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Separation of *Myzus* (*Nectarosiphon*) *antirrhinii* (Macchiati) from *Myzus* (*N.*) *persicae* (Sulzer) and related species in Europe (Homoptera: Aphididae)

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ABSTRACT. Multivariate morphometric analysis (canonical variates) was used to discriminate between closely related taxa within the *Myzus persicae* group. It is demonstrated that dark green, anholocyclic populations with a 2n=13 or 2n=14 karyotype in Europe, hitherto treated as a form or biotype of *M.persicae*, all conform to a discrete morphometric grouping and should therefore be treated as a separate taxonomic entity, permanently isolated from the *M.persicae* gene pool. It is suggested that this taxon was first described as *Siphonophora antirrhinii* by Macchiati in 1883. A discriminant function is provided to separate most individual apterae of *antirrhinii* from those of *persicae*. *Myzus icelandicus* Blackman sp.n., on Caryophyllaceae and other plants in Iceland, is distinguished from *M.polaris* H.R.L. and *M.certus* (Walker), and a key is given to apterous virginoparae of the species of the *M.persicae* group in Europe.

Introduction

Polyphagous aphids such as *Myzus persicae* (Sulzer) have in the past erroneously been described as new from many different plants, and numerous names have consequently been sunk as synonyms. Although many of these synonymies are undoubtedly correct, some failed to take account of features lost in museum preparations but recognized as different by the original describer, such as the appearance of the individual aphids or the colony as a whole, or aspects of behaviour or biology.

For many years one particular form, hitherto usually regarded as a race or biotype of *M.persicae*, has been recognized in Europe. This form is characterized by its consistently dark green colour, its obligate anholocycly, its relatively long antennal terminal process, its low level of alata production, and its abnormal karyotype (Waldhauer, 1953; Blackman, 1971). However, slide-mounted individuals of the dark green form could not be reliably separated from *M.persicae sensu stricto* on morphological characters alone, and in life it seemed to be just as polyphagous as the main species. Therefore uncertainty has remained about whether this form could be regarded as a single, discrete taxonomic entity. The name *dianthi* Schrank, allocated to this form by Börner (1952), also seemed incorrect, as the aphid described by Schrank (1801) was pale green in colour.

Multivariate morphometric techniques have therefore been used to clarify the taxonomic status of this aphid, and a name is applied to it. The separation of other species within the closely related *M.persicae* group is also difficult and the available keys do not take sufficient account of the variation now known to occur.

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Therefore a multivariate study was carried out on the most closely related members of this group in Europe, and a new key has been prepared to their apterous virginoparae.

Materials and Methods

The aphids used in this study comprised samples of thirty-two clones and fourteen field-collected, non-clonal populations of apterous virginoparae from seven putative taxa in the *M.persicae* group, and one hybrid clone between two of these taxa. Twenty-five of the clones and eight of the non-clonal samples were from various European countries, the others coming from North and South America, Iran, Japan and New Zealand. Samples of eight clones of *M.persicae* reared at different temperatures (10, 15 or 20°C) were also included in the analysis to assess the effect of temperature on morphology. In all, fifty-four separate samples were measured with five to twelve (usually twelve) aphids in each sample, yielding data on 616 individual specimens.

Fourteen characters were measured, chosen from preliminary studies and from experience as those most likely to show differences of taxonomic significance within the group. These were:

1. Length of third antennal segment (as 3).
2. Length of base of sixth antennal segment.
3. Length of terminal process of sixth antennal segment (pt).
4. Length of ultimate rostral segment (urs).
5. Number of accessory hairs on ultimate rostral segment.
6. Length of hind femur.
7. Length of hind tibia.
8. Length of second segment of hind tarsus (ht 2).
9. Length of siphunculus.
10. Maximum width of distal, swollen part of siphunculus.
11. Minimum width of proximal part ('stem') of siphunculus.
12. Length of cauda.
13. Length of longest hair on eighth abdominal tergite.
14. Length of longest hair on subgenital plate.

The data were analysed by the method of canonical variates, using firstly all fifty-four samples and then a selected subset (see Results). This method, which is the analogue for grouped data of the method of principal components for ungrouped data, followed the procedure described in Mardia *et al.* (1979).

Chromosome preparations were made from either fresh or prefixed material according to methods described previously (Blackman, 1980).

Results

Karyotype variation in the M.persicae group

This has been reviewed previously (Blackman, 1980). Holocyclic populations and species (*ajugae, certus, myosotidis, persicae*) generally have 2n=12, but a translocation heterozygote of *M.persicae* is widespread even in populations which go through the sexual phase, and in Japan an autosome dissociation also seems to be maintained in holocyclic populations of this species. A form related to *M.certus* occurring on *Cerastium* and *Stellaria* in Iceland, which has an obligate holocycle with an abbreviated parthenogenetic phase, has 2n=10. Permanently parthenogenetic populations within the group, however, seem invariably to be structurally heterozygous, either for one or more dissociations of autosomes or, in the case of *M.dianthicola,* for a more complex rearrangement of the karyotype.

In Europe, dark green anholocyclic aphids hitherto regarded as a form of *M.persicae* invariably have thirteen or fourteen chromosomes, thought to be due to either one or two

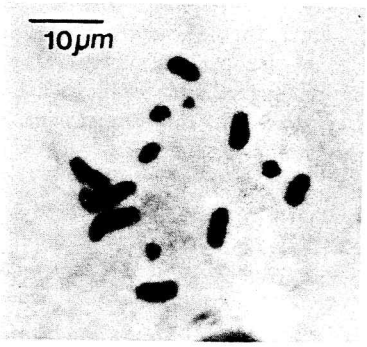

FIG. 1. Somatic metaphase cell of a clone of *M.antirrhinii* (see Discussion) from lupins at Reading. Of the thirteen chromosomes, five are short, and one of these is minute. Propionic acid squash, stained with Giemsa.

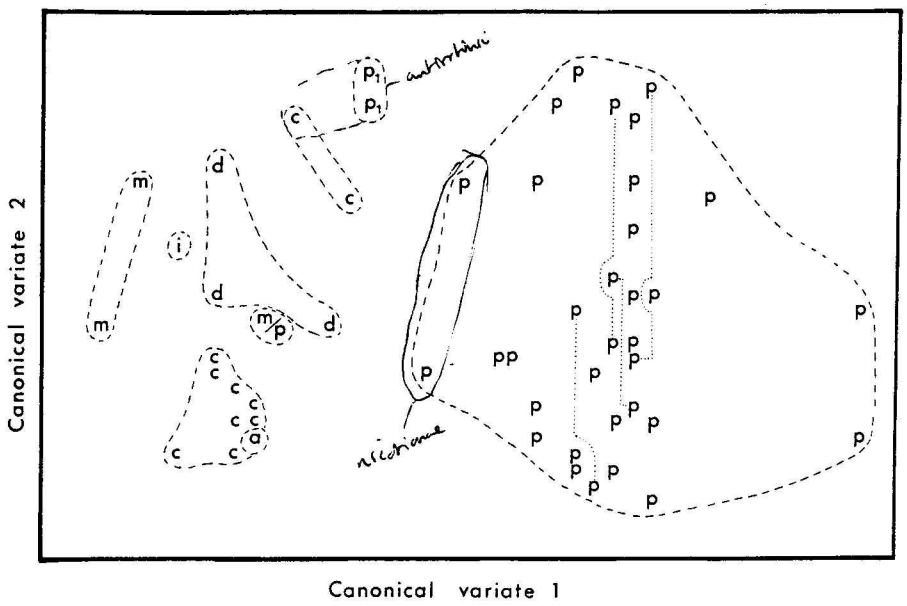

FIG. 2. Plot of the scores on the first and second canonical variates for fifty-four samples of *Myzus* (*Nectarosiphon*), based on fourteen variables (see text). Dotted lines join samples of the same clone reared at two different temperatures. a=*ajugae*, c=*certus*, d=*dianthicola*, i=*icelandicus* sp.n., m=*myosotidis*, m/p=hybrid clone between *myosotidis* and *persicae*, p=*persicae* (including *antirrhinii*), p_1=*persicae* group from Pittosporaceae in California (2n=13).

autosome dissociations respectively. These dissociations usually appear to involve breakpoints near the centre of autosomes 2 and 3, resulting in karyotypes in which the six or eight shortest elements are of similar size (Blackman, 1971). However, one population of this form recently discovered on lupins in a glasshouse at Reading University has a thirteen-chromosome karyotype, but with five short elements, one of these being minute (Fig. 1). This karyotype has presumably arisen by a rearrangement of the more usual thirteen-chromosome karyotype.

Morphometrics

Separation of the species of the M.persicae group

Fig. 2 is a plot of the scores on the first two canonical variates (cv) for all fifty-four samples, using all fourteen variables. It can be seen that these two variates, which together account for 55.5% of the total variation of the data, separate all samples of *M.persicae* (including the dark green, anholocyclic form) from all samples of other recognized taxa within the group. The first cv on its own almost provides a complete separation, but for two samples from Pittosporaceae in California with a 2n=13 karyotype. The second cv does not in fact contribute usefully to the separation of the putative taxa, splitting those samples provisionally assigned to *certus* into two groups. Scores of this cv are strongly dependant on rearing temperature, as is clearly demonstrated in Fig. 2 where the dotted lines join pairs of samples of the same clones of *M.persicae* reared at 10°C (upper point) and 20°C (lower point) respectively. The plot of the first two cv also fails to separate the single sample of *ajugae* from one of the *certus* groups.

Plots involving the third and fourth cv did not improve the separation between the putative taxa, but the groups obtained by plotting the first cv against the fifth (Fig. 3) agreed excellently with their expected taxonomic relationships. The fifth cv, which accounted for 6.5% of the total variation of the data, brought all samples of *certus* into one group well separated from *dianthicola* and *myosotidis*, as well as from *ajugae* and the Icelandic 2n=10 population. This plot also placed the hybrid clone obtained by crossing *myosotidis* and *persicae* mid-way

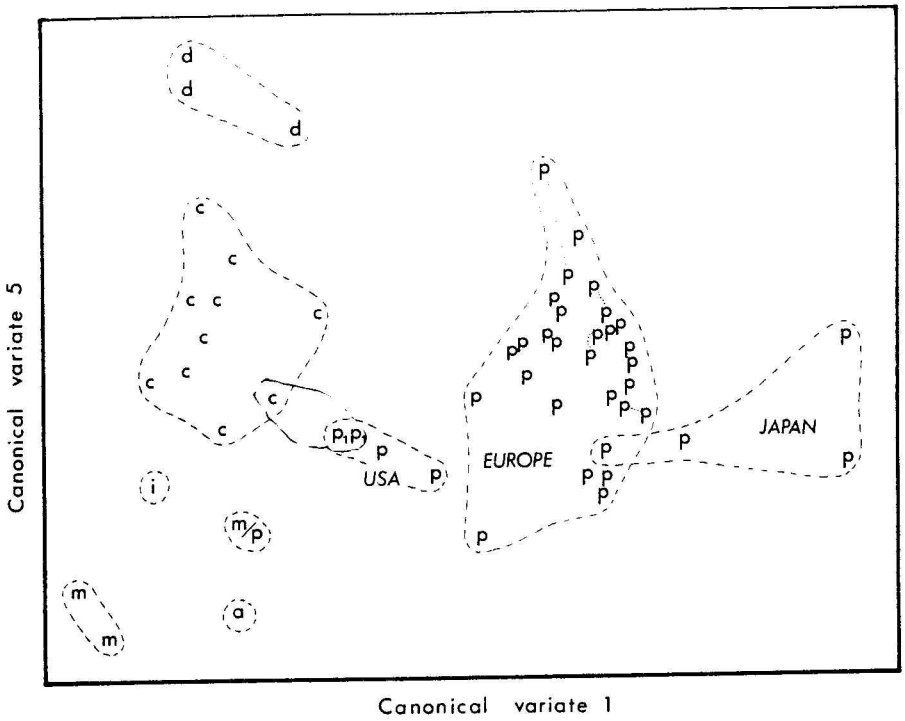

FIG. 3. Plot of the scores on the first and fifth canonical variates of fifty-four samples of *Myzus* (*Nectarosiphon*), based on fourteen variables (see text). Dotted lines join samples of the same clone reared at two different temperatures. For notation see Fig. 1.

between these two taxa. Samples of *persicae* clones reared at different temperatures were generally close to each other on this plot, indicating that environmental effects were minimal. Cv I and V together accounted for 45.8% of the total variation.

This analysis also provided an indication of possible geographical variation between *M.persicae* populations. All four samples from the U.S.A. formed a discrete group, although they included both 2n=12 and 2n=13 karyotypes. Scores of cv I for three of the four Japanese samples were outside the range of cv I scores of all the other (mainly European) clones and populations.

Separation of the dark green, anholocyclic form from *M.persicae* s.str.

Analysis of the data for all fifty-four samples failed to discriminate between the dark green anholocyclic 'form' of *M.persicae* and the main species. The analysis was therefore repeated leaving out the other species in the group and concentrating on the thirty-six samples of dark green and normal '*persicae*'.

With thirty-six groups, cv I, accounting for 30% of the total variation, had taken the place of cv II of the previous analysis as the variate whose scores were most influenced by the environment, and plots involving this variate did not produce any meaningful separations, pairs of samples of clones reared at different temperatures having widely different scores on cv I. When cv II was plotted against cv III (accounting together for 36% of the total variation), an absolute separation of the European samples of 2n=12 (normal and translocated) karyotype from those of 2n=13 or 14 karyotype (the anholocyclic, dark green form) was achieved (Fig. 4). The samples from outside Europe did not fit into this grouping whatever their karyotype, colour or life-cycle category (where known). Their taxonomy is being studied separately.

European samples were further investigated to select a discriminant function for separation

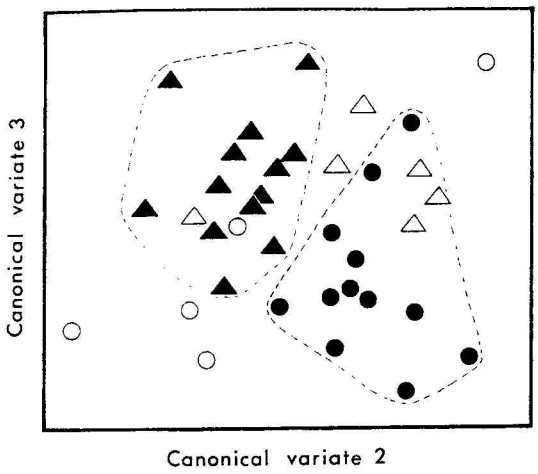

FIG. 4. Plot of the scores on the second and third canonical variates of thirty-six samples of the *Myzus persicae* group, based on fourteen variables (see text). Solid symbols represent European samples, open symbols represent samples from outside Europe; triangles are samples with 2n=13 or 14, circles are samples with 2n=12 (normal or translocated).

of 2n=13/14 and 2n=12 forms at the level of the individual aphid. The data set consisted of twenty-four samples totalling 286 individual specimens. To avoid the circularity of applying a discriminant function to the data set from which it was obtained, the specimens were partitioned randomly into two subsets: one a training set from which a discriminant function was calculated, and the other a test set on which we could see how well the function was working in terms of correct classifications. Partitioning was carried out using the MINITAB statistical package. Each subset had seventy-seven 2n=13/14 and sixty-six 2n=12 specimens.

Two types of discriminant analysis were investigated: parametric and non-parametric. For each type of analysis both linear (LDF) and quadratic (QDF) functions were tested (for a general discussion of the method see Fatti *et al.*, 1982). The results obtained by the non-parametric method, where the measurements were replaced by ranks, were similar to those using the parametric method, and are not presented here. In the parametric method, assumptions are made that the data come from a multivariate normal distribution, and that we can estimate means, covariance matrices and *a priori* probabilities that the data come from a given population. In theory a quadratic function should be used if the covariance matrices are unequal. The test for equality of covariance matrices was a straightforward likelihood ratio (Bartlett's) test. This was found to be highly significant at the 5% level indicating that the covariance matrices for the two groups were different. However, in practice LDFs performed

TABLE 1. Coefficients and performance with test set of a linear discriminant function (LDF) using all fourteen characters.

Character	Coefficient
1	−4.03
2	−385.52
3	140.56
4	731.91
5	0.50
6	−16.06
7	0.02
8	−165.52
9	−61.72
10	303.69
11	−431.53
12	78.28
13	136.69
14	188.26

Constant term: −61.72

Actual group	Predicted group 2n=13/14	2n=12
2n=13/14	76	1
2n=12	0	66

Percentage correctly classified= 99.3%.

TABLE 2. Coefficients and performance with test set of a linear discriminant function (LDF) using characters 1–4.

Character	Coefficient
1	−52.97
2	−499.46
3	137.58
4	707.52

Constant term: −57.92.

Actual group	Predicted group 2n=13/14	2n=12
2n=13/14	75	2
2n=12	1	65

Percentage correctly classified= 97.9%.

just as well as QDFs in separating the groups. Tests for skewness and kurtosis (Fatti *et al.*, 1982) showed that there was some skewness in the data, but LDFs are usually found to be robust for this, and this seemed to be true for our data.

Using the LDF method with all fourteen characters gave excellent separation, but it was clear from the relative sizes of the coefficients that several characters were contributing little to the separation (Table 1). By selecting characters with the highest value coefficients, subsets of six and seven characters could still provide good separation between the groups. An attempt was made to formalize this selection procedure, and reduce the number of variables further, by using regression techniques on MINITAB. A column was set up consisting of −1's for the 2n=12 form and +1's for the 2n=13/14 form, and then backward elimination and forward selection methods were used as well as conventional stepwise and regression techniques (Hand, 1981). Several LDFs obtained by these methods using only three or four characters gave over 95% of correct classifications. A subset consisting of the first four characters, which are all relatively easy to measure, and an LDF which correctly classified 97.9% of the test set, were finally chosen as providing the best practical discriminant between the groups (Table 2).

Discussion

There are obvious dangers of circularity in the use of multivariate analysis based on selected characters to confirm an interpretation of taxonomic relationships within a group, if the original interpretation was itself based to some extent on those same characters. However, in the *M.persicae* group as in certain other aphid species complexes, we are concerned mainly with species which are recognizable in the field by their appearance in life, specific host plant associations or life cycle differences, and which only become difficult to separate when they are preserved for morphological study. The selected characters have not been used before in any systematic way to separate members of the *M.persicae* group, but were included because they have been found useful either singly or in pairs in the taxonomy of other related species within the Aphididae.

The ability of scores on cv V to separate all members of the group except *persicae* (Fig. 2) is surprising, as usually in such analyses it is the first two cv which pick out most of the taxonomically meaningful variation. There are two probable reasons. First, the phenotype of the adult apterous aphid may be more strongly influenced by the environment than is usually the case in other animal groups. Scores on cv II, III and IV in the fifty-four-sample analysis, and the score on cv I in the thirty-six-sample analysis, all seem to be strongly temperature dependant. Second, genetic differences between groups would have contributed more to the total variation between samples if the group sizes had been larger for species other than *persicae* and *certus*.

The results of the thirty-six-sample analysis show that the dark green, anholocyclic 2n=13/14 form can be separated from 2n=12 populations of *persicae* in Europe by a combination of morphometric characters. Thus, in all probability it is a monophyletic grouping which should be regarded as a discrete taxonomic entity. The taxonomic status and naming of permanently parthenogenetic (uniparental) organisms is a long-standing problem. It has been argued (e.g. Dobzhansky, 1972) that uniparental species must be considered as conceptually distinct from biparental species, because they do not fit the biological species concept. However, populations of uniparental organisms do not exhibit a 'chaotic range of variation that defies analysis and classification' (White, 1978), but on the contrary can be grouped as definable 'species' in much the same way as sexually reproducing populations. This is explicable if

species are regarded primarily as functional units, maintained not so much by interbreeding and by the setting up of mating barriers between them, as by centripetal selection for gene combinations concentrated at or around an adaptive peak which best fulfils the functional 'role' of the species in the ecosystem. Such selection of functional gene combinations and elimination of deleterious mutations can occur in uniparental as well as in sexual systems. If uniparental species can be deliminated in much the same way as biparental ones, and the conceptual difficulties of regarding them as species can be overcome, then it seems justifiable to name them in the same way as biparental species. In fact, because their reproductive isolation from other taxa is assured the situation is simpler than when naming closely related species of biparental organisms, where possibilities of actual or potential interbreeding have to be considered, and may result in the erection of subspecies rather than full species. The subspecies concept is inapplicable to uniparental populations.

For these reasons it is proposed that the dark green form with 2n=13 or 2n=14 karyotype in Europe should be treated as a distinct species. Of the available names, most can be eliminated by examining type material where this is available, or by consulting the original descriptions, which often refer to pale green aphids. However, Macchiati (1883) described a glaucous green aphid, *Siphonophora antirrhinii*, on *Antirrhinum* spp. in southern Italy. True *M.persicae*, although very variable in colour, is unlikely to be described as glaucous green. Other aspects of Macchiati's description such as the pigmentation of the siphunculi fit the 2n=13/14 form, as does the fact that he did not observed any alatae, although recording several populations at different times of year on two different *Antirrhinum* species. Macchiati left no types.

Theobald (1926, p. 326) recognized Macchiati's *Antirrhinum* aphid, presumably from his description of the insect in life, and regarded it as a variety or biological form of *M.persicae*. Specimens in the Theobald collection from *Antirrhinum* in Scotland conform morphometrically to the 2n=13/14 form. However, Theobald's specimens from *Antirrhinum* at Moro, British East Africa, 16.i.12, which he also believed to be *antirrhinii*, appears to be genuine *persicae*. Although Theobald records the aphids doing much harm to *Antirrhinum* in Britain, the BM(NH) main collection contains only five European samples of *persicae*-like aphids from *Antirrhinum*. However, three of these agree morphometrically with the 2n=13/14 form, including the only sample from this host in Italy, collected by E. Tremblay at Portici, 21.v.67. We therefore propose that the correct name for this aphid is *Myzus* (*Nectarosiphon*) *antirrhinii* (Macchiati).

M.antirrhinii apparently arose at some time in the past from ancestral *M.persicae* stock; more than 100 years ago if the assumption that it is Macchiati's aphid is correct. Genetically isolated by total loss of the ability to produce sexual forms, it has diverged sufficiently in morphology, karyotype and other features to be recognizable as a distinct taxon. *M.persicae* itself frequently overwinters anholocyclically in regions with mild winters, but maintains a variable life cycle in which genotypes overwintering one year can potentially contribute genes, by male production, to the next year's sexual generation (Blackman, 1974). Thus populations of *M.persicae* in the long term maintain a common gene pool and do not necessarily diverge, so long as the sexual phase is not entirely lost.

M.antirrhinii has been collected from Buddlejaceae (*Buddleja*), Caprifoliaceae (*Lonicera*), Caryophyllaceae (*Dianthus, Silene*), Chenopodiaceae (*Beta*), Compositae (*Gynura*), Cruciferae (*Brassica, Raphanus*), Leguminosae (*Lupinus, Medicago*), Rubiaceae (*Galium*), Scrophulariaceae (*Antirrhinum*) and Solanaceae (*Solanum, Capsicum*), and may be just as polyphagous as *M.persicae*, although certain hosts and habitats (e.g. glasshouses and sheltered situations) may be favoured because of its obligate anholocycly and reluctance to produce alate females. *Antirrhinum*, as mentioned above, and also *Buddleja* (which is a host for several Scrophulariaceae-feeding insects), appear to be particularly favoured host plants. A population on *Lonicera* at Radcliffe-on-Trent, England, sampled several times during 1976 by J. H. Martin, was unusual in having a short antennal terminal process, but when reared in the laboratory on excised potato leaves it acquired the normal *antirrhinii* phenotype.

Simons & Eastop (1970) noted that one of five clones of *M.persicae* used in virus transmission experiments in California, U.S.A., was darker green than the others, had longer body hairs and a longer antennal terminal process, and rarely

produced alatae. Specimens of this clone preserved in the BM(NH) collection agree morphometrically with *M.antirrhinii*. In California, however, there are other anholocyclic *persicae*-like aphids with a 2n=13 karyotype which are morphologically distinct from *M.antirrhinii* and mainly found on Pittosporaceae. Apart from the Simons & Eastop clone, no other populations from outside Europe represented in the BM(NH) collection of *M.persicae* can be definitely assigned to *M.antirrhinii*.

Myzus (Nectarosiphon) icelandicus Blackman sp.n.

Hille Ris Lambers (1952) described *M.polaris* from Greenland as an apparently distinctive species with short, thick siphunculi, monoecious on *Cerastium alpinum* with an abbreviated parthenogenetic phase to the life cycle, males and oviparae occurring in July and August. Subsequently he recorded the occurrence of this species in Iceland (Hille Ris Lambers, 1955), but noted (in Prior & Stroyan, 1960, p. 285) that the Icelandic populations were much more like European *M.certus* than the type specimens of *polaris* from Greenland.

We have examined a long series of *polaris* collected in N.E. Greenland in 1970, 1974 and 1977 by M. J. Cotton, and more specimens from Iceland collected in 1979 by J. H. Martin, and re-examined the material studied by Hille Ris Lambers. We conclude that the Icelandic aphid is a species distinct from both *polaris* and *certus*, and give it the name *Myzus (Nectarosiphon) icelandicus*.

Populations of *polaris* from Greenland vary considerably in the shape of the siphunculi, but the part proximal to the swelling (the 'stem') is always very thick; at its narrowest point greater than 0.125 of the length of the siphunuculus in apterae, and in alatae thicker than the middle region of the hind tibiae. In *icelandicus* the stem of the siphunuculus in apterae is maximally 0.125 of its length, and in alatae thinner than the middle region of the hind tibiae. (This character can only be assessed where the cylindrical shape of the siphunculi has not been flattened or distorted in slide preparation.) Greenland *polaris* have 3–11 accessory hairs on the ultimate rostral segment whereas *icelandicus* has 3–7, which is the more normal range for *Myzus (Nectarosiphon)* species. Apterae viviparae from Greenland often have 5-segmented antennae, even in August in mixed populations with oviparae (which always have 6-segmented antennae), and alatae with 5-segmented antennae have also been recorded (Hille Ris Lambers, 1960). Individuals with 5-segmented antennae have not been collected in Iceland.

M.icelandicus is closely similar to *M.certus* in Britain and continental Europe, but tends to have a longer ultimate rostral segment (see key below). The chromosome number (2n female) is 2n=10, different from all other *Myzus (Nectarosiphon)* species. Compared with the basic 2n=12 karyotype of other *Myzus (Nectarosiphon)* species, *icelandicus* has only one short pair of autosomes, and has perhaps become homozygous for a fusion between one short and one medium-length autosome.

Like *M.polaris, M.icelandicus* has an abbreviated parthenogenetic phase, in tune with the short northern summer. Prior & Stroyan (1960) found it to be the most generally abundant aphid in their collections in Iceland in 1958. Although principally found on Caryophyllaceae (especially *Silene maritima, Stellaria media* and *Cerastium alpinum*), other plants in Cruciferae, Crassulaceae, Polygonaceae and Gentianaceae were also utilized as hosts, and sexuales were found on *Sedum villosum*. Thus as noted by Prior & Stroyan it is more polyphagous than *M.certus*, which is interesting in view of the fact that *M.persicae* has not established itself in Iceland. Several plants which are hosts of *persicae* in other parts of Europe are colonized by *icelandicus* in Iceland.

M.icelandicus is red-brown in life, like *certus* (J. H. Martin, pers. comm.). Neither the colour in life nor the karyotype of *M.polaris* are yet recorded.

Type material is restricted to specimens of known karyotype (2n=10):

Holotype, aptera vivipara, ICELAND: Reykjavick, *Cerastium ?alpinum*, 12.vii.79 (*Martin 2444*) (BMNH).

Paratypes, two apterae viviparae and two immatures, same collection data.

Key to apterous virginoparae of the *Myzus persicae* group in Europe

This key is devised to take account of morphological variation within European material of *Myzus (Nectarosiphon)*, and one other rel-

ated species, in the BM(NH) collection. It applies only to apterous virginoparae, alate virginoparae being in several cases more difficult to separate. One other nominal taxon currently placed in *Myzus (Nectarosiphon), titschacki* Börner 1942 described from the roots of a sedge or rush in Northern Germany, is omitted because we have not seen authentic material of this species. The key will work best with samples of several specimens from a population rather than with single individuals, as the range of variation in characters can then be assessed and compared with the values given in the key. Functions involving more than two variables require measurements in millimetres.

1 Siphunculi 0.22–0.30 mm long, 0.54–0.81 times as long as antennal segment 3 2

– Siphunculi 0.23–0.60 mm long, 0.84–1.34 times as long as antennal segment 3 3

2 Inner faces of antennal tubercles approximately parallel-sided in dorsal view. Narrowest part of 'stem' of siphunculus a little narrower than width of middle part of hind tibia. Dorsal cuticle smooth or slightly wrinkled, but not 'scaly'. Shiny pale greenish-brown, straw-coloured or dirty yellow in life. Polyphagous, but especially on Alliaceae, Caryophyllaceae and Compositae. Anholocyclic (no males known). 2n=12 ..... *ascalonicus*

– Inner faces of antennal tubercles with apices convergent in dorsal view. Narrowest part of 'stem' of siphunculus slightly broader than width of middle part of hind tibia. Dorsal cuticle wrinkled and with a 'scaly' appearance. Dull yellowish-green or yellowish brown to dark brown or crimson red (more pigmented in cold conditions). Polyphagous on similar range of host plants to *M. (N.) ascalonicus*. Anholocyclic, but males recorded. 2n=12 ..... *cymbalariae*

3 Siphunculus blackish on distal 0.3–0.5, contrasting with pale basal 0.5–0.7. Yellow in life, in rolled leaves of *Ligustrum vulgare*. Holocyclic and apparently monoecious on *Ligustrum*, but with alate males. 2n=12 ..... *ligustri*

– Siphunculus concolorous with body, or uniformly pigmented, or dark only at tip 4

4 Hairs on inner sides of antennal tubercles mostly pointed and at least 0.75 as long as basal diameter of antennal segment 3. Siphunculi 0.84–1.02 as long as antennal segment 3, less than 0.2 of body length. Green in life (with red oviparae), curling upper leaves of *Myosotis palustris*. Monoecious holocyclic with apterous males. 2n=12 *myosotidis*

– Hairs on inner sides of antennal tubercles short and blunt, less than 0.75 of basal diameter of antennal segment 3. Siphunculi 0.99–1.34 as long as antennal segment 3 and rarely less than 0.2 of body length 5

5 Cauda 0.37–0.49 times as long as antennal segment 3 (=as 3). Hind tarsus segment 2 (ht 2) 0.86–0.98 times as long as ultimate rostral segment (urs). Value of the function (ht 2×cauda)/(urs×as 3) in range 0.33–0.44. Green in life, on upper sides of leaves of *Ajuga* spp., folding leaves upward. 2n=12 *ajugae*

– Cauda 0.45–0.67 times as long as antennal segment 3. Hind tarsus segment 2 (ht 2) 0.78–1.58 times as long as ultimate rostral segment. Value of function (ht 2×cauda)/(urs×as 3) in range 0.44–0.89 6

6 Terminal process of antenna (pt) 0.44–1.16 times as long as (that is, usually shorter than) antennal segment 3 (=as 3) (measure several specimens). Value of the function, (cauda length)/(as 3×pt), within the range 1.20–2.70, but rarely less than 1.26 7

– Terminal process of antenna (pt) 0.90–1.49 times as long as (that is, usually longer than) antennal segment 3 (measure several specimens). Value of the function, (cauda length)/(as 3×pt), within the range 0.87–1.52 but rarely more than 1.25 10

7 Hind tarsus segment 2 0.32–0.39 times as long as antennal segment 3, and 1.14–1.58 times longer than ultimate rostral segment. Yellowish-green in life, on shoot apices and inflorescences of *Linaria* spp. Monoecious holocyclic with apterous males. 2n unknown ..... *linariae*

– Hind tarsus segment 2 0.22–0.33 times as long as antennal segment 3, and 0.78–1.29 times longer than ultimate rostral segment. On Caryophyllaceae, spotting and twisting leaves, sometimes on Violaceae or other plants 8

8 Terminal process of antenna 3.06–3.95 times (mostly more than 3.25 times) longer than base of last antennal segment (measure several specimens). Hind tarsus second segment 1.02–1.29 times (mostly more than 1.10 times) longer than ultimate rostral segment. Deep yellow green in life. Anholocyclic on *Dianthus caryophyllus*. 2n=14 (heterozygous) ..... *dianthicola*

– Terminal process of antenna 2.10–3.42 times (but mostly less than 3.25 times) longer than base of last antennal segment (measure several specimens). Hind tarsus second segment 0.78–1.15 times (but rarely more than 1.10 times) as long as ultimate rostral segment. Brown or red-brown in life 9

9 Ultimate rostral segment usually shorter than (0.85–1.10 times) base of last antennal segment. On Caryophyllaceae and Violaceae, Europe and North America. Monoecious holocyclic with apterous males, or anholocyclic. 2n=12 ..... *certus*

– Ultimate rostral segment usually longer than (1.00–1.19 times) base of last antennal segment. In Iceland, predominantly on Caryophyllaceae but sometimes on other plant families. Monoecious holocyclic with apterous males. Life cycle abbreviated. 2n=10 ..... *icelandicus*

10 Terminal process of antenna 3.75–4.95 times longer (usually more than 4.0 times longer) than

base of last antennal segment, and 0.84–1.38 times longer than siphunculus. Siphunculus rather evenly pigmented, with maximal width of swollen part usually more than 0.1 of length of siphunculus. Value of function (A+B)−(C+D) greater than 58 (see below). Mid-grey-green to dark green, sometimes dark red. Polyphagous. Anholocyclic, males unknown and alate females only sporadically produced. 2n=13 or 14 (heterozygous) *antirrhinii*

– Terminal process of antenna 3.14–4.10 times (usually less than 4.0 times) longer than base of last antennal segment, and 0.72–1.11 times as long as siphunculus. Siphunculus variably pigmented but usually pale except at apex, with maximal width of swollen part mostly less than 0.1 of length of siphunculus. Value of the function (A+B)−(C+D) less than 58 (see below). Pale green, yellow green, straw-coloured or pink. Polyphagous. Androcyclic or holocyclic heteroecious with sexual phase on *Prunus persica, P.serotina* or *Lycium halimifolium*. 2n=12 ..... *persicae*

A=terminal process length ×138
B=ultimate rostral segment length ×708
C=antennal segment 3 length ×53
D=base of last antennal segment length ×500

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