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Parasitoid assemblages reared from geometrid defoliators (lepidoptera: geometridae) of larch and fir in the alps

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Abstract

1 Geometrid larvae were collected from larch and fir in the Swiss Alps in 1991–94. Eight geometrid species were found in sufficient numbers to rear out parasitoids: *Agriopis aurantiaria*, *Bupalus piniarius*, *Epirrita autumnata*, *Eupithecia lariciata*, *Odontopera bidentata*, *Lycia isabellae* and *Semiothisa liturata* were collected from larch, and *Puengeleria capreolaria* was obtained from fir.

2 Parasitoid species belonging to five different guilds and four families were obtained; however, the taxonomic status of some of these is not completely resolved.

3 The parasitoid complex of the larch-feeding species was totally different from that of Tortricidae and Tenthredinidae, which feed on the same host tree. In general, there was little overlap in the parasitoid complexes of the larch geometrids, with the most dominant parasitoid of each species reared from only one host. By contrast, many parasitoid species found during our study are also known to attack the same hosts or closely related hosts on different host tree species in different environments, suggesting that host specificity in geometrid parasitoids is more related to host taxonomy than to host plant or habitat.

Keywords Geometridae, guild, host range, larch defoliators, parasitoids.

Introduction

Many looper species (Lep. Geometridae) occur in conifer forests in the Alps where they are not considered pests and very rarely reach outbreak density. However, some of these species are serious pests on other tree species in other regions. For example, *Epirrita autumnata* (Borkhausen), which feeds on European larch (*Larix decidua*) in the Alps, is considered to be the most important defoliator in birch (*Betula*) forests of Northern Fennoscandia (Haukioja *et al*., 1988). Another insignificant larch defoliator, *Agriopis aurantiaria* (Hübner), is part of the geometrid complex that frequently defoliates oak (*Quercus*) and other broadleaved trees in Europe (Kudler, 1978). Finally, *Bupalus piniarius* (L.) is often found in the Alps at low density on several conifer species, but is a serious pest of pine (*Pinus*) plantations elsewhere in Europe (Kudler, 1978).

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The present study is part of a biological control project against the eastern hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenée), an important defoliator of conifers in Canada. Our aim was to investigate the parasitoid complex of geometrids feeding on conifers in Europe and the potential of European parasitoids as classical biological control agents against the hemlock looper (West & Kenis, 1997; van Frankenhuyzen *et al*., 2002). Geometrid larvae were collected annually from larch, fir (*Abies alba*), spruce (*Picea abies*) and pine (*Pinus* spp.) in Switzerland, 1991–94. Eight of the 20 species collected (seven on larch, one on fir) were sampled in sufficient numbers to obtain data on parasitism. Some parasitoids were selected for further studies, but they were never released in Canada because of their incompatibility with the hemlock looper (West & Kenis, 1997).

The biology of the geometrids sampled during this study was studied by Herz (1994) (Table 1). More general information is also provided in Kudler (1978). All species are univoltine. *Epirrita autumnata* and *A. aurantiaria* overwinter as eggs, laid in autumn, and larvae are found from May to July. The other larch-feeding species overwinter as

Table 1 Biological characteristics of the geometrid species sampled in this study

	Host tree in this study	Other main host trees	Period of larval stage	Overwintering stage
Agriopis aurantiaria (Hübner)	Larix	Broadleaves	May to July	Egg
Bupalus piniarius (L.)	Larix	Pinus	July to Sept	Pupa
Epirrita autumnata (Borkhausen)	Larix	Betula	May to July	Egg
Eupithecia lariciata (Freyer)	Larix	–	July to Sept	Pupa
Odontopera bidentata (Clerck)	Larix	Polyphagous	July to Sept	Pupa
Lycia isabellae (Harrison)	Larix	–	June to August	Pupa
Semiothisa liturata (Clerck)	Larix	Pinus	July to August	Pupa
Puengeleria capreolaria (Denis & Schiffermüller)	Abies	–	August to July	Larva

pupae. Larvae of *Eupithecia lariciata* (Freyer), *Odontopera* (= *Gonodontis*) *bidentata* (Clerck), *Bupalus piniarius* and *Semiothisa liturata* (Clerck) are typically observed in July to September. However, due to early emergence and oviposition periods, larvae of *Lycia* (= *Poecilopsis*) *isabellae* (Harrison) can be found from early June onwards. The fir-feeding species, *Puengeleria capreolaria* (Denis & Schiffermüller), overwinters in the mid-larval stages and pupates in June to July. All larch-feeding species have five larval instars, whereas *P. capreolaria* has six larval instars, identified by their head capsule width (Herz, 1994).

This present study provides sampling data from Switzerland on the parasitoid complexes of seven larch-feeding and one fir-feeding looper species. These data are of great interest because, until now, very little was known on the parasitoids of these defoliators in the Alps. Some of these species (*E. autumnata*, *A. aurantiaria* and *B. piniarius*) have been studied on other host trees in other regions, which provides an interesting opportunity for a comparison of parasitism in different habitats. The other species have never been regarded as pests and their parasitoid complexes are very poorly known. However, data on their parasitoid complexes in their native range may be valuable because these insects may invade new regions and become new pests. Finally, data on parasitoids of larch geometrids complement previous studies on other larch defoliators in the Swiss Alps carried out by CABI Bioscience in Switzerland. Zinnert (1969) and Pschorn-Walcher & Zinnert (1971) provide extensive data on the parasitoid community of larch sawflies (Hym. Tenthredinidae) and Mills (1993) made similar studies on larch budmoth (Lep. Tortricidae). Taken as a whole, these studies on larch defoliators provide valuable information on the host and habitat specificity of parasitoids of exophytic insects.

Materials and methods

Sampling and rearing of hosts and parasitoids

All larvae were collected from 1991 to 1994 on European larch and silver fir located in two cantons in the Swiss Alps. Collection localities in the Canton Graubünden (south-eastern Switzerland) include Chamues-ch (altitude 1800 m), Surlej (altitude 1950 m), Susch (altitude 1700 m), Tschierv (altitude 1900 m) and Zuoz (altitude 1750 m). In the Canton Valais (south-western Switzerland), collections were carried out at Ayent (altitude 1350 m), Blatten (altitude 1650 m), Les Haudères (altitude 1500 m), Nufenen Pass (altitude 1550 m), Randa (altitude 1300 m), Saas Grund (altitude 1550 m), Sanetsch (altitude 1500 m), Simplon Dorf (altitude 1500 m) and Zinal (altitude 1800 m). Fir was sampled at Ayent, and larch at the other sites.

When possible, several collections were made at the same sites during the season to cover the whole spectrum of larval parasitoid guilds. When single collections were made, these were usually set to coincide with the occurrence of the late-larval instars. In total, approximately 15 000 larvae were obtained from 41 collections.

Larvae were sampled by beating the lower branches of conifers with a stick over a 1.2 m^2 canvas sheet attached to a wooden frame and held at chest height. Larvae were transported in styrofoam boxes containing fresh foliage to the laboratory, where they were sorted and reared separately, according to species. For each collection and species, an estimation of the number of larvae collected per person-hour was calculated. Some larvae were dissected and head-capsule widths measured to observe those instars that harbour parasitoids. Larvae were reared using three different methods. (i) The largest samples were usually reared in screened wooden cages of various sizes provided with fresh branches immersed in water and changed twice a week. Peat was placed at the base to allow parasitoid pupation or cocooning. (ii) Smaller samples were reared in groups of a maximum of 10 larvae in 1.3-L plastic cylinders, with shoots immersed in water and changed every 2–3 days. (iii) Small samples of various collections were selected for single rearing in small plastic vials (6 mm × 2.5 mm), with moistened foam stopper, and conifer twigs changed every 2–3 days. Each time the food was changed, host and parasitoid pupation/cocooning were monitored. Head capsules of larvae in single rearings and of larvae killed by a parasitoid were measured (Herz, 1994) to determine those stages that harbour and are killed by a parasitoid species.

Host pupae, wasp cocoons and fly puparia obtained by rearing were stored outdoors under natural conditions but protected from direct rain and sun. Host and parasitoid emergence was monitored daily. Those pupae, cocoons or puparia that did not emerge during the season were kept over the winter in a cold room at 2 °C, in a humid container, and incubated in the laboratory in the spring to obtain host and parasitoid adults. Parasitoids that emerged during the collection year were reared and kept in screened cages or plastic cylinders, and fed with honey and moistened cellulose paper. Mortality was monitored, and those that survived to autumn were kept over the winter in the cold room, in 1.3-L plastic cylinders within a humid plastic bag. Parasitoid adults belonging to the Microgastrinae and Rogadinae (both Braconidae) and some of the Ichneumonidae were identified by M. R. Shaw. The remaining adult specimens were sent to taxonomists for identification (see Acknowledgements).

Parasitoid guilds and parasitism rates

Each parasitoid species was assigned to a parasitoid guild, as described by Mills (1994). Parasitism is known to vary both qualitatively and quantitatively with time and methods of collection (Van Driesche, 1983). In particular, in external lepidopteran defoliators, some larval parasitoids kill their hosts before attacks by other parasitoids. Thus, only precise life table studies involving regular sampling during the whole larval stage could properly estimate the mortality inflicted by parasitoids on geometrid larvae. This was not the purpose of present study, where absolute numbers of parasitoids reared per collection site and an apparent level of parasitism for each collection site and species is provided. The latter was calculated by dividing the total number of parasitized larvae by the total number of larvae successfully reared to pupation or to parasitoid emergence or cocooning. Data from different collections at the same site and year were pooled. This figure for apparent parasitism largely underestimates actual parasitism because, at the time of collection, some of the early larval parasitoids had already killed their hosts whereas late larval parasitoids had not yet completed oviposition. Thus, parasitism rates given in this study must be considered with caution and regarded only as an indicator of parasitism in the different species, years and locations.

Results and Discussion

Parasitoid complexes of the geometrid species

Epirrita autumnata.

At least 12 parasitoid species belonging to four guilds were reared from larvae of *E. autumnata* (Table 2). In the Graubünden, where *E. autumnata* was most abundant, parasitism was dominated by the larval endoparasitoid *Aleiodes* cf. *gastritor* (Thunberg). It was the main species responsible for high parasitism rates at Tschierv and Surlej. This rogadine braconid attacks first- and second-instar larvae and emerges in summer from mummified third (3%), fourth (85%) and fifth (12%) instars ($n = 66$). Males die soon after mating and females overwinter. Egg maturation started in spring, suggesting that this species is strictly univoltine. Further details on the biology of *A.* cf. *gastritor* are provided in West & Kenis (1997). *Aleiodes gastritor sensu lato* is at first sight a polyphagous parasitoid of arboreal geometrids, but several cryptic species with restricted host range exist. In particular, this population obtained from *E. autumnata* was successfully crossed with a population from the same host collected on birch in Finland. By contrast, it was sexually incompatible with several other strains from other hosts and did not develop in the hosts of the other strains (M. R. Shaw, unpublished data). Other early larval parasitoids included microgastrine braconids, in particular *Protapanteles anchisiades* (Nixon) and *Cotesia salebrosa* (Marshall), which were bivoltine and emerged for a second generation (presumably in a different host species).

The second most important parasitoid of *E. autumnata* was the ichneumonid *Campoletis varians* (Thomson), which attacks unidentified larval stages and emerges from prepupae. In the insectory, a part of the population emerged in the summer (e.g. 16 of 70 in 1993) but, at high altitude in the field, probably all specimens are univoltine and overwinter in their cocoon. *Campoletis varians* is a known parasitoid of *E. autumnata* both on larch in the Alps (Delucchi *et al.*, 1974), and on birch in Finland (Ruohomäki, 1994).

Other parasitoids belonging to different guilds were reared in low numbers. Two undescribed or unidentified ichneumonids emerged in low numbers from larvae: *Casinaria* sp. 1, and *Phobocampe* sp. 1. *Agrypon flaveolatum* (Gravenhorst), a larval-pupal endoparasitoid, was reared from overwintered host pupae. It is best known as a common parasitoid of the closely related winter moth, *Operophtera brumata* (L.), but has been reared occasionally from various arboreal spring-feeding geometrids, including *E. autumnata*. Four specimens of a tachinid species were obtained, as well as a polyembryonic egg-prepupal parasitoid, *Copidosoma chalconotum* (Dalman) (Hym. Encyrtidae). Finally, two specimens of *Netelia* (*Bessobates*) *virgata* (Geoffroy) killed prepupae. This species is known from *E. autumnata* and, as all species of this genus, develops as a koinobiont larval-prepupal ectoparasitoid. (Shaw, 2001)

Agriopis aurantiaria.

This larch-feeding geometrid was the most abundant host found during this survey, with over 6000 larvae collected. It was particularly abundant in the Valais and at least 13 parasitoid species were obtained (Table 3). The main parasitoids belong to several guilds. Larval parasitoids included mainly the braconid *Protapanteles immunis* (Haliday) and an apparently undescribed ichneumonid, *Casinaria* sp. 1 (K. Horstmann, personal communication). Two *Phobocampe* spp. (*P. crassiuscula* (Gravenhorst) and *Phobocampe* sp. 1) and *Cotesia praepotens* (Haliday) were also reared in lower numbers. All larval parasitoids emerged in the insectary quickly in the summer, except *Phobocampe* sp. 1, a species also obtained from *E. autumnata*, which entered into diapause in its cocoon.

Table 2 Number and guild of parasitoids reared from *Epirrita autumnata* and rates of apparent parasitism

	Guild[a]	*Nufenen Pass*	*Les Haudères*	*Zinal*		*Saas Grund*	*Tschierv*	*Chamues-ch*	*Zuoz*		*Surlej*		*Sanetsch*		*Susch*	
Year of collection (no. of collections)		1991 (2)	1991 (1)	1992 (3)	1993 (4)	1992 (2)	1992 (2)	1993 (2)	1994 (1)	1993 (1)	1993 (2)	1994 (2)	1993 (2)	1994 (3)	1993 (1)	1994 (1)
No. of larvae collected		152	32	174	168[b]	100	242	141[b]	34	76	175[b]	267	374[b]	464	65	34
Host abundance (max. no. per man-hour)		10–20	< 10	< 10	10–20	10–20	50–100	< 10	< 10	< 10	10–20	20–50	10–20	20–50	< 10	< 10
Period of collection		20.6–10.7	20.6	4.6–2.7	27.5–5.7	2–16.6	8–25.6	3–17.6	6.6	18.6	2–17.6	7–15.6	18.6–1.7	7–28.6	28.5–10.6	15.6
No of unparasitized pupae reared		61	15	58	90	67	79	51	20	38	111	205	67	235	41	27
Ichneumonidae																
Agrypon flaveolatum (Gravenhorst)	L-P endo	–	–	–	–	–	–	9	–	1	4	–	–	–	–	1
Campoletis varians (Thomson)[c]	L-PP endo	20	1	2	17	1	11	14	3	2	3	4	28	10	3	2
Casinaria sp. 1	L endo	–	–	14	–	1	–	–	–	–	–	–	–	–	–	–
Netelia (Bessobates) virgata (Geoffroy)	L-PP ecto	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
Phobocampe sp. 1	L endo	–	–	–	–	–	–	–	–	–	–	5	9	18	–	–
Undetermined specimens		–	–	1	–	–	1	–	–	–	–	–	–	–	–	–
Braconidae																
Aleiodes cf. *gastritor* (Thunberg)[3]	L endo	–	–	–	–	–	47	39	4	16	13	13	160	67	2	1
Cotesia salebrosa (Marshall)	L endo	–	–	–	1	–	–	3	–	9	4	7	–	–	1	–
Protapanteles anchisiades (Nixon)	L endo	–	1	7	8	1	21	2	2	3	2	5	15	18	2	–
Undetermined specimens		–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Encyrtidae																
Copidosoma chalconotum (Dalman)	E-PP endo	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Tachinidae																
Undetermined Tachinidae 1	L-P endo	–	–	–	1	–	2	1	–	–	–	–	–	–	–	–
Apparent parasitism (%)		24.7	11.8	29.2	23.1	4.3	51.2	57.1	31.0	44.9	19.0	14.2	76.0	32.9	19.6	12.9

[a]Guild abbreviations: E, egg; L, larval; PP, prepupal; P, pupal; endo, endoparasitoid; ecto, ectoparasitoid.
[b]A part of the larvae were dissected at collection.
[c]Some parasitized by Mesochorinae.

Table 3 Number and guild of parasitoids reared from Agriopis aurantiaria and rates of apparent parasitism

	Guild[a]	Nufenen Pass	Simplon Pass	*Les Haudères*	*Tschierv*	*Saas Grund*		*Randa*			*Zinal*	
Year of collection (no. of collections)		1991 (2)	1991 (2)	1991 (1)	1992 (1)	1992 (3)	1993 (2)	1992 (2)	1993 (4)	1994 (2)	1992 (3)	1993 (5)
No. of larvae collected		131	588	36	18	585	95	170	875[b]	363	2610	787[b]
Host abundance (max. no. per man-hour)		10–20	50–100	< 10	< 10	20–50	< 10	10–20	> 100	20–50	> 100	50–100
Period of collection		20.6–10.7	19.6–16.7	20.6	25.6	2.6–1.7	26.5–24.6	3–17.6	20.5–6.7	15–10.6	4.6–2.7	27.5–16.7
No of unparasitized pupae reared		56	147	30	18	266	33	100	545	150	1451	431
Ichneumonidae												
Casinaria sp. 1	L endo	14	–	–	–	27	6	3	2	5	38	28
Dusona contumax (Förster)[c]	L-PP endo	1	38	1	–	17	21	–	44	61	1	–
Ophion minutus Kriechbaumer	L-PP endo	–	4	–	–	–	–	–	–	–	–	
Phobocampe crassiuscula (Gravenhorst)	L endo	–	–	–	–	–	–	4	–	1	–	–
Phobocampe sp. 1	L endo	–	5	–	–	–	–	–	4	15	3	5
Undetermined specimens		–	–	–	–	2	–	–	–	2	1	–
Braconidae												
Cotesia praepotens (Haliday)	L endo	–	–	–	–	1	–	–	–	3	–	–
Homolobus discolor (Wesmael)	L-PP endo	–	2	–	–	–	1	–	–	–	1	–
Homolobus infumator (Lyle)	L-PP endo	3	–	–	–	–	–	–	–	–	–	–
Protapanteles immunis (Haliday)	L endo	2	–	2	–	12	2	3	4	1	9	20
Undetermined specimen		–	–	–	–	1	–	–	–	–	–	–
Tachinidae												
Phryxe magnicornis (Zetterstedt)	L-P endo	–	3	–	–	4	–	2	3	4	49	–
Undetermined specimen		–	–	–	–	–	–	–	–	1	–	–
Apparent parasitism (%)		26.3	26.1	9.1	0.0	19.4	47.6	10.7	9.5	38,3	6.6	11.0

[a]Guild abbreviations: L, larval; PP, prepupal; P, pupal; endo, endoparasitoid.
[b]A part of the larvae were dissected at collection.
[c]Some parasitized by Mesochorinae.

A larval–pupal endoparasitoid was also occasionally abundant, the tachinid *Phryxe magnicornis* (Zetterstedt). Adults emerged in summer for a second generation on some other host. It has also been reared from *A. aurantiaria* and *Erannis defoliaria* on broadleaf trees in Germany (as *P. longicauda* Wainwright) (Herting, 1965). Other hosts reported in the literature include Geometridae, but also Zygaenidae, Tortricidae, Hesperiidae, Lycaenidae, Pieridae and Noctuidae (Tschorsnig & Herting, 1994; Ford *et al*., 2000).

One of the major parasitoids of *A. aurantiaria* in the Alps was the ichneumonid *Dusona contumax* (Förster). West & Kenis (1997) provide details on its biology. It apparently attacks only the last instar larvae because it was never obtained from larvae collected at an earlier stage and, in dissections, eggs were found exclusively in the last-instar larvae. Eggs hatch when the larvae have dropped to the soil to build their pupal chamber. Then the parasitoid larva develops rapidly and the prepupa is killed after 4–10 days. Larvae overwinter in a strong brown cocoon. In spring, it takes *D. contumax* 3–4 weeks at 21 °C in the laboratory to emerge. *D. contumax* was also reared from the same host on oak in Germany (Herting, 1965). Other parasitoids, the ichneumonid *Ophion minutus* Kriechbaumer, and the braconids *Homolobus discolor* (Wesmael) and *H. infumator* (Lyle), had a similar biology and were reared from *A. aurantiaria* in low numbers. *Ophion minutus* has already been reported from the same host on broadleaved trees (Thompson, 1945; Brock, 1982).

Lycia isabellae.

This was found mainly in the Valais. Parasitoids of this relatively rare species have never been studied in detail. Early instars were parasitized by the microgastrine braconid *Protapanteles immunis* and the apparently undescribed *Aleiodes* sp. 1 (Table 4). The biology of the latter is similar to that of *Aleiodes* cf. *gastritor* on *E. autumnata*. It attacks first- and, perhaps, second-instar larvae and emerges from mummified third- and fourth- (exceptionally second-) instar larvae (West & Kenis, 1997). Females overwinter and mature their eggs only in spring. *Casinaria moesta* (Gravenhorst) and the undetermined *Casinaria* sp. 1, which was also found commonly on *A. aurantiaria* and other geometrids, were obtained from late-instar larvae. The tachinid *Phryxe tenebrata* Herting, a larval-pupal endoparasitoid, was reared in higher numbers. It is the first host record for this parasitoid. The tachinid larva overwinters in the host pupa and adult flies emerge from the pupa in the next spring.

Finally, *Dusona stragifex* (Förster) was reared from prepupae. Its biology, described as *Dusona* sp. by West & Kenis (1997), is similar to that of *D. contumax* in *Agriopis aurantiaria*. Only last-instars are attacked, and larval development occurs when its host has stopped feeding. Then the host prepupa is killed rapidly, and the parasitoid larva overwinters in an obligatory diapause in its cocoon in the litter.

Eupithecia lariciata.

This was the second most abundant geometrid species found in this study, with over 3000 larvae collected in only 2 years. Twelve parasitoids representing five guilds were obtained (Table 5). Apparent parasitism was high, with rates over 50%. The most frequently collected parasitoid was the egg-prepupal parasitoid *Copidosoma cervius* (Walker), a polyembryonic species that oviposits into eggs and kills prepupae, in which it overwinters. Twenty-two to 74 wasps emerged from a single host. *Copidosoma cervius* is a parasitoid known mainly from *Eupithecia* spp. (Guerrieri & Noyes, 2005). Early larval stages of *E. lariciata* were parasitized by three microgastrine Braconidae, *Glyptapanteles vitripennis* (Curtis), *P. anchisiades* and a *Cotesia* species, which was tentatively determined as *C. errator* (Nixon), a rare species occasionally found on other *Eupithecia* spp. Because these microgastrine Braconidae usually kill their host before its last instar, and considering that most hosts were collected as mature larvae, parasitism by these early larval parasitoids is probably substantially underestimated. Other frequently collected parasitoids were the braconid *Zele caligatus* (Haliday) and the ichneumonid *Casinaria stygia* Tschek. This latter species attacks early larval stages and emerges from the last two instars. The biology of *Z. caligatus* was unobserved in this case, but it has been found to be a larval-prepupal parasitoid of other *Eupithecia* spp. (M. R. Shaw, unpublished data). Nothing further is known on the host range of *C. stygia*.

Last larval instars were attacked by the tachinid *Ceranthia lichtwardtiana* Villeneuve, whose larva emerges from the host pupa. Overwintering occurs in the puparium. *Ceranthia lichtwardtiana* is known mainly from *Eupithecia* spp. but it was recently recorded from *Geina didactyla* (L.) (Lep. Pterophoridae) (Bergsström, 1999). A few specimens of a larval-prepupal ectoparasitoid, *Netelia* (*Paropheltes*) ?*thomsonii* (Brauns) and the larval-pupal parasitoid *Platylabops lariciatae* (Kriechbaumer) were also obtained. *Platylabops lariciatae* had already been reared from *E. lariciata* in England (Styles, 1958; as *Aoplus*).

None of the parasitoids of *E. lariciata* emerged in the same year when reared under natural conditions. However, because larvae of this species occur late in summer, it is likely that at least some of its parasitoids have a first generation on other hosts occurring earlier in the season.

Odontopera bidentata.

This looper was reared in limited numbers, and only a few larvae were parasitized. However, seven parasitoid species were reared, all in low numbers (Table 6). The most abundant was the gregarious braconid *Cotesia spurius* (Wesmael). Between eight and 24 individuals emerged from a single mature larva. In addition, a few specimens of *Casinaria* sp. 1 (i.e. apparently identical to those obtained from *A. aurantiaria* and *E. autumnata*) and the two braconids *G. vitripennis* and *P. anchisiades* emerged from larvae; a *Dusona* sp., different from those attacking

Table 4 Number and guild of parasitoids reared from Lycia isabellae and rates of apparent parasitism

	Guild[a]	*Nufenen Pass*				*Simplon Dorf*	*Les Haudères*	*Randa*	*Zinal*	*Blatten*	
Year of collection (no. of collections)		1991 (1)	1992 (1)	1993 (3)	1994 (1)	1991 (2)	1991 (1)	1993 (4)	1993 (1)	1993 (2)	1994 (4)
No. of larvae collected		62	92	164	111	85	22	91	49	66	499
Host abundance (max. no. per man-hour)		< 10	< 10	< 10	10–20	< 10	< 10	< 10	< 10	< 10	10–20
Period of collection		10.7	11.8	15.7–4.8	13.7	19.6–16.7	20.6	24.6–5.8	16.7	17.8-1-9	13.7–19.8
No of unparasitized pupae reared		43	63	93	41	41	10	63	42	41	198
Ichneumonidae											
Casinaria moesta (Gravenhorst)	L endo	1	3	–	–	–	0.	0.	–	3	17
Casinaria sp. 1	L endo	1	3	8	–	–	0.	0.	–	1	1
Dusona stragifex (Förster)[b]	L-PP endo	–	–	3	2	1	–	1	–	16	–
Braconidae											
Aleiodes sp. 1	L endo	–	–	19	5	–	–	9	4	1	37
Protapanteles immunis (Haliday)	L endo	–	2	17	4	–	–	–	–	1	18
Tachinidae											
Phryxe tenebrata Herting	L-P endo	–	3	18	12	–	–	13	3	2	21
Apparent parasitism (%)		4.4	14.9	41.1	35.9	2.4	0.0	26.7	14.3	36.9	32.2

[a]Guild abbreviations: L, larval; PP, prepupal; P, pupal; endo, endoparasitoid.
[b]Some parasitized by Mesochorinae.

Table 5 Number and guild of parasitoids reared from Eupithecia lariciata and rates of apparent parasitism

	Guild[a]	Nufenen Pass		Blatten		Simplon Dorf		Randa	Saas Grund
Year of collection (no. of collections)		1992 (2)	1993 (4)	1992 (3)	1993 (3)	1992 (4)	1993 (5)	1993 (5)	1993 (2)
No. of larvae collected		177	147	402	243	914	839[b]	374	150
Host abundance (max. no. per man-hour)		< 10	< 10	20–50	10–20	50–100	20–50	20–50	< 10
Period of collection		11.8–12.9	27.7–30.8	1–28.9	17.8–17.9	18.8–28.9	5.8–4.10	17.7–31.8	16–31.8
No of unparasitized pupae reared		47	96	124	125	565	180	265	119
Ichneumonidae									
Platylabops lariciatae (Kriechbaumer)	L-P endo	–	–	–	–	5	–	–	–
Casinaria stygia Tschek[c]	L endo	6	–	14	2	8	12	–	–
Casinaria sp. 1	L endo	1	1	–	1	–	1	2	–
Netelia (*Paropheltes*) ?*thomsonii* (Brauns)	L-PP ecto	–	–	1	–	2	–	–	–
Undetermined specimens		–	–	2	3	3	2	–	–
Braconidae									
Aleiodes modestus (Reinhard)	L endo	1	2	–	–	1	1	1	1
Cotesia ? *errator* (Nixon)	L endo	20	23	139	44	28	34	4	6
Glyptapanteles vitripennis (Curtis)[c]	L endo	12	3	–	–	24	29	–	–
Protapanteles anchisiades (Dixon)	L endo	2	1	15	–	21	8	–	–
Zele caligatus (Haliday)[c]	L-PP endo	1	–	3	1	4	23	3	5
Encyrtidae									
Copidosoma cervius (Walker)	E-PP endo	8	7	7	12	77	191	10	4
Tachinidae									
Ceranthia lichtwardtiana Villeneuve	L-P endo	–	–	–	1	1	4	57	7
Apparent parasitism (%)		52.0	27.8	59.3	33.9	23.5	62.9	22.5	16.2

[a]Guild abbreviations: E, egg; L, larval; PP, prepupal; P, pupal; endo, endoparasitoid; ecto, ectoparasitoid.
[b]A part of the larvae were dissected at collection.
[a]Some parasitized by Mesochorinae.

other hosts in this study, from prepupae; and an undetermined tachinid fly from pupae.

Bupalus piniarius.

This species was also reared in limited numbers on larch and few parasitoids species were obtained (Table 7). The only species reared in significant numbers were a *Protapanteles* sp. (probably *P. immunis* but determined only from males) reared from middle instars, and *Dusona dubitor* Hinz reared from prepupae. Both species overwintered in their cocoons and emerged in the next spring. *Dusona dubitor* is known from *B. piniarius* on pine (Hinz, 1990).

Semiothisa liturata.

This was the rarest species encountered. Less than 100 individuals were collected on larch, at two sites in 1993

Table 6 Number and guild of parasitoids reared from Odontopera bidentata, and rates of apparent parasitism

	Guild[a]	Nufenen Pass		Simplon Dorf	
Year of collection (no. of collections)		1992 (1)	1993 (1)	1992 (1)	1993 (2)
No. of larvae collected		104	29	37	30
Host abundance (max. no. per man-hour)		< 10	< 10	< 10	< 10
Period of collection		11.8	16.8	1.9	5–16.8
No of unparasitized pupae reared		50	20	3	15
Ichneumonidae					
Casinaria sp. 1	L endo	1	–	–	4
Dusona sp. 1	L-PP endo	–	–	2	–
Undetermined species		–	–	–	1
Braconidae					
Cotesia spurius (Wesmael)	L endo	3	–	–	4
Glyptapanteles vitripennis (Curtis)	L endo	1	–	1	2
Protapanteles anchisiades (Nixon)	L endo	–	2	–	1
Tachinidae					
Undetermined Tachinidae 2	L endo	–	3	–	–
Apparent parasitism (%)		9.1	20.0	50.0	44.4

[a]Guild abbreviations: L, larval; PP, prepupal; endo, endoparasitoid.

Table 7 Number and guild of parasitoids reared from *Bupalus piniarius,* and rates of apparent parasitism

	Guild[a]	Nufenen Pass	Blatten	Simplon Dorf	
Year of collection (no. of collections)		1992 (1)	1992 (3)	1992 (3)	1993 (2)
No. of larvae collected		77	1187	31	104
Host abundance (max. no. per man-hour)		< 10	< 10	< 10	< 10
Period of collection		11–12.8	1–28.9	1–28.9	31.8–17.9
No of unparasitized pupae reared		44	64	14	76
Ichneumonidae					
Dusona dubitor Hinz	L-PP endo	–	9	2	8
Undetermined species		–	–	2	–
Braconidae					
Cotesia sp. 3	L endo	–	2	3	1
Protapanteles ? *immunis* (Nixon)[b]	L endo	–	18	1	–
Apparent parasitism (%)		0.0	31.2	41.7	10.6

[a]Guild abbreviations: L, larval; PP, prepupal; endo, endoparasitoid.
[b]Determined only from males.

(Table 8). Three early larval parasitoids were obtained. A *Protapanteles* sp. (probably *P. anchisiades* but determined only from males) and *Glyptapanteles vitripennis* were also reared from other geometrids during this study. *Aleiodes* sp. 1 was morphologically similar to, and may be conspecific with, the species reared from *Lycia isabellae*. It differs from *Aleiodes cantherius* (Lyle), a known parasitoid of *S. liturata*. Adults emerged in October and females overwintered. All three species killed mid-instar larvae. The fourth species, *Dusona inermis* (Förster), is a larval-prepupal parasitoid frequently reared from *S. liturata* (K. Horstmann, personal communication).

Peungeleria capreolaria.

This was the only geometrid found on fir in sufficient numbers to allow observations on parasitism. Eight parasitoid species were obtained from several collections at a single locality in the Valais (Table 9). Among larval parasitoids, *Aleiodes* sp. 3 was the most abundant. This species was distinct from those reared in higher numbers from *E. autumnata* and *P. isabellae*. Eggs and young larvae were already found in first- and second-instars in autumn, and adults emerged from mummified third and fourth instars in summer of the next year. The microgastrine *Glyptapanteles mygdonia* (Nixon) was reared in lower numbers. However, because this species usually emerges from mid instars, it is likely that our spring collections were made after some of them had already left their host. In the dissection of 50 young larvae on 30 September 1992, five microgastrine larvae were found. *Glyptapanteles mygdonia* is one of the only parasitoids already recorded from this poorly studied geometrid (Nixon, 1973). Another braconid, *Homolobus infumator* (Lyle), and a polyembryonic encyrtid, *Copidosoma serricorne* (Dalman), were reared from 26 and six prepupae, respectively. The other parasitoids were obtained in very low numbers.

Table 8 Number and guild of parasitoids reared from Semiothisa liturata, and rates of apparent parasitism

	Guild[a]	Randa	Simplon Dorf
Year of collection (no. of collections)		1993 (2)	1993 (3)
No. of larvae collected		35	51
Host abundance (max. no. per man-hour)		< 10	< 10
Period of collection		5–17.8	5–31.8
No of unparasitized pupae reared		25	29
Ichneumonidae			
Dusona inermis (Förster)	L-PP endo	–	2
Braconidae			
Aleiodes sp. 1[b]	L endo	3	6
Glyptapanteles vitripennis (Curtis)	L endo	–	5
Protapanteles ? *anchisiades* (Nixon)[c]	L endo	2	1
Apparent parasitism (%)		16.7	32.6

[a]Guild abbreviations: L, larval; PP, prepupal; endo, endoparasitoid.
[b]Some parasitized by Mesochorinae.
[c]Determined only from males.

Table 9 Number and guild of parasitoids reared from Puengeleria capreolaria, and rates of apparent parasitism

	Guild[a]	Ayent	
Year of collection (no. of collections)		1992 (2)	1993 (2)
No. of larvae collected		780	369[b]
Host abundance (max. no. per man-hour)		50–100	100–150
Period of collection		6–19.6	28.5–10.6
No of unparasitized pupae reared		542	192
Ichneumonidae			
Casinaria sp. 1	L endo	3	–
Braconidae			
Aleiodes sp. 3[c]	L endo	29	7
Glyptapanteles mygdonia (Curtis)	L endo	9	4
Homolobus discolor (Wesmael)	L-PP endo	1	–
Homolobus infumator (Lyle)	L-PP endo	20	6
Protapanteles sp.	L endo	1	1
Encyrtidae			
Copidosoma serricorne (Dalman)	E-PP endo	6	–
Tachinidae			
Undetermined Tachinidae 3		1	1
Apparent parasitism		11.4%	5.3%

[a]Guild abbreviations: E, egg; L, larval; PP, prepupal; endo, endoparasitoid.
[b]Includes larvae dissected in the laboratory.
[c]Some parasitized by Mesochorinae.

Hyperparasitism

Koinobiont, true hyperparasitoid species (i.e. those that are present in the primary parasitoid when it is still feeding) of the genera *Mesochorus* and *Astiphromma* (Hym. Ichneumonidae, Mesochorinae) were reared from cocoons of several primary parasitoids of the genera *Aleiodes*, *Glyptapanteles*, *Zele*, *Campoletis*, *Casinaria* and *Dusona* (Tables 2–9). Although these Mesochorinae were not determined to species level, it was clear that they were exhibiting considerable host specificity. *Aleiodes* cf. *gastritor* was parasitized by two distinct species. Hyperparasitism rates from Mesochorinae were not negligible, reaching, in 1993, 11% in *Aleiodes* cf. *gastritor* ($n = 230$) and 15% in *Campoletis varians* ($n = 67$) from *E. autumnata*, and 19% in *Zele caligatus* ($n = 32$) from *E. lariciata*. Pseudohyperparasitism (i.e. parasitism by idiobiont species that attack the cocoon stages of primary parasitoids) was not assessed.

Parasitoid host range

The parasitoids of larch and fir geometrids have received little study except by Delucchi *et al*. (1974) who provide a list of parasitoids reared from the major lepidopteran defoliators of larch in the Alps. Therefore, it is not surprising that a few of the parasitoids reared during this study, including some of the most abundant species, could not be determined to species level. Several are probably undescribed, in particular several *Aleoides* spp. and *Casinaria* sp. 1. This suggests that these parasitoids may be rather host or habitat specific. The host range of parasitoids is difficult to determine (Shaw, 1994; De Nardo & Hopper, 2004). The literature, in particular host – parasitoids lists, contains many errors, resulting from identification or rearing mistakes (e.g. arising from mass rearing of hosts), synonymies, etc. (Shaw, 1994; Noyes, 1994). Furthermore, different studies on parasitoid complexes of particular hosts cannot be easily compared because they have used different taxonomic expertise, and the same parasitoid species often appears under two or more different names. Therefore, single studies on the parasitoid community of taxonomically and/or ecologically related hosts are valuable to help determine parasitoid host range. This study on larch geometrids in the Alps is particularly useful because it complements previous studies carried out by the same laboratory on other larch defoliators in the same areas, Tenthredinidae (Zinnert, 1969; Pschorn-Walcher & Zinnert, 1971) and Tortricidae (Mills, 1993). Voucher specimens of these studies are still available for comparison (locations traceable through CABI Bioscience in Delémont).

Comparisons between the parasitoid complexes of the three different families (Tenthredinidae, Tortricidae and Geometridae) show hardly any overlap, even at the parasitoid genus level. The only species and genus mentioned for more than one host family is the ichneumonid *Campoletis varians*, a major parasitoid of the geometrid *E. autumnata* in the Alps. Three individuals were recorded from over 12 000 larvae of the tortricid *Zeiraphera diniana* by Mills (1993) in the same region. However, considering that larvae of the two host species are often found together at the same time, and because Mills reared field collected larvae in groups of 50–100 on larch foliage, it is likely that *C. varians* emerged from *E. autumnata* accidentally introduced into the rearing containers.

More surprisingly, this study showed limited overlap in the parasitoid complexes of larch feeding geometrids. Only the microgastrine braconids *P. anchisiades*, *P. immunis* and

G. vitripennis were found on at least two hosts in sizeable numbers. Another possibly polyphagous parasitoid is *Casinaria* sp.1, a species reared in high numbers from *A. aurantiaria*, and occasionally from several other species. However, for most geometrid species, the dominant parasitoids are apparently specific in this community. In particular, most *Aleiodes* spp., *Cotesia*, spp., *Dusona* spp. and Tachinidae were reared from single host species, although many Tachinidae are usually recognized as being more polyphagous than hymenopteran parasitoids. The vast majority of these species have been recorded from many other hosts, including from other families (for *Cotesia* spp., see Nixon, 1974; for *Dusona* spp., see Yu, 1999), but many of these records should be regarded as dubious.

Comparing our observations on the parasitoid complex of larch geometrids with other studies on the same species on other host plants in other environments is interesting, but it also faces the problems of identification errors and synonymies. *Epirrita autumnata* was studied on birch in Finland by Ruohomäki (1994) and Teder *et al.* (2000). The parasitoid complexes on larch in the Alps and on birch in northern Europe appear remarkably similar. The two most abundant parasitoids of *E. autumnata* on larch in Switzerland, *Aleiodes* cf. *gastritor* and *Campoletis varians*, were also found on birch in Finland. The polyembrionic *C. chalconotum*, which we reared in low numbers in the Alps, is also present on the same host in Finland (Teder *et al.*, 2000). Our *Phobocampe* sp. could be similar to the species determined as *Phobocampe neglecta* (Holmgren) or *Phobocampe bicingulata* (Gravenhorst) mentioned by Ruohomäki (1994) and Teder *et al.* (2000), respectively. Unfortunately, the taxonomy of this genus remains confused. As for Microgastrinae, we reared *P. anchisiades* and *Cotesia salebrosa*., whereas Ruohomäki (1994) mentions *P. immunis* and *C. jucunda* in Finland. However, the taxonomy of Microgastrinae is very confusing, and identification errors are likely. Specimens from *E. autumnata* from birch in Finland, previously identified as *P. immunis* and *Cotesia jucunda*, were provided by K. Ruohomäki for comparison with our *P. anchisiades* and *C. salebrosa* collected on larch in Switzerland. We consider that the same two species were present in Finland and Switzerland and identify them as *P. anchisiades* and *C. salebrosa*.

Similarities in parasitism were also observed between our *A. aurantiaria* populations on larch in the Alps and populations on broadleaf species in Germany (Herting, 1965). Two of the three most abundant parasitoids of *A. aurantiaria* on larch, *D. contumax* and *P. magnicornis*, were also recorded for broadleaf populations. *Phobocampe crassiuscula* (Gravenhorst) was also found in both environments in low numbers. Parasitism of broadleaf populations was dominated by the ichneumonid determined as *Ophion parvulus* Kriechbaumer, whereas we reared *O. minutus* from larch populations. Although these are two well-defined species, Herting (1965) mentions them as synonyms. Therefore, it is likely that his *O. parvulus* and our *O. minutus* are the same species. According to Brock (1982), *O. parvulus* is a parasitoid of Noctuidae, whereas *O. minutus* parasitizes the geometrid genera *Agriopis* and, probably, *Erannis*. Herting's study on parasitism of geometrid populations feeding on broadleaf species showed that the parasitoid complex of *A. aurantiaria* largely overlaps with that of the congeneric or closely related species *Agriopis marginata*, *Agriopis leucophaearia* and *Erannis defoliaria*, but much less with geometrids of other genera.

Egg-prepupal parasitoids of the genus *Copidosoma* are also specific to narrow taxonomic groups. *Copidosoma chalconotum*, obtained in our study from *E. autumnata,* is known for certain only from this genus. *Copidosoma cervius,* a major parasitoid of *Eupithecia lariciata,* attacks various *Eupithecia* spp. and other Eupitheciini*,* and *C. serricorne*, which we obtained from *P. capreolaria,* usually occurs on *Thera* spp. and relatives on Pinaceae (Guerrieri & Noyes, 2005).

These examples suggest that host range in geometrid parasitoids is generally more related to host taxon than to host habitat. In other words, the parasitoid complex of a given species on larch in the Alps is much more similar to that of the same species, or taxonomically closely related species, feeding on other trees species in different habitats and regions, than to other geometrid species feeding on the same tree in the same region. Indeed, although we found many parasitoid species that are probably species- or genus-specific, we failed to identify a species with more than one host that could be specific to a host tree or a particular habitat (i.e. that would be found on several larch geometrids but not known from any other host tree). Among the 'polyphagous' species found in our study, *P. anchisiades*, *P. immunis* and *G. vitripennis* are known from many other hosts in various environments (Nixon, 1973, 1976). The apparently undescribed species *Casinaria* sp.1, also collected from several larch geometrids, may be more habitat-specific. However, we also reared three individuals from the fir geometrid *P. capreolaria*, whereas larch and fir grow in very different habitats in the Alps.

Unfortunately, most studies of parasitoid complexes and parasitoid webs, including ours, focus on single habitats. Investigations should be carried out in various habitats to further assess traits determining parasitoid host range. Arboreal geometrids are particularly suitable for such studies, because many species are polyphagous, and several species are commonly found together on the same host tree.

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