Microgastrinae (Hymenoptera: Braconidae) parasitizing *Epirrita autumnata* (Lepidoptera: Geometridae) larvae in Fennoscandia with description of *Cotesia autumnatae* Shaw, sp. n.

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The microgastrine subset of hymenopteran parasitoids of the geometrid *Epirrita autumnata* is investigated in Fennoscandia. Ecology, including population dynamics, of the moth has been intensively studied in northern and mountainous Finland, Norway and Sweden. Recently supported hypotheses about the causes of its cyclic population dynamics stress the role of parasitoids, while the parasitoid complex with some 15 species is insufficiently known. The complex includes four solitary microgastrine species, *Protapanteles anchisiades* (Nixon), *P. immunis* (Wesmael), *Cotesia salebrosa* (Marshall) and *C. autumnatae* Shaw, **sp. n.** Here, we provide detailed figures for the latter, which is morphologically close to *C. jucunda* (Marshall), and describe the species as new to science. We also provide more general habitus figures of the other three species, as well as an identification key for the four species, aiming to aid recognition of these species by ecologists dealing with microgastrine parasitoids of *E. autumnata* and their alternative geometrid hosts.

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1. Introduction

Parasitoids play an important role in natural food webs (e.g. Morris *et al.* 2004) as well as in the application of biological control by often limiting and regulating the population sizes of their host insects (e.g. Stiling & Cornelissen 2005). In Fennoscandia (i.e. Norway, Sweden, Finland, and Russia: Kola Peninsula and Karelia), *Epirrita autumnata* (Lepidoptera: Geometridae) exhibits cyclic (period length 9–10 years), high-amplitude fluctuations in northern and mountainous areas which may culminate in devastating outbreak densities for 1–3 successive years (Tenow 1972, Haukioja *et al.* 1988, Ruohomäki *et al.* 2000). On the other hand, *E. autumnata* populations in southern Fennoscandia remain generally at low and relatively stable densities, although weakly cyclic, low-amplitude fluctuations in density have been reported for some populations outside the primary outbreak range (Klemola *et al.* 2006).

After years of active research on *E. autumnata* and population dynamic effects of their associated parasitoids (e.g. Ruohomäki 1994, Kaitaniemi & Ruohomäki 1999, Teder *et al.* 2000, Tanhuanpää *et al.* 2002, Klemola *et al.* 2007, 2008a, b, 2009), the most recent evidence from field experiments suggests that hymenopteran parasitoids act as causal agents for the delayed density-dependent component of the cyclic population dynamics (Klemola *et al.* 2010). These parasitoids are thus likely to drive regular population cycles of this moth species, at least in continental parts of northern Fennoscandia, according to the principles of the delayed density-dependent paradigm in population regulation of herbivores (Berryman *et al.* 1987, Turchin & Hanski 2001). Briefly, the scarcity of parasitoids allows *E. autumnata* to increase its abundance in the beginning of a cycle, while increasing levels of parasitism decrease moth numbers after the cyclic peak of the moth and maintain low density of the moth until the crash of parasitoid populations.

We have reared some 15 different species of parasitoids, including some species groups of closely-related species within a genus, from *E. autumnata* populations across Fennoscandia. They belong to the hymenopteran families Scelionidae and Encyrtidae (egg parasitoids), Braconidae (larval parasitoids), Eulophidae (larval parasitoids) and Ichneumonidae (larval and pupal parasitoids), and to the dipteran family Tachinidae (larval parasitoids).

In this paper we focus on microgastrine species (Braconidae: Microgastrinae) which have been among the most common larval parasitoids in *E. autumnata* populations sampled across Fennoscandia (Tenow 1972, Ruohomäki 1994, Kaitaniemi & Ruohomäki 1999, Teder *et al.* 2000, Klemola *et al.* 2007, 2008b, 2009, 2010, Vindstad *et al.* 2010, Schott *et al.* 2012) and in the Swiss Alps (Kenis *et al.* 2005). The cosmopolitan Microgastrinae comprise koinobiont larval endoparasitoids which attack a wide range of lepidopteran species and, with approximately 2,000 described species (Yu *et al.* 2012), it is undoubtedly one of the most species rich subfamilies of Braconidae. Mason (1981) estimated the total number of microgastrine species to fall between 5,000 and 10,000, but Rodriguez *et al.* (2012) have recently suggested a total in the range of 17,000 to over 46,000. This estimate takes account of the many new cryptic microgastrine species that have been revealed by integrating different species identification methods (morphology, DNA barcoding, ecology and behaviour; e.g. Kankare *et al.* 2005, Smith *et al.* 2008).

We have encountered four microgastrine species in our studies since 1987: *Protapanteles immunis* (Wesmael), *P. anchisiades* (Nixon), *Cotesia salebrosa* (Marshall) and *C. autumnatae* Shaw **sp. n.**, the latter species described in this paper. *Protapanteles* is a rather small (two or three dozen species) and mainly Holarctic genus (Mason 1981). *Cotesia*, on the other hand, is an enormous genus that encompasses over 250 described species (Yu *et al.* 2012), mainly from the Holarctic region, and probably at least 1,000 species overall.

The aim of this paper is a) to clarify the *Cotesia* and *Protapanteles* species parasitizing *E. autumnata* larvae, including the description of a new species, *Cotesia autumnatae* **sp. n.**, identified from our samples, and b) to provide practical means to recognise those species in ecological studies having to cope with large numbers of samples without sophisticated taxonomic tools. We also c) evaluate the potential importance of the microgastrine parasitoids in the population regulation of *E. autumnata*. This study is a part of

Table 1. Sampling sites in Finland (FI), Norway (NO) and Sweden (SE) and numbers analysed for DNA of parasitoids reared from the geometrid host *Epirrita autumnata* (No.). Additional data on all specimens are in Table 2.

Site-Id.	Site, Country	Coordinates	Alt. (m)	Trees*	No.
Outbreaking northern populations					
R3	Vittangi, SE	67°43’ 21°38’	318	PSB	9
R2	Sappisaasi, SE	67°53’ 21°35’	412	SPB	6(+1)
R4	Stenbacken, SE	68°13’ 19°37’	375	mB	3
R5	Stordalen, SE	68°18’ 19°12’	365	mB	3
V	Kuutsjärvi, FI	67°44’ 29°37’	355	PB	8(+1)
K	Kevo, FI	69°45’ 27°01’	113	mBP	11
R_{mas}	Kevo, FI	69°45’ 27°02’	141	PmB	5
MRP2	Skalluvaara, FI	69°48’ 27°08’	288	mB	5
Nuvv	Nuvvus, FI	69°49’ 26°15’	128	mB	1
Vets	Vetsikko, FI	69°57’ 27°19’	72	mBA	2
Pulm	Nuorgam, FI	70°04’ 27°52’	93	mB	3
Skip	Skiippagurra, NO	70°09’ 28°12’	35	mB	2
L_{th}	Luftjokk, NO	70°14’ 28°12’	42	mB	1
L_j	Hana, NO	70°14’ 28°27’	187	mB	1
L_k	Hana, NO	70°14’ 28°27’	216	mB	5(+1)
L	Hana, NO	70°14’ 28°30’	245	mB	4
L_{aut}	Luftjokkdalen, NO	70°15’ 28°23’	37	mB	1
Total, north					70(+3)
Non-outbreaking southern populations					
Na	Lähdesuo, FI	60°29’ 22°02’	13	BPSAl	7
Va05	Suoniitty, FI	60°42’ 22°21’	67	PB	4
Va18	Varjola, FI	60°41’ 22°24’	66	PSB	1
Va19	Hakula, FI	60°40’ 22°17’	70	PBS	5
Va42	Soisalo, FI	60°38’ 22°17’	56	PSBAl	4
Va43	Isokorpi, FI	60°39’ 22°18’	65	PB	4
Va46	Uusitalo, FI	60°39’ 22°21’	63	SBAl	4
Va54	Torikkala, FI	60°39’ 22°16’	47	BP	3
Va55	Järvijoki, FI	60°41’ 22°24’	62	PSB	1
Va56	Tortinmäki, FI	60°41’ 22°25’	61	SPBSaAl	7
Va57	Rauta-alho, FI	60°39’ 22°26’	57	PSB	1
Va58	Kiimassuonkulma, FI	60°38’ 22°22’	52	PBAlSa	5
Va59	Lapinkiuas, FI	60°38’ 22°21’	53	PSB	6
Total, south					52

* Trees are listed in order of abundance; abbreviations: B: *Betula pubescens* and/or in south *B. pendula*, mB: *Betula pubescens* ssp. *czerepanovii*, P: *Pinus sylvestris*, S: *Picea abies*, A: *Populus tremula*, Al: *Alnus incana*, Sa: *Salix* spp.

a broader attempt to specify all the parasitoid species that are involved in the dynamics of *E. autumnata* and *Operophtera brumata* (Linnaeus) in Fennoscandia.

2. Material and methods

2.1. Study species, study areas and field sampling

Larvae of the univoltine *E. autumnata* hatch in the spring simultaneously with the bud break of their deciduous host plants. The leaf-chewing larvae feed freely on foliage of many trees, shrubs and dwarf shrubs. After completing five instars the larvae descend from host plants by mid-summer and pupate in soil. In autumn, adults fly and females lay their eggs mostly on trunks and branches of trees and bushes where the essentially undeveloped eggs overwinter.

Our microgastrine samples were reared from *E. autumnata* collected as 3–5 instar larvae either from northern “outbreaking” or southern “non-outbreaking” populations of Fennoscandia (Table 1). All host larvae were reared on *Betula* leaves in the laboratory until they pupated, died,

Table 2. COI haplotypes of the four species of Microgastrinae reared from the geometrid host *Epirrita autumnata*. All specimens sequenced for COI are listed, with their sex, sampling sites and dates. Specifics for sampling sites are in Table 1, COI phylogram in Fig. 1.

Haplotype	Site-Id.	♀/♂	Date	Haplotype	Site-Id.	♀/♂	Date	Haplotype	Site-Id.	♀/♂	Date
Protapanteles immunis				*P. anchisiades* continued				*Cotesia autumnatae* **sp. n.**			
Pi I 6	K**	♀	24.VI.2005	Pa III 30	Vets	♀	25.VI.2005	Ca I 1	Va43**	♂	27.VI.2004
Pi I 6	Va05**	♀	3.VI.2005	Pa III 30	Va05	♀	1.VI.2006	Ca II 1	Va56**	♀	26.V.2004
Pi I 6	Va18	♀	26.V.2004	Pa III 30	Va19	♀	2.VI.2005	Ca III 2	Va42***	♀	31.V.2006
Pi I 6	Va46**	♀	25.V.2004	Pa III 30	Va19	♂	31.V.2006	Ca III 2	Va19***	♀	31.V.2006
Pi I 6	Va54	♂	27.V.2004	Pa III 30	Va42	♂	2.VI.2005				
Pi I 6	Va58**	♀	25.V.2004	Pa III 30	Va46	♀	1.VI.2005	*Cotesia salebrosa*			
Pi II 3	Va56	♀	26.V.2004	Pa III 30	Va46	♀	30.V.2006	Cs I 4	MRP2**	♀	24.VI.2004
Pi II 3	Va56**	♀	26.V.2004	Pa III 30	Va58	♀	1.VI.2005	Cs I 4	L_{k}^{**}	♀	9.VII.2004
Pi II 3	Va57	♀	25.V.2004	Pa III 30	Va58	♀	30.V.2006	Cs I 4	L_{k}	♂	17.VI.2003
Pi III 1	Va58	♀	25.V.2004	Pa IV 1	L_{th}	♀	14.VI.2006	Cs I 4	L	♀	28.VI.2004
Pi IV 7	Va19	♂	26.V.2004	Pa V 2	K	♂	18.VI.2005	Cs II 1	Pulm	♂	17.VI.2003
Pi IV 7	Va54	♂	27.V.2004	Pa V 2	K	♂	18.VI.2005	Cs III 3	K	♂	22.VI.2005
Pi IV 7	Va56	♀	26.V.2004	Pa VI 27	R3	♀	15.VI.2006	Cs III 3	Skip	♂	30.VI.2004
Pi IV 7	Va56	♀	26.V.2004	Pa VI 27	R3	♀	19.VI.2005	Cs III 3	L**	♂	28.VI.2004
Pi IV 7	Va59	♂	25.V.2004	Pa VI 27	R3	♀	23.VI.2004	Cs IV 1	L_{aut}	♀	3.VII.2003
Pi IV 7	Va59	♂	25.V.2004	Pa VI 27	R3	♀	23.VI.2004	Cs V 9	K	♂	20.VI.2005
Pi IV 7	Va59	♀	25.V.2004	Pa VI 27	R3	♀	23.VI.2004	Cs V 9	K**	♀	28.VI.2003
				Pa VI 27	R3	♀	23.VI.2004	Cs V 9	R_{mas}	♀	24.VI.2005
Protapanteles anchisiades				Pa VI 27	R4	♀	19.VI.2005	Cs V 9	MRP2	♂	1.VII.2003
Pa I 1	MRP2	♀	24.VI.2004	Pa VI 27	R4	♀	19.VI.2005	Cs V 9	Pulm	♂	30.VI.2004
Pa II 1	V	♂	12.VI.2006	Pa VI 27	R5	♂	19.VI.2005	Cs V 9	Pulm	♀	30.VI.2004
Pa III 30	R3	♂	19.VI.2005	Pa VI 27	V	♀	21.VI.2004	Cs V 9	Skip	♂	29.VI.2003
Pa III 30	R3	♀	23.VI.2004	Pa VI 27	V	♂	21.VI.2004	Cs V 9	Va05	♂	3.VI.2005
Pa III 30	R3	♂	23.VI.2004	Pa VI 27	V	♂	21.VI.2004	Cs V 9	Va54	♂	31.V.2006
Pa III 30	R2	♂	23.VI.2004	Pa VI 27	K**	♀	20.VI.2005	Cs VI 1	L_{k}	♂	4.VII.2005
Pa III 30	R2	♂	19.VI.2005	Pa VI 27	R_{mas}	♀	24.VI.2005	Cs VII 8	Na	♀	26.V.2006
Pa III 30	R2	♂	19.VI.2005	Pa VI 27	R_{mas}	♀	26.VI.2004	Cs VII 8	Na	♀	29.V.2005
Pa III 30	R2	♀	19.VI.2005	Pa VI 27	MRP2	♀	20.VI.2005	Cs VII 8	Na	♀	29.V.2005
Pa III 30	R4	♂	15.VI.2006	Pa VI 27	Va05	♀	1.VI.2006	Cs VII 8	Na**	♀	29.V.2005
Pa III 30	R5	♀	15.VI.2006	Pa VI 27	Va42	♀	31.V.2006	Cs VII 8	Na	♀	29.V.2005
Pa III 30	R5	♀	19.VI.2005	Pa VI 27	Va42	♀	27.V.2004	Cs VII 8	Na	♀	20.V.2004
Pa III 30	V	♀	21.VI.2004	Pa VI 27	Va43	♀	20.V.2006	Cs VII 8	Na	♂	20.V.2004
Pa III 30	V	♂	21.VI.2004	Pa VI 27	Va43	♀	1.VI.2005	Cs VII 8	Va56	♂	3.VI.2005
Pa III 30	V	♂	21.VI.2004	Pa VI 27	Va46	♀	30.V.2006	Cs VIII 3	L_{k}	♂	9.VII.2004
Pa III 30	V	♀	21.VI.2004	Pa VI 27	Va55	♀	1.VI.2005	Cs VIII 3	L	♀	28.VI.2004
Pa III 30	K	♂	18.VI.2005	Pa VI 27	Va56	♀	3.VI.2005	Cs VIII 3	L	♂	26.VI.2005
Pa III 30	K	♀	20.VI.2005	Pa VI 27	Va58	♂	25.V.2004	Cs IX 1	Va19	♀	26.V.2004
Pa III 30	K	♂	14.VI.2006	Pa VI 27	Va59	♀	30.V.2006	Cs X 2	K	♂	22.VI.2005
Pa III 30	R_{mas}^{**}	♀	24.VI.2005	Pa VI 27	Va59	♂	1.VI.2005	Cs X 2	L_{k}	♀	2.VII.2004
Pa III 30	MRP2	♀	19.VI.2006	Pa VII 1	R2	♀	19.VI.2005	Cs XI 3	L_{j}	♀	28.VI.2004
Pa III 30	Nuvv	♂	20.VI.2006	Pa VIII 1	R2	♂	15.VI.2006	Cs XI 3	Va43	♀	25.V.2010
Pa III 30	Vets	♀	25.VI.2005	Pa IX 1	R_{mas}	♂	14.VI.2006	Cs XI 3	Va59	♀	25.V.2010

* Paratypes S 24 and S 25.
** Checked morphologically by M. R. S.

or parasitoid larvae erupted and pupated. Because many parasitoid species overwinter inside their cocoons, parasitoid cocoons were retained intact in a ground cellar or refrigerator until the following summer when the adults emerged.

Several thousand microgastrine parasitoids have been reared during our long study. From these, 122 specimens, including samples from both northern and southern populations (Table 1) from the years 2003–2006 and 2010, were subjected to DNA barcoding and some to a closer morphological examination (Table 2). Adult parasitoids were killed almost immediately after their emergence, preserved in pure ethanol and stored refrigerated (close to +5°C) until DNA extraction in either autumn 2005, autumn 2006 or spring 2011. Four of the *Cotesia autumnatae* **sp. n.** specimens were included in the molecular analyses (Table 2).

2.2. Morphological identification

To find out whether there were morphologically cryptic species in our material, we studied the specimens by identifying them both morphologically and molecularly (DNA barcoding of mtDNA COI). Morphological identification of selected individuals (indicated in Table 2) was carried out by M.R.S., unaware of the results of molecular identification, using literature (Nixon 1973, 1974, 1976, Papp 1984, 1987, Kotenko & Tobias 1986) as well as reference material in the National Museums of Scotland, Edinburgh and the Natural History Museum, London.

In description of the new species, morphological terminology follows Nixon (1965, 1974) but for wing venation the terminology used by van Achterberg (1993) is added in parentheses.

2.3. Molecular identification

Genomic DNA was extracted from three legs of each individual using a DNeasy™ Tissue Kit (Qiagen). A ~1,500 bp portion of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified using two primer pairs: LCO2198 and HCO1490 (Folmer *et al.* 1994), and TL2-N-3014 alias “Pat” and C1-J-1859 alias “RonII” (Simon *et al.* 1994). Polymerase chain reaction (PCR) was conducted in 20 µl containing 5–20 ng of DNA template, 200 µM of each dNTP, 0.1 M of each primer, 0.25 mg/ml bovine serum albumin, 1× DyNAzyme™ buffer supplemented with 1.5 mM MgCl2 (Finnzymes Oy), and 1 U of DyNAzyme™ II DNA polymerase (Finnzymes Oy). PCRs were performed in PTC-100 Peltier Thermal Cycler (MJ Research Inc.) or in Eppendorf Mastercycler® gradient (Perkin-Elmer Corp.): an initial denaturation at 95°C for 5 min, 35 cycles of 30 s at 95°C, 1 min (LCO2198/HCO1490) or 1.30 min (Pat/RonII) at 47°C, and 1 min at 72°C, and a final extension at 72°C for 10 min. The PCR products were purified with the GFX™ PCR DNA and Gel Band Purification Kit (Amersham Pharmacia Biotech Inc., Piscataway, N.J.). The LCO2198/HCO1490 gene fragment was sequenced with the LCO2198 primer and the Pat/RonII gene fragment was sequenced with both primers using the automatic ABI PRISM® 3130xl DNA Sequencer with the ABI PRISM® BigDye® Terminator Kit (Applied Biosystems, Foster City, CA).

Using Sequencher® v.3.1.1 (Gene Codes Corp.), sequences were edited, and three fragments of the COI gene were assembled to obtain a consensus sequence for each individual.

The COI sequences were analyzed using the Neighbour Joining (NJ) method based on genetic distances corrected with the Kimura 2-parameter model in the program MEGA v4 (Tamura *et al.* 2007). The aim of this analysis was to investigate the clustering patterns of COI haplotypes in a DNA barcoding framework (Hebert *et al.* 2003). Only one copy of each unique haplotype was included in the analysis. All unique haplotypes (including that of *C. jucunda*) are available in GenBank under accession numbers KC414763–KC414790, which are presented in Fig. 1. We also included COI sequences of potentially related *Cotesia* species and *Microgaster canadensis* Muesebeck from GenBank.

3. Microgastrinae parasitoids of *Epirrita autumnata*

The NJ analysis of the 1,475 bp fragment of the COI gene of the braconids shows that the parasitoids reared from *E. autumnata* larvae fall into four distinct clusters that correspond to four species: *Protapanteles immunis*, *P. anchisiades*, *Cotesia salebrosa* and *C. autumnatae* **sp. n.** (Fig. 1), the latter one described below. This was entirely in accord with the result of the (more limited) morphological examination.

Within the *Cotesia* cluster, *C. salebrosa* and *C. autumnatae* **sp. n.** cluster closely with *C. marginiventris* (Cresson), *C. griffin* (Viereck) and *C. jucunda* (Marshall). (The specimen of *C. jucunda* concerned was reared from the geo-

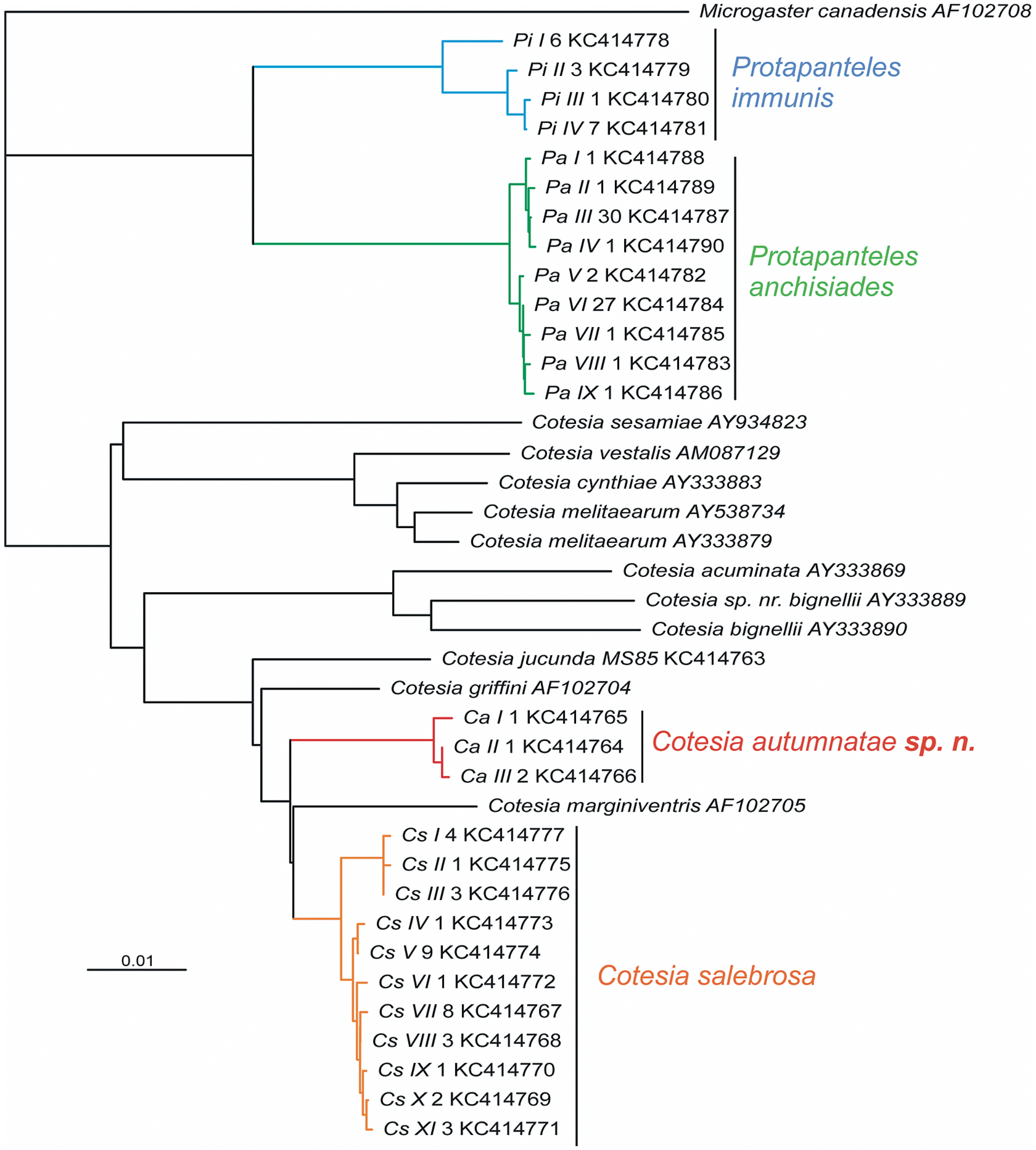

Fig. 1. The NJ dendrogram of COI haplotypes of four microgastrine species reared from larvae of the geometrid *Epirrita autumnata* in Fennoscandia. *Cotesia jucunda*, morphologically close to *C. autumnatae* **sp. n.**, has also been included as well as other *Cotesia* spp. and, as an out-group, *Microgaster canadensis*. The GenBank accession number is given for each sequence used in the analysis. For each haplotype of the four species reared from *E. autumnata*, the number just before the GenBank accession number shows the number of specimens in that haplotype; information of all specimens are listed in Table 2. Scale gives percentage divergence based on Kimura 2-parameter model corrected genetic distances.

metrid *Operophtera brumata* in Scotland, and has been compared with the type of *Apanteles jucundus* Marshall. It is also the specimen we have figured in this paper.) All four sequenced individuals of *C. autumnatae* **sp. n.** were from southern populations. Within the *C. salebrosa* cluster, two groups, a well-supported northern group (Cs haplotypes I–III) and a northern-southern mixed group (Cs haplotypes IV–XI), were found (Fig. 1). The northern *C. salebrosa* individ-

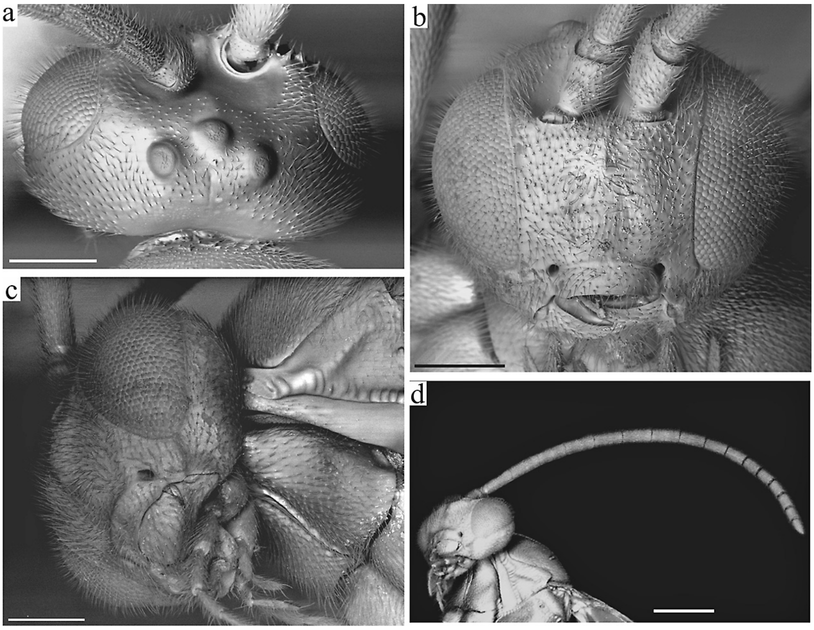

Fig. 2. *Cotesia autumnatae* **sp. n.**, paratype female. – a. Head, dorsal. – b. Head, facial. – c. Head, antero-latero-ventral. – d. Antenna. Scales 0.2 mm, except 0.5 mm in d.

uals, with one exception, overwintered in their cocoons, while none of the southern *C. salebrosa* or *C. autumnatae* **sp. n.** individuals did so.

The *Protapanteles* group formed two well-supported clusters corresponding to two species: *P. immunis* and *P. anchisiades* (Fig. 1). All *Protapanteles* individuals hatched during the same summer that they parasitized their host, regardless of the collection area.

4. Description of *Cotesia autumnatae* Shaw, sp. n. (Figs 2–6)

Material. Holotype ♀: “FINLAND: V: Vahto 60°41’N 22°24’E ex Epirrita autumnata, Betula, 29.5.[20]07, coc. 11.6.07, em. 20.6.07 K. Ruohomäki”; “S 29”, in NMS.

Paratypes: 10 ♀ 3 ♂, in NMS unless otherwise indicated. Same data as holotype, but coll. 4.VI.1999, coc. 11.VI.1999, em. 1999, S 21 (1 ♂); as holotype but 60°38’N 22°17’E, coll. 31.V.2006, coc. 26.VI.2006, em. 2006, S 24 (1 ♀); as holotype but 60°38’N 22°22’E, coll. 4.VI.2003, coc. 16.–25.VI.2003, em. 2003, 5 (1 ♀); as holotype but 60°39’N 22°21’E, coll. 20.V.2008, coc. 9.VI.2008, em. 20.VI.2008, E-08 59 (1 ♀); as holotype but 60°39’N 22°17’E, coll. 26.V.1998, coc V/VI.1998, em. 1998, S 23 (1♂, in ZMUT); as holotype but 60°40’N 22°21’E, coll. 23.V.2000, coc 31.V.2000, em. 2000, S 17 (1 ♀); Finland: V: Nousianen 60°40’N 22°17’E ex *Epirrita autumnata*, *Betula*, coll. 31.V.2006, coc. 26.VI.2006, em. 2006 (K. Ruohomäki, S 25) (1♀, in ZMUT); same data but coll. 3.VI.1999, coc. 19.VI.1999, em. 1999, S 22 (1 ♀); same data but coll. 29.V. 2007, em. 11.VI. 2007, S 26 (1 ♀); Finland: V: Masku 60°39’N 22°16’E ex *Epirrita autumnata*, *Betula*, coll. 23.V.2000, coc. 28.V. 2000, em. 2000 (K. Ruohomäki, S 19) (1 ♀); same data but coll. 26.V.2011, coc. 7.VI.2011, em. 20.VI.2011, S 40; same data but coll. 26.V.2011, coc. 10.VI.2011, em. 21.VI.2011, S 41; Finland: V: Naantali 6719:227 [60°29’N 22°02’E] ex *Epirrita autumnata*, *Betula*, coll. 1990, em. 1990 (K. Ruohomäki, S 18) (1 ♂). Several of the paratypes are in poor condition.

Description. Holotype, ♀: Length 3.0 mm.

Head in dorsal view (Fig. 2a; but slightly out of plane) 1.9 times as wide as long, widest at eyes, temple only gradually narrowing near eye then abruptly and roundly narrowing in posterior half, temple nearly as long as eye; clypeus rather well separated from face, face (excluding clypeus) 1.2–1.3 times wider than high (Fig. 2b), varying from rugulose and indistinctly punctate to dull (setose) and hardly sculptured; frons and vertex centrally tending to be smooth and shiny; ocelli in

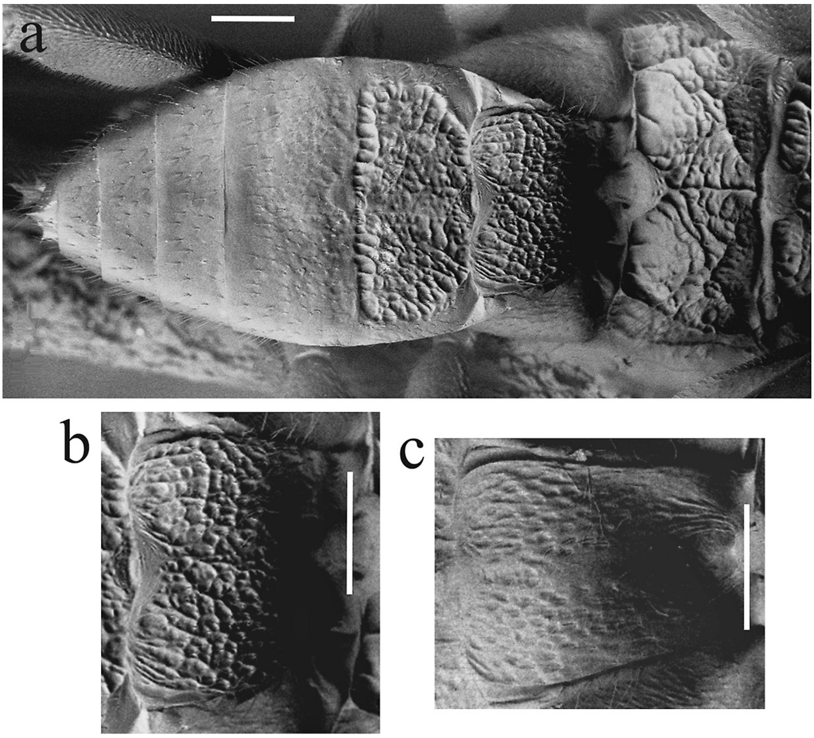

Fig. 3. – a. Propodeum and metasoma of *Cotesia autumnatae* **sp. n.**, paratype female, dorsal. – b. Tergite 1 of *C. autumnatae* **sp. n.**, paratype female, dorsal. – c. Tergite 1 of *Cotesia jucunda*, female, dorsal. Scales 0.2 mm.

a low triangle, imaginary tangent to posterior pair touching anterior ocellus, ocelli large, POL 2.1, distance between anterior and posterior ocellus 0.75, and OOL 2.0 times diameter of posterior ocellus, respectively; eyes extending to level of upper margin of clypeus or just below and weakly converging (Fig. 2b); malar space 0.8 times basal width of mandible (Fig. 2c); antenna (Fig. 2d) about as long as body, rather bristly, fourth segment about 2.8 times and penultimate segment about 1.3 times as long as wide.

Mesoscutum with weak hardly resolvable sculpture, only slightly shiny, notaulic courses even duller in some specimens but hardly detectable in others; scutellum more shiny but with similar vague sub-punctate sculpture; prescutellar sulcus well marked; phragma of scutellum moderately exposed (Fig. 3a); mesopleuron anteriorly with sculpture varying from rugulose to moderately strongly rugose with clear punctures, more shiny and with reduced sculpture below the weakly impressed and feebly crenulate precoxal sulcus and also onto mesosternum; propodeum moderately coarsely rugose (but variable), its median carina strong (Fig. 3a). Fore wing (Fig. 4) with pterostigma moderately broad, about 2.3 times as long as wide, issuing radius (r) beyond middle (about 0.6); metacarp (1-R1) 1.1 times as long as pterostigma and about 3.6 times as long as its distance from apex of radial cell (marginal cell); first abscissa of radius (r) rather long, as long as width of pterostigma and about 1.3 times as long as transverse cubitus (2-SR), ultimately practically vertical but sometimes weakly curved initially, its junction with transverse cubitus (2-SR) sharply angled at outer side (sometimes with a very slight stub); first abscissa of discoideus (1-CU1) 0.9– 1.0 times as long as second (2-CU1); discal cell (first discal cell) rather variable, about 1.1– 1.2 times wider than high; setae of median cell (basal cell) substantially reduced towards medius (M+CU1). Hind wing (Fig. 4) with cubitellan cell 1.5 times as long as wide; basella (cu-a) evenly curved; vannal lobe (plical lobe) beyond widest part lacking a hair fringe. Hind coxa weakly rugulose above and at side, subshiny above but matt and punctulate below; hind femur 3.4 times as long as wide (Fig. 5a); hind tibia with blunt spines rather evenly distributed, not especially dense; inner hind tibial spur longer than outer or spurs subequal (Fig. 5a), the inner one only sometimes reaching to middle of hind

Fig. 4. Wings of *Cotesia autumnatae* **sp. n.**, paratype female. Scale 0.5 mm.

basitarsus (rather variable in the specimens seen). Apical segment of front tarsus lacking a clear spine (though a thickened hair discernible by SEM, Fig. 5b).

Metasoma with first tergite (Fig. 3b) somewhat roundly widening towards apex, incurved only slightly at extreme apex, strongly convex in posterior half and rather deeply excavate basally (Fig. 3b), 1.1 times as long as apically wide (Fig. 3b); second tergite (Fig. 3a) about 2.5 times as wide as long, its basal field variable, 2.0–2.3 times as wide as long, with somewhat curved lateral sulci that are clear in some specimens (Fig. 3a) but in others indistinct leaving the basal field sometimes poorly defined; apical part of first and second tergite rugose, longitudinal element of sculpture best developed on first tergite; third tergite about 1.1 times as long as second (Fig. 3a), rather evenly long-setose (Fig. 3a), weakly rugulose in at least anterior half; hypopygium (Fig. 6) about half as long as hind tibia (but its base often concealed by laterotergites), rather densely setose ventrally, roundly sub-truncate apically, and not protruding beyond apex of metasoma; ovipositor sheath slightly protruding,

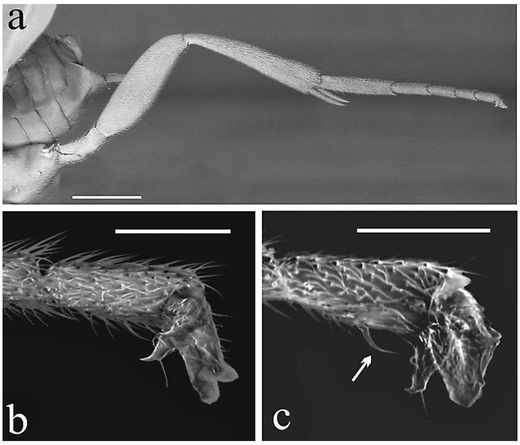

Fig. 5. – a. Hind leg of *Cotesia autumnatae* **sp. n.**, paratype female, lateral. – b. Apical segment of front tarsus of *C. autumnatae* **sp. n.**, paratype female, lateral. – c. Apical segment of front tarsus of *C. jucunda*, female, lateral. Scale 0.5 mm in a, 0.1 mm in b and c.

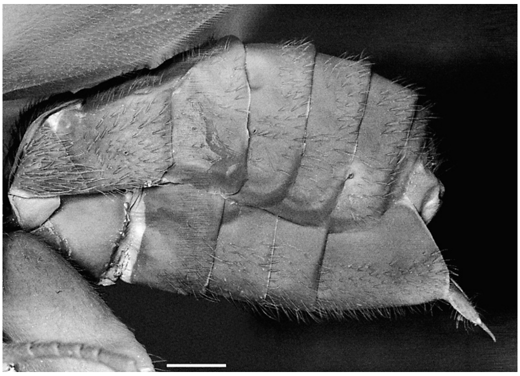

Fig. 6. Metasoma of *Cotesia autumnatae* **sp. n.**, paratype female, lateral. Scale 0.2 mm.

rather rounded and directed somewhat downwards (Fig. 6).

Colour: Black; mouthparts variably, all legs except usually coxae and most of trochanters (but excluding trochantelli) largely yellow/orange. Sometimes first, usually middle and hind femora infuscate at base below and to some extent along dorsal edge; hind tibia weakly infuscate apically below, and hind tarsi darkening apically. Tegulae essentially black; pterostigma dark greyish brown, vaguely paler at base and apex; venation in proximal half (including costa) largely yellowish and in distal half (including metacarp) greyish brown.

Male: Like female except for sexual characters, but legs darker (hind femur strongly flushed brown above and below).

Variation: The few females seen are very variable in the strength and extent of their sculpture (as expressed above). Some specimens have the coxae (especially front coxa) weakly marked with orange below.

Etymology. The name refers to the geometrid host, *Epirrita autumnata*, from which all specimens have hitherto been reared.

Host. All specimens have been reared as a solitary parasitoid of *Epirrita autumnata* (Borkhausen) collected on *Betula pubescens* or *B. pendula* in late May–early June, the adults emerging in the latter half of June the same year (indoors). The cocoons have invariably been of a strong lemon yellow colour. It is unclear how the parasitoid passes the winter. All specimens originate from the area without outbreaks of *E. autumnata*.

Remarks. There are several solitary European *Cotesia* species with a more or less impunctate, satiny mesoscutum, widening first tergite, rather evenly setose and partially sculptured third tergite, relatively long metacarp, hind wing vannal lobe lacking a hair fringe, moderate hind tibial spurs, and antennal characteristics similar to this species. However, these mostly are known from hosts other than Geometridae or are invariably dark-legged. Thus the new species differs from *Cotesia salebrosa* (Marshall), which is also a solitary parasitoid of *Epirrita* species and co-occurs with the new species, most obviously by its paler legs (hind femur blackish in *C. salebrosa*) and in its COI DNA sequence (see above). Nixon (1974) mentions pale-legged specimens of *Cotesia* (as *Apanteles*) *jucunda* (Marshall) [the dark-legged type of which has been examined], another solitary parasitoid of arboreal Geometridae, but in addition to being usually dark-legged this species has a narrower and more straight-sided first tergite (about 1.2–1.3 times as long as wide, Fig. 3c), a somewhat more apically truncate hypopygium, slightly slenderer legs and antenna and, most importantly, a characteristic though sometimes small spine on the apical segment on the front tarsus (Fig. 5c) – a character we have been unable to detect on any of the specimens here attributed to the new species, at most a thickened seta being visible under SEM (Fig. 5b). Although there are several points of similarity between these two species (and the cocoon of *C. jucunda* is also yellowish, though less bright) it also seems significant that *C. jucunda* is regularly a parasitoid of *Operophtera brumata* in Britain where it apparently does not parasitise *Epirrita* species (*cf.* Nixon, 1974; M. R. Shaw, unpublished). Also, the new species has not been reared from cooccuring *Operophtera*, or other geometrid species of the so-called winter moth group (e.g. Snäll *et al.* 2007), in Finland. However, the numbers reared in the areas where *C. autumnatae* **sp. n.** has been collected have been small (K. R. & T. K., unpubl.).

In Nixon's (1974) key to the "*Apanteles glomeratus*" group, the new species runs comfortably to couplet 59, but then founders. Its reddish yellow hind femur suggests *C. melanoscela* (Ratzeburg), from which however it differs by lacking the spine on the apical segment of the front tarsus. The alternates, *C. salebrosa* (as *callunae* (Nixon)) and *C. ancilla* (Nixon), both have the hind femur dark. If a different direction is taken at couplet 58, it will run to a yellow-legged form of *C. jucunda* (Marshall), but differs in lacking the spine on the apical segment on the front tarsus exhibited by that species. Couplet 59 of Nixon's key could be amended to accommodate the new species as follows:

59 Hind femur usually with at least a reddish flush along each side, sometimes almost entirely bright reddish yellow 59a
– Hind femur entirely blackish (apical segment of front tarsus without trace of a spine) 60

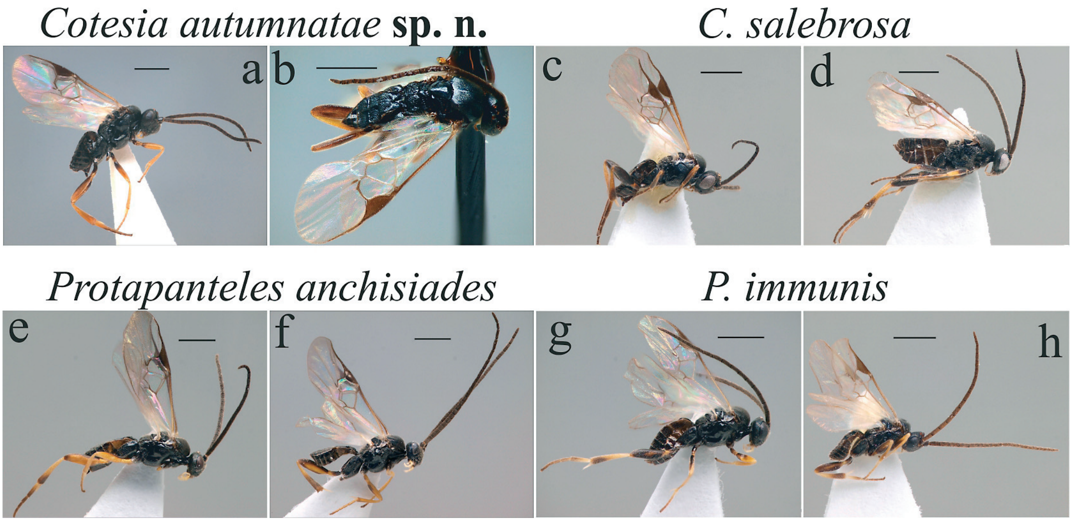

Fig. 7. Habitus of the four microgastrine species parasitizing *Epirrita autumnata* in Fennoscandia. In each pair, female (left) and male (right). Paratype for *Cotesia autumnatae* **sp. n.** Scales 1 mm.

59a Apical segment of front tarsus with a distinct though fine spine (hind femur often substantially darkened) *melanoscela* (Ratzeburg)

– Apical segment of front tarsus lacking a spine (hind femur practically completely reddish yellow) *autumnatae* **sp. n.**

5. Key to females of Microgastrinae reared from *Epirrita autumnata* in Fennoscandia. (Figs 7–9)

The general habitus of both sexes of the four species are shown in Fig. 7. The following key is aimed to serve mainly ecologists, using a stereo microscope for everyday species determination of samples reared from *E. autumnata*. Males tend to be much more variable than females, and consequently the key will work best for the female sex. Nevertheless, if allowance is made for sexual differences in dimensions (males are usually slenderer), males should also run satisfactorily.

1. Propodeum strongly rugose, usually with a clear median longitudinal carina (Fig. 8b); third metasomal tergite with more or less extensive (though sometimes rather fine) rugulose sculpture anteriorly (Fig. 8a) 2

– Propodeum weakly sculptured, sometimes smooth and shining, lacking a median longitudinal carina (Fig. 8e); third metasomal tergite almost as smooth anteriorly as posteriorly, lacking rugulose sculpture (Fig. 8d) 3

2. Hind femur black (sometimes narrowly orange/brown at extreme base and apex) (Fig. 9a); first three tergites of metasoma more robust and with stronger sculpture than alternate (Fig. 8a): T1 more strongly (sub)posteriorly widened (Fig. 8a); T2 rugose over practically its entire surface (Fig. 8a); T3 rugulose over at least anterior half where about as matt as T2, becoming medially smooth only in apical quarter (Fig. 8a) *Cotesia salebrosa* (Marshall)

– Hind femur predominantly yellowish orange, at most flushed dark along upper and lower margins (Fig. 9b); first three tergites (Fig. 8c) of metasoma less robust and with weaker sculpture: T1 less strongly widened (sub)posteriorly; T2 with a more or less trapezoid area of rugose sculpture [sometimes but not always clearly separated from the smoother lateral margins by deeply foveolate grooves (Fig. 3a)]; T3 anteriorly with sculpture clearly weaker than that on T2 (Fig. 8c) and here more shiny than sculptured part of T2 *Cotesia autumnatae* Shaw, **sp. n.**

3. First metasomal tergite almost twice as long as wide, parallel-sided for most of its length (Fig. 8d), roundly narrowing at extreme apex (Fig. 8d); second tergite with lateral sulci arising near middle of anterior margin then curv-

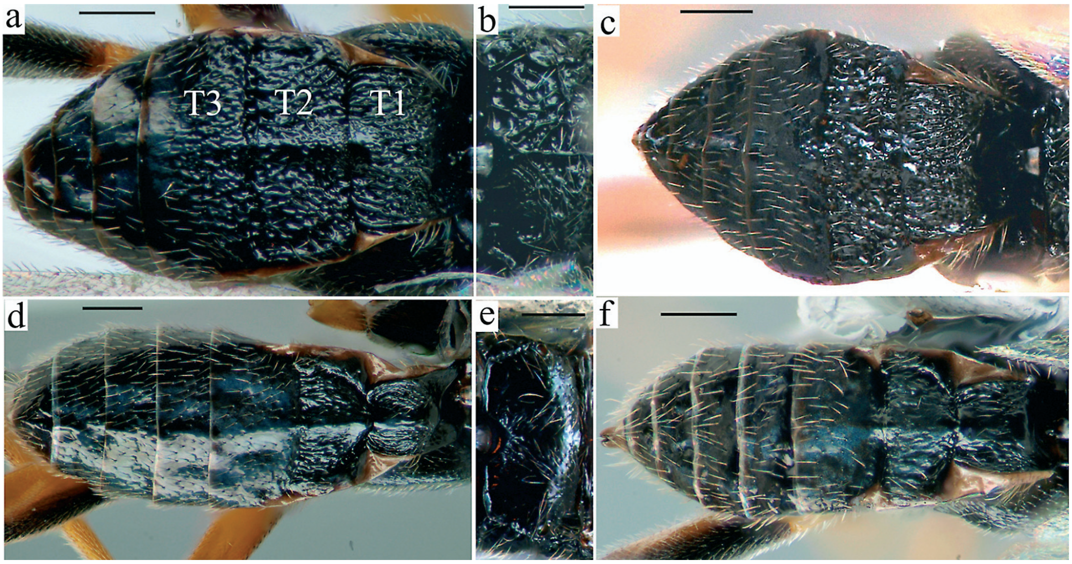

Fig. 8. – a. Metasoma of *Cotesia salebrosa*, with tergites 1–3 (T1–T3) indicated, female, dorsal. – b. Propodeum of *C. salebrosa*, female, dorsal. – c. Metasoma of *C. autumnatae* **sp. n.**, paratype female, dorsal. – d. Metasoma of *Protapanteles anchisiades*, female, dorsal. – e. Propodeum of *P. anchisiades*, female, dorsal. – f. Metasoma of *P. immunis*, female, dorsal. Scales 0.2 mm.

ing outwards and subsequently rather evenly towards the posterior margin of the tergite, defining a subtriangular or rather heart-shaped rugulose/striate area that is about three quarters as long as posteriorly wide (Fig. 8d) *Protapanteles anchisiades* (Nixon)

– First metasomal tergite broader (Fig. 8f), often widest near its midlength, about 1.3 times as long as wide, variably narrowing at its apex (Fig. 8f); second tergite with rather deep lateral sulci near anterior edge that are directed from near the midpoint towards sides of tergite, then weakening, to define a more strongly transverse rugulose/striate area about twice as wide as long (Fig. 8f) *Protapanteles immunis* (Wesmael)

6. Discussion

This is an article within a wider study dealing with all parasitoids of an ecologically much-studied geometrid moth, *Epirrita autumnata*, whose populations are outbreaking, cyclic, and/or remaining stable and at low densities, depending on the geographic area (Ruohomäki *et al.* 2000, Klemola *et al.* 2002, 2006). Therefore, the role of parasitoids may be different in these areas (Klemola *et al.* 2002), and the population dynamic role of different parasitoid species or parasitoid guilds may not be similar within or between the areas (Hagen *et al.* 2010, Schott *et al.* 2010, Klemola *et al.* 2010). Accordingly, knowledge of the parasitoid species involved may be crucial in thoroughly understanding the population dynamics of *E. autumnata* in different areas.

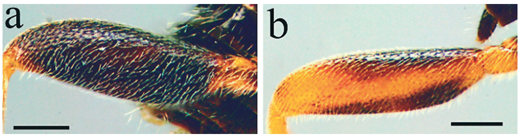

Fig. 9. – a. Hind femur of *Cotesia salebrosa*, female, lateral. – b. Hind femur of *C. autumnatae* **sp. n.**, paratype female, lateral. Scales 0.2 mm.

In both genera of Microgastrinae parasitizing *E. autumnata* larvae, there seems to be one abundant and another less numerous species (own unpublished data). The abundant ones are *P. anchisiades* and *C. salebrosa*. Of the other two, *P. immunis* and *C. autumnatae* **sp. n.**, the latter has been found only in south-western Finland (sites in Table 1), where its prevalence in *E. autumnata* larvae has been only some 1%. The indications

Table 3. Microgastrine parasitoids of *Epirrita autumnata* as named in published articles dealing with Fennoscandian populations. The right hand column gives the correctness of the published identification: +: correct, (+/–): Probably partly correct (for some specimens), –: not correct.

Species in the article	Reference*	
No name	1	
Apanteles solitarius (Ratzeburg) syn, *C. melanoscela* (Ratzeburg)	2, 3	–
Cotesia jucunda (Marshall)	4, 5, 6, 7, 8, 9, 10	–
Cotesia salebrosa (Marshall)	12, 13, 14, 15	+
Cotesia salebrosa (Marshall)	16, 17	(+/–)
Protapanteles immunis (Haliday)	4, 9, 11, 10, 16, 17	(+/–)
Protapanteles anchisiades (Nixon)	12, 14, 16, 17	(+/–)

* References: 1: Tenow 1956, 2: Tenow 1963, 3: Tenow 1972, 4: Ruohomäki 1994, 5: Ruohomäki *et al.* 1996, 6: Bylund 1997, 7: Karhu 1998, 8: Kaitaniemi & Ruohomäki 1999, 9: Teder *et al.* 2000, 10: Riihimäki *et al.* 2005, 11: Klemola *et al.* 2003, 12: Klemola *et al.* 2007, 13: Klemola *et al.* 2009, 14: Klemola *et al.* 2010, 15: Klemola *et al.* 2012, 16: Vindstad *et al.* 2010, 17: Schott *et al.* 2012.

are that *C. autumnatae* **sp. n.** may be more dependent on some other, as yet unknown, host species; certainly, its means of passing through the winter is undiscovered.

Of the three species found in northern areas with cyclic populations of the host, only *C. salebrosa* overwinters within cocoons spun by larvae that erupt from *E. autumnata* larvae. The population dynamics of this species must be relatively closely connected with that of the host, because the same cohort of parasitoids parasitizes the host in the following spring. Therefore, only *C. salebrosa* is an appropriate candidate, possibly along with some non-microgastrine parasitoid(s), some of which might be egg or pupal parasitoids, to have a primary role in causing a delayed density dependent component in the population dynamics of the host, i.e. in driving the high-amplitude population cycles of the host. Adults of both *Protapanteles* species emerge, after a brief pupal period (c. two weeks), soon after larval eruption from the host larvae. Because no microgastrine species is known to overwinter as adults and *E. autumnata* always overwinters as eggs, *Protapanteles* spp. seem to require some other host species in order to overwinter, especially because *E. autumnata* eggs overwinter without developed larva within and it is unlikely that these parasitoids can parasitize such eggs. According to the theory of population dynamics, population cycles, if driven by natural enemies, should be due to the action of specialists, because generalists also use other hosts or prey thereby making their populations partly uncoupled from populations of any particular host/prey species (Berryman *et al.* 1987, Ruohomäki *et al.* 2000, Tanhuanpää *et al.* 2002). The two *Protapanteles* species appear to be partly uncoupled from the population density of *E. autumnata*, in which case there cannot be direct roles for these two species in driving the cyclic dynamics of the host population.

All four microgastrines of this study probably have the potential for a wider host range among geometrids. However, we suggest that in the species-poor communities of the harsh environments of northern and mountainous Fennoscandia, i.e. where the population cycles of *E. autumnata* occur, densities of other potential hosts are too low to maintain high enough densities of parasitoids, forcing them to be specialists in practice. In some earlier articles we have called them “functional specialists” (Ruohomäki *et al.* 2000, Klemola *et al.* 2009), equivalent to local monophagy (Shaw 1994, 2006).

In non-outbreaking populations of *E. autumnata* in more southern latitudes, with more species-rich communities, the role of these very same microgastrine species could be crucially different, as there parasitoid species with the ability to use several host species play important roles in maintaining continuously low densities of hosts (e.g. Andersson & Erlinge 1977, Hanski *et* *al.* 1991), including those of *E. autumnata* (Klemola *et al.* 2002). For example, in these areas, contrary to the north, individuals of *C. salebrosa* do not overwinter in cocoons originating from *E. autumnata* larvae, but hatch as adults soon after cocoons have emerged, as do the three other microgastrines in these areas (there the specifics of overwintering of all the four species are unknown to us). However, our data do not allow us to claim that these four species, or other parasitoids, have a decisive role in maintaining stability and/or low density of *E. autumnata* outside the outbreak range (Teder *et al.* 2000). Instead, our results suggest and we assume that a variety of different biotic factors, including diseases, various kinds of predators (invertebrates and vertebrates), and parasitoids act in concert in keeping *E. autumnata* and most other folivorous Lepidoptera species at low densities (Tanhuanpää *et al.* 1999, 2001, 2003, Klemola *et al.* 2002).

Parasitoids are often difficult to determine, and the literature is full of mistakes concerning host relations (Shaw 1994). The parasitoids recorded from *E. autumnata* in various publications also include several microgastrines that were not correctly identified (Table 3; see also Kenis *et al.* 2005). In some cases a little detective work can lead to a clear understanding of the error: for example, Nixon (1974) did not know *Cotesia salebrosa* and had no doubt simply misidentified the specimens recorded in Tenow (1963) as [*Apanteles*] *solitarius* (now *Cotesia melanoscelus* (Ratzeburg), a parasitoid of Erebidae: Lymantriinae) on the grounds of its strongly rugose sculpture on the 3rd metasomal tergite, similar to that of *C. salebrosa*. In some other cases the precise identity of the regular parasitoid of *E. autumnata* in several ichneumonoid genera (e.g. *Aleiodes*, *Phobocampe*, *Agrypon*), is surrounded by taxonomic uncertainties, and/or biological anomalies, that still need careful research and clarification. Further discussion of these anomalies is beyond the scope of this paper. However, the fact that they exist – with the obvious corollary that the overall host relations of the parasitoid taxa are similarly unclear – does point to the great deal of taxonomic work (in which molecular studies as well as biological experimentation will no doubt play a part) that is still necessary before the effects of parasitoids in the population dynamics of their hosts, even in such well-studied cases as *E. autumnata*, can be properly understood.

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