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Sphaeroceridae (Diptera) reared from various types of carrion and other decaying substrates in Southern Germany, including new faunistic data on some rarely collected species

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Abstract. Rearing experiments were conducted in the vicinity of Ulm (Germany) using baits and samples of decaying organic matter collected in the field. Fifteen types of substrates consisted of vertebrate, mollusc and insect carrion (9 types), rotten plant material (3 types), fungi (2 types) and excrement. A total of 49,489 adult Sphaeroceridae belonging to 28 species emerged from these substrates. Seven species were reared for the first time, and for 22 species new larval feeding substrates are recorded. In addition, the occurrence of thirteen rarely-collected species in traps baited with carrion or fungi and emergence traps is reported. Five species are new to the German fauna: *Minilimosina gemella* Roháček, *Spelobia manicata* (Richards), *Telomerina eburnea* Roháček, *Opalimosina calcarifera* (Roháček) and an undescribed species of the genus *Elachisoma*.

INTRODUCTION

Coprophagy is a widespread larval feeding strategy in the Sphaeroceridae, as is reflected in their common name of "lesser dung flies". However, certain species are necrophagous or facultatively breed in carrion. The biology and ecology of coprophagous sphaerocerids is comparatively well known and has been investigated in various studies (e.g., Laurence, 1955; Papp, 1975, 1976, 1992). In contrast, little attention has been paid to the ecology of necrophagous species. Through the studies of Beaver (e.g., 1972) and Joswig (1985) some data have become available on the fauna of dead snails. Although it is well known that various species are attracted to vertebrate carrion (e.g., Smith, 1975; Pitkin, 1986; Kentner & Streit, 1990), there is little information upon which species actually breed there and which ones only visit carrion for adult feeding. Until now most carrion research focused on freely exposed vertebrate carcasses. This resource is mainly exploited by species of the family Calliphoridae (e.g., *Lucilia* and *Calliphora* spp.). Members of other dipteran families (e.g., Sphaeroceridae) are competitively inferior to the calliphorid larvae and normally emerge in very low numbers from this type of carrion (e.g., Fuller, 1934; Kneidel, 1984a,b). However, they play an important role in the decomposition of carrion inaccessible to blowflies (e.g., buried carrion, see Lundt, 1964; Payne et al., 1968; Nabagło, 1973) or unfavourable for blowflies (e.g., invertebrate carrion, see Kneidel, 1984a,b). Due to taxonomic problems, species composition and community structure of Sphaeroceridae has not been determined in these studies.

This paper presents part of the results of a more extensive study about saprophagous Diptera (with special reference to the fauna of buried and invertebrate carrion). The main subject of the paper is the emergence of Sphaeroceridae from various kinds of decaying substrates. Furthermore, some faunistically interesting species from simultaneous trapping experiments are included. The rearing data of other families (e.g., Phoridae) as well as specific ecological topics (e.g., niche partitioning within the carrion fly community) will be dealt with separately.

STUDY SITE

The experiments were conducted at four sites in the vicinity of Ulm (southern Germany). The sites were located near Senden Hittistetten, Dist. Neu-Ulm, Bavaria (48°20′N 10°07′E). Altitude: 490 m above sea-level.

(1) SF: A spruce forest, with a poor undergrowth of phanerogams. The forest floor was densely covered with mosses.

(2) DF: A humid deciduous forest of *Alnus glutinosa* (Betulaceae), *Fraxinus excelsior* (Oleaceae) and some *Prunus padus* (Rosaceae) lying alongside a stream. The herb layer was very well developed and rich in species. *Mercurialis perennis* (Euphorbiaceae) and *Phalaris arundinacea* (Poaceae) were the predominant plants.

(3) M: A seasonally wet meadow which was mown twice a year. Because of periodic fertilizing with liquid manure and artificial fertilizers, the plant community was dominated by nitrophilic herbs.

(4) F: An arable field planted with summer wheat in 1992 and rape in 1993. The management of the field was conventional, with the application of pesticides and fertilizers.

The four sites were situated close to each other (maximum distance 250 m).

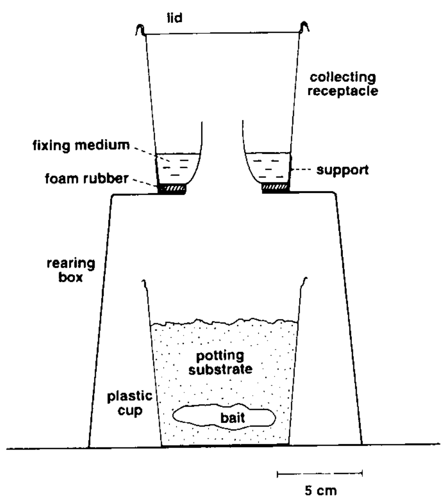

Fig. 1. Laboratory emergence trap. (Explanation: The rearing box consists of an inverted plastic flower pot in the bottom of which an aperture was cut. The collecting receptacle is a transparent polystyrene plastic cup whose bottom was invaginated by deep-drawing. The receptacle can be changed, and is held by a support. The support was cut from the same type of plastic cup. A solution of picric and nitric acid served as a fixing medium.)

MATERIALS AND METHODS

The data presented here were obtained from (1) rearing experiments with baits, (2) rearing experiments with decaying substrates collected in the field, and (3) trapping experiments with various trapping methods.

Rearing experiments with baits

During spring and summer of 1992–94 different types of baits were exposed in the field to allow colonization and oviposition by Diptera. The exposure period lasted 8 to 20 days (normally two weeks) and subsequently the baits were transferred to the laboratory. They were kept at room temperature (20–21°C) and the dipteran larvae in them were reared to the adult stage. To collect the emerging specimens, each bait was placed beneath a laboratory emergence trap (Fig. 1), which was of the photo-eclector type (for general information see Funke, 1971).

Table 1 gives an overview of the number of samples per bait, the mode of exposure, and the site where the experiments were conducted. Eight types of carrion served as baits: bovine liver, beef, snails (*Arianta arbustorum* and *Trichia striolata*, Helicidae; Clausiliidae gen. sp.), slugs (*Arion ater*, Arionidae), earthworms (*Lumbricus* sp., Lumbricidae) and crickets (*Acheta domesticus*, Gryllidae). For comparison some non-carrion substrates such as decaying fungi (*Agaricus bisporus*, Agaricaceae), rotten hay, thistle leaves (*Cirsium oleraceum*, Asteraceae) and steeped wheat grains (killed by freezing) were included in the experiments.

TABLE 1. Quantities, exposures and types of baits used in rearing experiments.

Type of bait	Exposure	N (samples)				Total (samples)
		SF	DF	M	F	
Liver (40 g)	freely exposed	–	23	–	–	23
Liver (40 g)	buried (2.5 or 5 cm)	5	40	10	–	55
Liver (15 g)	"	–	13	17	–	30
Liver (8 g)	"	–	12	–	–	12
Liver (5 g)	"	–	23	–	–	23
Beef (40 g)	"	–	–	–	4	4
Arion (15 g or 1 ind.)	"	5	33	16	–	54
Arion (5 g)	buried (2.5 cm)	–	12	–	–	12
Arianta (3 ind.)	"	–	6	–	–	6
Arianta (3 ind.)	freely exposed	5	16	10	–	31
Trichia (1 ind.)	"	–	15	–	–	15
Clausiliidae (1 ind.)	"	–	15	–	–	15
Lumbricus (1 ind.)	buried (1.5 cm)	–	15	15	–	30
Acheta (1 ind.)	freely exposed	–	15	15	–	30
Fungi (ca. 25 g)	"	5	5	5	–	15
Hay (10 g)	buried (1 cm)	–	7	7	–	14
Thistle leaves (20 g)	"	–	7	6	–	13
Wheat grains (30 g)	"	5	5	–	5	15
Total (samples)		25	262	101	9	397

Abbreviations: N – number of samples; sites: SF – spruce forest; DF – deciduous forest; M – meadow; F – arable field; ind. – individuals.

Baits were placed in plastic cups (diameter and height: 10 cm) which were sealed by a plastic screen (mesh size: 3.5 × 3.5 mm). The screen served to exclude larger carrion insects [mainly burying beetles of the genus *Nicrophorus* (Silphidae)] and vertebrate scavengers. The cups were filled with a commercially available potting substrate which served as pupariation substrate. The potting substrate consisted of sterilized peat with a small admixture of mineral soil. Simultaneous control experiments demonstrated clearly that the potting substrate alone did not sustain appreciable development of dipteran larvae (more than 139,700 dipterans were reared from baited potting substrate, but only a single specimen emerged from potting substrate alone). The majority of baits were buried in the substrate at a depth of 1 to 5 cm. A much smaller number was exposed freely on the surface of the substrate (some liver baits, most snails, crickets, decaying fungi). Very small baits (crickets and small snails) were exposed in small glass tubes (diameter: 3 cm).

Rearing experiments with substrates collected in the field

In 1993 larval and pupal tents of the ermine moth (*Yponomeuta* sp., Yponomeutidae) were collected from branches or trunk bases of their host plant (*Prunus padus*) at site DF. Due to food scarcity and a high rate of parasitism by Hymenoptera, a large number of dead and moribund individuals was present in each cluster. These were used as a breeding substrate by a high number of saprophagous dipteran species (including Sphaeroceridae).

By chance a small batch of vole excrement (from site M) and the decaying sporocarp of a lignicolous fungus (from another site near Senden, similar to DF) became available. They were also included in the rearing experiments. All samples were placed under laboratory emergence traps as in the bait experiments (see above).

Trapping

In addition to the rearing experiments, traps baited with decaying kidney (50 g), dead snails (*Helix pomatia*, Helicidae; 1 specimen) or fungi (*Agaricus bisporus*, 100 g) were operated at the four sites. The collecting period lasted from April 1993 to May 1994 (June until September in fungus traps). In this paper only some preliminary information will be provided (new records and remarks on some rare species). A more exhaustive presentation of the trapping results will be given in a subsequent publication.

From March 1992 until March 1993 emergence traps of the photo-eclector type (see Funke, 1971) were operated at the same sites. From this material only Phoridae have been determined. Nevertheless, some conspicuous sphaerocerid species have been extracted and are reported on below.

RESULTS

Rearing experiments

In Table 2 and 3 the results of the rearing experiments are presented for the woodland and open habitats. A total of 49,489 adult Sphaeroceridae representing 34.9% of the Diptera emerged from samples of both habitats. In different types of substrates the percentage of Sphaeroceridae ranged between 92% (excrement) and 0.2% (lignicolous fungus). In carrion the Sphaeroceridae were the most important family of Diptera in terms of individual numbers together with the Phoridae and Psychodidae. Altogether 28 species were reared: thirteen exclusively from substrates in the forest and six only from the open habitats. Nine species were present in baits from both habitat types. In the forest the highest number of species emerged from liver baits (18 spp.) and ermine moths (12 spp.). In open habitats the highest species numbers were reared from liver baits (12 spp.) and dead snails (6 spp.). Small snails (*Trichia*, Clausiliidae), earthworms, crickets and decaying herbaceous matter produced the poorest fauna (1–3 spp. per habitat type). In control experiments (blank baits with potting substrate alone) only one species (*Pullimosina moesta*, 1♂) emerged. However, it should be stressed that the sampling intensity was very different for the various types of substrates (e.g., 143 liver baits vs. one sample of rodent excrement). Without doubt, the number of recorded species per substrate is biased by the sampling intensity.

Not only the species number but also population density (adults reared per weight unit) was highest in the liver baits. In forest habitats slugs and fungi (*Agaricus*) showed, respectively, the second and third highest sphaerocerid densities. In open habitats this place was occupied by crickets and earthworms. The lowest densities were noticed in decaying plant material. The sphaerocerid density in dung could not be determined as the weight of the vole excrement sample is unknown. Considering the small size of the batch it appears to be very high.

Forest habitats (Table 2). The carrion breeding community of the forest habitats was dominated by four species, *Minilimosina parvula*, *Spelobia palmata*, *Telomerina flavipes* and *Spelobia luteilabris*. *Minilimosina parvula* was by far the most common species emerging from liver baits. In slug baits its number was not much higher than that of *Spelobia palmata*. The latter was the predominant species reared from snails (*Arianta*) and earthworms. The most important species bred from ermine moth larvae and cocoons were *Minilimosina parvula* and *Spelobia luteilabris*. *Telomerina flavipes* and *T. levifrons* were exclusively reared from liver, *Opalimosina liliputana* and *O. calcarifera* only from ermine moths. Slugs, snails (*Arianta*), earthworms and crickets had no exclusive species. *Crumomyia pedestris* emerged only from small snails (Clausiliidae) in the forest habitat.

TABLE 2. Number of sphaerocerid adults emerging from substrates exposed or collected at the woodland habitats.

	Specimens / substrate												Total	
Substrate	Liv	Slu	Sna	Ssn	Ewo	Cri	Erm*	Fng	LFn*	Hay	Thl	Wgr	Spm.	C.s.
Number of samples	116	50	27	30	15	15	6	10	1	7	7	10	294	≥ 207
Ischiolepta micropyga (Duda, 1938)	5	8	–	–	–	–	8	20	–	–	–	–	41	5
Crumomyia fimetaria (Meigen, 1830)	11	5	6	–	–	–	–	–	–	–	–	–	22	8
Crumomyia pedestris (Meigen, 1830)	–	–	–	2	–	–	–	–	–	–	–	–	2	≥ 1
Apteromyia claviventris (Strobl, 1909)+	109	240	77	–	–	–	1	54	–	–	–	3	484	29
Terrilimosina schmitzi (Duda, 1918)	1	–	–	–	–	–	–	–	–	–	–	–	1	1
Minilimosina splendens (Duda, 1928)	23	7	10	–	–	–	–	–	–	–	–	–	40	7
Minilimosina fungicola (Haliday, 1836)+	126	–	13	–	–	–	3	–	–	–	–	–	142	≥ 21
Minilimosina parvula (Stenhammar, 1855)+	24,506	2,011	185	–	–	–	65	760	–	–	–	–	27,527	≥ 132
Spelobia parapusio (Dahl, 1909)+	–	7	3	–	18	–	19	539	–	–	–	–	586	≥ 14
Spelobia palmata (Richards, 1927)+	3,233	1,770	274	2	198	–	2	111	–	–	–	23	5,613	≥ 177
Spelobia talparum (Richards, 1927)	2	–	–	–	–	–	–	–	–	–	–	–	2	1
Spelobia talis Roháček, 1983	1	–	–	–	–	–	–	–	–	–	–	–	1	1
Spelobia luteilabris (Rondani, 1880)+	767	156	42	–	–	–	58	–	–	–	–	–	1,023	≥ 81
Spelobia nana (Rondani, 1880)	4	–	–	–	–	–	–	–	–	–	–	–	4	4
Pullimosina pullula (Zetterstedt, 1847)	8	3	–	–	–	2	2	21	–	–	–	–	36	≥ 11
Pullimosina meijerei (Duda, 1918)	3	5	1	–	4	–	2	–	–	1	1	4	21	18
Pullimosina moesta (Villeneuve, 1918)	1	–	–	–	–	–	–	–	–	–	–	–	1	1
Telomerina levifrons (Spuler, 1925)	47	–	–	–	–	–	–	–	–	–	–	–	47	3
Telomerina flavipes (Meigen, 1830)	2,201	–	–	–	–	–	–	–	–	–	–	–	2,201	31
Telomerina eburnea Roháček, 1983+	139	–	–	–	–	–	15	–	–	–	–	–	154	14
Opalimosina liliputana (Rondani, 1880)	–	–	–	–	–	–	6	–	–	–	–	–	6	1
Opalimosina czernyi (Duda, 1918)	–	–	–	–	–	–	–	–	1	–	–	–	1	1
Opalimosina calcarifera (Roháček, 1975)	–	–	–	–	–	–	4	–	–	–	–	–	4	1
Total (individuals)	31,187	4,212	611	4	220	2	185	1,505	1	1	1	30	37,959	
% of total Diptera	44.9	17.1	28.6	6.6	68.1	4.3	18.0	22.6	0.2	33.3	33.3	17.0		
Specimens per sample	269	84.2	22.6	0.1	14.7	0.1	30.8	151	1.0	0.1	0.1	3.0		
Specimens per 10 g	99.8	67.9	34.7	8.6	35.8	3.9	n.d.	59.9	n.d.	0.1	0.1	1.0		
Total (species)	18	10	9	2	3	1	12	6	1	1	1	3	23	

Note: With exception of *O. czernyi* all species were present in samples from site DF. Species which also occurred in samples from site SF are marked with +. Abbreviations: Liv – liver; Slu – slugs (*Arion*); Sna – snails (*Arianta*); Ssn – small snails (*Trichia* and Clausiliidae); Ewo – earthworms (*Lumbricus*); Cri – crickets (*Acheta*); Erm – larval/pupal tents of ermine moths (*Yponomeuta*); Fng – fungi (*Agaricus*); LFn – lignicolous fungus; Hay – hay; Thl – thistle leaves (*Cirsium*); Wgr – wheat grains (*Triticum*); * – samples collected in the field; Spm. – specimens; C.s. – number of successfully colonized samples (samples of small snails, crickets and ermine moths were pooled); individuals per 10 g: refers to weight without shell in snails, n.d. – not determined.

TABLE 3. Number of sphaerocerid adults emerging from substrates exposed or collected at the open habitats.

	Specimens / substrate											Total	
Substrate	Liv	Bf	Slu	Sna	Ewo	Cri	Fng	Hay	Thl	Wgr	Exc*	Spm.	C.s.
Number of samples	27	4	16	10	15	15	5	7	6	5	1	111	≥ 77
Crumomyia pedestris (Meigen, 1830)	2	–	–	29	8	–	–	–	–	–	–	39	9
Copromyza stercoraria (Meigen, 1830)	–	–	–	–	–	–	–	–	–	–	61	61	1
Leptocera caenosa (Rondani, 1880)	33	–	–	–	–	–	–	–	–	–	–	33	2
Leptocera nigra Olivier, 1813	3	–	–	–	–	–	–	–	–	1	–	4	3
Herniosina bequaerti (Villeneuve, 1917)	–	–	–	–	–	–	1[1)]	–	–	–	–	1	1
Minilimosina fungicola (Haliday, 1836)	10	–	–	–	–	–	–	–	–	–	–	10	1
Minilimosina parvula (Stenhammar, 1855)	627	–	–	10	–	–	–	–	–	–	–	637	14
Spelobia palmata (Richards, 1927)	113	–	–	3	–	–	–	–	–	–	–	116	4
Spelobia czizeki (Duda, 1918)	–	–	–	–	–	–	–	–	–	–	4	4	1
Spelobia talparum (Richards, 1927)	6	–	–	–	–	–	–	–	–	–	–	6	1
Spelobia luteilabris (Rondani, 1880)	1,744	11	566	152	157	37	44	–	–	–	29	2,740	≥ 60
Spelobia nana (Rondani, 1880)	277	7	542	165	355	18	238	–	–	–	–	1,602	≥ 61
Pullimosina pullula (Zetterstedt, 1847)	1	–	1	–	–	4	149	5	2	2	32	196	≥ 13
Telomerina flavipes (Meigen, 1830)	37	218	–	–	–	–	–	–	–	–	–	255	4
Telomerina eburnea Roháček, 1983	5,560	201	–	65	–	–	–	–	–	–	–	5,826	17
Total (individuals)	8,413	437	1,109	424	520	59	432	5	2	3	126	11,530	
% of total Diptera	34.6	ca. 10	25.4	35.8	61.5	26.6	28.6	3.5	66.7	0.8	92.0		
Specimens per sample	312	109	69.3	42.4	34.7	3.9	86.4	0.7	0.3	0.6	126		
Specimens per 10 g	128	27.3	49.1	74.8	84.8	115	34.4	0.7	0.2	0.2	n.d.		
Total (species)	12	4	3	6	3	3	4	1	1	2	4	15	

Note: Samples of beef and wheat grains were exposed in the arable field, all other samples were exposed in the meadow. Abbreviations: see legend of Table 2; Bf – beef; Exc – rodent excrement (probably *Microtus*); [1)] – it is not certain whether the specimen actually emerged from the bait or was only attracted to it.

Opalimosina czernyi was the only species restricted to fungi. *Minilimosina parvula*, the most common species of liver baits, also predominated in the fungus (*Agaricus*) baits. *Spelobia parapusio*, the second most frequent species in fungi, was also reared from invertebrate carrion but was absent from the liver baits. *S. parapusio*, *Ischiolepta micropyga* and *Pullimosina pullula* mainly emerged from fungi. From decaying vegetable matter only three species were reared. Very few specimens of *Pullimosina pullula* were obtained from hay and thistle leaves. In wheat grains *Spelobia palmata* yielded the highest emergence. Obviously the adopted method was not very efficient for rearing phytosaprophagous species.

OPEN HABITATS (Table 3). The substrates exposed in open habitats were colonized by fewer species than those of the forest. The predominant carrion breeders of the meadow were *Telomerina eburnea*, *Spelobia luteilabris*, *S. nana* and *Minilimosina parvula*. The latter was much more common in the forest, whereas the other species apparently preferred the open habitats. In liver baits of the meadow *Telomerina eburnea* was the most frequent species. The individuals of this species were very unevenly distributed among the samples: three baits alone yielded 91.5% of the total emergence. The sphaerocerid community of beef baits (exposed in the arable field) differed from other baits by the high proportion of *T. flavipes*, which was even more common there than *T. eburnea*. Both *Telomerina* species emerged almost exclusively from vertebrate carrion. The community of invertebrate carrion was dominated by *Spelobia nana* and *S. luteilabris*. Both species were bred in approximately equal numbers from slug and snail carrion. In earthworm carrion *S. luteilabris* was clearly outnumbered by *S. nana*. As in the forest, slug, snail, earthworm and cricket carrion had no exclusive species. In contrast with *S. luteilabris*, *S. nana* and *Crumomyia pedestris* were better represented in invertebrate than in vertebrate carrion. The sphaerocerid community of fungi was very similar to that of invertebrate carrion, with exception of the high incidence of *Pullimosina pullula*. The latter was the second most common species in fungi after *Spelobia nana* but was quite rare in carrion. Only two species bred successfully in decaying plant material, viz. *Pullimosina pullula* and *Leptocera nigra*. The community of vole excrement was characterized by two exclusive species, *Copromyza stercoraria* and *Spelobia czizeki*. *C. stercoraria* was the predominant species in this sort of substrate and ranked before *Pullimosina pullula* and *Spelobia luteilabris*.

SEX RATIO OF REARED SPECIMENS. Only in four species a significant departure from the balanced sex ratio (50% ♂) was observed. These were *Telomerina eburnea* (51.4% ♂, $p < 0.05$, χ^2-test), *Minilimosina parvula* (51.2% ♂, $p < 0.01$), *Pullimosina pullula* (3.4% ♂, $p < 0.01$) and *Spelobia parapusio* (0% ♂, $p < 0.01$). In carrion traps the percentage of males of the normally parthenogenetic *Pullimosina pullula* was even higher (19.0% ♂ out of 200 collected individuals).

DEVELOPMENT TIMES. Notable differences in the development times of the reared species were observed. *Spelobia parapusio* was the species with the quickest development. Its emergence started already during the second week after baits were exposed. Adults of *Crumomyia pedestris*, *Pullimosina meijerei* and *Spelobia* spp. (excl. *S. parapusio*) began to emerge during the third week. The majority of species emerged from the fourth week onward. The longest development times were observed in the species of *Minilimosina* (subgenus *Minilimosina*) and *Telomerina* which did not emerge before the fifth week (sixth week in *T. levifrons*).

Species which only visited the baits. The following species visited the baits as adults but did not develop in them (Liv – liver, Fng – fungi, habitat abbreviations as in section Study site):

Sphaerocera monilis Haliday, 1836. – Fng: 1♀ (M).
Minilimosina bicuspis Roháček, 1993. – Fng: 3♂ (SF).
Opalimosina liliputana (Rondani, 1880). – Liv: 3 ♂, 2♀ (DF); Fng: 3♂, 2♀ (SF).
Opalimosina mirabilis (Collin, 1902). – Liv: 1♀ (DF); Fng: 1♀ (SF).
Opalimosina calcarifera (Roháček, 1975). – Liv: 1♀ (DF).
Trachyopella kuntzei (Duda, 1918). – Liv: 1♂, 2♀ (DF); Fng: 1♀ (SF), 6♂, 4♀ (M).
Trachyopella lineafrons (Spuler, 1925). – Liv: 5♂, 7♀ (DF).
Coproica hirticula Collin, 1956. – Fng: 1♀ (SF).

The above specimens were captured in laboratory emergence traps when baits were returned to laboratory. They could easily be distinguished by their coloration from the teneral flies which were reared from the same sample.

Remarkable species from the trapping experiments

The following noteworthy species have been collected in traps baited with kidney (KT), dead snails (ST) and fungi (FT), or in emergence traps set on soil (ET):

Leptocera oldenbergi (Duda, 1918). – ST: 2♂ (21.–28.iv.94), 1♀ (10.–17.iii.94) (DF).
Terrilimosina racovitzai (Bezzi, 1911). – KT: 1♀ (26.viii.–9.ix.93) (SF).
Minilimosina bicuspis Roháček, 1993. – KT: 1♂ (22.–29.vii.93) (SF).
Minilimosina gemella Roháček, 1983. – KT: 1♀ (19.–26.viii.93) (DF).
Spelobia manicata (Richards, 1927). – KT: 3♂, 2♀ (DF, M); ST: 3♂, FT: 1♀ (DF); (collected in v–vi, viii–ix.93, ii–iv.94).
Spelobia talis Roháček, 1983. – ET: 1♂, 1♀ (2.–16.ix.92), 1♂ (30.ix.–14.x.92) (M).
Spelobia pseudonivalis (Dahl, 1909). – KT: 1♀ (26.viii.–9.ix.93) (DF).
Telomerina levifrons (Spuler, 1925). – KT: 1♂, 4♀ (1.vii.–19.viii.93), 1♂ (27.v.–3.vi.94) (DF).
Opalimosina calcarifera (Roháček, 1975). – KT: 1♀ (22.–29.vii.93) (DF).
Opalimosina simplex (Richards, 1929). – KT: 1♀ (29.vii.–5.viii.93) (DF).
Opalimosina collini (Richards, 1929). – KT: 2♂ (1.–8.vii.93) (DF, M), 1♂ (12.–19.viii.93) (F).
Elachisoma sp. n. – KT: 1♂ (4.–11.vi.93) (SF).
Thoracochaeta zosterae (Haliday, 1833). – KT: 1♂ (24.–28.v.93) (SF), 1♂ (8.–15.vii.93) (M), 3♂, 2♀ (4.–17.vi.93, 1.–22.vii.93) (F).

DISCUSSION

New rearing records

In Table 4 the present knowledge (literature data) of the biology of the reared species has been summarized. In the present study new breeding substrates are reported for many species. These are listed below:

TABLE 4. Literature data of the reared sphaerocerid species: known breeding substrates and substrates visited by adult flies.

Species	Substrate							References
	VC	MC	IC	Fng	Veg	DL	DS	
Ischiolepta micropyga	○	–	–	–	○	○	–	R84 Hn/Ki90 Fl89
Crumomyia fimetaria	○	●	–	●●	●	○	○	R91 J85 Pa79 Fl89 O74 Pi86
Crumomyia pedestris	●[1]	●●	–	–	●[1]	○	–	R91 G39 D/Kn66 Pi88
Copromyza stercoraria	○	–	–	–	●	●	●●	R89 Hc67 Pi86 S78
Leptocera caenosa	○	○	–	–	○	●	–	R82 Pi86 Fl89 Kü86 Pa92
Leptocera nigra	●	–	–	–	○	●	–	R82 Fr92 Fl89 S78
Apteromyia claviventris	●	●	●	●	●	○	●	R83 J85 Hc63 Pa79 O74 Pi86
Herniosina bequaerti	●	–	–	●[2]	●	○	–	R83, 94 Pa/Pl76
Terrilimosina schmitzi	–	–	–	●	○	○	–	R83 Pa79 Fl89
Minilimosina splendens	○	–	–	○	○	○	–	R83 R/M88 C90 Fl89
Minilimosina fungicola	○	–	–	●	●●	○	–	R83 C90 Pi86 Fl89
Minilimosina parvula	○○	–	–	○	○	○	–	R83 M85 Pi86 Fl89
Spelobia parapusio	○	–	–	●●	○	○	○	R83 C90 Pi86 Fl89
Spelobia palmata	●●	●●	–	○	●	●	○	R83 Hc63 D/Kn66 Fl89 Pa92 Pi86
Spelobia czizeki	–	–	–	●	–	–	–	R83 Pa79
Spelobia talparum	●	–	–	○	●	●	●	R83 Fr92 Hc63, 67
Spelobia talis	–	–	–	–	–	–	–	R83
Spelobia luteilabris	●	●	–	●	●	●	●	R83 Bl/Bl90 Be72 C90 O74 Pa92
Spelobia nana	○	●	●	○	●	○	–	R83, 94 D/Kn66 Fl89 Hc67 Pi86
Pullimosina pullula	○	●	–	○	●●	●	●	R83 Ba77 J85 M/Br84 Pr92 Hc63
Pullimosina meijerei	–	●	–	–	○	–	–	R83 J85 Fl89
Pullimosina moesta	○	–	–	○	●●	●	–	R83 Kü78 Hc63 O74 Fl89 S78
Telomerina levifrons	○	–	–	○	○	○	–	R83, 94 Fl89
Telomerina flavipes	●●	●	–	●	○	●	●	R83 J85 C90 Fl89 Pa92 Pr92
Telomerina eburnea	○	–	–	–	○	–	–	R83 Fl89
Opalimosina liliputana	○	–	–	○	●	○	–	R83 C90 Pi86 O74 Fl89
Opalimosina czernyi	○	–	–	○○	○	○	–	R83, 94 C90 Pi86
Opalimosina calcarifera	–	–	–	–	○	●	–	R83 Pa92

Abbreviations: Substrates: VC – vertebrate carrion; MC – mollusc carrion; IC – insect carrion; Fng – fungal sporophores; Veg – decayed vegetation; DL – dung of large mammals (cows, horses, sheep, etc.); DS – dung of small mammals (rabbits, mice, voles, etc.); ● – breeding substrate; ●● – preferred breeding substrate; ○ – substrate visited by adults; ○○ – preferred substrate visited by adults; [1] – laboratory rearing; [2] – reared from fungal mycelia. Authors: Ba – Baumann; Be – Beaver; Bl/Bl – Blackith & Blackith; Br – Brown; C – Chandler; D/Kn – Deeming & Knutson; Fl – Florén; Fr – Froese; G – Guibé; Hc – Hackman; Hn/Ki – Han & Kim; J – Joswig; Kü – Kühlhorn; M – Marshall; O – Okely; Pa – Papp; Pi – Pitkin; Pl – Plachter; Pr – Prescher; R – Roháček; S – Skidmore.

FIRST REARING RECORD: *Ischiolepta micropyga, Minilimosina splendens, M. parvula, Spelobia talis, Telomerina levifrons, T. eburnea, Opalimosina czernyi* (a total of 7 out of 28 species).

NEW REARING RECORDS FROM VERTEBRATE CARRION: *Ischiolepta micropyga, Crumomyia fimetaria, Leptocera caenosa, Terrilimosina schmitzi, Minilimosina splendens, M. fungicola, M. parvula, Spelobia talis, S. nana, Pullimosina pullula, P. meijerei,* (*P. moesta*) (this species also emerged from a blank bait and is obviously not related to carrion), *Telomerina levifrons, T. eburnea* (a total of 13 out of 21 species).

NEW REARING RECORDS FROM MOLLUSC CARRION: *Ischiolepta micropyga, Minilimosina splendens, M. fungicola, M. parvula* (the rearing record of "*Limosina exigua*" in Joswig, 1985 probably refers to this species or to *M. fungicola*), *Spelobia parapusio, Telomerina eburnea* (a total of 6 out of 14 species).

NEW REARING RECORDS FROM ANNELID CARRION: *Crumomyia pedestris*, *Spelobia parapusio*, *S. palmata*, *S. luteilabris*, *S. nana*, *Pullimosina meijerei* (a total of 6 out of 6 species). The sphaerocerid fauna of dead earthworms had not been studied before.

NEW REARING RECORDS FROM INSECT CARRION: *Minilimosina fungicola*, *M. parvula*, *Spelobia parapusio*, *S. palmata*, *S. luteilabris*, *Pullimosina pullula*, *P. meijerei*, *Telomerina eburnea*, *Opalimosina liliputana*, *O. calcarifera* (a total of 11 out of 13 species).

NEW REARING RECORDS FROM FUNGI: *Ischiolepta micropyga*, *Minilimosina parvula* (some former rearing records of *M. fungicola* may actually refer to this species, see Roháček, 1983), *Spelobia palmata*, *S. nana*, *Pullimosina pullula*, *Opalimosina czernyi* (a total of 6 out of 10 species).

NEW REARING RECORDS FROM DECAYING PLANT MATTER: *Leptocera nigra*, *Pullimosina meijerei* (a total of 2 out of 5 species).

NEW REARING RECORD FROM EXCREMENT: *Spelobia czizeki* (a total of 1 out of 4 species).

Biology of the reared species

The most remarkable result of this study is the great number of species reared from carrion. Up to the present twenty-one European sphaerocerid species have been reported to breed in decaying animal matter. For eleven of them the carrion-breeding habits have been confirmed by their rearing. Ten species which were found to breed in carrion by previous workers have not been reared during the present study: *Ischiolepta vaporariorum* (snail carrion in laboratory: Beaver, 1972), *Herniosina bequaerti*, *Terrilimosina racovitzai* (vertebrate carrion: Papp & Plachter, 1976), *Minilimosina v-atrum* (snail carrion: Joswig, 1985), *Spelobia clunipes* (egg mass of *Succinea* snails: Deeming & Knutson, 1966), *Phthitia empirica* (vertebrate carrion: e.g., Blackith & Blackith, 1990), *Leptocera fontinalis* (snail carrion: e.g., Joswig, 1985), *Thoracochaeta brachystoma* (human corpse: Leclercq & Vaillant, 1992), *Coproica hirtula* (e.g., snail carrion: Beaver, 1987) and *C. vagans* (dead horseshoe crabs: Norrbom, 1983). In the present author's experiments, thirteen further species are reported, thus increasing the number of European carrion-breeding Sphaeroceridae to thirty-four. However, it is obvious that the majority of species only develop in carrion occasionally and that the number of primarily necrophagous species is quite restricted. Without doubt *Minilimosina parvula*, *Telomerina eburnea*, *T. flavipes*, *Spelobia palmata*, *S. nana* and *Crumomyia pedestris* belong to the latter group. It is curious that the two most important species of this investigation, *Minilimosina parvula* and *Telomerina eburnea*, have never been reared from carrion before. *Minilimosina parvula* was formerly classified as a mycetophagous species because it was often collected on decayed fungi "but much more rarely (five times) on carrion" (Roháček, 1983). Marshall (1985) was the first who noticed that *M. parvula* is strongly attracted to carrion and suggested that it "is a primarily necrophagous species". Although *M. parvula* was found to be a constant element of the fungus breeding community (Table 2), carrion is apparently the more important breeding substrate. *Telomerina eburnea*, the most common carrion breeder of the open habitats (Table 3) was only described in 1983 and its biology was unknown. Based on its close relationship to the necrophagous *T. flavipes* and collecting data from carrion, Roháček (1983) predicted its carrion-breeding habits. Among the predominantly necrophagous species, *Minilimosina parvula*, *Telomerina eburnea* and *T. flavipes* obviously prefer vertebrate carrion, while *Spelobia nana* and *Crumomyia pedestris* appeared to prefer invertebrate carrion (Tables 2–3). Already Roháček (1991) assumed that mollusc carrion is the preferred larval diet of *C. pedestris* under natural conditions. This species was quite infrequent in my rearing experiments. Phenological data from the trapping programme showed that *C. pedestris* was much more common during the winter months (December until March) which might have been the cause of its scarcity during the rearing experiments. *Spelobia palmata* shows a marked tendency towards polysaprophagy (rearing records from dung, decaying vegetable matter and fungi, cf. Papp, 1992; Roháček, 1983; and Table 2). Because of its predilection for carrion it is here treated with the necrophagous species. Little is known about the biology of *Minilimosina splendens* and *Telomerina levifrons*. Both species were occasionally reared from carrion during this study. In contrast, they have been rarely collected in my carrion traps and it is uncertain whether this is their optimum breeding substrate.

True polysaprophagous species are *Apteromyia claviventris*, *Spelobia luteilabris* and probably *Herniosina bequaerti*. These species breed indiscriminately in the most diverse kinds of decaying substrates (Roháček, 1983). Carrion appears to be a relatively important feeding substrate for *Spelobia luteilabris* and *Apteromyia claviventris*.

Two species, viz. *Spelobia parapusio* and *Opalimosina czernyi* must be regarded as predominantly mycetophagous. Although there is no previous rearing record of the latter, collecting data clearly suggest that fungi are the preferred larval substrate (Roháček, 1983; Chandler, 1990). *Spelobia parapusio*, a species which was believed to breed exclusively in fungi, was reared for the first time from non-fungal matter. As was pointed out in an earlier paper (Buck, 1994), the breeding in invertebrate carrion probably enables *S. parapusio* to reproduce in times when fungal sporophores are scarce or absent. Invertebrate carrion is also exploited by other typically mycetophagous species such as *Drosophila kuntzei* (Drosophilidae) (rearing record from dead snails: Joswig, 1985, and present study) and *Megaselia nigra* (Phoridae) (rearing record from dead snail: Disney, 1994). The absence of fungal sporophores and the increasing availability of snail carrion during drought periods might favour the selection of the less preferred breeding substrate (carrion) (Disney, 1994). From the above presented rearing data it could be inferred that *Spelobia nana* and *Pullimosina pullula* are regular fungus-breeders, too. Both species, however, clearly prefer open habitats and will, therefore, encounter fungal sporophores rarely under natural conditions. *Ischiolepta micropyga* and *Crumomyia fimetaria* are included tentatively in the group of primarily mycetophagous species (Table 2; Papp, 1979; Roháček, 1991). Further research is necessary to define the food preferences of these species.

The majority of species is supposed to be primarily phytosaprophagous as larva, viz. *Terrilimosina schmitzi*, *Minilimosina fungicola*, *Pullimosina* spp. and *Opalimosina liliputana* (Roháček, 1983). Rearing records of these species from carrion (Tables 2–3; Joswig, 1985) and fungi (*T. schmitzi*: Papp, 1979) must be regarded as occasional and atypical. Only *Minilimosina fungicola* seems to develop somewhat more regularly in carrion (Table 2). The absence of this species from my fungus baits combined with the frequent occurrence of *M. parvula* (Table 2) strengthen the suspicion of Roháček (1983) that earlier fungus rearing records of *M. fungicola* (e.g., Papp, 1979) are probably based on misidentified material of *M. parvula*. *Spelobia talparum* and *S. czizeki* seem to be intermediate as regards their way of life (see Hackman, 1963, for the former). Both were reared in approximately equal numbers from decaying vegetable matter and rodent dung (Franzen et al., 1997). Presumably, these will also be the preferred breeding substrates of the closely related *S. talis*. The carrion rearing records of *S. talis* (Table 2) and *S. talparum* (Tables 2–3;

Froese, 1992) and the fungus rearing record of *S. czizeki* (see Papp, 1979) are probably accidental.

The only typical coprophages which occurred during this study are *Copromyza stercoraria* and *Leptocera caenosa*. *Copromyza stercoraria* shows a distinct preference for the dung of small mammals and often inhabits their burrows (e.g., Hackman, 1967; Roháček, 1989). Apart from excrement, it also breeds in decaying herbaceous matter (e.g., nests and runway litter of voles: Hackman, 1967). *Leptocera caenosa* is mainly a synanthropic species developing in manure, dung, etc. (Roháček, 1982; Papp, 1992). Hackman (1963) classified it as a zoosaprophagous species without referring to rearing data. *Opalimosina calcarifera* was listed by Papp (1992) among the Hungarian species developing in pasture dung. However, it is not clear if this is the typical breeding substrate. The significance of carrion breeding in *O. calcarifera* and *Leptocera caenosa* (Tables 2–3) is probably low but merits further research.

The larvae of *Leptocera nigra* normally develop in mud and soil with a high proportion of organic matter (Roháček, 1982). The rearing records from carrion (Table 3; Froese, 1992) and dung (Skidmore, 1978) are probably accidental.

Faunistic notes on rarely collected species

Several species collected or reared during this study are of faunistic interest. *Minilimosina gemella*, *Spelobia manicata*, *Telomerina eburnea*, *Opalimosina calcarifera* and *Elachisoma* sp. n. are reported for the first time from Germany. *Minilimosina gemella* was considered as a boreo-alpine species restricted to mountains in Central Europe (Roháček, 1993). Its occurrence at the study site and a further lowland locality in northern Germany (Franzen et al., 1996) clearly demonstrates that it is not confined to montane regions. *Minilimosina bicuspis*, *Spelobia talis*, *Telomerina levifrons* and *Opalimosina collini* have only recently been discovered in Germany (Buck, 1994; Grundmann, 1991; Roháček et al., 1991). *Telomerina levifrons* is believed to be a typical species of *Sphagnum*-bogs in Europe (Marshall & Roháček, 1984). Based on its occurrence in the deciduous forest (site DF) it must be concluded that it also inhabits other damp habitats. For *Opalimosina simplex* only one general record from Germany has been published (Papp, 1984, locality not given). *Leptocera oldenbergi* is very rarely collected and has only been reported in a few instances from Germany (e.g., Kühlhorn, 1986; Roháček et al., 1991). The presence of *Thoracochaeta zosterae* in southern Germany is remarkable because it is mainly a coastal species. There is only one German inland record of this species (Grundmann, 1991). *Terrilimosina racovitzai* is troglophilous and lives in the aphotic interior part of caves (Papp & Plachter, 1976) and rarely in mine-galleries, cellars and mole nests (Roháček, 1983). Almost all previous German records were from caves. *Spelobia pseudonivalis* seems to be a eucoenic species of the burrows of small mammals (Hackman, 1967; Baumann, 1977). Very few German specimens have been collected outside this habitat (e.g., Grundmann, 1991; Feldmann, 1992; Buck, 1994).

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