Chapter 18

PARASITOIDS, PREDATORS, NEMATODES AND PATHOGENS ASSOCIATED WITH BARK WEEVIL PESTS

M. KENIS[1], R. WEGENSTEINER[2] & C. T. GRIFFIN[3]

[1]*CABI Bioscience Switzerland Centre, 2800 Delémont, Switzerland*
[2]*BOKU – University of Natural Resources & Applied Life Sciences, Vienna, Institute of Forest Entomology, Forest Pathology & Forest Protection, A-1190 Wien, Austria*
[3]*National University of Ireland, Maynooth, Co. Kildare, Ireland*

1. INTRODUCTION

Among the main bark weevil pests in Europe, *Hylobius abietis* L. and *Pissodes* spp. have been thesubject of several major studies regarding the biology, impact and use of their natural enemies. In particular, parasitoids and nematodes of *H. abietis*, and parasitoids of pine and fir *Pissodes* spp. have been extensively studied. In contrast, very little has been done on *Cryptorrhynchus lapathi L.*, and nothing on *Hylobius pinastri* (Gyllenhal), or on *Otiorrhynchus* spp. in the forest environment, probably reflecting their lower importance in forest protection.

2. *HYLOBIUS ABIETIS*

2.1. Parasitoids

Compared to other bark and wood boring insects, *H. abietis* has a very limited parasitoid complex. Eight to ten parasitoid species are recorded from the weevil, but no single study on the life history of *H. abietis* mentioned more than three parasitoids (e.g. Munro 1929; Hanson 1943; Elton *et al*. 1964; Gerdin and Hedqvist 1985; Henry 1995) (Table 1). This restricted parasitoid complex is probably due to the fact that larvae are concealed beneath soil and thick bark and, thus, are not accessible to polyphagous parasitoids attacking other bark weevils or bark beetles in conifers.

F. Lieutier et al. (eds), Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis, 395—414.

Table 1. Parasitoids recorded in the literature from Hylobius abietis *and their biology. Names in bold refer to frequent parasitoids reported from a least three different studies. Other names were mentioned in only one study. References are in the text..*

	Biology
Hym. Braconidae	
Allodorus lepidus (Haliday)	Egg-larval koinobiont endoparasitoid ?
Aspilota sp.	Adult endoparasitoid, very unlikely record. See text
***Bracon hylobii* Ratzeburg** [1]	Larval idiobiont ectoparasitoid
***Perilitus areolaris* Gerdin & Hedqvist**[2]	Adult endoparasitoid
Hym. Ichneumonidae	
***Dolichomitus tuberculatus* (Geoffroy)**	Larval (and pupal?) idiobiont ectoparasitoid
Stenarella gladiator (Scopoli)	Unknown, but very unlikely record. See text
Hym. Pteromalidae	
Tomicobia sp.	Adult endoparasitoid
Dipt. Phoridae	
Megaselia plurispinulosa Zetterstedt	Larval koinobiont endoparasitoid ?

[1] Some records as *Bracon brachycerus* Thomson, probably a misidentification
[2] Some records as *Perilitus rutilus* (Nees), probably a misidentification

Adults are commonly attacked by *Perilitus areolaris* Gerdin and Hedqvist (Hym.: Braconidae) (Gerdin and Hedqvist 1985; Starý *et al*. 1988). Earlier studies mentioned *Perilitus rutilus* (Nees) as parasitoid of *H. abietis* adults (e.g. Schindler 1964; Novák 1965; Slizynski 1969), but recent taxonomic studies (Starý *et al*. 1988; Haeselbarth 1999) suggested that *P. rutilus* was a misidentification of *P. areolaris*, which is known only from *H. abietis*, whereas *P. rutilus* is a parasitoid of weevils of the genera *Sitona* and *Phytonomus*. Schindler (1964) provides data on the life cycle of *P. areolaris* (as *P. rutilus*) in Germany. The parasitoid has two generations per year on *H. abietis*. It overwinters as a larva, in the adult weevil or in a cocoon. One to nine specimens emerge from a single host. Impact on beetle populations is difficult to measure for adult parasitoids. Schindler (1964) found 1-4% parasitism in field-collected samples in Germany, and Novák (1965) 15-16% in Czechoslovakia but, given the long life span of beetles, the short life of parasitized beetles and the two generations per year of parasitoids, the percentage of beetles eventually killed by the parasitoid is probably much higher. Further details on the biology of *P. areolaris*, such as larval development, mating and oviposition behaviour, are given in Slizynski (1969) and Gerdin and Hedqvist (1985). Schindler (1964) mentions *Aspilota* sp. (Hym.: Braconidae) as a rare parasitoid of adult *H. abietis*, but this record is very dubious because *Aspilota* species are known to parasitise Phoridae (Diptera). Långström (1972) also observed two parasitoids of adult *H. abietis* in Finland, *Pygostolus* sp. (Hym.: Braconidae) and *Tomicobia* sp. (Hym.: Pteromalidae). Since only larvae were obtained, *Pygostolus* sp. may be a misidentification for *Perilitus areolaris*. *Tomicobia* spp. are known parasitoids of Scolytidae and Curculionidae, but have not been reported elsewhere from *H. abietis*.

H. abietis larvae are attacked by at least two parasitoids, *Dolichomitus tuberculatus* (Geoffroy) (Hym.: Ichneumonidae) and *Bracon hylobii* Ratzeburg (Hym.: Braconidae). *D. tuberculatus* has often been reared from *H. abietis*, but always at low level (e.g. Munro 1929; Hanson 1943). Little is known of the biology of this parasitoid on *H. abietis*. It has also been reared from the weevil *C. lapathi* (see below) and from Cerambycidae (Fitton *et al*. 1988; Kenis and Hilszczanski, chapter 21) and, as other *Dolichomitus* species, it is most certainly an idiobiont ectoparasitoid of mature larvae or pupae.

B. hylobii is by far the most important and the most studied parasitoid of *H. abietis*. It is a gregarious ectoparasitoid of *H. abietis* larvae. Females lay four to 12 eggs on the weevil larvae. Laboratory experiments showed that females laid more eggs and spent much more time on larger larvae than on smaller larvae. Only larvae heavier than 100 mg were parasitized (Henry and Day 2000). In the laboratory, females gave rise to a maximum of 93 offspring and up to 17 host larvae were parasitised by a single female (Henry 1995). *B. hylobii* has five larval instars (Munro, in Hedqvist 1958). The last larval instar builds a cocoon in which it overwinters. Pupation and adult emergence occur in spring. In the UK, it was observed causing 30% parasitism in pine (Munro 1929) and an average of 47 % in Sitka spruce (Henry and Day 2001), but has a non-uniform distribution within sites. It was long assumed that *B. hylobii* is able to attack only larvae that occur at the level of the ground (Hedqvist 1958) and, therefore, would be incapable of parasitizing the majority of larvae that live under the bark deeper in the soil. However, a recent study (Henry and Day 2001) showed that, on Sitka spruce in the UK, most host larvae were reachable by *B. hylobii*. Parasitized larvae were found at depths of up to 15 cm and, on average, occurred at greater depth than healthy larvae.

B. hylobii seems to be rather specific. The only other hosts known are weevils of the genus *Pissodes* (Hedqvist 1958). A closely related species, *Bracon brachycerus* Thomson has been reported from *H. abietis* (see Hedqvist 1958; Herting 1973,) but Hedqvist (1958) supposes that these were misidentificatons for *B. hylobii*.

The use of *B. hylobii* as a biological control agent has often been discussed. Munro (in Hedqvist 1958) was the first to suggest its use as a mean of control. More recently, Henry and Day (2000, 2001) proposed and tested several control methods involving augmentation or conservation of *B. hylobii*. Some 40,000 adult parasitoids were reared in the laboratory and released onto forest clear fells in their first two summers. Parasitism in these plots was three times higher than in control plots (Henry and Day, 2001). However, the prospects of using *B. hylobii* in inundative releases are limited by the high costs usually related to mass production of specific parasitoids. Henry and Day (2000, 2001) also suggest sylvicultural methods to increase the impact of *B. hylobii*, which could be used in combination with other control methods. For example, *B. hylobii* will lay fewer eggs on smaller larvae, thus parasitizing higher numbers of small larvae than large larvae. Therefore, they anticipate that increasing resistance in the larval weevils' feeding substrate may have not only a direct effect on weevil mortality but also an indirect effect through an increase in parasitism rate. Provision of food for parasitoid adults has also been suggested. Finally, some forest site conditions known to reduce the level of parasitism, such as brash heaped on site after felling and needle litter lying over bark, could be easily modified to favour the activity of *B. hylobii*. However, more studies are needed, particularly on host-location behaviour and on reproduction in the field, to properly assess the possible impact of these methods.

A few other larval parasitoids were mentioned on single occasions in the literature. *Allodorus lepidus* Haliday (Hym.: Braconidae) was cited by Györfi (in Herting 1973), but we have found nothing on the status and biology of this species. Bramanis (1930) mentions *Steranella gladiator* (Scopoli) (as *Mesostenus gladiator*) (Hym.: Ichneumonidae) on *H. abietis* larvae or pupae in pine stumps in Latvia, with a parasitism rate of 3.5%. This record is also doubtful because *Steranella* species are usually parasitoids of aculeate Hymenoptera. In Sweden, Trägardh (1931) observed *Megaselia plurispinulosa* Zetterstedt (Dipt.: Phoridae) on *H. abietis* larvae in spruce stumps. Up to 54% of the larvae were found parasitized in one sample, with about 8 to 10 phorid larvae per host. It remains to be seen, however, whether it is a true parasitoid or a scavenger, as are the great majority of Phoridae. However, it belongs to a genus which is known to include several parasitoids of various insect orders (Disney 1994). Furthermore, the structure of its mouthparts suggests a truly parasitic behaviour (Trägardh 1931).

2.2. Predators

Little is known of predators of *H. abietis*. Reviews by Escherich (1923), Eidmann (1974) and Leather *et al*. (1999) provide lists of possible vertebrate and invertebrate predators, but nothing is known of their actual impact. Several birds have been observed feeding on larvae and adults, among which woodpeckers seem to be the most important (Eidmann 1974). Many insect predators were encountered in and around pine stumps attacked by *H. abietis* (list in Leather *et al*. 1999) but only few were observed feeding on the weevil. Notable exceptions are *Laphria* sp. (Dipt.: Asilidae), which was observed attacking adults, several Carabidae and Elateridae (Coleoptera), feeding on larvae and adults, and fly larvae, possibly of the genus *Brachyopa* (Dipt.: Syrphidae) found beside cadavers in larval galleries (Escherich 1923). The feeding habit of *H. abietis* larvae probably protects them against generalist predators. However, larvae may be caught when migrating from one food source to another. Experiments showed that, during migration, larvae are vulnerable to carabid predators (Salisbury and Leather 1998). But the real impact of predators in the field still needs to be evaluated.

2.3. Pathogens

Up to now the occurrence of pathogens in *Hylobius abietis* and closely related *Hylobius* species has been poorly studied, in spite of the importance of these forest pest insects. In Europe some reports have focused on the occurrence and action of entomopathogenic fungi in *H. abietis* but few authors have reported the occurrence of Protozoa. Pathogens have not been better studied in other species of the genus *Hylobius*, including the North America species. A few papers have focused on entomopathogenic fungi, and only one on a protozoan disease (in *H. pales* (Herbst): Walstad *et al*. 1970, Walstad and Anderson 1971, Schabel 1976, 1978, Schabel and Taft 1988; in *H. rhizophagus* Millers: Goyer and Benjamin 1971).

The results of early attempts to use the entomopathogenic fungus *Beauveria bassiana* (Bals., Vuill.) against *H. abietis* in laboratory and field tests were not always in agreement, and some of them were not very promising (Novák and Samsinakova 1964, Samsinakova and Novák 1967, Waldenfels 1975). Investigations on the occurrence of entomopathogenic fungi in field populations of *H. abietis* showed that *B. bassiana* can be found in *H. abietis* adults (Gerdin, 1977). In laboratory experiments, *B. bassiana* was tested against adult *H. abietis* and it was shown that high temperatures (> 30°C) were unfavourable (compared to 13° and 23°C). Inoculation with spore suspension led to higher infection rates compared to inoculation with dry spore powder (Wegensteiner and Führer 1988). The same study showed that sustained contact with *B. bassiana*-treated spruce bark caused high infection rates, and even limited contact of beetles with *B. bassiana*-treated bark for three days resulted in 100% infection, but with a long survival time of beetles (81.8 days). A comparative study of the efficacy of *B. bassiana* and two *Beauveria brongniartii* (Sacc., Petch.) strains showed differences in incubation time but high infection rates with all tested isolates (Wegensteiner 1989). Inoculation of *H. abietis* via fortuitous contact with spores of *B. bassiana* or *B. brongniartii* on fungus-overgrown beetles resulted in short survival time and high infection rates. This observation indicates the importance of a host passage, which is known to increase virulence (Wegensteiner 1992).

Metarhizium anisopliae (Metschn., Sorokin) has been reported to be very effective against *H. abietis*, achieving 100% mortality within 9 days, but significant strain-dependent differences were found in *H. abietis,* as well as differences in susceptibility of *H. abietis* compared to other insect species (Markova and Samsinakova 1990, Markova 2000). Some of these authors have mentioned that the tough, thick cuticle of *H. abietis* can be an exceptional problem for the effectiveness of entomopathogenic fungi, at least in prolonging the time to host death.

Pathogens other than fungi are reported from adult beetles. *Gregarina hylobii* (Fuchs) was found in the midgut lumen of *H. abietis*, and *Ophryocystis hylobii* (Purrini & Ormieres) in the Malpighian tubules (Fuchs 1915, Geus 1969, Purrini and Ormieres 1982). *Nosema hylobii* (Purrini) was described from the cells of the midgut epithelium of *H. abietis* (Purrini 1981). All those investigations were basic studies and concentrated on populations in Germany. Nothing is known of the effects of these pathogens on their hosts.

2.4. Nematodes

There is little evidence that parasitic nematodes are an important cause of natural mortality of forest weevils, but entomopathogenic nematodes (Rhabditida:

Heterorhabditidae and Steinernematidae) have potential as inundative biological control agents of *Hylobius abietis*.

Nematodes from three orders (Tylenchida, Diplogasterida and Rhabditida) have been reported from *Hylobius abietis* larvae. Up to 10% of insects collected in Denmark harboured *Allantonema miribile* Leuckart (Tylenchida: Allantonematidae), a parasite of the body cavity (Bovien 1937), but Wülker (1923) reported that *A. miribile* was not particularly pathogenic to pine weevils. *Dirhabdilaimus leuckarti* Fuchs (Diplogasterida: Diplogasteroididae) was isolated from dead or moribund "white, flaccid" larvae of *H. abietis* in Sweden, but when cultured and tested in the laboratory was unable to cause disease in *H. abietis* larvae (Pye and Burman, 1977). *Diplogaster* sp. (Diplogasterida: Diplogasteridae) was found in almost half of the dead *H. abietis* larvae field-collected in Sweden, but could not be confirmed as the cause of death (Gerdin 1977). Most members of the genus feed on dead material.

Entomopathogenic nematodes (*Steinernema* spp. and *Heterorhabditis* spp.) are parasites of insects that normally kill the host and develop in the resulting cadaver. Their natural hosts include the soil-dwelling stages of many insect species. They are also in commercial use for the control of several insect pests worldwide. *Steinernema feltiae* Filipjev was isolated from *H. abietis* in the Czech republic (Mracek *et al*. 1993); both adult and larval weevils were infected (Z. Mracek, pers. comm.). Entomopathogenic nematodes may in certain circumstances result in epizootics (Peters 1996). Epizootics have not been reported in *H. abietis*, but up to 30% of *Hylobius pales* sampled in North Carolina were infected with a *Steinernema* sp. (Thomas 1970).

Due largely to their mutualistic association with entomopathogenic bacteria (*Xenorhabdus* spp. and *Photorhabdus* spp., respectively), *Steinernema* spp. and *Heterorhabditis* spp. can result in rapid death of their insect hosts, and mass production is possible on a large scale for inundative application (Burnell and Stock 2000; Gaugler 2002). They have several other attributes that make them suitable as biological control agents, including safety to humans, plants and non-target organisms, and active host finding by the infective juvenile (making cryptic hosts, such as pine weevil larvae in tree stumps, potential targets). Entomopathogenic nematodes are applied inundatively, and recycling in the host environment is of secondary importance.

Field trials against adult *Hylobius abietis* in Sweden and *H. congener* in Canada showed that treating young seedlings with *Steinernema* spp. reduced damage due to adult weevils (Pye and Pye 1985; Eidt *et al*. 1995). However, extensive field trials in Scotland by the Forestry Commission using nematodes on containerised and bare root planting stock did not produce significant reduction in *H. abietis* feeding damage to the plants (Brixey 1997). Inadequate control of adult weevils might be due to failure of nematodes to survive at adequate numbers throughout the *Hylobius* feeding season, or may be accounted for by poor susceptibility of the adult weevils to entomopathogenic nematodes (a dose of 8,800 infective juvenile nematodes/insect was required to kill 50% of adult weevils (Collins 1993).

Early work in Sweden demonstrated the susceptibility of pine weevil larvae to *Steinernema carpocapsae* Weiser (Pye and Burman 1978) and preliminary field trials showed that application of this nematode had the potential to suppress numbers of weevils in stumps (Burman *et al*. 1979). In Scottish field trials, up to 70% of the population within treated stumps were infected and killed by nematodes (Brixey 1997). More extensive area-wide trials conducted in Scotland by the Forestry Commission confirm that *S. carpocapsae*, applied as a spot treatment to stumps, shows promise for area-wide suppression of *H. abietis* populations (S. Heritage, pers comm. 2002). Both the Swedish and Scottish work has concentrated largely on a single species of nematode, *S. carpocapsae*. In recent trials in Ireland, *Heterorhabditis downesi* Stock, Griffin and Burnell was the most successful of four nematode species tested in reducing numbers of adult pine weevil emerging from treated pine stumps (Dillon 2003). Stumps treated with this nematode produced an average of 8 adult weevils compared to 146 emerging from untreated stumps. Entomopathogenic nematodes on their own are unlikely to provide adequate control of pine weevil populations, but they may form an important component of an integrated pest management system for this pest.

3. *PISSODES* SPP.

3.1. Parasitoids

In the last 40 years, several extensive studies have been published on parasitoids of five of the eight European *Pissodes* spp. The pine trunk species *Pissodes castaneus* De Geer was studied by Alauzet (1982, 1987), Mills and Fisher (1986), Kenis and Mills (1994, 1998), Kenis *et al*. (1996) and Kenis (1996, 1997). Parasitoids of the two other pine trunk species, *P. pini* (L.) and *P. piniphilus* (Herbst) were investigated by Mills and Fisher (1986), Kenis and Mills (1994, 1998) and Kenis *et al*. (1996). The parasitoid complex of the fir trunk species *P. piceae* (Illiger) was studied by Haeselbarth (1962), Mills and Fisher (1986), Kenis and Mills (1994, 1998) and Kenis *et al*. (1996). *P. validirostris* (Salhberg), inhabiting pine cones, was the target of important studies by Annila (1975), Roques (1975), Mills and Fisher (1986), Kenis and Mills (1994, 1998), Kenis *et al*. (1996) and Kenis (1996, 1997). In contrast, very little has been done on the parasitoid complex of spruce trunk species, *P. harcyniae* (Herbst), *P. scabricollis* Miller and *P. gyllenhali* Gyllenhal, apart from some old parasitoid records (e.g. Lovaszy 1941; Zinovev 1958). However, unpublished data on parasitoids of *P. harcyniae* are provided in Table 2.

Table 2 shows the parasitoid complex of *Pissodes* spp. in Europe. *P. validorostris*, a pest of pine cones, is included in this review for comparison with congeneric species attacking conifer trunks. Only larval or pupal parasitoids are known. In all *Pissodes* spp., parasitism is usually dominated by braconids of the genera *Eubazus* and, to a lesser extent, *Coeloides*. In *Pissodes castaneus* however, the ichneumonid *Dolichomitus terebrans* (Ratzeburg) or the pteromalids *Rhopalicus tutela* (Walker) and *R. guttatus* (Ratzeburg) are occasionally more abundant than the braconids (Kenis and Mills, 1994). In general, parasitism on *Pissodes* spp. is higher than in other bark and wood boring beetles. Parasitism rates above 50% are common, whereas such high levels are rarely observed in Scolytidae, Cerambycidae or *Hylobius abietis*. These high rates can be explained by the accessibility of *Pissodes* eggs and larvae. Most parasitism is due to the egg-larval koinobiont parasitoids *Eubazus* spp. which have easy access to eggs in *Pissodes* feeding holes. Such egg-larval parasitism rarely afflicts Scolytidae, the eggs of which are hidden in galleries. The other parasitoids are all larval idiobiont ectoparasitoids and are usually also known from other bark and wood beetles. However, larvae of *Pissodes* weevils are particularly accessible because of their large size -compared to other bark beetles- and their proximity to the bark surface -compared to wood boring beetles.

The biology, ecology and taxonomy of the braconids *Eubazus* spp. and *Coeloides* spp. have been the focus of several studies. *Eubazus* spp. were investigated in detail by Haeselbarth (1962) on *P. piceae*, by Alauzet (1987) on *P. castaneus*, by Annila (1975), by Roques (1975) on *P. validirostris* and by Kenis *et al.* (1996) and Kenis and Mills (1998) on all *Pissodes* spp. *Eubazus* spp. attacking *Pissodes* spp. are specific to this genus and, perhaps, to the genus *Magdalis* (Achterberg and Kenis, 2000). They lay their eggs in *Pissodes* eggs, develop inside the host larva, and kill their host in the prepupal stage. Then, they build a cocoon in which to pupate under the bark or in the cone. Until recently, the taxonomy of the genus *Eubazus* was confusing. Several species had been described in the past, in many genera (*Eubadizon*, *Brachistes*, *Allodorus*, *Calyptus*), but many studies on *Pissodes* parasitoids had suggested that a single species attacks all European *Pissodes* spp. (Haeselbarth 1962; Annila 1975; Roques 1975; Alauzet 1982; Mills and Fisher 1986). Very recently, Kenis and his co-workers (Kenis *et al*. 1996; Kenis and Mills 1998) used morphometric, molecular and bio-ecological characters to show the occurrence of three sibling species, each of them being largely specialised in different hosts and microhabitats. *E. semirugosus* (Nees) is a parasitoid of those *Pissodes* spp. which develop in pine and spruce trunks, *E. robustus* (Ratzeburg) primarily attacks *P. validirostris* in pine cones and is occasionally found attacking *Pissodes* spp. in pine trunks, and the newly described species *E. abieticola* Achterberg and Kenis attacks only *P. piceae* in fir trunks. The taxonomy of the *Eubazus* spp. attacking *Pissodes* spp. throughout the world was revised by Achterberg and Kenis (2000). Interesting intraspecific variability in developmental responses was found in *Eubazus* spp. Mountain biotypes of *E. semirugosus* and *E. robustus* were found to have an obligatory diapause, in contrast to lowlands biotypes of the same species that were reared on the same hosts without diapause (Kenis *et al*. 1996). This variation is regarded as an adaptation to the phenology of their hosts in different climatic conditions. Indeed, the phenology of *Eubazus* populations is usually well synchronized with that of the corresponding *Pissodes* populations.

Three *Coeloides* spp. are found on *Pissodes* spp. (Haeselbarth 1967; Kenis and Mills 1994). *C. sordidator* (Ratzeburg), synonymous with *C. melanostigma* Strand and *C. stigmaticus* Hellén, is a major parasitoid of all pine-feeding *Pissodes* spp. It is also known from pine scolytids, cerambycids and buprestids (Haeselbarth 1967), but records from *Pissodes* spp. are much more frequent. In contrast, *C. abdominalis* (Zetterstedt) is a well-known parasitoid of pine bark beetles (Haeselbarth 1967; Mills 1983), but it has also been reared in sizeable numbers from *P. castaneus* and *P. pini* (Alauzet 1982, 1987; Kenis and Mills 1994). Finally, *C. forsteri* Haeselbarth is a rarer species, which has been reared exclusively from *P. pini*, *P. piceae*, *P. piniphilus* and *P. harcyniae* (Haeselbarth 1967; Kenis and Mills 1994). Details on the biology of *C. sordidator* are given in Annila (1975), Roques (1975), Alauzet (1987) and Kenis (1996, 1997). *C. abdominalis* was studied by Alauzet (1987) on *P. castaneus* and by Nuorteva (1957) on Scolytidae. The biology of *C. forsteri* on *P. piceae* was described by Haeselbarth (1962) as *Coeloides* sp. All *Coeloides* spp. are idiobiont ectoparasitoids of late instar larvae in feeding galleries. They paralyse and oviposit on *Pissodes* larvae through the bark. Parasitoid larvae develop quickly and build a cocoon in which they overwinter. One or two generations per year arerecorded by most authors, although Alauzet (1987) counted up to four generations in southern France. True diapause in *C. sordidator* was observed in the cocoon stage and was induced by short day photoperiod on the mother and by low temperature on larvae (Kenis 1997). In an attempt to develop rearing methods for *C. sordidator*, Kenis (1996) analysed the factors affecting sex ratio in laboratory rearing. Three factors were found to influence sex ratio: the host age, the age of ovipositing females, and the host of origin. Male-biased sex ratios were observed with young hosts, young females and with *C. sordidator* strains originally from *P. castaneus*. Female-biased sex-ratios were observed with older hosts, older females and with strains from *P. validirostris*. Competitive interactions between *C. sordidator* and *E. semirugosus* were studied by Kenis (1997). *C. sordidator* did not discriminate between healthy larvae and larvae containing *E. semirugosus* larvae suggesting that *C. sordidator*, and probably other ectoparasitoids, have a negative impact on *E. semirugosus* populations. Haeselbarth (1962) made similar observations with *Eubazus abieticola* and *Coeloides forsteri*.

Other braconids have occasionally been reported from *Pissodes* spp. *Bracon* spp. were reared from *P. piceae*, *P. pini* and *P. castaneus*. (Frediani, 1957, Haeselbarth 1962, Alauzet 1982; Kenis and Mills 1994). *B. palpebrator* Ratzeburg, *B. praetermissus* Marshall and *B. hylobii* have been mentioned as species, but the genus is in need of revision. Another species, *Spathius rubidus* (Rossi), was also reared in low numbers from *P. castaneus*, *P. pini* and *P. validirostris* (Annila 1975; Roques 1975; Alauzet 1982; Kenis and Mills 1994, M. Kenis, unpublished)

The ichneumonid *Dolichomitus terebrans* (Ratzeburg) is frequently associated with *P. castaneus* and has also been reared from *P. harcyniae*, *P. pini*, *P. piniphilus* and *P. piceae*. The few observations available on the parasitoid complex of *P. harcyniae* suggest that *D. terebrans* is a dominant species in this complex. It is also known from the scolytid *Dendroctonus micans* (Kugelann) (Gregoire 1976) as well as from several microlepidoptera (Aubert 1969), but several of these records may result from identification errors. In North America, a sub-species, *D. terebrans nubilipennis* (Viereck), occurs, which seems to be restricted to *Pissodes* spp. (Carlson 1979). *D. terebrans* is an ectoparasitoid attacking larvae, prepupae or pupae in pupal cells. In *P. validirostris*, it is replaced by three other pimpline ichneumonids, *Exeristes ruficollis* (Gravenhorst), *Scambus sudeticus* (Glowacki) and *S. sagax* (Hartig) (Roques 1975; Kenis and Mills 1994). A recent paper (Starzyk 1996) provides a list of ichneumonids supposedly reared from *P. piceae* in Poland: *Baranisobas ridibundus* (Gravenhorst), *Coleocentrus caligatus* (Gravenhorst), *Scambus brevicornis* (L.) and *Atractodes* sp. Since none of these species are known to attack Curculionidae, these records have to be considered cautiously.

The pteromalids *Rhopalicus tutela* (Walker), *R. guttatus* (Ratzeburg) and *Metacolus unifasciatus* Foerster are ectoparasitoids on larvae in galleries and are frequently found on *P. castaneus*. *R. tutela* has also been occasionally found on *P. pini*, *P. piniphilus,* and *P. harcyniae* (Kenis and Mills 1994, Kenis, unpublished). *R. guttatus* was sometimes reared from pine cones (Hedqvist 1963; Roques 1975), suggesting that it also attacks *P. validirostris*. However, Roques (1975) found it mainly in cones attacked by *Dioryctria mutatella* Fuchs (Lep.: Pyralidae). *M. unifasciatus* is usually associated with pine scolytids whereas *R. tutela* is a polyphagous species attacking a large number of bark beetle species (Mills 1983) and its abundance on *Pissodes* spp. probably depends on the density of its alternate hosts in the environment. Its biology, particularly host location mechanism, has been intensively studied on the scolytid beetle *Ips typographus* (L.) (e.g. Krüger and Mills 1990; Pettersson 2001; Pettersson et *al.* 2001).

Two species of *Eurytoma* spp. are reared from *Pissodes* spp. *Pissodes validirostris* is often heavily attacked by *E. annilai* Hedqvist (Annila 1975; Roques 1975). Roques (1976) showed that *E. annilai* (in Roques mentioned as *E. waachtli*) is a cleptoparasitoid of the ichneumonids *Scambus* spp. *E. annilai* and *E. wachtli* Mayr are occasionally reared from *P. castaneus*, but their biology is not known. Kenis and Mills (1994) suggest that they may act as clepto- or hyperparasitoids. An unidentified *Eurytoma* sp. has been reared in high numbers from *P. harcyniae* in Poland (M. Kenis, unpublished)

Two eupelmids, *Calosota aestivalis* Curtis and *Eupelmus urozonus* Dalman were reared from *P. castaneus* by Frediani (1957) (as *C. vernalis* Curtis) and Kenis and Mills (1994). Whereas Frediani describes them as primary parasitoids, Kenis and Mills reared them from cocoons of *D. terebrans* and *Coeloides* spp., respectively.

Finally, Alauzet (1982) mentions the tarsonemid mite *Pediculoides ventricosus* Newport as a parasite of *P. castaneus* pupae in southern France. However, its biology and incidence on *P. castaneus* have not been fully assessed.

High rates of parasitism observed in nearly all studies suggest an important impact on weevil populations. However, most studies on parasitoids were rather descriptive and no serious attempt has been made to evaluate the real impact of these parasitoids on the population dynamics of their hosts, or to develop methods to conserve or augment parasitoids. This perhaps reflects the relatively low importance of *Pissodes* spp. in European forestry compared to, e.g., bark beetles or *Hylobius abietis*. Ironically, the largest study on parasitoids of *Pissodes* spp. in Europe was carried out for the biological control project against the North American *Pissodes strobi*, a pest that is far more serious than any of its eight European congenerics (Kenis and Mills 1994; Hulme and Kenis 2002). Only two authors briefly explore the potential of parasitoids for the control of *Pissodes* spp. in Europe. Haeselbarth (1962) suggests that fir trees infested by *P. piceae* be cut in spring, between the emergence period of the parasitoids and that of the weevil. Annila (1975) suggests strategies to conserve parasitoids of *P. validirostris* in pine seed orchards in Finland.

Table 2. Parasitoids of Pissodes *spp. in Europe, with level of abundance: xxx = Dominant in at least two studies or samples, and present in >50% of the studies/samples; xx = Dominant in at least one study/sample or present in >50% of the studies/samples; x = Present in at least two studies/samples or reared for sure from Pissodes sp. by M. Kenis. Based on reviews by Mills and Fisher (1985), Kenis and Mills (1994) and unpublished surveys by M. Kenis from 1993-1998.*

		Pissodes species					
Parasitoid species	Biology[1]	*castaneus*	*pini*	*piniphilus*	*validirostris*	*piceae*	*harcyniae*
Hym.: Ichneumonidae							
Dolichomitus terebrans (Ratzeburg)	L. ec.	xxx	x	x		x	xxx
Exeristes ruficollis (Gravenhorst)	L. ec.				x		
Scambus sagax Hartig	L. ec				x		
Scambus sudeticus (Glowacki)	L. ec.				xx		
Hym.: Braconidae							
Bracon hylobii Ratzeburg	L. ec.			x		x	
Bracon praetermissus Marshall	L. ec.		x				
Undetermined *Bracon* spp.	L. ec.	x	x	x			
Coeloides abdominalis (Zetterstedt)	L. ec.	x	x				
Coeloides forsteri Haeselbarth	L. ec.		x	x		x	xx
Coeloides sordidator (Ratzeburg)	L. ec.	xxx	xx	xxx	xx		
Eubazus abieticola Achterberg & Kenis	E.-L. en.					xxx	
Eubazus robustus (Ratzeburg)	E.-L. en.	x		x	xxx		
Eubazus semirugosus (Nees)	E.-L. en.	xxx	xxx	xxx			xxx
Spathius rubidus (Rossi)	L. ec.	x	x		x		
Hym.: Pteromalidae							
Metacolus unifasciatus Foerster	L. ec.	xx					
Rhopalicus guttatus (Ratzeburg)	L. ec.	xx	x		x	x	
Rhopalicus tutela (Walker)	L. ec.	xx	x	x			xx
Hym.: Eupelmidae							
Calosota aestivalis Curtis	L. ec. (h)	x					
Eupelmus urozonus Dalman	L. ec. (h)	x					
Hym.: Eurytomidae							
Eurytoma annilai Hedqvist	*L. ec.*	x			x		
Eurytoma wachtli Mayr	*L. ec.*	x					
Undetermined *Eurytoma* spp.	L. ec.		x				xx
Acari: Tarsonemidae							
Pediculoides ventricosus Newport	*P. ec.*	x					

[1] Biology: L. ec. = Larval idiobiont ectoparasitoid; E.-L. en. =Egg-larval koinobiont endoparasitoid; P. ec. = Pupal ectoparasite; h = Facultative hyperparasitoid.

Should new control methods against *Pissodes* spp. be needed, the biology and ecology of *Pissodes* parasitoids are sufficiently known to apply this knowledge to the development of control methods. Similarly, this knowledge could be useful in case a European *Pissodes* species becomes invasive in another part of the world, such as *P. castaneus* which was introduced into Uruguay and Argentina (Abgrall *et* *al*. 1999). Then, some parasitoids, in particular the specific *Eubazus* spp., could be considered as valuable control agents.

3.2. Predators, nematodes and pathogens

Other natural enemies of *Pissodes* spp. have been studied in much less details than parasitoids. Undoubtedly, the most important predators are woodpeckers. These are particularly important for the large species *P. piceae* and *P. pini* attacking mature fir and pine trees. Quantifying their impact is difficult, but Haeselbarth (1962) suggests that, often, over 50% of overwintering larvae of *P. piceae* are destroyed by woodpeckers. Nuorteva and Saari (1980) observed similar damage on *P. pini* larvae overwintering in their pupal cell. Fir, pine and spruce trunks debarked by woodpeckers are a good indication of the presence of *Pissodes* spp. (M. Kenis, unpublished).

Insect predators are not considered important mortality factors in European *Pissodes* spp. in contrast to North America, where *Lonchaea corticis* Taylor (Dipt.: Lonchaeidae) is the main natural enemy of *Pissodes strobi* (Peck) (Hulme and Kenis 2002). Alauzet (1982) mentions *Thanasimus formicarius* (L.) feeding occasionally on young, emerging adults, whereas eggs and feeding larvae are difficult to reach. *T. formicarius* has been extensively studied as a predator of bark beetles (Kenis, Wermelinger and Grégoire, chapter 11). Lonchaeid flies (Haeselbarth 1962), *Nudobius lentus* (Gravenhorst) (Col.: Staphylinidae) and *Xylophagus cinctus* (De Geer) (Dipt.: Xylophagidae) (Starzyk 1996) were found attacking *P. piceae*, but nothing is known of their importance.

Tylenchid nematodes of the genera *Sphaerulariopsis* (Sphaerularidae) and *Neoparasitylenchus* (Allantonematidae) (Siddiqui 2000) are associated with *Pissodes* spp. It is notable that these genera also parasitise bark beetles, in which they may cause pathological effects (Kaya 1984). Other authors reported nematodes in *Pissodes* larvae and adults (e.g. Haeselbarth 1962), but nothing is known of the impact of these nematodes. The potential of entomopathogenic nematodes as a biological control agent for European *Pissodes* species has received little attention, but Laumond *et al.* (1979) showed that *Pissodes castaneus* larvae and pupae were very susceptible to *Steinernema carpocapsae* in the laboratory.

Dead larvae, pupae and teneral adults are sometimes found covered by fungi (Haeselbarth 1962; M. Kenis, unpublished), but their identity and role in weevil mortality has never been investigated. In contrast, dead larvae have often been observed enveloped in the growing mycelium of *Armillaria* spp., in particular in *P. piceae* (Starzyk 1996) and *P. castaneus* (M. Kenis, unpublished). Inundative biological control using pathogens has never been tested against *Pissodes* spp. in Europe.

4. *CRYPTORHYNCHUS LAPATHI*

To our knowledge, no specific studies have focused on the natural enemy complex of *C. lapathi*. Old parasitoid records are summarised in Szalay-Marzsó (1962) but, among the dozen parasitoid species listed in this publication, most are impossible to accept as parasitoids of *C. lapathi*. The only investigations on the life history of *C. lapathi* and its parasitoids are found in Strojny (1951), who described the oviposition behaviour of the ichneumonid *Dolichomitus tuberculatus* (Geoffroy) on *C. lapathi* larvae in willow branches, and in Szalay-Marszó (1962), who briefly described parasitism by the ichneumonid *Perosis* sp. (probably, but not certainly, *Schreineria* sp.) on 5th instar larvae. But there is no information on the abundance of these parasitoids. Since the review of Szalay-Marzsó (1962), only Schimitschek (1964) mentioned the braconid *Bracon immutator* Nees, var. *austriaca* Fahringer, as a larval parasitoid, but does not provide any data on its abundance and biology.

Szalay-Marzsó (1962) also briefly mentions predation by tits on adults, and by woodpeckers on larvae. Nothing is known about pathogens or nematodes under natural conditions; however, the potential of entomopathogenic nematodes for the control of *Cryptorhynchus lapathi* was tested by Cavalcaselle and Deseo (1984).

5. *OTIORRHYNCHUS* SPP.

No studies have focused on natural enemies of *Otiorrhynchus arcticus* Germar and *O. nodosus* (Müller), the two species of this large genus considered as seedling pests in northern Europe. However, information on their potential natural enemy complex can be gathered from the numerous data on natural enemies of other *Otiorrhynchus* spp. in horticulture. Lists of parasitoids are found in Herting (1973), Tschorsnig and Herting (1994) and Noyes (2001). Parasitoids of adult weevils belong to the genera *Perilitus* and *Pygostolus* (Hym.: Braconidae), *Dirhicnus* and *Tomicobia* (Hym.: Pteromalidae), *Pandelleia*, and *Rondania* (Dipt.: Tachinidae), and *Megaselia* (Dipt.: Phoridae). Predators are reviewed by Herting (1973) and include the genera *Cerceris* (Hym.: Sphecidae), *Broscus* and *Carabus* (Col.: Carabidae), *Hister* (Col.: Histeridae) and *Formica* (Hym.: Formicidae). In general, the parasitoid and predator complexes of *Otiorrhynchus* spp. are rather limited, and no attempt has been made to use these natural enemies as biological control agents.

In contrast, parasitic nematodes are important natural enemies of *Otiorrhynchus* spp. In Finland, natural populations of *Steinernema feltiae* killed 20% of *Otiorrhynchus dubius* (Ström) and *O. ovatus* (L.) larvae in strawberries (Vainio and Hokkanen 1993). Natural infections of *O. sulcatus* by entomopathogenic nematodes (*Steinernema carpocapsae S. feltiae* and *Heterorhabditis megidis* Poinar, Jackson and Klein have also been reported (Poinar 1986; Peters 1996). Numerous trials have demonstrated the success of entomopathogenic nematodes for the control of *Otiorrhynchus* spp. (particularly *O. sulcatus* (F.)) infesting hardy ornamentals and soft fruits (e.g. Klingler 1988; Landi 1990; Deseo and Costanzi 1987; Mracek *et al*. 1993; Fitters *et al*. 2001), and several nematode-based products are sold for this purpose. Trials in Ontario demonstrated the potential of heterorhabditids for control of *O. sulcatus* and *O. ovatus* in forest nurseries, provided soil temperatures were adequate (Rutherford *et al*. 1987). Considering the success of parasitic nematodes against *Otiorrhynchus* spp. in horticulture, it would be highly desirable to evaluate their potential against *O. arcticus* and *O. nodosus* in nurseries and plantations in northern Europe.

The main pathogens reported from *Otiorrhynchus* species (*O. ligustici* (L.), *O. ovatus, O. dubius*, *O. sulcatus*) are entomopathogenic fungi, which can be found in both larvae and adults of field populations, in some cases at high incidence (Marchal 1977, 1989). Therefore, the potential of such fungi to control *Otiorrhynchus* was tested: *Metarhizium anisopliae* and *Beauveria brongniartii* caused highest mortality of weevil larvae in laboratory and field tests (Workshop of the IOBC Study Group "Insect Pathogens and Insect-parasitic Nematodes" 1987 in Versailles 1989). *B. brongniartii* was reported to cause high mortality (up to 100%) of *O. sulcatus* in the lab and in the greenhouse (Coremanns-Pelseneer and Nef 1986, Tillemans *et al*. 1987). Various *M. anisopliae* strains were found to be effective (62% to 100% mortality) against *O. sulcatus* larvae in ornamentals (Zimmermann 1981, Sellenschlo 1984, Gillespie and Moorehouse 1989, Moorhouse *et al*. 1993a, 1993b). In addition, *M. anisopliae* was found to be also very effective under field conditions against *O. ovatus* and *O. dubius* larvae, whereas *B. bassiana* was less effective (Vainio and Hokkanen 1993). All of these results indicated the potential of entomopathogenic fungi for control of pest weevils in ornamentals, nurseries and various agricultural crops; today there are several commercial products on the market.

6. CONCLUSIONS

The information available on natural enemies of bark weevil pests in Europe varies with pest species and natural enemy category. The best studied systems are parasitoids of *Hylobius abietis* and *Pissodes* spp. The parasitoid complex of these insects is well known and the biology and ecology of their main parasitoids have been extensively studied. However, the role of parasitoids and other natural enemies in regulating weevil populations remains unclear. The impact of parasitoids is likely to be higher in *Pissodes* spp. than in *H. abietis*. *Pissodes* weevils are unusual among bark and wood-boring insects by suffering from high rates of parasitism. This is largely due to the specific egg-larval parasitoids *Eubazus* spp. Predators and pathogens have been less investigated. Even for the best studied systems, however, the impact and role of natural enemies on pest populations are not clearly understood.

Until now, little effort has been made to use these natural enemies in biological control programmes. Classical biological control, i.e. the introduction and establishment of an exotic natural enemy, has little prospect of success because the best targets for classical biological control are exotic pests whereas the main bark weevils in Europe are native. Inundative and conservation biological control are more promising strategies. Entomopathogenic nematodes and entomopathogenic fungi are used as biological pesticides against weevils in horticulture, and the techniques could be adapted to related forest pests. Particularly good targets would be *Otiorrhynchus* species and *H. abietis*. Promising results have already been achieved against *H. abietis* using entomopathogenic nematodes, but more research is needed before obtaining commercially competitive products. Parasitoids and predators show little prospects as inundative biological control agents because of the high production costs and the large areas involved in forestry. In contrast, sylvicultural methods could be developed, or modified, to enhance natural populations of parasitoids and predators, and increase their impact on the target pests. Such methods have already been suggested, in particular against *H. abietis*, but, so far, they have not been implemented.

7. ACKNOWLEDGEMENTS

We thank Mark Shaw and an anonymous reviewer for their useful comments on the manuscript. M. Kenis was supported by the Swiss Federal Office for Education and Science (project C99.0116).

8. REFERENCES

Abgrall, J.F., Villèn González, V., & Porcile, J.F. 1999. Estudios de investigación sobre gorgojo de los pinos (I parte). Peligro a la vista. Chile Forestal, 24, 9-13.

Achterberg, C. van, & Kenis, M. 2000. The Holarctic species of the subgenus *Allodorus* Foester s.s. of the genus *Eubazus* Nees (Hymenoptera: Braconidae). Zoologische Mededelingen Leiden, 73, 427-55.

Alauzet, C. 1982. Biocénose de *Pissodes notatus* F. ravageur des pins maritimes en forêt de Bouconne (Haute-Garonne: France). Nouvelle Revue d'Entomologie, 12, 81-89.

Alauzet, C. 1987. Bioécologie de *Eubazus semirugosus*, *Coeloides abdominalis* et *C. sordidator* (Hym. : Braconidae) parasites de *Pissodes notatus* (Col. : Curculionidae) dans le sud de la France. Entomophaga, 32, 39-47.

Annila, E. 1975. The biology of *Pissodes validirostris* Gyll. (Col., Curculionidae) and its harmfulness, especially in Scots pine seed orchards. Communicationes Instituti Forestalis Fenniae, 85, 1-95.

Aubert, J.F. 1969. *Les Ichneumonides Ouest-Palearctiques et leur Hôtes, I. Pimplinae, Xoridinae, Acaenitinae.* Alfortville, France: Quatres Feuilles Editeur.

Bovien, P. 1937. Some types of association between nematodes and insects. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kobenhavn, 101, 1-114.

Bramanis, L. 1930. Die Bedeutung der Kiefernstubben auf den Kahlschlägenfür die Entwicklung des Rüsselkäfers *Hylobius abietis* L. Folia zoologica et Hydrobiologica 1, 168-77. (Abstract in Review of Applied Entomology, 18, 695-96).

Brixey, J. 1997. The potential for biological control to reduce *Hylobius abietis* damage. Forestry Commission Research Information Note, 273.

Burman, M., Pye, A.E., & Nojd N.O. 1979. Preliminary field trial of the nematode *Neoaplectana carpocapsae* against larvae of the pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). Annales Entomologici Fennici, 45, 88.

Burnell, A.M., & Stock, S.P. 2000. *Heterorhabditis, Steinernema* and their bacterial symbionts - lethal pathogens of insects. Nematology, 2, 31-42.

Carlson, R.W. 1979. Ichneumonidae. In. *Catalog of Hymenoptera in America North of Mexico 1.* K.V. Krombein, P.D. Hurd, D.R. Smith, B.D. Burks (Eds.). Washington, D.C.: Smithsonian Institution Press.

Cavalcaselle, B., & Deseo, K.V. 1984. Prove di lotta conro le larve di insetti xilofagi del pioppo con nematodi entomopatogeni. Atti Giornate Fitopatologiche, 2, 393-402.

Collins, S. 1993. The potential of entomopathogenic nematodes to reduce damage by *Hylobious abietis L.* Ph.D Thesis, Universty of London, UK.

Coremanns-Pelseneer, J. & Nef, L. 1986. *Otiorrhynchus sulcatus* (Coleoptera): Larval control by the fungus *Beauveria* (first results). Mededelingen Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent, 51 (3a), 1049-56.

Deseo, K., & Costanzi, M. 1987. Impiego di nematodi entomoparassiti contro larve di curculionidi dannosa a coltore floricole ornamentali. *Difesa delle piante*, 10, 127-32.

Disney, R. H. L. 1994. *Scuttle Flies: the Phoridae*. Cambridge, UK: Cambridge University..

Dillon, A., 2003. Biological control of the large pine weevil, *Hylobius abietis* L., (Coleoptera, Curculionidae) using entomopathogenic nematodes. Ph.D Thesis, National University of Ireland, Maynooth, Ireland.

Eidmann, H.H. 1974. *Hylobius* Schönh. In. *Die Forstschädlinge Europas II. Käfer*. W. Schwenke (Ed.). Berlin: Paul Parey.

Eidt, D.C., Zervos S., Pye, A.E., & Finney Crawley, J.R. 1995. Control of *Hylobius congener* Dalle Torre, Shenkling, and Marshall (Coleoptera: Curculionidae) using entomopathogenic nematodes. Canadian Entomologist, 127, 431-38.

Escherich, K. 1923. *Die Forstinsekten Mitteleuropas, Band II*. Berlin: Paul Parey.

Elton, E.T.G., Blankwaardt, H.E.H., Burger, H.C., Steemers, W.F., & Tichelman, L.G. 1964. Insect communities in barked and unbarked pine stumps with special reference to the large pine weevil (*Hylobius abietis* L., Col., Curculonidae). Zeitschrift für Angewandte Entomologie, 55, 1-53.

Fitters, P.F.L., Dunne R., & Griffin C.T. 2001. Vine weevil control in Ireland with entomopathogenic nematodes: optimal time of application. Irish Journal of Agricultural and Food Research*,* 40, 199-213.

Fitton, M.G., Shaw, M.R., & Gauld, I.D. 1988. Pimpline Ichneumon-flies. Hymenoptera, Ichneumonidae (Pimplinae). Handbooks for the Identification of British Insects, 7 (1), 1-110.

Frediani, D. 1957. Su alcuni imenotteri pariti del *Pissodes notatus* F. nella Tuscana litoranea. Bolletino della Societa Entomologica Italiana 87, 92-97.

Fuchs, G. 1915. Die Naturgeschichte der Nematoden und einiger anderer Parasiten 1. des *Ips typographus* L., 2. des *Hylobius abietis* L. Zoologisches Jahrbuch, Abteilung für Systematik, 38, 109-222.

Gaugler, R. (Ed.) 2002. *Entomopathogenic nematology*. Wallingford, UK: CABI.

Gerdin, S. 1977. Observations on Pathogens and Parasites of *Hylobius abietis* (Coleoptera: Curculionidae) in Sweden. Journal of Invertebrate Pathology, 30, 263-64.

Gerdin, S., & Hedqvist, K.J. 1985. *Perilitus areolaris* sp. n. (Hymenoptera: Braconidae), an imago parasitoid of the large pine weevil, *Hylobius abietis* (Linnaeus) and its reproductive behaviour. Entomologica Scandinavica, 15, 363-69.

Goyer, R.A., & Benjamin, D.M. 1971. Infection of a Pine root weevil, *Hylobius rhizophagus*, by two muscardine fungi. Journal of Economic Entomology, 64 (2), 562.

Geus, A. 1969. Sporentierchen, Sporozoa. Die Gregarinida. In. *Die Tierwelt Deutschlands und der Angrenzenden Meeresteile*, 57. Teil. Jena, Germany: G. Fischer.

Gillespie, A., & Moorehouse, E. 1989. *Metarhizium anisopliae*: a promising biological control agent for black vine weevil, *Otiorrhynchus sulcatus*. IOBC/WPRS Bulletin, 14 (1), 53.

Grégoire, J.C. 1976. Note sur deux ennemis naturels de *Dendroctonus micans* Kug. en Belgique (Col. Scolytidae). Bulletin Annuel de la Société Royale d'Entomologie de Belgique, 112, 208-12.

Haeselbarth, E. 1962. Zur Biologie, Entwicklungsgeschichte und Oekologie von *Brachistes atricornis* Ratz. als eines Parasiter von *Pissodes piceae*. Zeitschrift für Angewandte Entomologie, 49, 233-89.

Haeselbarth, E. 1967. Zur Kenntnis der paläearktischen Arten der Gattung *Coeloides* Wesmael (Hymenoptera, Braconidae). Mitteilungen der Münchner Entomologischen Gesellschaft, 57, 20-53.

Haeselbarth, E. 1999. Zur Braconiden-Gattung *Perilitus* Nees, 1818. 2. Beitrag: Die Arten mit ausgebildetem ersten Cubitus-Abschnitt. Mitteilungen der Münchner Entomologischen Gesellschaft, 89, 11-46.

Hanson, H.S. 1943. The control of bark beetles and weevils in coniferous forests in Britain. Scottish Forestry Journal, 57, 19-45.

Hedqvist, K.J. 1958. Notes on *Bracon hylobii* Ratz. (Hym. Braconidae), a parasite of the pine weevil (*Hylobius abietis*). Annales Entomologici Fennici, 24, 73-83

Hedqvist, K.J. 1963. Die Feinde der Borkenkäfer in Schweden, 1. Erzwespen (Chalcidoidea). Studia Forestalia Suecica, 11, 1-176.

Henry, C.J. 1995. The effect of a braconid ectoparasitoid, *Bracon hylobii* Ratz., on larval populations of the large pine weevil, *Hylobius abietis* L. PhD thesis, University of Ulster, Coleraine, UK.

Henry, C.J., & Day, K.R. 2000. Egg allocation by *Bracon hylobii* Ratz., the principal parasitoid of the large pine weevil (*Hylobius abietis* L.) and implications for host suppression. Agricultural and Forest Entomology, 3, 11-18.

Henry, C.J., & Day, K.R. 2001. Biocontrol of the large pine weevil: structure of host (*Hylobius abietis* (L.)) and parasitoid (*Bracon hylobii* Ratz.) populations in felled stumps of Sitka spruce. IUFRO World Series Vol. 11, 1-12.

Herting, B. 1973. *A Catalogue of Parasites and Predators of Terrestrial Arthropods, Section A, Volume III, Coleoptera to Strepsiptera*. Farnham Royal, UK: Commonwealth Agricultural Bureaux.

Hulme, M.A., & Kenis, M. 2002. *Pissodes strobi* (Peck), White Pine Weevil (Coleoptera : Curculionidae). In. *Biological Control Programmes against Insects and Mites, Weeds, and Pathogens in Canada 1981-2000*. P. Mason, J. Huber (Eds.). Wallingford, UK: CABI.

Kaya, H.K. 1984. Nematode parasites of bark beetles. In. *Plant and insect nematodes*. W.R. Nickle (Ed.). New York: Marcel Dekker.

Kenis, M. 1996. Factors affecting sex ratio in rearing of *Coeloides sordidator* (Hymenoptera : Braconidae). Entomophaga, 41, 217-24.

Kenis, M. 1997. Biology of *Coeloides sordidator* (Hymenptera : Braconidae), a possible candidate for introduction against *Pissodes* strobi (Coleoptera : Curculionidae) in North America. Biocontrol Science and Technology, 7, 157-64.

Kenis, M., Hulme, M.A., & Mills, N.J. 1996. Comparative developmental biology of populations of three European and one North American *Eubazus* spp. (Hymenoptera: Braconidae), parasitoids of *Pissodes* spp. weevils (Coleoptera: Curculionidae). Bulletin of Entomological Research, 86, 143-53.

Kenis, M., & Mills, N.J. 1994. Parasitoids of European species of the genus *Pissodes* (Coleoptera: Curculionidae) and their potential for biological control of *Pissodes strobi* (Peck) in Canada. Biological control, 4, 14-21.

Kenis, M., & Mills, N.J. 1998. Evidence for the occurrence of sibling species in *Eubazus* spp. (Hymenoptera: Braconidae), parasitoids of Pissodes weevils (Coleoptera: Curculionidae). Bulletin of Entomological Research, 88, 149-63.

Klingler, J. 1988. Investigations on the parasitism of *Otiorrhynchus salicicola* and *O. sulcatus* [Col.: Curculionisdae] by *Heterorhabditis* sp. [Nematoda]. Entomophaga, 33, 325-31.

Krüger, K., & Mills, N.J. 1990. Observations on the biology of three parasitoids of the spruce bark beetle, *Ips typographus* (Col., Scolytidae), *Coeloides bostrichorum*, *Dendrosoter middendorffii* (Hym., Braconidae) and *Rhopalicus tutela* (Hym., Pteromalidae). Journal of Applied Entomology, 110, 281-91.

Landi, S., 1990. Possibilita di controllo biologico di *Otiorrhynchus* spp. su piante ornamentali in vivaio. Redia, 73, 261-73.

Långström, B. 1972. Snytbaggarnas (*Hylobius* spp., Col., Curculionidae) uppträdande på hyggen av varierande ålder och skogstyp i Finland 1970-1971. Licentiate-thesis at the Faculty of Forestry at the University of Helsinki, Finland. (In Swedish)

Laumond C., Mauléon H., & Kermarrec A. 1979. Données nouvelles sur le spectre d'hôtes et le parasitisme du nématode entomophage *Neoaplectana carpocapsae*. Entomophaga, 24, 13-27.

Leather, S.R., Day, K.R., & Salisbury, A.N. 1999. The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae): a problem of dispersal? Bulletin of Entomological Research, 89, 3-16.

Lovaszy, P. 1941. Zur Kenntnis der Schlupwespen einiger schädlicher Rüsselkäfer. Annales Entomologici Fennici, 7, 194-204.

Marchal, M. 1977. Fungi imperfecti isolés d'une population naturelle d'*Otiorrhynchus sulcatus* Fabr. (Col., Curculionidae). Revue de Zoologie Agricole et Pathologie Végétale, 76, 101-08.

Marchal, M. 1989. Endémisme des mycoses a *Beauveria bassiana* et *Metarhizium anisopliae* dans de populations naturelles d'*Otiorrhynchus sulcatus*. OILB/WPRS Bulletin, 12, 35.

Markova, G. 2000. Pathogenicity of several entomogenous fungi to some of the most serious forest insect pests in Europe. IOBC wprs Bulletin 23, 231-39.

Markova, G., & Samsinakova, A. 1990. Laboratory studies on the effect of the entomopathogenic fungus *Beauveria bassiana* on larvae of *Lymantria dispar*. Nauka za Gorata, 27, 81-84.

Mills, N.J. 1983. The natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. Biocontrol News and Information, 4, 305-28.

Mills, N.J., & Fischer, P. 1986. The entomophage complex of *Pissodes weevils*, with emphasis on the value of *P. validirostris* as a source of parasitoids for use in biological control. In. *Proceedings of the 2nd. International Conference IUFRO Cone and Seed Insects Working Party, Briançon, September 1986*. A. Roques (Ed.) Olivet, France: INRA.

Moorehouse, E., Gillespie, A., & Charnley, A. 1993a. The development of *Otiorrhynchus sulcatus* (Fabricius)(Coleoptera: Curculionidae) larvae on a range of ornamental pot-plant species and the potential for control using *Metarhizium anisopliae*. Journal of Horticultural Science, 68, 627-35.

Moorehouse, E., Gillespie, A., & Charnley, A. 1993b. Application of *Metarhizium anisopliae* (Metsch.) Sor. conidia to control *Otiorrhynchus sulcatus* (F.)(Coleoptera: Curculionidae) larvae on glasshouse plants. Annals of Applied Biology, 122, 623-36.

Mracek, Z., Jiskra K., & Kahouna L., 1993. Efficiency of steinernematid nematodes (Nematoda: Steinernematidae) in controlling larvae of the black vine weevil, *Otiorrhynchus sulcatus* (Coleoptera: Curculionidae) in laboratory and field experiments. European Journal of Entomology, 90, 71-76.

Munro, J.W. 1929. The biology and control of *Hylobius abietis* L. Part II. Forestry, 3, 61-65.

Novák, V. 1965. Beitrag zur Kenntnis der Fruchtbarkeit des brauen Rüsselkäfers (*Hylobius abietis* L.). P. 711. In. *Proceedings of the XII International Congress of Entomology, London 1964*. London UK.

Novák, V., & Samsinakova, A. 1964. Les essais d'application du champignon parasite *Beauveria bassiana* dans la lutte contre les parasites en agriculture et sylviculture en CSSR. Colloque International de Pathologie des Insectes, Paris 1962, 133-35.

Noyes, J.S. 2001. *Interactive Catalogue of World Chalcidoidea 2001*. CD Rom. Vancouver, Canada: Taxapad.

Nuorteva, M. 1957. Zur Kenntnis der parasitischen Hymenopteren der Borkenkäfer Finnlands. Annales Entomologici Fennici, 23, 47-71.

Nuorteva, M., & Saari, L. 1980. Larvae of *Acanthocinus*, *Pissodes* and *Tomicus* (Coleoptera) and the foraging behaviour of woodpeckers (Picidae). Annales Entomologici Fennici, 46, 107-10.

Peters, A., 1996. The natural host range of *Steinernema* and *Heterorhabditis* spp. and their impact on insect populations. Biocontrol Science and Technology, 6, 389-402.

Pettersson, E.M. 2001. Volatiles from potential hosts of *Rhopalicus tutela*, a bark beetle parasitoid. Journal of Chemical Ecology, 27, 2219-31.

Pettersson, E.M., Hallberg, E., & Birgersson, G. 2001. Evidence for the importance of odor-perception in the parasitoid *Rhopalicus tutela* (Walker) (Hymenoptera : Pteromalidae). Journal of Applied Entomology, 125, 293-301.

Poinar, G.O. Jr. 1986. Recognition of *Neoaplectana* spp. (Steinernematidae: Rhabditida). Proceedings of the Helminthological Society of Washington, 53, 121-29.

Purrini, K. 1981. *Nosema hylobii* n.sp. (Nosematidae, Microsporida), a new microsporidian parasite of *Hylobius abietis* L. (Curculionidae, Coleoptera). Zeitschrift für angewandte Entomologie, 92, 1-8.

Purrini, K., & Ormieres R. 1982. *Gregarina hylobii* and *Ophryocystis hylobii n.sp. (Ophryocystidae, Neogregarinida) Parasitizing Hylobius abietis* (Curculionidae, Coleoptera). Journal of Invertebrate Pathology, 39, 164-73.

Pye, A.E., & Burman M. 1977. Pathogenicity of the nematode *Neoaplectana carpocapsae* (Rhabditida, Steinernematidae) and certain microorganisms towards the large pine weevil, *Hylobius abietis* (Coleoptera, Curculionidae). Annales Entomologici Fennici, 43, 115-19.

Pye, A.E., & Burman M. 1978. *Neoaplectana carpocapsae*: infection and reproduction in large pine weevil larvae, *Hylobius abietis*. Experimental Parasitology, 46, 1-11.

Pye, A.E., & Pye N.L. 1985. Different applications of the insect parasitic nematode Neoaplectana *carpocapsae* to control the large pine weevil, *Hylobius abietis*. Nematologica, 31, 109-16.

Roques, A. 1975. Etude de la méroscénose des cônes de pin sylvestre en forêt de Fontainebleau. Thèse 3ème cycle, Paris VI. France.

Roques, A. 1976. Observations on the biology and cleptoparasitic behaviour of *Eurytoma waachtli* (Chalc. Eurytomidae) a parasite of *Pissodes validirostris* (Col. Curcul.) in the cones of Scots pine at Fontainebleau. Entomophaga, 21, 289-95.

Rutherford, T.A., Trotter D., & Webster J.M. 1987. The potential of heterorhabditid nematodes as control agents of root weevils. Canadian Entomology, 119, 67-73.

Salisbury, A.N., & Leather, S.R. 1998. Migration of larvae of the large pine weevil, *Hylobius abietis* L. (Col.: Curculionidae): Possible predation a lesser risk than dead by starvation? Journal of Applied Entomology, 122, 299-299.

Samsinakova, A., & Novák, V. 1967. Eine Methode zur integrierten Bekämpfung des Rüsselkäfers (*Hylobius abietis* L.). Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz, 40, 22-27.

Schabel, H.G. 1976. Green muscardine disease of *Hylobius pales* (Herbst) (Coleoptera: Curculionidae). Zeitschrift für angewandte Entomologie, 81, 413-21.

Schabel, H.G. 1978. Percutaneous infection of *Hylobius pales* by *Metarrhizium anisopliae*. Journal of Invertebrate Patholology, 31, 180-87.

Schabel, H.G., & Taft S.J. 1988. *Gregarina hylobii* (Sporozoa: Eugregarinida) in American pine reproduction weevils (Coleoptera: Curculionidae). Transactions of the American Microscopical Society, 107, 269-76.

Schimitschek, E. 1964. Liste der 1934-1936 und 1940-1953 gezogenen Parasiten und ihrer Wirte. Zeitschrift für angewandte Entomologie, 53, 320-41.

Schindler, U. 1964. Zur Imaginalparasitierung forstlicher Curculionidae. Zeitschrift für angewandte Zoologie, 51, 501-07.

Sellenschlo, U. 1984. Der gefurchte Dickmaulrüssler (*Otiorrhynchus sulcatus* (F., 1775)(Col.Curc.)), ein gefürchteter Schädling an Zierpflanzen. Praktische Schädlingsbekämpfer, 36, 22-24.

Siddiqui, M.R., 2000. *Tylenchida: Parasites of Plants* and *Insects*. 2nd ed. Wallingford, UK: CABI.

Slizinski, K. 1969. *Perilitus rutilus* Nees (Hym., Braconidae) – the parasite of imago of *Hylobius abietis* L. (Col., Curculionidae), new for the Polish fauna. Polskie Pismo Entomologiczne, 39 : 407-16.

Starý, P., Sterba, J., & Soldan, T. 1988. *Perilitus areolaris* G. & H. (Hymenoptera, Braconidae), a parasitoid of the pine weevil *Hylobius abietis* (L.) in Czechoslovakia. Acta Entomologica Bohemoslavaca, 85, 428-33.

Starzyk, J.R. 1996. Bionomics, ecology and economic importance of the fir weevil, *Pissodes piceae* (Ill.) (Col., Curculionidae) in mountain forests. Journal of Applied Entomology, 120, 65-75.

Strojny, W. 1951. Some observations on the egg-laying process of *Ephialtes tuberculatus* Fourcr. (Hym. Ichn.) – parasite of the larva of *Cryptorrhynchus lapathi* L. (Col. Curc.). Polskie Pismo Entomologiczne, 21, 140-43.

Szalay-Marzsó, L. 1962. Zur Morphologie, Biologie und Bekämpfung des Erlenwürgers *Cryptorrhynchus lapathi* L. (Col. Curculionidae) in Ungarn. Zeitschrift für angewandte Entomologie, 49, 163-194.

Thomas, H.A. 1970. Neoaplectanid nematodes as parasites of the pales weevil larva, *Hylobius pales*. Entomological News, 81, 91.

Tillemans, F., & Coremanns-Pelseneer J. 1987. *Beauveria brongniartii* (Fungus moniliale) as control agent against *Otiorrhynchus sulcatus* (Coleoptera, Curculionidae). Mededelingen Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent, 52, 379-84.

Trägardh, I. 1931. Zwei forstentomologisch wichtige Fliegen. Zeitschrift für angewandte Entomologie, 18, 672-90.

Tschorsnig, H.-P., & Herting, B. 1994. Die Raupenfliegen (Diptera: Tachinidae) Mitteleuropas: Bestimmungstabellen und Angaben zur Verbreitung und Ökologie der Einzelnen Arten. Stuttgarter Beiträge zur Naturkunde Serie A (Biologie), 506: 1-170.

Vainio, A., & Hokkanen H.M.T. 1993. The potential of entomopathogenic fungi and nematodes against *Otiorrhynchus ovatus* L. and *O. dubius* Strom (Col., Curculionidae) in the field. Journal of Applied Entomology, 115, 379-87.

Waldenfels, J. 1975. Versuche zur Bekämpfung von *Hylobius abietis* L. (Coleopt., Curculionidae). Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz, 48, 21-25.

Walstad, J.D., Anderson, R.F., & Stambaugh, W.J. 1970. Effects of Environmental Conditions on two species of Muscardine Fungi (*Beauveria bassiana* and *Metarrhizium anisopliae*). Journal of Invertebrate Pathology, 16, 221-25.

Walstad, J.D. & Anderson, R.F. 1971. Effectiveness of *Beauveria bassiana* and *Metarrhizium anisopliae* as control agents for the pales weevil. Journal of Economic Entomology, 64 (1), 322-23.

Wegensteiner, R. 1989. The efficacy of *Beauveria bassiana, B. brongniartii* and *B. tenella* against *Hylobius abietis* (Col., Curcul.). Proceedings of the International Conference on Biopesticides, Theory and Practice, 25.-28.09.1989, Ceske Budejovice, Czechoslovakia. 238-42.

Wegensteiner, R. 1992. Possibilities and efficacy of infection of *Hylobius abietis* (Col., Cuculionidae) with *Beauveria bassiana* and *Beauveria brongniartii*. Poster Abstract, XXV Annual Meeting of the Society for Invertebrate Pathology, Heidelberg, 16-21.08.1992. 225.

Wegensteiner, R. & Führer, E. 1988. Zur Wirksamkeit von *Beauveria bassiana* (Bals.) Vuill. gegen *Hylobius abietis* L. (Col.: Curculionidae). Entomophaga 33, 339-48.

Workshop of the IOBC Study Group "Insect Pathogens and Insect-parasitic Nematodes" 1987 in Versailles (1989): Control of weevils (Curculionidae) - b) Use of fungi. WPRS Bulletin, 12, 25-60.

Wülker, G. 1923. Ueber Fortpflanzung und Entwicklung von *Allantonema* und verwandte Nematoden. Ergebnisse und Fortschritte der Zoologie, 5, 389-507.

Zimmermann, G. 1981. Gewächshausversuche zur Bekämpfung des gefurchten Dickmaulrüsslers, *Otiorrhynchus sulcatus* F., mit dem Pilz *Metarhizium anisopliae* (Metsch.) Sorok. Nachrichtenblatt für den Deutschen Pflanzenschutzdienst 33, 103-08.

Zinovev, G.A. 1958. On the structure, dynamics and topology of the nuclei of bark beetle outbreaks. Zoologiceskij Zurnal, 37, 379-94.