

Oviposition, life cycle, and parasitoids of the spruce cone maggot, *Strobilomyia anthracina* (Diptera: Anthomyiidae), in the Alps

E.G. Brockerhoff* and M. Kenis

International Institute of Biological Control, European Station, 1 Chemin des Grillons, 2800 Delémont, Switzerland

Abstract

The life cycle of *Strobilomyia anthracina* (Czerny) which exploits Norway spruce seed cones was investigated in 1992 and 1993 in the Alps at c. 1800 m at Torgnon (Valle d'Aosta, Italy) and Lac de Tseuzier (Valais, Switzerland) by sampling cones at fortnightly intervals. Oviposition occurred primarily singly in the basal third of cones at the beginning of June when cone scales were open for pollination. Infestation rates were higher when cone crops were poor. Most larvae left the cones in August to pupate in the litter beneath trees, usually at a depth of 1–4 cm. Prolonged diapause of pupae coincided with failed or poor cone crops. Parasitism was investigated at these two and 27 additional sites in the Swiss, French and Italian Alps. Among several hundred host eggs only one was parasitized by *Trichogramma* sp. (Trichogrammatidae). Among the larval–pupal endoparasitoids, the figitid *Sarothrus areolatus* Hartig was more common than an ichneumonid, *Atractodes* sp., but parasitism by both was commonly below 10%. Parasitism by an ichneumonid larval ectoparasitoid, *Scambus* sp., also rarely exceeded 10%. Puparia of *S. anthracina* that were buried in the litter to detect pupal parasitoids revealed the gregarious pteromalid *Tritneptis* sp. near *lophyrorum* (Rushka). This is the first record of a pupal parasitoid of *Strobilomyia* species. Information on the biology of the three larval parasitoids is presented. The potential for biological control of North American *Strobilomyia neanthracina* Michelsen and *S. appalachensis* Michelsen by importation of natural enemies of *S. anthracina* appears limited.

Introduction

The recent development of seed orchards, to provide genetically superior seed for reforestation programmes, has increased concerns about seed losses to insect pests. *Strobilomyia* spp. (Diptera: Anthomyiidae), commonly known as cone maggots, are important pests of conifer seed cones and may destroy entire crops in Europe and North America (e.g. Stadnitskii *et al.*, 1978; Roques, 1983; Roques *et al.*, 1984;

de Groot *et al.*, 1994). All *Strobilomyia* species attack only one or a few conifer species of the same genus (Michelsen, 1988). *Strobilomyia anthracina* (Czerny) attacks cones of Norway spruce, *Picea abies*, in Europe and northern Asia (Stadnitskii *et al.*, 1978) and several other spruce species in eastern Asia (Suwa, 1971; Fang *et al.*, 1989). *Strobilomyia anthracina* was believed to be a Holarctic species, but a review identified the North American spruce cone maggots as *S. neanthracina* Michelsen and *S. appalachensis* Michelsen (Michelsen, 1988; Turgeon & Sweeney, 1993).

Chemical means for control of cone maggots are available (e.g. Annala, 1973; Miller & Hutcheson, 1981), but such treatments may have adverse environmental effects and

*Present address: Canadian Forest Service, Great Lakes Forestry Centre, PO Box 490, Sault Ste. Marie, Ontario, P6A 5M7, Canada.

require annual expenditure for control. Biological control could provide environmentally safe and long-lasting, and therefore potentially inexpensive control. Biocontrol programmes require detailed knowledge of the target species' biology and associated natural enemies. Some information on the biology of *S. anthracina* and its parasitoids is already available for parts of north-eastern Europe (Kangas & Leskinen, 1943; Stadnitskii *et al.*, 1978; Annila, 1981), but for central Europe it is limited (e.g. Roques, 1983). In particular, oviposition has not previously been studied in detail, and there is no information on pupal parasitism. This manuscript presents additional information on the life history of *S. anthracina* and its parasitoids and a description of the phenological relationships of Norway spruce seed cones, cone maggots and parasitoids in Central Europe. The prospects for biological control of North American spruce cone maggots by introduction of natural enemies of *S. anthracina* are also discussed.

Materials and methods

This study was carried out in parts of the Swiss, French

and Italian Alps (table 1). To investigate the phenology of *S. anthracina* and its parasitoids, cones of *P. abies* were collected at Torgnon and Tseuzier in 1992 and 1993, at fortnightly intervals from late May to the end of September. On each sampling date, cones were taken equally from five randomly selected trees per site, and trees were sampled once per year. Cones were collected systematically and evenly from all crown regions, either by climbing trees or, from smaller trees, with a pole pruner. From mid-July onwards, when infested cones became bent and resinous, only such cones were collected. Sample sizes per site ranged from 50 to 200 cones in 1992 and from 10 to 25 cones in 1993, when cones were scarce. To study egg parasitism, additional samples of 50 cones were taken at the end of the oviposition period of *S. anthracina* at Martigny and San Bernardino in spring 1993. All cones were kept at 2°C and dissected within a few days. Length of cones was determined prior to dissection and all observations were categorized into longitudinal thirds. Eggs were reared in petri dishes kept inside plastic containers with moist paper until the larvae hatched or the parasitoids emerged. All larvae were dissected for parasitoids.

Table 1. Collection sites of *Strobilomyia anthracina*, sample sizes and endoparasitism.

Country and location	Political district	Altitude (m)	Year	No. of <i>Strobilomyia</i> examined		No. of L3 and puparia parasitized by (% parasitism):	
				eggs and early instars	L3 and puparia	<i>Sarothrus arvolatus</i>	<i>Atractodes</i> sp.
Switzerland							
Cunter	Graubünden	1190	1992	–	7	–	–
Maloja	Graubünden	1810	1992	–	67	–	–
Mulegns	Graubünden	1460	1992	–	12	–	–
San Bernardino	Graubünden	1630	1992	–	46	–	–
S-chanf	Graubünden	1650	1992	–	64	1 (1.6)	–
Scuol	Graubünden	1520	1992	–	7	–	–
Susch	Graubünden	1530–1720	1992	–	106	–	–
			1993	–	33	6 (18.2)	–
Zernez	Graubünden	1510–1750	1992	–	147	1 (0.7)	3 (2.0)
Aven	Valais	1100	1994	–	4	–	–
Ayent	Valais	1150–1230	1992	–	124	–	2 (1.6)
			1994	–	16	–	–
Derborence	Valais	1400	1994	–	15	1 (6.7)	–
Grimentz	Valais	1520	1992	–	3	–	–
La Morge	Valais	1100	1994	–	21	–	–
Martigny	Valais	620	1993	8	31	2 (6.5)	2 (6.5)
Pomeiron	Valais	950	1994	–	3	–	–
Tseuzier (Lac de)	Valais	1500–1770	1992	186	171	5 (2.9)	4 (2.3)
			1993	4	29	3 (10.3)	–
Vercorin	Valais	1030	1994	–	9	–	–
Zinal	Valais	1700	1994	–	5	–	–
Col de la Croix	Vaud	1570	1992	–	6	–	–
Bedretto	Ticino	1660	1992	–	42	–	–
France							
Col du Corbier	Haute Savoie	1210	1992	–	8	2 (25.0)	–
La Rosière	Savoie	1440	1992	–	14	–	–
Les Saisies	Savoie	1650	1992	–	31	–	–
Roselend	Savoie	1590	1992	–	8	–	–
Villard sur Doron	Savoie	1480	1992	–	42	–	–
Italy							
Arpy	Aosta	1640	1992	–	16	–	–
La Thuile	Aosta	1780	1992	–	11	–	–
Torgnon	Aosta	1710–1950	1992	247	350	2 (0.6)	–
			1993	22	18	2 (11.1)	–
			1994	–	92	–	–
Vens	Aosta	1900	1992	–	27	–	–

To study the abundance and distribution of the endoparasitoids of *S. anthracina*, a total of 4693 infested cones (at least 50 per site) was sampled at 22 sites in 1992, four sites in 1993 and at eight sites in 1994 (table 1). These samples were taken shortly before the larvae left the cones to pupate in the litter, i.e. between the end of June and mid-August, depending on stand elevation. Cones were placed on an 8 mm mesh screen over water-filled plastic trays into which the larvae dropped when they exited the cones. Twice a day, larvae were removed from the trays and put on moist sifted soil in which they pupated. To assess mortality and parasitism, all puparia were dipped into water. This makes them translucent and easier to examine with a stereo microscope. (Healthy, dead or parasitized puparia contain either whitish pupae, an amorphous substance or air, or parasitoid larvae, respectively.) Puparia were overwintered outside in clay pots filled with sifted soil and covered with gauze (0.3 mm mesh) for protection from predators, but not from moisture. The following spring, all puparia were sifted from the soil, placed in petri dishes and allowed to complete their development in the laboratory. Unhatched puparia were re-examined to assess mortality that had occurred during overwintering.

At all collection sites, the size of the cone crop was recorded, using binoculars if necessary. For each stand, the number of seed cones per tree was counted or, if cone crops were high, estimated. The mean of at least ten trees was used to assign cone crops to one of four classes of cone production: none (0 cones per tree), low (1–10 cones per tree), medium (10–100 cones per tree), and high (more than 100 cones per tree).

Larval ectoparasitism was studied at Tseuzier and Torgnon in 1992 and 1993 and at Martigny in 1993 and calculated as follows: % ectoparasitism = no. of parasitized larvae / (total no. of larvae + no. of empty tunnels). As ectoparasitoids kill cone maggots before they can exit the cone, those that had left the cones to pupate in the litter (i.e. empty tunnels) were included in the total number of hosts.

Depth of pupation of *S. anthracina* was determined by placing c. 200 mature larvae onto moistened sifted soil in an 11 cm diameter plastic container buried outside in the ground. After pupation, layers of 1 cm were sifted to a depth of 24 cm to recover the puparia.

To investigate pupal parasitism and predation, a total of 527 mature larvae or fresh puparia were exposed at several sites (between 50 and 148 per site) c. 1 cm deep in wooden cages (30 × 30 × 5 cm) filled with sifted soil. Cages with a screen bottom (2 mm mesh) and top (8 mm mesh) to exclude vertebrate predators, were buried underneath spruce trees and covered with a 2 cm layer of forest litter. From September 1992 to April 1993, *S. anthracina* were exposed at Torgnon and Tseuzier and then transferred to the laboratory for emergence. Puparia were also exposed from July/August to September at Ayent in 1994 and 1995 and at Tseuzier in 1995. Additionally, puparia were extracted from five samples of forest litter and humus (50 × 50 cm, 10 cm deep) taken under infested trees at Tseuzier in September 1993 by sifting or soaking the samples in water.

Terminology for descriptions of parasitoid larvae is according to Short (1959) and Hagen (1964). Statistical analysis was performed using SYSTAT 5.03 for Windows™ or generated by hand. The frequency distribution of eggs was determined by goodness-of-fit comparison with a

Poisson distribution (Ludwig & Reynolds, 1988). If it deviated significantly, the index of dispersion and the d-statistic were calculated (Ludwig & Reynolds, 1988) to determine whether the distribution was clumped or regular.

Results and discussion

Oviposition and life cycle

The emergence of adult *S. anthracina* was not determined in the field, but they were observed flying around spruces and ovipositing in late May at Torgnon. The phenology presented (fig. 1) refers to observations made at Torgnon in 1992. The phenology was similar at Tseuzier in 1992, but in 1993 larval exit was already complete by mid-August at both Torgnon and Tseuzier (Brockerhoff, 1994). *Strobilomyia anthracina* oviposited between the cone scales of Norway spruce from late May onwards, usually when the scales were open.

Almost 70% of *S. anthracina* eggs were laid in the basal third of cones, none were found in the apical third (fig. 2). Single eggs were most common in infested cones (fig. 3), but when the cone crop was low, cones contained up to six *S. anthracina* eggs (1993 at Martigny). At Torgnon, eggs were not Poisson distributed ($\chi^2 = 8.56$, 2 df, $P < 0.01$) but had been laid regularly (index of dispersion = 0.74, d-statistic = -2.84, $P < 0.01$). However, at Tseuzier the frequency distribution did not significantly deviate from a Poisson distribution ($\chi^2 = 4.73$, 1 df, $0.1 > P > 0.05$). Single eggs were also most common in cones of *Picea mariana* attacked by *S. appalachensis* (Sweeney & Turgeon, 1994). Such regular oviposition may be due to an oviposition deterring pheromone (Sweeney & Turgeon, 1994) which reduces intraspecific competition.

Infestation rates, determined at the end of the oviposition period, appeared to be negatively correlated with the level of cone production. In 1992, when the cone crop was high at all sample sites, 35% of the cones (n=350) were infested by *S. anthracina* at Torgnon, and 50% at Tseuzier (n=200). In 1993, when cones were scarce, 58% were infested at Torgnon (n=50, $\chi^2 = 10.0$, $P = 0.002$), and 89% at Tseuzier (n=35, $\chi^2 = 18.0$, $P < 0.0001$). Maximum infestation rates (*S. anthracina* per cone \pm S.D.) were 0.41 ± 0.55 and 0.8 ± 0.8 at Torgnon and 0.83 ± 0.97 and 1.3 ± 0.8 at Tseuzier during 1992 and 1993, respectively.

First instar *S. anthracina* remained in the egg and larvae emerged as second instars. This was first observed by Tripp (1954) for *S. neanthracina* in North America. The larvae fed spirally around the cone axis destroying scale tissues and developing seed, and by the beginning of July, the majority were third instars (fig. 1). By mid-July, infested cones were readily identified as being typically bent and intensively resinous. Drops of brown frass-containing resin oozed from a hole made by the larva along the concave side of the cone bend. At the end of July, larvae began leaving the cones to pupate in the litter where they overwintered (fig. 1). Most larvae had left the cones by late August, but at Torgnon, a few larvae were found in cones until the end of September. Larvae usually exit during rain (Annala, 1981), which may reduce the risk of larval desiccation and predator attack (Sweeney & Turgeon, 1994) and may moreover assist entry into the litter.

Most larvae (two thirds) pupated at a depth of 1–4 cm, but some were found as deep as 8–9 cm (fig. 4). This distribution agrees with field observations obtained from

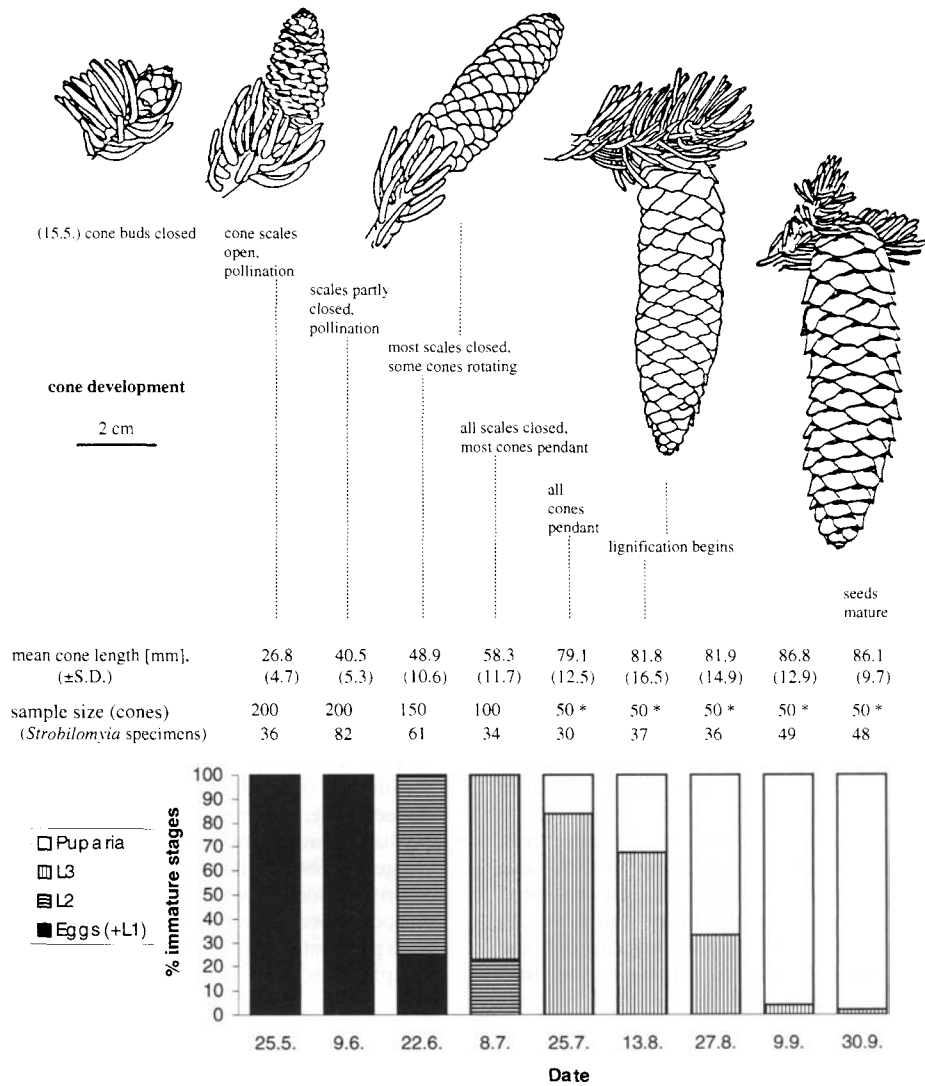


Fig. 1. Development of *Picea abies* cones and life cycle of *Strobilomyia anthracina* at Torgnon in 1992, indicating the percentage of eggs, larval instars and puparia. The latter have been determined by the presence of empty tunnels. * from 25 July on, only *S. anthracina* infested cones were sampled.

litter and soil samples. (This method is not recommended for collecting puparia, because only two to six were found per 0.1 m³ litter and humus, and the recovery process was impeded by large quantities of spruce needles and pieces of

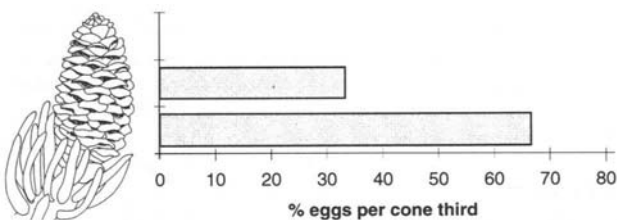


Fig. 2. Longitudinal distribution of eggs of *Strobilomyia anthracina* in spruce cones at Torgnon, 9 June 1992 (n = 200 cones, 82 eggs).

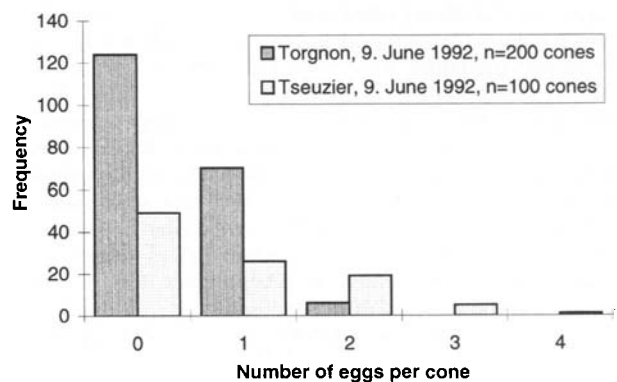


Fig. 3. Frequency distribution of *Strobilomyia anthracina* eggs at two sites.

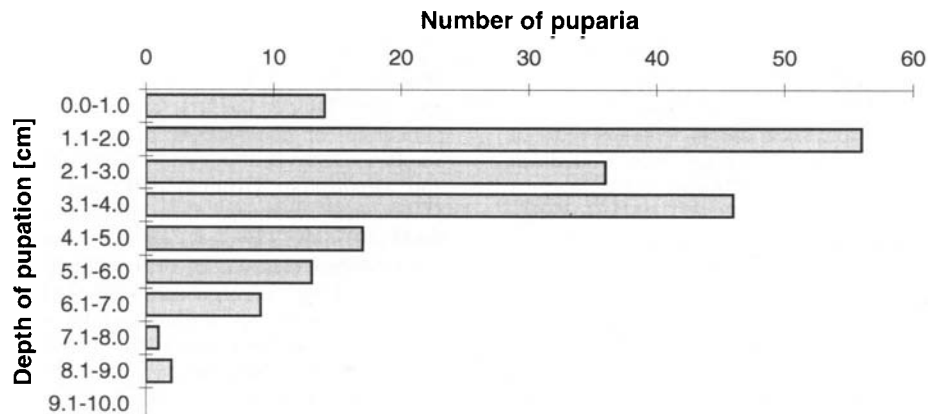


Fig. 4. Frequency distribution of *Strobilomyia anthracina* puparia in a soil layer of 10 cm depth (n = 191).

wood.) Similarly, Fogal (1986) found most puparia in the upper soil horizons.

Pupation occurred within a few days after the puparium was formed. Adults emerge either the following spring, at Torgnon and Tseuzier around early May, or stay in prolonged diapause. Annala (1981) observed prolonged diapause lasting up to two years. In our samples, 67–100% of *Strobilomyia* from 1992 and 1993 remained in diapause the following year, when the cone crop was rated 'none' or 'low.' Among *Strobilomyia* from 1994, only 0–20% remained in

diapause during 1995, when cone production was 'medium' at all sampling locations. Puparia that overwintered at the collection sites in exposure cages or in clay pots outside the laboratory had equal rates of prolonged diapause for Tseuzier but differed slightly for Torgnon (table 2). Overall, there was little difference between the two groups which suggests that the diapause behaviour had been determined prior to overwintering and overwintering in the laboratory yard did not alter it greatly. Prolonged diapause is frequently observed in conophytes (insects that feed exclusively on cone

Table 2. Comparison of mortality and prolonged diapause of *Strobilomyia anthracina* puparia from 1992 overwintered at the collection sites Tseuzier and Torgnon (altitudes 1770 m and 1800 m, respectively) and at the laboratory in Delémont (altitude 500 m) under semi-natural conditions.

Origin of puparia	Overwintering location	Overwintering mortality (%) ^a	Number of live puparia after overwintering	% in prolonged diapause after one winter ^b
Tseuzier	Tseuzier	41	38	100
	Delémont	9***	73	100
Torgnon	Torgnon	38	79	92
	Delémont	9***	191	99**

^aChi-square test of mortality between samples from the same origin (***, $P < 0.001$).

^bFisher's exact test of diapause rates between samples from same origin (**, $P < 0.01$).

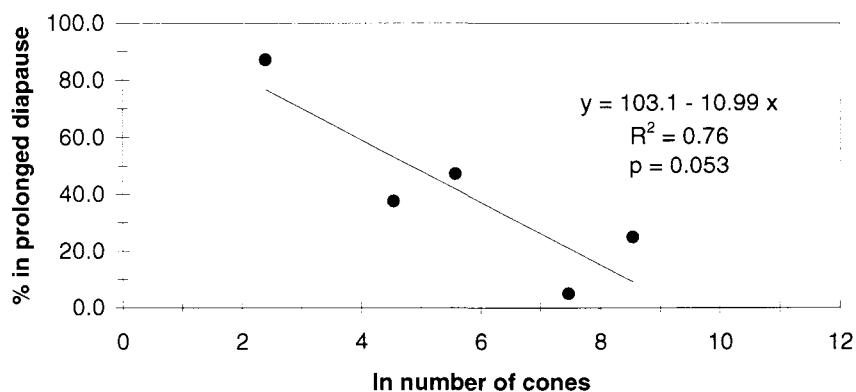


Fig. 5. Relationship between the percentage of *Strobilomyia anthracina* remaining in diapause for more than one year (i.e. in prolonged diapause) and the abundance of cones in the year following larval development (number of cones ln transformed). Data after Annala (1981).

structures; *sensu* Turgeon *et al.*, 1994), and is understood to be an adaptation to temporal fluctuations in the level of cone production (Bakke, 1963; Hanski, 1989; Roques, 1989).

In our samples, the occurrence of prolonged diapause coincided with failed or low cone crops, whereas rates of prolonged diapause were low when there was a medium cone crop. Similarly, data provided by Annala (1981) suggest that diapause is, to some degree, correlated with actual cone production, at least after the first overwintering (fig. 5). Hanski (1989) suggested that conspermatophages (insects feeding on both cones and seeds; *sensu* Turgeon *et al.*, 1994), like *Strobilomyia* spp., use 'risk spreading diapause', in which the length of diapause of the progeny of ovipositing females varies over several years within one generation. This would ensure that at least some of the offspring find cones for oviposition. However, we suggest that *S. anthracina* uses 'predictive diapause' rather than 'risk spreading diapause'. Predictive diapause was defined by Hanski (1989) for spermatophages (insects feeding only on seeds; *sensu* Turgeon *et al.*, 1994) that show a correlation between prolonged diapause and a lack of oviposition sites. It is clear that the correlation between conophyte emergence and presence of cones becomes weaker the longer the diapause lasts. *Strobilomyia* species are very likely to have difficulties adjusting their emergence to cone crops after more than one year, because they diapause in the litter where they are protected from cues provided either directly by the tree or by external factors (see Roques, 1989, for a discussion of probable mechanisms of diapause induction).

Parasitoids

Three specimens of a *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) developed in a single *S. anthracina* egg collected at Martigny in late May 1993 ($n=50$). Identification to the species level was not possible as only females emerged (identification is based on male characters). Many similar looking specimens were obtained from the same and other cones collected at Martigny, Torgnon and Tseuzier, but only from eggs of *Cydia strobilella* (Linnaeus) (Lepidoptera: Tortricidae) (Brockerhoff & Kenis, 1996), although several hundred eggs of *S. anthracina* were present. This is the first record of an egg parasitoid of *S. anthracina*.

Parasitism by other guilds was low, especially in 1992, when cones were very abundant (tables 1 and 3). Larval-pupal endoparasitoids were not found at two thirds of the sites, but some sample sizes may have been too small. Parasitism was higher in samples from 1993, when the cone crop was very low and the number of *Strobilomyia* per cone had increased, but the few cones available limited the sample sizes (tables 1 and 3). An inverse relationship of parasitism rate and cone crop has also been reported for *S. melania* Ackland (Roques, 1988).

Sarothrus areolatus Hartig (Hymenoptera: Figitidae), a larval-pupal endoparasitoid, was found at one third of the sites (table 1). Eggs and the characteristic eucoiliform first instar were found in third instars in July at Tseuzier. However, in North America, *Sarothrus* sp. (parasitizing *Strobilomyia neanthracina*) were observed attacking host eggs (Brockerhoff, unpublished data). Parasitized larvae developed normally and left the cones to pupate in the litter. Then, the parasitoid larva immediately consumed the host pupa externally while still remaining in the puparium. The mature larva is hymenopteriform ('grub-like'). After pupation in

spring, the parasitoid chewed a hole through the puparium and emerged, in the laboratory, two to four weeks after the host. Several specimens stayed in prolonged diapause for one year. This is the first record of *Sarothrus areolatus* as parasitoid of *Strobilomyia anthracina*, but other figitids, *Sarothrus abietis* Belizin, *Sarothrus* sp. (Stadnitzskii *et al.*, 1978) and *Melanips* sp. (Annala, 1981), have been reported from *Strobilomyia anthracina* from north-eastern Europe. Other hosts of *Sarothrus areolatus* are the anthomyiids *Pegohylemyia gnava* Meigen (Harwood, 1919; Wille, 1930; Blair, 1946) and *P. sonchii* (Hardy) (Fergusson, 1986; Kahlert, 1990).

An *Atractodes* sp. (Hymenoptera: Ichneumonidae) was rare in our samples (table 1). It could not be identified with certainty, but is probably *A. scutellatus* Hellén, a species known to parasitize *Strobilomyia anthracina* (Kangas & Leskinen, 1943; Stadnitzskii *et al.*, 1978). The phenology was identical to that of *Sarothrus areolatus*. First instars are caudate and mature larvae are hymenopteriform. Some specimens stayed in prolonged diapause for at least two years.

A *Scambus* sp. (Hymenoptera: Ichneumonidae) was found at all sites investigated for ectoparasitism (table 3). Identification was not possible because the larvae could not be reared to adults, but the cephalic structure indicated that it was a *Scambus* sp. (Short, 1959). It is most likely to be *S. strobilorum* Ratzeburg [= *S. sagax* var. *laticeps* (Ratzeburg)] which we often reared from infested spruce cones. Parasitisation of third instars paralysed before oviposition commenced between late May (Martigny) and July (Torgnon, Tseuzier). The parasitoid larva consumed its host within a few days and spun a cocoon within the tunnel made by the cone maggot. Adults emerged between April and May from cones kept outside (Brockerhoff & Kenis 1996). Other hosts of *S. strobilorum* are the pyralid *Dioryctria abietella* Fabricius (Stadnitzskii *et al.*, 1978), the tortricid *Petrova resinella* Linnaeus (Györfi, 1939, 1941) and the anobiid *Ernobius abietis* Fabricius (Györfi in Herting, 1973).

Tritneptis sp. near *lophyrorum* (Hymenoptera: Pteromalidae) was reared from *Strobilomyia anthracina* exposed at Ayent in 1994. This is the first record of a pupal parasitoid of *Strobilomyia* spp. Eight females and one male emerged from each of only two parasitized puparia, but this parasitoid might be more common since the exposure method was not exactly natural. *Tritneptis* spp. are usually associated with sawfly cocoons (Graham, 1969). Predation of cone maggots on the ground and puparia in the soil might also be important. In 1992, 1994 and 1995, we recovered only 63, 92 and 85%, respectively, of the puparia buried in the soil, the rest were probably preyed upon by invertebrates.

Recommendations for the biological control of North American *S. neanthracina* and *S. appalachensis* by introduction of natural enemies of *S. anthracina* cannot be made yet, because the natural enemies of North American *Strobilomyia*

Table 3. Ectoparasitism of *Strobilomyia anthracina* by *Scambus* sp. at three sites.

Location	1992		1993	
	N	No. parasitized	N	No. parasitized
Tseuzier	230	1 (0.4%)	19	2 (10.5%)
Martigny	—	—	35	5 (14.3%)
Torgnon	175	8 (4.6%)	16	1 (6.3%)

are only now being investigated. Based on the low levels of parasitism observed in this study, the prospects for biocontrol appear rather limited. However, higher parasitism rates of *S. anthracina* were reported from Finland and the former Soviet Union where endoparasitism alone reached up to 70% (Stadnitskii *et al.*, 1978; Annila, 1981). A braconid larval endoparasitoid *Phaenocarpa* sp. (Stadnitskii *et al.*, 1978) and a predator, *Earomyia schistopyga* Collin (Diptera: Lonchaeidae), (Kangas & Leskinen, 1943; Hackman, 1956), natural enemies of *S. anthracina* not encountered by us, could also be evaluated for biocontrol. However, preliminary results from North America (Brockerhoff, unpublished) suggest that the larval parasitoid complexes of *S. neanthracina* and *S. appalachensis* are similar to that of *S. anthracina*, with identical or closely related species. The potential for biological control by predators and pupal parasitoids remains to be determined.

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