Data Sheets on Quarantine Pests

Bursaphelenchus xylophilus

The vectors of *Bursaphelenchus xylophilus (Monochamus* spp.) are included in EU Directive 77/93. Since their importance only arises in relation to *B. xylophilus*, they are covered in this data sheet.

IDENTITY

• Bursaphelenchus xylophilus

Name: *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle Synonyms: *Aphelenchoides xylophilus* Steiner & Buhrer

Bursaphelenchus lignicolus Mamiya & Kiyohara

Taxonomic position: Nematoda: Aphelenchoididae

Common names: Pine wood nematode, pine wilt disease (English)

Nématode du bois de pin, nématode des pins, dépérissement des pins (French)

Kiefernholznematode (German)

Notes on taxonomy and nomenclature: B. xylophilus was first described in the USA as Aphelenchoides xylophilus (Steiner & Buhrer, 1934). Later it was described again, as Bursaphelenchus lignicolus, when determined to be the causal agent of pine wilt disease in Japan (Mamiya & Kiyohara, 1972). The synonymy was recognized in 1981 (Nickle et al., 1981). A very similar but non-pathogenic species, B. mucronatus, was described by Mamiya & Enda (1979), differing morphologically only in minor respects from B. *xylophilus* and most obviously by the presence in the female of a caudal mucro (finger-like projection) in the former species which was absent in the latter. However, populations of B. xylophilus were subsequently discovered in the USA which also carried a mucro on the tail. There has thus been much discussion about the taxonomic relationships between these two species, and also with B. fraudulentus Rühm, a nematode from deciduous trees in central Europe. Biochemical studies of several populations of these nematodes have clearly confirmed the distinctness of the three species (Webster et al., 1990; Abad et al., 1991). B. *xylophilus* is a native of North America, whereas the other two are Palaearctic species, one colonizing coniferous trees, the other deciduous. B. xylophilus found in Japan and other Asian countries is obviously an introduction from North America. Another apparently closely related species, Bursaphelenchus kolymensis Korenchenko, has been described from Larix from the far east of the former USSR (Korenchenko, 1980); this nematode has not been studied extensively but is possibly synonymous with B. mucronatus. A population of B. mucronatus has been detected in the Province of Quebec, Canada (Harmey & Harmey, 1993), but it is not known if this is an introduction.

Bayer computer code: BURSXY

EPPO A1 list: No. 158

EU Annex designation: II/A1

• *Monochamus* **spp. Taxonomic position**: Insecta: Coleoptera: Cerambycidae Names and **synonyms**: See Table 1.

EU Annex designation: I/A1 - as *Monochamus* spp. (non-European)

HOSTS

• Bursaphelenchus xylophilus

B. xylophilus is found mainly on *Pinus* spp. Apparently, the dead wood of all species of *Pinus* can act as a substrate for the development of *B. xylophilus*. However, only a limited number of species is susceptible to attack as living trees; the Far Eastern species *P. bungeana*, *P. densiflora*, *P. luchuensis*, *P. massoniana* and *P.thunbergii* (in their native habitats), and the European species *P. nigra* and *P. sylvestris* (planted in North America) and *P. pinaster* (planted in China) are the only species have been found to be damaged or killed by the nematode but only under experimental conditions (mainly as seedlings in glasshouses).

Other conifers can also act as hosts (primarily *Larix*, *Abies* and *Picea*) but reports of damage are rare. Isolated cases of death of *Picea* and *Pseudotsuga* due to this nematode have been reported in the USA (Malek & Appleby, 1984).

Within the EPPO region, *P. sylvestris* would be the species of *Pinus* most at risk in northern and central areas, whereas *P. nigra* and *P. pinaster* would be threatened in central and southern areas.

• Monochamus spp.

The *Monochamus* spp. which are of concern as known or possible vectors of *B. xylophilus* mainly develop in *Pinus* spp. but other coniferous genera can sometimes also act as hosts (see Table 1). They will, in addition, oviposit in most coniferous species, even those in which the possibilities for complete development to adult are limited. *Thuja plicata*, however, demonstrates insecticidal properties that prevents oviposition. Other species of *Monochamus* attack other plant hosts, but are of no relevance in the present context.

GEOGRAPHICAL DISTRIBUTION

• Bursaphelenchus xylophilus

It is presumed that *B. xylophilus* originated in North America and was transported from there to the southern Japanese island of Kyushu in infested timber at some time around the beginning of the 20th Century (Nickle *et al.*, 1981; Mamiya, 1983; Malek & Appleby, 1984). The fact that native American conifers are mostly resistant, while Japanese species are susceptible, tends to support this view. From Japan, *B. xylophilus* has spread to other Asian countries (Li *et al.*, 1983).

EPPO region: Absent. Surveys to determine whether *B. xylophilus* may be present have been conducted in several European countries (including Finland, Germany, Netherlands, Norway, Poland, Sweden, UK) but the species was not found. Furthermore, an examination in Finland of 150 consignments of conifer wood from European countries failed to detect the species. *B. xylophilus* was supposedly reported on *P. pinaster* in the south-west of France (Baujard *et al.*, 1979) but later microscopic and biochemical examination showed that the nematode present was, in fact, *B. mucronatus*. Although this species was found associated with dead or dying *Pinus*, it was concluded that it was not responsible for the mortality. As well as in France, *B. mucronatus* has been found in Austria, Finland, Norway, Sweden and Russia. See also De Guiran & Boulbria (1986).

Asia: China (Anhui, Guangdong, Jiangsu, Shandong, Zhejiang; Zhang & Huang, 1990), Hong Kong, Japan (Honshu, Kyushu, Ryukyu Archipelago, Shikoku), Korea Republic, Taiwan.

North America: Canada (Alberta, British Columbia, Manitoba, New Brunswick, Ontario, Quebec, Saskatchewan; probably throughout), Mexico, USA (recorded from at least 34 states, including Alabama, Arkansas, California, Connecticut,

Delaware, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Jersey, New York, North Carolina, Ohio, Oklahoma, Oregon (probably), Pennsylvania, South Carolina, Tennessee, Texas, Vermont, Virginia, Washington (probably), West Virginia, Wisconsin; probably wherever *Pinus* occurs, but not Hawaii). **EU**: Absent.

• Monochamus spp.

The species of *Monochamus* which are of concern as known or possible vectors of *B. xylophilus* occur only in the northern hemisphere. Table 1 provides a list, showing their geographical distribution, whether their range currently overlaps with that of *B. xylophilus* and whether they are known to be vectors of *B. xylophilus*. It may be noted that many species are very widely distributed, and that the genus is represented in most areas of the northern hemisphere. Exceptions are the islands of Great Britain and Ireland. The genus *Monochamus* is represented elsewhere in the world, but the species concerned do not attack conifers.

BIOLOGY

• Bursaphelenchus xylophilus

B. xylophilus is known to have two different modes in its life cycle, a propagative mode and a dispersal mode (Wingfield, 1983). In both cases, the nematodes are transmitted from one host to the next by species of *Monochamus* (see section on *Monochamus* spp. below). In the propagative life cycle, fourth-stage larvae of the nematodes are transmitted to recently dead or dying trees during oviposition by the female vector. The nematodes leave the beetle and enter the tree through the hole in the bark cut by the vector to lay its eggs. Within the wood the nematodes feed on the hyphae of fungi (usually *Ceratocystis* spp.) also transmitted to the wood by ovipositing beetles. Immediately on entering the wood the larval nematodes moult to adult and begin laying eggs. The population is composed of males, females and four larval stages in this propagative stage of rapid multiplication.

At a certain time after the initial invasion by the nematodes, the population ceases to multiply and begins to decline. A different type of third-stage larva is produced; this is called the "dispersal third-stage larva" (Mamiya, 1983), although it is more correctly a survival stage, being capable of resisting adverse conditions. It is likely that the onset of the dispersal mode is in reaction to a reduction in the availability of food, when the fungus has fully exploited the wood. The "dispersal" larvae gather in the wood surrounding the pupal chamber of the *Monochamus* vector, possibly under the influence of substances diffusing from the developing pupa. Close to the time of emergence of the beetle, the nematodes moult into the special fourth-stage larvae, called the "dauer larvae". Fungal hyphae also develop around the pupation chambers. The fungus forms long-necked perithecia projecting into the chamber, and the nematodes gather at the tips of the perithecia. When the young adult beetle emerges, it brushes against the perithecial necks, picking up the nematodes which settle below the elytra and, in particular, in the tracheae. The immature adult beetle then flies from the wood carrying nematodes.

The life cycle described above could be considered to be the "normal" life cycle of *B. xylophilus* and is similar to that of most other *Bursaphelenchus* spp. that have phoretic relationships with forest beetles. In North America, it is presumably the most common condition (Wingfield, 1983). On the other hand, in Asia, and also in North America wherever the nematode comes into contact with non-native or susceptible species of *Pinus*, a different type of transmission to tree hosts predominates. Under these conditions, the nematodes are transmitted from young adult beetles shortly after emergence from their pupal chambers, when they fly to feed on young *Pinus* shoots. The nematodes enter the

shoots through the feeding wounds. Why this form of transmission occurs only on certain *Pinus* species is not fully understood, but it is presumably because *Pinus* species native to the area where *B. xylophilus* occurs have developed physical or biochemical barriers to prevent direct invasion to healthy tissues.

In the young *Pinus* shoots, *B. xylophilus* then multiplies in the resin canals, attacking their epithelial cells. About 3 weeks later, the tree shows first symptoms of 'drying out', in the form of reduced oleoresin exudation. The nematodes can now move freely throughout the dying tree. As a consequence of the reduction of its defence mechanisms (e.g. reduced oleoresin), the tree becomes attractive to adult insects which gather on the trunks to mate. At this stage, intensified wilting and yellowing of the needles is seen. The tree dies 30-40 days after infection, and may then contain millions of nematodes throughout the trunk, branches and roots. The remainder of the life cycle is similar to that described for transmission during oviposition, as the nematodes locate the pupa of *Monochamus* just prior to emergence.

In the laboratory, *B. xylophilus* can be maintained on fungal cultures. It reproduces in 12 days at 15° C, 6 days at 20° C and 3 days at 30° C. Egg-laying starts on the 4th day after hatching, and the eggs hatch in 26-32 h at 25° C. The temperature threshold for development is 9.5° C.

• Monochamus spp.

Species of *Monochamus* from conifers are the principal vectors of *B. xylophilus*, and of these *M. alternatus* is the major vector in Japan, whereas *M. carolinensis* and *M. scutellatus* are the major vectors in North America. Other less efficient *Monochamus* vectors have been recorded in Japan and North America (Table 1). Many of the *Monochamus* spp. from conifers have been recorded as having non-pathogenic *Bursaphelenchus* spp. as associates; it is supposed, therefore, that most, if not all, species would also be capable of transmission of *B. xylophilus* to a greater or lesser extent. For example, the European *M. sutor* and *M. galloprovincialis* have been shown to transmit the related *B. mucronatus* and could, therefore, probably transmit *B. xylophilus* if it were introduced into Europe, as happened with *M. alternatus* in Asia.

Other genera of the Cerambycidae (e.g. Acalolepta, Acanthocinus, Amniscus, Arhopalus, Asemum, Corymbia, Neacanthocinus, Rhagium, Spondylis, Uraecha, Xylotrechus) and other Coleoptera (e.g. Chrysobothris, Hylobius, Pissodes) have been found to carry *B. xylophilus* in or on their bodies but there is no evidence that they have any role as vectors in nature.

Eggs of *Monochamus* spp. are laid in oviposition scars in the bark of the host tree and hatch within 4 to 12 days depending on temperature. The first-instar larva begins feeding on phloem and cambium in the sub-cortical zone. By the third instar, the larva begins to bore into the sapwood forming a gallery composed of an S-shaped horizontal portion perpendicular to the axis of the tree and a vertical portion parallel to the axis. Later larval stages complete the gallery by forming a wide pupal chamber in the vertical portion. *M. alternatus* has four larval instars, whereas 3-8 have been recorded for *M. carolinensis*.

The final larval instar plugs the opening of the tunnel with wood borings and begins pupation. The pupal stage lasts for up to 19 days and afterwards the fresh adult begins to chew through the xylem to emerge; between eclosion and emergence there may be an interval of 6-8 days. Any of the life stages (except the pupae) may hibernate and in *M. alternatus* it is usually the last larval stage. Where hibernation does not take place, the complete development from oviposition to adult emergence takes 8-12 weeks.

The newly emerged adult walks up the branch or log in which it has pupated and flies from the extremity to find current or one-year-old twigs where it feeds on the bark. This initial feeding stage, lasting about 10 days (but up to 3 weeks in some species), is essential for sexual maturation. Mature adults are attracted to weakened trees or recently felled logs where they mate and begin oviposition. The substances that attract the beetles to suitable host trees are monoterpenes and ethanol.

The female excavates a conical scar in the bark with the mandibles and deposits an egg by means of the ovipositor. There is usually one egg per scar although many scars are constructed that do not contain eggs. Females live for up to 83 days and continue egg-laying until death, laying 40-215 eggs.

M. alternatus usually has one generation per year but may require 2 years for development, especially in the cooler areas of Northern Japan. In Missouri, USA, *M. carolinensis* develops through two partially asynchronous generations per year. For further information on biology see Kobayashi *et al.* (1984) for *M. alternatus*, and Kondo *et al.* (1982) and Linit (1987) for *M. carolinensis*.

DETECTION AND IDENTIFICATION

Symptoms

• Bursaphelenchus xylophilus

The first indication of the presence of nematodes in the tree is a reduction of oleoresin production. Transpiration from the leaves decreases and later stops completely. The first obvious external symptom is the yellowing and wilting of the needles, leading to eventual death of the tree (Mamiya, 1983). The wilting may first appear on only one branch ("flag") although the whole tree may later show symptoms (Malek & Appleby, 1984). Note that "flagging" can also result from *Monochamus* feeding on the shoots.

• Monochamus spp.

These insects only oviposit on recently felled trees or trees already under stress. The feeding of the larvae produces feeding tracks on the sapwood under the bark and bore holes into the wood which may make the wood unsaleable.

Morphology

• Bursaphelenchus xylophilus

B. xylophilus shows the general characters of *Bursaphelenchus* spp.: lips high and offset; weakly developed stylet with reduced basal knobs; median bulb well developed; dorsal oesophageal gland opening inside median bulb. In the female, the post-uterine sac is long. In the male, the tail is curved ventrally, conoid and has a pointed terminus. A small bursa is situated terminally. The spicules are well developed, with a prominent rostrum.

B. xylophilus can be distinguished by the simultaneous presence of the following three characters: in the male the spicules are flattened into a disc-like structure (the cucullus) at their distal extremity. In the female the anterior vulval lip is a distinct overlapping flap and the posterior end of the body is rounded in nearly all individuals. This last character separates *B. xylophilus* from *B. mucronatus*, a non-pathogenic species in which the female has a mucronate posterior end. However morphological differentiation between *B. mucronatus* and populations of *B. xylophilus* with mucronate tails in North America is very difficult.

• Monochamus spp.

Larva

Larvae display the same facial features as other cerambycids. Body elongate, soft, with ten abdominal segments, including the anal mamilla. In *Monochamus* the length of the head is distinctly greater than the width. All the abdominal tergites are simple, without spines nor sclerified plates. The larva is apodous.

Adult

Adults of *Monochamus* are 15 to 30 mm long. Characteristics of the genus are: forehead transversal or sub-square; antennal protrusions very high, close together and separated by a

deep hollow. Antennae slender, very long for the male, distinctly longer than body for the female, the third segment being at least twice the length of the scape. Pronotum slightly convex, with a broad collar margin and a broad basilary margin marked by a groove, each side with a large lateral submedian conical protuberance. Anterior coxal cavities opening rearwards. Prosternal protuberances rounded, lower than coxae. Mesosternal process narrow. Elytra wider than pronotum at the base, shoulders protuberant, apices obsoletely truncated. Legs thin and elongate, especially in males where the anterior tibia is arched and tarsi bordered by hairs.

Detection and inspection methods

• Bursaphelenchus xylophilus

Before any symptoms appear in trees suspected of being infested, the reduction of oleoresin production can be detected by making a hole of 10-15 mm in diameter through the bark and cambium (Oda, 1967). Nematodes can be extracted from trees showing symptoms by taking trunk cores and then soaking the cores in water for several days; the nematodes will emerge from the wood into the water. Nematodes can be extracted from small chips of infested wood by use of the standard nematode extraction technique (the Baermann funnel).

• Monochamus spp.

From the exterior, the conical oviposition scars on the bark can show that a tree has been attacked. With the bark removed, young larvae can be seen producing feeding tracks in the sapwood. The oval entry holes in the wood caused by older larvae are characteristic, although they may be hidden by an accumulation of wood borings. The more obvious circular holes, visible in wood both with and without bark, are the exit holes and their presence indicates that the insects have completed their development in the wood and have departed.

MEANS OF MOVEMENT AND DISPERSAL

Within the wood tissues the nematodes can move actively and can leave one piece of wood to move into an adjoining piece. Without their vectors, however, they are incapable of moving from one host tree to another. Adults of the vector beetles can fly actively and a peak of flight activity is reached about 5 days after emergence. Beetles have been recorded as capable of flying for up to 3.3 km, but, in most cases, dispersal is only for a few hundred metres (Kobayashi *et al.*, 1984).

Infested wood is the most probable means of international transport of *B. xylophilus*, and the species has been intercepted on a number of occasions on sawn wood, round wood and wood chips imported into the EPPO region from the USA and Canada.

The most likely pathway of introduction of *B. xylophilus* is when imported together with vector insects which may carry the nematodes to coniferous trees. Such insects can only survive if the wood has a sufficient moisture content, greater than that needed by the nematode. The larger the pieces of timber, the longer insects are liable to survive, and therefore round wood and sawn wood present a greater risk than wood chips. Wood chips can have a high moisture content, allowing ready nematode survival, but the processing undergone in their preparation reduces the possibility of vectors surviving.

Whether introduced with or without a vector insect, it is still necessary for long-term establishment for the nematode to find a means of coming into contact with a native vector, and this can probably only be achieved if the nematode first invades wood which contains larvae or pupae of a potential vector. Nematodes can move very actively from wood chips or sawdust, and the connection with the vector could be made if such material were to come into contact with tree stumps or cut logs; within the wood processing industry, the

same means of transport is sometimes used for collecting both imported and local wood material (McNamara & Støen, 1988).

PEST SIGNIFICANCE

Economic impact

• Bursaphelenchus xylophilus

Pine wilt disease was first reported in Japan in 1913 in the Nagasaki region, but the causal agent was only identified as B. xylophilus in 1972 (Mamiya & Kiyohara, 1972). The symptoms were first attributed to wood-boring insects, which are found abundantly on infected trees, but it was then found that first symptoms precede attack by the insects. The disease then began to spread northwards causing very severe losses throughout the country. Over a million m^3 of wood were being lost per year at the end of the 1940s, but a campaign for destroying infected trees then brought this figure below 500 000 m³ per year (still a substantial loss). However, since industrialization has reduced the availability of manpower for the forests, and since wood has been replaced by oil as a fuel, infected trees are again remaining standing as reservoirs of the nematode. In consequence, the loss curve turned sharply upwards from 1970 and now even exceeds 2 million m^3 per year. Almost all of the Japanese archipelago is affected, from the Ryukyu Islands in the far south, where P. luchuensis is very susceptible, to the northern part of the island of Honshu, with much colder climates where the mean annual temperature is 10-12°C. It seems probable that this northward spread is due to heavy population pressure from the south. Only the most northern island of Hokkaido is still not affected. However, it is clear that serious pine wilt disease is associated with higher temperature (Rutherford *et al.*, 1990) and occurs only where the mean summer temperatures exceed 20°C.

In 1979, *B. xylophilus* was associated with death of *Pinus* in Missouri (USA), primarily of *P. sylvestris* growing in amenity plantings (Malek & Appleby, 1984), and, in North America in general, losses arise almost exclusively among exotic species and in artificial forest ecosystems like ornamental conifer plantings, wind-breaks and Christmas tree plantations. *B. xylophilus* is widespread in natural coniferous forests but significant losses are not recorded.

• Monochamus spp.

Monochamus larvae can cause economic losses to felled logs by forming bore holes in the wood. This is normally only of significance if the logs are left for a long time in the forest after felling. Under well-managed forest conditions, *Monochamus* spp. are not generally considered to be serious pests in their own right. Thus, the only economic impact arises in countries where *B. xylophilus* is present and damaging and the *Monochamus* species concerned transmit it.

Control

So far it has proved impossible to control *B. xylophilus* once introduced into a tree. Therefore, control of pine wilt disease in Japan has concentrated on a combination of cultural practices, in removing dead or dying trees from the forest to prevent their use as a source of further infection, and the control of the vector beetles by insecticidal treatment. The Japanese government has spent large amounts of money on extensive control programmes involving aerial spraying and removal of diseased trees (Ikeda, 1984). In the case of individual trees with a particular significance (e.g. religious), infection can be prevented by a prophylactic chemical treatment. Research is continuing to try to find alternative means of control, such as biological control agents for both nematodes and vectors, insect attractants, breeding of resistant *Pinus* clones, and inducing resistance by inoculation of non-pathogenic strains of *B. xylophilus*.

Phytosanitary risk

B. xylophilus and its vectors are listed as A1 quarantine pests by EPPO (OEPP/EPPO, 1986). The risk of introduction into the EPPO region has been discussed by several authors (including Magnusson, 1986; McNamara & Stoøen, 1988; Skwiercz, 1988). Evans et al. (1996) prepared a detailed analysis of the risk of *B. xylophilus* to the European Union. European Pinus species have proved very susceptible in North America and the introduction of B. xylophilus into Europe is considered to present a very serious risk. Several species of Monochamus are present in Europe and have already been shown to transmit the closely related B. mucronatus (Tomminen, 1990). In view of the non-specific nature of the phoretic relationship between Monochamus and Bursaphelenchus spp., it is probable that these European species would transmit B. xylophilus. Since the disease is favoured by hot summers, the southern areas are most threatened. Japanese experience suggests that an epidemic could spread from such areas to climatically less favourable areas provided susceptible tree species are present. Direct introduction of the nematode into northern Europe certainly also presents a risk, since symptoms could be expressed when trees suffer from any other form of stress (e.g. drought or occasional periods of high temperatures). Furthermore, an introduction into northern Europe would eventually lead to spread to the more susceptible southern areas.

The threat from *Monochamus* spp. is that they could carry *B. xylophilus* on entry. For this reason, the risk arises for the species from North America (see Table 1) and from the Far Eastern countries where *B. xylophilus* occurs (especially Japan). *M. alternatus*, the main vector in Japan, occurs in several Asian countries where the nematode is present. *M. saltuarius*, which is a known vector in Japan (Table 1), and M. urussovi which occurs in Japan but is not known to be a vector, have very wide ranges across northern Asia to Europe, but do not overlap in geographical distribution with B. xylophilus over this range. Other species occurring in Europe and Asia (*M. galloprovincialis*, *M. sutor*) do not overlap in geographical distribution with B. xylophilus at all. In principle, such species present no risk. However, there is a continuing risk that *B. xylophilus* will extend its range naturally in eastern Asia, and at a future date come into contact with these potential vectors.

PHYTOSANITARY MEASURES

EPPO's recommendations to prevent the introduction of *B. xylophilus* and its vectors cover plants and wood of all conifers, apart from *Thuja plicata*, from countries where the nematode occurs. It is recommended that coniferous

plants should be prohibited but that countries may choose whether to prohibit wood. If not prohibited, wood must have been heat treated to a core temperature of 56°C for 30 minutes. In the case of packing wood (crates, dunnage etc.), kiln drying could be accepted instead, whereas for particle wood, the alternative of fumigation is also acceptable.

Several quarantine treatments for wood chips have been proposed, such as steam/heat treatment or fumigation in transit with phosphine (Kinn, 1986). Such treatment can be expensive in relation to the value of the commodity. The main risk of infection of cut timber is in the period between felling and removal from the forest. Cut logs can be protected from oviposition (and thus from introduction of nematodes) by chemical treatment but such treatment is more effective in killing the insect larvae already present under the bark; in the latter case, the treatment is too late to prevent nematode infection. Other means of reducing the risk of attack are to cover logs after felling, to leave trap logs exposed nearby and to ensure that the felling is conducted outside the flight period of the beetles (Dominik, 1981; Raske, 1973).

The only known effective treatment for wood already infected with *B. xylophilus* and its vectors appears to be heat treatment, in which all parts of the wood reach a temperature

of 56°C for at least 30 min; commercial kiln practices normally achieve this. Inspection of timber does not always reveal the presence of insect larvae or pupae, which can be hidden within internal galleries.

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Monochamus species	Geographical distribution	Main hosts	Vector status
North America			
M. carolinensis	USA (eastern half),	Pinus	+
Olivier	Canada (east & US border), Mexico(north central)		
<i>M. clamator</i> LeConte	USA (west coast), Canada (British Columbia)	Pinus contorta	-
M. marmorator	USA, Canada	Abies, Picea	+
Kirby			
M. mutator	USA, Canada	Pinus	+
LeConte (syn. <i>M</i> .			
<i>maculosus</i> Haldeman)			
<i>M. notatus</i> (Drury)	USA, Canada	Pinus strobus	_
<i>M. obtusus</i> (Drury) <i>M. obtusus</i> Casey	USA (west coast), Canada	Pinus, Abies,	+
	(British Columbia)	Pseudotsuga	
M. rubigeneus	USA (south), Mexico,	Pinus	-
Bates	Guatemala, Honduras		
M. scutellatus Say	Eastern North America	Pinus, Picea, Abies,	+
subsp. scutellatus	(including parts of Mexico)	Larix	
M. scutellatus	USA (west coast), Canada	Picea	-
subsp. <i>oregonensis</i>	(British Columbia)		
LeConte	```'		
M. titillator	USA (centre, east & south-	Pinus, Abies, Picea	+
(Fabricius)	east), Canada (Ontario)		

Table 1. Monochamus species from coniferous trees, known to be vectors ofBursaphelenchus xylophilus or considered to be potential vectors

Monochamus species	Geographical distribution	Main hosts	Vector statu
Palaearctic region	(overlapping <i>B. xylophilus</i>))	
<i>M. alternatus</i> Hope	Japan, Korea Republic, Taiwan, Hong Kong, Lao, China (Anhui, Guangdong, Hunan, Jiangsu, Shandong, Zhejiang, i.e. east & centre)	Pinus, Cedrus, Abies, Picea, Larix	+
<i>M. nitens</i> Bates	Japan	Pinus	+
<i>M. saltuarius</i> Eschscholz	Japan, China (Heilongjiang; NE) Siberia, Lithuania, central & eastern Alps, central & eastern Europe and south to Italy	Picea	+
<i>M. tesserula</i> White	Japan, China	Pinus	-
<i>M. urussovii</i> (Fischer) (syn. <i>M.</i> <i>rosenmuelleri</i> Cederhielm)	Japan, China (Liaoning, Heilongjiang, Neimenggu; i.e. NE) Siberia, Russia (Caucasus), Finland, Poland	Abies, Larix, Picea, Pinus	-
Palaearctic region	(not overlapping B. xyloph	ilus)	
M. galloprovincialis (Olivier)	Portugal, North Africa, Italy, France, Greece, Germany, Poland, Sweden, Finland, Russia (European), Siberia	Pinus	-
<i>M. sartor</i> Fabricius	Central Europe (eastern France to western Ukraine)	Picea, Pinus	-
<i>M. sutor</i> (Linnaeus)	China (Heilongjiang, Liaoning; NE), Siberia, Russia (European), Georgia, the Nordic countries, central & eastern Europe, the Pyrenees, Alps	Pinus, Picea, Larix	-