

## Wing polymorphism in European species of Sphaeroceridae (Diptera)

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**Abstract.** The wing polymorphism is described in 8 European species of Sphaeroceridae (Diptera), viz. *Crumomyia pedestris* (Meigen, 1830), *Phthitia spinosa* (Collin, 1930), *Pteremis fenestralis* (Fallén, 1820), *Pullimosina mejerei* (Duda, 1918), *Puncticorpus cribratum* (Villeneuve, 1918), *Spelobia manicata* (Richards, 1927), *Spelobia pseudonivalis* (Dahl, 1909) and *Terrilimosina corivalis* (Villeneuve, 1918). These cases seem to belong to three types of alary polymorphism: i) species with separate macropterous and brachypterous forms – *Crumomyia pedestris*, *Pteremis fenestralis*, *Pullimosina mejerei*; ii) species with a continual series of wing forms ranging from brachypterous to macropterous – *Puncticorpus cribratum*, *Spelobia pseudonivalis*, *Terrilimosina corivalis*; iii) similar to the foregoing type but with only slightly reduced wing in the brachypterous form – *Phthitia spinosa*, *Spelobia manicata*. The variability of venation of wing polymorphic and brachypterous species of the West-Palaeartic species of Sphaeroceridae was examined and general trends in the reduction of veins during evolution are defined. These trends are found to be different in Copromyzinae (*C. pedestris*) and Limosiniinae (all other species) where 6 successive stages of reduction are recognized. The first case of a specimen (of *Pullimosina mejerei*) with unevenly developed wings (one normal, other reduced) is described in Sphaeroceridae. Causes of the origin of wing polymorphism, variability of wing polymorphic populations depending on geographical and climatic factors, importance of wing polymorphism in the evolution of brachypterous and apterous species and the probable genetic background of wing polymorphism in European species are discussed. *Pullimosina (Pullimosina) mejerei* is recorded for the first time from the Svalbard Islands (Norway) and *Terrilimosina corivalis* is newly recorded from Romania.

**Key words.** Diptera, Sphaeroceridae, wing polymorphism, evolution, wing venation, variability, Europe, Palaeartic Region

## Introduction

The recent discovery of a peculiar specimen of *Pullimosina mejerei* (Duda, 1918) with unevenly developed wings (one normal, the other shortened) initiated a return to my studies on wing polymorphic species of Sphaeroceridae performed in the 1990's. Results of this research have not been published except for an oral presentation at the Third International Congress of Dipterology held at the University of Guelph (Canada) in August 1994 (for abstract see ROHÁČEK 1994a). Therefore, they are presented in full here including additional information obtained subsequently in 1995–2012.

The polymorphism of wings occurring in both sexes (i.e. sexually independent) has long been considered a phenomenon rare in natural populations, not only of Sphaeroceridae but also of the Diptera as a whole (HACKMAN 1964). Within the European Diptera it has only been known in the families Anthomyzidae, Chloropidae and Sphaeroceridae. While only one wing polymorphic species, *Stiphrosoma sabulosum* (Haliday, 1837), was recorded in Anthomyzidae (for detail see ROHÁČEK 1996b, 2006; ROHÁČEK & BARBER 2005), in Chloropidae this type of alary polymorphism was noted by NARTSHUK (1987) in four species, viz. *Siphonellopsis lacteibasis* Strobl, 1906, *Elachiptera brevipennis* (Meigen, 1830), *Lasiosina parvipennis* Duda, 1933 and *Conioscinella zetterstedti* Andersson, 1966. However, only the latter case was studied in more detail (BRAUNS 1938, as *C. brachyptera* Zett.; WHEELER 1994).

Not more than two cases were known among European sphaerocerids up to the seventies, viz. *Pteremis fenestralis* (Fallén, 1820) and *Crumomyia pedestris* (Meigen, 1830), see ROHÁČEK (1975b). However, more extensive investigations on terricolous species of the family since 1980 resulted in finding that almost all continental European species that were originally considered brachypterous, are in fact wing polymorphic.

Because of the apparent evolutionary significance (as shown below) all these cases are dealt with here, with special regards to habitat selection of particular species and forms, to variability of wing venation of brachypterous forms and to changes of the structure of wing polymorphic populations in various geographical and climatic conditions. Wing polymorphism is here considered a transient stage preceding pure brachyptery. Therefore I should like to discuss the causality of its origin, its dependence on abiotic factors and ecological significance and its probable genetic basis.

## Material and methods

The material examined is given under each species with numbers of specimens studied, references to literature where the relevant localities were listed and a list of additional (hitherto unpublished) localities. New or interesting records of infrequent species are treated with full data. The majority of specimens examined are deposited in the Silesian Museum, Opava (Czech Republic), unless mentioned otherwise.

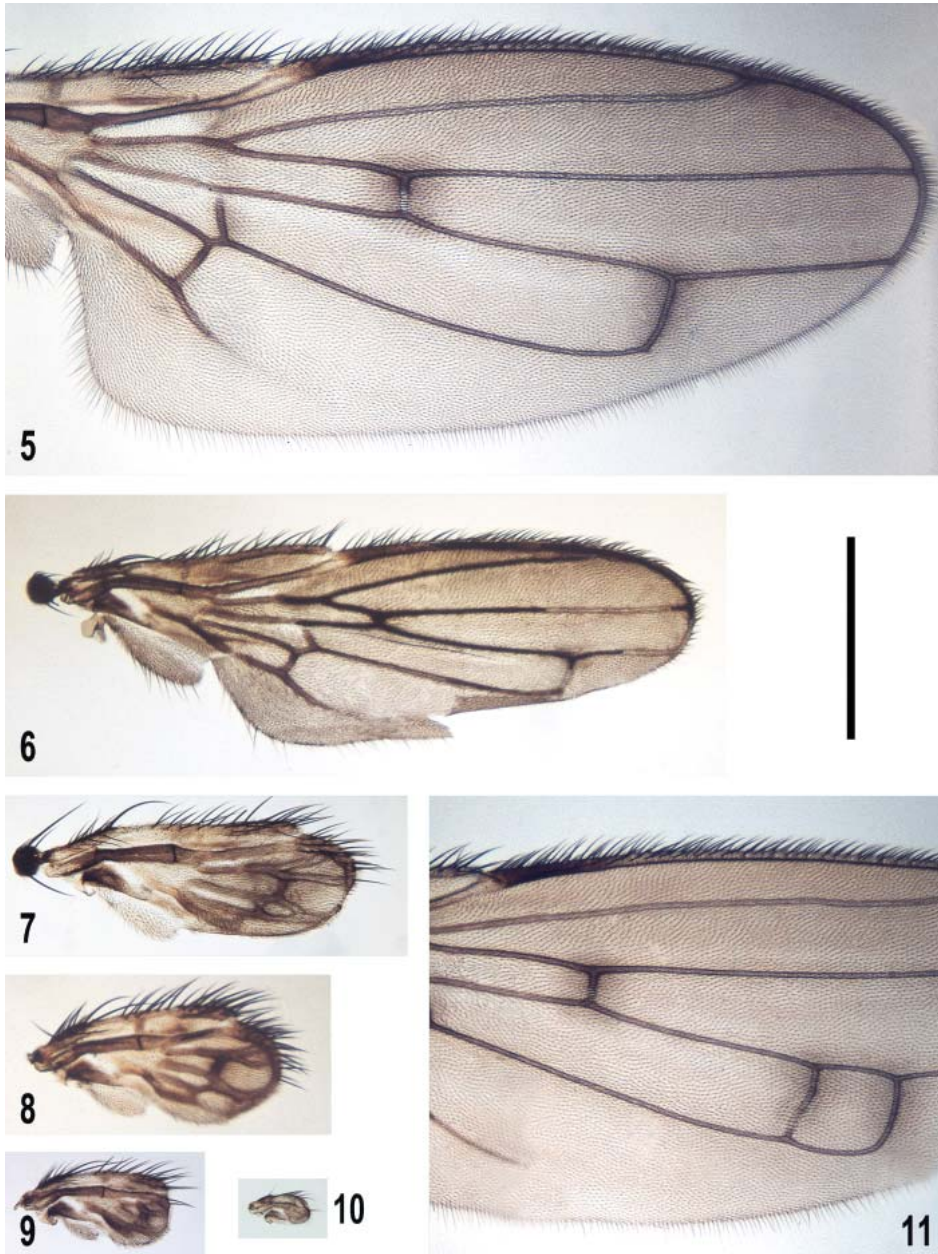
Wings were photographed on a compound microscope Jenaval with attached cameras (both classical and digital), using permanent or temporary microscopic slides. Macrophotographs of living specimens were taken by means of a Canon EOS 60D with macro lens (Canon MP-E 65 mm 1–5×) and ring macro flash (Canon MR-14ex). A dry mounted specimen of *Pullimosina mejerei* was photographed by means of a digital camera (UI-1485-LE-C CAMERA CMOS



Figs. 1–4. Wing polymorphic Sphaeroceridae. 1 – *Crumomyia pedestris* (Meigen, 1830), brachypterous male, body length 3.4 mm (Czech Republic: Úvalenské louky res. nr. Krnov); 2 – *Pteremis fenestralis* (Fallén, 1820), brachypterous male, body length 1.5 mm (Czech Republic: Jizerské hory Mts.– Jizerka); 3–4 – *Pullimosina* (*Pullimosina*) *mejerei* (Duda, 1918): 3 – macropterous female, body length 1.6 mm (Slovakia: Muránska planina Mts. – Šarkanica res.); 4 – male with ambiguous wings, body length 1.45 mm (Slovakia: Muránska planina Mts. – Bobačka cave env.). Photos by J. Roháček.

5Mpxl) on a trinocular stereomicroscope Olympus SZX16 using PROMICRA software QuickPHOTO CAMERA 2.3 with Deep Focus 3.1.

Terminology of the degree of wing reduction proposed by HACKMAN (1964) for Diptera is followed: *brachypterous* = wing reduced, shorter than abdomen, broad and more or less blunt, not permitting flight, with at least radial veins distinct; *stenopterous* = wing very narrow but sometimes long, not permitting flight, with at least radial veins distinct; *micropterous* = wing



Figs. 5–11. *Crumomyia pedestris* (Meigen, 1830), wings. 5 – macropterous female; 6 – submacropterous female (both Slovakia: Tatranská Kotlina – Šarpanec); 7 – large brachypterous female; 8 – medium brachypterous female; 9 – strongly brachypterous female; 10 – almost micropterous male (all Czech Republic: Úvalenské louky res. nr. Krnov); 11 – macropterous male with additional dm-cu cross-vein (Slovakia: Tatranská Kotlina – Šarpanec). Scale: 0.5 mm. Photo by J. Roháček.



reduced to small appendage of varying shape with at most traces of the radial vein; *apterous* = wing at most represented by minute scale, at most carrying some setae or totally absent. The following term is added: *submacropterous* = wing similarly shaped (including venation) as in normal macropterous specimens but distinctly shorter, darker, about as long as abdomen.

Wing venation terminology:  $A_1$  – anal vein; bm – basal medial cell;  $Cs_1$ ,  $Cs_2$ ,  $Cs_3$  – 1st, 2nd, 3rd costal sector;  $CuA_1$  – cubital vein; cup – posterior cubital cell (= basal cubital, anal cell); dm – discal medial cell; dm-cu – discal medial-cubital (= posterior,  $t_p$ ) cross-vein; M – medial vein;  $R_1$ ,  $R_{2+3}$ ,  $R_{4+5}$  – 1st, 2nd, 3rd branch of radial vein; r-m – radial-medial (= anterior,  $t_a$ ) cross-vein.

Nomenclature of taxa treated here follows that in ROHÁČEK et al. (2001), ROHÁČEK (2009b) and MARSHALL et al. (2011).

## A survey of the wing polymorphic species in Europe

### 1. *Crumomyia pedestris* (Meigen, 1830)

(Figs. 1, 5–11)

**Material examined.** More than 890 specimens (483 ♂♂ 410 ♀♀, with only 7 ♂♂ 3 ♀♀ macropterous, 2 ♂♂ 2 ♀♀ submacropterous and the rest brachypterous to almost micropterous) from Czech Republic, Slovakia – localities listed by ROHÁČEK (1975b, 1980, 1986, 1991, 1999, 2011) and ROHÁČEK & BARTÁK (2001). Additional localities: **CZECH REPUBLIC: MORAVIA:** Hrubý Jeseník Mts. – Rejvíz res. (V. Kavalcová leg.). **SLOVAKIA:** Velká Fatra Mts. – Rakša res. (J. Roháček leg.).

The species is usually strongly brachypterous to almost micropterous (Figs. 1, 7–10). Already GUIBÉ (1939) obtained macropterous specimens during his breeding experiments but suggested that they are less viable. On the basis of his results RICHARDS (1951) stated that only the dominant micropterous homozygotes and heterozygotes occur in the wild. However, since 1975 the macropterous specimens were also found in the field several times (ROHÁČEK 1975b, 1991; PAPP 1976). Originally (ROHÁČEK 1975b) I considered the macropterous and submacropterous forms (Figs. 5, 6) to be atavistic specimens very rarely occurring among the usual micropterous specimens in natural populations. This opinion proved to be incorrect in the light of recent findings. The macropterous forms (Fig. 5) seem to occur in only some populations, particularly in those living in drier habitats, e.g. in runs of small mammals. However, the preferred habitats of *Crumomyia pedestris* are very damp meadows and boggy alder forests where its larvae develop in dead snails. In my opinion the wing polymorphism and, subsequently, the now prevailing strong brachyptery evolved in consequence of the adaptation of this species to the extreme humidity of its preferred habitat niche where long wings are strongly disadvantageous.

### 2. *Phthitia (Collimosina) spinosa* (Collin, 1930)

(Figs. 12–14)

**Material examined.** Almost 80 specimens (34 ♂♂ 45 ♀♀, with 15 ♂♂ 18 ♀♀ slightly brachypterous, rest macropterous) from Great Britain (England), Czech Republic, Finland and Russia (North European Territory) – localities listed by ROHÁČEK (1983, 1996a), ROHÁČEK & BARTÁK (2001) and ROHÁČEK et al. (2005).

This species forms a fine example of a very initial stage of the development of wing polymorphism. The slightly brachypterous specimens were found in only two populations where they hardly predominated over fully winged ones. The wings of brachypterous specimens do

not reach beyond the tip of the abdomen and their venation is usually only slightly modified (Fig. 14), having a shortened 2<sup>nd</sup> costal sector and discal (dm) cell which represents the 2<sup>nd</sup> stage of reduction of the venation. However, also a vein mutant with lost terminal part of  $R_{2+3}$  was found (Fig. 13). This uncommon species is apparently associated with mosses in boggy and peat-bog meadows (ROHÁČEK 1983).

### 3. *Spelobia manicata* (Richards, 1927)

(Figs. 15–17)

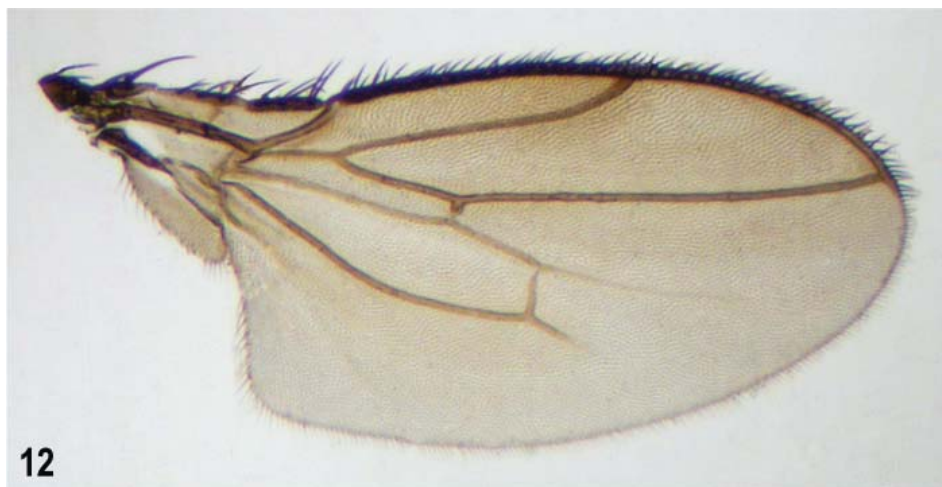
**Material examined.** 250 specimens (153 ♂♂ 97 ♀♀ with 91 ♂♂ 53 ♀♀ slightly brachypterous to submacropterous, rest macropterous) from Great Britain (England), Austria, Czech Republic, Slovakia – localities listed by ROHÁČEK (1980, 1983, 1984, 1995, 1999, 2009a, 2011), ROHÁČEK & BARTÁK (1999, 2001) and ROHÁČEK et al. (2005). Additional localities: **CZECH REPUBLIC:** MORAVIA: Karlova Pláň – Volárenský potok; Hradec nad Moravicí; Moravskoslezské Beskydy Mts. – Tanečnica Mt. (J. Roháček leg.). **SLOVAKIA:** Vysoké Tatry Mts. – Štrbské pleso, Vysoké Tatry Mts. – Velické pleso, Vysoké Tatry Mts. – Velická dolina valley (J. Roháček leg.).

This species is another example of a weak alary polymorphism. It is considered relatively young (ROHÁČEK 1983), only recently derived from the macropterous ancestor as it is very similar to *Spelobia clunipes* (Meigen, 1830). It should be noted that its macropterous form (Fig. 15) has somewhat on the average shorter wings than *S. clunipes*. Wings of brachypterous specimens are distinctly smaller, shortened, darkened, often with rounded outer corners of dm cell (Figs. 16, 17). *Spelobia manicata* is predominantly a microcavernicolous species living in burrows and runs of small mammals but also in leaf-litter, moss, etc. (ROHÁČEK 1983).

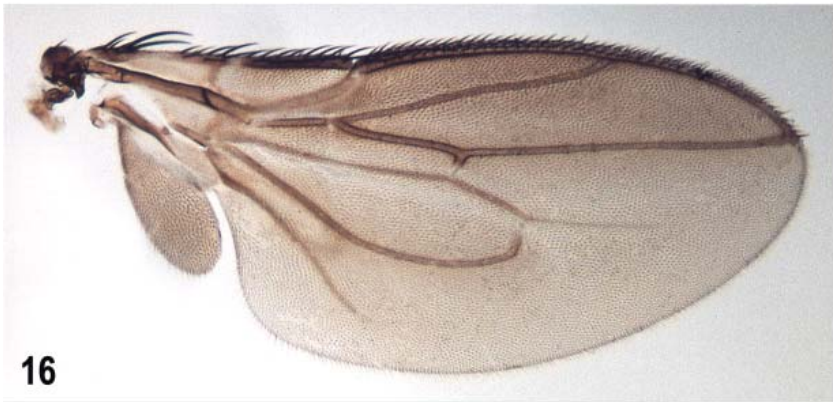
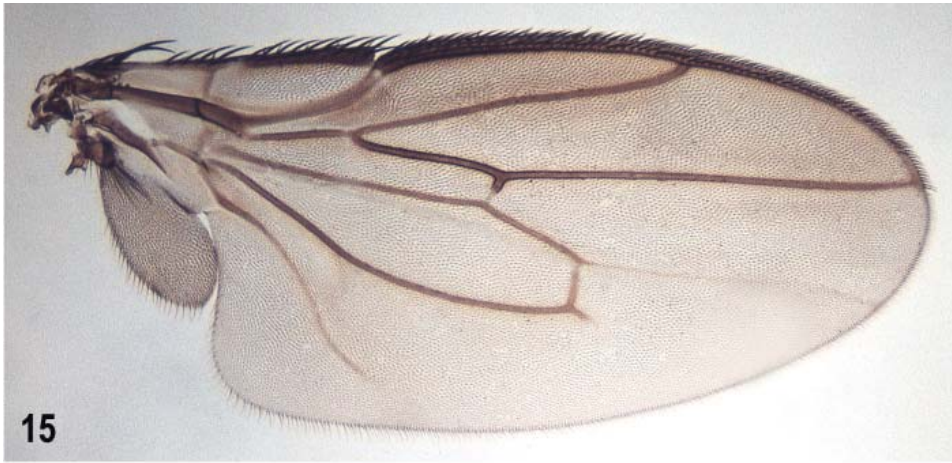
### 4. *Pteremis fenestralis* (Fallén, 1820)

(Figs. 2, 18–22)

**Material examined.** About 1,000 specimens (378 ♂♂ 630 ♀♀, with only 14 ♂♂ 32 ♀♀ brachypterous, rest macropterous) from Czech Republic and Slovakia – localities listed by ROHÁČEK (1980, 1984, 1986, 1995, 2009a, 2011), ROHÁČEK & BARTÁK (1999, 2001) and ROHÁČEK et al. (1998, 2005). Additional localities: **FINLAND:** Helsinki (L. Tiensuu, R. Frey leg.), Kyrkslätt (R. Frey leg.), Muonio (Sahlberg, Palmén leg.), Kajana (Hellén leg.), all in Zoological Museum, Helsinki. **GREAT BRITAIN:** ENGLAND: Oxford, University park (J. Roháček leg.). **AUSTRIA:** Tyrol, Obergurgl Mt. (H. Troger leg.), Hohe Tauern, Badgastein (H. Stockner leg.), in Zoologisches Institut, Universität Innsbruck. **CZECH REPUBLIC** (only examples of localities): **BOHEMIA:** Čistá u Sokolova (Dlabola leg.), Jelení u Karlových Var (Škaloudová leg.), Horská Kvilda, Ondřejov (M. Chvála, M. Barták leg.), Lipno nad Vltavou, Klášterec nr. Vimperk, Pěkná 2 km W, Doupovské hory – Lochotín (J. Roháček leg.), Žišov – Doubí (J. Máca leg.), Praha – Holešovice, Praha – Šárka, Jiloviště, Úvaly, Kunice, Velké Popovice, Veltrusy, Struhařov, Sokoleč, Třebotov, Předhrádk, Vlčkov nad Lužnicí (all M. Barták leg.), Hluboká nad Vltavou, Lešany (I. Kovář leg.), Jizerské hory Mts. – Jizerka, Bohdaneč (B. Mocek leg.), Malý Pěčín, Palupín u Strmilova (J. Roháček leg.). **MORAVIA:** Řásná u Telče, Třešť, Brno, Moravský kras – Mariánské údolí, Nedvědice, Vranovská přehrada – Cornštejn, Lednice, Moravičany, Kouty nad Desnou, Bělá pod Pradědem, Nýznerov, Vidnava, Úvalenská louky nr. Krnov, Opava, Chvalíkovice nr. Opava, Klokočov, Bílé Karpaty – Radějov, Moravskoslezské Beskydy Mts. – Tanečnica Mt. (J. Roháček leg.), Moravskoslezské Beskydy Mts. – Muřinkový vrch Mt. (M. Barták leg.), deposited in coll. Národní muzeum, Praha; Slezské zemské muzeum, Opava; Muzeum Soběslav; Muzeum východních Čech; coll. M. Barták, Praha. **SLOVAKIA:** Štúrovo, Hegyfarok, Bielá, Pribylina (M. Barták leg.), Stankovany nr. Kralovany, Vysoké Tatry Mts. – Štrbské pleso, Vysoké Tatry Mts. – Velická dolina, Regetovka nr. Bardejov (J. Roháček leg.), coll. Slezské zemské muzeum, Opava and coll. M. Barták, Praha. **POLAND:** E. Poland: Bondary, Białowieża – Budy 2 km NE, Białowieża 4 km S – Czerlon (J. Roháček leg.). **ROMANIA:** BANAT: Sfânta Elena 2.5 km NE (J. Roháček leg.). **GREECE:** PTERIA: Olympos Mts. – Karyá env. (J. Roháček leg.).

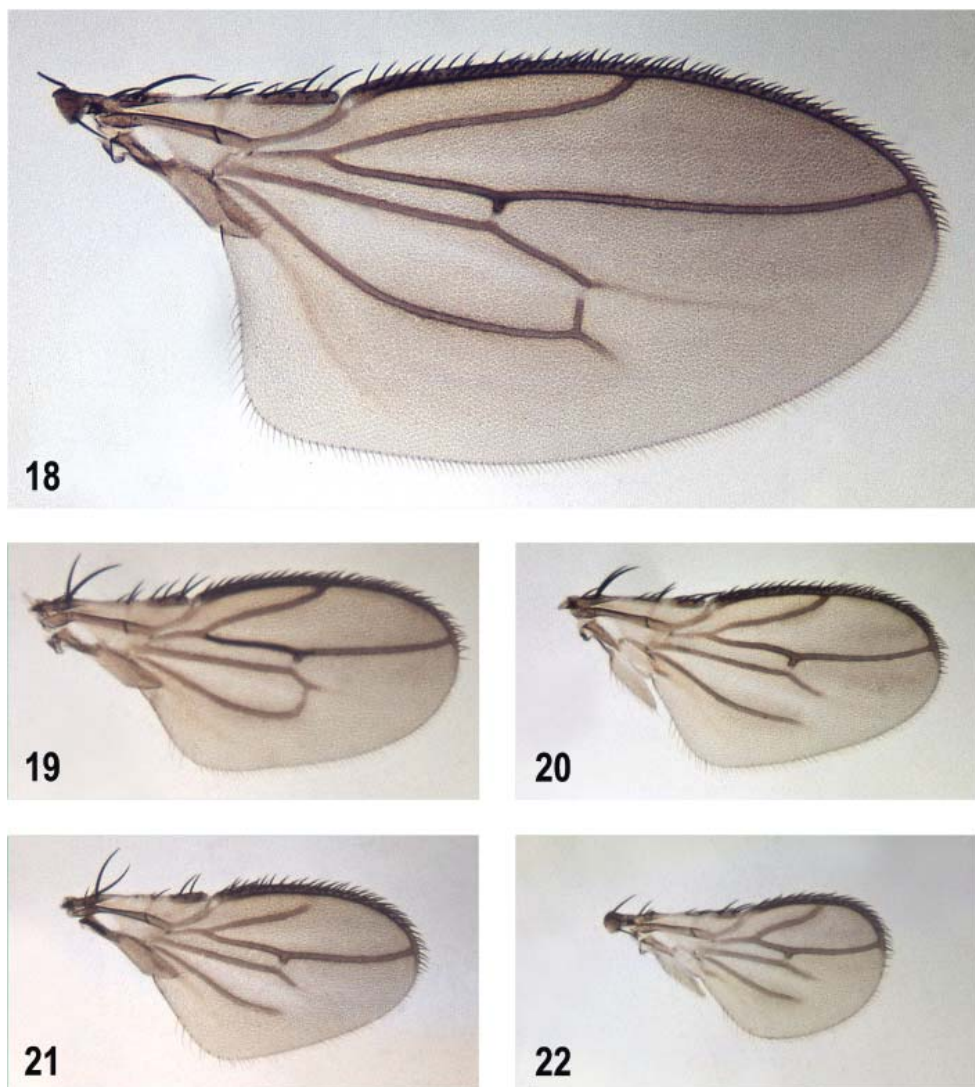


Figs. 12–14. *Phthitia (Collimosina) spinosa* (Collin, 1930), female wings. 12 – macropterous (Czech Republic: Řáská nr. Telč); 13 – slightly brachypterous, with apical part of  $R_{2+3}$  lost; 14 – distinctly brachypterous (both Czech Republic: Úvalenské louky res. nr. Krmov). Scale: 0.5 mm. Photo by J. Roháček.

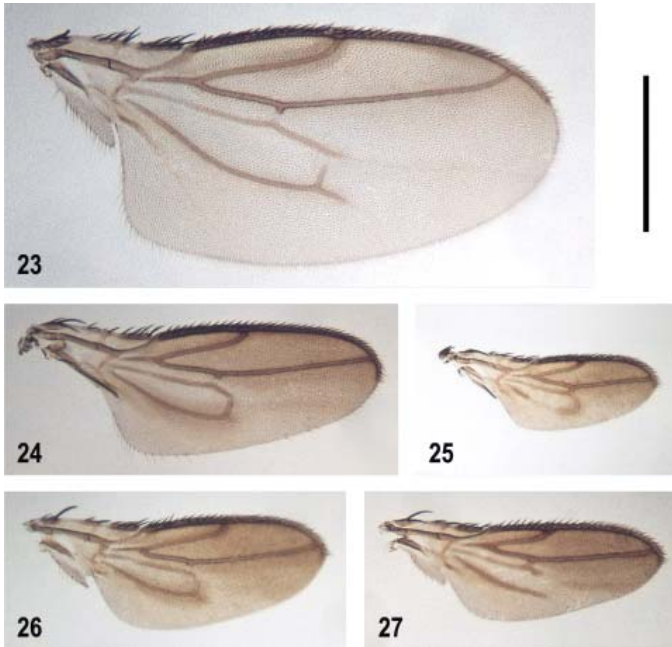


Figs. 15–17. *Spelobia manicata* (Richards, 1927), male wings. 15 – macropterous (Czech Republic: Třešť); 16 – submacropterous (Czech Republic: Hrubý Jeseník Mts. – Kouty nad Desnou); 17 – brachypterous (Czech Republic: Třešť – Pouště). Scale: 0.5 mm. Photo by J. Roháček.

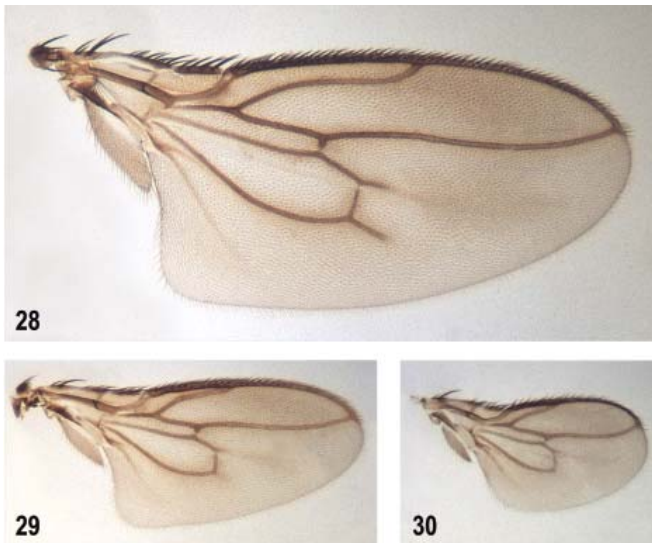




Figs. 18–22. *Pteremis fenestralis* (Fallén, 1820), female wings. 18 – macropterous; 19 – atypical brachypterous with dm-cu present; 20 – typical brachypterous (= *Borborus nivalis* Haliday, 1833); 21 – brachypterous with terminal part of  $R_{2+3}$  lost; 22 – strongly brachypterous (all Czech Republic: Hrubý Jeseník Mts.– Rejvíz res.). Scale: 0.5 mm. Photo by J. Roháček.



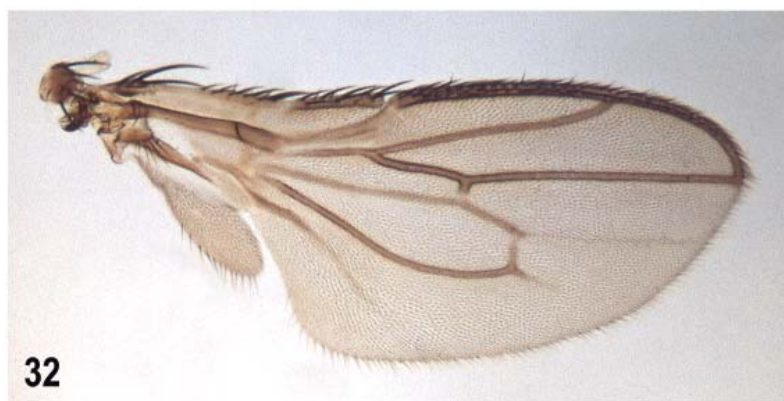
Figs. 23–27. *Pullimosina (Pullimosina) mejerei* (Duda, 1918), wings. 23 – macropterous female (Czech Republic: Třešť); 24 – largest brachypterous female (Czech Republic: Kunětická hora Mt.); 25 – brachypterous male with part of  $CuA_1$  lost; 26 – normal brachypterous male; 27 – brachypterous male with dm-cu cross-vein lost (all Czech Republic: Lednice – Kančí obora). Scale: 0.5 mm. Photo by J. Roháček.



Figs. 28–30. *Puncticorpus cribratum* (Villeneuve, 1918), wings. 28 – submacropterous (Hungary: Síkfökút); 29 – medium brachypterous, 30 – extremely brachypterous (both Slovakia: Vihorlat Mts.– Stakčín env.). Photo by J. Roháček.



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Figs. 31–34. *Spelobia pseudonivalis* (Dahl, 1909), wings. 31 – submacropterous male (Czech Republic: Nizký Jeseník Mts.– Slunečná Mt.); 32 – slightly brachypterous female (Czech Republic: Hrubý Jeseník – Kouty nad Desnou); 33 – typical brachypterous female (Czech Republic: Horní Benešov env.); 34 – strongly brachypterous female with dm-cu cross-vein lost (Czech Republic: Moravský kras – Babice). Scale: 0.5 mm. Photo by J. Roháček.



Figs. 35–37. *Terrilimosina corrivalis* (Villeneuve, 1918), male wings. 35 – almost macropterous (Romania: Banat, Sfânta Elena – Kulhavá skála); 36 – usual brachypterous (Slovakia: Bukovské vrchy Mts.– Stuzica res.); 37 – strongly brachypterous (Slovakia: Poľana Mts.– Hrončecký Grúň res.). Scale: 0.5 mm. Photo by J. Roháček.

A typical wing polymorphic species (HACKMAN 1964) but this phenomenon seems to be restricted only to North European and some, usually montane, Central European populations. The brachypterous form of *P. fenestralis* had long been considered a different species, *Pteremis nivalis* (Haliday, 1833), and COLLIN (1956) was the first to recognize its conspecificity with *P. fenestralis*. Also *Pteremis subabterus* Frey, 1946 was found to be another short-winged form of this species (HACKMAN 1964). The percentage of the brachypterous specimens clearly increases in more northern latitudes or higher altitudes (ROHÁČEK 1975b). The venation of brachypterous forms strongly vary in some populations (Figs. 19–22), which enabled speculation on the general trends in the modification of venation during the evolution of brachypterous species (see below). *P. fenestralis* chiefly lives in mosses, *Sphagnum* and grass tufts in wet open habitats as well as damp forests. It is common in mountains but rare in lowlands, particularly in southern Europe where the populations seem to be purely macropterous.



### 5. *Pullimosina (Pullimosina) mejerei* (Duda, 1918)

(Figs. 3, 4, 23–27)

**Material examined.** About 550 specimens (249 ♂♂ 304 ♀♀, with 139 ♂♂ 182 ♀♀ brachypterous, others macropterous) from Denmark, Austria, Czech Republic, Slovakia – localities listed by ROHÁČEK (1975a, 1978, 1980, 1983, 1984, 1986, 1995, 1999, 2009a, 2011), ROHÁČEK & BARTÁK (2001) and ROHÁČEK et al. (2005). Additional localities: **CZECH REPUBLIC: BOHEMIA:** Klášterec nr. Vimperk (J. Roháček leg.). **MORAVIA:** Hrubý Jeseník Mts. – Velká kotlina valley, Karlova Pláň – Volárenský potok, Šilheřovice – Černý les res., Moravskoslezské Beskydy Mts. – Tanečnica Mt. (J. Roháček leg.). **SLOVAKIA:** Velká Fatra Mts. – Rakša res., Malá Fatra Mts. – Šútovská dolina, Nízke Tatry Mts. – Donovaly 3 km E, Korytnica kúpele, Muránska planina NP – Šarkanica res.; Muránska planina NP – Muránska Huta 1 km NW, Bobačka cave, 48°46' 49"N, 20°06'16"E, 780 m a.s.l., sifting leaves in beech forest, 11.iv.2012, 1 ♂ with unevenly developed wings (J. Roháček leg.). **HUNGARY:** Kiskunsági N. P., Kunfehértó lake (J. Roháček leg.). **NORWAY: SVALBARD IS.** (= Spitzbergen), Colsbay, tundra, 15.vii.1983, 1 ♂ (f. brachyptera), R. I. Zlotin leg. (both in coll. J. Roháček, Opava). Note: The record from Svalbard Is. is the northernmost distribution limit of the species.

The species was originally described as brachypterous; the macropterous form was discovered only in 1975 but the species was confused (and synonymized) by ROHÁČEK (1975b) with the closely allied *P. pullula* (Zetterstedt, 1847), and this mistake was disproved subsequently by ROHÁČEK (1978, 1983). Both forms are clearly separated; no intermediate forms are known (ROHÁČEK 1975b, as *P. pullula*). The proportion of the brachypterous (Figs. 24–27) and macropterous (Figs. 3, 23) forms somewhat varies in samples taken in different habitats (e.g. in woodland with high leaf-litter layer the brachypterous form strongly predominate) but generally the short-winged specimens are more abundant in the majority of populations. The brachypterous form has the wing not only abbreviated but also somewhat narrowed (this the only case among European Limosiniinae). Besides the most common type, there are several other forms with more reduced venation (see Figs. 25, 27); that with rounded external corners of dm cell is rather common. *Pullimosina mejerei* is a typically terricolous species living in leaf-litter and other decayed plant matter, often in deep layers of detritus (ROHÁČEK 1983).

In spring 2012 a male specimen with unevenly developed wings, thus combining the macropterous and brachypterous form (see Fig. 4), was sifted from leaf-litter in the Muránska planina NP (Slovakia, see above). This is the first time that this peculiar phenomenon has been noted in Sphaeroceridae. Formerly, single specimens having one wing normal and the other shortened were only recorded in the wing polymorphic species *Stiphrosoma sabulosum* (Haliday, 1837) (Anthomyzidae), both in Europe (see COLLIN 1944; STACKELBERG 1958, 1970; ROHÁČEK 1996b) and USA: Michigan (ROHÁČEK & BARBER 2005), and one specimen with ambiguous wings was also recorded in a Canadian population of *Conioscinella zetterstedti* Andersson, 1966 (Chloropidae) (WHEELER 1994).

### 6. *Puncticorpus cribratum* (Villeneuve, 1918)

(Figs. 28–30)

**Material examined.** More than 450 specimens (197 ♂♂ 269 ♀♀, with 63 ♂♂ 81 ♀♀ submacropterous to macropterous, rest more or less brachypterous) from G. Britain (England), Denmark, Switzerland, Czech Republic, Slovakia, Hungary, Slovenia, Cyprus, Israel – localities listed by ROHÁČEK (1975a, 1986, 1999, 2001, 2004, 2011), ROHÁČEK & MARSHALL (1982), PAPP & ROHÁČEK (1988) and ROHÁČEK et al. (2005). Additional localities: **CZECH REPUBLIC: BOHEMIA:** Vyšší Brod – Čertova stěna (J. Roháček leg.). **SLOVAKIA:** Malá Fatra – Šútovská dolina,

Muránská planina NP – Muránska Huta 1 km NW, Nová Sedlica – Zbojský potok (J. Roháček leg.). **GREECE:** **PERIA:** Olympos Mts. – Karyá. **CRETE:** W. Crete: Prases 4 km SW, Prases 2 km W; SW Crete: Samaria gorge NW part, Omalos 3 km SW (all J. Roháček leg.).

The remarkable variability of wing length of this species has been described by ROHÁČEK & MARSHALL (1982); formerly the species was thought to be short-winged. This species represents another example of dependence of the degree of wing reduction on the geographical latitude and consequently on climatic conditions. The populations from northern areas or from higher altitudes of Central Europe have more abbreviated wings (Figs. 29, 30), while the submacropterous forms (Fig. 28) prevail in warm lowlands of Hungary and the almost full-winged specimens are known from the Mediterranean countries, viz. Israel (PAPP & ROHÁČEK 1988), Cyprus (ROHÁČEK 2004) and mainland Greece and Crete (new material examined). The type of wing polymorphism in *P. cribratum* is unlike that of *Pteremis fenestralis* or *Pullimosina meijerei* because intermediate forms are common and hence strongly brachypterous and macropterous forms are not sharply separated. *Puncticorpus cribratum* is a terricolous species associated with decaying sporophores and mycelia of fungi in forest litter (ROHÁČEK & MARSHALL 1982).

### 7. *Spelobia pseudonivalis* (Dahl, 1909)

(Figs. 31–34)

**Material examined.** 29 specimens (9 ♂♂ 20 ♀♀, with 1 ♀ macropterous, 1 ♂ 2 ♀♀ submacropterous, others brachypterous) from Germany, Czech Republic and Slovakia – localities listed by ROHÁČEK (1975a, 1980, 1983, 1999, 2009a) and ROHÁČEK et al. (2005).

The species was originally described as brachypterous (for typical wing see Fig. 33). The first longer-winged specimens (Fig. 31) were recorded by ROHÁČEK (1980) and its wing polymorphism was discussed by ROHÁČEK (1983). Unfortunately, the relatively small number of specimens available for study makes it impossible to study the phenomenon in *S. pseudonivalis* more thoroughly. It seems to be of a similar type to *Puncticorpus cribratum* but perhaps without geographical dependence and with a much rarer (sub)macropterous form. Among the brachypterous specimens a mutant female with strongly reduced wing and venation (dm-cu lost) was found (Fig. 34) and recently a fully winged female was recorded from Poľana Mts. in Slovakia (ROHÁČEK 2009a). Except for *Spelobia manicata*, *S. pseudonivalis* is the only microcavernicolous wing polymorphic species in Europe. It lives in burrows of small mammals, particularly in nests of moles (ROHÁČEK 1983).

### 8. *Terrilimosina corrivalis* (Villeneuve, 1918)

(Figs. 35–37)

**Material examined.** 80 specimens (44 ♂♂ 36 ♀♀, with only 1 ♂ macropterous, 2 ♂♂ 2 ♀♀ submacropterous, others slightly to strongly brachypterous) from Czech Republic, Slovakia, Ukraine – localities listed by ROHÁČEK (1975c, 1983, 1984, 1994b, 1995) and ROHÁČEK & BARTÁK (2001) – all as *Limosina* or *Terrilimosina sudetica* and by ROHÁČEK (2001, 2009a). Additional localities: **CZECH REPUBLIC:** **MORAVIA:** Hrubý Jeseník Mts.– Velká kotlina glacial cirque (V. Kavalcová leg.). **SLOVAKIA:** Velká Fatra Mts. – Rakša res., Malá Fatra Mts. – Šútovská dolina, Nízke Tatry Mts. – Donovaly 3 km E, Vysoké Tatry Mts – Popradské pleso (J. Roháček leg.). **ROMANIA:** Banat, Sfânta Elena – Kulhavá skála rock, at Vranovec cave, sifting decayed leaves by stream, 1.vi.2008, 1 ♂ (f. macroptera) (J. Roháček leg.).

A rather poorly known species. Originally described as slightly to distinctly brachypterous (VILLENEUVE 1918; ROHÁČEK 1975c – under the synonymous name *Limosina sudetica* Roháček, 1975), later the submacropterous form was recorded (ROHÁČEK 1983, as *T. sudetica*) and recently more strongly brachypterous (Fig. 37) and almost fully winged specimens (Fig. 35) were found. Thus, its wing polymorphism with prevailing brachypterous form and continual transition to rare macropterous form seems to be similar to that of *Spelobia pseudonivalis*. Venal mutants seem to be rather rare in the brachypterous form of *T. corrivalis* – only two specimens (1 ♂ 1 ♀) with posterior cross-vein lost were found in the Hrubý Jeseník Mts. (Czech Republic). *Terrilimosina corrivalis* is a terricolous species associated with leaf-litter, moss and other decayed vegetation in mountain forests of Central Europe; hitherto it has only been recorded from Switzerland, Germany, Czech Republic, Slovakia, and Western Ukraine (ROHÁČEK et al. 2001). It is newly recorded from Romania (new southernmost distribution limit).

### General trends in the reduction of wing venation with increasing brachyptery in European Sphaeroceridae

The evaluation of the modification of venation of all the above discussed wing polymorphic species as well as of other brachypterous species of the West Palaearctic area makes it possible to find some general trends in the reduction of venation during the evolution of brachypterous forms and species.

The reduction of venation with progressive abbreviation of the wing proceeds differently in the Copromyzinae (represented by *Crumomyia pedestris*) and in the species of Limosiniinae. In *C. pedestris* (Figs. 7–10) the proximal parts of the wing remain well preserved even in strongly brachypterous specimens (e.g. the very little reduced  $Cs_1$ ,  $R_1$ , the retention of both basal medial (bm) and posterior cubital (cup) cells, and alula are particularly interesting). On the contrary, the distal three-fourths of the wing are greatly modified by reduction in strongly brachypterous specimens:  $R_1$  terminates at the apex of wing (subcostal break is almost on its tip) while  $R_{2+3}$  and  $R_{4+5}$  end so close to  $R_1$  that  $Cs_2$  and  $Cs_3$  are not developed at all. Very interesting is the destiny of the discal (dm) cell which is first reduced to a small triangle (Fig. 7), and later completely replaced by fusion of M and  $A_1+CuA_1$  veins but with the retention of cross-vein r-m (Fig. 8). In almost micropterous forms only  $R_1$  is distinct, and other veins are fused to form a small basal (M, Cu, A) and apical (R) sclerites (Fig. 10).

In the Limosiniinae a greater generalization of evolutionary trends in the reduction of wing veins was possible because more cases had been studied. Besides the brachypterous forms of the wing polymorphic species also brachypterous species of the genus *Aptilotus* Mik, 1898 from the Canary Islands were taken into consideration. The probable successive sequence of reduction of veins in *Pteremis fenestralis* is shown in Fig. 38 and that in *Aptilotus* species in Fig. 39. Altogether 6 stages of the reduction of venation can be recognized as shown in the diagram on Fig. 40. Table 1 summarizes the distribution of the recognized stages in particular species. As shown in this table, the polymorphic species are those which occur in at least one of the other (brachypterous) stages besides the 1<sup>st</sup> stage (= macropterous or submacropterous form). On the other hand, the purely brachypterous species probably display much smaller variability as regards their venation (only 1–2 stages).

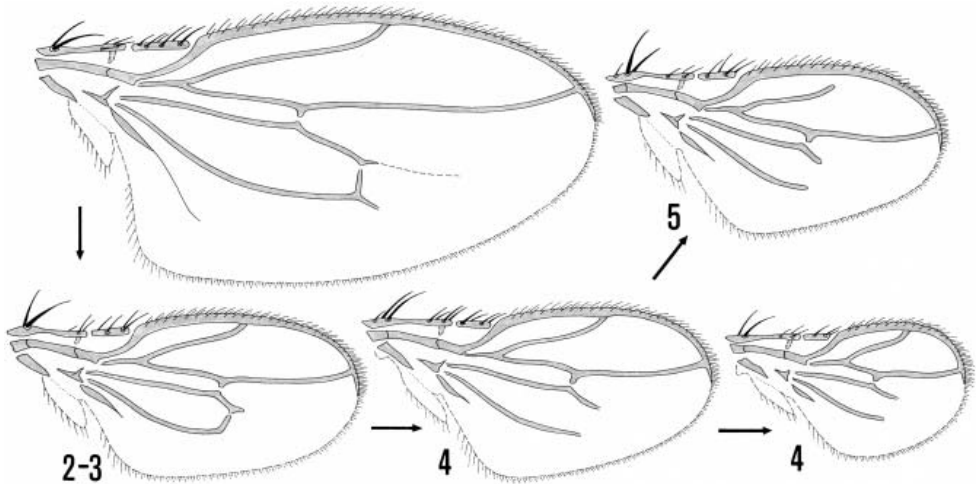


Fig. 38. Wings of *Pteremis fenestralis* (Fallén, 1820). Successive sequence of reduction of veins in wings with increasing brachyptery. The numbers 2–5 refers to stages of reduction of venation as defined in Fig. 40.

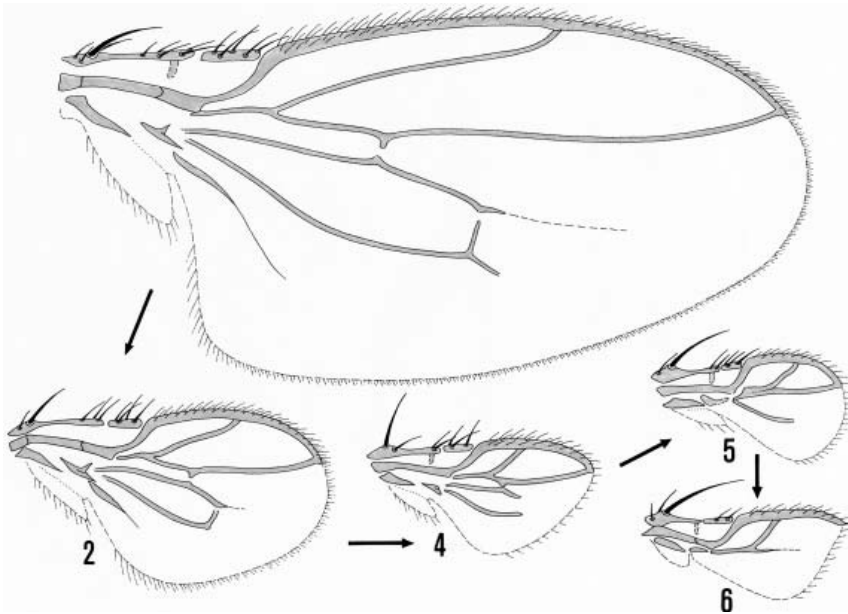


Fig. 39. Wings of *Atilotus* species from Canary Islands. Successive sequence of reduction of veins in wings in particular endemic species. The numbers 2–6 refers to stages of reduction of venation as defined in Fig. 40. *A. beckeri* (Duda, 1918) from Tenerife, a macropterous species (top wing); *A. avolans* (Roháček & Papp, 1983) from La Palma (left bottom); *A. gomerensis* (Papp & Roháček, 1981) from La Gomera (middle bottom); *A. franzi* (Papp & Roháček, 1981) from Tenerife (right bottom above, stage 5); *A. anapterus* (Papp & Roháček, 1981) from La Palma (right bottom below, stage 6).



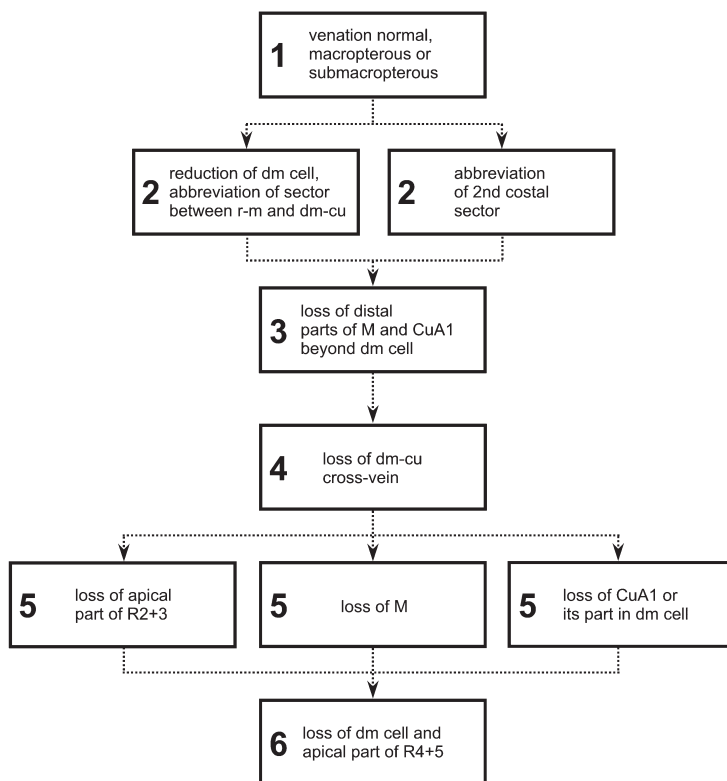


Fig. 40. Diagram with definition of 6 stages of reduction of venation in brachypterous and wing polymorphic species of Sphaeroceridae (West Palaearctic only).

## Discussion and conclusions

### 1. Causes of the origin of the wing polymorphism in Sphaeroceridae

HACKMAN (1964) recognized that the majority of brachypterous, apterous and wing polymorphic species of Sphaeroceridae are associated with terricolous and hypogean habitats. It is apparent that the adaptation of the originally macropterous species to an edaphic and hence flightless way of life had to reflect on the morphology of wings. Brachypterous mutants of both sexes proved to be more successful in colonizing terricolous habitat-niches, e.g. they were able to penetrate in deeper layers of the forest litter which are inaccessible to fully winged form. An important condition for preservation of the alary polymorphism in the population is a sufficient overlap of the habitat-niches of both macropterous and brachypterous forms making possible the free exchange of the genetic material between them. *Pullimosina meijerei* is a typical example; the short winged forms predominate in habitats with a deep leaf litter stratum. Most of the brachypterous and wing polymorphic species in the West Palaearctic area obviously evolved in the above way, including both microcavernicolous species (*Spelobia manicata*, *S. pseudonivalis*).

There is, however, a different case – *Crumomyia pedestris*. Its strongly brachypterous to micropterous forms are probably selected for the extremely wet terrestrial habitats such as boggy meadows and waterlogged forests. This opinion is supported by several pieces of evidence: i) It has purely brachypterous and very successful populations in damp marshy habitats; macropterous forms were probably eliminated from these populations long ago, and this state has become fixed genetically. ii) The rare wing polymorphic populations are restricted to drier terricolous habitats and the macropterous form may be well represented in them. If we accept GUIBÉ'S (1939) finding that the macropterous specimens are recessive homozygotes then the genetic structure of the polymorphic populations must be different from those formed only by brachypterous and micropterous individuals. iii) *C. pedestris* bears also other adaptations for survival in a strongly humid environment – e.g. the unusually densely and long finely haired body and legs being particularly well developed in brachypterous specimens.

## **2. Variability of the wing polymorphic populations in dependence upon geographical and climatic factors**

ROHÁČEK (1975b) was the first to discuss the influence of the geographical latitude on the ratio of the macropterous and brachypterous forms in populations of *Pteremis fenestralis*. The brachypterous form of this species is only common in northern Europe and Great Britain but rare in Central Europe and the more southern populations seem to be purely macropterous. The development of the brachyptery in *P. fenestralis* is perhaps affected by low temperature which inhibits the flying activity and, consequently, favours a transition of the species to a terricolous life-habit where the short wings are adaptive (this phenomenon was often discussed in brachypterous tipulids and limoniids, cf. BYERS 1961, HACKMAN 1964, MARTINOVSKÝ & STARÝ 1969). In Central Europe *P. fenestralis* lives as a muscicolous species and most of populations are macropterous. The wing polymorphic populations were noted at higher altitudes with colder climate, e.g. in upland peat-bogs. The macropterous specimens inhabit the warm surface layer while the brachypterous can be mainly found in the deeper, wet and cold layers of grass, *Sphagnum* and mosses.

A similar correlation between the wing length (or the proportion of short winged specimens) and climate was also described in *Puncticorpus cribratum* (see ROHÁČEK & MARSHALL 1982). In this terricolous species the macropterous and submacropterous form prevail in more southern lowland situations and the populations in the Mediterranean subregion (cf. PAPP & ROHÁČEK 1988, ROHÁČEK 2004) seem to be purely macropterous. The species is generally thermophilous and did not penetrate into high mountains but its populations from northern latitudes are distinctly shorter winged on the average. Possibly the influence of climatic and geographical factors upon the structure of populations of other wing polymorphic species will be detected in the future.

## **3. Wing polymorphism as a transient and temporary stage in the evolution of the brachypterous and apterous species**

The present study of the reduction of venation in the brachypterous forms of European wing polymorphic species showed distinct similarity between their venation and that of bra-

chpterous species of the genus *Aptilotus* Mik, 1898 from Canary Islands. The comparison of the successive stages of vein reduction found in *Pteremis fenestralis* with those of *Aptilotus* species (cf. Figs. 38, 39) indicates that the wing polymorphism is to be considered a transient and temporary stage antecedent to full brachyptery and/or aptery.

The brachypterous species can evolve either if its wing polymorphic ancestor colonized a habitat-niche where only brachypterous mutants can compete with its native inhabitants or if the macropterous form becomes extinct because it is unable to tolerate changes in microclimatic conditions (e.g. increasing humidity), or if the original habitat-niche of the macropterous form became separate from the new one colonized by the brachypterous form – example: cavernicolous *Aptilotus martini* Wheeler & Marshall, 1989 versus *A. beckeri* (Duda, 1918).

It seems that the evolutionary process of brachypterous species is probably very slow in the continental habitats of the temperate climatic zone or, in other words, the wing polymorphic populations remain long stabilized there because of the overlap of habitat-niches and relatively constant microclimatic conditions. On the other hand, this process may be rapid in more extreme situations, for instance in high mountains (particularly in the tropics) or on islands.

The *Aptilotus* species from the Canary Islands are a fine example. As noted by ROHÁČEK & PAPP (1983) and ROHÁČEK et al. (2003) two macropterous ancestral species gave rise to 7 closely allied species, 6 being brachypterous (see Table 1) and restricted to particular islands of the archipelago (ROHÁČEK et al. 2003). They are specialized terricolous and cavernicolous species. Both ancestral species (surely tending to wing polymorphism) possibly colonized

Table 1. Distribution of particular stages with various degree of reduction of venation in the wing polymorphic (P) and/or brachypterous (B) species of the West Palaearctic Limosininae (solid circle). *Aptilotus beckeri* (Duda, 1918) is a macropterous species (M) representing the ancestral-like type of venation in the genus *Aptilotus*. For the characteristics of the stages 1–6 see diagram on Fig. 40. Submacropterous forms are included in stage 1. In species where a true macropterous form was not found the occurrence of a submacropterous form is indicated by 2 solid circles in stage 1.

Species	Wing	Stages of reduction					
		1	2	3	4	5	6
<i>Phthitia (C.) spinosa</i> (Collin, 1930)	P	●●●	●●●	○○○	○○○	○○○	○○○
<i>Spelobia manicata</i> (Richards, 1927)	P	●●●	●●●	●●●	○○○	○○○	○○○
<i>Pteremis fenestralis</i> (Fallén, 1820)	P	●●●	●●●	●●●	●●●	●●●	○○○
<i>Pullimosina mejerei</i> (Duda, 1918)	P	●●●	●●●	●●●	●●●	●●●	○○○
<i>Puncticorpus cribratum</i> (Villeneuve, 1918)	P	●●●	●●●	●●●	○○○	○○○	○○○
<i>Spelobia pseudonivalis</i> (Dahl, 1909)	P	○●●	●●●	●●●	●○○	○○○	○○○
<i>Terrilimosina corrivalis</i> (Villeneuve, 1918)	P	○●●	●●●	●●●	●○○	○○○	○○○
<i>Aptilotus beckeri</i> (Duda, 1918)	M	●●●	○○○	○○○	○○○	○○○	○○○
<i>Aptilotus avolans</i> (Roháček & Papp, 1983)	B	○○○	●●●	●●●	○○○	○○○	○○○
<i>Aptilotus gomerensis</i> (Papp & Roháček, 1981)	B	○○○	○○○	○○○	●●●	○○○	○○○
<i>Aptilotus martini</i> Wheeler & Marshall, 1989	B	○○○	○○○	○○○	●●●	○○○	○○○
<i>Aptilotus pilifemoratus</i> (Papp & Roháček, 1981)	B	○○○	○○○	○○○	○○○	●●●	○○○
<i>Aptilotus franzi</i> (Papp & Roháček, 1981)	B	○○○	○○○	○○○	○○○	●●●	○○○
<i>Aptilotus anapterus</i> (Papp & Roháček, 1981)	B	○○○	○○○	○○○	○○○	○○○	●●●

most of the islands and produced brachypterous forms at least on three of them (Tenerife, La Palma, La Gomera). These, after the early extinction of the macropterous form, rapidly developed into distinct species. There is a purely macropterous species in this group, *Aptilotus beckeri*, that is considered a descendant of the macropterous form of one of these ancestors (it is closely related to 4 brachypterous species). It occurs on more islands, among them also on Tenerife but it apparently colonized this island only after its brachypterous relative endemic here, viz. *Aptilotus franzi* (Papp & Roháček, 1981), had already become specifically different. Interestingly, the reduction of venation in the discussed brachypterous species occurs in different stages; this indicating not only the ancestral wing polymorphism but also different duration and speed of evolution.

#### 4. Probable genetic background of wing polymorphism in European species of Sphaeroceridae

Wing polymorphism of insects is undoubtedly determined genetically (for review see ROFF 1986) as has also been demonstrated in Sphaeroceridae by GUIBÉ (1939) in his breeding experiments with *Crumomyia pedestris*. Only analyses of crossings of all forms might clarify the genetic background of wing polymorphism. However, except for *Crumomyia pedestris*, none of the other European wing polymorphic species has been bred in the laboratory till now. Therefore the following results are only hypotheses inferred from the studies of the natural populations that should be tested by crossing experiments in future. ROFF (1986) mentioned two models for the genetic determination of wing polymorphism: i) a single locus with two alleles (with macroptery being either dominant or recessive). ii) a polygenic mode of inheritance being apparently the more general situation (the number of loci involved may be very variable).

Three types of wing polymorphism are recognized here in the European species of Sphaeroceridae. The first type is characterized by distinctly separated macropterous and brachypterous forms. It was genetically interpreted by GUIBÉ (1939) for *Crumomyia pedestris*. GUIBÉ (1939) believed that the macropterous specimens are recessive homozygotes while the brachypterous and micropterous forms are heterozygotes and dominant homozygotes. However, considering the existence of submacropterous forms and the high variability of brachypterous forms (see Figs. 6–10) the genetic basis of this type of wing polymorphism is probably more complex. Undoubtedly, the oligogenes (possibly more than one) play the primary role but the cooperation of the polygenes is highly plausible.

The problem of almost purely brachypterous wild populations of this species could only be explained by their extremely humid habitat. In that environment a certain kind of directed selection has to occur, which results in the elimination of the macropterous phenotype from the population. However, because of genetic homeostasis, it is unlikely that the recessive alleles may be completely eliminated in this way, thus only the micropterous dominantly homozygous specimens remain in the population. In this connection Guibé's finding of reduced viability of the macropterous specimens seems to be rather important. If the relevant recessive alleles had pleiotropic effects and caused a decrease of the vitality or even the lethality in the homozygous state, it would result in the elimination of the macropterous phenotype



from the population even with the retention of the genetic homeostasis. However, the rare pterygopolymorphic populations are apparently genetically different. It is obvious that the recessive alleles of genes which control the wing polymorphism cannot have pleiotropic effects in these populations. Only under this presumption the macropterous specimens can be ecologically successful in habitats where no selective stress (pressure) operates against the macropterous phenotype. Indeed, the wing polymorphic populations were found to prefer a relatively dry terrestrial and hypogean habitats.

In my opinion, generally the same type of wing polymorphism also occurs in two European species of Limosininae, *Pullimosina mejerei* and *Pteremis fenestralis*. As regards *P. mejerei* the brachypterous form predominates in most populations; indicating a complementary operation of oligogenes while the brachypterous specimens ought to be dominantly homozygous or heterozygous. The variability of the mutual representation of both the brachypterous and macropterous forms in populations can be explained by the structure of the inhabited environment. In this case the so-called dispersive selection could also cooperate, because the macropterous specimens prefer the surface layer of the leaf litter while the brachypterous ones prevail deeper in detritus. However, these habitat-niches overlap, which enables free crossing of both forms and, consequently, also high genetic variability of the relevant population.

The genetic background of contemporary presence of wings of both macropterous and brachypterous type in a single specimen (as also found in *Pullimosina mejerei*, Fig. 4) has, to my knowledge, hitherto not been discussed. Inasmuch as this phenomenon only occurs in species with distinctly separate macropterous and brachypterous forms where the alary polymorphism obviously is governed by a single or a few oligogenes these extremely rare specimens probably possess a genetic mosaic of tissues. Thus, the genetic apparatus should be different in the left and right side of the body so that the normally long wing and the shortened wing can simultaneously develop in these specimens.

The wing polymorphism of *Pteremis fenestralis* is obviously also primarily controlled by oligogenes. The representation of the brachypterous phenotype in populations strongly varies depending on the geographical and climatic conditions. The purely macropterous populations living in southern latitudes possibly do not possess the (probably recessive) alleles determining the brachyptery. In case the brachypterous mutant specimen evolves in such population, it is probably soon eliminated by stabilizing (centripetal) selection. It seems that the northern and montane polymorphic populations inhabit habitat-niches with different microclimatic conditions (more humid, colder) where the brachypterous specimens can successfully survive, e.g. in deeper layers of mosses, in runs of rodents. In this way the mutant recessive alleles (determining the brachyptery) become fixed in the population. There is a remarkable variability of the venation in brachypterous specimens of *P. fenestralis*. Although these modifications undoubtedly depend on the degree of the wing reduction, they may have their own genetic basis because the venal mutants are also known in macropterous species.

Another type of wing polymorphism is that represented by *Puncticorpus cribratum*, *Spelobia pseudonivalis* and *Terrilimosina corrivalis*. In these species the macropterous (or submacropterous) to strongly brachypterous forms occur in a continuum, with various transient types. The genetic background of this type of wing polymorphism cannot be explained easily. Because the moderately brachypterous specimens seem to be the most common, it is probable

that the wing length is determined by polygenes which, according to ROFF (1986), seems to be a more general situation in insect wing polymorphism. In some of the above species the true full-winged form does not occur; despite this they display a remarkable variability of the phenotypes (wing length, venation). In *Puncticorpus cribratum* the polymorphic structure of populations is distinctly influenced by climatic conditions, with strongly brachypterous forms prevailing in northern, the submacropterous to macropterous ones in southern latitudes.

The last type of wing polymorphism was found in two European species, *Spelobia manicata* and *Phthitia spinosa*. Because both these species have a macropterous form, submacropterous transient (intermediate) forms and an only slightly brachypterous form, they seem to represent an initial stage of the wing polymorphism of the second type, probably genetically determined by polygenes.

All the above discussed types of wing polymorphism have likely evolved in consequence of the changes of the environment or of the way of life of the relevant species. According to the theory of population genetics, the mutant alleles have an evolutionary significance only when the environment (or conditions) changes so much that the old adaptive values also change, so that the mutant genotypes acquire high fitness. The above mentioned process then produces alterations of the genetic structure of the population and hence rapid evolution.

In the original environment inhabited by the macropterous population the mutant brachypterous specimens are probably quickly eliminated by means of the stabilized selection because their genotypes have lower adaptive values. However, after the change of the habitat or in consequence of the penetration into new habitat-niches (e.g. in deeper layers of detritus) the fitness (= ability to survive and reproduce) of brachypterous mutants strongly increases. This leads to the fixation of mutant alleles and, subsequently (owing to selection which operates against the macropterous specimens in a new habitat-niche because they have a lower fitness there) to the transformation of the genetic structure of the population in favour of the brachypterous form, particularly when the brachyptery is associated with dominant alleles (as is in *Crumomyia pedestris*). In some cases, where the new and original habitat-niche overlap, a distinctive effect of the dispersive selection may occur, which in one niche favours the macropterous form, in the other the brachypterous one. In this way the genetic variability of the population essentially increases which may result in the evolvement of further mutant forms (e.g. venal mutants).

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### References

- BRAUNSA. 1938: Die Flügelrückbildung bei der Strandfliege *Conioscinella brachyptera* Zett. (Diptera; Chloropidae) und die Beziehungen zur Ausbildung der Flügelsinneskuppeln. *Zoologischer Anzeiger* **123**: 281–295.
- BYERS G. W. 1961: Biology and classification of *Chionea*. Pp. 188–191. *Verhandlungen des XI. Internationaler Kongress für Entomologie, Wien 1960, Vol. 1*. Wien.

- COLLIN J. E. 1944: The British species of Anthomyzidae (Diptera). *Entomologist's Monthly Magazine* **80**: 265–272.
- COLLIN J. E. 1956: Some new British Borboridae (Diptera). *Journal of the Society for British Entomology* **5(5)**: 172–178.
- GUIBÉ J. 1939: Contribution à l'étude d'une espèce: *Apterina pedestris* Meigen (Diptère). *Bulletin Biologique de la France et de la Belgique, Supplément* **29**: 1–112.
- HACKMAN W. 1964: On reduction and loss of wings in Diptera. *Notulae Entomologicae* **44**: 73–93.
- MARSHALL S. A., ROHÁČEK J., DONG H. & BUCK M. 2011: The state of Sphaeroceridae (Diptera: Acalyptratae): a world catalog update covering the years 2000–2010, with new generic synonymy, new combinations, and new distributions. *Acta Entomologica Musei Nationalis Pragae* **51**: 217–298.
- MARTINOVSKÝ J. & STARÝ J. 1969: The discovery of brachypterous females of *Limnophila platyptera* (Macquart), with notes on the classification of this species (Diptera, Tipulidae). *Acta Entomologica Bohemoslovaca* **66**: 381–386.
- NARTSHUK E. P. 1987: Zlakovye mukhi (Diptera: Chloropoidea), ikh sistema, evolyuciya i svyazi s rasteniyami. [Grassflies (Diptera: Chloropidae), their system, evolution and plant associations]. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **136**: 1–279 (in Russian).
- PAPP L. 1976: Some terricolous Sphaerocerids and Drosophilids from Hungary (Diptera: Sphaeroceridae and Drosophilidae). *Folia Entomologica Hungarica, S. N.* **29(1)**: 75–86.
- PAPP L. & ROHÁČEK J. 1988: The Sphaeroceridae (Diptera) of Israel. *Israel Journal of Entomology* **21** (1987): 77–109.
- RICHARDS O. W. 1951: Brachypterous Sphaeroceridae. *British Museum (Natural History) Ruwenzori Expedition, 1934–1935*, **2(8)**: 829–851.
- ROFF D. A. 1986: The evolution of wing dimorphism in insects. *Evolution* **40**: 1009–1020.
- ROHÁČEK J. 1975a: Über das Vorkommen einiger Sphaeroceridenarten (Diptera) in einem Auenwald. *Folia Facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis* **15(1)**, *Biologia* **43** (1974): 91–95.
- ROHÁČEK J. 1975b: Die Flügelpolymorphie bei den europäischen Sphaeroceridenarten und Taxonomie der Limosina heteroneura-Gruppe (Diptera). *Acta Entomologica Bohemoslovaca* **72**: 196–207.
- ROHÁČEK J. 1975c: Three new species of the genus *Limosina* Macq. (Sphaeroceridae, Diptera) from Czechoslovakia. *Scripta Facultatis Scientiarum Naturalium Universitatis J. E. Purkynianae Brunensis, Biologia* **2**, **5**: 115–126.
- ROHÁČEK J. 1978: Revision of the European species of the *Limosina heteroneura*-group (Diptera, Sphaeroceridae). *Časopis Slezského Muzea, Opava (A)* **27**: 125–151.
- ROHÁČEK J. 1980: Sphaeroceridae (Diptera) collected by the soil trap method in submountain areas of North Moravia (Czechoslovakia). *Časopis Slezského Muzea, Opava (A)* **29**: 145–160.
- ROHÁČEK J. 1983: A monograph and re-classification of the previous genus *Limosina* Macquart (Diptera, Sphaeroceridae) of Europe. Part II. *Beiträge zur Entomologie* **33**: 3–195.
- ROHÁČEK J. 1984: Acalyptrate Diptera of peat-bogs in North Moravia (Czechoslovakia). Part 6. Sphaeroceridae. *Časopis Slezského Muzea, Opava (A)* **33**: 97–131.
- ROHÁČEK J. 1986: Čelad' Sphaeroceridae. Pp. 149–164. In: ČEPELÁK J. (ed.): *Diptera Slovenska II*. Veda, Bratislava, 435 pp (in Slovak).
- ROHÁČEK J. 1991: Sphaeroceridae (Diptera) of Czechoslovakia. Part 2. *Crumomyia* Macquart. *Časopis Slezského Zemského Muzea, Opava (A)* **40**: 1–27.
- ROHÁČEK J. 1994a: Wing polymorphism in European species of Sphaeroceridae (Diptera). Pp. 187–188. In: O'HARA J. E. (ed.): *Third International Congress of Dipterology, 15–19 August 1994, University of Guelph; Abstract Volume*. Guelph, 270 pp.
- ROHÁČEK J. 1994b: Sphaeroceridae (Diptera) of Slovakia: corrections and additions to faunal list. *Entomological Problems* **25**: 83–91.
- ROHÁČEK J. 1995: Sphaeroceridae. Pp. 163–171. In: ROHÁČEK J., STARÝ J., MARTINOVSKÝ J. & VÁLA M. (eds.): *Diptera Bukovských vrchov (Diptera of the Bukovské Hills)*. SAŽP – Správa CHKO a BR Východné Karpaty, Humenné, 232 pp (in Slovak, with English summary).
- ROHÁČEK J. 1996a: Sphaeroceridae (Diptera) of the Czech Republic: corrections and additions to the faunal list, with taxonomical notes. *Časopis Slezského Zemského Muzea, Opava (A)* **44** (1995): 219–240.
- ROHÁČEK J. 1996b: Revision of Palaearctic Stiphrosoma, including the *Anthomyza laeta*-group (Diptera: Anthomyzidae). *European Journal of Entomology* **93**: 89–120.

- ROHÁČEK J. 1999: Sphaeroceridae. Pp. 347–357. In: ROZKOŠNÝ R. & VAŇHARA J. (eds.): Diptera of the Pálava Biosphere Reserve of UNESCO, II. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia* **100**: 221–458.
- ROHÁČEK J. 2001: The type material of Sphaeroceridae described by J. Villeneuve with lectotype designations and nomenclatural and taxonomic notes (Diptera). *Bulletin de la Société Entomologique de France* **105(5)** (2000): 467–478.
- ROHÁČEK J. 2004: New records of Clusiidae, Anthomyzidae and Sphaeroceridae (Diptera) from Cyprus, with distributional and taxonomic notes. In: KUBÍK Š. & BARTÁK M. (eds.): Dipterologica bohemoslovaca 11. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia* **109**: 247–264.
- ROHÁČEK J. 2006: A monograph of Palaearctic Anthomyzidae (Diptera). Part 1. *Časopis Slezského Zemského Muzea, Opava (A)* **55(supplement 1)**: 1–328.
- ROHÁČEK J. 2009a: Sphaeroceridae. Pp. 260–271. In: ROHÁČEK J. & ŠEVČÍK J. (eds.): *Diptera of the Poľana Protected Landscape Area – Biosphere Reserve (Central Slovakia)*. SNC SR, Administration of the PLA – BR Poľana, Zvolen, 340 pp.
- ROHÁČEK J. 2009b: Sphaeroceridae Macquart, 1835. In: JEDLIČKA L., KÚDELA M. & STLOUKALOVÁ V. (eds.): *Checklist of Diptera of the Czech Republic and Slovakia*. Electronic version 2. <http://zoology.fns.uniba.sk/diptera2009> (accessed on 6.vi.2012).
- ROHÁČEK J. 2011: The fauna of Sphaeroceridae (Diptera) in the Gemer area (Central Slovakia). *Časopis Slezského Zemského Muzea, Opava (A)* **60**: 25–40.
- ROHÁČEK J., BÁEZ M. & BUCK M. 2003: The Sphaeroceridae (Diptera) of the Canary Islands and their biogeography. *Studia Dipterologica* **10**: 51–76.
- ROHÁČEK J. & BARBER K. N. 2005: Revision of the New World species of Stiphrosoma Czerny (Diptera: Anthomyzidae). *Beiträge zur Entomologie* **55**: 1–107.
- ROHÁČEK J. & BARTÁK M. 1999: Sphaeroceridae (Diptera) of peat-bogs in the Šumava Mts. (SW Bohemia, Czech Republic). *Časopis Slezského Zemského Muzea, Opava (A)* **48**: 9–32.
- ROHÁČEK J. & BARTÁK M. 2001: Sphaeroceridae. In: BARTÁK M. & VAŇHARA J. (eds.): Diptera in an industrially affected region (north-western Bohemia, Bílina and Duchcov environs), II. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia* **105**: 415–423.
- ROHÁČEK J., BARTÁK M. & KUBÍK Š. 1998: Diptera Acalyprata of the Hraniční (Luzenská) slat' peat-bog in the Šumava Mts. (Czech Republic). *Časopis Slezského Zemského Muzea, Opava (A)* **47**: 1–12.
- ROHÁČEK J., KUBÍK Š. & BARTÁK M. 2005: Sphaeroceridae. Pp. 335–348. In: BARTÁK M. & KUBÍK Š. (eds.): *Diptera of Podyjí National Park and its Environs*. Česká zemědělská univerzita v Praze, Praha, 434 pp.
- ROHÁČEK J. & MARSHALL S. A. 1982: A monograph of the genera Puncticorpus Duda, 1918 and Nearcticorpus gen. n. (Diptera, Sphaeroceridae). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* **109**: 357–398.
- ROHÁČEK J., MARSHALL S. A., NORRBOM A. L., BUCK M., QUIROS D. I. & SMITH I. 2001: *World catalog of Sphaeroceridae (Diptera)*. Slezské zemské muzeum, Opava, 414 pp.
- ROHÁČEK J. & PAPP L. 1983: Another new species of the Paralimosina beckeri-group from the Canary Islands (Diptera: Sphaeroceridae). *Folia Entomologica Hungarica* **44**: 147–152.
- STACKELBERG A. A. 1958: Materialy po faune dvukrylykh Leningradskoy oblasti. III. Diptera Acalyprata, ch. 1. [List of Diptera of the Leningrad Region, III. Acalyprata, part 1.]. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **24**: 103–191 (in Russian).
- STACKELBERG A. A. 1970: 83. sem. Anthomyzidae. Pp. 326–329. In: BEI-BIENKO G. YA. (ed.): *Opredelitel nasekomykh evropeiskoy chasti SSSR*. [Key to the insects of the European part of the USSR]. Vol. 5, pt. 2, Nauka, Leningrad, 943 pp (in Russian).
- VILLENEUVE J. 1918: Descriptions de deux espèces nouvelles du genre Limosina (Leptocera) Macq. (Dipt.). *Bulletin de la Société Entomologique de France* **1918**: 79–82.
- WHEELER T. A. 1994: Conioscinella zetterstedti Andersson (Diptera: Chloropidae), a chloropid fly with polymorphic wing reduction, new to the Nearctic and Central Palaearctic regions. *Canadian Entomologist* **126**: 1377–1381.