Chapter 11

RESEARCH ON PARASITOIDS AND PREDATORS OF SCOLYTIDAE – A REVIEW

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1. INTRODUCTION

Scolytidae are major forest pests in Europe. For example, *Ips typographus* (L.) is considered the main pest problem in forestry in many central and northern European countries. Consequently, there is a long tradition of forest entomology studying various aspects of bark beetle ecology, including their natural enemy complexes, with a view to developing control methods. In recent years, the need for the development of sustainable pest management methods, taking into account the whole forest ecosystem, has enhanced the interest in natural mortality factors.

Mills (1983) provided an extensive review of the natural enemies of conifer feeding bark beetles in Europe. In contrast, natural enemies of broadleaf-feeding species have never been reviewed. Furthermore, much research has been carried out in the last 20 years, in particular in fields such as host/prey location or tritrophic interactions. Other noteworthy reviews include two books by Hedqvist (1963; 1998) on chalcid and braconid parasitoids of Scolytidae in Sweden, and a publication by Nuorteva (1957) on parasitoids of bark beetles in Finland. Data are also available in general parasitoid and predator catalogues such as Thompson (1943), Herting (1973), and Noyes (2001), although these often repeat errors contained in primary publications.

This review will focus primarily on parasitoids and predators of bark beetle species considered to be pests of living trees in Europe, although it may also consider relevant research in other continents. A list of these European species is given in chapter 1. Pathogens of scolytids are reviewed in another chapter (Wegensteiner, chapter 12).

F. Lieutier et al. (eds), Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis, 237—290.

2. PARASITOIDS

2.1. Parasitoid complexes

Tables 1, 2 and 3 list the hymenopteran parasitoids of European Scolytidae living on Pinaceae, Cupressaceae and broadleaf trees, respectively. In addition to Hymenoptera, mites can also be parasitic on eggs, larvae or pupae of bark beetles. However, it is often difficult to properly assess the exact biology of mites, which may either be parasites, parasitoids, predators, saprophytes or commensals. In this review, mites will be reviewed in the predator section.

There is a large variation in the knowledge of the parasitoids of European bark beetles. As expected, the parasitoid complexes of the most important pests have been the target of specific studies. Parasitoids of *Ips typographus* have been studied, among others, by Sachtleben (1952), Bombosch (1954), Mills and Schlup (1989), and Weslien (1992) and those of *Tomicus piniperda* (L.) and *Ips acuminatus* (Gyll.) by Hérard and Mercadier (1996) and Balazy *et al.* (1987). *Scolytus* species have been investigated as well because of their importance as vectors of the Dutch elm disease (e.g. Beaver 1967a; Schroeder 1974; Maksimovic 1979; Merlin 1984, Manojlovic *et al.* 2000a, 2000b). *Phloeotribus scarabaeoides* (Bernard) was studied extensively by several authors for its importance in olive plantations (Russo 1938; González and Campos 1990a, 1991). Hintze-Podufal and Druschke (1988), Mills (1991) and Lozano and Campos (1991) provide significant data on the parasitoid complex of *Leperisinus varius* (F.) and Eichhorn and Graf (1974) on the ambrosia beetles *Trypodendron* spp. In addition, Nuorteva (1957), Hedqvist (1963, 1998), and Mendel (1986) provide numerous rearing records for bark beetles in Finland, Sweden, and Israel, respectively. For many European bark beetles, however, information on their parasitoid complex is usually restricted to parasitoid-host lists, catalogues and general studies which provide incomplete or erroneous records. No mention of parasitoids was found in the European literature for the following scolytid species: *Gnathotricus materiarius* (Fitch), *Hylastes* spp., *Hylurgus ligniperda* (F.), *Trypodendron signatum* (F.) and *Xylosandrus germanus* (Blandford). Larvae of these species either live in the root system (*Hylastes* spp., *H. ligniperda*) or in the sapwood (*G. materiarius*, *T. signatum*, *X. germanus*) and are thus probably less susceptible to generalist larval parasitoids. In addition, *G. materiarius* and *X. germanus* are exotic species recently introduced into Europe, which may have not yet been adopted by European parasitoids.

The parasitoid complex of a particular scolytid host is difficult to evaluate because of the cryptic habit of bark beetle larvae and because a scolytid species usually shares the same breeding resource with a range of other insects. In most studies, parasitoids were reared from entire logs and attributed to the most abundant or most likely host, which resulted in many erroneous records. The most obvious mistakes are easily detected. For example, the braconid parasitoid *Eubazus semirugosus* (Nees) has often been associated with scolytids (Herting, 1973; Hedqvist, 1998) whereas it is a common egg-prepupal parasitoid of weevils of the genus *Pissodes* that cannot parasitize eggs of scolytids in galleries (Kenis and Mills, 1998). Similarly, most records of Ichneumonidae on Scolytidae are erroneous, with the exception of the large spruce species *Dendroctonus micans* (Kug.), which is commonly attacked by the ichneumonid *Dolichomitus terebrans* (Ratzeburg) (Grégoire 1976). However, errors are often more difficult to trace, especially when two or more scolytid species occur simultaneously. Ideally, parasitism should be evaluated by the debarking of infested wood, observation and determination of host galleries and single rearing of parasitoid larvae, pupae or cocoons. Unfortunately, only few studies were based on log dissection and individual rearing (e.g. Schroeder 1974; Mendel 1986). Another method to study parasitoids and other natural enemies consists of the exposure of sentinel hosts for a short period of time, as was carried out by Weslien (1992) with *I. typographus*.

2.2. Parasitoid guilds and general biology

A parasitoid guild can be defined by the host stage attacked, the host stage killed, and the mode of parasitism (endo- or ectoparasitism) (Mills, 1994). Four parasitoid guilds are found on Scolytidae.

2.2.1. Egg parasitoids

Only one true hymenopteran egg parasitoid has been undoubtedly reared from scolytids in Europe. *Trichogramma semblidis* (Aurivillius) is a well-known parasitoid of the ash bark beetle *Leperisinus varius* (= *Hylesinus fraxini* Panzer = *H. orni* Fuchs) and the closely related ash species *Hylesinus crenatus* F. (e.g. Michalski and Seniczak 1974; Hintze-Podufal and Druschke 1988). It is also reported from 56 species of Lepidoptera, Diptera and Coeloptera (Noyes, 2001). However, the genus *Trichogramma* is a taxonomically difficult group, and sibling species within this complex with a narrower host range cannot be ruled out. *T. semblidis* was very common on ash bark beetles in Poland, with mean parasitism rates of 11-14% (Michalski and Seniczak 1974). Parasitoid females were found in galleries ovipositing in freshly laid beetle eggs.

2.2.2. Egg-larval endoparasitoids

The only confirmed egg-larval parasitoid of Scolytidae in Europe is the eulophid *Entedon ergias* Walker (= *leucogramma* (Ratzeburg)), one of the most abundant parasitoids of broad-leaf scolytids of the genus *Scolytus* (Hedqvist 1963; Schroeder 1974; Merlin 1984; Yates, 1984). Other *Entedon* spp. have been reported from bark beetles (Tables 1 and 3), but their biology is unknown. The biology of *E. ergias* has been described in detail by Beaver (1966a) on *Scolytus scolytus* (F.). The female enters the scolytid maternal gallery to oviposit in the egg. The parasitoid development occurs internally. Parasitised larvae are usually killed in the 4th, penultimate instar. Parasitism induces a modification of the behaviour of the parasitised larva, which moves to the outer bark before the unparasitised ones. Overwintering occurs as a larva in the host larva or as a pupa in the gallery. There are one or two generations per year. *E. ergias* has also be studied extensively in the

USA, where it was accidentally introduced and became established on the elm beetle, *Scolytus multistriatus* (Van Driesche *et al.* 1996)

2.2.3. Larval ectoparasitoids

Most of the parasitoids of Scolytidae belong to this guild. Two different strategies are observed. Larval ectoparasitoids can either enter bark beetle galleries to find and parasitize host larvae ("cryptoparasitoids"), or can locate and parasitise their host through the bark. The best known cryptoparasitoid is the holarctic *Roptrocerus xylophagorum* (Ratz.), a common and polyphagous parasitoid of conifer bark beetles. Its biology has been extensively studied, both in Europe and the USA (e.g. Hedqvist 1963; Samson 1984; Pettersson *et al.* 2000; Sullivan *et al.* 1999). Eggs are laid on bark beetle larvae and, occasionally, on pupae in the galleries. Two other species, *Roptrocerus mirus* (Walker) and *R. brevicornis* (Thomson), occur on conifers in Europe (Hedqvist 1963). They have never been studied in detail and have been cited much less frequently and from fewer hosts than *R. xylophagorum* (Table 1). However, this may result from identification errors since recent studies showed that *R. mirus* is nearly as frequent as *R. xylophagorum*, particularly on spruce (Wermelinger 2002; M. Kenis, unpublished). The pteromalid *Cerocephala eccoptogastri* Masi and several Bethylidae are mentioned as cryptoparasitoids of scolytid larvae and pupae by Mendel (1986), and seem to be particularly abundant in southern Europe and the Mediterranean region (Tables 2, 3) (Russo 1938; Mendel 1986). Other probable cryptoparasitoids are the species that attack ambrosia beetles in the sapwood, *Perniphora robusta* (Ruschka) and *Eurytoma polygraphi* (Ashmead), although their oviposition behaviour has never been clearly described.

The majority of the larval parasitoids attack their host through the bark. This biology is encountered mainly in Braconidae and Pteromalidae, but also in Ichneumonidae, Eurytomidae, Torymidae and Eupelmidae. Nuorteva (1957), Hedqvist (1963, 1998) and Mills (1983) provide general overviews of the biology of these parasitoids, but some species have been studied in greater detail, for example, *Coeloides bostrichorum* Giraud, *Rhopalicus tutela* (Walker) and *Dendrosoter middendorffii* (Ratzeburg) as parasitoids of *Ips typographus* (Sachtleben 1952; Bombosch 1954; Krüger and Mills 1990; Hougardy and Grégoire 2001), *Cheiropachus quadrum* (F.) and *Rhaphitelus maculatus* Walker on *Phloeotribus scarabaeoides* (Russo 1938; Campos and Gonzalez 1990, 1991; Gonzalez and Campos 1990b; Campos and Lozano 1994), and *Dendrosoter protuberans* (Nees), a parasitoid of *Scolytus* species (Kennedy, 1970). The general biology is similar for most species. Parasitoids usually locate their host by walking on the bark, paralysing the larvae or pupae by injecting venom, and laying a single egg on the paralysed host. Eggs and larvae develop quickly. Overwintering usually occurs as prepupae or pupae, in the host gallery. Braconids and ichneumonids build a cocoon in the gallery, whereas chalcids pupate directly in the host gallery. Several ectoparasitoids act as facultative or obligatory hyper- or cleptoparasitoids on other parasitoids of the same guild (see section 2.6 below).

2.2.4. Adult endoparasitoids

Adult parasitism is a relatively rare event in endopterygote insects. Bark beetles, however, are frequently parasitized in the adult stage by a range of Braconidae and Pteromalidae (Table 1). Interestingly, adult parasitism seems to be restricted to conifer bark beetles whereas there is no record from broadleaf species, apart from the dubious notification of *Centistes cuspitatus* Hal. on *Leperisinus varius* (Hintze-Podufal and Druschke 1988). The most studied adult parasitoid is the pteromalid *Tomicobia seitneri* (Ruschka), a frequent parasitoid of *Ips typographus* and, possibly, some other *Ips* spp. Faccoli (2000a, 2001a) provides a review of its biology. Females oviposit into adult beetles of various ages on the bark. Parasitized beetles are still able to bore into the bark and lay eggs, but fecundity is reduced by an average of 30% (Sachtleben 1952). The parasitoid kills its host and emerges from it in the gallery. It has usually two generations per year. Overwintering occurs as a larva in the host beetle. *T. seitneri* seems to be present in most *I. typographus* populations and parasitism rates vary from 20% to 100% (Faccoli 2000a). *T. seitneri* is often parasitized in the host beetle by another pteromalid, *Mesopolobus typographi* (Ruschka) (Balazy and Michalski 1962; Seitner, in Hedqvist 1963). Several other *Tomicobia* spp. are reported from conifer bark beetles in the world (Faccoli 2001a). In Europe, *T. acuminati* Hedqvist is found on *Ips acuminatus* and *T. pityophthori* (Boucek) on *Pityogenes chalcographus* (L.) (Hedqvist 1963; Lobinger and Feicht 1999).

Braconid adult parasitoids all belong to the sub-family Euphorinae. *Ropalophorus clavicornis* (Wesmael) is a frequently encountered parasitoid of *I. typographus* (Nuorteva 1957; Hedqvist 1998; Faccoli 2001a). Its biology has been poorly studied but seems to be very similar to that of *T. seitneri* (Bombosch 1954; Nuorteva 1957; Faccoli 2001a). There is very little information on the level of parasitism by *R. clavicornis*, except from Bombosch (1954) who mentions 18% parasitism in Bavaria. In a large collection of parasitoids from spruce infested by *I. typographus* in Switzerland, *R. clavicornis* was the main adult parasitoid, and the third most abundant species of the whole parasitoid complex (Wermelinger 2002). The genus *Cosmophorus* comprises several species apparently specialised on conifer bark beetles. Five of them occur in Europe. Hedqvist (1998) and van Achterberg and Quicke (2000) provide determination keys, host lists and general data on their biology, which is apparently similar to the other adult parasitoids. Finally, another euphorine braconid, *Cryptoxilos cracoviensis* (Capek and Capecki), has been reared from adults of *Cryphalus piceae* (Ratz.) in Poland (Capek and Capecki 1979).

2.3. Host specificity

Host range is among the most difficult characteristics to determine in parasitoid ecology (Shaw 1994). The literature is full of identification mistakes and erroneous host-parasitoid associations, especially in bark beetles and their parasitoids, which are usually associated merely because they emerge from the same logs. The most obvious errors were removed from Tables 1, 2 and 3, but these undoubtedly still contain many wrong associations. However, patterns in host specificity can emerge from the most serious studies. For example, adult parasitoids and the egg-larval parasitoid *Entedon ergias* are probably more specific than the majority of the larval ectoparasitoids. *E. ergias* seems to be restricted to the genus *Scolytus*. *Tomicobia seitneri* and *Ropalophorus clavicornis* are usually associated with *I. typographus*, *Tomicobia acuminati* with *Ips acuminatus* and *Tomicobia pityophtori* with *Pityogenes chalcographus*. The host specificity of *Cosmophorus* spp. is less clear, and at least some species have been reared from several bark beetle hosts (Hedqvist 1998). The high specificity of parasitoids attacking eggs and adults could be explained by the fact that females probably locate their host by their aggregative pheromone, as shown for *T. seitneri* (Mills and Schlup 1989; Faccoli 2000a), *T. pityophthori* (Lobinger and Feicht 1999) and *R. clavicornis* (Faccoli 2001a). More generally, koinobiont endoparasitoids tend to be more specific than idiobiont ectoparasitoids because the former live in close interaction with the hormonal system of their host.

Larval ectoparasitoids of Scolytidae are thought to be rather more host-tree specific than host-specific, but this is highly variable. Few parasitoids are commonly found on conifer and broad-leaf species. The main examples include Eurytomidae (e.g. *Eurytoma morio* Boheman) and Eupelmidae (e.g. *Eupelmus urozonus* Dalman), which are known to be facultative or obligatory hyperparasitoids, but also some Pteromalidae such as *Heydenia pretiosa* Forster, *Dinotiscus colon* (L.), and the braconid *Ecphylus silesiacus* (Ratzeburg), although the existence of cryptic species cannot be ruled out. The pteromalid, *Perniphora robusta*, and the eurytomid *Eurytoma polygraphi* are specialised in ambrosia beetles living in the sapwood, but are found equally in conifers and broad-leaf trees. Other overlaps are probably the result of identification errors or accidental parasitism. Within conifers or broad-leaf trees, some parasitoids are reported to be polyphagous and to attack beetles on various tree genera (e.g. *Rhopalicus tutela*, *Roptrocerus* spp., *Dendrosoter middendorffii*), whereas others seem to be confined to a single tree genus (e.g. *Metacolus unifasciatus* Forster, *Coeloides abdominalis* (Zetterstedt) and *C. sordidator* (Ratzeburg) on pine, and *Coleoides bostrichorum*, on spruce). Some larval ectoparasitoids are strongly linked to a host species, such as *C. bostrichorum* with *I. typographus*, although other host records are sometimes found. However, it remains to be seen whether the apparent association between a parasitoid and a particular host tree is due to the tree itself or to the host beetle, or a combination of the two. Interestingly, when *I. typographus*, a typical spruce bark beetle, occasionally attacks pine, it is followed by its whole range of parasitoids, including those that are usually associated with spruce rather than pine, such as *C. bostrichorum*, *D. eupterus*, *T. seitneri* and *R. clavicornis* (Turcani and Capek, 2000; Turcani and Kenis, unpublished). Inversely, during an outbreak of the pine bark beetle *Ips sexdentatus* (Boern.) on oriental spruce (*Picea orientalis*) in Turkey, Schimitschek (1940) reared a parasitoid complex very similar to that usually observed on pine, including *C. abdominalis*, a species usually associated with various pine beetles.

Very few studies have focused on parasitoid host range in Scolytidae. A notable exception is Mendel (1986) who, in Israel, collected 26 parasitoid species from 15 bark beetle species on 17 different members of the Pinaceae, Cupressaceae and various broad-leaf families. He reared parasitoids singly from identified larval galleries, which prevented errors in host-parasitoid associations. Interestingly, there was little overlap between the parasitoid complexes in Pinaceae and other trees, but the overlap was much larger between Cupressaceae and broad-leaves. All levels of host specificity were found, from highly polyphagous species (e.g. *H. pretiosa*) to species specific to a single beetle (e.g. *Ecphylus caudatus* Rushka on *Hypoborus ficus* (Erichson), to a single genus (e.g. *Entedon ergias* on *Scolytus* spp.), or restricted to a single tree species but polyphagous within this tree (e.g. *D. middendorffii*, or *R. xylophagorum* in *Pinus*). The mechanisms leading to polyphagy or monophagy in larval ectoparasitoids are not clear, but probably include multiple factors such as host- and host tree location (both long range and short range), and physical constrains such as bark thickness and host size. Host location is the subject of the following section. The influence of bark thickness on host range has been investigated by Manojlovic *et al.* (2000a) in *E. silesiacus*, a parasitoid of *Scolytus* spp. on elm. *E. silesiacus*, the species living in the thickest bark, was the least parasitized and the least preferred host.

2.4. Host location

The topics of host location and, more generally, tri-trophic interactions, have provided some of the most interesting studies on bark beetle parasitoids in recent years. Host location mechanisms have been studied because they are supposed to be the key to understanding parasitoid host ranges, and also because their better understanding would allow the development of new control methods aiming at conserving and augmenting natural enemies in the field. In addition, Mills and his colleagues studied host location mechanisms in *Ips typographus* parasitoids to evaluate their potential as biological control agents against new hosts in North America (Mills and Krüger, 1989; Mills and Schlup, 1989; Mills *et al.*, 1991). The location of bark beetles by parasitoids involves two distinct steps. Firstly, the parasitoid must locate the host habitat, i.e. an infested tree (long-range host location). Secondly, the parasitoid must be able to locate a particular host at a suitable developmental stage (short-range host location).

The attraction of the adult parasitoid *Tomicobia seitneri* to the aggregation pheromone of *Ips typographus* was shown in field conditions by Mills and Schlup (1989) and Faccoli (2000a). Mills and Schlup also tested pheromones of American *Dendroctonus* spp., to which *T. seitneri* did not respond, suggesting that this host location mechanism involves specific interactions, and may be responsible for the higher specificity in adult parasitoids compared to larval parasitoids. Lobinger and Feicht (1999) showed that *Tomicobia pityophthori* was strongly attracted by the pheromone of its host, *Pityogenes chalcographus*. It is likely that other adult parasitoids also locate their hosts using the host pheromone as kairomone, as suggested by Faccoli (2001a) for *Ropalophorus clavicornis*. In contrast, it seems that aggregation pheromones do not attract larval ectoparasitoids, as shown by Mills and Schlup (1989) for *I. typographus* parasitoids. However, multistriatin, a component of the aggregation pheromone of *Scolytus multistriatus* is known to be attractive for several larval ectoparasitoids of this elm-feeding scolytid (Kennedy, 1984; Gonzales *et al.*, 1999). The mechanisms and cues involved in long-range host location in larval ectoparasitoids are unclear. Mills and Schlup (1989) suggested that the cues could be emitted by the host-associated fungi. However, in a field experiment, *Rhopalicus tutela* was attracted by spruce logs and isolated bark infested with *I. typographus* larvae, but not by spruce wood containing the associated fungi alone.

In Spain, Lozano *et al.* (2000) showed that the larval ectoparasitoids *Dendrosoter protuberans* and *Cheiropachus quadrum* and their host, *Phloeotribus scarabaeoides* are attracted by the same compounds, alpha-pinene and 2-decanone. They suggest that these parasitoids could use these compounds to locate their host.

Mechanisms of short-range host location in larval ectoparasitoid have been studied more extensively, especially on *I. typographus* and its main parasitoids (Mills *et al.* 1991; Pettersson 2001a, 2001b; Pettersson *et al.* 2000, 2001a, 2001b). They followed interesting observations by Ryan and Rudinsky (1962) and Richerson and Borden (1972) on *Coeloides vancouverensis* (D.T.) (= *C. brunneri* Vier.) and its host *Dendroctonus pseudosugae* Hopkins in North America, providing evidence for the role of sound and infra-red radiation, respectively, as cues for locating host larvae beneath the bark. However, in a series of experiments on *I. typographus* parasitoids (*Coeloides bostrichorum*, *Dendrosoter middendorffii* and *Rhopalicus tutela*), Mills *et al.* (1991) rejected the role of sound, vibration and infrared radiation, and showed evidence that volatile cues play the major role. However, they were not able to isolate the source of these volatiles, nor the volatiles themselves. Pettersson and co-authors (Pettersson *et al.* 2000, 2001a, 2001b; Pettersson 2001a, 2001b) confirmed the role of volatiles in host location in *C. bostrichorum*, *R. tutela*, *Roptrocerus mirus* and *R. xylophagorum*. They revealed odour perceptive sensillae on antennae of *R. tutela* (Pettersson *et al.* 2001a), and showed that, for all parasitoids investigated, the attractive compounds were mainly oxygenated monoterpenes present in infested trees. These are probably involved in both short-range and long-range attraction, and seem not to arise from the insect hosts, but from the host-plant complex, including associated fungi.

2.5. Dispersal, longevity and feeding behaviour in the field

Most knowledge on the biology and ecology of parasitoid adults has been gathered from laboratory rearing (e.g. Kennedy 1970; Krüger and Mills 1990; Campos and Gonzales 1990; 1991; Gonzales and Campos 1990b, Manojlovic *et al.* 2000a), or from observations of adult behaviour on infested logs (e.g. Hedqvist 1963, Mills 1991). However, the ecology and biology of adults of bark beetle parasitoids remain largely unknown, especially in relation to dispersal capacities, longevity in natural conditions and feeding habits in the field. These characteristics, however, are essential in the development of new management methods taking into account the roles and impacts of parasitoids and other natural mortality factors. Hougardy and Grégoire (2000) suggested that food sources such as nectar, pollen and honeydew are available in abundance in spruce forests and that searching for food is probably not time and energy consuming.

Dispersal behaviour could be studied using rubidium as an internal marker. Promising results were obtained by Hougardy *et al.* (2003) who marked larval parasitoids of *Ips typographus* by introducing rubidium chloride into spruce vascular systems. In another recent field study, Lobinger and Feicht (1999) used traps baited by the pheromone of *Pityogenes chalcographus* related to an electronic design to study the swarming behaviour of the adult parasitoid *Tomicobia pityophthori*.

2.6. Competitive interactions and other mortality factors in parasitoids

Larval ectoparasitoids are often subject to hyper- or cleptoparasitism. Antagonistic interactions between parasitoids of scolytids have been discussed by Mills (1991). *Eurytoma morio* and *Eurytoma arctica* Thomson, polyphagous parasitoids of conifer and broad-leaf tree scolytids, may act as primary parasitoids (e.g. Nuorteva 1957; Hedqvist 1963; Pettersen 1976a), cleptoparasitoids (Mills 1991) and hyperparasitoids through Braconidae and Pteromalidae (Sachtleben 1952; Nuorteva 1957). Eupelmidae of the genera *Calosota* and *Eupelmus* have been frequently reared from logs attacked by bark beetles (e.g. Hedqvist 1963, Pettersen 1976b; Mendel 1986) but the few data available on their biology suggest that they act mainly as hyperparasitoids (Hedqvist 1963). Kenis and Mills (1994) observed that *Calosota aestivalis* Curtis and *Eupelmus urozonu*s, the most often cited eupelmid parasitoids of bark beetles in Europe, parasitized cocoons of *Dolichomitus terebrans* and *Coeloides* spp., respectively, in galleries of *Pissodes castaneus* De Geer (Col.: Curculionidae) in pine logs. Rarely, primary pteromalid parasitoids may also act as facultative hyperparasitoids of braconids, as observed with *Dinotiscus eupterus* on *Dendrosoter middendorffii* (Sachtleben 1952).

Cleptoparasitism is probably a common behaviour among parasitoids of bark beetles. Mills (1991) showed that females of *Cheiropachus quadrum* and *E. morio* commonly displaced females of *Coeloides filiformis* Ratz. ovipositing on the ash bark beetle *Leperisinus varius*. Hougardy and Grégoire (2003) observed that, on *Ips typographus*, *R. tutela* females were able to displace *C. bostrichorum* from the oviposition sites to steal the host previously located by the braconid. Hougardy (2003) also investigated the niche partitioning mechanisms in the main parasitoids of *I. typographus*, i.e. *Coeloides bostrichorum*, *Rhopalicus tutela*, and *Roptrocerus xylophagorum*. She analysed between-stand, between-tree and within-tree distributions, as well as habitat preferences and interactions with other species.

Competitive interactions among parasitoids of adults have been poorly studied. *Mesopolobus typographi* is known as a hyperparasitoid of *Tomicobia seitneri* (Seitner, in Hedqvist, 1963), but its biology is largely unknown.

Table 1. Parasitoids reared reared from scolytid species feeding on living Pinaceae in Europe and the Near East. xx = Particularly reliable association, i.e. mentioned in at least four different studies, or obtained by log dissection. x = other records. (x) = Association that appears dubious to the senior author because it comes from an unreliable study and the biology of the parasitoid makes this association unlikely. Totally unlikely associations are not mentioned in this table.

	Guild[1]	*Cryphalus piceae*	*Dendroctonus micans*	*Ips acuminatus*	*Ips amitinus*	*Ips cembrae*	*Ips duplicatus*	*Ips sexdentatus*	*Ips typographus*	*Orthotomicus erosus*	*Pityogenes conjunctus*	*Pityogenes chalcographus*	*Pityogenes trepanatus*	*Pityokteines curvidens*	*Pityokteines spinidens*	*Pityokteines vorontzovi*	*Pityophtorus pityographus*	*Polygraphus poligraphus*	*Tomicus minor*	*Tomicus piniperda*[2]	*Tripodendron lineatum*
Main references[3]		a, b c,f ,g h,i	a, b c,f ,j k,l	a, b c, d e,f ,ly	a,b c,f ,ln	a,b c,f	a, b c,f ,l	a,b c,d e,f ,lz	a,b c,d e,f l,n op q,r st wx	a u	a b c	a,b c,d e,f ,ln ,s	b c f	a, b c, g	a, b c	a, b g, §	a,c g	a,b c,d e,f	a,b c,d e,f, l	a,b c,d e,f,l,m, u	a,b d,v
<u>Braconidae</u>																					
Blacus humilis (Nees)	?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.
Bracon instabilis (Marshall)	L.ec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(x)	(x)	.
B. hylobii Ratzeburg	L.ec.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
B. osculator Nees	L.ec.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
B. palpebrator Ratzeburg	L.ec.	.	.	.	.	(x)	.	.	(x)	.	.	.	.	.	.	.	.	.	x	x	.
B. stabilis (Wesmael)	L.ec.	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.
Coeloides abdominalis (Zetterstedt)	L.ec.	.	.	xx	.	x.	.	xx	.x	.	.	.	.	.	.	.	.	.	xx	xx	.
C. bostrichorum Giraud	L.ec.	x	.	.	x.	x	x	x.	xx	.	.	xx	.	x	.	.	.	.	.	x	.
C. scolyticida Wesmael	L.ec.	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	(x)	.	.
C. sordidator (Ratzeburg)	L.ec.	.	.	.x	.	.	.	x.	(x)	.	.	.	.	.	.	.	.	.	xx	xx	.

Table 1. (cont.).

		C. piceae	*D. micans*	*I. acuminatus*	*I. amitinus*	*I. cembrae*	*I.. duplicatus*	*I. sexdentatus*	*I.. typographus*	*O. erosus*	*P. conjunctus*	*P. chalcographus*	*P. trepanatus*	*P. curvidens*	*P. spinidens*	*P. vorontzovi*	*P. pityographus*	*P. poligraphus*	*T. minor*	*T. piniperda*^{2}	*T. lineatum*
Cosmophorus cembrae Ruschka	A.en.	x	.	.	.	.	.	.	.	.	.	xx	.	.	x	x	.	(x)	.	.	.
C. klugi Ratzeburg	A.en.	.	.	.	.	.	.	.	xx	.	.	.	.	.	x	x	.	xx	.	.	.
Cosmophorus regius Niezabitowski	A.en.	.	.	.	.	.	.	.	xx	.	.	.	.	.	.	.	.	xx	.	.	x
Cryptoxilos crocoviensis (Cap. & C.)	A.en.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dendrosoter flaviventris Förster	L.ec.	.	.	.	.	.	.	.	.	xx	.	.	x	.	.	.	.	.	.	xx	.
(= *caenopachoides* Ruschka)																					
D. hartigi (Ratzeburg)	L.ec.	.	.	x	.	.	.	.	.	xx	.	x	x	.	.	.	.	x	xx	.	.
D. middendorfi (Ratzeburg)	L.ec.	x	x	x	x	x	x	x	xx	xx	.	x	.	x	.	x	x	xx	xx	xx	(x)
D. protuberans (Nees)	L.ec.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	(x)	(x)	.
Dendrosotinus similes Boucek	L.ec.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Doryctes leucogaster (Nees)	L.ec.	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.
D. mutilator (Thunb.) (= *obliteratus*	L.ec.	.	.	.	.	.	.	(x)	(x)	.	.	.	.	.	.	.	.	.	.	(x)	.
Nees = *strigztus* Kokujev)																					
D. pomarius Reinhard	L.ec.	.	.	.	.	(x)	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.
D. striatellus (Nees)	L.ec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(x)	.
Ecphylus caudatus Ruschka	L.ec.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
E. hylesini (Ratzeburg)	L.ec.	.	.	x	.	.	.	.	x	.	.	xx	.	.	x	x	x	xx	x	.	.
E. silesiacus (Ratzeburg)	L.ec.	x	.	.	.	.	.	.	.	.	.	x	.	.	.	x	x	.	.	.	.
Heterospilus sicanus (Marshall)	L.ec.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lysitermus pallidus Förster	L.ec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	xx	.	.	.

Table 1. (cont.).

		C. piceae	*D. micans*	*I. acuminatus*	*I. amitinus*	*I. cembrae*	*I.. duplicatus*	*I. sexdentatus*	*I.. typographus*	*O. erosus*	*P. conjunctus*	*P. chalcographus*	*P. trepanatus*	*P. curvidens*	*P. spinidens*	*P. vorontzovi*	*P. pityographus*	*P. poligraphus*	*T. minor*	*T. piniperda*[2]	*T. lineatum*
Lestricus secalis (L.)	?	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.
(= *Cenocoelus agricolator* L.)																					
Ontsira antica (Wollaston)	L.ec..	.	.	(x)	.	.	.	.	.	.	.		.	.	.	.	.	.	.	(x)	.
O. imperator (Haliday)	L.ec..	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(x)	(x)	.
Perilitus rutilus (Nees)	A.en.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.
Ropalophorus clavicornis (Wesm.)	A.en.	.	.	.	x	.	.	.	xx	.	.	.	.	.	.	.	.	.	.	.	.
Spathius brevicaudis Ratzeburg	L.ec.	.	.	(x)	.	.	.	.	(x)	.	.	(x)	.	.	.	.	.	.	.	(x)	.
S. exarator (L.)	L.ec.	.	.	.	.	(x)	.	.	(x)	.	.	.	.	.	.	.	.	.	(x)	.	.
S. rubidus Rossi	L.ec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(x)	.	.
<u>Ichneumonidae</u>																					
Dolichomitus terebrans (Ratz.)	L.ec.	.	xx	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Neoxorides collaris (Gravenhorst)	L.ec.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Xorides irrigator (F.)	L.ec.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<u>Pteromalidae</u>																					
Cheiropachus quadrum (F.)	L.ec.	.	.	(x)	(x)	.	.	(x)	x	.	.	(x)	.	.	.	.	.	.	(x)	(x)	.
Dinotiscus aponius (Walker)	L.ec.	.	(x)	.	.	.	.	(x)	(x)	.	.	.	.	.	.	.	.	.	.	(x)	.
D. colon (L.)	L.ec.	.	.	xx	.	.	.	.	.	.	.	.	.	.	.	.	.	.	xx	x	.
Dinotiscus eupterus (Waljer)	L.ec.	x	.	x	x	.	.	(x)	xx	.	x	xx	.	.	x	x	x	xx	(x)	.	.
Heydenia pretiosa Forster	L.ec.	.	.	x	.	.	.	.	xx	xx	.	.	.	.	.	x	.	.	xx	.	.
Macromesus amphiterus Walker	L.ec.?	.	.	.	.	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	.

Table 1. (cont.).

		C. piceae	*D. micans*	*I. acuminatus*	*I. amitinus*	*I. cembrae*	*I.. duplicatus*	*I. sexdentatus*	*I.. typographus*	*O. erosus*	*P. conjunctus*	*P. chalcographus*	*P. trepanatus*	*P. curvidens*	*P. spinidens*	*P. vorontzovi*	*P. pityographus*	*P. poligraphus*	*T. minor*	*T. piniperda*^{2}	*T. lineatum*
Mesopolobus typographi (Ruschka)	A.en. (h).	.	.	x	x	.	.	.	xx	.	.	x	.	.	.	.	.	x	.	(x)	.
Metacolus azureus (Ratzeburg)	L.ec.	.	.	x	.	.	.	.	.	xx	x	x	.	.	.	.	.	.	x	xx	.
M. unifasciatus Forster	L.ec.	.	.	xx	.	.	.	.	(x)	xx	.	.	.	.	.	.	.	.	xx	xx	.
Perniphora robusta Ruschka	L.ec. c.?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x x
Platygerrhus affinis (Walker)	L.ec.?	.	.	.	.	.	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.
Psychophagus omnivorus (Walker)	(h) ?	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.
Pteromalus abieticola Ratzeburg	?	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
P. puparum (L.)	?	.	.	.	.	.	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.
*Rhaphitelus ladenbergii (*Ratz.)	L.ec.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(x)	.
Rhopalicus guttatus (Ratzeburg)	L.ec.	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	x	.
R. quadratus (Ratzeburg)	L.ec.	.	.	xx	xx	.	.	.	.	.	.	xx	.	.	.	.	.	.	xx	xx	.
R. tutela (Walker)	L.ec.	.	x	xx	xx	.	xx	xx	xx	.	.	xx	.	x	.	.	.	x	xx	xx	.
Roptrocerus brevicornis Thomson	L.ec.c.	.	.	xx	.	.	.	.	.	.	.	xx	.	.	.	.	.	.	xx	xx	.
R. mirus (Walker)	L.ec.c.	.	.	.	.	.	.	.	xx	.	.	x	.	.	.	.	.	x	.	x	.
R. xylophagorum (Ratzeburg)	L.ec.c.	xx	.	xx	xx	x	xx	.	xx	xx	.	xx	.	x	x	x	.	x	.	xx	.
Tomicobia acuminate Hedqvist	A.en.	.	.	xx	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
T. pityophthori (Boucek)	A.en.	.	.	x	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
T. seitneri (Ruschka)	A.en.	.	.	x	x	.	x	.	x	.	.	.	.	.	.	.	.	.	.	.	.
Eulophidae																					
Aprostocetus hedqvisti Graham	?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.

Table 1. (cont.).

		C. piceae	*D. micans*	*I. acuminatus*	*I. amitinus*	*I. cembrae*	*I.. duplicatus*	*I. sexdentatus*	*I.. typographus*	*O. erosus*	*P. conjunctus*	*P. chalcographus*	*P. trepanatus*	*P. curvidens*	*P. spinidens*	*P. vorontzovi*	*P. pityographus*	*P. poligraphus*	*T. minor*	*T. piniperda*[2]	*T. lineatum*
Entedon methion (Walker)	E-L.en.?	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
E. pinetorum Ratzeburg	E-L.en.?	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
Eupelmidae																					
Calosata aestivalis Curtis	L.ec. (h)	.	.	.	.	.	.	.	.	xx	.	.	.	.	.	.	.	.	.	.	.
Eupelmus urozonus Dalman	L.ec. (h)	.	.	x	.	.	.	.	x	.	.	.	.	.	.	x	.	x	.	.	.
Eurytomidae																.					
Eurytoma abieticola Ratzeburg	L.ec.?	.	.	.	.	(x)	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	.
E. arctica Thomson	L.ec.	.	.	xx	x	.	.	x	xx	.	.	x	.	.	.	.	.	.	xx	xx	.
E. blastophagi Hedqvist	L.ec.	.	.	.	.	.	.	.	xx	.	.	.	.	.	.	.	.	.	.	.	.
E. crassinervis Thomson	L.ec.?	.	.	.	.	.	.	.	(x)	.	.	(x)	.	.	.	.	.	.	.	.	.
E. morio Baheman	L.ec.	.	.	x	.	.	.	.	xx	xx	.	xx	.	.	.	.	.	.	.	.	.
E. polygraphi (Ashmead)	L.ec.?	.	.	.	.	.	.	.	(x)	.	.	.	.	.	.	.	.	.	.	.	xx
(= *spessivtsevi* Bouc. & Novicky)																					
E. rufipes Walker	L.ec.?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(x)	.

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[1] Parasitoid guilds: L.ec. = Larval ectoparasitoid; L.ec.c. = Larval ectoparasitoid, cryptoparasitoid; E-L.-en. = Egg-larval endoparasitoid; (h) = Essentially hyperparasitoid. See text for more details.

[2] Includes data of the cryptic species *T. piniperda and T. destruens*

[3] Refereses: a: Noyes (2001); b: Herting (1973); c: Mills (1983); d: Hedqvist (1963); e: Hedqvist (1998); f: Thomson (1943); g: Faccoli (2000b); h: Hedqvist (1967); i: Capeck & Capecki (1979); j: Grégoire (1976); k: Voolma (1986); l: Nuorteva (1957); m: Hérard & Mercadier (1996); n: Grodski (1997); o: Bombosch (1954); p: Faccoli (2001a); q: Hougardy & Grégoire (2003); r: Mills & Schlup (1989); s: Pettersen (1976a); t: Sachtleben (1952); u: Mendel (1986); v: Eichhorn & Graf (1974); w: Weslien (1992); x: Wermelinger (2002); y: Balazy *et al.* (1987); z: Schimitschek (1940); §: Capek (1955).

Predators and diseases are also responsible for mortality in bark beetle parasitoids. Many generalist predators, such as clerid beetles and dolichopodid flies, feed indiscriminately on both hosts and parasitoids (Mills 1983), but their impact on parasitoid populations has never been measured. Very little is known on pathogens of bark beetle parasitoids, although researchers often observe dead parasitoid larvae and pupae in galleries (M. Kenis, unpublished). Winter mortality is important. Faccoli (2002) measured mortality rates of 47-48 % in *C. bostrichorum* and *R. xylophagorum* in Italy. In Colorado, the winter mortality rate of *Dendrosoter protuberans* varied between 79 and 89 % (Hostetler and Brewer 1976). The mortality factors could not be firmly established, although low temperatures were suspected to play a major role, especially in *D. protuberans*.

Table 2. Parasitoids reared from scolytid species feeding on living Cupressaceae in Europe and the Near East. xx = Particularly reliable association, i.e. mentioned in at least four different studies, or obtained by log dissection. x = other records. Totally unlikely associations are not mentioned in this table. Records from Ruschka (1916), Lichtenstein and Picard (1920), Herting (1973), Mendel (1986), and Noyes (2001).

	Guild[1]	*Phloeosinus armatus*	*Phloeosinus bicolor*	*Phloeosinus thujae*
Braconidae				
Dendrosoter protuberans (Nees)	L.ec.	xx	xx	.
Hecabolus sulcatus Curtis	L.ec.	.	x	x
Heterospilus incompletus (Ratzeburg)	L.ec.	.	.	x
Pteromalidae				
Cerocephala eccoptogastri Masi	L.ec.c.	xx	xx	.
Heydenia pretiosa Forster	L.ec.c.	xx	xx	.
Metacolus unifasciatus Forster	L.ec.	xx	xx	x
Rhaphitelus maculatus Walker	L.ec.	xx	xx	x
Rhopalicus quadratus (Ratzeburg)	L.ec.	.	.	x
Eulophidae				
Entedon ergias Walker	E-L.en.	.	x	.
Eupelmidae				
Calosota aestivalis Curtis	L.ec. (h)	xx	xx	.
Eurytomidae				
Eurytoma morio Boheman	L.ec.	xx	xx	x
Bethylidae				
Cephalonomia hypobori Kieffer	L.ec.c.	.	xx	x

[1] Parasitoid guilds: L.ec. = Larval ectoparasitoid; L.ec.c. = Larval ectoparasitoid, cryptoparasitoid; E-L.-en. = Egg-larval endoparasitoid; (h) = Essentially hyperparasitoid. See text for more details.

Table 3. Parasitoids reared from scolytid species feeding on living broad-leaved trees in Europe and the Near East. XX = Particularly reliable association, i.e. mentioned in at least four different studies, or obtained by log dissection. X = other records. (X) = Association that appears dubious to the senior author because it comes from an unreliable study and the biology of the parasitoid makes this association unlikely. Totally unlikely associations are not mentioned in this table.

	Guild[1]	*Hylesinus crenatus*	*Leperesinus varius*[2]	*Phloeotribus scarabaeoides*	*Scolytus intricatus*	*Scolytus laevis*	*Scolytus multistriatus*	*Scolytus ratzeburgi*	*Scolytus scolytus*	*Trypodendron domesticum*	*Xyleborus dispar*
Main references[3]		a,b,c e,f	a,b,c g,h,i	a,j, k,l	a,b,d, f, m, s, v	a,b, d, e	a,b,d e,f,n, o,p,q,r	a,b ,d,e, f,s	a,b,e ,f,o,p, q,t	a,b, d,u	f,u
<u>Braconidae</u>											
Bracon caudatus Ratzeburg	L.ec.	.	(x)	.	.	.	.	.	.	.	.
B. obscurator Nees	L.ec.	.	(x)	.	.	.	.	.	.	.	.
B. palpebrator Ratzeburg	L.ec.	.	.	.	(x)	.	.	.	.	.	.
B. ratzeburgii Dalla Torre	L.ec.	.	(x)	.	.	.	.	.	.	.	.
B. stabilis Wesmael	L.ec.	xx	xx	.	.	.	.	.	.	.	.
B. tenuicornis Wesmael	L.ec.	.	.	x	.	.	.	.	.	.	.
Centistes cuspidatus (Haliday)	A.en.?	.	x	.	.	.	.	.	.	.	.
Coeloides abdominalis (Zetterstedt)	L.ec.	.	(x)	.	.	.	.	(x)	.	.	.
C. filiformis Ratzeburg	L.ec.	xx	xx	xx	.	.	.	.	.	.	.
C. melanotus Wesmael	L.ec.	x	xx	x	.	.	.	.	(x)	.	.
C. scolyticida Wesmael	L.ec.	.	x	.	.	.	xx	x	xx	.	.
C. sordidator (Ratzeburg)	L.ec.	.	.	.	(x)	.	.	.	.	.	.
C. subconcolor (Russo)	L.ec.	.	x	xx	.	.	.	.	.	.	.
C. ungularis Thomson	L.ec.	.	.	.	.	.	.	xx	.	.	.
Dendrosoter ferrugineus (Marshall)	L.ec.	.	.	x	.	.	.	.	.	.	.
D. protuberans (Nees)	L.ec.	xx	xx	xx	x	.	xx	x	x	.	.

Table 3. (cont.).

	Guild[1]	*Hylesinus crenatus*	*Leperesinus varius*[2]	*Phloeotribus scarabaeoides*	*Scolytus intricatus*	*Scolytus laevis*	*Scolytus multistriatus*	*Scolytus ratzeburgi*	*Scolytus scolytus*	*Trypodendron domesticum*	*Xyleborus dispar*
Doryctes undulatus (Ratzeburg) (=*brachyurus* Marshall)	L.ec.	.	.	.	(x)	.	.	.	.	.	.
Doryctes pomarius Reinhard	L.ec.	.	.	.	.	.	x	.	x	.	.
D. rex Marshall	L.ec.	.	.	.	.	.	.	(x)	.	.	.
Ecphylus eccoptogastri Ratzeburg	L.ec.	.	.	xx	.	.	xx	.	x	.	.
E. hylesini (Ratz.)	L.ec.	(x)	(x)	.	.	.	.	.	.	.	.
E. silesiacus (Ratzeburg)	L.ec.	.	.	xx	x	.	xx	.	x	.	.
Hecabolus sulcatus Curtis	L.ec.?	.	(x)	.	.	.	.	.	.	.	.
Meteorus consimilis (Nees)	?	.	.	.	.	.	x	.	.	.	.
M. obfuscatus (Nees)	?	.	.	.	.	.	.	x	x	.	.
Monolexis fuscicornis Förstrer (=*Hecabolus doderoi* (Mantero))	L.ec.?	.	.	x	.	.	.	.	.	.	.
Ontsira imperator (Haliday)	L.ec.	.	.	.	.	.	.	(x)	.	.	.
Rhoptrocentrus piceus Marshall	L.ec.?	.	.	x	.	.	.	.	.	.	.
Spathius brevicaudis Ratzeburg	L.ec.	.	(x)	.	x	(x)	x	.	.	.	.
S. curvicaudis Ratzeburg	L.ec.	.	.	.	.	.	x	.	.	.	.
S. exarator (L.)	L.ec.	(x)	(x)	.	.	.	(x)	.	.	.	.
S.rubidus (Rossi)	L.ec.	.	(x)	x	.	.	x	.	.	.	.

Table 3. (cont.).

	Guild[1]	*Hylesinus crenatus*	*Leperesinus varius*[2]	*Phloeotribus scarabaeoides*	*Scolytus intricatus*	*Scolytus laevis*	*Scolytus multistriatus*	*Scolytus ratzeburgi*	*Scolytus scolytus*	*Trypodendron domesticum*	*Xyleborus dispar*
Ichneumonidae											
Nematopodius formosus Gravenhorst (= *Pseudopimpla anisandri* (Fahringer))	?	.	.	.	.	.	.	.	.	.	(x)
Pteromalidae											
Acrocormus semifasciatus Thomson	L.ec.?	.	.	.	xx	.	.	.	.	.	.
Agrilocida ferrierei Stephan	L.ec.?	.	.	.	.	.	xx	.	.	.	.
Cerocephala cornigera Westwood	L.ec.c.?	.	xx	xx	.	.	x	.	.	.	.
C. eccoptogastri Masi	L.ec.c.	.	x	xx	.	.	xx	.	.	.	.
Cheiropachus obscuripes Brues	L.ec.	.	(x)	.	.	.	.	.	.	.	.
C. quadrum (F.)	L.ec.	.	xx	xx	xx	x	xx	x	xx	.	.
Cleonymus obscurus (Walker)	L.ec.?	.	.	.	.	.	.	.	x	.	.
Dinotiscus aponius (Walker)	L.ec.	x	xx	.	.	x	x	xx	x	.	.
D. colon (L.)	L.ec.	.	.	x	.	.	.	xx	.	.	.
Dinotiscus eupterus (Walker)	L.ec.	.	x	.	.	.	.	.	(x)	.	.
Habritys brevicornis (Ratzeburg)	L.ec.?	.	.	.	.	.	.	.	.	x	x
Heydenia pretiosa Förster	L.ec.	.	x	xx	.	.	xx	x	.	.	.
Perniphora robusta Ruschka	L.ec.c.?	.	.	.	.	.	.	.	.	xx	xx
Platygerrhus ductilis (Walker)	L.ec.?	.	.	.	x	.	.	.	.	.	.
P. maculatus Erdös	L.ec.?	.	.	.	x	.	.	.	.	.	.

Table 3. (cont.).

	Guild[1]	*Hylesinus crenatus*	*Leperesinus varius*[2]	*Phloeotribus scarabaeoides*	*Scolytus intricatus*	*Scolytus laevis*	*Scolytus multistriatus*	*Scolytus ratzeburgi*	*Scolytus scolytus*	*Trypodendron domesticum*	*Xyleborus dispar*
Pteromalus brunnicans Ratzeburg	L.ec.?	.	.	.	.	.	.	.	x	.	.
Rhaphitelus ladenbergii Ratzeburg	L.ec.	.	(x)	.	x	.	x	.	.	.	.
R. maculatus Walker	L.ec.	.	x	xx	x	.	xx	.	x	.	.
Rhopalicus tutela (Walker)	L.ec.	.	(x)	.	x	.	(x)	.	(x)	.	.
Roptrocerus mirus (Walker)	L.ec.c.	.	.	.	(x)	.	.	.	.	.	.
R.xylophagorum Ratzeburg	L.ec.c.	.	.	.	(x)	.	.	.	.	.	.
Theocolax formiciformis Westwood	?	.	(x)	.	.	.	.	.	.	.	.
Trigonoderus cyanescens (Förster)	?	.	.	.	(x)	.	.	.	.	.	.
T.princeps Westwood	?	.	.	.	.	.	.	x	.	.	.
<u>Eulophidae</u>											
Aulogymnus bivestigatus (Ratzeburg)	?	.	x	.	.	.	.	.	.	.	.
Baryscapus hylesini Graham	?	.	x	.	.	.	.	.	.	.	.
Entedon armigerae Graham	E-L.en.?	.	.	.	.	(x)	.	.	.	.	.
E.ergias Walker	E-L.en.	.	.	.	xx	xx	xx	xx	xx	.	.
E.tibialis (Nees)	E-L.en.?	.	.	.	x	.	.	.	.	.	.
Euderus albitarsis (Zetterstedt)	?	.	.	.	(x)	.	.	.	.	.	.
Stenomesius rufescens (Retzius)	?	.	.	(x)	.	.	.	.	.	.	.
<u>Eupelmidae</u>											
Calymmochilus russoi Gibson	?	.	.	x	.	.	.	.	.	.	.

Table 3. (cont.).

	Guild[1]	*Hylesinus crenatus*	*Leperesinus varius*[2]	*Phloeotribus scarabaeoides*	*Scolytus intricatus*	*Scolytus laevis*	*Scolytus multistriatus*	*Scolytus ratzeburgi*	*Scolytus scolytus*	*Trypodendron domesticum*	*Xyleborus dispar*
Eusandalum merceti Bolivar & Pieltrain	(h)	.	.	.	.	.	x	.	.	.	.
Eupelmus aloysii Russo	L.ec. (h)	.	.	x	.		.	.	.	.	.
E. annulatus Nees	L.ec. (h)?	.	.	.	.	.	.	x	.	.	.
E. urozonus Dalman	L.ec. (h)	.	x	x	x	.	.	.	.	.	.
E.vesicularis (Retzius)	L.ec. (h)	.	x	x	.	.	.	.	.	.	.
Eurytomidae											
Bruchophagus maurus (Boheman)	L.ec.?	.	.	.	.	.	x	.	.	.	.
Eurytoma aloisfilippoi (Russo)	L.ec.	.	x	xx	.	.	.	.	.	.	.
E. arctica Thomson	L.ec.	x	xx	.	.	.	x	.	.	.	.
E.eccoptogastri Ratzeburg	L.ec.	.	(x)	.	.	.	.	.	.	.	.
E.flavoscapularis Ratzeburg	L.ec.	.	x	.	.	.	.	.	.	.	.
E.morio Boheman	L.ec.	x	xx	xx	x	x	xx	.	x	.	.
E. polygraphi (Ashmead)	L.ec.?	.	.	.	.	.	.	.	.	xx	.
(= *spessivtsevi* Bouc. & Novicky)											
Torymidae											
Torymus arundinis (Walker)	L.ec.?	.	x	.	.	.	.	.	.	.	.
T. hylesini Graham	L.ec.?		x	.	.	.	.	.	.	.	.
Trichogrammatidae											
Trichogramma semblidis Auriv.	E.en.	xx	xx	.	.	.	.	.	.	.	.

Table 3. (cont.).

	Guild[1]	*Hylesinus crenatus*	*Leperesinus varius*[2]	*Phloeotribus scarabaeoides*	*Scolytus intricatus*	*Scolytus laevis*	*Scolytus multistriatus*	*Scolytus ratzeburgi*	*Scolytus scolytus*	*Trypodendron domesticum*	*Xyleborus dispar*
Bethylidae											
Cephalonomia cursor Westwood	L.ec.c.?	.	.	xx	.	.	.	.	.	.	.
C. hypobori Kieffer	L.ec.c.	.	.	xx	.	.	xx	.	.	.	.
Laelius elisae (Russo)	L.ec.c.?	.	x	xx	.	.	.	.	.	.	.
Plastanoxus westwoodi (Kieffer)	L.ec.c.?	.	.	xx	.	.	.	.	.	.	.
Sclerodermus brevicornis Kieffer	L.ec.c.?	.	.	x	.	.	.	.	.	.	.
S. domesticus Latreille	L.ec.c.	.	.	.	.	.	xx	.	.	.	.

[1] Parasitoid guilds: E.en = Egg endoparasitoid; L.ec. = Larval ectoparasitoid; L.ec.c. = Larval ectoparasitoid, cryptoparasitoid; E-L.- en. = Egg-larval endoparasitoid; A.en. = Adult endoparasitoid; (h) = Essentially hyperparasitoid. See text for more details.

[2] Many records from *Hylesinus fraxini* Panzer, synonym with *Leperisinus varius* (F.)

[3] References: a: Noyes (2001); b: Herting (1973); c: Michalski and Seniczak (1974); d: Hedqvist, 1963; e: Hedqvist, 1998; f: Thomoson, (1943); g: Mills (1991); h: Hintze-Podufal and Druschke (1988); i: Lozano and Campos (1991); j: Russo (1938); k: Mendel (1986); l: Gonzales and Campos (1990); m: Markovic and Stojanovic (1996); n: Manohlovic (2000); o: Maksimovic (1979); p: Merlin (1984); q: Schroeder (1974); r: Mendel (1986); s: Nuorteva (1957); t: Beaver (1967a); u: Eichhorn and Graf (1974); v: Yates (1984)

3. PREDATORS

Predators are defined as carnivorous organisms killing several prey during their development. Since most problems with bark beetles occur in conifers, most investigations on predators were carried out on conifers, and little information is available on predators of Scolytidae on broad-leaf trees. In general, predators have a larger range of prey species than parasitoids. They can be efficient antagonists because many species are more mobile and active during wintertime than their prey. Like parasitoids, many predators are known to locate their prey by semiochemicals, i.e. by bark beetle pheromones or tree volatiles. They are the first to arrive at newly infested trees - often concomitantly with their prey - while most parasitoids arrive later (Stephen and Dahlsten, 1976; Ohmart and Voigt, 1982; Linit and Stephen, 1983). Insect predators do not seem to prefer specific tree parts, but rather colonise the lower parts of bolts (Wermelinger 2002), in contrast to parasitoids, which often prefer the upper parts of a tree where the bark is thinner (Ball and Dahlsten 1973; Stephen and Dahlsten 1976; Gargiullo and Berisford 1981; Wermelinger 2002). Many insect predators produce only one generation per year (Nicolai 1996).

3.1. The predatory taxa

Many species have been found associated with bark beetle galleries but only a few are definitely known to forage on living eggs, larvae, pupae, or adults of bark beetles. Many species may be facultative predators, preying also on other subcortical taxa, and others may be solely scavengers. Most predatory species belong to the Coleoptera and Diptera. Some important coleopteran families include Cleridae, Rhizophagidae, and Trogossitidae (=Ostomidae). Many species of other families are also associated with bark beetles. Among the Diptera, the Dolichopodidae and Lonchaeidae are the most relevant families.

Furthermore, predatory bugs in the heteropteran family Anthocoridae suck on juvenile and adult scolytids. A few species of Raphidiidae (Neuroptera) live in their larval stage in the brood galleries of bark beetles and feed on scolytid larvae. There are also mite species that are predatory or parasitic on eggs and larvae of scolytids. The only relevant vertebrate group foraging on bark beetles is the woodpeckers.

Previous compilations of insect predators were provided by Herting (1973) and Mills (1983). The present synopsis mainly reviews the literature of the last five decades including also that on woodpeckers. The most important taxa are discussed in more detail below while a comprehensive list is given in Table 4.

3.1.1 Coleoptera (beetles)

Beetles are among the most important and most investigated predators of scolytids. Both their larvae and adults may feed on prey larvae or adults. They usually show less specificity for prey or tree species than parasitoids. Many predators are attracted by prey-emitted pheromones, modulated by tree volatiles (Erbilgin and Raffa 2001). Predacious beetles in conifers often respond to alpha-pinene and ethanol (Schroeder and Weslien 1994). In addition, they can detect anti-aggregation pheromones such as verbenone emitted by bark beetles. This is hypothesised to deter predators specialised on early successional scolytid species and to be indifferent or attractive to generalist predators (Lindgren and Miller, 2002). Among the most extensively investigated beetle species are *Thanasimus* spp. (Cleridae), *Rhizophagus* spp. (Rhizophagidae), and *Nemosoma elongatum* (L.) (Trogossitidae).

Cleridae (checkered beetles). This family includes two genera, among which three species of *Thanasimus* Latreille are known to be predators of bark beetles (Table 4). Among these, *T. formicarius* (L.) has been the most intensively studied. Experimental studies showed that it can reduce a brood of *Tomicus piniperda* by 81% (Schroeder 1997) and a brood of *Ips typographus* by 18% (Mills 1985). However, in field exclusion experiments involving *Ips typographus japonicus* Niijima, its impact was somewhat mixed with that of intraspecific competition (Lawson *et al.* 1997). *T. formicarius* starts flying early in the season, and forages throughout the summer, attacking a wide range of prey. In Germany, the females oviposit from early April to late August (Gauss 1954). This author mentions more than 20 species of bark-beetle prey in the following genera; *Ips*, *Pityogenes*, *Tomicus*, *Polygraphus*, *Hylesinus*, *Hylastes*, *Scolytus* and *Dendroctonus*. The predators are attracted to their prey by their aggregation pheromones (Bakke and Kvamme 1978, 1981; Köhnle and Vité 1984; Tømmerås 1988). Tømmerås (1985) observed that predator antennae have receptors keyed to a high number of prey pheromones [(+)- and (-)-ipsdienol, (S)-*cis*-verbenol, (-)-ipsenol, (+)-lineatin, (-)-verbenone, *exo*-brevicomin, frontalin, etc] and host-tree volatiles [(+)- and (-)-□-pinene, myrcene, terpineol, limonene, □-pinene, camphor, pino-camphone, (+)- and (-)-linalol]. This sometimes resulted in high catches in pheromone traps (up to a 1:4 *T. formicarius* : *Ips typographus* ratio according to Bakke and Kvamme 1978). Responding to the pheromones and host-tree volatiles, the predators land on the attacked trees, feed on the attacking bark beetles and oviposit on the bark surface. *T. formicarius* was caught in equal numbers in pine stands attacked the previous year by *Tomicus piniperda* and in unattacked stands, suggesting that they are extremely mobile (Schroeder 1997). Their appearance early in the year and their response to aggregation pheromones allows them to be one of the first species to colonise bark-beetle broods (Lawson *et al.* 1997; Hérard and Mercadier 1996). *T. formicarius*' high impact can be explained by its high fecundity (106 eggs/female: Dippel *et al.* 1997), and high voracity; one adult consumes 3 adult *Ips typographus* per day (Gauss 1954), and each larva consumes 44 to 57 prey larvae during its whole larval life (Mills 1985; Hérard and Mercadier 1996; Dippel *et al.* 1997). Predator densities attacking *I. typographus* were estimated at 1.3 to 11 larvae/1000 cm^2 (Mills, 1985; Thalenhorst 1958). Combining these larval prey consumption figures with associated predator densities, we conclude that the larvae of *T. formicarius* kill 57 - 627 *I. typographus* larvae per 1000 cm^2. For comparison, *I. typographus* density has been estimated at 84 – 189 individuals/1000 cm^2 by Hougardy and Grégoire (2000) and 227/1000 cm^2 by Gonzalez *et al.* (1996). Adult *T. formicarius* live for 4-10 months and the life cycle takes one year (Gauss 1954) or two years in Scandinavia

(Schroeder 1999a). The beetles overwinter either as prepupae or as young adults in pupal niches within the bark.

Rhizophagidae (root-eating beetles). The family is represented among bark-beetle associates by the genus *Rhizophagus* Hrbst. Vogt (1966) lists 14 European species, most of which live under the bark of conifers or broadleaves. *R. depressus* (F.) and *R. dispar* (Payk.) are associated with *Trypodendron lineatum*, *Pityogenes chalcographus, Ips typographus, Ips acuminatus, Ips sexdentatus, Dendroctonus micans, Tomicus piniperda, T. minor* (Kolomiets and Bogdanova 1980) or respond to the pheromones of these species and/or to ethanol (Byers 1992; Kubisz 1992). They are probably only partly predacious, although there is documented evidence for predation. Hanson (1937) observed in the laboratory a single adult *R ferrugineus* (Payk.) consuming 79 eggs of *Hylastes* sp. Hérard and Mercadier (1986) found that the larvae of *R depressus* are partly mycetophagous or saprophagous, and partly predacious on *T. piniperda* (the larvae consumed 14 prey larvae, the adults 1 prey larva; all stages were also observed to feed on bark-beetle eggs). A similar observation was made by Merlin *et al.* (1986) on *Rhizophagus dispar* Gyll., which grew and developed either when reared on fungal cultures or when provided with living or dead bark beetle larvae. Schroeder (1996) found in an exclusion experiment that *R. depressus* reduced *T. piniperda* broods by 41%.

The biology and feeding habits of *Rhizophagus grandis,* one of the rare examples of a specific predator, are much clearer, because of the wide interest in this insect as a biological control agent against *Dendroctonus micans*. Except for specificity, the major features of *R. grandis*' life cycle are probably similar to those of the other species. The adults find the prey brood chambers using chemical clues (Wyatt *et al.* 1993; Tømmerås *et al.* 1984; Grégoire *et al.* 1992); this prey location mechanism is so finely tuned that a high proportion of the prey broods is eventually discovered (Fielding *et al.* 1991b; Van averbeke and Grégoire 1995). Oviposition is regulated both by chemical stimuli and inhibitors (Baisier 1990; Grégoire *et al.* 1991). Adults and larvae feed on the eggs, larvae, pupae and callow adults of the prey. The larvae aggregate on wounded prey but, when food is scarce, they become cannibalistic (Baisier *et al.* 1984; Baisier 1990). Merlin *et al.* (1984) observed that, during its whole larval life, each individual *R. grandis* consumes the equivalent of one fully grown *D. micans* larva. The prepupae become photopositive, leave the brood chambers and pupate in the ground or in the bark at the stem base of the trees. There is at least one generation per year (King *et al.* 1991).

Trogossitidae (bark-gnawing beetles). Most trogossitids live underneath the bark. However, there is only one species reported to be predatory on scolytids, i.e. *Nemosoma elongatum.* This is a well-known and widespread predator foraging on a wide range of bark beetles on both conifers and broadleaf trees (cf. Table 4). It is most often found associated with *Pityogenes chalcographus* in spruce and considered to be a very important predator of this bark beetle. The predator's biology and ecology have been investigated quite extensively (Baier 1991; Wigger 1994; Dippel 1995, 1996; Dippel *et al.* 1997). The adults are attracted by kairomonal cues and boring dust of bark beetles. Its long-term abundance is, with a time lag, closely related to that of *P. chalcographus* (Kopf and Funke 1998) while its seasonal phenology shows much variation (cf. Baier 1991; Wigger 1996). However, in spring, oviposition of both prey and predator start at the same time. In *P. chalcographus* pheromone baited traps *N. elongatum* can reach up to 20 % of the total catches (Wigger 1996). Trogossitid predators of bark beetles respond to single kairomone compounds (Billings and Cameron 1984; Köhnle and Vité 1984).

Staphylinidae (rove beetles). A large number of species have been described associated with bark beetles, or were caught in bark beetle pheromone traps. However, they feed on a wide range of prey species and the precise biology is often unclear. The fact that they can be reared on bark beetles in the laboratory does not mean that they actually forage on bark beetles in the field. Some may also feed on tree sap (Nuorteva 1956). The most frequent staphylinid predators are *Nudobius lentus* (Grav.) and *Placusa* spp. (Rauhut *et al.* 1993). They forage facultatively on bark beetles and their larvae. *N. lentus* is frequently found in pheromone traps for spruce bark beetles.

Histeridae (hister beetles). The histerids most frequently associated with bark beetles in Europe are *Platysoma* spp. and *Plegaderus* spp. They are attracted to pheromone traps of spruce bark beetles (Rauhut *et al.* 1993) as well as to plant volatiles (Schroeder and Weslien, 1994). The foraging behaviour of *Eblisia minor* (Rossi) (= *Platysoma frontale* Paykull) was studied in more detail (Hérard and Mercadier 1996). During the three larval stages it consumed an average of 44 scolytid larvae. The adults are also predacious.

Nitidulidae (sap beetles). Various species of *Epuraea, Glischrochilus* and other genera are reported to be attracted to scolytid pheromones (Zumr 1983; Rauhut *et al.* 1993; Faccoli 2001b) or to plant volatiles (Schroeder and Weslien 1994). Both their adults and larvae may feed on eggs of bark beetles or other prey (Nuorteva 1956; Schroeder 1999). Many species are endangered and recorded on red lists.

Tenebrionidae (darkling beetles). Only a few tenebrionids exhibit a predatory feeding behaviour. Various *Corticeus* species are facultatively predacious on eggs and larvae of bark beetles (Nuorteva 1956; Goyer and Smith 1981; Smith and Goyer 1982; Hérard and Mercadier 1996). *Corticeus fraxini* (Kug.) was reared in the lab and some life history parameters were investigated (Hérard and Mercadier 1996). Both its larvae and adults are predacious. They respond to prey pheromones (Rauhut *et al.* 1993).

There are a few additional coleopteran families which include bark beetle predators. Within the Colydiidae, two *Aulonium* and one *Bitoma* species have been reported from European scolytids. Although the Carabidae are a large predatory group, only

Dromius and *Calodromius* species are frequently found associated with bark beetles. Various species from other predatory families are attracted by either prey- or host tree semiochemicals: *Salpingus planirostris* (F.) (Salpingidae) was found in high numbers in pheromone traps for spruce bark beetles (Rauhut *et al.* 1993). *Pytho depressus* (L.) (Pythidae) was strongly attracted by the host tree volatiles alpha-pinene and ethanol (Schroeder and Weslien 1994). Further coleopteran families with potential bark beetle predators are Laemophloeidae, Mycetophagidae, and Silvanidae (see Table 4).

3.1.2 Diptera (flies)

Most predatory Diptera feed on bark beetles in their larval stage. They often outnumber other subcortically living predatory taxa (Morge 1961). On the other hand, their prey consumption is usually lower than that of beetles. They do not feed exclusively on bark beetles but also on larvae of cerambycids, curculionids, other Diptera and Hymenoptera. The main families are described below. Other dipteran taxa occasionally associated with bark beetles are found in Table 4.

Dolichopodidae (long legged flies). The most relevant genus is *Medetera*. The adult flies are predatory on small insects with a soft integument (Nuorteva 1956; Lieutier 1979; Nicolai 1995a). Mating occurs on the infested trunks and the females deposit their eggs in bark crevices and under scales of bark beetle infested trees (Hopping 1947). *Medetera dendrobaena* Kowarz produces up to 120 eggs per female (Dippel *et al.* 1997). This species is mono- to bivoltine. The arrival of dolichopodids on infested logs occurs shortly after colonisation by bark beetles but their presence and oviposition extends through the summer (Stephen and Dahlsten 1976; Lieutier 1979; Nicolai 1995c).

Most species are known to prey on scolytid larvae, pupae, and teneral adults. They overwinter in the larval stage and emerge simultaneously with the bark beetles (Beaver 1966c; Lieutier 1979). Winter mortality in the maggots can be substantial (Hopping 1947; Nuorteva 1959; Beaver 1966c). *Medetera* has been found to be associated with many bark beetle species in different tree species (cf. Table 1; Capek 1957; Nuorteva 1959; Ounap 1992b). The genus is not necessarily restricted to scolytid diets but also feeds on other taxa. The prey consumption of *M. dendrobaena* showed a functional response, i.e. prey consumption increased with increasing bark beetle density (Nicolai 1995b). When prey is abundant, dolichopodids kill more prey than necessary (Beaver 1966c). With low prey supply they can act cannibalistically.

The impact of dolichopodid flies on scolytid survival is discussed controversially in the literature. Bark beetle mortality imposed by *Medetera* species was assessed to be minor (Mills 1986) and to be independent of *Medetera* densities (Mills 1985). At low densities the access of dolichopodid larvae to bark beetle larvae may be restricted by intact pieces of phloem (Nagel and Fitzgerald, 1975). However, they can reach densities of up to 10 larvae per 100 cm^2 (Dippel *et al.* 1997) and cause mortality rates of 70-90 % (Hopping 1947; Nuorteva 1959).

Lonchaeidae (lance flies). Among the Lonchaeidae, only the genus *Lonchaea* lives subcortically (Morge 1963). The feeding behaviour of these species is controversially discussed in the literature. They are often considered to be saprophagous or coprophagous (Lieutier 1979). Most species of this genus, however, have developed from saprophagous to predatory behaviour. Morge (1961, 1963) and Hérard and Mercadier (1996) investigated extensively the predatory behaviour of these species. They are specialised in colonising certain species and conditions of trees rather than in preying on specific species of bark beetles. More species live in broadleaves than in conifers. *Lonchaea* species occur in smaller numbers and feed on detritus rather than on living bark beetle larvae (Morge 1961). In conifers, however, some species are known to be obligatory predators, occurring in high numbers. They can feed on eggs, larvae, and adults as well (Morge 1967). Like the Dolichopodidae, they are very voracious, killing more prey individuals than they can eat. When prey individuals are rare, cannibalism occurs. (Hérard and Mercadier 1996).

Pallopteridae (pictured-wing flies). *Toxoneura usta* (Meigen) is known to forage on scolytid larvae (Morge 1967; Martinek 1977; Chandler 1991). It is able to feed on eggs, larvae, pupae, and even adult bark beetles, killing many more prey than it can actually eat (Morge 1967). It is not specialised on any particular tree or prey.

Asilidae (robber flies). Asilid flies are not specialised predators of bark beetles. However, scolytids may be among their prey (Wichmann 1956; Dennis 1979). The adult flies insert their stylet before or behind the pronotum or between the elytra, inject paralysing saliva into the body and suck up the liquefied contents. Their larvae are predacious on other subcortical insect larvae (Wichmann 1956).

3.1.3 Other insect groups

Among the Heteroptera, the predatory behaviour of *Scoloposcelis* species and *Xylocoris cursitans* (Fallén) (Anthocoridae) has been studied in some detail (Heidger 1994; Hérard and Mercadier 1996; Dippel *et al.* 1997). Both larvae and adults are very voracious, killing more prey than they can consume (Hérard and Mercadier 1996). *Scoloposcelis pulchella* can produce two generations per year. They respond to the same lures as their prey (Heidger 1994).

The larvae of some Raphidioptera prey on or underneath the bark. A few species of Raphidiidae are known to forage non-specifically on cerambycids, bark beetles and other subcortically living organisms (Schimitschek 1931; Wichmann 1957). They may be able to access scolytid galleries only after the bark is loosened, e.g. by maturation feeding of bark beetles or by woodpeckers (Wichmann 1957). For further predatory insects see Table 4.

3.1.4 Acari (mites)

Mites can be associated with bark beetles in two ways. The first group feeds on substrates other than living bark beetles, e.g. fungi or nematodes. Therefore, some of these may even be beneficial to bark beetles (Hirschmann and Wisniewski 1983). These mites depend in a phoretic way on bark beetles, i.e. in a given stage they attach themselves to the emerging bark beetles and use them as transport vehicles to reach new habitats. The second group is parasitic or predacious on various scolytid stages. Adult females and deutonymphs may be phoretic as well.

In general, the ecology of acarine species associated with bark beetles is poorly understood. It may range from mutualistic to parasitic behaviour with all possible combinations of the two. Many mites are parasites rather than predators. A large number of mite species has been found associated with European bark beetles (Hirschmann 1971; Hirschmann and Wisniewski 1983; Kielczewski *et al.* 1983; Moser and Bogenschütz 1984; Moser *et al.* 1989), but only a few are known to actually feed on scolytids. In a study on *Ips typographus,* some 30 % of trapped beetles carried an average of 3 phoretic mites (Moser and Bogenschütz 1984). Common acarine predators such as *Iponemus* spp. and *Paracarophenax* spp. are known to be specialised on bark beetle eggs, whereas *Pyemotes* spp. and *Digamasellus* spp. feed on larvae and pupae. Some adults are commensals while their larvae feed on eggs (Hintze-Podufal and Druschke 1988). Adult bark beetles are not attacked (Moser 1975). The mites are transported to new habitats by adult beetles beneath their elytra or attached to the thorax or elytral declivity. Egg parasites seem to be more host specific than larval parasites (Lindquist 1969). Many species are specific in terms of habitats rather than in terms of hosts (Lindquist 1970). The impact of mites on bark beetle population dynamics is largely unexplored but often considered substantial. Mortality by *Pyemotes* spp. and *Iponemus* spp. reached up to 90 % (Gäbler 1947; Lipa and Chmielewski 1977; Kielczewski *et al.* 1983; Moser *et al.* 1989).

3.1.5 Aves (birds)

Among birds, the woodpeckers (Picidae) are the most important predators on scolytids. Most quantitative studies have been made in America, mainly in *Dendroctonus* spp. infestations. In Europe species like the black *(Dryocopus martius* L.), the great spotted *(Dendrocopos major* (L.)), and the three-toed woodpecker *(Picoides tridactylus* (Hemp. and Ehr)) are commonly observed foraging on bark beetles on conifers (Schimitschek 1931; Nuorteva 1956; Pechacek 1994) and on broadleaves (Yates 1984). In general, they seem to prefer larger prey species than scolytid larvae or beetles (Nuorteva and Saari 1980). In an American study, 89 % of

Table 4. List of European predatory species, their host trees, and their bark beetle preys. Observation type represents character of information: f= observed feeding on respective prey or prey found in faeces, a= associated in galleries or on bodies of respective prey, s= attracted to semiochemicals (pheromones or allelochemicals). Killing rate denotes prey consumption or killing by the respective predator (A= adult, L= larva), an asterisk indicates unclear feeding behaviour. For a summary of further older data see Herting & Simmonds (1973) and Mills (1983). Coleopteran taxonomy follows basically Freude et al. (1965-1998)

Table 4

Predator	Host tree	*Dendroctonus micans*	*Hylurgops palliatus*	*Ips acuminatus*	*Ips cembrae*	*Ips sexdentatus*	*Ips typographus*	*Orthotomicus erosus*	*Pityogenes calcaratus*	*Pityogenes chalcographus*	*Polygraphus poligraphus*	*Scolytus intricatu*	*Scolytus spp.*	*Taphrorychus bicolor*	*Tomicus spp.*	*Trypodendron lineatum*	*Other species*	Observation type	Killing rate	References[1]
COLEOPTERA																				
Carabidae																				
Calodromius spilotus (Ill.)	*Pn*	.	.	.	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
(=*Dromius quadrinotatus*)																				
Dromius quadrimaculatus (L.)	*Pn*	.	.	.	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
Carabidae spp.*	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	a		36
Cleridae																				
Allonyx quadrimaculatus (Sch.)	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	a		22
Thanasimus femoralis (Zett.)		.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	s		77
T. formicarius (L.)	*Pc,Fr*	x	.	x	.	x	x	.	.	x	.	.	x	.	x	.	x	a,f,s	44-57 larvae/L 2.9 adults/A/day 74-109 adults/A	11,15,18, 21,22,23, 45, 46, 63, 67,68,70, 72,76
T. rufipes (Brahm)	*Pc*	.	.	.	.	.	x	.	.	x	.	.	.	.	.	x	.	a,s		63, 76
Colydiidae																				
Aulonium ruficorne (Ol.)	*Pn*	.	.	x	.	x	.	x	x	.	.	.	.	.	.	.	x	a,f,s		22, 40, 41
A. trisulcum (Fourcr.)	*Ul*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	a		1
Bitoma crenata (F.)	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
Histeridae																				
Eblisia minor (Rossi) *(=Platysoma frontale)*	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a,f	44 larvae/L 1.5 larvae/A/day	22
Paromalus parallelepipedus (Hbst)	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	a,s		36, 37, 38, 63

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obs tye	Killing rate	References[1]
Platysoma angustatum (Thunb.)* *(=Cylister ferrugineum)*	*Pn,Pc*	.	.	x	.	x	x	x	x	x	.	.	.		x	x	.	a,s		22,36,40,42,63
P. elongatum (Thunb.)*	*Pn*	..	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	a		22, 42
P. lineare (Er.)*	*Pn,Pc*	.	.	.	.	.	x	.	.	x	.	.	.	.	x	x	.	a,s		63, 67
Plegaderus discisus Er.	*Pn*	..	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	s		40, 42
Plegaderus vulneratus (Panz.)	*Pn,Pc*	..	x	.	.	.	x	.	.	.	.	.	.	.	x		x	a,f,s		18,37,55,63, 67,7 78
<u>Laemophloeidae</u>																				
Cryptolestes fractipennis Motsc	*Pn*	..	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	a		22
C. spartii (Curt.)	*Pn*	..	.	.	.	.	.	x	x	.	.	.	.	.	x	.	.	a		42
Placonotus (Laemophloeus) *testaceus* (F.)	*Fa*	x .	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	a		20
<u>Mycetophagidae</u>																				
Litargus connexus (Fourcr.)	*Pn*	..	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
<u>Nitidulidae</u>		.																		
Epuraea angustula Sturm	*Pc*	..	x	.	.	.	.	.	.	.	.	.	.	.	.	.	x	a		55
E. laeviuscula (Gyll.)*	*Pc*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	a		55
E. marseuli Rtt. (=*E. pusilla* (Ill.))	*Pn*	.	x	x	.	x	x	.	.	x	.	.	.	.	x	x	.	a,f,s	23 eggs/L/day	22,36,55,67,68,77
E. pygmaea (Gyll.)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	x	a,f,s	9 eggs/L/day	55,77,78
E. rufomarginata (Steph.)	*Pn*	.	.	x	.	x	x	.	.	.	.	.	.	.	x	.	.	a,s		22,87
E. silacea (Hbst.)	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
E. thoracica Tourn.*	*Pc,Pn*	.	x	x	.	.	x	.	.	.	.	.	.	.	x	.	.	a		55,78
E. unicolor (Ol.)	*Fa*	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	a		20
Epuraea spp.*	*Pn,Pc*	.	x	.	.	.	x	.	.	x	.	.	.	.	x	x	.	a,f,s		18,55,63,67,70,78 87
Glischrochilus quadripunctatus (L.)* (=*quadripustulatus* (L.))	*Pn,La,Pc*	..	.	.	x	.	.	.	.	.	.	.	.	.	x	.	.	a,f,s		18,36,55,64,67

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obst ye	Killing rate	References[1]
G. hortensis (Fourcr.)*	*Pc*	.	.	.	.	.	x	.	.	x	.	.	.	.	.	x	.	s		63
Ipidia binotata (Rtt.)	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	a		22
(= *Quadrimaculata* Quensel)																				
Pityophagus ferrugineus (L.)	*Pn,Fa*	.	.	.	.	.	x	.	.	.	.	.	.	x	x	.	.	a,s		36,53,67,77
<u>Pythidae</u>																				
Pytho depressus (L.)	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	s		67
<u>Rhizophagidae (=Monotomidae)</u>																				
Rhizophagus bipustulatus F.	*Pc,Pn,Fr*	.	.	.	.	.	x	x	x	.	.	.	.	.	x	.	x	a,s		23,29,36,40,42
R. cribratus Gyll.	*Pc,Pn*	.	x	.	.	x	x	.	.	.	.	.	.	.	.	.	x	a		27
R. depressus (F.)	*Pn,Pc*	x	x	x	.	x	x	.	.	x	.	.	.	.	x	x	.	a,f,s	14 larvae/L 1 larva/A/day 16 eggs/A/day	18,22,27,29,38,55 63,67,68,87
R. dispar (Payk.)	*Pn,Pc*	x	x	x	.	x	x	.	.	.	.	.	.	.	x	x	.	a,f,s	15 eggs/L/day	18,27,29,36,44,55 63,76,78
R. ferrugineus (Payk.)	*Pn,Pc*	.	x	x	.	x	x	.	.	.	.	.	.	.	x	.	x	a,s	79 eggs/A	7,19,22,55,67,77, 87
R. grandis Gyll.	*Pc,Pn*	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	a,f,s	1 larva/L	6,13,14,16,17,25, 26,27,43,73,74,84
R. nitidulus (F.)	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	x	x	a,s		29,36,63,64
R parvulus Payk.	*Pc*	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	s		29
R. perforatus Er.	*Fr,Ul*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	x	s		29
R. puncticollis Sahlb.	*Pc*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	s		27
<u>Salpingidae</u>																				
Rabocerus foveolatus (Liungh)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		76
R. gabrieli (Gerh.)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		76
Salpingus (Rhinosimus) planirostris F.	*Pc*	.	.	.	.	.	x	.	.	x	.	.	.	.	.	x	.	s		63
S. (Rhinosimus) ruficollis (L)	*Pc*	.	.	.	.	.	x	.	.	x	.	.	.	.	.	x	.	s		63

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obst ye	Killing rate	References[1]
Sphaeriestes (Salpingus) castaneus Panz	*Pc*	.	.	.	.	.	x	.	.	x	.	.	.	.		x	.	s		63
Silvanidae																				
Silvanus bidentatus (F.)	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
S. unidentatus (F.)	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
Staphylinidae																				
Aleochara sparsa Heer	*Pc*	.	.	.	.	.	x	.	.	x	.	.	.	.	.	x	.	s		63
Metoponcus brevicornis (Er.)	*Ab*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	s		8
Nudobius lentus (Grav.)	*Pn,La,Pc*	.	x	.	x	.	x	.	.	x	x	.	.	.	x	.	x	a,f,s		18,36,55,58,63,64 70,78,87
Phloeonomus spp.*	*Pn,Pc*	.	x	.	.	.	x	.	.	.	.	.	.	.	x	.	.	a		38,55,78
Phloeopora testacea (Mannh.)	*Pc,Pn*	.	x	.	.	.	x	.	.	.	.	.	.	.	x	.	.	a		55,70
Phloeostiba lapponicus (Zett.)*	*Pc*	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.	a		55
Placusa adscita Er.	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
P. atrata (Mannh.)	*Pc,Be*	.	x	.	.	.	.	.	.	.	.	.	x	.	.	.	x	a,f		55
P. depressa Maekl.	*Pc*	.	x	.	.	.	x	.	.	x	.	.	.	.	x	x	x	a,s	2 eggs/L/day	18,38,55,63
P. tachyporoides (Waltl.)		.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	s		87
Quedius laevigatus Gyll.	*Pc*	.	x	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a,s	7 larvae/A/day	55,87
Q. plagiatus Mannh.	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	s		78
Staphylinidae spp.*	*Pn,Pc, La*	.	.	.	.	.	x	.	.	x	.	.	.	.	x	x	.	a,s		36,38,55,63,64,77 78
Tenebrionidae																				
Corticeus fraxini Kug	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a,f	93 larvae/L 1 larva/A/day	22
C. (Hypophloeus) linearis F.*		.	.	x	.	x	x	.	.	x	.	.	.	.	.	x	.	a,s		18,22,63
C. longulus Gyll.*	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.			62
C. pini Panz.*	*Pn*	.	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	a		42
C. suberis (Luc.)* (= *rufulus* Ros.)	*Pn*	.	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	a		42

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obst ye	Killing rate	References[1]
*C. unicolor** (Pill. Mitt.)	*Pn*	.	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	a		42
Trogossitidae																				
Nemosoma elongatum (L.)	*Pc,Al,* *Pn,Fa*	.	.	.	.	.	x	.	.	x	.	.	.	x	.	.	x	a,f,s	1-2 beetles/A/day 30-45 larvae+pupae+ teneral beetles/L	2,3,10,11,20,28 42,63,69,70,75,81 82,87
DERMAPTERA																				
Forficulidae																				
Forficula auricularia L.		.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	f		64
DIPTERA																				
Asilidae																				
Laphria flava (L.)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	f		79
Choerades (Laphria) gilva (L.)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	f	7 beetles/A/day	79
Tolmerus (Machimus) atricapillus (Fallén)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	f		79
Dolichopodidae																				
Dolichopus sp.	*Qu*	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.	a		85
Medetera ambigua (Zett.)	*Pc,Pn*	.	.	.	.	x	x	.	.	.	.	.	.	.	.	.	.	a		32
M. adjaniae (Goss.)(=*breviseta* Par.)	*Pc*	.	x	.	.	.	x	.	.	x	.	.	.	.	.	.	x	a		46,56,76,78
M. dendrobaena Kowarz	*Pc,Fa*	.	.	.	.	.	x	.	.	x	.	.	.	x	.	x	.	a,s	0.5-10 larvae/L/day	11,52,53,54
M. dichrocera Kowarz	*Pc,Pn*	.	x	.	.	.	x	.	.	x	.	.	.	.	x	.	.	a,f		55,56
M. excellens Frey	*La,Pc*	.	.	.	x	.	x	.	.	.	.	.	.	.	.	.	.	a,f		64,76,78
M. impigra Collin	*Ul,La,Fa*	.	.	.	.	.	.	.	.	.	.	.	x	x	.	.	.	a,f	4-7 larvae/L	4,20
M. infumata Loew	*Pn,Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	x	.	.	a,s		55,77
M. melancholica Lundb.*	*Al,Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	a		55
M. nitida (Macqu.)	*Ul*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	x	a,f	7-11 larvae/L	4,66
M. obscura Zett.*	*Pn*	.	x	.	.	.	.	.	.	.	.	.	.	.	x	.	.	a		55

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obst ye	Killing rate	References[1]
M. pinicola Kow. (=*nuortevai* Thun)	*Pn,Pc*	.	x	.	.	.	x	.	.	.	.	.	.	.	x	.	.	a		55,56,76
M. setiventris Thun.	*Pc,Pn*	.	x	.	.	.	.	.	.	x	.	.	.	.	.	.	x	a		55
M. signaticornis Loew	*Pc,Pn*	.	.	.	.	x	x	.	.	.	.	.	.	.	.	.	.	a		18,32,55,59,70,72 76,77,78
M. striata Parent	*Pn*	.	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.	a		42,55
M. thunebergi Negrob.	*Pc,Pn*	.	.	.	.	x	x	.	.	.	.	.	.	.	.	.	.	a		32
M. vagans Beck.* (=*fennica* Thun.)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	x	a		55
Medetera spp.	*Pc,Pn,Ab* *Qu,Fa*	.	x	.	.	.	x	x	x	x	x	x	.	x	.	.	x	a,f	7-20 larvae+pupae/L 1 larva/L/day	3,20,22,40,54,55 56,58,65,78,85,86
Empididae																				
Drapetis sp.	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22
Lonchaeidae																				
L. bruggeri Morge	*Con*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		48,76,78
L. collini Hackman	*Con*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a,f	1 larva/L/day	22,48
L. fugax Becker	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		70
L. helvetica MacGowan	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		76
L. laticornis Meigen*	*Ab*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	a		8
L. scutellaris Rondani	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		48,76
L. seitneri Hendel	*Con*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	a		48
L. zetterstedti Becker*	*Pc,Pn*	.	.	.	.	x	x	.	.	.	.	.	.	.	.	.	.	a		32,48,76
Milichiidae																				
Madiza glabra Fallén*	*La*	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	a		64
Muscidae																				
Phaonia gobertii (Mik)*	*Pn,La*	.	.	.	x	.	x	.	.	.	.	.	.	.	.	.	.	a		32,64
Phaonia sp.	*Pn*	.	.	.	.	x	x	.	.	x	x	.	.	.	x	.	.	a,f		22,58
Pallopteridae																				

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obst ye	Killing rate	References[1]
Palloptera ustulata Fallén		.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.			34
Toxoneura (Palloptera) usta (Meig.)	*Con*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	a,s		9,49,70,76
Stratiomyidae																				
Zabrachia minutissima (Zett.)*		.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a,s		77
Z. tenella (Jaenn.)*		.	.	.		.	.	.	.	.	.	.	.	.	.	.	.	a		35
HETEROPTERA																				
Anthocoridae																				
Lyctocoris campestris (F.)	*Pn*	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	a		22
Scoloposcelis obscurella (Zett.)	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a	4.7 larvae/L/day 25 larvae/A/day	22
S. pulchella (Zett.)	*Pn,Pc*	.	x	x	.	x	x	x	x	x	x	.	.	.	x	.	.	a,f	39-144 larvae/L	11,21,22,40,42,58
Xylocoris cursitans (Fallén)	*Pn*	.	.	x	.	x	.	.	.	.	.	.	.	.	x	.	.	a,f	44 larvae/L 4 larvae/A/day	22
HYMENOPTERA																				
Formicidae																				
Formicidae spp.		.	.	.	.	.	.	x	.	.	.	.	.	.	.	.	x	f		39,83
NEUROPTERA																				
Chrysopidae																				
Chrysoperla carnea (Steph.)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		76
ODONATA																				
Anisoptera spp	*Pn*	.	.	x	.	.	.	.	.	x	x	.	.	.	x	x	x	f		30
RAPHIDIOPTERA																				
Raphidiidae																				
Dichrostigma (Raphidia) flavipes (Stein)	*Pc*	.	.	.	x	.	x	.	.	.	.	.	.	.	.	.	.	a		64,80
Phaeostigma (Raphidia) notata (F.)	*Pc*	.	.	.	x	.	x	.	.	.	.	.	.	.	.	.	.	a		64,80
Phaeostigma sp.	*Pn*	.	.	.	.	x	.	.	.	.	.	.	.	.	x	.	.	a		22

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obst ye	Killing rate	References[1]
Puncha ratzeburgi (Brau.)	*Pc*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	a		76
ACARI																				
Acarophenacidae																				
Paracarophenax ipidarius (Redik.)*		.	.	.	x	.	x	.	.	.	.	.	.	.	.	.	x	a		24,50,51
Ascidae																				
Lasioseius ometes Oud.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	a		71
Proctolaelaps fiseri (Vitzt.)		.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	a		71
P. pini Hirsch.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	a		71
P. xyloteri Sams.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	a		71
Digamasellidae																				
Dendrolaelaps apophyseosimilis Hirsch		.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	a		71
Dendrolaelaps spp.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.	a		71
Pyemotidae																				
Pyemotes dryas (Vitzt.)		.	.	.	.	.	x	.	.	x	x	.	.	.	.	.	.	a		24,50,51
P. herfsi (Oud.)		.	.	.	.	.	.	.	.	.	.	.	x	.	x	.	.	a		24
P. scolyti (Oud.)	*Ul*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	a,f		5,12,24,33
Tarsonemidae																				
Iponemus gaebleri (Schaar.)		.	.	.	.	x	x	.	.	.	.	.	.	.	.	.	x	a		24,31,50,51
Uropodidae																				
Trichouropoda bipilis (Vitzt.)	*Fr*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x	a		23
ARANEAE																				
Erigonidae																				
Troxochrus nasutus Schenkel		.	x	.	.	.	.	.	.	x	.	.	.	.	.	.	.	a		47
AVES																				
Fringillidae																				
Fringilla coelebs L.		.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.	f		72

Table 4 (cont.)

Predator	Host tree	*D. mic.*	*H. pal.*	*I. acu.*	*I. cem.*	*I. sex.*	*I. typ.*	*O. ero.*	*P. cal.*	*P. cha.*	*P. pol.*	*S. int.*	*S. spp.*	*T. bic.*	*T. spp.*	*T. lin.*	*Spp*	Obst ye	Killing rate	References[1]
Picidae																				
Dendrocopos major (L.)	*La,Qu*	.	.	.	x	.	.	.	.	.	.	x	.	.	.	.	.	f		64,60
Dryocopus martius L.	*La*	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.	f		64
Picoides syriacus (Hemp. & Ehr.)	*Pn,Ol,Pr Cu,Ul*	.	.	.	.	.	.	x	x	.	.	.	x	.	x	.	.	f		39
P. tridactylus (L.)	*Con*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.	x	f	1200 adults/day (estimate)	57,61
Picoides sp.	*Qu*	.	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.			85

[1] References: 1 Allen (1975); 2 Baier (1991); 3 Baier (1994); 4 Beaver (1966); 5 Beaver (1967); 6 Bergmiller (1903); 7 Byers (1992); 8 Capek (1957); 9 Chandler (1991); 10 Dippel (1996); 11 Dippel *et al.* (1997); 12 Doberski (1980); 13 Fielding and Evans (1997); 14 Fielding *et al.* (1991b); 15 Gauss (1954); 16 Grégoire *et al.* (1991); 17 Grégoire *et al.* (1992b); 18 Grodzki (1997); 19 Hanson (1937); 20 Harz and Topp (1999); 21 Heidger (1994); 22 Herard and Mercadier (1996); 23 Hintze-Podufal and Druschke (1988); 24 Kielczewski *et al.* (1983); 25 King *et al.* (1991); 26 Kobakhidze (1965); 27 Kolomiets and Bogdanova (1980); 28 Kopf and Funke (1998); 29 Kubisz (1992); 30 Labedzki (1989); 31 Levieux *et al.* (1989); 32 Lieutier (1979); 33 Lipa and Chmielewski (1977); 34 Martinek (1977); 35 Matile (1993); 36 Mazur (1973); 37 Mazur (1975); 38 Mazur (1979); 39 Mendel (1985); 40 Mendel (1988); 41 Mendel *et al.* (1989); 42 Mendel *et al.* (1990); 43 Merlin *et al.* (1984); 44 Merlin *et al.* (1986); 45 Mills (1985); 46 Mills (1986); 47 Moor and Nyffeler (1983); 48 Morge (1963); 49 Morge (1967); 50 Moser and Bogenschütz (1984); 51 Moser *et al.* (1989); 52 Nicolai (1995c); 53 Nicolai (1996); 54 Nicolai *et al.* (1992); 55 Nuorteva (1956); 56 Nuorteva (1959); 57 Otvos and Stark (1985); 58 Ounap (1992a); 59 Ounap (1992b); 60 Pavlik (1999); 61 Pechacek (1994); 62 Pishchik (1980); 63 Rauhut *et al.* (1993); 64 Schimitschek (1931); 65 Schopf and Köhler (1995); 66 Schröder (1974); 67 Schroeder and Weslien (1994); 68 Schroeder (1996); 69 Schumacher and Pohris (2000); 70 Seitner (1924); 71 Strube and Benner (1984); 72 Thalenhorst (1958); 73 Tømmerås *et al.* (1984); 74 Wainhouse *et al.* (1992); 75 Wegensteiner and Führer (1991); 76 Wermelinger (2002); 77 Weslien and Schroeder (1999); 78 Weslien (1992); 79 Wichmann (1956); 80 Wichmann (1957); 81 Wigger (1993); 82 Wigger (1996); 83 Wilkinson *et al.* (1978); 84 Wyatt *et al.* (1993); 85 Yates (1984); 86 Zinovjev (1957) [in Morge (1961)]; 87 Zumr (1983°;

[2] Host trees: *Ab: Abies; Al: Alnus; Be: Betulus;* Con: Conifers*; Cu: Cupressus; Fa: Fagus; Fr: Fraxinus; La: Larix; Ol: Olea; Pc: Picea; Pn: Pinus; Pr: Prunus; Qu: Quercus;Ul: Ulmus*

the prey in the gizzard of three-toed woodpeckers were larvae of buprestid beetles (Otvos and Stark 1985) while in a German study, the faeces of the same species consisted of 89 % of *I. typographus* (Pechacek 1994). When foraging on bark beetle broods, woodpeckers prefer the later and larger instars (Kroll and Fleet 1979). At the same time, they also devour predatory and parasitic insects living underneath the bark.

Indirect effects of woodpecker activity by puncturing, loosening and removing bark can cause more bark beetle mortality (due to desiccation, other predation, diseases) than direct woodpecker foraging (Moore 1972; Otvos 1979). They can debark large proportions of infested trunks (Hintze-Podufal and Druschke 1988). Only a fraction of the brood in bark flakes dropping to the ground survives to emergence (Kroll and Fleet 1979). Mortality imposed by woodpeckers may vary significantly among single trees, ranging from 5 to 70 % (Shook and Baldwin 1970; Moore 1972; Massey and Wygant 1973; Berryman 1976; Amman 1984; Pavlik 1999). They are most significant in endemic situations, in local outbreaks, or during the decline of an outbreak (Otvos 1979). Woodpecker impact is highest in the upper tree parts where bark beetle densities are highest, during winter and spring (Moore 1972). Woodpecker populations are positively influenced by bark beetle outbreaks.

4. QUANTITATIVE ASSESSMENT OF PARASITOIDS AND PREDATORS AND THEIR ROLES IN THE POPULATION DYNAMICS OF SCOLYTIDAE.

It is difficult to quantify the effects of predators on bark beetles. The consumption of prey in the field is hard to measure, and predators may not only forage on the target bark beetle, but also on other subcortical insects, including predators and parasitoids (Mendel *et al.* 1990) and therefore reduce the overall detrimental effect on a bark beetle population. For example, *Thanasimus formicarius* is an important mortality factor for *Medetera* larvae (Nuorteva 1959).

In contrast, most studies on parasitoids of Scolytidae have provided some quantitative evaluations of parasitism, either as parasitism rates, or as relative abundance of parasitoid species. Parasitism rates varying from 0 to 100% have been found. However, parasitism rates and consumption rates are poor indicators of the real impact of natural enemies on bark beetle populations. Several authors state that natural enemies do not play an important role in regulating bark beetle populations (e.g. Sachtleben 1952; Bombosch 1954; Faccoli 2001a) whereas a few others affirm the contrary (e.g. Mendel 1987), but few of these statements are based on solid data. To better evaluate the impact of parasitoids and predators on bark beetle populations, various methods have been used, such as consumption rate based assessments (e.g. Dippel *et al.* 1997; Wermelinger 2002), life table analyses, and natural enemy exclusion experiments. Life tables are not easy to construct for bark beetles because of the problem of overlapping generations. On the other hand, their cryptic biology may facilitate population studies because the cause of death and the stage at which it occurs can usually be assessed through regular bark examination. Furthermore, the effect of population densities on mortality factors can be assessed easily because sample logs can be considered as separate populations, with different beetle densities. In his study on *Scolytus scolytus* in the UK, Beaver (1966b, 1967b) was among the first to use a life table (or, better, population table) approach to assess the various mortality factors on bark beetles and their role in population regulation. He stated that populations are likely to be regulated by different mechanisms at different population densities. Among the main mortality factors were subcortical predators (mainly *Medetera* spp.) and larval ectoparasitoids (mainly *Coeloides scolyticida* Wesmael). Predators showed a density-dependent response at low beetle densities, but became inversely density-dependent at higher densities. In contrast, the ectoparasitoids showed a density-dependent response only above a certain host density. This suggests that subcortical predators have regulatory power at low beetle densities whereas ectoparasitoids compensate at high densities, together with other factors such as intraspecific competition. The roles of woodpeckers and the egg-larval endoparasitoid *Entedon ergias* were less clear. Similar studies on *Leperisinus varius* (Lozano *et al.* 1993, 1994) and *Phloeotribus scarabaeoides* (Lozano *et al.* 1996a, 1996b) showed that populations were regulated by density-dependent larval mortality, due to larval competition and ectoparasitism. However, in both bark beetles, larval parasitism alone tended to show an inversely density-dependent response. Other similar studies were made in North America. In a time-series analysis of populations and antagonists of the North American bark beetle *Dendroctonus frontalis* Zimmermann, delayed density dependency was shown (Turchin *et al.* 1999), suggesting that antagonists are more important during the decline phase of an outbreak than at the beginning. This is supported by another study on *Dendroctonus ponderosae* Hopk. that assigned predators (except clerids) and parasitoids a more significant role in epidemics than in endemic situations (Amman 1984). In a two-year study during an *Ips typographus* infestation in Switzerland, Wermelinger (2002) observed that predators were more abundant in the first year, at the peak of bark beetle density, whereas parasitoids dominated in the second year, when overall beetle mortality increased and populations collapsed.

Mills (1986) and Mills and Schlup (1989) produced basic partial life tables of *I. typographus* in Switzerland and Germany. They suggested that clerid predators *Thanasimus* spp. and larval ectoparasitoids had a significant influence on brood survival. They showed that parasitism may vary with tree height (e.g. parasitism by braconids being much higher at the top of the tree), although the relation between parasitism and bark thickness was unclear. Wermelinger (2002) also found higher parasitism on *I. typographus* at the top of the tree than at the bottom.

Natural enemy exclusion experiments provide an elegant method to better assess the impact of natural enemies on bark beetle populations, but have rarely been carried out in Europe. Notable exceptions are the works by Weslien (1992) and Schroeder and Weslien (1994) who, in Sweden, observed a reduction of *I. typographus* and *Tomicus piniperda* populations of 83-89% compared to caged populations where parasitoids and predators were excluded. Related studies in North America also showed that parasitoids and predators can reduce bark beetle populations to a similar extent (e.g. Linit and Stephen 1983; Riley and Goyer 1986).

5. UTILISATION OF PARASITOIDS AND PREDATORS IN BIOLOGICAL CONTROL PROGRAMMES

Although the justification of most studies on parasitoids was their potential use in biological control strategies against scolytids, only few biological control programmes have been implemented. The most important has been the biological control of *Dendroctonus micans* in Georgia, Turkey, UK and France.

D. micans, originally a Siberian species, has been increasing its range continuously during the 20th century, and most of the time it was closely followed by *Rhizophagus grandis*. The impact of this predator was observed very early in Germany, after the establishment of both species (Bergmiller 1903). The first biocontrol programme involving *R. grandis* was developed in the Georgian SSR, after *Dendroctonus micans* invaded the region during the 1950s (Kobakhidze 1965). A small number of adult and larval predators was imported from Czechoslovakia, released in 1963 and established successfully in the local *D. micans* infestations. By 1970, 54,000 predators had been released (Tvaradze 1976), and by 1976 a series of rearing units was established, producing insects on logs infested with *D. micans*. From Georgia, *D. micans* progressed into Turkey, where a biocontrol programme has also been implemented.

In 1983, as *D. micans* was progressing through the French Massif Central, a Belgian-French programme was developed (Grégoire *et al.* 1985). Semi-artificial rearing methods using an artificial diet and oviposition stimulants were established and, in the period 1983-1991, 659 sites (12,275 ha; public as well as private forest) had been treated, usually with rather large releases (500-1000 pairs/site). The sites situated at the borders of the infested area were treated first, to take advantage of the lower pest density there, and to try limiting the spread of the pest. During 1983-99, a total of 530.000 insects were produced and released. Predator establishment and impact were closely followed in a series of permanent plots and in more temporary surveys. The predator releases were always followed by establishment and, within 6-8 years, by the collapse of the bark-beetle populations (see e.g. Van averbeke and Grégoire 1995). At present, *D. micans* is still expanding (Aveyron, Orne), justifying the need for further releases. A potential development is the monitoring of pest and predator movements using kairomone traps that attract *R. grandis* (Grégoire *et al.* 1992).

Also in 1983, following the discovery of *D. micans* in the north-west of England and in Wales (Bevan and King 1983), a rearing and release programme started in the UK (Fielding *et al.* 1991; Evans and Fielding 1994; Fielding and Evans 1997). Combined with internal quarantine procedures and the deployment of a pest-free zone around the infested area, predators were released in all sites. In order to cover as many sites as possible, release rates were adjusted to 10-50 pairs/site (average: 57 individuals/site). Between 1984 and 1995, 156,400 insects were released in 2,741 sites (public and private forest). Establishment of *R. grandis* and subsequent control of *D. micans* was observed at the same rates as elsewhere. As *D. micans* is still expanding, the biocontrol programme is continuing.

Finally, *R. grandis* is also being used in a neo-classical biological control programme against a close relative of *D. micans*, *D. valens*, a north-American species which invaded China in the late 1990's. Following promising laboratory results (Miller *et al.* 1987), *R. grandis* is presently being mass-reared in China for releases in the Shanxi Province (Yang Zhong-qi, pers. comm.).

The programme against *D. micans* was the only classical biological control (i.e. the introduction and establishment of exotic natural enemies to control a pest), that has ever been carried out against scolytids in Europe, mainly because few exotic scolytids have invaded Europe, and these are, presently, not the most damaging species. Conversely, European parasitoids have often been considered for release against European scolytids that have established in other parts of the world. Several parasitoids of the European elm bark beetle, *Scolytus multistriatus*, vector of the Dutch elm disease, were introduced into North America, either accidentally (*Entedon ergias* and *Cheiropachus quadrum*) or intentionally (*Dendrosoter protuberans, Ecphylus silesiacus* and *Coeloides scolyticida*, but only *D. protuberans* became established) (Van Driesche *et al.* 1996). A full evaluation of the biological control programme was not made. The pteromalid parasitoid *Rhopalicus tutela* and several predators, *Thanasimus formicarius*, *Rhizophagus dispar*, *R. bipustulatus* and *R. ferrugineus*, were introduced against *Hylastes ater* in New Zealand, after its accidental introduction from Europe, despite the fact that these natural enemies were rarely, or never found in association with *H. ater* in Europe. Only *T. formicarius* became established, but its incidence appears limited. (Faulds 1989). *Metacolus unifasciatus*, *Dendrosoter chaenopachoides* and several predators were released against the European *Orthotomicus erosus* in South Africa (Kfir 1986). *D. chaenopachoides* became established and is now spreading (Tribe and Kfir 2001).

T. formicarius was sent from Germany to the US in 1882-83 against *Dendroctonus frontalis*, but this attempt did not succeed (Moeck and Safranyik 1984). Later, Mills and his colleagues (e.g. Mills 1985; Mills and Schlup 1989; Krüger and Mills 1990; Mills *et al.* 1991) studied the parasitoids and predators of European conifer bark beetles in relation to potential biological control of *Dendroctonus* spp. in North America. *T. formicarius* was sent to Canada for laboratory studies and rearing (Safranyik *et al.* 2002). It was decided not to release it because of its possible impact on other bark-beetle competitors of *D. ponderosae*, and because laboratory experiments had demonstrated that crossbreeding with the native *T. undatulus* to produce fertile hybrids was possible. Later on, in 1995-96, *T. formicarius* was again considered for classical biological control, against *Tomicus piniperda* in the US. However, its introduction was postponed because of its possible impact on non-target prey and the risk of competitive displacement of native predators (Haack *et al.* 1997). Interestingly, *T. formicarius* was also introduced in 1908 from Great-Britain into Sri Lanka against *Xyleborus fornicatus* on tea, but was never retrieved from the field (Clausen 1978).

Programmes to conserve or augment parasitoids and predators of scolytids have never been seriously attempted in Europe, with the notable exception of mass releases of parasitoids against the small elm bark beetle, *S. multistriatus*, in Granada, southern Spain, as part of integrated management of Dutch elm disease (González *et al.* 1999). Over 1 million specimens of seven parasitoid species were released from 1995 to 1997. Parasitism increased from 6 to 20 %, and, at the same time, the level of tree infection and of bark beetle populations decreased substantially, but it is not clear whether the release of parasitoids played any role in these decreases.

In Sweden, Weslien (1992) observed that less than 10% of *Ips typographus* populations overwinter in logs, whereas the large majority of its natural enemies do. He suggested that log removal after the emergence of bark beetles in summer should be avoided, to preserve parasitoids and predators. Similarly, to control the olive beetle *Phloeotribus scarabaeoides*, in southern Spain, González and Campos (1991) suggested removal of infested wood in late June, just before the emergence of the beetle, when most of the parasitoids have already emerged.

Kairomones may be used to attract natural enemies and augment their impact. Schroeder and Weslien (1994) used logs baited with ethanol and alpha-pinene to attract antagonists of *T. piniperda*, and observed a significant reduction of beetle populations compared to unbaited logs. Grégoire *et al.* (1992) and Pettersson (2001a, 2001b) determined that oxygenated monoterpenes present in infested trees play an important role in host/prey location in *Rhizophagus grandis* on *Dendroctonus micans* and in parasitoids of *I. typographus,* respectively*,* and suggested the use of these compounds to enhance the role of natural enemies.

Control methods may be detrimental to parasitoids and predators and efforts should be made to limit these detrimental effects. Weslien and Schroeder (1999) observed that predators were more numerous in unmanaged than in managed spruce stands. Similarly, the application of pheromone traps may pose a problem in integrated bark beetle management. Since many predators and parasitoids react to the same semiochemicals as their prey or host, commercial pheromone traps may trap out significant amounts of these beneficials (Nebeker *et al.*, 1984). For pheromone traps against bark beetles it was calculated that the *Nemosoma elongatum* individuals caught in the traps would have eaten a multiple of the number of bark beetles caught in these traps (Baier 1991; Wigger 1993; Schumacher and Pohris 2000). Optimised blends of semiochemicals and application times may minimise such detrimental effects (Raffa 1991; Aukema *et al.* 2000).

6. CONCLUSIONS AND FUTURE RESEARCH

Parasitoids and predators have been studied more extensively in bark beetles than in any other forest insect pests in Europe, which illustrates the significance of Scolytidae in European forestry. Substantial progress was made in recent years in the understanding of various aspects of the ecology of parasitoids, such as host location, competitive interactions, etc. However, many gaps in our knowledge remain. First of all, most studies concentrated on a few scolytid species whereas the natural enemy complex of many others is largely unknown. This probably reflects the relative importance of the different pest species. However, most natural enemies are not host- or prey-specific and a better knowledge of the natural enemies of secondary pests would help in understanding the natural control of the primary pests, which can lead to the development of control strategies. Secondly, there is wide variation in knowledge of the different groups of natural enemies. In general, parasitoids have been more extensively studied than predators, although there is no evidence suggesting that parasitoids are more important natural regulators than predators. Among parasitoids, adult parasitism has been much less investigated than parasitism on larvae. Most studies on predators focused on *Thanasimus formicarius* and *Rhizophagus grandis*, whereas the biology, ecology and impact of other species and groups remain largely unknown. More generally, the role of natural enemies in the population dynamics of scolytids needs to be better assessed, to evaluate their importance as regulatory factors and to develop strategies to enhance their impact.

Despite extensive research on the natural enemies of scolytids, few attempts have been made to use this knowledge in biological control strategies, with the notable exception of the *Dendroctonus micans*/*Rhizophagus grandis* programmes. Classical biological control (i.e. the introduction of an exotic natural enemy into a new area for permanent control) is better used against exotic species and, thus, is not targeted for the main scolytid pests in Europe. However, because of the increase of international wood trade, introductions of exotic bark- and wood boring insects are rising worldwide. New introductions are expected in Europe, both from other continents and other European regions (e.g. many European bark beetles, including *Ips typographus,* are still absent from the British Isles). Classical biological control could be envisaged as part of management strategies against new introduction. Biological control by augmentation (i.e. regular releases of laboratory reared/produced natural enemies) is technically possible, since many parasitoids and predators can be mass reared, but it will probably never be economically profitable in forestry, given the large areas involved and their low productivity. However, it may be considered for protection of particularly valuable trees, such as the elm trees of the Alhambra in Granada (González *et al.* 1999), or in orchards (e.g. *Phloeotribus scarabaeoides* and *Leperisinus varius* in olive groves). Biological control by conservation (i.e. the conservation and enhancement of native natural enemies already present on-site) is probably the most promising strategy against scolytid pests. Forestry practices could be modified to favour the action of native parasitoids and predators and to enhance the natural control of forest pests. Various techniques have been suggested, based on, for example, wood removal dates, use of kairomones, etc. (see section 5, above), and many more could be developed. These strategies, however, require an excellent knowledge of the biology and ecology of parasitoids and predators. More data still need to be gathered on many traits, such as natural enemy impact and population dynamics, host location mechanisms, biologies of adult parasitoids and predators in the field, specificity and interactions with alternative hosts and prey, etc. Furthermore, since such strategies would have to be adapted to particular regions and field situations, they would rely on the skills of foresters and other forest practitioners, who would have to be trained specifically for these tasks.

Taxonomy and identification of natural enemies is another field that would need more research. There is a serious lack of knowledge, particularly in the systematics of parasitoids attacking bark beetles. There are too few specialists in Europe, too many groups of parasitoids that are not properly covered, and the identification keys are not accessible for applied entomologists. A correct identification of natural enemies is an essential component of any biological control programme.

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