Chapter 18

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

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1. INTRODUCTION

Among the main bark weevil pests in Europe, Hyllobius abietis L. and Pissodes spp. have been the subject 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 Hyllobius pinastris (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.

395

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 study. References are in the text..

<table>
<thead>
<tr>
<th>Parasitoid Species</th>
<th>Biology</th>
</tr>
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<tr>
<td><strong>Hym. Braconidae</strong></td>
<td></td>
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<tr>
<td><em>Allodoras lepidus</em> (Haliday)</td>
<td>Egg-larval koinobiont endoparasitoid ?</td>
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<tr>
<td><em>Aspilota sp.</em></td>
<td>Adult endoparasitoid, very unlikely record.</td>
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<tr>
<td><em>Bracon hylobii Ratzeburg</em> ¹</td>
<td>See text</td>
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<tr>
<td><em>Perilitus areolaris Gerdin &amp; Hedqvist</em>²</td>
<td>Larval idiobiont ectoparasitoid</td>
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<tr>
<td><em>Perilitus areolaris Gerdin &amp; Hedqvist</em>²</td>
<td>Adult endoparasitoid</td>
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<td><strong>Hym. Ichneumonidae</strong></td>
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<tr>
<td><em>Dolichomitus tuberculatus</em> (Geoffroy)</td>
<td>Larval (and pupal?) idiobiont ectoparasitoid</td>
</tr>
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<td><em>Stenarella gladiator</em> (Scopoli)</td>
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<td><strong>Hym. Pteromalidae</strong></td>
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<tr>
<td><em>Tomicobia sp.</em></td>
<td>Unknown, but very unlikely record. See text</td>
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<td><strong>Dipt. Pteroidae</strong></td>
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<tr>
<td><em>Megaselia plurispinulosa</em> Zetterstedt</td>
<td>Larval koinobiont endoparasitoid ?</td>
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¹ Some records as *Bracon brachytarsus* Thomson, probably a misidentification
² Some records as *Perilitus rutillus* (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 rutillus* (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. rutillus* was a misidentification of *P. areolaris*, which is known only from *H. abietis*, whereas *P. rutillus* is a parasitoid of weevils of the genera *Sitona* and *Phytonomus*. Schindler (1964) provides data on the life cycle of *P. areolaris* (as *P. rutillus*) 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 Pterididae (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) supposed that these were misidentifications 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 inulative 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. *Alloeorus lepidus* Haliday (Hym.: Bracidae) 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 *Brachypoda* (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

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 inudnative biological control agents of *Hyalobius abietis*.

Nematodes from three orders (Tylenchida, Diplogasterida and Rhabditida) have been reported from *Hyalobius 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 *Hyalobius 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 inudnative 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 inudnatively, and recycling in the host environment is of secondary importance.

Field trials against adult *Hyalobius 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 *Hyalobius* 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 (Burban 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 (Salvberg), 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. gyllenhalii Gyllenhal, apart from some old parasitoid records (e.g. Lovaszy 1941; Znovev 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. validirostris, 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 Enbazus 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 *Hylóbius 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 *Coeloïdes* 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* (Ratzburg) 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 *Coeloïdes* spp. are found on *Pissodes* spp. (Haeselbarth 1967; Kenis and Mills 1994). *C. sordidator* (Ratzburg), 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. harcyiae* (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 are recorded 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. praeternisus* 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. harcyiae, P. pini, P. piniphilus* and *P. piceae*. The few observations available on the parasitoid complex of *P. harcyiae* 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 nubilipes* (Viereck), occurs, which seems to be restricted to *Pissodes* spp. (Carlson 1979). *D. terebrans* is an ectoparasitoid attacking larvae, prepupa 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), *Coleocterus caligatus* (Gravenhorst), *N. Enemies of Bark Weevils* 403
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 Forster are ectoparasitoids on larvae in galleries and are frequently found on P. castaneus. R. tutela has also been occasionally found on P. pini, P. pinipilus, 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 Pissodex 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 Pissodex spp. Pissodex validirostris is often heavily attacked by E. annilai Hedqvist (Annila 1975; Roques 1975). Roques (1976) showed that E. annilai (in Roques mentioned as E. waechti) is a cleptoparasitoid of the ichneumonids Scambus spp. E. annilai and E. waechti 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 eulophids, 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 tarsenemid 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 Pissodex spp. in European forestry compared to, e.g., bark beetles or Hyllobius abietis. Ironically, the largest study on parasitoids of Pissodex spp. in Europe was carried out for the biological control project against the North American Pissodex 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 Pissodex 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.

<table>
<thead>
<tr>
<th>Parasitoid species</th>
<th>Biologe</th>
<th>castaneus</th>
<th>pini</th>
<th>pinipalidae</th>
<th>xuvaldebrusci</th>
<th>pipecote</th>
<th>harrywite</th>
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</thead>
<tbody>
<tr>
<td>Hym.: Ichneumonidae</td>
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<tr>
<td>Dolichomitus terebrans (Ratzeburg)</td>
<td>L. ec.</td>
<td>xxx</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>xxx</td>
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<tr>
<td>Exeristes ruficollis (Gravenhorst)</td>
<td>L. ec.</td>
<td>x</td>
<td></td>
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<tr>
<td>Scambus sagax Hartig</td>
<td>L. ec.</td>
<td>x</td>
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<tr>
<td>Scambus sudeticus (Glowacki)</td>
<td>L. ec.</td>
<td>xx</td>
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<td></td>
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<tr>
<td>Hym.: Braconidae</td>
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<tr>
<td>Bracon hylobii Ratzeburg</td>
<td>L. ec.</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Bracon praermissus Marshall</td>
<td>L. ec.</td>
<td>x</td>
<td></td>
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<tr>
<td>Undetermined Bracon spp.</td>
<td>L. ec.</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Coeloides abdominalis (Zetterstedt)</td>
<td>L. ec.</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Coeloides forsteri Haeselbarth</td>
<td>L. ec.</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Coeloides sordidator (Ratzeburg)</td>
<td>L. ec.</td>
<td>xxx</td>
<td>xx</td>
<td>xxx</td>
<td>xx</td>
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<tr>
<td>Euhazus abieticola Acherberg &amp; Kenis</td>
<td>E.-L. en.</td>
<td></td>
<td></td>
<td></td>
<td>xxx</td>
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<tr>
<td>Euhazus robustus (Ratzeburg)</td>
<td>E.-L. en.</td>
<td>x</td>
<td>x</td>
<td>xxx</td>
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<tr>
<td>Euhazus semirugosus (Nees)</td>
<td>E.-L. en.</td>
<td>xxx</td>
<td>xxx</td>
<td>xxx</td>
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<tr>
<td>Spaltius rubidus (Rossi)</td>
<td>L. ec.</td>
<td>x</td>
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<tr>
<td>Hym.: Pteromalidae</td>
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<tr>
<td>Metacolus unifasciatus Foerster</td>
<td>L. ec.</td>
<td>xx</td>
<td></td>
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<tr>
<td>Rhopalicus guttatus (Ratzeburg)</td>
<td>L. ec.</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Rhopalicus tatea (Walker)</td>
<td>L. ec.</td>
<td>xx</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Hym.: Eupelmidae</td>
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<tr>
<td>Calosota aenivalis Curtis</td>
<td>L. ec. (h)</td>
<td>x</td>
<td></td>
<td></td>
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<tr>
<td>Eupelmus urozonus Dalman</td>
<td>L. ec. (h)</td>
<td>x</td>
<td></td>
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<tr>
<td>Hym.: Eurytomidae</td>
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<tr>
<td>Eurytoma annulata Hedges</td>
<td>L. ec.</td>
<td>x</td>
<td></td>
<td></td>
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<tr>
<td>Eurytoma wachelli Mayr</td>
<td>L. ec.</td>
<td>x</td>
<td></td>
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<tr>
<td>Undetermined Eurytoma spp.</td>
<td>L. ec.</td>
<td>x</td>
<td></td>
<td></td>
<td>xx</td>
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<tr>
<td>Acari: Taronemidae</td>
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<tr>
<td>Pedicularis ventricosus Newport</td>
<td>P. ec.</td>
<td>x</td>
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</table>


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 tender 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-Marszó (1962), only Schmitschek (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-Marszó (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 Perilicus and Pygostolus (Hym.: Braconidae), Dirhinus and Tomocidus (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 Costanzo 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 *Otioryynchus* 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 *Otioryynchus* 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 *Hylaeus 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 *Euphasus* 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 *Otioryynchus* 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 inauditive 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).

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