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Global chorotypes of European black flies (Diptera: Simuliidae)

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SUMMARY

Data on the distribution of 238 European black fly taxa recorded in 97 operational geographical units (OGUs), of which 54 are European, were taken from published primary and secondary sources, summarised, numerically analysed and evaluated for chorotype identification. In continental Europe, 225 species have been recorded, of which 91 were registered only on the mainland. On the European islands, 70 species have been recorded, 13 of which are exclusively there; among them, 10 are European endemics (5 on the Mediterranean islands and 5 in Macaronesia). The individual species were recorded in 1–64 OGUs, the observed frequency distribution of species, according to the occupied OGUs, is strongly asymmetric and skewed to the right. This distribution does not fit the Fisher's log-series distribution, the zero-truncated negative binomial, or the zero truncated Poisson distributions. The prevailing number of European black flies has a clear tendency to occupy small ranges. More than half of all species (128) are known from six or fewer OGUs (median = 6) and more than one-third of the species (35.5%) are from only 1–3 OGUs. One-quarter of all species, including 11 species complexes, are known from 14 or more OGUs (Q3 = 14). Only 12 species (~ 5%) are known from 39 or more OGUs; half of them being recognised species complexes. A wide range can be considered a property of a species complex, and by abduction, a taxon with such a range can be considered a species complex. Splitting a species complex into separate species can result in a range-splitting effect, i.e. the disintegration of the original large range into a number of overlapping or non-overlapping smaller species ranges can result in existing chorotypes disappearing or new ones arising. Cluster analysis C1 (CLC = complete linkage clustering, Baroni-Urbani & Buser index of similarity) provided 30 significant clusters, 26 of them isolated, with 1 to 24 species each (median = 5.5). Cluster analysis C2 (CLC, Jaccard's index of similarity) provided 53 significant clusters, 26 of them isolated, with 1 to 20 species each (median = 3). The cophenetic correlation coefficient r_{coph} between C1 and C2 was 0.8015, indicating a high agreement between the two classifications. In an expert assessment based on cluster analysis, 29 global chorotypes were distinguished. According to the overall range extent and its location on the continents, the chorotypes were arranged into seven groups as follows: Holarctic (26 spp., American–European, Pan-Holarctic,

Holarctic boreal, Palaearctic–East Beringian chorotypes), Palaearctic (40 spp., Pan-Palaearctic, Euro–Asian, Sibero–European), West–Central Palaearctic group (10 spp., Central Asian–Euro–Mediterranean, Central Asian–Turano–Euxinian, Turano–Caucasian), Western Palaearctic (18 spp., Euro–Mediterranean, Mediterranean–Macaronesian, Macaronesian–West Mediterranean), European (86 spp., Pan-European, Western European, Northern European, Central European, Apenninian, Balkan, Eastern European), Mediterranean group (53 spp., Pan-Mediterranean, West Mediterranean, East Mediterranean, Euxinian, Crimean, Caucasian), and the Macaronesian group (5 spp., Azorean, Madeiran, Canarian). The main result of the analysis of ranges of European black flies is the description of 29 global chorotypes. The analysis shows that the chorological structure of the European black fly fauna is complex and it varies significantly in different parts of the continent and adjacent islands. This can be the start for further zoogeographical, phylogeographical and other analyses in this area of research.

INTRODUCTION

Black flies (Diptera: Simuliidae), with almost 2,400 extant species (Adler 2022), are prominent and economically serious annoying pests of birds and mammals, as well as vectors of their parasitic diseases. At the same time, black flies are a considerable part of food webs especially in boreal ecosystems.

For several centuries, the simuliids have attracted interest primarily as pests of humans and both domestic and wild animals. Females of approximately 98% of the species are obligately anautogenous or primiparous autogenous and attack humans, mammals, and birds as blood donors. However, anthropophilic species represent only up to 10% of all species (Crosskey 1990, Malmqvist et al. 2004, Adler and McCreadie 2019). High biting activity with a daily biting rate of up to several thousand or tens of thousands of attacks (Jedlička and Halgoš 1978, 1982, Jedlička 1988, Országh et al. 1994) can annoy hosts to such an extent that there may be subsequent reductions in outdoor work and recreational activities of humans, as well as reduced livestock production leading to severe economic losses (Wilhelmi 1920, Gräfner et al. 1976, Jedlička 1988, Jedlička and Stloukalová 2003, Betke 2003, Adler and McCreadie 2019). Mass sucking of blood associated with the injection of salivary haemolytic, anticoagulative, and vasodilatory secretions results in various skin manifestations such as haemorrhagic erythema and edema. It can lead to simuliosis

(black fly fever) associated with symptoms such as headache, nausea, fever, and even general intoxication. In more severe cases, haemorrhagic shock and death may occur. As bloodsuckers, simuliids are also proven, or hypothetical vectors of some viruses (Mead et al. 2004, Kuzmin et al. 2009) and specific vectors of several parasitic diseases of humans, domestic, and wild animals, such as blood protists and filarial nematodes (Reeves et al. 2007, Santiago-Alarcon et al. 2012, Adler and McCreadie 2019). However, the most severe disease transmitted by black flies as specific vectors is human onchocerciasis, known as river blindness, according to the last stage of the disease. Based on recent estimates (WHO 2020, 2021), more than 240 million people in sub-Saharan Africa, Yemen, and tropical Latin America are exposed to human onchocerciasis. Out of this population, more than 14.6 million people have experienced skin manifestations as a result of the disease, and 1.15 million have lost vision.

The second and less common reason for studying simuliids is their role in running waters. The eggs, larvae, and pupae of black flies are adapted to life in lotic waters (Rubtsov 1956, Crosskey 1990, Adler et al. 2004). Larvae are overwhelmingly filter-feeding, but scraping and predation occur also (Crosskey 1990). They ingest fine particulate organic matter of size 0.1-350 μm, like bacteria, algae, and diatoms, and are able to receive dissolved organic material (Fredeen 1960, Carlsson 1962, Wotton 1976,

2009, Wallace and Merritt 1980). They can catch about 1% of the seston floating around them (Malmqvist et al. 2004). The assimilation efficiency of energy from food is estimated very differently, that is from 2 to 90% depending on food type (Wotton 1978, Ladle and Hansford 1981). In addition, a large part of the organic material is transferred to a higher level in the more concentrated form of larger faecal pellets usable in the next parts of the detrital food chain (Wotton et al. 1996; 1998). Black fly larvae and pupae are also an important component of food for carnivorous insects, fish, and birds (e.g. Malmqvist 1994, Einarsson et al. 2006).

Simuliids are distributed worldwide, with the exception of Antarctica and some islands and deserts without watercourses (Crosskey 1990, Currie and Adler 2008).

Biogeography, initially the study of the distribution of organisms, has recently aimed to understand "the temporal and spatial patterns of life on Earth" (Schickhoff et al. 2014). Knowledge of the distribution of taxa of different levels has been and is used primarily in the biogeographical regionalization of the Earth at different levels up to the global level (e.g. Wallace 1876, Holt et al. 2013, Morrone 2015, Rueda et al. 2013, Escalante 2017), however, animal distribution data were one of the starting points and are still mutually informative with many disciplines, such as evolutionary biology (e.g. Darwin 1859, Darlington 1957, Morrone 2009), ecology (e.g. Hardie and Hutschings 2010, Heads 2015), parasitology and medicine (e.g. Nieberding et al. 2008, Scheiner 2009, Smith 2009, Morand and Krasnov 2010), conservation (e.g. Whittaker et al. 2005, Hurlbert and Jetz 2007) and other fields of the study of life.

Descriptive or systematic biogeography has two objectives: The identification of areas (regionalisation) using species distribution as a variable and the opposite procedure, the systemization of species according to their ranges with the aim of defining distribution types (Fattorini 2016). In biogeography, the geographic range of a species or a higher taxon is the basic unit, and with its static and dynamic properties and processes, the most general geographical characteristics of the taxon (de Lattin 1967, Kryzhanovskiy and Starobogatov 1974, Brown et al. 1996). The subject of chorology is the description of the location and form of the range on the Earth's surface. Its task is to "accurately and correctly describe the distribution ranges of animals" (de Lattin 1967). The synthetic result of chorology is the definition and classification of chorotypes as the first stage of biogeographical analysis (Hausdorf 2002) and the basis for clarifying history and finding the causes of their formation (Passalacqua 2015).

The classification categories of taxon ranges have not been and are not always understood clearly and uniformly (for an overview, history and critical discussion see Morrone 2014a, Fattorini 2015, 2016, and Passalacqua 2015). The term chorotype and its content are still understood in at least two ways: 1) as a group of species with a similar overall distribution with recurrent distribution ranges called global chorotype (Fattorini 2015), corresponding to similar terms (Verbreitungstype, Arealtype, chorological type, etc.); and 2) as a group of species with a similar distribution in a certain delimited territory, the local chorotype according to Fattorini (2015). Global chorotypes are basal forms of ranges from a purely geographical point of view without any assumption about their origin, formation, and dynamics. Global simuliid chorotypes in this sense are the subject of the present study.

The classification of species ranges and their types is one of the complex issues of zoogeography (Kryzhanovskiy and Starobogatov 1974). In the chorology of plants, the arrangement of species ranges into chorotypes was considered impossible (Meusel 1943, Meusel et al. 1965), and the distribution of the species was characterized by the diagnosis of the range presented by a formula in which the nominal values of the four variables express the

location of the range, its relation to climatic zones, oceanity and continentality, and altitude. Such an indication of the range location can be considered as analogous to the ordination of individual range in the multidimensional space of four nominal axes. However, this approach also has its pitfalls (e.g., Jäger 1968). Nevertheless, Holub and Jirásek (1968) considered range typification and its organization into a system important. This method has not been adopted in zoogeography. To indicate the type of distribution, it is used almost exclusively or as a simple toponymic naming of the range, perhaps with a faunagenetic background, or various detailed systems of chorotypes.

Various definitions and names of different types of distribution have been used in the past for European species, including in part chorotypes (for an overview see Vigna Taglianti et al. 1992, 1999, Fattorini 2015, 2016, Passalacqua 2015). In order to unify terminology and define a limited number of chorotypes involving all types of ranges, Vigna Taglianti et al. (1992, 1999) designed a hierarchical three-level system based on the size of the ranges and their location, with three units at the highest level, i.e. a) the main chorotypes of the Western Palaearctic fauna, with special reference to the Near East, b) cosmopolitan and subcosmopolitan, and c) endemic ranges. Within the first of them (main chorotypes of the Western Palaearctic […]), they distinguish five major groups (Holarctic, European, Mediterranean, Palaeotropical extending to the Mediterranean, and Palaearctic with peripheral extension to the Western Palaearctic) and 38 chorotypes at the third level in total (cosmopolitan and endemic units are not detailed nor counted). This system was commonly used (e.g. Parenzan 1994, Stoch and Vigna Taglianti 2006, Bukejs 2012, Fattorini 2013, Pellizzari et al. 2015, Hubenov 2021, and others).

In addition to various earlier proposals, two decades before the later more widely accepted system of Vigna Taglianti et al. (1999), two other proposals were published that remained unknown or did not find a wider response, but were accepted and used mainly in Russian-written publications.

The first of them, the hierarchical classification of insect ranges based on the regionalization of the Palearctic, was designed by Emelyanov (1974). At the highest level, the ranges are arranged in two groups (1. large and 2. narrow). Within the main group of large ranges, three subgroups are defined, viz. 1a) the largest (5 types based on the main Palaearctic trans-zonal and trans-sectorial regions: Palaearctic, Hyadian, Northern Palaearctic, Southern Palaearctic, Tethydian), 1b) zonal ranges (6 types based on latitudinal zones: arctic, arctoboreal, boreal, boreo-subtropical, subboreal, subtropical), and 1c) moderately large (usually not exceeding two or three neighbouring provinces). Range types within 1c and 2 and their names are formed according to the provincial divisions of the Palaearctic. Putting emphasis on latitude, he followed Meusel (1943) and Holub and Jirásek (1967, 1968). Although, according to Kryzhanovskiy (2002), this scheme is quite controversial, it has found application, especially among Russian authors (e.g. Krivokhatsky and Emelyanov 2000, Kustov 2006, 2013, Plotnikov et al. 2013, Mikhailichenko 2014, Mikhailichenko et al. 2013, and others). The proposed system of chorotypes also contains draft rules for creating their names.

About a decade later, Gorodkov (1983, 1984) came up with a formalized concept of the hierarchical system of chorotypes (range types). Based on Meusel's (1943) concept of the three-dimensional range, he used a three-level hierarchic system with four types at the highest level according to the range size, i.e. cosmopolitan, polyregional, Holarctic, and Palaearctic. Within each type of the first level, depending on the form and location of the range (in particular longitudinal), he distinguished between 0 and 7 types of the second level, and within these, 0 to 2 types of the third level. The disadvantage of this system is that it has been developed for the northern, humid part of the

Palaearctic whereas the southern part is absent. However, it was used more often than the previous one, mainly in Russian arachno-entomology, including dipterology (Esyunin et al. 1993, Medvedev 2009, Esyunin and Marusik 2011, Sushko 2012, Barkalov 2012, 2016, Dedyukhin 2016,) and has also been reused for simuliids (e.g., Panchenko 1999, 2003, Aibulatov 2014a, b, 2016a, b, Petrozhitskaya and Mirzaeva 2019). Based on the principles of Gorodkov, some authors developed his system, especially with greater use of formalization and hierarchization (Panchenko 1999, 2003, Ryndevich 2013).

Regarding black flies, four ways of characterizing the species distribution are used. First, the distribution of the species is given as a list of regions of different hierarchical levels in which the species is present (e.g. Rubtsov 1956, 1959-1964, Rubzow and Yankovsky 1988, Budaeva and Khitsova 2010a, Aibulatov 2014a, Budaeva et al. 2016, Crosskey 2017, Adler 2022). This type of data is a usable source of information on species distribution for further analysis.

Ranges of superspecific taxa (e.g. Rubtsov 1956, 1959–1964) are certain type of generalization and cannot usually be used in the typology of species ranges.

In parallel with the previous method, Rubtsov (1956, 1959–1964) also used a second one. He tried to characterize the types of species distribution using not the geographical, but the ecological point of view at the highest level using the category of stream (arctic, mountain-taiga, taiga-forest, steppe, Mediterranean mountain, and Mediterranean lowland) and river species (boreal and Mediterranean). He did not list the distribution types for all species; however, 57 European species can be found in the examples.

In the third approach, the authors used the category of faunistic or zoogeographical complex, i.e. a set of species that was formed in a single territory in the conditions of a single landscape and during a single period (e.g.

Kryzhanovskiy and Starobogatov 1974), which is a category corresponding approximately to the category Faunenkreis (de Lattin 1967) or close to the cenocron (Morrone 2014a), respectively. In various studies, 5-6 complexes out of about 10 are used in various combinations, often bound to latitudinal zones (polyzonal, boreal, boreal-polyzonal, boreal-forest, boreo-montane, mountain-plain steppe, steppe, ancient-mediterranean, mediterranean, subarid). This approach was used in the zoogeographic analysis of black flies of the Belarusian-Ukrainian Polesie (Kaplich et al. 2011), the subzone of (Eastern) European mixed forests (Kaplich et al. 2014, 2015), Ukraine (Sukhomlin 2013, Sukhomlin and Zinchenko 2013) and the forest-steppe zone of Central Russia (Budaeva and Khitsova 2010b).

The fourth approach is the detection and definition of (global) chorotypes (range types in some studies). Studies on black fly chorotypes are relatively rare and mostly devoted to chorotypes of non-European regions – North America (Currie (1997) and Palaearctic Asia or their parts (Halgoš 2005, Aibulatov 2014a, b, 2016a, b, Petrozhitskaya and Mirzaeva 2019). For the 77 species found in the Yukon Territories, Currie (1997) identified 11 chorotypes, four of which may hypothetically occur in Europe. For Mongolian black flies, Halgoš (2005) used a two-level system with 11 range types, in eight of them 26 species occurring in Europe were also included. A two-level system was also applied by Aibulatov (2014a, b, 2016a) in studies on the black flies of Yakutia (Sakha). In two higher-level groups (Holarctic and Palaearctic), he used 17 range types, 9 of which also included European species. In a study on 38 species in southern Evenkia, Petrozhitskaya and Mirzaeva (2019) consistently applied Gorodkov's principle. From a combination of seven longitudinal (2 Holarctic and 5 Palaearctic) and five latitudinal zones, 35 chorotypes were hypothetically possible, but only 14 of them were actually found, seven of which extend into Europe.

Chorological studies on European black flies are similarly scarce. In a preliminary analysis of the distribution of black flies in the Western Carpathians, six types were recognized (Jedlička 2000), viz. Holarctic, Palaearctic, Euro-Siberian, West Palaearctic, Sub-Mediterranean (incl. Euro–Mediterranean) and European. A more detailed system of simuliid chorotypes using Gorodkov's principles (1983, 1984), although not explicitly stated, was developed by Panchenko in the analysis of the distribution of black flies of Crimea and the whole of Ukraine, respectively. Panchenko used a formalized three-level hierarchical system of phyla, classes, and groups. In the first study (Panchenko 1999), he defined four phyla, eight classes, and 16 range groups for 36 Crimean species. In his second study of the whole of Ukraine (Panchenko 2003), he also used a three-level system, but substantially restructured it defining only two phyla, eight classes and 53 range groups with 105 nominal species.

Black fly chorotypes appear only marginally in more broadly designed studies. In a study on terrestrial Diptera from NW Caucasus, Mikhailichenko et al. (2013) listed a single black fly species, *Simulium tarnogradskii* Rubtsov, in the Euxine chorotype. Hubenov (2021) summarized data on the distribution of Diptera in Bulgaria including 74 black fly species (some doubtful species/records or both), for which he used 42 chorotypes (range types), mostly according to Vigna Taglianti et al. (1999) and also taking into account Gorodkov (1984). In other studies, only the numbers of species in chorotypes are reported, e.g. the review study on the fauna of haematophagous dipterans from North-western Russia (Medvedev 2009) used 13 range types, seven of which are also known for black flies, but only the numbers of species and several examples in each type was given, which are not always consistent with current records.

The aim of the present study is:

- to summarise and update data on the distribution and species richness of European black flies,

- to analyse their distributional patterns,

- based on this analysis, to identify global chorotypes as the first step in a further study of the species distribution, and

- to stimulate the study and analysis of the distribution of black flies, which are currently not at the forefront of interest.

MATERIALS AND METHODS

Data

The data on species distribution were taken mainly from two sources – the 2022 version of "World Blackflies (Diptera: Simuliidae): a Comprehensive Revision of the Taxonomic and Geographical Inventory [2022]" (Adler 2022, Inventory in the following text) and Simuliidae in Fauna Europaea (Crosskey 2017, FaEu). Both sources contain secondary data summarizing primary data on the occurrence of species mostly at the country level, in the cases of large countries in their geographically defined parts. However, the data concerning black flies in the recently displayed version of FaEu are partly out of date, being transferred from the original edition (Crosskey 2004) with no or minor changes.

Additional data were found for Armenia (Andrianov et al. 2015), Belgium (Lock 2018), Bulgaria (Kovachev 1973, 1976, 1979, 2000, Russev et al. 1976), Croatia (Đuknič et al. 2019), Finland (Aibulatov 2009a), Italy (Rivosecchi et al. 2007), Kazakhstan (Makatov 2007, 2008a, 2008b), Kyrgyzstan (Aibulatov 2014a), Macedonia (Kovachev et al. 1999), Mongolia (Aibulatov 2014a, Yadamsuren et al. 2020), Montenegro (Đuknič et al. 2019), Netherlands (Lock and van Maanen 2014) Romania (Jedlička 2019), Russia, both the European part and Siberia (Rubtsov 1956, Usova 1961, Mitrokhin 1973, Patrusheva 1974, 1982, Bodrova 1978, Ostroushko et al. 2007, Petrozhitskaya and Rodkina 2007a, b, 2009a, b, Aibulatov 2009a, b, 2013, 2014a, b, Budaeva and Khitsova 2010a, b, 2016, Kaplich et al. 2011, Aibulatov and Baryshev 2016, Budaeva et al. 2016, Vasilevich

and Kaplich 2016, Yankovsky 2006), Spain (Rivosecchi et al. 2007, López-Peña and Jiménez-Peydró 2017), Turkey (Basören and Kazanci 2016) and Ukraine (Rubtsov 1959-1964, Panchenko 1991, 1999, 2000, 2003, 2005, 2012, 2013, 2016, Sukhomlin and Zinchenko 2008, 2013, 2016, Sukhomlin et al. 2008, Kaplich et al. 2011, Teplyuk and Sukhomlin 2018, Usova and Panchenko 1973).

Territory and geographical operational units

The extent of the territory of Europe is adopted as defined in FaEu (de Jong et al. 2014), i.e. the European mainland and islands, incl. the Macaronesian islands (excluding Cape Verde Is.), with the addition of Caucasus (Kustov 2015).

As operational geographical units (OGUs), countries or their parts as used in the Inventory were used in the analyses. Regarding the non-European Palaearctic, only those where species known from Europe have been registered were included. In the case of Denmark, Greece, France, Portugal, Spain, and Italy, only the mainland without islands is included, i.e. the Azores, Balearic Islands, Canary Islands, Caucasus, Crimea, Faeroe Islands, and Madeira, as well as in the case of Ukraine without the Crimea peninsula, all of which are treated as separate OGUs for zoogeographic reasons. Great Britain was treated as three OGUs: England, Scotland, and Wales. The European part of Russia was subdivided into five units – Karelia and Murmansk region, Northern Russia, Central Russia, Southern Russia, and the Caucasus; the Asiatic part was subdivided into Western Siberia, Eastern Siberia, and the Far East (Adler 2022, Soós and Papp 1984). China was treated as four OGUs: North-western China, North-eastern China, Northern China, and Central and Southern China. The territory of Canada was divided into Yukon, Northwest Territories (CAN-NWT), Nunavut (CAN-Nun), the Cordilleran part (CAN-Cord), Prairie Provinces (CAN-prair), and Eastern Canada (CAN-East). The territory of the USA is treated as Alaska, and three zones from the north-west to the south-east states (USA1-3). Seven territories – Albania, Andorra, the Channel Islands, Kosovo, Liechtenstein, and Malta – have not been included due to missing or scarce data on limited species' numbers and/or the very small area concerned. After these adjustments, 97 OGUs were used in the analyses.

We use the toponymic term Middle Asia as used in biogeography (e.g. Cowan 2007, Ryndevych 2013, Hurka et al. 2019).

Species included

The initial list of 255 extant species (described and named) and species-level taxa (formally undescribed and unnamed morphoforms and cytospecies considered species, as defined by Adler 2022) registered in Europe was extracted from the Inventory (Adler 2022). Additional seven species (*Helodon rubicundus* Rubzov, *Prosimulium tridentatum* Rubtsov, *Simulium delizhanense* (Rubtsov), *S. malyschevi* Dorogostaisky, Rubtsov and Vlasenko, *S. kurense* Rubtsov and Djafarov, *S. aemulum* Rubtsov, *S. curvitarse* Rubtsov) with no European entries in the Inventory were added from other published sources (see above). From this extended list of species, we omitted two nomina nuda (*S.*? *anomalum* Eversmann and *S.*? *laticornis* Knoz). Four other questionable species (*S. parvum* Enderlein, *S.*? *canescens* Bréme, *S.*? *incanum* Loew, and *S.*? *lividum* (Schellenberg)) were also excluded from the list in FaEu (Crosskey 2017). All of them were described a long time ago and were not reliably reported in modern times.

Furthermore, we omitted two morphoforms, i.e. *Simulium* 'aff. *monticola*' Dušinský, Kúdela, Stloukalová and Jedlička and 'II' Grenier (*Simulium* sp. 'A', attrib. Dorier), as well as four cytospecies ('Crete' Procunier (*Metacnephia*), 'K' Leonhardt (*aureum* cytospecies); 'IL-8' Adler, Belqat, González, Pérez and Seitz (*vernum* group cytospecies), *S.* (*Nevermannia*) '4' (Chubareva and Petrova)), all

not being described and named formally as species.

We divided two species from the list into two taxa each for our analysis. In addition to the true *Simulium tuberosum* (Lundström) distributed in the Nearctic and northern Palaearctic, a second, formally unnamed taxon, was included here under the name *S.* aff. *tuberosum*. It is recorded in many European countries as *S. tuberosum*, but is distinct from the *S. tuberosum s. str.* (Adler and Kuusela 1994) and marked by a question mark in country records in the Inventory. In the case of *S. ruficorne* Macquart, we accept the opinion of Cherairia and Adler (2018) on the probable identity of two cytoforms (of five recently recognised), and instead of *S. ruficorne* we included *S. beckeri* Roubad (cytoform A1/A2) and *S. annulipes* Becker (cytoform C).

In the next step, this adapted list containing 252 species or species-level taxa was checked for doubtful entries, namely, records marked with a question mark in the Inventory (Adler 2022) as well as records isolated in Europe and outside of known and accepted distribution range of the species. Such records in a single country may have been the results of misidentification or error. Therefore, we omitted *Metacnephia persica* (Rubtsov), *M. ramificata* (Rubtsov), *M. sommermannae* (Stone), *Simulium brachyanterum* Rubtsov, *S. fluviatile* Radzivilovskaya, *S. alajense* Rubtsov, *S. latimentum* (Rubtsov), *S. bimaculatum* (Rubtsov), and *S. exile* (Rubtsov) recorded from Romania, and *S. delizhanense* (Rubtsov), *S. desertorum* Rubtsov, and *S. kurense* Rubtsov & Djafarov from Bulgaria. The exclusion of Ukrainian records of *S. pavlovskii* Rubtsov is based on recent revisions (Panchenko 2016, Sukhomlin and Zinchenko 2016). A half-century-old record of *S. deserticola* Rubtsov was not confirmed later and needs revision (K. B. Sukhomlin, pers. com.), and we have omitted it from the species list. This procedure in total resulted in the exclusion of 14 taxa from the analysis.

The most recent records published after 2021 could no longer be taken into account.

After all these adjustments, the final list analysed in the study consists of 238 species-level taxa.

Data processing

Source data available in text format were coded into the presence/absence (1/0) matrix of 238 species x 97 OGUs using standard MS Excel functions. This primary data matrix consisting of 23,086/fields contained 2,523 positive entries.

The data matrix was analysed using a three-step procedure consisting of 1) empirical assessment, 2) numerical cluster analysis, and 3) the final chorotype identification, definition and species assignment.

1. Empirical assessment

In the first step, each author separately and independently assigned each species empirically according to its distributional data to one of the chorotypes according to Gorodkov (1983, 1984) and one according to Vigna Taglianti et al. (1992, 1999). Assignments were compared, and in case of differences among the authors, the differing assignments were discussed and unified by consensus. If the numerical classification provided a controversial assignment, this was used in the third step as an auxiliary criterion.

2. Cluster analysis

As similarity measures for cluster analysis, two indices mainly used in zoogeography were selected, viz. the second index of Baroni-Urbani and Buser (1976, originally S**, further BB2) and Jaccard's index (Jaccard 1901, JAC). BB2 considers both positive and (down-weighted) negative matches of species presences, JAC is based on positive matches only (Hubálek 1982). Both indices satisfying the theoretical axiomatic conditions are admissible for use in cluster

analysis (Baroni-Urbani and Buser 1976, Hubálek 1982), they have known and tabulated critical values (Baroni-Urbani and Buser 1976, Real 1999), and are commonly used in biogeography (Márquez et al. 2001).

Similarity matrices were transformed into dissimilarities in the clustering procedure.

As cluster analysis, complete linkage clustering (CLC) was used. This method is not affected by cluster size and dilates the clustering space, thus accentuating the differences among clustered objects (Borcard et al. 2011). The results were two classifications: C1 (CLC+BB2, cluster numbers 101-130) and C2 (CLC+JAC, cluster numbers 201-253).

The BB2 was calculated in RMacoqui (Olivero et al. 2015), JAC in R environment using the stats package hclust (R Core Team 2021). The cluster analysis was performed and graphically adjusted in R environment using packages hclust, stats, and dendextend (Galili 2015, R Core Team 2021). Other calculations were performed using standard statistical and text functions in MS Excel (version 12, Microsoft Corporation 2019).

In both classifications, only clusters branched below the critical value of the similarity index used, referred to as significant, were taken into account and accepted. Clusters with a similarity of zero to all other clusters are a special case, hereinafter referred to as isolated clusters.

3. Chorotype identification and assignment of species

The resulting accepted clusters of C1 and C2 analyses were cross-tabulated and then the intersections of clusters were used as a basis for chorotype identification in this step. In ambiguous cases and/or outlying species, these species were assigned to chorotypes according to the expert evaluation of species range from the first step, considering the criteria specified for individual chorotypes or groups of chorotypes in the Results. In defining and arranging groups of chorotypes, we used the longitudinal aspect of ranges following Gorodkov (1983, 1984). The identified chorotypes and chorotype groups were depicted on the maps using Adobe Photoshop, version 25.9.1. The map from Natural Earth (https://www.naturalearthdata.com, accessed on 3 June 2024) was used as the background. The boundaries of the chorotypes are generalized and do not always show potential gaps and outliers.

RESULTS

Data on the distribution of European black flies compiled from several sources are summarized and numerically analysed for the first time. We analysed the data in three interrelated directions: species richness in Europe, the size of the range of European species, and the definition of global chorotypes including the assignment of species to them.

Species richness

Of black flies registered in Europe, 238 taxa were included in the analysis, among them, three forms were treated here as species, i.e. *Simulium beckeri*, *S. annulipes*, and *S.* aff. *tuberosum*.

Of all the species analysed, only 102 are endemic to Europe (incl. Macaronesia), representing 42.9% of the species registered in Europe. Europe shares 96 species with Palaearctic Asia, 23 of which are also known from North America. Three other species known from both Europe and North America are missing in Asia. Only one of them, *Simulium vittatum* Zetterstedt, with the core of its range on the American continent, also known from Greenland, Iceland, and the Faeroe Is., does not enter the European mainland or the more southern Atlantic islands. Europe has 39 species in common with Palaearctic Africa (except for questionable records), only two of which are missing in continental Europe (*S. velutinum* (Santos Abreu) and *S. ibleum* (Rivosecchi)) and 15 of them are not known from the Mediterranean islands.

In continental Europe, 225 species were recorded, 91 of which were recorded only on the mainland. 70 species are known from the European islands (Mediterranean islands 41 spp., British Isles 35, Macaronesia 10, and North Atlantic islands 4), 13 of which are exclusively present there. Among them, ten are European endemics: five are known from the Mediterranean islands and five from Macaronesia. The other three species registered only on the European islands are also known from Africa, Asia or America. At present, there are no species registered exclusively in the British Isles (incl. the Channel Islands). A more detailed look at species richness, however, is beyond the scope of this study and will be published separately elsewhere.

Range size and splitting effect

The range size of a species is one of the basic characteristics used to define chorotypes. The data used do not allow us to directly assess the range size according to the areas in which the individual species have been recorded, as the size of the OGUs is very different, ranging from several hundred (e.g., Madeira) up to more than 7 million km^2 (Eastern Siberia). Nevertheless, the number of OGUs in which the species occurs indicates the relative size of the range compared to other species.

The occurrence of species in OGUs shows frequency distribution strongly skewed to the right (skewness = 1.78, Fig. 1). The observed frequencies do not fit Fisher's log-series (Pearson's goodness of fit test $\chi^2 = 104.235$, P < 10^{-3}), zero-truncated negative binomial ($\chi^2 = 114.021$, P < 10^{-4}), nor the zero-truncated Poisson distributions ($\chi^2 = 3.3922 \times 10^{17}$, P < 10^{-5}). Experimental frequencies are closest to Fisher's log-series distribution (Fig. 1). The biggest difference is in the frequencies of the first three classes, where the observed frequencies are significantly lower than expected. On the contrary, on the right side of the distribution, observed frequencies predominate over expected, in some classes this is across all compared distributions.

In European black flies, the species range sizes vary widely from 1 to 64 OGUs. More than half of all species (128, that is 53.78%) are known from six or fewer OGUs (median = 6).

In a single OGU, 53 species (22.3%, first quartile = 2) were registered, 16 species (6.7%) occurred each in two and three OGUs, thus more than one-third of the species (35.7%) were registered in one to three OGUs. These data suggest that European black fly species have a clear tendency to occupy small ranges.

This trend is even more distinct in European endemics, of which more than half (53, that is 51.96%) are known from only one OGU (median = 1), 16 species (15.68%) from two, 7 species (6.86%) from three OGUs, 6 species from 4 OGUs (5.88%). In summary, almost three-quarters of European endemic species (74.50%) were recorded in less than four OGUs (third quartile = 4).

Only one-quarter of all species, including 11 species complexes (out of 15 known from Europe), is known from 14 or more OGUs (third quartile = 14), and 12 species (~ 5%) are known from 39 or more OGUs (percentile 0.95= 38.4). Half of them are recognized species complexes with described infraspecific forms *Simulum ornatum* (Meigen)–64 OGUs *S. vernum* Macquart–53), *S. noelleri* Friederichs–50, *S. cryophilum* (Rubtsov)–47, *S. pseudequinum* Séguy–47, *S. reptans* (Linnaeus)–45), and the other half are species not listed among species complexes (*S. equinum* (Linnaeus)–49, *S. angustitarse* (Lundström)–46, *S. erythrocephalum* (De Geer)–45, *S. angustipes* Edwards–44, *S. aureum* Fries–40, *S. rubzovianum* (Sherban)–40) but according to the known variability and/or known infraspecific forms, they can be assumed to be complexes. The other five European species complexes (*S. bezzii* (Corti)–34, *Prosimulium rufipes* (Meigen)–24, *S. paraequinum* Puri–23, *P. latimucro* (Enderlein)–22, *Stegopterna trigonium* (Lundström)–18) also fall into the

fourth quarter of the distribution. The last four species complexes (*S. colombaschense* (Scopoli)–13, *P. ursinum* (Edwards)–12, *S. reptantoides* Carlsson–10, *P. rachiliense* Djafarov–9) fall into the upper half of the distribution.
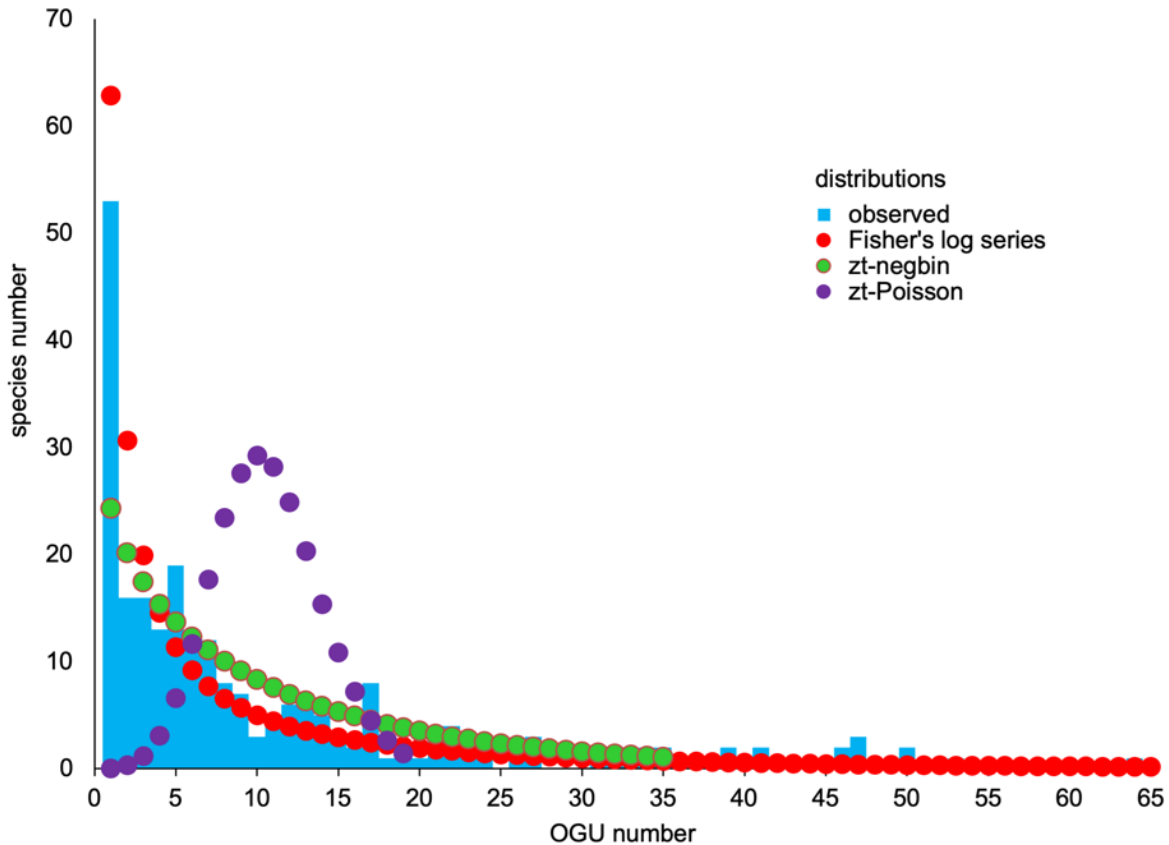

Figure 1. Observed and expected frequencies of the species in OGUs. On the right side, the class marks are omitted in classes with expected frequency below 1 in zero truncated negative binomial distribution (zt-negbin) for k ≥ 36, and in zero truncated distribution (zt-Poisson) for k ≥ 20.

A wide range seems to be one of the zoogeographical features of a species complex. Based on this premise, it can be abducted that any taxon with such a large range may probably be a species complex. As shown in the past, two extreme situations may arise from a chorological point of view, if after taxonomic analysis such a species complex is divided, and its forms are erected to valid species. First, with complete sympatry of the newly erected species, their ranges, and thus the chorotype will not change significantly; only the number of species allocated in it will increase. Second, if the erected species are completely allopatric with smaller ranges, they may be reassigned to other known or new chorotypes, and the current chorotype with high probability may disappear. The options outlined can be considered to be extreme possibilities, and in reality, rather diverse transitional states will arise. In any case, the disappearance of some of the current chorotypes is likely in black flies. This phenomenon is hereinafter referred to as the splitting effect. The splitting effect could eventually shift the observed frequencies closer to the expected theoretical ones.

Clustering results

Numerical analysis (NC) performed as cluster analyses C1 (CLC + BB2) and C2 (CLC + JAC) resulted in several dozen clusters at different levels. In the analysis, we only accepted significant clusters.

C1 provided 26 isolated clusters (Fig. 2 and Supplementary Material Fig. S1). Three of them are further branched in the zone of statistically significant dissimilarity into two, two, and three significant clusters respectively. The result was 30 accepted clusters (numbered 101–130) with 1 to 24 species each (median = 5.5); six clusters consisting of one species each, 14 clusters containing 2–8 species, and 10 clusters containing 10 or more species. The index of cophenetic correlation was 0.5662.

C2 provided 26 isolated clusters (Fig. 3 and Supplementary Material Fig. S2), 14 of them being further branched into another 41 significant clusters in the zone of statistically significant dissimilarity. The resulting 53 accepted significant clusters (201–253) contain from 1 to 20 species (median = 3), only seven clusters contain 10 or more species, only the two most numerous clusters contain 17 and 20 species, respectively, and 13 clusters consist of one species each. The index of cophenetic correlation was 0.7418.
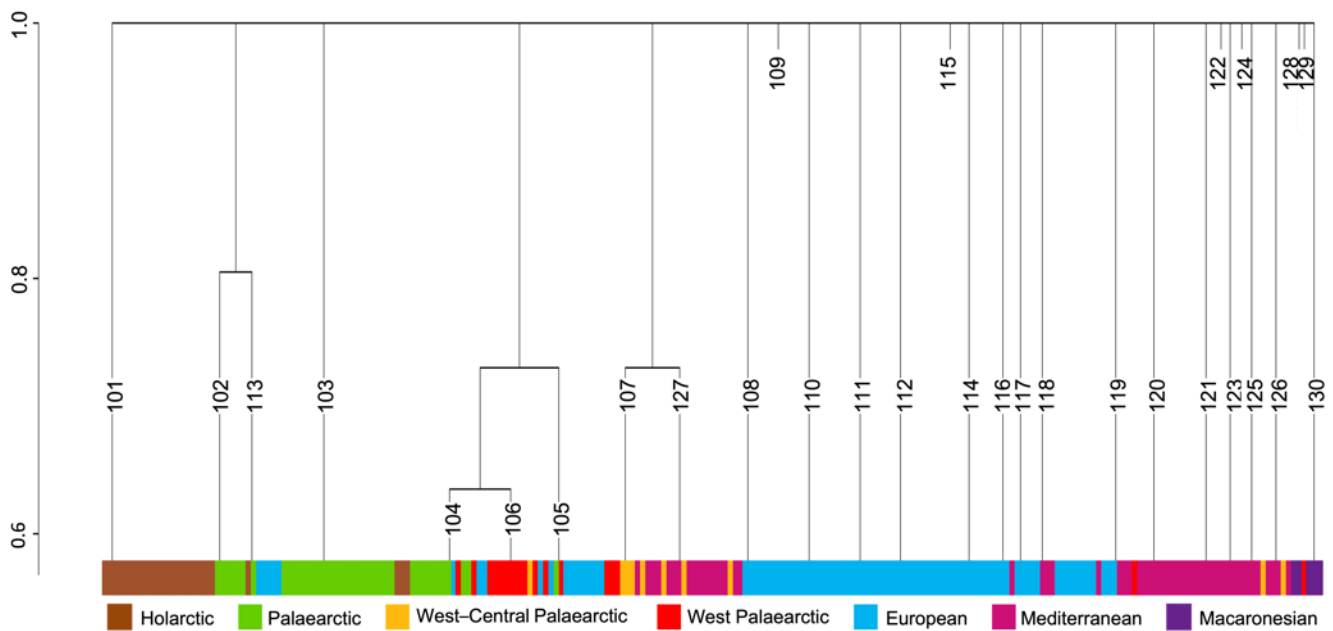

Figure 2. Dendrogram of classification C1 (Baroni-Urban and Buser index 2, complete linkage clustering). Only branches above the level of significance are displayed (the complete dendrogram including species labels is in the Supplementary Material Fig. S1). The numbers of significant C1 clusters are displayed on the dendrogram branches (corresponding to the text and Supplementary Material Figs S1 and S3). The coloured band beneath the dendrogram consists of bars for each species according to the chorotype group to which the species belongs.
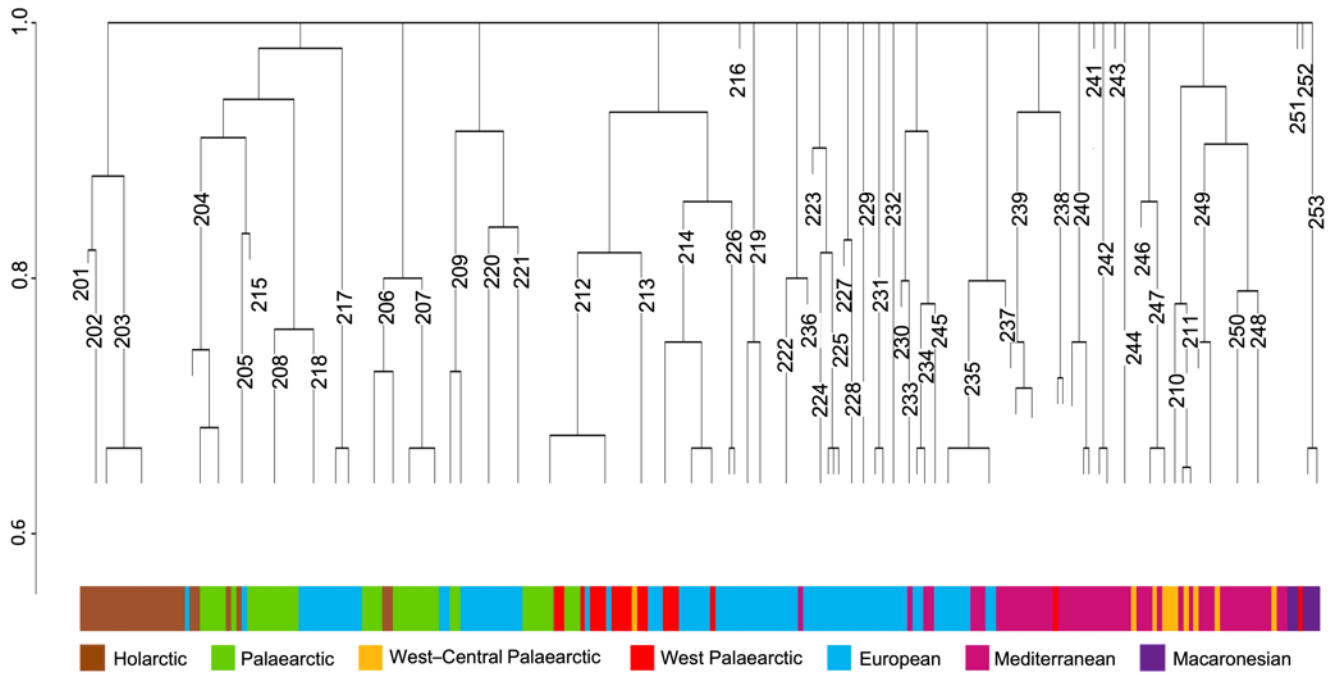
Figure 3. Dendrogram of classification C2 (Jaccard index, complete linkage clustering). Only branches above the level of significance are displayed (the complete dendrogram including species labels is in the Supplementary Material Fig. S2). The numbers of significant C1 clusters are displayed on the dendrogram branches (corresponding to the text and Supplementary Material Figs S2 and S3). The coloured band beneath the species labels consists of bars for each species according to the chorotype group to which the species belongs.

C1 with a lower cluster number was more compact than C2 (Supplementary Material Fig. S3). The differences between C1 and C2 were statistically nonsignificant (test of independence $\chi^2 = 6551.33$, P < 10^{-5}), the Pearson's index of cophenetic correlation coefficient between both classifications was 0.8015, indicating a high agreement between the two classifications, and the difference between the two classifications was statistically non-significant (P (r_{coph} = 0) < 10^{-5}). Only in 14 cases were the C1 and C2 clusters identical (Supplementary Material Fig. S3) of which 11 and 10 were isolated, respectively. All of them were small clusters containing 1–7 species (median = 2) with small, non-disjunctive ranges. In other cases, the C1 clusters were divided into 2–4 clusters in C2. The C2 clusters contained fewer species, their core coinciding with the C1 clusters, sometimes they highlighted a more detailed structure. In other cases, they separate species with larger

extensions from the C1 core range as distinct clusters. In both C1 and C2, species-rich clusters were partly a mixture of species with wide ranges, for example, two Holarctic species are assigned to cluster 103 with 22 Sibero–European species, and another two to cluster 104 containing a mixture of 20 species of Pan-Holarctic, Pan-Palaearctic, Euro–Asian, Euro–Mediterranean, and Pan-European species. On the contrary, species with narrow ranges are usually distinguished reliably, e.g. Western European (108 and 223–225 in C1 and C2 resp.), East Mediterranean (124∩243), Macaronesian (128–130 and 251–253), and others. This was one of the reasons why we used the NC as a starting point, and we further adjusted its results according to the occurrence of species and newly proposed chorotypes in the OGUs (Supplementary Material Fig. S4), taking into account the existing chorotype systems used in zoogeography. The results of the cluster analysis

including cluster numbers are summarized in Supplementary Material Fig. S3.

Chorotypes of European black flies

Chorotypes, as basic forms of ranges, were defined based on a comparison of individual recent species ranges exclusively from a geographical point of view. In the final classification, we distinguished 29 chorotypes, arranged into seven groups, i.e. in the Holarctic, Palaearctic, West–Central Palaearctic group, Western Palaearctic, European, Mediterranean, and Macaronesian groups.

The main criterion for grouping chorotypes was the longitudinal extent of distribution, i.e. the total size of the ranges and their location on the continents in the main large zoogeographic units, which is considered the basic criterion in this field (Gorodkov 1984, Esyunin et al. 2010). In the first step, the distribution in the Nearctic and the longitudinal sectors of the Palaearctic (west, central, and east) was taken into account; in the second step, the zonal latitudinal distribution (if applicable) or at least the distinction between the Mediterranean and the boreo-temperate zone was considered. In the next step, the results of the cluster analyses were taken into account. The resulting 29 chorotypes were arranged into seven groups (Fig. 4). The assignment of species to chorotypes and chorotype groups is in Table 1.

Table 1. Chorotypes and chorotype groups of European black fly species.

Chorotype groups
chorotypes
and species assigned

1.[1] **Holarctic group** (26 spp.)[2]

1.1.[3] **American–European chorotype** (3 spp.)[2]
P.[4] *ursinum* (Edwards), *S. (He.) usovae* (Golini), *S. (Ps.) vittatum* Zetterstedt

1.2. Pan-Holarctic chorotype (9 spp.)
S. (Bs.) annulus (Lundström), *S. (Bs.) baffinense* Twinn, *S. (N.) silvestre* (Rubtsov), *S. (S.) noelleri* Friederichs, *S. (S.) murmanum* Enderlein, *S. (S.) tuberosum* (Lundström), *S. (S.) vulgare* Dorogostaisky, Rubtsov & Vlasenko, *S. (S.) rostratum* (Lundström), *S. (S.) truncatum* (Lundström)

1.3. Holarctic boreal chorotype (10 spp.)
C. eremites Shewell, *M. bilineata* (Rubtsov), *S. (N.) dendrofilum* (Patrusheva), *S. (N.) fontinale* Radzivilovskaya, *S. (Sb.) giganteum* Rubtsov, *S. (Sb.) subpusillum* Rubtsov, *S. (S.) malyschevi* Dorogostaisky, Rubtsov & Vlasenko, *S. (S.) transiens* Rubtsov, *S. (S.) annulitarse* Zetterstedt, *St. trigonium* (Lundström)

1.4. Palaearctic–East Beringian chorotype (4 spp.)
S. (B.) maculatum (Meigen), *S. (He.) dogieli* (Rubtsov), *S. (N.) bicorne* Dorogostaisky, Rubtsov & Vlasenko, *S. (S.) rubtzovi* Smart

2. Palaearctic group (40 spp.)

2.1. Pan-Palaearctic chorotype (7 spp.)
S. (E.) angustipes Edwards, *S. (N.) angustitarse* (Lundström), *S. (N.) lundstromi* (Enderlein), *S. (N.) vernum* Macquart, *S. (S.) ornatum* Meigen, *S. (S.) reptans* (Linnaeus), *S. (W.) equinum* (Linnaeus)

2.2. Euro–Asian chorotype (7 spp.)
P. hirtipes (Fries), *S. (Bo.) erythrocephalum* (De Geer), *S. (E.) aureum* Fries, *S. (Sb.) nigrum* (Meigen), *S. (S.) morsitans* Edwards, *S. (S.) paramorsitans* Rubtsov, *S. (S.) posticatum* Meigen

2.3. Sibero–European chorotype (26 spp.)
H. (H.) rubicundus Rubzov, *P. tridentatum* Rubtsov, *P. macropyga* (Lundström), *C. pallipes* (Fries), *G. ivanovae* (Ivashchenko), *M. lyra* (Lundström), *S. (Bs.) arctium* (Rubtsov), *S. (Bs.) crassum* (Rubtsov), *S. (He.) meigeni* (Rubtsov & Carlsson), *S. (N.) beltukovae* (Rubtsov), *S. (N.) curvans* (Rubtsov & Carlsson), *S. (Sb.) pusillum* Fries, *S. (Sb.)*

rangiferinum (Rubtsov), *S. (S.) cholodkovskii* Rubtsov, *S. (S.) decimatum* Dorogostaisky, Rubtsov & Vlasenko, 1935, *S. (S.) palustre* Rubtsov, *S. (S.) frigidum* Rubtsov, *S. (S.) polare* Rubtsov, *S. (S.) splendidum* Rubtsov, *S. (S.) tumulosum* Rubtsov, *S. (S.) aemulum* Rubtsov, *S. (S.) curvitarse* Rubtsov, *S. (S.) longipalpe* Beltyukova, *S. (S.) promorsitans* Rubtsov, *S. (S.) simulans* Rubtsov, *St. duodecimata* (Rubtsov)

3. West–Central Palaearctic group (10 spp.)

3.1. Central Asian–Euro–Mediterranean chorotype (1 sp.)
S. (W.) pseudequinum Séguy

3.2. Central Asian–Turano–Euxinian (6 spp.)
M. nigra (Rubtsov), *S. (S.) kerisorum* (Rubtsov), *S. (S.) kiritshenkoi* Rubtsov, *S. (W.) paraequinum* Puri, *S. (W.) turgaicum* Rubtsov, *S. (W.) veltistshevi* Rubtsov

3.3. Turano–Caucasian chorotype (3 spp.)
S. (Ms.) montium Rubtsov, *S. (N.) crassicaulum* (Rubtsov), *S. (S.) tarnogradskii* Rubtsov

4. Western Palaearctic group (18 spp.)

4.1. Euro–Mediterranean chorotype (16 spp.)
P. latimucro (Enderlein), *P. rufipes* (Meigen), *P. tomosvaryi* (Enderlein), *S. (E.) petricolum* (Rivosecchi), *S. (E.) rubzovianum* (Sherban), *S. (N.) brevidens* (Rubtsov), *S. (N.) carthusiense* Grenier & Dorier, *S. (N.) costatum* Friederichs, *S. (N.) cryophilum* (Rubtsov), *S. (S.) argenteostriatum* Strobl, *S. (S.) bezzii* (Corti), *S. (S.) intermedium* Roubaud, *S. (S.) trifasciatum* Curtis, *S. (S.) monticola* Friederichs, *S. (S.) variegatum* Meigen, *S. (To.) auricoma* Meigen

4.2. Mediterranean–Macaronesian chorotype (1 sp.)
S. (N.) beckeri (Roubad)

4.3. West Mediterranean–Macaronesian chorotype (1 sp.)
S. (E.) velutinum (Santos Abreu)

5. European group (86 spp.)

5.1. Pan-European chorotype (9 spp.)
S. (He.) latipes (Meigen), *S. (N.) bertrandi* Grenier & Dorier, *S. (S.) degrangei* Dorier & Grenier, *S. (S.) reptantoides* Carlsson, *S. (S.) janzeni* Enderlein *S. (S.)* aff. *tuberosum* (auct. non Lundström), *S. (S.) argyreatum* Meigen, *S. (W.) balcanicum* (Enderlein), *S. (W.) lineatum* (Meigen)

5.2. Western European chorotype (6 spp.)
M. amphora Ladle & Bass, *S. (N.) armoricanum* Doby & David, *S. (N.) dunfellense* Davies, *S. (N.) juxtacrenobium* Bass & Brockhouse, *S. (N.) naturale* Davies, *S. (N.) urbanum* Davies

5.3. Northern European chorotype (20 spp.)
H. (H.) ferrugineus (Wahlberg), *P. luganicum* Rubtsov, *P. nenetz* Yankovsky, *G. brachiata* (Rubtsov), *G. zverevae* Rubtsov, *M. breevi* (Rubtsov), *M. tredecimata* (Edwards), *S. (Bs.) annae* (Rubtsov), *S. (Bs.) olonicum* (Usova), *S. (Bs.) annuliforme* (Rubtsov), *S. (He.) tsheburovae* (Rubtsov), *S. (N.) fuscipes* (Fries), *S. (N.) kuznetzovi* Rubtsov, *S. (S.) gabovae* (Rubtsov), *S. (S.) tshuni* (Yankovsky), *S. (S.) bronchiale* (Rubtsov), *S. (S.) fuscum* (Rubtsov), *S. (S.) rotundatum* (Rubtsov), *S. (S.) zetterstedti* Carlsson, *S. (S.) laplandicum* (Chubareva & Yankovsky)

5.4. Central European chorotype (17 spp.)
P. fulvipes (Edwards), *T. hydroides* (Novák), *S. (He.) sedecimfistulata* Rubtsov, *S. (N.) angustatum* (Rubtsov), *S. (N.) arminii* Seitz & Adler, *S. (N.) bavaricum* Seitz & Adler, *S. (N.) berchtesgadense* Seitz, *S. (N.) codreanui* (Sherban), *S. (N.) crenobium* (Knoz), *S. (N.) dolomitense* (Rivosecchi), *S. (N.) hasekei* Seitz, Adler & Remschak, *S. (N.) oligotuberculatum* (Knoz), *S. (N.) quasidecolletum* Crosskey, *S. (S.) ibariense* Zivkovitch & Grenier, *S. (S.) colombaschense* (Scopoli), *S. (S.) voilense* Sherban, *S. (S.) maximum* (Knoz)

5.5. Apenninian chorotype (8 spp.)
P. calabrum Rivosecchi, *P. italicum* Rivosecchi, *S. (N.) fucense* (Rivosecchi), *S. (N.) marsicanum* (Rivosecchi), *S. (S.) pontinum* Rivosecchi, *S. (S.) liriense* Rivosecchi, *S. (S.) rivosecchii* Rubtsov, *S. (To.) segusinum* (Couvert)

5.6. Balkan chorotype (8 spp.)
M. danubica (Rubtsov), *M. uzunovi* Kovachev, *S. (S.) vigintifile* (Dinulescu), *S. (S.) baracorne* Smart, *S. (S.) croaticum* (Baranov), *S. (S.) savici* (Baranov), *S. (S.) simoffi* (Enderlein), *S. (S.) banaticum* Dinulescu

5.7. Eastern European chorotype (18 spp.)

C. toptchievi Yankovsky, *S. (E.) argentipile* (Rubtsov), *S. (E.) silvaticum* (Rubtsov), *S. (He.) rivi* (Ivashchenko), *S. (N.) volhynicum* (Usova & Sukhomlin), *S. (N.) lidiae* (Semushin & Usova), *S. (Sb.) ivashchenkoi* (Yankovsky), *S. (Sb.) patrushevae* (Ivashchenko), *S. (Sb.) raastadi* (Usova & Reva), *S. (Sb.) rubzovium* (Ivashchenko), *S. (Sb.) suchomlinae* (Usova & Reva), *S. (S.) dolini* Usova & Sukhomlin, *S. (S.) corpulentum* Rubtsov, *S. (S.) gusevi* Rubtsov, *S. (S.) abbreviatum* Rubtsov, *S. (S.) kachvorjanae* Usova & Zinchenko, *S. (S.) lugense* Yankovsky, *S. (S.) shevtshenkovae* Rubtsov

6. Mediterranean group (53 spp.)

6.1. Pan-Mediterranean chorotype (5 spp.)

S. (N.) ibleum (Rivosecchi), *S. (S.) hispaniola* Grenier & Bertrand, *S. (S.) subtile* Rubtsov, *S. (T.) brevifile* (Rubtsov), *S. (To.) galloprovinciale* Giudicelli

6.2. West Mediterranean chorotype (19 spp.)

P. albense Rivosecchi, *U. aculeatum* (Rivosecchi), *U. faurei* (Bernard), *U. juccii* Contini, *G. fabri* Doby & David, *M. blanci* (Grenier & Theodorides), *M. nuragica* Rivosecchi, *M. sardoa* (Rivosecchi & Contini), *S. (He.) saccai* (Rivosecchi), *S. (N.) pinhaoi* Santos Grácio, *S. (N.) ichnusae* Rivosecchi & Contini, *S. (N.) timondavidi* Giudicelli, *S. (R.) lamachi* Doby & David, *S. (S.) sicanum* (Rivosecchi), *S. (S.) xanthinum* Edwards, *S. (To.) continii* (Rivosecchi & Cardinali), *S. (To.) ibericum* Crosskey & Santos Grácio, *S. (W.) quadrifila* Grenier, *S. (W.) sergenti* Edwards.

6.3. East Mediterranean chorotype (1 sp.)

S. (E.) flexibranchium Crosskey

6.4. Euxinian chorotype (9 spp.)

P. petrosum Rubtsov, *P. rachiliense* Djafarov, *S. (N.) florae* (Djafarov), *S. (S.) bukovskii* Rubtsov, *S. (S.) fontanum* Terteryan, *S. (S.) debacli* Terteryan, *S. (S.) monticoloides* (Rubtsov), *S. (To.) popowae* Rubtsov, *S. (W.) angustifurca* (Rubtsov)

6.5. Crimean chorotype (5 spp.)

S. (E.) krymense (Rubtsov), *S. (N.) chodakovi* (Panchenko), *S. (N.) karajimae* (Panchenko), *S. (N.) tauricum* (Rubtsov), *S. (To.) karasuae* (Panchenko)

6.6. Caucasian chorotype (14 spp.)

P. gigas Rubtsov, *S. (E.) maritimum* (Rubtsov), *S. (Ms.) alizadei* (Djafarov), *S. (N.) australe* (Rubtsov), *S. (N.) djafarovi* (Rubtsov), *S. (N.) elatum* (Rubtsov), *S. (N.) fontium* (Rubtsov), *S. (N.) gejgelense* (Djafarov), *S. (N.) gomphocorne* (Rubtsov), *S. (N.) murvanidzei* (Rubtsov), *S. (S.) schamili* (Rubtsov), *S. (S.) bergi* Rubtsov, *S. (To.) adornatum* (Rubtsov), *S. (W.) dahestanicum* (Rubtsov)

7. Macaronesian group (5 spp.)

7.1. Azorean chorotype (1 sp.)
S. (E.) azorense (Carlsson)

7.2. Madeiran chorotype (1 sp.)
S. (R.) joanae Seitz

7.3. Canarian chorotype (3 spp.)
S. (E.) guimari Becker, *S. (N.) annulipes* Becker, *S. (R.) paraloutetense* Crosskey

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[1] groups of chorotypes are numbered at first level.

[2] number of included species

[3] chorotype has a two-level number: the first is the group number and the second is the order within the group.

[4] Abbreviations for genus group names: *B – Byssodon, Bo – Boophthora, Bs – Boreosimulium, C – Cnephia, E – Eusimulium, G – Greniera, H – Helodon, He – Hellichiella, M – Metacnephia, Ms – Montisimulium, N – Nevermannia, P – Prosimulium, Ps – Psilozia, R – Rubzovia, S – Simulium, Sb – Schoenbaueria, St – Stegopterna, T – Twinnia, To – Trichodagmia, U – Urosimulium, W – Wilhelmia.*
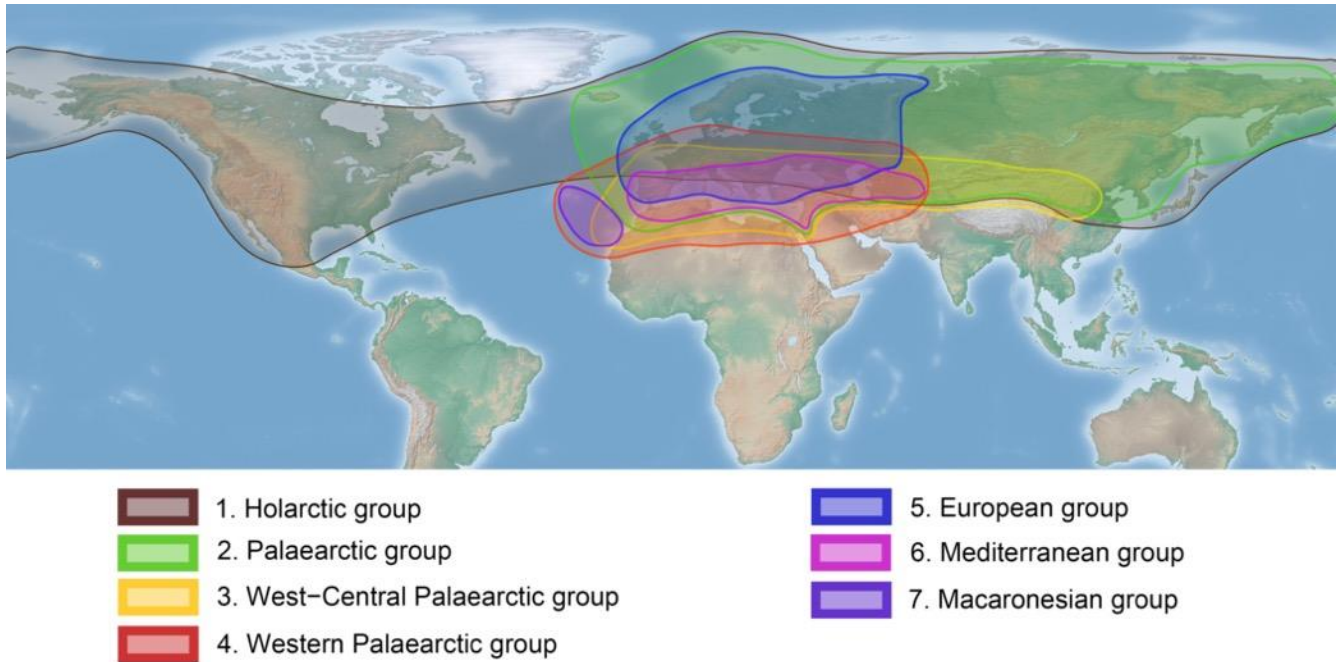
Figure 4. Boundaries of chorotype groups of European black fly species.

We decided not to follow a strictly formal system of chorotypes with formally named categories like phylum, class, etc., as used by Panchenko (1999, 2003), Ryndevich (2013), and others. With this arrangement and at this stage of the study of chorotypes, we do not imply any assumptions about the origin and development of species and chorotype ranges.

1. Holarctic group

The Holarctic group includes four chorotypes of 26 species that are widespread, at least in parts of both the Palaearctic and the Nearctic (Fig. 5). All of them are missing in South Europe, the Mediterranean, and Macaronesia, and most of them also in Central and Western Europe. We accepted Currie's (1997) opinion of Holarctic chorotypes, but we differ from Vigna Taglianti et al. (1999) who also included the chorotypes restricted to the Palaearctic or one of its larger parts in the Holarctic group, although they are missing in the Nearctic. In C1, 20 species represent a well-defined isolated cluster 101 (Fig. 2, Supplementary Material Fig. S3), but another six species are displaced to Pan-

Palaearctic, Euro–Asian, and Sibero–European chorotypes in three other clusters (102–104). Only the American–European chorotype is differentiated in C2 into two significant clusters 201 and 202, with another 17 species forming the core of cluster 203. The division of other chorotypes occurs at a nonsignificant level. We differentiate them according to the extent of their range in the Nearctic and with regard to Currie (1997).

1.1. American–European chorotype

This chorotype, markedly different from other Holarctic chorotypes, includes three European species with a known distribution in the Nearctic, mainly in the boreal (*S. usovae* only in Nunavut, *P. ursinum* up to British Columbia and Quebec), the range of *S. vittatum* extending to Mexico in the south. In the Palearctic, they are known only from North-western Europe including some North Atlantic islands (except *S. usovae*) and they are absent in Europe except for Scandinavia, as well as Asia and Africa. *S. vittatum* in the east of its range does not reach mainland Europe and is known only from the North Atlantic Islands. The species of this

chorotype are well distinguished in C2 as two significant clusters 201 and 202. In C1 they form one nonsignificant subcluster within cluster 101 of the Holarctic species. After resolving the status of intraspecific forms, the assignment of the chorotype of the species could change as a result of the splitting effect.

1.2. Pan-Holarctic chorotype

A chorotype of nine European species known from substantial parts of the Palaearctic and Nearctic (with possible discontinuities). In the Nearctic their range can extend up to the Eastern Forests, the Grassland Great Basin, and/or Sonoran provinces; in Europe, it covers almost the entire continent apart from some southern parts; species with this type of distribution are missing in the Mediterranean and Macaronesia. In C1, this chorotype partly overlaps with the other Holarctic chorotypes (101). *Simulium vulgare* Dorogostaisky, Rubtsov & Vlasenko and *S. rostratum* (Lundström) have a slightly isolated position being included in cluster 102 of Euro–Asian species, and *S. noelleri* with Pan-Palaearctic species (104), which may be related to the fact that the core of their distribution is in Europe. The existence of cytoforms suggests a division of the taxa and a subsequent splitting effect.

1.3. Holarctic boreal chorotype

A chorotype of ten European species distributed mainly in Northern Europe (from Fennoscandia and Northern Russia up to Ukraine), Asia (Siberia, possibly extending to Central Asia), and Northern Nearctic (Canadian taiga, Rocky Mts.). They are missing in Central, Western and Southern Europe, the Mediterranean, Macaronesia, and the USA (except Alaska). In NC, this chorotype overlaps with the Pan-Holarctic and Palaearctic–East Beringian chorotype in 101∩203. Two species, *Simulium giganteum* and *S. annulitarse*, are included in the cluster of Siberoeuropean species (103∩206) apparently due to their massive presence in Siberia and scattered records in Nunavut and Northern Europe. The existence of the cytoforms in *Metacnephia bilineata* and *Stegopterna*

trigonium may indicate a change in their assignment to the chorotype due to the splitting effect.

1.4. Palaearctic–East Beringian chorotype

The core of the distribution of four European species is in the northern Palaearctic: in Europe in the north, centre and east of the continent, in Asia from Siberia and Kazakhstan to China, and in Nearctic, in contrast to the previous chorotype, only extending to East Beringia, eastwards approximately to the Mackenzie River, with possible extension to the western part of the Northwest Territories. In C1, the three species are part of the cluster of Holarctic chorotypes (101∩203), only *Simulium maculatum* being assigned to the heterogeneous cluster 102 of widely distributed Euro–Asian and Sibero–European species with scattered records but partly differentiated in C2 (205). In defining the chorotype, we accept the opinion of Currie (1997).

2. Palaearctic group

The Palaearctic group consists of chorotypes distributed in at least two longitudinal sectors of the Palaearctic (typically in Western and Central Palaearctic) but missing in the Nearctic. Vigna Taglianti et al. (1999) assigned all such chorotypes to the Holarctic group. The group of Palaearctic chorotypes is analytically complicated. The ranges of these chorotypes overlap widely and differ either in the core of their distribution or by extension to other marginal territories (Fig. 5). To distinguish between Pan-Palaearctic and Euro–Asian chorotypes, we arbitrarily chose presence/absence in Palaearctic Africa.

2.1. Pan-Palaearctic chorotype

A chorotype of seven species whose ranges cover (with possible disjunction) all three longitudinal sectors of the Palaearctic latitudinally from the boreal to the Mediterranean, including Mediterranean Africa. All are missing in Macaronesia. In NC, this chorotype is clustered with other widely

distributed Pan-Palearctic, Euro–Asian, Euro–Mediterranean, and Pan-European species being a significant part of the core of the intersection 104∩212. *Simulium vernum* and *S. ornatum* are species complexes, and intraspecific forms are also known in other species. The splitting effect in these cases can be expected with the possible disappearance of this chorotype in black flies.
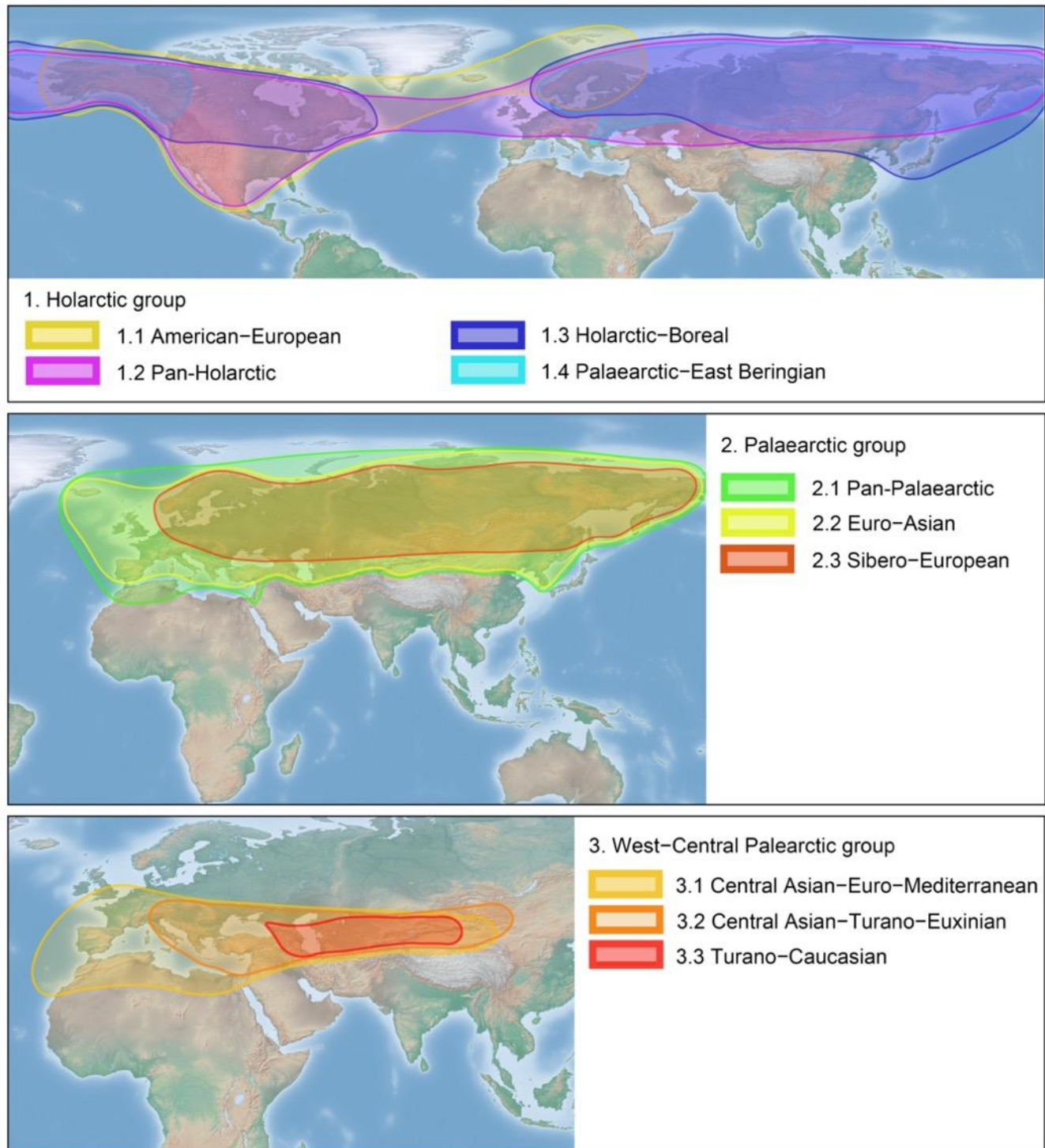

Figure 5. Boundaries of chorotypes of European black fly species from the Holarctic, Palearctic, and West–Central Palaearctic groups.

2.2. Euro–Asian chorotype

A chorotype of seven species widespread throughout all three sectors of the Palaearctic. In Europe, they are distributed from the British Isles to the Caucasus, mostly except for the Mediterranean islands; in Palaearctic Asia, their ranges mainly reach its northern part (Siberia, Far East, and Northern China) with extensions to Kazakhstan, Turan, and Anatolia. None of these species has been recorded in Macaronesia or the Near East. The chorotype range overlaps widely with the previous chorotype, from which it differs by its absence in Northern Africa. A similar overlap exists with Pan-European and Euro–Mediterranean chorotypes (104∩212). Some published data indicate taxonomic intraspecific diversity and/or doubtful records and their revision could result in the splitting effect.

2.3. Sibero–European chorotype

A chorotype of 26 species obligatory distributed in Siberia and in Northern and/or North-eastern Europe (Fennoscandia, Northern/Central Russia, Belarus, Ukraine). Most species are also known from the Far East, ten species from Mongolia and/or Northern China, and seven species extend to Kazakhstan and Middle Asia. In Europe, most species are also known from Central Russia, some occur in Ukraine, only five species in Germany and Poland, only three species extend to the south of Central Europe and/or northern Balkans, and only *Simulium beltukovae* is known from France and Italy. In C1, 22 species form the nucleus of an isolated cluster 103 with two Holarctic boreal species added (*S. giganteum*, *S. annulitarse*). *S. pusillum*, *S. promorsitans* and *S. simulans* form a branch with Eurasian and Pan-Holarctic species from which they are distinctly separated as intersections 102∩207 and 102∩209. *S. beltukovae* is linked to Pan-European and Euro–Mediterranean species. The inclusion of *S. beltukovae* in this chorotype preliminary relates to records from Eastern and Western Siberia as well as the isolated position in NC (105∩204). However,

the core of the species range is in Europe (Northern and Central Europe, the Balkans, France, Italy, Ukraine, and Central Russia) which indicates rather the Pan-European chorotype. There may exist two taxa originally described: *S. beltukovae* in Northern Europe and Siberia, and *S. carpathicum* Knoz in Central and Southern Europe; the record from Kazakhstan needs to be verified.

3. West–Central Palaearctic group

A group of three chorotypes with ten species distributed in the Western and Central Palaearctic, with possible minor extensions to the Eastern Palaearctic (Fig. 5). All species have a more southern distribution. In Europe, they are missing in arctic and boreal regions as well as in most parts of the Atlantic, Continental, and Steppic regions.

3.1. Central Asian–Euro–Mediterranean chorotype

A chorotype of a single species, *Simulium pseudequinum*, known from Western Palaearctic up to Central China longitudinally and from the British Isles to Northern Africa, Pakistan, and Punjab latitudinally. It is missing in Northern Europe (Fennoscandia, Poland, Baltic, Central and Northern Russia) and Siberia. In NC the species was assigned to a compact cluster intersection 106∩213 of Euro–Mediterranean species. Such an atypical range along with the existence of intraspecific forms (Inci et al. 2017, Đuknić et al. 2019) indicates a possible splitting effect.

3.2. Central Asian–Turano–Euxinian chorotype

A chorotype of six species with a very specific range from Pakistan through Middle Asia (except *Simulium paraequinum*), Iran, Iraq (except *Metacnephia nigra*, *S. kerisorum*), Transcaucasia and Caucasus, Crimea (*S. paraequinum*, *S. veltistshevi*), Anatolia, and the Near East (*S. paraequinum*, *S. turgaicum*) to the Balkans, *S. paraequinum* also to Northern Italy. *S. veltistshevi* is distributed eastward to Xinjiang

(Uyghur) and Inner Mongolia, reaching Europe only marginally. All species are absent in Northern, Western and Mediterranean Europe and Northern Africa. Four species (*S. kiritshenkoi*, *S. paraequinum*, *S. turgaicum*, *S. veltistshevi*) form the significant cluster 107 (with intermixed Euxinian *S. fontanum*). *S. nigra*, and *S. kerisorum* are in the cluster 127 consisting mostly of Caucasian, Euxinian, and one Turano–Caucasian species. Cytological and molecular data indicate the existence of cryptic species (Petrova et al. 2003, Inci et al. 2017, Đuknić et al. 2019), which is also indicated by the range and so the splitting effect could be supposed. If the presence of *M. nigra* and *S. kerisorum* in the Eastern Balkans is not confirmed after the revision, they will be deleted from the list of European species.

3.3. Turano–Caucasian chorotype

The chorotype includes three species known from Pakistan (*Simulium montium* only), parts of Middle Asia, Iran, Transcaucasia, and the Caucasus; the record of *S. tarnogradskii* in China (Xinjiang) needs verification. This chorotype reaches the south-eastern borders of Europe only in the Caucasus and does not extend deeper into Europe. In NC only *S. montium* forms a separated intersection 126∩246, the other two species are clustered with Caucasian and Euxinian species.

4. Western Palaearctic group

A group of three chorotypes distributed in the Western Palaearctic in at least two of the following: the European mainland, the Mediterranean and/or Macaronesia (Fig. 6).

4.1. Euro–Mediterranean chorotype

A chorotype of 16 species distributed mainly in Central and Southern Europe and the Mediterranean (obligatory in Northern Africa) with extensions to the British Isles, Scandinavia, Baltic, Crimea, Macaronesia or to the Caucasus. All species, except *Simulium brevidens*, are present in the Mediterranean Isles. A large proportion of species are missing in the British

Isles (7 spp.), the Baltic (9), Fennoscandia (9), and five in both the Baltic and Fennoscandia. Species of this chorotype are classified into significant clusters in C1 (104–106) and C2 (212–214) intermixed with Pan-Palearctic, Euro–Asian and Pan-European species.

4.2. Mediterranean–Macaronesian chorotype

A chorotype of a single taxon, *Simulium beckeri*. The expected distribution includes Madeira, the Canary Islands, the Iberian Peninsula, the Balearic Islands, North Africa, the Near East and Iraq. In the numerical classification, it is linked to Pan- and West Mediterranean species (120) but forms an isolated intersection 120∩238 with Pan-Mediterranean *S. ibleum*. In the case of a further division of this taxon, this chorotype can be expected to disappear as a result of the splitting effect.

4.3. West Mediterranean–Macaronesian chorotype

We include here the single species *Simulium velutinum*, which is reliably known only from the Canary Islands, Algeria, and Morocco; other data on the distribution of this species result from the misidentification of cytospecies (Adler et al. 2015a). In NC it forms a separate nonsignificant branch in the cluster of endemic Canarian species 130∩253, from which it differs by its presence in North Africa.

5. European group

A group of seven European chorotypes with ranges restricted to non-Mediterranean Europe (Fig. 6). With 86 included species, it is the chorotype group richest in species.

5.1. Pan-European chorotype

A chorotype of nine species with ranges covering substantial parts of Europe with minor extensions to Western Siberia, Anatolia, Caucasus, and Western Kazakhstan (*Simulium lineatum* only). The range of this chorotype is largely nested in the range of the Euro–Mediterranean, Sibero–European, Euro–Asian, and Pan-Palearctic chorotypes, but it is limited

to Europe. The largest range overlap is with the Euro–Mediterranean chorotype, from which it differs only by its absence in Palaearctic Africa.

Most species are absent from the Mediterranean islands but are known from continental Italy. We also assign here species with a disjunctive range if current knowledge allows the interpolation to territories where they have not yet been registered (e.g. *Simulium reptantoides*). The occurrence of *S. latipes* in Western Siberia is based on a single record in the Northeast Urals (Patrusheva 1982) and may be a misidentification. In the current understanding, *S. janzeni* seems to be rather a central European species, but its true identity remains unresolved. In the NC it was classified as an outlier to the north European species in isolated intersection 110∩215, however, its occurrence in the Northern (incl. Karelia–Murmansk Region) and Central Russia, as well as in Romania, needs verification. In NC, the chorotype does not form a separate cluster, the species are dispersed in neighbouring clusters of Pan-Palearctic and Euro–Asian and/or Euro–Mediterranean, rarely with Central European (105∩214) species that have partly overlapping ranges.

5.2. Western European chorotype

A chorotype of six species distributed in western Europe from the British Isles and Denmark to the Iberian Peninsula with minor extensions to Scandinavia (*Simulium juxtacrenobium*, *S. urbanum*) and the Baltic (*S. naturale*); they do not reach Central, Eastern, and Southern Europe. In C1 they form an isolated cluster 108 divided in C2 into three parts 223-225, according to distribution details.

5.3. Northern European chorotype

A chorotype of 20 species distributed in Northern Europe (Fennoscandia, Northern Russia) and partly in Central Russia (5 species), with scarce extension to the Baltic (*Helodon ferrugineus*, *Prosimulium luganicum*), Western Siberia (*H. ferrugineus*, only in Polar Ural, Patrusheva 1982), or Northern Ukraine

(*Simulium rotundatum*); the presence of the latter species in Bulgaria and Romania needs verification. The occurrence of five species in Central Russia can be expected as the border between Northern and Central Russia is set at 60° N arbitrarily, which may not fully correspond to the natural limit of biomes. In C1, all species are classified into well-separated intersections: 12 species form a cluster of species occurring in Northern Russia with extensions to Fennoscandia and/or Central Russia 110∩(217&218), seven species form a separated intersection 111∩219 distributed almost exclusively in the Karelia and Murmansk region, and *S. zetterstedti* has an isolated position (109∩216) due to a single record from Sweden.

5.4. Central European chorotype

A chorotype of 17 species distributed in Central Europe. The range of any of the included species does not extend to northern and western continental Europe nor to the British Isles, some of them extend into the mountain areas of the Balkans, France and/or Spain (e.g., *S. maximum*), Crimea, and Caucasus (*S. angustatum*); the known range of some species is strongly limited (e.g. the Alps). In NC, the chorotype overlaps with Pan-European, Euro–Mediterranean, and Balkan ones. Nine prevailing mountain species form two isolated intersections 114∩227, 115∩214, 228–229), and 118∩230; seven species are in clusters with Euro–Mediterranean and Pan-European and/or Balkan species. *S. dolomitense* is clustered with the Apenninian species because of its occurrence in North-eastern Italy (Dolomites) only (119∩235). The assignment of *S. voilense* is questionable, as its range is close to the Balkan species, with extensions to Slovakia, Italy, and Ukraine. *S. angustatum*, originally described from Crimea, has also been reported from China (Liaoning); the record needs to be verified. *P. fulvipes* and *S. codreanui* have also been reported in Anatolia; in the first case, the identity of the taxon is not clear.
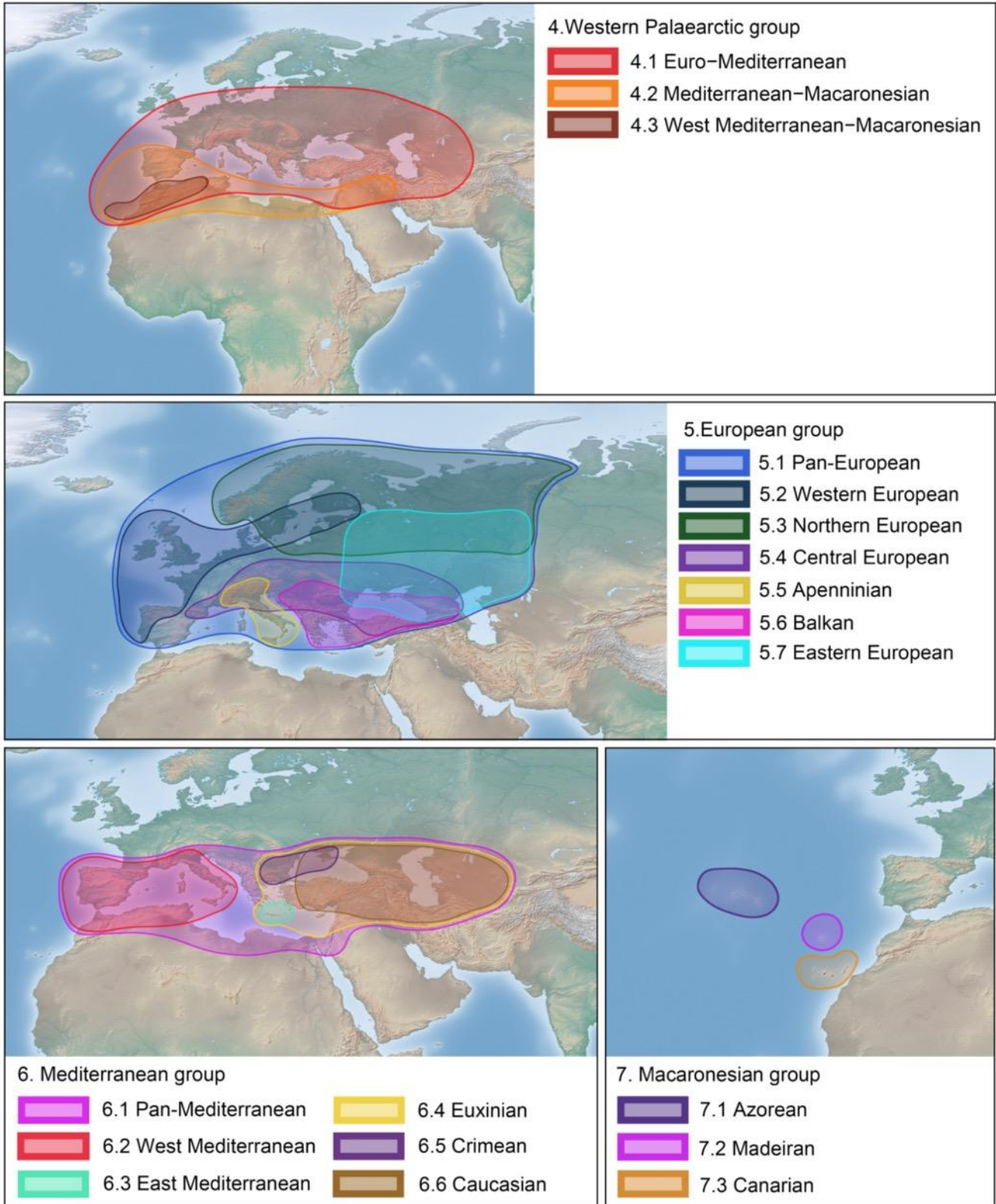
Figure 6. Boundaries of chorotypes of European black fly species from the Western Palaearctic, European, Mediterranean, and Macaronesian groups.

5.5. Apenninian chorotype

A distribution type of eight species occurring in the northern and inner regions of the Apennine Peninsula; in C1 they form an isolated cluster 119 with three West Mediterranean and one Central European (119∩235), and one Pan-Mediterranean species included (119∩236). *S. marsicanum* (present in southern Italy and Sicily) has an intermediate position between the Apenninian and West Mediterranean chorotypes.

5.6. Balkan chorotype

A chorotype of eight species known almost exclusively from the Balkans. Only *Simulium baracorne* is also reported from Central Europe, Anatolia, Ukraine, and Uzbekistan. The records would require verification due to the uncertain status of the taxon. In NC they form a separate cluster 117∩232 (2 spp.) or subcluster 116∩231 (3 spp.), the other three species are partly mixed with some Central European, Crimean, and Euxinian chorotypes in cluster 118, not being differentiated from them even in C2.

5.7. Eastern European chorotype

The range of most of the 18 species of this chorotype is limited to Central Russia and Ukraine, with only five species being rarely recorded in Belarus (two species), Karelia (a single record), Crimea (*Simulium volhynicum* only), and Southern Russia (three species). An isolated record of *S. lugense* in Eastern Siberia needs revision (Lena basin, Vorobets and Potapova 1988, Aibulatov, Zoological Institute RAS, personal communication). In C1, they form two well-defined isolated clusters: 12 species mainly from Central Russia (112) and five species known mainly from Ukraine (113). The position of *S. silvaticum* is uncertain; in C1 it is misclassified in 116 as Balkan but in C2 correctly in 221 as an Eastern European species; according to records from Northern Italy, Romania, and Serbia it cannot be ruled out that it is a species complex. After analysing more detailed data on the distribution of all species, the chorotype is likely to be divided into northern and southern chorotypes.

6. Mediterranean group

The Mediterranean group includes six chorotypes (Fig. 6) of 53 European species with ranges lying entirely or substantially in the Mediterranean sensu Vigna Taglianti et al. (1999).

6.1. Pan-Mediterranean chorotype

A chorotype of five species with ranges extending, sometimes disjunct, into the whole Mediterranean with extensions to Crimea and Caucasus. The species are a non-uniform group (at present) with an incompletely known distribution. The typical Pan-Mediterranean range has *Simulium ibleum* (from northern Africa through the Mediterranean islands to Lebanon). *S. hispaniola* and *S. galloprovinciale* have the core of their range in the western Mediterranean, where they are also included in NC, and only on the basis of records from Turkey have they been assigned to this chorotype. The ranges of the remaining two species, *S. subtile* (Northern Italy, Romania, Caucasus) and *S. brevifile* (Southern Italy, incl. Sardinia and Sicily, Ukraine incl. Crimea), are probably only fragmentarily known, and we rank them here only according to the convex polygon of their known distribution. *Prosimulium rachiliense* cytoform B (Morocco, Western Turkey, and probable Turkish Thrace) may likely belong to this chorotype, but we currently assign this species, according to the records of cytoform A, to the Euxinian chorotype. In NC they do not form a separate cluster, but are individually linked to Mediterranean–Macaronesian, West Mediterranean, Apenninian or Balkan species.

6.2. West Mediterranean chorotype

The chorotype includes 19 species distributed from the Iberian Peninsula to the southern coast of the Apennine Peninsula including the islands (cf. Rivosecchi 2004) and western North Africa. Only the range of *Simulium lamachi* surprisingly

extends to the Berchtesgaden Alps (Germany). In C1, this chorotype is divided into five isolated clusters 119–123 due to the narrow ranges of endemics. Three intersections (121∩240, 122∩241, 123∩242) are composed exclusively of nine West Mediterranean species, in the C1 cluster 120 the Pan-Mediterranean species *S. ibleum* and Mediterranean–Macaronesian *S. beckeri* are assigned to seven West Mediterranean species in a nonsignificant subcluster but both these species are well distinguished as intersection 120∩238 from 120∩239. Another three West Mediterranean species are arranged together with the prevailing Apenninian and one Central European species in the intersection 119∩235.

6.3. East Mediterranean chorotype

This type of distribution has just *Simulium flexibranchium*, which is known only from the Greek islands of Rhodes, Crete, Kithira, and Naxos. In NC it forms an isolated intersection 124∩243.

6.4. Euxinian chorotype

A chorotype of nine species known from the Eastern Balkans, Crimea, Caucasus, Transcaucasia, and Anatolia; *Simulium fontanum* has been also reported from the Ukrainian Carpathians and Iran. The record of *S. angustifurca* from Inner Mongolia is far outlying; if its identity is confirmed and new records cover the disjunction, the species will probably have to be reassigned to the Central Asian–Euro–Mediterranean chorotype. *Prosimulium rachiliense* is a species complex with two distinct cytoforms, of which cytoform A is probably non-European (Transcaucasia, Anatolia); cytoform B currently assigned to this chorotype, is also reported from Morocco, suggesting a relationship to the Pan-Mediterranean chorotype. In NC, five Euxinian species are grouped together with Caucasian, Turano-Caucasian and Centralasian-Turano-Euxinian species in 127∩248−249, another four species (*P. rachiliense*, *S. bukovskii*, *S. fontanum*, and *S. angustifurca*) are scattered among Balkan, Crimean, Central Asian–

Turano–Euxinian, Central European and Azorean species. The assignment of taxa into the Euxinian chorotype is a matter of criteria and discussion.

6.5. Crimean chorotype

The chorotype includes four Crimean endemics as well as *Simulium krymense* (Crimea and the Balkans). Four species form an isolated intersection 125∩244, whereby *S. krymense* is classified within a significant cluster 118 consisting mainly of Balkan species but in a separate intersection 118∩245 with *S. bukovskii*. Its inclusion in this chorotype is equivocal due to its position as a possible older synonym of *S. petricolum* and also due to questionable records from the Balkans.

6.6. Caucasian chorotype

The chorotype of 14 species distributed in the Caucasus and Transcaucasia, with scarce extensions to Southern Russia, Crimea, Ukraine, Anatolia, and Austria (*Simulium maritimum*). Eight of them are endemic to the Caucasus and Transcaucasia, *S. dahestanicum* is also known from Iraq and Iran, and after an analysis of non-European species it can be assigned to another chorotype. The other three species have also been recorded from China (Sichuan: *S. alizadei*, *S. gejgelense*, Liaoning: *S. maritimum*), but these records are far outlying with a huge gap from the Caucasian range core and therefore need to be revised. In NC, species are grouped with Euxinian, Turano–Caucasian, and Central Asian–Euxino–Caucasian species into two isolated clusters 126 and 127 in C1 and four significant clusters 247–250 in C2.

7. Macaronesian group

A group of three chorotypes with distribution limited to Macaronesia (Fig. 6).

7.1. Azorean chorotype

This is the chorotype of a single species, *Simulium azorense*, which is endemic to the Azores. The chorotype is well defined as isolated intersection 128∩251.

7.2. Madeiran chorotype

This type of distribution has *Simulium joanae* only, endemic to Madeira. In NC it forms isolated intersection 129∩252.

7.3. Canarian chorotype

The chorotype includes endemic *Simulium guimari*, *S. annulipes*, and *S. paraloutetense*. In addition to Canarian endemics, the isolated intersection 130∩253 contains the outlying *S. velutinum*, which differs by its presence in Algeria and Morocco.

DISCUSSION

Data quality

Analysis of black fly species distribution, like any other zoogeographic analysis, is mainly biased by two shortfalls: Linnaean and Wallacean ones (Lomolino 2004, Whittaker et al. 2005, Hortal et al. 2015). Both mean that gaps in the data could affect the results of the analyses. The other shortfalls (Hortal et al. 2015) are perhaps less biasing.

The Linnaean shortfall is that many species are unknown and have not yet been described (Lomolino 2004, Whittaker et al. 2005), so we are analysing an incomplete set of species, which is especially important in regionalization. The existence of such species can hypothetically be expected in every group and every territory. For black flies, though, this bias also has a slightly different form: some of the named species are accepted complexes of cryptic species, which (at least some of their populations) can be distinguished by chromosome structure (cytospecies, cytoforms, cytotypes) and/or gene sequences (molecular forms). Adler (2022) lists 51 such complexes worldwide, 15 of which (without *Simulium ruficorne*, see later) are also known from Europe (*Prosimulium latimucro*, *P. rachiliense*, *P. rufipes*, *P. ursinum*, *S. cryophilum*, *S. vernum*. *S. bezzii*, *S. noelleri*, *S. ornatum*, *S. colombaschense*, *S. reptans*, *S. reptantoides*, *S. paraequinum*, *S. pseudequinum*, *Stegopterna*

trigonium). However, it is not a finite number. Based on the karyological studies and analyses of about 250 Nearctic species, Currie and Adler (2008) estimated that the number of such hidden species could represent up to a third of currently named species worldwide. Moreover, the Linnaean shortfall affects also the estimation of the range size and the assignment of species to chorotypes (see below).

The Wallacean shortfall, which means that the distribution of the described species is incomplete and only partly known, may represent a similar bias (Lomolino 2004, Whittaker et al. 2005). If this occurs in well-known groups such as vertebrates (e.g. Rueda et al. 2013) or vascular plants (Finnie et al. 2007), it must be all the more common in black flies. Even in Europe, there are countries where data on black flies are missing or incomplete. The Wallacean shortfall is more accentuated, especially in some more detailed biogeographic analyses using smaller OGUs, e.g. the study of local chorotypes (sensu Fattorini 2015, 2016) requires more precise and equivalent information than large-scale analyses (cf. Morrone and Escalante 2002, Jetz et al., 2008, da Silva et al. 2016).

At first sight, the primary data matrix could give the impression of a massive Wallacean shortfall impact. The data matrix of 238×97, that is 23,086 fields, contained 2,523 positive (10.9%) and 20,563 zero entries (89.1%). However, many of the zero values are true ones. If we take into account 85 narrow endemics (of them 79 European only), which objectively occur in one to three OGUs and are absent in all others, their absence represents 8,112 true zeros. If another 24 endemic European species are really missing outside of Europe, this represents another 1,080 true zeros. These 11,715 true zeros plus positive values fill the data matrix with valid values up to 50.8%.

The data matrix also contains false positive values, both suspected and unrecognized. False positive values are usually caused by misidentification of the species and

can only be reliably detected by a complete revision of the material. Based on suspicious data on distribution or species identity, some false positive values may be excluded with only a small probability of error. We have evaluated as likely false positive records and excluded species whose presence in Europe is based on poorly documented records from Romania (Dinulescu 1966, c.f. Stloukalová and Jedlička 2007), the following: *Metacnephia persica*, *M. ramificata*, *M. sommermannae*, *Simulium brachyantherum*, *S. fluviatile*, *S. alajense*, *S. latimentum*, *S. bimaculatum*, and *S. exile*. We followed a similar procedure for *S. brachyantherum*, *S. delizhanense*, *S. desertorum*, and *S. kurense* reported from Bulgaria, and *S. deserticola* from Ukraine. The omission of Ukrainian records of *S. pavlovskii* is based on recent revisions (Panchenko 2016, Sukhomlin and Zinchenko 2016). A more detailed view will be published in the forthcoming study on species richness (Jedlička et al., in prep.).

Data processing

The conversion of primary data to binary in OGUs is basically a transformation to a coarse extent of occurrence (EOO, Gaston 1991). When using administrative boundaries, extrapolation may result in an overestimation of the real EOO, but it is only a minor bias when assessing general distribution in broad and coarse scales (Hurlbert and Jetz 2007, Jetz et al. 2008, Morrone 2014b).

The use of numerical methods in zoogeography, especially in regionalization, is now a standard (Kreft and Jetz 2010, Morrone 2018) which helps to reveal the hidden structure of analysed OGUs partly hidden by unknown and/or unrecognized influences, partly random noise, or a too complex structure. There are several procedures available, but the preference for applying some of them is not theoretically justified (Escalante 2017), their use is occasionally discussed, and there is no clear agreement in either the index of similarity or the clustering methods used (Rueda et al. 2013).

Few procedures have been developed specifically for biogeography (e.g. Olivero et al. 2011, 2013, Gatto and Cohn-Haft 2021). Nevertheless, the combination of available methods can be a "best strategy" (Morrone 2018), and expert synthesis is also accepted in regionalization (Cox 2001, Whittaker et al. 2013). In determining the chorotypes, we finally proceeded to an expert assessment of the intersection of clusters of two NCs.

In general, the index of similarity remains a matter of choice and should be appropriate to the problem addressed (Slonim et al. 2005), but it may affect the results of clustering (Moore and Russell 1967). Hubálek (1982) recommends using two or three alternative indices of similarity and comparing the outcome; the basic criterion for choice being the biological interpretability of the results. Both the BB2 and JAC meet theoretical conditions and are admissible in biological analyses (Hubálek 1982), both are suitable choices and commonly used in biogeography (e.g. Márquez et al. 2001).

Range size and splitting effect

The range size can be estimated in different ways, such as the number of occupied locations or squares, the range of geographical coordinates of the marginal points of occurrence, EOO, etc. (Gaston 1991, 1994). Gaston (1991) considers EOO to be the simplest and, to a first approximation, an acceptable, albeit rough estimate of range size. As a rule, EOO interpolates the range inwards, but with the use of administrative boundaries, it can extrapolate the size of the range and thus cause its overestimation, especially for species with a small distribution (Jetz et al. 2008, Morrone 2014b). This is also known in black flies, e.g. in *Twinnia hydroides* or *Prosimulium latimucro* (Stloukalová and Jedlička 2001, Jedlička and Stloukalová 2004).

Given the objectives of this study, true range size is not necessary as an absolute value

of the actual area, but rather as the overall extent of distribution of a species in relation to other species. In this sense, the frequency of a species in OGUs can be used as a rough estimate of the relative range size and the limits of the species' distribution (Gaston 1994, Hurlbert and Jetz 2007, Gaston and Fuller 2009).

The right-skewed frequency distribution of species ranges is prevalent but not the only known type of distribution (Brown et al. 1996, Quinn et al. 1996, Gaston and He 2002). It was also confirmed for simuliids in our data, where the smallest frequency class is modal, i.e. the largest group of species consists of species known only from one OGU. Most species have a narrow range and only a few species are widespread distributed, as generally accepted (Anderson 1985, Brown et al. 1996, Gaston and He 2002, Borregaard et al. 2012).

Two features of the observed frequency distribution are noticeable – observed frequencies lower than expected in the first three classes and exceeding expected on the right side of the distribution. This last feature, and the position of the substantial majority of species complexes on the right side of the distribution, may lead to the assumption that a wide range can be considered for the feature of species complexes and vice versa; that is a species with such a wide range can be a species complex.

In general, a species complex assessed as one unit usually has a wide range (e.g. *Simulium noelleri* Pan-Holarctic, *Stegopterna trigonium* Holarctic boreal, *Simulium vernum* and *S. ornatum* Pan-Palaearctic, *S. reptans* Euro–Asian, *S. pseudequinum* Central Asian–Euro-Mediterranean), which is often different from other species. By abduction, we can assume that species with unusually wide ranges are species complexes (c.f. Adler et al. 2010, 2015b), even if the existence of a species complex in them is not yet known or presumed (e.g., *S. angustitarse*, *S. maculatum*, *S. equinum*, and others). In the complexes, the division into species, and subsequently the range splitting effect is assumed, i.e., dividing the previous species

complex range into smaller parts. Our understanding of the splitting effect can be demonstrated in *S. ruficorne*, which is considered a species with the largest distribution among black flies. For this species consisting of five cytoforms, four distinct species were recognized (Cherairia and Adler 2018). Although the forms were not formally named and erected to species, we accepted the well-argued opinion of Cherairia and Adler (2018) and used two taxa instead of the *S. ruficorne* species complex. As a result, the originally supposed polyregional Macaronesian–Mediterranean–Afrotropical chorotype (if we consider *S. ruficorne* as one species) has disappeared. In Europe, *S. beckeri* (cytoform A1/A2) represents a new Macaronesian–Mediterranean chorotype, thus leaving *S. annulipes* (cytoform C) to become part of the Canarian chorotype. The same phenomenon was observed in the past for *S. aureum s.l.*, sometimes regarded as a Holarctic taxon (e.g. Panchenko 2003). After the establishment of several cytoforms as distinct species with significantly smaller ranges, *S. aureum s.l.* as currently understood remains Euro–Asian in distribution (present study), however, we expect the process to continue. We can assume a similar situation for *Prosimulium hirtipes*, *P. italicum* and *S. colombaschense* (Adler et al. 2016, Kúdela et al. 2018), as well as for the subgenera *Eusimulium* and *Wilhelmia* (Adler et al. 2015a, 2015b) and others. The prevalence of small ranges suggests allopatric speciation (Gaston 1998, Takashina et al. 2022, Adler and Reeves 2023), however, because sympatric and parapatric speciation with large range overlap was confirmed in black flies (Shields and Procunier 2019), the result of splitting may be very different in different taxa.

Chorotypes

In this study, we aimed to identify the global chorotypes of European black flies, as the chorotypes are recently understood (Vigna Taglianti et al. 1992, 1999, Fattorini 2015,

2016). The relevant studies analyse the distribution of another and a usually smaller set of species and cover a different area (e.g. Panchenko 1999, 2003, Jedlička 2000, Hubenov 2021), or evaluate other aspects of distribution (e.g. Rubtsov 1956, 1959–1964, Usova 1987, and others). Even if we agree with them regarding the concept of global chorotypes as a type of global range, several questions remain open. Among them, the most problematic is the accurateness of range agreement which is complicated by the presence of different ranges of various sizes with outlying extensions, as well as the size of the areas when smaller ranges are nested inside of larger ones.

In a hypothetical case, the system of chorotypes could be strictly hierarchical (Esyunin et al. 2010) and correspond to biogeographical regions if species distribution strictly follows regionalization. However, chorotypes either exceed these regions or do not reach their size, often having vague boundaries, and are overlapping or nested. Nevertheless, they can be arranged in hierarchically nested groups, but they do not represent a true hierarchy (Meusel and Jäger 1992, Passalacqua 2015). When arranging chorotypes in a transparent system, we started (with some reservations) from Gorodkov's (1983, 1984) principle of prioritizing the longitudinal aspect of the range, as it has been shown that it leads to simpler, more compact and informative chorotype groups and their systematic arrangement at the highest level, compared to other approaches (Esyunin et al. 2010). An attempt to use latitude consequently as a criterion for distinguishing chorotypes or their groups as the primary (Emelyanov 1974) or secondary criterion (Gorodkov 1983, 1984), encountered problems with the known transzonal distribution of many black fly species (Usova 1976, 1987, Jedlička and Halgoš 1992). In addition, the data used do not provide a reliable basis for such a procedure. In studies of Palaearctic black fly chorotypes, most authors used explicitly or implicitly Gorodkov's approach. Petrozhitskaya and Mirzaeva (2019) used it strictly, however, out of 35 hypothetical combinations, they found only 14 real chorotypes, seven of which also extend to Europe. Halgoš (2005) has declared a mix of both, Gorodkov's and Yemelyanov's approaches.

There is no generally accepted principle of ordering of the chorotype system. Many European authors accept the system proposed by Vigna Taglianti et al. (1992, 1999) with three units at the highest level, i.e., "a) main chorotypes of Western Palearctic fauna [...], b) cosmopolitan and subcosmopolitan, and c) endemics (to the Near East)", which partly resembles the application of one of Gorodkov's (1983, 1984) principles of classification based on the range size and the location of the range core. We do not share this view regarding the inclusion of all endemics in a separate unit at the highest level. Although this could apply specifically to the Near East, from a broader perspective, e.g. European, such an assessment cannot be accepted in our view. In Europe, and maybe in any larger area, specific endemics exist for its different parts, and if assigned into a separate unit at the highest level, they would represent a very heterogeneous group with a limited range as the only common feature. In our opinion, endemic ranges belong to the core of broader chorotypes, if they exist, and thus we follow the view conceded by Vigna Taglianti et al. (1999) as the possible alternative solution. Cosmopolitan and subcosmopolitan chorotypes of Vigna Taglianti et al. (1999) corresponding to Gorodkov's category of polyregional chorotypes, were not found in European black flies. For these reasons, we have decided to omit the highest level used by Vigna Taglianti et al. (1999).

For European black flies, most of the chorotypes reported from the Middle East (Vigna Taglianti et al. 1999) were not detected, and in some cases we have adopted another solution. In this system, our three chorotypes of the Macaronesian group as well as the Mediterranean–Macaronesian and Macaronesian–West Mediterranean chorotypes, fall into the Mediterranean chorotype (according

to the definition "Some extensions occur west to Macaronesia") and the Caucasian chorotype according to the range borders extending to the South-western Asiatic or Turanian chorotypes. The Central Asian–Turano–Euxinian chorotype could be assigned to the Centralsiatic–European chorotype but with a restricted range, and the Turano–Caucasian chorotype is explicitly listed as part of the Turanian chorotype. The Apenninian and Balkan chorotypes are not distinguished and would fall into the Southern European chorotype, as those species assigned to them are separated into both C1 and C2, but we prefer their separate status. The Crimean chorotype is not mentioned; perhaps it falls within the broadly understood Eastern European or East Mediterranean chorotype.

However, the group of Holarctic chorotypes is broader and a more detailed analysis including all Holarctic species is needed and being prepared. In addition, our four chorotypes of the Holarctic group are listed as a single chorotype, but we prefer their separate status also with regard to the system used by Currie (1997). However, the group of Holarctic chorotypes is broader and requires a more detailed analysis including all the Holarctic species.

Most authors use a two-level system for black fly chorotypes, only Petrozhitskaya and Mirzaeva (2019) used a linear list of chorotypes resulting from the combination of longitudinal and latitudinal dimensions. Finally, Hubenov (2021) used a one-level list of regionally characterized chorotypes.

When arranging chorotypes, different systems of categories have been used, in general, a system of chorotypes organised into groups and classes (Esyunin et al. 2010), groups and families (Esyunin and Marusik 2011) or groups and complexes (Ryndevich 2013) is applied. Esyunin's opinion (pers. com.) is that "groups and classes should be universal and [choro]types may be different". In black flies, only Panchenko (1999, 2003) has previously used such a system of formal categories of classes and phyla,

however, with a different number and content of the categories. In his first study on Crimean black flies, Panchenko (1999) used four phyla, whereas in the extended and revised study covering the whole of Ukraine (Panchenko 2003) he used only two phyla – the circumpolyzonal (panholarctic) phylum containing a single (circumtemperate) class with three groups, and the Palaearctic phylum with five classes and 50 groups. In general, categories have been defined and understood ambiguously.

With respect to the nonexistence of general rules (cf. Esyunin et al. 2010), we have omitted the use of formalized categories; instead, we use an informal two-level system of chorotypes organised into groups based on longitudinal/sectorial range size.

The number of studies dealing with chorotypes of black flies does not exceed a dozen, they have been published over more than the last two decades and both the Linnean and Wallacean shortfalls must have left their mark. During this period, both the concept of some species and the data on their distribution have changed significantly which had to be appropriately reflected in the recognition of chorotypes.

The area of interest in these studies covered only a smaller part of Palaearctic or Nearctic and accordingly, in each study, a different set of species was used that only partially overlaps with the set of European species. From non-European territories, this overlap is, as expected, smaller. Our set has 20 species (8.4%) in common with Yukon territories (Currie 1997, 77 species in total) as well as with Evenkia (Petrozhitskaya and Mirzaeva 2019, 38 spp.), 26 species (10.9%) with Mongolia (Halgoš 2005, 57 spp.), and 48 (20.2%) with Yakutia (Aibulatov 2014a, b, 2016a, b, 90 spp.). There is a greater overlap of the species analysed in four studies from the territory of Europe: from Crimea and the whole of Ukraine (Panchenko 1999, 2003, 103 spp., 44% overlap), from Bulgaria (Hubenov 2021, 74 spp., 67 in common, 28.2%), and a preliminary

report from the Western Carpathians (Jedlička 2000, 44 species, 18.5% of the present set). This is due to the fact that only smaller areas were studied and that a large part of Europe was not included.

All studies on black fly chorotypes agree on the separation of Holarctic chorotypes s. str. as a separate group, which supports our position in contrast to Vigna Taglianti et al. (1999) who included a single Holarctic chorotype in their second-level major group "1. Chorotypes of species widely spread in the Holarctic Region" along with 12 other chorotypes at the same level (e.g., the Palaearctic, the Western Palaearctic, the Asiatic–European, the Sibero–European, the Centralasiatic–Europeo–Mediterranean, the Centralasiatic–Mediterranean, etc.). In addition to erecting Holarctic chorotypes as a separate group, we also differ to some extent in the arrangement and defining other chorotypes, which reflects the data on the distribution of black flies.

The further arrangement of the Holarctic chorotypes differs, which is partly due to changes in the distributional data. As a result, for example, Currie's Palaearctic–Cordilleran chorotype disappeared because new data on distribution led to the inclusion of *Simulium bicorne* to the Palaearctic–East Beringian chorotype and three other species to other broader Holarctic chorotypes. For a similar reason, some species have not been recognized as Holarctic chorotypes, such as *S. annulus* (known from Mongolia, Ukraine, and Yakutia), *S. maculatum*, *S. silvestre*, *S. noelleri*, *S. vulgare*, *S. rubtzovi* (all five from Mongolia and Ukraine), *S. malyschevi* (from Evenkia as Sibero–American boreal and Mongolia), *S. transiens* (from Mongolia), and *S. subpusillum*, *S. tuberosum*, *S. truncatum*, *Stegopterna trigonium* (from Ukraine). Currie alone could have distinguished the American–European chorotype, but did not do so and therefore the species assigned currently to that chorotype he considered as Holarctic (*Prosimulium ursinum*, missing in Asia) or Nearctic (*Simulium vittatum*). In the last case, its only known occurrence in the Palaearctic is in Iceland and the Faeroe Islands, and the existence of cytoforms and molecular forms (Adler 2022) could support Currie's view. No study other than Currie's distinguishes the Palaearctic–East Beringian chorotype and species of this chorotype are assigned to the broader Holarctic chorotypes, although their known distribution in the Nearctic is limited. Petrozhitskaya and Mirzaeva (2019) recognised three (circum)Holarctic chorotypes (boreal, boreo-montane, and temperate), but for *S. malyschevi* the European records have been overlooked and it is therefore included in the Sibero–American boreal chorotype. Panchenko (2003) recognized Holarctic chorotypes at the phylum level with one class (circumtemperate) and three chorotypes, but this assessment is inconsistent with today's data on distribution and taxonomy.

Another group of chorotypes that could be taken into account in all cited studies (except Currie's) is our Palaearctic group with Pan-Palaearctic, Euro–Asian, and Sibero–European chorotypes, which correspond to Aibulatov's (2014a, b, 2016a) Transpalaearctic, Euro–Asian–North African, Euro–Asian, and Euro–Siberian, Euro–Siberian–Central Asian–East Asian, Euro–Siberian–Central Asian, Euro–Siberian–Turano–East Asian, Euro–Siberian–East Asian by Aibulatov, or Transpalaearctic polyzonal, Transeuroasiatic temperate, West–Central Palaearctic boreal and West–Central Palaearctic temperate by Petrozhitskaya and Mirzaeva. The main difference in the evaluation of the Sibero–European chorotype is that Aibulatov separates species with range extensions to Mongolia (e.g. *Helodon rubicundus*, *Prosimulium tridentatum*), Kyrgyzstan, and/or Kazakhstan as distinct chorotypes. In our opinion, a more detailed analysis of the distribution of these species is needed.

A similar tendency in the delimitation of more detailed chorotypes can be observed in studies by Panchenko (2003) and Hubenov (2021). Panchenko (2003) defined 45 chorotypes (his groups) for 83 species (after the exclusion of

taxa regarded at present as synonyms, Adler 2022) and most of them (32, i.e. 60.4%) consist of a single species. Similarly, Hubenov (2021) used 42 range types (versus 17 in the present study) for a common subset of species, for 12 species he indicates 2–3 possible range types. In both cases, chorotypes are more detailed than used here taking into account minor extensions outside the centre of the distribution, e.g. our Central European chorotype is partitioned into six range types, Euxinian into five, and Euro–Mediterranean and Sibero–European into three each. Probably the consideration of marginal records in order to cover the distribution in detail, sometimes in one (or a few) outlying OTUs, led to constructions such as the East European–Siberian range type (due to one record in Inner Mongolia?) for *Simulium angustifurca* (Euxinian in the present study based on records from Bulgaria, Caucasus, Ukraine), or Central and Southeast European–Turanian for *S. baracorne* (the Balkan chorotype in the present study, an outlying record in Uzbekistan being disregarded). This tendency evidently follows the effort to define the chorotypes so that they cover the whole known range(s) of assigned species as much as possible, including range extensions, but this is contrary to the basic goal of defining chorotypes as similar, not equal distribution types (Fattorini 2015, 2016).

The other groups of chorotypes limited to Europe could not be found in Asian faunas. However, some studies were published earlier and therefore the data on the distribution of some species used do not match the present knowledge (e.g. *Prosimulium hirtipes*, *Simulium erythrocephalum*, *S. aureum*, and others) or are based on older misidentifications common in Europe earlier (*S. venustum* and *S. verecundum*). Except for such differences, the assignment of species to chorotypes is comparable.

In zoogeographic analyses from Eastern Europe (Ukraine, Belarus, Central Russia) (e.g. Budaeva and Khitsova 2010b, Kaplich et al. 2011, 2014, 2015, Sukhomlin 2013, Sukhomlin and Zinchenko 2013), the authors recognize 4–6 faunistic complexes (in different combinations),

like boreal, boreo-montane, Mediterranean, ancient-Mediterranean and steppe or Mediterranean-steppe. However, the concept of a faunistic complex is different from the concept of global chorotypes, so a direct comparison with chorotypes is not entirely possible due to the fact that the faunistic complex takes into account the history and development of fauna and distribution.

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