal, in addition to being vectored by insects. Species producing chlamydospores are usually soilborne (Rossetto and Ribeiro 1990, Kile 1993), whereas those that sporulate aerially are dispersed by wind and water splash (Baker and Thomas 1946, Vigouroux and Stojadinovic 1990). Species that cause vascular wilts and woodstain can also be transmitted through root grafts (Gibbs and French 1980, Accordi 1986) and by pruning tools. This is especially important for the spread of *Ceratocystis* pathogens in agricultural crops and forest plantations (Walter, Rex and Schreiber 1952, Matasci and Gessler 1997).

Most *Ceratocystis* species are well adapted to dispersal by insects. Many species produce volatile metabolites with sweet fruity odours that attract a wide range of insects to infected tissues (Hanssen 1993, Kile 1993). However, the intimacy ot the association between insects and *Ceratocystis* species is highly variable. Species such as *C. polonica, Ceratocystis laricicola* Redfern & Minter and *Ceratocystis rufipenni* Wingfield, Harrington & Solheim, seem to have a mutualistic relationship with their bark beetle vectors (Redfern *et al*. 1987, Solheim 1988, Wingfield, Harrington and Solheim 1997). On the other hand, species such as *C. paradoxa* (Chang and Jensen 1974), *C. fagacearum* (Juzwik and French 1983, Appel, Kurdyla and Lewis

Junior 1990), *C. fimbriata* (Crone and Bachelder 1961, Hinds 1972) and *C. moniliformis* (Hinds and Davidson 1972) have non-specific associations with fungivorous or sap-feeding insects such as nitidulid beetles (Coleoptera: Nitidulidae), flies (Diptera: Drosophilae) and ambrosia beetles (Peplinski and Merril 1974, Kile 1993).

Different modes of reproduction are found among *Ceratocystis* species, including heterothallism, homothallism and exclusive asexual reproduction (Harrington, Steimel and Kile 1998). Genetic studies have shown that sexuality in these species is controlled by two mating-type genes designated MAT-1 and MAT-2 (Harrington and McNew 1997,1998). In strictly heterothallic species, such as *C. eucalypti* and *C. fagacearum*, sexual progeny are only produced upon mating of strains representing different mating types (Kile *et al*. 1996, Harrington, Steimel and Kile 1998). Other species, such as *Ch. australis* and *Chalara neocaledoniae* Kiffer & Delon, are known only by their anamorph states, and supposedly only reproduce asexually (Kile *et al*. 1996, Harrington, Steimel and Kile 1998). However, most *Ceratocystis* species, including among others, *C. fimbriata*, *C. coerulescens*, *C. virescens*, *C. polonica* and *Ceratocystis pinicola* Harrington & Wingfield, are homothallic and also undergo unidirectional mating type switching (Harrington and McNew 1997,1998). In these species, selffertile strains that contain both mating type idiomorphs give rise to both selffertile and self-sterile strains. The latter contain only the MAT-1 gene, and these MAT-1 strains can cross with the selffertile strains. Progeny of selfing and crossing events segregate in a 1:1 ratio, with half the ascorpores being selffertile (MAT-1 and MAT-2) and the other half selfsterile (MAT-1). It has been shown that self sterile strains are produced as the result of a deletion of the MAT-2 idiomorph, which then results in the expression of only the MAT-1 mating type (Witthuhn *et al*. 2000).

The close morphological similarity between many *Ceratocystis* species contributes to poorly defined species boundaries within the genus (Harrington, Wingfield and Kile 1996). Phylogenetic studies using DNA sequence data from the rRNA operon (Wingfield *et al*. 1994, Visser *et al*. 1995, Wingfield *et al*. 1996, Witthuhn *et al*. 1998, 1999, Barnes *et al*. 2003), mating type genes (Witthuhn *et al*. 2000, Harrington *et al*. 2002) and microsatellite DNA regions (Barnes *et al*. 2001) have suggested that some *Ceratocystis* species that have been regarded as single entities in the past, actually represent complexes of cryptic species. Two of these species complexes, the *C. coerulescens* and *C. fimbriata* complex, are treated in more detail below (Figure 1).

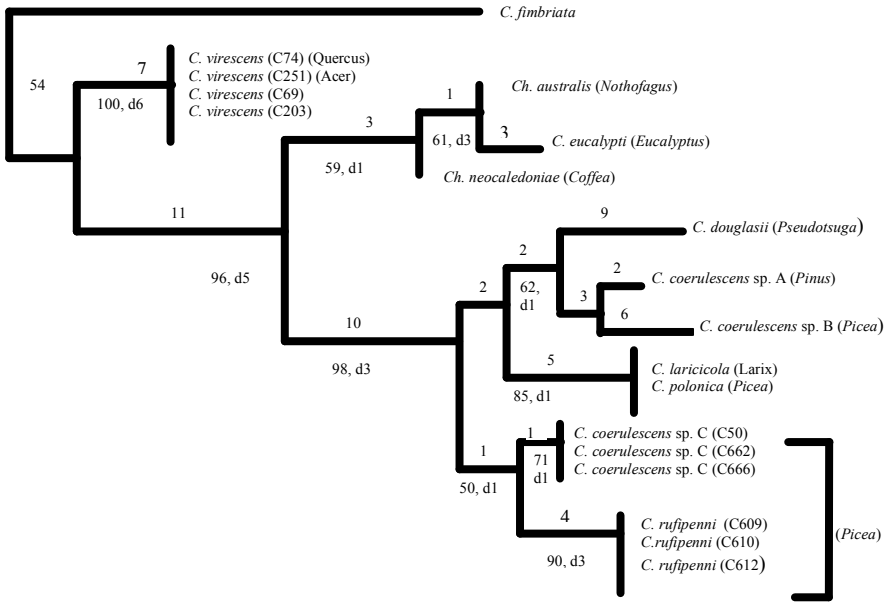

Figure 1. Phylogeny of the *Ceratocystis coerulescens* species complex and its relationship with *Ceratocystis fimbriata*. The phylogenetic tree was produced from the DNA sequence of a 565 bp region of the ribosomal RNA operon using PAUP (Witthuhn et al. 1998).

***Ceratocystis coerulescens* complex.** Eleven species have been grouped in the *Ceratocystis coerulescens* complex. These species have similar morphology and are closely related based on DNA sequence data and isozyme profiles (Harrington, Wingfield and Kile 1996, Harrington and Wingfield 1998, Witthuhn *et al*. 1999, 2000). Seven species cause sap stain on conifers in the family Pinaceae, while four species are pathogens or incite sap stain on hardwood trees. Phylogenetic analysis using sequences of the rRNA operon and MAT-2 HMG box have shown that the species occurring on conifers form a single monophyletic clade, with the hardwood species as their basal ancestor (Witthuhn *et al*. 1998, 2000). It has thus been suggested that adaptation to conifer hosts occurred once in the evolutionary history of *Ceratocystis* (Witthuhn *et al*. 1998, 2000).

Ceratocystis coerulescens was the first species described in the group colonizing conifers (Münch 1907). This fungus causes blue-stain of

spruce and pine sapwood in Europe and North America (Münch 1907, Harrington, Wingfield and Kile 1996, Harrington and Wingfield 1998). *Ceratocystis pinicola* occurs in Britain and is an agent of blue-stain on pine logs and lumber (Gibbs 1993, Harrington and Wingfield 1998). *Ceratocystis rufipenni* was described from Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and white spruce (*Picea glauca* (Moench) Voss) infested by the North American spruce bark beetle, *Dendroctonus rufipennis* Kirby in British Columbia (Wingfield, Harrington and Solheim 1997). It is virulent on Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and can kill trees that have been inoculated in sufficiently high dosages (Solheim and Safranyik 1997). *Ceratocystis resinifera* Harrington & Wingfield has been found in continental Europe and North America and colonizes wounds of live spruce trees (Harrington, Wingfield and Kile 1996, Harrington and Wingfield 1998). *Ceratocystis douglasii* has originally been recognized as a form of *C. coerulescens* (Davidson 1953), but has subsequently been described as a new species (Wingfield, Harrington and Solheim 1997). This fungus stains the sapwood of Douglas-fir in western North America, and appears to be restricted to the natural range f its host (Wingfield, Harrington and Solheim 1997, Harrington and Wingfield 1998). *Ceratocystis laricicola* infests larch (*Larix* spp.) and has a mutualistic association with the bark beetle *Ips cembrae* Heer in Europe and Japan (Redfern *et al*. 1987, Yamaoka *et al*. 1998, Kirisits 2001, Stauffer *et al*. 2001). The remaining species in the conifer subgroup is *C. polonica,* which is a pathogen and agent of blue-stain on Norway spruce and other spruce species in Europe and Japan (Solheim 1986, Yamaoka *et al*. 1997). This *Ceratocystis* species is primarily vectored by the aggressive bark beetle *Ips typographus* L. (Siemaszko 1939, Furniss, Solheim and Christiansen 1990). In addition, *Ips typographus* f. *japo-nicus* Niijima in Japan (Yamaoka *et al*. 1997) as well as *Ips amitinus* Eichhoff (Kirisits 2001) and *Ips duplicatus* Sahlberg (Krokene and Solheim 1996) in Europe have recently been identified as important vectors of *C. polonica*.

The four *Ceratocystis* species occurring on hardwoods include *C. virescens* that causes sapstreak in maple and other hardwood species in eastern North America (Davidson 1944, Harrington and Wingfield 1998), *C. eucalypti* that is a wound colonist on *Eucalyptus* spp. in Tasmania and Victoria, Australia (Kile *et al*. 1996), and two asexual species occurring in Australia, *Ch. australis* and *Ch. neocaledoniae*. The first of these is a virulent pathogen causing myrtle wilt on *Nothofagus cunninghamii* in Tasmania (Kile *et al*. 1996). The latter species produces a vascular wilt disease on coffee (*Coffea robusta* Linden ex Wild.) and guava trees (*Psidium guajava* L.) (Kile and Walker 1987).

The *Ceratocystis* species occurring on hardwoods and conifers can be distinguished morphologically, based on conidiophore characteristics. The hardwood group has tapering and proliferating phialides, while the conifer species lack these phialide characters (Harrington, Wingfield and Kile 1996). The conifer species can be reliably subdivided into two morphologically well-defined groups: *C. coerulescens sensu lato,* where the ascospores are surrounded by an even sheath that is wider at the ends than at the sides, and *C. polonica sensu lato*, where ascospore sheaths are wider at the sides than at the ends (Harrington and Wingfield 1998). Within *Ceratocystis coerulescens sensu lato* on conifers, small morphological differences exist (Harrington and Wingfield 1998), however, unequivocal separation of the entire conifer colonizing species is practically only possible through isozyme and DNA sequence comparisons (Harrington, Wingfield and Kile 1996, Witthuhn *et al*. 1998, 2000, Harrington *et al*. 2002).

Ceratocystis polonica sensu lato. As discussed above, species in the *C. coerulescens* complex have been widely studied during the course of the past decade. These studies have included several phenotypic and genotypic characters (Harrington, Wingfield and Kile 1996, Harrington and McNew 1998, Witthuhn *et al*. 1998, 2000, Harrington and Wingfield 1998, Harrington *et al*. 2002). They have added considerable resolution to the taxonomy of nine of these species, but problems have remained in distinguishing between *C. polonica* and *C. laricicola.*

Ceratocystis polonica was first isolated from Norway spruce in Poland and described by Siemaszko 1939 as *Ophiostoma polonicum.* Visser *et al*. 1995 reported the presence of a *Chalara* (*Thielaviopsis*) anamorph in cultures of *O. polonicum*, and this characteristic, together with DNA sequence comparisons, clearly showed that this fungus is a species of *Ceratocystis*. *Ceratocystis laricicola*, on the other hand, was correctly described by Redfern *et al*. 1987. It was, however, not compared with *C. polonica,* probably due to the fact that *C. polonica* was not recognised as having a *Chalara* state at the time when *C. laricicola* was described (Harrington and Wingfield 1998). Later studies showed the two species were morphologically indistinguishable (Harrington and Wingfield 1998), had identical ITS sequences (Witthuhn *et al*. 1998), and a low level of isozyme variation (Harrington, Wingfield and Kile 1996). However, they represent distinct ecological entities (Siemaszko 1939, Solheim 1986, Redfern *et al*. 1987) and are true biological species, as interspecific crosses between MAT-1 and MAT-2 strains of both species fail to produce viable progeny (Harrington and

McNew 1998, Harrington *et al*. 2002).

These two fungi, together with *C. rufipenni* are especially important for forestry, because they are associated with aggressive tree-killing bark beetles. *Ceratocystis polonica* is a mutualistic associate of the Eurasian spruce bark beetle, *I. typographus*, which is a highly destructive pest of Norway spruce throughout Eurasia (Postner 1974, Chrisiansen and Bakke 1988). Since the 18th century *I. typographus* has caused large-scale outbreaks with millions of killed trees (Klimetzek and Yue 1997) in Scan-dinavia and central Europe (Postner 1974, Christiansen and Bakke 1988, Führer 1996, Kirisits 2001). The most recent and still ongoing outbreak of *I. typographus* in central and western Europe started around 1992 and has been triggered by destructive wind-throws, followed by years with warm and dry climate (Führer 1996, Kirisits 2001). From 1985 to 1994, the *I. typographus – C. polonica* complex has been responsible for losses of about 14,1 million cubic meters of spruce wood in Austria, Switzerland and the German province Baden-Württemberg alone (Führer 1996).

Ceratocystis laricicola is vectored by the eight spined larch bark beetle, *I. cembrae* (Redfern *et al*. 1987, Yamaoka *et al*. 1998, Stauffer *et al*. 2001, Kirisits 2001), which is distri-buted across continental Europe and Asia (Postner 1974, Pfeffer 1995) and has been introduced to Scotland and Denmark (Crooke and Bevan 1957, Redfern et al. 1987, Stauffer *et al*. 2001). This bark beetle is regarded as a secondary although important pest of larch and plays a particularly important role in regions outside the natural range of European larch (Schimitschek 1931, Postner 1974, Stauffer *et al*. 2001). For example, *I. cembrae* and *C. laricicola* have become principal pests of larch in Scotland, after their introduction in 1955 with imported timber from Germany (Crooke and Bevan 1957, Redfern *et al*. 1987).

Mass inoculation experiments that aim to mimic natural mass-attacks by bark beetles, have demonstrated that both *C. polonica* (Christiansen 1985, Solheim 1988, Kirisits 1998, Krokene and Solheim 1998, Yamaoka, Taka-hashi and Iguchi 2000, Kirisits and Offenthaler 2002) and *C. laricicola* (Redfern *et al*. 1987, Yamaoka *et al*. 1998, Kirisits 2001) are able to kill their respective host trees. It is thought that through the mutualistic association between these bark beetles and the specific *Ceratocystis* spp. that they carry, the fungus increases the impact of each beetle attack and thereby contributes to exhaust the host defences and makes the tree suitable for bark-beetle reproduction (Whitney 1982, Harrington 1993b, Paine, Raffa and Harrington 1997). Reciprocally, these fungi benefit by being dispersed and introduced into suitable host trees by their beetle vectors (Whitney 1982,

Malloch and Blackwell 1993, Krokene 1996). Ironically, the less virulent pathogenic *Ophiostoma* spp. associated with these insects (Solheim 1986, Krokene 1996, Krokene and Solheim 1998, Kirisits 2001, Viiri 2002) gain the same dispersal advantage, simply by being present in this environment.

Mechanisms of fungal colonization and host responses have been particularly well studied in the *C. polonica* – Norway spruce system. Fungal succession studies have shown that *C. polonica* is the first species to invade the sapwood after *I. typographus* has attacked a tree (Solheim 1992). This is probably due to its rapid growth and its ability to tolerate the low oxygen levels found in living sapwood (Solheim 1991). However, not all isolates of *C. polonica* have the same ability to kill trees and to induce intensive blue-stain in the spwood of its host tree. Isolates with low levels of virulence have been reported from independent mass inoculation experiments in Austria (Kirisits and Anglberger 1999, Baier *et al*. 2002) and Norway (Krokene and Solheim 2001). Kirisits and Anglberger 1999 considered the low level of virulence as a general characteristic of the particular isolate used in their experiment. Likewise, in the Norwegian study loss of pathogenicity was attributed to senescence of the isolates after several transfers of cultures during routine storage or, alternatively, to long periods of storage of the isolates (Krokene and Solheim 2001). However, mycoviral infections, such as those reported in the forest tree pathogens *Ophiostoma novoulmi* (Rogers, Buck, and Braiser 1987, Cole *et al*. 1998) and *Cryphonectria parasitica* (Nuss 1992, 2000), might have been involved but were not considered.

Spruce trees infected by *C. polonica* respond in several ways to contain the fungus. Responses such as cellular proliferation, mobilization of polyphenolic parenchyma cells, formation of traumatic resin ducts, lignification (Nagy *et al*. 2000, Evensen *et al*. 2000, Krokene, Solheim and Christiansen 2003) as well as translocation of starch reserves (Christiansen and Ericsson 1986) have been shown to be part of the defence mechanisms. Furthermore, experiments have shown that preinoculation of spruce trees with non lethal dosages of *C. polonica* inoculum induces disease resistance that protects trees against subsequent mass infections of the same fungus (Christiansen *et al*. 1999, Krokene and Solheim 2001). The mechanisms underlying this induced resistance differ from the systemic acquired resistance (SAR) present in angiosperms, since it is non-systemic and non-specific (Krokene, Solheim and Christiansen 2003). The induced resistance of Norway spruce is due to anatomical and biochemical reactions in the phloem and the sapwood, in which polyphenolic parenchyma cells and traumatic resin ducts are involved (Krokene, Solheim and Christiansen 2003). Different ne-

crotizing fungi, chemical elicitors and even mechanical wounding can activate a similar defence response compared to that induced by pre-treatment with *C. polonica* (Christiansen *et al*. 1999, Krokene and Solheim 2001, Franceschi, Krekling and Christiansen 2002).

The *Ceratocystis fimbriata* complex. *Ceratocystis fimbriata* was first reported causing rot of sweet potato (*Ipomoea batatas* L.) in 1890 in New Jersey, USA (Halsted 1890). It is the type species of the genus *Ceratocystis* and as in the case of other *Ceratocystis* species, its taxonomy was unclear for more than fifty years. Saccardo 1892 reclassified this fungus as *Sphaeronaema fimbriatum*, while Zimmerman 1900 described a strain of *C. fimbriata* causing coffee canker in Java (Indonesia) as a separate species, *Rostrella coffea* Zimmermann. Elliott 1923 renamed *C. fimbriata* as *Ceratostomella fimbriata*, but when Nannfeldt 1932 erected the family Ophiostomataceae, the species was transferred to the genus *Ophiostoma*, and later, based on the presence of endoconida (now recognised as the *Thielaviopsis* state) to *Endoconidiophora* (Davidson 1935). The name *Ceratocystis fimbriata* was recognized again by Bakshi 1950, who revived the generic name *Ceratocystis* and considered *Ophiostoma*, *Endoconidiophora*, *Rostrella*, *Linostoma* and *Grosmannia* as synonyms of *Ceratocystis*. When Hunt 1956 accepted Bakshi's 1950 amendment, the name *C. fimbriata* became widely accepted (Griffin 1968, Von Arx 1974, Upadhyay 1981).

Morphologically, *C. fimbriata* is characterised by perithecia with long necks that taper towards the tips and terminate in 8 to 15 convergent ostiolar hyphae. Perithecial bases are dark and globose, surrounded by a dense network of hyphae. Asci are evanescent in the early stages of development, while ascospores are characteristically hat-shaped and exuded through the perithecial necks in sticky masses (Hunt 1956, Upadhyay 1981). The fungus also produces chains of cylindrical conidia and aleurioconidia (chlamydospores) that play an important role in the survival of this fungus in the soil (Pontis 1951, Webster and Butler 1967, Accordi 1989). The anamorph of *C. fimbriata* has for many years been accommodated in *Chalara* (Hunt 1956, Nag Raj and Kendrick 1975, Upadhyay 1981), but recently, based on a phylogenetic analysis of DNA sequence data, has been recognised as best residing in *Thielaviopsis* (Paulin-Mahady *et al*. 2002).

Ceratocystis fimbriata is one of the most aggressive plant pathogens in the genus *Ceratocystis*, causing wilt, canker-stain diseases as well as tissue rot on a wide variety of perennial as well as agronomic crop plants, worldwide (Kile 1993). More than 30 economically important plants are attacked by this pathogen (Baker and

Harrington 2000) including, among others, plane trees (Walter, Rex and Schreiber 1952, Panconesi 1981), *Eucalyptus* spp. (Roux *et al*. 1999, Roux *et al*. 2001), aspen (*Populus tremuloides* Michx.) (Zalasky 1965, Hinds 1972), rubber (*Hevea brasiliensis* (Wiild: Juss.) Mull-Arg.) (Silveira *et al*. 1994), mango (*Mangifera indica* L.) (Batista 1960), almond (*Prunus amygdalus* Batsch.) (De Vay *et al*. 1968, Teviotdale and Harper 1991), *Syngonium* spp. (Walker *et al*. 1988) and pimento trees (*Pimenta officinalis* L.) (Leather 1966).

Ceratocystis fimbriata is particularly important in Latin America, where it causes substantial losses in three of the main perennial crops that are grown in this region: coffee, cocoa and citrus (*Citrus* spp.). Coffee canker has been reported from Colombia (Obregon 1936), Venezuela (Pontis 1951), Guatemala (Szkolnik 1951) and Costa Rica (Echandi and Segall 1956). Symptoms of diseased plants include yellowing of foliage, dieback and wilt. When the outer surface of the stem bark of infected trees is removed, dark lesions are obvious and these usually extend downwards towards the roots and girdle the trunks, causing tree death (Pontis 1951, Castro 1991). Coffee canker has become one of the most important threats to coffee production in Colombia, where more than 800000 hectares of this crop are planted (Castro 1998). The principal mode of ingress for *C. fimbriata* into coffee trunks is through mechanical wounds (Pontis 1951). The fungus is easily transported on agricultural tools or with soil. Thus, a major factor associated with spread of coffee canker in Colombia is infection through wounds on the lower stems made by the shoes of farmers needing to secure themselves on the steep slopes on which coffee is cultivated (Castro 1991).

Ceratocystis fimbriata was first reported on cacao in Ecuador in 1918, causing a serious wilt disease (Desrosiers 1958). This disease was subsequently found in Venezuela (Malaguti 1952), Colombia (Idrobo 1958), Trinidad (Goberdhan 1959), Costa Rica (Havord 1962) and the Dominican Republic (Schieber 1969). Recently, cacao wilt disease has also been detected in Brazil, in plantations from South Bahia (Bezerra 1997). Cacao wilt is frequently associated with wounds made by machetes and other tools. The mycelium and spores enter the xylem and ray parenchyma cells through such fresh wounds, and cause dark reddish to purple staining that may develop into a vascular wilt. Externally, the disease is easily recognized because wilted leaves be-come dry, curled and remain attached to the trees for several weeks (Montes de Oca 1975). The incidence of cacao wilt has been reduced significantly in Latin America in recent years, especially because resistant varieties have become widely available for planting (Delgado and Echandi 1965, Ocampo, Mafla and Victoria 1982, Simmonds 1994).

The first report of *C. fimbriata* in citrus orchards was made in 1981, when it caused serious dieback on lime trees (*Citrus aurantifolia* (Christm.) Swing) in the central region of Colombia (Instituto Colombiano Agropecuario 1993). Three years later, it was also found on lemon trees (*Citrus limon* Burmman) in Argentina (Contreras and Marmelioz 1984). By 1994, about 10% of the citrus trees in Colombia had been killed by the pathogen (Mourichon 1994). The disease is characterised by a general yellowing of the foliage, followed by heavy defoliation and prominent shoot proliferation. Internally, brown to reddish lesions are evident in the stele of the trunk, and, as the disease progresses, lesions converge and become flame shaped, black in colour, and trees are eventually killed (Mourichon 1994).

The taxonomic complexity of what has been referred to as *C. fimbriata* in Latin America became evident in a recent study based on ITS sequence comparisons and microsatellite analysis (Barnes *et al*. 2001). Isolates of *C. fimbriata* from coffee in Colombia were found to reside in two genetically isolated groups that might represent different species. However, apart from this study and scattered information that is not widely available in the scientific literature, very little is known regarding the biology, ecology or genetic background of *C. fimbriata* in Latin America. For example, in countries such as Colombia and Costa Rica, several native hosts (e.g. *Inga* sp., *Herrania* sp., *Annona muricata* L., *Caryodendron orinocense* Karst.) are infected by this pathogen (Montes de Oca 1975, Pardo-Cardona 1995 and Buriticá 1999), but their role as alternative hosts and sources of inoculum for susceptible agricultural crops remains uncertain.

Ceratocystis fimbriata has long been recognised as a variable fungus consisting of distinct, host-specialized strains (Webster and Butler 1967, Harrington 2000). The best studied of these host specific races is *C. fimbriata forma specialis platani*, which causes a canker stain disease of plane trees in the Northern hemisphere (Walter, Rex and Schreiber 1952, Santini and Capretti 2000). Similarly, reciprocal inoculation experiments have demonstrated the existence of host-specific isolates on pimento (Leather 1966), sweet potato (Kojima and Uritani 1976), *Syngonium* (Vogelzang and Scott 1991) and cocoa (Baker and Harrington 2000). Earlier genetic analyses indicated that such host-specialized isolates could represent distinct, but closely related species (Olsen and Martin 1949, Webster and Butler 1967). The view that the host is an important factor separating strains of *C. fimbriata sensu lato* has recently also been confirmed based on DNA sequence data (Wingfield *et al*. 1996, Witthuhn *et al*. 1998, Santini and Capretti 2000, Barnes *et al*. 2001 2003). Witthuhn *et al*. 1999

found that isolates of *C. fimbriata* from *Populus* spp., *Prunus* spp. and *Platanus* spp. could be separated based on RFLP analysis of the ITS regions of the rRNA operon. Similar results were obtained by Santini and Capretti 2000 and Barnes *et al*. 2001, using RAPD / minisatellite markers and microsatellite markers, respectively. Thus, *C. fimbriata* strains from different hosts and geographical regions grouped in separated clades in accordance with their respective hosts and origins.

The view that *C. fimbriata* may represent a complex of cryptic species has gained further support by the recent description of two new *Ceratocystis* species that probably used to be treated within *C. fimbriata*. *Ceratocystis albofundus* Wingfield, De Beer & Morris was reported causing wilt and die-back of *Acacia mearnsii* Wildeman in South Africa (Morris, Wingfield and De Beer 1993, De Beer 1994). Detailed morphological and molecular comparisons showed that the fungus represents a distinct *Ceratocystis* species that is characterised by light-coloured perithecial bases, dark necks, divergent ostiolar hyphae and distinct ITS sequences (Wingfield *et al*. 1996, Roux *et al*. 1999). The other new species from wounds on *Eucalyptus* in Australia has recently been described as *Ceratocystis pirilliformis* Barnes & Wingfield (Barnes *et al*. 2003). This species has hat-shaped ascospores similar to those found in *C. fimbriata*, but differs from this species in its pear-shaped perithecial bases. Phylogenetic analysis of the rRNA ITS regions also supported the definition of this fungus as a new *Ceratocystis* species (Barnes *et al*. 2003).

CONCLUSIONS

Selection pressure for insect dispersion has resulted in convergent morphological characteristics in the ophiostomatoid fungi, which has made it difficult to establish reliable taxonomic characters for this group of fungi. Thus, the classification of these fungi has been the subject of substantial debate since the first ophiostomatoid species was described in 1890. In recent years, phylogenetic analyses using DNA sequence data have provided new clarity to classification of these fungi and have facilitated more accurate identification of them.

The genus *Ceratocystis sensu stricto* is reserved for those ophiostomatoid fungi that have *Thielaviopsis* anamorphs, that are intolerant to the antibiotic cycloheximide in culture and that lack cellulose and rhamnose in their cell walls. Some of these species are economically important plant pathogens of both agricultural crops and forest plantation trees. As species of *Ceratocystis* have been more intensively studied, it has become evident that some of the species in fact represent a complex of several host-specialized forms and

cryptic taxa. This has important implications, especially in designing for quarantine measures against these pathogens.

Nine of the eleven species thus far identified in the *C. coerulescens* complex have been unequivocally delimited using a wide variety of phenotypic and genotypic characteristics. Nevertheless, problems have been experienced in separate *C. polonica* and *C. laricicola*. This is because they are morphologically indistinguishable, have similar isozyme profiles and identical ITS sequences. Both species are associated with aggressive conifer bark beetles and are able to kill their hosts, which justifies a more intensive study of them. Improved taxonomy of these species and an extended knowledge regarding their population characteristics would expand our understanding of their epidemiological relationships with insect vectors and host trees.

Ceratocystis fimbriata represents one of the most virulent and economically important vascular pathogens in many agricultural crops and forest trees. Genetic and pathological studies have suggested that this fungus comprises a complex of several host-specialized forms. Two of these "forms" have already been described as new species based on molecular and detailed morphological comparisons. It is clear that further investigations are required to delimitate other species within this complex of important plant pathogens.

Much literature has been generated for *Ceratocystis sensu stricto*. During the last decade, research dealing with these fungi was especially focused in understanding the phylogenetic relationships amongst *Ceratocystis* species. However, a few studies deal with the population biology of *Ceratocystis* species. The knowledge of the level of variability and degree of genetic structure of natural populations of plant pathogens is important to establish hypothesis regarding their origin, movement and reproduction strategies. This information is likely to be required in the planning and implementation of management strategies against diseases caused by species of *Ceratocystis*, including generation of resistant plant material, development of quarantine strategies and appropriate use of chemical control measures.

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