Acta Soc. Zool. Bohem. **73**: 87–156, 2009
ISSN 1211-376X

Species richness of gall midges (Diptera: Cecidomyiidae) in Europe (West Palaearctic): biogeography and coevolution with host plants

Marcela Skuhravá & Václav Skuhravý

Bítovská 1227, CZ–140 00 Praha 4, Czech Republic; skuhrava@quick.cz

Received 25 September 2009; *accepted 21 December 2009*
Published 2 December 2010

Abstract. The present fauna of the family Cecidomyiidae Macquart, 1838 in Europe includes 1800 valid species in 270 genera. It is divided into three subfamilies: Lestremiinae Rondani, 1840 with 280 species in 33 genera, Porricondylinae Enderlein, 1936 with 310 species in 62 genera and Cecidomyiinae Rondani, 1840 with 1210 species in 175 genera. Only the last subfamily includes gall-causing and plant-inhabiting species. For the family Cecidomyiidae, Europe is the most species-rich continent of the world. On average, each gall midge genus contains 6,6 species. The most species-rich genus is *Dasineura* Rondani, 1840, with 230 species, followed by *Contarinia* Rondani, 1860, with 135 species. On the basis of the larval feeding habits, the family Cecidomyiidae may be divided into three biological groups: 51% of species are phytophagous, 39% mycophagous, 8% zoophagous and the biology of about 2% remains unknown. All species of the subfamilies Lestremiinae and Porricondylinae are mycophagous.

Fundamental sources for evaluation of the family Cecidomyiidae in Europe are 40,000 records about their occurrence and distribution gathered by the present authors at more than 1850 localities in 17 countries of mainland Europe and nine islands in the Mediterranean at altitudes from sea level up to 2645 m a. s. l. in the Alps in the period 1955–2009. All samples were obtained using the time and area unit collection method and results were enriched by data collected by earlier researchers. Evaluation was based on identified and valid species, not on unidentified and unnamed gall-inducing organisms.

This abundant data enabled production of maps of occurrence of individual gall midge species of the Czech Republic, Slovakia, France, Spain, Portugal, Poland and Austria, and also graphs showing the vertical occurrences of some species in several countries of Europe. These were published in several summarizing articles (Skuhravá 1991, 1994a, b, Skuhravá & Skuhravý 2009a, Skuhravá et al. 2005, 2006). The accumulated data makes it possible to determine zoogeographical characteristics of single species occurring in Europe.

Here we summarize information about the occurrence of gall midge species of the main genera in Europe and present results in maps of the following genera: *Dasineura* Rondani, 1840, *Contarinia* Rondani, 1860, *Asphondylia* Loew, 1850, *Rhopalomyia* Rübsaamen, 1892, *Lasioptera* Meigen, 1818, *Stefaniola* Kieffer, 1913, *Rabdophaga* Westwood, 1847, *Jaapiella* Rübsaamen, 1915, *Resseliella* Seitner, 1906, *Macrolabis* Kieffer, 1892, *Baldratia* Kieffer, 1897, and *Mayetiola* Kieffer, 1896.

Evaluation of species richness using the average species number per locality showed that Hungary, with 29 species, France with 28 species and the Czech Republic with 26 species are the countries with the highest gall midge species richness in Europe. The average species number decreases to the north and to the south of Europe. Evaluation of species richness using the species density calculated for country or island unit area of 1000 km^2 makes it possible to divide countries into five density groups. The Czech Republic and South Tyrol (northern Italy) are the countries with the highest species density, each with 189 gall midge species occurring per 1000 km^2. Gall midges of Europe belong to the following zoogeographic or biogeographic units: 71% are European species, 12% Eurosiberian, 9.5% Mediterranean including Submediterranean, 1.3% Palaearctic or Euroasian, 4.5% Holarctic, 0.4% cosmopolitan and 1.3% are alien species.

Gall midge species are not uniformly distributed in Europe. Many species were found only once at the type locality, some species are rare, others occur moderately frequently and only a few species occur very frequently. It is possible to divide all species found in the area under study into six frequency groups by using the first six members of the geometrical progression with quotient "2" and coefficient "a", as follows: $a.2^0 + a.2^1 + a.2^2 + a.2^3 + a.2^4 + a.2^5$. The most frequent species in the whole of Europe is *Jaapiella veronicae* (Vallot, 1827) causing galls on *Veronica chamaedrys*; in northern Europe it is *Iteomyia capreae* (Winnertz, 1853) on *Salix caprea*; in southern Europe both *Phyllodiplosis cocciferae* (Tavares, 1901) and *Dryomyia lichtensteinii* (Löw, 1878) causing galls on

Quercus coccifera, Q. ilex and Q. suber are equally frequent. Each part of Europe has its own gall midge species which is the most frequent in the area characterized by particular conditions of the environment. Species number changes with geographic position. The highest species number occurs in the temperate part of Europe covered with mixed forests between latitudes 45° and 52° North. Species number decreases to the north and to the south and is influenced importantly by climatic factors. Central Europe has favourable weather with mild temperatures and with a relatively sufficient amount of rainfall. Species number changes with increasing altitude of localities together with changes in composition of vegetation: in lower parts the gall midge species number is relatively high and it decreases with increasing altitude. *Rhopalomyia luetkemuelleri* (Thomas, 1893) causing galls on *Artemisia spicata* and *Jaapiella alpina* (Löw, 1885) inducing galls on *Silene acaulis* are two gall midge species found at the highest altitudes in Europe – at elevations of 2500–2700 m a. s. l. in the Alpine and subnivale zones. *Oligotrophus juniperinus* (Linnaeus, 1758) inducing galls on *Juniperus communis*, occurs over a large altitudinal span including sites in the planare zone at 190 m a. s. l. up to 2348 m a. s. l. in the Alps. It has considerable ecological tolerance and has been recorded over a vertical range of more than 2000 m. Gall-inducing gall midges of Europe are one of the best known gall-causing groups of animals in the world. They have to be the most suitable group for prognosis of gall midge species numbers and their galls in the future. On the basis of data on the occurrence and distribution of gall midge species gathered from the times of Linnaeus to the present it may be predicted that in Europe the number of valid species in the family Cecidomyiidae may be increased by about four hundred to 2200 valid species and the number of galls caused by gall midges by about two hundred to 1400 sorts of galls by the year 2050.

In Europe 915 gall-causing and plant-inhabiting species of the subfamily Cecidomyiinae are associated with 280 genera of host plants that belong in 72 plant families. On average one plant genus hosts 3,26 species of gall midges. Only two gall midge species are associated with the Pteridophyta, 27 species with the Gymnospermae, 886 species with the Angiospermae, of which 109 species are on Monocotyledones, and 777 species on Dicotyledones. Gall midges are more closely associated with some plant families in which they find more favourable host plant species and genera for their development. The family Fabaceae hosts the highest number of gall midge species – 123 species – and the family Asteraceae hosts 104 gall midge species. In Europe about 70% of gall-inducing species and plant inhabiting species of the subfamily Cecidomyiinae are associated with herbaceous plants and only 30% with trees and shrubs. For the comparison of relationships between gall midges and host plants we introduce the formula – the index of mutual gall midge species and plant species occurrence:

IGS-PSO= NPS/NGMS where NPS is the number of plant species in a particular country and NGMS is the number of gall midge species occurring in the country. This index indicates the degree of mutual occurrence of gall midges on host plants in particular parts of Europe. The analysis of relationships between gall midges and host plants produced the surprising finding that although the species number of flowering plants in Europe increases towards the south, the species number of gall midges decreases.

Galls of gall midge species are not equally distributed on the organs of their host plants. Species of the genus *Dasineura* Rondani, 1840 cause galls mainly on buds and leaves; of the genus *Contarinia* Rondani, 1860 on flowers; of *Asphondylia* Loew, 1850 on flowers and fruits, of *Rabdophaga* Westwood, 1847 on stems and buds; of *Rhopalomyia* Rübsaamen, 1892 on buds; of *Jaapiella* Rübsaamen, 1915 on buds and flowers, species of the genus *Macrolabis* Kieffer, 1892 are mainly inquilines in galls of other gall midges and the species of *Mayetiola* Kieffer, 1896, *Lasioptera* Meigen, 1818, *Planetella* Westwood, 1840 and *Resseliella* Seitner, 1906 develop in galls mainly on stems. In Europe 94 gall midge species are associated with twelve main broad-leaved tree species and 23 gall midge species with six coniferous tree species. *Quercus robur* is the host tree species with the highest species gall midge number (15 species), followed by *Populus tremula* and *Quercus cerris* (each with 13 species), *Betula pendula* and *Tilia platyphyllos* (each with 10 species).

Coevolution of gall-inducing and plant inhabiting species of the family Cecidomyiidae developed in parallel with two groups of vascular plants, the Pteridophyta and the Spermatophyta, a long time ago in the geological history of the Earth. One fossil record of *Sequoiomyia kraeuseli* (Möhn, 1960) found in fossil cones of *Sequoia langsdorfii* (Taxodiaceae) supports the early coevolution of gall midges with conifers. Fossil galls of ten gall midge species provide evidence of the coevolution of gall midges with flowering plants in the Miocene and Pliocene of the Tertiary in various parts of Europe. The gall-inducing and plant inhabiting gall midges of the subfamily Cecidomyiinae probably started to develop at the end of the Mesozoic when they entered into interactions with developing groups of flowering plants. The main development of gall-inducing and plant inhabiting gall midges came in the Pliocene and Miocene of the Tertiary.

This article is illustrated with 40 figures, including maps of geographical distribution of the main genera of the subfamily Cecidomyiinae, maps of distribution areas of several interesting gall midge species and graphs illustrating summaries of results obtained during investigations in Europe.

Distribution, Diptera, Cecidomyiidae, Lestremiinae, Porricondylinae, Cecidomyiinae, Palaearctic, West Palaearctic, Europe, species number, species richness, frequency, geographic gradients, biogeography, zoogeography, plant-animal relations, coevolution with host plants.

CONTENTS

Abstract 87
Introduction 89
Material and methods 92
Results 95
Fauna 95
Species richness 97
Species density 103
Species richness of the main genera 106
Geographic distribution 113
Geographic position and geographic gradients 123
Climatic factors 125
Vertical distribution 126
Frequency 130
Possibilities of finding additional gall midge species number in Europe 132
Gall midges and host plants 134
Mutual occurrence of gall midges and host plants 142
Distribution of galls on host plants 144
Abundance of gall midge species on host plant species 144
Coevolution of the family Cecidomyiidae with plants 145
Factors affecting gall midge species richness 148
Acknowledgements 150
References 150

INTRODUCTION

The Cecidomyiidae is one of the most species-rich families of Diptera and also contains the largest group of gall-inducing animals in the world. Gagné (2004), in his World Catalog, listed 5451 species in 598 genera of living and fossil gall midges. Altogether 3113 species in 344 genera occur in the Palaearctic Region of which more than 1800 species in 270 genera occur in Europe (Skuhravá 2006a). The family Cecidomyiidae Macquart, 1838 is currently classified under three subfamilies: Lestremiinae Rondani, 1840, Porricondylinae Enderlein, 1936 and Cecidomyiinae Rondani, 1840. Only larvae of Cecidomyiinae are able to induce galls on host plants, larvae of three subfamilies are mycophagous or mycosaprophagous. Adults are usually very small, inconspicuous flies but the galls (in Latin: cecidium) that are caused by their larvae on various organs of host plants are strange and striking formation (hence the common name "gall midges"). Larvae of some species live free in flower heads or stems of plants without making galls and others are mycophagous or saprophagous. Zoophagous larvae are predators of larvae of other gall midges, of aphids, mites, coccids, or other small arthropods and some of them may be used in biological control of pests. Larvae of some species live as inquilines in galls of other gall midges or other insects. The biology of many species of gall midges caught as adults in nature is completely unknown (Skuhravá 1986, 1997a, Skuhravá et al. 1984a, b). In Europe about sixty gall midge species are economically important, of them forty species cause damage to agricultural plants (Darvas et al. 2000) and twenty to forest trees (Skuhravá & Roques 2000).

The Palaearctic Region is the largest zoogeographic or biogeographic region of the world occupying an area of about 52 millions km^2 (about 39% of the Earth surface). It includes arctic and temperate Eurasia and all islands surrounding the continent in the Arctic, in the sea of Japan and the eastern half of the North Atlantic, the Mediterranean North Africa and the northern and central parts of the Arabian Peninsula. In Asia the customary boundary has the High Himalayas chain as main divider and the boundary in China and Japan runs at Northern Latitude 30° (Udvardy 1975, Soós & Papp 1986). The Palaearctic Region is usually divided into two parts, namely the West

Palaearctic, and the East Palaearctic (*sensu lato*), that includes an extensive area from the Ural Mountains across Siberia to the Kamchatka Peninsula in the most eastern part of Russia, or into four subregions, viz. Euro-Siberian, Mediterranean, Central-Asian, and East-Palaearctic (*sensu stricto*), situated in eastern Asia and including Japan and its islands, the Korean Peninsula, part of Russia and part of China.

The West Palaearctic consists of the western part of the Euro-Siberian subregion (i.e. Europe) and of the Mediterranean subregion, together including 48 countries and several islands that differ substantially from each other by the geographic position and mainly by various areas. It is very difficult to compare gall midge species numbers of these countries and to evaluate them. For example, France is the largest European country, occupying an area of 551,255 km^2 and the gall midge fauna includes 668 species of which 581 belong to Cecidomyiinae including gall-inducing species (Skuhravá et al. 2005). On the other hand, Liechtenstein situated between Austria and Switzerland is the smallest country occupying an area of 157 km^2 and its gall midge fauna includes 65 species (Skuhravá & Skuhravý 1993a). It was therefore necessary to find a method that would make it possible to compare these values. We used two methods for evaluation of species numbers of individual country: **species number per unit area** and **average species number per locality of area** under study.

Europe is one of the five continents of the Earth covering an area of about 10,180,000 km^2. It is bounded to the north by the Arctic Ocean, to the west by the Atlantic Ocean, to the south by the Mediterranean Sea, to the southeast by the Caucasus Mountains and the Black Sea and the waterways connecting the Black Sea to the Mediterranean. To the east, Europe is divided from Asia by the water divide of the Ural Mountains, the Ural River, and by the Caspian Sea. For the project *Fauna Europaea*, the external geographic boundaries are defined as follows: the defined area consists of the European mainland and Mediterranean islands, plus the Macaronesian islands (Azores, Canary Islands, Madeira; excluding Cape Verde Islands), Franz Josef Land and Novaya Zemlya, with Western Kazakhstan excluded (Fig. 1).

In Europe the main natural vegetation is forest. In temperate Europe, mixed forests with both broadleaved and coniferous trees dominate. The most important species in central and western Europe are broadleaved trees of *Fagus sylvatica*, *Quercus robur* and *Q. petraea*. In the north, the taiga is a mixed forest with dominant trees of *Picea abies*, *Pinus sylvestris* and *Betula* spp.; further north within Russia and extreme northern Scandinavia, the taiga changes to tundra. In the Mediterranean the dominant tree is *Olea europaea* which is very well adapted to its arid climate. In the semi-arid Mediterranean region scrub forests occur. a narrow east-west oriented strip of Eurasian grassland, the steppe, extends eastwards from Ukraine and southern Russia as far as Hungary. In Europe animals and plants have been substantially affected by the presence and activities of man since ancient times. With the exception of Scandinavia and northern Russia, few areas of untouched wilderness and original nature are at present found here, except for various national parks. In the past, most (about 90%) of Europe was covered by forests. They extended from the Mediterranean to the Arctic Ocean in the north. About half of these original forests disappeared through the centuries owing to deforestration.

Southern parts of Europe, forming a zoogeographic sub-unit called the Mediterranean subregion partly borders the Mediterranean Sea and also includes the northern part of Africa and part of western Asia. The climate of this part is mild, winters are rainy and summers are hot and dry. The landscape is covered with forests, woodlands and scrub. This part is one of the world‘s most endangered biogeographic regions. Only about 4% of the original vegetation remains. Man and his activities, including overgrazing, deforestation and conversion of lands for pasture, agriculture, or urbanization, have degraded much of the region. Formerly this region was mostly covered with forests and woodlands, but heavy human use has reduced much of the region to the sclerophyll

shrublands known as chaparral, matorral, maquis and garrigue. At present, 48 countries of various size comprise Europe. Of them, the European part of Russia is the largest both in area and population. The level of knowledge about galls on plants and gall-inducing organisms is very uneven in Europe. Some countries have a long tradition and many researchers contributed to the knowledge which resulted in high species numbers of the family Cecidomyiidae being recorded in Germany, France, United Kingdom, Czech Republic, Poland and Austria. Up to the end of the twentieth century only a few records of gall midge species and their galls were known from Greece and islands in the Mediterranean Sea. At present we have little information about gall midges and their galls in Albania and Moldova.

Gall midges are the richest group of gall-inducing animals in Europe. Houard (1908–1909) in his two-volume book on plant galls of Europe and the Mediterranean included 6239 sorts of galls that are induced by 1450 species of animals belonging to various taxonomical groups. Gall midges (Diptera: Cecidomyiidae) totalled 420 species are the richest group of all gall-inducing animals, constituting 29%. Buhr (1964–1965), in identification keys for galls on the plants of Central and Northern Europe, recorded gall midges as the richest group, including 580 species, i.e. 36% of all insect species inducing galls. Kolomoets et al. (1989) recorded 328 gall-inducing species of Diptera associated with plants in the European part of the USSR. Of those, 301 species (92%) belong to Cecidomyiidae and 25 species to six other dipteran families. In Japan, situated in the Eastern Palaearctic, the gall midges with 628 species (44%), including described and undescribed species, are the richest group of gall-inducing arthropods (Yukawa & Masuda 1996). Of those, only 176 species are described species.

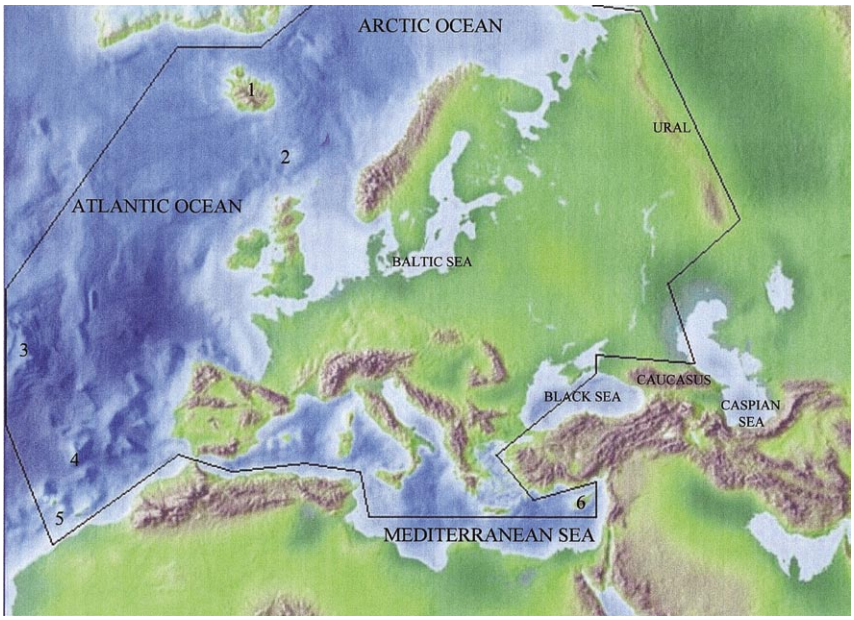


Fig. 1. Europe and its boundary (black line) as defined in the *Fauna Europaea* (2007) and its main geographical features shown in different colours: lowlands from sea level to 200 m a. s. l. (green); hilly country from 200 to 500 m a. s. l. (yellow); uplands from 500 to 900 m a. s. l. (pale brown); lower mountains from 900 to 1800 m a. s. l. (brown); upper mountains from 1800 to 2400 m a. s. l. and over (dark brown). Important islands: 1 – Iceland; 2 – Faroe Islands; 3 – Azores; 4 – Madeira; 5 – Canary Islands; 6 – Cyprus.

We summarized knowledge about gall midges in several European countries from various points of view, including a review of the history of research, evaluation of contributions of earlier researchers to the progress of studies, the biology, zoogeography, relations of gall midges to host plants and economic importance of gall midges. We published such summarizing articles about gall midges of Slovakia (Skuhravá 1991), of the Czech Republic (Skuhravá 1994a, b), of Greece (Skuhravá & Skuhravý 1997), of France (Skuhravá et al. 2005), of Denmark (Skuhravá et al. 2006), of the Iberian Peninsula (Skuhravá et al. 2006), of Poland (Skuhravá et al. 2008) and of Austria (Skuhravá & Skuhravý 2009a).

The aim of our present article is to show the species richness of gall midges in Europe and the West Palaearctic, the abundance, density and frequency of gall midges and factors influencing them, including geographic distribution and the effect of geographic gradients for distribution of species numbers, the influence of climatic factors on species distribution and to predict increasing of species number in the future. We analyse relations of gall midges to host plants and their botanical families, try to elucide causes of their diversity and to indicate the probable process of coevolution of the family Cecidomyiidae with plants in the history of the Earth.

MATERIAL AND METHODS

During the period 1955–2009 we investigated gall midges in 17 countries and nine islands at more than 1850 localities spread throughout Europe from the northernmost situated locality at Harstad in the island Hinnoya in northern Norway to the southernmost situated locality in Malta in the Mediterranean. Localities for our investigations were selected from the sea level – some at the seaside of the Atlantic Ocean and many along the coast of the Mediterranean, and at various altitudinal zones starting with lowlands up to mountains with the highest situated locality at an altitude of 2645 m a. s. l. at Col du Galibier in Hautes Alpes in France. We gathered about 40,000 records about the occurrence of gall midge species in Europe and in nine islands in the Mediterranean. These records are a unique collection of such data dealing with a group of gall-inducing arthopods and they make it possible to evaluate the Cecidomyiidae from several points of view and to determine factors that influence their species richness in Europe. Important is the fact that our considerations on species richness and evaluations of factors influencing them are based on **valid species,** e.i. on **identified species**, not on unidentified and unnamed gall-inducing organisms (Fig. 2).

During our faunistic investigations in various countries of Europe and in Asia we used at each locality the **time and area unit collection method** that we established in 1955. This involves surveying each selected locality visually by walking through it slowly over a period of at least one up to three hours. Two persons walk through various biotopes at the locality and search for gall midges galls and collect them on herbs, shrubs and trees and examine visually buds, leaves, flowers, fruits and stems of herbaceous plants, shrubs and trees. The altitude and short characteristics of biotopes are noted. All findings are recorded, including notes about the local abundance of species. Each locality was investigated only once by this method. During excursions, several specimens of each host plant with galls were put in separate small plastic bags. All species that were found were recorded in the protocol and all collected material was prepared. Several specimens of each host plant with galls were preserved as herbarium items, several plants with galls were kept in plastic bags to obtain living larvae, several plants with galls were placed in small emergence cages to obtain adults and finally several galls with larvae were put into vials with 75% alcohol for future morphological studies or for studies of the digestive system of larvae. Such samples taken from various habitats or microhabitats are very important.

The localities where we investigated gall midges in the Czech Republic, Slovakia and Austria are given in Fig. 3. Localities were selected throughout the whole territory using the map with Ehrendorfer's network (Ehrendorfer 1973), as far as possible examining one locality in each oblong of a size 11×12 km. In a similar way we prepared our investigations in Italy, Switzerland, Greece and other countries.

All data obtained during our investigations of gall midge faunas in Europe, was augmented with data of earlier authors, and evaluated and analysed from two points of view, viz. from the geographic and from the zoological points of view using the methods of Skuhravá (1987, 1994a, b, 1997b). From the geographic point of view, the horizontal occurrence is presented by various species numbers (absolute species numbers found) and by average species numbers in countries of Europe and by numbers of species related to area unit of 1000 km^2. The vertical occurrence is shown as average species numbers in the rising altitudinal zones. From the zoological point of view, it is possible to elaborate the characterization of a particular species (zoogeographic diagnosis) and elaborate maps of distribution areas of a particular species which may be compared with distribution areas of pertinent host plant species.

We gathered not only our own data on occurrence of gall midges in European countries that we obtained in the course of our expeditions but we collected also data on occurrence of gall midge species in countries of Europe found by earlier researchers from the middle of the nineteenth century, when various researchers started investigations of galls, up to the present. These data about occurrence were included in the part devoted to distribution of each gall midge species in the Catalogue of Palaearctic Diptera (Skuhravá 1986). The paucity of records of gall midge species in some countries motivated us to investigate in countries where the species number was low, as for example in Norway, Greece, northern Italy (South Tyrol) and the islands in the Mediterranean.

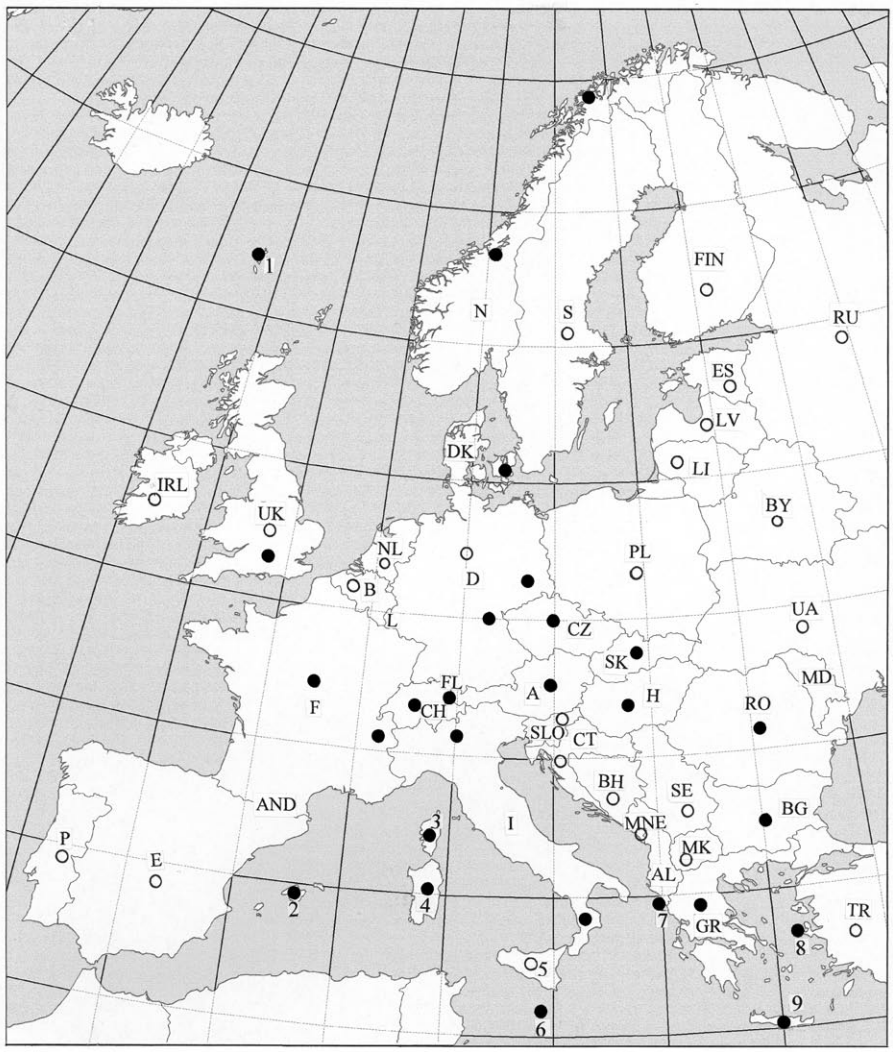


Fig. 2. Distribution of sites in Western Europe where the investigations of the family Cecidomyiidae were carried out in countries and islands by the present authors (black circles) in the period 1955–2009, or where summaries of information were published by other authors (white circles). See Table 1 for the abbreviations for countries; numbers for islands: 1 – Faroe Islands, 2 – Mallorca, 3 – Corsica, 4 – Sardinia, 5 – Sicily, 6 – Malta, 7 – Corfu, 8 – Samos, 9 – Crete.

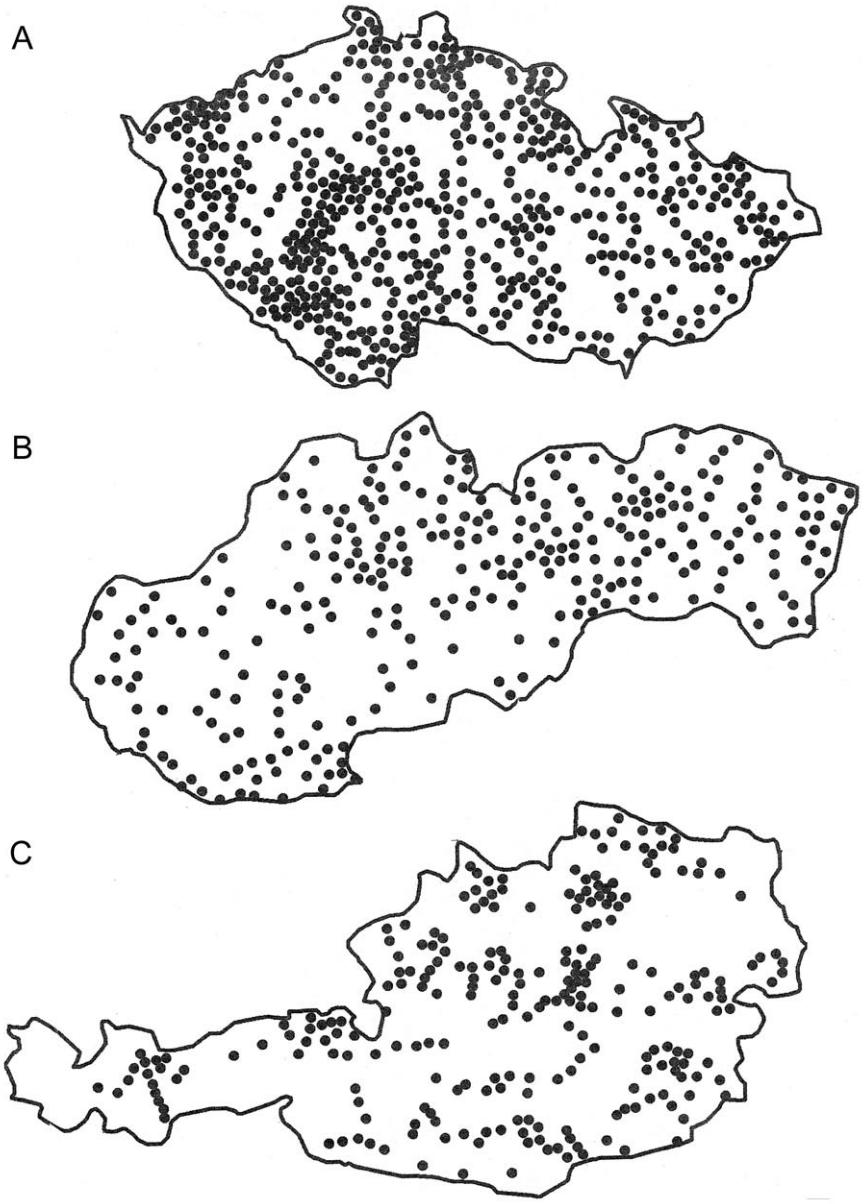


Fig. 3. A–C. Distribution of localities in Central Europe where planned systematic faunistic investigations of the family Cecidomyiidae were carried out by the present authors: a – in the Czech Republic investigations were made at 670 localities at altitudes from 116 m a. s. l. to 1603 m a. s. l. at Mount Sněžka, in the Giant Mountains, the highest point of the country, in 1957–1982 (Skuhravá 1994a, b); b – in Slovakia investigations were made at 336 localities at altitudes from 110 m a. s. l. to 2000 m a. s. l. in the High Tatras in 1969–1976 (Skuhravá 1991); c – in Austria investigations were made at 274 localities situated at altitudes from 115 m a. s. l. up to 2500 m a. s. l. in the Alps in 1967 and 1991–1993 (Skuhravá & Skuhravý 2009a).

In Table 1, we summarized fundamental data and source of information on the Cecidomyiidae in alphabetical order of countries and islands of Europe, abbreviations of countries as used in the maps; total gall midge species of Cecidomyiidae, followed totals for the three subfamilies, the Lestremiinae, Porricondylinae and Cecidomyiinae; number of localities examined by the present authors and the references. Islands belonging to Europe are here considered to be independent geographic units, although some of them are components of continental countries as indicated in parentheses; for Spain and Portugal, see the chapter "Area of study" in the catalog of Carles-Tolrá Hjorth-Andersen (2002). Cyprus and Malta are independent island countries. The present level of knowledge in countries of Europe and in islands in the Mediterranean, given as species numbers of Cecidomyiidae, is shown in Fig. 4.

It is necessary to emphasize that we comprehend and interpret the family Cecidomyiidae as a whole mainly in the introductory parts of our article. In the parts devoted to evaluation of results we deal mainly with part of it – the subfamily Cecidomyiinae – that includes gall-inducing and plant-inhabiting species which are associated with host plants. Members of the subfamilies Lestremiinae and Porricondylinae are mycophagous and are not associated directly with host plants.

RESULTS

Fauna

The fauna includes all the species of animals found in a particular region, period, or special environment. The following six faunal regions or realms are recognized on the basis of terrestrial animal species. The fauna of the Diptera is known from each of these regions and relevant catalogues have been published. We give in the following part the authors that prepared the family Cecidomyiidae for catalogues of various parts of the world.

The fauna of Cecidomyiidae of the Palaearctic region including Eurasia, i.e.Europe and Asia north of the tropics, and northern Africa, was prepared by Skuhravá (1986); the fauna of the Nearctic region consisting of North America except for tropical Mexico by Foote (1965) and Gagné (1989a); of the Neotropical region (situated in South and Central America including tropical Mexico) by Gagné (1968, 1994); of the Afrotropical or Ethiopian region of Africa south of the Sahara and part of southern Arabia by Harris (1980); of the Indomalayan or Oriental region covering tropical Asia and associated continental islands by Gagné (1973) and Grover (1981); of the Austral-Asian and Oceanian regions including Australia, New Guinea and islands in Oceania by Gagné (1989b). In addition, Nearctic and Palaeartic (including Eurasia and northern Africa) regions are usually combined into the Holarctic region. Many changes have occurred in the composition of faunas of all regions in the last twenty years. They are reflected in the world catalog of Gagné (2004) and in the analysis of world faunas in the article by Skuhravá (2006a).

The present or contemporary or extant fauna of the family Cecidomyiidae known in Europe totals 1800 species in 270 genera (Table 2). Europe, a small continent if it is classified by size, is the most species-rich continent of the world in terms of known species of gall midges. On average each gall midge genus includes 6,6 species. Most genera are monotypic, containing only a single species. On the other hand there are several large genera with many species, as follows: the species richest genus *Dasineura* (230 species), followed by *Contarinia* (135 species), *Asphondylia* (50 species) and *Rabdophaga* (40 species) (see Table 7). The distribution of gall midge species in Europe where they form single small faunas of countries and islands is given in Fig. 4.

The gall midges occurring in Europe may be divided into three main biological groups on the basis of the larval feeding habits. If we evaluate the family Cecidomyiidae as the whole, we obtain the following data: 51% of species are phytophagous, larvae of which feed on or in plant tissue, forming galls or inhabiting plant organs without making galls; 39% are mycophagous, larvae of which are associated with various fungi; in this group are usually included xylophagous species; 8% are zoophagous, larvae of which feed as predators on small animals, especially insects, and the biology of about 2% remains unknown. See Table 2 and Figs 5, 6. If we evaluate the subfamily Cecidomyiinae as separate unit that contains 1210 species, the separation of species into

Table 1. Sources of information on the family Cecidomyiidae in Europe. Abbreviations: CA – country abbreviation; T – total species number; L – Lestremiinae; P – Porricondylinae; C – Cecidomyiinae; n – number of localities

country	CA	T	L	P	C	n	references
Andorra	AND	30	2		28		Skuhravá et al. 1996, 2002, 2006
Albania	AL	19			19		Skuhravá 1986 (including 8 alien species)
Austria	A	396	31	13	352	274	Skuhravá & Skuhravý 1967, 1992c, 1995, 2009a, Skuhravá & Franz 1989
Belarus	BY	38	0	0	38		Fiedorowiczówna 1931, Perepeczko-Baumanowa 1935
Belgium	B	140	5	5	130		Lambinon 1957, 1958, 1976, Gosseries 1991
Bosnia and Herzegovina	BH	169			169		Simova-Tošič et al. 2007
Bulgaria	BG	240			240	46	Skuhravá et al.1991
Canary Is. (Spain)		3			3		Skuhravá et al. 2002
Corfu (Greece)		49			49	8	Skuhravá & Skuhravý 2006b
Corsica (France)		60			60	10	Skuhravá & Skuhravý (in prep.)
Crete (Greece)		38			38	10	Skuhravá & Skuhravý 1997a
Croatia	CR	232			232		Simova-Tošič et al. 2004
Cyprus	CY	32			32	17	Skuhravá & Skuhravý 2004a
Czech Republic	CZ	590	13	13	564	670	Skuhravá 1994a, 1994b, 2006b, 2009
Denmark	DK	307	18	14	275	22	Skuhravá et al. 2006
Estonia		93	48	45	0		Spungis 1998, Spungis & Jaschhof 2000
Faroe Is. (Denmark)		5			5	5	Skuhravá & Skuhravý 2009c
Finland	FIN	135	4	27	104		Hackman 1980
France	F	668	33	54	581	17	Skuhravá & Skuhravý 2004c, d, Skuhravá et al. 2005
Germany	D	836	125	58	653	26	Meyer & Jaschhof 1999
Greece	GR	167				56	Skuhravá & Skuhravý 1997a, 2009b
		211					Skuhravá & Skuhravý (unpubl.)
Hungary	H	332			332	22	Skuhravá & Skuhravý 1999
Ireland	IRL	87			87		O'Connor et al. 1999
Italy	I	324	7	2	315		Skuhravá & Skuhravý 1994, Skuhravá 1995
		508	27	10	471	14	Skuhravá & Skuhravý (unpubl.)
Italy, South Tyrol		312			312	124	Skuhravá et al. 2001, 2002, Skuhravá & Skuhravý 2003, 2005a, b, 2006a, 2007b, 2009d
Latvia	LV	506	113	129	264		Spungis 2002, 2003, Spungis & Jaschhof 2000
Liechtenstein	FL	65			65	9	Skuhravá & Skuhravý 1993a
Lithuania	LI	224	25	35	164		Pakalniškis et al. 2000, Spungis & Jaschhof 2000
Luxembourg	L	75			75		Lambinon et al. 2001
Macedonia	MK	148			148		Simova-Tošič et al. 2007
Madeira (Portugal)		18			18		Skuhravá 2008
Mallorca (Spain)		33			33	7	Skuhravá & Skuhravý 2004b
Malta	M	36			36	17	Skuhravá et al. 2002
Moldova	MD	5			5		
Montenegro	MNE	85			85		Simova-Tošič & Skuhravá 2001
Netherlands	NL	340	20	15	305		Nijveldt & Beuk 2002
Norway	N	170	48	4	112	15	Skuhravá & Skuhravý (in preparation)
Poland	PL	320	17			397	Skuhravá & Skrzypczyńska 1983, Skuhravá et al.
		463	49				2008
Portugal	P	122			122		Skuhravá et al. 1996, 2002, 2006
Romania	RO	315	2	9	304	23	Skuhravá et al. 1972
Russia (European)	RU	650	122	128	400		Skuhravá, Skuhravý & Przboro (in prep.)
Samos (Greece)		34			34	8	Skuhravá & Skuhravý 2006b
Sardinia (Italy)		44			44	15	Skuhravá & Skuhravý 2002
Serbia	SE	283			283		Simova-Tošič et al. 2000, Skuhravá & Skuhravý 1964
Sicily (Italy)		89			89		Skuhravá et al. 2007
Slovakia	SK	362	2	5	355	336	Skuhravá 1991, 2006b, 2009

Table 1. (continued)

country	CA	T	L	P	C	n	references
Slovenia	SLO	219			219		Simova-Tošič et al. 1996, Skuhravá & Skuhravý 1964
Spain	E	229	17	0	212		Skuhravá et al. 1996, 2002, 2006, Skuhravý & Skuhravá 1999
Sweden	S	378	102	7	266		Skuhravá & Skuhravý (in prep.)
Switzerland	CH	237	3	6	228	56	Skuhravá & Skuhravý 1997b, Merz et al. 1998
Turkey	TR	70			70		Skuhravá et al. 2005
Ukraine	UA	298	93	39	166		Skuhravá, Skuhravý & Berest (in prep.)
United Kingdom	UK	620	62	32	526	7	Harris 1976, Chandler 1998, Skuhravá & Skuhravý 2007b

biological groups is quite different: phytophagous gall midges comprise 76%, zoophagous 12%, mycophagous including xylophagous 9% and for 3% the larval biology remains unknown.

Species richness

The term **species richness** is used here for the records of all species occurring in Europe, compared with species numbers of other parts of Palaearctic Region or with other continents. The term **species density** is used for the number of species calculated for each country on a unit area of 1000 km^2 (i.e. 31.62×31.62 km).

A total of 1800 gall midge species (i.e. valid, described species) of the family Cecidomyiidae are known from the whole territory of Europe (Table 2). Species are not equally distributed in European countries. The occurrence of gall midge species in a country may be influenced by several factors, mainly by the geographic position, size of the country, composition of vegetation, environmental changes and also by investigations that were done in a country by researchers in the past and by investigations that are carried out at present. We tried to analyse some of these factors on the basis of our rich experience obtained during long-term studies of this group in Europe.

In Table 3 we compare species numbers in countries of Europe ranked according to **geographic area** and simultaneously we evaluate the level of knowledge and level of recent reseach of the family in each country. In the column called **level of knowledge** we evaluate results of investigations of the family obtained by researchers in the past which are expressed in the present species number of the family. For evaluation of the level of knowledge we use the adapted classification scale given in the publication of Merz et al. (1998) where they evaluate the quality of knowledge of dipteran families in Switzerland, viz. as very good, good, medium, poor or very poor. The **level of recent research** in the last column of the table is evaluated for the period of

Table 2. Number of species and genera of Cecidomyiidae in Europe (Skuhravá 2010, unpublished data) and separation of gall midge species into biological groups. Abbreviations: n – number of, myco – mycophagous, phyto – phytophagous, xylo – xylophagous, zoo – zoophagous, un – unknown biology

subfamily	n genera	n species	myco	xylo	phyto	zoo	un
Lestremiinae	33	280	280	0	0	0	0
Porricondylinae	62	310	310	0	0	0	0
Cecidomyiinae	175	1210	75	35	915	150	35
total	270	1800	665	35	915	150	35
%		100	37	2	51	8	2

about the last twenty years (1989–2009). We use the following three categories: no, few or many investigations (Table 3).

The species number does not depend directly on the **size of the country**. European part of Russia has the largest area but from the point of view of its species richness (600 species) is in third place. Ukraine is second in area but with about 300 species only in the sixteenth place from the point of species richness. Two large countries, France and Germany, are among the first five

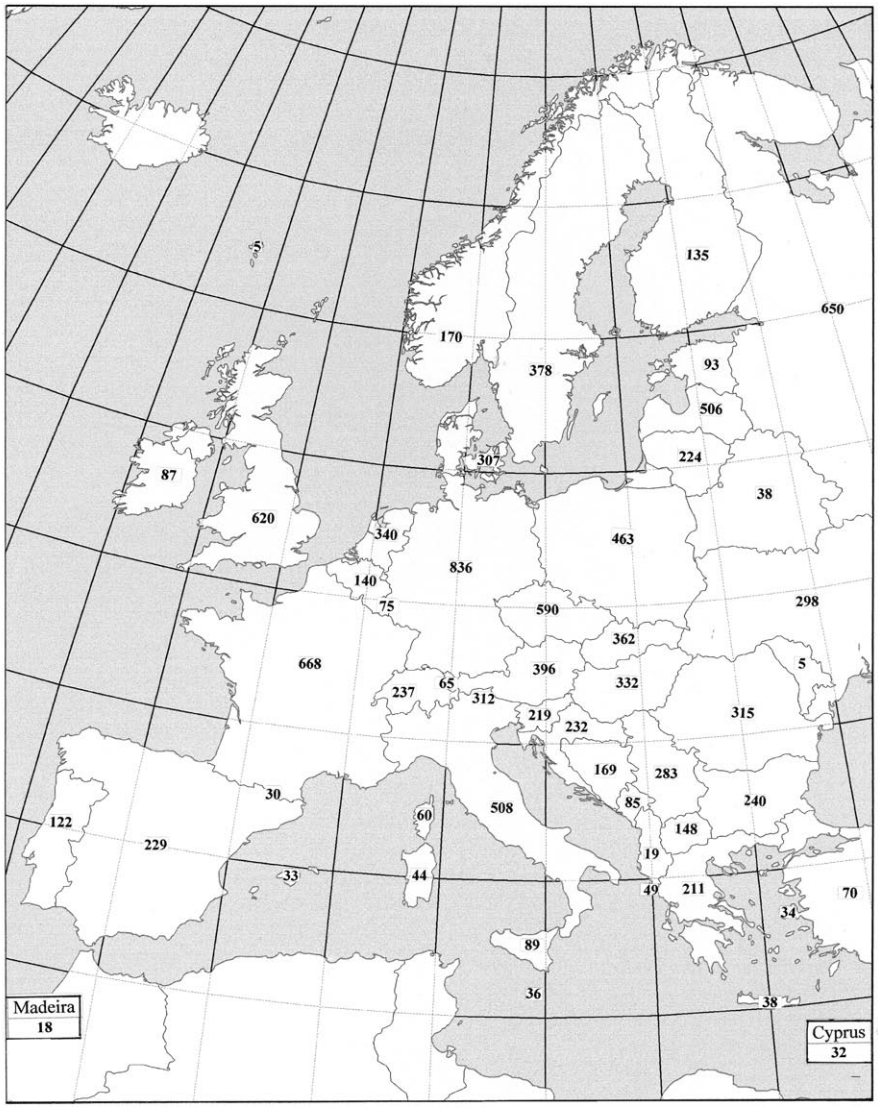


Fig. 4. Distribution of species of the family Cecidomyiidae in countries and islands of Europe in 2009; islands belonging to Europe are here considered to be independent geographic units although some of them are components of continental countries. Cyprus and Malta are independent island countries.

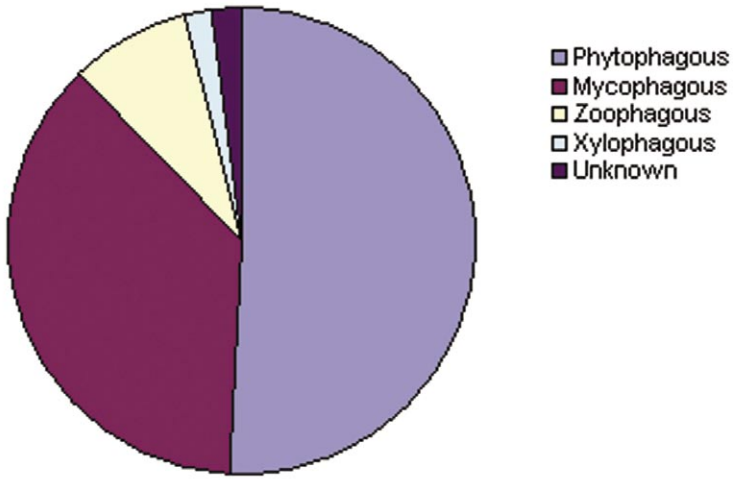


Fig. 5. Biological groups of gall midges of the family Cecidomyiidae in Europe.

countries both from the point of view of area and species numbers. Finland with a large area of 337,030 km^2 has only 135 species, in contrast to Bulgaria occupying a much smaller area (about one third the area of Finland) where 240 species are known to occur. On the other hand, from Slovenia, a relatively small country situated in the western part of the Balkan Peninsula, with an area of 20,273 km^2, a relatively high species number is known (219 species). Species numbers of countries occupying quite similar areas may differ substantially, as for example 590 gall midge species are known to occur in the Czech Republic with an area of 78,900 km^2 (Skuhravá 2006b), 283 species in Serbia with an area of 77,500 km^2 (Simova-Tošić et al. 2000) and only 87 species in Ireland with an area 70,280 km^2 (O'Connor et al. 1999).

Species richness of countries in Europe is importantly influenced by the **level of knowledge**, by the number of researchers who contributed to increasing known species numbers in the past and also by the level of recent research. Germany, France, United Kingdom and other countries given in the upper part of Table 3 are countries where investigations of gall midges have a long tradition and where many researchers contributed to the high level of knowledge of this group. On the other hand, Albania, Finland, Ireland and Norway may be counted as countries where gall midge faunas are poorly known and only a few researchers have investigated gall midges. In Belarus and Moldova gall midges are very poorly known. Lestremiinae and Porricondylinae of Estonia are well known, in contrast to Cecidomyiinae the number of which are not known to us at present.

An important measurement for evaluating of species numbers of areas under study is the **average species number per locality.** It may be calculated for a particular area of the country where investigations were carried out at particular number of localities and gall midge galls were collected by the time and area unit collection method. The average species number per locality may be calculated according to the formula: **ASN=sf/nl**, where **ASN** is the average species number per locality, **sf** is the total of all species found at all examined localities in the course of investigations in this area and **nl** is the number of localities where investigations were carried out. Average species numbers of Cecidomyiidae in countries of Europe where investigations of present authors

Table 3. Species numbers of Cecidomyiidae related to country area and evaluation of the level of knowledge and recent research. For distribution of the Cecidomyiidae in three subfamilies see Table 1

country	country area (km^2)	number of species	level of knowledge	level of recent research
Russia (European)	3,960,000	650	medium	few
Ukraine	603,700	300	medium	many
France	547,030	668	very good	many
Spain	505,992	229	medium	few
Sweden	449,964	378	good	few
Norway	385,155	170	poor	few
Germany	357,050	836	very good	many
Finland	338,145	135	poor	no
Poland	312,685	463	very good	many
Italy	301,318	508	very good	many
United Kingdom	244,820	620	very good	many
Romania	238,392	315	medium	no
Belarus	207,600	38	poor	no
Greece	131,940	211	good	many
Bulgaria	110,910	240	good	few
Iceland	103,000	0	unknown	no
Hungary	93,030	332	very good	few
Portugal	91,568	122	medium	no
Austria	83,858	396	very good	few
Czech Republic	78,866	590	very good	few
Serbia	77,474	283	good	many
Ireland	70,280	87	poor	few
Lithuania	65,200	224	medium	many
Latvia	64,589	506	very good	many
Croatia	56,542	232	good	many
Bosnia and Herzegovina	51,129	169	good	many
Slovakia	48,845	362	very good	few
Estonia*	45,226	93	see the note*	
Denmark	43,094	307	good	few
Netherlands	41,526	340	very good	few
Switzerland	41,290	273	very good	few
Moldova	33,843	8	very poor	no
Belgium	30,510	140	medium	few
Albania	28,748	19	poor	no
Macedonia	25,333	148	medium	many
Slovenia	20,273	219	good	many
Montenegro	13,812	85	medium	few
Cyprus	9,251	32	good	no
Luxembourg	2,586	75	medium	few
Andorra	468	30	good	no
Malta	316	36	good	no
Liechtenstein	160	65	good	no

* Note. Estonia: Level of knowledge: medium for Lestremiinae and Porricondylinae, unknown for Cecidomyiinae; no investigations of the subfamily Cecidomyiinae have been done.

have been done are shown in Fig. 7. The highest value of average gall midge species numbers was found in central and western Europe. In central Europe the highest value was calculated for Hungary (29 species) and the Czech Republic (26), in western Europe for central France (28 species) and south-eastern France (25). This fact may be conditioned or resulted from the highly

varied topography and ecology of these parts of Europe. Many varied factors influence the biodiversity of organisms, both plants and animals. Central Europe has heterogeneous geological substrata and considerable differences in composition of natural vegetation. In addition, Central Europe is situated at the crossroads of routes of plant species that penetrate to this part from all directions, viz. from southern and northern Europe, from western and eastern parts. The average species numbers decreases to the north and also to the south of Europe. In the northern part of the Scandinavian Peninsula the average species number was found to be from 1 to 5, in southern parts of Europe, and in some islands in the Mediterranean (Corsica, Crete, Mallorca) the average species number is around 9, in Malta 4.5 and in Cyprus 3 species.

In Table 4 the countries of Europe are arranged according to the present species numbers and these numbers are compared with data obtained 25 years ago during the preparation of the section on the family Cecidomyiidae for the *Catalogue of Palaearctic Diptera* (Skuhravá 1986, Skuhravá et al. 1984).

At present, Germany is the country with the highest species number, followed by France, European part of Russia, United Kingdom, Czech Republic, Italy, Latvia and Poland. Seven other countries (Austria, Sweden, Slovakia, the Netherlands, Hungary, Romania, Denmark) have a relative high species numbers from 307 to 396 species, nine countries (Ukraine, Serbia, Bulgaria, Switzerland, Croatia, Spain, Lithuania, Slovenia and Greece) have medium species number from 211 to 298 species, six other countries (Norway, Bosnia and Herzegovina, Macedonia, Belgium, Finland and Portugal) are species poor having from 122 to 170 species and the remaining countries characterized by decreasing species numbers from 93 to 11 per country may be considered to be species poor within the framework of Europe. It is clear that it is necessary to include into the evaluation of species numbers not only simple species numbers but also other criteria.

We included in evaluation of species numbers of Europe also the **historical aspect**. We compared species numbers of countries in Europe and their changes during the last 25 years (Table 4).

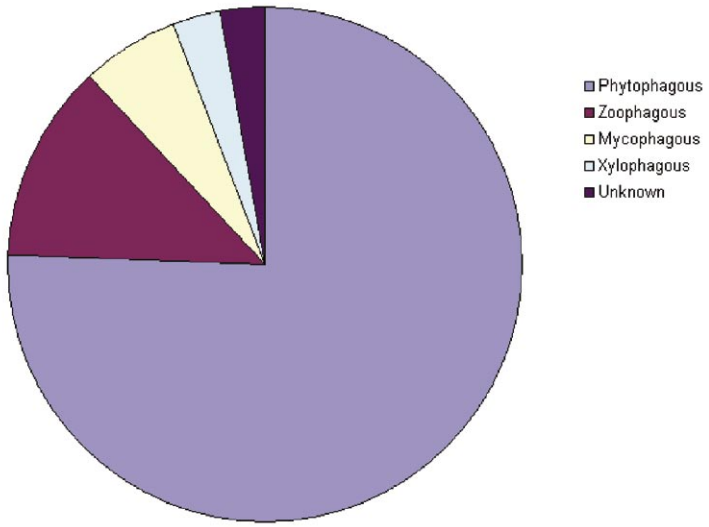


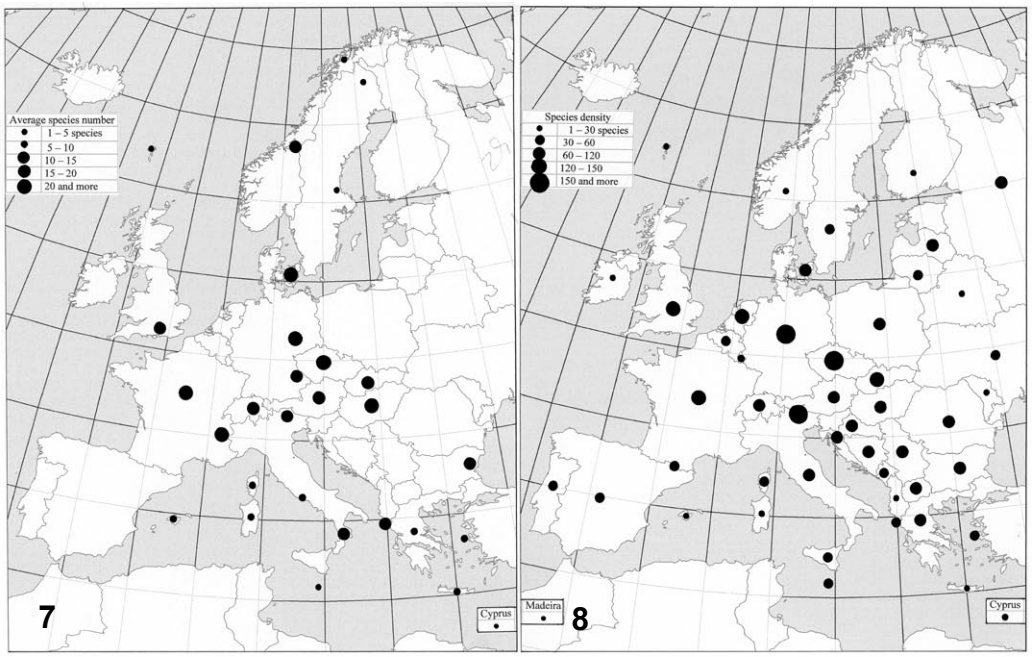
Fig. 6. Biological groups of gall midges belonging to the subfamily Cecidomyiinae in Europe.

Table 4. Species numbers of Cecidomyiidae in Europe in 2009 and comparison with species numbers known in 1984

	country	number of species		number of species change
		1984	2009	1984–2009 [%]
1	Germany[1]	586, 406	836	21
2	France	523	668	28
3	Russia (European Part)[2]	524	650	24
4	United Kingdom	603	620	3
5	Czech Republic	504	590	17
6	Italy	334	508	52
7	Latvia		506	
8	Poland	360	463	29
9	Austria	256	396	55
10	Sweden	261	378	45
11	Slovakia	350	362	3.5
12	Netherlands	295	340	15
13	Hungary	240	332	38
14	Romania	294	315	7
15	Denmark	160	307	92
16	Ukraine		298	
17	former Yugoslavia[3]	287	400	39
18	Serbia		283	
19	Bulgaria	104	240	130
20	Switzerland	81	237	192
21	Croatia		232	
22	Spain	80	229	186
23	Lithuania		224	
24	Slovenia		219	
25	Greece	19	211	1000
26	Norway	65	170	162
27	Bosnia and Herzegovina		169	
28	Macedonia		148	
29	Belgium	89	140	57
30	Finland	135	135	0
31	Portugal	118	122	3
32	Estonia		93	
33	Ireland		87	
34	Montenegro		85	
35	Turkey	34	70	105
36	Liechtenstein		65	
37	Belarus		38	
38	Malta		36	
39	Andorra		30	
40	Cyprus	9	32	255
41	Albania	11	19	72

Notes: [1)] In 1984 the German Federal Republic included 586 species and the German Democratic Republic 406 species; [2)] In 1984 the European part of the Soviet Union was formed of the following parts using the recent country names: Russia, Ukraine, Belarus, Moldova, Estonia, Latvia, Lithuania; each of them is now an independent country;
[3)] The former Yugoslavia is formed at present of six independent countries: Bosnia and Herzegovina, Croatia, Macedonia, Montenegro, Serbia, Slovenia.

Additions of recorded species are expressed in percentages of the species numbers given in 1984. Greece and Cyprus are two countries with the highest additional species numbers during the period 1984–2009. Greece was the country where only 19 species were known in 1984. All species were discovered only by chance. In 1994 we started our systematic faunal investigations at localities



Figs. 7, 8. Evaluation of gall midge species richness. 7 (left) – average species numbers of the family Cecidomyiidae in countries of Europe where systematic faunal investigations have been made during 1955–2009. 8 (right) – species density of gall-inducing and plant-inhabiting species of the family Cecidomyiidae in Europe calculated per unit area of 1000 km^2 for each country and island.

spread over the whole of Greece and on several islands. In the course of several years we raised species number to 211 species, i.e. more than ten times (1000%). Only nine species were known in Cyprus in 1984. After our investigations the species number increased to 32 species (an increase of 255%). Bulgaria, Switzerland, Spain, Norway and Denmark are countries where the progress in investigations of gall midges is expressed in increasing species numbers from 90 to 200%. Other countries with lower increasing additional species during this time period usually posses a relatively high species number that were gathered mainly in previous time periods. The species number of Finland remains at the same level as before 25 years.

Species density

Species density refers to the number of species per unit area. We use this term for the number of gall midge species calculated for each country or island per unit of 1000 km^2, that is for a square with four equal sides each long 31.62 km. This method makes it possible to compare species numbers occurring in various parts of Europe, determine where the area or areas with the highest species numbers occur and to elucidate reasons that cause inequalities in distribution of species numbers in Europe.

Species density for gall midge species occurring per 1000 km^2 may be calculated using the formula of MacArthur & Wilson (1967): $\mathbf{S = x/a^{0.25}}$ where **S** is the number of species per area of

Table 5. Species density of gall-inducing and plant-inhabiting members of the subfamily Cecidomyiinae in countries and islands of Europe

country or island	area (km^2)	n species	species density per 1000 km^2
Albania	28,748	19	8.2
Andorra	468	30	37.5
Austria	83,858	352	116.5
Belgium	30,510	130	55.3
Bosnia and Herzegovina	51,129	169	63.3
Bulgaria	110,910	240	74.1
Canary Islands (Spain)	7,273	3	1.9
Corfu (Greece)	592	49	56.3
Corsica (France)	8,680	60	35.1
Crete (Greece)	8,260	38	22.3
Croatia	56,542	232	84.7
Cyprus	9,251	32	18.3
Czech Republic	78,866	564	189.2
Denmark	43,094	275	107.4
Faroe Islands (Denmark)	1,399	5	4.6
Finland	336,593	104	24.2
France	547,030	581	120.3
Germany	357,021	653	150.5
Greece	131,940	211	62.1
Hungary	93,030	332	107.1
Ireland	70,280	87	29.0
Italy	301,230	471	114.9
Italy, South Tyrol	7,400	312	189.1
Latvia	64,589	264	94.1
Liechtenstein	160	65	103.0
Lithuania	65,200	164	57.7
Luxembourg	2,586	75	57.7
Macedonia	25,333	148	66.1
Madeira (Portugal)	740	18	21.7
Mallorca (Spain)	3,411	33	24.4
Malta	316	36	48.6
Moldova	33,843	5	2.1
Montenegro	13,812	85	44.7
Netherlands	41,524	305	120.1
Norway	324,220	112	26.4
Poland	312,685	397	94.5
Portugal	91,568	122	39.4
Romania	238,391	304	76.0
Russia (European)	3,960,000	400	50.6
Samos (Greece)	479	34	42.5
Sardinia (Italy)	23,813	44	20.0
Serbia	88,361	283	91.3
Sicily (Italy)	25,426	89	40.1
Slovakia	48,845	355	134.5
Slovenia	20,273	219	104.2
Spain	504,851	212	42.9
Sweden	449,964	266	46.0
Switzerland	41,290	228	90.1
Ukraine	603,700	166	33.8
United Kingdom (GB)	244,820	526	132.8

1000 km^2, **x** is the number of gall midge species found in the country and **a** is the whole area of the country expressed in 1000 km^2.

Results and calculations are given in Tables 5, 6 and in Fig. 8. Only countries of Europe where investigations were carried out or the summary of knowledge is available are given. Species numbers in the third column involves only the species of the subfamily Cecidomyiinae including gall-inducing and plant-inhabiting gall midges and inquilines, not the species of subfamilies Lestremiinae and Porricondylinae, larvae of which do not induce galls.

On the basis of our calculations, two countries situated in Central Europe, the Czech Republic and South Tyrol, the autonomous province in northern Italy, have the highest species density, each with 189 gall midge species occurring per 1000 km^2. Germany with 150 species in an area of 1000 km^2 is at third place. United Kingdom, France, the Netherlands, situated in western Europe, and Slovakia in Central Europe, also have a high level of species density, including 120–150 species per area of 1000 km^2. The countries of Central and western Europe have a higher species density than the countries situated to the north and to the south. The very low species density have been recorded in countries situated in northern Europe, viz. Finland, Norway, Sweden, and in the Faroe Islands, situated in the Atlantic Ocean far from the European continent, and on the other hand the countries and islands in southern Europe, viz. Madeira, Sardinia, Crete and Cyprus.

Species richness of gall midges in Europe is influenced by many factors. Above all by the geographic position on the continent with different natural conditions of the realm. The number of gall midges is much lower in the tundra and taiga covered with species-poor vegetation. In countries of northern Europe, i.e. in Finland, Sweden and Norway, the relatively low gall midge species number is the result of lower occurrence and poorer species composition of plants. In temperate parts of Europe, i.e. in United Kingdom, Germany, France, Czech Republic, Slovakia, Poland, Hungary, Romania and countries of the former Yugoslavia (Bosnia-Herzegovina, Croatia, Serbia, Slovenia, Macedonia, Montenegro) broad-leaved and mixed forests cover large areas and these forests contain many plant species which may be hosts of gall midges.

Table 6. Evaluation of gall-inducing and plant-inhabiting species of the family Cecidomyiinae occurring in countries of Europe into five density groups according to the species density

density groups				
very high 150 and more species	high 120–150 species	medium 60–120 species	low 30–60 species	very low 1–30 species
Czech Republic	France	Austria	Andorra	Albania
South Tyrol	Netherlands	Denmark	Belgium	Canary Is.
Germany	Slovakia	Hungary	Corfu	Crete
	United Kingdom	Italy	Corsica	Cyprus
		Latvia	Lithuania	Faroe Islands
		Liechtenstein	Luxembourg	Finland
		Poland	Malta	Ireland
		Serbia	Montenegro	Madeira
		Slovenia	Portugal	Mallorca
		Switzerland	Samos	Moldova
		Bosna and Herzegovina	Sicily	Norway
		Bulgaria	Spain	Sardinia
		Croatia	Sweden	Belarus
		Greece	Ukraine	
		Macedonia		
		Romania		
		Russia		

Species numbers per 1000 km^2 in the southern parts of Europe, the so called Mediterranean subregion, including southern parts of Greece, southern parts of Italy, southern part of the Iberian Peninsula and islands in the Mediterranean Sea, are much lower than in Central Europe. For example, the total value of species density for nine islands in the Mediterranean Sea is seven. Large parts of these countries and islands were deforested in ancient times and at present the landscape is covered mainly with sclerophyll vegetation (garrigue or maquis). Relations between plants bearing galls to plants without galls are from 1:50 up to 1:80. We can confirm that low numbers of galls occurs in these areas on the basis of our own experience. During our investigations when we used the time-area collecting method, we could speak about a success when we found 5 to 10 galls of gall midges at one locality, whereas in Central Europe we usually found galls of 15 to 30 species at one locality.

Species richness of a country, zoogeographic region, continent or their parts is expressively influenced by the level of knowledge and degree of exploration of such area. Germany, France, United Kingdom, Italy, Poland, Czech Republic and Austria are countries with a relative long tradition in the study of gall midges and with many researchers who devoted their efforts to the study of gall midges and their galls in the past. These countries have also the highest species numbers of gall midges. On the other hand there are many countries where the study of gall midges does not have so long a tradition or is in the initial phase.

Gall midge species numbers in Greece, South Tyrol and Austria were relatively low before our investigations. Only 20 gall midge species were known from Greece before 1994. After our exploration the species number increased to 210. In South Tyrol the species number increased from 24 to 312 and in Austria from 170 to 396. The number of gall midge species in Greece and South Tyrol increased more than ten times after using the time-area collecting method.

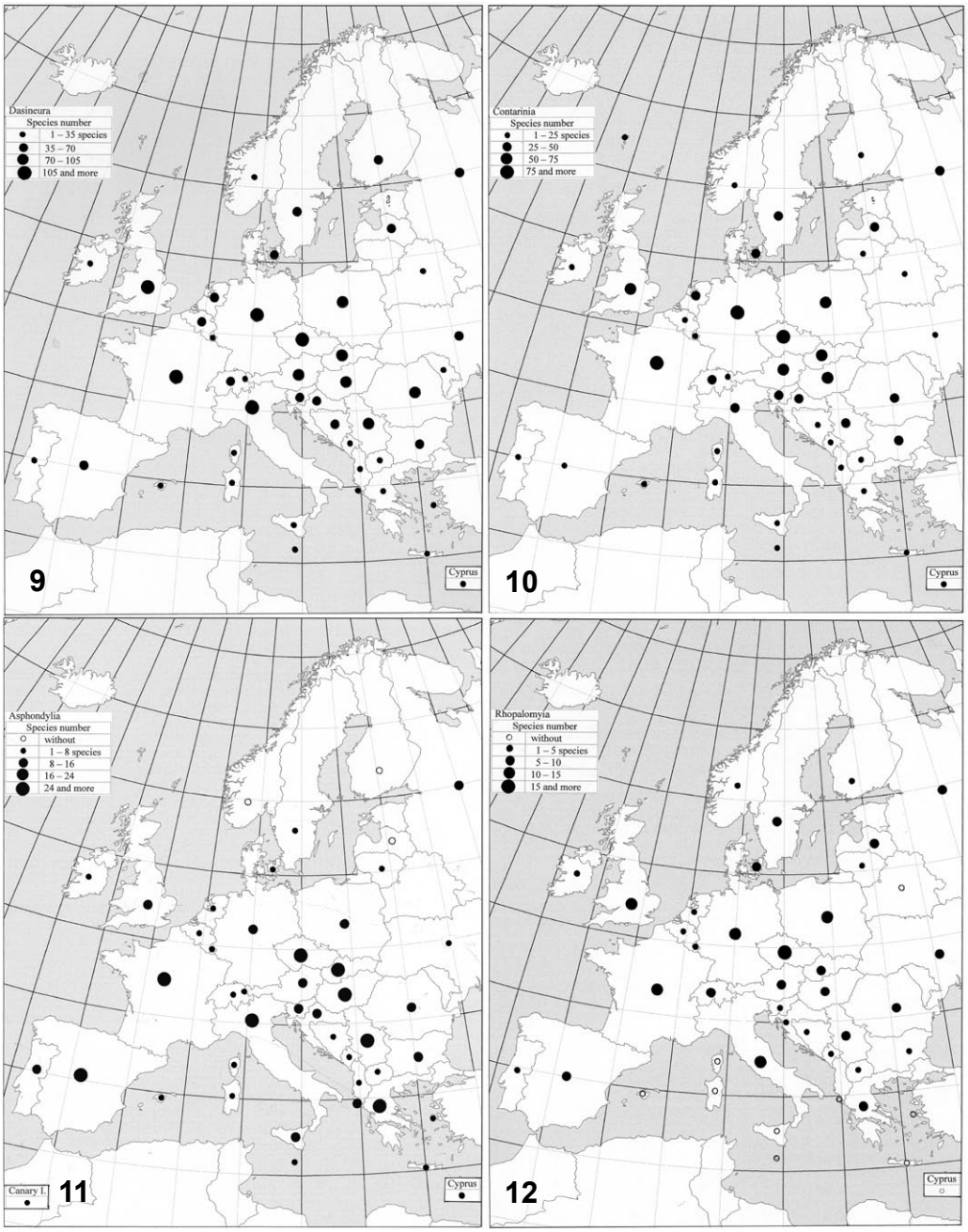
Surprising is the high abundance of gall midges in Kazakhstan. Fedotova (2000) gave 804 gall midge species occurring on the area of 2,780,000 km^2 where the exploration was made at more than 60 localities. Kazakhstan with 112 gall midge species occurring in the area unit per 1000 km^2 is one of the very well explored countries in Central Asia, the western part of which is adjacent to eastern Europe. Richness of gall midge species in that area is connected with relatively species rich vegetation. The flora of Kazakhstan includes about 6000 plant species in 1118 genera and 161 families (Ryabushkina et al. 2008).

If we compare the species density of Europe with other parts of the Palaearctic region, species richness of the family Cecidomyiidae in the East Palaearctic Region is known mainly owing to the studies of Yukawa (1971). He treated in his revision 167 named and 17 unnamed gall midge species, forming a collection of 184 gall-inducing species of the family Cecidomyiidae. After twenty five years of intensive studies Yukawa and his students (so called Yukawa's Cecidological School) were able to broaden the knowledge of Cecidomyiidae in Japan and to increase the species number from 184 to 628 (which is the number of sorts of galls caused by gall midges, including described and undescribed species), that is 3.4 times (Yukawa & Masuda 1996, Paik et al. 2004). Japan extending over an area of 377,835 km^2 in the temperate to subtropical zones of the East Palaearctic, is of quite similar size to Norway in the West Palaearctic where only 170 gall midge species were found. In contrast, Norway is situated in the boreal part of northern Europe. Its northernmost part has a mostly maritime subarctic climate and arctic tundra with species poor vegetation that does not give enough host plants for gall midges.

Also of interest is the comparison of species numbers found in Europe with species richness of gall midges occurring in North America. It occupies a territory of 24,490,000 km^2, of which the USA has an area of 9,400,000 km^2 and Canada 9,976,139 km^2. Gagné (1989) in his book gives 891 gall midge species associated with 350 plant genera of 87 plant families. If we count relations between gall midge species number known and the territory according to the formula of MacArthur and Wilson, we obtain an average of 76 gall midge species per 1000 km^2.

Species richness of the main genera

Numbers of species assigned to the genera of gall-inducing gall midges differ in the countries of western and eastern Europe. In Table 7 we give species numbers of twelve of the most species-



Figs. 9–12. Distribution of species of the main genera of the family Cecidomyiidae in countries of Europe. 9 – *Dasineura* Rondani, 1840. 10 – *Contarinia* Rondani, 1860. 11 – *Asphondylia* Loew, 1850. 12 – *Rhopalomyia* Rübsaamen, 1892.

Table 7. Species numbers of the main genera of gall-inducing Cecidomyiinae in the world, in the Palaearctic Region, Western and Eastern Europe in comparison with Kazakhstan (Central Asia)

genus	World	Palaearctic	Europe		Kazakhstan
			Western	Eastern	
Dasineura Rondani, 1840	490	335	230	61	92
Contarinia Rondani, 1860	340	225	135	42	79
Asphondylia Loew, 1850	270	66	50	20	9
Rhopalomyia Rübsaamen, 1892	260	161	38	9	60
Lasioptera Meigen, 1818	125	50	27	9	3
Stefaniola Kieffer, 1913	108	108	6	0	74
Rabdophaga Westwood, 1847	80	40	40	18	11
Jaapiella Rübsaamen, 1915	80	80	35	9	51
Resseliella Seitner, 1906	47	27	23	9	1
Macrolabis Kieffer, 1892	50	50	35	5	22
Baldratia Kieffer, 1897	38	36	3	1	20
Mayetiola Kieffer, 1896	31	30	28	1	1

-rich genera of the world and compare these numbers with numbers in the Palaearctic, Western and Eastern Europe and in Kazakhstan, situated in south-western Asia, the area of which is greater than western Europe.

Dasineura is the largest genus of the family Cecidomyiidae containing 490 species spread over all the world. Most of these species – 335 – occur in the Palaearctic Region, 112 species in the Nearctic Region and only a few species in other biogeographic regions. Larvae induce galls mainly on leaves, on leaf and flower buds on host plants of various plant families. In Europe most species are associated with Fabaceae, Rosaceae, Asteracae, Brassicaceae and Lamiaceae. *Dasineura* is the most species-rich genus in the Palaearctic Region and is abundant in Western Europe where 230 species occur. The species number is much lower in Eastern Europe (Fig. 9). In Kazakhstan it is also the most species-rich genus and is in first position, together with the genus *Halodiplosis*.

Contarinia with 340 species described in the world is in second place. In Western Europe 135 species were found. Larvae induce galls mainly on flowers, flower and leaf buds and leaves or live freely in flower heads of many host plants of various plant families. In Europe most species are associated with Fabaceae, Asteraceae and Poaceae. Species are abundant in Western and Central Europe, their number decreases to the east, southeast and southwest but they are relatively abundant in Kazakhstan. Of 230 species that are distributed mainly in Central Europe, the highest species numbers are found in Germany, Czech Republic, France and United Kingdom in the latitudinal belt between 35^0 and 54^0 North. Lower species numbers were found in Norway, Sweden and Finland and, on the other hand, species are relatively abundant in eastern parts of southern Europe (Fig. 10).

Asphondylia with 270 species occurring in the world is in third place. Of these, 50 species occur in Central and Western Europe (Fig. 11). Species number decreases to the south and east. In Kazakhstan only nine species were found. Larvae induce galls on flower or leaf buds and fruits on host plants of various plant families. Galls are usually associated with fungal mycelia (so called ambrosia galls). In Europe the galls are induced on host plants belonging mainly to Fabaceae and Lamiaceae. *Asphondylia* is considered to have its origin in the Neotropical Region and then to have spread throughout the world (Möhn 1961, Tokuda & Yukawa 2007). We suppose that at least one centre of the origin of the genus *Asphondylia* is in the Mediterranean area in southern Europe in the western part of the Palaearctic Region. This area is considered to be one of the cen-

tres of origin of plant and animal species in Europe. In this area 50 described species and several undescribed species of the genus *Asphondylia* are distributed which are associated with 13 plant families. Interestingly, most species of this genus are associated with herbaceous plants, only a few with trees and shrubs. No species have been found in Norway and Finland and the species numbers in northern parts of Europe are low. Species of the genus *Asphondylia* occur abundantly in southern Europe. This fact supports our hypothesis that at least one of the centres of diversity of the genus *Asphondylia* is situated in Europe. In the Fig. 21 there are shown distribution areas of several species of this genus.

Rhopalomyia, including 260 species in the world, is relatively species-rich in central, southeast and western Europe where it contains 38 species (Fig. 12). Its number decreases markedly to the south. No species were found in the islands of the Mediterranean Sea. Many *Rhopalomyia* species were found and occur in Central Asia, mainly in Kazakhstan. Larvae induce galls on stems, buds and leaves of host plants mainly of the family Asteraceae. Galls often occur on several organs of the same host plant species. Alternation of plant organs is connected with the development of several generations per year.

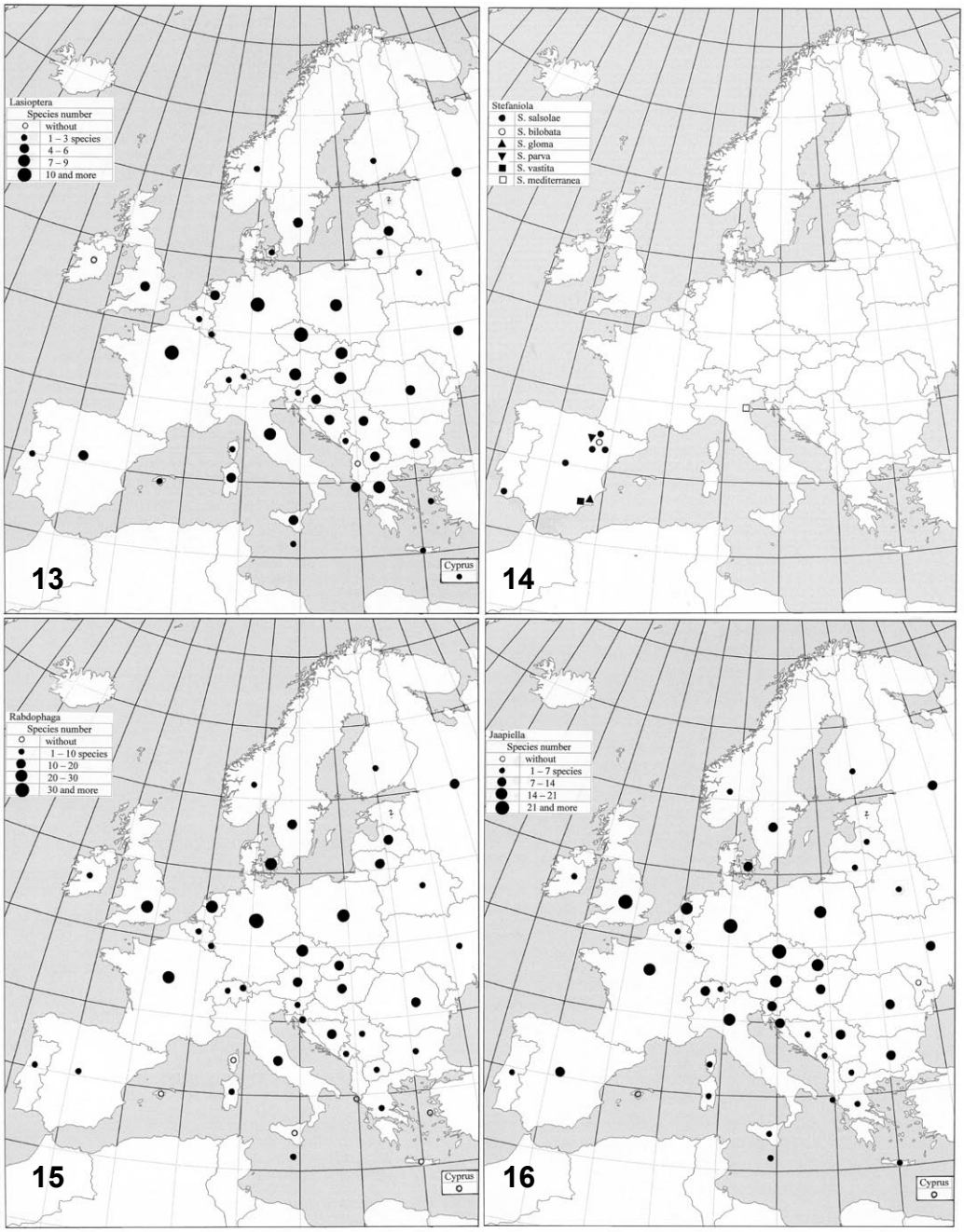
The genus *Lasioptera* includes 50 species in the Palaearctic Region and 27 of them occur in Western Europe (Fig. 13). Larvae induce galls on stems of host plants of various families, mainly on Poaceae and Apiaceae, or develop in fruits without making galls. Galls are usually associated with fungal mycelia (so called ambrosia galls). Larvae of *Lasioptera buhri* develop in stems of host plants belonging to several genera of three different families. Species of the genus *Lasioptera* are relatively abundant in Central and Western Europe and numbers decreases northwards and southwards. Also in Central Asia its numbers are low – only three species occur in Kazakhstan.

Stefaniola contains 108 species and is a Palaearctic genus. Species are distributed in Central Asia, mainly in Kazakhstan and adjacent countries, and in North Africa. Only six species reach to Europe where they occur in southwestern parts, in Spain and Portugal (five species) and in Italy (one species), all very rare. Larvae induce leaf and bud galls on various species of Chenopodiaceae. Four species are associated with *Salsola vermiculata*, viz. *Stefaniola bilobata*, *S. gloma*, *S. parva* and *S. salsolae*, *S. vastita* cause galls on *Anabasis*. All these species occur in the Iberian Peninsula. *Stefaniola mediterranea*, causing galls on stems of *Salicornia europaea* and *Halocnemum strobilaceum*, was found in Italy (Fig. 14).

Rabdophaga is a Holarctic genus with 40 species occurring in the Palaearctic Region and with the same species number occurring in North America. Larvae cause stem, bud and leaf galls on various species of *Salix* and one species, *Rabdophaga giraudiana*, is known to be associated with *Populus tremula* and *P. alba*. Both genera of host plants belong to the family Salicaceae. The species are abundant in central and northern parts of Western Europe and their number decreases to the south and southwest (Fig. 15). Only one species was found in Sardinia and Mallorca in the Mediterranean and no species was found in the remaining seven islands in the Mediterranean. a relatively low species number was found in Kazakhstan.

Jaapiella is a Palaearctic genus with 80 species of which 35 species occur in Western Europe (Fig. 16). Larvae induce galls on leaf and flower buds and leaves of host plants of various plant families. Some species are inquilines in galls of other gall midges. Higher species numbers occur in Central and Western Europe and species numbers reduces towards the marginal parts of Europe. Only a few species were found in northern and southern Europe, on islands in the Mediterranean and no species was found in Mallorca in the Mediterranean Sea. a relatively large number of species occurs in Kazakhstan.

Macrolabis is also a Palaearctic genus with 35 species distributed in Western Europe (Fig. 17). Larvae induce galls on leaf and flower buds on host plants of various families. About one half of species are inquilines in galls of other gall midges. Species numbers decrease from Central



Figs. 13–16. Distribution of species of the main genera of the family Cecidomyiidae in countries of Europe. 13 – *Lasioptera* Meigen, 1818. 14 – *Stefaniola* Kieffer, 1913. 15 – *Rabdophaga* Westwood, 1847. 16 – *Jaapiella* Rübsaamen, 1915.

Table 8. Distribution of species of the family Cecidomyiidae occurring in Europe and in zoogeographical units of the world

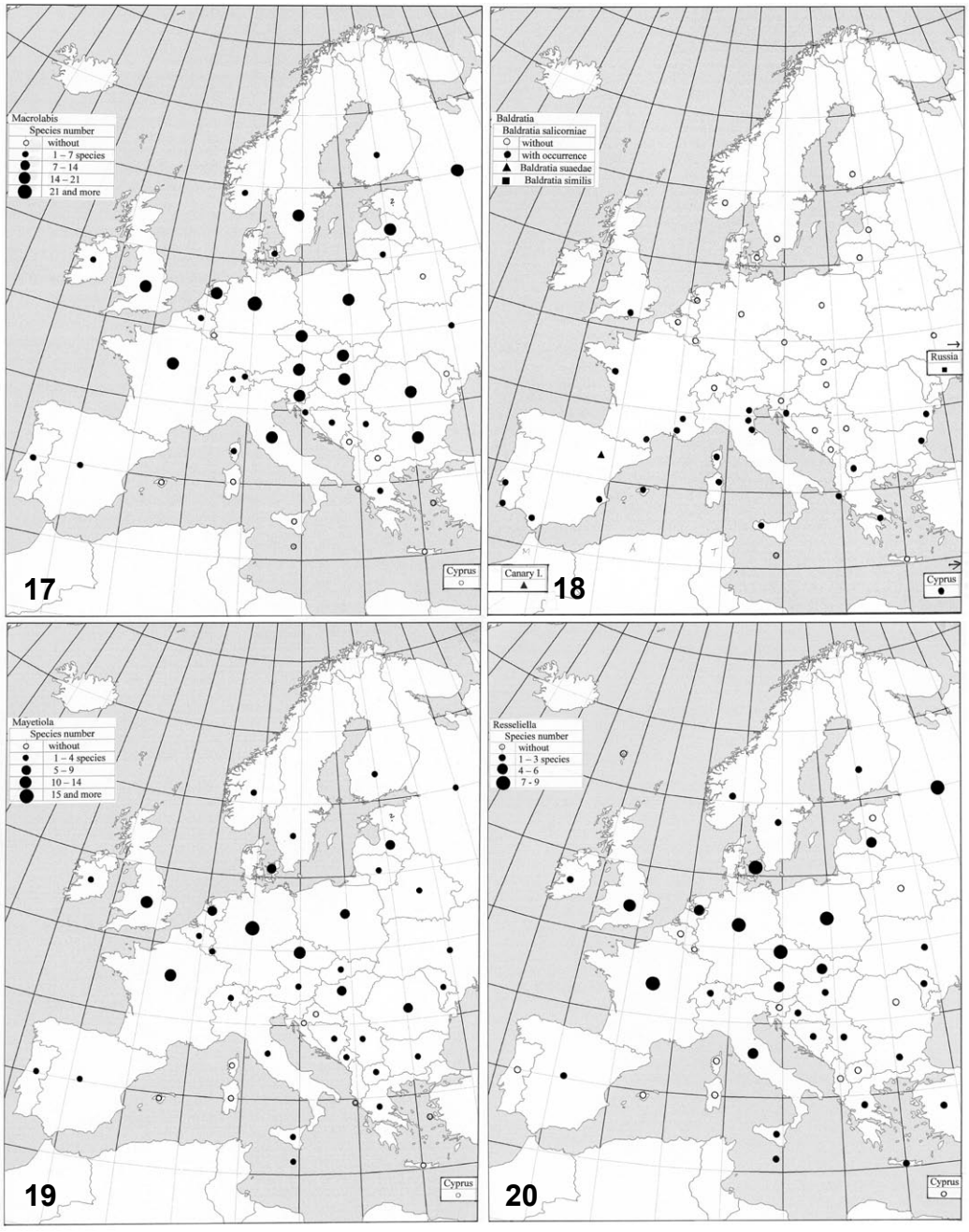
taxon	zoogeographical unit						
	European	Euro-siberian	Mediter-ranean	Palaearctic	Holarctic	cosmopolitan	alien
Cecidomyiidae							
(1800 species)	1278	216	170	25	81	7	23
%	71.0	12.0	9.5	1.3	4.5	0.4	1.3
Lestremiinae							
(280 species)	181	54	0	0	43	2	0
%	64.6	19.3			15.4	0.7	
Porricondylinae							
(310 species)	280	12	0	5	13	0	0
%	90.3	3.9		1.6	4.2		
Cecidomyiinae							
(1210 species)	817	150	170	20	25	5	23
%	67.5	12.5	14.0	1.7	2.0	0.4	1.9

and Western Europe to the south and no species was found in Macedonia and Montenegro in the Balkan Peninsula and in the islands in the Mediterranean, with the exception of Corsica. Species of this genus were found abundantly in Kazakhstan.

Baldratia is a Palaearctic genus with 36 species and with two species occurring in Africa. Larvae induce galls on stems of various Chenopodiaceae in Central Asia and only three species occur in Western Europe. Only one species, *Baldratia salicorniae*, causing galls on *Salicornia fruticosa*, is native to Europe and occurs scattered along the coast of the Black Sea, along the coasts of the Mediterranean Sea and in several islands in this sea. Galls of *B. salicorniae* were found also at several localities in southern France, Spain, Portugal and in southern parts of England on the coast of the Atlantic Ocean. *Baldratia suaedae* and *B. similis* are species which have their origin in the Middle East. Galls of *Baldratia suaedae* on *Suaeda vera*, described from material found in Israel, were discovered at two localities in Europe, viz. on the Canary Islands and in Monegros in north-eastern Spain. Galls of *Baldratia similis* causing galls on *Anabasis aphylla*, described from material found in Iran, were found at one locality in south-eastern Russia (Fig. 18).

Mayetiola is a Palaearctic genus containing 30 species with only one species native to North America. Larvae induce galls on stems of various species and genera of Poaceae. *Mayetiola destructor*, a serious pest of cereals that occurred abundantly in Europe in the past, is considered to have its origin in south-eastern Europe, probably in the Ukraine. It has been accidentally introduced with cereals into other biogeographic regions where it causes serious damage. Most species were described from western Europe, only one species occurs in eastern Europe and in Kazakhstan. Species of this genus occur abundantly in Central and Western Europe, their number reduces northwards and southwards and no species were found in Croatia and Slovenia in the Balkan Peninsula or on seven islands in the Mediterranean. *Mayetiola destructor* is the only species known to occur in Sardinia and Malta. It has been probably introduced there with cereals (Fig. 19).

Resseliella is a genus with cosmopolitan distribution and diverse biology. Of 43 species occurring in the Holarctic, 27 occur in the Palaearctic and 16 in the Nearctic region. Larvae of many Palaearctic species live under the bark of trees and shrubs, causing them damage, and some species are considered to be pests. Several species are associated with resin of coniferous trees or with cambium liquid flowing from stems of young broad-leaved trees that were primarily wounded



Figs. 17–20. Distribution of species of the main genera of the family Cecidomyiidae in countries of Europe. 17 – *Macrolabis* Kieffer, 1892. 18 – *Baldratia* Kieffer, 1897. 19 – *Mayetiola* Kieffer, 1896. 20 – *Resseliella* Seitner, 1906.

by animals (Dengler 2004). European species are associated with 11 plant families: six species with Pinaceae and four with Rosaceae, other families each hosting one gall midge species. The biology of several species remains unknown. Most species are distributed in Central and Western Europe, their number decreases in southern Europe and no species was found in Mallorca, Corsica and Sardinia and Cyprus (Fig. 20).

Geographic distribution

The gall midge species occurring in Europe may be divided, according to their overall distribution in the world, into six zoogeographic units: European, Eurosiberian, Mediterranean (including Submediterranean), Palaearctic or Euroasian, Holarctic and cosmopolitan (Table 8). In addition, species that penetrated into Europe from other continents and are members of the present European

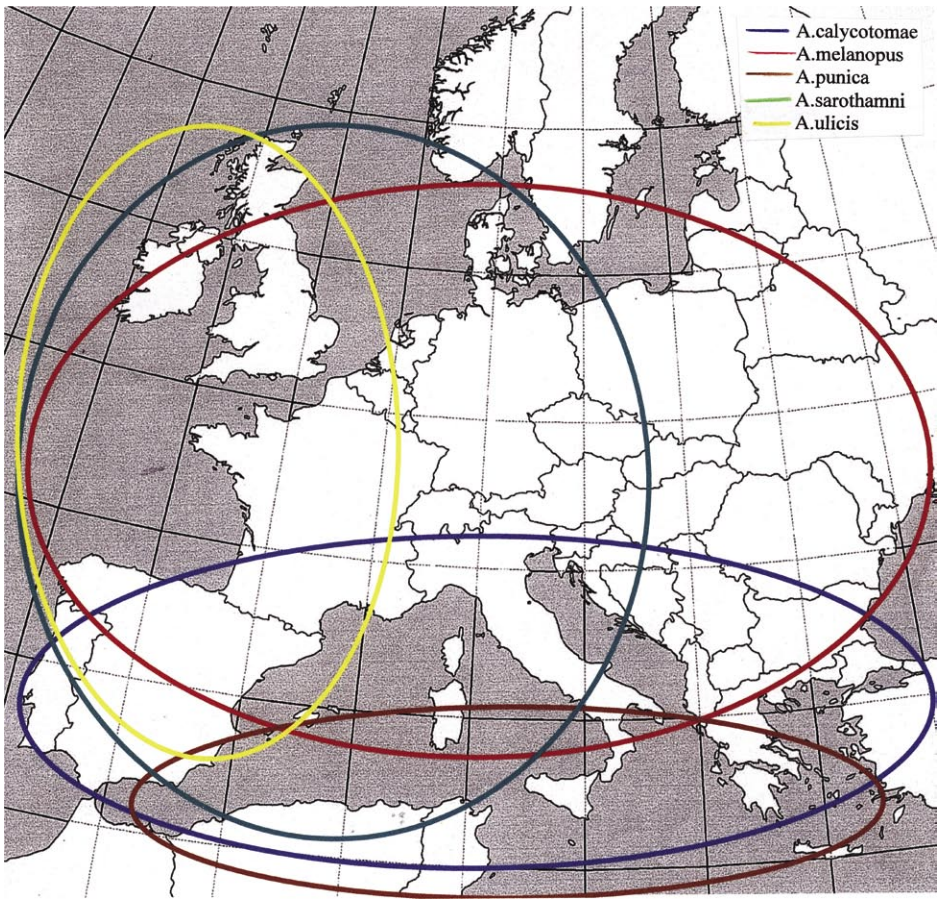


Fig. 21. Distribution areas of five species of the genus *Asphondylia* Loew, 1850 in Europe shown by lines of their limits: *A. calycotomae* Kieffer, 1912 causing galls on *Calycotome spinosa* (Fabaceae) (blue line); *A. melanopus* Kieffer, 1890 inducing galls on *Lotus corniculatus* (Fabaceae) (red line); *A. punica* Marchal, 1897 evoking galls on *Atriplex halimus* (Chenopodiaceae) (brown line); *A. sarothamni* (Loew, 1850) producing galls on *Cytisus* (*Sarothamnus*) *scoparius* (Fabaceae) (green line); *A. ulicis* Trail, 1873 causing galls on *Ulex europaeus* (Fabaceae) (yellow line). *A. calycotomae* and *A. punica* are Mediterranean species, *A. ulicis* is an Atlantic species, *A. sarothamni* is a sub-Atlantic species and *A. melanopus* a European species.

gall midge fauna are designated as alien. On the other hand, some European gall midge species that spread into other continents are considered to be immigrants there and some European gall midge species were introduced in other continents of the world as agents for biological control of pests or of weeds. The distribution of species of the subfamily Cecidomyiinae including the gall-causing and plant inhabiting species is better known than the distribution of species belonging to subfamilies Lestremiinae and Porricondylinae that require different sampling methods.

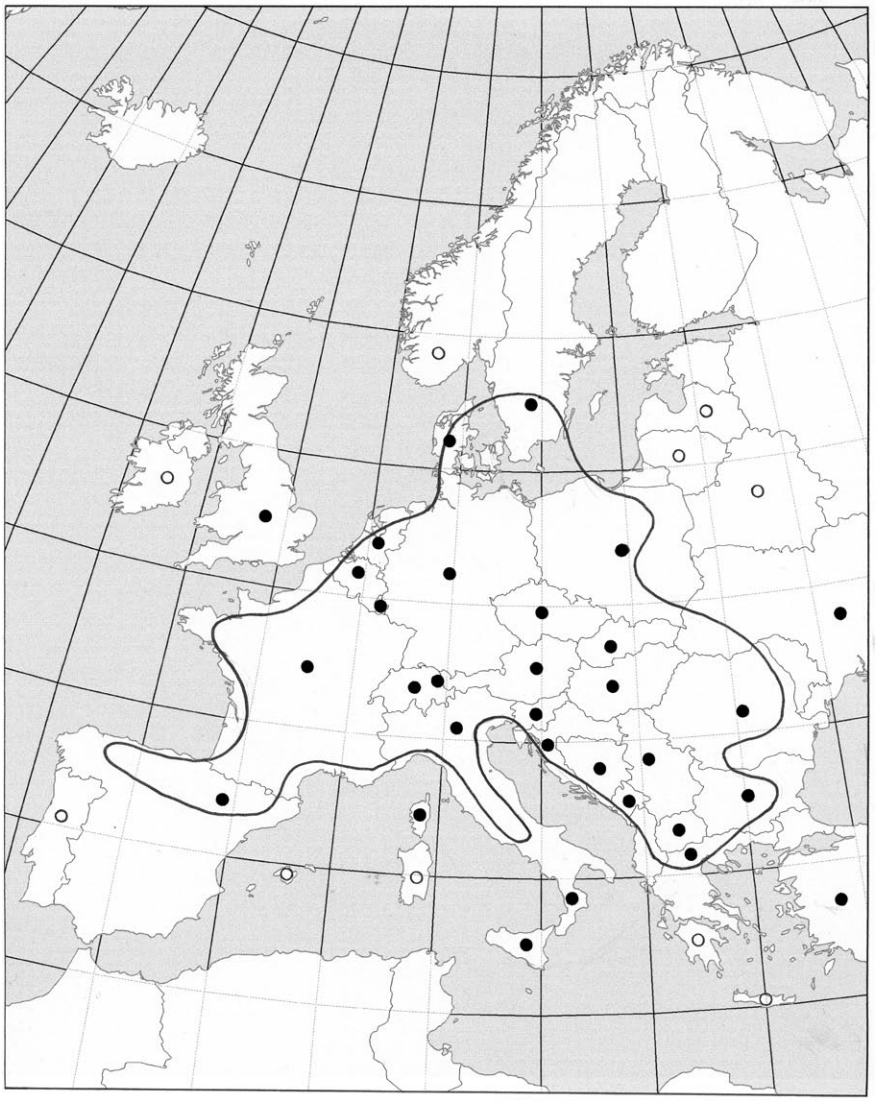


Fig. 22. Distribution area of *Mikiola fagi* (Hartig, 1839) in countries of Europe including its occurrence in single countries (black circles) and its absence (white circles), and distribution area of its host plant, *Fagus sylvatica* L. (Fagaceae) (black line). Distribution area of the host plant after Meusel et al. (1965–1992).

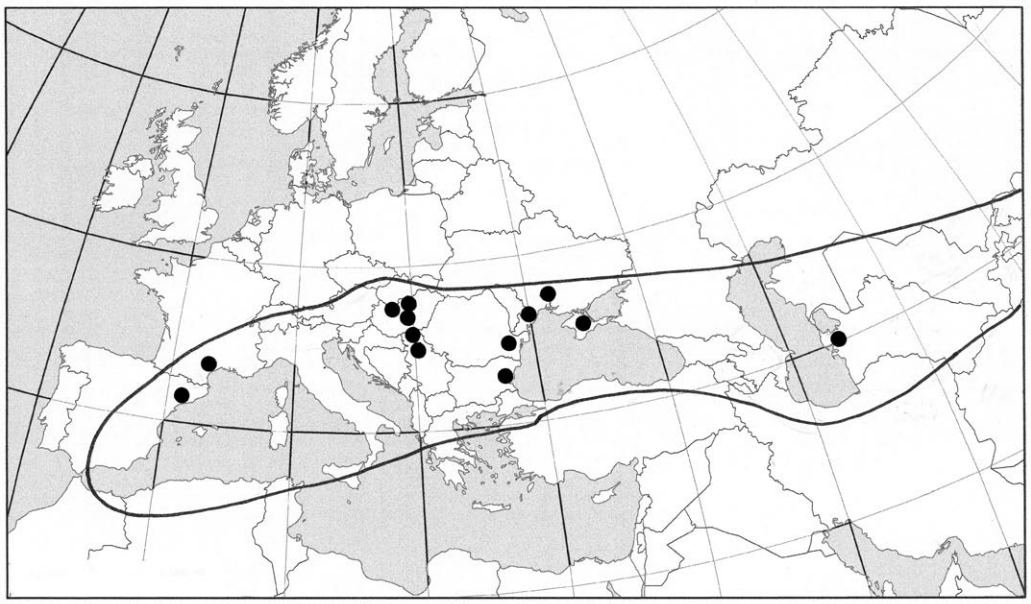


Fig. 23. Distribution area of *Kochiomyia kochiae* (Kieffer, 1909) (black circles) on *Bassia prostrata* (L.) Scott (= *Kochia prostrata* (L.) Schrad.) (Chenopodiaceae) (black line), a Pontic-Pannonian species. Distribution area of the host plant after Meusel et al. (1965–1992).

Of 1800 species of the family Cecidomyiidae forming the present fauna of Europe, 71% are European, 12% Eurosiberian, 9.5% Mediterranean and Submediterranean, 4.5% Holarctic, 1.3% Palaearctic, 0.4% cosmopolitan and 1.3% alien species. In the best known group of gall midges, in the subfamily Cecidomyiinae, we found all types of distribution. Of interest is the fact that in the subfamilies Lestremiinae and Porricondylinae there were not found gall midge species with Mediterranean or Submediterranean types of distribution and only a few European species occur or have been found beyond the boundary of Europe, in Asia or in North America.

European species occur only in Europe and are considered to have the centres of their origin in Europe. Altogether 1278 species (71%) of the family Cecidomyiidae known to occur in Europe belong in this group, i.e. nearly three quarters of all species. Areas of their distribution may range from very small to large. Most of them are known only from the type locality in some country of Europe and have never been recorded again after the original description. Several species have small areas of distribution, occurring only in the country where they were discovered and in one or two adjacent countries. Some species occur abundantly in several countries of Central Europe and some of them extend southwards to the Mediterranean and even to North Africa, others extend to south-east or to western Turkey or the Caucasus. Typical representatives of European gall midges are *Mikiola fagi* galling leaves of *Fagus sylvatica* (Fig. 22), *Macrodiplosis pustularis* with galls on leaves of *Quercus robur* and its relatives, *Acericecis vitrina* causing galls on leaves of *Acer pseudoplatanus*, *Zygiobia carpini* inducing galls on leaves of *Carpinus betulus*, and *Taxomyia taxi* causing galls on buds of *Taxus baccata*. Most species of the subfamily Porricondylinae and about two thirds of species of the subfamily Lestremiinae have European distributions.

Several gall midge species that are members of the European fauna have a particular or strange distribution area. Gall midge species associated with *Cytisus* (*Sarothamnus*) *scoparius*,

viz. *Asphondylia sarothamni*, *Contarinia scoparii*, *Dasineura tubicoloides*, *Jaapiella sarothamni* and *Janetiella tuberculi*, are European and **sub-Atlantic species** occurring abundantly along the shores of the Atlantic Ocean, penetrating inland and reaching, with their host plant, eastwards to the Czech Republic. *Kochiomyia kochiae* is a **Pontic-Pannonian species** causing galls on *Bassia prostrata* (= *Kochia prostrata*) (Fig. 23). It occurs abundantly along the shores of the Black Sea (Pontus Euxinus) and in the Pannonian lowlands in Hungary (Skuhravá & Skuhravý 1999). The galls were found also in southern France and in north-eastern Spain where this species reaches the

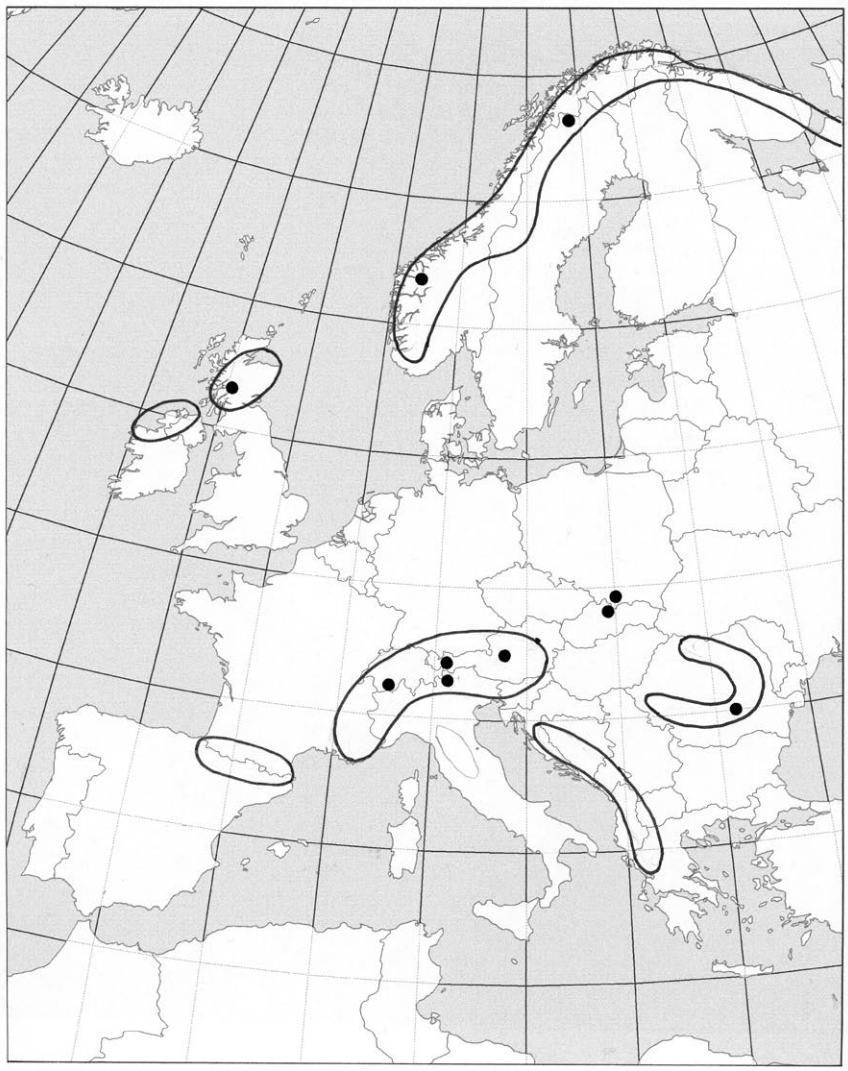


Fig. 24. Disjunct area of distribution of *Jaapiella alpina* (Löw, 1877) (black circles) and its host plant *Silene acaulis* (L.) Jacq. (Caryophyllaceae) (black line) in Europe. Distribution area of the host plant after Meusel et al. (1965–1992).

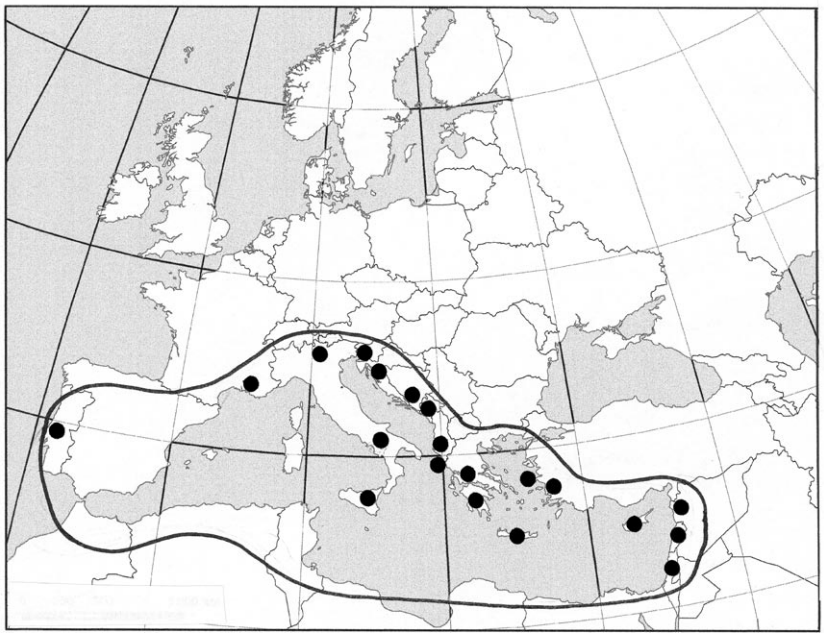


Fig. 25. Mediterranean distribution area of *Dasineura oleae* (Angelini, 1831) (black circles) and its host plant, *Olea europaea* L. (Oleaceae) (black line) in the southern part of Europe and westernmost Asia. Distribution area of the host plant after Meusel et al. (1965–1992).

most western limits of its remarkable distribution area. The gall midge *Jaapiella alpina* causing galls on *Silene acaulis*, the host plant species of typical arctic-alpine distribution, has a disjunct distribution area with scattered occurrence at very high elevations in the mountains of Europe (Fig. 24).

Eurosiberian species inhabit the Eurosiberian subregion of the Palaearctic region. About one eighth, i.e. 216 species (12%) of the Cecidomyiidae known to occur in Europe belong in this group. They have centres of origin in Europe where they occur usually abundantly and extend at least to Western Siberia, with some of them reaching to Central Siberia and only few reaching to Eastern Siberia and to the most eastern part of the Palaearctic Region, to the Far East. Typical representatives of Eurosiberian species are *Harmandiola cavernosa*, *H. globuli*, *H. populi* causing galls on leaves of *Populus tremula*, *Lasioptera rubi* inducing galls on stems of *Rubus idaeus* and its relatives, *Iteomyia capreae* on *Salix caprea* (Fig. 26), *Geocrypta galii* on *Galium mollugo* and *Dasineura urticae* on *Urtica dioica*. *Thecodiplosis brachyntera* galling needles of *Pinus sylvestris* and *Pinus mugo* occurs abundantly in Central Europe where it is classed as a pest causing serious outbreaks from time to time (Skuhravý 1991). Its occurrence decreases eastwards and the galls were found in southern part of Central Siberia (Skuhravá & Skuhravý 1993b).

Mediterranean species have centres of origin in the Mediterranean area. About 170 species, i.e. 9.5% of the family Cecidomyiidae known to occur in Europe belong in this group. They occur along the shores of the Mediterranean and are associated with Mediterranean host plant species. Some of them occur over greater areas and a few species reach the northern limits of their distribution

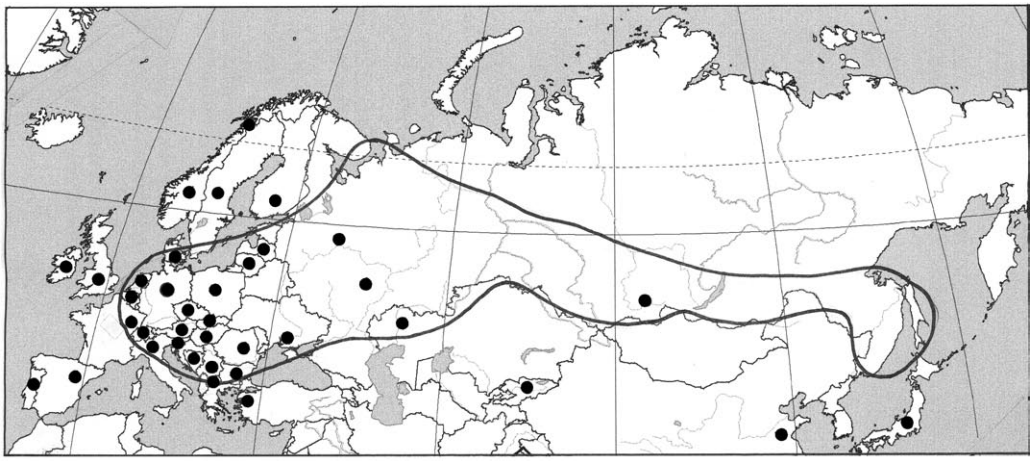


Fig. 26. Eurosiberian distribution area of *Iteomyia capreae* (Winnertz, 1853) (black circles) and its host plant, *Salix caprea* L. (Salicaceae) (black line) including Europe, Siberia and the East-Palaearctic subregion. Distribution area of the host plant after Meusel et al. (1965–1992).

areas in Central Europe. In such case they are defined as **Submediterranean species.** Nine gall midges associated with *Quercus cerris*, viz. *Dryomyia circinans*, *Contarinia quercicola*, *C. subulifex*, *Dasineura tubularis*, *Janetia cerris*, *J. homocera*, *J. nervicola*, *J. pustularis* and *J. szepligetii* that occur abundantly in the Mediterranean area reach the northern limits of their distribution in the eastern part of Austria, southern part of the Czech Republic and of the Slovak Republic.

Typical Mediterranean species are *Dasineura oleae* inducing galls on leaves of *Olea europaea* (Fig. 25), *Phyllodiplosis cocciferae* and *Dryomyia cocciferae* causing galls on leaves of *Quercus coccifera*; four species associated with *Quercus ilex*, viz. *Contarinia ilicis*, *C. luteola*, *Dasineura ilicis* and *Dryomyia lichtensteinii*; *Dasineura asparagi* causing galls on *Asparagus aphyllus*; four species associated with *Artemisia herba-alba*, viz. *Rhopalomyia hispanica*, *R. navasi*, *R. producticeps* and *R. tavaresi*; *Braueriella phillyreae*, *Dasineura rufescens* and *Probruggmanniella phillyreae* which are associated with various species of *Phillyrea*. Also six gall midge species associated with various *Erica* spp. have Mediterranean type distributions. *Dasineura broteri*, *D. elegans* and *D. zimmermanni* occupy only small distribution areas. In contrast, *Dasineura ericaescopariae*, *Myricomyia mediterranea* and *Wachtliella ericina* occupy larger areas in the Mediterranean. *W. ericina* reaches up to southern England, to southern Denmark and to the southern part of the Czech Republic in Central Europe. *Asphondylia coronillae* causing galls on buds and pods of *Coronilla emerus* is a Mediterranean species that occurs abundantly in southern Europe and penetrates up to Switzerland and northern Italy. *Lasioptera eryngii* causing large galls on stems of *Eryngium campestre* occurs scattered in the whole Mediterranean and occupies a large area reaching up to Turkey. It penetrates northwards up to the Czech and Slovak Republics where the most northern boundary of its distribution area runs. It may be designated as a typical Submediterranean species.

Palaearctic or Euro-Asian species are species that inhabit Europe or the Eurosiberian subregion and at least one of the other Palaearctic subregions, i.e. Central Asian or East Palaearctic subregion. Only about 25 species (1.3%) of the family Cecidomyiidae known to occur in Europe belong in this group, mainly species caught as adults, viz. *Trisopsis abdominalis*, *T. karelini*, *T. punctiven-*

tris, *T. tyroglyphi*, *Stomatosema kamali* of the subfamily Cecidomyiinae and *Peromyia truncata* and *Polyardis bispinosa* of the subfamily Lestremiinae. Of gall-causing species of the subfamily Cecidomyiinae, *Etsuhoa sabinae* and *Xerephedromyia ustjurtensis*, have disjunct Euro-Asian areas of distribution. Galls of *Etsuhoa sabinae* on *Juniperus sabina* occur rarely in mountains of Europe and were also found in mountains of eastern Kazakhstan. Galls of *Xerephedromyia ustjurtensis* on *Ephedra distachya* were discovered in western Kazakhstan near the Caspian Sea, in Turkmenistan, Jordan, in southern Ukraine, northern Spain and southern France and Italy. Such types of disjunct distribution may be denominated as Mediterraneo-Turanian. Also *Lasioptera umbelliferarum* causing galls on *Hippomarathrum* (formerly *Seseli*) has a disjunct distribution area. Galls were found in Sicily (southern Italy), in southern Russia, Georgia, Azerbaijan, Iran and Israel.

Holarctic species occur simultaneously in the Palaearctic and in the Nearctic regions. 81 species (4.5%) of the family Cecidomyiidae known to occur in Europe belong in this group. The most abundant are the Lestremiinae with 43 species, followed by the Cecidomyiinae with 25 species and at the last position are the Porricondylinae with only 13 species. *Camptomyia multinoda* and *Porricondyla nigripennis* of the subfamily Porricondylinae, *Aphidoletes aphidimyza*, *A. thompsoni* and *A. urticaria*, *Coquillettomyia dentata* and *C. lobata*, *Mycodiplosis coniophaga* and *M. inimica* of the subfamily Cecidomyiinae may be considered to be truly Holarctic species. These species are mycophagous or zoophagous and are not associated with specific host plants. On the other hand, several gall midge species associated with their host plants, mainly with cereals, fruit trees and fodder crops, that occur in both regions, may be classed as secondarily Holarctic because their host plants are of European origin and gall midges were imported from Europe into North America with their host plants. For example: *Contarinia pyrivora* and *Dasineura pyri* causing galls on *Pyrus communis*; *Dasineura mali* on *Pyrus malus* (Fig. 28); *Dasineura alopecuri* developing in inflorescences of *Alopecurus pratensis*; *D. gentneri* and *D. leguminicola* associated with

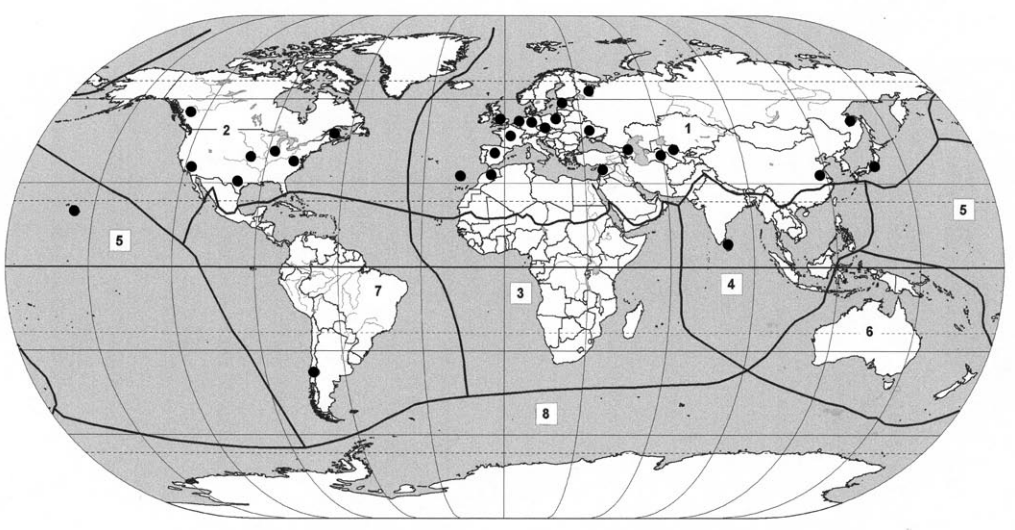


Fig. 27. Cosmopolitan distribution of the gall midge *Lestremia cinerea* Macquart, 1826 (black circles) in the biogeographical regions of the world: 1 – Palaearctic, 2 – Nearctic, 3 – Afrotropical, 4 – Indomalayan, 5 – Oceanian, 6 – Australian, 7 – Neotropical, 8 – Antarctic regions.

Table 9. Alien gall midge species occurring in Europe, their host species, plant family and origin; zoophagous species are marked by an asterisk before the species name

gall midge species	host species	plant family	origin
Asphondylia buddleia Felt, 1935	*Buddleia racemosa*	Loganiaceae	North America
Clinodiplosis cattleyae (Molliard, 1903)	*Cattleia*	Orchidaceae	Central and South Americas
Contarinia citri Barnes, 1944	*Citrus* spp.	Rutaceae	Africa
Contarinia quinquenotata (Löw, 1888)	*Hemerocallis fulva*	Liliaceae	temperate Asia
Dasineura gibsoni Felt, 1911	*Cirsium*	Asteraceae	North America
Dasineura gleditchiae (Osten Sacken, 1866)	*Gleditchia triacanthos*	Caesalpiniaceae	North America
Dasineura oxycoccana (Smith, 1890)	*Vaccinium* spp.	Ericaceae	North America
**Dicrodiplosis pseudococci* (Felt, 1914)	*Planococcus citri* (Pseudococcidae)		Africa
**Epidiplosis filifera* (Nijveldt, 1965)	*Ceratoplates floridensis* (Coccidae)		Eastern Asia
**Feltiella acarisuga* (Vallot, 1827)	Tetranychidae (Acari)		unknown
Horidiplosis ficifolii Harris, 2003	*Ficus benjamina*	Moraceae	tropical Asia
Janetiella siskiyou Felt, 1917	*Chamaecyparis lawsoniana*	Cupressaceae	North America
**Lestodiplosis aonidiellae* Harris, 1968	*Aonidiella aurantii* (Diaspidae)		Africa
Obolodiplosis robiniae (Haldeman, 1847)	*Robinia pseudoacacia*	Fabaceae	North America
Orseolia cynodontis Kieffer et Massalongo, 1902	*Cynodon dactylon*	Poaceae	Africa
Procontarinia matteiana Kieffer et Cecconi, 1906	*Mangifera indica*	Anacardiaceae	tropical Asia
Prodiplosis vaccinii (Felt, 1926)	*Vaccinium* spp.	Ericaceae	North America
Prodiplosis violicola (Coquillett, 1900)	*Viola* spp.	Violaceae	North America
Resseliella conicola (Foote, 1956)	*Picea sitchensis*	Pinaceae	North America
Rhopalomyia chrysanthemi (Ahlberg, 1939)	cultivated *Chrysanthemum*	Asteraceae	temperate Asia
Rhopalomyia grossulariae Felt, 1911	*Ribes grossularia*	Grossulariaceae	North America
Stenodiplosis panici Plotnikov, 1926	*Panicum* spp.	Poaceae	temperate Asia
Stenodiplosis sorghicola (Coquillett, 1899)	*Sorghum* spp.	Poaceae	Africa

Trifolium spp. In some cases it is not quite clear where a particular gall midge species is native and to which part it was introduced.

Cosmopolitan species are species that occur on all continents of the Earth having a world-wide distribution. Only seven species of the family Cecidomyiidae known to occur in Europe may be assigned to this group: *Anarete johnsoni*, *Lestremia cinerea* (Fig. 27) and *Monardia modesta* (Lestremiinae), *Didactylomyia longimana*, *Feltiella acarisuga*, *Stomatosema obscura* and *Silvestriola cincta* (Cecidomyiinae) were found on several continents and are considered to be cosmopolitan in distribution. The origin of most of them is unknown. *Mayetiola destructor* developing on cereals is considered to be a primarily European species that has been imported into other continents probably with straw.

Alien species (non-native, exotic, non-indigenous, foreign) are species introduced outside their normal distribution. Invasive alien species are alien species whose establishment and spread modify ecosystems, habitats, or species (DAISIE 2009). In the fauna of gall midges of Europe 23 species were found that are noted as **alien** or **invasive** species (Table 9). Most of them are associated with various plant families and four species are predators. They were introduced into

Europe unintentionally from other parts of the world. Typical representatives are *Obolodiplosis robiniae* causing galls on leaflets of *Robinia pseudoacacia* (Fig. 29), and *Dasineura gleditchiae*, causing galls on leaflets of *Gleditchia triacanthos*, both originally Nearctic species that have been imported into Europe unintentionally, probably with seedlings of their host plant. Ten species came to Europe from North America, one species from Central and South America, six from Asia, five from Africa and the origin of one species is unknown (Skuhravá et al. 2007, 2010).

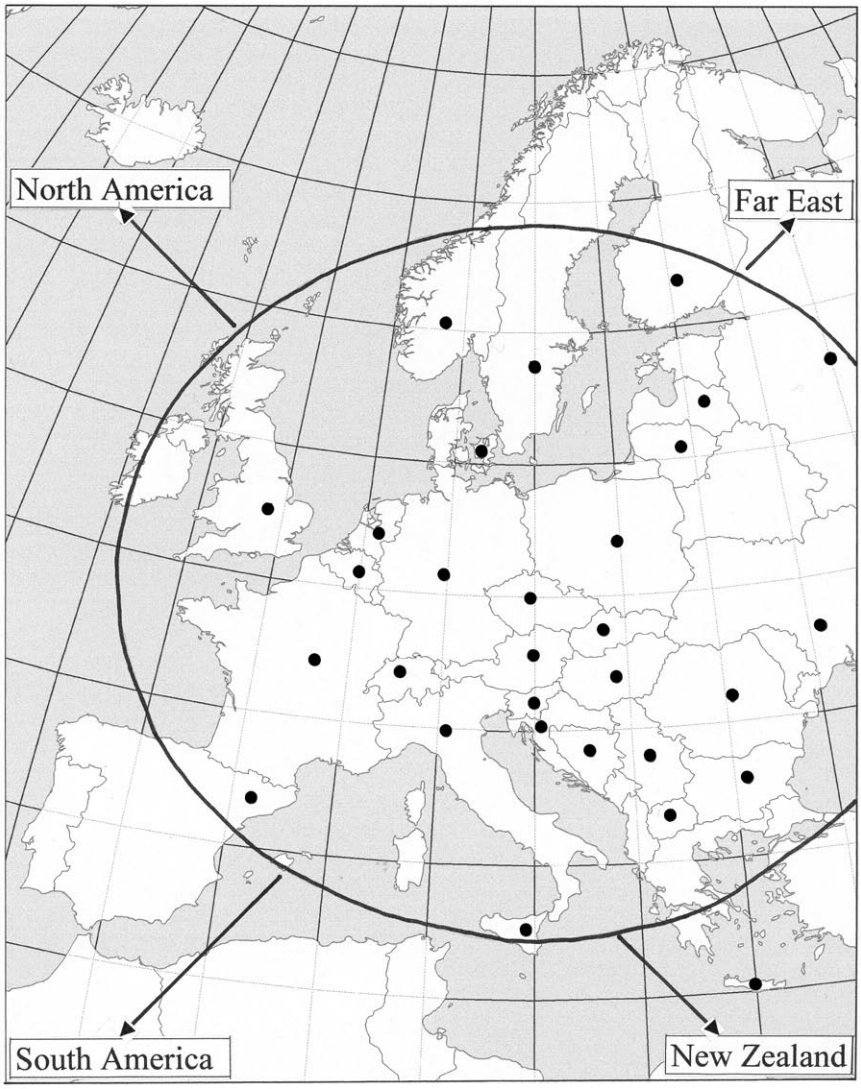


Fig. 28. Distribution of *Dasineura mali* (Kieffer, 1904) (black circles) on apple trees *Malus sylvestris* Mill. and *Malus domestica* Borkh. (Rosaceae) in Europe (black line). *D. mali* probably originates, as do its host plants, from southern Europe and western Asia which are primary areas of its distribution, and it was imported secondarily to other parts of the world. Distribution area of the host plant after Meusel et al. (1965–1992).

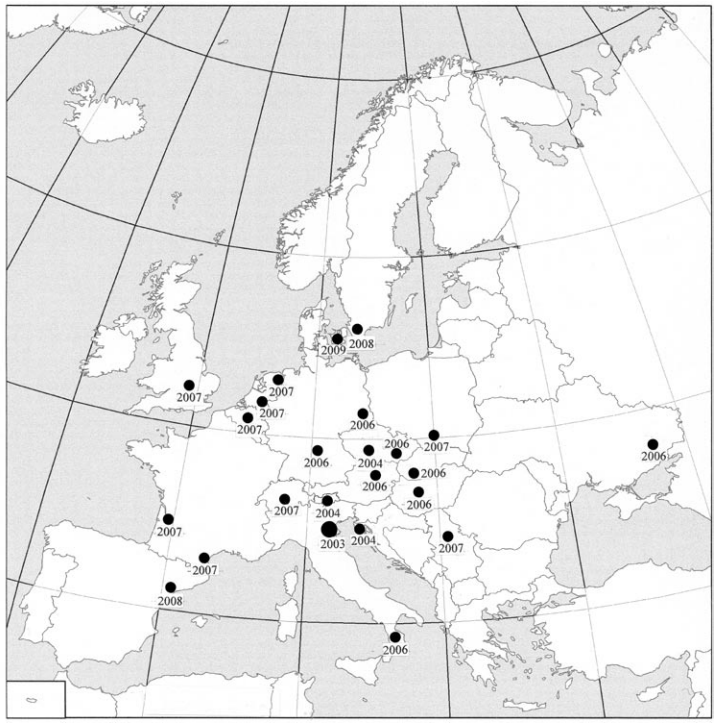


Fig. 29. Occurrence of *Obolodiplosis robiniae* (Haldeman, 1847) (black circles) causing galls on *Robinia pseudoacacia* L. (Fabaceae) and its spread throughout Europe. *O. robiniae* is a Nearctic species, alien to Europe. It has been imported into Europe, probably with seedlings, and its galls were discovered for the first time in 2003 in northern Italy. Since then it has spread quickly over large areas of Europe up to Doneck in Ukraine in 2006, to southern England in 2007, northern Spain and southern Sweden in 2008.

Five European gall midge species were intentionally introduced into other continents for **biological control of weeds**: *Cystiphora sonchi* against *Sonchus arvensis* in Canada (Peschken 1982); *Cystiphora schmidti* against skeleton weed (*Chondrilla juncea*) in Australia, California and Argentina; *Zeuxidiplosis giardi* against St. John's wort (*Hypericum perforatum*) in Hawaii, New Zealand and Australia; *Spurgia euphorbiae* against leafy spurge (*Euphorbia esula*) in North America (North Dakota) (Sobhian et al. 2000); *Rhopalomyia tripleurospermi* against scentless chamomile (*Tripleurospermum perforatum*) in Canada (Skuhravá & Hinz 2000). On the other hand, the European species *Gephyraulus raphanistri* which was tested as a potential control agent of *Raphanus raphanistrum*, one of the most important weeds of crops in Australia, was found to have unsuitable phenological characteristics (Vitou et al. 2008).

Endemic species form a special category. Such species are native to a particular geographical region or their occurrence is restricted to such region. In Europe it is possible to class thirty eight gall midge species as endemic. They are known so far only from the Iberian Peninsula. They have not been recorded in any other country and seem to be restricted to the Iberian Peninsula. It is necessary to emphasize that they may be revealed in some of other countries in the future. As

a true endemic may be regarded only such species which are associated with host plants endemic to the Iberian Peninsula, as for example *Dasineura halimii* and *D. herminii* causing galls on *Halimium* spp. (Skuhravá et al. 2006).

We have prepared maps showing the distribution areas of more than 500 gall midge species. Some of them were published in our articles and the larger part await publication in the future. In addition, we have drawn several hundreds of maps showing the occurrence of gall midge species in several countries of Europe where we summarized previous knowledge, i.e. of the Czech Republic (Skuhravá 1994a, b), Slovakia (Skuhravá 1991), France (Skuhravá et al. 2005), Spain and Portugal (Skuhravá et al. 2006), Poland (Skuhravá et al. 2008) and Austria (Skuhravá & Skuhravý 2009a).

Geographic position and gradients

Gall midge species richness changes with composition of natural vegetation and with geographic position, mainly along a north-south axis (Skuhravá & Skuhravý 1998). We tested both geographic gradients, latitudinal and longitudinal, using the **average species numbers per locality** obtained from samples taken by the time unit area collection method at localities with precisely determined geographic positions. Fundamental data for the analysis are given in Table 10 and results are shown in Figs 30 and 31.

The occurrence of gall midges given by average species numbers along **the latitudinal gradient** produces interesting results (Fig. 30). The average species numbers of gall-inducing Cecidomyiidae

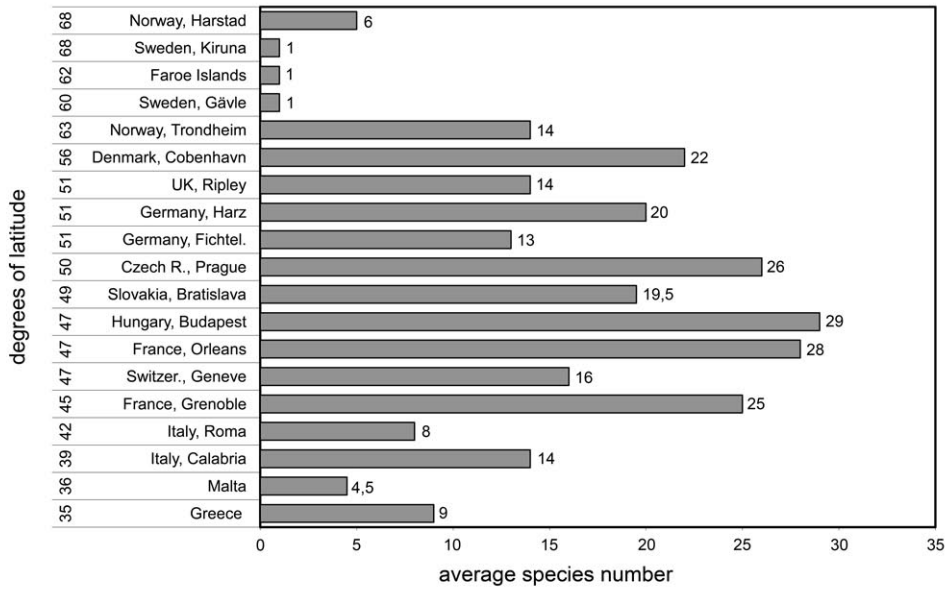


Fig. 30. Average species numbers of gall-inducing and plant inhabiting species of the subfamily Cecidomyiinae in countries of Europe along the latitudinal gradient of 3800 km from the northernmost investigated area in northern Norway (Harstad) to the southernmost investigated area in the island of Malta in the Mediterranean Sea. All samples have been taken by the time and area unit collection method.

Table 10. European countries where systematic faunal investigations have been undertaken by the present authors during the period 1955–2009, important characteristics of countries and average species numbers of Cecidomyiidae. Geographic coordinates (latitude and longitude) are related as far as it is possible to the area or town situated nearest to the study area. Altitudes include the lowest and the highest elevations of examined localities. Biogeographic provinces are given according to Udvardy (1975), types of natural vegetation according to Noirfalise (1987). At the end of the table there are added data obtained in the course of investigations in the southern part of Central Siberia (Asia) for comparison with data obtained in Europe. ASN – average species number

country	lat. N	long. E	altitude m a.s.l.	biogeographic provinces	type of natural vegetation	ASN	references
Austria, Wien	48°12’	16°22’	240 115–2500	Central European Highlands	mixed forest, conifer forests	17.0	Skuhravá & Skuhravý 2009a
Bulgaria, Sofia	42°40’	23°19’	1–2000	Balkan Highlands	mixed forest, oak forest	14.0	Skuhravá et al. 1991
Bulgaria, Varna	43°13’	27°55’	1–180	Black Sea Coast	Pontic beech forest	14.0	Skuhravá et al. 1991
Corfu (Greece)	39°37’	20°02’	1–250	Mediterranean Sclerophyll	Hellenic oakwood	12.6	Skuhravá & Skuhravý 2006b
Corsica (France)	41°55’	08°44’	1–1000	Mediterranean	sclerophyll	9.8	Skuhravá & Skuhravý (in prep.)
Crete (Greece)	35°20’	28°08’	1–800	Mediterranean	sclerophyll	9.2	Skuhravá & Skuhravý 1997a
Cyprus	35°00’	33°00’	1–150	Mediterranean	sclerophyll	3.1	Skuhravá & Skuhravý 2004a
Czech Republic, Prague	50°05’	14°25’	120–1603	Central European Highlands	mixed forest	26.0	Skuhravá 1994a, b
Denmark, Sjæland (Copenhagen)	55°66’	12°34’	1–75	Atlantic Province Boreo-nemoral	beech forest	22.0	Skuhravá et al. 2006
Faroe Islands, Tórshavn (Denmark)	62°00’	6°46’W	0–300	Arctic-Alpine	blanket bogs	1.0	Skuhravá & Skuhravý 2009
France, Orleans	47°54’	01°54’	110–630	Atlantic Province	oak forest	28.0	Skuhravá & Skuhravý 2004d
France, Hautes Alpes, Grenoble	45°10’	05°43’	850–2645	Central European Highlands	beech-fir forest	25.0	Skuhravá & Skuhravý 2004c
Germany, Bayerischer Wald	48°32’	09°03’	650–1450	Middle European Forest	coniferous, mixed forest	13.0	Skuhravá & Skuhravý 1992b
Germany, Harz	51°41’	10°58’	450–550	Middle European Forest	Hercynian beech forest	20.0	Skuhravá & Skuhravý 1988
Germany, Fichtelgebirge	50°07’	12°00’	528–875	Middle European Forest	Hercynian beech forest	13.0	Skuhravá & Skuhravý 1992a
Greece, Athens	38°03’	23°40’	140 1–1100	Balkan Highlands, Mediterranean	oak forest, sclerophyll	9.3	Skuhravá & Skuhravý 1997a
Hungary, Budapest	47°30’	19°04’	116–1015	Pannonian	Danubian thermophilous oak forest	29	Skuhravá & Skuhravý 1999
Italy, Central part (Roma)	41°58’	12°40’	10–13	Mediterranean	*Quercus ilex* forest	8.0	Skuhravá & Skuhravý (unpubl.)
Italy, Calabria, Cetraro	39°31’	15°56’	1–560	Mediterranean	*Quercus ilex* forest	14.0	Skuhravá & Skuhravý (in prep.)
Italy, South Tyrol, Bolzano	46°20’	11°14’	224–2340	Central European Highlands	spruce forest	15.0	Skuhravá & Skuhravý 2001–2009
Liechtenstein, Vaduz	47°07’	09°31’	476–620	Central European Highlands	spruce forest	19.5	Skuhravá & Skuhravý 1993a
Mallorca (Spain)	39°33’	02°44’	1–400	Mediterranean	sclerophyll	9.5	Skuhravá & Skuhravý 2004b
Malta, La Valetta	35°54’	14°30’	1–240	Mediterranean	sclerophll	4.5	Skuhravá et al. 2002
Norway, Harstad	68°48’	06°30’	1–3	West European taiga	blanket bogs	5	Skuhravá & Skuhravý (in prep.)
Norway, Trondheim	63°25’	10°25’	5–560	West European taiga	boreal spruce forest	14.0	Skuhravá & Skuhravý (in prep.)

Samos (Greece)	37°41'	27°00'	1–600	Mediterranean	sclerophyll	8.8	Skuhravá & Skuhravý 2006b
Sardinia (Italy)	40°55'	09°00'	0-700	Mediterranean	sclerophyll	6.5	Skuhravá & Skuhravý 2002
Slovakia, Bratislava	48°08'	17°07'	110–2000	Middle European forest, Pannonian	Carpathian forest, Danubian thermophilous oak forest	19.5	Skuhravá 1991
Sweden, Kiruna	67°51'	20°13'	330	West European taiga	subarctic pine-birch woodland	1.0	Skuhravá (unpubl.)
Sweden, Gävle	60°40'	17°10'	1–10	West European taiga	subarctic pine-birch woodland	1.0	Skuhravá (unpubl.)
Switzerland, Zurich	47°23'	08°33'	208–2044	Central European Highlands	montane Scotts pine forest, beech forest	16.0	Skuhravá & Skuhravý 1997b
United Kingdom, Ripley, Surrey (GB)	51°30'	00°12'	20–150	British Islands	beech and oak forest	14.2	Skuhravá & Skuhravý 2007b
Asia: Siberia, Krasnojarsk	56°00'	92°00'	350– 1400	Central Asian taiga	East Siberian taiga	13.5	Skuhravá & Skuhravý 1993b

in countries of Europe arranged along the latitudinal gradient over a distance of about 3800 km from the northernmost investigated area in Norway (Harstad) to the southernmost investigated area in the island of Malta shows **the highest value between latitudes 45° and 52° North**. Species numbers in the northernmost localities were low, mainly in tundral parts of Scandinavia. In contrast, gall midge species numbers found at the coast in northern Norway were relatively high owing to the influence of the warm Gulf Stream. Average species numbers decrease rapidly to the south and in Malta the average species number per locality was only 5.

On the other hand, the occurrence of gall midge species along **the longitudinal gradient** does not produce such clear results (Fig. 31). The average species numbers of gall-inducing Cecidomyiidae in countries of Europe along the longitudinal gradient of 2000 km from the westernmost investigated area in England to the easternmost area in Bulgaria at the Black Sea coast in comparison with average species number in the southern part of Central Siberia seems to be nearly equal, with two higher values (peaks), viz. in France, where average species number was 29 owing to the influence of the Atlantic Ocean, and in Central Europe where the highest average species number was found in Hungary situated in the warmer part of the Pannonian lowland.

Climatic factors

Climate and climatic factors have an important influence on the occurrence and distribution of gall midges in Europe. Climate includes temperature, humidity, atmospheric pressure, wind, rainfall and some other elements in a given region over long periods of time. The climate of a locality is affected by its latitude, terrain, altitude, ice or snow cover, as well as nearby water bodies and their currents. Climates can be classified according to the average and typical ranges of different variables, most commonly temperature and precipitation which may be shown in graphs, so called **climatograms**. They represent the sum of two climatic variables, e.g. temperature and rainfall for a particular geographical locality and for a specified period, with measurements taken at regular intervals, usually monthly. In the climatogram are given the long-term monthly average temperatures (in a graph on the left side) and the monthly precipitations (in a graph on the right side) in relation 10° C = 20 mm. When the precipitation curve falls below the temperature curve, it is a dry period.

The average species number of gall midges is highest in Central Europe and decreases towards the south, as was described in the previous chapters. We compared decreasing

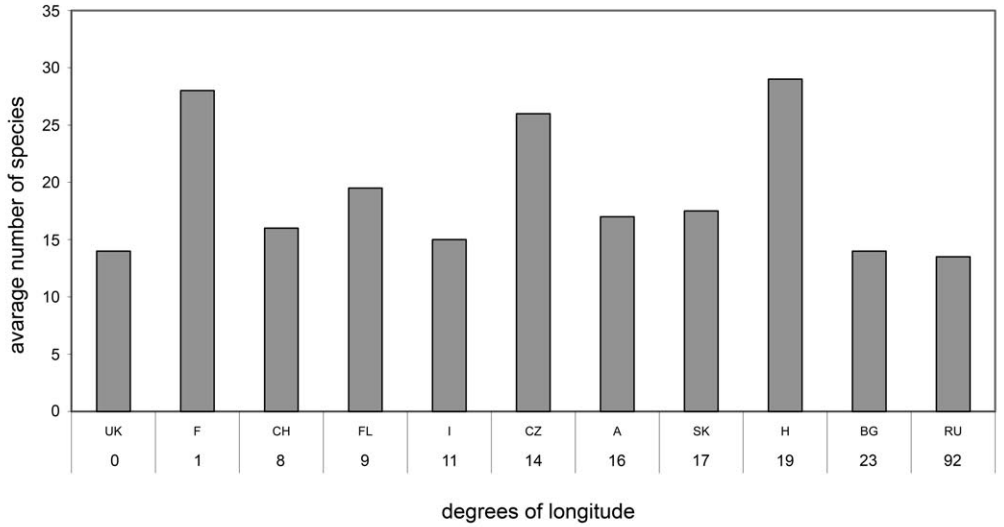


Fig. 31. Average species numbers of gall-inducing and plant inhabiting species of the subfamily Cecidomyiinae in countries of Europe along the longitudinal gradient of 2000 km from the westernmost investigated area in southern England to the eastermost area in Bulgaria at the Black Sea compared with average species number in the southern part of Central Siberia. All samples have been taken by the time and area unit collection method. For abbreviations of country names see Table 1.

average gall midge species numbers per locality with climatograms of several parts of Europe and found that this phenomenon is correlated with climatic conditions and with the temperature and rainfall (Fig. 32). Central Europe has favourable weather during the year which is characterized with mild, i.e. not too high temperatures and with a relative sufficient amount of rainfall. The average gall midge species number in Central Europe is very high, i.e. 26 species in the Czech Republic and 29 species in Hungary.

The average temperature increses to the south of Europe and, on the other hand, the average rainfall decreases, which is shown on climatograms for southern Europe where the middle part of a year with hot and dry weather is figured in black. Hot and dry weather is not too suitable for the development of gall midges and their galls on host plants. It may be shown that low average gall midge species numbers occur in the islands of the Mediterranean, viz. only 9.5 species on average in Mallorca, 9.2 in Crete and even only 4.5 species in Malta.

Long winter periods of cold with low temperatures and short summer periods in northern Europe do not give suitable conditions for the development of gall midges and their galls on host plants. On the other hand, a narrow strip (several kilometres only) along the coast in northern Europe which is under the influence of the Gulf Stream provides suitable conditions for development of gall midges on host plants and the gall midge species number is there much higher than in inland parts at the same latitude.

Vertical distribution

The composition of vegetation, including availability of various plant species as potential hosts for gall-inducing gall midge species, changes with increasing altitude. It is an important value for zoogeographic analysis. Europe is very varied; the configuration of terrain changes very quickly

in some parts and large differences in altitudes occur in relatively small areas. We analyzed the vertical distribution of the gall midge species from localities in several parts of Europe according to the altitudinal zones proposed by Ellenberg (1978) that we adapted for different areas. In Central Europe we usually use eight zones for the area under study, viz. planare zone (from the sea level–200 m a. s. l.), colline (200–500 m a. s. l.), submountain (500–900 m a. s. l.), mountain (900–1500 m a. s. l.), sub-Alpine (1500–1700 m a. s. l.), Alpine (1700–2400 m a. s. l.), subnivale and nivale zones (over 2400 m a. s. l.). Each of these zones is indicated by different abiotic factors, mainly climatic, and by characteristic composition of vegetation in which there may be present plant species suitable as hosts for gall-inducing Cecidomyiidae. Altitudinal range of these zones differ in slopes of mountains or mountain ranges oriented south and north, and with geographic position.

Elevations of localities at which particular species have been found are an essential basis for zoogeographic evaluation. For example, in Austria the lowest point is at Neusiedler See at 115 m a. s. l. and the highest point is the mount Grossglockner at 3797 m a. s. l. We collected galls of

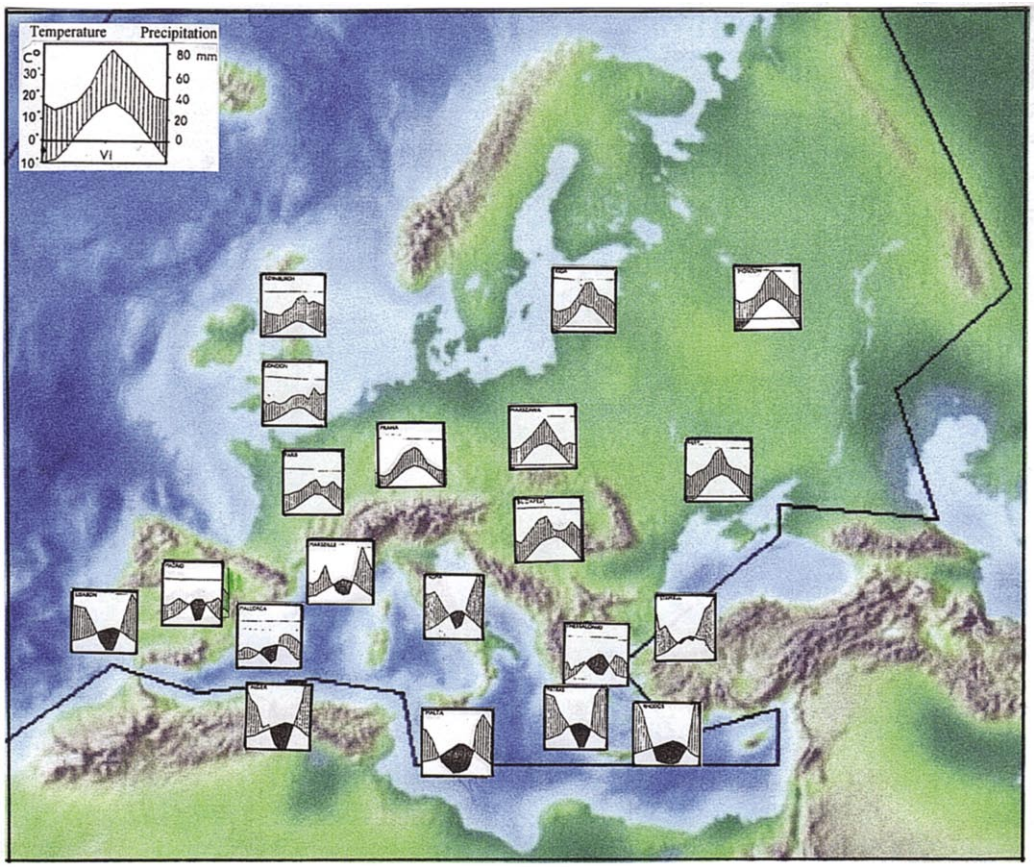


Fig. 32. Europe and its climatic conditions shown in several climatograms. Mild weather conditions in Central Europe are suitable for development of gall midges. In southern Europe, on islands in the Mediterranean Sea and in northern Africa dry and hot climates prevail which are not suitable for development of gall midges and for their galls on host plants.

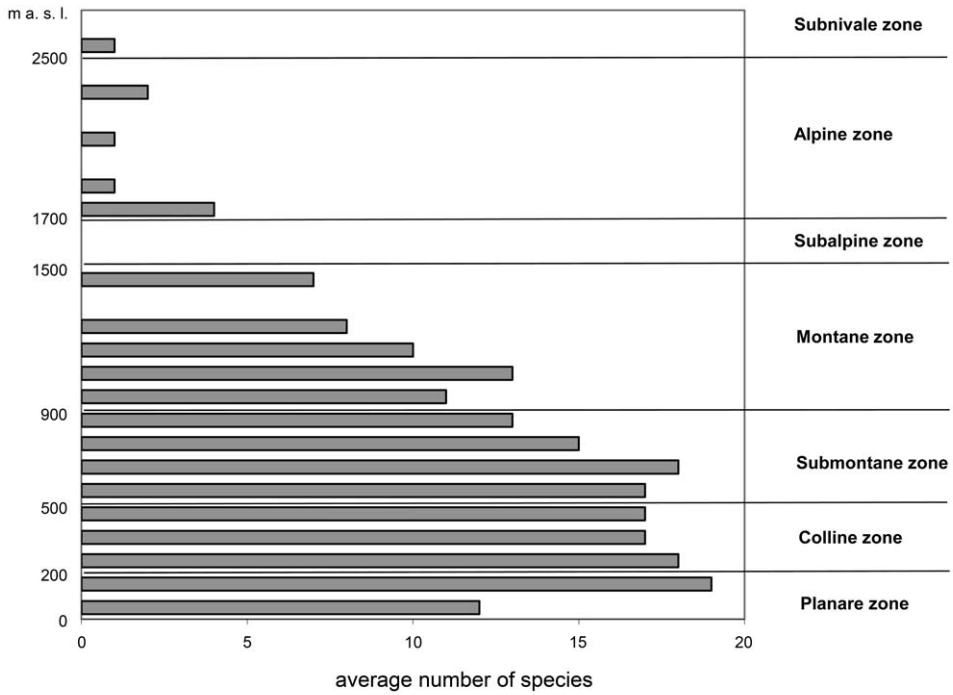


Fig. 33. Vertical distribution of gall midges (Cecidomyiidae) shown as average species numbers in belts of 100 meters in altitudinal zones of Austria in Central Europe. The average species number falls with rising elevation from the planare zone up to the subnivale zone where only one gall midge species, *Jaapiella alpina* causing galls on *Silene acaulis* (Caryophyllaceae) has been found at altitudes of 2500 m a. s. l. Span of altitudinal zones according to Ellenberg (1978).

gall midges at localities situated in planare zone at 120 m up to the Alpine zone at 2400 to 2500 m. Only a few gall midge species and their associated host plants occur in narrow altitudinal spans of one zone. Most species occupy larger areas of distribution both in horizontal and vertical directions and usually are able to occur with their host plants over a relatively large altitudinal range (Skuhravá & Skuhravý 2009a).

Gall midge species numbers in the planare zone of Europe are usually low and numbers are usually much higher in colline, submontane and montane zones. Above the boundary of forests, the so-called timber line (this altitude differs in various parts of Europe in connection with geographic position), the gall midge species number falls abruptly and only two to four species occur in the higher zones, i.e. in the sub-Alpine and Alpine zones. The number of gall midge species therefore decreases with rising altitude.

Of 396 gall midge species forming the fauna of Austria (Skuhravá & Skuhravý 2009a), the majority occur in colline, submontane and montane zones, only 20 species occur in the sub-Alpine zone and 13 species in the Alpine zone. *Jaapiella alpina* causing galls on *Silene acaulis*, *Dasineura bistortae* on *Polygonum viviparum* and *Hygrodiplosis vaccinii* on *Vaccinium uligi-*

nosum, found at elevations from 2300–2500 m a. s. l., are true Alpine species associated with Alpine host plants. In South Tyrol, where intensive investigations were carried out in the Alpine zone (Skuhravá & Skuhravý, in press) 33 species were found in the Alpine zone. The galls of *Rhopalomyia luetkemuelleri* on *Artemisia spicata* and *Jaapiella alpina* on *Silene acaulis* were found in the subnivale zone at altitudes of 2700 m a. s. l. and are gall midge species found at the highest altitudes in Europe.

The vertical distribution of gall midges in Europe is shown by **average species numbers** recorded at localities in separate successive altitudinal belts of 100 meters (Fig. 33). The basis of calculations are totals of all species numbers obtained during our own investigations at localities situated in particular altitudinal zones.

We recognized twenty three types of vertical distribution in the gall midge fauna of Austria on the basis of their **altitudinal span** which is given by elevations of the lowest and the highest situated locality where a particular species was found (Fig. 34). Two fundamental patterns of vertical distribution were found in each of the lower zones, viz. the occurrence of a species only inside a particular zone and the occurrence of a species exceeding this zone and reaching higher zones or running across them to higher altitudinal zones. Few gall midge species and their associated host plants occur in narrow altitudinal spans of one zone. These may be named **monozonal species.** Most species occupy larger areas of distribution both in horizontal and vertical directions and usually are able to occur with their host plants in relative large altitudinal range. They may be named **bi-, tri-,** or **polyzonal species.**

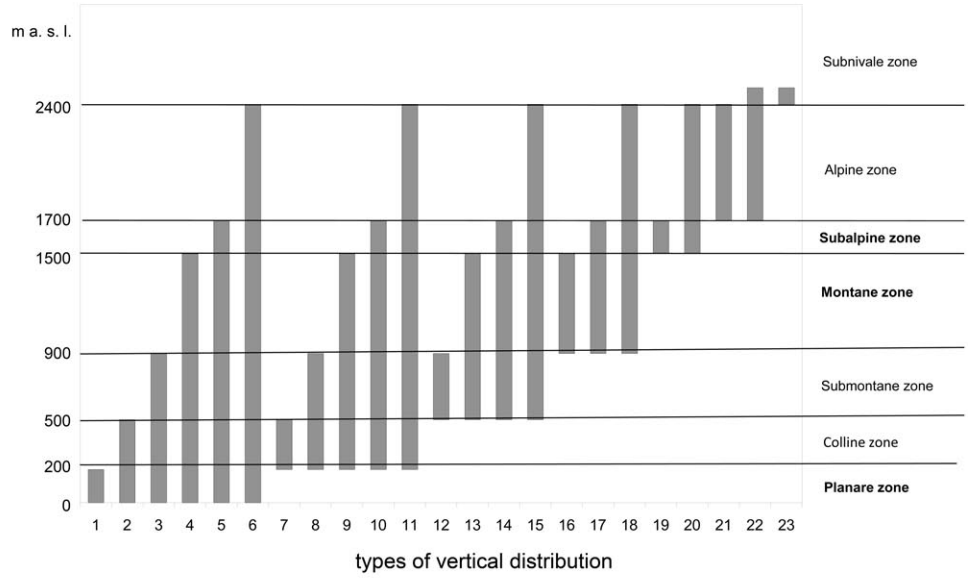


Fig. 34. Diagram of twenty-three types of vertical distribution in seven altitudinal zones of Europe recognized in the gall midge fauna in the course of investigations carried out by present authors at 1821 localities in the years 1955–2009.

For example, the gall midges associated with *Quercus cerris* in Central Europe may be considered to be monozonal and colline species, *Macrodiplosis pustularis* causing galls on *Quercus robur* and *Q. petraea* is a bizonal species occurring in colline and submontane zones and *Oligotrophus juniperinus* inducing galls on *Juniperus communis* a polyzonal species. It occurs over a large altitudinal span, including sites in the planare zone up to sites in the Alpine zone. Bisamberg, 190 m a. s. l. in north-eastern Austria was the lowest situated locality where galls were found and Mount Kanzel, 2348 m a. s. l. in the Alps in northern Italy is the highest point of its known vertical occurrence (Skuhravá 1987, 1997, Skuhravá & Franz 1989, Skuhravá et al. 2002). *O. juniperinus* has a large ecological tolerance and is able to inhabit places that are distant vertically from each other by more than 2000 meters. *O. juniperinus* may be considered to be a sub-boreal and Alpine species.

The occurrence of gall midges in single altitudinal zones may change with geographical position in Europe. For example, *Asphondylia verbasci* causing flower galls on various *Verbascum* species is in the Czech Republic a colline species occurring from 198 m a. s. l. to 510 m a. s. l., but in southern Europe, in Bulgaria, it occurs at altitudes of 1400 m a. s. l. in the montane zone.

We prepared detailed analyses of the vertical distribution of gall midge species occurring in the Czech Republic, Slovakia and Austria and expressed them in graphs (Skuhravá 1991, 1994a, b, Skuhravá & Skuhravý 2009a).

Frequency

Frequency in ecology is the number of individuals of a species within a given area. In our case, the frequency is the number of occurrences (given as the number of localities where the species was found) of a particular gall midge species within a given area. The area under study may be of varied size from small, including e.g. district, county, region, mount, mountains, island, protected part of landscape, up to large, e.g. country, Western Europe, Central Europe, zoogeographic or biogeographic subregion and region, continent. The basis for such analysis is the number of localities at which a particular species was found, without determining the local abundance of species. The frequency of animals is usually expressed only by words: very scarce, scarce, moderately frequent, frequent and very frequent.

For example, if a particular species was found in the area under study at only one locality out of 60 localities that had been investigated, it is designated as very rare and a species found at 30 localities is designated as very frequent. Species between these two value are denominated by the terms: scarce, moderately frequent or frequent based only on the experience of the researcher.

On the basis of our rich experiences with the evaluation of frequency of gall midge species in areas of various size in Europe we developed a unified method for evaluation of frequency of a particular species in a given area where a particular number of localities was investigated.

If we plotted the occurrence of all species found in the area at localities under study, we received always the same configuration in the graph, as in Fig. 35. The highest column on the left includes species each of which was found at only one locality in the course of our investigations, the number of localities per species reduces very quickly, only a few species occur at more localities and usually one or two species occur very frequently, each being found at many localities (small column on the right) (Skuhravá & Skuhravý 2009a). It is possible to divide all species found in the area under study into six frequency groups by using the first six members of the geometrical progression with quotient "2" and coefficient "a":

$$a.2^0 + a.2^1 + a.2^2 + a.2^3 + a.2^4 + a.2^5 = 63.a \text{ (a sum of the progression).}$$
$$1a + 2a + 4a + 8a + 16a + 32\ a = 63\ a \text{ (simplified)}$$

Table 11. Frequency groups of gall midges found in Austria (after Skuhravá & Skuhravý 2009a)

frequency group	1	2	3	4	5	6
members of geometrical progression	$a.2^0$	$a.2^1$	$a.2^2$	$a.2^3$	$a.2^4$	$a.2^5$
simplified	1a	2a	4a	8a	16a	32a
number of localities (if a=300)	1–5	6–14	15–33	34–71	72–147	148≤
verbal denomination	very scarce	scarce	medium frequent	frequent	very frequent	most frequent

The value of the coefficient may be determinated from a sum of the geometrical progression. If we investigate an area at 63 localities, the coefficient "a" has the value 1. In other cases it is possible to count the coefficient "a" from the number of localities that we investigated which is equal to 63a. The extent of each of six frequency group is given by one member of this progression. Details are given in the article of Skuhravá (1994a, b). It is possible to assign verbal denominations to each of the six group. As an example we give here the calculation of the frequency groups for Austria in Table 11.

The frequency of gall midge species in Europe is noted for the following shared characters (Fig. 35). On one side is the group of many very scarcely occurring species that were found only once in the area under study, some of them were found only at the type locality and have not been

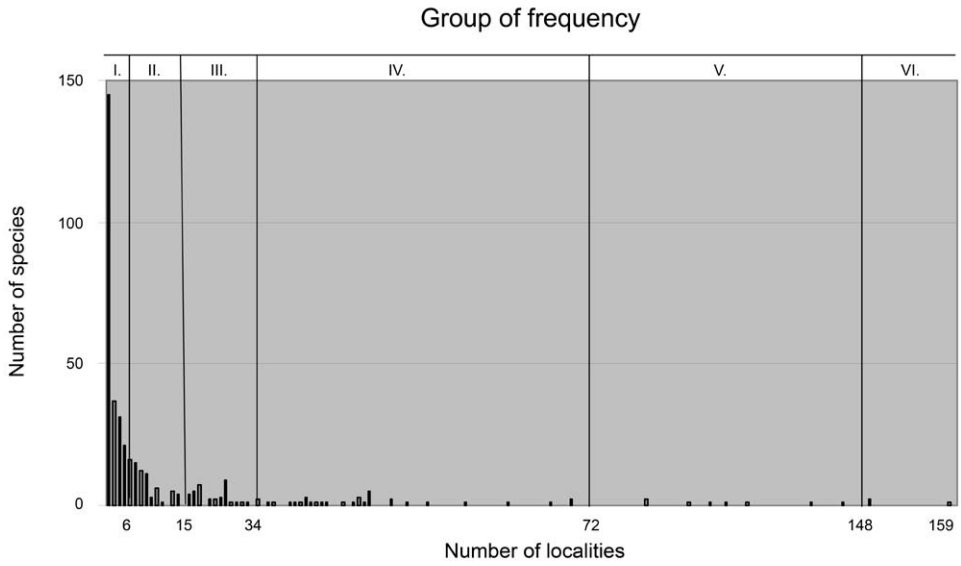


Fig. 35. Species of the family Cecidomyiidae found in Austria in the period 1834–2004 arranged in six frequency groups according to the number of localities at which each species was found. The first column on the left includes 145 gall midge species which have been found at only one locality. The last column on the right (in the form of a black point) shows one species, *Macrolabis heraclei* (Kaltenbach, 1862), causing galls on *Heracleum sphondylium* (Apiaceae), the most frequent species in Austria, which was found at 159 localities.

found again since that time. They are figured in the graph on the left side. On the opposite side is the group of a small number of species, sometimes only one or two species, that were found many times (= at many localities) and are the most frequent species in the area under study. In the graph they are figured at the right side. Each of four groups between these two extreme groups includes decreasing numbers of species each of which was found at more and more localities.

We have determined the frequency of gall midges occurring in Europe in some of the countries where we have carried out investigations, viz. in Slovakia (Skuhravá 1991), Bulgaria (Skuhravá et al. 1991), the Czech Republic (Skuhravá 1994a, b), Switzerland (1997), Hungary (Skuhravá & Skuhravý 1999), Denmark (Skuhravá et al. 2006) and Austria (Skuhravá & Skuhravý 2009a). If there are not such data at our disposal, it is possible to use the number of citations in the literature to evaluate the frequency of occurrence, as we have done for Portugal and Spain (Skuhravá et al. 2006) and for Poland (Skuhravá et al. 2008), or to combine both methods, as we have done for France (Skuhravá et al. 2005).

Each part of Europe is characterized by the occurrence of the different groupings of the most frequent gall midge species. The most frequent gall midge species in the whole of Europe is *Jaapiella veronicae* causing galls on leaf buds of *Veronica chamaedrys*. The galls of this species were found at 501 localities (of 670 explored) in the Czech Republic (Central Europe) during investigations in the years 1957–1982 (Fig. 36). In Northern Europe, in Norway, the most frequent species is *Iteomyia capreae* causing galls on leaves of *Salix caprea* and related species, in Denmark *Mikiola fagi* inducing galls on leaves of *Fagus sylvatica* and in Poland *Lasioptera rubi* causing galls on stems of *Rubus idaeus* and related species. In France the most frequent species is *Dasineura rosae* causing galls on various species of *Rosa*, in Switzerland *Dasineura fraxinea* producing pustule galls on leaves of *Fraxinus excelsior*, in Austria *Macrolabis heraclei* causing galls on leaves of *Heracleum sphondylium*, in Slovakia *Geocrypta galii* evoking galls on stems of *Galium mollugo* and related species, in Hungary *Lasioptera rubi* and *Dasineura rosae*, in Bulgaria also *D. rosae* and *D. hyperici* which causes galls on *Hypericum perforatum*. All above mentioned gall midge species belong to faunal elements of the Middle European Forest Province (Fig. 37).

The most frequent gall midge species in the western part of the Mediterranean area – in the Iberian Peninsula, that is in Spain and Portugal – are *Phyllodiplosis cocciferae* and *Dryomyia lichtensteinii* causing galls on leaves and buds of south-European oaks, viz. *Quercus coccifera*, *Q. ilex* and *Q. suber*, whereas in the eastern part of this area – in Greece – the most frequent species is *Dasineura turionum* changing stems of *Asparagus acutifolius* into galls. These gall midges belong to faunal elements of the Mediterranean Sclerophyll Province.

Possibilities of finding additional gall midge species in Europe

Gall-inducing gall midges of Europe are one of the best known gall-causing group of animals in the world. They can be used therefore as the most suitable group for estimating the number of gall midges and their galls that may be found in future studies. We try to determine this prognosis using data from the literature and also data obtained in the course of our investigations in Europe.

We use as the starting point for our prognosis of the increasing species number of the family Cecidomyiidae in Europe five gall midge species given in Linnaeus (1758) whose 10th edition of *Systema Naturae* is the starting point of zoological nomenclature. Bergenstamm & Löw (1876) summarized knowledge of that time and gave 606 species of the family Cecidomyiidae from all the world (Table 12). For Europe they gave 492 species. In the subsequent period of 120 years the number of known gall midges was increased by about five hundred species. Of those, 45 species belonged to the subfamily Lestremiinae, 357 to the subfamily Cecidomyiinae and 90 to undescribed species causing galls. The two last groups form together a group of 447 gall causing and plant inhabiting species.

Kieffer (1898) gave 650 species in his list of the family Cecidomyiidae of Europe and Algeria where Lestremiinae included 88 species and Cecidomyiinae 562 species, of which 492 species caused galls or inhabited plants without making galls. From 1876 to 1898 the number of Lestremiinae increased importantly from 45 to 88 species, i.e. by about 100%, on the other hand the number of gall-causing species was increased only moderately from 447 to 492, i.e. by about 10%.

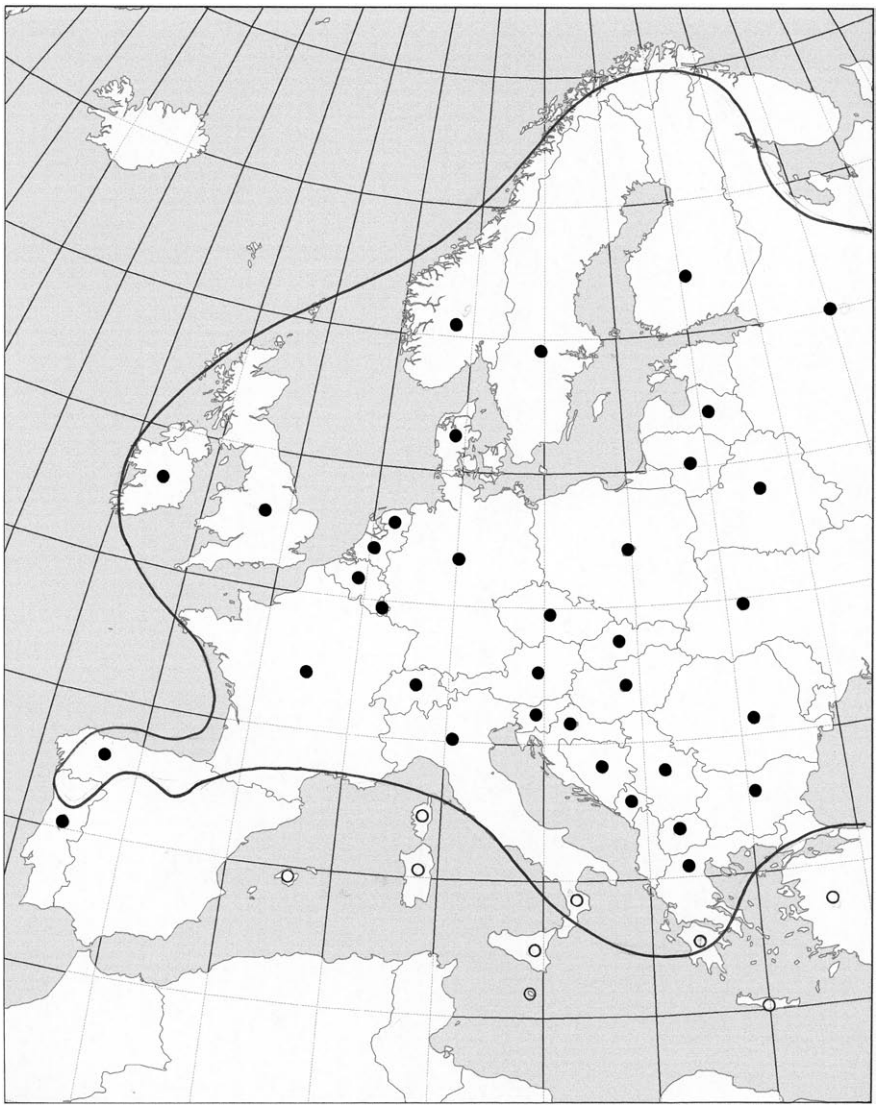


Fig. 36. Occurrence of *Jaapiella veronicae* (Vallot, 1827), causing galls on *Veronica chamaedrys* L. (Scrophulariaceae), the most frequent species in Central Europe (black circles). Its galls were found at 510 localities in the Czech Republic. The density of its occurrence decreases southwards and this species does not occur in the Mediterranean area. White circles indicate absence of the species. Distribution area of the host plant (black line) after Meusel et al. (1965–1992).

Table 12. Number of species of the family Cecidomyiidae in various parts of the world, as given by Bergenstamm & Löw (1876)

Cecidomyiidae	number of species						total
	Europe	N America	S America	Africa	Orient	Australia	
Lestremiinae	45	1	1	0	0	1	48
Cecidomyiinae	357	42	4	6	4	2	415
unidentified species	90	45	0	7	1	0	143
total	492	88	5	13	5	3	606

Kieffer (1901) summarized knowledge of galls in Europe and gave in his synopsis 1067 species of animals belonging to various groups as causers of galls. The family Cecidomyiidae with 364 species was the most species-rich group of gall-inducing animals.

Houard (1908–1909) recorded from Europe and the Mediterranean area 6239 sorts of galls caused by 1450 species belonging to various groups of animals of which 420 were gall-causing species of the family Cecidomyiidae (i.e. valid, described species). In addition, he listed about 300 galls, the causers of which were unknown, on various host plants.

Buhr (1964–1965) included 580 valid species (65%) of the family Cecidomyiidae as causers of galls on various host plants in Central and Northern Europe and about 320 undescribed species (35%) the causers of which had not been identified because larvae were not known and adults had not been reared at that time. The relation between described species and undescribed species is 2:1. It is possible to assume that these unknown causers will be found, reared from galls, identified and described in the future. The gall midge fauna of Europe will thus be enriched in the future by about 300 species known at the time of Buhr and by another 100 undescribed species associated with various plant species discovered mainly in the southern parts of Europe from the second half of 20th century until the present. It is therefore possible to expect about a 50% increase in the number of valid gall midge species and their galls in the future.

Skuhravá (1986) recorded in the Catalogue of Palaearctic Diptera 1500 species in the family Cecidomyiidae in Europe of which 170 belong to the subfamily Lestremiinae, 215 to the subfamily Porricondylinae and 1115 to the subfamily Cecidomyiinae. After 25 years, the number has increased to 1800 species (Skuhravá 2010, unpublished). The subfamily Lestremiinae includes 280 species, the subfamily Porricondylinae 310 and the subfamily Cecidomyiinae 1210 species.

In Fig. 38 we show the increasing species numbers of gall midges and increasing number of galls caused by gall midges during the last 150 years and the lines show the trends of increase. On the basis of summarized facts we predict that in Europe between the years 2010 and 2050 the number of gall midges species recorded will increase by about four hundred to 2200 valid species and the number of galls caused by gall midges by about two hundred to 1400 sorts of galls caused by gall midges. This is based on the assumption that in the future most of the unidentified causers of galls will be recognized as good species and described and that new galls and new gall midge species will be found by future researchers.

Gall midges and host plants

The vegetation covering Europe is relatively species-rich. Tutin et al. (1964–1980) give the following numbers of plant taxa: 11,557 species, 1541 genera and 203 families. 915 gall midges species (i.e. valid, described species) forming the subfamily Cecidomyiinae are associated with 280 host plant genera belonging to 72 plant families, i.e. with 18% of plant genera and 35% of plant families known to occur in Europe. Undescribed gall midge species and species identified to the

genus level that are known on the morphology of the gall only are not included in our consideration. On average one plant genus hosts 3,26 species of gall midges. We analyse relations between gall midges and their host plant from several points of view, viz. from the phylogenetical system of plants, abundance of gall midges associated with host plant families and relations between gall midges and their host plants in different countries of Europe, and the distribution and abundance of galls on different organs of host plants. See tables 13, 14 and 15.

In Europe only two gall midge species are associated with the Pteridophyta and 27 species with the Gymnospermae. The majority of gall midges, 886 species, are associated with the Angi-

Fig. 37. The most frequent species of the family Cecidomyiidae in several countries of Europe. See comments in the text p. 132.

Table 13. Gall-inducing and plant inhabiting species of the subfamily Cecidomyiinae associated with plant families and plant genera in Europe, arranged according to the phylogenetical system of plants according to Tutin et al. (1964–1980) in *Flora Europaea*; n1 – number of plant genera; n2 – number of gall midge species

host plants taxa		n1	n2	host plants taxa		n1	n2
Pteridophyta	Dennstaedtiaceae	1	2	Rhamnales	Rhamnaceae	2	5
Spermatophyta					Vitaceae	1	3
Gymnospermae				Malvales	Tiliaceae	1	8
Coniferales				Hypericales	Hypericaceae	1	6
	Pinaceae	4	17	Thymelaeales	Thymelaeaceae	1	2
	Cupressaceae	2	8	Violales	Violaceae	1	5
Taxales	Taxaceae	1	1		Cistaceae	2	4
Gnetales	Ephedraceae	1	1		Tamaricaceae	1	5
Angiospermae				Cucurbitales	Cucurbitaceae	1	2
Dicotylenodes				Myrtales	Lythraceae	1	1
Salicales	Salicaceae	2	64		Onagraceae	1	2
Fagales	Betulaceae	2	14	Umbelliflorae	Araliaceae	1	1
	Corylaceae	2	10		Cornaceae	1	1
	Fagaceae	2	49		Apiaceae	18	28
Urticales	Ulmaceae	1	4	Ericales	Pyrolaceae	1	1
	Moraceae	1	1		Ericaceae	3	15
	Cannabaceae	1	1	Primulales	Primulaceae	1	1
	Urticaceae	1	3	Oleales	Oleaceae	4	1
Santalales	Loganiaceae	1	1	Gentianales	Gentianaceae	1	1
Polygonales	Polygonaceae	2	10		Apocyanaceae	1	1
Centrospermae	Chenopodiaceae	7	21		Asclepiadaceae	1	2
	Caryophyllaceae	9	23		Rubiaceae	2	14
Ranales	Ranunculaceae	7	13	Tubiflorae	Boraginaceae	4	8
	Berberidaceae	1	2		Lamiaceae	20	42
Rhoeadales	Papaveraceae	1	1		Solanaceae	1	3
	Capparidaceae	1	1		Scrophulariaceae	7	16
	Brassicaceae	20	28	Plantaginales	Plantaginaceae	1	1
Rosales	Saxifragaceae	2	1	Dipsacales	Caprifoliaceae	3	11
	Grossulariaceae	1	5		Valerianaceae	1	2
	Rosaceae	11	49		Dipsaceae	3	4
	Fabaceae	28	123	Campanulales	Campanulaceae	2	11
Geraniales	Geraniaceae	1	2		Asteraceae	25	104
	Linaceae	1	1	**Monocotyledones**			
	Euphorbiaceae	1	9	Liliiflorae	Liliaceae	7	10
Rutales	Rutaceae	2	2		Dioscoreaceae	1	1
	Polygalaceae	2	1	Juncales	Juncaceae	1	1
Sapindales	Anacardiaceae	2	3	Graminales	Poaceae	31	69
	Aceraceae	1	9	Cyperales	Cyperaceae	2	27
Celastrales	Buxaceae	1	1	Microspermae	Orchideaceae	1	1

total 72 plant families, 280 host plant genera, 915 gall midge species

ospermae, of which a smaller part, including 109 species, cause galls or develop in plant organs of host plants belonging to the Monocotyledones and a larger part, including 777 species, develop on Dicotyledones.

The **Pteridophyta** in Europe comprise 25 families of which only one family, Dennstaedtiaceae (Polypodiaceae), contains only one species – *Pteridium aquilinum* – that is the host plant of two gall midge species, *Dasineura pteridis* and *D. pteridicola*. Larvae of both species cause simple galls on leaf margins (bent or rolled parts of leaf margins). These two gall midge species form only 0,21% of all gall midge species associated with host plants in Europe.

The **Gymnospermae** in Europe comprise five families of which four include host plant species for 27 gall midge species, i.e.2,95% of all gall midge species associated with host plants in Europe. The family Pinaceae hosts 17 gall midge species which are associated with four plant genera of coniferous trees (*Abies*, *Larix*, *Picea* and *Pinus*). The family Cupressaceae hosts eight gall midge species associated with two plant genera, viz. *Juniperus*, hosting seven gall midge species, and *Chamaecyparis*, hosting only one gall midge species, which is of North American origin. The family Taxaceae hosts only one gall midge species, *Taxomyia taxi*, developing in galls on *Taxus baccata* and the family Ephedraceae includes the host plant for only one species, *Xerephedromyia ustjurtensis*, causing galls on *Ephedra distachya*.

About one half of gall midge species developing on host plants of Gymnospermae do not cause galls at all: two species develop inside seed, five species in cones and five species are associated with resin. Fifteen gall midge species developing in various plant organs cause galls: two species induce stem galls, four species cause galls on needles and nine species induce galls in buds. The galls on Gymnospermae are of various shape. The most primitive seem to be simple swellings on the bark of *Picea abies* caused by larvae of *Dasineura abietiperda*. More complicated are the galls of *Xerephedromyia ustjurtensis* caused on stems of *Ephedra distachya*, which are formed by swellings of stems with large central chambers containing the larva of the causer. The larvae of *Paradiplosis abietispectinatae* induce swellings of needles on *Abies alba* and the larvae of *Thecodiplosis brachyntera* cause swellings at the base of needle pairs on *Pinus sylvestris* and *P. mugo*. Seven species of gall midges cause bud galls on various species of *Juniperus*, the larvae of *Dasineura kellneri* induce galls on buds of *Larix decidua* and the larvae of *Taxomyia taxi* change leaf buds of *Taxus baccata* into galls.

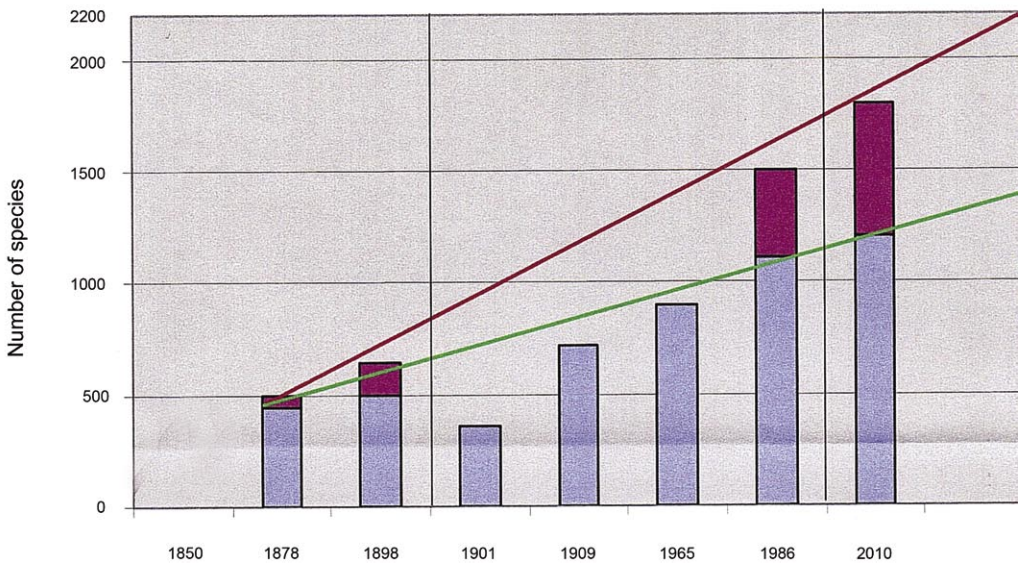


Fig. 38. Increasing species number of the family Cecidomyiidae during the 19th and 20th centuries and the prognosis for the future.

Table 14. Species numbers of gall-inducing and plant-inhabiting gall midges of the subfamily Cecidomyiinae associated with host plant families in Europe and comparison with occurrence of gall midge species numbers of the same families in Kazakhstan (Central Asia). Abbreviations: WE – Western Europe; EE – Eastern Europe; MD – Mediterranean; KZ – Kazakhstan

plant family	number of gall midge species				plant family	number of gall midge species			
	WE	EE	MD	KZ		WE	EE	MD	KZ
Fabaceae	123	60	22	114	Vitaceae	3	0	2	0
Asteraceae	104	33	8	139	Urticaceae	3	1	2	1
Poaceae	69	14	6	16	Solanaceae	3	1	1	3
Salicaceae	64	26	3	18	Anacardiaceae	3	0	1	0
Fagaceae	49	9	18	2	Asclepiadaceae	2	0	0	0
Rosaceae	49	30	16	39	Berberidaceae	2	0	0	2
Lamiaceae	41	15	5	25	Cucurbitaceae	2	0	1	1
Apiaceae	28	7	6	33	Dennstaedtiaceae	2	0	1	0
Brassicaceae	28	8	5	44	Geraniaceae	2	0	1	6
Cyperaceae	27	3	1	1	Onagracceae	2	2	0	1
Caryophyllaceae	23	4	2	15	Rutaceae	2	0	1	0
Chenopodiaceae	21	2	8	90	Thymelaeaceae	2	1	0	0
Pinaceae	17	7	1	2	Valerianaceae	2	0	0	0
Scrophulariaceae	16	9	2	11	Apocyanaceae	1	0	0	0
Ericaceae	15	3	4	0	Araliaceae	1	0	0	0
Oleaceae	15	3	9	0	Buddlejaceae	1	0	0	0
Betulaceae	14	5	0	2	Buxaceae	1	1	0	0
Rubiaceae	14	4	4	14	Cannabaceae	1	0	0	0
Ranunculaceae	13	5	1	14	Capparidaceae	1	0	1	1
Caprifoliaceae	11	3	1	7	Cornaceae	1	0	0	0
Campanulaceae	11	1	0	2	Dioscoreaceae	1	0	0	0
Corylaceae	10	0	2	0	Ephedraceae	1	0	0	9
Polygonaceae	10	1	2	28	Gentianaceae	1	0	0	1
Liliaceae	10	0	2	1	Juncaceae	1	0	0	0
Aceraceae	9	4	3	0	Linaceae	1	0	0	2
Euphorbiaceae	9	3	2	14	Lythraceae	1	0	0	0
Tiliaceae	8	5	0	0	Loganiaceae	1	0	0	0
Cupressaceae	8	2	1	6	Moraceae	1	0	0	0
Boraginaceae	8	1	1	4	Orchideaceae	1	0	0	0
Hypericaceae	6	1	3	0	Papaveraceae	1	0	1	2
Grossulariaceae	5	3	0	3	Plantaginaceae	1	1	0	1
Rhamnaceae	5	1	1	1	Polygalaceae	1	2	0	1
Tamaricaceae	5	0	1	12	Primulaceae	1	1	0	1
Violaceae	5	1	1	1	Pyrolaceae	1	0	0	0
Cistaceae	4	0	0	1	Saxifragaceae	1	0	0	0
Dipsacaceae	4	2	0	0	Taxaceae	1	0	0	0
Ulmaceae	4	2	0	0	**total families**	**73**	**41**	**40**	**54**

Of the flowering plants, the **Angiospermae** are represented by 173 families in Europe, 68 of which provide host plants for 886 gall midge species, i.e. 96.84% of all gall midge species associated with host plants in Europe.

Of the **Monocotyledonae**, that contain 34 families, only six provide host plants for 109 gall midge species, i.e. 11.92% of all gall midge species associated with host plants in Europe. Most of them, totalling 69 species, are associated with various species and genera of Poaceae, 27 gall midge species with Cyperaceae and 10 gall midge species with Liliaceae. Each of three families, viz. Dioscoreaceae, Juncaceae and Orchideaceae, hosts only one gall midge species. Most gall

midges totalling 777 species, i.e. 84.92% of all gall midge species associated with host plants in Europe, are associated with 62 families of the **Dicotyledones** that contains a total of 139 plant families.

Gall midges are more diverse on some plant families in which they find more favourable host plant species and genera for their development. Of the Dicotyledones, the family Fabaceae hosts the highest number of gall midges – 123 species, followed by Asteraceae with 104 gall midge species, Salicaceae with 64 species, Fagaceae and Rosaceae, each with 49 species, and Lamiaceae with 41 species. About two thirds of gall midge species are associated with 12 large plant families and the remaining third of gall midge species with 61 plant families.

The family Fabaceae hosts 123 gall midge species on plant species belonging to 28 genera, for example *Lathyrus* hosts 17 gall midge species, *Vicia* 14 species, *Medicago* 11 species, *Genista* 10 species, and *Trifolium* 8 species. The family Asteraceae hosts 104 gall midge species on 25 genera of host plants, for example *Artemisia* hosts 24 gall midge species, *Achillea* 7 species, *Hieracium* 7 species, *Chrysanthemum* 6 species, *Erigeron* 5 species. The family Poaceae hosts 69 gall midge species on 31 genera of host plants, for example *Poa* 9 gall midge species, *Dactylis* and

Table 15. Relations of gall-inducing and plant-inhabiting gall midges of the subfamily Cecidomyiinae to host plant species in countries of Europe given as the index of mutual gall midge species and plant species occurrence (IGS-PSO); ng – number of gall midge species; np – number of plant species; index – index of mutual occurrence

country	ng	np	index	references to botanical articles
Austria	352	3400	9	Tutin et al. 1964–1980
Belgium	130	1400	11	Tutin et al. 1964–1980
Bulgaria	240	3560	15	Jordanov 1976
Corsica	60	1625	27	Rikli 1946
Crete	38	2200	58	Rikli 1946, Sfikas 1987
Cyprus	32	1800	56	Sinclair 1991
Czech Republic	564	2200	4	Kubát 2002
Faroe Islands	5	400	80	Fosaa 2000
France	581	4500	8	Tutin et al. 1964–1980, Rikli 1946
Germany	653	2800	4	Jäger & Werner 2007
Greece	211	6700	32	Rikli 1946
Hungary	332	4200	13	Soó 1973
Italy	315	5600	18	Pignatti 1982
Italy (South Tyrol)	312	2361	7	Wilhalm & Hilpold 2006
Latvia	264	1385	5	Flora of Latvia 1953–1959
Mallorca	33	1250	37	Tutin et al. 1964–1980
Malta	36	1250	35	Haslam et al. 1977
Netherlands	305	1500	5	Tutin et al. 1964–1980
Poland	397	2500	6	Szafer et al. 1986, Mirek et al. 2002
Portugal	122	2735	22	Rikli 1946, Castroviejo 1986–2005
Romania	304	3600	12	Hayek 1927–1933, Savulescu 1952
Russia (European)	400	6500	16	Tutin et al. 1964–1980
Sardinia	44	2000	45	Tutin et al. 1964–1980
Sicily	89	2200	25	Tutin et al. 1964–1980
Slovakia	355	3352	10	Baláž et al. 2001
Slovenia	219	3200	15	Martinčič & Sušnik 1999
Spain	212	6500	30	Castroviejo 1986–2005
Sweden	266	2000	8	Karlsson 1998
Switzerland	228	3500	15	Lauber & Wagner 2001
Ukraine	166	3700	22	Bordzilowskij 1938
United Kingdom	526	2200	4	Fitter & Peat 1994

Festuca each 5 species, *Alopecurus*, *Bromus*, *Calamagrostis* and *Phragmites* each 4 gall midge species. In contrast, the family Salicaceae hosts 64 gall midge species which are associated with only two plant genera: *Populus* with 14 gall midge species and *Salix* with 50 gall midge species. Also in the family Fagaceae only two plant genera are associated with gall midges: *Fagus* hosts 6 gall midge species and *Quercus* 43 gall midge species.

Most gall midges that are associated with Angiospermae induce galls on various plant organs and only a few develop on or in organs of host plants without inducing gall development. Larvae of plant-inhabiting, i.e. not gall-inducing gall midges, live under the leaf sheaths of grasses, inside plant stems, under the bark of living, injured or dying trees, in resin masses, in inflorescences, in or on seeds and in cones. About one half of gall-inducing gall midge species cause galls on flowers and leaf buds, others induce galls on leaves and only a small part develop inside fruits.

In Western Europe 915 gall midge species are associated with 72 plant families and 12.5 is the average number of gall midge species per plant family; in Eastern Europe 287 gall midge species are associated with 41 plant families and 7 is the average number of gall midge species per plant family; in the Mediterranean 153 gall midge species are associated with 40 plant families and 3.8 is the average number of gall midge species per plant family. As it is shown, the western part of Europe is more species rich than the eastern part and the Mediterranean is notably species poorer. Surprisingly, the gall midge fauna of Kazakhstan in Central Asia is more species rich including 714 gall midge species that are associated with 52 families (according to Fedotova 2000), and 13.5 is the average gall midge species number per family.

In Western Europe 115 gall midge species are associated with Fabaceae and 100 species with Asteraceae. Host plants of the family Fabaceae, with 60 gall midge species, are also in first place in Eastern Europe and in the Mediterranean. On the other hand, in Kazakhstan the highest species number of gall-inducing gall midges – 139 species – is associated with the family Asteraceae the species of which form the main plant associations in desert and semidesert areas of Central Asia. In Western Europe a large amount – 69 species – are associated with Poaceae, 64 species with Salicaceae and 49 species with Fagaceae. Gall midge species associated with plant families including trees and shrubs (Salicaceae, Fagaceae, Pinaceae, Oleaceae, Betulaceae, Corylaceae, Aceraceae, Tiliaceae, Cupressaceae, Rhamnaceae, Tamaricaceae and Ulmaceae) and including about 200 gall-inducing species markedly predominate gall midge species associated with herbaceous plants.

The gall midge fauna of Eastern Europe including 287 gall-inducing species that are associated with 41 plant families is similar to that occurring in Western Europe but the species number associated with trees and plants is much lower. For example, only 26 gall midge species are known to occur on Salicaceae, in contrast to 64 species occurring in Western Europe and 9 species on Fagaceae in contrast to 49 species in Western Europe.

The gall midge fauna occurring in nine islands situated in the Mediterranean Sea and including 153 gall midge species that are associated with 40 plant families is relatively poor.

Gall midge species cause galls mainly on herbaceous plants of the family Fabaceae and on trees and shrubs of the family Fagaceae in second place. Islands in the Mediterranea area are densely covered with broad-leaved forests with dominant tree species of the genus *Quercus* including many species that are host plants of many gall midge species.

Kazakhstan is a large country situated in Central Asia and with only a small part in Eastern Europe. It occupies an area of 2,727,300 km² which is greater than Western Europe. It includes very diverse types of landscape: lowlands with steppes, taigas, rock-canyons, hills, deltas, mountains, snow-capped mountains and deserts. The flora of Kazakhstan is rich and includes about 6000 plant species in 1118 genera and 161 families (Ryabushkina et al. 2008). Gall midge fauna occurring in Kazakhstan is also rich: 714 gall-inducing species are associated with 54 plant families, i.e. with

33% of all plant families known in Kazakhstan (Fedotova 2000). Asteraceae with 139 gall-inducing species is the richest family, followed by Fabaceae hosting 114 species, Chenopodiaceae with 90 species, Brassicaceae with 44 species and Rosaceae with 39 gall midge species. In Kazakhstan, compared with Western and Eastern Europe, the majority of gall-inducing gall midge species are associated with herbaceous plants and only a few species cause galls on trees and shrubs.

If we compare the species richness of gall midges in the four mentioned areas using the average species number per one host plant family, Western Europe with 12.5 gall midge species associa-

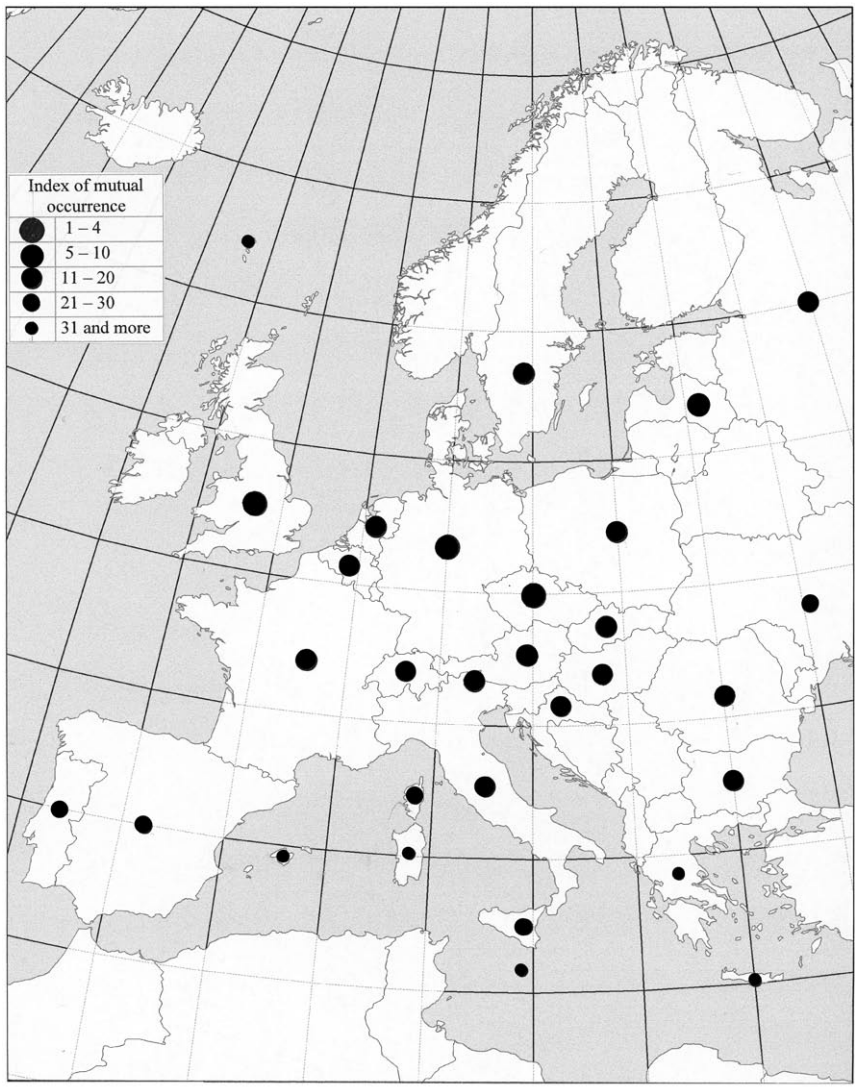


Fig. 39. Relations of gall-inducing and plant-inhabiting gall midges of the subfamily Cecidomyiinae to host plant species in countries of Europe given by the index of mutual occurrence.

Table 16. Distribution of galls of eleven major genera of gall-inducing Cecidomyiinae on different organs of host plants in Europe

gall midges genus	n species	organs of host plants					inquiline	biology unknown
		stem	bud	leaf	flower	fruit		
Dasineura	230	20	62	62	56	19	17	
Contarinia	135	6	18	17	80	9	3	
Asphondylia	50	0	13	1	20	19	0	
Rabdophaga	40	20	16	4	0	1	1	
Rhopalomyia	38	4	18	7	5	0	4	
Jaapiella	35	0	10	8	12	1	4	
Macrolabis	35	0	9	5	5	0	15	
Mayetiola	28	27	0	0	0	0	0	1
Lasioptera	27	16	0	2	0	0	5	4
Planetella	27	8	0	6	0	0	0	13
Resseliella	23	13	1	0	0	4	2	3
total	668	114	147	112	178	53	51	21

ted with one plant family is in first place, followed by Eastern Europe with 7 gall midge species associated with one plant family and the Mediterranean with 3.8 gall midge species associated with one plant family in last place in Europe. Of interest is the comparison of data from Europe with data obtained in Kazakhstan situated in Central Asia where it has been found that an average 13.5 gall midge species are associated with one plant family.

Mutual occurrence of gall midges and host plants

As we have shown in previous sections, gall midges are not equally distributed in countries of Europe. We try to analyse the relations between the species numbers of gall midges and the numbers of plant species in particular countries and islands of Europe (Table 15). It is necessary to mention that the numbers of species of flowering plants occurring in particular country given by various authors sometimes differ importantly. For some countries we were not able to obtain recent data of species numbers of flowering plants.

For the comparison of relations between gall midges and host plants we introduce here the formula – the **index of mutual gall midge species and plant species occurrence** (IGS-PSO), as follows:

$$\text{IGS-PSO} = \text{NPS}/\text{NGMS}$$

where **NPS** is the number of plant species in a particular country and **NGMS** is the number of gall midge species occurring in the same part. This index indicates the degree of mutual occurrence of gall midges on host plants in particular parts of Europe (Table 15, Fig. 39).

For example. If 5000 plant species have been recorded in a particular country and the fauna of gall midges of that country includes 500 gall midge species, the index is IGS-PSO=5000/500 and the result after calculating is 10. This number indicates a high value of mutual occurrence of gall midge species and host plants in that country. It means that we may find in such a country an average of one gall midge species on every tenth plant species. If in such a country the gall midge fauna includes only 100 gall midge species, the index IGS-PSO=5000/100 and the result after calculating is 50. In such a case we should find one gall midge species on every 50th plant species. Such a result indicates that the fauna of gall midges associated with plant species in a particular country is poor.

It is necessary to note that the value of the index is greatly influenced by the intensity of investigation of the gall midge faunas of the various countries and islands as well as by the diversity of the flora. For example, the UK low figure results from the combination of a depauperate post--glacial flora and long-term study of galls (K. M. Harris, pers. comm.).

Countries in Europe with an index value from 1 to 4 are noted for the highest mutual occurrence of gall midges and host plants. The United Kingdom, Germany and the Czech Republic having an index number of 4 are the countries with the highest mutual occurrence of gall midges and host plants in Europe. Countries characterized by an index value from 5 to 10 are noted for high mutual occurrence, viz. Latvia, the Netherlands, Poland, South Tyrol, France, Sweden, Austria and Slovakia. Eight countries, viz. Belgium, Romania, Hungary, Bulgaria, Slovenia, Switzerland, European part of Russia and Italy having been characterized by the index numbers from 11 to 20 may be evaluated as countries with medium mutual occurrence of gall midges and host plants. Five countries, viz. Spain and Portugal, Corsica, Sicily and Ukraine, characterized by the index numbers from 21 to 30, are countries of weak mutual occurrence of gall midges and host plants. Greece and five islands in the Mediterrranean Sea (Mallorca, Sardinia, Crete, Malta and Cyprus) with index numbers from 31 to 60 are countries with poor mutual occurrence of gall midges and host plants. The Faroe Islands situated in the Atlantic Ocean in northern Europe have a very poor mutual occurrence of gall midges and host plants characterized with the index number 80.

Although Greece is in Europe the country with the richest flora, including 6700 species of flowering plants, the gall midge fauna of Greece, including 211 species, may be classed as poor.

Table 17. Species numbers of gall-inducing Cecidomyiinae associated with main broad-leaved and coniferous trees in Europe. Abbreviations of countries: A – Austria, CH – Switzerland, CZ – Czech Republic, D – Denmark, F – France, P – Poland (data from Skuhravá & Skuhravý 1997a, b, 2009a, Skuhravá et al. 2002, 2005, 2006, 2007, 2009, Skuhravý & Skuhravá 1998)

	gall midge species number									
	Europe	F	A	CH	CZ	P	D	Sicily	Malta	Crete
broad-leaved trees										
Fagus sylvatica	4	4	4	3	4	4	4	2	0	0
Quercus robur	15	14	8	3	6	7	7	0	0	0
Acer pseudoplatanus	4	4	4	4	4	4	3	1	0	0
Fraxinus excelsior	5	4	4	3	4	4	3	0	0	0
Tilia platyphyllos	8	5	6	5	5	5	5	0	0	0
Betula pubescens	10	6	4	2	5	4	5	0	0	0
Carpinus betulus	6	5	4	4	5	4	3	0	0	0
Populus tremula	13	11	9	8	9	10	7	0	0	0
Salix caprea	7	13	6	2	7	9	9	0	0	0
Olea europaea	4	2	0	0	0	0	0	4	1	2
Quercus cerris	13	2	9	0	8	1	0	1	0	0
Quercus ilex	5	5	0	0	0	0	0	4	0	0
total	94	75	58	34	57	52	46	12	1	2
coniferous trees										
Picea abies	5	4	4	3	4	5	5	0	0	0
Pinus sylvestris	5	3	4	3	3	3	4	0	0	0
Abies alba	3	2	2	0	2	2	3	0	0	0
Larix decidua	3	2	2	1	2	3	2	0	0	0
Juniperus communis	7	4	2	2	3	4	3	0	0	0
Taxus baccata	1	1	1	1	1	1	1	0	0	0
total	23	16	15	10	15	18	18	0	0	0

We obtain similar relations between the rich flora of Spain including 6500 species of flowering plants and 212 gall midge species found. Similar relations between rich floras and poor gall midge faunas were found in islands in the Mediterranean Sea, viz. in Mallorca, Corsica, Sardinie, Sicily, Malta, Corfu, Crete and Cyprus.

The analysis of the relationship between gall-inducing and plant-inhabiting gall midges of the subfamily Cecidomyiinae and potential host plant species in the countries of Europe produced a surprising result: although number of species of flowering plants increases from north to south, the species number of gall midges decreases.

Distribution of galls on host plants

Galls of gall-inducing species of the subfamily Cecidomyiinae are not equally distributed on organs of their host plants. We analysed eleven genera of gall-inducing Cecidomyiinae occurring in Europe on the basis of which organ of host plant is used for development of their larvae (Table 16). Of 668 species belonging to these eleven genera, 90% induce galls on various plant organs, 7% are inquilines in galls of other gall midges or insects and the biology of 3% is completely unknown. Species of the genus *Dasineura* cause galls mainly on buds and leaves, of the genus *Contarinia* on flowers, of *Asphondylia* on flowers and fruits, of *Rabdophaga* on stem and buds, of *Rhopalomyia* on buds, of *Jaapiella* on buds and flowers, species of the genus *Macrolabis* are mainly inquilines in galls of other gall midges and species of *Mayetiola*, *Lasioptera*, *Planetella* and *Resseliella* develop in galls mainly on stems. Some species that have two or more generations per year may cause galls on two or more different organs of their host plant and therefore the sum of inhabited plant organs in the table does not equal the number of gall midge species.

Abundance of gall midge species on host plant species

We use the term abundance here for the number of species associated with one host plant species. Different numbers of species or genera of gall-inducing gall midges may develop on one host plant species. The occurrence of gall midges (Cecidomyiidae) on host plants, mainly on trees, is not so abundant as that of gall wasps (Cynipidae, Hymenoptera). For example, about 130 different gall--inducing species of gall wasps, belonging to several genera, are associated with *Quercus robur* and *Quercus petraea* (Fagaceae) in Europe but only fifteen gall-inducing species of gall midges, also belonging to several genera (Skuhravá et al. 1998).

If we analyse the gall midge faunas of European countries from the point of view of association with host plants, we find that herbaceous plants are more frequently host plants than trees and shrubs. Although trees and shrubs host fewer gall midge species than herbaceous plants, their galls on leaves are usually more conspicuous and, therefore, much better known than small and inconspicuous galls on herbaceous plants that are hidden among grasses near the soil.

For example: the gall midge fauna of Poland includes 397 species of the subfamily Cecidomyiinae that are associated with 257 species of host plants belonging to 48 plant families of which 197 species (76%) are herbaceous plants and 60 species (24%) trees and shrubs (Skuhravá et al. 2008). Similar relationships between number of herbaceous plants and trees/ shrubs as host plants were found in the gall midge fauna of Austria (Skuhravá & Skuhravý 2009a) and of Denmark (Skuhravá et al. 2006). In Europe about 70% of gall-inducing species of the subfamily Cecidomyiinae are associated with herbaceous plants and only 30% with trees and shrubs.

Many tree species are hosts of one, two, three or more gall midge species. Some gall midge species are monophagous and are associated with only one host plant species, some are oligophagous having been associated with several species of one host plant genus and only a few gall midge species are polyphagous and are associated with species of several genera belonging to

one or more plant families. Gall midge species associated with twelve main broad-leaved tree species and six coniferous trees in Europe are given in the Table 17.

Altogether one hundred and seventeen gall-inducing and plant inhabiting species are associated with eighteen main tree species in Europe. Ninety four gall midge species are associated with twelve main broad-leaved host tree species and twenty three gall midge species with six coniferous trees. These trees are not distributed equally in Europe and, naturally, gall midge species coincide with their host plants in distribution. *Quercus robur* is the host tree species with the highest species number of Cecidomyiidae (15 species), followed by *Populus tremula* and *Quercus cerris*, each with thirteen gall midge species, then *Betula pendula* with ten gall midge species and *Tilia platyphyllos* with ten gall midge species. *Olea europaea* is the south-European plant species and the boundary of its distribution area are considered to be the boundary of the Mediterranean subregion. Gall midge species associated with broad-leaved trees occurring in Sicily, Malta and Crete, parts of the Mediterranean subregion, form a characteristic species composition which differs substantially from the gall midge species composition in other parts of Europe.

France, situated in the most western part of Europe bordering the Atlantic Ocean has the richest gall midge species composition including 75 species that are associated with broad-leaves trees and also the highest species numbers of gall midges associated with one species of host plant. It is composed not only of gall midge species abundantly distributed in Central Europe but also includes nine gall midge species associated with *Quercus cerris*, *Q. ilex* and *Olea europaea* originating from the Mediterranean area and distributed only in the southernmost part of France. Some of these gall midges reach to the southern parts of Austria and of the Czech Republic.

In Poland and Germany, situated in the northern part of continental Europe, there was found the highest gall midge species number associated with coniferous trees. This is in harmony with character of vegetation in this part of Europe. No gall midge species associated with coniferous tree was found in Sicily, Malta and Crete that are situated in the Mediterranean area.

Coevolution of the family Cecidomyiidae with plants

Coevolution is defined by Lincoln et al. (1982) as the independent evolution of two or more species having an obvious ecological relationship, usually restricted to cases in which the interactions are beneficial to both species; it is also used for the evolutionary interactions between species with some degree of independence, such as parasites and their hosts. Such relationships may be observed between the gall midges and their host plants, host animals or other host organisms in the course of their evolution.

No members of the family Cecidomyiidae are known to be associated with the most primitive groups of organisms, i.e. with Prokaryota and Algae, and no gall midges have been found to be directly associated with lichens (Lichenes) (Table 18, Fig. 40). It seems that at least two main developmental lines of gall midges appeared during their evolution. In the past, members of the family Cecidomyiidae were probably involved in interactions with three groups of fungi, i.e. with Ascomycetes, Basidiomycetes and Deuteromycetes. This is supported by the fact that in the recent time we have evidence that the larvae of gall midges develop in association with various groups of fungi (Nijveldt 1969, Skuhravá et al. 1984, Yakovlev 1994, Ševčík 2006).

The current associations may result from more than one coevolutionary event. We know that the ability of organisms to induce galls has arisen on many separate occasions so the same may be true within cecidomyiid lineages. Coevolution of gall-inducing and plant inhabiting species of the family Cecidomyiidae with two groups of vascular plants, Pteridophyta and Spermatophyta, is shown on Fig. 40. Plant groups marked by red frames indicate host plant species suitable for development of gall midges.

The ferns (Pteridophyta) first appeared in the fossil record in the early-Carboniferous period. By the Triassic, the first evidence of ferns related to several modern families appeared. The "great fern radiation" occurred in the late-Cretaceous, when many modern families of ferns first appeared. There is no fossil evidence of galls of gall midges on ferns and only two extant gall midge species are known to occur on ferns in Europe, viz *Dasineura pteridis* and *D. pteridicola*, both causing galls on *Pteridium aquilinum* of the family Dennstaedtiaceae.

The seed plants (Spermatophyta, Gymnospermae) originated in the late Carboniferous Period. Early characteristics of seed plants were evident in fossil Progymnospermes of the late Devonian period around 380 million years ago. Conifers are by far the most abundant gymnosperms with around 600 plant species. Only one fossil record supports the coevolution of gall midges with conifers – *Sequoiomyia kraeuseli* found in fossil cones of *Sequoia langsdorfii* of the family Taxodiaceae. A relatively low species number of twenty six gall midge species currently occurring in Europe indicates a low degree of coevolution.

Cycads are the next most abundant group with about 130 plant species and without fossil evidence of coevolution with gall midges. Gnetales included approximately 75–80 species. There is no fossil evidence about the galls of gall midges on Gnetales. Only one recent gall midge species is known – *Xerephedromyia ustjurtensis* inducing galls on *Ephedra distachya* of the family Ephedraceae in Europe.

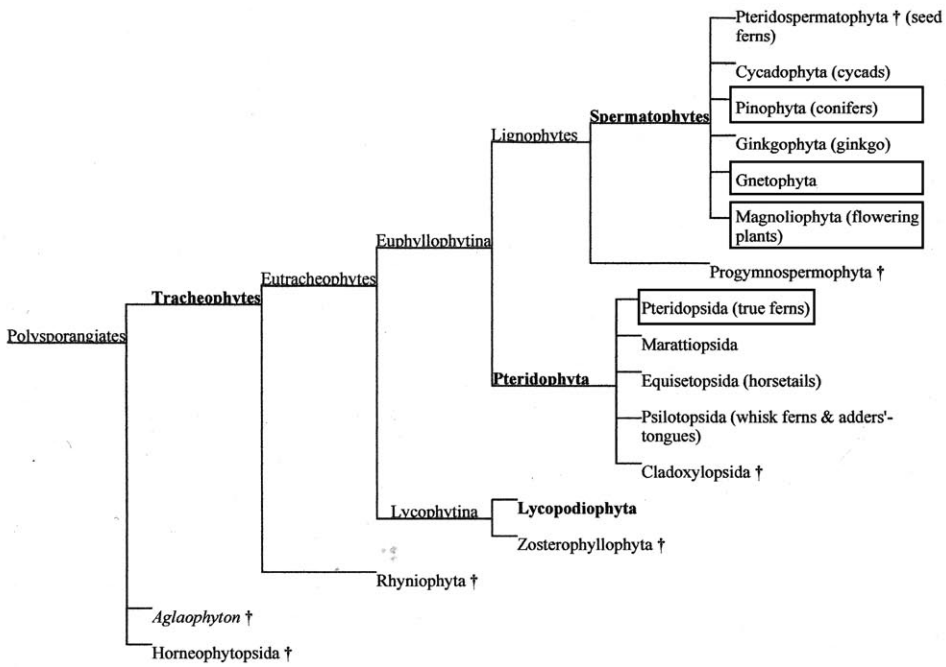


Fig. 40. Coevolution of gall-inducing and plant inhabiting species of the family Cecidomyiidae with two groups of vascular plants, Pteridophyta and Spermatophyta, according to the phylogenetic system proposed by Kenrick & Crane (1997) and Smith et al. (2006). Plant groups marked by red frames indicate host plant species of gall midges.

Table 18. Recent species numbers of the family Cecidomyiidae associated with the main groups and subgroups of organisms in Europe. Groups of vascular plants are given according to the phylogenetical system proposed by Kenrick & Crane (1997) and Smith et al. (2006)

phylogenetical group or subgroup of organisms and plants			recent species number of gall midges
Prokaryota	Cyanophyta		0
	Bacteriophyta		0
Algae			0
Mycophyta (fungi)	Ascomycetes		7
	Basidiomycetes		70
	Deuteromycetes		0
	Lichenes		0
Bryophyta (mosses)			0
Vascular plants	Pteridophyta (ferns)	Pteridopsida (true ferns)	2
(897 gall midge species)	Spermatophyta	Cycadophyta	0
	(Gymnospermae)	Pinophyta (conifers)	26
	(seed plants)	Ginkgophyta	0
		Gnetophyta	1
		Magnoliophyta (Angiospermae)	
		(flowering plants)	870

The flowering plants (Magnoliophyta, Angiospermae) are the most abundant group of plants, including about 260,000 recent and many fossil species. Most gall midges known to occur in Europe, including 870 recent species, are associated with this group of plants. Fossil galls of ten gall midge species provide evidence of their coevolution with flowering plants in the Miocene and Pliocene of the Tertiary in various parts of Europe.

Adults of eighty-nine fossil species of 54 genera of the family Cecidomyiidae are known from various parts of the world (Evenhuis 1994, Skuhravá 2006). Fossil gall midge adults were found mainly in amber and copal and are dated from the Upper Jurassic, Lower Cretaceous, Upper Cretaceous, Eocene, Oligocene, Miocene, Pliocene and Holocene. Fossil gall midge adults were found scattered in all biogeographic regions except the Australasian and Oceanian regions. The oldest fossil gall midge species, *Catotricha mesozoica* Kovalev, 1990, found in Siberia from the Upper Jurassic and Lower Cretaceous, provides evidence that members of the Lestremiinae and Porricondylinae probably originated and developed in the Mesozoic (Kovalev 1990).

In Europe, fossil gall midge adults were found mainly in amber of the Baltic Region. They belong mainly to the subfamilies Porricondylinae and Lestremiinae and only a very few species are Cecidomyiinae. Single species, sometimes identified to the genus level only, were found in the UK, Denmark, Germany, France, Austria and Italy. Fossil adults of several gall midge species were discovered in the earliest Eocene amber in northern France (Nel & Prokop 2006) and in later Eocene amber in western Ukraine (Fedotova & Perkovsky 2004, 2005, Perkovsky & Fedotova 2004).

There are only a few data about fossil galls induced by gall midges on organs of fossil host plants in the world (Larew 1992). In Europe the galls of ten gall-causing species were found, mainly in the form of the leaf impressions of host plant trees from the Tertiary Upper Miocene and Pliocene (Trotter 1903, Rübsaamen 1929). Möhn (1960) discovered the fossil gall midge species *Sequoiomyia kraeuseli* in the cone seeds of the fossil plant *Sequoia langsdorfii* (Taxodiaceae) in Rheinland (Germany) from the Miocene. Straus (1977) mentioned among fossil galls

Table 19. Fossil galls induced by gall midges of the subfamily Cecidomyiinae on host plants found in Europe

gall midge species	host plant	host family	host organ	locality	age	reference
Sequoiomyia kraeuseli	*Sequoia langsdorfii*	Taxodiaceae	cones	Germany: Duren	Miocene?	Möhn 1960
Asphondylia sarothamni	*Sarothamnus*	Fabaceae	leaf	Europe, not precised	tertiary	Rübsaamen 1929
Cecidomyia sp.	*Populus*	Salicaceae	leaf	Switzerland: Oeningen	tertiary	Trotter 1903
Contarinia carpini (misidentification)	*Betula*	Betulaceae	leaf	Germany: Willershausen	pliocene	Straus 1977
Dasineura fraxini	*Fraxinus*	Oleaceae	leaf	Germany: Willershausen	pliocene	Straus 1977
Dasineura ruebsaameni?	*Carpinus*	Corylaceae	leaf	Germany: Willershausen	pliocene	Straus 1977
Didymomyia tiliacea	*Tilia*	Tiliaceae	leaf	Germany: Willershausen	pliocene	Straus 1977
Mikiola fagi	*Fagus pliocenica*	Fagaceae	leaf	France: Pas-de-la-Mougudo	pliocene	Marty 1894
Mikiola fagi	*Fagus*	Fagaceae	leaf	Europe, not precised	tertiary	Rübsaamen 1929
Phegomyia fagicola (misidentified) as *Mikiola? pontiensis*	*Fagus castaneaefolia*	Fagaceae	leaf	Spain: Cerdãna	miocene	Villalta 1957, Skuhravá 2006
Phegomyia fagicola (misidentification)	*Quercus*	Fagaceae	leaf	Germany: Willershausen	pliocene	Straus 1977

found at Willershausen in Harz (Germany) in the Pliocene also six fossil galls that were probably caused by species of the family Cecidomyiidae. Villalta (1957) found in Spain traces of galls which he identified as *Mikiola pontiensis*. It was a misidentification. On the basis of their form, these galls were caused by another gall midge species – *Phegomyia fagicola* (Kieffer, 1913), an extant species (Skuhravá 2006). Information about fossil galls caused by gall midge species is summarised in Table 19.

Fossil galls of ten gall midge species were found on nine genera of host plants belonging to eight plant families. Most gall midges induced galls on leaves and only one species inhabited cones. Fagaceae are the plant family hosting the highest number of gall midges – four species, and each of the other families hosts only one gall midge species.

It is necessary to note that three gall midge species given in Table 19 were incorrectly identified in the past. Identification of the species causing galls on leaves of *Fagus castaneifolia* was corrected by Skuhravá (2006). The galls on leaves of *Betula* are caused by another species, not by *Contarinia carpini* which is specifically associated with *Carpinus*. Also the galls on leaves of *Quercus* given as *Phegomyia fagicola* were incorrectly identified. *P. fagicola* is specifically restricted to *Fagus* and could not cause galls on leaves of *Quercus*.

During evolution, the gall-inducing and plant inhabiting gall midges of the subfamily Cecidomyiinae probably started to develop at the end of the Mesozoic when they entered into interactions with developing groups of plants, started to inhabit suitable parts of plants, their organs

and tissues inducing there changes that initiated the formation of galls. The main development of gall-inducing and plant inhabiting gall midges came in the Pliocene and Miocene of the Tertiary, together and in parallel with the development of flowering plants, as is supported by the evidence of several fossil galls of gall midges.

Factors affecting gall midge species richness

From our observations and literature research we conclude that gall midge species richness is influenced mainly by **abiotic factors,** i.e. by geographic and altitudinal position of the area under study that are associated with changing climatic variables including sunshine, temperature and rainfall; by **biotic factors,** i.e. mainly by the type of vegetation cover and composition of natural vegetation; and **by anthropic factors**, involving various human activities. The present species richness and distribution of gall midge species in Europe are results of all these influences which are briefly commented on below. In most cases detailed information is provided in earlier sections of this article.

Geographic position. In Europe the most suitable area for gall midges is the temperate zone situated between latitudes 45° and 52° North, which is covered with broadleaved, coniferous and mixed forests. Gall midge species number changes with geographical position and decreases both northwards and southwards. On the other hand, species numbers of gall midges are relatively stable along the west-east axis. The exceptionally low gall midge species number in the Faroe Islands, situated in the Atlantic Ocean far off the European continent, is the result of geographical isolation.

Altitude. Generally speaking, the number of gall midge species decreases with rising altitude. Species numbers in the planare zone of Europe are usually low and are much higher in colline, submontane and montane zones. Above the timber line, usually at an altitude of about 1500 m in Europe (this altitude differs in various parts of Europe with geographic position) the species number falls abruptly and only a few species occur in the sub-Alpine and Alpine zones.

Climatic factors. Gall midge species number is relative high in Central, Western and Eastern Europe and falls to the south. This corresponds with changing climatic factors that are shown in climatograms: the temperature increases to the south and, on the other hand, the rainfall decreases and the hot and dry weather in southern Europe may be unsuitable for the development of gall midges and their galls on host plants.

Composition of vegetation. Richness of plant species, providing plenty of potential hosts for gall midges, is the most important prerequisite of richness of gall midges in the area. When we compared the number of plant species in various parts of Europe with the number of gall midge species, we discovered a very surprising fact that the number of gall midge species decreases to the south of Europe although the number of plant species increases.

Association with host plant species. Most gall-inducing gall midges are specifically restricted to their host plants and usually mirror the distribution of their host plants in their native environments, but in a few cases their distribution may be extended into new areas when their host plants become established in distant areas, such as Siberia, the Far East or even North America.

Anthropic factors. People have changed landscapes in Europe for a long time. Mediterranean areas have been exploited in ancient times by clearing, burning and grazing and natural forests have been replaced by olive trees, carob, wine grapes and citrus trees. Also landscapes in other parts of Europe changed under influence of man which gradually decreased the number of gall

midge species. Some species that were abundant in the past disappeared as a result of the degradation and destruction of biotopes, the use of chemical agents in plant protection against pests and intensive fertilization of fields, cutting and burning of grass on headlands and fallows, destruction of small forest areas, use of land for new building activities, park and orchard arrangements with regular cutting of grass, cutting of grass on slopes, formerly left without human interventions, cutting of reeds and adjustment of littoral growths, amelioration of wetlands and wet meadows. In the course of all these activities, the natural growth and multiplication of host plants of gall midges is restricted and thus, the populations of plants and animals that are dependent on them (including Cecidomyiidae) are progressively reduced (Skuhravá 2005).

Intensity of investigations. Results of gall midge species numbers in the area under study are affected also by the number of investigations and by selection of suitable sites for collection of gall midges. More investigations and more samples usually result in increased species numbers, new records and also discovery of new species. It is necessary also to emphasize the importance of the researchers, their ability, experience, knowledge and enthusiasm that make it possible to discover gradually additional gall midge species and hidden factors influencing gall midge species richness.

Acknowledgements

We would like to express our thanks to Keith M. Harris (Ripley, Woking, Surrey, England) for valuable comments on the manuscript and for improvements of the English text. We thank Jan Zárybnický, Agency for Nature Conservation and Landscape Protection of the Czech Republic, Prague, for all advice and for preparing maps according to the map basis of © ESRI® & NASA, 2007. We thank Torbjörn Tyler, Botanical Museum, Lund, Sweden, for data on recent and past plant species numbers of Sweden. We are grateful to our daughter, Ivana Vaněčková, and our granddaughter, Pavla Kosová, for their help in preparing computer version of graphs.

REFERENCES

Baláž D., Marhold K. & Urban P. (eds.) 2001: Red list of plants and animals of Slovakia. *Nature Conservation* **20** (Suppl.), 160 pp.

Bergenstamm J. E. & Löw P. 1976: Synopsis Cecidomyidarum. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft*, *Wien* **26**: 1–104.

Bordzilowskij E. 1938: *Flora RSS UCR* [Flora of Ukraine]. Kiev: Naukova Dumka, 197 pp.

Buhr H. 1964–1965: *Bestimmungstabellen der Gallen* (*Zoo- und Phytocecidien*) *an Pflanzen Mittel- und Nordeuropas*. Jena: Fischer Verlag, 1572 pp.

Castroviejo S. (ed.) 1986–2005: *Flora Ibérica*. *Plantas vasculares de la Península Ibérica e Islas Baleares*. (12 volumes). Madrid: Real Jardín Botánico-C.S.I.C.

Chandler P. (ed.) 1998: *Checklists of Insects of the British Isles* (*New Series*). *Part 1*: *Diptera* (*Incorporating a List of Irish Diptera*). London: Royal Entomological Society, 234 pp. (Cecidomyiidae. Pp.: 24–43).

DAISIE 2009: *Handbook of Alien Species in Europe*. Dordrecht, Netherlands: Springer, 399 pp.

Darvas B., Skuhravá M. & Andersen A. 2000: Agricultural dipteran pests of the Palaearctic region. Pp.: 565–650. In: Papp L. & Darvas B. (eds.): *Contributions to a Manual of Palaearctic Diptera*. *Vol. 1*. *General and Applied Dipterology*. Budapest: Science Herald, 978 pp.

Dengler K. 2004: Forschungen zur kambiophagen Gallmücke Resseliella quercivora (Mamaev, 1965) (Cecidomyiidae, Diptera). Biologie, Ökologie, Verbreitung, Schädlichkeit. *Schriftenreihe der Fachhochschule Rottenburg* **19**: 1–111.

Ehrendorfer F. 1973: *Liste der Gefässpflanzen Mitteleuropas*. Stuttgart: Gustav Fischer, 318 pp.

Ellenberg H. 1978: *Vegetation Mitteleuropas mit den Alpen*. Second Edition. Stuttgart: Ulmer, 981 pp.

Evanhuis N. L.1994: *Catalogue of the Fossil Flies of the world* (*Insecta*: *Diptera*). Leiden: Backhuys Publishers, 600 pp.

Fauna Europaea 2007: version 1.1, available on line http://www.faunaeur.org

Fedotova Z. A. 2000: *Gallicy-fitofagi* (*Diptera*, *Cecidomyiidae*) *pustyn i gor Kazakhstana*: *morfologija*, *biologija*, *rasprostranenie*, *filogenija i sistematika* [*Plant-feeding gall midges* (*Diptera*, *Cecidomyiidae*) *of the deserts and mountains of Kazakhstan*: *Morphology*, *biology*, *distribution*, *phylogeny and systematics*]. Samara: Samarskaja GSCHA, 803 pp (in Russian).

Fedotova Z. A. & Perkovsky E. E. 2004: New gall midges (Diptera: Cecidomyiidae) from the Rovno amber: subfamily Lestremiinae, tribes Strobliellini and Campylomyzini; subfamily Porricondylinae, tribes Diadocidiini and Asynaptini. *Paleontological Journal* **38**: 538–547.

Fedotova Z. A. & Perkovsky E. E. 2005: New gall midges (Diptera: Cecidomyiidae) from the Rovno amber: subfamily Porricondylinae (tribes Bryocryptini and Winnertziini) and subfamily Lasiopterinae (tribes Brachineurini and Oligotrophini). *Paleontological Journal* **39**: 41–51.

Fiedorowiczowna Z. 1931: Zoocecidia na roslinach zebranych w powiecie dzisnienskim i braslawskim Ziemi Wilenskej. *Prace Towarysztwa Przyjaciol Nauk*, *Wilno* **6:** 25–39.

Fitter A.H. & Peat H. J. 1994: The Ecological Flora Database. (Ecological Database of the British Isles). *Journal of Ecology* **82**: 415–425.

Flora of Latvia 1953–1959: 4 Volumes. Riga.

Foote R. H. 1965: Family Cecidomyiidae (Itonididae). Pp.: 241–296. In: Stone A., Sabrosky C. W., Wirth W. W., Foote R. H. & Coulson J. R. (eds.): *A Catalog of the Diptera of America North of Mexico*. Washington, D. C.: U. S. Government Printing Office:1696 pp.

Fosaa M. A. 2000. *Wildflowers in the Faroe Islands*. *Checklist*. Tórshavn: Føroya Náttúrugripasavn, 34 pp.

Gagné R. J. 1968: Family Cecidomyiidae. Fascicle 23. Pp.:1–62. In: Papavero N. (ed.): *A Catalogue of the Diptera of the Americas South of the United States*. São Paulo: Departamento de Zoologia, Secretaria da Agricultura, 62 pp.

Gagné R. J. 1973: Family Cecidomyiidae. Pp.: 480–517. In: Delfinado M. D. & Hardy D.E. (eds.): *A Catalog of the Diptera of the Oriental Region*. *Vol. 1*. *Order Nematocera*. Honolulu: The University Press of Hawaii, 628 pp.

Gagné R. J. 1989a: *The Plant Feeding Gall Midges of North America*. Ithaca and London: Cornell Univ. Press, 356 pp.

Gagné R. J.: 1989b: Family Cecidomyiidae. Pp.: 152–163. In: Evenhuis N. L. (ed.): *Catalog of the Diptera of the Australasian and Oceanian Regions*. Honolulu, Hawaii: Bishop Museum Press, 1155 pp.

Gagné R. J. 1994: *The Gall Midges of the Neotropical Region*. Ithaca and London: Comstock Publishing Associates and Cornell University Press, 352 pp.

Gagné R. J. 2004: A Catalog of the Cecidomyiidae (Diptera) of the World. *Memoirs of the Entomological Society of Washington* **25**: 1–408.

Gosseries J. 1991: Cecidomyiidae. Pp.: 61–64. In: Grootaert P., De Bruyn L. & De Meyer M. (eds.): Catalogue of the Diptera of Belgium. *Studiendocumenten van het K. I. B. N.* **70:** 1–338.

Grover P. 1981: Studies on gall midges of India XLIV: A catalogue of Indian gall-midges. *Cecidologia Internationale* **2**: 63–108.

Hackman W. 1980: A check list of the Finnish Diptera I. Nematocera and Brachycera (s.str.) *Notulae Entomologicae* **60**: 17–48. (Cecidomyiidae. Pp.: 38–40).

Harris K. M. 1976: Cecidomyiidae. Pp.: 32–42. In: Kloet G. S. & Hincks W. D. (eds.): *A Check List of British Insects*. *Part 5*. *Diptera and Siphonaptera*. London: Royal Entomological Society, 139 pp.

Harris K. M. 1980: Family Cecidomyiidae. Pp.: 238–251. In: Crosskey R. W. (ed.): *Catalogue of the Diptera of the Afrotropical Region*. London: British Museum (Natural History), 1437 pp.

Haslam S. M., Sell P. D. & Wolseley P. A. 1977: *A Flora of the Maltese Islands*. Malta: Malta University Press, 560 pp.

Hayek A. 1927–1933: *Prodromus Florae Peninsulae Balkanicae*. **1** (1927): 1193 pp.; **2** (1928–1931): 1152 pp.; **3** (1932–1933). Berlin: Springer Verlag, 472 pp.

Houard C. 1908–1909: *Les Zoocécidies des Plantes d'Europe et du Bassin de la Méditerranée*. 2 Volumes. Paris: A. Hermann et Fils, 1247 pp.

Jäger E. J. & Werner K. (eds.) 2007: *Rothmaler – Exkursionsflora von Deutschlands*. *Band 3*. Gefässpflanzen. Berlin: Spektrum Acad. Verlag, 753 pp.

Jordanov D. (ed.) 1976: *Flora of Bulgaria*. Vol. 6. Sofia: Bulgarian Academy of Sciences Publishing House, 590 pp.

Karlsson T. 1998: Förteckning över svenska kärlväxter. *Svensk Botanisk Tidskrift* **91**: 241–560.

Kenrick P. & Crane P. R. 1997. *The Origin and Early Diversification of Land Plants*: *A Cladistic Study*. Washington, D.C.: Smithsonian Institution Press, 150 pp.

Kieffer J. J. 1898: Synopse des Cécidomyies d'Europe et d'Algérie. *Bulletin de la Société Histoire Naturelle Metz* **2**(8): 1–64.

Kieffer J. J. 1901: Synopsis des Zoocécidies d'Europe. *Annales de la Société Entomologique de France* **70**: 234–579.

Kolomoets T. P., Mamaev B. M., Zerova M. D., Nartshuk E. P., Jermolenko B. M. & Djakonchuk L. A. 1989: *Nasekomye – galloobrazovateli kulturnych i dikorastuschich rastenij evropeiskoi chasti SSSR*. *Dvukrylye*. [*Insects – Gall-inducers of Cultural and Free-growing Plants in European Part of the USSR*. *Diptera*]. Kiev: Naukovaja dumka, 167 pp (in Russian).

Kovalev V. 1990: Dvukrylye [Diptera]. Pp.: 123–177. In: Rasnitsyn A. P. (ed.): *Pozdnemezozzojskie nasekomye Vostočnogo Zabajkalia* [*Late Mesozoic Insects of Eastern Transbaikalia*]. Moskva: Nauka, 224 pp (in Russian).

Kubát K. (ed.) 2002: *Klíč ke květeně České republiky* [*Key to the Flora of the Czech Republic*]. Praha: Academia, 926 pp (in Czech).

Lambinon J. 1957: Contribution a l'étude des zoocécidies de la Belgique II. Une excursion cécidologique dans La Vallée de la Meuse a Houx et Bouvignes. *Lejeunia*, *Revue de Botanique* **21**: 65–71.
Lambinon J. 1958: Contribution a l'étude des zoocécidies de la Belgique I. Récoltes cécidologiques dans Le Bassin de L'Ourthe, aux environs de Barvaux. *Bulletin de la Sociéte Royale de Botanique de Belgique* **90**: 323–334.
Lambinon J. 1976: Contribution a l'étude des zoocécidies de la Belgique III. Zoocécidies recueillies dans les vallées de la Houille et de la Hulle au cours de l'excursion du 31 août 1975. *Lejeunia*, *Revue de Botanique* **79**: 15–32.
Lambinon J., Schneider N. & Feitz F. 2001: Contribution à la connaissance des galles de Diptères (Insecta, Diptera) du Luxembourg. *Bulletin de la Societe Naturelle Luxembourg* **102**: 51–76.
Larew H. G. 1992: Fossil galls. Pp.: 50–59. In: Shorthouse J. D. & Rohfritsch O. (eds.): *Biology of Insect-induced galls*. New York, Oxford: Oxford University Press, 285 pp.
Lauber K. & Wagner G. 2001: *Flora Helvetica*. Bern, Stuttgart, Wien: Verlag Paul Haupt, 1615 pp.
Lincoln R. J., Boxshall G. A. & Clark P. F. 1982: *A Dictionary of Ecology*, *Evolution and Systematics*. Cambridge: Cambridge University Press, 298 pp.
Linnaeus C. 1758: *Systema naturae per regna tria naturae secundum classes*, *ordines*, *genera*, *species*, *cum characteribus*, *differentiis*, *synonymis*, *locis*. Editio decima. Holmiae [= Stockholm], 824 pp.
Mac Arthur R. H. & Wilson E. O. 1967: *Island Biogeography*. Princeton: Princeton University Press, 203 pp.
Martinčič A. & Sušnik F. 1999: *A Concise Flora of Slovenia*. *Gymnosperms and Angiosperms*. Ljubljana: Cankavaja zalozba, 515 pp.
Merz B., Bächli G., Haenni J.-P. & Gonseth Y. (eds.) 1998: *Diptera-Checklist. Fauna Helvetica*. *Vol. 1*. Neuchâtel: Centre Suisse de Cartographie de la Faune, 369 pp.
Meusel H., Jäger E. & Weinert E. 1965–1992: *Vergleichende Chorologie der zentraleuropäischen Flora*. *Band 1–3*. Jena: Gustav Fischer, 258; 418; 133 pp.
Meyer H. & Jaschhof M. 1999: Cecidomyiidae. Pp.: 18–32. In: Schumann H., Bährmann R. & Stark A. (eds.): Entomofauna Germanica 2. Checkliste der Dipteren Deutschlands. *Studia Dipterologica*, Suppl. **2**, 354 pp.
Mirek Z., Piękoś-Mirkowa H., Zając A. & Zając M. 2002: *Flowering Plants and Pteridophytes of Poland*. *Krytyczna lista roślin naczyniowych Polski*. Kraków: W. Szafer Institute of Botany, Polish Academy of Science, 442 pp.
Möhn E. 1960: Eine neue Gallmücke aus der niederrheinischen Braunkohle, Sequoiomyia kraeuseli n.g., n.sp. (Diptera, Itonididae). *Senckenbergina Biologica* **41**: 513–522.
Nel A. & Prokop J. 2006: New fossil gall midges from the earliest Eocene French amber (Insecta, Diptera, Cecidomyiidae). *Geodiversitas* **28**: 37–54.
Nijveldt W. 1969: *Gall Midges of Economic Importance*. *Vol. 8*. *Miscellaneous* (*Zoophagous*, *Fungivorous*, *and Those That Attack Weeds*). London: Crosby Lockwood & Son ltd., 221 pp.
Nijveldt W. & Beuk P.L.Th. 2002: Family Cecidomyiidae. Pp.: 69–84. In: Beuk P. L. T. (ed.): *Checklist of the Diptera of the Netherlands*. Utrecht: KNNV Uitgeverij, 448 pp.
Noirfalise A. 1987: *Map of the Natural Vegetation of the Member Countries of the European Community and the Council of Europe*. Strasbourg: Council of Europe, 80 pp.
O'Connor J. P., Wistow S., Ashe P. & O'Connor M. A. 1999: A review of the Irish gall-inducing Cecidomyiidae (Diptera) and their inquilines. *Irish Naturalists' Journal* **26[**1998]: 81–92.
Paik J-Ch., Yukawa J., Uechi N., Sato S. & Ganaha T. 2004: Gall-inducing species of the family Cecidomyiidae (Diptera) recorded from the Korean Peninsula and surrounding islands, in comparison with the gall midge fauna of Japan. *Esakia* **44**: 57–66.
Pakalniškis S., Rimšaité J., Sprangauskaite-Bernotiene R., Butautaite R. & Podenas S. 2000: Checklist of Lithuanian Diptera. (Cecidomyiidae. Pp.: 20–27). *Acta Zoologica Lithuanica* **10**(1): 3–58.
Perepeczko-Baumanowa J. 1935: Zoocecidia zobrane w Oszmianie i najblizszych okolicach (zoocecidii Oszmiany, Belarus). *Prace Towarysztwa Przyjaciol Nauk*, *Wilno* **9**: 239–261.
Perkovsky E. E. & Fedotova Z. A. & 2004: New species of gall midges (Diptera: Cecidomyiidae) from Rovno amber: subfamily Lestremiinae, tribes Micromyiini and Peromyiini. *Paleontological Journal* **38**: 396–406.
Peschken D. P. 1982: Host specificity and biology of Cystiphora sonchi (Diptera: Cecidomyiidae), a candidate for the biological control of Sonchus species. *Entomophaga* **27**: 405–416.
Pignatti S. 1982: *Flora d'Italia*. 3 Volumes. Bologna: Edagricole, 1280 pp.
Rikli M. 1946: *Das Pflanzenkleid der Mittelmeerländer*. 2 Volumes. Bern: Verlag H. Huber, 1093 pp.
Rübsaamen E. H. 1929: Gallbildungen. Pp.: 219–248. In: *C. Schröder's Handbuch der Entomologie*. Jena: G. Fischer, 350 pp.
Ryabushkina N., Gemedzhieva N., Kobaisy M. & Cantrell C. L. 2008: Brief review of Kazakhstan flora and use of its wild species. *Asian and Australasian Journal of Plant Science and Biotechnology* **2** (2): 64–71.
Savulescu T. (ed.) 1952: *Flora Republicae Popularis Romanicae*. Vol. 1. Bucuresti: Romanian Academy Publishing House, 656 pp. (In Romanian).
Sfikas G. 1987: *Wild Flowers of Crete*. Athens: Efstathiadis Group S. A., 310 pp.

Simova-Tošić D., Skuhravá M. & Skuhravý V. 1996: Gall midges (Diptera: Cecidomyiidae) of Slovenia. *Scopolia* **36**: 1–23.
Simova-Tošić D., Skuhravá M. & Skuhravý V. 2000: Gall midges (Diptera: Cecidomyiidae) of Serbia. *Acta Entomologica Serbica* **5**: 47–93.
Simova-Tošić, D. & Skuhravá, M. 2001: Gall midges (Diptera: Cecidomyiidae) of Montenegro. *Acta Entomologica Serbica* **6**: 65–82.
Simova-Tošić D., Skuhravá M. & Skuhravý V. 2004: Gall midges (Diptera, Cecidomyiidae) of Croatia. *Acta Societatis Zoologicae Bohemicae* **68**: 133–152.
Simova-Tošić D., Skuhravá M. & Skuhravý V. 2007: Gall midges (Diptera: Cecidomyiidae) of Bosnia and Hercegovina. *Acta Societatis Zoologicae Bohemicae* **71**: 27–43.
Simova-Tošić D., Skuhravá M. & Skuhravý V. & Postolovski M. 2007: Gall midges (Diptera: Cecidomyiidae) of Macedonia. *Acta Societatis Zoologicae Bohemicae* **71**: 45–60.
Sinclair V. 1991: *The Floral Charm of Cyprus*. New Barnet, Hertfordshire: Interworld Publications, 207 pp.
Skuhravá M. 1986: Family: Cecidomyiidae. Pp.: 72–297. In: Soós Á. & Papp L. (eds.): *Catalogue of Palaearctic Diptera*. Vol. 4. Budapest: Akadémiai Kiadó & Amsterdam: Elsevier, 441 pp.
Skuhravá M. 1987: Analysis of areas of distribution of some Palaearctic gall midge species (Cecidomyiidae, Diptera). *Cecidologia Internationale* **8**: 1–48.
Skuhravá M. 1991: Gallmücken der Slowakei (Cecidomyiidae, Diptera). VI. Die Zoogeographie der Gallmücken. *Zborník Slovenského Národného Múzea*, *Prírodne Vedy*, *Bratislava* **37**: 85–178.
Skuhravá M. 1994a: The zoogeography of gall midges (Cecidomyiidae, Diptera) of the Czech Republic. I. Evaluation of the faunistic researches in the 1855–1990 period. *Acta Societatis Zoologicae Bohemicae* **57**[1993]: 211–293.
Skuhravá M. 1994b: The zoogeography of gall midges (Cecidomyiidae, Diptera) of the Czech Republic. II. Review of gall midge species including zoogeographic diagnoses. *Acta Societatis Zoologicae Bohemicae* **58**: 41–88.
Skuhravá M. 1995: Cecidomyiidae. Pp.: 23–32. In: Minelli A., Ruffo S. & La Posta S. (eds.): *Checklist delle species della fauna Italiana*. Fasc. **64.** Bologna: Calderini: 1–39.
Skuhravá M. 1997a: Cecidomyiidae. Pp.: 71–204. In: Papp L. & Darvas B. (eds.): *Contributions to a Manual of Palaearctic Diptera* (*with special reference to flies of economic importance*). *Vol. 2. Nematocera and Lower Brachycera*. Budapest: Science Herald, 592 pp.
Skuhravá M. 1997b: Gall midges (Diptera, Cecidomyiidae) of the Czech and Slovak Republics as members of zoogeographical units in the Palaearctic Region. Pp.: 149-171. In: Vaňhara J. & Rozkošný R. (eds.): Dipterologica bohemoslovaca **8.** *Folia Facultatis Scientiarium Naturalium Universitatis Masarykianae Brunensis*, *Biologica* **95**: 1–236.
Skuhravá M. 2006a: Species richness of gall midges (Diptera: Cecidomyidae) in the main biogeographic regions of the world. *Acta Societatis Zoologicae Bohemicae* **69**: 327–372.
Skuhravá M. 2006b: Cecidomyiidae Macquart, 1838. In: Jedlička L., Stloukalová V. & Kúdela M. (eds.): *Checklist of Diptera of the Czech Republic and Slovakia*. *Electronic version 1*. URL: http://zoology.fns.uniba.sk/diptera.
Skuhravá M. 2008: Cecidomyiidae. Pp.: 264–265, 329. In: Borges P. A.V., Abreu C., Aguiar A. M. F., Carvalho P., Jardim R., Melo I., Oliveira P., Sérgio C., Serrano A. R. M. & Vieira P. (eds.): *A List of the Terrestrial Fungi*, *Flora and Fauna of Madeira and Selvagens Archipelagos*. Funchal and Angra do Heroísmo: Direcção Regional do Ambiente da Madeira and Universidade dos Açores, 356 pp.
Skuhravá M. 2009: Cecidomyiidae Macquart, 1838. In: Jedlička L., Kúdela M. & Stloukalová V. (eds.): *Checklist of Diptera of the Czech Republic and Slovakia*. *Electronic version 2*. URL: http://zoology.fns.uniba.sk/diptera2009.
Skuhravá M.: The list of gall midges (Diptera: Cecidomyiidae) of Europe. (In prep.)
Skuhravá M., Bayram S., Cam H., Tezcan S. & Can P. 2005: Gall midges (Cecidomyiidae, Diptera) of Turkey. *Turkish Journal of Entomology* **29**(1): 17–34.
Skuhravá M., Blasco-Zumeta J. & Pujade-Villar J. 2002: Cecidomyiidae. Pp.: 21–25. In: Carles-Tolrá Hjorth-Andersen M. (ed.): *Catálogo de los Diptera de Espana*, *Portugal y Andorra* (*Insecta*). (*Catalogue of Diptera of Spain*, *Portugal and Andorra*). Monografías de la Sociedad Entomológica Aragonesa, Zaragoza **8**, 323 pp.
Skuhravá M. & Franz H. 1989: Familie Cecidomyiidae (Itonididae). Pp.: 67–97. In: Franz H. (ed.): *Die Nordost-Alpen im Spiegel ihrer Landtierwelt*. *Eine Gebietsmonographie*. *Band VI/I*. Innsbruck: Universitätsverlag Wagner, 413 pp.
Skuhravá M. & Hinz H. 2000: Rhopalomyia tripleurospermi sp. n. (Diptera: Cecidomyiidae), a new gall midge species on Tripleurospermum perforatum (Asteraceae, Antheminae) in Europe, and a biological control agent in Canada. *Acta Societatis Zoologicae Bohemicae* **64**: 425–435.
Skuhravá M. & Roques A. 2000: Palaearctic Dipteran Forest Pests. Pp.: 651–692. In: Papp L. & Darvas B. (eds.): *Contribution to a Manual of Palaearctic Diptera*. Vol. 1. *General and applied Dipterology*. Budapest: Sciece Herald, 978 pp.
Skuhravá M., Martinez M. & Roques A. 2010: Chapter 10. Diptera. In: Roques A., Rasplus J. Y., Rabitsch W., Lopez-Vaamonde C., Kenis M. & Nentwig W. (eds.): *Terrestrial Invertebrate Invasions in Europe*. in press.

Skuhravá M. & Skrzypczyńska M. 1983: Przeglad prysczarkow (Cecidomyiidae, Diptera) Polski. (A review of gall midges (Cecidomyiidae, Diptera) of Poland). *Acta Zoologica Cracoviensia* **26** (12): 387–420 (in Polish, with English summary).
Skuhravá M. & Skuhravý V. 1964: Verbreitung der Gallmücken in Jugoslavien (Diptera, Itonididae). *Deutsche Entomologische Zeitschrift* **11**: 449–458.
Skuhravá M. & Skuhravý V. 1967: Beitrag zur Gallmückenfauna von Österreich. *Marcellia* **34**: 213–227.
Skuhravá M. & Skuhravý V. 1988: Die Gallmücken (Cecidomyiidae, Diptera) des Harzes. *Entomologische Nachrichten und Berichte* **32**: 29–33.
Skuhravá M. & Skuhravý V. 1992a: Die Gallmücken (Cecidomyiidae, Diptera) des Naturparkes Fichtelgebirge. *Entomologische Nachrichten und Berichte* **36**: 1–8.
Skuhravá M. & Skuhravý V. 1992b: Zwei an Ahorn lebende Gallmückenarten und weitere Gallmücken (Cecidomyiidae, Diptera) im Nationalpark Bayerischer Wald. *Entomologische Nachrichten und Berichte* **36**: 97–101.
Skuhravá M. & Skuhravý V. 1992c: Die Gallmücken (Cecidomyiidae, Diptera) der Kalkalpen und des Waldviertels in Ost-Österreich. *Sitzungsberichte der Österreichische Akademie der Wissenschaften* **199[**1991–1992]: 27–57.
Skuhravá M. & Skuhravý V. 1993a: *Die Gallmücken* (*Diptera*: *Cecidomyiidae*) *des Fürstentums Liechtenstein*. Praha, Tschechische Republik. Vaduz, Fürstentum Liechtenstein, 18 pp.
Skuhravá M. & Skuhravý V. 1993b: Gall midges (Cecidomyiidae, Diptera) of the southern part of Central Siberia. Pp.: 93–100. In: Jedlička L., Rozkošný R. & Vaňhara J. (eds.): *Dipterologica Bohemoslovaca* **5.** Bratislava: Slovak Entomological Society, 130 pp.
Skuhravá M. & Skuhravý V. 1994: Gall midges (Cecidomyiidae, Diptera) of Italy. *Entomologica*, *Bari* **28**: 45–76.
Skuhravá M. & Skuhravý V. 1995: Die Gallmücken (Cecidomyiidae, Diptera) von Österreich II. *Sitzungsberichte der Österreichische Academie der Wissenschaften* **201**: 3-34.
Skuhravá M. & Skuhravý V. 1997a: Gall midges (Diptera: Cecidomyiidae) of Greece. *Entomologica*, *Bari* **31**: 7–68.
Skuhravá M. & Skuhravý V., 1997b: Gall midges (Diptera, Cecidomyiidae) of Switzerland. *Mitteilungen der Schweitzerischen Entomologischen Gesellschaft* **70**: 133–176.
Skuhravá M. & Skuhravý V. 1998: The zoogeographic significance of European and Asian gall midge faunas (Diptera: Cecidomyiidae). Pp.: 12–17. In: Csóka G., Mattson W., Stone G. & Price W. (eds.): *The Biology of Gall-inducing Arthropods*. St. Paul, MN: General Technical Report NC-199. U.S. Dep. Agric., Forest Service, North Central Research Station, 329 pp.
Skuhravá M. & Skuhravý V. 1999: Gall midges (Diptera: Cecidomyiidae) of Hungary. *Annales Historico-Naturales Musei Nationalis Hungarici* **91**: 105–139.
Skuhravá M. & Skuhravý V. 2002: Gall midges (Diptera: Cecidomyiidae) of Sardinia – second contribution to the gall midge fauna of Italy. *Entomologica*, *Bari* **36**: 5–22.
Skuhravá M. & Skuhravý V. 2003: Die Gallmückenfauna (Cecidomyiidae, Diptera) Südtirols: 3. Die Gallmücken der Sextener Dolomiten. *Gredleriana* **3**: 49–76.
Skuhravá M. & Skuhravý V. 2004a: Gall midges (Diptera: Cecidomyiidae) of Cyprus. Pp.: 265–283. In: Kubík Š. & Barták M. (eds.): *Dipterologica bohemoslovaca* **11**. *Folia Facultatis Scientiarium Naturalium Universitatis Masarykianae Brunensis*, *Biol*. **109**: 1-346.
Skuhravá M. & Skuhravý V. 2004b: Gall midges (Diptera: Cecidomyiidae) of Mallorca (Balearic Islands, Spain). *Boletin de la Asociacion Espanola de Entomologia* **28**: 105–119.
Skuhravá M. & Skuhravý V. 2004c: Gall midges (Diptera: Cecidomyiidae) of the Hautes Alpes (south-eastern France). *Bulletin de la Société Linnéenne de Bordeaux* **32**: 47–65.
Skuhravá M. & Skuhravý V. 2004d: Gall midges of the department Loiret (central France). *Bulletin de la Société Linnéenne de Bordeaux* **32**: 291–301.
Skuhravá M. & Skuhravý V. 2005a: Die Gallmückenfauna (Diptera: Cecidomyiidae) Südtirols: 4. Gallmücken des Tauferer- Ahrntales und Tales (Zillertaler Alpen). *Gredleriana* **5**: 263–284.
Skuhravá M. & Skuhravý V. 2005b: Die Gallmückenfauna (Diptera: Cecidomyiidae) Südtirols: 5. Gallmücken des Unterlandes. *Gredleriana* **5**: 285–310.
Skuhravá M. & Skuhravý V. 2006a: Die Gallmückenfauna (Diptera, Cecidomyiidae) Südtirols 6. Gallmücken im Westen: Burggrafenamt – Vinschgau. *Gredleriana* **6**: 317–342.
Skuhravá M. & Skuhravý V. 2006b: Gall midge (Diptera: Cecidomyiidae) of the islands Corfu and Samos (Greece). *Acta Universitatis Carolinae*, *Biologica* **50**: 109–123.
Skuhravá M. & Skuhravý V. 2007a: Die Gallmückenfauna (Diptera, Cecidomyiidae) Südtirols: 7. Gallmücken des Schlerngebietes in den westlichen Dolomiten. *Gredleriana* **7**: 307–324.
Skuhravá M. & Skuhravý V. 2007b: Records of gall midges (Cecidomyiidae, Diptera) in and around Ripley, Surrey, England. *Cecidology* **22**: 32–33.
Skuhravá M. & Skuhravý V. 2009a: Gall midges (Diptera: Cecidomyiidae) of Austria. – Annotated list of species and zoogeographic analysis. *Studia Dipterologica* **15** (2008): 49–150.

Skuhravá M. & Skuhravý V. 2009b: Gall midges (Diptera: Cecidomyiidae) of the Olympos Mountains (northern Greece). *Acta Societatis Zoologicae Bohemicae* **72** (2008): 227–244.
Skuhravá M. & Skuhravý V. 2009c: Plant galls and gall midges (Diptera: Cecidomyiidae) of the Faroe Islands in the Atlantic Ocean. *Fróðskapparrit* **57**: 115–127.
Skuhravá M. & Skuhravý V. 2009d: Die Gallmückenfauna (Diptera, Cecidomyiidae) Südtirols: 8. Gallmücken der Östlichen Dolomiten. *Gredleriana* **9**: 259–278.
Skuhravá M. & Skuhravý V.: Die Gallmückenfauna (Diptera, Cecidomyiidae) Südtirols: 9. Gallmücken der Sarntaler Alpen. *Gredleriana* (in press).
Skuhravá M. & Skuhravý V.: Gall midges (Diptera: Cecidomyiidae) of South Tyrol (Italy) – summary results and zoogeographical analysis. *Gredleriana* (in press).
Skuhravá M. & Skuhravý V.: Gall midges (Diptera: Cecidomyiidae) of Corsica (France). *Bulletin de la Sociéte Linnéenne de Bordeaux* (in press).
Skuhravá M. & Skuhravý V.: Gall midges (Diptera: Cecidomyiidae) of Norway. (In prep.).
Skuhravá M. & Skuhravý V.: Gall midges (Diptera: Cecidomyiidae) of Sweden. (In prep.).
Skuhravá M., Skuhravý V. & Neacsu P. 1972: Verbreitung der Gallmücken in Rumänien (Diptera, Cecidomyiidae). *Deutsche Entomologische Zeitschrift* **19**: 375–392.
Skuhravá M., Skuhravý V. & Brewer J. W. 1984a: Biology of Gall Midges. Pp.: 169–222. In: Ananthakrishnan T. N. (ed.): *Biology of Gall Insects*. New Delhi, Bombay, Calcutta: Oxford + IBH Publishing Co., 362 pp.
Skuhravá M., Skuhravý V. & Brewer J. W. 1984b: The distribution and long-term changes in population dynamics of gall midges (Cecidomyiidae, Diptera) on cereals in Europe. *Cecidologia Internationale* **5**: 1–5.
Skuhravá M., Skuhravý V., Dončev K. D. & Dimitrova B. D. 1991: Gall midges (Cecidomyiidae, Diptera) of Bulgaria. I. Faunistic researches in the 1978–1987 period. *Acta Zoologica Bulgarica* **42**: 3–26.
Skuhravá M., Skuhravý V., Blasco-Zumeta J. & Pujade J. 1996: Gall midges (Diptera: Cecidomyiidae) of Iberian Peninsula. *Boletin de la Asociation Espanola de Entomologia* **20**(1–2): 41–61.
Skuhravá M., Skuhravý V. & Dengler K. 1998: Gall inducing and other gall midge species (Cecidomyiidae, Diptera) associated with oaks (Quercus spp.) (Fagaceae) in the Palaearctic Region. Pp.: 1–11. In: Csóka G., Mattson W., Stone G. & Price W. (eds.): The biology of gall inducing arthropods. *St. Paul*, *MN*: *General Technical Report NC-199*.: *U.S. Dep. Agric*., *Forest Service*, *North Central Research Station*, 329 pp.
Skuhravá M., Skuhravý V. & Hellrigl K. 2001: Gallmückenfauna (Cecidomyiidae, Diptera) des Südtirols – ein Beitrag zur Gallmückenfauna Italiens. *Gredleriana* **1**: 83–132.
Skuhravá M., Skuhravý V. & Ebejer M. 2002: Gall midges (Cecidomyiidae, Diptera) of Malta. *Entomologica*, *Bari* **36**: 25–43.
Skuhravá M., Skuhravý V. & Hellrigl K. 2002: Die Gallmückenfauna (Cecidomyiidae, Diptera) Südtirols (2): Gallmücken des Nationalparks Stilfser Joch und der Gadertaler Dolomiten. *Gredleriana* **2**: 103–136.
Skuhravá M., Skuhravý V., Dauphin P. & Coutin R. 2005: Gall midges of France. Les Cécidomyies de France (Diptera: Cecidomyiidae). *Mémoires de la Société Linnéenne de Bordaeaux* **5**: 1–212.
Skuhravá M., Skuhravý V., Blasco-Zumeta J. & Pujade J. 2006: Gall midges (Diptera: Cecidomyiidae) of the Iberian Peninsula. 2. Zoogeographic analysis of the gall midge fauna. *Boletin de la Asociation Espanola de Entomologia* **30**: 93–159.
Skuhravá M., Skuhravý V. & Jörgensen J. 2006: Gall midges (Diptera: Cecidomyiidae) of Denmark. *Entomologiske Meddelelser* **74** (Special issue): 1–94.
Skuhravá M., Skuhravý V. & Csóka G., 2007: The invasive spread of the gall midge *Obolodiplosis robiniae* in Europe. *Cecidology* **22**: 84–90.
Skuhravá M., Skuhravý V. & Massa B. 2007: Gall midges (Diptera Cecidomyiidae) of Sicily. *Naturalista Siciliano* **31**: 215–263.
Skuhravá M., Skuhravý V., Skrzypczyńska M. & Szadziewski R. 2008: Gall midges (Cecidomyiidae, Diptera) of Poland. Pryszczarki (Cecidomyiidae, Diptera) Polski. *Annals of the Upper Silesian Museum*, *Bytom* (*Entomology*) **16**: 5–160.
Skuhravá M., Skuhravý V. & Berest Z.: Gall midges (Diptera: Cecidomyiidae) of Ukraine. (In prep.).
Skuhravá M. & Skuhravý V. & Przhiboro A. A.: Gall midges (Diptera: Cecidomyiidae) of the European part of Russia. (In prep.).
Skuhravý V. 1991: The needle-shortening gall midge Thecodiplosis brachyntera (Schwägr.) on the genus Pinus. *Rozpravy Československé Akademie Věd*, *Řada Matematických a Přírodních Věd* **10**: 1–104.
Skuhravý V. & Skuhravá M. 1999: Gall midges (Cecidomyiidae, Diptera) of Los Monegros require protection of their biotops. Pp.: 131-135. In: Melic A. & Blasco-Zumeta J. (eds.): Manifiesto Científico por Los Monegros. *Boletin de la Sociedad Entomologica Aragonesa* **24** (1998): 131–135.
Skuhravý V., Skuhravá M. & Brewer J. W. 1996: Some survival adaptations of gall-inducing gall midges (Diptera: Cecidomyiidae). *Journal of Applied Entomology* **120**: 237–239.

Smith A. R., Pryer K. M., Schuettpelz E., Korall P., Schneider H. & Wolf P.G., 2006: A classification for extant ferns. *Taxon* **55**(3): 705–731.
Sobhian R., Littlefield J., Cristofaro M. & Mann K. 2000: Biology and host specificity of Spurgia capitigena (Bremi) (Diptera: Cecidomyiidae) for the biological control of Euphorbia esula L. in North America. *Journal of Applied Entomology* **124**: 333–338.
Soó R. 1973: *Synopsis systematico-geobotanica florae vegetationisque Hungariae* V. Budapest: Akadémiai Kiadó, 150 pp.
Soós Á. & Papp L. (eds.) 1986: *Catalog of Palaearctic Diptera*. *Vol. 4. Sciaridae – Anisopodidae*. Budapest: Akadémiai Kiadó, 441 pp.
Spungis V. 1998: New species of gall midges (Diptera, Cecidomyiidae, Porricondylinae) from Estonia. *Latvijas Entomologs* **36**: 21–26.
Spungis V. 2002: A check-list of Latvian Porricondylinae (Diptera, Cecidomyiidae) with notes on new records. *Latvijas Entomologs* **39**: 56–60.
Spungis V. 2003: a checklist of Latvian Cecidomyiinae (Diptera, Cecidomyiidae) with notes on new records. *Latvijas Entomologs* **40**: 5–11.
Spungis V. & Jaschhof M. 2000: Gall midges of the subfamily Lestremiinae from Estonia, Latvia and Lithuania: checklist and description of new species. *Beiträge zur Entomologie* **50**: 283–316.
Straus A. 1977: Gallen, Minen und andere Frassspuren im Pliokän von Willershausen am Harz. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* **113**: 43–80.
Szafer W., Kulczyński S. & Pawłowski B. 1986. *Rośliny polskie* [*Polish Plants*]. Vol. 1+2. Warszawa: PWN, 1019 pp (in Polish).
Ševčík J. 2006: Diptera associated with fungi in the Czech and Slovak Republics. *Časopis Slezského Muzea Opava* (A) **55**, Suppl. **2**: 1–84.
Trotter A. 1903: Studi cecidologici: Le galle ed i cecidozoi fossili. *Rivista Italiana di Paleontologia* **9**: 12–22.
Tutin T. G., Heywood V. H., Burges N. A., Valentine D. H., Walters S. M. & Webb A. A. (eds.) 1964–1980: *Flora Europaea*. Cambridge: Univ. Press, **1** (1964): 428 pp, **2** (1968): 420 pp., **3** (1972): 370 pp., **4** (1976): 505 pp., **5** (1980): 510 pp.
Udvardy M. D. F. 1975: *A Classification of the Biogeographic Provinces of the World*. IUCN Occasional Paper **18**, 48 pp.
Villalta J. F. 1957: Dos zoocecidías fósiles del Mioceno de Cerdana (Prov. De Lérida). *Cursillos y Conferencias del Instituto* "*Lucas Mallada*" **4:** 63–64.
Vitou J., Skuhravá M., Skuhravý V., Scott J. & Sheppard A. 2008: The role of plant phenology in the field host specifity of Gephyraulus raphanistri (Diptera: Cecidomyiidae) associated with Raphanus spp. (Brassicaceae). *European Journal of Entomology* **105**: 113–119.
Wilhalm T. & Hilpold A. 2006: Rote Liste der gefährdeten Gefässpflanzen Südtirols. *Gredleriana* **6**: 115–198.
Yakovlev E. B. 1994: *Dvukrylye Palearktiki*, *svjazannye s gribami i miksomicetami* [*Palaearctic Diptera associated with Fungi and Myxomycetes*]. Petrozavodsk: Karelian Research Center, Russian Academy of Sciences, Forest Research Institute, 126 pp (in Russian, English summary).
Yukawa J. 1971: A revision of the Japanese gall midges (Diptera: Cecidomyiidae). *Memoirs of the Faculty of Agriculture*, *Kagoshima Univ*. **8**(1): 1–203.
Yukawa J. & Masuda H. 1996: *Insect and mite galls of Japan in colors*. Tokyo: Zenkoku Nôson Kyôiku, Kyôkai, 826 pp (in Japanese).