







Overlooked insects in neglected ecosystem: new records of Phoridae for Slovakia discovered in rural environment

Bernd Grundmann¹, Peter Manko², Jozef Oboňa³

(1) Dickstraße 6, D – 33824 Werther (Westf.), Germany, bernd.grundmann@hotmail.com 
<https://orcid.org/0009-0007-8478-0188> 

(2) Department of Ecology, Faculty of Humanities and Natural Sciences, University of Prešov, 17. novembra 1, SK – 08116 Prešov, Slovakia, peter.manko@unipo.sk 
<https://orcid.org/0000-0003-1862-9117> 

(3) [Corresponding author] Department of Ecology, Faculty of Humanities and Natural Sciences, University of Prešov, 17. novembra 1, SK – 08116 Prešov, Slovakia, jozef.obona@unipo.sk 
<https://orcid.org/0000-0002-1185-658X> 

Abstract: An understudied ecosystem such as a rural area can hold many surprises. In this paper we report the results of a collection at a rural site in eastern Slovakia using a single Malaise trap over a five-month period. From May to September 2023, 70 species of the Diptera family Phoridae were found there, 19 of which represent new species for the Slovak fauna (one sp. of the genus *Aenigmatias* and 18 spp. of the genus *Megaselia*). The species richness of the Phoridae fauna in Slovakia has thus increased by almost 9% to 229 species. It is very likely that more intensive research will yield many more interesting records and greatly increase our knowledge of Slovakia's biodiversity.

Keywords: faunistic, new records, Phoridae, scuttle flies, Slovakia

Introduction

Urban and rural areas are not usually considered to be biodiversity-rich environments. These highly degraded remnants of native habitats, together with highly altered areas occupied by non-native species, are often neglected by researchers, leaving the biodiversity of most towns and villages unstudied or understudied (Hartop et al., 2015). The same applies to the study of Diptera biodiversity (e.g. Hartop et al., 2015).

Inadequate knowledge of the fauna of regions and gaps in information on the occurrence of species may limit the achievement of international biodiversity goals (Girardello et al., 2018; Sánchez-Fernández et al., 2011 and references therein). Comprehensive biological databases based on relevant data are a primary tool in ecological and biogeographical research, as good quality distribution data are required for the development of reliable designs and conservation strategies (Prendergast et al., 1993; Soberón & Peterson,

2004; Guralnick et al., 2007; Hortal et al., 2007). Even though it is challenging (Fattorini, 2013), any faunal information on a little-known group, and especially from an understudied region and ecosystem, is very important. What Hartop et al. (2015) write about urban ecosystems in their excellently titled article 'Opportunity in our Ignorance...' also applies to the rural habitats of scuttle flies, as documented in several papers (Durska, 1981; Prescher & Weber, 1996; Disney, 2001; Langourov, 2004; Hartop et al., 2015; Brown & Hartop, 2017; Grundmann & Kappert, 2023).

Flies of the family Phoridae (Diptera), also known as scuttle flies, are small to medium-sized (0.5–6 mm), often somewhat curved and more or less robust, with characteristic wing venation (Disney, 1983). Adults are conspicuous for their rapid and somewhat abrupt movements (Disney, 1983). Most adults feed on nectar, honeydew and sap oozing from fresh carrion and faeces; some feed on the body juices of live beetle larvae and pupae.



Fig. 1. Malaise trap set on PM's private land.

Phorid flies belong to the lower family Cyclo-rhapha, a superfamily of Platypezoidea with about 35 genera and more than 700 species in Europe (Oosterbroek, 2006). Recently, 210 species are known from Slovakia (Mocek, 1997, 2009; Grundmann et al., 2023).

Material and methods

Locality data

Slovakia, Prešov District, Lažany Village. Malaise trap (Townes' type) (Fig. 1), 49°02'13.7"N 21°05'45.6"E, leg P. Manko. The trap was placed in a shaded area about 3 m from a small forest stream at the edge of the forest (mainly oak (*Quercus*), hornbeam (*Carpinus*), lime (*Tilia*), with hazel (*Corylus*), birch (*Betula*), poplar (*Populus*), elder (*Sambucus*) and willow (*Salix*) on the edges with a lot of dead wood and standing dry trees and diverse other microhabitats – leaf litter and decomposing leaves, bare soil and stands of moss and herbaceous vegetation) in the immediate vicinity of a mowed lawn (backyard), an orchard, and a compost heap. Considering that the paper deals with the family Phoridae, it is probably

worth mentioning that the trap was located near the local cemetery, the nearest graves being less than 50 m away.

Sampling

Phorid flies were sampled together with other insects using a Malaise trap (see locality data) exposed for one week (7-day period) in each month from May to September 2023 (May (12–16.5.2023), June (16–23.6.2023), July (20–29.7.2023), August (19–23.8.2023), September (19–25.9.2023)). The material collected in ethanol was transported to the laboratory. Collected flies were sorted to family level, fixed in 75% alcohol and identified by group specialists. Phorid flies belong to the dominant dipteran groups in the collected material. Specimens were identified to species level by B. Grundmann using keys (Schmitz, 1943, 1951; Disney, 1983, 1989, 1994, 1999). BG also kept the collection of scuttle flies.

Data on larval biology and feeding ecology were drawn from the following publications: Donisthorpe (1927), Picard (1930), Örösi-Pal (1938), Schmitz (1941, 1943, 1949), Schmutterer (1952), Decou-Burghelle (1961), Lundt (1964), Spradbery (1973),

Disney (1976, 1977, 1991, 1994), Hackman (1963), Yarkulov (1972), Hackman & Meinander (1979), Yakovlev (1986), Köhlhorn (1987), Gemesi & Disney, (1991), Durska (1996, 2001, 2009, 2013, 2015, 2020), Buck (1997), Werner (1997), Ayre (2002), Coupland & Barker (2004), Durska et al. (2005), Craik (2009), Grundmann & Kappert (2023).

Results

A total of 554 scuttle flies were found in the trap (May – 117 individuals, June – 145, July – 160, August – 63, September – 69) belonging to 70 species (see the Annotated list of recorded species). 19 species are recorded for the first time in Slovakia. 31 species were recorded on the basis of only 1 individual. The most abundant species was *Diplonevra nitidula* (Meigen, 1830) with 113 specimens (20% of all recorded specimens), followed by *Megaselia consetigera* (Schmitz, 1925) with 61 specimens (11%), *Chaetopleurophora erythronota* (Strobl, 1892) with 59 specimens (10%) and *Diplonevra abbreviata* (von Roser, 1840) with 48 specimens (8%). Only 5 species were recorded in all seasons and more than half of the species (39) were recorded in only one sampling period (month).

Annotated list of recorded species

For species records only the months are given, for the exact collection period in which the species was caught see Materials and methods. For species new to the Slovak fauna, we also provide some information on the feeding ecology of their larvae, if known. For more abundant species, where it was possible to display and interpret seasonal activity we also provide information on it along with information on feeding ecology, if known.

Diptera

Phoridae

Aenigmatias lubbocki (Verrall, 1877) (Fig. 2). Material examined: May, 1 ♂. Note: First record for Slovakia. Zoophagous (Durska, 2015). All species of the genus *Aenigmatias* are myrmecophilous. They are



Fig. 2. A male and a wingless female of *Aenigmatias lubbocki* in copula (photo by www.spessart-fliegen.de .

parasitic on ant pupae (Donisthorpe, 1927; Schmitz, 1941).

Anevrina thoracica (Meigen, 1804). Material examined: July, 1 ♂; September, 2 ♂♂, 1 ♀. Note: The saprophagous species is known to fly in two generations from April to July, hibernation as pupa. It is widely distributed all over Europe (Schmitz, 1941). It has been recorded from mammal's nests (Hackman, 1963) and from corpses of small vertebrates (Disney, 1994).

Anevrina urbana (Meigen, 1830). Material examined: May, 1 ♂. Note: Saprophagous, as the previous species (Hackman, 1963; Disney, 1994).

Borophaga femorata (Meigen, 1830). Material examined: May, 4 ♂♂; June, 2 ♂♂. Note: The life history of this species is still unknown (Craik, 2009).

Borophaga germanica (Schmitz, 1918). Material examined: May, 1 ♀; June, 8 ♀♀. Note: The species was only active at the site in spring and early summer. After the peak in June, it was no longer recorded. Zoophagous, recorded to be a parasitoid of larval Bibionidae (Gemesi & Disney, 1991; Langourov, 2004).

Borophaga incrassata (Meigen, 1830). Material examined: August, 4 ♂♂. Note: This species is also known to be a parasitoid of the larvae of Bibionidae (Morris, 1922). Later Grozdanic (1936) reported it as a parasitoid of honey-bees, but this was a misidentification of *Megaselia rufipes* (Örösi-Pal, 1938).

Chaetopleurophora erythronota (Strobl, 1892). Material examined: June, 16 ♂♂, 1 ♀; July, 20 ♂♂, 8 ♀♀; August, 7 ♂♂, 2 ♀♀; September, 1 ♂, 3 ♀♀. Note: The species was active at the site in summer

and autumn, with peak activity in July. Zoophagous (molluscivore). *Chaetopleurophora* larvae develop in dead molluscs (Coupland & Barker, 2004, and many references therein).

Conicera tarsalis Schmitz, 1920. Material examined: May, 1 ♂.

Diplonevra abbreviata (von Roser, 1840). Material examined: June, 3 ♂♂, 1 ♀; July, 34 ♂♂, 2 ♀♀; August, 8 ♂♂. Note: The species was only active in summer, with a peak in activity in July.

Diplonevra concinna (Meigen, 1830). Material examined: July, 1 ♂. Note: The larvae of this saprophagous species have been found in vasp's nests (Spradbery, 1973).

Diplonevra florescens (Turton, 1801). Material examined: May, 1 ♂, 1 ♀; June, 1 ♂; July, 1 ♀; September, 1 ♂. Note: Necrophagous, developing in all kinds of carrion. Three generations from May to October (Schmitz, 1949).

Diplonevra glabra (Schmitz, 1927). Material examined: May, 7 ♂♂, 3 ♀♀. Note: This species is limited to one generation in April and May after Schmitz (1949). But there may be three generations from April to late August (Disney, 1983).

Diplonevra nitidula (Meigen, 1830). Material examined: May, 5 ♂♂, 5 ♀♀; June, 15 ♂♂, 23 ♀♀; July, 26 ♂♂, 6 ♀♀; August, 13 ♂♂, 3 ♀♀; September, 15 ♂♂, 1 ♀. Note: The species was active throughout the sampling season, with peak activity in June and July. Has been reared from compost (Werner, 1997). The zoophagous larvae have found to be parasitoids of earthworms (Disney, 1991).

Diplonevra pilosella (Schmitz, 1927). Material examined: June, 1 ♂, 2 ♀♀; September, 1 ♀. Note: Species whose larvae are reported to be parasitoids of earthworms (Colyer, 1950; Disney, 1991).

Gymnophora arcuata (Meigen, 1830). Material examined: May, 2 ♂♂, 6 ♀♀; June, 2 ♂♂, 5 ♀♀; July, 3 ♂♂, 3 ♀♀; August, 2 ♂♂, 5 ♀♀; September, 2 ♂♂, 1 ♀. Note: The species was active throughout the sampling period from May to September, with a marked decrease in activity in September. Saprophagous, breeding in carrion and other decaying material (Coupland & Barker, 2004, and references therein).

Gymnophora integralis Schmitz, 1920. Material examined: September, 1 ♂.

Metopina braueri (Strobl, 1880). Material examined: May, 1 ♂. Note: Zoophagous (Durska, 2013), the diet of this species remains unknown.

Phora atra (Meigen, 1804). Material examined: May, 5 ♂♂; June, 1 ♂. Note: Saprophagous (Durska et al., 2005). Kühlnhorn (1987) reported it from cat dung, thus probably coprophagous as well.

Phora edentata Schmitz, 1920. Material examined: May, 4 ♂♂; June, 1 ♂; July, 2 ♂♂.

Phora holosericea Schmitz, 1920. Material examined: May, 5 ♂♂; June, 2 ♂♂. Note: Zoophagous (Durska, 2013). Reported to be a predator of root aphids (Yarkulov, 1972).

Spiniphora bergenstammi (Mik, 1864). Material examined: May, 1 ♂; June, 2 ♂♂; July, 1 ♂. Note: This and the following species are saprophagous. Development in all kinds of carrion (Disney, 1994).

Spiniphora excisa (Becker, 1901). Material examined: June, 1 ♂.

Triphleba distinguenda (Strobl, 1892). Material examined: May, 2 ♀♀; September, 2 ♀♀. Note: Most abundant species of the genus, it is known to fly in three generations from May to November, hibernation as pupa. It is saprophagous and widely distributed in Europe (Schmitz, 1943).

Triphleba dudai (Schmitz, 1918). Material examined: May, 2 ♂♂; June, 2 ♂♂, 1 ♀; July, 1 ♂, 1 ♀; August, 1 ♂; September, 1 ♂, 2 ♀♀. Note: Saprophagous (Lundt, 1964).

Megaselia abdita Schmitz, 1959. Material examined: June, 1 ♂. Note: First record for Slovakia. Saprophagous (necrophagous) (Durska, 1996, 2013, 2020; Disney & Manlove, 2005; Manlove & Disney, 2008) or coprophagous (Disney, 1994). The forensic use is described in Greenberg & Wells (1998).

Megaselia aculeata (Schmitz, 1919). Material examined: August, 1 ♂. Note: First record for Slovakia.

Megaselia albiclava Schmitz, 1926. Material examined: August, 2 ♂♂. Note: First record for Slovakia.

Megaselia breviterga (Lundbeck, 1920). Material examined: May, 1 ♂, 4 ♀♀; June, 3 ♀♀; July, 1 ♀; September, 1 ♂. Note: Saprophagous.

Megaselia campestris (Wood, 1908). Material examined: September, 1 ♂.

Megaselia ciliata (Zetterstedt, 1848). Material examined: July, 1 ♀. Note: Zoophagous, this species is known to attack the eggs of land snails (Disney, 1977; Ayre, 2002).

Megaselia clemonsi Disney, 1984. Material examined: July, 1 ♂. Note: First record for Slovakia.

Megaselia consetigera (Schmitz, 1925). Material examined: May, 7 ♂♂; June, 10 ♂♂; July, 22 ♂♂, 3

♀♀; August, 7 ♂♂; September, 12 ♂♂. Note: The species was active throughout the sampling season with a peak in activity in July and a further increase in activity in September.

Megaselia diversa (Wood, 1909). Material examined: May, 1 ♂. Note: First record for Slovakia.

Megaselia elongata (Wood, 1914). Material examined: May, 1 ♂. Note: Zoophagous, reported as a parasitoid of Myriapoda (Picard, 1930; Disney, 1994).

Megaselia emarginata (Wood, 1908). Material examined: May, 1 ♂, 3 ♀♀; June, 2 ♂♂, 7 ♀♀; July, 2 ♀♀. Note: The species was active throughout the spring and summer, with a peak in activity in July.

Megaselia errata (Wood, 1912). Material examined: May, 1 ♂; August, 1 ♂.

Megaselia flava (Fallén, 1823). Material examined: July, 2 ♀♀. Note: Mycetophagous (Hackman & Meinander, 1979).

Megaselia flavicans Schmitz, 1935. Material examined: June, 1 ♀; July, 1 ♂, 1 ♀; September, 3 ♂♂, 4 ♀♀. Note: The species was active in June and July, with a peak in activity in September after being absent in the August sample. The flight activity of this species indicates two generations per season at the sampling site. Mycetophagous (Disney, 1994).

Megaselia flavicoxa (Zetterstedt, 1848). Material examined: May, 1 ♂; June, 1 ♂; September, 2 ♂♂. Note: Zoophagous, reported as a parasitoid of Sciariidae (Diptera Nematocera) (Disney, 1976).

Megaselia frontalis (Wood, 1909). Material examined: August, 1 ♂.

Megaselia fusca (Wood, 1909). Material examined: May, 5 ♂♂; June, 1 ♂. Note: Saprophagous (coprophagous) (Hackman, 1963).

Megaselia fuscinervis (Wood, 1908). Material examined: June, 6 ♂♂.

Megaselia hortensis (Wood, 1909). Material examined: July, 1 ♂.

Megaselia infrapospita (Wood, 1909). Material examined: September, 1 ♂.

Megaselia latifrons (Wood, 1910). Material examined: July, 1 ♂. Note: First record for Slovakia.

Megaselia latior Schmitz, 1936. Material examined: August, 1 ♂. Note: First record for Slovakia. Mycetophagous (Disney & Evans, 1979).

Megaselia ledburiensis Brues, 1915. Material examined: June, 1 ♂. Note: First record for Slovakia. This is the valid name of the species formerly known as *Megaselia subfuscipes* Schmitz, 1935 (Disney, 2014). Zoosaprophagous (Buck, 1997).



Fig. 3. A male of *Megaselia melanocephala*, one of the largest and most striking species in the genus (photo by www.spessart-fliegen.de). Scale bar: 1 mm.

Megaselia lutea (Meigen, 1830). Material examined: May, 2 ♂♂, 8 ♀♀; June, 1 ♂, 2 ♀♀; July, 1 ♂, 2 ♀♀; August, 1 ♀; September, 1 ♂. Note: The species was active throughout the sampling period with a peak in May and a decreasing trend in activity during the summer and autumn. Mycetophagous (Disney, 1994).

Megaselia lutescens (Wood, 1910). Material examined: September, 1 ♂. Note: First record for Slovakia. Mycetophagous (Disney, 1994).

Megaselia manicata (Wood, 1910). Material examined: July, 1 ♂. Note: First record for Slovakia.

Megaselia melanocephala (von Roser, 1840) (Fig. 3). Material examined: May, 1 ♀; June, 1 ♀; July, 2 ♂♂; August, 1 ♂. Note: First record for Slovakia. This zoophagous species is known to be a predator of spider eggs (Decou-Burghelle, 1961).

Megaselia nigriceps (Loew, 1866). Material examined: July, 1 ♀; September, 2 ♂♂, 1 ♀. Note: Zoosaprophagous (Durska, 2013).

Megaselia obscuripennis (Wood, 1909). Material examined: August, 1 ♂. Note: Zoophagous.

Megaselia picta (Lehmann, 1822). Material examined: June, 1 ♂; July, 1 ♂; August, 1 ♀.

Megaselia pleuralis (Wood, 1909). Material examined: May, 3 ♂♂; June, 1 ♂; July, 1 ♂. Note: Saprophagous (Disney, 1994).

Megaselia plurispinulosa (Zetterstedt, 1860). Material examined: July, 1 ♂, 1 ♀. Note: Mycetophagous.

Megaselia producta (Schmitz, 1921). Material examined: May, 1 ♂. Note: First record for Slovakia.

Megaselia protarsalis Schmitz, 1927. Material examined: June, 1 ♂, 1 ♀. Note: First record for Slovakia.

Megaselia pseudogiraudii (Schmitz, 1920). Material examined: May, 3 ♂♂, 2 ♀♀; June, 3 ♂♂. Note: First record for Slovakia.

Megaselia rubescens (Wood, 1912). Material examined: May, 1 ♂; July, 1 ♂. Note: First record for Slovakia. Mycetophagous (Yakovlev, 1986).

Megaselia rufa (Wood, 1908). Material examined: May, 1 ♂, 4 ♀♀. Note: This species is known to be a parasite of Coccoidea (Schmutterer, 1952).

Megaselia ruficornis (Meigen, 1830). Material examined: May, 2 ♂♂, 2 ♀♀; June, 1 ♂, 7 ♀♀; July, 1 ♀; August, 1 ♂, 1 ♀. Note: The species was active from May to August with a peak in June.

Megaselia scutellaris (Wood, 1909). Material examined: September, 2 ♂♂. Note: Mycetophagous.

Megaselia simulans (Wood, 1912). Material examined: September, 1 ♂.

Megaselia spinata (Wood, 1910). Material examined: June, 2 ♂♂, 1 ♀; August, 1 ♂. Note: First record for Slovakia.

Megaselia subpleuralis (Wood, 1909). Material examined: September, 1 ♂.

Megaselia subtumida (Wood, 1909). Material examined: September, 1 ♀.

Megaselia tarsalis (Wood, 1910). Material examined: July, 1 ♂. Note: First record for Slovakia.

Megaselia uliginosa (Wood, 1909). Material examined: September, 1 ♂.

Megaselia variana Schmitz, 1926. Material examined: May, 3 ♂♂, 1 ♀. Note: First record for Slovakia.

Discussion

In our rapidly changing world, the fauna of towns and villages remains poorly known (Hartop et al., 2015). Similarly, the lack of financial support for local faunistic research and the shortage of specialists means that these ecosystems are understudied.

In this study we report the results of a single Malaise trap catch. 70 species of the family Phoridae have been recorded from a single trap from March to September 2023 in the eastern part of Slovakia. 19 species are recorded for the fauna of Slovakia for the first time. This increases the number of the known phorid species in the country from 210 to 229.

The 554 fly specimens were identified to species level. They belong to 70 species. This is a relatively high number considering that more comprehensive studies have been carried out. For example, two other studies have identified 99 species from 42,000 individuals (Brown & Hartop, 2017) or 52 species from 6,000 individuals (Durska, 2009). According to the results of the first two publications cited above, only about 40 species would be detected with a similar number of individuals as we collected in this study. On the other hand, there are studies that have also recorded very high numbers of species. As an example, Grundmann & Kappert (2023) have found 71 species belonging to other genera than *Megaselia* (from 24,000 individuals). Although differences in species diversity are certainly largely due to differences in the geographical location of sites, but also to differences in approaches and methodologies, local conditions play a particularly important role. Rural landscapes with different landscape features (habitats, habitat types), which differ in terms of management, the presence of different sources of organic matter and potential larval hosts, are therefore likely to provide very suitable conditions for a large number of ecologically diverse species.

The species composition and representation differs from other works, which is a logical consequence of the different approaches to collecting the material and the local conditions at the study sites. Our findings are similar to the results of Grundmann & Kappert (2023), the most abundant species is *Diplonevra nitidula*. If *Megaselia* species were included in their results, the relative abundance of *Diplonevra nitidula* would be exactly the same as we found: 20%. There is also a difference in the abundance of low abundant species, which in our case accounted for up to more than half of the total number of individuals in May and more than a third in September. It is this trend (many low abundance species in spring, a decline in abundance in summer and a resurgence in autumn) that suggests the very real possibility that if we had set the trap throughout the year we would probably have detected significantly more species, especially low abundant or rare species.

In terms of feeding groups, most of the species detected are still unexplored (35), 13 species belonged to zoophages (parasites, parasitoids), 14 to saprophages (including species referred to as necrophages) and 8 to mycetophages. It is pointless to discuss in detail the temporal changes in the representa-

tion of these groups, as the feeding ecology of more than half of the species is unknown and, moreover, the relative abundance of these species varied from close to 30% to more than 50%. Also, given the “patchy” heterogenous pattern of habitat representation at the material collection site, the figure itself is not comparable to the results of other studies conducted in uniform large-scale habitats (e.g., Durska, 2001, 2013, 2015, 2020).

Looking at the sex ratio, we obtained results confirming the overall dominance of males, but the proportions varied from species to species – mostly males dominated, but in some cases females, and in extreme cases only females appeared in the samples. Several authors have found similar and the others different results, and it is generally accepted that the reason for this is a combination of differences in male and female behaviour (and here we add that it certainly differs between species, as we can see in our results) and collection methods (Disney, 1994; Prescher et al., 2002; Durska et al., 2010; Durska, 2013). However, differences in the use of the same method are also interesting. In contrast to the study by Grundmann and Kappert (2023), we found a large number of females (up to 35% of the total number of individuals).

Acknowledgements

We would especially like to thank the anonymous reviewers for providing constructive comments and for improving the manuscript. Our thanks also go to Jürgen Kappert, for permission to use his beautiful photos (<http://www.spessart-fliegen.de>). This work was supported by the Slovak Scientific Grant Agency, contracts no. VEGA-1/0012/20, VEGA 1/0213/22, and by the Slovak Research and Development Agency under the contract no. APVV-20-0140.

References

- Ayre K. 2002 *Megaselia ciliata* (Zetterstedt) (Dipt., Phoridae) attacking eggs of *Deroceras reticulatum* (Müller) (Gastropoda: Limacidae). *Entomologist's monthly Magazine* 138: 17–18.
- Brown B.V., Hartop E.A. 2017 Big data from tiny flies: patterns revealed from over 42,000 phorid flies (Insecta: Diptera: Phoridae) collected over one year in Los Angeles, California, USA. *Urban Ecosystems* 20: 521–534.
<https://doi.org/10.1007/s11252-016-0612-7>
- Buck M. 1997 Untersuchungen zur ökologischen Einnischung saprophager Dipteren unter besonderer Berücksichtigung der Phoridae und Sphaeroceridae (Brachycera/Cyclorrhapha). Dissertation Universität Ulm, 194 pp.
- Chao A. 1984 Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11: 265–270.
<http://www.jstor.org/stable/4615964>
- Chiu C.H., Wang Y.T., Walther B.A., Chao A. 2014 Improved nonparametric lower bound of species richness via a modified Good-Turing frequency formula. *Biometrics* 70: 671–682.
<https://doi.org/10.1111/biom.12200>
- Colyer C.N. 1950 Notes on the breeding of *Diploneura pilosella* Schmitz and *Megaselia rufipes* Mg. (Dipt., Phoridae) and of the puparium of the former. *Entomologist's Monthly Magazine* 86: 320–322.
- Coupland J.B., Barker G.M. 2004 Diptera as predators and parasitoids of terrestrial gastropods, with emphasis on Phoridae, Calliphoridae, Sarcophagidae, Muscidae and Fanniidae. pp. 85–158. In: *Natural enemies of terrestrial molluscs*. CABI Publishing, Wallingford.
- Craik J.C.A. 2009 Larvae of *Borophaga femorata* (Meigen, 1830) (Diptera, Phoridae) in larval columns of *Sciara militaris* in west Scotland in 2009. *Dipterist's Digest* 16 (2): 100.
- Decou-Burghelle A. 1961 Sur la biologie de *Megaselia melanocephala* von Roser, phoride parasite des cocons de *Meta menardi* Latr. *Annales du Laboratoire Souterrain, Hans-sur-Lesse* 11: 16–22.
- Disney R.H.L. 1976 A further case of a nematoceran fly (Diptera: Sciaridae) parasitised by a species of scuttle fly (Diptera, Phoridae). *Entomologist's Gazette* 27: 91–98.
- Disney R.H.L. 1977 A further case of a scuttle fly (Dipt., Phoridae) whose larvae attack slug eggs. *Entomologist's Monthly Magazine* 112: 174.
- Disney R.H.L. 1983 Scuttle flies – Diptera, Phoridae (except *Megaselia*). *Handbooks for the Identification of British Insects* 10 (6): 1–81.
- Disney R.H.L. 1989 Scuttle Flies – Diptera Phoridae Genus *Megaselia*. *Handbooks for the Identification of British Insects* 10 (8): 1–155.

- Disney R.H.L. 1991 Scuttle flies (Diptera: Phoridae) as parasites of earthworms (Oligochaeta: Lumbricidae). *British Journal of Entomology and Natural History* 4: 11–13.
- Disney R.H.L. 1993 Notes on European Phoridae (Diptera). *British Journal of Entomology and Natural History* 6: 107–118.
- Disney R.H.L. 1994 Scuttle Flies: The Phoridae. Chapman & Hall, London – Glasgow, 467 pp.
- Disney R.H.L. 1999 A troublesome sibling species complex of scuttle flies (Diptera, Phoridae) revisited. *Journal of Natural History* 33 (8): 1159–1216.
- Disney R.H.L. 2001 The scuttle flies (Diptera: Phoridae) of Buckingham Palace Garden. *Supplement to London Naturalist* 80: 248–258.
- Disney R.H.L. 2014 Revisionary notes on the *Megaselia sulphuripes* (Meigen) species group (Diptera: Phoridae). *Entomologist's Monthly Magazine* 150: 211–225.
- Disney R.H.L., Evans R.E. 1979 Further records of Phoridae (Dipt.) reared from fungi. *Entomologist's Monthly Magazine* 114: 166.
- Disney R.H.L., Manlove J.D. 2005 First occurrences of the Phorid, *Megaselia abdita*, in forensic cases in Britain. *Medical and Veterinary Entomology* 19: 489–491.
<https://doi.org/10.1111/j.1365-2915.2005.00593.x>
- Donisthorpe H.S.J.K. 1927 *The Guests of British Ants: Their Habits and Life-Histories*. G. Routledge and Sons, London, xxxiii + 244 pp.
- Durska E. 1981 Phoridae (Diptera) of Warsaw. *Memorabilia Zoologica* 35: 47–56.
- Durska E. 1996 The species composition and structure of scuttle fly communities (Diptera: Phoridae) in mature tree stands in pine forests at different stages of habitat degradation. *Fragmenta faunistica* 39 (19): 267–285.
- Durska E. 2001 Secondary succession of scuttle fly communities (Diptera: Phoridae) in moist pine forest in Białowieża Forest. *Fragmenta faunistica* 44 (1): 79–128.
- Durska E. 2009 The scuttle fly (Diptera: Phoridae) assemblages of pine plantations of the Biała Forest (Poland). *Entomologica Fennica* 20 (3): 170–178.
- Durska E. 2013 Effects of disturbances on scuttle flies (Diptera: Phoridae) in Pine Forests. *Biodiversity and Conservation* 22: 1991–2021.
<https://doi.org/10.1007/s10531-013-0522-4>
- Durska E. 2015 Effects of fire on scuttle flies (Diptera: Phoridae) in a pine forest in Poland. *Entomologica Fennica* 26 (4): 181–193.
<https://doi.org/10.33338/ef.84645>
- Durska E. 2020 Preliminary data of the scuttle flies (Diptera: Phoridae) in the linden-oak-hornbeam forest of the Wigry National Park, North East Poland. *Fragmenta Faunistica* 63 (1): 47–52.
<https://doi.org/10.3161/00159301FF2020.63.1.047>
- Durska E., Kaczorowska E., Disney R.H.L. 2005 Scuttle flies (Diptera: Phoridae) of saline habitats of the Gulf of Gdansk, Poland. *Entomologica Fennica* 16: 159–164.
<https://doi.org/10.33338/ef.84250>
- Fattorini S. 2013 Regional insect inventories require long time, extensive spatial sampling and good will. *PLoS One* 8 (4): p.e62118.
<https://doi.org/10.1371/journal.pone.0062118>
- Gemesi O., Disney R.H.L. 1991 A further case of parasitisation of larval Bibionidae by a scuttle fly (Diptera: Phoridae). *Entomologist's Gazette* 42 (1): 67–69.
- Girardello M., Martellos S., Pardo A., Bertolino S. 2018 Gaps in biodiversity occurrence information may hamper the achievement of international biodiversity targets: insights from a cross-taxon analysis. *Environmental Conservation* 45 (4): 370–377.
<https://doi.org/10.1017/S0376892918000115>
- Greenberg B., Wells J.D. 1998 Forensic use of *Megaselia abdita* and *M. scalaris* (Phoridae: Diptera): case studies, developmental rates, and egg structure. *Journal of Medical Entomology* 35: 205–209.
<https://doi.org/10.1093/jmedent/35.3.205>
- Grozdanic S. 1936 Die Bienenbuckelfliege (*Phora incrassata*). *Glasnik Hrvatskoga Prirodoslovnoga Društva Zagreb* 41–48: 160.
- Grundmann B., Kappert J. 2023 The Phoridae (Diptera) of NE-Westphalia: a field study over five years. *Fragmenta Faunistica* 66 (1): 15–36.
<https://doi.org/10.3161/00159301FF2023.66.1.015>
- Grundmann B., Oboňa J., Mocek B., Mock A. 2023 Scuttle flies (Diptera: Phoridae) of subterranean habitats in Slovakia: a review and a case study. *Biologia* 78: 3591–3597.
<https://doi.org/10.1007/s11756-023-01486-4>

- Guralnick R.P., Hill A.W., Lane M. 2007 Towards a collaborative, global infrastructure for biodiversity assessment. *Ecology letters* 10 (8): 663–672. <https://doi.org/10.1111/j.1461-0248.2007.01063.x>
- Hackman W. 1963 Studies on the dipterous fauna in burrows of voles (*Microtus*, *Clethrionomys*) in Finland. *Acta Zoologica Fennica* 102: 1–64.
- Hackman W., Meinander M. 1979 Diptera feeding as larvae on macrofungi in Finland. *Annales Zoologici Fennici* 16: 50–83.
- Hartop E.A., Brown B.V., Disney R.H.L. 2015 Opportunity in our ignorance: urban biodiversity study reveals 30 new species and one new Nearctic record for *Megaselia* (Diptera: Phoridae) in Los Angeles (California, USA). *Zootaxa* 3941 (4): 451–484. <https://doi.org/10.11646/zootaxa.3941.4.1>
- Hortal J., Lobo J.M., Jiménez-Valverde A. 2007 Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology* 21 (3): 853–863. <https://doi.org/10.1111/j.1523-1739.2007.00686.x>
- Kühlhorn F. von 1987 Über den Dipterenbeflug von Katzenkot und dessen mögliche hygienische Bedeutung. *Angewandte Parasitologie* 28: 93–101.
- Langourov M. 2004 Scuttle flies (Diptera: Phoridae) from urban and suburban areas in the Sofia Plain. In: Penev L., Niemelä J., Kotze D.J., Chipev N. (eds) *Ecology of the City of Sofia. Species and Communities in an Urban Environment*, Pensoft Publishers, Sofia–Moscow, 429–436.
- Lundt H. 1964 Ökologische Untersuchungen über die tierische Besiedlung von Aas im Boden. *Pedobiologia* 4: 158–180.
- Manlove J.D., Disney R.H.L. 2008 The use of *Megaselia abdita* (Diptera: Phoridae) in winter forensic entomology. *Forensic Science International* 175: 83–84. <https://doi.org/10.1016/j.forsciint.2007.08.001>
- Mocek B. 1997 Faunistic records from the Czech and Slovak Republics: Diptera, Phoridae. In: Vaňhara M., Rozkošný V. (eds) *Dipterologica Bohemoslovaca*, 8. Folia Fac Sci Nat Univ Masarykianae Brunensis, *Biologia* 95: 220–222.
- Mocek B. 2009 Phoridae Latreille, 1796. In: Jedlička L., Kúdela M., Stloukalová V. (eds) *Checklist of Diptera of the Czech Republic and Slovakia*. <http://www.edvis.sk/diptera2009/families/phoridae.htm> (accessed 31.10.2023).
- Morris H.M. 1922 On the larva and pupa of a parasitic phorid fly – *Hypocera incrassata* Mg. *Parasitology* 14 (1): 70–74.
- Oosterbroek P. 2006 *The European Families of the Diptera. Identification, diagnosis, biology*. KNNV Publishing, Utrecht, 205 pp.
- Örösi-Pal Z. 1938 Humpbacked flies and the honey bee. *Bee World* 19: 64–68.
- Picard F. 1930 Sur le parasitisme d'un Phoridae (*Megaselia cuspidata* Schmitz) aux dépens d'un Myriapode. *Bulletin de la Société Zoologique de France* 55: 180–183.
- Prendergast J.R., Quinn R.M., Lawton J.H., Eversham B.C., Gibbons D.W. 1993 Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365 (6444): 335–337. <https://doi.org/10.1038/365335a0>
- Prescher S., Moretti M., Duelli P. 2002 Scuttle flies (Diptera, Phoridae) in *Castanea sativa* forests in the southern Alps (Ticino, Switzerland), with thirteen species new to Switzerland. *Bulletin De La Société Entomologique Suisse* 75: 289–298. <https://doi.org/10.5169/seals-402834>
- Prescher S., Weber G. 1996 Zur Kenntnis der Buckelfliegen-Fauna (Diptera: Phoridae) ausgewählter Standorte in Köln – Frühjahrsaspekt. *Decheniana-Beihefte* 35: 415–421.
- Sánchez-Fernández D., Lobo J.M., Abellán P., Millán A. 2011 How to identify future sampling areas when information is biased and scarce: An example using predictive models for species richness of Iberian water beetles. *Journal for Nature Conservation* 19 (1): 54–59. <https://doi.org/10.1016/j.jnc.2010.05.003>
- Schmitz H. 1941 33. Phoridae (1. Teilband). Lieferung 141. In: Lindner E. (ed.) *Die Fliegen der paläarktischen Region* 4 (33): 65–128.
- Schmitz H. 1943 33. Phoridae (1. Teilband). Lieferung 147+149. In: Lindner E. (ed.) *Die Fliegen der paläarktischen Region* 4 (33): 129–192.
- Schmitz H. 1949 33. Phoridae (1. Teilband). Lieferung 160. In: Lindner E. (ed.) *Die Fliegen der paläarktischen Region* 4 (33): 193–240.
- Schmitz H. 1951 33. Phoridae (1. Teilband). Lieferung 165. In: Lindner E. (ed.) *Die Fliegen der paläarktischen Region* 4 (33): 241–272.

- Schmutterer H. 1952 *Plastophora rufa* (Wood) (Dipt., Phoridae) als Eiräuber und Parasit von *Eulecanium corni* (Bché) (Homoptera, Coccoidea). Anzeiger für Schädlingskunde 145: 148.
- Scholtz T., Choudhury A. 2014 Parasites of freshwater fishes in North America: Why so neglected? Journal of Parasitology 100: 26–45. <https://www.jstor.org/stable/24624673>
- Soberón J., Peterson T. 2004 Biodiversity informatics: managing and applying primary biodiversity data. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 359 (1444): 689–698. <https://doi.org/10.1098/rstb.2003.1439>
- Spradbery J.P. 1973 Wasps: An account of the biology and natural history of social and solitary wasps. University of Washington Press, Seattle, 235 pp.
- Werner D. 1997 Die Dipterenfauna verschiedener Mülldeponien und Kompostierungsanlagen in der Umgebung von Berlin unter besonderer Berücksichtigung ihrer Ökologie und Bionomie. Studia dipterologica, Supplementum 1: 1–176.
- Yakovlev E.B. 1986 Nasekomye-mitsebionty yuzhoi Karelii (ekologofaunistichestii spisok). In: Yakovlev E.B., Uzenbaev S.D. (eds) Fauna i ekologiya chlenistonogikh Karelii, 83–123. (In Russian)
- Yarkulov F. 1972 Mukha-gorbatka *Phora holosericea* (Diptera, Phoridae) – khishchnik kornevykh tley. Zoologicheskii Zhurnal 51 (9): 1415–1418. (In Russian)
-