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The Genetics of Mimetic Colour Polymorphism in the Large Narcissus Bulb Fly, Merodon equestris Fab. (Diptera: Syrphidae)

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THE GENETICS OF MIMETIC COLOUR POLYMORPHISM IN THE LARGE NARCISSUS BULB FLY, *MERODON EQUESTRIS* FAB. (DIPTERA: SYRPHIDAE)

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[Plate 39]

CONTENTS

Genetical studies have revealed six gene loci concerned with body hair colour in *Merodon equestris*. These are:

(i) *Bulborum*. Darkens all the thorax including the scutellum except the anterior. The dark allele is dominant.

(ii) The modifier U. In conjunction with *bulborum* this produces the morph *subvalidus*. This is characterized by some sexual dimorphism. These are certain sex differences in the degree of darkening of the second abdominal segment and the female shows a degree of darkening of the anterior thorax. The dominant dark allele only expresses itself when the dominant allele of *bulborum* is present.

(iii) The modifier V. In conjunction with the dominant alleles of *bulborum* and the modifier U only the dominant allele of the modifier V gives the sexually dimorphic colour type *validus*. The second abdominal segment is more or less completely blackened and in the female only the anterior of the thorax is completely blackened.

(iv) *Equestris*. The dominant allele produces a black thoracic band like *bulborum* except that the scutellum is coloured.

(v) *Transversalis*. Expression is limited to the female, although the locus is inherited autosomally. There is a black band on the third abdominal segment.

(vi) Ground colour. There are three alleles determining the distribution of orange and yellow over

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the thorax and abdomen. They are YOYO, OOYY and OOOO, the letters referring to yellow or orange coloration from the anterior of the thorax to the abdomen tip. The dominance is simple: YOYO is dominant to OOYY and OOOO and OOYY is dominant to OOOO. Within the colour types YOYO and OOYY there are colour variants YYYO, YOYY, YYYY and OOOY, OOYO respectively. Orange is dominant to yellow in the YOYO category and yellow dominant to orange in the OOYY category. The OOOO can be regarded as a universal recessive and can be treated as a separate category or as a variant of the OOYY category.

Linkage has been detected between three of the loci. These are *equestris*, *bulborum* and ground colour and the order of mention is the order of linkage on the chromosome. Linkage, however, is not very strong so that some recombination occurs.

Some aspects of the population genetics of the colour polymorphism have been studied using such little data as are available. Linkage disequilibrium has been found in the field for the linked genes *bulborum* and ground colour appears to be strongly maintained.

A listing of potential models for the 34 colour types of *M. equestris* reveals that the colour types most commonly occurring, and maintained at high frequency and in linkage disequilibrium, are the best mimics of bumble bees in the United Kingdom. Some aspects of the evolution of the colour polymorphism in Europe, particularly in relation to the related species *M. flavus* are discussed.

The chromosome number found confirms that found by other workers ($2n = 12$) and polytene chromosomes have been demonstrated in a variety of tissues.

INTRODUCTION

Flies of the family Syrphidae are mostly striking in appearance and some are pests or beneficial predators. Consequently this family is among the best known in the Diptera. Its taxonomy has been reviewed by Verrall (1901), Shannon (1921 *a*, *b*, 1922) and Coe (1953) and general data for Britain are well covered by Colyer & Hammond (1968). Much biological information can be found in papers by Metcalf (1913, 1916, 1917), Heiss (1938) and Schneider (1969). Recently Boyes, Brink & Mehta have made great progress with the cytogenetics of the group (1964, 1966, 1967, 1968, 1970).

Merodon equestris qualifies both as a striking fly and as a pest. Most of the research performed on it to date has been concerned with its role as a pest of daffodil bulbs. The biology was especially well studied in the United States in the 1920s after the bulb-growing industry had been affected by fairly severe outbreaks. Broadbent (1927, 1928), Wilcox & Mote (1927) and Weigel (1926) may be cited here, and these authors, together with Weigel (1928) and Cole (1929), discussed methods of control. In Britain the biology was dealt with by Fryer (1914) and Hodson (1932) and the latter author outlined control measures. For recent work oriented towards chemical control the series of papers by Woodville in *Plant Pathology* (see most recent, 1967) may be cited.

In all this work the remarkable colour polymorphism of the fly has received comment but very little study. Apart from taxonomists who named the major colour varieties (see Hodson (1932) and Coe (1953)), Verrall (1901), Gabritchevsky (1924) and Brown (1951) list the colour types – the last author with some errors. The mimetic polymorphism of another bee-mimicking syrphid, *Volucella bombylans*, L., was probably an early species to be analysed genetically (Gabritchevsky 1924). Another example seems to have been the tropical and very spectacular case of *Papilio dardanus* Brown (Ford 1936), Clark & Sheppard (1959, 1960 *a*, *b*, *c*, 1963). The long neglect of a multiple polymorphism in *M. equestris*, a common pest species in Europe and America (and now also carried with bulbs to Australasia and Japan (Commonwealth Institute of Entomology 1960)), seems surprising.

Gabritchevsky's work on *V. bombylans* is well summarized by Keeler (1926). The basic genetics is very simple but from the data that Gabritchevsky presented it would appear that the system might merit re-examination particularly as the minor modifications in colour are controlled in a manner as yet unknown. Here there are two major interacting loci. One locus produces black or yellow hairs on the thorax and abdomen anterior and the other produces white or red abdomen tip colour. In the first case black hair colour is dominant to yellow and in the second white is dominant to red when the black hair allele of the first locus is absent. In its presence expression of the white hair allele of the second locus is suppressed and the abdomen is always red. The system of control that I found in *M. equestris* (Conn 1971) is quite different as the following results show.

Materials and methods

Pairs of adults were placed in plastic boxes (23 cm long × 14 cm wide × 9 cm high). Pollen food was provided in the form of buttercups held in a glass tube with moist folded filter paper. Sugar solution (or in 1970 honey solution) was provided in the plastic caps of small specimen tubes. The cages were kept in a constant temperature room at 25 °C, 60 cm below a bank of five 25 W fluorescent tubes. At this distance the cages were stacked without any apparent effect on mating behaviour. Buttercups were changed at least every 2 days and the sugar solution changed almost as often, as it frequently became mouldy.

Copulation was frequently seen in the cages and even occurred in specimen tubes when the flies were removed in the course of cleaning the cages. Females laid eggs freely in the foliage of the buttercups and under the caps holding the sugar solution. These eggs were removed daily using a fine camel hair brush to sweep them into 0.6 cm × 2.5 cm tubes – one tube for each cross. These tubes were then kept in the laboratory where the temperature was usually about 20 °C and were examined daily. The larvae usually emerged within a week and these were placed on *Narcissus* bulbs in seed boxes (37.5 cm × 25 cm) or plastic pots (23 cm) grown in an unsterilized mixture of 3 loam : 2 peat : 1 sand kept in an unheated greenhouse. The larvae were left to find their own way into the bulbs.

The following January, February and March the bulbs were cut open. Larvae were collected from these or else the pupae were sifted from the soil. They were placed in 6.25 cm plastic cups containing a 5 cm deep layer of peat. The cups were covered with muslin and stacked on sheets of Perspex.

Adults emerged in May and June and males and females were separated daily and placed in spare mating cages for use that year. Records were kept of the crosses and where possible the flies, after use, were pinned and preserved so that it was usually possible to refer back to ancestral broods and flies when necessary. Not all desirable crosses have been satisfactorily performed because only about half of the crosses were viable and because adult flies are not fertile for very long and so cannot be mated in the most desirable way if the best partner does not emerge.

Results and discussion

(A) *Mendelian genetics*

The factors determining the colour types only affect the colour of the hairs of the tergites and not the colour of the exoskeleton, which is always black, except for limited areas of the second abdominal segment at the sides and anterior of the tergite which are translucent pale yellow. The basic morphs are described in isolation (see figure 1). In every case where black hairs occur the black-haired patterns (usually bands) can be considered as superimposed on a ground colour pattern which involves combinations of yellow and orange distributed (again in bands) over the whole body. The basic morphs are described together with as many deviants as possible. The first abdominal segment does not possess many hairs at all on the dorsal surface and is largely overshadowed by the scutellum and so does not play any significant part in mimicry and determination of the colour type. Hence it is omitted from figure 1.

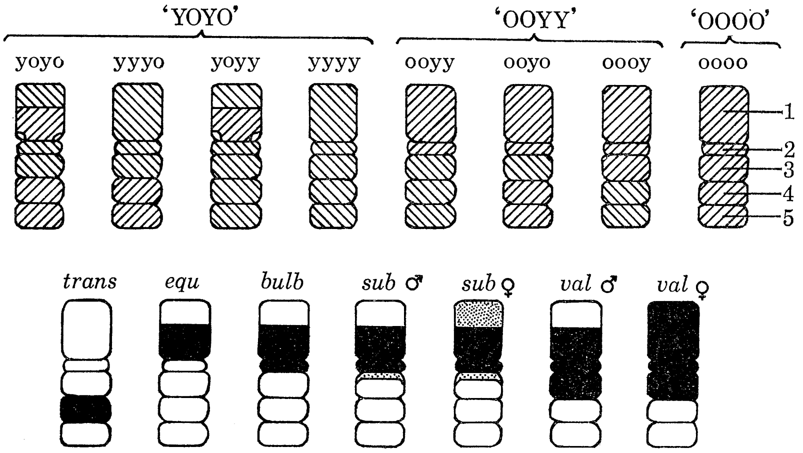

FIGURE 1. Diagram to show the effects of the different gene loci. Each locus is illustrated in isolation. 'YOYO', 'OOYY', 'OOOO' indicate major alleles at the ground colour locus. yoyo, yyyo, etc. indicate actual colour patterns from the anterior of the thorax to the posterior of the abdomen.

trans = *transversalis.*
equ = *equestris.*
bulb = *bulborum.*
sub ♂ = *subvalidus* male.
sub ♀ = *subvalidus* female.
val ♂ = *validus* male.
val ♀ = *validus* female.
1, 2 = components of thorax.
2 = scutellum.

3–5 = components of abdomen.
3 = second abdominal segment.
4 = third abdominal segment.
5 = fourth abdominal segment.
▧ = yellow.
▨ = orange.
■ = black.
▦ = black hairs mixed with ground coloration.
□ = ground coloration visible.

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Some females caught in the wild in 1966 which provided offspring for the 1967 crosses provide results shown in table A8 and are included for the sake of completeness.

(i) Bulborum, subvalidus *and* validus

Bulborum converts the hair on most of the thorax including the scutellum to black leaving only the anterior third coloured orange or yellow. There is no sexual dimorphism and there is little variation except that occasionally there may be very few black hairs on the second abdominal segment and in some families the colour is 'diluted' to an extent that allows the ground colour (orange or yellow) to become faintly discernible. Most authors (Hodson, Brown and Gabritchevsky) include two other morphs (male *subvalidus* and *validus*) under *bulborum*, but these prove to be genetically quite distinct.

Subvalidus shows sexual dimorphism. The male is as *bulborum* except that the second abdominal segment has a mixture of black and coloured hairs arranged in a fairly constant pattern. The basic colour of the second abdominal segment is black with large areas of coloured hairs antero-laterally where the exoskeleton is also pale. The female is harder to define and is more variable. The anterior of the thorax is darkened, although not black, and there are sombre and black hairs as well as normal coloured ones. The abdomen anterior (second abdominal segment) has coloured hairs mixed with black hairs. Usually, as with the male, the paler hairs are more prevalent on the anterior of the segment but the markings are not so prominent or so definite.

Validus extends the sexual dimorphism further. The male is as *subvalidus* except that the second abdominal segment is completely black except for a few isolated paler hairs. The female has a completely black thorax and abdomen anterior except occasionally for a few isolated paler hairs on the abdomen anterior. The darkening in both sexes may extend to the third abdominal segment in a few instances but never covers more than the anterior half. There may be a narrow band in which a gradation of colour occurs where the hairs are not black but are darker than normal (the line between black and ground colour is always sharp on the thorax of the male).

The following is probably the simplest explanation of the data listed in table A1; there is a major gene acting together with two modifier loci to produce the *bulborum*, *subvalidus*, *validus* range of colour types. The *bulborum* morph is an expression of the dominant allele of the major gene (designated the *bulborum* locus). The *subvalidus* morph is an expression of the dominant allele of the *bulborum* locus together the dominant allele of a modifier U which shows some degree of sex-limited expression. Absence of the dominant allele at the *bulborum* locus means that the modifier is not expressed even if the dominant allele is present. The *validus* morph is an expression of the dominant alleles at the *bulborum* and modifier U loci together with the dominant allele of a second modifier locus V which further enhances the sexual dimorphism. All three loci are autosomal.

On the basis of the above hypothesis certain predictions can be made.

(1) It should be possible to 'synthesize' *validus* by crossing *subvalidus* × other and *bulborum* × other phenotypes from appropriate backgrounds (where other means any colour type other than *validus*, *subvalidus* or *bulborum*). The two modifiers should be carried in some of the other-type individuals in the dominant state but should be unexpressed so that on crossing other-type individuals with individuals carrying the dominant *bulborum* allele the alleles of the different loci would combine in the progeny and this expression would often take the form of *subvalidus* or *validus* types. This is supported by the evidence of crosses 68–79, 67–75, 68–154 amongst others. Crosses 67–7 and 67–34 support the view that the dominant allele of the modifier locus V requires the dominant alleles of *bulborum* and modifier U to be present for expression and that an individual that carries the dominant alleles of *bulborum* and the modifier V and is homozygous recessive for the modifier U is phenotypically *bulborum*.

(2) Some *subvalidus* × *subvalidus* and *subvalidus* × other crosses should yield 3 *subvalidus*: 1 *bulborum* and 1 *subvalidus*: 1 *bulborum* in the same way as some *validus* × *validus* crosses should yield 3 *validus*: 1 *subvalidus*/*bulborum*. 68–33 is probably a cross in which the female parent carried the U locus in a heterozygous condition thus giving a ratio (12:2) approximating to 3 *subvalidus*: 1 *bulborum*. 67–43, 67–63, 68–37 and 68–60 are probably crosses of the second type. 67–43 and 68–60 possibly are *validus* × *validus* crosses yielding ratios approximating to 9 *validus*: 3 *subvalidus*: 4 *bulborum* (assuming the loci segregate independently).

It is often possible to predict the outcome of a cross, particularly when considering the basic elements such as just the *bulborum* locus alone. If a cross of *validus* × other yields all *validus* in the F_1 generation than one of these F_1 types crossed with an other-type individual should yield 1 *validus*/*subvalidus*/*bulborum*: 1 other type. This is shown in cross 68–142 whose progeny were used in crosses 69–39, 69–40, 69–62, 69–63, 69–89 and all these except possibly 69–40 gave ratios not far from 1:1.

(ii) Equestris

This character affects the same parts as *bulborum* except for the scutellum which is coloured yellow or orange. The hairs of the affected parts are black. It shows very little variation except that, like *bulborum*, a few individuals show 'dilution' of the blackness and in these the underlying ground colour may be faintly apparent as well. What is involved in 'dilution' is not clear. The *equestris* character does not affect hair length.

It is clear from the data (table A 2) that the gene behaves as a simple autosomal dominant and from crosses such as 68–109, 68–150, 69–20 and 69–73 is not allelic to *bulborum*. It is also not allelic to either of the modifiers U or V (see crosses 69–19, 69–51 and cross refer between table A 1 and table A 2).

(iii) Transversalis

This colour type is only expressed in the female but inheritance is autosomal. Hodson mistakenly referred to it as sex-linked instead sex-limited. The hairs of the third abdominal segment are affected and expression is variable. The hairs on the dorsal parts of the tergite are affected, those along the lateral edges are unaffected. There are two separate effects. The hairs are shorter and finer than normal, showing the black tergite underneath, and they are also darkened. Variation in expression is shown by the fact that there are variable numbers of normal coloured hairs of normal length interspersed in patches with the shorter hairs.

Crosses demonstrating that this gene is sex-limited in expression are to be found in the male × non-*transversalis* female crosses (table A 3) which yield *transversalis* in their female progeny.

The position as regards dominance is, as yet, not entirely clear. From the evidence of the pedigrees of crosses such as those involving 68–32 it would appear that the black band is produced by the recessive allele. However pedigrees such as 68–109 tend to refute this suggestion. Generally all that could be classified as *transversalis* were classified as such – even those with weak expressivity (in the case of 68–32 F_1 the individuals were quite easily distinguished). It seems possible that this locus may show dominance in the process of evolution – selection being hampered by the effects of sex-limited expression. The possibility is strengthened by the variations in expressivity, particularly by differences involving whole families.

(iv) *Ground colour*

There are three basic colour types and certain variations of these which, on the basis of their inheritance, can be placed with one or other of the three main groups. All the colour varieties are conveniently given names in which the letters refer to the colour of the bands in order running from head to tail.

(*a*) YOYO yellow hairs on the thorax and the second abdominal segment, orange hairs as a transverse bar on the thorax where *equestris* is positioned (except for a pair of lateral tufts of yellow hair just anterior to the scutellum: these tufts are black when *equestris* is present) and an orange haired abdomen tip. The letters of the name YOYO refer to the colours of the bands in order.

(*b*) OOYY orange hairs on all the thorax, the abdomen is wholly yellow.

(*c*) OOOO wholly orange haired.

The other colour types, which are variants of the above, included in (*a*) are: (1) as (*a*) but without orange thoracic band of hairs (YYYO); (2) wholly yellow (YYYY), (3) as (*a*) but abdomen tip yellow (YOYY). Included in (*b*) are: (1) as (*b*) but abdomen tip orange (OOYO); (2) as (*b*) but abdomen anterior orange haired (OOOY).

The table A4 has been set up classifying all specimens as belonging to categories *a*, *b* or *c*. The variants have been included in these tables in the appropriate places. The results left little doubt as to the existence of a simple dominance heirarchy of YOYO > OOYY > OOOO and the table is arranged to emphasize this conclusion.

The genetics of the variants within each category is less easy to study. However, some preliminary results (table A5) indicate that within the YOYO category the orange thoracic band and the orange abdomen tip are dominant, and that within the OOYY category the yellow abdomen tip and yellow abdomen anterior are dominant and it would of course be justifiable to put OOO at the end of this series in the OOYY category as its universal recessive. Possibly there is some type of switch gene that interacts with the loci determining the colour variants. This would be confirmed if it was found that the abdomen tip colour is determined by one locus and orange is dominant to yellow in the YOYO category and yellow dominant to orange in the OOYY category.

(v) *Other colour types*

There are other colour types that appear occasionally. One of these is the 'dilution' type. Occasionally an *equestris* or *bulborum* individual appears in which the hairs are sombre rather than black. This often permits the underlying ground colours to be discerned.

Another unusual colour type has simply been referred to as 'odd'. It appears in females only and effects the colour of the scutellum and second abdominal segment. These parts become sombre in colour but not black in the affected individuals. From table A6 it would appear that the character is an autosomal dominant sex-limited to the female. It is quite possible that it is one of the *bulborum* modifiers (possibly U to judge from its affect) which can express itself independently of *bulborum* on the right genetic background. The crosses that it has appeared in come largely from one wild female caught and retained because of its 'odd' coloration (the female parent of cross 68–90). Other 'odd' types have appeared in 68–109 and 68–118. The 68–109 male parent is from 67–36 and appears to be normal. The female parent of this cross probably emerged from the bulbs taken from the field but there is no record of this. The 68–118 male parent is from 67–54 and the normal female is from 67–67. By crossing the 'odd' type with *bulborum* it may be possible to synthesize *validus* or *subvalidus*. Alternatively, it should be possible to select a genetic background to suppress the 'odd' colour and cross the suppressed 'odd' colour type to pure bred *bulborum* to see if it still gives *subvalidus* or *validus*.

(vi) *Evidence for non-allelism*

Fundamentally the evidence for non-allelism is the independent segregation of loci. The arrangement of data in the tables so far aims to compress the evidence for segregation. This arrangement is far from ideal as regards presenting evidence on allelism. Table A7 re-presents the data more suitably.

The list of possible relationships is as follows:

Bulborum and modifier V
modifier U
equestris
transversalis
ground colour

Modifier V and modifier U
equestris
transversalis
ground colour
Modifier U and *equestris*
transversalis
ground colour
Equestris and *transversalis*
ground colour
Transversalis and ground colour

Formal proof is provided in crosses of the heterozygous double dominant with the double recessive. If four types are produced in the F_1 then there can be no allelism.

Independent segregation can be seen in the tables of crosses for *bulborum* and the modifier V, *bulborum* and the modifier U, *bulborum* and *equestris*. Modifiers U and V are probably not allelic to *equestris* (demonstrated by 69–19 and 69–51) (tables A1, A2). The modifiers U and V are not allelic: if they were there would be simple segregation of *validus*, *subvalidus* and *bulborum*.

The remainder of the relationships are analysed with the help of crosses in table A7 on allelism. The allelism relationships of the modifier U to *transversalis* and to ground colour are unclear because of the lack of suitable crosses. However allelism here seems unlikely.

(B) *Linkage*

Linkage between genes determining colour types may suggest the course of evolution of a set of mimetic patterns. Most authors agree that various closely linked systems ('supergenes') that have been found in mimetic polymorphisms have evolved to reduce the segregational load of genetic polymorphism. In other words, linkage has evolved because it reduces the production of non-mimetic combinations.

Most of the crosses were not set up specifically for the study of linkage, but were to elucidate the Mendelian genetics as hypotheses concerning linkage could not be completely formulated until the basic system was known. In *M. equestris* the search for linkage is often complicated by sex-limited expression and epistatic interaction. So far data are scant. A list of conditions required for each component of the linkage study is drawn up below. The word 'truncation' as used below applies to the classes of families obtained in the F_1 generation. The distribution is described as truncated when for one reason or another one or more particular classes of family cannot be considered as far as linkage is concerned, with consequent complications for the linkage calculations. Details of the results are included later (subsection vi).

(i) Bulborum *and other loci.*

(1) Bulborum *and the modifier V.*

This is one of the relationships that has complications as the V locus depends for its expression on the presence of the B and U dominant alleles so that in each cross U must be present in all individuals (in the absence of evidence that it is inherited completely independently of both B and V). Thus this rules out the double backcross since U is not expressed in the absence of B and it is not clear whether the supposed double recessive *bbvv* has the U locus in the dominant or recessive states. Deciding the point by a breeding test is hardly feasible in a species with a long life cycle such as *M. equestris*.

The intercross-backcross may be employed (phenotypically *validus* × *subvalidus*) with certain restrictions. These are that there must be no *bulborum* types in the F_1 – locus U must not show segregation: families yielding only *validus* types and no *subvalidus* types are not included as the *validus* parents might be homozygous *VV*. This category will include a number of crosses in which the *validus* parent was heterozygous *Vv* but all the F_1 types were *validus* by chance. Thus the distribution of the F_1 progeny ratios is truncated. Families yielding no 'non-*bulborum* types are also not included as one of the parents may then be homozygous *BB*. This excludes a cross in which both parents were heterozygous *Bb* but happened not to produce any *bb* offspring. Since only a quarter of the offspring are expected to be *bb*, this exclusion and its further truncation of the F_1 progeny ratios is more serious than the last. Hence any detailed study would benefit greatly from a prior knowledge of the genotypes of the parents.

(2) Bulborum *and the modifier U*

Similar problems occur here with respect to the simple double backcross so that the intercross–backcross is best used in the study of this relationship also. The conditions set on the parents are: (*a*) that they are *validus* or *subvalidus* × *bulborum*, (*b*) that families yielding only *validus* or *subvalidus* types are excluded as the *validus* or *subvalidus* parent may be homozygous *UU* (as this category will include a certain number of crosses in which the parent in question was in fact heterozygous *Uu* but all the F_1 progeny were *validus* or *subvalidus* there is truncation of this class), and (*c*) that families yielding no 'non-*bulborum*' types are also not included as one of the parents may then be homozygous *BB* (this produces a similar truncation to that seen in the last relationship).

(3) Bulborum *and* equestris

The double backcross is of greater use here than the intercross–backcross in spite of the complication of masking of the *equestris* phenotype by the *bulborum* phenotype. If the parental genotypes are not known then the requirements are that one parent must be *bulborum*, *subvalidus* or *validus*, while the other parent must be *narcissi* or *transversalis*, and that as a result of the *bulborum* parent carrying the *equestris* gene E some of the progeny are *equestris*. This means that the distribution of the classes of the F_1 families is truncated as some of the *bulborum* parents carrying E will fail to give *equestris* types in the F_1 generation so these crosses will be excluded. Also all F_1 families that do not contain *narcissi* or *transversalis* are excluded as this type of result can be obtained if the *bulborum* parent is homozygous *EE* or occasionally if it is *Ee*. Hence each tail of the distribution of F_1 families is removed.

As a condition for the above families to be observed not all the F_1 generation can be *bulborum*. At least two of the F_1 generation must be non-*bulborum* for a mixed family of the right type to be considered. Hence here there is a further truncation.

(4) Bulborum *and* transversalis

As *transversalis* is sex limited in expression to the female the study of linkage must be confined to the females of the F_1 generation. The type of cross easiest to use is *bulborum* (or *subvalidus* or *validus*) male × double recessive female (assuming for the moment that the allele of *transversalis* causing the dark band is dominant). Progenies are selected for analysis if they contain both *transversalis* and non-*transversalis*. This causes truncation of both ends of the family of F_1 ratios for *transversalis* and one must take into account truncation of the F_1 distributions for the *bulborum* locus, wholly *bulborum* progenies being excluded as outlined previously.

(5) Bulborum *and ground colour*

The only crosses that cannot be used are those containing female *validus* parents masking the ground colour types and those containing *validus* females in the F_1 for the same reason. Other than this there are no complications except for truncations arising if the parental genotypes are not known. Only then do progenies containing none of one or the other or both of the recessive phenotypes have to be excluded.

(ii) *The modifier V and other loci*

(1) *The modifier V and the modifier U*

Both modifiers are dependent upon the presence of *bulborum* for expression so to avoid the complications that would arise if *bulborum* is linked to either of the modifier loci one must set the requirement that all offspring manifest the dominant *bulborum* allele. The intercross–backcross is preferable to the double backcross as in the latter the status of the V locus is uncertain in the absence of the dominant allele of the modifier U.

Truncation of the F_1 ratios excludes families containing only *validus* or lacking *bulborum* from consideration.

(2) *The modifier V and* equestris

The relationship cannot be studied directly either by use of the double backcross or the intercross–backcross as the progeny cannot be classified as recombinant and non-recombinant.

(3) *The modifier V and* transversalis

The sex-limited expression of *transversalis* must be taken into account. Crosses of *validus* males with *subvalidus* females can provide evidence if the male is heterozygous for *transversalis*, as shown either by the progeny or by deduction from relatives.

Truncation of the F_1 distributions is usual owing to uncertainty about the parental genotypes. The families have to be selected on the basis of the F_1 containing some *subvalidus* and mixed *transversalis* and non-*transversalis*.

(4) *The modifier V and ground colour*

The double heterozygote parent (*validus*, dominant ground colour) is preferably male as in the equivalent female the phenotypes are often harder to distinguish because of masking. Likewise, in the F_1 generation the male *validus* can be studied but the female *validus* cannot, whereas both male and female *subvalidus* can be studied.

The F_1 distribution is often truncated as one often does not know the status of the *V* gene in the supposedly heterozygous parent so one selects families that are not all *validus*. The distribution may also be truncated with respect to ground colour if one does not know the genotype of the parent (in this case the families which do not have individuals expressing the recessive phenotype are not considered).

(iii) *The modifier U and other loci*

(1) *The modifier U and* equestris

This relationship is impossible to study directly for similar reasons to those outlined in (ii) (2).

(2) *The modifier U and* transversalis

The problems hence are similar to those of the relationship of the modifier V and *transversalis* except that the necessary crosses are now *subvalidus* or *validus* males with *bulborum* females.

(3) *The modifier U and ground colour*

In this case the complication that accompanies the study of the relationship of the modifier V to ground colour, namely the ground colour phenotype of female *validus* parents and progeny is not necessarily present. Only in crosses involving the female *validus* colour type in the parents or the progeny must one allow for it. Apart from this truncation involves only those families that do not have individuals expressing the recessive phenotypes of both the loci.

(iv) Equestris *and other loci*

(1) Equestris *and* transversalis

Parental genotypes are often known in crosses appropriate for this locus pair, and when they are, there are no complications except that for, convenience, the double heterozygote parent should be male. Truncation is only necessary if the parental genotypes are not certain.

(2) Equestris *and ground colour*

Again unless the parental genotypes are not clear no truncation is necessary and there are no complications.

(v) Transversalis *and other loci*

(1) Transversalis *and ground colour*

Except in crosses in which female *validus* appears this is as simple to study as the relationship of *equestris* and *transversalis*. Only the females of the F_1 are of interest and the male parent should be the double heterozygote parent as before.

(vi) *Statistical analysis of linkage*

As is evident from the data tabulated in table A9, p. 392 the crosses useful to the study of linkage are sparse in the total list. This is due to the many and various conditions, discussed above, that have to be satisfied. Those crosses with the most conditions attached are the most poorly represented.

Because of these difficulties and because families tend to be small methods of linkage analysis developed in human genetics are useful. The maximum likelihood estimate outlined in Stern (1960) and Morton's sequential analysis (1955, 1956) seem most appropriate. However, Morton had calculated his values for families up to seven and many families here were larger than this. Thus for simplicity the method outlined by Stern was employed. As the data are so scant only approximate results can be expected.

In this method, if x is assigned to the recombination frequency, the basic approach is to look at the probability of obtaining a given family as x is given successively changing *a priori* values. The value $x = 0.5$ corresponds to the unlinked condition and if this gives the highest probability then no linkage is the 'most-likely' hypothesis. However, before drawing conclusions, 'odds on linkage' ($P_x/P_{x=0.5}$) are calculated and joint estimates of the relationship of the loci are obtained from the product of the odds of many families.

From the results obtained (tables A 9, A 10) it can be safely concluded already that some of the gene loci behave as if they are linked. *Bulborum* and ground colour are linked fairly closely with a recombination fraction of 15 to 20 % applying apparently both in males and females separately and together. *Bulborum* and *equestris* are linked with a recombination fraction of 20 to 25 % and *equestris* and ground colour are linked with a recombination fraction of about 30 % so that the gene order *equestris–bulborum*–ground colour is indicated. Such indications as there are suggest that *transversalis* is unlinked to this system and from the results shown few other definite conclusions can be drawn.

The relationship of *bulborum* and *equestris* is difficult to study as families have been selected to exclude the three extreme classes of family (see above). Hence linkage is probably closer than the calculations show. Coincidence of cross-overs cannot be calculated until the results are strictly comparable for the relationships between the three linked loci. Truncation was not accounted for in the above calculations as the results are too scant to merit such attention. However, as a whole the linkage results so far provide a basis for planning more decisive experiments.

(C) *Population genetics*

Both genetics and evolutionary biology have profited greatly from the study of natural genetic polymorphisms (Ford 1964; Sheppard 1958). As regards colour polymorphisms Lepidoptera have probably attracted most attention (Ford 1953; Sheppard 1961), but as regards population structure and nature of selective forces no case is, as yet, fully understood. The following studies on morph frequencies of *M. equestris* in the wild are at an early stage. There have been problems of the time available and of catching the adults in sufficient numbers, and as the number of morphs is large the sample sizes of individual morphs tend to be small.

The flies were caught for a specific period (usually 1 h) at a specific time of the day (usually around 14.00 h B.S.T.). They were caught over plots of bulbs in Church Field on the Field Station by means of a long handled insect net. They were usually caught by stalking individuals that had landed, as attempts to capture free-flying individuals were almost fruitless. The flies were labelled by cellulose paint applied on the tibia with a piece of dry grass. In 1968 and 1969 the flies were taken indoors and chilled in a 10 °C C.T. room but in 1970 they were anaesthetized by carbon dioxide from a 'Corkmaster'. They were labelled differently each day – different paints and tibiae being used. They were sought in the field as soon as they started emerging in the laboratory and collections were continued for so long as any could be found.

Besides these samples from the field, others were collected from bulbs lifted from Church Field. In this case the larvae and pupae were stored in peat until the adults emerged, when they were killed, pinned and preserved.

Accepting the conditions outlined in Mendelian genetics and assuming 'linkage equilibrium' between loci, the formulae for calculating the gene frequencies from the phenotype frequencies can be derived. If a locus is in linkage disequilibrium with an epistatic locus, then the frequency of a recessive morph among morphs that are able to express the recessive does not correctly estimate the frequency of the recessive allele in the population as a whole. Hence formulae for the calculation of gene frequency are simple to derive only on the assumption of linkage equilibrium.

Gene frequencies have been calculated for the results presented (table A 11, table A 12). These results assume that the Hardy–Weinberg law holds and that there is no selection operating (i.e. no linkage disequilibrium). As will be seen later this does not hold and so at best they can only be used as a guide to the gene frequencies, given the sample sizes, especially as they often depend on the size of the smallest class, particularly when studying ground colour (table A 11, A 12*f*).

The formulae for calculation of gene frequencies are set out below.

Bulborum

$$\frac{\textit{Validus}+\textit{subvalidus}+\textit{bulborum}\text{ types}}{\text{total sample}} = p_b^2+2p_b q_b,$$

$$\frac{\text{other types}}{\text{total sample}} = q_b^2.$$

Hence q_b and p_b where p_b is the frequency of the *bulborum* allele.

Modifier V

$$\frac{\textit{Subvalidus}\text{ types}}{\textit{Validus}+\textit{subvalidus}\text{ types}} = q_v^2.$$

Hence q_v and p_v.

Modifier U

$$\frac{\textit{Bulborum}\text{ types}}{\textit{Validus}+\textit{subvalidus}+\textit{bulborum}\text{ types}} = q_u^2.$$

Hence q_u and p_u.

Equestris

$$\frac{\text{non-}\textit{equestris}\text{ types among those able to express }\textit{equestris}}{\text{all types except those unable to express }\textit{equestris}} = q_e^2.$$

Hence q_e and p_e.

Transversalis

If *transversalis* allele is dominant

$$\frac{\text{non-}\textit{transversalis}\text{ type females}}{\text{all females}} = q_t^2.$$

Hence q_t and p_t.

Ground colour

Let p_g be the frequency of the YOYO gene and q_g and r_g be the frequencies of the OOYY and OOOO genes respectively.

Then

$$\frac{\text{OOOO types among all able to express ground colour}}{\text{all able to express ground colour}} = r_g^2$$

and

$$\frac{\text{OOYY and OOOO types among all able to express ground colour}}{\text{all able to express ground colour}}$$

$$= q_g^2+r_g^2+2q_g r_g = (r_g+q_g)^2$$

$$= (1-p_g^2).$$

Calculations were also made of the chromosome frequencies with respect to the *bulborum* and ground colour loci (tables A 13, A 14, A 15). These can be compared with the chromosome frequencies expected on the basis of the gene frequencies, assuming independent assortment and no selection (table A 16), of the alleles of the two loci, that is, multiplying together the values of the gene frequencies of the two loci allowing for female *validus*. Calculations were not made with regard to the other two linkage relationships (viz. *equestris* and ground colour, *bulborum* and *equestris*) as disequilibrium certainly present in the *bulborum*–ground-colour relationship combined with masking creates a very confused situation. To obtain results here progeny tests are probably called for.

With two alleles at the *bulborum* locus and three alleles at the ground-colour locus six different chromosome types can be made up and the formulae for calculating their frequencies are set out below.

TABLE 1

chromosome type	chromosome frequency
B-YOYO	p
B-OOYY	q
B-OOOO	r
b-YOYO	s
b-OOYY	t
b-OOOO	u
Total	1

TABLE 2. PHENOTYPES OF THE F_1 OF PARTICULAR GENOTYPE COMBINATIONS

male genotype	female gamete genotype					
	B-YOYO	*B-OOYY*	*B-OOOO*	*b-YOYO*	*b-OOYY*	*b-OOOO*
B-YOYO	*B-YOYO*	*B-YOYO*	*B-YOYO*	*B-YOYO*	*B-YOYO*	*B-YOYO*
B-OOYY	*B-YOYO*	*B-OOYY*	*B-OOYY*	*B-YOYO*	*B-OOYY*	*B-OOYY*
B-OOOO	*B-YOYO*	*B-OOYY*	*B-OOOO*	*B-YOYO*	*B-OOYY*	*B-OOOO*
b-YOYO	*B-YOYO*	*B-YOYO*	*B-YOYO*	*b-YOYO*	*b-YOYO*	*b-YOYO*
b-OOYY	*B-YOYO*	*B-OOYY*	*B-OOYY*	*b-YOYO*	*b-OOYY*	*b-OOYY*
b-OOOO	*B-YOYO*	*B-OOYY*	*B-OOOO*	*b-YOYO*	*b-OOYY*	*b-OOOO*

TABLE 3

colour type	frequency expected	overall frequency of colour type
Bulborum YOYO	$p^2+2p(q+r+s+t+u)+2s(q+r)$	a
Bulborum OOYY	$q^2+2q(r+t+u)+2rt$	b
Bulborum OOOO	r^2+2ru	c
non-*bulborum* YOYO	$s^2+2s(t+u)$	d
non-*bulborum* OOYY	t^2+2ut	e
non-*bulborum* OOOO	u^2	f

Setting out parental genotypes it becomes possible to find the colour types of the F_1 expected (shown in the body of table 2).

Hence one can now derive formulae for p, q, r, s, t, u from data on observed frequencies of colour types a, b, c, d, e, f.

So when random mating occurs,

$$f = u^2 \quad \text{hence } u;$$

$$f+e = (t+u)^2 \quad \text{hence } t;$$

$$f+e+d = s^2+2s(t+u)+t^2+2tu+u^2,$$

$$= (s+t+u)^2 \quad \text{hence } s.$$

Quadratic equations are however required to solve for p, q, r, i.e.

$$c = r^2+2ru,$$

so

$$r^2+2ru-c = 0;$$

and

$$b = q^2+2q(r+t+u)+2rt,$$

so

$$q^2+2q(r+t+u)+2rt-b = 0;$$

and

$$a = p^2+2p(q+r+s+t+u)+2s(q+r),$$

so

$$p^2+2p(q+r+s+t+u)+2s(q+r)-a = 0$$

hence

$$-p^2+2p+2s(q+r)-a = 0.$$

χ^2 tests on changes in the proportions of the different morphs from year to year show some interesting results (table A 17*a*). None of the loci gave significant changes from year to year except for the proportions of the three ground colour morphs and the modifier U in the males. With respect to the modifier U males the contributions to the final values of χ^2 from the various years was very similar so that one cannot attribute this to differences between field captures and laboratory emergences but possibly to fluctuating optima for the morph frequencies. The major contributions to the values of χ^2 for the ground-colour males, females and total come from different samples so that no one sample was extraordinarily different from any of the others.

Using χ^2 tests to examine morph frequencies and sex reveals (table A 17*b*) significant differences between the sexes in both the 1969–70 and 1970 samples as far as the modifier V is concerned. There is a deficiency of female *subvalidus*. It may be significant here that as female *subvalidus* is not a particularly striking mimetic type, selection may favour *validus* or *subvalidus* types that cannot be readily distinguished from *validus*. As regards ground colour it is remarkable that the two laboratory reared samples showed significant differences between the sexes, whereas the differences are not significant in field-caught samples. In both cases there is an excess of male YOYO and OOOO and female OOYY. In the field-caught samples 1968 and 1969 this is not so, although in 1970 it is so but not statistically significant.

Considering the combined colour types of *bulborum* and ground colour (table A 17*c*) there are significant changes from year to year in males, females and when the sexes are considered together. These results stand out in spite of the necessity to lump together classes where expectations were less than 5. Most of the variation was from within the non-*bulborum* group of colour types, the *bulborum* group of colour types being constantly predominantly YOYO with a few OOYY and OOOO types. Probably what is happening is that selection is maintaining the *bulborum* YOYO colour type at a high frequency, the *bulborum* OOYY and OOOO types being highly disadvantageous; that crossing with non-*bulborum*, *bulborum* types produce many recombinants, especially non-*bulborum* YOYO, and that the selective forces acting on these non-*bulborum* types vary greatly from year to year.

There are no significant differences between the sexes for the six colour types expressed by the *bulborum* and ground colour loci (table A 17*d*) except in the 1969–70 sample (allowing for female *validus* by removing male *validus*). In this sample there is an excess of all *bulborum* male types, non-*bulborum* OOOO males and non-*bulborum* OOYY and OOOO females observed to the number expected. The reasons for these results are not clear particularly as this pattern is not found in other samples.

Linkage equilibrium implies that the ratios of the ground-colour phenotypes should be the same in *bulborum* and non-*bulborum* classes. Thus if one compares the sizes of classes as in table A 18 χ^2 is found to be significant in every case even where classes have been lumped together when expected values have been less than 5. Occasionally even after lumping together as far as one can, the expected value was still less than 5. These results have been included for continuity. From these results a table has been drawn up (table A 19) showing which classes are in excess to their expectations under linkage equilibrium. *Bulborum* YOYO, non-*bulborum* OOYY and OOOO are in excess and other classes are deficient. These three classes are probably the best mimetic patterns (see below) and this provides tentative evidence that mimicry 'works' in the wild. How and for what predators it works is far from clear. In my sampling area bumble bees, the supposed models, were seen so seldom while I was catching the flies that it seemed not worth while to pursue them. However, pesticide experiments in parts of this field may partly account for their rarity.

(D) *Mimicry*

Since animal mimicry was recognized by Bates & Muller and seen to be a special case of the action of natural selection the phenomenon has been extensively studied and discussed. Important reviews have been given by Dixey (1908), Carpenter & Ford (1933), Sheppard (1963), Ford (1964), Wickler (1968), Rettenmeyer (1970) and many others. The genetics and evolution of mimicry have been analysed and discussed by Ford (1953), Fisher (1958), Goldschmidt (1945), Clarke & Sheppard (1960*a*, *b*, *c*) and Sheppard (1958, 1959, 1960, 1961, 1963). Behavioural studies have made by Brower (1960) and Brower & Brower (1962, 1965), Brower, Brower & Westcott (1960), Brower, Cook & Croze (1967), Morrell & Turner (1970) and theoretical aspects of it have been considered by Fisher (1958) and Emlen (1968). As mentioned in the Introduction the only major study of mimicry in the Syrphidae is that performed by Gabritchevsky (1924, 1926).

No practical studies on mimicry were performed in my work. Thus it is not known for certain that *M. equestris* is a Batesian rather a Mullerian mimic, but this seems likely from the demonstration by Brower & Brower (1965) that syrphids in the related genus *Eristalis* are Batesian mimics of honey bees. This section lists some potential models and mimics and discusses the implications of these groupings. Table 4 and plate 39 give an indication of how well the colour types of *M. equestris* cover the range of important British models (Alford 1971), but do not in themselves indicate the relative success of the different colour types as the various species of bumble bee have different distributions, and some have colour variants also. Further complexity is suggested by the fact that although bumble bees have a large mimetic following among other insects they are themselves far from adopting a common pattern through Mullerian mimicry. In some species the males do not even mimic the females. Although lacking the protection of a sting the male bumble bee is often more flamboyantly coloured than the corresponding queen and worker. The table shows, nevertheless, that there are common bumble-bee patterns corresponding to most of the morphs of *M. equestris*.

The number of mimetic patterns of *M. equestris* seems unnecessarily large (34 common morphs as well as the few unusual ones) especially when compared to most mimetic species, for example, the recently described example of *Oxycarenus multiformis* (Hemiptera: Lygaeidae) (Abdel–Aziz 1968; Samy 1969, 1971) in which there are four morphs: red, banded, spotted and black with a dominance hierarchy in the order listed. From the table it would appear that some morphs of *M. equestris* lack models. However, models are often to be found in bumble bees that are less recorded. *Subvalidus* males and females are similar to many of the cuckoo bees, e.g. *Psithyrus bohemicus* Seidl. and *P. vestalis* Fourcroy which were not included in the table as they were not regarded as common by Alford.

M. equestris originated in continental Europe and was only introduced to Britain about 100 years ago (Verrall 1901). Museum specimens indicate that the colour types found in this country have not altered noticeably since the last century so that what selection has occurred must have been largely for changes in the frequencies and relationships of the alleles of the different loci. Certainly *equestris* which has only the rare *Bombus distinguendus* Morawitz, as a model in the United Kingdom has many models on the continent. It remains fairly frequent in Britain perhaps because when combined with *transversalis* it is not unlike *bulborum-transversalis* and can gain protection from some of the same models (but see on). With bumble bees themselves so varied, possibly some predators come to treat all hairy flies with caution so that morphs, such as *equestris*, that apparently lack close models gain some protection. This would weaken

TABLE 4. THE RESEMBLANCE OF THE MORPHS OF *MERODON EQUESTRIS* FAB. TO SOME COMMON SPECIES OF BUMBLE BEES

	some common bumble bees						
morphs of *Merodon equestris*	*Bombus ruderarius* (Müller)	*B. pascuorum* (Scop.)	*B. hortorum* (L.)	*B. lapidarius* (L.)	*B. pratorum* (L.)	*B. lucorum* (Fabr.)	*B. terrestris* (L.)
narcissi YOYO	.	■	.	.	.	.	.
OOYY	.	●	.	.	.	.	.
OOOO	.	●	.	.	.	.	.
transversalis YOYO	.	■	.	.	.	.	.
OOYY	.	●	.	.	.	.	.
OOOO	.	●	.	.	.	.	.
equestris YOYO	.	.	.	.	.	.	.
OOYY	.	.	.	.	.	.	.
OOOO	.	.	.	.	.	.	.
equestris–transversalis YOYO	□	.	.	○	○	.	.
OOYY	.	.	●	.	.	■	.
OOOO	.	.	.	.	.	.	.
bulborum YOYO	.	.	.	.	.	.	.
OOYY	.	.	.	.	.	.	.
OOOO	.	.	.	.	.	.	.
bulborum–transversalis YOYO	□	.	.	○	●	▲	□
OOYY	.	.	●	.	.	●	■
OOOO	.	.	.	.	.	.	.
subvalidus male YOYO	.	.	.	.	.	.	.
OOYY	.	.	.	.	.	.	.
OOOO	.	.	.	.	.	.	.
subvalidus female YOYO	.	.	.	.	.	.	.
OOYY	.	.	.	.	.	.	.
OOOO	.	.	.	.	.	.	.
subvalidus–transversalis YOYO	○	.	.	■	■	.	●
OOYY	.	.	▲	.	.	▲	●
OOOO	.	.	.	.	.	.	■
validus male YOYO	.	.	.	.	●	.	.
OOYY	.	.	.	.	.	.	.
OOOO	.	.	.	.	.	.	.
validus female orange tail	●	.	.	●	.	.	.
yellow tail	●	.	.	▲	.	.	.
validus transversalis orange tail	●	.	.	●	.	.	.
yellow tail	●	.	.	▲	.	.	.

good resemblance, ●; fair resemblance, ■; poor resemblance, ▲; others, .
Resemblance to male bumble bees only is indicated by an open figure.
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DESCRIPTION OF PLATE 39

FIGURE 2. *Merodon equestris* morphs

	narcissi			*subvalidus* males	
YOYO	OOYY	OOOO	YOYO	OOYY	OOOO
YOYO	*transversalis* OOYY	OOOO	YOYO	*subvalidus* females *	OOOO
YOYO	*equestris* OOYY	OOOO	YOYO	*subvalidus–transversalis* OOYY	*
YOYO	*equestris–transversalis* OOYY	OOOO	YOYO	*validus* males OOYY	OOOO
YOYO	*bulborum* OOYY	OOOO	yellow tail	*validus* females	orange tail
YOYO	*bulborum–transversalis* OOYY	OOOO	yellow tail	*validus–transversalis*	orange tail
			‘odd’ YOYO		‘odd’-*transversalis* OOOO

scale = 1 cm

* = no reasonable specimens available. Some specimens that have battered wings have been used in crosses and are the best available.
N.B. Disposition of key follows that of insects.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

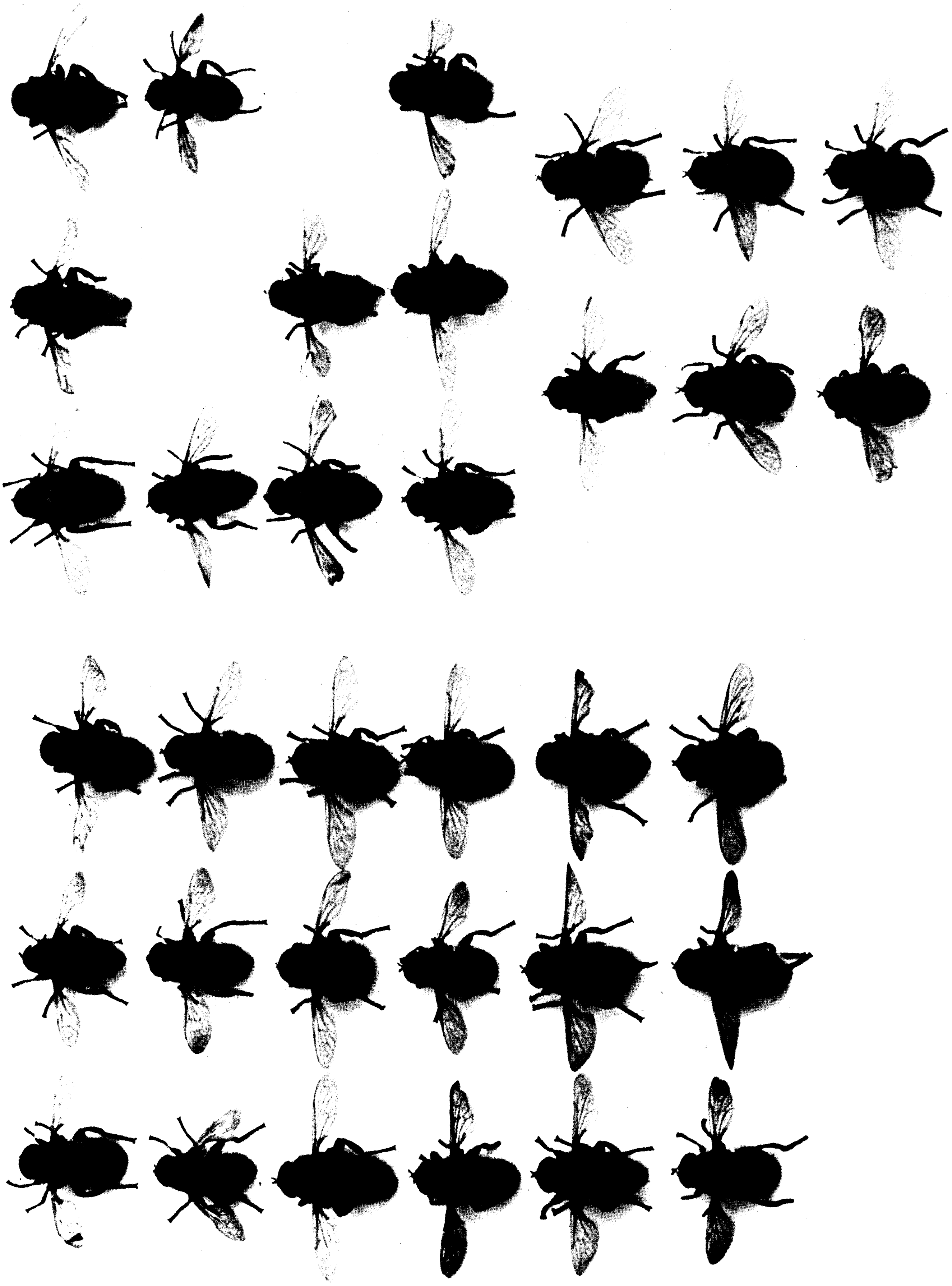

FIGURE 2. For legend see facing pag

any tendency for selection to tighten linkage and create supergenes. Such generalization (or lack of discrimination) by predators might help to explain the weak linkages found in *M. equestris* which so far as I know are without precedent in the study of mimetic polymorphism. However, against this tentative hypothesis two considerations must be opposed.

One is that a more 'classical' situation suggestive of supergenes seems to exist in the other bee-mimicking polymorphic syrphid that has been investigated. In *V. bombylans* each locus produces sweeping changes in the entire pattern. The dominant allele of one locus gives an excellent mimic of the black-with-red tail pattern of *Bombus lapidarius* L. The other allele when homozygous gives a paler stripey pattern which may be white tailed or red tailed depending on the state of a second locus. This is apparently not linked to the first and is epistatic to it so that the '*lapidarius*' morph always has a red tail. Apart from this epistasis at the second locus white is dominant to red and the resulting morphs have generalized resemblance to bees such as *B. hortorum* L. and *B. pratorum* L. respectively. Thus *V. bombylans* mimicks three common bumblebee patterns but, unlike *M. equestris* (and various other syrphids such as *Criorrhina berberina* Fab. and *Eristalis intricaria* L.) it fails to take advantage of another of the commonest patterns – the pale and basically unstripey pattern typified by *B. pascuorum* Scop. On the other hand, *V. bombylans* produces no non-mimetic or poorly mimetic forms.

The other point against generalized avoidance as the explanation of weak linkage is that it seems not to occur. If *M. equestris* is a Batesian mimic, and if the predators are not deceived by generalized resemblance, then in any particular area where only a limited number of bumblebee species are common it should be possible to show that selection is favouring the most mimetic morphs. The intensity of selection would be indicated by the degree of linkage disequilibrium. In fact referring back to the studies on the population genetics linkage disequilibrium is evident (*bulborum* and ground colour) and is quite marked.

These finds make the presence of the *equestris* morph in Britain somewhat puzzling unless it has some other advantages that more than compensate for its imperfections as a mimic. It is certainly maintained at a frequency far too high to be accounted for by repeated introduction from continental Europe particularly as from my own experience the fly does not migrate far from a particular isolated semi-naturalized plot of *Narcissus* bulbs. However, this is just one of several puzzles still unsolved with regard to *M. equestris* mimicry. To mention another, why is *transversalis* sex-limited? This question could also be extended to include the sex-limited effects of the modifiers V and U. Sexual selection by the females for sex-limited expression of these characters has been suggested as the reason for this phenomenon in other mimetic insects (Wickler 1968). The best known example is *P. dardanus*. However in *P. dardanus* the male is completely non-mimetic, whereas in *M. equestris* all the males are mimetic but certain types are not produced.

Possibly one reason why there is no epistatic interaction between *bulborum* and ground colour is that there is linkage between the loci. Also the most favoured morphs in this country are *bulborum* YOYO and non-*bulborum* OOYY and OOOO. In continental Europe there is some evidence that this may not be so and that non-*bulborum* YOYO in the form of *equestris* YOYO may be favoured. Certainly there are bumble bees such as *B. ruderarius* Müller which have colour types on the continent that would form good models for this combination. It is conceivable that this is a comparatively young case of mimicry still in the process of becoming stabilized or that has been made more fluid as a result of being carried by man, together with the *Narcissus* bulbs, into areas where the bee faunas are quite different from those of Europe. It has thus reached N. America, Australasia and Japan (Commonwealth Institute of Entomology 1960). It would be interesting to find out what has happened in North America where the bumble bees present a different spectrum of patterns.

The genus *Merodon* is well represented in Europe, particularly central and eastern Europe. Other species of *Merodon* apart from *M. equestris* are also mimetic. *M. clavipes* is an example. This species tends to occur farther south and east than *M. equestris*. In this species the male resembles *M. equestris* form *equestris* YOYO and the female resembles *narcissi* OOYY. It also has a longer abdomen and in that respect appears less bumble bee-like. *M. flavus* is a sibling species that can only be distinguished from *M. equestris* in the male (Sack 1913; H. Gloor 1971, personal communication). It seems to prefer higher altitudes (in the Alps and the Pyrenees) than *M. equestris*, but overlaps with it and has the same colour types as *M. equestris* except that it lacks the *bulborum*, modifier U and modifier V group. It is reasonable to suggest that *M. equestris* originated from an alpine species like *M. flavus* and in the course of evolution evolved the additional range of colour types to extend the mimicry to bumble bees inhabiting lower grounds. Certainly the range of colour types given for *M. flavus* covers most of the alpine bees. I have caught a few specimens of bees not covered by *M. flavus* but these were mimicked by species of *Volucella*. Moreover, the *Volucella* were very common suggesting that these models are already well loaded, so that selection to establish the same pattern in another species would be weak or absent.

In the United Kingdom adult *M. equestris* are out in May, June and very early July – before most of the young birds have left the nest and also before most bumble-bee populations have built up. This means that naïve young birds have a greater likelihood than otherwise of learning about bee-like coloration from bees than from mimics. The following year forgetful birds could get a reminder from the queen bumble bees in the spring. Thus by the time the bulb fly emerges, birds should be experienced (see also Waldbauer & Sheldon 1971). Other workers have found that an experience with an aposematic insect is remembered for a long time. Crows remember for at least 9 months (Rothschild 1964) and two species of tit remembered an aposematic moth after 12 months during which they did not see it. Lizards can remember aposematic models after 11 months of no experience (Sexton 1964). Thus long memory in the predators of *M. equestris* cannot be excluded and it raises the question, pertinent for birds, of whether the predators learnt their bees in the areas where they are apt to feed on the flies. It needs to be added that some animals can eat bumble bees and so will not be deterred from sampling *M. equestris*. I have witnessed a large toad (*Bufo bufo* L.) gulp a *B. lucorum* Fabr. queen with no ill effect and this is reported also elsewhere (Beddard 1892).

M. equestris, like many syrphids, mimics by behaviour as well as appearance. It produces a bee-like buzz when touched and also mimics bee behaviour by waving its abdomen occasionally when walking, and, touched in chilly conditions (10 to 15 °C) that are not conducive to flight, it raises its middle leg on one side and buzzes. This simulates well the threatening appearance of a bumble bee when similarly molested, the threat in the case of the bee being the real one that it is about to grapple with the offending object and sting it. Gaul (1952) and the Browers (1965) have studied sound mimicry. Brower & Brower's work seems to indicate that sound seems to decrease the likelihood of a predator taking a mimic when in conjunction with visual stimuli.

(E) *Cytology*

The chromosome numbers in syrphids have been analysed in great detail by Boyes & Brink (1964, 1966, 1967, 1968 (with Mehta), 1970) in a series of publications. A good summary of results before 1951 is given by Makino, and Metz (1916) and Stevens (1908) are two early workers who obtained good results with simple techniques. My results agree with those of Boyes & Brink as to number and types of chromosomes ($2n = 12$) and I have also detected polytene chromosomes in many organs. Material was dissected under 0.73 % saline (Sharma & Sharma 1965), passed through 1N HCl for 5 to 10 min and then placed in acetic orcein (G. T. Gurr) at full commercial strength for a period of time dependent on the tissue – usually not longer than 15 min. The tissue was then squashed under a coverslip and left for 5 min, taken through absolute alcohol and mounted in Euparal. To examine chromosome numbers, germinal primordia, 'brain' tissue and imaginal disks of overwintering last instar larvae, it was found that pupating larvae and pupae were useful material. Polytene chromosomes were in abundance in the fat body tissue of the last larval stage. They were also observed in Malpighian tubules but usually this tissue did not prove easy to study. In the study of polytene chromosomes fat droplets were found to be a problem, but keeping the tissue as long as possible in HCl (but not so long that the chromosomes break easily and do not stain) tended to counteract this. Acetic orcein and absolute alcohol also affected the droplets so that one could often remove most of them.

Ordinary chromosomes were examined under oil immersion, whilst polytene chromosomes were examined under fairly low power. The polytene chromosomes are large and difficult to separate from each other to that it may be quicker to build up montage photographs from tissues of individual larvae than to try to find single good examples.

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APPENDIX TABLES

TABLE A1. *VALIDUS, SUBVALIDUS* AND *BULBORUM*

cross no.	parental phenotypes		parental origins		progeny												total no. of progeny
					♂				♀				total				
	♂	♀	♂	♀	1	2	3	4	1	2	3	4	1	2	3	4	
67–2	*VAL*	*VAL*	?	?	2	0	0	0	0	0	0	0	2	0	0	0	2
67–43			no. 18	no. 9	6	2	0	1	9	0	1	0	15	2	1	1	19
67–63			no. 18	H VII	2	0	0	0	3	0	3	0	5	0	3	0	8
67–72			+	F VI	11	0	0	2	7	0	0	3	18	0	0	5	23
68–37			67–56	67–7	11	2	0	2	17	0	0	3	28	2	0	5	35
68–42			67–43	67–35	4	0	0	0	3	0	0	0	7	0	0	0	7
68–60			67–62	67–56	3	2	0	1	3	1	1	2	6	3	1	3	13
68–74			67–34	67 -30	0	0	0	0	1	0	0	0	1	0	0	0	1
67–44	*VAL*	*SUB*	H VII	E V	2	0	0	0	1	0	0	0	3	0	0	0	3
68–45			67–52	67–52	10	6	0	3	8	5	2	6	18	11	2	9	40
68–115			67–54	67–35	8	8	0	3	8	7	0	6	16	15	0	9	40
H VII	*SUB*	*VAL*	+	+	1	0	0	0	1	0	2	0	2	0	2	0	4
67–33			no. 9	E V	3	0	0	1	0	0	0	1	3	0	0	2	5
67–35			no. 12	F VI	3	0	0	2	1	0	0	2	4	0	0	4	8
67–45			no. 12	no. 5	0	0	0	2	4	0	0	0	4	0	0	2	6
67–65			+	no. 9	1	0	0	0	4	0	0	0	5	0	0	0	5
68–152			+	+	6	0	0	1	5	0	1	2	11	0	1	3	15
67–7	*SUB*	*BULB*	no. 5	no. 10	0	0	0	1	1	0	3	1	1	0	3	2	6
67–34	*BULB*	*SUB*	no. 4	no. 10	3	0	0	0	2	0	0	0	5	0	0	0	5
67–62	*VAL*	OTHER	+	no. 8	3	1	0	4	5	5	3	0	8	6	3	4	21
67–66			F VI	D IV	1	0	0	0	0	0	0	0	1	0	0	0	1
68–32			67–68	67–67	10	0	2	9	9	0	0	11	19	0	2	20	41
68–68			67–72	67–30	0	0	0	0	1	0	0	1	1	0	0	1	2
68–78			67–36	?	0	1	1	0	0	0	1	1	0	1	2	1	4
68–109			67–36	?	4	1	0	5	8	1	5	7	12	2	5	12	31
69–25			68–37	+	5	0	0	0	11	1	0	0	16	1	0	0	17
69–26			68–42	?	1	2	0	0	5	0	0	0	6	2	0	0	8
69–28			68–33	+	2	8	1	12	0	1	3	7	2	9	4	19	34
69–33			68–45	+	3	3	1	7	3	0	0	6	6	3	1	13	23
69–34			68–37	+	0	2	0	4	10	0	0	5	10	2	0	9	21
69–35			68–37	+	0	0	0	2	0	0	0	1	0	0	0	3	3
69–42			68–42	68–50	3	3	0	0	6	3	0	0	9	6	0	0	15
69–43			68–45	68–32	0	0	0	0	1	0	0	0	1	0	0	0	1
69–48			68–32	68–32	2	3	0	12	9	0	0	2	11	3	0	14	28
69–59			68–45	68–50	2	10	0	0	5	7	0	0	7	17	0	0	24
69–63			68–142	68–32	4	0	0	2	0	0	0	4	4	0	0	6	10
69–114			68–109	68–92	0	0	0	0	0	0	0	2	0	0	0	2	2
69–115			68–150	68–137	2	0	0	1	2	0	0	1	4	0	0	2	6
69–117			68–154	68–154	1	1	1	2	1	0	2	1	2	1	3	3	9
69–122			68–54	68–91	0	3	0	4	0	0	1	3	0	3	1	7	11
69–125			68–152	68–149	2	0	0	0	1	0	0	0	3	0	0	0	3
69–127			68–146	68–149	0	0	0	0	0	0	1	1	0	0	1	1	2
E V	OTHER	*VAL*	+	+	0	0	0	0	1	1	1	0	1	1	1	0	3
F VI			+	+	0	0	0	1	0	0	0	3	0	0	0	4	4
67–1			?	?	3	0	1	1	2	0	0	1	5	0	1	2	8
67–16			no. 4	no. 9	4	0	0	0	5	0	0	0	9	0	0	0	9
67–19			no. 12	no. 9	0	0	0	0	2	0	0	0	2	0	0	0	2
67–46			no. 5	no. 5	2	0	0	1	1	0	0	1	3	0	0	2	5
67–52			D IV	no. 9	4	0	0	0	5	1	0	1	9	1	0	1	11
67–53			no. 12	no. 12	4	0	0	1	0	0	0	5	4	0	0	6	10

Table A 1 (*cont.*)

cross no.	parental phenotypes		parental origins		progeny												total no. of progeny
					♂				♀				total				
	♂	♀	♂	♀	1	2	3	4	1	2	3	4	1	2	3	4	
67–56			D IV	no. 9	5	0	0	0	6	0	0	0	11	0	0	0	11
67–68			+	no. 8	5	0	0	4	3	0	0	2	8	0	0	6	14
67–73			+	no. 9	4	0	0	5	5	0	0	3	9	0	0	8	17
68–19			67–45	67–45	0	0	0	1	0	0	0	0	0	0	0	1	1
68–54			67–31	67–31	0	0	0	0	1	0	0	0	1	0	0	0	1
68–86			67–68	67–68	1	1	0	3	3	0	0	1	4	1	0	4	9
68–96			?	?	0	0	0	0	1	0	0	1	1	0	0	1	2
68–137			67–35	67–59	4	0	0	1	5	0	0	4	9	0	0	5	14
68–142			+	67–63	5	0	0	0	11	0	0	0	16	0	0	0	16
68–150			+	+	2	0	0	2	2	0	0	3	4	0	0	5	9
69–13			68–50	68–32	0	1	1	1	1	0	0	3	1	1	1	4	7
69–14			68–16	68–37	5	2	0	5	8	0	0	5	13	2	0	10	25
69–19			68–33	68–37	3	10	1	16	12	0	0	12	15	10	1	28	54
69–20			68–33	68–37	0	0	2	4	1	0	0	4	1	0	2	8	11
69–31			68–50	68–37	0	0	0	2	0	0	0	1	0	0	0	3	3
69–39			68–50	68–142	0	0	0	1	0	0	0	0	0	0	0	1	1
69–40			68–50	68–142	0	0	0	1	1	0	0	7	1	0	0	8	9
69–49			68–32	68–32	0	0	2	4	2	2	0	5	2	2	2	9	15
69–51			68–32	68–37	2	2	0	4	7	0	0	7	9	2	0	11	22
69–53			68–32	68–32	1	0	0	4	2	0	0	3	3	0	0	7	10
69–58			68–50	68–45	0	4	0	0	4	1	0	0	4	5	0	0	9
69–62			68–16	68–142	2	3	0	6	4	0	1	3	6	3	1	9	19
69–73			68–16	68–32	1	2	0	10	4	0	0	4	5	2	0	14	21
69–77			68–101	68–37	0	3	0	5	2	0	0	1	2	3	0	6	11
69–89			68–142	68–16	0	1	0	0	1	0	0	2	1	1	0	2	4
69–121			68–154	68–150	0	3	0	4	6	0	0	5	6	3	0	9	18
69–124			68–154	68–154	0	2	0	2	0	0	0	2	0	2	0	4	6
69-139			68–82	68-137	2	0	0	4	4	0	0	3	6	0	0	7	13
B II	*SUB*	OTHER	+	+	0	2	0	0	0	0	0	2	0	2	0	2	4
67–11			cage 3	no. 1	2	0	0	1	1	0	0	1	3	0	0	2	5
67–18			no. 10	no. 10	0	0	2	1	0	0	0	1	0	0	2	2	4
67–36			no. 9	?	4	0	0	2	1	0	1	1	5	0	1	3	9
68–16			67–77	67–3	1	0	1	8	0	0	0	4	1	0	1	12	14
68–33			67–77	67–30	0	8	0	5	0	4	2	7	0	12	2	12	26
68–118			67–54	67–67	0	2	0	3	0	2	1	2	0	4	1	5	10
68–145			+	+	0	4	0	0	0	6	0	2	0	10	0	2	12
68–153			+	+	1	0	2	2	0	0	0	1	1	0	2	3	6
68–155			+	+	0	3	0	4	2	0	0	0	2	3	0	4	9
69–12			68–33	68–26	0	1	1	4	1	0	3	0	1	1	4	4	10
69–110			68–154	68–154	0	2	0	2	0	0	2	2	0	2	2	4	8
69–129			68–146	68–149	0	0	4	5	0	0	7	3	0	0	11	8	19
68–79	*BULB*	OTHER	67–69	67–69	0	3	0	4	0	1	0	1	0	4	0	5	9
68–98			67–18	67–28	0	1	0	0	0	0	1	0	0	1	1	0	2
68–117			67–54	67–46	0	0	0	0	0	0	2	2	0	0	2	2	4
69–117			68–154	68–154	0	0	0	0	0	0	2	2	0	0	2	2	4
69–128			68–146	68–117	0	0	1	0	0	0	0	0	0	0	1	0	1
69–132			68–60	68–144	0	2	0	1	1	2	0	1	1	4	0	2	7
67–54	OTHER	*BULB*	D IV	A I	1	2	0	3	0	0	2	1	1	2	2	4	9
67–69			D IV	A I	0	0	1	1	0	0	1	3	0	0	2	4	6
67–75			+	H VII	1	2	0	2	0	2	1	3	1	4	1	5	11
68–26			67–36	67-43	0	1	2	7	0	0	5	7	0	1	7	14	22
68–57			67–62	67–62	0	0	0	0	0	0	0	1	0	0	0	1	1
68–146			+	67–75	2	2	1	3	0	0	2	0	2	2	3	3	10
68–154			+	+	8	0	0	5	1	1	0	3	9	1	0	8	18

Table A 1 (*cont.*)

					progeny												
	parental phenotypes		parental origins		♂				♀				total				
cross no.	♂	♀	♂	♀	1	2	3	4	1	2	3	4	1	2	3	4	total no. of progeny
69–4			68–46	68–26	0	0	4	6	0	0	4	3	0	0	8	9	17
69–80			68–146	68–146	0	0	0	2	0	0	0	0	0	0	0	2	2
C III	OTHER	OTHER	+	+	0	0	0	1	0	0	0	0	0	0	0	1	1
D IV			+	+	0	0	0	12	0	0	0	9	0	0	0	21	21
67–3			D IV	no. 1	0	0	0	9	0	0	0	9	0	0	0	18	18
67–6			no. 4	no. 13	0	0	0	3	0	0	0	4	0	0	0	7	7
67–10			no. 4	D IV	0	0	0	8	0	0	0	3	0	0	0	11	11
67–13			no. 1	no. 10	0	0	0	1	0	0	0	3	0	0	0	4	4
67–14			no. 13	no. 1	0	0	0	0	0	0	0	5	0	0	0	5	5
67–15			no. 3	no. 11	0	0	0	1	0	0	0	0	0	0	0	1	1
67–17			A I	no. 3	0	0	0	1	0	0	0	2	0	0	0	3	3
67–27			A I	no. 10	0	0	0	4	0	0	0	2	0	0	0	6	6
67–28			no. 10	no. 3	0	0	0	1	0	0	0	1	0	0	0	2	2
67–30			no. 8	no. 4	0	0	0	2	0	0	0	3	0	0	0	5	5
67–49			no. 12	no. 4	0	0	0	2	0	0	0	2	0	0	0	4	4
67–55			no. 4	no. 11	0	0	0	5	0	0	0	3	0	0	0	8	8
67–59			no. 5	no. 5	0	0	0	4	0	0	0	1	0	0	0	5	5
67–64			?	D IV	0	0	0	2	0	0	0	1	0	0	0	3	3
67–67			+	D IV	0	0	0	12	1*	0	0	9	1*	0	0	21	22
67–76			+	D IV	0	0	0	10	0	0	0	9	0	0	0	19	19
68–18			67–67	67–67	0	0	0	5	0	0	0	0	0	0	0	5	5
68–21			67–7	67–3	0	0	0	4	0	0	0	10	0	0	0	14	14
68–46			67–55	67–55	0	0	0	3	0	0	0	1	0	0	0	4	4
68–50			67–33	67–67	0	0	0	20	0	0	0	13	0	0	0	33	33
68–66			67–30	67–31	0	0	0	8	0	0	0	9	0	0	0	17	17
68–82			67–54	67–76	0	0	0	18	0	0	0	9	0	0	0	27	27
68–92			?	67–36	0	0	0	8	0	0	0	7	0	0	0	15	15
68–93			67–3	67–31	0	0	0	1	0	0	0	2	0	0	0	3	3
68–101			67–68	67–13	0	0	0	10	0	0	0	13	0	0	0	23	23
68–115			67–54	67–35	0	0	0	3	0	0	0	2	0	0	0	5	5
68–129			67–64	67–76	0	0	0	8	0	0	0	8	0	0	0	16	16
68–114			?	+	0	0	0	6	0	0	0	10	0	0	0	16	16
68–149			?	+	0	0	0	5	0	0	0	7	0	0	0	12	12
69–11			68–50	68–33	0	0	0	7	0	0	0	10	0	0	0	17	17
69–17			+	68–50	0	0	0	13	0	0	0	0	0	0	0	13	13
69–27			68–66	68–16	0	0	0	5	0	0	0	10	0	0	0	15	15
69–29			68–46	68–90	0	0	0	6	0	0	0	5	0	0	0	11	11
69–32			68–50	68–66	0	0	0	7	0	0	0	8	0	0	0	16*	16*
69–46			68–50	68–45	0	0	0	4	0	0	0	3	0	0	0	7	7
69–47			68–50	68–50	0	0	0	10	0	0	0	6	0	0	0	16	16
69–60			68–50	68–50	0	0	0	6	0	0	0	7	0	0	0	13	13
69–61			68–109	68–109	0	0	0	22	0	0	0	22	0	0	0	44	44
69–64			68–129	68–129	0	0	0	14	0	0	0	9	0	0	0	23	23
69–67			68–50	68–109	0	0	0	9	0	0	0	7	0	0	0	17*	17*
69–69			?	68–66	0	0	0	12	0	0	0	3	0	0	0	15	15
69–70			68–101	68–50	0	0	0	9	0	0	0	11	0	0	0	20	20
69–71			68–66	68–45	0	0	0	1	0	0	0	2	0	0	0	3	3
69–74			68–16	68–145	0	0	0	2	0	0	0	1	0	0	0	3	3
69–75			68–93	68–50	0	0	0	27	0	0	0	16	0	0	0	43	43
69–84			68–50	68–50	0	0	0	3	0	0	0	3	0	0	0	6	6
69–105			68–149	68–118	0	0	0	3	0	0	0	0	0	0	0	3	3
69–107			68–154	68–153	0	0	0	3	0	0	0	2	0	0	0	5	5
69–116			68–60	68–93	0	0	0	1	0	0	0	2	0	0	0	3	3
69–130			68–101	68–101	0	0	0	2	0	0	0	0	0	0	0	2	2

TABLE A1 (*cont.*)

cross no.	parental phenotypes ♂	parental phenotypes ♀	parental origins ♂	parental origins ♀	progeny ♂ 1	♂ 2	♂ 3	♂ 4	♀ 1	♀ 2	♀ 3	♀ 4	total 1	total 2	total 3	total 4	total no. of progeny
69–138			68–92	68–144	0	0	0	6	0	0	0	4	0	0	0	10	10
69–146			68–82	68–82	0	0	0	4	0	0	0	1	0	0	0	5	5
69–156			68–149	68–149	0	0	0	1	0	0	0	0	0	0	0	1	1
69–157			68–82	68–82	0	0	0	1	0	0	0	3	0	0	0	4	4

Odd and aberrant crosses

cross no.	parental phenotypes ♂	parental phenotypes ♀	parental origins ♂	parental origins ♀	progeny ♂ 1	♂ 2	♂ 3	♂ 4	♀ 1	♀ 2	♀ 3	♀ 4	total 1	total 2	total 3	total 4	total no. of progeny
A I	(1)	OTHER	+	+	0	1	1	4	0	0	2	1	0	1	3	5	9
68–52	OTHER (2)	OTHER	67–67	67–6	0	0	0	0	1	0	0	0	1	0	0	0	1
68–76	OTHER	OTHER†	67–67	67–3	0	0	0	0	0	0	1	0	0	0	1	0	1
68–90	OTHER	(6)	67–69	+	2	0	0	2	2	0	0	6	4	0	0	8	12
68–91	OTHER	(7)	67–54	67–46	1	0	0	4	1	2	1	3	2	2	1	7	12
69–37	OTHER	(3)	68–66	68–90	0	0	0	2	0	0	0	2	0	0	0	4	4
69–38	OTHER	(3)	68–50	68–90	0	0	0	12	0	0	0	15	0	0	0	27	27
69–41	OTHER	(3)	68–50	68–90	0	0	0	7	0	0	0	2	0	0	0	9	9
69–72	OTHER	(4)	68–50	68–109	0	0	0	9	0	0	0	11	0	0	0	20	20
69–87	OTHER	(4)	68–146	68–109	0	0	0	4	0	0	0	4	0	0	0	8	8
69–90	OTHER	(5)	68–101	68–118	0	0	1	0	0	0	0	1	0	0	1	1	2

Key to the above tables on *validus*, *subvalidus* and *bulborum* crosses:

VAL = *validus*.
SUB = *subvalidus*.
BULB = *bulborum*.
OTHER = not of the first three types.
1 = *validus* type F_1.
2 = *subvalidus* type F_1.
3 = *bulborum* type F_1.
4 = other type F_1.
† = contamination probable.
* = sex of one insect could not be determined.
? = origins unknown or uncertain.
\+ = wild type obtained from the field.
(1) = precise phenotype not known as abdomen of insect lost.
(2) = no record of the cross being fertile – labelling mix-up suspected.
(3) = from 68–90 cross – odd colour type.
(4) = from 68–109 cross – odd colour type.
(5) = from 68–118 cross – *subvalidus*.
(6) = wild type and probably not virgin – odd coloration.
(7) = labelling suspect.

Table A2. *Equestris*

	parental phenotypes		parental origins		progeny						total no. of progeny
					♂		♀		total		
cross no.	♂	♀	♂	♀	1	2	1	2	1	2	
67–13	*EQU*	*EQU*	no. 1	no. 10	1	0	3	0	4	0	4
69–69			?	68–66	8	4	2	1	10	5	15
C III	*EQU*	*NARC*	+	+	0	0	0	1	0	1	1
67–49			no. 12	no. 4	2	0	0	2	2	2	4
68–21			67–7	67–3	2	2	5	5	7	7	14
68–129			67–64	67–76	4	4	7	1	11	5	16
69–27			68–66	68–16	2	3	3	7	5	10	15
69–70			68–101	68–50	2	7	2	9	4	16	20
69–71			68–66	68–45	1	0	0	2	1	2	3
67–14	*NARC*	*EQU*	no. 13	no. 1	0	0	2	3	2	3	5
68–66			67–30	67–31	8	0	9	0	17	0	17
68–92			?	67–36	0	8	2	5	2	13	15
68–93			67–3	67–31	0	2	1	0	1	2	3
68–101			67–68	67–13	4	6	3	10	7	16	23
68–144			?	+	5	1	4	6	9	7	16
69–32			68–50	68–66	3	4	4	4	8*	8	16*
69–61			68–109	68–109	10	12	15	7	25	19	44
69–64			68–129	68–129	7	7	7	2	14	9	23
69–107			68–154	68–153	0	3	1	1	1	4	5
69–116			68–60	68–93	0	1	2	0	2	1	3
D IV	*NARC*	*NARC*	+	+	0	12	0	9	0	21	21
67–3			D IV	no. 1	0	9	0	9	0	18	18
67–6			no. 4	no. 13	0	3	0	4	0	7	7
67–10			no. 4	D IV	0	8	0	3	0	11	11
67–15			no. 3	no. 11	0	1	0	0	0	1	1
67–17			A I	no. 3	0	1	0	2	0	3	3
67–27			A I	no. 10	0	4	0	2	0	6	6
67–28			no. 10	no. 3	0	1	0	1	0	2	2
67–30			no. 8	no. 4	0	2	0	3	0	5	5
67–55			no. 4	no. 11	0	5	0	3	0	8	8
67–59			no. 5	no. 5	0	4	0	1	0	5	5
67–67			+	D IV	0	12	0	9	0	21	21
67–76			+	D IV	0	10	0	9	0	19	19
68–18			67–67	67–67	0	5	0	0	0	5	5
68–46			67–55	67–55	0	3	0	1	0	4	4
68–50			67–33	67–67	0	20	0	13	0	33	33
68–82			67–54	67–76	0	18	0	9	0	27	27
68–115			67–54	67–35	0	3	0	2	0	5	5
68–149			?	+	0	5	0	7	0	12	12
69–11			68–50	68–33	0	7	0	10	0	17	17
69–17			+	68–50	0	13	0	0	0	13	13
69–29			68–46	68–90	0	6	0	5	0	11	11
69–46			68–50	68–45	0	4	0	3	0	7	7
69–47			68–50	68–50	0	10	0	6	0	16	16
69–60			68–50	68–50	0	6	0	7	0	13	13
69–74			68–16	68–145	0	2	0	1	0	3	3
69–75			68–93	68–50	0	27	0	16	0	43	43
69–84			68–50	68–50	0	3	0	3	0	6	6
69–105			68–149	68–118	0	3	0	0	0	3	3
69–130			68–101	68–101	0	2	0	0	0	2	2
69–138			68–92	68–144	0	6	0	4	0	10	10
69–146			68–82	68–82	0	4	0	1	0	5	5
69–156			68–149	68–149	0	1	0	0	0	1	1
69–157			68–82	68–82	0	1	0	3	0	4	4

TABLE A2 (*cont.*)

CROSSES INVOLVING *VALIDUS*, *SUBVALIDUS* OR *BULBORUM*

	parental phenotypes		parental origins		progeny									total no. of progeny
					♂			♀			total			
cross no.	♂	♀	♂	♀	*VAL*	1	2	*VAL*	1	2	*VAL*	1	2	
67–7	*VAL*	*VAL*	no. 5	no. 10	0	1	0	4	1	0	4	2	0	6
67–45			no. 12	no. 5	0	1	1	4	0	0	4	1	1	6
68–37			67–56	67–3	13	2	0	17	0	3	30	2	3	35
67–11	*VAL*	*EQU*	cage 3	no. 1	2	1	0	1	1	0	3	2	0	5
67–18			no. 10	no. 10	2	0	1	0	1	0	2	1	1	4
67–36			no. 9	?	4	0	2	2	1	0	6	1	2	9
68–117			67–54	67–46	0	0	0	2	1	1	2	1	1	4
67–46	*EQU*	*VAL*	no. 5	no. 5	2	1	0	1	1	0	3	2	0	5
67–53			no. 12	no. 12	4	0	1	0	4	1	4	4	2	10
68–78	*VAL*	*NARC*	67–36	?	2	0	0	1	1	0	3	1	0	4
68–109			67–36	?	5	1	4	14	6	1	19	7	5	31
69–110			68–154	68–154	2	2	0	2	2	0	4	4	0	8
69–114			68–109	68–92	0	0	0	0	1	1	0	1	1	2
69–115			68–150	68–137	2	0	1	2	1	0	4	1	1	6
67–52	*NARC*	*VAL*	D IV	no. 9	4	0	0	6	1	0	10	1	0	11
68–137			67–35	67–59	4	0	1	5	1	3	9	1	4	14
68–150			+	+	2	1	1	2	0	3	4	1	4	9
68–154			+	+	8	0	5	2	1	2	10	1	7	18
69–13			68–50	68–32	2	0	1	1	1	2	3	1	3	7
69–14			68–16	68–37	7	5	0	8	5	0	15	10	0	25
69–19			68–33	68–37	14	16	0	12	12	0	26	28	0	54
69–20			68–33	68–37	2	4	0	1	3	1	3	7	1	11
69–51			68–32	68–37	4	4	0	7	7	0	11	11	0	22
69–73			68–16	68–32	3	1	9	4	0	4	7	1	13	21
69–77			68–101	68–37	3	5	0	2	1	0	5	6	0	11
69–80			68–146	68–146	0	2	0	0	0	0	0	2	0	2

Key to the above tables on *equestris* crosses:

EQU = *equestris*.
NARC = non-*equestris*, non-*validus*, *subvalidus* or *bulborum*, i.e. either *narcissi* or *transversalis*.
VAL = *validus*, *subvalidus* or *bulborum* – any one of these types can mask the presence or absence of *equestris*.
1 = *equestris* F_1.
2 = non-*equestris* F_1 – recessive types.
* = sex of one of F_1 could not be determined.
? = origins unknown or uncertain.
\+ = wild type obtained from the field.

Table A3. *Transversalis*

cross no.	♀ parental phenotype only	parental origins		progeny ♀ only		total no. of progeny
		♂	♀	*TRANS*	NON-*T*	
B II	*TRANS*	+	+	1	1	2
D IV		+	+	7	2	9
E V		+	+	0	3	3
H VII		+	+	2	1	3
67–1		?	?	1	2	3
67–6		no. 4	no. 13	1	3	4
67–10		no. 4	D IV	1	2	3
67–11		cage 3	no. 1	1	1	2
67–13		no. 1	no. 10	1	2	3
67–14		no. 13	no. 1	2	3	5
67–16		no. 4	no. 9	4	0	4
67–17		A I	no. 3	0	2	2
67–18		no. 10	no. 10	0	1	1
67–19		no. 12	no. 9	2	0	2
67–27		A I	no. 3	2	0	2
67–33		no. 9	E V	0	1	1
67–45		no. 12	no. 5	1	3	4
67–46		no. 5	no. 5	2	0	2
67–52		D IV	no. 9	2	5	7
67–53		no. 12	no. 12	5	0	5
67–54		D IV	A I	3	0	3
67–55		no. 4	no. 11	2	1	3
67–56		D IV	no. 9	5	1	6
67–63		no. 18	H VII	0	6	6
67–64		?	D IV	0	1	1
67–65		+	no. 9	0	4	4
67–67		+	D IV	5	4	9
67–75		+	H VII	5	1	6
67–76		+	D IV	9	0	9
68–21		67–7	67–3	9	1	10
68–26		67–36	67–43	5	7	12
68–32		67–68	67–67	5	15	20
68–33		67–77	67–30	7	6	13
68–57		67–62	67–62	0	1	1
68–66		67–30	67–31	8	1	9
68–82		67–54	67–76	7	2	9
68–93		67–3	67–31	1	0	1
68–117		67–54	67–46	2	2	4
68–129		67–64	67–76	6	2	8
68–145		+	+	5	3	8
68–146		+	67–75	2	0	2
68–149		?	+	5	2	7
68–153		+	+	0	1	1
69–11		68–50	68–33	3	7	10
69–25		68–37	+	2	10	12
69–28		68–33	+	5	6	11
69–32		68–50	68–66	3	5	8
69–33		68–45	+	2	7	9
69–34		68–37	+	2	13	15
69–37		68–66	68–90	2	0	2
69–40		68–50	68–142	2	6	8
69–41		68–50	68–90	2	0	2
69–42		68–42	68–50	0	9	9
69–51		68–32	68–37	6	8	14
69–53		68–32	68–32	2	3	5
69–60		68–50	68–50	2	5	7

TABLE A3 (*cont.*)

		parental origins		progeny ♀ only		total no. of progeny
cross no.	♀ parental phenotype only	♂	♀	*TRANS*	NON-*T*	
69–61		68–109	68–109	18	4	22
69–64		68–129	68–129	5	4	9
69–69		?	68–66	3	0	3
69–74		68–16	68–145	1	0	1
69–75		68–93	68–50	23	0	23
69–77		68–101	68–37	1	2	3
69–89		68–142	68–16	2	1	3
69–116		68–60	68–93	2	0	2
69–117		68–154	68–154	3	1	4
69–122		68–54	68–91	1	3	4
69–125		68–152	68–149	0	1	1
69–127		68–146	68–149	1	1	2
69–129		68–146	68–149	8	2	10
69–132		68–60	68–144	2	2	4
69–146		68–82	68–82	1	0	1
69–157		68–82	68–82	3	0	3
A I	NON-*TRANS*	+	+	2	1	3
C III		+	+	0	1	1
F VII		+	+	0	3	3
67–3		D IV	no. 1	5	4	9
67–7		no. 5	no. 10	2	3	5
67–28		no. 10	no. 3	0	1	1
67–30		no. 8	no. 4	1	2	3
67–34		no. 4	no. 10	0	2	2
67–35		no. 12	F VI	1	2	3
67–36		no. 9	?	1	2	3
67–43		no. 18	no. 9	3	7	10
67–44		H VIII	E V	1	0	1
67–49		no. 12	no. 4	2	0	2
67–59		no. 5	no. 5	0	1	1
67–62		+	no. 8	2	11	13
67–68		+	no. 8	2	3	5
67–72		+	F VI	8	2	10
67–73		+	no. 9	4	4	8
68–16		67–77	67–3	0	4	4
68–37		67–56	67–7	6	14	20
68–42		67–43	67–35	0	3	3
68–45		67–52	67–52	8	11	19
68–46		67–55	67–55	0	1	1
68–50		67–33	67–67	6	7	13
68–54		67–31	67–31	0	1	1
68–60		67–62	67–56	5	2	7
68–68		67–72	67–30	0	2	2
68–74		67–34	67–30	1	0	1
68–78		67–36	?	1	1	2
68–79		67–69	67–69	1	1	2
68–86		67–68	67–68	0	4	4
68–92		?	67–36	3	4	7
68–96		?	?	1	1	2
68–98		67–18	67–28	0	1	1
68–101		67–68	67–13	5	7	12
68–109		67–36	?	11	10	21
68–115		67–54	67–35	1	1	2
68–118		67–54	67–67	2	3	5
68–137		67–35	67–59	4	5	9

TABLE A 3 (*cont.*)

cross no.	♀ parental phenotype only	parental origins ♂	parental origins ♀	progeny ♀ only *TRANS*	progeny ♀ only NON-*T*	total no. of progeny
68–142		+	67–63	7	4	11
68–144		?	+	7	3	10
68–150		+	+	4	1	5
68–152		+	+	3	5	8
68–154		+	+	2	3	5
68–155		+	+	0	2	2
69–4		68–46	68–26	4	3	7
69–12		68–33	68–26	0	4	4
69–13		68–50	68–32	0	4	4
69–14		68–16	68–37	3	10	13
69–19		68–33	68–37	11	13	24
69–20		68–33	68–37	0	5	5
69–26		68–42	?	0	5	5
69–27		68–66	68–16	2	8	10
69–29		68–46	68–90	3	2	5
69–31		68–50	68–37	1	0	1
69–35		68–37	+	1	0	1
69–38		68–50	68–90	9	6	15
69–43		68–45	68–32	0	1	1
69–46		68–50	68–45	0	3	3
69–47		68–50	68–50	0	6	6
69–48		68–32	68–32	2	9	11
69–49		68–32	68–32	1	8	9
69–58		68–50	68–45	0	5	5
69–59		68–45	68–50	0	12	12
69–62		68–16	68–142	2	6	8
69–63		68–142	68–32	0	4	4
69–67		68–50	68–109	3	4	7
69–70		68–101	68–50	6	5	11
69–71		68–66	68–45	0	2	2
69–72		68–50	68–109	0	11	11
69–73		68–16	68–32	3	5	8
69–84		68–50	68–50	1	1	2
69–87		68–146	68–109	2	2	4
69–90		68–101	68–118	1	0	1
69–107		68–154	68–153	0	2	2
69–110		68–154	68–154	4	0	4
69–114		68–109	68–92	1	1	2
69–115		68–150	68–137	2	1	3
69–121		68–154	68–150	0	11	11
69–124		68–154	68–154	2	0	2
69–138		68–92	68–144	4	0	4
69–139		68–82	68–137	3	4	7

Key to the above tables on *transversalis* crosses:

TRANS = *transversalis*.

NON-*TRANS*, NON-*T* = non-*transversalis*.

? = origins unknown or uncertain.

\+ = wild type obtained from the field.

Table A4. Ground colour

	parental phenotypes		parental origins		progeny									total no. of progeny
					♂			♀			total			
cross no.	♂	♀	♂	♀	1	2	3	1	2	3	1	2	3	
68–92	YOYO	YOYO	?	67–36	6	2	0	2	5	0	8	7	0	15
69–17			+	68–50	11	0	2	0	0	0	11	0	2	13
69–29			68–46	68–90	5	1	0	5	0	0	10	1	0	11
69–67			68–50	68–109	8	0	1	4	0	3	12	0	4	16
69–84			68–50	68–50	2	0	1	3	0	0	5	0	1	6
69–138			68–92	68–144	6	0	0	4	0	0	10	0	0	10
69–156			68–149	68–149	1	0	0	0	0	0	1	0	0	1
C III	YOYO	OOYY	+	+	0	0	0	0	1	0	0	1	0	1
D IV			+	+	6	2	4	4	5	0	10	7	4	21
67–3			D IV	no. 1	2	4	3	4	5	0	6	9	3	18
67–14			no. 13	no. 1	0	0	0	2	3	0	2	3	0	5
67–15			no. 3	no. 11	0	0	1	0	0	0	0	0	1	1
67–30			no. 8	no. 4	1	0	1	0	3	0	1	3	1	5
67–64			?	no. 4	0	2	0	0	1	0	0	3	0	3
67–67			+	D IV	7	3	2	0	8	1	7	11	3	21
67–76			+	D IV	6	1	3	4	5	0	10	6	3	19
68–82			67–54	67–76	8	4	6	5	4	0	13	8	6	27
68–115			67–54	67–35	2	0	1	1	1	0	3	1	1	5
68–144			?	+	3	3	0	6	4	0	9	7	0	16
68–149			?	+	4	1	0	1	6	0	5	7	0	12
69–61			68–109	68–109	13	2	7	7	5	10	20	7	17	44
67–10	OOYY	YOYO	no. 4	D IV	4	4	0	2	1	0	6	5	0	11
67–49			no. 12	no. 4	2	0	0	0	2	0	2	2	0	4
68–129			67–64	67–76	2	3	3	3	5	0	5	8	3	16
69–27			68–66	68–16	1	1	3	6	0	4	7	1	7	15
69–70			68–101	68–50	4	1	4	6	5	0	10	6	4	20
68–50	YOYO	OOOO	67–33	67–67	11	0	9	6	0	7	17	0	16	33
69–60			68–50	68–50	5	0	1	4	0	3	9	0	4	13
69–105			68–149	68–118	2	0	1	0	0	0	2	0	1	3
67–55	OOOO	YOYO	no. 4	no. 11	1	0	4	2	0	1	3	0	5	8
68–46			67–55	67–55	2	0	1	0	0	1	2	0	2	4
67–13	OOYY	OOYY	no. 1	no. 10	0	1	0	0	3	0	0	4	0	4
67–59			no. 5	no. 5	0	2	2	0	1	0	0	3	2	5
68–21			67–7	67–3	0	2	2	0	10	0	0	12	2	14
69–69			?	68–66	0	3	9	0	3	0	0	6	9	15
69–157			68–82	68–82	0	0	1	0	3	0	0	3	1	4
69–71	OOYY	OOOO	68–66	68–45	0	1	0	0	2	0	0	3	0	3
67–6	OOOO	OOYY	no. 4	no. 13	0	0	3	0	4	0	0	4	3	7
67–17			A I	no. 3	0	1	0	0	2	0	0	3	0	3
67–27			A I	no. 10	0	3	1	0	2	0	0	5	1	6
67–28			no. 10	no. 3	0	0	1	0	1	0	0	1	1	2
68–18			67–67	67–67	0	2	3	0	0	0	0	2	3	5
68–66			67–30	67–31	0	4	4	0	9	0	0	13	4	17
68–101			67–67	67–13	0	4	6	0	11	2	0	15	8	23
69–11			68–50	68–33	0	0	7	0	5	5	0	5	12	17
69–32			68–50	68–66	0	2	5	0	4	4	0	7*	9	16*
69–64			68–129	68–129	0	7	7	0	4	5	0	11	12	23
69–107			68–154	68–153	0	0	3	0	1	1	0	1	4	5
69–130			68–101	68–101	0	0	2	0	0	0	0	0	2	2
69–146			68–82	68–82	0	1	3	0	1	0	0	2	3	5
68–93	OOOO	OOOO	67–3	67–31	0	0	2	0	0	1	0	0	3	3
69–46			68–50	68–45	0	0	4	0	0	3	0	0	7	7
69–47			68–50	68–50	0	0	10	0	0	6	0	0	16	16
69–74			68–16	68–145	0	0	2	0	0	1	0	0	3	3
69–75			68–93	68–50	0	0	27	0	0	16	0	0	43	43
69–116			68–60	68–93	0	0	1	0	0	2	0	0	3	3

TABLE A4 (*cont.*)

CROSSES INVOLVING *VALIDUS*, *SUBVALIDAS* OR *BULBORUM* (1)

	parental phenotypes		parental origins		progeny									total no. of progeny
					♂			♀			total			
cross no.	♂	♀	♂	♀	1	2	3	1	2	3	1	2	3	
67–36	YOYO	YOYO	no. 9	?	5	0	1	2	0	0	7	0	1	8
67–44			H VII	E V	2	0	0	0	0	0	2	0	0	2
67–66			F VI	D IV	1	0	0	0	0	0	1	0	0	1
68–45			67–52	67–52	16	0	3	7	0	6	23	0	9	32
68–57			67–62	67–62	0	0	0	1	0	0	0	0	0	1
69–4			68–46	68–26	8	2	0	7	0	0	15	2	0	17
69–26			68–42	?	3	0	0	0	0	0	3	0	0	3
69–33			68–45	+	11	0	3	2	0	4	13	0	7	20
69–42			68–42	68–50	6	0	0	3	0	0	9	0	0	9
69–59			68–45	68–50	12	0	0	7	0	0	19	0	0	19
69–63			68–142	68–32	4	0	1	2	0	3	6	0	4	10
B II	YOYO	OOYY	+	+	1	0	1	0	2	0	1	2	1	4
67–7			no. 5	no. 10	0	1	0	3	1	0	3	2	0	5
67–18			no. 10	no. 10	2	0	1	0	1	0	2	1	1	4
67–54			D IV	A I	3	0	3	2	1	0	5	1	3	9
67–62			+	no. 8	8	0	0	8	0	0	16	0	0	16
68–32			67–68	67–67	10	6	5	11	0	0	21	6	5	32
68–68			67–72	67–30	0	0	0	0	1	0	0	1	0	1
68–78			67–36	?	2	0	0	2	0	0	4	0	0	4
68–98			67–18	67–28	1	0	0	1	0	0	2	0	0	2
68–109			67–36	?	9	1	0	11	2	0	20	3	0	23
68–117			67–54	67–46	0	0	0	1	3	0	1	3	0	4
68–145			+	+	4	0	0	6	2	0	10	2	0	12
68–153			+	+	3	2	0	0	1	0	3	3	0	6
68–155			+	+	2	5	0	0	0	0	2	5	0	7
69–25			68–37	+	3	0	2	1	0	0	4	0	2	6
69–34			68–37	+	2	0	4	0	0	5	2	0	9	11
69–35			68–37	+	2	0	0	0	0	1	2	0	1	3
69–110			68–154	68–154	2	2	0	2	2	0	4	4	0	8
69–114			68–109	68–92	0	0	0	0	2	0	0	2	0	2
69–117			68–154	68–154	1	4	0	0	3	0	1	7	0	8
69–122			68–54	68–91	3	0	4	1	0	3	4	0	7	11
69–125			68–152	68–149	2	0	0	0	0	0	2	0	0	2
69–132			68–60	68–144	2	1	0	2	0	0	4	1	0	5
67–34	OOYY	YOYO	no. 4	no. 10	3	0	0	0	0	0	3	0	0	3
68–26			67–36	67–43	3	7	0	5	7	0	8	14	0	22
68–154			+	+	8	3	2	1	3	0	9	6	2	17
69–48			68–32	68–32	6	0	11	1	0	1	7	0	12	19
68–16	OOOO	YOYO	67–77	67–3	6	0	5	1	0	3	7	0	8	15
68–118			67–54	67–67	4	0	1	4	0	1	8	0	2	10
69–128			68–146	68–117	1	0	0	0	0	0	1	0	0	1
67–11	OOYY	OOYY	cage 3	no. 1	0	2	1	0	1	0	0	3	1	4
68–79			67–69	67–69	0	4	3	0	2	0	0	6	3	9
68–146			+	67–75	0	4	4	0	2	0	0	6	4	10
69–127			68–146	68–149	0	0	0	0	1	1	0	1	1	2
67–75	OOOO	OOYY	+	H VII	0	3	2	0	6	0	0	9	2	11
68–33			67–77	67–30	0	4	9	0	13	0	0	17	9	26
69–12			68–33	68–26	0	0	6	0	1	2	0	1	8	9
69–28			68–33	+	0	7	16	0	3	8	0	10	24	34
69–80			68–146	68–146	0	0	2	0	0	0	0	0	2	2
69–115			68–150	68–137	0	3	0	0	0	0	0	3	0	3
69–129			68–146	68–149	0	1	8	0	3	7	0	4	15	19

TABLE A4 (*cont.*)

	parental phenotypes		parental origins		progeny									total no. of progeny
					♂			♀			total			
cross no.	♂	♀	♂	♀	1	2	3	1	2	3	1	2	3	
E V	YOYO	NOT CLEAR	+	+	0	0	0	2	0	0	2	0	0	2
H VII			+	+	1	0	0	0	2	0	1	2	0	3
67–2			?	?	2	0	0	0	0	0	2	0	0	2
67–16			no. 4	no. 9	5	0	0	0	0	0	5	0	0	5
67–33			no. 9	E V	4	0	0	1	0	0	5	0	0	5
67–35			no. 12	F VI	3	2	0	0	2	0	3	4	0	7
67–43			no. 18	no. 9	8	1	0	1	0	0	9	1	0	10
67–53			no. 12	no. 12	5	0	0	1	4	0	6	4	0	10
67–63			no. 18	H VII	2	0	0	3	0	0	5	0	0	5
67–65			+	no. 9	1	0	0	0	0	0	1	0	0	1
67–68			+	no. 8	6	1	2	0	2	0	6	3	2	11
67–72			+	F VI	8	2	3	0	3	0	8	5	3	16
67–73			+	no. 9	5	3	1	1	3	0	6	6	1	13
68–37			67–56	67–7	13	2	0	0	3	0	13	5	0	18
68–42			67–43	67–35	3	0	0	0	0	0	3	0	0	3
68–60			67–62	67–56	4	1	1	2	1	1	6	2	2	10
68–86			67–68	67–68	4	0	1	1	0	0	5	0	1	6
68–152			+	+	5	0	2	1	2	0	6	2	2	10
69–39			68–50	68–142	1	0	0	0	0	0	1	0	0	1
69–40			68–50	68–142	1	0	0	2	4	1	3	4	1	8
69–49			68–32	68–32	3	0	3	1	0	6	4	0	9	13
69–51			68–32	68–37	5	2	1	0	7	0	5	9	1	15
69–53			68–32	68–32	4	0	1	1	0	2	5	0	3	8
69–58			68–50	68–45	4	0	0	1	0	0	5	0	0	5
69–62			68–16	68–142	8	0	3	2	0	2	10	0	5	16
69–139			68–82	68–137	3	0	3	1	0	2	4	0	5	9
67–1	OOYY	NOT CLEAR	?	?	4	1	0	0	1	0	4	2	0	6
67–45			no. 12	no. 5	0	2	0	0	0	0	0	2	0	2
67–46			no. 5	no. 5	2	1	0	0	1	0	2	2	0	4
67–56			D IV	no. 9	5	0	0	0	0	0	5	0	0	5
68–19			67–45	67–45	0	1	0	0	0	0	0	1	0	1
68–137			67–35	67–59	4	1	0	0	4	0	4	5	0	9
68–142			+	67–63	5	0	0	0	0	0	5	0	0	5
68–150			+	+	0	0	4	0	3	0	0	3	4	7
69–124			68–154	68–154	0	4	0	0	2	0	0	6	0	6
F VI	OOOO	NOT CLEAR	+	+	1	0	0	0	0	0	1	0	0	1
67–52			D IV	no. 9	5	0	0	0	1	0	5	1	0	6
69–13			68–50	68–32	0	0	2	0	2	2	0	2	4	6
69–14			68–16	68–37	7	5	0	0	5	0	7	10	0	17
69–19			68–33	68–37	14	16	0	0	12	0	14	28	0	42
69–20			68–33	68–37	2	4	0	0	4	0	2	8	0	10
69–31			68–50	68–37	0	0	2	0	1	0	0	1	2	3
69–73			68–16	68–32	0	0	13	0	0	4	0	0	17	17
69–77			68–101	68–37	3	5	0	0	1	0	3	6	0	9
69–89			68–142	68–16	1	0	0	0	2	0	1	2	0	3
69–121			68–154	68–150	0	0	7	0	0	5	0	0	12	12

Table A4 (*cont.*)

Odd and aberrant crosses

	parental phenotypes		parental origins		progeny									total no. of pro-geny
					♂			♀			total			
cross no.	♂	♀	♂	♀	1	2	3	1	2	3	1	2	3	
A I	(2)	OOYY	+	+	2	0	4	0	3	0	2	3	4	9
68–76	YOYO	YOYO (3)	67–67	67–3	1	0	0	0	0	0	1	0	0	1
68–90	OOYY	OOYY (4)	67–69	+	4	0	0	5	1	0	9	1	0	10
68–91	YOYO	OOYY (3)	67–54	67–46	3	0	1	4	3	0	7	3	1	11
69–37	OOOO	YOYO (5)	68–66	68–90	2	0	0	1	1	0	3	1	0	4
69–38	YOYO	YOYO (5)	68–50	68–90	12	0	0	15	0	0	27	0	0	27
69–41			68–50	68–90	7	0	0	2	0	0	9	0	0	9
69–72			68–50	68–109	6	0	3	10	0	1	16	0	4	20
69–87	OOOO	YOYO (5)	68–146	68–109	1	0	3	1	0	3	2	0	6	8
69–90			68–101	68–118	0	0	1	1	0	0	1	0	1	2

Key to the above tables on ground colour:

1 = YOYO.
2 = OOYY.
3 = OOOO.
? = origins unknown or uncertain.
+ = wild type obtained from the field.
(1) = Separated as ♀ *validus* types with phenotypes 1–3 can be difficult to distinguish as groups 1 and 2 can vary in tail colour.
NOT CLEAR = not clear for the reasons stated in (1) above.
(2) = probably YOYO.
(3) = labelling mix-up suspected.
(4) = ♀ parent wild type and probably not virgin.
(5) = some of females showed odd colour type and so were not included in the two categories in the main parts of the table – those not involving and those involving *validus, subvalidus* and *bulborum.*

Table A5. Ground colour variants

(*a*) *Parents of the same category*

	parental phenotypes		parental origins		progeny												total no. of progeny
					♂				♀				total				
cross no.	♂	♀	♂	♀	1	2	3	4	1	2	3	4	1	2	3	4	
68–92	YOYO	YOYO	?	67–36	4	2	0	0	0	0	0	0	4	2	0	0	6
69–67			68–50	68–109	8	0	0	0	4	0	0	0	12	0	0	0	12
69–84			68–50	68–50	2	0	0	0	3	0	0	0	5	0	0	0	5
69–156			68–149	68--149	1	0	0	0	0	0	0	0	1	0	0	0	1
69–29	YOYO	YYYO	68–46	68–90	3	2	0	1	3	2	0	0	6	4	0	1	11
69–138	YYYO	YOYO	68–92	68–144	6	0	0	0	4	0	0	0	10	0	0	0	10
69–17			+	68–50	11	0	0	0	0	0	0	0	0	0	0	0	11

1 = YOYO. 2 = YYYO. 3 = YOYY. 4 = YYYY.

cross no.	♂	♀	♂	♀	1	2	3	4	1	2	3	4	1	2	3	4	total no. of progeny
68–21	OOYY	OOYY	67–7	67–3	2	0	0	2	10	0	0	0	12	0	0	2	14
69–69			?	68–66	3	0	0	9	3	0	0	0	6	0	0	9	15
67–13	OOYY	OOOY	no. 1	no. 10	0	1	0	0	3	0	0	0	3	1	0	0	4
67–59	OOOY	OOYY	no. 5	no. 5	0	0	0	0	0	1	0	0	0	1	0	0	1
69–157			68–82	68–82	0	0	0	1	3	0	0	0	3	0	0	1	4
68–93	OOOO	OOOO	67–3	67–31	0	0	0	2	0	0	0	1	0	0	0	3	3
69–46			68–50	68–45	0	0	0	4	0	0	0	3	0	0	0	7	7
69–47			68–50	68–50	0	0	0	10	0	0	0	6	0	0	0	16	16
69–74			68–16	68–145	0	0	0	2	0	0	0	1	0	0	0	3	3
69–75			69–93	68–50	0	.0	0	27	0	0	0	16	0	0	0	43	43
69–116			68–60	68–93	0	0	0	1	0	0	0	2	0	0	0	3	3

1 = OOYY. 2 = OOOY. 3 = OOYO. 4 = OOOO.

TABLE A5 (*cont.*)

(*b*) *Parents of different categories*

cross no.	parental phenotypes ♂	parental phenotypes ♀	parental origins ♂	parental origins ♀	progeny ♂ 1	♂ 2	♂ 3	♂ 4	♂ 5	♀ 1	♀ 2	♀ 3	♀ 4	♀ 5	total 1	total 2	total 3	total 4	total 5	total no. of progeny
D IV	YOYO	OOYY	+	+	6	0	0	0	6	4	0	0	0	5	10	0	0	0	11	21
67–3			D IV	no. 1	2	0	0	0	7	4	0	0	0	5	6	0	0	0	12	12
67–14			no. 13	no. 1	0	0	0	0	0	2	0	0	0	3	2	0	0	0	3	5
67–15			no. 3	no. 11	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1
67–64			?	no. 4	0	0	0	0	2	0	0	0	0	1	0	0	0	0	3	3
67–67			+	D IV	5	2	0	0	5	0	0	0	0	9	5	2	0	0	14	21
67–76			+	D IV	3	3	0	0	4	1	2	0	1	5	4	5	0	1	9	19
69–61			68–109	68–109	8	0	0	0	9	1	0	0	0	15	9	0	0	0	24	33*
67–30	YOYO	OOOY	no. 8	no. 4	1	0	0	0	1	0	0	0	0	3	1	0	0	0	4	5
68–82			67–54	67–76	8	0	0	0	10	5	0	0	0	4	13	0	0	0	14	27
68–115			67–54	67–35	0	0	2	0	1	0	0	1	0	1	0	0	3	0	2	5
68–114	YOYY	OOYY	?	+	0	0	0	0	3	3	0	0	0	4	3	0	0	0	7	10†
68–149			?	+	4	0	0	0	1	1	0	0	0	6	5	0	0	0	7	12
C III	Y–YY[1]	OOYY	+	+	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
67–10	OOYY	YOYO	no. 4	D IV	0	1	1	2	4	0	2	0	0	1	0	3	1	2	5	11
68–129			67–64	67–76	0	0	0	0	6	0	0	0	0	5	0	0	0	0	11	11[2]
69–27			68–66	68–16	0	0	0	0	4	0	0	0	0	4	4	0	0	0	8	12[3]
69–70	OOOY	YOYO	68–101	68–50	4	0	0	0	5	5	0	0	0	5	9	0	0	0	10	19[4]
67–49	OOOY	YOYY	no. 12	no. 4	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	2[5]
68–50	YOYO	OOOO	67–33	67–67	11	0	0	0	9	6	0	0	0	7	17	0	0	0	16	33
69–60			68–50	68–50	5	0	0	0	1	4	0	0	0	3	9	0	0	0	4	13
69–105			68–149	68–118	2	0	0	0	1	0	0	0	0	0	2	0	0	0	1	3
67–55	OOOO	YOYY	no. 4	no. 11	1	0	0	0	4	0	0	1	1	1	1	0	1	1	5	8
68–46	OOOO	YYYO	67–55	67–55	2	0	0	0	1	0	0	0	0	1	2	0	0	0	2	4

1 = YOYO, 2 = YYYO, 3 = YOYY, 4 = YYYY, 5 = colour type in the other two categories.
* = 4♂Y–YO, 1♂Y–YY, 4♀Y–YO, 2♀Y–YY not included in the classes above.
† = 3♂Y–YO, 3♀Y–YO not included in the classes above.
[1] = masked colour type.
[2] = 2♂Y–YY, 3♀Y–YY not included in the classes above.
[3] = 1♂Y–YO, 1♀Y–YO, 1♀Y–YY not included in the classes above.
[4] = 1♀Y–YO not included in the classes above.
[5] = 2♂Y–YO not included in the classes above.
? = origins unknown or uncertain.
\+ = wild type obtained from the field.

cross no.	parental phenotypes ♂	parental phenotypes ♀	parental origins ♂	parental origins ♀	progeny ♂ 1	♂ 2	♂ 3	♂ 4	♀ 1	♀ 2	♀ 3	♀ 4	total 1	total 2	total 3	total 4	total no. of progeny
69–71	OOYY	OOOO	68–66	68–45	1	0	0	0	2	0	0	0	3	0	0	0	3
67–17	OOOO	OOYY	A I	no. 3	1	0	0	0	2	0	0	0	3	0	0	0	3
68–18			67–67	67–67	0	2	0	3	0	0	0	0	0	2	0	3	5
68–66			67–30	67–31	4	0	0	4	9	0	0	0	13	0	0	4	17
68–101			67–67	67–13	2	2	0	6	9	2	0	2	11	4	0	8	23
69–11			68–50	68–33	0	0	0	7	5	0	0	5	5	0	0	12	17
69–32			68–50	68–66	2	0	0	5	3	1	0	4	6*	1	0	9	16*
69–64			68–129	68–129	7	0	0	7	4	0	0	5	11	0	0	12	23
69–107			68–154	68–153	0	0	0	3	0	1	0	1	0	1	0	4	5
69–130			68–101	68–101	0	0	0	2	0	0	0	0	0	0	0	2	2
67–6	OOOO	OOOY	no. 4	no. 13	0	0	0	3	2	2	0	0	2	2	0	3	7
67–27			A I	no. 10	2	1	0	1	2	0	0	0	4	1	0	1	6
67–28			no. 10	no. 3	0	0	0	1	0	1	0	0	0	1	0	1	2
69–146	OOOO	OOOY	68–82	68–82	1	0	0	3	1	0	0	0	2	0	0	3	5

* = 1 OOYY sex not determined.
1 = OOYY. 2 = OOOY. 3 = OOYO. 4 = OOOO.

Table A 6. ‘Odd’ colour type

	parental phenotypes		parental origins		progeny									
					♂			♀			total			total no. of progeny
cross no.	♂	♀	♂	♀	1	2	3	1	2	3	1	2	3	
68–90	*narc*	‘odd’	67–69	+	2	0	2	2	3	3	4	3	5	12
69–37	*narc*	‘odd’	68–66	68–90	0	0	2	0	2	0	0	2	2	4
69–38	*narc*	‘odd’	68–50	68–90	0	0	12	0	8	7	0	8	19	27
69–41	*narc*	‘odd’	68–50	68–90	0	0	7	0	1	1	0	1	8	9
69–72	*narc*	‘odd’	68–50	68–109	0	0	9	0	2*	9	0	2	18	20
69–87	*narc*	‘odd’	68–146	68–109	0	0	4	0	1	3	0	1	7	8
69–90	*narc*	*sub*	68–101	68–118	1	0	0	0	1	0	1	1	0	2

Key to above table on ‘odd’ colour types:

1 = *validus*, *subvalidus* and *bulborum*.
2 = ‘odd’ colour type.
3 = other colour types – *narcissi*, *equestris*, etc.
+ = wild type obtained from the field.
* = one of these looks more like ‘diluted’ *equestris*.
narc = *narcissi* type.
sub = *subvalidus*.

TABLE A7. ALLELISM

	parental types – both loci specified		nos. of F$_1$ with respect to types specified				
cross no.	♂	♀	double dom.	dom. A	dom. B	double rec.	total no. of progeny
(1)							
69–48	*BULB* (*T*?)	DOUBLE REC. (*NARC*)	2	7	0	2	11
68–118	*BULB* (*T*)	DOUBLE REC. (*NARC*)	2	1	1	1	5
67–62	*BULB* (*T*)	DOUBLE REC. (*NARC*)	2	11	0	0	13
(2)							
68–32	*BULB* YOYO	DOUBLE REC.	0	12	20	0	32
69–34	*BULB* YOYO	DOUBLE REC.	2	0	0	9	11
69–110	*BULB* YOYO	DOUBLE REC.	4	0	0	4	8
69–117	*BULB* YOYO	DOUBLE REC.	1	4	0	3	8
69–122	*BULB* YOYO	DOUBLE REC.	4	0	0	7	11
(3)							
67–7	*U* (*TRANS*)	DOUBLE REC.	0	1	3	0	4
(4)							
67–7	U YOYO	DOUBLE REC.	0	0	3	0	3
(5)							
68–45	V (*T*?)	DOUBLE REC.	2	6	1	1	10
(6)							
67–49	E (*T*)	DOUBLE REC.	0	0	2	0	2
69–27	E (*T*)	DOUBLE REC.	0	3	2	5	10
69–70	E (*T*)	DOUBLE REC.	0	2	6	3	11
(7)							
68–66	E OOYY	DOUBLE REC.	13	4	0	0	17
68–101	E OOYY	DOUBLE REC.	7	1	8	7	23
69–32	DOUBLE REC.	E OOYY	6	2	1	7	16
69–64	DOUBLE REC.	E OOYY	11	3	0	9	23
(8)							
67–3	YOYO (*T*)	DOUBLE REC.	0	4	5	0	9
67–30	YOYO (*T*)	DOUBLE REC.	0	0	1	2	3
68–50	YOYO (*T*)	DOUBLE REC.	2	4	4	3	13
68–144	YOYO (*T*)	DOUBLE REC.	4	2	3	1	10

(1) *Bulborum* and *transversalis* – non-allelic.
(2) *Bulborum* and ground colour – non-allelic.
(3) Modifier U and *transversalis* – poor evidence.
(4) Modifier U and ground colour – poor evidence.
(5) Modifier V and *transversalis* – non-allelic.
(6) *Equestris* and *transversalis* – non-allelic.
(7) *Equestris* and ground colour – non-allelic.
(8) Ground colour and *transversalis* – non-allelic.

Dominant A = first-named dominant only (*bulborum* of *bulborum-transversalis* table).
Dominant B = second-named dominant only.

Table A8. Early crosses (1966)

(Separated from the other crosses because of lack of knowledge of the origins of the parents – females were taken from the wild, their male mates were not known)

		progeny	
cross no.	parental phenotype (♀ only)	males	females
1	*equ* OOYY	2 *equ* OOYY	1 *val* yellow tail, 4 *e-t* OOYY 2 *narc* OOYY
2	*v-t* orange tail	1 *sub* OOOO	1 *v-t* orange tail
3	*narc* OO—*	1 *narc* YOYO	1 *trans* YOYY, 1 *trans* OOYY, 2 *narc* OOYY
4	*narc* OOYY	1 *bulb* OOYY, 1 *narc* YOYY, 1 *narc* OOYY, 1 *narc* OOOO	1 *narc* YOYY, 1 *narc* OOYY, 1 *narc* OOOY
5	*trans* OOYY	1 *sub* Y-YO, 1 *equ* OOYY, 1 *narc* OOYY, 1 *narc* OOOY, 1 *narc* OOOO	1 *v-t* yellow tail, 1 *val* yellow tail, 1 *trans* OOOY, 1 *narc* OOYY
8	*narc* OOYY	1 *equ* OOYY, 1 *narc* YOYO, 1 *narc* OOYO	1 *val* yellow tail, 1 *bulb* OOOO 1 *equ* (diluted) Y-YO, 1 *trans* OOOO, 1 *narc* OOOY
9	*val* orange tail	2 *sub* Y-YO	2 *v-t* yellow tail, 4 *v-t* orange tail, 2 *val* yellow tail
10	*e-t* OOYY	1 *sub* Y-YO, 1 *equ* OOYY, 1 *narc* OOOO	1 *sub* Y-YY, 1 *bulb* Y-YY, 1 *bulb* OOYY, 3 *e-t* OOYY, 1 *equ* OOYY, 1 *trans* OOYY
11	*trans* OOYY	1 *narc* OOYY	1 *trans* YOYY, 1 *narc* OOYY
12	*trans* OOYY	1 *sub* Y-YO, 1 *sub* Y-YY, 1 *sub* OOYY, 2 *equ* Y-YO, 1 *equ* OOYY, 1 *narc* YOYO	1 *v-t* yellow tail, 1 *val* yellow tail, 1 *e-t* Y-YY
13	*equ* OOYY	1 *equ* OOYY, 1 *narc* YOYO, 1 *narc* OOOY, 1 *narc* OOOO	1 *e-t* OOYY, 1 *trans* OOYY, 2 *narc* OOYY
17	*trans* OOYY		1 *trans* OOOY
18	*val* orange tail	1 *val* Y-YO	
A I	♀ *narc* OOOY X ♂ *bulb*, *sub* or *val* Y—*	1 *sub* OOOO, 1 *bulb*, OOOO, 1 *narc* YOYO, 1 *narc* YYYY, 1 *narc* OOOO	2 *b-t* OOYY, 1 *narc* OOYY

* Abdomen absent so that the rest of the colour type could not be distinguished (A I was included here for this reason).

Table A9. Families providing evidence on linkage

(1) *Bulborum* and the modifier V:

		1	2	3	4
validus × *subvalidus*	68–45	16	15	0	9

1 = *validus*. 2 = *subvalidus*. 3 = *bulborum*. 4 = ‘non-*bulborum*’.

(2) *Bulborum* and the modifier U:

		1	2	3	4
subvalidus × *bulborum*	67–7	1	0	3	2

1 = *validus*. 2 = *subvalidus*. 3 = *bulborum*. 4 = ‘non-*bulborum*’.

(3) *Bulborum* and *equestris*:

		1	2	3
validus/subvalidus/bulborum × *narcissi*	68–109	19	7	5
	69–115	4	1	1
narcissi × *validus/subvalidus/bulborum*	68–137	9	1	4
	68–150	4	1	4
	68–154	10	1	7
	69–13	3	1	3
	69–20	3	7	1
	69–73	7	1	13

1 = *bulborum/subvalidus/validus*. 2 = *equestris*. 3 = *narcissi/transversalis*.

TABLE A 9 (*cont.*)

(4) *Bulborum* and *transversalis*:

		1	2	3	4
validus × ‘other’	67–62	2	11	0	0
	68–78	0	1	1	0
	68–109	6	8	5	2
	69–48	2	7	0	2
	69–114	0	0	1	1
subvalidus × ‘other’	67–36	1	1	0	1
	68–118	2	1	1	1
bulborum × ‘other’	68–79	1	0	0	1

1 = *validus/subvalidus/bulborum–transversalis*.
2 = *validus/subvalidus/bulborum*.
3 = *transversalis*.
4 = double recessive.

(5) *Bulborum* and ground colour:

		1	2	3	4	5
validus × ‘other’	68–32	1	11	20	0	9
	68–109	11	0	9	3	8
	69–34	2	0	0	9	10
	69–114	0	0	0	2	0
	69–117	1	4	0	3	1
	69–122	4	0	0	7	0
subvalidus × ‘other’	67–18	2	0	0	2	0
	68–145	10	0	0	2	0
	68–153	3	0	0	3	0
	68–155	2	1	0	4	2
	69–110	4	0	0	4	0
bulborum × ‘other’	68–117	0	2	1	1	0
	69–132	3	0	1	1	2
‘other × *bulborum*	67–75	4	2	5	0	0
	68–26	8	0	0	14	0
	68–154	9	0	0	8	1
	69–80	0	0	0	2	0

1 = double dominant.
2 = *bulborum* dominant.
3 = ground colour dominant, *bulborum* recessive.
4 = double recessive.
5 = number of *validus* females excluded.

(6) Modifier V and modifier U:

		1	2	3	4
subvalidus × *validus*	68–152	11	0	1	3

1 = *validus*. 2 = *subvalidus*. 3 = *bulborum*. 4 = *narcissi*.

The problem with the above cross is that one must assume independent segregation of *bulborum* from the two modifier loci.

(7) Modifier V and *transversalis*:

		1	2	3	4
validus × *subvalidus*	68–45	2	6	0	5

1 = *validus–transversalis*. 2 = *validus*. 3 = *subvalidus–transversalis*. 4 = *subvalidus*.

As 5 female F_1 were *transversalis* one must assume independence of these loci from *bulborum* for this cross to be of use.

(8) Modifier V and ground colour:

No even remotely suitable crosses set up yet.

(9) Modifier U and *transversalis*:

		1	2	3	4
subvalidus × *bulborum*	67–7	1	0	2	1

1 = *validus/subvalidus–transversalis*. 2 = *validus/subvalidus*. 3 = *bulborum–transversalis*. 4 = *bulborum*.

As one female F_1 was *equestris* and not *transversalis* the above is only of use if neither locus is linked to *bulborum*.

TABLE A 9 (*cont.*)

(10) Modifier U and ground colour:

		1	2	3	4
subvalidus dom. × *bulborum* rec.	67–7	0	0	3	0

1 = *validus/subvalidus* and dominant ground colour.
2 = *validus/subvalidus* and recessive ground colour.
3 = *bulborum* and dominant ground colour.
4 = *bulborum* and recessive ground colour.

As two of the F_1 individuals were *equestris* and another *validus* then the above is only of use if neither locus is linked to *bulborum*.

(11) *Equestris* and *transversalis*:

		1	2	3	4
equestris × *narcissi*	69–27	0	3	2	5
	69–70	0	2	6	3

1 = *equestris–transversalis*. 2 = *equestris*. 3 = *transversalis*. 4 = *narcissi*.

(12) *Equestris* and ground colour:

		1	2	3	4
narcissi × *equestris*	68–93	0	1	0	2
	68–101	7	1	8	6
	69–32	6	2	1	8
	69–64	11	3	0	9
	69–107	1	0	0	4

1 = double dominant.
2 = *equestris* dominant, ground colour recessive.
3 = ground colour dominant, *equestris* recessive.
4 = double recessive.

(13) *Transversalis* and ground colour:

		1	2	3	4
YOYO × OOYY (no *bulborum*)	67–3	0	5	4	0
	67–30	0	1	0	2
	68–115	1	0	0	1
	68–144	4	2	3	1
YOYO × OOOO (no *bulborum*)	68–50	2	4	4	3
YOYO × OOYY (*bulborum* involved)	67–7	2	0	1	1
	67–62	2	0	6	0
	68–78	1	0	1	0
	68–109	6	1	5	1
	69–114	1	1	0	1

1 = double dominant.
2 = *transversalis* dominant, ground colour recessive.
3 = ground colour dominant, *transversalis* recessive.
4 = double recessive.

The male parent is given before the female parent.

BULBORUM AND GROUND-COLOUR RELATIONSHIP

(Numbers present of the different types – dividing the sexes.)

	males				females				total				
cross no.	1	2	3	4	1	2	3	4	1	2	3	4	5
68–32	1	11	9	0	0	0	11	0	1	11	20	0	9
68–109	5	0	4	1	6	0	5	2	11	0	9	3	8
69–34	2	0	0	4	0	0	0	5	2	0	0	9	10
69–114		—			0	0	0	2	0	0	0	2	0
69–117	1	2	0	2	0	2	0	1	1	4	0	3	1
69–122	3	0	0	4	1	0	0	3	4	0	0	7	0
67–18	2	0	0	1		—			2	0	0	2	0
68–145	4	0	0	0	6	0	0	2	10	0	0	2	0
68–153	3	0	0	2		—			3	0	0	2	0
68–155	2	1	0	4		—			2	1	0	4	0
69–110	2	0	0	2	2	0	0	2	4	0	0	4	0
68–117		—			0	2	1	1	0	2	1	1	0
69–132	2	0	0	1	1	0	1	0	3	0	1	1	2
67–75	1	2	2	0	3	0	3	0	4	2	5	0	0
68–26	3	0	0	7	5	0	0	7	8	0	0	14	0
68–154	8	0	0	5	1	0	0	3	9	0	0	8	1
69–80	0	0	0	2		—			0	0	0	2	0

Divisions of males and females as in the main table.
— = Less than two individuals so of no use for calculations.

Table A10. Likelihood ratios

(*a*) *Bulborum–equestris* linkage

	ratio of probabilities of obtaining that family with that value of x to its probability when $x = 0.5$ ($P_x/P_{x=0.5}$)								
value of x	68–109	69–115	68–137	68–150	68–154	69–113	69–20	69–73	overall
0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	0.0099	0.36	1.05	1.05	11.5	0.60	11.5	208.0	64.0
0.2	0.15	0.64	1.33	1.33	5.37	0.87	5.37	90.1	374.0
0.3	0.49	0.84	1.24	1.24	3.18	0.97	3.18	23.8	149.0
0.4	0.85	0.96	1.08	1.08	1.57	1.00	1.57	4.31	7.36
0.5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

x = frequency of recombination.

Figures to two decimal places only except where essential for the meaning of the table. Also where figures are greater than 10 then figures are taken to one decimal place only and where they are over 100 figures are taken to no decimal places.

(*b*) *Bulborum–transversalis* linkage

	$P_x/P_{x=0.5}$								
value of x	67–62	68–78	68–109	69–48	69–114	67–36	68–118	68–79	overall
0.0	0.00	2.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00
0.1	12.8	1.64	0.003	0.05	0.36	0.36	0.13	1.64	0.000087
0.2	14.1	1.36	0.02	0.38	0.64	0.64	0.41	1.36	0.033
0.3	5.81	1.16	0.68	0.74	0.84	0.84	0.71	1.16	1.97
0.4	2.44	1.04	1.01	0.95	0.96	0.96	0.92	1.04	2.15
0.5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

(*c*) *Bulborum*-ground colour linkage – males only

	$P_x/P_{x=0.5}$															
value of x	68–32	68–109	69–34	69–117	69–122	67–18	68–145	68–153	68–155	69–110	69–132	67–75	68–26	68–154	69–80	overall
0.0	0.00	0.00	32.0	0.00	64.0	4.00	8.00	16.0	0.00	8.00	4.00	0.00	512.0	4096.0	2.00	0.00
0.1	12602.0	0.027	17.0	0.13	30.6	2.92	5.25	9.45	3.40	5.25	2.92	1.05	178.0	1041.0	1.64	5.66×10^{13}
0.2	2390.0	0.23	8.4	0.41	13.4	2.08	3.29	5.25	3.36	3.29	2.08	1.33	55.0	225.0	1.36	4.91×10^{11}
0.3	248.0	0.58	3.8	0.71	5.28	1.48	1.99	2.73	2.29	1.99	1.48	1.24	14.5	39.7	1.16	9.27×10^{7}
0.4	15.2	0.88	1.62	0.95	1.90	1.12	1.24	1.41	1.35	1.24	1.12	1.08	3.15	5.4	1.06	2.81×10^{3}
0.5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

(*d*) *Bulborum*-ground colour linkage – females only

	$P_x/P_{x=0.5}$													
value of x	68–32	68–109	69–34	69–114	69–117	69–122	69–145	69–110	68–117	69–132	67–75	68–26	68–154	overall
0.0	1024.0	0.00	16.0	2.00	0.00	8.00	128.0	8.00	0.00	0.00	0.00	2048.0	8.00	0.00
0.1	321.0	0.018	9.45	1.64	0.36	5.25	55.1	5.25	0.59	0.36	0.047	578.0	5.25	1.461×10^{6}
0.2	88.0	0.22	5.25	1.36	0.64	3.29	21.5	3.29	0.87	0.64	0.26	141.0	3.29	1.378×10^{6}
0.3	20.2	0.62	2.73	1.16	0.84	1.99	7.39	1.99	0.97	0.84	0.59	28.4	1.99	2.578×10^{4}
0.4	3.80	0.91	1.41	1.06	0.96	1.24	2.23	1.24	1.00	0.96	0.88	4.49	1.24	8.00×10^{2}
0.5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table A10 (*cont.*)

(*e*) *Bulborum*–ground colour – males and females together

value of x	$P_x/P_{x=0.5}$							
	68–32	68–109	69–34	69–114	69–117	69–122	67–18	68–145
0.0	0.00	0.00	1024.0	2.00	0.00	1024.0	8.00	2048.0
0.1	9572000	0.000000026	321.0	1.64	0.017	321.0	5.25	578.0
0.2	427900	0.09	88.0	1.36	0.17	88.0	3.29	141.0
0.3	10210	0.57	20.2	1.16	0.50	20.2	1.99	28.35
0.4	114.0	0.98	3.80	1.06	0.85	3.80	1.24	4.49
0.5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

	$P_x/P_{x=0.5}$							
	68–153	68–155	69–110	68–117	69–132	67–75	68–26	68–154
0.0	32.0	0.00	128.0	0.00	0.00	0.00	2095000	69358
0.1	17.0	3.40	55.1	0.59	1.05	0.017	206800	11567
0.2	8.39	3.36	22.0	0.87	1.33	0.17	15530.0	1481
0.3	3.79	2.29	7.39	0.97	1.24	0.50	823.0	152.0
0.4	1.62	1.35	2.23	1.00	1.07	0.85	27.6	11.1
0.5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

	$P_x/P_{x=0.5}$		
	69–80	overall	product of male and female-considered-alone tables
0.0	2.00	0.00	0.00
0.1	1.64	2.83×10^{17}	8.27×10^{19}
0.2	1.36	1.23×10^{20}	6.76×10^{17}
0.3	1.16	4.35×10^{14}	2.39×10^{12}
0.4	1.06	1.17×10^{7}	2.25×10^{6}
0.5	1.00	1.00	1.00

(*f*) *Equestris*–*transversalis* linkage

value of x	$P_x/P_{x=0.5}$		
	69–27	69–70	overall
0.0	0.00	0.00	0.00
0.1	0.06	0.44	0.027
0.2	0.11	1.37	0.15
0.3	0.42	1.62	0.68
0.4	0.86	1.25	1.02
0.5	1.00	1.00	1.00

(*g*) *Equestris*–ground colour linkage

value of x	$P_x/P_{x=0.5}$					
	68–93	68–101	69–32	69–64	69–107	overall
0.0	0.00	0.00	0.00	0.00	16.0	0.00
0.1	0.36	0.0011	0.24	362.0	9.47	0.32
0.2	0.64	0.12	0.86	275.0	5.29	95.2
0.3	0.84	2.59	1.18	64.0	2.73	448.0
0.4	0.96	1.72	1.08	7.00	1.41	17.6
0.5	1.00	1.00	1.00	1.00	1.00	1.00

(*h*) *Transversalis*–ground colour linkage

value of x	$P_x/P_{x=0.5}$					
	67–3	67–30	68–115	68–144	68–50	overall
0.0	256.0	0.00	2.00	0.00	0.00	0.00
0.1	99.2	0.36	1.64	0.006	0.018	0.0062
0.2	34.4	0.64	1.36	0.11	0.22	0.72
0.3	10.3	0.84	1.16	0.42	0.57	2.42
0.4	2.65	0.96	1.04	0.82	0.91	1.96
0.5	1.00	1.00	1.00	1.00	1.00	1.00

TABLE A11

colour type	(*a*) numbers of different colour types caught in Church Field, 1968			(*b*) lab. emergences 1968–69 from bulbs removed from Church Field		
	male	female	total	male	female	total
validus	14	20	34	28	19	47
non-*validus*	30	58	88	39	47	86
subvalidus	0	0	0	0	0	0
non-*subvalidus*	30	58	88*	39	47	86*
bulborum	3	11	14	2	5	7
non-*bulborum*	27	47	74	37	42	79
equestris	7	18	25	6	10	16
non-*equestris*	20	29	49	31	32	63
transversalis	—	35	—	—	35	—
non-*transversalis*	—	43	—	—	31	—
ground colour YOYO	20	22	42	38	11	49
OOYY	20	36	56	19	36	55
OOOO	4	0	4	10	0	10
total	44	78	122	67	66	133

colour type	(*c*) numbers of different colour types caught in Church Field, 1969			(*d*) lab. emergences 1969–70 from bulbs removed from Church Field		
	male	female	total	male	female	total
validus	7	4	11	27	62	89
non-*validus*	28	22	50	215	165	380
subvalidus	0	0	0	43	7	50
non-*subvalidus*	28	22	50*	172	158	330
bulborum	4	3	7	25	16	41
non-*bulborum*	24	19	43	147	142	289
equestris	5	4	9	46	45	91
non-*equestris*	19	15	34	101	97	198
transversalis	—	12	-	—	105	—
non-*transversalis*	—	14	—	—	122	—
ground colour YOYO	20	14	34	107	41	148
OOYY	11	8	19	58	93	151
OOOO	4	0	4	77	31	108
total	35	26	61	242	227	469

colour type	(*e*) numbers of different colour types caught in Church Field, 1970			grand total of five previous samples		
	male	female	total	male	female	total
validus	20	29	49	96	134	230
non-*validus*	97	69	166	409	361	770
subvalidus	18	5	23	61	12	73
non-*subvalidus*	79	64	143	251	222	473†
bulborum	4	9	13	38	44	82
non-*bulborum*	75	55	130	310	305	615
equestris	21	13	34	85	90	175
non-*equestris*	54	42	96	225	215	440
transversalis	—	38	—	—	225	—
non-*transversalis*	—	60	—	—	270	—
ground colour YOYO	59	19	78	244	107	351
OOYY	42	43	85	150	216	366
OOOO	16	7	23	111	38	149
total	117	98	215	505	495	1000

* = *subvalidus* were not distinguished from *validus* in these samples. † Only for 1969–70 and 1970 samples. Note that the figure for ground colour in the columns of females and total do not add up to the overall totals as the female *validus* have been excluded.

Table A 12. Gene frequencies calculated using the formulae outlined in the text

(*a*) Bulborum

	males		females		total	
date	p	q	p	q	p	q
1968	0.217	0.783	0.224	0.776	0.221	0.779
1968–69	0.257	0.743	0.202	0.798	0.229	0.771
1969	0.106	0.894	0.145	0.855	0.295	0.705
1969–70	0.221	0.779	0.209	0.791	0.215	0.785
1970	0.199	0.801	0.251	0.749	0.222	0.778
overall	0.217	0.793	0.215	0.785	0.216	0.784

p = frequency of dominant allele.
q = frequency of recessive allele.

(*b*) *Modifier U*

	males		females		total	
	p	q	p	q	p	q
1968	0.580	0.420	0.404	0.596	0.460	0.540
1968–69	0.742	0.258	0.544	0.456	0.640	0.360
1969	0.397	0.603	0.345	0.655	0.376	0.624
1969–70	0.487	0.513	0.566	0.434	0.523	0.477
1970	0.691	0.309	0.543	0.457	0.609	0.391
overall	0.559	0.441	0.519	0.481	0.538	0.462

p = frequency of dominant allele.
q = frequency of recessive allele.

In earlier years (up to and including 1969) *subvalidus* was placed with *validus* so calculations of gene frequencies of the modifier U are unaffected.

(*c*) *Modifier V*

	males		females		total	
date	p	q	p	q	p	q
1969–70	0.216	0.794	0.681	0.319	0.400	0.600
1970	0.312	0.688	0.617	0.383	0.435	0.565
overall	0.248	0.752	0.659	0.341	0.412	0.588

p = frequency of dominant allele.
q = frequency of recessive allele.

In earlier years (up to and including 1969) *subvalidus* and *validus* types were not distinguished so that there are no records for the modifier V.

(*d*) Equestris

	males		females		total	
date	p	q	p	p	p	q
1968	0.139	0.861	0.214	0.786	0.186	0.814
1968–69	0.085	0.915	0.127	0.873	0.107	0.893
1969	0.110	0.890	0.111	0.889	0.111	0.889
1969–70	0.171	0.829	0.174	0.826	0.172	0.828
1970	0.151	0.849	0.126	0.874	0.141	0.859
overall	0.148	0.852	0.160	0.840	0.154	0.846

p = frequency of dominant allele.
q = frequency of recessive allele.

TABLE A12 (*cont.*)

(*e*) Transversalis

	females only	
date	p	q
1968	0.258	0.742
1968–69	0.315	0.685
1969	0.266	0.734
1969–70	0.267	0.733
1970	0.218	0.782
overall	0.261	0.759

p = frequency of *transversalis* allele.
q = frequency of recessive allele.

(*f*) *Ground colour*

	males			females			total		
date	p	q	r	p	q	r	p	q	r
1968	0.261	0.437	0.302	0.212	0.788	0.000	0.233	0.569	0.198
1968–69	0.342	0.272	0.386	0.125	0.875	0.000	0.245	0.459	0.296
1969	0.345	0.317	0.338	0.397	0.603	0.000	0.365	0.370	0.265
1969–70	0.253	0.183	0.564	0.133	0.434	0.433	0.202	0.283	0.515
1970	0.296	0.334	0.370	0.149	0.532	0.319	0.238	0.410	0.352
overall	0.281	0.250	0.469	0.161	0.515	0.324	0.229	0.356	0.415

p = frequency of YOYO allele.
q = frequency of OOYY allele.
r = frequency of OOOO allele.

(*g*) Bulborum (*female* validus *not considered*)

	females		total	
date	p	q	p	q
1968	0.100	0.900	0.148	0.852
1968–69	0.055	0.945	0.167	0.833
1969	0.071	0.929	0.131	0.189
1969–70	0.072	0.928	0.157	0.843
1970	0.107	0.893	0.164	0.836

p = frequency of dominant allele.
q = frequency of recessive allele.

TABLE A13. NUMBERS OF FLIES WITH COMBINED COLOUR TYPES OF *BULBORUM* AND GROUND COLOUR (EXCLUDING FEMALE *VALIDUS*)

	1968			1968–69			1969			1969–70			1970		
colour type	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
B–YOYO	13	9	22	30	5	35	10	3	13	82	19	101	41	13	54
B–OOYY	3	2	5	0	0	0	1	0	1	9	3	12	1	1	2
B–OOOO	1	0	1	0	0	0	0	0	0	4	1	5	0	0	0
b–YOYO	7	13	20	8	6	14	10	11	21	25	22	47	18	6	24
b–OOYY	17	34	51	19	36	55	10	8	18	49	90	139	41	42	83
b–OOOO	3	0	3	10	0	10	4	0	4	73	30	103	16	7	23
total	44	58	102	67	47	114	35	22	57	242	165	407	117	69	186

M = males. F = females. T = total.

Table A14. Morph frequencies of flies with combined colour types of *bulborum* and ground colour (excluding female *validus*)

morph	symbol in formulae	1968			1968–69		
		M	F	T	M	F	T
bulborum YOYO	a	0.295	0.155	0.216	0.448	0.106	0.307
bulborum OOYY	b	0.068	0.034	0.049	0.000	0.000	0.000
bulborum OOOO	c	0.023	0.000	0.010	0.000	0.000	0.000
non-*bulborum* YOYO	d	0.159	0.224	0.196	0.119	0.128	0.123
non-*bulborum* OOYY	e	0.386	0.586	0.500	0.284	0.766	0.482
non-*bulborum* OOOO	f	0.068	0.000	0.029	0.149	0.000	0.083

continued	1969			1969–70			1970		
	M	F	T	M	F	T	M	F	T
a	0.286	0.136	0.228	0.368	0.115	0.248	0.350	0.188	0.290
b	0.029	0.000	0.018	0.037	0.018	0.029	0.009	0.014	0.011
c	0.000	0.000	0.000	0.017	0.006	0.012	0.000	0.000	0.000
d	0.286	0.500	0.368	0.103	0.133	0.115	0.154	0.087	0.129
e	0.286	0.364	0.316	0.202	0.545	0.342	0.350	0.609	0.446
f	0.114	0.000	0.070	0.302	0.182	0.253	0.137	0.101	0.124

Table A15. Chromosome frequencies (excluding female *validus*)

chromosome	symbol in formulae	1968			1968–69		
		M	F	T	M	F	T
B–YOYO	p	0.152	0.078	0.109	0.257	0.054	0.168
B–OOYY	q	0.024	0.022	0.013	0.000	0.000	0.000
B–OOOO	r	0.041	0.000	0.027	0.000	0.000	0.000
b–YOYO	s	0.110	0.134	0.124	0.085	0.071	0.077
b–OOYY	t	0.412	0.766	0.557	0.272	0.875	0.458
b–OOOO	u	0.261	0.000	0.170	0.386	0.000	0.297

continued	1969			1969–70			1970		
	M	F	T	M	F	T	M	F	T
p	0.140	0.070	0.113	0.184	0.055	0.131	0.193	0.099	0.157
q	0.023	0.000	0.014	0.022	0.007	0.014	0.006	0.008	0.007
r	0.000	0.000	0.000	0.013	0.007	0.012	0.000	0.000	0.000
s	0.196	0.327	0.252	0.069	0.079	0.072	0.103	0.050	0.081
t	0.294	0.603	0.356	0.160	0.425	0.368	0.328	0.525	0.403
u	0.338	0.000	0.265	0.550	0.427	0.503	0.370	0.318	0.352

Table A16. Expected chromosome frequencies (on the basis of gene frequencies)

chromosome type	1968			1968–69			1969		
	M	F	T	M	F	T	M	F	T
B–YOYO	0.057	0.021	0.035	0.088	0.007	0.041	0.034	0.028	0.048
B–OOYY	0.095	0.079	0.084	0.070	0.048	0.077	0.034	0.043	0.049
B–OOOO	0.065	0.000	0.029	0.099	0.000	0.050	0.036	0.000	0.035
b–YOYO	0.204	0.191	0.198	0.254	0.118	0.204	0.308	0.369	0.317
b–OOYY	0.342	0.709	0.485	0.202	0.827	0.382	0.283	0.560	0.321
b–OOOO	0.236	0.000	0.169	0.287	0.000	0.246	0.302	0.000	0.230

TABLE A 16 (*cont.*)

	1969–70			1970		
continued	M	F	T	M	F	T
B–YOYO	0.056	0.010	0.032	0.059	0.016	0.039
B–OOYY	0.040	0.031	0.045	0.066	0.057	0.067
B–OOOO	0.125	0.031	0.081	0.074	0.034	0.058
b–YOYO	0.197	0.123	0.170	0.237	0.133	0.199
b–OOYY	0.143	0.403	0.238	0.267	0.475	0.343
b–OOOO	0.439	0.403	0.434	0.296	0.285	0.294

These figures are calculated on the basis of all morphs except female *validus* which is excluded as one cannot distinguish ground colour on the basis of an orange or a yellow tail only.

TABLE A 17. χ^2 TESTS

(*a*) *Changes in morph frequencies between years, each locus considered separately*

locus producing change in colour type considered	male	female	total
bulborum	N.S.	N.S.	N.S.
modifier U	*	N.S.	N.S.
modifier V	N.S.	N.S.	N.S.
equestris	N.S.	N.S.	N.S.
transversalis		N.S.	
ground colour	***	**	***

(*b*) *Morph frequencies and sex*

locus producing change in colour type considered	1968	1968–69	1969	1969–70	1970
bulborum	N.S.	N.S.	N.S.	N.S.	N.S.
modifier U	N.S.	N.S.	N.S.	N.S.	N.S.
modifier V	†	†	†	***	**
equestris	N.S.	N.S.	N.S.	N.S.	N.S.
ground colour	N.S.	***	N.S.	***	N.S.

(*c*) *Changes in morph frequencies between years, considering* bulborum *and ground colour together*

	male	total
(i) including male *validus*	***	***
(ii) excluding male *validus*	***	***
(iii) females only **		

(*d*) bulborum *and ground colour*

Question of whether there are significant differences of the double colour types between the sexes (after removing male *validus*)

1968	1968–69	1969	1969–70	1970
N.S.	N.S.	N.S.	***	N.S.

N.S. = not statistically significant. * = $0.05 > p$. ** = $0.01 > p$. *** = $0.001 > p$. † = no results obtained.

TABLE A18. VALUES OF χ^2 (*BULBORUM* AND GROUND COLOUR COMBINED MORPH FREQUENCIES)

(χ^2 was calculated as described in the text)

	1968			1968–69			1969		
sample	M	F	T	M	F	T	M	F	T
χ^2	10.86	8.56	22.42	42.40	11.21	69.86	5.67	0.83	6.79
degrees of freedom	1	1	1	1	1	1	1	1	1
significance	***	**	***	***	***	***	*	N.S.	**
were parts of sample combined?	yes	yes	yes	yes	yes	yes	yes	yes	yes
after combination of sample were any expected values still less than 5?	no	yes	no	no	yes	no	yes	yes	no

	1969–70			1970		
sample	M	F	T	M	F	T
χ^2	113.87	47.93	222.37	58.28	23.71	97.64
degrees of freedom	2	1	2	2	1	2
significance	***	***	***	***	***	***
were parts of sample combined?	no	yes	no	no	yes	no
after combination of sample were any expected values still less than 5?	no	no	no	no	yes	no

* = $0.05 > p$. ** = $0.01 > p$. *** = $0.001 > p$. N.S. = not significant.

TABLE A19. EXCESS OR DEFICIENCY OF DOUBLE COLOUR PHENOTYPES

(observed to expected by χ^2)

	1968			1968–69			1969			1969–70			1970		
colour type	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
bulborum YOYO	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
bulborum OOYY	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
bulborum OOOO	−	X								−		−	−		−
non-*bulborum* YOYO	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
non-*bulborum* OOYY	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
non-*bulborum* OOOO	+	X								+		+	+		+

+ = excess of observed to expected.
− = deficiency of observed to expected.
X = none observed or expected.
Where there is only one + or − sign opposite *bulborum* OOYY and *bulborum* OOOO and non-*bulborum* OOYY and non-*bulborum* OOOO, then these two classes have been combined as the expected values of one or both of the classes fell below 5.

FIGURE 2. For legend see facing page.