BIOSYSTEMATICS OF THE *MUELLERIANELLA* COMPLEX (HOMOPTERA, DELPHACIDAE), TAXONOMY, MORPHOLOGY AND DISTRIBUTION

by

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SUMMARY

The closely related species and forms of the plant-hopper genus *Muellerianella* have been studied. In Western Europe this complex consists of three bisexual species and a number of triploid forms which reproduce by gynogenesis. *M. extrusa* Scott 1871 appears to be a distinct species which lives on *Molinia caerulea*. It is here taken out of synonymy from *M. fairmairei* Perris 1857, which lives on *Holcus lanatus*. The third species, *M. brevipennis* Boheman 1847, lives on *Deschampsia cespitosa*. Intra- and interspecific morphological differences in males and females are described in detail, including geographic variation. Triploid forms, which are usually associated with *M. fairmairei* cannot be distinguished from bisexual females of this species. Distribution maps are given for each bisexual species and for the triploid forms which are based on an evaluation of literature data, museum collections and on 150 new samples taken all over Europe.

INTRODUCTION

Earlier investigations on two sibling species of the genus *Muellerianella* (Auchenorrhyncha, Delphacidae) have shown, that this genus is highly interesting for biosystematic and evolutionary studies. DROSOPOULOS (1976, 1977) discovered that the excess of females, which is often found in populations of *M. fairmairei* is caused by triploid females which coexist with *M. fairmairei* and reproduce by gynogenesis (pseudogamy). This mode of reproduction, which is very rare in insects (WHITE 1978), is asexual, but the eggs can only develop after the female has been inseminated by a male of a related bisexual species. From crossing experiments DROSOPOULOS (1978) concluded that these triploid gynogenetic forms arose by hybridization between *M. fairmairei* and *M. brevipennis*. The ecological differences between these two bisexual species have been extensively studied by DROSOPOULOS (1977). However, most of his work has been based on populations from only two localities in the Netherlands, and many questions were left open.

The striking similarity between the species of this genus has led to great confusion in the past. In the autumn of 1978 we found that *M. extrusa*, previously being regarded identical with *M. fairmairei* (living on *Holcus lanatus*), represents a distinct species which lives on *Molinia caerulea*. Moreover, no reliable differences were known between females of the *Muellerianella* species. The complexity of the genus is further increased by extensive variation between triploid females which resemble *M. fairmairei*.

For the understanding of the evolution of this complex of bisexual and asexual forms much information is needed. Since the process of speciation and differentiation is very complicated, all relevant aspects should be studied.

Ideally, one should have information on past and present distribution, detailed morphological descriptions including geographic variation, ecological data on hostplants, habitat and phenology, information on pre- and postmating isolation mechanisms, results of hybridization experiments, detailed descriptions of karyotypes, and data on biochemical (allelic) differentiation (WHITE, 1978).

Although it is hardly possible to obtain all this information even for a small number of species, we have tried to apply this multidisciplinary approach in our studies on the genus *Muellerianella*, without going into much detail or being too superficial.

The work of DROSOPOULOS (1976, 1977, 1978) formed a good starting-point to extend the work to a wider geographic scale and to go more deeply into some special problems. The results of the investigations of last years will be presented in a series of papers of which this is the first. In the present paper, a taxonomic revision of the genus is given, morphological differences between the species are described and distributional data are evaluated. Later papers will give information on ecology, acoustic behaviour, hybridization, cytogenetics and on the ecological differentiation and coexistence between bisexual and asexual forms.

NOMENCLATURE

Present knowledge of the *Muellerianella* complex necessitates some corrections in the nomenclature of this genus. Because the sibling species *M. extrusa* and *M. fairmairei* have not been recognized in the past, several unjustified synonyms have been made.

The genus *Muellerianella* was erected by WAGNER (1963). Two species were recognized: *M. fairmairei* Perris 1857 and *M. brevipennis* Boheman 1847. Recently a third species has been described from the Caucasus, named *M. relicta* Logvinenko 1976.

Previously, the name *M. fairmairei* has been used for the species living on *Holcus*, the species which lives on *Molinia caerulea*, and for triploid females which cannot be distinguished from the *Holcus*-species. The original description of *M. fairmairei* Perris 1857 was based on one female which was taken from La Teste (near Bordeaux), France. I this female which is deposited in the zoological museum o the École National Supérieur d'Agronomie in Montpellier. It strongl resembles to bisexual species which lives on *Holcus* but it might also be triploid female. Because it is impossible to discriminate between di ploid and triploid forms in museum-material, the taxonomic identity o the holotype cannot be determined with certainty.

Since the nomenclature for parthenogenetic organisms is proble matic and the biological species concept cannot be applied to par thenogenetic forms, it seems best to preserve the name *M. fairmaire* Perris 1857 for the bisexual species which lives on *Holcus lanatus*. In order to prevent confusion in the future we have deposited two labele males of the species from *Holcus* with the holotype female in the Perri collection.

Nast (1971) listed three other names as synonyms for *M. fairmairei*: *Delphax neglecta* Flor 1861, *Liburnia extrusa* Scott 1871 and *Delphax fair mairei signicollis* Rey 1894.

The description of *Delphax neglecta* is based on a series of specimen from the Eastern Baltic. No holotype was designated. Unfortunately the type material contains a mixture of males and females of *M. brevipenni* and a number of females which resemble "*M. fairmairei*" (Vilbaste pers. comm.). Therefore *D. neglecta* was listed as a synonym for both *M. brevipennis* and *M. fairmairei* by Nast (1971), which is not justified however. Since the bisexual species from *Holcus* probably does not occur in the Eastern Baltic, the "*M. fairmairei*" females in the type series may belong to the species from *Molinia* or they might be triploid gynogenetic females. Since in the original publication of Flor (1861) both males and females of *M. brevipennis* are described and the unclear females in the series cannot be easily identified, I prefer to regard the name *M. neglecta* as a synonym for *M. brevipennis* Boheman 1847. On my request Dr. Vilbaste designated one *M. brevipennis* male in the type series as lectotype for *D. neglecta*. The type series is in the Museum of Tartu (Estonia).

The second name which has been published as synonym for *M. fairmairei* is *Liburnia extrusa* Scott 1871. Males and females of *Liburnia extrusa* were described from England. The type material is stored at the British Museum (Natural History), London. Examination of these series revealed that the holotype and paratypes belong to the species from *Molinia*. Therefore the name *Liburnia extrusa* is not a synonym of *M. fairmairei* and the name for the species from *Molinia* should be *Muellerianella extrusa* Scott 1871.

The present nomenclature for the bisexual species of the genus *Muellerianella* should be as follows:

1. *Muellerianella brevipennis* Boheman 1847, originally described as *Delphax brevipennis* Boheman 1847. Other previously used invalid names for this species are: *Fulgora flavescens* Fabricius 1794 (primary homonym), *Delphax bivittata* Boheman 1850, *Delphax hyalinipennis* Stål 1854, and Delphax neglecta Flor 1861.
2. *Muellerianella fairmairei* Perris 1857, originally described as: *Delphax fairmairei* Perris 1857.
3. *Muellerianella extrusa* Scott 1871, originally described as *Liburnia extrusa* Scott 1871.
4. *Muellerianella relicta* Logvinenko 1976.

With regard to the triploid gynogenetic forms a lot of difficulties arise in naming these taxa. Since the biological species concept is based on the presence or absence of interbreeding between populations it cannot be applied appropriately to asexual reproducing organisms (Maslin 1968, Mayr 1969, White 1978). Following Schultz (1969) the common triploid forms which coöccur with *M. fairmáirei*, were called *M.2-fairmairei-brevipennis* by Drosopoulos (1977). In this name the possible hybrid origin of the triploid forms is incorporated. Triploid forms were obtained after hybridization and backcrossing of *M. fairmairei* and *M. brevipennis* (Drosopoulos 1979). Despite of extensive crossing experiments the synthesis of triploid females could not be repeated however (Booij in prep.). If the hybrid character of the triploid forms can be confirmed by biochemical methods the terminology proposed by Drosopoulos (1977, 1979) seems to be appropriate. On the other hand there is much variation between triploid *Muellerianella* clones (this paper and Booij in prep.). Some triploid forms might have evolved from hybridization between *M. brevipennis* and *M. extrusa* or even by autopolyploidy. As long as the genetic structure of the different triploid forms is not fully understood, I prefer a very neutral terminology. In this paper the term "*triploid form*" or "*triploid females*" will be used for all triploid gynogenetic females which resemble *M. fairmairei* morphologically.

TABLE I

Simplified overview of the *Muellerianella* complex as it is known at present.

	M. brevipennis	*M. extrusa*	*M. fairmairei*	*Triploid forms*
hostplant	*Deschampsia cespitosa*	*Molinia caerulea*	*Holcus lanatus*	*Holcus lanatus*
wintereggs in	*Deschampsia cespitosa*	*Molinia caerulea*	*Juncus effusus*	*Juncus effusus*
generations/year	1–2	1	1–4	1–2
distribution	temperate and northern Europe	temperate and northern Europe	atlantic-mediterranean	atlantic
reproduction	bisexual	bisexual	bisexual	gynogenetic

The basic biological features of *M. brevipennis*, *M. fairmairei*, *M. extrusa*, and the triploid forms are given in Table 1. In the rest of this paper names of these species and forms will be abbreviated as *Mb*, *Mf*, *Me* and *M3* respectively.

MORPHOLOGY

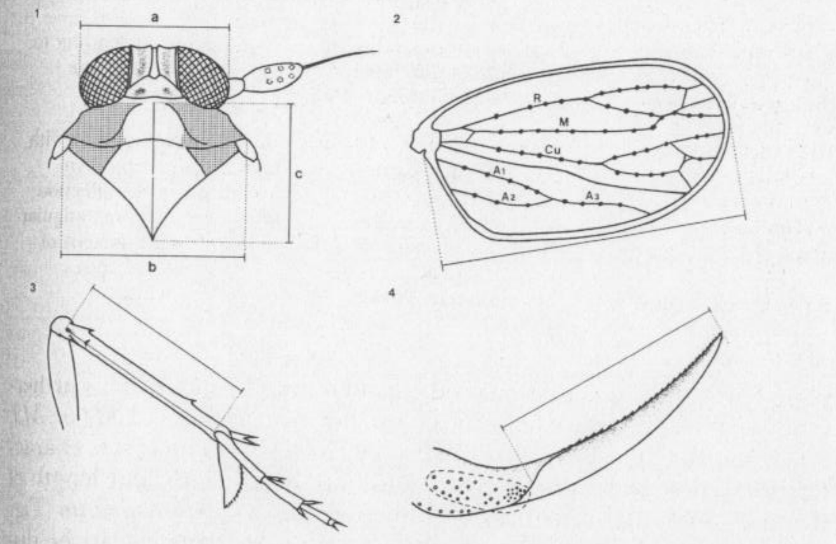
In several genera of Delphacidae like *Javesella*, *Muellerianella*, and *Ribautodelphax*, species can only be distinguished by examination of the male genitalia. Although even small differences between species tend to be very constant and characteristic, one should bear in mind that even genital characters can reveal considerable variation due to geographical or environmental factors. This has been shown for several leafhopper-species (LeQuesne and Woodroffe 1976, Müller 1956). Identification of females of *Muellerianella* is very difficult. Differences in the form of the gonocoxae and genital scales, as used by Ossianninilsson (1978) for *Javesella* and *Ribautodelphax*, were found not to be suitable. The gonocoxae are too variable and genital scales are reduced.

The high similarity between *Me* and *Mf*, the difficulties in identifying females, and the association of *M3* and *Mf* in the field which are morphologically extremely alike, necessitated a detailed morphological analysis. The availability of material from different parts of Europe made it possible to include geographic variation in the analysis. *Me* has been studied in less detail because this species was discovered after most of the morphological studies and collecting had been done.

Methods

For morphological investigations males and females were collected by hand from their hos plants in the field. In some cases fieldcollected third to fifth instar larvae were reared to adults under optimal conditions in the laboratory. For females, mainly freshly killed material was used because triploid females and diploid (bisexual) females can only be discriminated by cytological methods. These methods, developed by Drosopoulos (1977) and improved afterwards, will be described in detail in a future paper. Most of the males were measured after mounting. Apart from overall length and the clarity of pigmentation patterns, the characters used are hardly affected by longer preservation. Measurements and observations were made with a binocular microscope (Wild M5) at 50 × magnification and a stereo microscope (Leitz-Dialux 20 EB) at 100 × and 400 × magnification. The measuring-fault of size characters was maximal 0.01 mm for head-width, spur-length, and length of the ovipositor-saw, and maximal 0.02 mm for the other size characters.

Genital characters have been studied after maceration at 100° C in 20% KOH for about 5 minutes or at 60° C in 50% lactic acid for several hours.



Figs. 1–4. Some quantitative characters used for morphometrics in *Muellerianella*. 1, head-width (a), thorax-width (b), and thorax-length (c). 2, winglength and number of hairspots on veins. 3, length of hind-tibia. 4, sawblade of the ovipositor: length, number of sensillae at base, number of teeth.

Morphology of females

Because no reliable differences between females were known, the morphology of females was studied in great detail. From a variety of 45 characters which were examined in some test-series of *Mb* and *Mf*, 28 were found to be suitable for final analysis. These characters are partly quantitative, like size-characters and meristic characters (Figs 1–4), and partly qualitative like colour and pigmentation characters (Figs 5–20).

After examination of many females it appeared that *Mb* females can be easily distinguished from *Me*, *Mf* and *M3* females by several qualitative characters which are listed in Table 2. Most *Mb* females are darker than females of the other species and the pigmentation patterns are less clearly demarcated and not contrasting with the ground-colour. The pigmentation on the genae differs most characteristically (Figs 5–10), but also the pigmentation on the frons and the abdomen can be used to distinguish *Mb*. In macropterous females, which are always intensively

TABLE 2

Qualitative morphological characters which differentiate females of *M. brevipennis* from females of *M. extrusa*, *M. fairmairei* and *triploid forms*.

	M. brevipennis	*M. extrusa/M. fairmairei/triploids*
genae pigmentation	vague, not extending to base of antennae	contrasting, extending to base of antennae
dark streak between eyes and keels	always absent	always present
frons pigmentation	vague, mottled, without a distinct pattern	weakly developed or with a distinct pattern
eye colour	black-brown	with greenish reflection
ocellus spot	small, circular	often extended, rectangular
abdomen pigmentation	with broad, dark lateral bands.	lighter with pattern of stripes and spots.
inner wing margins	semi-transparant	white

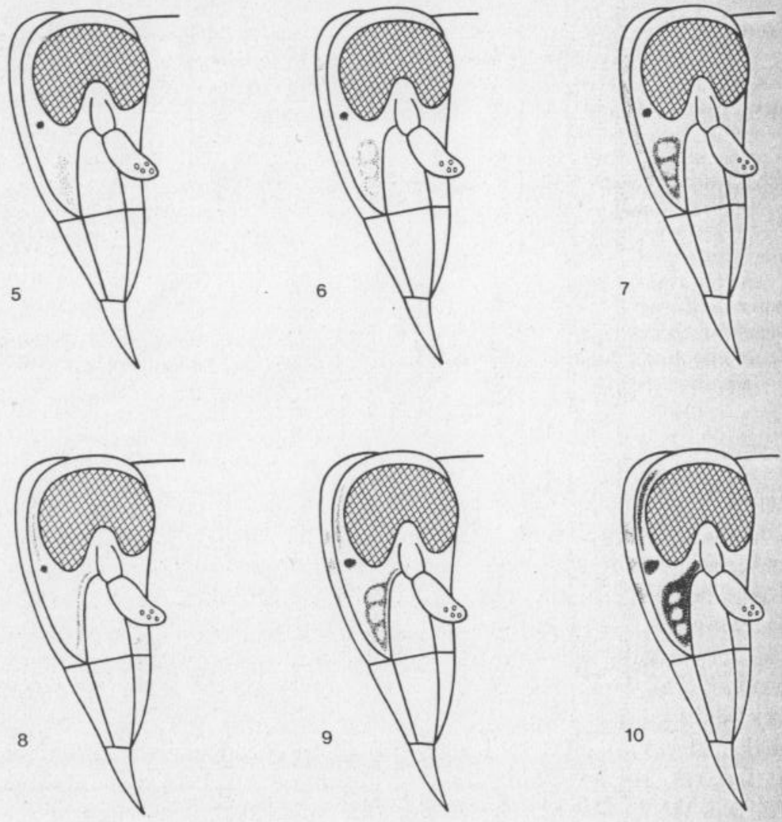
pigmented, the pigmentation on the head is most pronounced. Furthermore females of *Mb* are on average smaller than females of *Mf* or *M3*, but larger than females of *Me* (Table 3). However, in most size characters there is considerable overlap, and only head-width and length of the hind-tibia can be used to discriminate females of *Muellerianella* (Fig. 21). From this figure it can also be seen that *Me* females can be distinguished from *Mf* females by the length of their hindtibia. Since large females of *Me* can be easily confused with small females of *Mf* or *M3* one should be cautious to use this character. Differences in colour or pigmentation patterns could not be found between *Me*, *Mf* and *M3*.

The score of 28 characters for many individuals of *Mf* and *M3* in samples from Ireland and the Netherlands did not yield any differences which could be used to distinguish these females. Although the mean value of several characters differed significantly between *M3* and *Mf* females, the ranges are strongly overlapping (Table 4). Moreover some differences which were found in Ireland, appeared to be absent or reversed in the Dutch sample. From table 3 and 4 it can be seen that some characters might indicate whether a female is more likely to be a *M3* or a *Mf* female. These are: head-width, thorax-width, number of hairspots on the wings, number of sensilla on base of the ovipositorsaw and number of teeth on the ovipositorsaw. Two of these characters have been assessed in a great number of animals from different sites in the Netherlands. It appeared that in all samples the mean winglength of *M3* females is significantly shorter than that of *Mf* females (*Mf*: 1.56 ± 0.11 mm (n = 187) and *M3*: 1.50 ± 0.11 mm (n = 356), t = 6.04, P > 0.001) and that the mean number of hairspots was higher in *Mf* than in *M3* females (*Mf*: 35.5 ± 6.0 (n = 178) and *M3*: 26.8 ± 4.7 (n =

TABLE 3

Size differences between females of the *Muellerianella* species and forms. Mean values and standard deviations for different size characters are given in mm. Material used: *Me* Denmark, Germany, Ireland, Great Britain and the Netherlands; *Mf* Spain, Yugoslavia, France, Ireland and the Netherlands; *Mb* Sweden, Finland, Denmark, Poland, Yugoslavia, France, Ireland and the Netherlands; *M3* the Netherlands, Ireland, France and Yugoslavia.

	M. extrusa	*M. fairmairei*	*Triploid forms*	*M. brevipennis*
	$\bar{x}$ s_x n	$\bar{x}$ s_x n	$\bar{x}$ s_x n	$\bar{x}$ s_x n
headwidth	0.72 ± 0.03 (60)	0.76 ± 0.03 (85)	0.79 ± 0.02 (53)	0.81 ± 0.03 (131)
thorax-width	0.78 ± 0.03 (60)	0.84 ± 0.04 (85)	0.89 ± 0.03 (53)	0.88 ± 0.04 (131)
hind-tibia length	0.88 ± 0.04 (60)	1.08 ± 0.05 (85)	1.09 ± 0.07 (53)	0.91 ± 0.05 (131)
wing-length (brachypterous)	1.34 ± 0.10 (60)	1.59 ± 0.13 (85)	1.55 ± 0.11 (53)	1.43 ± 0.10 (131)
overall-length brachypters				
freshly killed	3.00 ± 0.14 (54)	3.54 ± 0.20 (96)	3.52 ± 0.21 (66)	3.28 ± 0.16 (72)
mounted	2.62 ± 0.21 (55)	3.12 ± 0.17 (45)		2.75 ± 0.17 (79)
overall-length macropters				
fresh or mounted	3.98 ± 0.20 (20)	4.53 ± 0.20 (36)		4.08 ± 0.27 (12)

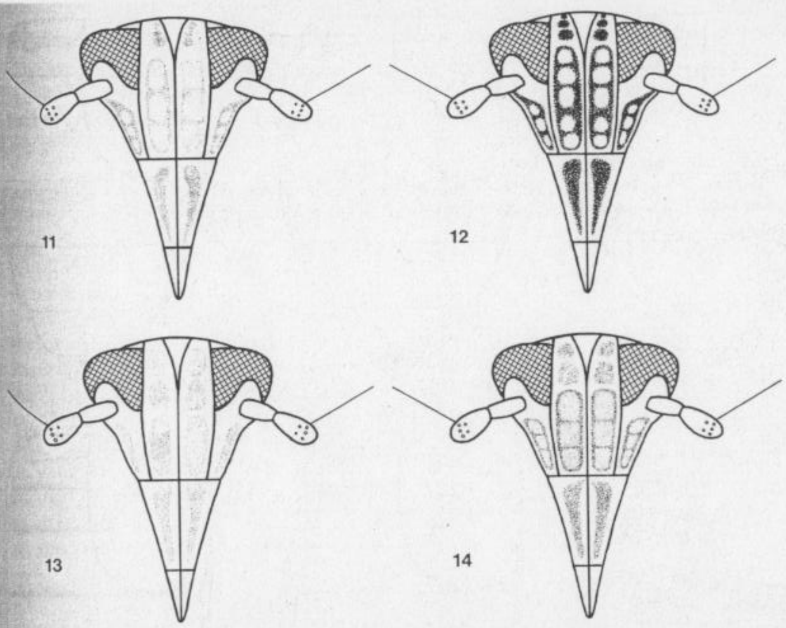


Figs. 5–10. Pigmentation patterns on the genae of *Muellerianella* species. Figs. 5–7 *M. brevipennis*. 5, light specimen. 6, average specimen. 7, dark specimen. Figs. 8–10 *M. extrusa*, *M. fairmairei* and *triploid forms*. 8, light specimen. 9, average specimen. 10, dark specimen.

347), t = 16.9, $P < 0.001$). However, the variation within and between samples is so great that the diagnostic value of these characters is too low to be useful.

Some differences found, can be interpreted as evidence for the hypothesis that *M3* arose by hybridization between *Mf* and *Mb*. Thorax width, head-width, wing-length, number of hairspots on the wings, number of sensillae and teeth on ovipositorsaw are on average intermediate between *Mf* and *Mb* (table 3). However, the length of hind tibia and of the ovipositor tend to be longer in *M3* than in *Mf* whereas they are shorter in *Mb*.

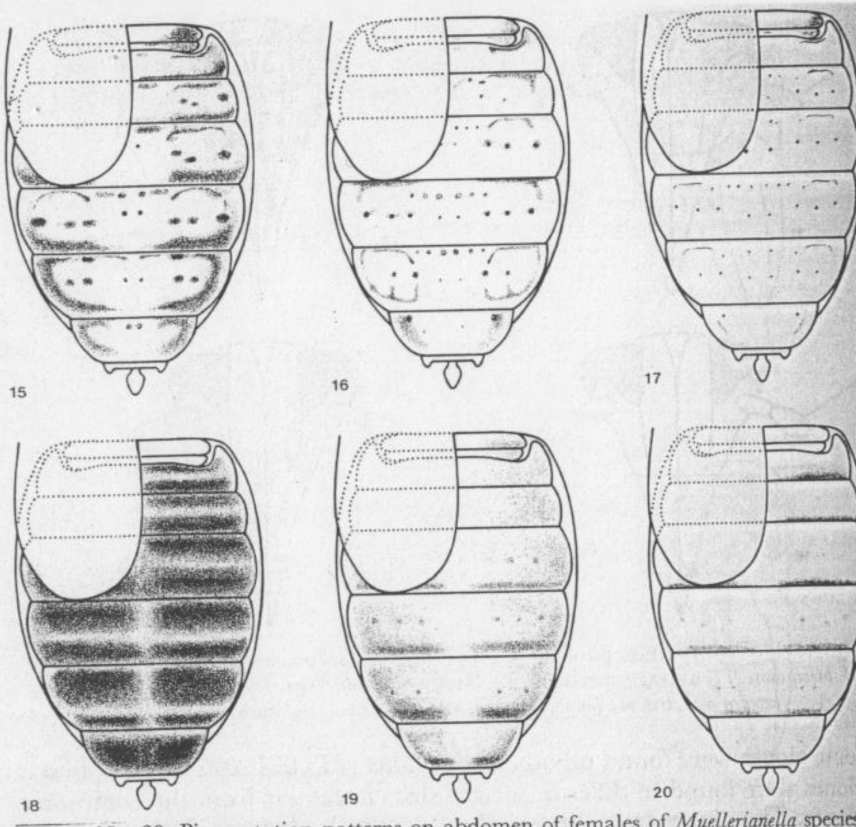
Apart from the most common triploid forms which live on *Holcus* some clones were found on other hostplants (*M3* 071, 072, 073). These clones were found to differ in several size characters from the common clones. The clones from *Bromus ramosus* and *Deschampsia flexuosa* had a smaller headwidth and shorter legs, and can be easily confused with *Me*-females.



Figs. 11–14. Pigmentation patterns on the frons of *Muellerianella* species. Figs. 11–12, *M. brevipennis*. 11, average specimen. 12, dark specimen. Figs. 13–14, *M. fairmairei*, *M. extrusa* and *triploid forms*. 13, average specimen. 14, dark specimen.

	mean head-width	*mean hindtibia-length*	
M3 Holcus lanatus	0.79	1.08	(n = 85)
M3 Bromus ramosus	0.75	0.90	(n = 10)
M3 Deschampsia flexuosa	0.76	0.91	(n = 10)

For 24 characters measured in *Mf* and *M3* (including those presented in Table 4), coëfficients of variation have been calculated in order to compare the degree of variation between *M3* and *Mf*. Of the 24 coëfficients calculated, 8 were greater in *Mf*, 10 were greater in *M3* and 6 were about the same in *M3* and *Mf*. From this we can conclude that the



Figs. 15—20. Pigmentation patterns on abdomen of females of *Muellerianella* species. Figs. 15–17 *M. extrusa*, *M. fairmairei* and *triploid forms*. 15, dark specimen. 16, average specimen. 17, light specimen. Figs. 18–20 *M. brevipennis*. 18, dark specimen. 19, average specimen. 20, light specimen.

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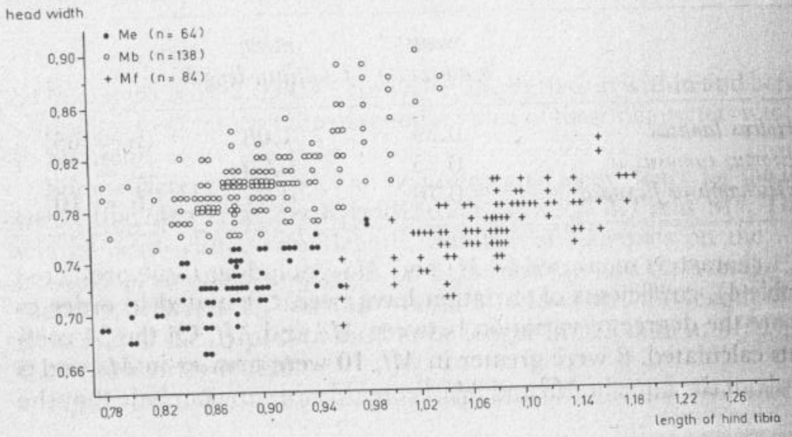


Fig. 21. Differences in some size characters between females of *M. extrusa* (*Me*), *M. brevipennis* (*Mb*), and *M. fairmairei* (*Mf*). Based on material from different parts of Europe.

Morphological differences between females of *M. fairmairei* and *triploid* females in samples from Glenga riff (Ireland) and Leersum (The Netherlands). Means and standard deviations are given. An asterix indicates that the difference between *Mf* and *M3* is significant at least at the 0.05% level.

	Glengarriff		*Leersum*	
	M. fairmairei (n = 25)	*Triploids* (n = 13)	*M. fairmairei* (n = 24)	*Triploids* (n = 60)
overall length	3.66 ± 0.14	3.74 ± 0.18	3.53 ± 0.18	3.41 ± 0.16*
thorax length	0.77 ± 0.04	0.81 ± 0.04*	0.75 ± 0.05	0.75 ± 0.04
thorax width	0.86 ± 0.04	0.89 ± 0.03*	0.87 ± 0.03	0.89 ± 0.03*
head width	0.78 ± 0.02	0.81 ± 0.02*	0.77 ± 0.02	0.77 ± 0.02
length fore tibia	0.75 ± 0.03	0.77 ± 0.04	0.74 ± 0.04	0.71 ± 0.04*
length hind tibia	1.10 ± 0.04	1.16 ± 0.05*	1.07 ± 0.04	1.05 ± 0.05*
wing length	1.55 ± 0.09	1.64 ± 0.10*	1.59 ± 0.09	1.50 ± 0.08*
ovipositor length	0.85 ± 0.03	0.86 ± 0.05	0.84 ± 0.02	0.86 ± 0.04
no. wing hairspots	61.9 ± 8.3	59.5 ± 6.7	59.4 ± 9.7	47.0 ± 7.6*
no. ovip. sensillae	25.1 ± 3.1	22.5 ± 2.9*	26.1 ± 2.4	18.4 ± 1.6*
no. ovip. teeth	29.3 ± 2.3	25.5 ± 1.8*	28.8 ± 3.3	24.2 ± 2.1*
no. spur teeth	13.4 ± 2.7	14.5 ± 2.3	15.0 ± 1.7	14.5 ± 1.7

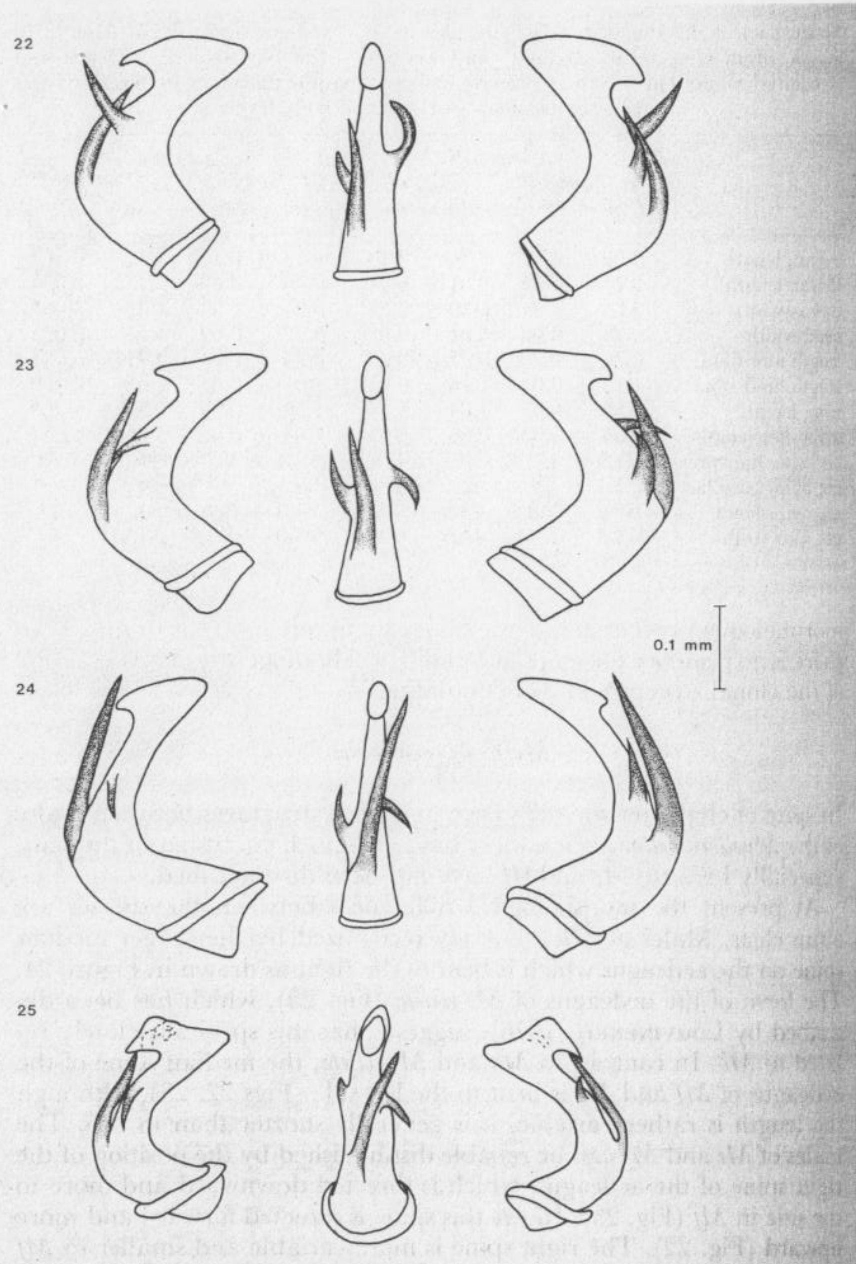
morphological variation is of the same magnitude in *Mf* as in *M3*. Thus there is no evidence for more morphological homogeneity in *M3* despite of the clonal structure of *M3* populations.

Morphology of males

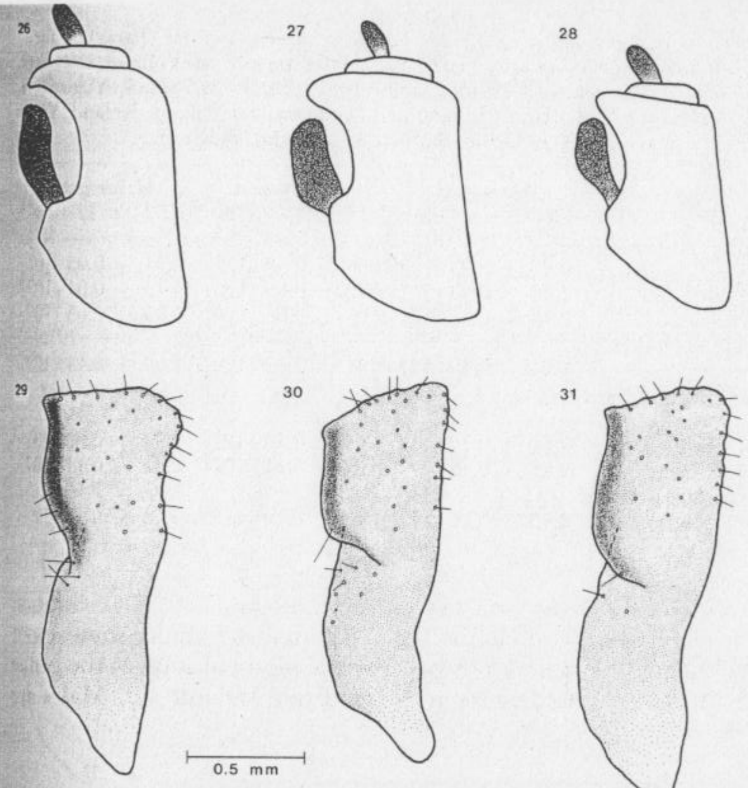
In spite of characteristic difference in genital structures between males of the *Muellerianella* species, there has been much confusion in the past, expecially because *Me* and*Mf* have not been distinguished.

At present the morphological differences between the species are quite clear. Males of *Mb* are easily recognized by the longer median spine on the aedeagus which is bent to the right as drawn in Figure 24. The form of the aedeagus of *M. relicta* (Fig. 25), which has been described by LOGVINENKO (1976), suggests that this species is closely related to *Mb*. In contrast to *Mb* and *M. relicta*, the median spine of the aedeagus of *Mf* and *Me* is bent to the left side (Figs 22, 23). Although the length is rather variable, it is generally shorter than in *Mb*. The males of *Me* and *Mf* can be reliable distinguished by the position of the right spine of the aedeagus, which is directed downward and more to the side in *Mf* (Fig. 23). In *Me* this spine is directed forward and more upward (Fig. 22). The right spine is more variable and smaller in *Mf* than in *Me*.

As shown in Figures 26–28, the lateral concavity of the genital cap-



Figs. 22–25. Various views of the aedeagus of the Muellerianella species. 22, *M. extrusa.* 23, *M. fairmairei.* 24, *M. brevipennis.* 25, *M. relicta* (redrawn after Logvinenko, 1976).



Figs. 26–31. Genital segments and parameres of the *Muellerianella* species. Figs. 26–28 Genital segments. 26, *M. brevipennis.* 27, *M. extrusa.* 28, *M. fairmairei.* Figs. 29–31 Parameres. 29, *M. brevipennis.* 30, *M. extrusa.* 31, *M. fairmairei.*

sule formed by the caudal margin is deeper in *Mb* than in the other species. In *Me* the lateral concavity tends to be somewhat deeper and more angular than in *Mf* (Figs. 27, 28), but this difference is not fully reliable due to variation. The dorso-caudal projection of the genital capsule is sharp and poinyed downward in *Mb*, while it is blunt and not pointed downward in *Me* and *Mf* (figs. 26–28).

In Figures 29–31 the most common form of the parameres is given for each species. However, since there is considerable variation within and between populations (see below), and the observed form depends on the angle at which it is viewed, these forms are not reliable for identification.

Males of *Mb*, *Me* and *Mf* can be further characterized by a number of size characters of which especially headwidth and length of the hind

TABLE 5

Size differences between males of the *Muellerianella* species. For all characters mean values and standard deviations are given in mm. Material used: *Me* Finland, Denmark, Great Britain, W. Germany, Ireland and the Netherlands; *Mf* Spain, Yugoslavia, Andorra, France, the Netherlands, Ireland and Denmark; *Mb* Poland, Ireland, Yugoslavia, France, Denmark, Sweden, Finland, Belgium.

	M. extrusa	*M. fairmairei*	*M. brevipennis*
	$\bar{x}$ s_x n	$\bar{x}$ s_x n	$\bar{x}$ s_x n
head-with	0.65 ± 0.03 (57)	0.68 ± 0.03 (120)	0.74 ± 0.03 (107)
thorax-width	0.69 ± 0.03 (57)	0.72 ± 0.03 (120)	0.79 ± 0.04 (107)
hind-tibia length	0.78 ± 0.05 (57)	0.96 ± 0.05 (120)	0.83 ± 0.05 (107)
wing-length (brachypterous)	1.24 ± 0.19 (57)	1.45 ± 0.13 (120)	1.55 ± 0.14 (107)
overall-length brachypters			
freshly killed	2.59 ± 0.10 (51)	2.65 ± 0.13 (42)	2.90 ± 0.09 (43)
mounted	2.26 ± 0.12 (47)	2.35 ± 0.11 (107)	2.51 ± 0.11 (107)
overall-length macropters			
fresh or mounted	3.73 ± 0.16 (11)	3.73 ± 0.10 (7)	4.05 ± 0.17 (12)

tibia are useful for identification (Table 5 and Fig. 32). Pigmentation patterns which are useful characters to distinguish females show about the same differences in males. Especially the pigmentation of the genae (Figs. 5–10) can be used to separate *Mb* from *Me* and *Mf*. Males are generally more intensively pigmented than females and the ground-colours are more orange-brown in stead of yellowish, especially in *Me* and *Mf* which are often deeply orange and black pigmented.

32

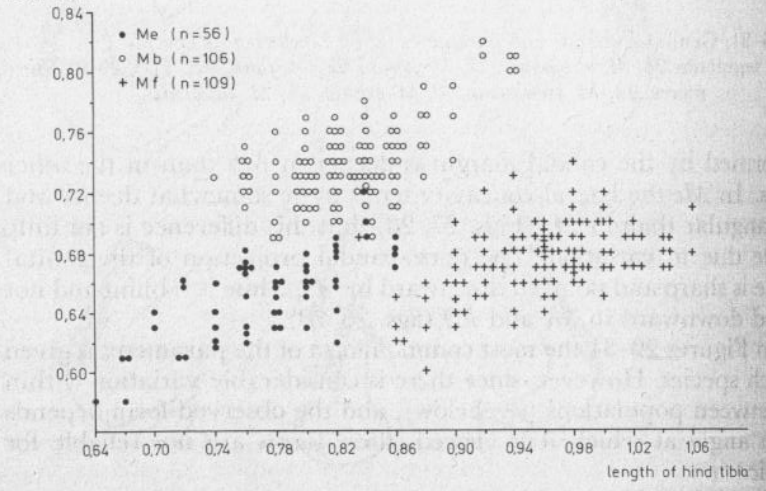
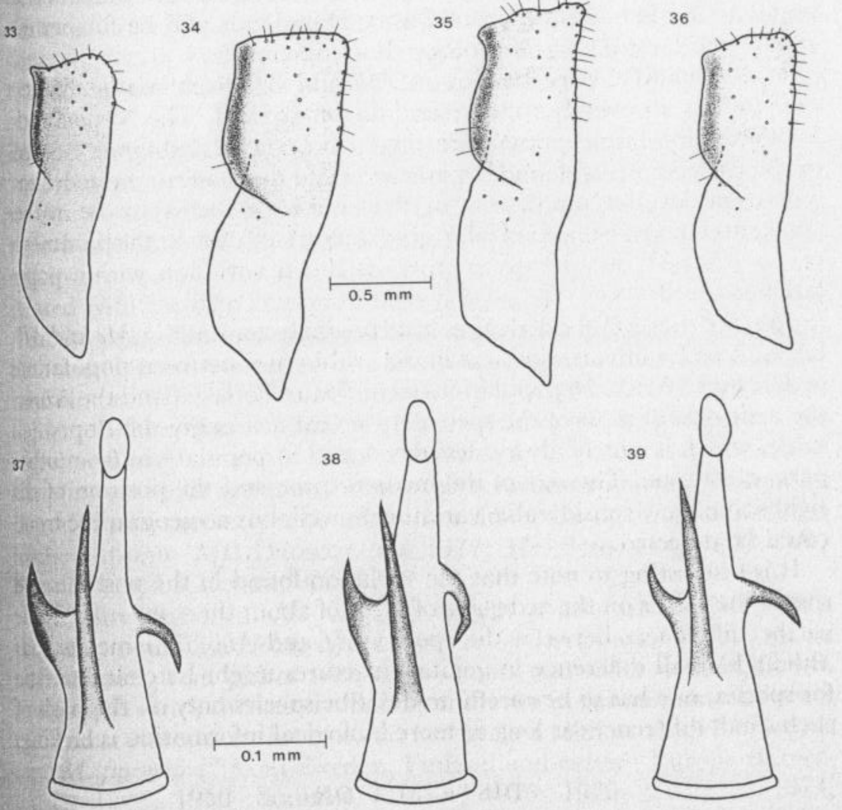


Fig. 32. Differences in some size characters between males of *M. extrusa* (Me), *M. brevipennis* (Mb) and *M. fairmairei* (Mf).

Geographic variation in morphology

In order to study the geographic variation, material from different parts of Europe was measured and morphologically compared. For this purpose seven size characters were selected: thorax-width, thorax-length, head-width, length of fore- and hind-tibia, wing-length and overall-length. From each sample both males and females were measured. Moreover, variation in male genitalia was studied.

From the analysis of size characters, no interesting geographic trends



Figs. 33–39. Intraspecific variation in genital structures of *M. fairmairei*. Figs. 33–36 Parameres of specimen from S. Spain, Greece, S. Sweden, and S. France, respectively. Figs. 37–39 Aedeagus of specimen from S. Spain, Greece and S. Sweden, respectively.

of patterns were found. In both males and females mean values for characters varied between populations and although the differences were often significant, they appeared to be very irregular and not correlated with macroclimatic conditions. Even on a smaller scale, for example between Dutch populations of *Mf*, we found similar differences. Therefore it seems likely that the size characters are strongly influenced by local conditions (e.g. hostplant quality and microclimate). Therefore one might doubt upon the biosystematic value of geographic analysis of such characters in insects.

One of the populations of *Me* clearly deviates from the other samples of *Me*. This sample was taken from the Castor Hanglands (Cambridgeshire, Great Britain) by Morris. Although the measurements were taken from alcohol material, which might slightly affect some characters, the specimens are strikingly bigger than specimens of the other *Me* populations. The samples from Castor Hanglands will be further discussed in a later paper on ecology (Booy in prep.).

Male genitalia were studied in *Mb* and *Mf* from many different populations all over Europe (Scandinavia, Ireland, The Netherlands, W. Germany, France, Spain, Portugal, Yugoslavia and Greece). Geographic variation was found in parameres and the shape of the aedeagus. The form of the parameres in *Me* and *Mb* seems to be rather constant, but there is appreciable geographic variation in the parameres of *Mf* (Figs 33–36). However, there is much variation within populations as well.

Also the shape of the aedeagus is surprisingly constant in *Me* and *Mb*, but quite a lot of variation was found within and between populations of *Mf* (Figs 37–39). In populations from Spain, Portugal and the Azores the aedeagus of most of the specimens reveal a strongly developed left spine, which is nearly always less developed in populations from other parts of Europe. The size of the median spine and the position of the right spine show considerable variation as well, but no geographic trend could be detected.

It is interesting to note that the variation found in the position and size of the spines on the aedeagus of *Mf* is of about the same magnitude as the differences between the species *Mf* and *Me*. This means that although small difference in genital structures might be characteristic for species, one has to be careful to describe species only on the basis of such small differences as long as more biological information is lacking.

DISTRIBUTION

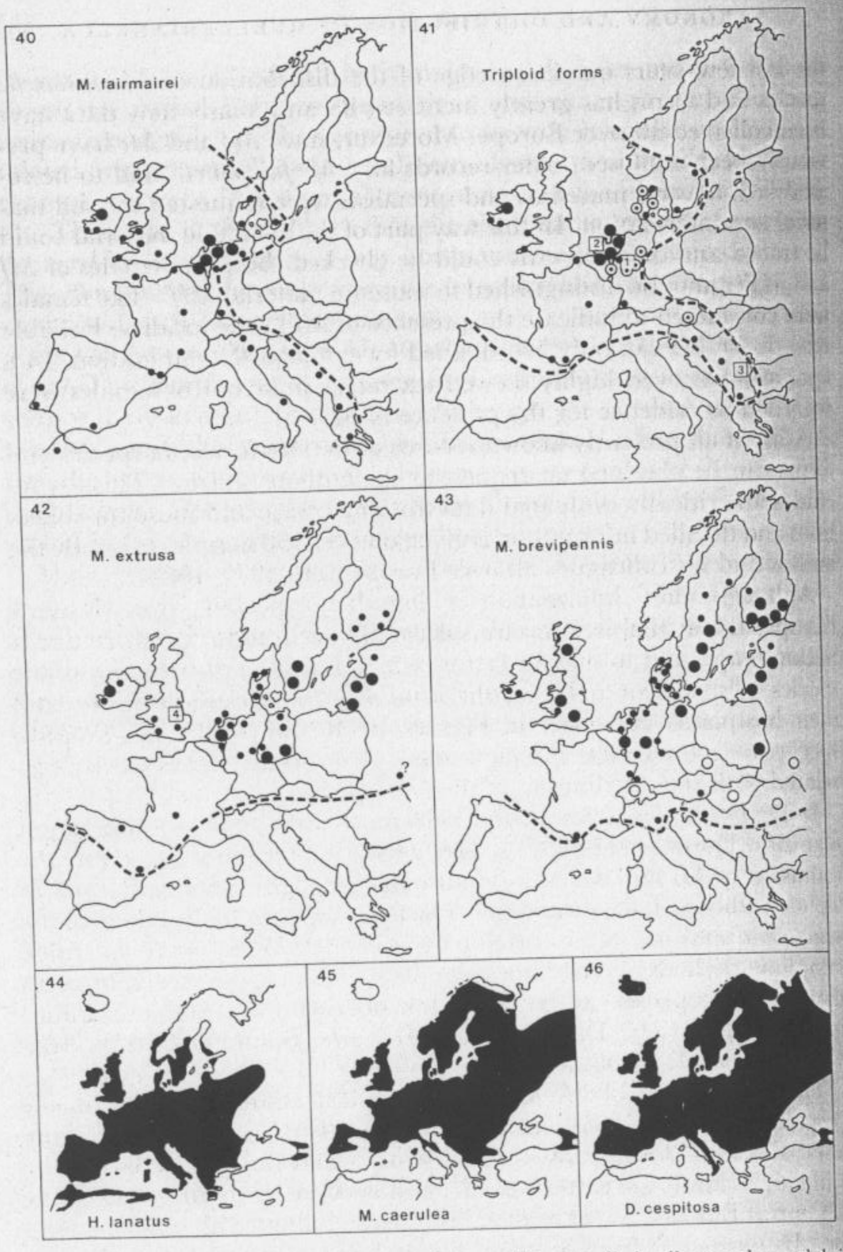
Distributional data for *M. brevipennis* and *M. fairmairei* have been listed by Nast (1972) and subsequently discussed by Drosopoulos (1977). In the last few years our knowledge of the distribution of *Muellerianella* species and forms has greatly increased because many new data have been collected all over Europe. Moreover, since *Mf* and *Me* have previously been confused, older records for "*M. fairmairei*" had to be reanalysed. Several museums and specialists were requested to send material and information. In this way part of the available material could be traced and older records could be checked. Because females of *Mf* and *M3* cannot be distinguished in museum material, *Mf*—like females were considered to indicate the presence of *Mf* at the locality. Reliable records for *M3* can only be obtained by cytological examination. In a few cases however, highly skewed sex-ratio's in favour of females were regarded as evidence for the presence of *M3*.

A list of all presently known records of the *Muellerianella* species and forms can be obtained on request at the authors address. This list includes all critically evaluated data from literature and museum-collections and detailed information is given on over 150 samples taken by the author and his colleagues all over Europe from 1977–1980.

Although more information is desirable, especially from Eastern Europe, the available data are sufficiently accurate to produce distribution maps, and to suggest factors which limit the distribution of the species. Distribution maps for the *Muellerianella* species and forms, and their hostplants are given in Figures 40–46. Since the *Muellerianella* species are more or less specific feeders, their occurrence is closely correlated with the distribution of their hostplants.

In the past *Mf* was considered to be more widespread and abundant than *Mb* (Drosopoulos 1977). This wrong impression is caused by the confusion of *Mf* and *Me* and because *Mf* is caught more easily and in higher numbers than *Mb* and *Me*. The latter two species live deep in the vegetation and are rarely caught by sweepnet. When more intensive sampling methods are used, for example a suction apparatus, it appears that all three species can be influent or dominant at suitable localities in the autumn (*Mf:* Drosopoulos 1977; *Me:* Schiemenz 1971; *Mb:* Törmälä and Raatikainen 1976).

The distribution of *M. fairmairei* is typical atlantic-mediterranean (Fig. 40). Although *Holcus lanatus* extends farther N and NE, *Mf* seems to be absent from places with cold winters and short seasons, like S. Finland, Poland, the eastern Baltic, and even in submontaneous areas of Central Europe. As far as could be checked allmost all older records for "*M. fairmairei*" from Sweden, Finland and eastern Europe (Kontkanen 1947, 1950, Schiemenz 1971, 1975, 1976, Vilbaste 1974, Hiebsch et al 1978, Ossiannilsson 1978) refer to *M. extrusa*. Other records from Ireland (Morris 1974) and W. Germany (Remane 1958) refer to both species.



Figs. 40–46. Distribution of the species and forms of the *Muellerianella* complex and their hostplants. 40, *M. fairmairei*. 41, *Triploid forms*. 42, *M. extrusa*. 43, *M. brevipennis*. Small solid circles indicate records from 1–3 sites, large solid circles records from 3–10 sites, large open circles not confirmed records for countries and open circles with points indicate records of triploid forms coexisting with *M. brevipennis*. Specialized hostplant-clone of triploid forms on *deschampsia flexuosa*, *Calamagrostis canescens* and *Bromus ramosus* are indicated by $\boxed{1}$, $\boxed{2}$ and $\boxed{3}$ respectively. $\boxed{4}$ indicates a population of *M. extrusa*

In spite of the recent discovery (1978) of *M. extrusa*, we have been able to collect quite a lot of data for this species, from which a distribution map could be produced (Fig. 42). The available data suggest that the distribution of *Me* is closely correlated with that of the hostplant *Molinia caerulea*. In Northern Europe *Me* is widespread in bogs, moors and related habitats and presumably extends far to the east. In S. Europe the species is probably restricted to mountainous habitats with a humid climate. Former data of "*M. fairmairei*" from Finland, E. Germany, the Eastern Baltic and Russia refer to *Me*. Material from Sakhalin (E. Russia) is very similar to *Me* (VILBASTE pers. comm.). More material from Siberia and Japan should be examined to see to what extent *Me* is distributed in the boreal and temperate zones of the Eastern Palaearctic.

For *M. brevipennis* many reliable records are given in literature (KUNTZE 1937, KONTKANEN 1952, LOGVINENKO 1975, TORMÄLÄ and RAATIKAINEN 1976, LE QUESNE 1960, BITTNER and REMANE 1977, OSSIANNILSSON 1978). The distribution of *M. brevipennis* is closely similar to that of *M. extrusa* (Fig. 43). The species is widely distributed in temperate and boreal regions of Europe. In southern Europe the species is restricted to higher elevations.

M3. Since triploid forms are mainly associated with *Mf*, the distribution of *M3* is closely correlated with that of *Mf* (Fig. 41). It has been shown, however, that in samples of *Mf* from Spain, Portugal and Greece no *M3* females were found. Thus it seems that *M3* extends less southwards than *Mf*. On the other hand M3 is occasionally found in association with *Mb* in areas where *Mf* is absent, like in Denmark and in submountainous areas of Germany. It is not likely that *M3* extends much farther NE since *H. lanatus* becomes rarer there. it can be concluded that the distribution of *M3* is somewhat intermediate between *Mf* and *Mb*. The ecological and geographic relations between *Mf*, *Mb* and *M3* will be more fully discussed in another paper.

When the bisexual species are compared on a wider geographic scale it can be concluded that *Mb* and *Me* are sympatric, and that *Mf* is partly sympatric with *Mb* and *Me*. The degree of sympatry between *Mf* and both other species is less than suggested by the distribution maps since they occur, like their hostplants, at different altitudes in S. Europe. Syntopic populations of *Mb* and *Mf* or *Me* and *Mf* are mainly found in NW Europe (Ireland, Great Britain, the Netherlands, Denmark, NW Germany).

DISCUSSION

In this paper it was shown that the species of the genus *Muellerianella* can be distinguished by several small but reliable differences, most of which are non-genital in females. The importance of ecological and ethological characters in systematics is illustrated by the fact that *M. extrusa* and *M. fairmairei* were found to be distinct species because they differ in ecology and acoustic behaviour (Booy in prep.). Only afterwards morphological differences between these species were found.

The minor differences between *M. extrusa* and *M. fairmairei* suggest that these species are closely related, although morphological differences are not necessarily correlated with genetic differentiation. *M. brevipennis* is morphologically much more diverged, and can hardly be regarded as sibling species of *M. fairmairei* or *M. extrusa*, as was done before (Drosopoulos 1977). Populations of *Muellerianella* from Eastern Europe, Siberia and Japan should be further studied to elucidate the taxonomic structure of this genus completely.

As has been shown in this paper, the morphological variation of triploid gynogenetic females, which is at least partly genetic, is just as wide as in the bisexual females of *M. fairmairei*. This suggests that different clones are present in the field. Although these clones might have differentiated by mutation (recombination is absent), it seems unlikely that they all originated from one single individual and differentiated to such an extent that they could adapt to the variety of habitats and climates in all parts of Europe where they occur now. Presumably they arose several times.

The extensive variation found between triploid forms, makes it very unlikely that morphological characters can be used to distinguish *M3* from *Mf*. At this moment cytological examination is indispensable for the recognition and discovery of *M3* females in samples of *Muellerianella*.

It seems likely that most of the thelytokous reproducing animals are of hybrid origin (White 1978). From crossing experiments, Drosopoulos (1978) concluded that the triploid gynogenetic forms of *Muellerianella* arose by hybridization between *M. fairmairei* and *M. brevipennis*. The fact that some morphological characters are intermediate between these species supports this hypothesis, but most other characters are not intermediate. Much stronger evidence for a hybrid origin is formed by the distribution of the triploid forms. They occur mainly in the region where the bisexual species are sympatric, and they extend their range somewhat NE by accepting *M. brevipennis* as host species, where *M. fairmairei* is absent. If these triploid forms are of hybrid origin indeed, it seems likely that they arose when *M. fairmairei* and *M. brevipennis* became sympatric after the extension of *Holcus lanatus* to the North. Since this extension is closely correlated with the evolution of anthropogenic grasslands in Europe (Scholz 1975), it is possible that these forms are not older than a few thousand years. The ecological and geographic relations between *M. brevipennis*, *M. fairmairei* and *triploid forms* will be further discussed in later papers.

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REFERENCES

Bittner, C. & Remane, R., 1977. Beiträge zur Kenntnis der Zikadenfauna (Homoptera, Auchenorrhyncha, Cicadina) des Roten Moores/Rhön.—Beitr. Naturk. Osthessen **11/12**: 141–162.

Drosopoulos, S., 1976. Triploid pseudogamous biotype of the leafhopper *Muellerianella fairmairei*.—Nature **263**: 499–500.

Drosopoulos, S., 1977. Biosystematic studies on the *Muellerianella* complex (Delphacidae, Homoptera, Auchenorrhyncha).—Meded. Landbouwhogeschool Wageningen **77**: 1–133.

Drosopoulos, S., 1978. Laboratory synthesis of a pseudogamous triploid "species" of the genus *Muellerianella* (Homoptera, Delphacidae).—Evolution: **32**: 916–920.

Flor, 1861. Die Rynchoten Livlands in systematischer Folge beschrieben. Zweiter Teil: *Rhynchota gulaerostria* Zett. (Homoptera) Cicadina und Psyllodea.—Arch. Nat. Kurklands. **4**: 1–567.

Hiebsch, H., Emmerich, R., Krause R., 1978. Zur Fauna einiger Arthropodengruppen des Flächennaturdenkmals "Saugartenmoor" in der Dresdender Heide.—Ent. abh. Staatl. Mus. Tierk. **42**: 212–249.

Kontkanen, P., 1947. Beiträge zur Kenntnis der Zikadenfauna Finnlands II.—Ann. Ent. Fenn. **13**: 170–175.

Kontkanen, P., 1950. Quantitative and seasonal studies on the leafhopperfauna of the fieldstratum on open areas in North Karelia.—Ann. Zool. Soc. Zool. Bot. Fenn. "Vanamo" **13**: 1–91.

Kontkanen, P., 1952. Beiträge zur Kenntnis der Zikadenfauna Finnlands.—Ann. Ent. Fenn. **18**: 26–24.

Kuntze, H. A., 1937. Die Zikaden Mecklenburg, eine faunistisch-ökologische Untersuchung.—Arch. für Naturgesch. N.F. **6**: 299–388.

LeQuesne, W. J., 1960. Handbook for the identification of British insects.—Vol. II, part 3, Hemiptera, Fulgomorpha. Royal Entomological Society of London. 68 pp.

LeQuesne, W. J. & Woodroffe, G. E., 1976. Geographical variation in the genitalia of three species of Cicadellidae (Hemiptera).—Syst. Entom. **1**: 169–172.

Logvinenko, V. M., 1975. Fauna Ukrainii.—Vol. 20, part 2, Kiev: 1–141.

Logvinenko, V. M., 1976. New species of leafhoppers of the superfamily Fulgoroidae (Auchenorrhyncha) from the Caucasus.—Rev. d'Entom de l'URSS, **55**: 602–609.

Marchand, H., 1953. Die Bedeutung der Heuschrecken und Schnabelkerfe als Indikatoren verschiedener Grasslandtypen.—Beitr. Ent. **3**: 116–162.

Maslin, T. P. 1968. Taxonomic problems in parthenogenetic vertebrates.—Syst. Zool. **17**: 219–231.

Mayr, E., 1969. Principles of Systematic Zoology.—McGraw-Hill New York. 428 pp.

Morris, M. G., 1974. Auchenorrhyncha (Hemiptera) of the Burren, with special reference to species associations of the grasslands.—Proc. R. Ir. Acad. **74**, Section B: 7–30.

Müller, H. J., 1965. The taxonomic value of the male genetalia in the light of new studies on the seasonal forms of *Euscelis*.—Proc. 10th Intern. Congr. Entom. **1**: 357—362.

Nast, J., 1972. Palaeartic Auchenorrhyncha (Homoptera), an annotated checklist.—Polish Scientific Publishers Warsaw. 550 pp.

Nast, J., 1979. Auchenorrhyncha (Homoptera) Wyzyny Lubelskiej i Roctocza, Czesc I–Fulgoroidea.—Frag. Faun. **25**: 1–13.

Ossiannilsson, F., 1978. Fauna entomologica Scandinavia 7, part 1, The Auchenorrhyncha (Homoptera) of Fennoscandia and Denmark.—Scandinavian Science Press Ltd., Klampenborg Denmark. 222 pp.

Perris, 1857. Nouvelles excursions dans les Grandes Landes.—Ann. Soc. Linn. Lyon, **4**: 83–180.

Remane, R., 1958. Die Besiedlung von Grünlandflächen verschiedener Herkunft durch Wanzen und Zikaden im Weser-Ems Gebiet.—Z. Angew. Entom., **42**: 353–400.

Schiemenz, H., 1971. Die Zikadenfauna (Homoptera, Auchenorrhyncha) der Erzgebirgshochmoore.—Zool. Jb. Syst. **98**: 397–417.

Schiemenz, H., 1975. Die Zikadenfauna der Hochmoore im Thüringer Wald und Harz (Homoptera, Auchenorrhyncha).—Faun. Abh. Staatl. Mus. Tierk. Dresden **5**: 215–233.

Schiemenz, H., 1976. Die Zikadenfauna von Heide- und Hochmoore des Flachlandes der DDR.—Faun. Abh. Staatl. Mus. Tierk. Dresden **6**: 39–54.

Scholz, H., 1975. Grassland evolution in Europe.—Taxon **24**: 81–90.

Scott, 1871. On certain British Hemiptera-Homoptera. Revision of the family Delphacidae and description of several new species of the genus *Delphax* and others.—Ent. Month. Mag. **7**: 193–196.

Servadei, A., 1968. Contributo alla corologia dei Rhynchota Homoptera Auchenorrhyncha d'Italia.—Est. Ann. Mus. di storia Nat. Genova **77**: 138–183.

Törmälä, I. & Raatikainen, N., 1976. Primary production and seasonal dynamics of the flora and the fauna of the fieldstratum in a reserved field in Middle Finland.—Maataloust. Aikakousk. **48**: 363–385.

Vilbaste, J., 1974. Preliminary list of Homoptera-Cicadina of Latvia and Lithuania.—ENSV TA Toimet, Biol. **23**: 131–163.

Wagner, W., 1963. Dynamische Taxionomie, angewandt auf die Delphacidae Mitteleuropas.—Mitt. Hamburg. Zool. Mus. Inst. **60**: 111–180.

White, M. D., 1978. Modes of speciation.—W. H. Freeman & Company San Francisco. 455 pp.

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