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ORIGINAL ARTICLE

A case study of Heleomyzidae (Diptera) recorded on snow in Poland with a review of their winter activity in Europe

AGNIESZKA SOSZYŃSKA-MAJ[1] and ANDRZEJ J. WOŹNICA[2]

[1] Department of Invertebrate Zoology and Hydrobiology, University of Łódź, Banacha 12/16, 90-237 Łódź, Poland; e-mail: agasosz@biol.uni.lodz.pl

[2] Institute of Biology, Wrocław University of Environmental and Life Sciences, Kożuchowska 5b, 51-631 Wrocław, Poland; e-mail: andrzej.woznica@up.wroc.pl

Key words. Diptera, Heleomyzidae, Europe, Poland, winter activity, snow fauna, phenology, review

Abstract. Twenty eight species of winter-active Heleomyzidae were collected during a long-term study in Poland. More than 130 samples of insects, including Heleomyzidae, were collected from the surface of snow in lowland and mountain areas using a semi-quantitative method. Lowland and mountain assemblages of Heleomyzidae recorded on snow were quite different. *Heleomyza modesta* (Meigen, 1835) and *Scoliocentra* (*Leriola*) *brachypterna* (Loew, 1873) dominated in the mountains, *Tephrochlamys rufiventris* (Meigen, 1830) mainly in the lowlands and *Heteromyza rotundicornis* (Zetterstedt, 1846) was common in both habitats. Heleomyzidae were found on snow during the whole period of snow cover, but the catches peaked from late November to the beginning of February. In late winter and early spring the occurrence of heleomyzids on snow decreased. Most individuals were active on snow at air temperatures between –2 and +2.5°C. A checklist of 78 winter active European Heleomyzidae is presented. *Helomyza nivalis* Wahlgren, 1918 is herein considered as a new junior synonym of *Helomyza caesia* Meigen, 1830, syn. n.

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INTRODUCTION

Heleomyzidae, a small family of Diptera, comprises 151 species in Europe (Lo Giudice & Woźnica, 2013; Woźnica, 2013). It is widely distributed around the world, but is especially numerous in areas with a cool, temperate climate (Woźnica, 2008). Many representatives of this family, especially from the tribe Heleomyzini, are cold-adapted and have a typical boreo-alpine distribution, being abundant in mountains and the north of Europe. Heleomyzid flies are one of the most common groups of insects active in winter and are often recorded on the surface of snow in Poland (Soszyńska, 2004; Soszyńska-Maj & Woźnica, 2012) and Scandinavia (Hågvar & Greve, 2003). In the warmer areas of southern Europe they are active at low temperatures, mostly in autumn and winter, at higher altitudes (above 1,000 m a.s.l.) or in caves (Erhard & Spötl, 2010).

Diptera dominate the fauna in cold regions (Oliver, 1968), at high altitudes or in caves (Jefferson, 1983; Weber & Weber, 2013). Most snow-active flies belong to five dipteran families, which are definitely the best adapted for activity at low temperatures and are recorded on snow: Trichoceridae (e.g. Hågvar & Krzemińska, 2008), Chironomidae (Koshima, 1984, 1985; Anderson et al., 2013; Giłka et al., 2013; Soszyńska-Maj et al., 2016), Limoniidae (Hågvar, 1971, 1976), Heleomyzidae and Sphaeroceridae (Hågvar & Greve, 2003; Soszyńska-Maj & Woźnica, 2012). Apart from flies, springtails (Collembola), snow scorpionflies (Mecoptera: Boreidae), spiders (Araneae), ice crawlers (Grylloblattidae), beetles (Coleoptera), psyllids (Psylloidea), bugs (Heteroptera), earwigs (Dermaptera) and even moths (Lepidoptera) belong to the assemblage of snow-active insects (Aitchison, 2001; Hågvar, 2001, 2007, 2010; Hågvar & Aakra, 2006; Soszyńska-Maj, 2008; Jaskuła & Soszyńska-Maj, 2011; Soszyńska-Maj & Buszko, 2011; Soszyńska-Maj & Jaskuła, 2013). Winter-emerging aquatic insects are regularly observed on snow and are a significant subgroup within this community, with stoneflies (Plecoptera) and caddisflies (Trichoptera) being the most abundant members besides Chironomidae (Bouchard et al., 2009; Hågvar, 2010; Soszyńska-Maj, pers. observ.).

Best adapted to snow activity are brachypterous or apterous insects belonging to the genera *Boreus* (Mecoptera), *Chionea* (Diptera: Limoniidae) and *Diamesa* (Diptera: Chironomidae). Their morphological adaptations include enlargement of the legs for walking instead of flying, melanism, size reduction and hairy bodies (Hermann et al., 1987; Lencioni, 2004; Giłka et al., 2013). Heleomyzidae

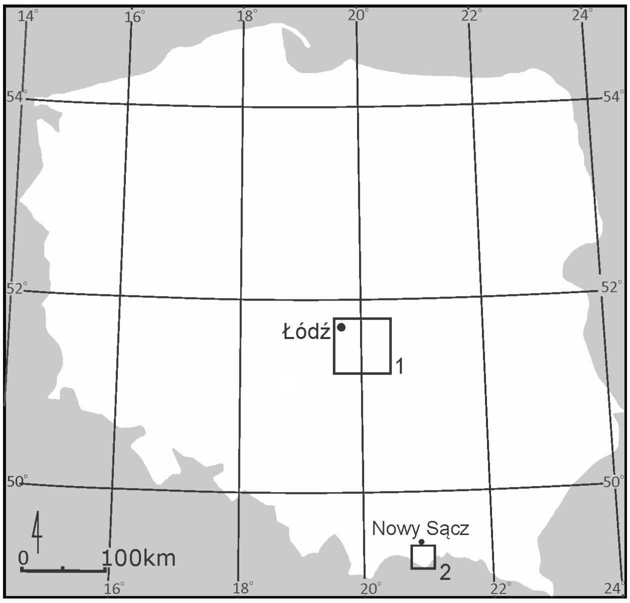

Fig. 1. Map of Poland showing the location of the sites studied: 1 – central Poland (lowland), 2 – Beskid Sądecki Mountains.

do not show any morphological adaptions to snow activity, but they are adapted to low temperatures. Adults of *Scoliocentra nigrinervis* had the second lowest supercooling point of snow-active insects studied (mean –16.5°C, range –20.5/–13°C) (Sømme & Østbye, 1969). The lowest supercooling point was reported for the chironomid *Diamesa mendotae* Muttkowski (–21.6°C) (Bouchard et al., 2006). It is noteworthy that some flies can survive even long, severe and snowy winters as immature stages: for example, larvae of *Heleomyza borealis*, a snow-active fly especially widely distributed in the Arctic, can survive temperatures as low as –60°C and need a lower than –15°C temperature stimulus and thereafter warmer period to pupate (Block, 2002). Despite the known low temperature preferences of the species of this family, snow-recorded Heleomyzidae have been intensively studied only by Hågvar & Greve (2003). During an almost 20-year-long study in southern Norway, they found Heleomyzidae to be the dominant brachyceran family among the Diptera recorded on snow and identified 13 species of these flies. Four heleomyzid species were observed on snow in southern Finland (Frey, 1913), one in central Finland (Tahvonen, 1942) and two in mountain areas in Bulgaria (Czerny, 1930). The snow activity of Heleomyzidae was recorded in central Poland (Soszyńska, 2004). Von der Dunk (2006), in his work on Bavarian heleomyzids, noted 10 heleomyzids species on snow. Finally, seven species were recorded from the European part of Russia (Pavlov, 2006).

Winter activity has until now been studied only in Germany; however, the appearance on snow was not studied. Nine species of Heleomyzidae were found by Broen & Mohrig (1965), and 27 species were caught using various collecting methods by Bährmann & Adaschkiewitz (2003). Twenty five species of winter-active heleomyzids were recorded in Germany using seven sampling methods, such as sweep nets, pitfall traps, Moericke traps (yellow pan traps) and cave traps (Bährmann, 1996). However, in these papers no information on snow cover was provided.

Although the snow and winter activity of Heleomyzidae are frequently discussed, no comprehensive research including quantitative or statistical analyses has been published to date. The main aim of this study was to describe the structure of the heleomyzid community recorded on snow in Poland, to compare the heleomyzid assemblage recorded on snow in the Polish lowlands and mountains, determine what influence particular weather conditions have on the winter activity of Heleomyzidae in the study area and present a checklist of winter-active Heleomyzidae in Europe.

MATERIAL AND METHODS

This investigation was carried out from 1997 to 2013, with different intensities of sampling in different years from November to the first half of April, depending on the weather and presence of snow cover. This was part of a more general, long-term research project on snow-active invertebrates in Poland. Depending on favourable atmospheric conditions samples were collected regularly, at 10 or 14 day intervals. The lowland assemblage was studied in central Poland at regular intervals in 1999–2003 and 2005–2007. The assemblage in the Beskid Sądecki Mountains (mountain community) was sampled regularly over three winter seasons 2010–2013. Other samples were collected intermittently in different years and at different localities. Only samples containing at least one heleomyzid were included in the present analysis.

The material was collected at 24 sites in central Poland (Figs 1, 2C) and at 15 sites in the Beskid Sądecki Mountains (Figs 1, 2A, B, D, E). Additional data come from isolated samples collected in the Tatra, Gorce, Bieszczady and Bialskie Mountains and the Polish uplands.

All study sites in central Poland, with the highest point of 284 m a.s.l., were located in large forests, mostly protected as Nature Reserves (e.g. Fig. 2C). Several forest associations, such as mixed deciduous forest with fir, beech and spruce, mixed coniferous forest, riparian forest (*Circeo-Alnetum*), acidophilous beech woods (*Luzulo pilosae-Fagetum*) and dry-ground forest (*Tilio-Carpinetum*), are characteristic of this part of Poland. The Beskid Sądecki is a mountain range in the western Carpathians with the highest peak 1262 m a.s.l. The study areas were situated in the lower montane forest zone at altitudes of 650–750 m, covered with stands of beech with some fir and spruce (*Dentario glandulosae-Fagetum*) (Fig. 2A, B, D). The climates in the regions studied is presented in Table 1 (Liszewski, 2001; Durło, 2003).

A total of 131 samples of Heleomyzidae were collected on snow: 51 samples from snow in the lowlands, 64 in the Beskid Sądecki Mountains and 16 from the other study sites. The insects were picked off the snow surface by hand or with tweezers. The

Table 1. Climate in the regions studied based on Liszewski (2001) and Durło (2003).

	Average annual air temperature	Snowfall	Duration of snow cover (per year)	Average thickness of snow cover	Maximum thickness of snow cover
Central Poland	+7.6–8.0°C	ca 70 days a year	40–45 days	unstable, ca 8–18 cm	30–40 cm
Beskid Sądecki 600–1100 m a.s.l.	+4.5°C	ca 70 days a year	130 days	ca 30–35 cm	60 cm (locally 100 cm)

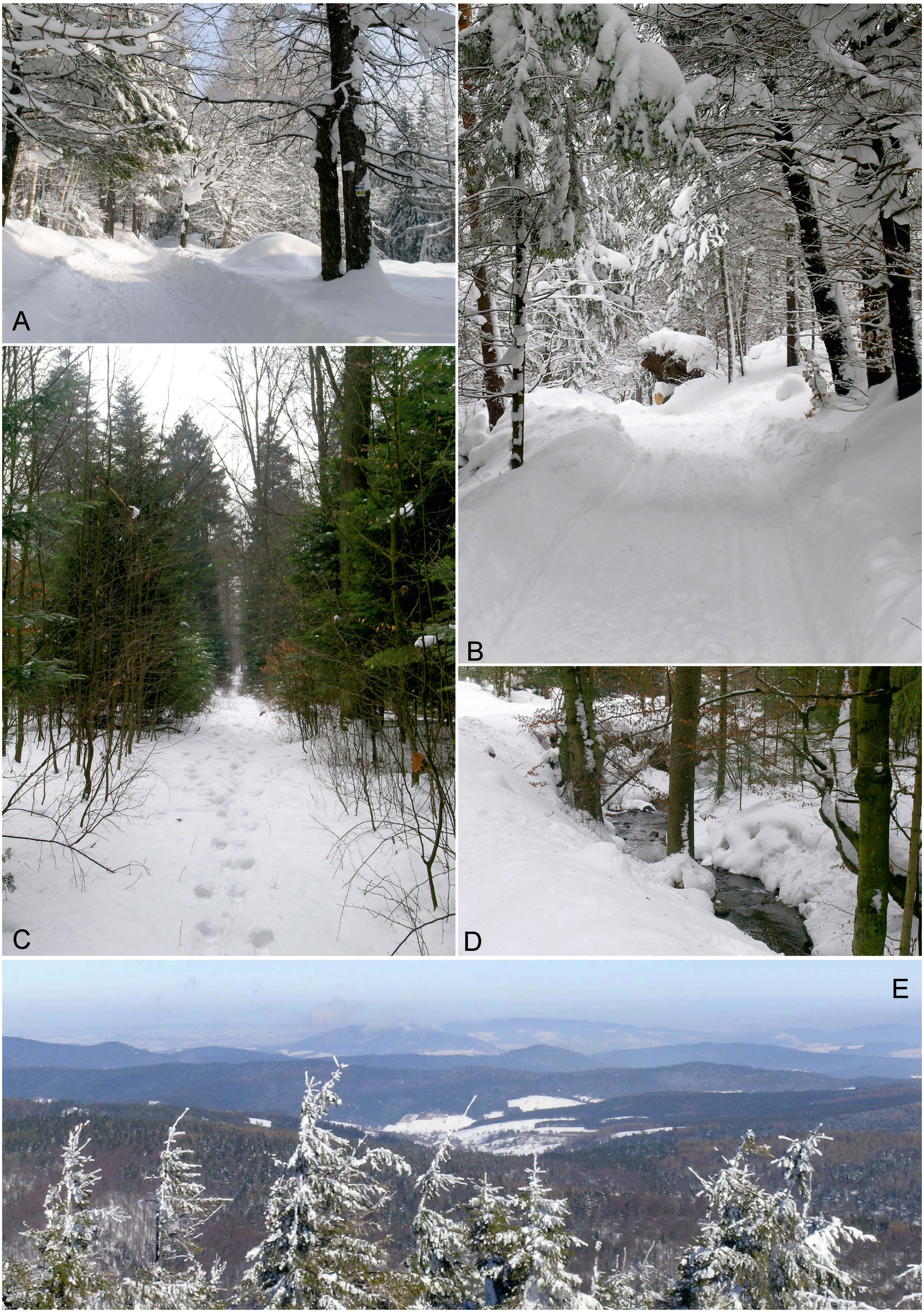

Fig. 2. Photographs taken at the sites studied. A, B, D, E – mountain forest in the Beskid Sądecki area (A – Parkowa Mountain, B – Jaworzyna Krynicka, D – Czarny Potok River, E – Beskid Sądecki Mountains); C – Molenda nature reserve in central Poland lowland.

Table 2. List of Heleomyzidae recorded on snow in Poland, with data on the number of individuals and biocenotic indices: D – dominance, F – frequency, Q – ecological significance; L – lowlands, BSM – Beskid Sądecki Mountains, M – other Polish mountains.

No.	Species	Indiv.	♂	♀	L	BSM	M	D	F	Q
	HELEOMYZINAE									
1	*Eccoptomera longiseta* Loew, 1862	4	2	2	4			0.98	3.05	1.73
2	*Eccoptomera obscura* (Meigen, 1830)	38	15	23	34	3		9.31	11.45	10.33
3	*Eccoptomera ornata* Loew, 1862	3		3	3			0.74	1.53	1.06
4	*Eccoptomera pallescens* (Meigen, 1830)	1	1		1			0.25	0.76	0.43
5	*Gymnomus caesius* (Meigen, 1830)	18	9	9	1	8	5	4.41	10.69	6.87
6	*Gymnomus spectabilis* (Loew, 1862)	3		3		3		0.74	2.29	1.3
7	*Heleomyza* (*Heleomyza*) *captiosa* (Gorodkov, 1962)	13	7	6		16		3.19	6.87	4.68
8	*Heleomyza modesta* (Meigen, 1835)	64	45	19		55	7	15.69	28.24	21.05
9	*Morpholeria* (*Spanoparea*) *kerteszii* Czerny, 1924	1		1		0	1	0.25	0.76	0.43
10	*Oldenbergiella brumalis* Czerny, 1924	17	7	10	11	4		4.17	7.63	5.64
11	*Orbellia cuniculorum* Robineau-Desvoidy,1830	6	3	3	6			1.47	0.76	1.06
12	*Orbellia hiemalis* (Loew, 1862)	11	5	6	11			2.7	3.05	2.87
13	*Orbellia myiopiformis* Robineau-Desvoidy, 1830	8	3	7	5	3		1.96	3.82	2.74
14	*Schroederella iners* (Meigen, 1830)	1	1		1			0.25	0.76	0.43
15	*Scoliocentra* (*Leriola*) *brachypterna* (Loew, 1873)	61	26	33		58	3	14.95	15.27	15.11
16	*Scoliocentra* (*Leriola*) *nigrinervis* (Wahlgren, 1918)	7	4	3		5	2	1.72	5.34	3.03
17	*Scoliocentra* (*Scoliocentra*) *villosa* (Meigen, 1830)	5	3	2	1	4		1.23	3.82	2.16
	HETEROMYZINAE									
18	*Heteromyza atricornis* Meigen, 1830	5	1	4		5		1.23	2.29	1.68
19	*Heteromyza rotundicornis* (Zetterstedt, 1846)	60	40	20	28	32		14.71	17.56	16.07
20	*Tephrochlamys flavipes* (Zetterstedt, 1838)	14	1	13	14			3.43	2.29	2.8
21	*Tephrochlamys rufiventris* (Meigen, 1830)	57	40	17	53	3	1	13.97	20.61	16.97
22	*Tephrochlamys tarsalis* (Zetterstedt, 1847)	1	1		1			0.25	0.76	0.43
	SUILLIINAE									
23	*Suillia cepelaki* Martinek, 1985	2	2			0	2	0.49	1.53	0.87
24	*Suillia pallida* (Fallen, 1820)	2	1	1	2			0.49	1.53	0.87
25	*Suillia parva* (Loew, 1862)	2		2		2		0.49	1.53	0.87
26	*Suillia ustulata* (Meigen, 1830)	2	2		2			0.49	1.53	0.87
27	*Suillia vaginata* (Loew, 1862)	2	2		2			0.49	1.53	0.87
	TOTAL	408	221	187	180	201	21			

air temperature and humidity was measured. A thermo-hygrometer was installed in the shade, about 1 m above the ground. Only live flies were collected from the snow. The time spent collecting was limited (up to 1.5 h) so that the samples could be compared semi-quantitatively.

Specimens were also collected using pitfall traps, which caught ground-active invertebrates, under snow cover in the lowland area. Heleomyzidae were caught using this method only in winter 2005/2006 on xerothermic wasteland and in marshy meadows every two weeks. The traps were constructed as described by Aitchison (1974) and in more detail by Soszyńska-Maj & Jaskuła (2013). They contained ethylene glycol (freezing point: –30°C) to preserve the insects with addition of a small amount of detergent to reduce surface tension. They were protected with a roof against snow and rain. These samples, together with qualitative samples only (not subject to a time limit), were excluded from the environmental analysis and only used in the compilation of the list of species and analysis of seasonal dynamics. These traps were operated wherever there was snow cover.

In order to analyse the biocenotic structure of the catches, dominance (D), frequency (F) and Q index (geometric mean of frequency and dominance) were calculated. To explain the relationship between the ambient temperature and number of active Heleomyzidae, Pearson's correlation coefficients at a significance level $p < 0.05$ were calculated. Variables such as the number of individuals and the maximum number of species were included in this calculation. The null hypothesis of no correlation between the activity of heleomyzids on snow and air temperature was tested. All the statistical calculations were done in Statistica 10.0 (StatSoft, 2011).

A checklist of winter active European Heleomyzidae was drawn up. The list was based on data from 71 papers (numbered in References) and the records reported in this study. It included all information about their occurrence on snow, in pitfall traps, yellow traps or just on their activity between November and March/April.

Table 3. Heleomyzidae collected in central Poland using pitfall traps when there was no snow; X – xerothermic wasteland, WM – marshy meadow.

Species	1–15 Nov.	16–30 Nov.	1–15 Dec.	16–31 Dec.	15–31 Mar.	
Eccoptomera obscura	2♂		1♂1♀		1♀	X
Eccoptomera pallescens			3♀	1♀		WM
Orbellia hiemalis	2♀					X
Schroederella iners	1♀					X
Tephrochlamys rufiventris			1♂			WM

RESULTS

A total of 408 adult individuals were sampled, which belonged to 27 species and three subfamilies: Heleomyzinae, Heteromyzinae and Suilliinae. Heleomyzinae were eu-

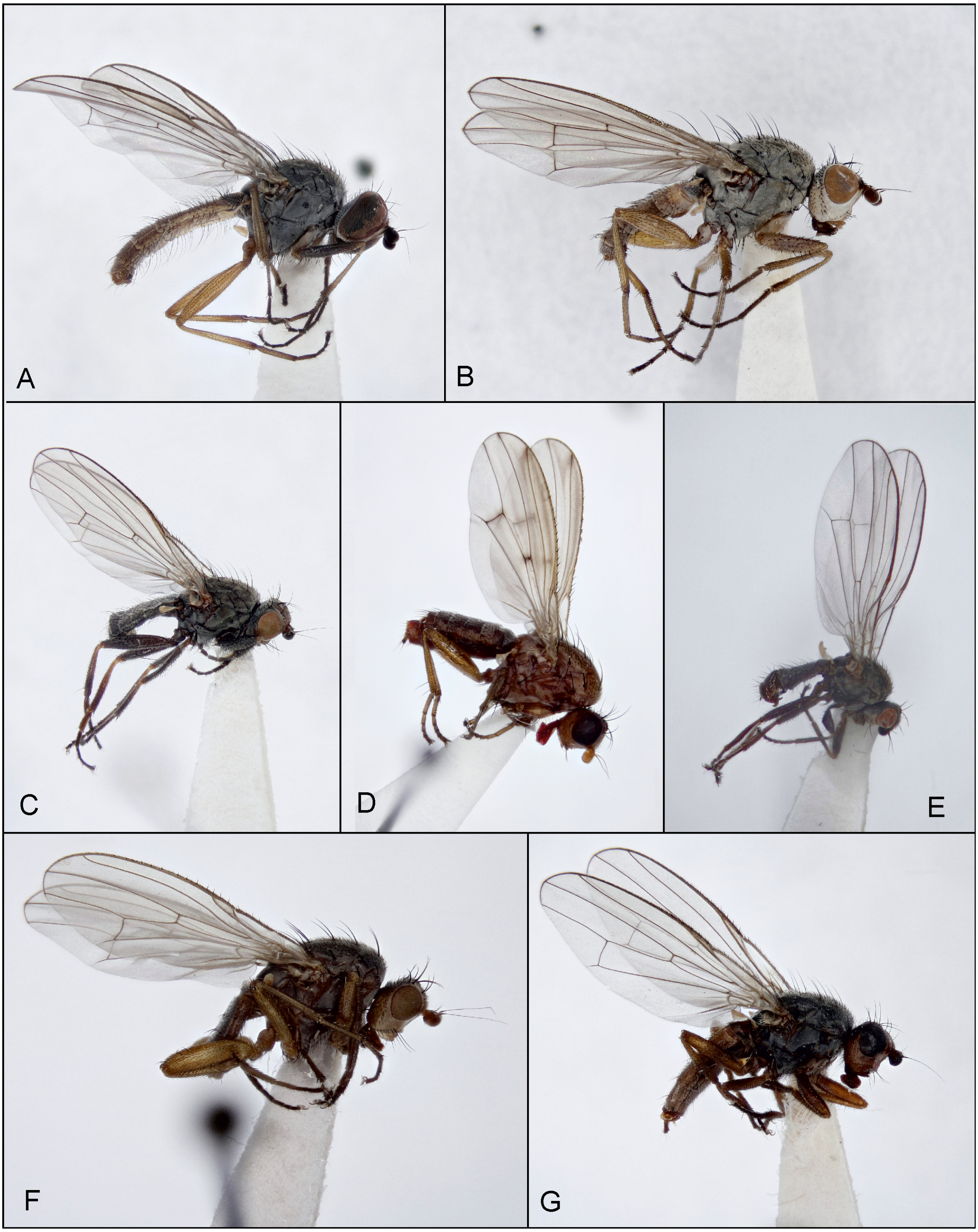

Fig. 3. Photographs of the characteristic species of Heleomyzidae recorded on snow. A – *Heteromyza rotundicornis*, male; B – *Tephrochlamys rufiventris*, male; C – *Heleomyza modesta*, male; D – *Suillia parva*, female; E – *Oldenbergiella brumalis*, male; F – *Eccoptomera obscura*, male; G – *Scoliocentra* (*Leriola*) *brachypterna*, female.

dominant in the material (17 species and 64% of individuals). Detailed data on the species and the structure of the assemblage are listed in Table 2. More males (221 indiv.) than females (187 indiv.) were collected on snow.

Four of the species appeared almost equally dominant in the combined material from lowland and mountains, although they differed in frequency. *Heleomyza modesta* (Fig. 3C) was the most abundant and most frequent species among all the Heleomyzidae collected on snow. *Heteromyza rotundicornis* (Fig. 3A), *Scoliocentra brachyptera* (Fig. 3G) and *Tephrochlamys rufiventris* (Fig. 3B) were similarly abundant but less frequent. The Q index, a geometric mean of frequency and dominance, indicated these four species as the most characteristic for the assemblage investigated.

Lowland and mountain assemblages differed in species composition and community structure. Among the 18 species recorded in the lowlands *T. rufiventris* was predominant, followed by *Eccoptomera obscura* (Fig. 3F) and *Heteromyza rotundicornis*. Fourteen species were recorded in the Beskid Sądecki Mts community. Here, *Heleomyza modesta* and *S. brachyptera* predominated, followed by *Heteromyza rotundicornis*. Two more heleomyzids were caught in other montane areas: *Suillia cepelaki* and *Morpholeria kerteszii*. Among the five heleomyzids that were recorded in both lowland and mountain communities, only *Heteromyza rotundicornis* was almost equally represented in both regions. Two other species were abundant only in the lowlands (*T. rufiventris* and *E. obscura*) and one mainly in the mountains (*Gymnomus caesius*).

Pitfall traps

No heleomyzids were caught by the Moericke traps placed on snow during winter, neither in the lowlands nor the mountains. However, five species were recorded in pitfall traps in the lowlands (meadows at the edge of a forest) during a period when there was no snow present (Table 3).

Seasonal variation

The study of snow active flies was carried out whenever snow was present, from the second half of November to March (in the lowlands) and April (in the mountains). Separate samples for late October, early November and mid-April, were collected following abnormally early or late snowfalls.

In the lowlands, Heleomyzidae began to appear on snow in late November and continued to occur there until the end of December, but later on their number decreased. In the mountains the number of specimens collected increased from the second half of December and reached a peak at the beginning of February (Fig. 4). Table 4 shows the seasonal variation in catches on snow throughout winter. The Heleomyzidae differed in their seasonal activity. One group of species, which occurred in late autumn/early winter and disappeared in mid-December, consisted of *Orbellia cuniculorum*, *Morpholeria kerteszii*, *Suillia vaginata*, *S. pallida*, *O. hiemalis* and *Tephrochlamys flavipes*. However, the abundance of these species was so low that their occurrence then may be accidental. The other group consisted of winter species, which were active during almost the whole autumn/spring period, i.e. the dominant species and the less abundant *Gymnomus caesius*. Another group of species consisting of *Orbellia myopiformis*, *Scoliocentra brachyptera*, *S. nigrinervis*, *G. spectabilis* and *Eccoptomera longiseta* were mainly collected in mid-winter. A few species started or increased their activity in March

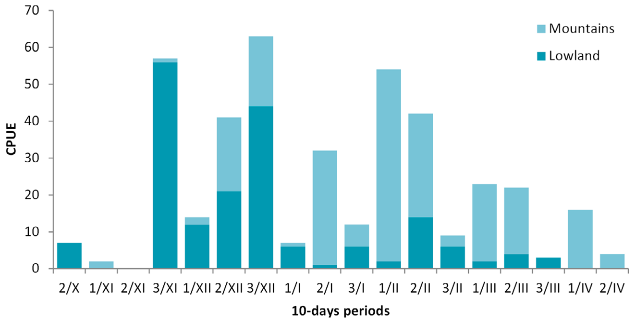

Fig. 4. Phenology of Heleomyzidae recorded on snow in Poland, (CPUE – catch per unit effort). Ten-day periods and months are as follows: e.g. 2/XII stands for mid-December. The slight differences in the colour of each of the columns indicate the catches recorded in the lowlands and mountains.

and April: *Suillia parva* (Fig. 3D), *Heteromyza atricornis*, *Heleomyza captiosa* and *Scoliocentra villosa*. This group includes a few individuals of accidentally occurring species.

Influence of weather

Heleomyzidae were found alive on the surface of snow at temperatures between –5°C and +8°C (Fig. 5) and at 53–100% air humidity. However, the largest number of individuals and species were collected between –2.5°C and +2°C and at a high humidity (80–100%) (Fig. 6). Three species of Heleomyzidae were recorded when the samples were collected at the lowest temperatures: *Scoliocentra nigrinervis* (–5°C), *Heleomyza modesta* (–4°C) and *Orbellia myopiformis* (–4°C). All of the most important taxa in the assemblage studied were recorded between –5°C and +2°C. Above +2°C, mainly accidental and less abundant species were recorded (Table 5, Fig. 5).

All the Heleomyzidae collected on snow were alive. As air temperatures increased, there was always a greater tendency for the flies to fly away when disturbed. Flying heleomyzids were observed at air temperatures higher than about 2°C. However, part of the population was still sitting in the characteristic "starting position" (Fig. 7C), very often on the higher sites on natural piles or banks of snow. Flying Heleomyzidae were not collected.

Regression analysis of the activity of heleomyzids over the range of air temperatures from –5°C (the lowest recorded temperature) to c. +2°C, the temperature when flying heleomyzids were observed, (Fig. 8A) confirmed the positive effect of an increase in air temperature ($R^2 = 0.7264$; $P = 0.0072$) on the number of specimens recorded on snow, on maximum species richness ($R^2 = 0.8578$; $P = 0.0010$), on the number of males ($R^2 = 0.7651$; $P = 0.0045$) and females ($R^2 = 0.6331$; $P = 0.0182$), and on abundance in the lowlands ($R^2 = 0.6133$; $P = 0.0215$) and mountains ($R^2 = 0.5698$; $P = 0.0304$). The same positive statistical confirmation (Fig. 8B) was obtained for the relation between increasing air humidity and the number of Heleomyzidae specimens ($R^2 = 0.8359$; $P = 0.0298$) and species diversity ($R^2 = 0.9055$; $P = 0.0344$).

Table 4. Heleomyzidae recorded on snow in Poland during this study. Ten-day periods and months are given; e.g., 2/XII stands for second decade of December.

Species	3/X	1/XI	2/XI	3/XI	1/XII	2/XII	3/XII	1/I	2/I	3/I	1/II	2/II	3/II	1/III	2/III	3/III	1/IV	2/IV
Orbellia cuniculorum	6																	
Morpholeria kerteszii				1														
Suillia vaginata				1	1													
Orbellia hiemalis				1		1												
Suillia pallida				1		1												
Tephrochlamys flavipes				13			1											
Suilla cepelaki					1		1											
Suillia ustulata					1								1					
Eccoptomera ornata						2		1										
Schroederella iners							1											
Oldenbergiella brumalis	1					12	1			1	3							
Gymnomus spectabilis								1			2							
Scoliocentra nigrinervis							3		1		3							
Scoliocentra brachypterna						13	5		4		25	8	1	5				
Gymnomus caesius		1				2	4		1	1	2	5				1		1
Tephrochlamys rufiventris		1		12		2	22	4		3		5	5		1	1		1
Eccoptomera obscura				13	1		13		1			6	1	2	1			
Heteromyza rotundicornis				4	9	4	7		14	2	7	3			2		8	
Heleomyza modesta					1	2	3		8	4	5	7	1	15	16	1	1	
Orbellia myiopiformis				2		1	1		3		1							
Eccoptomera longiseta								1		1		1	1					
Eccoptomera pallescens												1						
Tephrochlamys tarsalis												1						
Heteromyza atricornis												4			1			
Scoliocentra villosa						1								1	1		2	
Heleomyza captiosa						1	1				5						4	2
Suillia parva											1						1	
	3/X	1/XI	2/XI	3/XI	1/XII	2/XII	3/XII	1/I	2/I	3/I	1/II	2/II	3/II	1/III	2/III	3/III	1/IV	2/IV

Taxonomic comments on the species list of winter-active Heleomyzid flies

Gymnomus caesius (Meigen, 1830)

Helomyza caesia Meigen, 1830: 56.
= *Helomyza nivalis* Wahlgren, 1918: 4, syn. n.

The junior author had the opportunity to study the holotype of *Helomyza nivalis* Wahlgren, 1918 during his stay in Lund in 2002. This revealed that *H. nivalis* is a junior synonym of *Helomyza caesia* Meigen, 1830, later transferred to the genus *Gymnomus* Loew by Papp & Woźnica (1993). *H. nivalis* was considered a nomen dubium in the Catalogue of Palaearctic Diptera (Gorodkov, 1984).

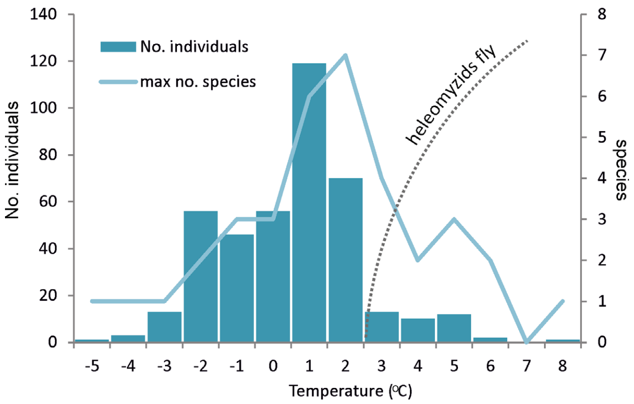

Fig. 5. Total numbers of individuals and species of Heleomyzidae recorded on snow at different air temperatures; curved dotted line indicates the temperature when Heleomyzidae were recorded flying.

Supplementary description of *Helomyza nivalis*

Body length: 4.5 mm. Cheek-eye ratio: 0.5. Anterior orbital seta about 0.5 of the length of the second orbital bristle. Antenna: scape and pedicel brick-reddish in colour, first flagellomere brown distally. Arista longer than head width. Fourteen small hairs in anterior corner of anepisternum. Dorsocentral bristles on dark brown (brownish-black) spots. Wing medial vein ratio: 1.24. Head ratio: 1.1. Fore femora more greyish-brown distally. Four dorsal bristles on hind femur. Male terminalia typical of *Gymnomus caesius* (Meigen, 1830) as described by Papp & Woźnica (1993). According to the femoral chaetotaxy and grey postpronotal area this species corresponds exactly to couplet 16(–) in Woźnica's (2011) key.

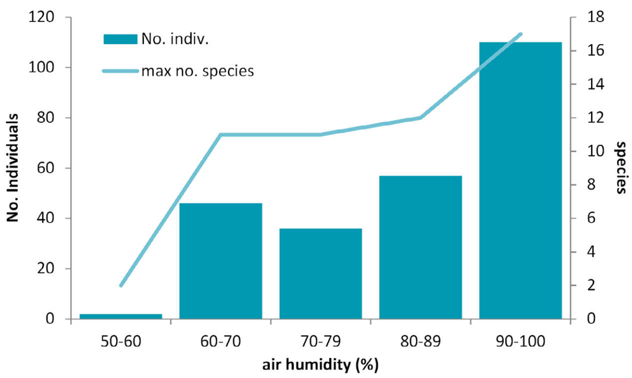

Fig. 6. The relationship between numbers of Heleomyzidae recorded on the snow and humidity.

Table 5. Heleomyzidae recorded on snow in Poland: numbers of specimens and temperatures (°C) at which they were recorded.

Species	–5	–4	–3	–2	–1	0	1	2	3	4	5	6	7	8
Scoliocentra nigrinervis	1		1	2			2	1						
Orbellia myiopiformis		1		3	1		3							
Heleomyza modesta		2	3	20	4	8	11	11	1	3	1			
Tephrochlamys rufiventris			4	13	12	14	10	1		1	1			
Heteromyza rotundicornis			4	7	7	8	24	8						1
Eccoptomera ornata			1			2								
Oldenbergiella brumalis				8	3	2	3		1					
Scoliocentra brachypterna				1	3	4	30	21		2				
Suilla cepelaki				1			1							
Scoliocentra villosa				1			1	3						
Tephrochlamys flavipes					13	1								
Orbellia hiemalis					1	2	5	3						
Suillia vaginata					1		1							
Suillia ustulata					1							1		
Schroederella iners						1								
Gymnomus spectabilis						1		1						
Eccoptomera pallescens							1							
Morpholeria kerteszii							1							
Suillia parva							1							
Orbellia cuniculorum									6					
Heteromyza atricornis							2	2						1
Eccoptomera obscura						10	13	14		1				
Heleomyza captiosa						3	4	1		1	4			
Gymnomus caesius							7	5	1	2	2			
Suillia pallida								1			1			
Eccoptomera longiseta								1			1	1		
Tephrochlamys tarsalis								1						
	–5	–4	–3	–2	–1	0	1	2	3	4	5	6	7	8

Fig. 7. Photographs of Heleomyzidae recorded on the surface of snow. A – *Tephrochlamys rufiventris*, male; B – *Orbellia hiemalis*, female (photo Ł. Mielczarek); C – *Scoliocentra* (*Leriola*) *nigrinervis*, female (photo C. Ovidiu-Manci).

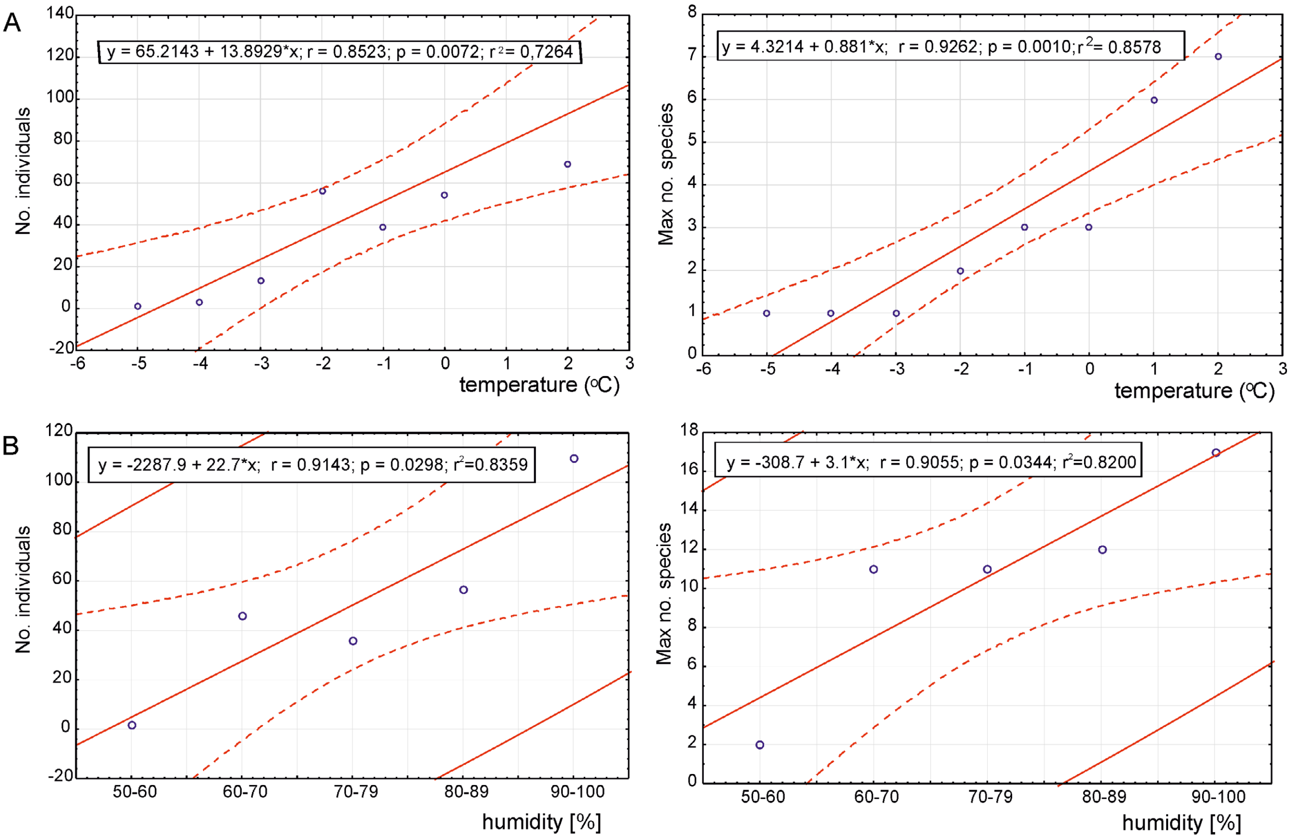

Fig. 8. Linear regression analysis showing the correlation between the number of individuals and species of Heleomyzidae recorded on snow and temperatures up to 2°C (A) and humidity (B), at $p < 0.05$.

Material examined. Holotype ♂, labelled: Nkpy [= Nyköping] 31/12, Suö [white (yellowish due to age)]; Holotypus (red), *Helomyza nivalis* Wahlgr.; ZML 2001, 234 (green).

Remarks. Left hind tarsus missing. Specimen minutia pinned. Genitalia dissected and stored in a microvial of glycerine.

Scoliocentra (*Leriola*) *nigrinervis* (Wahlgren, 1918)

Helomyza nigrinervis Wahlgren, 1918: 3.
Scoliocentra bipunctata Müller, 1924 (1923): 88.

According to Gorodkov (1962a) this species is recorded under the name *Leria maculipennis* Becker, 1897 by Frey (1913), who did not include it in volume VI of Enumeratio Insectorum Fenniae (Frey, 1941). The last published Checklist of the Fly Families Chyromyidae and Heleomyzidae (Diptera) of Finland (Kahanpää, 2014) also does not include this species name, although it should be mentioned that Tahvonen (1942) cites *Leria maculipennis* from Jyväskylä, central Finland. The distribution of *Sc.* (*Leriola*) *maculipennis*, given in detail by Gorodkov (1962a), indicates that it is an Arctic species probably widely distributed in the Holarctic Region (Gorodkov, 1984). Tahvonen's data are included in the list under the name *Scoliocentra nigrinervis*.

Suillia univittata (von Roser, 1840)

Helomyza univittata von Roser, 1840: 61.
Helomyza agaricina Rondani, 1867: 119.

Some specimens of *Suillia univittata* (von Roser, 1840) are placed in collections under the species name *Suillia lurida* (Meigen, 1830) (Martinek, 1972); however we follow the interpretation of Séguy (1934) and Martinek (1972) in regarding them as well separated species. Therefore, all published data where *Suillia univittata* is quoted as *lurida* (specified in Martinek, 1972) are included under *univittata* in the species list (see Table 6).

DISCUSSION

Heleomyzidae – a cold adapted and winter active group

Heleomyzids are known to prefer cold and extreme habitats, such as caves, cold mountains and snow-covered areas. Their most northerly locality is Spitsbergen (Czerny, 1924; Papp, 1981). The preference for a cool climate may have been a characteristic of the Heleomyzidae from early in their evolution, which began in the Cenozoic in northern Europe (Gorodkov, 1972). The current distribution of western Palearctic heleomyzids indicates that the recent European fauna developed in a mountainous area south of the Polar Circle and survived the glaciation in numerous isolated refuges in mountains in Western and Central Europe. It concerns mostly species now classified within the subfamily Heleomyzinae and belonging to the genus *Gymnomus* (Woźnica, 1996). With all probability the Heleomyzid fauna dispersed from south to north during the interglacial periods (Gorodkov, 1972). This may explain the disjunctive distribution of some snow-active

Heleomyzidae, such as *Heleomyza modesta*, *Scoliocentra brachypterna*, *Suillia parva* and *Scoliocentra nigrinervis*. The last mentioned species is very common in Scandinavia (Hågvar & Greve, 2003), while in the rest of Europe it occurs only in the Western Carpatians, above 700 m a.s.l. (Soszyńska & Woźnica, 2012). Apparently, *Scoliocentra nigrinervis* did not colonize lowland regions when the glaciers retreated but remained in the cooler mountainous habitats.

As many as 27 species of heleomyzids were recorded on snow in Poland. Dominant species were *Heleomyza modesta*, *Heteromyza rotundicornis*, *T. rufiventris*, *Scoliocentra brachypterna* and to a lesser extent *E. obscura*. Ten of the 14 Heleomyzidae species recorded on snow in southern Norway (Hågvar & Greve, 2003; Frey, 1913) were also recorded in Poland with the same dominant taxon – *Scoliocentra brachypterna*. In Germany, Bährmann & Adaschkiewitz (2003) stated that some taxa are typically winter-active: *Heleomyza modesta*, *G. caesius*, *E. obscura*, *Suillia oxyphora*, *S. pallida*, *S. vaginata*, *Schroederella iners* and *Tephrochlamys laeta*. In Poland, several species of this cold-adapted family were recorded only in mountains (Table 2). Species of the genera *Gymnomus*, *Heleomyza*, *Scoliocentra*, and *Suillia cepelaki* are most abundant in natural forests in the mountains. These flies naturally occur in wooded areas (Woźnica, 1996). In contrast, species of the genera *Eccoptomera*, *Oldenbergiella* and *Orbellia* occur mainly in less forested areas, and dominate in the lowlands.

Additional results from our winter study are the new faunistic records of Heleomyzidae in Poland. One species of Heleomyzidae is new to the Polish fauna – *Suillia cepelaki* (Woźnica & Soszyńska-Maj, in press), one was previously known only from a single Polish record – *Scoliocentra nigrinervis* (Soszyńska-Maj & Woźnica, 2012). The record of *Suillia cepelaki* in Polish mountains is the most northern known occurrence of this species in Europe, and probably also the northernmost border of its distribution (Woźnica & Soszyńska-Maj, in press). Among the lowland species, records of *E. ornata* are especially noteworthy. This species was recorded in this study for the first time both on the snow and in the lowlands. Previously, it was recorded in Poland exclusively in the mountains (Woźnica, 2007). These results demonstrate the importance of winter studies when updating lists of some groups of insects, particularly those that are mainly active in cold weather. This was previously demonstrated for winter emerging Chironomidae (Soszyńska-Maj et al., 2016).

On the basis of the new data from Poland and literature on winter-active flies and Heleomyzidae recorded on snow, a list of 78 winter-active Heleomyzidae in Europe was compiled (Table 6) (papers are numbered in References and cited in Table 6 by those numbers). One species recorded on snow in Poland had never previously been noted for its winter activity. Every species in the list of 78 winter-active taxa could be potentially recorded on snow. Winter-active Heleomyzidae make up almost 52% of the whole family, making these flies the most winter active group of Diptera other than the Trichoceridae (Soszyńska-Maj et al., in prep.).

The absence of Heleomyzidae in pitfall traps under snow leads to the conclusion that these flies do not seek protection from the weather in the subnivean space beneath the snow as other insects do (Koshima, 1984, 1985). This is undoubtedly due to their wings, which are significantly longer than the abdomen and would make boring into deep snow cover impossible.

Phenology

Records of Heleomyzidae on snow in the lowlands were highest in late November and December. In the mountains, however, they appeared at the end of December and peaked at the beginning of February. These differences are mainly determined by the dominant species. All the dominant species in the lowlands were recorded on snow throughout the autumn-spring period (*T. rufiventris*, *E. obscura*, *Heteromyza rotundicornis*), but were more abundant in late autumn and early winter. However, the activity on snow of the two most abundant species in the mountains (*Heleomyza modesta* and *Scoliocentra brachypterna*) peaked in mid-winter, i.e. January and February. Hågvar & Greve (2003) also report *Scoliocentra brachypterna* and *T. rufiventris* occurring on snow in Norway at this time. In Germany, Bährmann & Adaschkiewitz (2003) reports collecting 27 species of Heleomyzidae in winter and provides details of the winter phenology of 10 species. The phenology they cite for *Heleomyza modesta* corresponds with our data.

Response to weather conditions

The group of species recorded at the lowest temperatures included those that occur only in the mountains (*Scoliocentra nigrinervis*, –5°C and *Heleomyza modesta*, –4°C) and those that were present both in mountain and lowland assemblages (*O. myiopiformis*, *E. ornata*, *T. rufiventris*). A single species, *Heteromyza rotundicornis*, common in both assemblages, had the widest temperature range. Species that were recorded in the lowlands predominated at the highest winter temperatures.

Highest number of individuals and species of Heleomyzidae were collected between –2°C and 2°C and at from 91 to 100% humidity. The positive effect of rising air temperature and humidity were statistically confirmed. Very often, heleomyzids were collected when the weather was cloudy or even foggy, which indicates stable weather without rapid temperature changes. At air temperatures lower than –3.5°C, heleomyzids were only recorded on the snow occasionally, while above 2°C they were commonly seen flying. The lowest temperature at which they are recorded is reported by Svensson (1966), who found *Scoliocentra nigrinervis* at –8°C, and this species can survive down to –16°C in a supercoooled state (Sømme & Østbye, 1969). Our study in Poland confirmed that this species was active at the lowest temperature recorded (–5°C). The majority of other field observations of these insects on snow were made at temperatures between –2 and + 2°C (Frey, 1913; Tahvonen, 1942; Hågvar & Greve, 2003). However, *Sco-*

Table 6. A checklist of European Heleomyzidae, including species recorded in winter, based on this study and records in the literature. Sources are numbered in References. * – this paper, S – recorded on snow but no record of the month collected, W – recorded in winter but without a specific date.

No.	Species	Snow cover	Pitfall traps	Winter activity	Source
1	*Acantholeria vockerothi* Hackman, 1969			XII–II	(19)
2	*Eccoptomera emarginata* Loew, 1862	S		XI–XII	(67)
3	*Eccoptomera longiseta* (Meigen, 1830)	II	X–III	I–II	*(09,35,49,59,)
4	*Eccoptomera microps* (Meigen, 1830)	XII		X–II	(19,35,44,58,63,67)
5	*Eccoptomera obscura* (Meigen, 1830)	XI–III	XI–XII,III,W	X–XII,IV, W	*(01,02,19,27,48,66)
6	*Eccoptomera ornata* Loew, 1862	XII–I			*
7	*Eccoptomera pallescens* (Meigen, 1830)	XI,II	X,XII,W	X–IV	*(01,02,20,35,36)
8	*Gymnomus amplicornis* (Czerny, 1924)			II–III,W	(02,12,63)
9	*Gymnomus caesius* (Meigen, 1830)	XI–II	W	XII–II,W	*(01,02,19,24,28,36,39,40,54,68)
10	*Gymnomus ceianui* (Martinek, 1985)			X,XII–II	(07,15,52,54)
11	*Gymnomus martineki* Papp & Woźnica, 1993			II	(19)
12	*Gymnomus sabroskyi* (Gill, 1962)		IV	W	(45)
13	*Gymnomus spectabilis* (Loew, 1862)	I–II,W		XII	*(01,06)
14	*Heleomyza borealis* (Boheman, 1865)	III–IV	V	II–IV	(05,36,60)
15	*Heleomyza captiosa* (Gorodkov, 1962)	II,IV	W	X–IV	*(01,02,09,12,19,20)
16	*Heleomyza modesta* (Meigen, 1835)	XII–IV	I–II	X–IV	*(01,02,07,12,15,19,24,28,32,39,57,63,66)
17	*Heleomyza serrata* (Linnaeus, 1758)	XI,II–IV	W	XII–III,W	(01,02,12,33,36,39,41,60)
18	*Heteromyza atricornis* Meigen, 1830	III		X–III,W	*(02,07,09,16,19,38)
19	*Heteromyza commixta* Collin, 1901	IV			(36)
20	*Heteromyza oculata* Fallen, 1820	XII		XI–XII	(36,19)
21	*Heteromyza rotundicornis* (Zetterstedt, 1846)	XI–IV		XI–III	*(10,21,29,48)
22	*Morpholeria kerteszii* Czerny, 1924	XI			*
23	*Morpholeria ruficornis* (Meigen, 1830)		X	XI,XII,W	(02,04,08,19,28)
24	*Neoleria flavicornis* (Loew, 1862)			I–III	(09,20)
25	*Neoleria maritima* (Villeneuve, 1921)			XI–XII,II	(06,09)
26	*Neoleria propinqua* Collin, 1943			XII	(41)
27	*Neoleria ruficauda* (Zetterstedt, 1847)			XI–I–III	(06,12,20)
28	*Neoleria ruficeps* (Zetterstedt, 1838)			XI–XII	(06,15,41,66)
29	*Oecothea fenestralis* (Fallen, 1820)	XII	W	X–IV	(01,02,09,40,55,59)
30	*Oecothea ushinskii* Gorodkov, 1959			XII	(15)
31	*Oldenbergiella blascoi* Carles-Tolrá, 1995			XII,II	(15,19)
32	*Oldenbergiella brumalis* Czerny, 1924	X–II		X–XI	*(57,69)
33	*Oldenbergiella calcacifera* Papp, 1980			X–III	(12,20,47,48,51,57)
34	*Oldenbergiella canalicata* Carles-Tolrá, 1998			I,III	(12,20)
35	*Oldenbergiella pappi* Carles-Tolrá, 1992			XII,II	(09,15)
36	*Oldenbergiella seticerca* Papp,1980			X–XII,II–III	(12,20,47,55,66)
37	*Orbellia borisregis* Czerny, 1930	II		II	(25)
38	*Orbellia cuniculorum* Robineau-Desvoidy,1830	X		XII,III	*(12,56)
39	*Orbellia hiemalis* (Loew, 1862)	X–XII	XI	XI–II	*(24,39,48,55,66,71)
40	*Orbellia myiopiformis* Robineau-Desvoidy, 1830	XI–II		XI–IV	*(12,20,24,36,48,55,59,63, 69)
41	*Orbellia nivicola* (Frey, 1913)	XI–I			(30,36,55,64)
42	*Schroederella bifida* Papp & Carles-Tolrá, 1994			XI–XII	(15)
43	*Schroederella iners* (Meigen, 1830)	XI–XII	X–XI,W	X–III	*(01,02,23,50,53,66,69)
44	*Schroederella hispanica* Papp & Carles-Tolrá, 1994			XII–III	(15)
45	*Schroederella hungarica* Papp & Carles-Tolrá, 1994			I	(66)
46	*Scoliocentra* (*Leriola*) *brachypterna* (Loew, 1873)	I–IV		X,II–III	*(02,36)
47	*Scoliocentra* (*Leriola*) *nigrinervis* (Wahlgren, 1918)	XI–IV		I–III*,W	*(01,25,30,31,36,43,56,62,63,65)
48	*Scoliocentra (Scoliocentra) dupliciseta* (Strobl, 1898)			I	(46,59,69)
49	*Scoliocentra* (*Scoliocentra*) *villosa* (Meigen, 1830)	II–IV		W	*(02,61)
50	*Suillia affinis* (Meigen, 1830)		X,W	X–XII,IV	(01,02,04,11,28)
51	*Suillia atricornis* (Meigen, 1830)			X–XI,II	(19)
52	*Suillia bicolor* (Zetterstedt, 1838)			W	(02)
53	*Suillia cepelaki* Martinek, 1985	XII		?–IV	*(56)
54	*Suillia discolor* Czerny, 1927			XII	(11)
55	*Suillia gigantea* (Meigen, 1830)		W	I	(01,15)
56	*Suillia flagripes* (Czerny, 1904)			XI–I	(17,41)
57	*Suillia flava* (Meigen, 1830)		W	W	(01,02)
58	*Suillia flavifrons* (Zetterstedt, 1838)	X–II,IV		W	(02,30,36,55,67)
59	*Suillia fuscicornis* (Zetterstedt, 1847)		X–XI,II,W	X–II,W	(01,02,04,17,28,41,60)
60	*Suillia humilis* (Meigen, 1830)		X–XI,W	X–III,W	(01,02,04,07,08,12,15,19,28,34,35)
61	*Suillia laevifrons* (Loew, 1862)		X–XI,W	X,W	(01,02, 04,28)
62	*Suillia notata* (Meigen, 1830)		W	X–II	(01,04,08,09,11,17,41)
63	*Suillia oxyphora* (Mik, 1900)		W	X–I	(01,02)
64	*Suillia pallida* (Fallen, 1820)	XI–XII	X,W	X– IV	*(01,02,19,28,36,48,70)
65	*Suillia parva* (Loew, 1862)	I–II		XII,II–III	*(12,36,63)
66	*Suillia setitarsis* (Czerny,1904)			II–III	(26)
67	*Suillia similis* (Meigen, 1838)		W	W	(01,02)
68	*Suillia tuberiperda* (Rondani,1867)	I		I–III	(37)
69	*Suillia ustulata* (Meigen, 1830)	XII,II		III	*(48)
70	*Suillia umbratica* (Meigen, 1835)			W	(01,28)
71	*Suillia univittata* (von Roser, 1840) [= *lurida* auct.]			I–X	(22,24,59)
72	*Suillia variegata* (Loew, 1862)			XII–II	(09,11,18,19,41)
73	*Suillia vaginata* (Loew, 1862)	XI–XII	W	XI–XII	*(01,02)
74	*Tephrochlaena oraria* (Collin, 1943)			I	(16)
75	*Tephrochlamys flavipes* (Zetterstedt, 1838)	XI–I	X	XII–III,W	*(02,09,11,12,14,16,19,20,29,34,40,41,48,55)
76	*Tephrochlamys laeta* (Meigen, 1830)	XI–XII	W	W	(01,02,67)
77	*Tephrochlamys rufiventris* (Meigen, 1830)	XI–IV	XI–XII,II	X–IV	*(01,02,04,06,09,11,19,24,26, 29, 30,36,39,40,48,55, 59,60, 63,67)
78	*Tephrochlamys tarsalis* (Zetterstedt, 1847)	II		X–XII,II–IV	*(48,60,67)

liocentra brachypterna, *Heleomyza borealis*, *H. serrata* and *Heteromyza commixta* were also recorded at higher temperatures (up to 5 or even 10°C) on snow in southern Finland (Hågvar & Greve, 2003).

Ecology

For some specialized arthropods, snow cover is an important refuge from extreme weather, e.g. wingless females of Geometridae (Soszyńska-Maj & Buszko, 2011) and rich communities of Chironomidae (Soszyńska-Maj et al., 2016) and *Triphleba trinervis* (Phoridae) (Soszyńska & Durska, 2002). The genera *Boreus* (Mecoptera) (Hågvar, 2001) and *Chionea* (Limoniidae) (Hågvar, 1971, 1976) also use snow surface as a refuge, as do many Collembola (review by Hågvar, 2010). The snow surface is also a stage for sexual behaviour and copulation for some taxa, such as, species of wingless and fully-winged Chironomidae (Jonsson & Sandlung, 1975; Bouchard & Ferrington, 2009; Giłka et al., 2013; Soszyńska-Maj et al., 2015).

During our study, we did not observe heleomyzids either copulating or walking on snow as is reported for winged Chironomidae (copulating and moving), Phoridae (walking) and Sphaeroceridae (walking) (Soszyńska & Durska, 2002, Soszyńska-Maj, unpubl. data, Soszyńska-Maj et al., 2016). Only Svensson (1966) reports *Scoliocentra nigrinervis* moving on snow at a rate of 8–10 cm per minute. All Heleomyzidae collected in Poland were standing on the snow motionless, unless they were disturbed. Hågvar & Greve (2003) also note that Heleomyzidae recorded on snow do not use the snow surface for walking, migration, copulation or sexual behaviour (only one such record), or for feeding or basking.

All available data on the biology of Heleomyzidae indicates their larvae are either saprophagous or mycetophagous, and this influences the phenology and habitat preferences of the adult. The adults of mycetophagous species of the genus *Suillia* occur in forests and in cool and shady places during autumn, which is confirmed by our results (Table 5). Autumnal and winter species whose larvae are necrophagous feed on carrion and prefer grassy and steppe areas (viz. *Neoleria* spp., *Oldenbergiella* spp., *Orbellia* spp. and *Schroederella* spp.). Larvae of the genera *Heleomyza* and *Scoliocentra*, some species of *Heteromyza* and *Tephrochlamys rufiventris* are probably saprophagous. Their adults appear in early spring and as the temperature rises they find shelter in caves and diapause there in summer. Locally, they stay permanently in caves as troglophiles. *Heleomyza serrata*, *H. borealis*, *Scoliocentra brachypterna* and *S. villosa* are mostly regarded as troglophiles and *Heleomyza modesta* and *Eccoptomera pallescens* as trogloxenes and are often recorded in caves in Norway, Austria and Poland (Østbye et al., 1987; Kjaerandsen, 1993; Christian & Spötl, 2010; Østbye & Lauritzen, 2013; Weber & Weber, 2013). Populations of some heleomyzids also occur in burrows and soil tunnels made by small rodents or rabbits, in birds' nests, on guano in caves or even in old-fashioned toilets where they reproduce. Their saprophagous larvae develop in excrement, e.g. the larvae of *Eccoptomera* spp. in droppings of winter active rodents (Czerny, 1924; Papp, 1981; Woźnica, 2008; Carles-Tolrá, 2011). The habitats that winter active Heleomyzidae prefer make them possible prey for shrews, which are active beneath the snow. Shrews feed on winter-active species rather than hibernating invertebrates (Ackefors, 1964; Randolph, 1973; Pernetta, 1977; Aitchison, 1984; Itämies & Lindgren, 1989). Heleomyzidae may also be a source of food for bats in caves, as the winter diet of bats consists mainly of winter-active Diptera (Kaňuch et al., 2005; Williams et al., 2011).

During this study in Poland, slightly more males than females were collected on snow (male-to-female sex ratio is 1.2), which indicates that both sexes overwinter and copulate either in winter or not until spring. It should also be mentioned that some freshly emerged specimens with a balloon on the front of their heads were seen on the snow – *Scoliocentra nigrinervis* (end of December) and *Scoliocentra brachypterna* (beginning of March). The latest studies on Diptera collected on carcasses in winter (Carles-Tolrá, 2011; Carles-Tolrá & Prado e Castro, 2011) show that there are several species of Heleomyzidae that lay eggs in winter, and can be classified as cadaver colonizers [viz. *O. brumalis* Czerny (Fig. 3E)] with imagines common in late autumn and winter (Carles-Tolrá, 2011; Carles-Tolrá et al., 2011; Roháček, 1997).

Hågvar & Greve (2003) point to the fact that during winter, the snow cover accumulates excrements and carrion like a big freezer, which is released when the snow melts. They hypothesized that cold-tolerant Heleomyzidae could be the first to colonize these resources at snow melt. In this way they could outcompete more heat demanding saprophagous insects which exploit the same food source, for example beetles and other Diptera. In support of this hypothesis, Hågvar & Greve (2003) show that females of *Scoliocentra nigrinervis* contain mature eggs throughout winter, which they lay as soon as a favourable substrate becomes available. The occurrence on snow might reflect their continuous search for possible substrates, even at low temperatures. The overwintering of males furthermore indicates copulation when the substrate is available. We support this hypothesis. Also, some species may be able to find substrates for egg-laying in burrows or in caves, and stay active throughout the whole winter. However, we have not dissected females of Heleomyzidae to determine the number of egg they contain or the status of their ovaries.

Much is still left to learn about the ecology of this interesting, cold-tolerant family of flies. It would be interesting to determine whether carrion or dung placed in typical Heleomyzidae habitats during late winter is first colonized by these species and whether they are winners in utilizing resources exposed when snow melts.

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