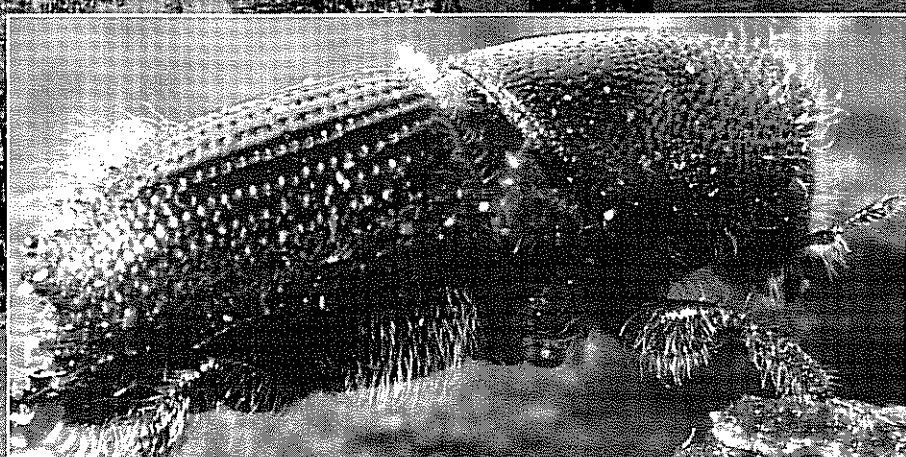


Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis

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Ips sexdentatus (six-spined engraver beetle), a bark beetle attacking pines (photo taken by Janin – INRA).

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Chapter 10

FUNGAL ASSOCIATES OF EUROPEAN BARK BEETLES WITH SPECIAL EMPHASIS ON THE OPHIOSTOMATOID FUNGI

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1. INTRODUCTION

Fungi are common and well-known associates of bark beetles (Coleoptera: Scolytidae). The relationship between fungi and scolytids was recognized relatively long ago. Schmidberger (1836) described an “ambrosia” in the galleries of the wood-inhabiting bark beetle *Xyleborus dispar*, and Hartig (1844) discovered the fungal nature of this “ambrosia” lining the tunnels of the insects. Likewise, Hartig (1878) first recognized the interrelationships between insect damage, discoloration of wood and fungi, and during his studies on blue-stain in the sapwood of conifers, Münch (1907, 1908) observed that blue-stain in living trees and lumber is associated with attack by bark beetles. Since these early discoveries a large number of investigations on various aspects of the association of fungi with bark beetles have been carried out.

Scolytids are among the most economically important pests of the world's forests, especially conifer forests in the boreal and temperate regions of the Northern hemisphere (Postner 1974; Schwerdtfeger 1981; Wood 1982; Wood and Bright 1992). A considerable number of fungal associates of bark beetles are known as forest pathogens in their own right, causing vascular wilt or vascular stain diseases (Webber and Gibbs 1989; Harrington 1993a, 1993b; Wingfield *et al.* 1993). Many other species give rise to discoloration in the sapwood of conifers and cause enormous losses to forestry and wood industry worldwide (Whitney 1982; Seifert 1993; Butin 1996).

Although the association between scolytids and fungi has been recognised for more than one century, many fundamental aspects of this relationship are still poorly

known. A key question pertaining to the symbiosis between bark beetles and fungi is that regarding the degree of dependence of the partners on each other. Many fungi are totally dependent on their associated insects for dissemination and they have not been found outside the bark beetle habitat (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Whitney 1982; Kirschner 1998; Six 2003). Similarly, one group of scolytids, the ambrosia beetles, are obligatorily dependant on certain fungi, the ambrosia fungi, for nutrition (Francke-Grosmann 1967; Postner 1974; Norris 1979; Beaver 1989). However, the role of fungi associated with bark beetles that colonize the phloem of trees has been the subject of considerable debate, and arguments exist both for and against the view that the insects and the fungi they carry are mutualists (e. g. Francke-Grosmann 1967; Whitney 1982; Christiansen *et al.* 1987; Harding 1989; Harrington 1993a, Wingfield *et al.* 1995; Krokene 1996; Paine *et al.* 1997).

In this chapter a synthesis of the knowledge regarding the association of fungi with bark beetles is presented. This synthesis will focus on European scolytids and it deals mainly with fungal associates of conifer bark beetles. This is because they have been most intensively studied, in contrast to scolytids on hardwoods where much less knowledge is available. This review also highlights the ophiostomatoid fungi which include the ascomycete genera *Ceratocystis*, *Ceratocystiopsis* and *Ophiostoma* and related anamorph genera, causing tree diseases and blue-stain on trees and lumber. Fungal pathogens of bark beetles are treated by Wegensteiner (chapter 12) and are thus excluded here.

2. OVERVIEW OF THE ASSOCIATION OF FUNGI WITH BARK BEETLES IN RELATION TO BARK BEETLE ECOLOGY

The large majority of bark beetle species fulfil most of their life cycle in the wood or secondary phloem underneath the bark of conifer and deciduous trees (Postner 1974; Schwerdtfeger 1981; Wood 1982; Wood and Bright 1992; Pfeffer 1995). Two major groups, ambrosia beetles and phloeophagous bark beetles, are commonly distinguished based on their habitats and larval feeding habits (Francke-Grosmann 1966, 1967; Postner 1974; Beaver 1989; Wood 1982; Pfeffer 1995). These two groups differ greatly in their nutrition biology and also show fundamental differences in their association with fungi. Another group, the phloeomycetophagous bark beetles that feed both on phloem and on associated fungi are also considered (Francke-Grosmann 1952, 1966, 1967; see below and 6.2.2.).

One group of bark beetles, termed "ambrosia beetles" or "xylomycetophagous bark beetles" breeds in the wood of trees (Francke-Grosmann 1966, 1967; Postner 1974; Beaver 1989; Pfeffer 1995). The ambrosia beetles also include the platypodid beetles (Coleoptera: Platypodidae) with only one species, *Platypus cylindrus* occurring in Europe (Postner 1974; Pfeffer 1995). Wood is a poor substrate for nutrition of insects, since they are not able to digest lignin, cellulose and hemicelluloses, which are the main constituents of the xylem (Francke-Grosmann 1967; Graham 1967; Beaver 1989). Ambrosia beetles have overcome this problem through ectosymbiosis with nutritionally obligate fungi (Francke-Grosmann 1966, 1967; Graham 1967; Postner 1974; Beaver 1989; Berryman 1989; Six 2003). The

larvae of ambrosia beetles feed on specific fungi, known as "ambrosia fungi" that are transported to newly colonised trees and cultivated by the adult insects. Although ambrosia beetles can sometimes attack and kill living trees they usually breed on dying or recently killed trees and fresh logs and degrade timber (Postner 1974; Schwerdtfeger 1981).

The second, much larger group of bark beetles lives in the phloem of hardwood and conifer trees. They are referred to as "phloeophagous", "phloem-feeding" or "true bark beetles" (Postner 1974; Schwerdtfeger 1981; Wood 1982; Wood and Bright 1992; Pfeffer 1995). Phloem provides a nutrient-rich source of nutrition for the insects and in contrast to ambrosia beetles most phloem-feeding bark beetles are most likely not dependent on their fungal associates for nutrition (Francke-Grosmann 1967; Whitney 1982; Harding 1989). However, phloem-feeding bark beetles are commonly associated with various fungi, in particular blue-stain fungi belonging to the ascomycete genera *Ophiostoma* and *Ceratocystis* and their anamorphs (e. g. Mathiesen-Käärik 1953; Francke-Grosmann 1967; Whitney 1982; Beaver 1989; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997; Kirschner 1998; Jacobs and Wingfield 2001; Six 2003).

Some phloem-feeding bark beetles, especially on conifers, are amongst the most economically important forest pests. Under certain circumstances these scolytids attack living trees and cause long-lasting and destructive outbreaks. In Europe, *Ips typographus* on Norway spruce is considered as the most aggressive and most economically important bark beetle species (Christiansen and Bakke 1988), but there are also many other scolytids that cause considerable damage to European forestry (Postner 1974; Schwerdtfeger 1981).

In order to utilize living trees for breeding, bark beetles must overcome the tree's defence systems and kill their hosts (Postner 1974; Christiansen *et al.* 1987; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997; Lieutier 2002 and chapter 9). Overcoming the resistance of the host tree is accomplished by a co-ordinated mass attack of many individuals, which exhausts the anatomical and biochemical host defenses and is followed by tree death (Christiansen *et al.* 1987; Raffa and Klepzig 1992; Lieutier 2002 and chapter 9). For bark beetle species that attack living trees and kill them by this "cooperative strategy" (Lieutier 2002 and chapter 9) the association with pathogenic blue-stain fungi has always been suspected to be of great significance (Berryman 1972; Whitney 1982; Christiansen *et al.* 1987; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997; Lieutier 2002 and chapter 9). Associated blue-stain fungi might help their insect vectors to overcome and kill their host trees by contributing to exhaust the tree's defense mechanisms (see 3.3.1. and 6.2.1.; Lieutier chapter 9). Among true bark beetles in Europe, one species, *Dendroctonus micans* is unusual, because it individually attacks trees and behaves like a true parasite that initially does not kill its host (Gregoire 1988; Lieutier 2002 and chapter 9). As part of the solitary, "defence-avoiding attack strategy" (Lieutier 2002 and chapter 9), associated blue-stain fungi do not play an important role in the successful breeding of *D. micans* in living trees (Lieutier *et al.* 1992; Lieutier 2002 and chapter 9).

Despite the traditional distinction between xylomycetophagous and phloeophagous bark beetles, some species seem to be intermediate between these

two groups. In Europe, two species on pine, *Tomicus minor* and *Ips acuminatus* share characteristics of both mycetophagous and phloeophagous scolytids and one may best refer to them as phloeomycetophagous bark beetles (Francke-Grosmann 1952, 1966, 1967; see 6.2.2.). Consequently, they are regularly associated with *Ambrosiella* species that are typical ambrosia fungi of xylmycetophagous scolytids and with blue-stain fungi in the genus *Ophiostoma* that are common associates of phloeophagous bark beetles (Mathiesen-Käärik 1953; Francke-Grosmann 1952, 1967).

One form of behaviour in some phloem-feeding bark beetles has important consequences regarding the transmission of virulent forest pathogens. Elm bark beetles in the genus *Scolytus* fulfil their maturation feeding requirements on twig crotches in the crown of trees and this leads to efficient transmission of the Dutch elm disease pathogens *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* from diseased to healthy elm trees (Postner 1974; Webber and Brasier 1984; Webber and Gibbs 1989). *Scolytus intricatus* on *Quercus* spp. shows a similar behaviour and might thus be an efficient vector of the oak wilt pathogen *Ceratocystis fagacearum*, if it were accidentally introduced from North America into Europe (Webber and Gibbs 1989).

3. TAXONOMY, BIOLOGY AND ECOLOGY OF FUNGI ASSOCIATED WITH BARK BEETLES

Fungi associated with bark beetles have been grouped based on various characteristics. They have been classified as mycangial or non-mycangial, describing whether they are disseminated in mycangia (see 4.) or not (Paine *et al.* 1997; Six 2003). The term "ambrosia fungi" is used for those fungal associates of ambrosia beetles, which are cultivated in the galleries of the insects and on which the beetles depend for nutrition (Francke-Grosmann 1967; Norris 1979; Beaver 1989). Both classifications refer to the ecology of the fungi, but do not consider their taxonomy. The various fungi associated with bark beetles belong to the yeasts (3.1.), basidiomycetes (3.2.), ascomycetes (3.3.) and anamorphic fungi without sexual states (3.4.). Zygomycetes have occasionally also been reported as associates of bark beetles (Whitney 1982; Harding 1989; Kirschner 1998; Jankowiak 2004), but they are casual and inconsistent elements in this ecological niche and will not be treated in detail here.

3.1. Yeasts

Yeasts are commonly associated with phloeophagous bark and ambrosia beetles (Grosmann 1931; Siemaszko 1939; Callahan and Shiffine 1960; Francke-Grosmann 1967; Zimmermann 1973; Whitney 1971, 1982; Bridges *et al.* 1984; Harding 1989; Leufvén and Nehls 1986; Furniss *et al.* 1990; Six 2003). Very little is known about the taxonomy of yeasts associated with scolytids, the species assemblages occurring with bark beetles and the effects of yeasts on the insects. Taxonomically, all yeasts associated with bark beetles probably belong to the ascomycetes (Six 2003).

In many studies on the mycobiota of bark beetles yeasts have been recorded, but their identity has only rarely been determined (e. g. Grosmann 1931; Bramble and Holst 1940; Callaham and Shifrine 1960; Zimmermann 1973; Bridges *et al.* 1984; Leufvén and Nehls 1986; Furniss *et al.*, 1990; Solheim 1992b; Krokene 1996; Six 2003). Species that are associated with ambrosia beetles have occasionally been reported as ambrosia fungi, thus being nutritionally important for the insects (Francke-Grosmann 1967). They are also suspected to be nutritionally important for phloeophagous bark beetles (Whitney 1982; Strongman 1986; Pignal *et al.* 1988; Harding 1989). Yeasts have been isolated from the outer surface of adult beetles and their immature stages as well as from the digestive tracts of larvae and mature insects (Grosmann 1931; Leufvén and Nehls 1986; Furniss *et al.* 1990; Six 2003). They are also common in the breeding galleries and pupal chambers of bark beetles (Bridges *et al.* 1984). In early stages of the breeding development of bark beetles, yeasts are among the most frequent micro-organisms that can be isolated from the phloem and xylem adjacent to the insect galleries (Bramble and Holst 1940; Käärik 1975; Bridges *et al.* 1984; Kirisits 1996), but they do not display pathogenicity to their host trees (Callaham and Shifrine 1960). In isolations directly from bark beetles, yeasts occur more frequently than the blue-stain fungi, while the opposite is true for isolations from the wood of bark beetle-infested trees (Furniss *et al.* 1990; Solheim 1992b).

Individual bark beetle species often carry not only one, but two or several yeast taxa (Callaham and Shifrine 1960; Whitney 1982; Leufvén and Nehls 1986; Six 2003). The yeasts associated with bark beetles are relatively unspecific and one fungal species is usually associated with several insect species (Callaham and Shifrine 1960; Six 2003). Most bark beetle-associated yeasts belong to the genera *Candida*, *Pichia*, *Hansenula*, *Saccharomyces* and *Cryptococcus* (Callaham and Shifrine 1960; Whitney 1982; Leufvén & Nehls 1986; Harding 1989; Six 2003). The most detailed study on yeasts associated with bark beetles in Europe was carried out by Leufvén and Nehls (1986) who studied the yeasts occurring with *I. typographus*. At least six different yeasts were recorded, with *Hansenula holstii* and *Candida diddensii* type yeasts being most prevalent (Leufvén and Nehls 1986).

3.2. Basidiomycetes

Basidiomycetes have only occasionally been mentioned as associates of bark beetles (Siemaszko 1939; Whitney 1982; Klepzig *et al.* 2001a, 2001b; Six 2003), but their diversity in this habitat may have been underestimated thus far (Kirschner 1998, 2001). In Europe, *Gloeocystidium ipidophilum* was described from galleries of *I. typographus* on Norway spruce in Poland (Siemaszko 1939). This fungus was not mentioned again for a long time, but it was recently also found in Germany (Kirschner 1998) Poland (Jankowiak 2004) and Austria (Grubelnik 1998), in the same niche as the one originally reported for it. A hymenomycete similar, but not identical to *G. ipidophilum* was isolated from the sapwood of *Picea abies* infested by *I. typographus* in Norway (Solheim 1992b). *Heterobasidion annosum*, the causal agent of Annosum root rot (Butin 1996) has occasionally been found to be

associated with bark and ambrosia beetles on conifers (Bakshi 1950; Harding 1989; Kirschner 1998). The vector relationships between bark beetles and *H. annosum* are likely only casual.

Recently, knowledge on the association of basidiomycetes with bark beetles in Europe has been improved by Kirschner (1998, 2001) who isolated 20 kryptic basidiomycetes from the insects or from bark beetle galleries. Most of these basidiomycetes represent new taxa and at least some of them are suspected to be consistently associated with bark beetles. Their trophic roles may be diverse, and many of these newly detected basidiomycetes are likely mycoparasites or mycophilous fungi (Kirschner 1998). A few North American bark beetle species, particularly *Dendroctonus* species and *Ips avulsus* appear to be intimately associated with basidiomycetes, which is in contrast to the situation in Europe (Six 2003 and references therein). These basidiomycetes belong to the genus *Entomocorticium*, including five species known to be associated with bark beetles (Whitney *et al.* 1987; Klepzig *et al.* 2001a, 2001b; Six 2003 and references therein).

3.3. Filamentous ascomycetes

Filamentous ascomycetes have long been known as common associates of bark beetles. Fungi belonging to the genera *Ceratocystis*, *Ceratocystiopsis* and *Ophiostoma* are the most prevalent and most important associates of phloeophagous bark beetles and they are also known to occur in the galleries of wood-inhabiting scolytids (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Zimmermann 1973; Upadhyay 1981; Whitney 1982; Wingfield *et al.* 1993; Krokene 1996; Paine *et al.* 1997; Kirschner 1998; Six 2003). These principal fungal associates of phloem feeding bark beetles have received most attention, which is not surprising considering their economic importance as tree pathogens and agents of sapstain. However, it is worth mentioning that diverse assemblages of other ascomycetes with various trophic roles are associated with bark beetles, some of which seem to have a consistent relationship with the insects (Kirschner 1998, Malloch and Blackwell 1993). In this review, I focus on the ophiostomatoid fungi and refer to Kirschner (1998, 2001) and Malloch and Blackwell (1993) for an overview of other ascomycetes associated with bark beetles.

3.3.1 The ophiostomatoid fungi

Together with other ascomycetes, *Ophiostoma*, *Ceratocystis* and *Ceratocystiopsis* as well as related asexual fungi in the genera *Leptographium*, *Pesotum*, *Hyalorhinocladiella*, *Sporothrix* and *Thielaviopsis* are known as the "ophiostomatoid fungi" (Wingfield *et al.* 1993). This common name was introduced in the 1990s taking the similarities of these fungi into account. Ophiostomatoid fungi associated with bark beetles are also commonly known as "blue-stain fungi", referring to the damage these fungi cause, namely blue, gray, brown or even black discoloration of the sapwood of trees, mostly on conifers (Münch 1907; Lagerberg *et al.* 1927; Seifert 1993; Butin 1996; Fig. 1).

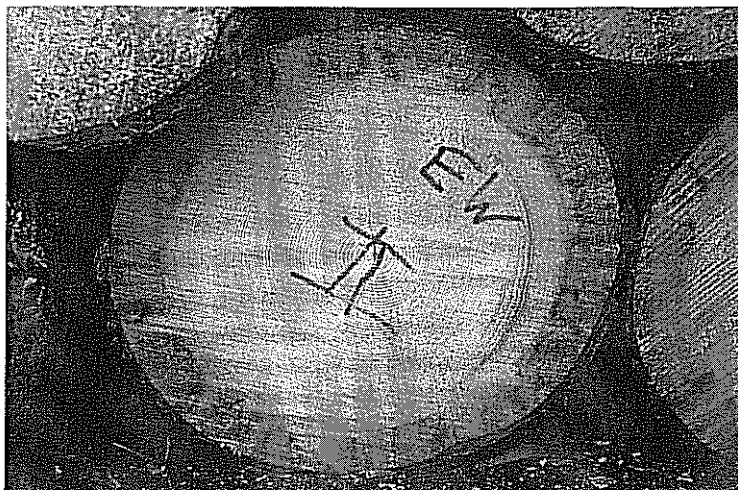


Figure 1. Blue-stain in the sapwood of Norway spruce infested by the bark beetle *Ips typographus*.

Blue-stain is considered as serious problem in conifer trees (Seifert 1993; Butin 1996), however, hardwoods are also affected (Butin and Zimmermann 1972; Kowalski and Butin 1989; Kowalski 1991; Seifert 1993). On hardwoods, these fungi more often cause vascular wilt and vascular stain diseases (Kile 1993; Harrington 1993; Brasier 2000). Sap stain is caused by fungal hyphae, which are concentrated in the ray parenchyma cells and resin ducts of infected sapwood (Münch 1907; Liese and Schmid 1961; Ballard *et al.* 1984; Seifert 1993; Gibbs 1993). Tracheids are also colonized, especially at later stages of infection (Liese and Schmid 1961; Ballard *et al.* 1982; Seifert 1993; Gibbs 1993).

Blue-stain fungi utilise assimilates stored in the living ray parenchyma cells of the sapwood (Seifert 1993; Butin 1996). In contrast to decay fungi, they do not decompose the structural components of the wood (cellulose, lignin and hemicelluloses) (Münch 1908; Seifert 1993). The moisture content of the sapwood is important for the development of blue-stain. Most blue-stain fungi grow at moisture content between 30-40 % and 130-140 % of the dry weight, with different fungal species having different requirements (Münch 1908; Lagerberg *et al.* 1927; Butin 1996). Pathogenic blue-stain fungi that cause stain in living trees are able to infect fresh sapwood with high moisture content and low oxygen levels (Münch 1908; Lagerberg *et al.* 1927; Scheffer 1986; Solheim 1991).

Taxonomy of the phoiostomatoid fungi. *Ophiostoma* and *Ceratocystis* have many morphological characters in common, including perithecia with globose or pear-shaped bases and long perithecial necks (Fig. 2), evanescent asci and hyaline, one-celled, small ascospores, which vary in their shape and possess or lack sheaths (Hunt 1956; Upadhyay 1981; De Hoog and Scheffer 1984; Wingfield *et al.* 1993;

Harrington and Wingfield 1998; Jacobs and Wingfield 2001). Based on their similarities *Ophiostoma* and *Ceratocystis* have been considered as synonyms for long periods of their taxonomic history. The third related genus, *Ceratocystiopsis* forms a morphologically well-defined group and is characterised by a unique combination of features, namely relatively small ascocarps, short perithecial necks with convergent ostiolar hyphae and sickle-shaped, sheathed ascospores (De Hoog and Scheffer 1984; Upadhyay and Kendrick 1975; Upadhyay 1981; Wingfield 1993). There are, however, various arguments relating to whether these fungi should be treated together with *Ophiostoma*.

It is now widely accepted that *Ceratocystis* is not closely related to *Ophiostoma* and *Ceratocystiopsis*, despite the similarities in their perithecial characteristics (De Hoog and Scheffer 1984; Wingfield *et al.* 1993; Jacobs and Wingfield 2001). Phylogenetic studies based on analyses of the rDNA sequence data placed *Ophiostoma* in a monophyletic group close to the Diaporthales, while *Ceratocystis* is closely related to taxa in the Microascales (Spatafora and Blackwell 1993; Hausner *et al.* 1993b; Paulin-Mahady *et al.* 2002). *Ceratocystiopsis*, though morphologically well defined, groups phylogenetically together with *Ophiostoma* and these genera have thus been synonymized (Hausner *et al.* 1993a). However, *Ceratocystiopsis* is still widely used as genus name and it is also treated as separate from *Ophiostoma* in the present review.

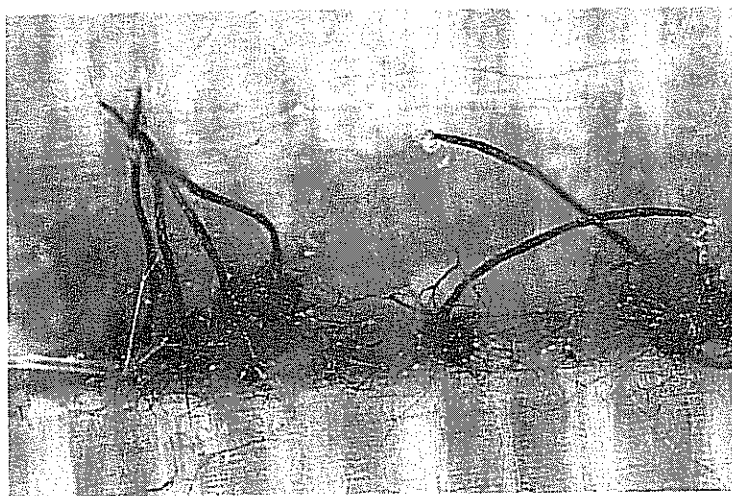


Figure 2. Perithecia of *Ceratocystis polonica*.

The similar ascocarps of *Ceratocystis*, *Ophiostoma* and *Ceratocystiopsis* evolved separately from each other, likely as adaptations to the bark beetle habitat. Besides molecular markers the separation of *Ceratocystis* from *Ophiostoma* and *Ceratocystiopsis* is supported by several lines of evidence. Most distinctively, these genera can be differentiated based on their asexual stages. *Ceratocystis* species have *Thielaviopsis* anamorphs (De Hoog and Scheffer 1984; until very recently known as

Chalara, Paulin-Mahady *et al.* 2002), with endogenous conidium development by "ring wall building" (Minter *et al.* 1983). In contrast, asexual stages of *Ophiostoma* belong to a variety of hyphomycete genera including *Leptographium*, *Pesotum* (until recently known as *Graphium*; Okada *et al.* 1998, 2000), *Sporothrix* and *Hyalorhinocladiella* (De Hoog and Scheffer 1984), and conidium development is always exogenic by "apical wall building" (Minter *et al.* 1982). Similarly, *Ceratocystis* spp. have *Hyalorhinocladiella* and *Sporothrix* anamorphs, but not *Leptographium* and *Pesotum* states (Upadhyay 1981; De Hoog and Scheffer 1984; Wingfield 1993). Other than these characteristics *Ophiostoma* and *Ceratocystis* are very similar, if not identical (De Hoog and Scheffer 1984; Wingfield 1993), and therefore, subsequent discussion will deal with *Ophiostoma* as including *Ceratocystis*. There are also differences between *Ophiostoma* and *Ceratocystis* in the development of the ascospores and the arrangement and organisation of the asci in the perithecium (Van Wyk and Wingfield 1990; Van Wyk *et al.* 1993).

Species of *Ophiostoma* and *Ceratocystis* also differ in the chemical composition of their cell walls (De Hoog and Scheffer 1984 and references therein). *Ophiostoma* spp. are unusual within the ascomycetes, since their cell walls contain besides chitin also cellulose and rhamnose (De Hoog and Scheffer 1984). In contrast, the cell walls of *Ceratocystis* consist mainly of chitin and do not contain any detectable amounts of cellulose and rhamnose (De Hoog and Scheffer 1984). In addition, *Ophiostoma* and *Ceratocystis* differ in their tolerance to the antibiotic cycloheximide that inhibits the protein synthesis in most eucaryotic organisms (Harrington 1981). While *Ceratocystis* is very sensitive to even low concentrations of cycloheximide, species of *Ophiostoma* tolerate high concentrations of this antibiotic (Harrington 1981; De Hoog and Scheffer 1984).

Ecology of the ophiostomatoid fungi. *Ceratocystis* and *Ophiostoma* also display differences in their ecology and their relationships with insects (Harrington 1987, 1993a; Kile 1993). *Ceratocystis* species colonize a variety of herbaceous and woody plants (Kile 1993). Many species are distributed in subtropical and tropical regions of the world and some others occur on woody plants in temperate and boreal regions, causing blue-stain in the sapwood of conifers (Harrington 1987; Kile 1993; Harrington and Wingfield 1998). Apart from bark beetles, a wide variety of insects such as flies (Diptera) or nitidulid beetles (Nitidulidae) are known as vectors of *Ceratocystis* spp. (Harrington 1987). Generally, *Ceratocystis* species have a relatively loose and unspecific relationship with insects. This is exemplified by the causal agent of oak wilt in North America, *C. fagacearum*, which is transmitted at low frequencies by nitidulid beetles (Juzwik and French 1983). However, there are also exceptions to this characteristic. There are three *Ceratocystis* species, which are consistently associated with conifer bark beetles (Solheim 1986; Redfern *et al.* 1987; Wingfield *et al.* 1997; Harrington and Wingfield 1998). Intriguingly, these three species are relatively virulent pathogens (Christiansen 1985; Redfern *et al.* 1987; Harrington and Wingfield 1998; Solheim and Safranyik 1997; Yamaoka *et al.* 1997; 1998).

Species of *Ophiostoma* and *Ceratocystiopsis* and their anamorphs are, in contrast to *Ceratocystis* spp., mainly distributed in temperate and boreal regions of the Northern hemisphere (Harrington 1987, 1993a; Jacobs and Wingfield 2001). Most of these fungi live in the phloem and in the sapwood of conifers and hardwoods and they rarely occur on other substrates such as herbaceous plants (Hunt 1956; Upadhyay 1981; Jacobs and Wingfield 2001). *Ophiostoma* spp. are predominantly known as fungal associates of phloeophagous bark beetles, with which they often form intimate and relatively specific relationships (Mathiesen-Käärrik 1953; Whitney 1982; Paine *et al.* 1997; Kirschner 1998; Jacobs and Wingfield 2001). *Ophiostoma* species also occur in association with ambrosia beetles (Bakshi 1950; Mathiesen-Käärrik 1953; Zimmermann 1973; Kirschner 1998), cerambycid beetles (Mathiesen-Käärrik 1953; Jacobs and Wingfield 2001; Jacobs and Kirisits 2003; Jacobs *et al.* 2003a), weevils (Mathiesen-Käärrik 1953; Jacobs and Wingfield 2001; Viiri, chapter 17) and phoretic mites carried by bark beetles (Bridges and Moser 1983, 1986; Léveux *et al.* 1989; Moser *et al.* 1989, 1997). A number of ophiostomatoid fungi are not specifically associated with insects, but disseminated through the air or by rain-splash inoculum (Mathiesen-Käärrik 1953; Kile 1993; Dowding 1969; Gibbs 1993). These species also occur in galleries of bark beetles, in particular at late stages of brood development, but their relationship with the insects is relatively loose and unspecific (Mathiesen-Käärrik 1953; Kirisits 1996; Kirschner 1998).

The association of blue-stain fungi with bark beetles can easily be recognized on trees or logs infested by the insects, especially on conifers. At advanced stages of breeding activity, blue-stain can be seen in the phloem and in the sapwood (Fig. 1) around and underneath insect galleries. Perithecia and anamorph structures of the ophiostomatoid fungi develop in the phloem and sapwood in and around female and larval galleries and in pupal chambers (Fig. 3).

Blue-stain fungi are primary colonizers of the sapwood of dying and recently killed trees. A number of studies have treated the characteristic succession of colonization of the sapwood by blue-stain fungi, following attack by bark beetles (Bramble and Holst 1940; Käärrik 1975; Solheim 1992a, 1992b). The most virulent blue-stain fungi are the first to grow into the fresh sapwood of trees that have been infested by the insects. Other, less virulent blue-stain fungi follow these primary invaders. During this temporal succession, primary and secondary invaders are rapidly replaced by other fungi, including wood-decay fungi and saprotrophic species (Solheim 1992b). In contrast to their pathogenic abilities, most blue-stain fungi are poorly adapted to live and survive saprophytically in host tissues (Gibbs and Inman 1991; Gibbs 1993; Solheim 1992b). They are thus quickly replaced by other fungi, which are better adapted to live saprophytically.

Pathogenicity of ophiostomatoid fungi. There are a considerable number of economically important plant and tree pathogens among the ophiostomatoid fungi (Wingfield *et al.* 1993; Kile 1993a; Harrington 1993a). Among these, the most aggressive tree pathogens are those that cause vascular wilt diseases. They are disseminated by insect vectors or abiotic agents, infect the vascular system of living trees, which leads to disruption of the water transport and finally to death of trees.

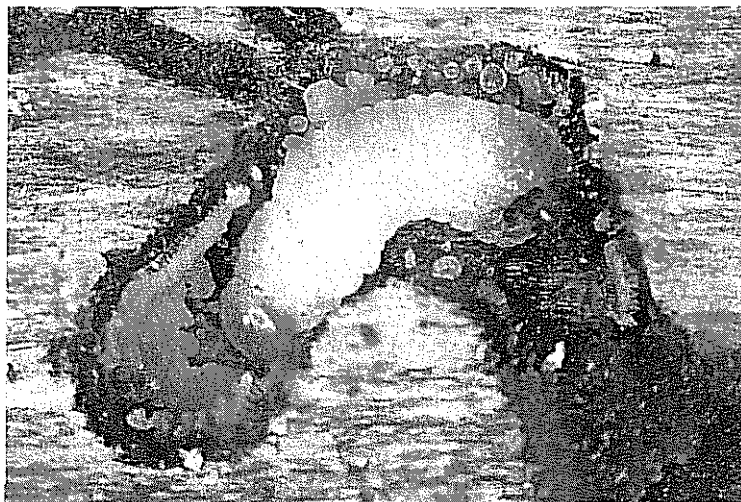


Figure 3. Larva of the spruce bark beetle *Ips typographus* prior to pupation in a pupal chamber. Plentiful sporulation of *Leptographium penicillatum* is seen along the walls of the gallery.

The best known examples of vascular wilt pathogens are *O. ulmi* and *O. novo-ulmi* that are effectively transmitted by elm bark beetles and have been responsible for various pandemics of Dutch elm disease in Europe, North America and parts of Asia (Brasier 1991, 2000; Webber and Gibbs 1989). Other examples of aggressive wilt pathogens within the ophiostomatoid fungi include *C. fagacearum*, the causal agent of oak wilt in North America (Webber and Gibbs 1989; Kile 1993), *Leptographium wageneri*, which is responsible for black stain root disease on conifers in western North America (Harrington 1993a; Viiri, chapter 17) and *Ceratocystis fimbriata*, which causes vascular stain and canker diseases on a wide range of economically important woody plants, including tree species of great economic importance (Kile 1993; Roux *et al.* 2000; Marin 2004). While the Dutch elm disease pathogens are consistently associated with insect vectors, the relationships of *C. fagacearum* and *C. fimbriata* with insects are loose and unspecific, and *L. wageneri* is probably intermediate between these two extremes (Webber and Gibbs 1989; Harrington 1993a; Kile 1993; Viiri, chapter 17).

Most ophiostomatoid fungi causing blue-stain in the sapwood of conifers are moderately or weakly virulent pathogens, or they are saprophytes that cause damage to stored logs, timber and other wood products (Seifert 1993; Gibbs 1993; Butin 1996). However, some species display relatively high levels of virulence to their hosts and can kill trees when inoculated at sufficiently high dosages (Horntvedt *et al.* 1983; Christiansen 1985; Christiansen *et al.* 1987; Harrington 1993a; Paine *et al.* 1997; Lieutier 2002, chapter 9). Generally, bark beetle-associated blue-stain fungi are much less virulent than the aforementioned aggressive wilt pathogens. In contrast to typical vascular wilt pathogens, pathogenic blue-stain fungi mainly

colonize the ray parenchyma cells of the sapwood which leads to disruption of the sap flow of infected trees (Ballard *et al.* 1982; Horntvedt *et al.* 1983; Webber and Gibbs 1989; Harrington 1993a; Paine *et al.* 1997; Kirisits and Offenthaler 2002). Colonization of xylem vessels or tracheids is very limited at early stages of pathogenesis and occurs extensively only at late stages of infection (Ballard *et al.* 1984; Webber and Gibbs 1989). Simultaneously to infection of the xylem the phloem of trees is also colonized by blue-stain fungi, which can lead to bark girdling of the host trees (Webber and Gibbs 1989). Due to the patterns of colonization of the xylem, pathogenic blue-stain fungi have been referred to as "vascular stain pathogens" (Webber and Gibbs 1989). The type of disease caused by these fungi has also been called "canker stain", because disease symptoms include both necrotic lesions in the phloem and stain in the sapwood (Wingfield *et al.* 1993; Fig. 4).

Systemic vascular wilt pathogens and non-systemic vascular stain pathogens differ substantially in the modes of inoculation and infection as well as in their pathogenesis. While infection of vascular wilt pathogens can start from a single inoculation point and progresses systemically, pathogenic blue-stain fungi are simultaneously inoculated into the host tissues during the mass attack of trees by bark beetles (Webber and Gibbs 1989). The host tree can always resist single or low numbers of inoculations of blue-stain fungi which lead to discrete necrotic lesions in the phloem and to limited desiccation or stain in the sapwood (Redfern *et al.* 1987; Lieutier *et al.* 1989a, 1989b; Krokene 1996; Lieutier 2002, chapter 9). However, it has been demonstrated in mass inoculation experiments that the defense mechanisms, in particular the induced, hypersensitive wound response of the host trees get exhausted, which can finally result in tree death (Horntvedt *et al.* 1983; Christiansen 1985; Christiansen *et al.* 1987; Croisé *et al.* 1998; Lieutier 2002, chapter 9). After mass inoculation, necrotic lesions develop in the phloem and the sapwood becomes blue-stained and dysfunctional (Fig. 4).

Examples of relatively virulent ophiostomatoid fungi associated with bark beetles in Europe include *Ceratocystis polonica* (associated with *Ips* spp. on *Picea* spp.; e. g. Horntvedt *et al.* 1983; Christiansen 1985; Solheim 1988; Harding 1989; Christiansen and Solheim 1990; Krokene and Solheim 1998; Kirisits 1998; Kirisits and Offenthaler 2002), *Ceratocystis laricicola* (associated with *Ips cembrae* on *Larix* spp.; Redfern *et al.* 1987; Kirisits *et al.* 2000) as well as *Leptographium wingfieldii* and *Ophiostoma minus* (associated with *Tomicus piniperda* on *Pinus* spp.; Solheim *et al.* 1993, 2001; Croisé *et al.* 1998). Other bark beetle-associated blue-stain fungi also display varying levels of virulence to their host trees. Most of them also stimulate the tree's defense reactions to some extent. However, they are less virulent as the aforementioned blue-stain fungi and can kill trees, if at all, only at very high inoculation dosages. Such less virulent bark beetle-associated blue-stain fungi in Europe include *Ambrosiella* sp., *Ophiostoma bicolor*, *O. penicillatum*, *O. piceaperdum*, *O. piceae* and *Pesotum* sp. on Norway spruce (Horntvedt *et al.* 1983; Solheim 1988; Harding 1989; Krokene and Solheim 1998; Kirisits 1996, 1998), *O. canum*, *O. ips* and *O. brunneo-ciliatum* on pine (Lieutier *et al.* 1989a, 1989b; Guérard *et al.* 2000; Solheim *et al.* 2001) as well as *Graphium laricis* and *O. brunneo-ciliatum* on European larch (Redfern *et al.* 1987; Kirisits *et al.* 2000). Within the fungal assemblages of particular bark beetles there are often one or

sometimes two relatively virulent fungal associates, while other associated fungi are less virulent. European scolytids with such patterns of virulence among fungal associates include *I. typographus*, *I. amitinus*, *I. cembrae*, *I. duplicatus* and *T. piniperda* (Hornthvedt *et al.* 1983; Solheim 1988; Solheim *et al.* 1993, 2001; Kirsits *et al.* 2000; Krokene and Solheim 1996, 1998).



Figure 4. Necrotic lesions in the secondary phloem and blue-stain in the sapwood of a Norway spruce tree after mass inoculation with *Ceratocystis polonica*.

The results of various inoculation studies suggest that there is considerable variation in the virulence of different isolates of the same blue-stain fungus. Isolates of *L. wingfieldii* collected within the forest of Orléans varied greatly in their virulence to Scots pine (Lieutier *et al.* 2004). Likewise, low levels of virulence and loss of virulence have been described for isolates of *C. polonica* (Kirsits and Anglberger 1998; Krokene and Solheim 2001). Recently, hypovirulence caused by infections of dsRNA mycoviruses has been detected in isolates of *C. polonica* and *C. laricicola* (Marin 2004). This intriguing finding raises questions about the impact of the virus on the ecology and epidemiology of these pathogenic blue-stain fungi and also about possible indirect effects on the relationship between the fungi and their insect vectors.

Pathogenic blue-stain fungi are also known to be associated with North American bark beetles, but I will not treat them in detail here and refer to recent overviews provided by Krokene (1996) and Paine *et al.* (1997). In Asia, the best-

known examples of pathogenic blue-stain fungi associated with bark beetles are *C. polonica* (associated with *Ips typographus* f. *japonicus* on *Picea* spp. in Japan; Yamaoka *et al.* 2000), *C. laricicola* (associated with *Ips subelongatus* on *Larix kaempferi* in Japan; Yamaoka *et al.* 1998) and *Leptographium yunnanensis* (associated with *Tomicus piniperda* in China; Lieutier 2002).

3.4. Anamorphic Fungi

Among the anamorphic fungi associated with bark beetles almost all belong to the hyphomycetes (Francke-Grosmann 1967; Batra 1967; Beaver 1989; Whitney 1982; Kirschner 1998). Many asexual fungi have been known to be associated with bark beetles, but often the relationship between the insects and the fungi seem to be fortuitous and inconsistent (Zimmermann 1973; Whitney 1982; Kirschner 1998; Six 2003). However, some non-ophiostomatoid hyphomycetes are commonly associated with bark beetles (Kirschner 1998, 2001). The way, in which these more regularly associated hyphomycete taxa interact with their insect associates and with other fungi in the bark beetle habitat is unknown. But they may be significant, for example as antagonists and mycoparasites of more intimate associates such as ambrosia fungi and blue-stain fungi (Kirschner 1998; Six 2003).

For many ophiostomatoid species that are phylogenetically related to *Ophiostoma* no sexual state is known to occur and these taxa are thus known under the generic name of their anamorph state, *Leptographium*, *Pesotum*, *Sporothrix* and *Hyalorhinocladiella*. Among these, *Leptographium* species are probably best known (Jacobs and Wingfield 2001), but there are also numerous *Pesotum* species that are consistently associated with bark beetles (e. g. Mathiesen-Käärik 1953; Solheim 1992a, 1992b; Krokene and Solheim 1996; Kirisits *et al.* 2000). Synnematos anamorphs of *Ophiostoma* have until recently been classified in the genus *Graphium*, but phylogenetic studies based on sequence analyses of the rDNA placed *Graphium penicillioides*, the type species of the genus *Graphium*, within the Microascales (Okada *et al.* 1998, 2000). *Graphium* is thus only distantly related to *Ophiostoma*, and consequently, synnematos anamorphs of *Ophiostoma* were transferred to *Pesotum* (Okada *et al.* 1998, 2000). In addition to *Pesotum* spp., a few *Graphium* species are closely associated with bark beetles (Kirschner 1998; Kirisits *et al.* 2000; Jacobs *et al.* 2003b).

Besides a few species where teleomorphs are known, ambrosia fungi generally belong to various genera of hyphomycetes. Major ambrosia fungi belong to the genera *Ambrosiella*, *Raffaelea* and *Fusarium* (Francke-Grosmann 1967; Batra 1967; Zimmermann 1973; Norris 1979; Beaver 1989). The principal ambrosia fungi of European xylomycetophagous bark beetles are *Ambrosiella* spp. (Table 1). Analyses of rDNA sequence data of *Ambrosiella* species have shown that this genus is polyphyletic, with two lineages closely related to *Ceratocystis* and *Ophiostoma*, respectively (Cassar and Blackwell 1996; Rollins *et al.* 2001, Paulin-Mahady *et al.* 2002). Three *Ambrosiella* species, including *A. xylebori* (the type species of the genus), *A. ferruginea* and *A. hartigii* are related to *Ceratocystis*, whereas eight other taxa, *A. brunnea*, *A. gnathotrichi*, *A. ips*, *A. macrospora*, *A. sulcati*, *A. sulfurea*, *A.*

tingens, and an *Ambrosiella* sp. associated with *Hylurgops palliatus* and *Polygraphus poligraphus* (Krokene and Solheim 1996) show affinities to *Ophiostoma* (Cassar and Blackwell 1996; Rollins *et al.* 2001). Similarly, *Raffaelea* species have proven to be closely related to *Ophiostoma* (Jones and Blackwell 1998). The close phylogenetic relationships of *Ambrosiella* and *Raffaelea* species to *Ophiostoma* and *Ceratocystis* clearly demonstrate that the most common associates of phloeophagous and xylomycetophagous bark beetles share common ancestors.

A significant characteristic of the ambrosia fungi is their pleomorphism. In the breeding systems of the ambrosia beetles they form "ambrosial" layers along the gallery walls, representing the "ambrosia" first described by Schmidberger (1936). The "ambrosia" consists of a dense, palisade-like layer of hyphae, on the top of which numerous conidia are formed in chains (Francke-Grosmann 1967; Batra 1967; Zimmermann 1973; Beaver 1989). Beetles and larvae feed on this ambrosial layer and sporulation of the ambrosia fungi is greatly enhanced by the browsing activity of the insects (Mathiesen-Käärrik 1953; Francke-Grosmann 1967; Beaver 1989). Likewise, ambrosial growth seems to be influenced by the physical contact between the insect and the fungus. The control of the growth form of the ambrosia fungi by the insects may be explained by secretions of the adult beetles and their larvae (Francke-Grosmann 1967; Beaver 1989). Slow "ambrosial" growth with intensive sporulation may also occur in culture, and can be stimulated by cultivation of the fungi on certain media (Francke-Grosmann 1967 and references therein; Batra 1967; Beaver 1989). However, in cultures ambrosia fungi often form fast-growing and sterile mycelia. A third growth form is commonly observed in the mycangium of the beetles, where ambrosia fungi form yeast-like stages (Francke-Grosmann 1967; Beaver 1989).

Ambrosia fungi are relatively sensitive to various environmental factors such as relative humidity, moisture content of the sapwood and extreme temperatures. Many ambrosia fungi including *Ambrosiella* species are extremely sensitive to desiccation as well as exposure to high and low temperatures (Zimmermann 1973; Zimmermann and Butin 1973). Ambrosia fungi and thus also ambrosia beetles have specific requirements on the moisture content of the sapwood of their host trees. Generally, this is one of the most decisive factors for establishment and successful breeding of the insects, since the fungus cannot grow when the moisture content is too low (Francke-Grosmann 1967). In the wood of their host trees ambrosia fungi usually penetrate only a few mm into the xylem and their growth is usually restricted to areas surrounding the galleries (Francke-Grosmann 1967; Zimmermann 1973). However, *Ambrosiella ferruginea*, the ambrosia fungus of *Xyloterus lineatus*, penetrates several cm into the sapwood of its conifer hosts and causes a reddish-brown discoloration in the xylem (Mathiesen-Käärrik 1953; Francke-Grosmann 1956a).

4. TRANSMISSION OF FUNGI

Both bark beetles and their intimately associated fungi have evolved morphological adaptations to ensure maintenance of symbiosis from generation to generation. The

most obvious adaptations of the insects for consistent dispersal of certain fungi are specialized structures in the integument of the beetles associated with gland or secretory cells that are used for the storage, transport and transmission of fungi. These structures have been defined as mycangia or mycetangia (Batra 1963a; Francke-Grosmann 1967; Beaver 1989; Berryman 1989). In the strict sense, mycangia consist of more or less spacious tubes, pouches or cavities in the integument lined with glandular cells that produce secretions which protect and preserve the spores of associated fungi (Francke-Grosmann 1956a, 1956b, 1963a, 1963b, 1967; Batra 1963a; Beaver 1989; Léveux *et al.* 1991; Six 2003). More broadly defined the term mycangium refers to any structure that functions in the transport and protection of fungi, regardless whether glandular cells are present or not (Whitney 1982; Six 2003).

Besides protecting fungal spores from detrimental environmental influences (e. g. drought, UV light) and effectively disseminating fungal associates to new habitats, mycangia also act selectively towards certain fungi, since spores of mutualistic species are favoured and detrimental or neutral symbionts are excluded (Batra 1963a; Francke-Grosmann 1967; Beaver 1989). The fungi consistently occurring in the mycangia (= mycangial fungi) are biologically highly or obligately significant for the insects. Probably all mycangial fungi have a decisive role for the nutrition of their associated insects (Francke-Grosmann 1967; Beaver 1989; Paine *et al.* 1997; Six 2003).

Mycangia are commonly classified on the basis of their location on the beetles and structural characteristics. There is a great diversity in the location, form, structure and size of mycangia in xylomycetophagous and phloeophagous bark beetles, which supports the view that these organs have evolved numerous times and independently in different scolytid genera and species (Batra 1963a; Francke-Grosmann 1967; Beaver 1989; Berryman 1989). Mycangia can be present on both sexes, only on the males or only on the females, depending on scolytid species (Francke-Grosmann 1967; Beaver 1989). Xylomycetophagous bark beetles generally possess mycangia, in which they disseminate their ambrosia fungi. Although mycangia play a primary role in dissemination of fungi by ambrosia beetles, other means of fungal dissemination, in particular through the gut, may also be important in this group of scolytids (Francke-Grosmann 1975; Beaver 1989).

Only a small number of the European xylomycetophagous bark beetles have thus far been investigated for the type of mycangium that they bear. These include the economically important species, *Xyleborus dispar*, *X. monographus*, *X. saxeseni*, *Xyloterus domesticus*, *X. lineatus* and *X. signatus*, as well as the introduced *Xyleborus germanus* and *Gnathotrichus materiarius* (Table 1 and references therein). With exception of *G. materiarius* where the mycangium occurs in the male, only the females of European xylomycetophagous scolytids possess a mycangium. There is a considerable variation in the types of mycangia present on European ambrosia beetles (Table 1 and references therein). In *Xyloterus* spp. the mycangium consists of a pair of glandular tubes in the prothorax (Francke-Grosmann 1956a, 1958, 1967). In *Xyleborus dispar* and *X. germanus* the mycangium is represented by intersegmental pouches located between the pro- and mesonotum (Francke-Grosmann 1956a, 1958, 1967), while in *X. monographus* it consists of membranous

pouches at the base of the mandibles (Schedl 1964, Francke-Grosmann 1967). Another type of mycangium is seen in *X. saxeseni* that possesses sclerotized pouches at the base of the elytra (Francke-Grosmann 1956a, 1967). Finally, the mycangium of *G. materiarius* consists of an enlargement of the precoxal cavity (Farris 1963; Francke-Grosmann 1966, 1967).

Mycangia are also known in a number of true bark beetles, although they occur only in a few species (Francke-Grosmann 1967; Whitney 1982; Beaver 1989; Paine *et al.* 1997; Six 2003). For example, various types of mycangia occur in some, but not all North American *Dendroctonus* species (Whitney 1982; Paine *et al.* 1997; Six 2003). In Europe, mycangia have been described for five true bark beetle species (Table 1 and references therein). In *I. acuminatus* which has a phloeomycetophagous feeding habit (Francke-Grosmann 1952; see 6.2.2.), females possess paired membranous pouches at the base of the mandibles (Francke-Grosmann 1963b, 1967). In the mycangium of *I. acuminatus* the nutritionally important fungus, *Ambrosiella macrospora* is transmitted. Primitive mycangia, consisting of secretion-filled punctures of the integument, especially on the elytra, have been described in both sexes of *Hylurgops palliatus*, *Hylastes ater* and *Hylastes cunicularius* (Francke-Grosmann 1956b, 1963a, 1967). Likewise, puncture pits on the mandibles, the pronotum and the elytra function as mycangia in *I. sexdentatus* (Lévieux *et al.* 1991).

For the majority of phloeophagous bark beetles that regularly carry particular fungi, mycangia have not been found. In these non-mycangial scolytid species dissemination of fungi is thus suspected to occur either epizooically by conidia and ascospores adhering to the insect's exoskeleton or endozooically through spores passing the gut undigested (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Whitney 1982; Furniss *et al.* 1990; Paine *et al.* 1997). Apparently, this form of fungal transmission is as efficient as in scolytids which possess mycangia, since relatively specific and relatively constant assemblages of fungi also occur with non-mycangial bark beetles. However, it is also possible that relatively simple, unobvious pit mycangia, similar to those of *Ips sexdentatus* (Lévieux *et al.* 1991) may also occur in other scolytids, but have so far not been recognized.

Phoretic mites often also play an important role in the transmission of ophiostomatoid fungi (Bridges and Moser 1983, 1986; Lévieux *et al.* 1989; Moser *et al.* 1989, 1997). Some mites in the genus *Tarsonemus* even possess specialized structures, called sporothecae which are organs for transmission of fungi (Moser 1985). Likewise, in some cases phoretic mites may even be more intimately associated with a particular fungus than the bark beetles themselves. The best known examples are *D. frontalis*, its hyperphoretic mites *Tarsonemus krantzi* and *T. ips* (which both have sporothecae) and *Ophiostoma minus* which is more closely associated with the mites than with the southern pine beetle (Bridges and Moser 1983; Moser 1985; Klepzig *et al.* 2001a, 2001b).

Fungi associated with bark beetles have also evolved adaptations to the symbiosis with their insect partners. Morphological features of *Ophiostoma*, *Ceratocystis* and *Ceratocystiopsis* such as long perithecial necks (Fig. 2) and sticky ascospores and conidia are viewed as adaptations to the bark beetle habitat (Francke-Grosmann 1967; Whitney 1982; Beaver 1989; Malloch and Blackwell 1993; Six 2003). Ascospores

Table 1. *Ambrosia fungi of European scolytids and types of mycangia occurring in European bark beetle species*

Bark beetle species	Principal ambrosia fungus ¹	Type of mycangium	References
Ambrosia beetles (xylomycetophagous)²			
<i>Gnathotrichus materiarius</i>	<i>Ambrosiizima monospora</i> ³	Enlargement of precoxal cavity in male	Farris 1963; Francke-Grosmann 1966, 1967
<i>Xyleborus dispar</i>	<i>Ambrosiella hartigii</i>	Intersegmental pouches between pro- and mesonotum in female	Francke-Grosmann 1956a, 1958, 1967
<i>Xyleborus germanus</i>	<i>Ambrosiella hartigii</i>	Intersegmental pouches between pro- and mesonotum in female	Francke-Grosmann 1956a, 1958, 1967
<i>Xyleborus monographus</i>	'Yellowish moniloid fungus'	Paired membranous pouches at base of mandible in female	Schedl 1964; Francke-Grosmann 1967
<i>Xyleborus sexeseni</i>	<i>Ambrosiella sulfurea</i>	Sclerotized pouches in base of elytra in female	Francke-Grosmann 1956a, 1967
<i>Xyloterus domesticus</i>	<i>Ambrosiella ferruginea</i>	A pair of glandular tubes in prothorax of female	Francke-Grosmann 1956a, 1958, 1967
<i>Xyloterus lineatus</i>	<i>Ambrosiella ferruginea</i>	A pair of glandular tubes in prothorax of female	Francke-Grosmann 1956a, 1958, 1967
<i>Xyloterus signatus</i>	<i>Ambrosiella ferruginea</i>	A pair of glandular tubes in prothorax of female	Francke-Grosmann 1956a, 1958, 1967
True bark beetle (phloeophagous)			
<i>Hylastes ater</i>	-	Secretion-filled punctures of the integument, especially on the elytra	Francke-Grosmann 1956b, 1967
<i>Hylastes cunicularius</i>	-	Secretion-filled punctures of the integument, especially on the elytra	Francke-Grosmann 1956b, 1967
<i>Hylurgops palliatus</i>	-	Secretion-filled punctures of the integument, especially on the elytra	Francke-Grosmann 1956b, 1967
<i>Ips acuminatus</i> ⁴	<i>Ambrosiella macrospora</i>	Paired membranous pouches at base of mandible in female	Francke-Grosmann 1963b, 1967
<i>Ips sexdentatus</i>	-	Puncture pits on the proximal part of the mandible, the sides of the pronotum and the elytra	Lévieux <i>et al.</i> , 1991

Notes: ¹ See also table 2 and references therein. ² European scolytids with xylomycetophagous feeding habits (Postner 1974; Pfeffer 1995), for which neither the ambrosia fungus nor the type of mycangium has been investigated: *Xyleborus cryptographus*, *X. alni*, *X. eurygraphus*, *X. dryographus*, *X. pfeili*, *X. levae*.

³ references: Batra 1963b; Kischner 1998, 2001. ⁴ *I. acuminatus* is suggested to have a "phloeomycetophagous" feeding habit (Francke-Grosmann 1952).

and conidia easily adhere to the bodies of the insects. Ascospores often possess well developed sheaths, which may protect the spore from digestion in the gut of the beetles (Francke-Grosmann 1967; Malloch and Blackwell 1993). Ophiostomatoid fungi and ambrosia fungi are pleomorphic and show both mycelial and yeast-like growth forms. In the mycangium of the beetles the fungi are usually present in their slow-growing yeast stage (Francke-Grosmann 1967; Beaver 1989; Six 2003). The loss of the sexual stage in almost all known ambrosia fungi and in some ophiostomatoid fungi may also be viewed as extreme adaption to the symbiosis with bark beetles (Six 2003).

5. ASSEMBLAGES OF FUNGI ASSOCIATED WITH EUROPEAN BARK BEETLES

Since the discovery of the association of fungi with bark beetles numerous studies on the mycobiota associated with European scolytids have been carried out. An overview of the assemblages of fungi and especially the ophiostomatoid fungi associated with xylomycetophagous (5.1.) and phloeophagous bark beetles (5.2.) is presented.

5.1. Assemblages of fungi associated with xylomycetophagous bark beetles

For six xylomycetophagous beetles that are native in Europe and for two species that have been introduced into Europe their principal ambrosia fungi are known (Tables 1 and 2 and references therein). Their identity has not been determined for the other seven xylomycetophagous species in Europe (Table 1) that are economically less important. Most European scolytids with xylomycetophagous feeding habit are associated with species in the genus *Ambrosiella* (Tables 1 and 2) that includes taxa related to *Ceratocystis* or *Ophiostoma* (Cassar and Blackwell 1996; Rollins *et al.* 2001; Paulin-Mahady *et al.* 2002). *Xyleborus dispar* and the introduced *X. germanus* live in symbiosis with *A. hartigii*, whereas *X. domesticus*, *X. lineatus* and *X. signatus* are associated with *A. ferruginea*. Both *A. hartigii* and *A. ferruginea* are closely related to species in the genus *Ceratocystis* (Cassar and Blackwell 1996; Rollins *et al.* 2001). *Ambrosiella sulfurea*, which has affinities to the genus *Ophiostoma* (Cassar and Blackwell 1996; Rollins *et al.* 2001) is transmitted by *X. saxeseni*. The ambrosia fungus of *Xyleborus monographus* has been referred to as "yellowish moniloid fungus" (Francke-Grosmann 1967). A *Raffaelea* species has also been reported to be associated with this scolytid (Kowalski 1991). The introduced *G. materiaris* is associated with a non-ophiostomatoid ambrosia fungus, the yeast *Ambrosiozyma monospora* (Batra 1963b; Kirschner 1998). As seen in European ambrosia beetles the association between the insects and their principal ambrosia fungi is not species-specific, since several beetle species can be associated with the same *Ambrosiella* species.

In addition to their principal fungal associates, ambrosia beetles are also known to carry *Ophiostoma* species and other non-ambrosial ophiostomatoid fungi. These fungi have also been proposed to represent ambrosia fungi with nutritional

importance for the insects (Bakshi 1950), but most authors consider them as "weed fungi" that are ecologically insignificant for the beetles (Francke-Grosmann 1966, 1967; Beaver 1989). The spectrum of ophiostomatoid fungi occurring together with xylomycetophagous bark beetles comprises a considerable number of species, most of which are generalists that occur in association with a wide range of insects on several host trees (Table 2).

5.2. Assemblages of fungi associated with phloeophagous bark beetles

A synthesis of the numerous investigations on the assemblages of ophiostomatoid fungi associated with phloem-feeding bark beetles in Europe is provided in Table 2. Thus far, 27 true bark beetle species, 23 on conifers and 4 on hardwoods have been examined for the ophiostomatoid fungi they carry. The best-studied European bark beetle regarding its fungal associates is *I. typographus* which has been included in many investigations within its distribution range in Europe (Table 2 and references therein) and also in Japan (Yamaoka *et al.* 1997). I will subsequently often refer to this species as example.

5.2.1. Overview about ophiostomatoid fungi associated with phloeophagous bark beetles

Ophiostomatoid fungi associated with true bark beetles in Europe mainly belong to the genus *Ophiostoma*, which is represented by a large number of species (Table 2). Several *Leptographium* and *Pesotum* species are also associated with phloeophagous bark beetles (Table 2). A few European bark beetles transmit *Ceratocystis* species, namely *C. polonica* and *C. laricicola*. *Ceratocystis polonica* is mainly associated with *I. typographus*, *I. amitinus* and *I. duplicatus* on Norway spruce, although it is occasionally also transmitted at low frequencies by other spruce bark beetles (Table 2). Likewise, *C. laricicola* is associated with *I. cembrae* on *Larix* spp. *Ceratocystis polonica* and *C. laricicola* are unusual, since they are among the few *Ceratocystis* species that are regularly transmitted by bark beetles. The only other known example is *C. rufipenni* that is associated with *D. rufipennis* on *Picea* spp. in North America (Wingfield *et al.* 1997). A few conifer bark beetles, including particularly *H. palliatus*, *I. acuminatus*, *I. sexdentatus* and *T. minor* transmit *Ambrosiella* species that are phylogenetically related to *Ophiostoma* (Table 2; see 3.4.). Species of *Graphium* as associates of bark beetles are also included in Table 2, despite the fact *Graphium* is not closely related to *Ophiostoma* and other ophiostomatoid fungi (Okada *et al.* 1998, 2000; Harrington *et al.* 2001). In particular, four *Graphium* species are common associates of European bark beetles. These include *G. pseudormiticum* associated with several pine bark beetles, *G. fimbriisporum*, associated with various spruce bark beetles, *G. laricis*, occurring with *I. cembrae* on larch and *G. penicillioides*, associated with *Taphrorychus bicolor* on beech and *Scolytus* spp. on elm (Kirschner 1998; Kirisits *et al.* 2000; Jacobs *et al.* 2003b; Table 2).

5.2.2. Intimacy of association between ophiostomatoid fungi and phloem-feeding bark beetles

Based on the intimacy of association with ophiostomatoid fungi, scolytids can broadly be divided into two groups. One of these groups includes bark beetle species that are relatively loosely associated with fungi, in the sense that only a low portion of individuals in a population carries fungi. The pine shoot beetle, *Tomicus piniperda* may be a typical example for a scolytid with a relatively loose relationship with blue-stain fungi. Although this bark beetle transmits numerous ophiostomatoid fungi (Table 2), none of these occur at consistently high frequencies in populations of the insect (Mathiesen-Käärik 1953; Lieutier *et al.* 1989b; Solheim and Långström 1991; Gibbs and Inman 1991). Even *L. wingfieldii*, *O. minus* and *Hormonema dematoides*, the most consistent associates of *T. piniperda* are usually isolated at relatively low frequencies, compared to other conifer bark beetle-fungus-systems (Lieutier *et al.* 1989b; Solheim and Långström 1991; Gibbs and Inman 1991). Other examples of conifer bark beetles with relatively loose association with fungi include the solitary *D. micans* on Norway spruce (Lieutier *et al.* 1992), *Cryphalus abietis* on Silver fir (Kirschner 1998), and *Pityogenes quadridens* on Scots pine (Mathiesen-Käärik 1953) (Table 2). Among bark beetle species on deciduous trees, *Leperisinus varius* on ash and *Scolytus intricatus* on oak infrequently disseminate unspecific *Ophiostoma* species (Kirschner 1998).

The second group of bark beetles comprises species that are intimately associated with blue-stain fungi, meaning that a large percentage of individuals (up to 100 %) carry spores of ophiostomatoid fungi. This does not necessarily mean that one particular blue-stain fungus is always present at such high frequencies, but that the majority of beetles usually carry at least one fungus out of the whole assemblage of fungi associated with a particular bark beetle species. For conifer bark beetles intensive association with blue-stain fungi is the rule rather than the exception. A typical example is *I. typographus* on Norway spruce. A diverse assemblage of fungi is associated with this economically extremely important bark beetle. Despite the fact that there is a great variation in the composition of the mycobiota reported in various investigations (see 5.2.5), all studies agree that *I. typographus* very consistently and regularly carries blue-stain fungi (Table 2). The same is true for many other conifer bark beetles, including *Crypturgus cinereus*, *Crypturgus pusillus*, *Dryocoetes autographus*, *Hylastes ater*, *Hylastes cunicularius*, *Hylurgops palliatus*, *Hylurgops glabratus*, *Ips acuminatus*, *Ips amitinus*, *Ips cembrae*, *Ips duplicatus*, *Ips sexdentatus*, *Orthotomicus laricis*, *Orthotomicus proximus*, *Pityogenes chalcographus*, *Polygraphus poligraphus* and *Tomicus minor* (Table 2).

Among bark beetles on hardwoods, *Scolytus* spp. on elm seem to be rather intimately associated with ophiostomatoid fungi, in particular with the introduced Dutch elm disease pathogens *O. ulmi* and *O. novo-ulmi* and with *G. penicilliioides* (Table 2). However, the different *Scolytus* species vary greatly in their efficiency as vectors of the Dutch elm disease pathogens, with *Scolytus scolytus* being the most effective vector (Webber and Brasier 1984; Webber and Gibbs 1989; Webber 1990, 2000). On beech, the secondary *Taphrorychus bicolor* may be relatively regularly associated with *G. penicilliioides* (Table 2).

5.2.3. Elements of the mycobiota of phloephagous bark beetles

The symbiosis between ophiostomatoid fungi and bark beetles is usually not a "one fungus – one insect" relationship. Hence, most bark beetle species are associated with an assemblage of several fungi. Typically, some fungal species occur at high frequencies and/or constantly together with a given bark beetle species, while others are rare and/or casual components of the mycobiota. For example, a very high number of fungi has been reported to occur together with *I. typographus* in Europe, but many of the recorded species are generally rare in this niche or have been found only by one or a few investigators (Table 2). Only a few species are mentioned as relatively constant associates in the majority of the studies on the mycobiota of *I. typographus*. Thus, despite different results of the various investigations (see 5.2.5.), *C. polonica*, *O. ainoae*, *O. bicolor*, *O. penicillatum* and *O. piceaperdum* are probably the most common and ecologically most significant fungi associated with *I. typographus* in Europe (Table 2). Very similar patterns also occur in many other bark beetle-fungus systems (Table 2).

Table 2: Ophiostomatoid fungi associated with bark beetles (Coleoptera: Scolytidae) in Europe. Species of *Graphium*, which were formerly known as anamorphs of *Ophiostoma* are also included.

Bark beetle (Host trees) ^a	Fungus ^b	References ¹
<i>Cryphalus abietis</i> ^{b,f} (Conifers [<i>Abies alba</i>])	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001
	(<i>Ophiostoma piceaperdum</i>)	Kirschner 1998, 2001
<i>Crypturgus cinereus</i> ^{b,c} (Conifers [<i>Picea abies</i> , <i>Pinus sylvestris</i>])	<i>Ceratocystiopsis alba</i>	Kirschner 1998, 2001
	<i>Ceratocystiopsis minima</i>	Kirschner 1998, 2001
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	<i>Ceratocystis leucocarpa</i>	Kirschner 1998, 2001
	<i>Ophiostoma neglectum</i>	Kirschner 1998, Kirschner and Oberwinkler 1999
	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001
	<i>Ophiostoma</i> cf. <i>piceae</i>	Kirschner 1998, 2001
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001
	<i>Ophiostoma stenoceras</i>	Kirschner 1998, 2001
<i>Crypturgus pusillus</i> ^{b,c} (Conifers [<i>Picea abies</i>])	<i>Ceratocystiopsis alba</i>	Kirschner 1998, 2001
	<i>Ceratocystiopsis minima</i>	Kirschner 1998
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ceratocystis leucocarpa</i>	Kirschner 1998
	<i>Graphium pseudormiticum</i> (= <i>G. fimbriisporum</i> ?)	Kirschner 1998, 2001
	<i>Ophiostoma ainoae</i>	Kirschner 1998, 2001
	<i>Ophiostoma araucariae</i>	Kirschner 1998, 2001
	<i>Ophiostoma bicolor</i>	Kirschner 1998, 2001
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	<i>Ophiostoma neglectum</i>	Kirschner 1998, Kirschner and Oberwinkler 1999
	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001
	<i>Ophiostoma</i> cf. <i>piceae</i>	Kirschner 1998

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^c
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001
	<i>Ophiostoma simplex</i>	Kirschner 1998
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
	<i>Ophiostoma torulosum</i>	Kirschner 1998
<i>Dendroctonus micans</i> ^{b,f} (<i>Picea abies</i>)	<i>Ophiostoma canum</i>	Lieutier <i>et al.</i> 1992
	(<i>Ophiostoma penicillatum</i>)	Lieutier <i>et al.</i> 1992
	(<i>Ophiostoma minus</i>)	Lieutier <i>et al.</i> 1992
	(<i>Ophiostoma</i> sp.)	Lieutier <i>et al.</i> 1992
<i>Dryocoetes autographus</i> ^{b,e} (Conifers [<i>Picea abies</i> , <i>Pinus sylvestris</i>])	<i>Ceratocystiopsis alba</i>	Kirschner 1998, 2001
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ceratocystis autographa</i>	Bakshi 1951
	<i>Graphium adustum</i>	Grosmann 1931
	<i>Graphium fimbriisporum</i>	Kirisits <i>et al.</i> 2000, Jacobs <i>et al.</i> 2003b
	<i>Graphium pseudormiticum</i> (= <i>G. fimbriisporum</i> ?)	Kirschner 1998, 2001
	<i>Leptographium guttulatum</i>	Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001; Jacobs <i>et al.</i> 2001a
	<i>Ophiostoma ainiae</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma araucariae</i>	Kirschner 1998, 2001
	<i>Ophiostoma cucullatum</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma galeiformis</i>	Bakshi 1951
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	<i>Ophiostoma obscura</i>	
	<i>Ophiostoma neglectum</i>	Kirschner 1998; Kirschner and Oberwinkler 1999
	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma</i> cf. <i>piceae</i>	Kirschner 1998
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma simplex</i>	Kirschner 1998
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
<i>Gnathotrichus materiarius</i> ^{d,e} (Conifers [<i>Larix decidua</i> , <i>Pinus sylvestris</i>])	<i>Leptographium</i> sp.	Kirschner 1998
	<i>Ophiostoma araucariae</i>	Kirschner 1998
	<i>Ophiostoma cucullatum</i>	Kirschner 1998
	<i>Ophiostoma obscura</i>	Kirschner 1998
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998
	<i>Ophiostoma piceae</i>	Kirschner 1998
<i>Hylastes ater</i> ^{b,e} (<i>Pinus sylvestris</i>)	[<i>Graphium</i> (<i>Pesotum</i> ?) <i>aureum</i>]	Mathiesen-Käärik 1953
	<i>Leptographium guttulatum</i>	Wingfield and Gibbs 1991, Jacobs and Wingfield 2001
	<i>Leptographium lundbergii</i>	Dowding 1973; Mathiesen 1950; Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Leptographium serpens</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	(<i>Ophiostoma ips</i>)	Mathiesen-Käärik 1953
	<i>Ophiostoma minus</i>	Mathiesen 1950; Mathiesen-Käärik 1953

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ¹
	<i>Ophiostoma penicillatum</i>	Mathiesen 1950; Mathiesen-Käärik 1953, Jacobs and Wingfield 2001
	[<i>Ophiostoma penicillatum</i> f. <i>chalcographi</i>]	Mathiesen 1950
	[<i>Ophiostoma penicillatum</i> f. <i>pini</i>]	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	(<i>Ophiostoma piliferum</i>)	Mathiesen-Käärik 1953
<i>Hylastes opacus</i> ^{b,e} (<i>Pinus sylvestris</i>)	<i>Graphium</i> (<i>Pesotum</i> ?) sp.	Wingfield and Gibbs 1991
	<i>Leptographium guttulatum</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium lundbergii</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium procerum</i>	Wingfield & Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium wingfieldii</i>	Wingfield & Gibbs 1991; Jacobs and Wingfield 2001
<i>Hylastes cunicularius</i> ^{b,e} (<i>Picea abies</i>)	<i>Ophiostoma galeiformis</i>	Mathiesen-Käärik 1953; Zhou <i>et al.</i> 2004
	<i>Ophiostoma olivaceum</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma penicillatum</i>	Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Ophiostoma piceae</i>	Mathiesen-Käärik 1953
<i>Hylurgops palliatus</i> ^{b,e} (Conifers [<i>Picea abies</i> , <i>Pinus sylvestris</i> , <i>Larix kaempferi</i>])	<i>Ambrosiella</i> sp.	Krokene and Solheim 1996; Rollins <i>et al.</i> 2001
	<i>Ceratocystiopsis alba</i>	Kirschner 1998, 2001
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ceratocystis autographa</i>	Bakshi 1951
	<i>Ceratocystis polonica</i>	Krokene and Solheim 1996
	<i>Graphium fimbriisporum</i>	Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2003b
	<i>Graphium pseudodormiticum</i>	Kirschner 1998, 2001
	(= <i>G. fimbriisporum</i> ?)	
	<i>Graphium</i> (<i>Pesotum</i> ?)	Mathiesen 1950, Mathiesen-Käärik 1953
	<i>pyknocephalum</i>	
	<i>Graphium</i> (<i>Pesotum</i> ?) spp.	Wingfield and Gibbs 1991
	<i>Leptographium guttulatum</i>	Mathiesen 1950; Harding 1989; Wingfield and Gibbs 1991; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001; Jacobs <i>et al.</i> 2001b
	<i>Leptographium lundbergii</i>	Kotýnková-Sychrová 1966; Harding 1989; Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium procerum</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Leptographium wingfieldii</i>	Wingfield and Gibbs 1991; Jacobs and Wingfield 2001
	<i>Ophiostoma atroae</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma bicolor</i>	Harding 1989; Kirschner 1998, 2001
	<i>Ophiostoma cucullatum</i>	Kirschner 1998, Kirisits <i>et al.</i> 2000
	<i>Ophiostoma galeiformis</i>	Bakshi 1951
	<i>Ophiostoma japonicum</i>	Kirschner 1998, 2001
	(= <i>O. arborea</i> ?)	
	<i>Ophiostoma neglectum</i>	Kirschner 1998, 2001; Kirisits,

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^c
	<i>Ophiostoma penicillatum</i>	unpublished Mathiesen 1950; Mathiesen-Käärik 1953; Kirschner 1998; Jacobs and Wingfield 2001 Mathiesen 1950
	[<i>Ophiostoma penicillatum</i> f. <i>palliatum</i>] (= <i>Leptographium guttulatum</i>)	
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Harding 1989; Krokene and Solheim 1996; Kirschner 1998, 2001; Kirisits et al. 2000 Kirschner 1998
	<i>Ophiostoma</i> cf. <i>piceae</i>	
	<i>Ophiostoma piceaperdum</i>	Davidson et al. 1967; Harding 1989; Krokene and Solheim 1996; Kirschner 1998, 2001; Kirisits et al., 2000; Jacobs and Wingfield 2001
	<i>Ophiostoma simplex</i>	Kirschner 1998
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
<i>Hylurgops glabratus</i> ^{b,c} (Conifers [<i>Picea abies</i>])	<i>Graphium fimbriisporum</i>	Kirisits 1996; Kirisits et al. 2000; Jacobs et al. 2003b
	<i>Leptographium guttulatum</i>	Kirisits 1996; Kirisits et al. 2000; Jacobs and Wingfield 2001; Jacobs et al., 2001b
	<i>Ophiostoma ainoae</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma cucullatum</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma flexuosum</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma floccosum</i>	Lin 2003
	<i>Ophiostoma piceae</i>	Kirisits 1996; Kirisits et al. 2000
	<i>Ophiostoma piceaperdum</i>	Kirisits 1996; Kirisits et al. 2000
<i>Ips acuminatus</i> ^{c,c} (<i>Pinus</i> spp.)	<i>Ambrosiella macrospora</i>	Mathiesen 1950; Francke-Grosmann 1952, 1963b; Cassar and Blackwell 1996
	<i>Ceratocystiopsis minima</i>	Lieutier et al. 1991
	<i>Ceratocystiopsis minuta</i>	Mathiesen 1951
	(<i>Ceratocystis coerulescens</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	(<i>Graphium</i> (<i>Pesotum</i> ?) <i>pyknocephalum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Leptographium lundbergii</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Jacobs and Wingfield 2001 Lieutier et al. 1991
	<i>Ophiostoma brunneo-ciliatum</i>	
	(<i>Ophiostoma canum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma clavatum</i>	Rennerfelt 1950; Mathiesen 1950, 1951; Mathiesen-Käärik 1953; Francke-Grosmann 1952, 1963b
	<i>Ophiostoma ips</i>	Lieutier et al. 1991; Mathiesen-Käärik 1953
	<i>Ophiostoma minus</i>	Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Lieutier et al. 1991
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Francke-Grosmann 1952
	<i>Ophiostoma piliferum</i>	Mathiesen 1950, Mathiesen-Käärik 1953; Francke-Grosmann 1952, 1963
	<i>Ophiostoma</i> sp.	Lieutier et al. 1991
	<i>Ophiostoma</i> spp.	Rennerfelt 1950; Mathiesen 1950

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^c
<i>Ips amitinus</i> ^{b,c} (<i>Picea abies</i> , <i>Pinus cembra</i>)	<i>Ceratocystiopsis</i> cf. <i>alba</i>	Kirisits <i>et al.</i> 2000
	<i>Ceratocystiopsis minuta</i>	Kirisits <i>et al.</i> 2000
	<i>Ceratocystis polonica</i>	Kirisits <i>et al.</i> 2000
	<i>Graphium fimbriisporum</i>	Kirisits <i>et al.</i> 2000 ; Jacobs <i>et al.</i> 2003b
	<i>Graphium</i> (<i>Pesotum</i> ?) spp.	Grosmann 1931
	<i>Leptographium lundbergii</i>	Grosmann 1931
	<i>Leptographium</i> spp.	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma bicolor</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma brunneo-ciliatum</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma cucullatum</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma minus</i>	Grosmann 1931
	<i>Ophiostoma penicillatum</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piceae</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piceaperdum</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma</i> cf. <i>piceaperdum</i>	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piliferum</i>	Grosmann 1931
<i>Ips cembrae</i> ^{b,c} (<i>Larix decidua</i> , <i>Larix kaempferi</i>)	<i>Ceratocystiopsis</i> cf. <i>alba</i>	Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
	<i>Ceratocystiopsis minuta</i>	Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
	<i>Ceratocystis laricicola</i>	Redfern <i>et al.</i> 1987; Redfern 1989; Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
	<i>Graphium laricis</i>	Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001; Jacobs <i>et al.</i> 2003b
	<i>Ophiostoma bicolor</i>	Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
	<i>Ophiostoma brunneo-ciliatum</i>	Redfern <i>et al.</i> 1987; Redfern 1989; Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
	(<i>Ophiostoma fusiforme</i>)	Agayeva <i>et al.</i> 2004
	(<i>Ophiostoma lunatum</i>)	Agayeva <i>et al.</i> 2004
	<i>Ophiostoma piceae</i>	Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
	<i>Ophiostoma</i> cf. <i>piceaperdum</i>	Kirisits <i>et al.</i> 2000; Stauffer <i>et al.</i> 2001
<i>Ips duplicatus</i> ^{b,c} (<i>Picea abies</i>)	<i>Ceratocystis polonica</i>	Valkama 1995; Krokene and Solheim 1996
	<i>Ophiostoma bicolor</i>	Valkama 1995; Krokene and Solheim 1996
	<i>Ophiostoma penicillatum</i>	Valkama 1995; Krokene and Solheim 1996; Jacobs and Wingfield 2001
	<i>Ophiostoma piceae</i>	Valkama 1995; Krokene and Solheim 1996
	<i>Ophiostoma piceaperdum</i>	Krokene and Solheim 1996; Jacobs and Wingfield 2001
	(<i>Ophiostoma</i> sp.)	Mathiesen 1950
	<i>Pesotum</i> sp.	Krokene and Solheim 1996
<i>Ips sexdentatus</i> ^{b,c} (<i>Pinus</i> spp.)	<i>Ambrosiella ips</i>	Siemaszko 1939; Mathiesen-Käärik 1953
	<i>Ambrosiella tingens</i>	Mathiesen-Käärik 1953
	<i>Graphium pseudormiticum</i>	Kirschner 1998, 2001; Kirisits, unpublished
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Leptographium</i> sp.	Lieutier <i>et al.</i> 1989
	<i>Ophiostoma ainoae</i>	Kirschner 1998, 2001

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^h	References ^j
	(= <i>O. brunneo-ciliatum</i> ?)	
	<i>Ophiostoma araucariae</i>	Kirschner 1998, 2001
	<i>Ophiostoma brunneo-ciliatum</i>	Mathiesen-Käärik 1953; Lieutier <i>et al.</i> 1989, 1991; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma clavatum</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma ips</i>	Siemaszko 1939; Francke-Grosmann 1952; Lieutier <i>et al.</i> 1989, 1991; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma japonicum</i>	Kirschner 1998, 2001
	(= <i>O. arborea</i> ?)	
	<i>Ophiostoma minus</i>	Siemaszko 1939; Lieutier <i>et al.</i> 1989
	<i>Ophiostoma obscura</i>	Kirschner 1998, 2001
	<i>Ophiostoma piceae</i>	Kirisits, unpublished
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001
	<i>Ophiostoma</i> sp.	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Pesotum fragrans</i>	Mathiesen-Käärik 1953
<i>Ips typographus</i> ^{b,c} (<i>Picea abies</i>)	<i>Ceratocystopsis alba</i>	Kirschner 1998, 2001; Kirisits, unpublished
	<i>Ceratocystopsis minuta</i>	Siemaszko 1939; Mathiesen 1950; 1951, Kotýnková-Sychrová 1966; Käärik 1975; Solheim 1986, 1992b, 1993; Harding 1989; Kirisits 1996; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Jankowiak 2004
	<i>Ceratocystis polonica</i>	Siemaszko 1939; Mathiesen 1950, 1951; Mathiesen-Käärik 1953; Käärik 1975; Solheim 1986, 1992a, 1992b, 1993; Harding 1985, 1989, 1995; Furniss <i>et al.</i> 1990; Krokene and Solheim 1996; Viiri and Weissenberg 1995; Kirisits 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Salle <i>et al.</i> 2003; Jankowiak 2004
	<i>Graphium fimbriisporum</i>	Morelet 1995; Kirisits 1996; Grubelnik 1998; Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2003b
	<i>Graphium pseudorniticum</i>	Kirschner 1998, 2001
	(= <i>G. fimbriisporum</i> ?)	
	<i>Graphium</i> (<i>Pesotum</i> ?)	Grosmann 1931; Siemaszko 1939, Mathiesen 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Jankowiak 2004
	<i>pycnocephalum</i>	Jankowiak 2004
	<i>Leptographium euphyes</i>	Jankowiak 2004
	<i>Leptographium lundbergii</i>	Harding 1989
	<i>Leptographium</i> spp.	Rennerfelt 1950; Kirschner 1998; Viiri and Weissenberg 1995; Viiri 1997; Viiri and Lieutier 2004
	<i>Ophiostoma ainoae</i>	Solheim 1986, 1992a, 1992b, 1993; Harding 1989; Viiri and Weissenberg 1995; Kirisits 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ¹
	<i>Ophiostoma araucariae</i>	2004; Jankowiak 2004
	<i>Ophiostoma bicolor</i>	Kirschner 1998, 2001 Kotýnková-Sychrová 1966; Davidson <i>et al.</i> 1967; Käärik 1975; Solheim 1986, 1992a, 1992b, 1993; Harding 1985, 1989; Furniss <i>et al.</i> 1990; Viiri and Weissenberg 1995; Kirisits 1996; Krokene and Solheim 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Salle <i>et al.</i> 2003; Jankowiak 2004
	<i>Ophiostoma cainii</i>	Harding 1989
	<i>Ophiostoma cucullatum</i>	Solheim 1986; Harding 1989; Kirisits 1996; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Jankowiak 2004
	<i>Ophiostoma flexuosum</i>	Solheim 1986; Harding 1989; Jankowiak 2004
	<i>Ophiostoma floccosum</i>	Mathiesen 1950, 1951; Mathiesen-Käärik 1953
	<i>Ophiostoma japonicum</i> (= <i>O. arborea</i> ?)	Kirschner 1998, 2001
	(<i>Ophiostoma minus</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma neglectum</i>	Kirschner 1998; Kirscher and Oberwinkler 1999
	(<i>Ophiostoma obscura</i>)	Kirschner 1998, 2001
	<i>Ophiostoma penicillatum</i>	Grosmann 1931, 1932; Goidānich 1936; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Davidson <i>et al.</i> 1967; Käärik 1975; Solheim 1986, 1992a, 1992b, 1993; Harding 1985, 1989; Furniss <i>et al.</i> 1990; Viiri and Weissenberg 1995; Kirisits 1996; Krokene and Solheim 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001; Viiri and Lieutier 2004; Jankowiak 2004
	[<i>Ophiostoma penicillatum</i> f. <i>chalcographi</i>]	Mathiesen 1950
	<i>Ophiostoma piceae</i>	Grosmann 1931; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Käärik 1975; Solheim 1986, 1992b, 1993; Harding 1985, 1989; Viiri and Weissenberg 1995; Kirisits 1996; Krokene and Solheim 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Viiri and Lieutier 2004; Jankowiak 2004
	<i>Ophiostoma</i> cf. <i>piceae</i>	Kirschner 1998
	<i>Ophiostoma piceaperdum</i>	Kotýnková-Sychrová 1966; Solheim 1986, 1992b, 1993; Harding 1989, 1995; Viiri and Weissenberg 1995;

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ¹
		Kirisits 1996; Viiri 1997; Grubelnik 1998; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001; Viiri and Lieutier 2004; Salle <i>et al.</i> 2003; Jankowiak 2004
	<i>(Ophiostoma pluriannulatum)</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma serpens</i>	Kotýnková-Sychrová 1966
	<i>Ophiostoma stenoceras</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Kirschner 1998
	<i>Ophiostoma tetropii</i>	Käärik 1975; Solheim 1986, 1992b; Viiri and Weissenberg 1995; Viiri 1997, Kirschner 1998; Salle <i>et al.</i> 2003
	<i>Ophiostoma</i> spp.	Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Harding 1989; Viiri and Lieutier 2004
	<i>Pesotum fragrans</i>	Solheim 1992b
	<i>Pesotum</i> sp.	Furniss <i>et al.</i> 1990; Solheim, 1992a, 1992b, 1993; Krokene and Solheim 1996
	<i>Pesotum (Graphium?)</i> spp.	Harding 1985, 1989; Furniss <i>et al.</i> 1990; Solheim 1992b, 1993; Viiri and Weissenberg 1995; Viiri 1997; Viiri and Lieutier 2004; Jankowiak 2004
<i>Leperisinus varius</i> ^{b,f} (<i>Fraxinus excelsior</i>)	<i>(Ophiostoma quercus)</i>	Kirschner 1998
<i>Orthotomicus laricis</i> ^{b,c} (<i>Pinus sylvestris</i>)	<i>Ceratocystiopsis falcata</i>	Kirschner 1998
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ceratocystis leucocarpa</i>	Kirschner 1998
	<i>Graphium pseudormiticum</i>	Kirschner 1998, 2001
	<i>Leptographium</i> sp.	Kirschner 1998
	<i>Ophiostoma ainoae</i>	Kirschner 1998, 2001
	<i>Ophiostoma araucariae</i>	Kirschner 1998, 2001
	<i>Ophiostoma bicolor</i>	Kirschner 1998, 2001
	<i>Ophiostoma cucullatum</i>	Kirschner 1998, 2001
	<i>Ophiostoma ips</i>	Kirschner 1998, 2001
	<i>Ophiostoma japonicum</i> (= <i>O. arborea?</i>)	Kirschner 1998, 2001
	<i>Ophiostoma obscura</i>	Kirschner 1998, 2001
	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001
<i>Orthotomicus proximus</i> ^{b,c} (<i>Pinus sylvestris</i>)	<i>(Ceratocstis coerulescens)</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Graphium (Pesotum?) pycnocephalum</i>	Mathiesen-Käärik 1953
	<i>(Leptographium lundbergii)</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>(Ophiostoma clavatum)</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma ips</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma minus</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma piliferum</i>	Mathiesen-Käärik 1953
	<i>(Ophiostoma</i> sp.)	Mathiesen 1950

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ¹
	(<i>Pesotum fragrans</i>)	Mathiesen-Käärik 1953
<i>Pityogenes chalcographus</i> ^{b,c} (<i>Picea abies</i>)	<i>Ceratocystiopsis minuta</i>	Kirisits 1996; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	(<i>Ceratocystis coerulescens</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ceratocystis polonica</i>	Krokene and Solheim 1996; Kirisits 1996, Kirisits <i>et al.</i> 2000
	<i>Graphium fimbriisporum</i>	Kirisits 1996; Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2003b
	<i>Graphium pseudormiticum</i> (= <i>G. fimbriisporum</i> ?)	Kirschner 1998, 2001
	<i>Graphium</i> (<i>Pesotum</i> ?) <i>pycnocephalum</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Leptographium</i> sp.	Kirisits <i>et al.</i> 2000
	<i>Ophiostoma ainoae</i>	Kirisits 1996; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000;
	<i>Ophiostoma araucariae</i>	Kirschner 1998, 2001
	<i>Ophiostoma bicolor</i>	Krokene and Solheim 1996; Kirisits 1996; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma cucullatum</i>	Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma floccosum</i>	Mathiesen 1950, 1951; Mathiesen-Käärik 1953; Lin 2003
	<i>Ophiostoma neglectum</i>	Kirschner 1998; Kirscher and Oberwinkler 1999
	(<i>Ophiostoma obscura</i>)	Kirschner 1998, 2001
	<i>Ophiostoma penicillatum</i>	Grosman 1931; Goidanich 1936; Mathiesen 1950; Mathiesen-Käärik 1953; Kirschner 1998; Jacobs and Wingfield 2001
	[<i>Ophiostoma penicillatum</i> f. <i>chalcographi</i>]	Mathiesen 1950
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Krokene and Solheim 1996; Kirisits, 1996; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma</i> cf. <i>piceae</i>	Kirschner 1998
	<i>Ophiostoma piceaperdum</i>	Kotýnková-Sychrová 1966; Davidson <i>et al.</i> 1967; Kirisits 1996; Kirschner 1998, 2001; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001
	<i>Ophiostoma serpens</i>	Kotýnková-Sychrová 1966
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
	<i>Pesotum</i> sp.	Kirisits 1996; Kirisits <i>et al.</i> 2000
	<i>Pesotum</i> (<i>Graphium</i> ?) sp.	Mathiesen 1950; Mathiesen-Käärik 1953
<i>Pityogenes quadridens</i> ^{b,g} (<i>Pinus sylvestris</i>)	(<i>Ambrosiella tingens</i>)	Mathiesen 1950, Mathiesen-Käärik 1953
	<i>Leptographium hundertbergii</i>	Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Ophiostoma canum</i> (<i>Ophiostoma minus</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	[<i>Ophiostoma penicillatum</i> f. <i>pini</i>]	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Mathiesen-Käärik 1953

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^c
<i>Polygraphus poligraphus</i> ^{b,e} (<i>Picea abies</i>)	<i>Ambrosiella</i> sp.	Krokene and Solheim 1996; Rollins <i>et al.</i> 2001
	<i>Ceratocystiopsis minuta</i>	Kirschner 1998, 2001
	<i>Ceratocystis polonica</i>	Krokene and Solheim 1996
	<i>Graphium pseudormiticum</i> (= <i>G. fimbriisporum</i> ?)	Kirschner 1998
	<i>Ophiostoma bicolor</i>	Krokene and Solheim 1996; Kirschner 1998, 2001;
	<i>Ophiostoma penicillatum</i>	Krokene and Solheim 1996; Jacobs and Wingfield 2001
	<i>Ophiostoma piceae</i>	Kirschner 1998, 2001
	<i>Ophiostoma piceaperdum</i>	Kirschner 1998, 2001; Jacobs and Wingfield 2001
<i>Scolytus intricatus</i> ^{b,f} (<i>Quercus</i> spp.)	<i>Ophiostoma quercus</i>	Kirschner 1998
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
<i>Scolytus</i> spp. ^{b,e} (<i>Ulmus</i> spp.)	<i>Ceratocystiopsis</i> cf. <i>falcata</i>	Kirisits and Konrad, unpublished
	<i>Graphium penicillioides</i>	Brasier 1990; Kirisits <i>et al.</i> 2000; Kirisits and Konrad, unpublished
	<i>Ophiostoma quercus</i>	Brasier 1990; Brasier & Kirk 1993; Kirisits <i>et al.</i> 2000; Kirisits, unpublished
	<i>Ophiostoma piceae</i>	Brasier and Kirk 1993; Lin 2003
	<i>Ophiostoma ulmi</i>	e. g. Siemaszko 1939; Webber and Brasier 1984; Webber and Gibbs 1989; Webber 1990, 2000; Brasier 1990, 1991
	<i>Ophiostoma novo-ulmi</i>	e. g. Webber and Brasier 1984; Webber and Gibbs 1989; Webber 1990, 2000; Brasier 1990, 1991
<i>Taphrorychus bicolor</i> ^{b,e} (<i>Fagus sylvatica</i>)	<i>Graphium penicillioides</i>	Kirschner 1998; Kirisits <i>et al.</i> 2000
	<i>Leptographium</i> sp.	Kirisits, unpublished
	<i>Ophiostoma</i> cf. <i>acericola</i>	Kirschner 1998; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma quercus</i>	Kirschner 1998; Kirisits <i>et al.</i> 2000; Lin 2003
	<i>Ophiostoma piceae</i>	Lin 2003
	<i>Ophiostoma</i> cf. <i>stenoceras</i>	Kirisits, unpublished
<i>Tomicus minor</i> ^{c,e} (<i>Pinus</i> spp.)	<i>Ambrosiella tingens</i>	Rennerfelt 1950; Mathiesen 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953; Rollins <i>et al.</i> 2001; Kirisits, unpublished
	<i>Ceratocystiopsis minuta</i>	Mathiesen 1950, 1951; Mathiesen-Käärik 1953
	<i>Graphium pseudormiticum</i>	Jacobs <i>et al.</i> 2003b
	<i>Leptographium guttulatum</i>	Kirisits <i>et al.</i> 2000; Jacobs <i>et al.</i> 2001b; Jacobs and Wingfield 2001
	<i>Leptographium lundbergii</i>	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma canum</i>	Rennerfelt 1950; Mathiesen 1950, 1951; Francke-Grosmann 1952; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Kirisits <i>et al.</i> 2000
	(<i>Ophiostoma floccosum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma minus</i>	Grosmann 1931; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^c
	<i>Ophiostoma piceae</i>	Mathiesen 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953
	<i>Ophiostoma piliferum</i>	Grosmann 1931; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Francke-Grosmann 1952; Mathiesen-Käärik 1953
	(<i>Ophiostoma pluriannulatum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma</i> spp.	Rennerfelt 1950
<i>Tomicus piniperda</i> ^{b,f} (<i>Pinus</i> spp.)	<i>Ambrosiella tingens</i>	Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ceratocystiopsis minuta</i>	Mathiesen-Käärik 1953; Kirisits <i>et al.</i> 2000
	<i>Ceratocystis autographa</i>	Kotýnková-Sychrová 1966
	<i>Graphium</i> (<i>Pesotum</i> ?) spp.	Gibbs and Inman 1991; Wingfield and Gibbs 1991
	<i>Leptographium euphyes</i>	Jacobs <i>et al.</i> 2001a; Jacobs and Wingfield 2001
	<i>Leptographium guttulatum</i>	Jacobs <i>et al.</i> 2001b; Jacobs and Wingfield 2001
	<i>Leptographium lundbergii</i>	Mathiesen 1950; Mathiesen-Käärik 1953; Gibbs and Inman 1991; Jacobs and Wingfield 2001
	<i>Leptographium procerum</i>	Gibbs and Inman 1991; Jacobs and Wingfield 2001
	<i>Leptographium wingfieldii</i>	Morelet 1988; Piou <i>et al.</i> 1989; Lieutier <i>et al.</i> 1989; Solheim and Långström 1991; Gibbs and Inman 1991; Wingfield and Gibbs 1991; Kirisits <i>et al.</i> 2000; Jacobs and Wingfield 2001
	<i>Leptographium</i> sp.	Kirschner 1998
	<i>Ophiostoma canum</i>	Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Kirschner 1998
	(<i>Ophiostoma clavatum</i>)	Mathiesen 1950; Mathiesen-Käärik 1953
	<i>Ophiostoma floccosum</i>	Lin 2003
	<i>Ophiostoma galeiformis</i>	Zhou <i>et al.</i> 2004
	<i>Ophiostoma huntii</i>	Gibbs and Inman 1991; Jacobs and Wingfield 2001
	<i>Ophiostoma ips</i>	Mathiesen-Käärik 1953
	<i>Ophiostoma minus</i>	MacCallum 1922; Grosmann 1931; Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrová 1966; Solheim and Långström 1991; Piou <i>et al.</i> 1989; Lieutier <i>et al.</i> 1989; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piceae</i>	MacCallum 1922; Siemaszko 1939; Mathiesen 1950; Mathiesen-Käärik 1953; Solheim and Långström 1991; Gibbs and Inman 1991; Kirschner 1998; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piceaperdum</i>	Solheim & Långström 1991; Kirisits <i>et al.</i> 2000
	<i>Ophiostoma piliferum</i>	Siemaszko 1939; Rennerfelt 1950; Mathiesen 1950; Mathiesen-Käärik

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ⁱ
	<i>Ophiostoma</i> spp.	1953; Kotýnková-Sychrová 1966; Solheim and Långström 1991; Gibbs and Inman 1991; Kirisits, unpublished; Rennerfelt 1950; Mathiesen 1950, Mathiesen-Käärik 1953
<i>Xyleborus dispar</i> ^{d,e} (Deciduous trees, rarely also conifers)	<i>Ambrosiella hartigii</i> ⁱ	Hartig 1844; Francke-Grosmann 1958, 1967, Batra 1967; Zimmermann 1973; Cassar and Blackwell 1996
	<i>Ceratocystis</i> (<i>Ophiostoma</i>) sp.	Zimmermann 1973
<i>Xyleborus dryographus</i> ^{d,e} (Deciduous trees)	<i>Ophiostoma verrucosum</i>	Gebhardt <i>et al.</i> 2002
<i>Xyleborus germanus</i> ^{d,e} (Deciduous trees and conifers)	<i>Ambrosiella hartigii</i> ⁱ	Francke-Grosmann 1958, 1967, Batra 1967; Cassar and Blackwell 1996
<i>Xyleborus monographus</i> ^{d,e} (Deciduous trees [<i>Quercus</i> sp.])	"Yellowish monilioid fungus" ⁱ	Francke-Grosmann 1958; 1966, 1967; Kirschner 1998
	<i>Ophiostoma grandicarpa</i>	Kirschner 1998
	<i>Ophiostoma quercus</i>	Kowalski 1991
	<i>Ophiostoma stenoceras</i>	Kirschner 1998
	<i>Raffaelea</i> sp. ⁱ	Kowalski 1991
<i>Xyleborus saxeseni</i> ^{d,e} (Deciduous trees and conifers)	<i>Ambrosiella sulfurea</i> ⁱ	Francke-Grosmann 1958, 1967; Batra 1967; Cassar and Blackwell 1996
<i>Xyloterus domesticus</i> ^{d,e} (Deciduous trees [<i>Fagus sylvatica</i> , <i>Quercus</i> sp., <i>Betula</i> sp.])	<i>Ambrosiella ferruginea</i> ⁱ	Hartig 1872b; Francke-Grosmann 1956a, 1958, 1967; Batra 1967; Zimmermann 1973; Cassar and Blackwell 1996
	<i>Graphium penicillioides</i>	Zimmermann 1973
	<i>Graphium</i> (<i>Pesotum</i> ?) sp.	Zimmermann 1973
	<i>Ophiostoma ambrosia</i> (= <i>Ophiostoma piliferum</i>)	Bakshi 1950
	<i>Ophiostoma bacillisporum</i>	Butin and Zimmermann 1972; Zimmermann 1973
	<i>Ophiostoma piceae</i> (<i>Ophiostoma quercus</i> ?)	Zimmermann 1973
	<i>Ophiostoma torulosum</i>	Butin and Zimmermann 1972; Zimmermann 1973; Kirisits, unpublished
<i>Xyloterus lineatus</i> ^{d,e} (Conifers [<i>Picea abies</i> , <i>Larix decidua</i> , <i>Larix kaempferi</i>])	<i>Ambrosiella ferruginea</i> ⁱ	Hartig 1872a; Mathiesen-Käärik 1953; Francke Grosmann 1956a, 1958, 1967; Batra 1967; Kirschner 1998, 2001
	(<i>Ceratocystis autographa</i>)	Bakshi 1951
	(<i>Graphium pseudormiticum</i>)	Kirschner 1998, 2001
	<i>Leptographium lundbergii</i>	Bakshi 1950; Kotýnková-Sychrová 1966; Jacobs and Wingfield 2001
	(<i>Ophiostoma cucullatum</i>)	Kirschner 1998, 2001
	(<i>Ophiostoma galeiformis</i>)	Bakshi 1951
	<i>Ophiostoma neglectum</i>	Kirschner 1998, Kirschner and

Table 2 continued

Bark beetle (Host trees) ^a	Fungus ^b	References ^j
	<i>Ophiostoma penicillatum</i>	Oberwinkler 1999
	<i>Ophiostoma piceae</i>	Mathiesen-Käärik 1953; Jacobs and Wingfield 2001
	<i>Ophiostoma piceaperdum</i>	Bakshi 1950; Mathiesen-Käärik 1953; Kirschner 1998, 2001
	<i>Ophiostoma piliferum</i> (<i>Ophiostoma torulosum</i>)	Kotýnková-Sychrová 1966; Kirschner 1998, 2001
		Bakshi 1950
		Kirschner 1998
<i>Xyloterus signatus</i> ^{a,e} (Deciduous trees)	<i>Ambrosiella ferruginea</i> ⁱ	Francke-Grosmann 1956a, 1958, 1967; Batra 1967

Notes: ^a Host trees of particular bark beetle species follow Postner (1974) and Pfeffer (1995). Hosts in brackets refer to the tree species, from which insects originated for the studies on the associated fungi and/or from which fungi were isolated. ^{b, c, d} Feeding habit of the respective bark beetle species: ^b phloeophagous, ^c phloeomycetophagous, ^d xylomycetophagous. ^{e, f, g} Level of intensity of association with ophiostomatoid fungi for the respective bark beetle species: ^e intimately associated, ^f loosely associated, ^g intensity of association not precisely known. Xylomycetophagous bark beetles have always been assigned to the group of scolytids with intimate association with fungi, since they nutritionally depend on ambrosia fungi. ^h Fungal species in bold font are appraised to be commonly associated with a given bark beetles species. Fungi in parenthesis are extremely rare elements of the mycobiota of a bark beetle species. Fungi in brackets are of doubtful taxonomic status. ⁱ Nutritionally important ambrosia fungus. ^j In the case of different reports by various authors regarding the abundance/importance of a particular fungus associated with a particular bark beetle species, the references, which reported the fungus as relatively common associate are printed in bold font.

Ophiostomatoid fungi vary greatly in the specificity of association with certain bark beetle species and the occurrence on different host trees. Some fungi are specifically associated with one or a few scolytid species on one host trees, while others occur with a wide range of insects and even on several host trees (Table 2). Originally, many blue-stain fungi were thought to be very specific in their association with bark beetles (Mathiesen-Käärik 1953; Francke-Grosmann 1967; Whitney 1982). As surveys of the mycobiota of scolytids have increased in number, it has become clear that strict specificity of fungi regarding their associated insects is rare and rather the exception than the rule (Table 2; Krokene and Solheim 1996; Kirisits 1996; Kirschner 1998; Kirisits *et al.* 2000; Jacobs and Wingfield 2001).

Despite the finding that some blue-stain fungi are less specific than previously believed, there are still fungal species showing a relatively narrow range of insect associates and host trees (Table 2). This is in clear contrast to other fungi, which are associated with a broad range of bark beetles and often occur on more than one host tree. Typical examples for the latter fungi are *Ceratocystiopsis minuta* and *O. piceaperdum*, which occur together with an extremely wide spectrum of European bark beetles on at least two conifer hosts (Table 2). Despite occurring in a wide range of niches, *C. minuta* and *O. piceaperdum* rely on their insect associates for transmission. However, another group of blue-stain fungi consists of unspecific species, which occur both in association with insects as well as on logs without insect attacks, indicating that they are both transmitted by bark beetles and by airborne or rain-splash inoculum (Mathiesen-Käärik 1953; Dowding 1969; Gibbs 1993).

Examples for such unspecific ophiostomatioid fungi include *Ophiostoma piceae*, *O. floccosum* and *O. piliferum* on conifers as well as *O. quercus* on hardwoods (Table 2).

5.2.4. Comparisons of the fungal assemblages of different bark beetle species

The synthesis presented in Table 2 allows for qualitative and quantitative comparisons of the differences in the whole mycobiota of different bark beetle species occurring on the same or on different host trees. This is a question, which is directly connected to the specificity of blue-stain fungi regarding their associated insects and hosts discussed above. Here, I also believe that specificity of the assemblages of fungi with individual bark beetles has previously been overestimated (e. g. Mathiesen-Käärik 1953; Francke-Grosmann 1967) and in many cases, differences of the mycobiota between scolytids occurring on the same host are relatively small and often mainly quantitative. For example, various spruce bark beetles have many elements of their mycobiota in common (Table 2). One major quantitative difference between the various bark beetles on Norway spruce refers to *C. polonica* that is more commonly associated with *I. typographus*, *I. duplicatus* and *I. amitinus*, while other spruce bark beetles rarely, if at all carry this blue-stain fungus (e. g. Solheim 1986; Harding 1989; Krokene and Solheim 1996; Kirschner 1998; Kirisits *et al.* 2000; Table 2 and references therein).

Certain elements of the fungal assemblages of bark beetles on pine also overlap between individual species, e. g. *Ophiostoma ips*, *O. brunneo-ciliatum*, *O. minus* and *C. minuta*, but there are also fungi that are relatively specific for individual scolytid species (Table 2). For example, the mycobiota of *T. minor* and *I. acuminatus* differ considerably, even though these two scolytids often occur together on thin-barked parts of the bole or branches of pines. Despite some overlap, the spectrum of fungi associated with bark beetles on different host trees (e. g. spruce, pine and larch; Table 2) generally shows large differences, which might suggest that the host tree is more important than the associated insects, in driving specificity and speciation of ophiostomatoid fungi.

5.2.5. Variation in the mycobiota of bark beetles

An intriguing aspect of the association of blue-stain fungi with phloem-feeding bark beetles is the variation of the assemblages of fungi associated with the same bark beetle species at different localities in Europe (Table 2 and references therein). Various factors might be responsible for this variation. Among these, the methodology employed in different studies may often be very important. Every method of fungal isolation is selective. Thus, the species spectrum and frequency of fungal associates of bark beetles can vary considerably depending on the sources and the methods of isolation employed by different researchers (e. g. Furniss *et al.* 1990; Krokene 1996; Yamaoka *et al.* 1997; Grubelnik 1998, Kirschner 1998). Methodological factors should be considered, when comparing results of different studies on the mycobiota of bark beetles (Table 2). In addition, mycological studies always have a strong "human component". Thus, the experience, skills and focus of the researcher can have a strong influence on the outcome of a study.

The investigations by Kirschner (1998, 2001) may be a good example to illustrate the influence of the isolation methods on the results of a study. Kirscher (1998, 2001) used a specific medium for isolation, consisting mainly of pieces of inner bark of *Picea abies* embedded in water agar, onto which adult, living bark beetles were placed individually. Such an isolation procedure was not used in any other study on the mycobiota of European bark beetles and this may be the reason that numerous fungi recorded by Kirschner (1998, 2001) have not been reported in any other investigation.

The variation of the mycobiota of bark beetles at different localities in Europe has been best-known for *I. typographus* and this scolytid is again used as an example to illustrate this phenomenon further, although variation in the spectrum of blue-stain fungi between different localities is also known for other bark beetle species (see Table 2 and references therein). An extremely diverse assemblage of blue-stain fungi is associated with *I. typographus* in Europe. A similar spectrum of fungi has been reported to occur together with this bark beetle in various parts of the continent, but remarkable qualitative and quantitative differences in the composition of the mycobiota of this insect between study sites have also been documented. Differences are most obvious for the most virulent fungal associate of *I. typographus*, *C. polonica*. Other differences in the mycobiota of *I. typographus* are also well-known, in particular for *O. piceaperdum* (Table 2), but they will not be discussed further here.

Thus-far, *C. polonica* only has been found as common associate of *I. typographus* in Poland (Siemaszko 1939), Norway (e. g. Solheim 1986, 1992a, 1992b; Krokene and Solheim 1996), in samples from Belgium (Harding 1989) and at some localities in Austria (Kirisits 1996, 2001; Grubelnik 1998; Kirisits *et al.* 2000). In contrast, it was not recorded at all in some studies (Rennerfelt 1950; Kotýnková-Sychrová 1966), or occurred rarely in investigations performed in Sweden (Mathiesen-Käärík 1953; Harding 1989), Denmark (Harding 1989), Finland (Viiri 1997), Germany (Harding 1989; Kirschner 1998) and France (Salle *et al.* 2003). It was also relatively rare in a recent study conducted in Southern Poland (Jankowiak 2004). In another French study, *C. polonica* occurred at moderately high frequencies (Viiri and Lieutier 2003). While it was the dominant fungal associate of *I. typographus* in South-Eastern Norway (Solheim 1986, 1992a, 1992b), *C. polonica* was less frequently isolated at six localities in Central Norway (Solheim 1993). Likewise, the fungus was rare or only moderately frequent in several study sites in Austria, in contrast to other localities where it was the dominant fungus associated with *I. typographus* (Kirisits 1996, 2001; Grubelnik 1998; Kirisits *et al.* 2000). It is particularly interesting that *C. polonica* is the most virulent blue-stain fungus associated with *I. typographus* (e. g. Horntvedt *et al.* 1983; Christiansen 1985; Solheim 1988; Krokene and Solheim 1998), which gives rise to speculation about the ecological consequences of the variation of the occurrence of *C. polonica* within the distribution range of *I. typographus* (Harding 1989; Solheim 1993).

There is no clear geographic pattern in the occurrence of *C. polonica* in Europe, since the fungus was both reported as frequent associate of *I. typographus* in some studies in Northern (e. g. Solheim 1986, 1992a, 1992b; Krokene and Solheim 1996) and Central Europe, while it occurred rarely or not at all in studies in adjacent

countries (e. g. Rennerfeldt 1950; Mathiesen-Käärik 1953; Kotýnková-Sychrova 1966; Harding 1989; Viiri 1997; Kirschner 1998). Furthermore, *C. polonica* has also been found together with *I. typographus* f. *japonicus* in Japan (Yamaoka *et al.* 1997; Marin 2004), which suggests that the fungus follows the distribution range of its vectors and host trees in Eurasia. Differences in the methodology between various studies might also explain some of the varying results concerning the mycobiota of *I. typographus* (see above), and in particular those regarding *C. polonica*. However, the conflicting results about the occurrence and frequency of fungi associated with *I. typographus* in Europe cannot be ascribed exclusively to differences in the methodology employed in the various studies.

It has been suggested that the population dynamics of *I. typographus* has a strong influence on the incidence and frequency of *C. polonica* or that *C. polonica* may even play a role in the initiation and development of outbreaks of *I. typographus* (Harding 1989; Solheim 1993). Following this hypothesis, *C. polonica* occurs at low frequencies during non-outbreak periods of *I. typographus*, but its frequency increases during the course of outbreaks. As increasing numbers of healthy trees are attacked, *C. polonica* gains a habitat, in which it is more competitive than other fungal associates of the spruce bark beetle (Harding 1989; Solheim 1993). This competitive advantage is probably due to its ability to maintain growth in the wet sapwood of healthy trees, which contains low levels of oxygen (Solheim 1991). Thus-far, there is only weak evidence supporting this hypothesis. Solheim (1993) developed this theory to explain differences in the frequency of *C. polonica* between South-Eastern Norway, where a severe outbreak of *I. typographus* occurred in the 1970s and Central Norway where the spruce bark beetle never caused large-scale damage. However, Harding (1989) did not find obvious differences in the frequency of *C. polonica* between sites varying in the outbreak status of *I. typographus*. Studies in Austria also provided no support for the view that the occurrence of *C. polonica* is related to damage levels by *I. typographus*. Here, *C. polonica* occurred at low frequencies in stands outside the natural range of Norway spruce, which have been suffering most severely during the outbreak of *I. typographus* since 1992 (Grubelnik 1998; Kirisits *et al.* 2000; Kirisits 2001). In these Austrian studies, *C. polonica* was more frequently recorded at localities within the natural range of Norway spruce. This pattern of diffusion could be due to climatic influences. *Ceratocystis polonica* has a relatively low temperature maximum around 31–32°C (Marin 2004) which may inhibit its vigour and give other fungi such as *O. bicolor* with higher growth maximum (Solheim 1991) competitive advantages at localities with high spring and summer temperatures, such as at the Austrian localities in the foothills of and outside the Alps. This hypothesis certainly requires thorough study.

Some authors have suggested that the vigour/vitality of Norway spruce may have a strong influence on the spectrum of fungi that are isolated from the phloem and sapwood following attack by *I. typographus* (Harding 1989; Solheim 1992b; Jankowiak 2004). According to this view, vigorous trees may favour the development of *C. polonica*, whereas other ophiostomatoid fungi are more competitive than *C. polonica* on low vigorous, wind-thrown and wind-broken trees as well as logs. This hypothesis is connected to the other hypothesis that *C. polonica* increases its frequency during outbreak periods of *I. typographus* (Harding 1989;

Solheim 1993; see above). Harding (1989) found no relationship between the occurrence of *C. polonica* and the health status of Norway spruce trees. In a recent study in Poland, *C. polonica* was relatively rare, but it occurred more frequently on healthy trees compared to weakened or dead trees as well as wind-thrown, wind-broken and trap trees (Jankowiak 2004). Despite a few hypotheses have been suggested to explain the variation of the frequency of *C. polonica* as associate of *I. typographus* at different localities in Europe, this phenomenon seems to be very complex and is not fully understood thus-far. This intriguing question, therefore, deserves continuing and careful study in the future.

6. SYMBIOSIS BETWEEN BARK BEETLES AND FUNGI

The term "symbiosis" has been used with different meanings in various scientific disciplines, either in a strict or broad sense. For the present discourse on fungal associates of bark beetles I follow the terminology of Whitney (1982). In its original definition symbiosis refers to the more or less continuous living together of different species, regardless of the benefits or disadvantages to the partners. This broad definition includes mutualism, antagonism and other symbiotic relationships. Mutualism, often referred to as symbiosis in its strict sense, is defined as relationship between two separate species where both partners benefit. In antagonistic relationships, one or both partners are detrimentally affected. The symbiotic relationships between xylomycetophagous bark beetles and ambrosia fungi (6.1) and between true bark beetles and fungi (6.2) are discussed below.

6.1. Symbiosis between xylomycetophagous bark beetles and ambrosia fungi

The relationship between xylomycetophagous bark beetles and ambrosia fungi clearly represents a symbiosis, since the two partners are in close physical contact with each other throughout their life and do not become separated at any stage of their life histories (Francke-Grosmann 1967; Beaver 1989; Berryman 1989). Moreover, beetles and fungi are mutualistic symbionts, which benefit from and obligately depend on each other (Francke-Grosmann 1967; Berryman 1989).

Ambrosia fungi mainly benefit from the association with ambrosia beetles by the consistent dissemination of fungal spores and their inoculation into new, suitable habitats (Francke-Grosmann 1967; Norris 1979; Beaver 1989). The fungi are also selectively protected and nourished in the beetle's mycangium. In the galleries, ambrosia beetles actively take care of their ambrosia fungi and protect them from other "weed" fungi which leads to the dominance of ambrosia fungi in the galleries of xylomycetophagous bark beetles (Francke-Grosmann 1967; Beaver 1989).

For the beetles the advantage of the association with their domesticated ambrosia fungi is obvious. The fungi provide the only source of food for the adult ambrosia beetles and their larvae (Francke-Grosmann 1967; Norris 1979; Beaver 1989; Berryman 1989). Ambrosia fungi derive nutrients from the wood of their host trees, concentrate them in their mycelium and make them available to the ambrosia beetles that feed on ambrosial layers formed along the galleries. Apart from converting

nutrients from the wood and providing them in a nutrient form (sugars and other carbohydrates, lipids and proteins) that can be digested by the beetles, fungi produce and concentrate nutrients essential for the beetles that are not at all or only at very low concentrations present in the wood. Nutritionally beneficial fungi provide a very rich source of protein, nitrogen and amino acids to the beetles (Beaver 1989; Six 2003 and references therein). Likewise, ambrosia fungi supply the beetles with sterols (especially ergosterol) that are very essential for growth, molting, and reproduction (Beaver 1989; Six 2003 and references therein). The fungal diet is probably also important for fulfilling some of the vitamin requirements of the insects (Beaver 1989). The total nutritional dependence of the xylomycetophagous bark beetles on their associated fungi makes it possible to successfully rear the insects on artificial cultures of their ambrosia fungi (Francke-Grosman 1967; Beaver 1989; Norris 1979).

6.2. Symbiosis between phloeophagous bark beetles and fungi

As in the ambrosia beetles and their associated ambrosia fungi, the relationship between phloeophagous bark beetles and certain fungi, mainly ophiostomatoid fungi, yeasts and occasionally basidiomycetes, represents in many cases also a symbiosis, since the partners are more or less consistently and continuously associated with each other. Only for a short period of time, during some stages of larval development in the phloem, insects and fungi can physically become separated from each other, and the larvae feed ahead of the front of fungal colonization in the phloem (Whitney 1971; Yearian *et al.* 1972). Contact between them is re-established after pupation of the insects in the pupal chambers where the fungi often form dense layers of conidiophores and sometimes also ascocarps, and young adults become inoculated with conidia and ascospores (Whitney 1971; Webber and Gibbs 1989; Yearian *et al.* 1972) (see also Fig. 3).

While the association between phloeophagous bark beetles and certain fungi clearly fulfills the criteria of a symbiosis, there is no unequivocal agreement whether their relationship represents mutualism (Whitney 1982; Harding 1989; Harrington 1993a; Paine *et al.* 1997). True bark beetles form a heterogenous group and various species differ considerably in their nutrition biology (phloeophagous versus phloeomycetophagous), aggressiveness, attack strategies and range of vigour of host trees selected for breeding. It is thus reasonable to assume that there is no universal model describing the interactions between phloem-feeding bark beetles and associated fungi. Bark beetle species may vary considerably in their dependence on fungi and many different forms of symbiosis may be encountered in different bark beetle-fungal complexes.

Fungal associates of true bark beetles benefit in similar ways from the association with their insect partners as ambrosia fungi benefit from the relationship with xylomycetophagous scolytids (Whitney 1982; Krokene 1996; Paine *et al.* 1997; Six 2003). The fungi are transmitted and inoculated to new, appropriate habitats by the beetles. The insects not only disseminate fungal spores, but also create wounds in the bark, and enable blue-stain fungi and other fungal associates to infect the

tissues of their host trees. Many blue-stain fungi occur exclusively in association with bark beetles and obligately depend on the beetles to be transmitted to suitable habitats (Francke-Grosmann 1967; Krokene 1996; Paine *et al.* 1997; Upadhyay 1981; Kirschner 1998; Six 2003).

The ecological significance of the fungi for the bark beetles is less clear and in most cases still not fully understood. Different groups of fungi may be beneficial or inimical to the insects in various ways (Paine *et al.* 1997). I will discuss four modes of action how bark beetles can gain benefits from their associated fungi: involvement of fungi in tree killing and in exhaustion of the defense mechanisms of the host tree during bark beetle attack (6.2.1.), nutrition (6.2.2.), protection from detrimental fungi (6.2.3.), and involvement in pheromone production (6.2.4).

6.2.1. Involvement of fungi in tree killing and in exhaustion of the defense mechanisms of the host during attack by bark beetles

Blue-stain fungi have long been suspected to play an important role in killing of conifer trees attacked by bark beetles (e. g. Nelson and Beal 1929; Nelson 1934; Bramble and Holst 1940). Many researchers considered the involvement of the fungi in tree killing and in exhaustion of the defence mechanisms of the host as the main mode of action from which bark beetles benefit from the association with fungi (e. g. Berryman 1972; Whitney 1982; Christiansen *et al.* 1987; Christiansen and Bakke 1988; Harding 1989; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997). Association with phytopathogenic fungi has also been mentioned as an important characteristic of aggressive bark beetle species and even as a prerequisite for scolytids to display aggressive behaviour (Christiansen *et al.* 1987; Krokene 1996). The high level of virulence of some fungal associates to their host trees (see 3.3.1.) is the primary argument in support of the hypothesis that fungi are important components in the ability of bark beetles to kill trees (e. g. Berryman 1972; Whitney 1982; Christiansen *et al.* 1987; Raffa and Klepzig 1992; Krokene 1996).

However, the general importance of fungi to help bark beetles in overcoming the defense mechanisms of the host trees has also been questioned by several authors (e. g. Harrington 1993a; Wingfield *et al.* 1995; Paine *et al.* 1997; Lieutier 2002, chapter 9). This view is based on several lines of evidence. Here, I will mention only a few examples of the arguments that have been presented. Harrington (1993a) considers the virulence of ophiostomatoid fungi merely as adaption to the habitat of bark beetles on living trees that might have been evolved as result of interspecific competition between various ophiostomatoid fungi, but not primarily through coevolution with bark beetles. By their fast growth, tolerance against host chemicals and their ability to grow under anaerobic conditions in moist sapwood, pathogenic species gain competitive advantages over other fungal associates (Harrington 1993a). Other arguments refer to the intimacy of association between bark beetles and associated blue-stain fungi. For example, *T. piniperda* is so loosely associated with *L. wingfieldii* and other ophiostomatoid fungi that it is difficult to understand, how fungi could contribute to exhaust the defence mechanisms of pine trees during natural attack of the pine shoot beetle (Lieutier *et al.* 1989a; Lieutier 1993, 2002, chapter 9). In *I. typographus*, the pathogenic blue-stain fungus *C. polonica* has been

suggested to be essential to overcome the defense mechanisms of Norway spruce (Christiansen *et al.* 1987; Christiansen and Bakke 1988; Krokene 1996; Krokene and Solheim 1998). However, the frequency of *C. polonica* varies considerably between different localities and in many areas in Europe this pathogenic fungus is only rarely associated with *I. typographus* (see 5.2.5.). This clearly demonstrates that the spruce bark beetle does not obligately need *C. polonica* to successfully colonize living trees. Even in areas, where *C. polonica* occurs rarely, *I. typographus* is associated with numerous ophiostomatoid fungi, in particular *O. bicolor*, *O. penicillatum* and *O. piceaperdum* (Table 2). Thus, *I. typographus* always transmits fungi when attacking living host trees. However, these species are less virulent than *C. polonica* (Hornftvedt *et al.* 1983; Harding 1989; Kirisits 1998) and probably less efficient to exhaust the defense systems of Norway spruce.

Apart from the few examples mentioned above, no attempt is made in this chapter to extensively review the role of ophiostomatoid fungi in tree killing and in exhaustion of the defense mechanism of the host during bark beetle attack. This is because this aspect of bark beetle-fungus relationship has recently been extensively treated by Lieutier (2002) and Lieutier (chapter 9) and I also refer to other recent reviews of this topic (Whitney 1982; Harding 1989; Harrington 1993a; Raffa and Klepzig 1992; Krokene 1996; Paine *et al.* 1997). I believe that the various lines of evidence justify to assume that bark beetle species greatly differ in the dependence on fungi to interfere with the defense mechanisms of their host trees. It is easy to predict that the debates on the role of fungi in overcoming the defense systems of host trees will continue in the future. Simultaneously, the conflicting views will likely stimulate research in various scolytid-fungus-host-systems, which will contribute to improve our current understanding of the intriguing interactions between bark beetles, fungi and live conifer trees.

The association of the Dutch elm disease pathogens *O. ulmi* and *O. novo-ulmi* with elm bark beetles represents a bark beetle-fungus relationship that differs from that of conifer bark beetles with blue-stain fungi. *Scolytus* species transmit *O. ulmi* and *O. novo-ulmi* during maturation feeding from diseased to healthy trees (Webber and Brasier 1984; Webber and Gibbs 1989). These healthy trees get infected, decline due to Dutch elm disease and become susceptible to attack by the next generation of elm bark beetles, which breed in the bark of diseased elm trees. The pandemics of Dutch elm disease since the early 20th century have created large amounts of susceptible host trees for the elm bark beetles and the fungi thus provided benefits to the populations of these scolytids (Webber and Brasier 1984; Webber and Gibbs 1989; Webber 2000). It should be considered, however, that the association of *O. ulmi* and *O. novo-ulmi* with *Scolytus* spp. is an untypical bark beetle-fungus-host relationship, since it is driven by an introduced pathogen that came in contact with highly susceptible host trees (Brasier 2000).

6.2.2. Nutrition

Concerning their nutritional biology, it is reasonable to further distinguish two groups within bark beetles colonizing the phloem of trees. One group of species feeds both on the phloem of the host trees, but also on associated fungi, and it is

probably justified to describe their feeding habit as "phloeomycetophagous" (Francke-Grosmann 1952, 1966, 1967). Some, but not all species in this group possess mycangia in which nutritionally relevant fungi are carried (Francke-Grosmann 1952, 1963b; Whitney 1982; Paine *et al.* 1997; Six 2003). These scolytids share characteristics of true bark beetles and xylomycetophagous bark beetles (Francke-Grosmann 1952, 1966, 1967; Six 2003 and references therein).

Within the European bark beetle fauna, two species on pine, *T. minor* and *I. acuminatus* have been reported to have a phloeomycetophagous feeding habit (Francke-Grosmann 1952, 1967). The larvae of these bark beetle species create very short galleries in the phloem and move later in the outer sapwood where they pupate. Initially the larvae feed in the phloem, but at later stages of their development they feed on conidia and mycelium of fungi, *I. acuminatus* on *Ambrosiella macrospora* and *T. minor* on *A. tingens*. The fungi form dense conidial layers in the larval galleries of *I. acuminatus* and *T. minor*, very similar to ambrosia fungi associated with ambrosia beetles. In *I. acuminatus* an oral mycangium has been detected in which the conidia of *Ambrosiella tingens* are transported (Francke-Grosmann 1963b). No mycangium has so far been found in *T. minor* (Francke-Grosmann 1952, 1963b). Scolytids with phloeomycetophagous feeding habit are probably more numerous represented in the North American bark beetle fauna. Although they have not explicitly referred to as phloeomycetophagous, *D. frontalis* and *D. ponderosae* likely belong to this group, since they both possess a mycangium and feed on phloem as well as on fungi, upon which they are largely dependent for nutrition (Barras 1973; Klepzig 2001a, 2001b; Six 2003).

Most bark beetle species that breed in the phloem of trees are truly phloeophagous and thus feed mainly on the phloem of their host trees, which is a nutrient-rich substrate. Typically, they do not possess a mycangium and are less - and in many cases not obligately - dependent on fungal associates for nutrition, although the fungi may provide an additional food source for larvae and teneral adults (Francke-Grosmann 1967; Harding 1989; Whitney 1982; Six 2003). Different groups of fungi may vary in their importance for the insects. Yeasts are suspected to be essential as suppliers of vitamins, especially B-group vitamins (Strongman 1986; Pignal *et al.* 1988; Beaver 1989; Harding 1989 and references therein), while non-mycangial ophiostomatoid fungi are generally thought to be less, if at all, important for nutrition of phloeophagous bark beetles (Grosmann 1931; Yearian *et al.* 1972; Whitney 1982; Harding 1989; Fox *et al.* 1993). Some blue-stain fungi even display antagonism against bark beetles (Barras 1970; Yearian *et al.* 1972; Klepzig *et al.* 2001a, 2001b).

The nutritional relevance of yeasts and blue-stain fungi for phloeophagous bark beetles in Europe is poorly known, but the few studies that have been conducted so far, suggest that the insects can be reared successfully in the absence of blue-stain fungi, while a positive influence of yeasts cannot be excluded (Grosmann 1931; Harding 1989; Colineau and Lieutier 1994; Simsek and Führer 1993; Simsek 1994). Grosmann (1931) concluded that yeasts and blue-stain fungi are not obligately needed for the development of *I. typographus*, since a single larva free of micro-organisms developed into an adult insect. This conclusion is questionable, however, due to the limited scope of the study and because the fecundity and behaviour of

progeny was not tested. Harding (1989) was able to rear *I. typographus* in the complete absence of blue-stain fungi through two generations, however, yeast were occasionally isolated from parent and offspring beetles. Simsek and Führer (1993) and Simsek (1994) successfully reared *I. typographus* from eggs to mature adults on a semi-artificial medium based on ground phloem, in which the development of associated fungi was suppressed by fungicides. Finally, *Ips sexdentatus* showed normal breeding behaviour and reproduced successfully in absence of its fungal associates, *O. brunneo-ciliatum* and *O. ips* (Colineau and Lieutier 1993). Besides these European studies, Yearian *et al.* (1972) successfully reared *I. avulsus*, *I. calligraphus* and *I. grandicollis* through 3 to 4 generations in the absence of *O. ips* on pine logs. In summary, the nutritional role of associated fungi for phloeophagous bark beetles has received relatively little attention in Europe thus-far, and this topic should, therefore, be investigated more intensively in the future.

Studies in North America have shown that certain blue-stain fungi are antagonists of bark beetles by making the phloem unsuitable for larval nutrition or inhibiting oviposition of adult beetles. In phloem colonized by *O. minus* larval development of *D. frontalis* was negatively affected in various ways, resulting in lower reproductive success (Barras 1970; Klepzig *et al.* 2001a, 2001b). Similarly, oviposition of *Ips avulsus*, *Ips calligraphus* and *Ips grandicollis* was almost totally inhibited in the phloem of pine logs that had been preinfected by *O. ips* (Yearian *et al.* 1972). Among conifer bark beetles in Europe it is generally not known, if blue-stain fungi could have negative effects on brood development, but Webber and Gibbs (1989) reported that larvae of elm bark beetles (*Scolytus* spp.) avoided areas of elm bark that had previously been colonized by *O. ulmi*. Possible antagonistic effects of blue-stain fungi on bark beetles in Europe form an uninvestigated area of research that deserves attention in the future.

6.2.3. Protection from detrimental fungi

The idea that mutualistic fungi protect bark beetle galleries from invasion by detrimental fungi originally comes from *D. frontalis* and its associated fungi and phoretic mites (Klepzig *et al.* 2001a, 2001b). In this system, the two mycangial fungi of *D. frontalis*, *Entomocorticium* sp. and *C. ranaculosus* compete with the nonmycangial and antagonistic fungus, *O. minus* for resources in the phloem of trees attacked by the southern pine beetle. The two mycangial fungi, especially *Entomocorticium* sp. and to a lesser extent *C. ranaculosus*, provide some protection from the detrimental *O. minus* to the developing larvae. Other examples of such competitive interactions are mentioned by Six (2003).

I speculate that protection of the developing broods from antagonists by associated fungi could be important in many beetle-fungus-systems. Blue-stain fungi quickly colonize the gallery systems and the adjacent phloem after attack by bark beetles and likely occupy this niche at least until the young insects have left their host trees. Thus, ophiostomatoid fungi might play a considerable role in preventing the establishment of fungi that are deleterious to the developing larvae. This postulate certainly requires confirmation by thorough studies.

6.2.4. Involvement in pheromone production

A few studies provided evidence that fungi may be involved in the production of pheromones (Whitney 1982 and references therein; Harding 1989 and references therein; Six 2003). The only investigation addressing this question in an European bark beetle-fungus system is that of Leufvén *et al.* (1984) who showed in laboratory assays that yeasts associated with *I. typographus* can convert cis/trans-verbenol, an aggregation pheromone of this bark beetle, to verbenone, which functions as an antiaggregation pheromone. The abundance of yeasts increased during later phases of bark beetle attack and this increase occurred at the same time as the increase of the amount of verbenone, which suggests that yeasts could be important in interfering with the chemical communication of *I. typographus* under field conditions (Leufvén and Nehls 1986).

Many species of *Ophiostoma* and *Ceratocystis* produce volatile metabolites that give fungal cultures characteristic odors (Hanssen 1993). These metabolites include short-chain alcohols and esters, mono- and sesquiterpenes as well as other miscellaneous compounds (Hanssen 1993). The production of intensive aromas by ophiostomatoid fungi and especially by *Ceratocystis* species is viewed as an adaption to attract various insects that are unspecifically involved in dissemination of these fungi (Kile 1993; Harrington and Wingfield 1998). It is attractive to think that volatiles produced by ophiostomatoid fungi might also play a role in the chemical communication of bark beetles, but so far this assumption is speculative and requires investigation (Hanssen 1993).

7. PERSPECTIVES FOR FUTURE RESEARCH

The association of fungi with bark beetles is a fascinating example of symbiosis that has received much attention in the past. It is easy to predict that the fungi transmitted by bark beetles and the relationship with their associated insects and host trees will continue to fascinate scientists in various disciplines. The fact that bark beetles are important forest pests and that many fungal associates of scolytids cause destructive tree diseases or are economically important agents of blue-stain, will likely help to justify allocation of research resources to continue studying these fungi thoroughly and in an interdisciplinary manner. Below I will present a few ideas for future research, from a personal, very subjective perspective.

Despite tremendous research efforts in the past I feel that we still can learn a lot about the diversity of fungi in the bark beetle habitat. So far, only a minor portion of the 154 European bark beetle species (Postner 1974) have been examined regarding the fungi they carry. It is, therefore, likely that a large number of ophiostomatoid fungi and other fungi associated with bark beetles remain to be discovered, even in a relatively well-studied region as Europe. Further surveys of ophiostomatoid species associated with bark beetles in Europe could greatly improve the knowledge on the taxonomy, ecology and biogeography of these fungi.

It is only a little more than a decade ago that the issue of "sibling species" within the ophiostomatoid fungi has started to receive considerable attention (Brasier and Kirk 1993). They represent morphologically similar or even indistinguishable fungi

that are ecologically and genetically isolated and represent different biological species. Examples of such sibling species in Europe are *O. quercus* and *O. piceae* as well as the bark beetle-vectored blue-stain fungi, *C. polonica* and *C. laricicola* (Brasier and Kirk 1993; Kirisits 2001; Harrington *et al.* 2002; Marin 2004). Due to the rapid progress in the development of reliable molecular markers, it is likely that many more sibling and kryptic species within the ophiostomatoid fungi will be identified in the near future. Genetic studies, mating experiments, studies on the host specialization of fungi and growth experiments can be effectively combined to provide several lines of evidence to distinguish "sibling species". These discoveries will also improve the understanding of speciation within the ophiostomatoid fungi and will provide new insights in their ecology and relationships with insects.

The synthesis of studies on the fungal assemblages of European bark beetles (Table 2) has clearly shown that remarkable variation in the composition of the mycobiota of the same bark beetle species at different localities in Europe can occur. *Ips typographus* has been mainly used as a model to illustrate this phenomenon, but it is also documented for other European scolytids. The factors, which drive the variation of the mycobiota of *I. typographus* as well as the resulting implications for the ecology and population dynamics of the spruce bark beetle still remain poorly known. Thus, further studies on the variation of the mycobiota of *I. typographus* in various parts of Europe will represent an intriguing area for future research. Although I have focussed on *I. typographus*, comparisons of the mycobiota of scolytids in various parts of Europe are certainly also of interest for other economically important bark beetle species. I also believe that the role of phoretic mites associated with bark beetles in transmission of blue-stain fungi should be further investigated, since mites have been shown to be very important in driving the transmission and frequency of ophiostomatoid fungi in bark beetle-fungus-mite-systems in North America (Bridges and Moser 1983, 1986; Klepzig *et al.* 2001a, 2001b).

The relationships between phloem-feeding bark beetles and fungi represent in most cases a "polysymbiosis". Typically, at least two, and often more fungal species are consistently associated with one scolytid species. It is reasonable to assume that different fungi interact in various ways with their bark beetle partners, with some fungi being beneficial for the insects, while others being neutral or antagonistic symbionts (Six 2003). Likewise, fungal associates strongly compete with each other for space and resources in the bark beetle habitat (Klepzig *et al.* 2001a, 2001b). These competitive interactions may influence the frequency of occurrence of fungal associates, which likely also has some consequences for the insect-fungal relationships. I think that we have presently just started to understand the interactions between various fungal associates of bark beetles at varying ecological situations (Klepzig *et al.* 2001a, 2001b; Six 2003). Therefore, the competitive interactions between fungi associated with scolytids *in vitro* and *in vivo* form a largely uninvestigated and highly intriguing area for future research that will provide essential information for characterizing the bark beetle-fungus symbiosis (Klepzig 1998; Klepzig and Wilkins 1997; Klepzig *et al.* 2001a, 2001b; Six 2003).

Although much is already known about the phytopathogenicity of bark beetle-associated blue-stain fungi, there is still a need for further studies. The pathogenicity

of some potentially important fungal species and the ability of these fungi to stimulate the defense reactions of their host trees should be tested, considering especially the variation of virulence displayed by different isolates of the same fungal species (see Lieutier *et al.* 2004). Likewise, the recently discovered mycovirus-mediated hypovirulence in *C. polonica* and *C. laricicola* (Marin 2004) offers many possibilities for future research. This includes the possible ecological implications of dsRNA mycovirus infections on populations of these *Ceratocystis* species and possible chances for implementation of biological control strategies. It may also be very intriguing to screen other pathogenic blue-stain fungi for the presence of dsRNA mycoviruses and to study the possible effects of the viruses on the pathogenicity and fitness of the fungi.

Pathogenic blue-stain fungi have been an invaluable tool to study the defense mechanisms of conifers against bark beetles and fungi (Lieutier 2002, chapter 9 and references therein) and I look forward to the progresses in the understanding of the resistance mechanisms of conifers that will be made in the future. In addition, studies should consider the processes of inoculation and infection of blue-stain fungi under natural conditions. For many conifer bark beetle species it is well established that they carry blue-stain fungi, however, the spore load of associated fungi transmitted by individual beetles is not known for most beetle-fungus-systems (but see Webber and Brasier 1984; Webber and Gibbs 1989; Webber 1990, 2000). For a few blue-stain fungi (*L. wingfieldii* and *O. brunneo-ciliatum*) a relationship between the number of spores inoculated and the intensity of the defense reaction has been established (Lieutier *et al.* 1989a; Lieutier 1993, 2002, chapter 9), but such a relationship has not been investigated for many other bark beetle-associated blue-stain fungi. Both the spore load carried by the beetles as well as possible relationships between the number of spores inoculated by the insects to the tree and the intensity of the tree's defense reactions are essential to understand inoculation and infection of blue-stain fungi by bark beetles under field conditions.

Recent reviews of the symbiosis between bark beetles and fungi, including the present one, have proposed that there may be great differences between various bark beetle-blue-stain fungus-systems in terms of the relevance of the fungi (Wingfield *et al.* 1995; Krokene 1996; Paine *et al.* 1997; Lieutier 2002, chapter 9; Six 2003). In order to improve our understanding of the relationship between bark beetles and blue-stain fungi, additional studies should be initiated aimed at investigating the direct effects of association with fungi for phloeom-feeding bark beetles. Whitney (1982) proposed that the role of associated fungi for bark beetles could be revealed by production of aseptic, microbe-free insects and by comparing them in biological experiments with specifically fungus-inoculated insects or beetles from field populations. The production of microbe-free insects is extremely difficult to achieve and includes the risk of failure. However, I believe that studies using aseptic bark beetles will be a main approach in the future to make progress in the understanding of the complex relationships between fungi, bark beetles and their host trees.

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