

The structure of a high latitude plant-flower visitor system: the dominance of flies

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Elberling, H. and Olesen, J. M. 1999. The structure of a high latitude plant-flower visitor system: the dominance of flies. – *Ecography* 22: 314–323.

The species richness of insect flower visitors to all angiosperms at a subarctic-alpine site in northern Sweden was described and the plant-flower visitor matrix was analysed and compared to other high latitude systems and with systems from lower latitudes. In the habitat, 23 plant species had a total of 242 interactions with 388 flower-visiting insects, belonging to 118 taxa. Connectance of the plant-flower visitor matrix was 8.9. Comparing our findings with other studies, we get that the proportion of dipteran species of the total pollinator fauna increases with latitude but that the proportions of species of Diptera, Hymenoptera and Lepidoptera do not vary significantly among high latitude systems. Muscidae and Empididae were more abundant and generalised than other dipteran families visiting flowers in the arctic, their proportions of the total Diptera fauna increase with latitude and they are the most widespread families of flower-visiting insects in the arctic. Several Muscidae species are typical to alpine habitats in the arctic-subarctic zone. These species have special pollen feeding behaviour and an elongated proboscis, which improves access to closed flowers.

Compared to other published pollination system studies, the connectance of low latitude systems ranges between 3.4 and 28.1, whereas high latitude and high altitude systems vary between 8.6 and 19 (–60).

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In all natural systems, communities of species interact with one other. These interactions, whether classified as mutualistic, antagonistic or neutral, vary in space and time in their specificity and intensity (C. M. Herrera 1988, Olesen 1992, Warncke et al. 1993, Bronstein 1994, Thompson 1994). The interaction structure of many systems has been analysed (cf. e.g. Briand 1983, Sugihara et al. 1989). However, many of the generalisations produced are still disputable, provide only static pictures, and need more data and thought.

Most studies on interacting communities concern predator-prey systems. The structure of mutualistic interactions, for example between plants and their pollinators, has been less intensively studied (however, see Jordano 1987, Waser et al. 1996). Most literature on pollination biology focuses on single plant species and

their associated fauna of flower visitors. The scarcity of research in pollination ecology at the community or system level is largely due to labour-intensive sampling procedures, tedious observation protocols, and difficulties posed by taxonomically resolving an entire community of animal species.

Jordano (1987) reviewed a set of mutualism studies involving communities of interacting plants and flower-visiting or fruit-eating animals. He concluded that facultative interactions of high generality were frequent. He also suggested that many of the null interactions observed in system matrices might be due to reduced phenological overlap between plant and animal species, incompatible plant-animal morphology, or insufficient observations. However, most of the systems included in Jordano's analysis were only subsets or compartments

Accepted 9 September 1998

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ISSN 0906-7590

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Table 1. Structure of the plant-flower visitor system at Abisko, northern Sweden.

Number of animal species (a)	118
Number of plant species (p)	23
System size ($M = ap$)	2714
Total number of species interactions (I)	242
Connectance ($C = 100I/(ap)$)	8.92
Number of species interactions per animal species	
mean \pm SD	2.05 ± 0.18
skewness	2.42 ± 0.22
Number of species interactions per plant species	
mean \pm SD	10.52 ± 1.63
skewness	1.15 ± 0.47

of total systems, e.g. *Heliconia* flowers-hummingbirds (Stiles 1975). This bias was more pronounced among pollination systems than in dispersal systems. Of the studies reviewed by Jordano (1987), only the interaction system of J. Herrera (1988) could be regarded as total, i.e. including all plants within the habitat and their flower-visiting animals.

Since 1987 several studies of total pollination systems have been published. Olesen (unpubl.) reviews 19 systems from 15 studies, all including the entire communities of flowering plants and flower-visiting animals within defined and limited habitats. These studies span widely in both latitude and altitude. The review points out that lowland tropical and arctic systems are severely understudied. For obvious reasons, no study of any total lowland tropical plant-pollinator system exists, though studies of spectacular compartments have been made, e.g., the euglossine bee-orchid system (e.g. Roubik and Ackerman 1987). On the other hand, a few arctic-subarctic studies are available (three Canadian studies by Mosquin and Martin (1967), Hocking (1968) and Kevan (1970, 1972)). However, Mosquin and Martin (1967) sampled for only three days. The latter two were both made at Hazen Camp and may here be regarded as replicates. Thus more information is needed about total pollination systems at high latitudes, especially from regions outside Canada, to make more valid cross-latitudinal and -longitudinal comparisons.

The present paper reports on a study at a species-rich site in the subarctic-alpine zone in northern Sweden. It describes and analyses the total plant-flower visitor interaction matrix and compares its characteristics with

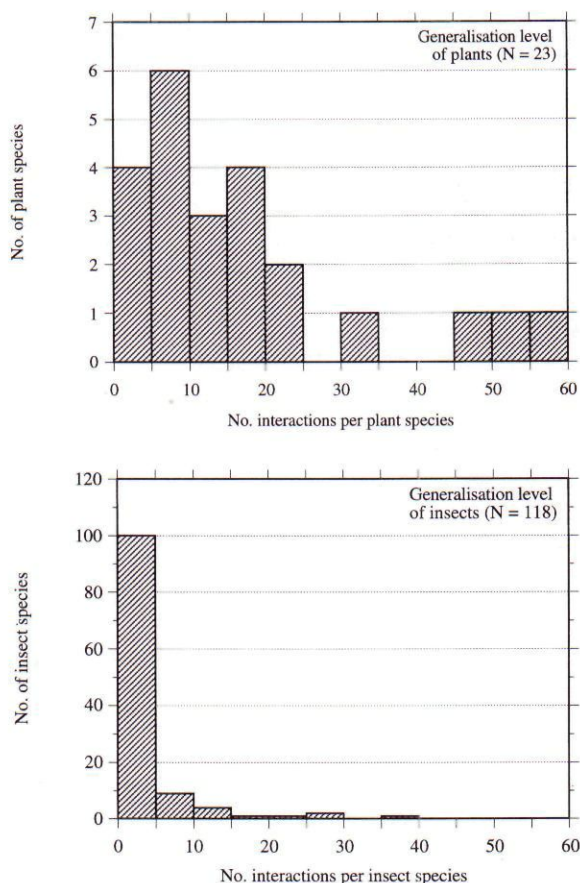


Fig. 1. Frequency distributions of generalisation level, i.e. number of interactions per plant and insect species respectively.

other subarctic-arctic-alpine systems and with pollination systems of lower latitudes especially in relation to the role of flies as flower visitors at high latitudes.

Material and methods

The study was carried out at Latnjajaure, an alpine site in the subarctic zone in northern Sweden ($68^{\circ}21'N$, $18^{\circ}30'E$) at an altitude of 985 m, 15 km due west of Abisko. The study site consisted of a 30×50 m plot of rocks and low vegetation on the calcareous species-rich

Table 2. Species richness and abundance of orders of flower visitors from Abisko, Sweden.

Order	No. of species	(%)	No. of specimens	(%)
Diptera	88	(75)	322	(83)
Hymenoptera	23	(19)	43	(11)
Lepidoptera	3	(2.5)	6	(1.5)
Coleoptera	2	(1.7)	9	(2.3)
Trichoptera	1	(0.85)	3	(0.77)
Thysanoptera	1	(0.85)	5	(1.3)

Table 3. Comparison of flower specialisation among the most abundant families of Diptera, Abisko, Sweden. Mean \pm SD.

	No. of plant spp. visited per Diptera sp.	No. of visiting indi- viduals per Diptera sp.
Empididae	4.2 \pm 4.0	8.8 \pm 11.5
Muscidae	3.9 \pm 2.9	7.7 \pm 9.5
Chironomidae	1.9 \pm 2.0	3.1 \pm 5.9
Phoridae	1.8 \pm 1.3	2.2 \pm 1.9
Anthomyiidae	1.4 \pm 1.2	1.4 \pm 1.5
Sciaridae	1.1 \pm 0.29	2.8 \pm 4.5

westward slope of Mt. Latnjatjärro. Field work was conducted from 21 May to 23 August, 1994. Throughout the flowering season, we observed flower-visiting insects daily by regularly sampling along transect lines which ran across the plot, spending a total of ca 10 h of observation and insect sampling time on each plant species. Between days, visitation sequence was randomised to correct for differences in visitation during the course of the day. Regardless of whether insects were observed to forage for nectar and pollen or to perform sun-basking, they were all classified as flower visitors and potential pollinators and the plant species visited were recorded. Very few flower visitors could be identified to species in the field, so they were caught and preserved for later identification. Insects were identified by taxonomists specialising in the various families and genera (see Acknowledgements). All the material is deposited at our department and in the collections of the assisting taxonomists. Numbers of sampled flower-visiting individuals of a species were used as a measure of its overall abundance.

The total number of species-species interactions in the matrix (I) and its connectance ($C = 100I/ap$, where a and p are number of animal and plant species respectively) were calculated. These measures may be very sensitive to sample size, since the number of insect species visiting a plant species depends on the number of individuals observed. Many interactions in our matrix are represented by single observations and additional field time would almost certainly result in some of the 0's (absent interaction) being replaced by 1's (observed interaction), and thus higher connectance estimates. However, additional observation effort would also add novel insect species to the matrix, decreasing

connectance. In general, connectance decreases hyperbolically with increasing matrix size, but even at moderately small matrix sizes connectance becomes relatively robust to sample size (Olesen unpubl.). Despite these shortcomings in estimation of system measures our comparisons between systems are unlikely to be affected seriously by these problems.

Statistical analyses were performed with SYSTAT (Wilkinson 1992).

Results

A total of 388 flower-visiting insects, belonging to 118 taxa, visited 23 of the 47 plant species that flowered at the study site (cf. Appendix). Fifty-eight percent of the insect taxa and 78% of the specimens were identified to species, 28% of the taxa and 15% of the specimens were identified to genus, and the rest to higher levels only. Most of the parasitoid Hymenoptera were identified only to tribe. The appendix gives the interaction matrix between the communities of flowering plants and insects, and Table 1 summarizes the system characteristics.

Diptera was by far the most abundant and species-rich order of flower visitors (Table 2). Anthomyiidae (17 spp.), Chironomidae (16 spp.), Muscidae (14 spp.), Sciaridae (12 spp.), Phoridae (9 spp.) and Empididae (5 spp.) were the most abundant and species-rich Diptera families (cf. Appendix).

Number of species interactions per species varied considerably. The plant species visited by most insect species were *Dryas octopetala* (28 visitor species), *Diapensia lapponica* (25), *Saxifraga aizoides* (25), and *Potentilla crantzii* (24). The insect species visiting the largest number of plant species were *Thricops hirtulus* (10 plant species), *Smittia aterrima* (9), *Rhamphomyia morio* (9), *Coenosia atritibia* (9), and *Chamaepsila morio* (9). Each plant species had on average 5.1 times as many interactions as each insect species. This was an effect of the difference in size of the two communities, $a:p = 5.1$ (Table 1). However, the distribution of interactions per plant species was less skewed than that of insect species (Kolmogorov-Smirnov two-sample test: Unsigned difference $D = 0.713 > D_{0.001} = 0.637^{***}$;

Table 4. Comparison of relative insect species richness among high latitude systems.

	Present study	Proportion of total insect species number (in %)*		
		Mosquin and Martin 1967	Hocking 1968	Kevan 1970, 1972
Diptera	77	72	74	67
Hymenoptera	20	6	13	19
Lepidoptera	3	22	12	14
Coleoptera	2	0	1	0

* Other insect orders were excluded. G-test of goodness of fit (Diptera): $G = 1.637$, $DF = 3$, $0.5 < p < 0.9$; (Hymenoptera + Lepidoptera): $G = 5.356$, $DF = 3$, $0.1 < p < 0.5$ (Sokal and Rohlf 1995: 697).

Table 5. Comparison of relative fly species richness among high latitude systems. Only families constituting $\geq 10\%$ of total Diptera fauna at ≥ 1 site were tabulated.

	Present study	Proportion of total Diptera species (in %)		
		Mosquin Martin 1967	Hocking 1968	Kevan 1970, 1972
Anthomyiidae	19			8
Calliphoridae	1	15	3	4
Chironomidae	18		45	15
Empididae	6	8	7	12
Muscidae	17	77	21	23
Phoridae	10			
Sciaridae	14		2	4
Syrphidae			5	15

Fig. 1). Therefore, even after correcting for differences in community size (by looking at the fraction of the community visited), plants were more generalised than insects.

The species of the various families of Diptera varied greatly in abundance and in number of food-plant species visited. Species of Empididae and Muscidae visited more plant species and were more abundant than species of other dipteran families (Table 3). Numbers of flower-visiting individuals per dipteran species (abundance) and numbers of plant species visited per dipteran species (level of generalisation) were highly significantly correlated (Spearman rank correlation: $r_s = 0.89$, $Z = 7.98$ (after correcting for ties), $p \leq 0.0001$). Thus level of plant generalisation of a fly was strongly influenced by its abundance.

Discussion

Comparison between high and low altitudinal pollination systems at the study site in northern Sweden

So far, 165 Muscidae species have been found in the entire Abisko area, and 26 of their plant species from the lower mountain birch zone (385–750 m a.s.l.) are listed by Pont (1993). If we compare our data with those of Pont (1993), Muscidae species from the two sites do not differ in average generalisation level (3.9 plant species per Muscidae species at our study site and 4.2 in the birch zone). Half the Muscidae species common to both Pont's (1993) and our sites were more generalised at our site and half were more generalised in the birch zone. Thus among the Muscidae we find no indications of any change in the level of flower generalisation with altitude. *Thricops furcatus* was found only at our site and also at Totland's (1993) temperate Norwegian sites at 1300 m a.s.l. and thus seems to be a high altitude specialist.

Pont (1993) stated that the proportion of Muscidae species generally increases with altitude, whereas the proportions of Syrphidae and bumblebees decrease. Thus above the timberline the Muscidae are probably the most important flower visitors, in particular the genera

Thricops, *Spilogona* and *Phaonia* (cf. Appendix). Muscidae may, in general, be an important high alpine pollinator group. For example, flies of this family have been observed as flower-visitors at 4840 m a.s.l. in the Andes (Olesen et al. unpubl.).

At Abisko, the *Phaonia* species, three of the five *Thricops*, the *Spilogona* species, and *Fannia mollissima* (Fanniidae) might constitute an arctic guild of flower visitors. These species possess a characteristic set of morphological and flower behavioural traits selected for life above the timberline, e.g. special pollen feeding behaviour and an elongated proboscis, which improves access to closed flowers (Pont 1993). Generally, the scarcity of flower visitors with long proboscis in the Arctic may have opened a niche for flies and put a selection premium on a longer proboscis and more shallow flowers. Among plants, selection may favour flowers with wider corolla and a more parabolic shape, facilitating access of shorter-tongued flies to nectar and enhancing heat uptake and visitation from sun-basking insects. The flower behaviour of arctic flies may, to some extent, be explained by sun-basking, since most Muscidae (according to Pont 1993) do not visit flowers for feeding but only for thermal energy uptake.

Comparison between different high latitudinal pollination systems

The results of the present study were compared to those of three other high latitude studies (Mosquin and Martin 1967, Hocking 1968, and Kevan 1970, 1972). The proportions of species of Diptera, and Hymenoptera and Lepidoptera combined did not vary significantly among high latitude systems (Table 4). We also compared the most species-rich families of dipteran flower-visitors (Table 5). Muscidae contributed the largest proportion of species, and Anthomyiidae and Syrphidae were the second and third most species-rich families. Only Muscidae and Empididae were common to all four systems.

Latitudinal comparison between pollination systems

The proportion of dipteran species of the total pollinator fauna increases with latitude (data from Olesen unpubl.,

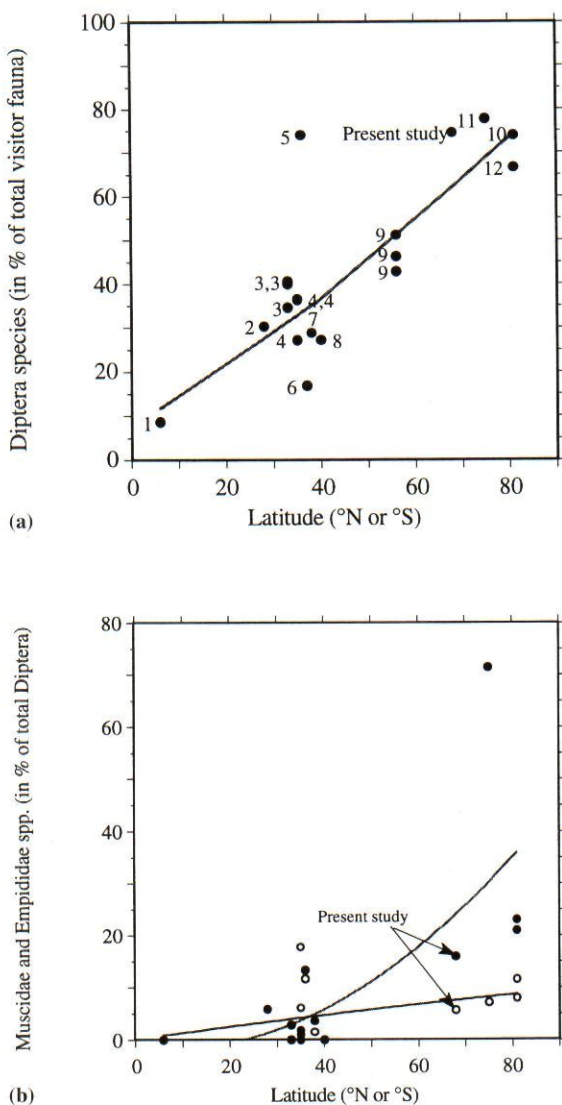


Fig. 2. Latitudinal gradients in a) relative frequency of Diptera species, and b) Muscidae (closed circles) and Empididae species (open circles) as flower visitors. Effect of latitude on relative frequency was estimated by logistic regression analysis (Quasi-Newton minimisation, maximum likelihood estimation and rescaling of the mean square error to one, Wilkinson (1992: 410, 436) and Sokal and Rohlf (1995: 760)):

$$y = \frac{e^{-2.15 + 0.0443x}}{1 + e^{-2.15 + 0.0443x}} 100 \text{ (Diptera);}$$

$$y = \frac{e^{-5.37 + 0.0652x}}{1 + e^{-5.37 + 0.0652x}} 100 \text{ (Muscidae);}$$

$$y = \frac{e^{-4.16 + 0.0232x}}{1 + e^{-4.16 + 0.0232x}} 100 \text{ (Empididae);}$$

all are highly significant, $p = 0.001$ for all three regressions. 1) Ramirez (1989, tropical montane forest), 2) Forfang and Olesen (unpubl., subtropical mist forest), 3) Arroyo et al. (1982, alpine meadows) – three sites, 4) Inoue et al. (1990, subtropical forest), Kato et al. (1990, subtropical forest) and Kakutani et al. (1990, urban site), 5) Inouye and Pyke (1988, alpine meadow), 6) J. Herrera (1988, mediterranean shrubland), 7) Petanidou (1991, phrygana), 8) Schemske et al. (1978, temperate forest), 9) Olesen (unpubl., temperate forest, bog and fallow) – three sites, 10)

Fig. 2). The logistic regression of the proportion of dipteran species with latitude predicts that dipteran species constitute 70% of the total flower-visitor fauna in the present study, close to the 77% observed. Even after correcting for the effect of latitude on the size of the flower-visiting dipteran fauna, Arctic and alpine systems are relatively rich in Diptera as pollinators (Mosquin and Martin 1967, Kevan 1970, 1972, Arroyo et al. 1982, Inouye and Pyke 1988, Totland 1993), whereas Mediterranean and temperate systems are Diptera-poor (Schemske et al. 1978, J. Herrera 1988, Inoue et al. 1990, Kakutani et al. 1990, Kato et al. 1990, Petanidou 1991, Olesen unpubl., Fig. 2). Thus, compared to lower latitudes, dipterans are very frequent flower-visitors in the Arctic.

The proportions of Muscidae and Empididae (as percentages of the total number of species of Diptera) increase with latitude (Fig. 2). On Melville Island (75°N) for example, Mosquin and Martin (1967) found that Muscidae constituted up to 77% of the total Diptera flower-visitor fauna. Thus Muscidae and Empididae are more abundant and generalised than other dipteran families visiting flowers in the arctic (Table 2), their proportions of the total Diptera fauna increase with latitude (Fig. 2) and they are the most widespread families of flower-visiting insects in the Arctic (Table 5).

We used regression equations from Olesen (unpubl.) to predict parameters for the high latitude systems and to compare with the observed ones. In our study, estimated and observed values for connectance (C), and number of interactions (I) were very similar. All four high latitude systems varied markedly in a , p , M , I , and C (Table 6). Although, it is premature to say anything about latitudinal gradients of mutualism variables in general (Olesen unpubl.) the connectance of low latitude systems ranges between 3.4 and 28.1, whereas high latitude and high altitude-systems vary between 8.6 and 19.

In general, number of interactions per species varies considerably among plant-pollinator systems (Olesen unpubl.). The ratio between average number of interactions per plant species and per animal species is equal to the ratio between numbers of animal and plant species

$$\left(\frac{I_p}{I_a} = \frac{I}{p/a} = \frac{a}{p} \right)$$

$a > p$ in 9 out of 36 plant-pollinator systems (Jordano 1987), in 17 out of 19 plant-pollinator systems (Olesen unpubl.), in 9 out of 19 plant-fruit disperser systems (Jordano 1987), and in one plant-ant system (Fonseca and Ganade 1996), i.e. $a > p$ in 36 out of 75 mutualism systems. In three systems $a = p$, thus in exactly half of all studies animals are more generalised because the

Hocking (1968, tundra and southern slopes), 11) Mosquin and Martin (1967, arctic tundra), 12) Kevan (1970, 1972, arctic tundra).

Table 6. Comparison of plant-flower visitor system characteristics of high latitude systems. a = no. of insect species, p = no. of plant species, M = ap, I = no. of interactions, C = 100I/M = connectance, lat = latitude, and Exp and Obs = expected and observed values respectively. Regression equations between system variables (Olesen unpubl.): $I = \exp(0.611 + 0.808 \ln a + 0.353 \ln p - 0.00097 \ln \text{lat})$ and $C = \exp(5.201 - 0.191 \ln a - 0.646 \ln p - 0.0009 \ln \text{lat})$.

	Present study		Mosquin and Martin 1967		Hocking 1968		Kevan 1970, 1972	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Latitude	68		75		81		81	
a:p	5.1		1.6		2.8		4.0	
M	2714		198		2349		1914	
I	242	249	38	41	179	195	225	187
C (%)	8.6	8.8	19	21	7.6	8.3	12	10

systems contain more plants than animals and vice versa. In general, average differences in generalisation levels between partners in mutualistic systems can be explained by the relative size of the interacting communities whereas the actual level of generalisation of the individual species and its evolutionary background remains unknown.

Acknowledgements – We would like to thank U. Molau and B. Elberling for their kind assistance. M. Stenström is thanked for his comments on the manuscript. We are also grateful to A. C. Pont for identifying the insects to order and family and for identifying species of the dipteran families Fanniidae and Muscidae. We would also thank the following for identifying the remaining Diptera: D. J. Henshaw (Agromyzidae), D. M. Ackland (Anthomyiidae), K. Rognes (Calliphoridae), O. A. Sæther (Cecidomyiidae, Chironomidae), J. W. Ismay (Chloropidae), C. E. Dyte (Dolichopodidae), M. Chavela (Empididae, Hybotidae), P. Oosterbroek (Limoniidae), P. J. Chandler (Mycetophilidae), H. Disney (Phoridae), P. L. T. Beuk (Pipophilidae, Psilidae), H. Andersson (Scathophagidae), H. Hippa (Sciariidae), S. Andersen (Tachinidae), and P. B. Jensen for identifying the Hymenoptera, excluding Apidae. The study was supported financially by the Danish Natural Science Council and The Swedish Academy of Sciences. D. Clayre has provided linguistic advice.

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DIPTERA																											
Agromyzidae	Phytomyza aquilonia	Frey																									
	Alliopsis glacialis	Zetterstedt																									
	Botanophila bidens	Ringdahl																									
	Delai piliventris	Pokorny																									
	Egle minuta	Meigen																									
	Egle parva	Robineau-Desv.																									
	Egle sp. indet.																										
	Paradelia sp. indet.																										
	Pegomya haemorrhoum																										
	Pegomya sp. indet.	Zetterstedt																									
Anthomyiidae	Pegoplata aestiva	Meigen																									
	sp. indet. 1																										
	sp. indet. 2																										
	sp. indet. 3																										
	Zaphne barbiventris	Zetterstedt																									
	Zaphne frontata	Zetterstedt																									
	Zaphne sp. indet. 1																										
	Zaphne sp. indet. 2																										
	Bellardia pubicornis	Zetterstedt																									
	Dasineura sp. indet.																										
Cecidomyiidae	Acanptocladius submontanus	Edwards																									
Chironomidae	Corynoneura scutella	Winnertz																									
	Heterotriassocladus subpilosus																										
	Limnophyes brachytomus	Kieffer																									
	Limnophyes natalensis	Kieffer																									
	Limnophyes niniae (a)	Sæther																									
	Limnophyes schnelli (a)	Sæther																									
	Micropsectra radialis	Goetghebuer																									
	Micropsectra sp. indet. 1																										
	Micropsectra sp. indet. 2																										
	Oliveridia tricornis (b)	Oliver																									
Pseudosmittia oxoniama (c)	Edwards																										
Total																											

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(a) A new record for Sweden. (b) New for Europe. (c) In Abisko, individuals of this species have previously been identified as *P. rutneri*. (d) Only known from the Abisko-area in northern Sweden. (e) The identification of female specimens of this species is uncertain. (f) Only 6–7 specimens have previously been found.

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