VIII.—On the Life-History and Bionomics of *Myzus ribis*, Linn. (Red-Currant Aphis). By Maud D. Haviland, Bathurst Student of Newnham College. Communicated by Professor F. O. BOWER, F.R.S.

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SYNONYMY.

<i>Aphis ribis</i> , Linn., Fabr., Schrank, Kalt.,	<i>Aphis galeopsidis</i> , Kalt., Walker.
Flogel.	<i>Phorodon galeopsidis</i> , Pass., Buckton.
<i>Myzus ribis</i> , Pass.? Buckton.	<i>Myzus whitei</i> , Theobald?
<i>Rhopalosiphum ribis</i> , Koch.	<i>Myzus dispar</i> , Patch?

INTRODUCTION.

Myzus ribis, Linn. (red-currant aphis), has attracted the attention of entomologists for more than a hundred and fifty years. But in spite of its abundance, wide geographical distribution, and economic importance as a pest of bush fruits, the complete life-cycle has never been determined. It was with the view of settling the disputed question of the fate of the aphis in the summer, and in the hope that elucidation of the bionomics of this species would throw further light on some uncertain points in the life-history of other migratory *Aphidinae*—notably on the production of the sexuales—that these researches were undertaken.

I must express my sincere thanks to Professor J. Stanley Gardiner, who gave me facilities to carry out the work in the Zoological Laboratory, Cambridge, and to Miss Stephen, Principal of Newnham College, who permitted the use of her garden for the cultivation of the necessary material.

Mr F. Balfour-Browne has helped me with much useful suggestion and criticism, and I would particularly express my thanks to Mr H. H. Brindley for his advice and assistance. I must also thank the Trustees of the Balfour Fund for a grant awarded to me for the prosecution of the work.

THE NATURE OF THE ATTACK AND ITS REMEDY.

Myzus ribis is commonly, though not invariably, associated with the presence of large red blisters on the leaves, but it is still an open question whether these are always caused by the aphides. The deformity and discoloration are generally apparent as soon as the buds open and before the leaves are fully unfolded. The red colour of these blisters is due to anthocyanin, a soluble pigment common in plants. It is possible that

mechanical injury to the tissues, which involves the phloem but not the xylem, may result in an accumulation of sugars and other products of photosynthesis within the affected area, and under certain circumstances these may give rise to anthocyanin. If this is so, the reaction of the plant to the punctures of the aphid's rostrum would account for the malformation without supposing that the injected saliva of the insect acts as an irritant to the leaf cells.

I am inclined to think that most of the damage is done by the stem mother while the buds are opening. My observations go to show that she hatches in April, and has a larval period lasting for three weeks or a month. When she begins to produce young at the beginning of May, the leaves already show the red swellings which characterise the attack of this pest. When once the leaves are fully unfolded, the sucking of the aphides has little effect upon them. The actual damage to the bushes is sometimes very considerable. The functions of the injured leaves are interrupted and the fruit ripens prematurely. Davidson (4) says that the stem mothers of *Myzus ribifoliae* cause similar blisters on *Ribes glutinosum* in America.

Koch, Kaltenbach, and other older writers attribute the red blisters to *M. ribis*, but Theobald (27, p. 96) is doubtful whether it actually causes them. But he adds (p. 110): "I have never found this species except under the red blisters." This is a mistake, for, as I hope to show, *M. ribis* is equally common under green undeformed leaves. Flogel (11), though he holds that the blisters are caused by the aphides, recognises that they feed also upon normal leaves, but he considers that only the later generations do so. He propounds the curious theory that those feeding under the red blisters have a gregarious disposition (*Socialtendenz*) which turns to vagrant habit (*Dissipationstendenz*) in their descendants. The fact really is that if the aphides be taken from the diseased leaves and fed on healthy ones, they distribute themselves all over the surface and *vice versa*. If surplus foodstuffs are massed in the blisters, possibly the aphides are induced to congregate there, while outside they remain scattered because every spot is alike. Moreover, from the first generation onwards, *M. ribis* can be found on healthy leaves where its sucking seems to do little harm, but it is more readily overlooked. I have also found the stem mothers on unblistered leaves, and this inclines me to the view that the blisters when present are the work of the fundatrix on the opening bud. When the *Myzus* is associated with undistorted leaves, it is either that the stem mother has hatched after the buds are open, or else that the lice have migrated thither at a stage when the leaves are impervious to attack.

M. ribis is known to feed upon black currant and gooseberry, but it is less damaging to these than to *Ribes rubrum*. In 1918, black currant and gooseberry growing beside observation bushes of red currant in my garden were unaffected. A colony artificially founded upon gooseberry died out in the first generation after transference; and the third generation on black currant resulted in a swarm of winged forms which left the bushes at the end of May after producing a slight curling of the leaves.

The only effective remedial measure against *M. ribis* is to spray the bushes with soft soap, or nicotine solution, or paraffin emulsion in April as soon as the buds open. Where possible, it is advisable to pick off the blistered leaves by hand, as these afford shelter to the pest; and in case any aphides escape the first spraying, a second should be given early in May. Theobald recommends spraying the bushes with paraffin jelly early in October, to destroy the sexuales; but as my observations go to show that currant-reared sexuales may appear in September, and be succeeded in October by an immigration from the summer host plant, this method is uncertain, for oviposition may have taken place before the remedy is applied, and the egg is impervious to the wash. Ridding the neighbouring ground of such weeds as *Lamium*, *Polygonum*, and *Veronica*, which harbour the aphides in the late summer, might also be beneficial, but little reliance can be placed on this method of control.

THE DIMORPHISM OF THE RED BLISTER AND GREEN LEAF FORMS.

Myzus ribis has already been so exhaustively described by Kaltenbach (16), Flogel (10, 11), Patch (23), and others, that an account of the general characteristics of the parthenogenetic forms is unnecessary here. But in 1918 I noticed a dimorphism in this species, which, though it has not been treated as such by other observers, seems sufficiently remarkable to be described in detail.

When dealing with four fundatrices in April, a difference had already appeared between two which were found upon red-blistered leaves and two taken from green undistorted leaves. Briefly, the stem mothers on the former were pale yellow, with round abdomens, while those on the latter were green and more oval in shape. One of each form was chosen for breeding the generation series, and the other two were mounted alive in balsam and measured.

The breadth of the head is taken as the standard in calculating the proportions of the fundatrices, as subsequent results with the succeeding apterous generations, have shown that it is the least variable of the dimensions chosen for measurement. It can be seen from Table A that

TABLE A.

The dimensions of two fundatrices from red blister and green leaf respectively.

	Red Blister Form.		Green Leaf Form.	
	Absolute Dimensions.	Dimensions expressed as per cent. of Breadth of Head between Eyes.	Absolute Dimensions.	Dimensions expressed as per cent. of Breadth of Head between Eyes.
	mm.		mm.	
Breadth of head between eyes .	·29	100	·28	100
Length of body	2·30	790	2·77	989
Greatest breadth of abdomen .	1·38	475	·98	350
Breadth between cornicles . .	·70	241	·57	203
Length of cornicles	·40	130	·33	117
Total length of antenna . . .	1·85	637	1·40	500
Femur (metathoracic leg) . . .	·65	224	·50	178
Tibia (metathoracic leg) . . .	·90	310	·90	321

the form from the green leaf is actually, as well as proportionately, longer and narrower than that from the blistered leaves—a difference appreciable even to the naked eye.

TABLE B.

The average dimensions of twelve apterous females from red blister compared with those of twelve similar forms from green leaf.

	Red Blister Form.		Green Leaf Form.	
	Average Absolute Dimensions.	Dimensions expressed as per cent. of Width of Head between Eyes.	Average Absolute Dimensions.	Dimensions expressed as per cent. of Width of Head between Eyes.
	mm.		mm.	
Width of head between eyes .	·31	100	·31	100
Length of body	2·01	648	2·18	700
Greatest breadth of abdomen .	·95	300	·83	267
Breadth between cornicles . .	·67	200	·50	161
Total length of antenna . . .	2·36	671	2·37	764
Length of cornicles	·30	96	·31	100
Length of femur	·56	180	·57	183
Length of tibia	1·31	422	1·41	454

This disparity is maintained in the succeeding apterous generations (Table B). Henceforth, for the sake of brevity, the two forms will be distinguished as “red blister” and “green leaf” respectively. It will be seen that the most striking difference again occurs in the length and breadth of the abdomen. The dimensions of this part in insects are

variable and depend much on the amount of "telescoping" of the posterior segments in the individual. This holds good also for the Aphidæ, but it does not explain the divergence between the two forms. It merely shifts

FIG. 1.—Fifth joint of the antenna of two winged females.
A, from green leaf, and B, from red blister.

p.s. = permanent sensorium.

the difficulty of explanation to the problem of why an aphid which feeds on red blister should retract the cauda further than one which does not. Actually the difference might be expected to tend in the opposite direction, for if the blisters contain specially abundant food (and apart from the question of shelter, I think there can be no doubt that they are

the favourite feeding-ground), greater extension of the abdomen might be expected there than is found in the forms from normal leaves. That any aphides remain on the green leaves may perhaps be explained by the overcrowding of the blisters, which are filled as early as the first generation.

The colour difference between the forms is quite striking, but I am inclined to think that it is merely transitory, for if both forms be fed for a time on the same food, the distinction disappears. How far the dimensions of the abdomen remain constant under such conditions I have not yet determined for the apterous forms.

The same disparity in abdominal dimensions is not maintained among the winged females; but, on the average, forms from green leaves are rather the larger as regards the body and wing length, while those from red blisters have longer antennæ both actually and proportionately.

The difference in body dimensions is correlated with a difference in the number and arrangement of the sensoria on the fifth and sixth joints of the antenna. These sensoria have been described by several writers, but, so far as I know, Flogel (11) is the only one who has investigated their histology. They consist of a circular opening closed by a membrane, like a tympanum, and are surrounded by a fringe of minute hairs. Flogel says that the peculiar cells lying beneath this membrane are supplied by a branch of the antennary nerve, and the whole structure is evidently specialised for a particular function. He calls it an organ of smell (*Geruchsorgan*), but the structure is unlike that of any known olfactory organ, and the researches of Häuser (14) on the Heteroptera, and some as yet incomplete experiments of my own on *Macrosiphum pelargonii* (Aphidæ) tend to show that the sense of smell, if it exists at all in the Hemiptera, is not located in the antennæ.

In *Myzus ribis* there are two kinds of sensoria on Joint V. At the distal end is a large sensorium which may be called the permanent sensorium. A similar sensorium is found at the base of the spur on Joint VI, but under the high power of the microscope this is found to be a compound structure, composed of several small ones crowded together. In addition, in the red blister form, six to nine smaller sensoria occur along the shaft of Joint V. These do not appear until after the final moult, and may be called supplementary sensoria. On the other hand, in females from green leaves, besides the permanent sensorium, Joint V bears typically only imbricating scales, and a few stiff hairs which are possibly sensory in function. It is, however, not unusual to find a green leaf female which has three or four supplementary sensoria on Joint V,

TABLE C.

Dimensions of winged females of *Myzus ribis* from red blister and green leaf, of *Ribes rubrum* from *Galeopsis tetrahit*, and of *Aphis galeopsidis* of Kalténbach.

Average of twelve individuals in each case.

	Red Blister Form.		Green Leaf Form.		Fourth Generation after Transference to <i>Galeopsis tetrahit</i> .		<i>Aphis galeopsidis</i> Kalt.	
	Average Absolute Dimensions.	Dimensions expressed as per cent. of Length of Forewing.	Average Absolute Dimensions.	Dimensions expressed as per cent. of Length of Forewing.	Average Absolute Dimensions.	Dimensions expressed as per cent. of Length of Forewing.	Average Absolute Dimensions.	Dimensions expressed as per cent. of Length of Forewing.
Length of forewing	mm. 2·31	100	mm. 2·61	100	mm. 3·06	100	mm. 3·27	100
Length of body	1·59	68	1·84	70	2·10	68	2·35	71
Greatest breadth of abdomen.	·52	22	·59	22	·68	22	·71	21
Breadth between cornicles.	·32	14	·30	11	·36	11	·37	11
Total length of antenna.	1·99	86	1·87	71	2·87	93	3·03	92
Length of cornicles	·23	10	19	7	·20	6	·22	6

but these are always small and never tuberculate, as in the red blister forms. Fig. 2 shows the range of variation in this feature in seventeen sister females—granddaughters of a female with the typical form of open-leaf joint. Five of these had no sensoria on Joint V of either antenna. Of the remainder—

4 had 4 sensoria
 4 „ 3 „
 3 „ 2 „
 1 „ 1 sensorium.

But of these twelve females, only three had additional sensoria on each antenna. In the rest, the other antenna was of the typical green leaf type.

Besides the absence of sensoria on Joint V, the green-leaf form differs from that from the red blister in the smaller size of the sensoria on Joint III and Joint IV. This variation in the antenna is not alluded to by the older writers on *Myzus ribis*. Buckton does not mention it, and

Flogel (10, 11), who described the structure of the species minutely, asserted positively that "on the fifth joint are about eight sensoria."

(For the views of later observers see section *Myzus whitei* and *Myzus dispar*.)

FIG. 2.—Range of variation in Joint V of the antennæ, in respect of the sensoria, of seventeen sister females of the green-leaf type.

Between June 8th and June 23rd I made a collection of winged forms from my garden; the results are set out in the table below.

TABLE D.

Collections of winged females from red blister and green leaf to show the type of antenna.

	Total Number collected.	Red Blister Type.		Green Leaf Type.		Undetermined.	
		Number.	Per cent. of Total.	Number.	Per cent. of Total.	Number.	Per cent. of Total.
Red blister collection .	174	173	99.4	1	.05	...	...
Green leaf collection .	73	6	7.19	65	78.2	12	14.3

The occurrence of the red blister type in the collection from green leaves may possibly be explained by the fact that the winged females are

more vagrant than the apterous, and crawl away soon after emerging; but as the blisters are already crowded with nymphs and larvæ, they cannot establish themselves elsewhere. Hence it is not surprising that some were taken resting on the surrounding leaves. The green leaf collection is smaller than that from the red blister because the former migrants emerged a few days earlier than the latter, and their maximum swarm was already past.

Correlated with the absence of supplementary sensoria on Joint V is the greater distance of the permanent sensoria of V and VI from the articulation of these two joints. This will be best understood by reference to fig. 3, where the curve of error of sixty females from red blisters is compared with that of the same number from green leaves; or to Table E, which shows the average distance between the articulation and the sensoria of both joints.*

TABLE E.

Variation in respect of the distance between the permanent sensoria of, and the articulation between, Joint V and Joint VI.

	Total Number taken.	Average Dis- tance between Sensorium of V and Articulation.	Average Dis- tance between Sensorium of VI and Articulation.	Average Total Distance between the two Permanent Sensoria.
Red blister collection .	60	mm. 3.20	mm. 7.09	mm. 10.39
Red blister stock trans- ferred in first instar to green leaves.	38	3.23	7.24	10.26
Red blister stock, first gen- eration reared on green leaves.	60	3.40	7.52	11.34
Green leaf collection . .	60	5.42	8.13	14.14

The foregoing data show that there is foundation for the distinction between red blister and green leaf types; and the generation series of observations show conclusively that they are dimorphic forms of the same

* Some writers consider that the form of the cornicles is of taxonomic value in determining *M. ribis* and allied species; but after examination of all the material at my disposal, it is evident that forms with clavate and cylindrical cornicles may occur in the same brood, and that food does not seem to be entirely the determining factor. There is certainly a decided preponderance of cylindrical cornicles among forms with the red blister type of antenna, and of clavate cornicles among those from green leaves; but the two features are not altogether correlated, and at present I am inclined to regard the difference in cornicles merely as an individual variation.

FIG. 3.—Curves showing the relations of the permanent sensoria to the articulation of Joints V and VI. Sixty individuals in each curve.

— = Red blister form.
 - - - = " " First generation on green leaf.
 = Green leaf form.

FIG. 4.—Curves showing the relations of the permanent sensoria to the articulation of Joints V and VI.

— = Red blister form (60 individuals).
 = Their progeny transferred in first-instar to green leaves (38 individuals).

The abscissæ represent the difference in $\frac{1}{100}$ mm. between the sensorium and the articulation. The lower curves refer to the fifth, and the upper to the sixth, joint.

species. Here the descendants of two stem mothers were followed down in each case through four lines of descent. Six of these lines of both stocks were fed entirely on green leaves, but the seventh and eighth (by a coincidence in both instances it was the youngest of both series) were fed on blistered leaves. The result was that all the latter had the red blister type of antenna, while all the rest, irrespective of generation, had the green leaf type. That position in the brood had nothing to do with the modification is shown by the A II, B II, A III, and B III lines of descent. Here

FIG. 5.—Curve showing the relation of the permanent sensoria to the articulation of Joints V and VI in nine females of red blister stock reared for three generations on green leaves.

The abscissæ represent the difference in $\frac{1}{100}$ mm. between the sensorium and the articulation. The lower curves refer to the fifth, and the upper to the sixth, joint.

(see generation series) an attempt was made to check the eldest of eldest and youngest of youngest lines by choosing alternately the eldest and youngest of the brood as parent to the next generation.

All the winged forms of these four “control” lines of descent have the green leaf type of antenna.

The question arises what is the cause of the modification of the antenna in this species? Taking as a working hypothesis that it is due to something in the food, I tried the effect of rearing thirty-eight young of a female of red blister stock on green leaves from their first instar; but the result was on the whole negative, although the range of variation in the

sixth joint was rather greater (fig. 4). In dealing with sixty females of red blister stock, whose apterous parents had been transferred to green leaves (=first generation on green leaf) the result was a little more conclusive (fig. 3). The mode remains the same, but the curve has a tendency to form a "shoulder" falling near the mode of the green leaf curve. The second generation on green leaves were all apterous, and in the third generation only nine winged forms appeared. This number is too small for any conclusion to be drawn, though a tendency to shift the mode of the curve towards the mode of the green leaf type is apparent (fig. 5).

A defect in these feeding experiments in 1918 was that I did not recognise the significance of the character of the food until the production of the winged forms was at its height. This occurred in the third and fourth generations, after which, for the rest of the summer, reproduction was limited to apterous forms which do not show the required characters. Next year it is hoped to carry out the feeding experiments from the first, and thus obtain more data on the subject.

TABLE F.

Table for comparison with Table D, to show the effect of rearing the red blister form on green leaves. Only the presence or absence of supplementary sensoria is considered here. For the position of the permanent sensoria, see Table E.

	Total Number examined.	Red Blister Type (many Sensoria).		Green Leaf Type (few Sensoria).		Undetermined.	
		Number.	Per cent. of Total.	Number.	Per cent. of Total.	Number.	Per cent. of Total.
Red blister form: transferred in first instar to green leaf.	47	36	76	10	21	1	.01
Red blister form: first generation on green leaf.	73	56	76	17	23	...	...
Red blister form: third generation on green leaf.	9	...	...	9	100	...	...

Kelly (18) recorded a difference in the ratio of Joint III to Joint IV of the antenna between forms of *Aphis rumicis* reared on opium poppy and nasturtium respectively; but he did not ascertain whether this was due to the nature of the food, or to dealing with two different strains of aphides. The conclusion from his further researches among the progeny of poppy-fed females only, was that the progeny of somatically different mothers tend on the average to be alike, and that somatic variations in the par-

thenogenetic line are not inherited; but the number was small, and it was not shown whether the somatic variations recorded were adaptations to the special environment of the parent, or to a fixed characteristic of the strain employed. If the latter, the results were in accordance with the known rule that children of much varying parents tend to regress to the mean of the race.

MYZUS WHITEI, THEOBALD, AND MYZUS DISPAR, PATCH.

Two species closely resembling *M. ribis*, Linn., have been recorded from England and America respectively.

Theobald (27, p. 110) describes *M. whitei*, taken in the winged form only, on black and red currants. He says that it might be mistaken for *M. ribis*, but it is darker, the three to seven sensoria occur only on the proximal half of Joint V, the abdominal markings are distinctive, and the eyes are dark. A coloured plate of the two species is given, in which, however, both are figured with the red eyes of *M. ribis*. It has been shown already that the sensoria on Joint V are extremely variable, and therefore cannot alone be made the basis of a new species. As regards the abdominal markings, *M. ribis* is figured with three distinct transverse bands on segments 5-7, and four lateral spots on each side of segments 2-5, *M. whitei* is shown with a single large patch on segments 4-6, and two lateral spots on 2-3. Hitherto all the specimens that I have seen of *M. ribis* have had the square abdominal patch ascribed by Theobald to *M. whitei*. The lateral spots vary, but are generally three in number on segments 3-5, though some specimens have two (on 4-5) or four (on 2-5). I thought at first that the green leaf form might be identical with *M. whitei*; but this explanation will not cover the discrepancy of the colour of the eyes and abdominal markings. Flogel (11) does not mention the abdominal pattern in the parthenogenetic female, but he figures the winged male with a single large spot, exactly similar to that of *M. whitei*. Kaltenbach (16) says that *M. ribis* has a square patch in the middle of the abdomen, and three or four smaller ones at the sides. Koch's figure (19) resembles Theobald's *M. ribis* in having three distinct regular bands, but in the text he says: "On the back of the abdomen is a confluent black mark ('ein gemeinschaftlicher Fleck') on the 4th, 5th, and 6th segments; and in addition, at the side of the four anterior segments, a small mark also black." These descriptions apply better to the *M. whitei* than to the *M. ribis* of Theobald's figures; and I am inclined to think that *M. whitei* may prove to be only a variety of *M. ribis*, especially as Patch (23) remarks that in some collections of the latter species the

markings "extend across the abdomen in transverse bands instead of a solid patch."

M. dispar was first described by Miss Patch (23) from specimens taken together with *M. ribis* on gooseberry and currant in America. Dobrovliansky (9) also records it from black currant in Russia. The apterous form is green, and the alate form is very pale green, with three vivid longitudinal lines and a few blackish transverse markings on the caudal half of the abdomen. The pupa is pale green, and when nearly ready for the final moult, it has the thoracic lobes pellucid brown like the thorax of the winged female. I have already remarked that the colour of *M. ribis* varies with the character of the food, and therefore specific distinctions cannot be based on the colour of the wingless female; but the abdominal markings of the winged form do not correspond with those of *M. ribis*, nor does the dark thorax of the nymph. But for these differences, I should have been inclined to think that *M. dispar* was nothing but the green leaf form of *M. ribis*, for the author goes on to make a distinction between the antennal joints of the two species, which is precisely the difference which I have shown to exist between the two forms of *M. ribis*. She says: "In *ribis*, the terminal sensorium in Joint V and the sensorium at the base of the spur in Joint VI approximate the articulation between V and VI much more closely than is the case with *dispar*. Joint III is more slender in *ribis*, and the sensoria are proportionately larger. . . . The cornicles of *dispar* are relatively shorter and less slender than those of *ribis*."

It was this observation of Patch which led me to take the measurements between the permanent sensoria (fig. 3). Before, I had based the distinction between the green leaf and red blister forms only on the presence or absence of supplementary sensoria on Joint V. Patch does not mention the latter feature in the text, but she gives two excellent figures, in which *M. ribis* is shown with supplementary sensoria on this joint, and *M. dispar* with none at all. With regard to the cornicles—the cornicles of the green leaf form of *ribis* are proportionately shorter than those from the red blister.

In spite of the difference in colouring, which possibly may be accounted for by another climate, I incline to the view that *M. dispar* may prove to be identical with the green leaf form of *M. ribis*.

THE LIFE-CYCLE.

The life-cycle of *M. ribis* has been treated by several writers, notably by Kaltenbach, Koch, and Flogel in Germany, by Buckton and Theobald

in England, and by E. M. Patch in America, but until recently the fate of the aphid in the late summer has been a mystery. It was well known that this species appeared on the currant as the stem mother at the end of March or beginning of April, and reached its maximum abundance in June. During July it became scarcer, the red blisters were emptied, and in August it vanished altogether except for an occasional apterous female. It was an open question whether these remaining females were able to maintain the race until the autumn, when they gave birth to the winged males and wingless females, which, after copulation, produced the winter eggs; or whether there was an emigration to a second host plant in June, followed by a return migration in autumn of males and gynoparae, such as Börner (1) has shown for *Rhopalosiphum ribis*.

On June 21st, in a cornfield near Cambridge, I found a plant of *Galeopsis tetrahit* infested with the apterous forms and nymphs of a species first described by Kaltenbach as *Aphis galeopsidis*, and later by Passerini and Buckton as *Phorodon galeopsidis*. In spite of their greater size, I was struck at once by their resemblance to *M. ribis*, and this impression was confirmed a few days later when the winged females appeared.

I took six apterous, and two alate, females of *M. ribis* from the generation series (A. I, 7) and transferred them to a potted plant of *Galeopsis*.* In two or three hours they had all settled down to feed, and by the next morning were producing young freely. Both *P. galeopsidis* and the transferred *M. ribis* attach themselves closely to the under side of the leaves, which when young have a tendency to curl round the aphides in the axis of the mid-rib. I continued to rear this stock of transferred *M. ribis* throughout the summer. During drought, when it became difficult to obtain fresh plants of *Galeopsis*, I substituted *Lamium purpureum* with complete success, but the aphides died within twenty-four hours when placed on such aromatic Labiatae as *Mentha* or *Nepeta*.

About the same time, I collected plants of *Galeopsis* infested with *P. galeopsidis* in two other places near Cambridge, and likewise found this species on *Lamium purpureum* and *Lamium amplexicaule*. Early in July I observed the apterous forms swarming under the leaves of *Veronica*

* At this time I was not aware of the experiments of Gillette and Bragg (*Jour. Econ. Ent.*, Concord, vol. x, 1917, p. 388), who successfully transferred examples of *M. ribis* from *Ribes* to *Stachys* and *Leonurus*, and autumn forms back from these plants to currant. The writers suggest that Kaltenbach and Koch may have had this species under observation as *galeopsidis*, but do not discuss the discrepancies in the description of the two forms by the first-named observer. Kaltenbach (*Die Pflanzenfeinde*, p. 484) gives *Aphis lamii*, Koch, as a possible synonym of his own *galeopsidis*; but Koch cannot have referred to this species, since he describes his *lamii* with dark cornicles.

polita. They had already been severely parasitised by a hymenopteron, and a fortnight later had completely disappeared. During August and September I failed to find this species on any plant in the open.

P. galeopsidis was first described by Kaltenbach in his monograph (16, p. 35), and the description does not differ fundamentally from that of *M. ribis* in the same work. He says that in the apterous forms, *ribis* is citron-yellow with a very short cauda, while *galeopsidis* is green and the cauda is "small." Further on he mentions that *ribis* is found under swellings on the leaves, and the explanation suggests itself that he wrote his account of *ribis* from the form from the red blisters, which, as I have

FIG. 6.—The development of the frontal tubercles. Semi-diagrammatic.

- (a) *Myzus ribis*, winged ♀ from red blister.
 (b) " " " " " green leaf.
 (c) " " " " " first generation after transference to *Galeopsis tetrahit*.
 (d) *Phorodon galeopsidis*, Kalt., winged ♀ from *Galeopsis tetrahit*.
 (e) *Myzus ribis*, ♂ from currant.

already shown, is yellow, and shorter in the body than the form from the green leaves. As regards the winged female, he says that the rostrum reaches to the second coxæ in *ribis*, whereas in *galeopsidis* it does not; but in all the examples that I found on *Galeopsis* the rostrum is indistinguishable from that of *ribis*. Moreover, he continues that the first antennal joint is drawn into a strong tooth. This accounts for the subsequent inclusion of the species by Passerini in his genus *Phorodon*, which, as Buckton points out, differs from *Myzus* only in the possession of a tooth on Joint I. It will be seen from fig. 6 that no distinction can be made between the forms in this respect. Furthermore, Kaltenbach describes *M. ribis* with a large dorsal patch on the abdomen, and three

or four smaller spots at the sides; and *galeopsidis* with a threefold spot in front of the cornicles, and two separate bands anterior to it. An examination of the twelve examples of each form measured in Table C shows that lateral spots may occur in *galeopsidis*, and bands on the anterior segments of the abdomen of *ribis*. The latter vary much, and in the red blister form often appear only as a narrow streak behind the metathorax, but in some specimens from green leaves they are nearly as pronounced

FIG. 7.—Diagrams of the abdominal pattern of

- (a) *Myzus ribis*, winged ♀ from red blister.
 (b) " " " " " green leaf.
 (c) " " " " " of the first generation after transference to *Galeopsis tetrahit*.
 (d) *Phorodon galeopsidis*, Kalt., from *Galeopsis tetrahit*.

as in *galeopsidis*. In fact, when females from red-blistered currants and *Galeopsis* are compared, it would be a pardonable mistake to refer them to different species. It is only when a series is examined that the differences are found to be linked together completely by a chain of intermediate forms (fig. 7).

The first females of *M. ribis* transferred to *Galeopsis* did not show any appreciable effects of the change, but their progeny (A. I, 8 from the fundatrix on currant) were remarkable for an increase of size in both winged and wingless forms. The latter, breeding females and nymphs, were indistinguishable from similar examples of *P. galeopsidis*.

With regard to the winged females, circumstances prevented me from taking the average dimensions of a number when living; and as abdominal measurements of spirit specimens are unreliable, the lengths of the antenna, forewing, and cornicle alone are given in Table H, as these structures do not shrink in alcohol. However, I include the dimensions of a single female of this generation, mounted alive in balsam (Table G). The decrease in size of the later generation in Table H is perhaps due to malnutrition, for during drought in August it was sometimes difficult to procure sufficient fresh food.

It seems, then, that the summer host-plants of *M. ribis* are certain of the Labiatae and other weeds, and that this aphid has been described previously during its second cycle as a different species, *P. galeopsidis*, Kalténbach. The synonymy of this species is rather involved. Davis (6) records *P. galeopsidis* from *Polygonum* in America. His description closely resembles that of the form I have identified as *P. galeopsidis*, except that he says the pupa has a dorsal longitudinal red line, which is even more marked in the immature male. But Gillette (13) points out that Davis was actually describing *Rhopalosiphum hippophææ*, Koch, and he gives *P. galeopsidis* as a synonym of that species. In America *Hippophææ* is the winter host of two allied species—*R. hippophææ*, with clavate cornicles, migrating to *Polygonum*, and *M. braggi*, Gillette, with cylindrical cornicles, migrating to Compositae. It is just possible that the latter may be identical with *M. carthusianus*, of which I described an apterous female taken from the thistle (15). Gillette believes that Buckton confused these two species under the name *galeopsidis*, figuring the apterous form of *braggi* and the alate form of *hippophææ*. Mordwilko (20) discusses the life-history of *R. hippophææ*, and says that Ferrari took the summer migrants from *Inula graveola*. Altogether the synonymy of this group is by no means clear; but it cannot be settled without further knowledge of the bionomics and of the sexual forms of these species, both in Europe and America. Until then, the best course seems to be to identify the summer migrants of *M. ribis* with the *P. galeopsidis* of Kalténbach.

The following is a list of plants from which the latter species has been described by other writers:—

<i>Galeopsis tetrahit</i>	.	.	.	Kalténbach.
„ <i>bifida</i>	.	.	.	„
„ <i>versicolor</i>	.	.	.	„
<i>Lamium album</i>	.	.	.	„ and Buckton.
„ <i>purpureum</i>	.	.	.	„
„ <i>amplexicaule</i>	.	.	.	„

<i>Stachys sylvatica</i>	.	.	.	Kaltenbach and Buckton.
<i>Polygonum persicaria</i>	.	.	.	Buckton.
„ <i>hydropiper</i>	.	.	.	Kaltenbach.
„ <i>laxiflorum</i>	.	.	.	„
„ <i>lapathifolium</i>	.	.	.	„

With regard to the distribution of the sensoria on Joint V, out of forty-one specimens collected in the field on June 25th, thirteen had the red blister and twenty-eight the green leaf type. From this it may be inferred that both forms are migratory from the currant, for the early date precludes the idea that they could have been established on the *Galeopsis* long enough for the change of host to have affected the antennal development. I was not able to determine whether the type remained constant through several generations on *Galeopsis*, because in the laboratory this stock produced a few apterous generations only and then died out. The green leaf form introduced from currant produced only the green leaf type of Joint V, though in the first generation on *Galeopsis*, nine examples out of thirty-eight had a number of small sensoria all over the shaft of the joint, but this did not appear in the later generations.

I made several attempts to transfer different generations of this stock back to currant, but they were invariably unsuccessful, as the following extracts from my notes show :—

July 18. Transferred two winged and five wingless females (second generation on *Galeopsis*) back to currant.

July 19. Feeding and produced two young.

July 21. All dead but two wingless forms which have lost their green translucent colour and become yellow and opaque.

July 25. Both females dead.

Later experiments always failed, and the aphides died in a few days without reproducing. Even in autumn, when it might have been supposed that a return migration to currant would take place, neither winged nor wingless forms re-established themselves, but crawled about the cage until they died of exhaustion. This inability to live on the first host after transference to the second is curious. At first I thought it might be explained by a structural change, such as is suggested by Kaltenbach's statement of a shortened rostrum in *galeopsidis* as compared with *ribis*, but on examination both of these, and of transferred forms, I can find no difference at all.

TABLE G.

Dimensions of alate female of *Myzus ribis*. First generation on *Galeopsis tetrahit*.

	Absolute Dimensions.	Dimensions expressed as per cent. of Length of Forewing.
	mm.	per cent.
Length of forewing	3.13	100
Length of body	2.26	7
Breadth across abdomen	.72	23
Breadth between cornicles	.30	9
Total length of antenna	2.80	89
Length of cornicles	.20	6

TABLE H.

Average dimensions of twelve alate females of *Myzus ribis*. First generation on *Galeopsis tetrahit*.

	Average Absolute Dimensions.	Dimensions expressed as per cent. of Length of Forewing.
	mm.	per cent.
Length of forewing	3.43	100
Total length of antenna	2.91	84
Length of cornicles	.25	7

THE GENERATION SERIES.

The generations descended from two stem mothers, A and B, were followed throughout the summer. Four lines of descent were chosen from each stock:—

A (B) I = eldest-born of eldest-born.

A (B) II = } eldest- and youngest-born chosen alternately from
A (B) III = } each generation.

A (B) IV = youngest-born of youngest-born.

The second and third lines were intended only as controls in case it should prove desirable to obtain a mean between the eldest and youngest series.

These observations were made on aphides kept in the laboratory. I intended to have identical series, founded from the laboratory stock, "sleeved" on currant bushes in the garden under entirely natural conditions; but in wet, windy weather it was found impossible to make accurate records each day of the number of young, etc. Details were therefore discontinued, but the garden series were maintained as controls for the

laboratory observations, the eldest-born of each generation being chosen as the parent of the next. The three garden series became extinct in August. In the nine weeks from June 2nd to August 10th they passed through five and four and five generations respectively, while during approximately the same time the A. I and B. I series in the laboratory passed through seven and five generations. I am inclined to account for their survival when the controls in the open disappeared, by the fact that they were better protected against enemies; for the well-known disappearance of the red-currant aphid in the late summer seems to be partly natural, and due to the diminished birth-rate, and partly accidental, owing to the increase of insect enemies.

The laboratory series passed altogether through fifteen of the eldest, and five of the youngest, generations. Eight of the A. I, 7 generation were transferred to *Galeopsis tetrahit*, and (including the cycle on the second host) this line of descent passed through eighteen generations. The B. I series passed through only eleven generations. Throughout the summer it was noticeably less productive than the other, and at the B. I, 5 generation there was a long period of inactivity. The parent—the apterous progeny of a winged female—delayed the fourth moult for over three weeks, and then died after producing three young at irregular intervals.

Winged females may occur in the first generation, but my records show that the maximum of these forms appeared in the fourth generation in each eldest line of descent (fig. 8), but in A. IV and B. IV it occurred in the third and second respectively. From this it may be inferred that the appearance of winged individuals is not governed by position in the line of descent. On the observation bushes in the garden, the maximum appearance of the winged forms was some days earlier on green leaves than on red blisters.

In mixed generations, the earlier births seem to be composed as a rule of both alate and apterous forms, while the later ones are nearly all alate. This rather supports the view that exhaustion of the parent may induce their appearance, but this is not borne out by the control lines (A. II, A. III, B. II, B. III), in which eldest and youngest were taken alternately in each generation. Mordwilko (22, p. 82) says that the appearance of winged females is accelerated by lack of food; and this view is held by Davis (5, p. 132) for *Aphis maidi-radici*, by Webster and Phillips (28, p. 82) for *Toxoptera graminum*, and by Buckton. As much evidence can be found against as for this theory, which rests on general statements and not on facts established by experiment. For instance, in *M. ribis* the maximum swarm of winged forms occurs just when food is most plentiful.

Börner (1) points out that in autumn *Rhopalosiphum lactucae* produces a host of apterous females, whose attack causes the plant to sicken and die, and yet no winged forms appear. He also records some observations on the "hop louse," where a healthy plant produced more alate females than a sickly one, but more evidence is needed on this subject. It is most probable that a change in the metabolic products of the host plant, such

FIG. 8.—Curves showing the proportion of alate to apterous forms in the generation series, A.I.

— = Apterous forms.
 = Alate forms.

The abscissæ = the generations.

as a seasonal increase of tannins, may tend to the development of winged forms, but at present we are quite in the dark as to what this change may be. It is certain only that insufficiency of food alone cannot produce this result.

The average number of young per day per aphid throughout the productive period was 2.8; and the largest number of births from a single aphid in twenty-four hours was 12. Fertility diminished towards the end of the life of the female until there was sometimes an interval of several

days between the births. Fig. 9 shows the total number of progeny in each of the A. I generations. The maxima occur in the third, fifth, and eighth generations, and are succeeded by a gradual decline as autumn approaches. The curve formed by the total length of life of the parent

FIG. 9.—Curves to show the total number of young produced in each of the A. I generation series, and the longevity of the mother.

— = Total number of young of each ♀.
 = Length of life of ♀.

The abscissæ = the number of the generations.

is superimposed, and shows that the diminution in the birth-curve is a real decrease in fertility, and not a shortening of the life of the mother. This agrees with the observations of Davis on *Macrosiphum pisi* and *Aphis maidi-radici*, and of Webster on *Toxoptera graminum*.

Fig. 9 represents as nearly as possible the total number of young born

in each generation. Fig. 8 shows only those identified as alate or apterous. Thus the numbers are not the same for the two curves, because the forms cannot be distinguished from one another until the third instar. As I have remarked elsewhere, there is a large mortality in the early stages, and therefore only a proportion of the actual number born were available in making fig. 8. From a comparison of the figures this mortality seems to have been about 25-35 per cent.

M. ribis is prolific, and an apterous female may give birth to over a hundred young. The generation records show no difference in fertility between the eldest and youngest lines of descent. In fact, the highest number was 128, born of a female of the B. IV, 1 generation. The average number of young per aphid in the two eldest lines was 33.2, and in the two youngest 48.7. The B. I generations were less prolific than the A. I, although they were kept under similar conditions, and this was also the case when the other lines of the two stocks were compared, except as regards B. IV, 1. To test the relative fertility and longevity of the red blister and green leaf mothers, I made a number of observations apart from the generation series, but there seemed to be no constant difference between them.

The winged forms are less productive than the wingless, and on the whole they are not so long-lived. In the former respect my observations agree with those of Webster on *Toxoptera* (28, p. 75). The alate females are more vagrant than those of most aphides and scatter their young promiscuously over the leaves. Their progeny may be either winged or wingless; but the only exact data I have as to the proportions in which the two forms occur in such a brood is from the generation series, where A. I, 5, B. I, 3, and B. I, 5 were derived from winged mothers, and the percentage of winged forms in these were 68, 40, and 13 respectively.

Reproduction by the winged forms does not begin for some hours, or even days, after emerging; but the insects are very sensitive to light, and after a period of sterility may sometimes be induced to give birth by removal to bright sunshine. In the case of A. I, 4, the aphid, after producing two young, remained inactive for four days. She was then put in the sun, and within ten minutes had dropped three larvæ. The winged aphides are distinctly phototropic and invariably fly to the window or other source of light. The apterous forms seem much less sensitive in this respect.

After transference to *Galeopsis*, the fertility of the females does not change much. During July and August five females under observation produced on an average 38.3 young each, with a maximum of eight in the twenty-four hours. On the other hand, the proportion of winged forms was high and appeared in each generation, although exact numbers

were not taken. These females, soon after emerging, began to reproduce on their birth plant.

It is worth remarking that apterous females of *M. ribis* were transferred to *Galeopsis*, for this disposes of the view sometimes held that only certain forms are morphologically or physiologically suited to live on the second host plant, and that the winged migrants leave the first host because they are unfitted to feed there. Last summer I proved that the apterous females of *Rhopalosiphum capreae*, Fab. can live equally well upon *Salix* or *Umbelliferae*. Mordwilko (20) showed that *Aphis sambuci*, Linn., from the elder tree, could live and reproduce upon *Lychnis*, and I have repeated his experiment, using the apterous forms with complete success.

It is the more remarkable that attempts to transfer *M. ribis* back from *Labiatae* to currant invariably failed, although no structural difference beyond an increase in size could be detected between forms reared on the two plants. A similar and even more striking case is that of *Aphis grossulariae*, Kalt. (= *viburni*, Schrank). Here, after the first generation from the migrants, it is impossible artificially to establish the currant form back on the parent *viburnum*, although the *viburnum* form can, with some difficulty, be cultivated on the currant. Meanwhile two stocks, both founded by natural migrants from *viburnum*, breed throughout the summer on currant and *viburnum* respectively, and are structurally indistinguishable.*

TABLE I.

Control lines of descent showing per cent. of winged forms in each generation.

Generation.	Parent.	Per cent. of Winged Forms.	Generation.	Parent.	Per cent. of Winged Forms.
A. II, 2 . .	Youngest	40	B. II, 2 . .	Eldest	74
A. II, 3 . .	Eldest	33	B. II, 3 . .	Youngest	11
A. II, 4 . .	Youngest	16	B. II, 4 . .	Eldest	52
A. II, 5 . .	Eldest	17	B. II, 5 . .	Youngest	0
A. II, 6 . .	Youngest	7	B. II, 6 . .	Eldest	0
A. II, 7 . .	Eldest	0	B. II, 7 . .	Eldest	0
A. III, 2 . .	Youngest	51	B. III, 2 . .	Youngest	27
A. III, 3 . .	Eldest	48	B. III, 3 . .	Eldest	27
A. III, 4 . .	Youngest	29	B. III, 4 . .	Youngest	7
A. III, 5 . .	Eldest	7	B. III, 5 . .	Eldest	38
A. III, 6 . .	Youngest	9	B. III, 6 . .	Youngest	0
A. III, 7 . .	Eldest	0	B. III, 7 . .	Eldest	0

* Since the above went to press, I have found young fundatrices of *Aphis grossulariae* on red currant. It is possible, therefore, that this species may undergo a complete cycle on *Ribes*.

TABLE J.
The Generation Series.

Generation Number.	Date of Birth.	Age at Birth of Young.	Reproductive Period.	Number of Young.	Average Number of Young per Day of Productive Period.	Largest Number of Young per Day.	Date of Death.	Total Length of Life.
A.	...	...	17 days	77	4.9	7	20/v/18	...
B.	...	...	+ 17 "	44	...	4	20/v/18	...
A. I, 1	3/v/18	13 days	5 "	24	4.4	7	20/v/18	17 days
B. I, 1	3/v/18	14 "	3 "	11	3.2	6	20/v/18	17 "
A. I, 2	15/v/18	5 "	13 "	61	4.9	9	8/vi/18	24 "
*B. I, 2	16/v/18	12 "	5 "	5	1	4	3/vi/18	18 "
A. I, 3	19/v/18	2 "	33 "	102	3.3	9	27/vi/18	39 "
B. I, 3	27/v/18	11 "	12 "	40	3.4	6	18/vi/18	22 "
*A. I, 4	21/v/18	11 "	6 "	24	4.0	12	8/vi/18	18 "
*B. I, 4	6/vi/18	15 "	10 "	20	2.0	5	30/vi/18	24 "
A. I, 5	1/vi/18	11 "	25 "	80	3.5	8	6/vii/18	36 "
B. I, 5	20/vi/18	14 "	8 "	7	.7	1	13/vii/18	23 "
A. I, 6	11/vi/18	8 "	17 "	41	2.7	6	6/vii/18	25 "
B. I, 6	3/vii/18	24 "	21 "	19	.9	6	16/viii/18	44 "
A. I, 7	18/vi/18	11 "	8 "	39	4.9	9	6/vii/18	18 "
B. I, 7	26/vii/18	17 "	13 "	32	2.6	7	26/viii/18	31 "
A. I, 8	29/vi/18	11 "	18 "	97	5.7	10	27/vii/18	28 "
B. I, 8	10/viii/18	10 "	5 "	16	3.1	7	26/viii/18	16 "
A. I, 9	9/vii/18	15 "	12 "	50	4.2	10	6/viii/18	28 "
B. I, 9	20/viii/18	12 "	9 "	7	.7	2	9/ix/18	21 "
A. I, 10	23/vii/18	6 "	3 "	30	10	10	1/viii/18	9 "
B. I, 10	31/viii/18	10 "	9 "	3	.3	1	19/ix/18	19 "
A. I, 11	28/vii/18	6 "	18 "	35	1.17	7	23/viii/18	26 "
A. I, 12	3/viii/18	21 "	16 "	20	1.4	4	18/ix/18	46 "
A. I, 13	23/viii/18	23 "	2 "	9	4.1	6	24/ix/18	32 "
A. I, 14	14/ix/18	11 "	4 "	6	1.2	3	23/x/18	40 "
A. I, 15	25/ix/18			Sexual forms				
A. IV, 1	19/v/18	4 "	19 "	50	2.12	7	12/vi/18	24 "
B. IV, 1	13/v/18	7 "	28 "	120	4.8	10	18/vi/18	36 "
A. IV, 2	10/vi/18	15 "	37 "	104	2.30	6	6/vii/18	26 "
B. IV, 2	18/vi/18	12 "	16 "	11	.6	3	18/vii/18	30 "
A. IV, 3	31/vii/18	3 "	23 "	62	2.16	5	25/viii/18	25 "
B. IV, 3	15/vii/18	29 "	17 "	13	.7	3	31/viii/18	47 "
A. IV, 4	24/viii/18	4 "	7 "	28	4.0	9	8/ix/18	15 "
B. IV, 4	28/viii/18	11 "	2 "	2	1.0	1	22/ix/18	25 "

* The asterisk denotes a winged female.

ECDYSIS.

M. ribis has a large mortality in the first and second instars, and during observations on the moulting of sixteen individuals, only nine reached maturity. The aphides were frequently found dead in the first and second moults. Mr Brindley tells me that he has observed an appreciable mortality among cockroaches from entanglement with the tracheal tubes during ecdysis, and it is possible that this may hold for aphides also.

This aphid, whether alate or apterous, like all others whose post-embryonic development is known, normally moults four times. The period of immaturity is variable and may be anything between six and nineteen days.

TABLE K.
Variation in the duration of the different instars.

Date of Birth.	Period between Birth and First Moul.	Period between First and Second Moults.	Period between Second and Third Moults.	Period between Third and Fourth Moults.	Period between Fourth and Fifth Moults.	Period between last Moul and Birth of Young.	Total Length of Immaturity.
June 22, 3 p.m. . . .	5 days + 19 hours.	4 days.	3 days.	2 days.	...	5 days.	19 + days.
July 2, 6 p.m.	2 days + 16 hours.	1 day.	2 "	1 day.	8 days.	6 "	20 + "
June 9, noon (winged female).	1 day + 22 hours.	4 days.	3 "	3 days.	...	...	12 "
May 29, 3.30 p.m. . .	1 day + 19 hours.	3 "	2 "	6 "	...	3 "	15 + "
June 21, 6.30 p.m. . .	15 hours.	3 "	4 "	1 day.	...	1 day.	10 "
June 9	2 days.	3 "	2 "	3 days.	...	3 days.	13 "
July 2, 3 p.m.	1 day + 19 hours.	1 day.	1 day.	1 day.	1 day.	...	5 + "
July 10	2 days.	2 days.	4 days.	4 days.	...	4 "	16 "
July 11, 5 p.m. . . .	Two moults in first 24 hours.	...	6 "	4 "	...	5 "	16 "
Averages.	2 days + 4 hours.	2 "	3 "	2 "	...	4 "	14 + "

Only one of the nine aphides included in Table K was winged, and she became mature in twelve days. Subsequent observations on the generation series showed that protracted development does not necessarily

result in winged forms. For instance, five apterous females of the fifth generation took twenty-three days to complete their ecdyses, while alate forms of the second and fourth generations were respectively eleven and ten days in attaining maturity.

Moreover, these observations on *M. ribis* show that in certain cases the female may have a fifth moult subsequent to the birth of young. It is claimed that a fifth moult has likewise been noticed exceptionally in *Macrosiphum pisi*; and Davis records a case where an apterous female of *Aphis maidi-radici*s produced six young, then moulted, became winged, and gave birth to twenty-one more.

As two of the nine examples of *M. ribis* under observation thus underwent a fifth moult, it seems likely that this is not an uncommon occurrence; but unless looked for, it is easily missed. Moreover, on May 25th, an apterous female of the generation series, which had already produced twelve young, was found in ecdysis.

THE SEXUAL FORMS.

The sexual forms have been already figured and minutely described by Flogel (11), and further description is unnecessary here except as regards the frontal tubercles in the male. Flogel remarks that they are almost absent in this sex, and his figure and that of Buckton (2, Plate xxxii, fig. 6) represent the head nearly as flat as in *Aphis*. In the males from my collection, including individuals from both first and second host plants, the tubercles are quite well developed, although less conspicuous than in the viviparous females. Moreover, a winged female occurred in the A. IV, 3 generation, whose head much resembled that of Flogel's figure. Hence the presence or absence of frontal tubercles is not always a sexual character.

Sexual forms first appeared in the generation series on August 22nd. The apterous mother, A. I, 11, produced thirty-five young, of which the eight eldest were males. At this time no oviparous females had appeared and the males died without mating. A few days later (September 5th) three oviparous females occurred in the B. II, 9 generation, which was the progeny of an apterous female, while the rest of the brood were wingless viviparous forms. After this oviparous females appeared in generations A. I, 14, A. II, 9, A. III, 8, A. IV, 5, and B. II, 10. In every case the mother was apterous, and the rest of the brood were wingless and viviparous. In mixed broods the sexual forms occurred among the earlier births. At the end of September an apterous female, A. I, 14, produced thirteen young. Nine died soon after birth; of the remaining four, two

were males and two were females. From the first these larvæ, which were reared on the same leaf, were distinct in colour—the males being bright green and the females pale yellow. Subsequently mating took place and eggs were laid.

The period of development of the oviparous females varied between sixteen and forty-five days. That of the males was twenty to twenty-five days. The total length of life ranged from twenty-nine to sixty days for females, and from thirty to thirty-five days for males. Oviposition did not take place until two or three days after copulation. Dissections of eight females yielded on an average five large eggs each, with others at various stages in the ovary. The eggs were occasionally deposited on the leaves, but for the most part the aphides crawled to the stem or into the axils of the buds for the purpose. One male may fertilise two, or probably more, females.

Thus it is clear that migration to the second host plant is not obligatory in this species, since the sexual forms can be produced after an unbroken cycle on currant. Mordwilko (20) writing of *A. sambuci*, Linn., says: "If this species is proved to migrate from elder, we should have the interesting problem of the sexuparæ produced on the first host plant; and this does not occur in any other of the migratory *Aphidinae*." As the foregoing observations show, this is the case with *M. ribis*, a form unique in this respect in the sub-family. Moreover, the males and oviparous females may be produced on the second host plant also, a condition which, as far as I know, does not obtain with any other of the *Aphidinae*.

Winged males appeared at the beginning of October upon *Galeopsis*. They were the progeny of two winged females of the A. I, 17 generation (*ribis* stock transferred to *Galeopsis*) and were indistinguishable from the males born on currant. Buckton (2, p. 172) says that the nymph of the male of *Phorodon galeopsidis* is very small and has a broad head, but these nymphs were identical with those of the winged viviparous females. The males from *Labiatae* mated when placed with oviparous females from currant, and eggs were laid after such unions, but the females were unable to live or oviposit on *Labiatae*.

Until the end of October, no oviparous females appeared among the *Galeopsis* stock. The researches of Mordwilko and others show that in other species of migratory *Aphidinae* the male alone is born on the second host, and that the eggs are never laid there. The observations of Van der Goot (*Beiträge zur Kenntniss des Holländischen Blattlause*) seemed to confirm this for *M. ribis*. He records that migrants of *P. galeopsidis* appeared on currant in the autumn, and that oviposition took place on

that plant; but he doubted whether the species is identical with *M. ribis*, because he failed to establish *M. ribis* upon *Labiatae* in the spring. Buckton (2, p. 172) remarks that he failed to find the oviparous female of *P. galeopsisidis*, and as all observers are agreed that this form appears only from July to September, it seemed to me probable that the males and viviparous mothers of the sexual females returned to currant, and that the eggs were laid there. In the hope of verifying this, I tried repeatedly to transfer the last two viviparous generations to currant, but in every case they died in a day or two without reproducing. It is worth remarking that the males transferred from *Galeopsis* to *Ribes* lived only three or four days, although they fed readily, while on their birth plant they survived for a week or even longer.

On October 26th, an oviparous female (A. I, 18 generation) was found upon *Galeopsis*. Unfortunately it is not certain whether the parent was winged or wingless. This female differed from the oviparous females on *ribis* only by a vivid green and somewhat interrupted line extending along the dorsum. I put her into a tube with a newly-emerged male from *Galeopsis* and copulation took place within two hours. The following day she laid three eggs upon *Lamium* leaves, and died twenty-four hours later.*

It must not be overlooked that this female came of captive stock, and it is quite conceivable that her parent may have been a migrant, who, kept in confinement, was unable to reach the first host plant, and so of necessity produced her young on the second. At the same time it is clear that the oviparous forms of this species may be born, and can oviposit upon *Labiatae* in the laboratory, and there seems no reason why this should not happen in the open, if from any cause *Ribes* is not attainable. The migratory stock from currant might thus under certain circumstances continue indefinitely upon *Labiatae*. The difficulty in the way of this view is that *Galeopsis* and *Lamium* are both annuals, and therefore, even if the egg survived the winter, the fundatrix would be faced with starvation when she appeared in spring. Against this must be put the fact that *Lamium* at any rate is a very common weed, and in sheltered situations seems to flourish all the year round. On the whole, I incline to the view that while permanent colonisation of the second host plant is not usual, it is by no means impossible under certain circumstances.

* Since the above was written, these eggs, which were kept over the winter, have shrivelled up without hatching. Steven ("Biology of the Chermes of Spruce and Larch, and their Relation to Forestry," *Proc. Roy. Soc. Edin.*, vol. xxxvii, 1917, pp. 356-381) remarks that the eggs of *Gallicolæ migrantes* laid on spruce, and of *Gallicolæ non-migrantes* laid on larch, do not hatch. The failure of aphid eggs to hatch on certain food-plants requires further investigation.

The fate of the viviparous forms that remain on Labiatae after the appearance of the sexuales is uncertain, but granted mild weather and sufficient food, there is no reason why they should not continue to reproduce viviparously through the winter. Several *Aphidinae* are known to be able to do this. For instance, Webster and Phillips (28, p. 93) have shown that in the mild winter of the Southern States of America, *Toxoptera graminum* seldom produces sexual forms, but multiplies parthenogenetically throughout the year. Börner (1) has shown that the viviparous generations of *Aphis pruni*, *Hyalopterus trirhodus*, *Rhopalosiphum lactuce*, etc., may live far into, or even survive, the winter; and Mordwilko (20) says the same of *Pemphigus affinis*. Probably this is rare in our climate, for although aphides can stand a good deal of cold, prolonged freezing kills them, as is shown by the experiments of Webster and Phillips (28, p. 92).

Thus the persistence of the viviparous line after the production of the sexuales is really dependent on accidents of temperature. The whole viviparous cycle indeed may be compared biologically to the soma of the individual animal. It exists merely as a vehicle of the germ plasm, and when the future of the species has been ensured by the production of the zygote, it may persist for a time under favourable conditions, but sooner or later disappears.

NATURAL ENEMIES.

More than a hundred and fifty years ago, Bonnet wrote: "Like as we sow grain to provide for our own subsistence, so it appears that nature sows plant-lice on all kinds of trees and plants for the nourishment of multitudes of different insects."

M. ribis has a large share of natural enemies, both predaceous and parasitic. To the former class belong the larvæ of certain Cecidomyiidæ, which devour numbers of the aphides from June onwards. Theobald (27) points out that Syrphid and Coccinellid larvæ seldom attack this species; but I once took two larvæ of the lacewing (*Chrysopa*) from a red blister. Individuals of all ages are persecuted by a mite, *Anystus cornigera*, Koch, though there is no evidence that it ever causes the death of its host. In July, the fungus *Empusa aphidis*, introduced into the laboratory on some aphides taken from *Galeopsis* in the field, was very prevalent for a time on the generation series on Labiatae. Those on currant suffered very little, though kept under identical conditions, and I have seldom found aphides on currant killed by this fungus in the open.

But the principal enemy of *M. ribis* is a small parasitic Braconid,

Aphidius ribis, Haliday. Kaltenbach (16) remarks that out of no aphid did he rear so many Aphidiidæ. My observations on the embryonic and post-embryonic development of this parasite are incomplete, and it is intended here to offer only a few preliminary remarks on a subject which I hope to investigate more fully in the future.

Aphides struck by the *Aphidius* were first found on July 3rd, and were common until the end of August. The female *Aphidius* oviposits within twelve hours after emerging from the pupa, but I never induced her to do so without a previous meal of either "honey-dew" from the aphides, or sugar syrup. If a male is present, mating then takes place and oviposition begins within a few minutes. If no male is at hand, she lays a number of eggs parthenogenetically, varying in number from four to twenty. The number of ovipositions after mating was difficult to determine, but seems to be between thirty and forty. Aphides parasitised in the second and third instars frequently die with the larval Braconid within them. Hence the number of dried and bloated aphid skins found on the leaves cannot be taken as representing by any means the whole control of this pest by the *Aphidius*, for there is undoubtedly a large mortality of the hosts, and incidentally of the parasites within them, which is not recognised as due to this cause. An alate *Myzus* was invariably ignored by the *Aphidius*, and I have never found a winged female or nymph containing the parasite; but whether these forms are not attacked in the early stages, or whether they are unable to complete their development after parasitisation, I am unable to say. The apterous females of *M. ribis* are nearly, if not quite, sterile after the attack. On July 16th I isolated seven mature females which had been exposed to an *Aphidius* two days previously. After eight days, one which seemed healthy had produced twenty-five young, four had died, and three contained the pupæ of the parasite.

The larval life of individuals from the parthenogenetic eggs is about fifteen days, and the pupation is between seven and fifteen days. The larval life of individuals from fertilised eggs is about ten days (though in one exceptional case it was twenty-five days), and pupation is six or seven days. Hence the forms from parthenogenetic eggs develop rather more slowly than the others. Both sexes may arise from unfertilised eggs. From thirty-three parthenogenetic ovipositions I was able to rear only five males and two females. The life of the male is three to four days; that of the female is longer and she may live for a week. I have reared *Aphidius ribis* through three generations in the summer.

The *Myzus* is attacked both in the red blisters and on the green leaves, but my observations go to show a greater number of victims on the latter.

Diagram of the life-cycle of *Myzus ribis*, Linn., from observations on the A.I line

Frequently a parasitised aphid is found clinging to the edge of a leaf—a position it seldom chooses when alive; but it is not known whether aphides who have placed themselves thus are more liable to be struck, or whether they crawl thither at the approach of death. The female *Aphidius* is very indiscriminating, and will not only attack the cast skins of the *Myzus*, but will also try to oviposit in a spot where an aphid has been sucking. She also attacks the same victim repeatedly.

I obtained an *Aphidius* indistinguishable from *A. ribis* from *P. galeopsidis* collected in the field in July, and these oviposited in *M. ribis*, both from currant and Labiatae. I also obtained a single example of a species nearly allied to, if not identical with, *A. roseæ*, Hal.

SUMMARY.

M. ribis, Linn. (red-currant aphid), on *Ribes rubrum* is dimorphic in respect of certain features of the antenna and of abdominal and wing dimensions.

The nature of the food, whether healthy or blistered by the attack of the fundatrix, seems to be the determining factor of this dimorphism.

The form from healthy leaves is probably identical with *M. whitei*, Theobald, and *M. dispar*, Patch.

M. ribis is migratory, and in summer colonises certain Labiatae and other weeds; but this migration is not obligatory, and the entire life-cycle may be passed on currant.

On its summer host plant this species has been previously described as *Phorodon galeopsidis*, Kaltenbach.

There is a decline in fertility in the later part of the summer among the forms remaining on currant.

This is caused by a lower birth-rate, and not by the shortening of the life of the parent.

This decline, together with the attacks of predaceous and parasitic enemies, accounts for the frequent disappearance of the species from currant in August and September.

Both sexual forms may be produced, and eggs may be laid, on either host plant. Males transferred from Labiatae to *Ribes* can fertilise the females on the latter plant.

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