Table 2. Joint segregation for different characters in F_2 generation

Characters		XY	Xy	xY	xy	χ^2	p
Habit (45:19) and inflorescence type (45:19) (3 genes common)	Obs.	869.0	3.00	0.00	345.00	3.9420	0.30–0.20
	Exp.	855.70	0.00	0.00	361.30		
Habit and pod form (57:7)	Obs.	769.00	103.00	299.00	49.00	4.8950	0.20–0.10
	Exp.	762.11	93.59	321.78	39.52		
Habit and pod colour (63:1)	Obs.	855.00	17.00	340.00	5.00	1.9274	0.70–0.50
	Exp.	842.33	13.39	355.65	5.65		
Inflorescence type (45:19) and pod form (57:7)	Obs.	766.00	102.00	302.00	47.00	3.4039	0.50–0.30
	Exp.	762.11	93.59	321.78	39.52		
Inflorescence type and pod colour (63:1)	Obs.	851.00	17.00	344.00	5.00	1.5187	0.70–0.50
	Exp.	842.33	13.39	355.65	5.65		
Pod form (57:7) and pod colour (63:1)	Obs.	1050.00	18.00	145.00	4.00	3.6278	0.50–0.30
	Exp.	1066.95	16.93	131.02	2.07		

was twining in habit with the flowers borne in the axils of every leaf, and with flat pods, green in colour. The F_2 population consisted of 1217 plants and the observations were recorded on the following characters: Habit of plant, inflorescence type, pod form, and pod colour. Ratios obtained for various characters indicate the interaction of 3 pairs of factors. Habit of the plant and the type of inflorescence both segregated in the ratio of 45:19 indicating that 1 gene is basic and the remaining 2 are complementary duplicates in action. A ratio of 57:7 was realized for the form of the pod suggesting the interaction of 1 independent dominant gene and complementary action of remaining 2 genes. Colour of the pod is governed by 3 duplicate factors giving 63:1 ratio. Analysis of the combined ratios (table 2) applied for colour and form of the pod showed that they are independent and did not show association with plant habit and inflorescence type. But the plant habit with inflorescence type showed the presence of 3 genes common for both these characters with a modified ratio of 45:0:0:9. D'Cruz and Ponnaiyya[2], Rangaswamy and Nambiar[3,4] observed monogenic segregation for pod form and pod colour. Meenakshi and Sundaresan[5] reported digenic ratio for pod colour. But in the present investigation, trigenic ratios have been reported for these 2 characters. Habit of the plant and inflorescence type are also governed by 3 pairs of factors (45:19), the gene symbols may be designated as T_h for twining plant habit and A_x for axillary inflorescence respectively. The trigenic ratios have been reported here for the first time for the above-mentioned characters.

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2 R. D'Cruz and V.T. Ponnaiyya, Indian J. Genet. Pl. Breed *29*, 139 (1969).
3 A. Rangaswamy and K.K. Nambiar, Proc. Indian Acad. Sci. *1*, 857 (1935a).
4 A. Rangaswamy and K.K. Nambiar. Proc. Indian Acad. Sci. *2*, 74 (1935 b).
5 K. Meenakshi and R. Sundaresan, Madras Agric. J. *51*, 71 (1964).

Cytological and genetic localization of a Y-autosome translocation in an Australian strain of the housefly, *Musca domestica*

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Summary. The Australian housefly strain *KIN* lacks a separate Y-chromosome and both males and females have 2 X-chromosomes. Genetic analyses showed the presence of the male-determining factor on autosome II, while cytological analyses demonstrated that part of the Y-chromosome has become attached to the same autosome. The Y-chromosome material is thus indicated as the site of the male-determining factor in this strain.

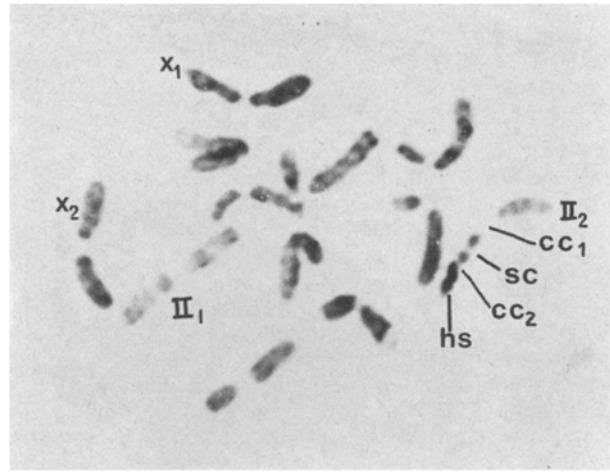
Translocations involving the Y-chromosome and any of the 5 autosomes of the housefly chromosome complement can be induced by X-rays[2]. Where chromosome IV is involved, the resulting experimental strain has 2 X-chromosomes in both sexes, with the males carrying the remainder of the Y-chromosome[2]. However, in naturally occurring strains in which the males carry 2 X-chromosomes (termed holandric), no Y could be found, nor could any Y-material be detected cytologically on the autosome showing sex-linkage[3]. Hiroyoshi[3] suggested that a male-determining factor and a viability factor were both attached to autosome-III with subsequent loss of the Y-chromosome. Kerr[4], on the other hand, found sex-linkage of autosome-II markers in a Canberra, Australian strain, and found that males showed both X-chromosomes, but was unable to detect any Y-material.

We analyzed an Australian strain, *KIN*, both genetically and cytologically in crosses with reference strains (table 1). We found sex-ratios not differing significantly from 1:1 for all within-strain crosses and crosses between-non-Australian strains, and, in these cases, within-mutant classes. However, we also found marked viability effects for a

number of mutant classes. The expected Mendelian ratios were not found for test crosses involving *KIN* and the marker strains, *WTIN* and *608Q*.

For both crosses involving marker strains and *KIN*, marked sex-ratio distortion among the appropriate mutants implicated autosome-II as carrying a male-determining factor (tables 2 and 3). High levels of recombination in males were found in the *608Q × 608Q/KIN* cross and will be discussed elsewhere[9].

In this cross, we also found high frequencies of a new genotype, which we have termed *absent thoracic bristles (atb)*, characterized by the absence of thoracic bristles, shiny black thorax and small body size. We attempted to start an *atb* strain, but all individuals died within 3 days of emergence; possibly *atb* is an example of a synthetic lethal[5]. We used late larval or prepupal 'brains' and pharate adult testes for air-dried chromosome preparations using a technique modified from that of Imai et al.[5]. (Our cytological methods and observations are being published separately[10].



The karyotype of the male *KIN* housefly strain. The 2 X-chromosomes are noted, X_1 and X_2. Autosome II_2 is carrying the male-determining factor. Indicated is the centromeric constriction (cc_1) of autosome II, and the secondary constriction (sc) on the long arm. Proximal to the secondary constriction is another constriction (cc_2), considered to be the centromeric constriction of the translocated Y-chromosome. The presence of the translocated Y is further verified by the presence of the heterochromatic segment (hs) proximal to cc_2 which is not found in the homologue, autosome II_1. The diploid number is 12. The part of the Y-chromosome not joined to autosome II_2 is considered lost.

Table 1. Strains of houseflies used in genetic crosses to locate the male-determining factor

Strain	Description
WHO	Wild-type from the World Health Organization laboratories in Pavia (Italy)
KIN	Wild-type, collected at Kingsford, Australia. Males have XX-sex chromosome complement (H.T. Imai, personal communication), suggesting the study
WTIN	*stw* = stubble wing, chromosome II; *w* = white-eye colour, chromosome III. Obtained from Dr A.W. Farnham, Rothamstead Experimental Station, Harpenden, England
608Q	*ac* = alicurve wings, chromosome I; *ar* = aristapedia, chromosome II; *bwb* = brown body colour, chromosome III; *oc* = ocra-eye colour, chromosome V. Obtained from Dr. A.W. Farnham

Table 2. Determination of the location of the male-determining factor from the cross, *WTIN × WTIN/KIN*

Phenotype	Males	Females	Total
Wild-type (+)	964	99	1063
White-eye (*w*)	1025	263	1288
Stubble wings (*stw*)	1	681	682
White-eye, stubble wings (*wstw*)	-	882	882
	1990	1925	3915

Table 3. Determination of the location of the male-determining factor from the cross, *608Q × 608Q/KIN*

Phenotype	Males	Females	Total
Wild-type (+)	606	465	1071
Ocra-eye (*oc*)	38	42	80
Ali-curve (*ac*)	109	88	197
Brown body (*bwb*)	42	110	152
Aristapedia (*ar*)	5	93	98
Absent thoracic bristle (*atb*)	60	14	74
	860	812	1672

The *absent thoracic bristle* phenotype was a new mutant resulting from this cross.

Cells both from *KIN* and *WHO* were analyzed. *WHO* males have the normal XY-karyotype (10 autosomes plus an X and a Y), whereas *KIN* males have 10 autosomes plus 2 X-chromosomes, no free Y, and a terminal heterochromatic region on one member of an autosomal pair (II). This autosome was identified as autosome-II due to the presence of the prominent secondary constriction, characteristic of this chromosome[7,8]. In some *KIN* male cells, a further constriction occurs, distal to the secondary constriction, and proximal to the heterochromatic segment (figure). These results strongly indicate that part of the Y-chromosome is attached to autosome-II in *KIN* males. The fragment involved is too small greatly to affect length measurements, which may account for previous authors[3,8] inability to locate it, without the use of banding techniques. This model resembles the Y-reciprocal autosomal translocation schematically represented by Hiroyoshi[2], but we are providing the necessary cytological evidence to qualify it.

Our results thus implicate autosome-II as the autosome involved in the translocation with the Y in giving rise to the *KIN* karyotype, and also the small remaining Y-fragment as the site of the male-determiner in this strain.

1 Present address: Department of Zoology, Hebrew University of Jerusalem, Jerusalem, Israel.
2 D.E. Wagoner, Genetics *62*, 115 (1969).
3 T. Hiroyoshi, Genetics *50*, 373 (1964).
4 R.W. Kerr, Aust. J. biol. Sci. *23*, 377 (1970).
5 H.T. Imai, R.H. Crozier and R.W. Taylor, Chromosoma *59*, (4), 341 (1977).
6 T. Dobzhansky, The Genetics of the Evolutionary Process. Columbia University Press, New York 1970.
7 A.M. Perje, Hereditas *34*, 209 (1948).
8 J.W. Boyes, in: Genetics of Insect Disease Vectors, p.371. Ed. J.W. Wright and R. Pal. Elsevier, Amsterdam 1967.
9 D.S. Lester, R.H. Crozier and E. Shipp, Experientia *35*, 175 (1979).
10 D.S. Lester, R.H. Crozier and E. Shipp, Experientia *35*, 174 (1979).