GENETIC DIVERGENCE AMONG TUMOROUS-HEAD STRAINS OF *DROSOPHILA MELANOGASTER*¹

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THE tumorous-head strain (symbolized tu-h) of *Drosophila melanogaster* has been the subject of a large number of investigations. An introduction to the literature can be found in GARDNER (1959), WOOLF, KNOWLES and JARVIS (1964), and JOHNSON and GARDNER (1965). Abnormal head growths occur in the flies of this strain because of the presence of a semidominant gene (*tu-3*) in the right arm of chromosome 3. The penetrance of this gene can be increased by a maternal effect produced by a sex-linked recessive gene (*tu-1*), by polygenic modifiers, and by high temperature during an early developmental stage.

The strain originated from a collection made at Acahuizotla, Mexico, in 1941, by field workers from the University of Texas. In 1945, abnormal head growths were noted in some of the flies of this strain being maintained at the University of Texas. The strain, was sent to DR. W. W. NEWBY at the University of Utah in 1946 through the courtesy of DR. W. S. STONE of the University of Texas. Genetic studies were initiated at the University of Utah by DR. E. J. GARDNER and his students. A sample of the strain was sent from the University of Utah to DR. W. J. BURDETTE, then of Louisiana State University. DR. BURDETTE sent a sample to the California Institute of Technology in 1949 and about the same time to The Institute for Cancer Research, Philadelphia, Pa. In 1949, DR. E. J. GARDNER moved to Utah State University where he and his students continued investigations with the strain. In 1951, a stock was shipped from Utah State University to Johns Hopkins University. The stock maintained at the University of Utah was taken to Arizona State University by the present author in 1961.

Two different types of third chromosomes are present in the tumorous-head strain formerly maintained at the University of Utah and now symbolized by tu-h(ASU). About 80% of the flies from stock bottles are heterozygous for a chromosome (symbolized 3B) containing, in addition to *tu-3*, the Payne inversion [*In(3L)P*] and the recessive gene (*st*) for scarlet eyes which is located (position 44.0) between the centromere and the proximal break of the inversion. The other chromosome (symbolized by 3A) contains *tu-3*, but lacks *In(3L)P* and *st*. Since the 3B chromosome is homozygous lethal, there are only two types of adult flies: homokaryotypes (3A/3A) and heterokaryotypes (3A/3B). WOOLF and CHURCH (1963) demonstrated that the 3B chromosome is maintained in the

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tu-h(ASU) strain at a high frequency because female heterokaryotypes produce significantly more offspring than female homokaryotypes and both female and male heterokaryotypes are more viable than the corresponding homokaryotypes.

WOOLF and KNOWLES (1964) concluded that the reduced productivity of female homokaryotypes is determined by an interchromosomal effect. In addition to a major region near roughoid (*ru*) at position 0.0 on chromosome 3, reduced productivity of these types is also influenced by one or more regions on chromosome 2. A polygenic system appears to be interacting. The importance of genetic background on female productivity was shown further by WOOLF, KNOWLES and JARVIS (1964), by comparing the productivity of females from the tu-h(ASU) strain with those from the tumorous-head strain [symbolized tu-h(CT)] maintained at the California Institute of Technology. Female homokaryotypes from the tu-h(CT) strain are even less productive than females from the tu-h(ASU) strain. Females homozygous for the 3A chromosome from the tu-h(ASU) strain but who possess chromosomes 1 and 2 (and probably 4) from the tu-h(CT) strain show a productivity which is characteristic of homokaryotypes from the tu-h(CT) strain. Conversely, females homozygous for the 3A chromosome from the tu-h(CT) strain, but who possess chromosomes 1 and 2 (and probably 4) from the tu-h(ASU) strain show a productivity characteristic of the homokaryotypes from the tu-h(ASU) strain.

The tu-h(ASU) strain also differs from the tu-h(CT) strain in the frequency of sterile males (WOOLF, KNOWLES and JARVIS 1964). About 20% of the males from the tu-h(ASU) strain are aspermic, while less than 2% of the males from the tu-h(CT) strain show this trait. The high frequency of aspermia in the tu-h(ASU) strain is attributed to a polygenic system involving mainly chromosome 2.

The striking differences between the tu-h(ASU) and tu-h(CT) strains in regard to the productivity of female homokaryotypes and the frequency of aspermia led to an investigation of other tumorous-head strains. The objective of the present paper is to demonstrate that divergence has occurred among the strains maintained at different institutions, and even between strains kept at the same institutions, for genetic systems affecting important fitness characters.

PROCEDURE

In addition to the tu-h(ASU) and tu-h(CT) strains which were already available for study (WOOLF, KNOWLES and JARVIS 1964), strains were obtained from Utah State University, Johns Hopkins University, and The Institute for Cancer Research. In this paper, these various strains will be symbolized as follows:

<i>Symbol</i>	<i>Institution</i>
tu-h(ASU)	Arizona State University, Tempe
tu-h(CT)	California Institute of Technology, Pasadena
tu-h(JH)	Johns Hopkins University, Baltimore, Maryland
tu-h(Phil)	The Institute for Cancer Research, Philadelphia, Pennsylvania
tu-h(60)	Utah State University, Logan
tu-h(90)	Utah State University, Logan

Each strain was subcultured, selected for abnormal head growths for two or more generations, and then compared for the frequency of flies showing some expression of the *tu-3* gene (pene-

trance), frequency of aspermia, and the relative productivity of the female homokaryotypes and heterokaryotypes. Unless otherwise stated, the cultures were maintained at 22°C.

The frequency of aspermia was determined by dissecting the testes in insect Ringers solution from males that had been isolated from females for 3 to 5 days. The testes were then placed in a drop of this solution on a microscopic slide. A cover slip was placed over the testes and tapped gently in order to rupture the walls of the testes and seminal vesicles. An examination was then made for spermatozoa following the technique of WOOLF, KNOWLES and JARVIS (1964).

A comparison of the productivity of the female homokaryotypes and heterokaryotypes from each strain was made by mating in vials single virgin females from each strain with three *bw;st* (*bw* = brown eyes) males. The females and males had been aged 3 to 5 days before the matings were made. After five days the parents were removed from the vials. If the female parent was dead at this time, the vial was discarded. Seventeen days after the matings were made, the vials were examined for offspring. If the offspring were all non-scarlet, the female parent was classified as a homokaryotype. If scarlet and non-scarlet offspring appeared, the female parent was classified as a heterokaryotype. The number of offspring produced by female homokaryotypes and heterokaryotypes was then compared. Instead of counting all flies in all vials, the procedure was to select the vials randomly until one containing only non-scarlet offspring was encountered. The flies in this vial were counted. The next vial containing scarlet and non-scarlet offspring was used as a control, and the flies were counted. By using this method, only a few minutes elapsed between the counting of the flies in the two vials. Since many hours were required to complete the countings in a series of vials and the number of flies eclosing in a vial increases with time, a comparison of the average number of flies produced by female homokaryotypes and heterokaryotypes was carried out using Friedman two-way nonparametric analysis of variance (SEGEL 1956), which corrects for the positive covariance between paired measurements. As in previous studies (WOOLF and KNOWLES 1964; WOOLF, KNOWLES, and JARVIS 1964) the median was used as the measure of central tendency.

RESULTS

The results of the penetrance studies are shown in Table 1. Over 80% of the flies from the tu-h(ASU), tu-h(60), and tu-h(90) strains showed one or more abnormal head growths. The tu-h(JH) strain ranked fourth with a value of 74.4%. About 61% of the flies from the tu-h(Phil) strain exhibited an amorphous growth, while the penetrance in the tu-h(CT) strain was only 21%. For each strain, the penetrance was higher in females than males, as noted for the original tu-h strain by GARDNER and WOOLF (1949).

Aspermic frequencies also varied widely in the various strains (Table 2). The value of about 20% ($n = 102$) for the tu-h(ASU) strain agrees well with

TABLE 1

Percentage of flies in the tu-h(ASU), tu-h(60), tu-h(90), tu-h(CT), tu-h(JH) and tu-h(Phil) strains showing the tumorous-head abnormality

Strain	Females		Males		Total	
	n	Percent abnormal	n	Percent abnormal	n	Percent abnormal
tu-h(ASU)	484	91.3	695	75.8	1179	82.2
tu-h(60)	483	91.3	551	78.0	1034	84.7
tu-h(90)	464	92.9	517	79.5	981	85.8
tu-h(CT)	275	22.5	301	19.6	576	21.0
tu-h(JH)	591	80.4	621	68.8	1212	74.4
tu-h(Phil)	383	70.0	381	51.7	764	60.9

TABLE 2

Percentage of males showing aspermia in the tu-h(ASU), tu-h(60), tu-h(90), tu-h(CT), tu-h(JH), and tu-h(Phil) strains

Strain	Number	Percent
tu-h(ASU)	102	20.6
tu-h(60)	501	34.7
tu-h(90)	476	17.0
tu-h(CT)	211	2.4
tu-h(JH)	102	0.0
tu-h(Phil)	297	1.7

the value of 21.3% based on 872 flies observed by WOOLF, KNOWLES and JARVIS (1964). The highest frequency of aspermia was noted for the tu-h(60) strain. Almost 35% ($n = 501$) were aspermic. Seventeen percent ($n = 476$) of the tu-h(90) males showed this trait. The other three strains showed a relatively low frequency of aspermia: tu-h(CT), 2.4% ($n = 211$); tu-h(JH), 0.0% ($n = 102$); tu-h(Phil), 1.7% ($n = 297$).

The results of the female productivity studies are given in Table 3. The data for the tu-h(ASU) and tu-h(CT) are taken from the paper by WOOLF, KNOWLES and JARVIS (1964). An unexpected discovery is the lack of heterokaryotypes in the tu-h(Phil) strain. In terms of the relative productivity of the female homokaryotypes, the other strains fall into three categories. The tu-h(90) strain is similar to the tu-h(CT) strain. A large proportion of the female homokaryotypes failed to produce offspring; and when offspring did appear, the median number per vial was small: 5 for tu-h(90) and 11 for tu-h(CT). On the other extreme are the tu-h(60) and tu-h(JH) strains. Although the difference in productivity of the homokaryotypes and heterokaryotypes for each strain is still highly significant, the homokaryotypes are relatively productive. The median numbers per vial were 64 for tu-h(60) and 55 for tu-h(JH). The tu-h(ASU) strain, which has been the most extensively studied for male and female productivity (WOOLF

TABLE 3

Productivity of female homokaryotypes and heterokaryotypes from the various tu-h strains

Mating	Total number of matings	Sterile matings	Frequency of female homokaryotypes	Median number of offspring produced by		P*
				Homokaryotypes	Heterokaryotypes	
1 tu-h(ASU) ♀ × 3 <i>bw;st</i> ♂ ♂	362	5.0%	21.2%	26	84.5	<0.01
1 tu-h(60) ♀ × 3 <i>bw;st</i> ♂ ♂	263	5.3%	31.6%	64	81	<0.01
1 tu-h(90) ♀ × 3 <i>bw;st</i> ♂ ♂	357	27.5%	3.8%	5	71	<0.01
1 tu-h(CT) ♀ × 3 <i>bw;st</i> ♂ ♂	290	32.0%	3.6%	11	78	<0.01
1 tu-h(JH) ♀ × 3 <i>bw;st</i> ♂ ♂	115	0.9%	33.0%	55	64	<0.01
1 tu-h(Phil) ♀ × 3 <i>bw;st</i> ♂ ♂	523	23.3%	100%	48	..	...

* Probability associated with the null hypothesis of no difference in productivity of homokaryotypes and heterokaryotypes as determined by Friedman two-way analysis of variance.

and CHURCH 1963; WOOLF and KNOWLES 1964; WOOLF, KNOWLES and JARVIS 1964) represents an intermediate condition with the homokaryotypes being moderately productive (median = 26).

It is concluded that the homokaryotypes from the various studies can be classified as showing very low productivity, moderate productivity, or relatively high productivity, when compared with each other and with the heterokaryotypes from each respective strain.

DISCUSSION

The results indicate that genetic divergence for important fitness characters has occurred among the tumorous-head strains maintained at the different institutions, and even between sublimes maintained at the same institution. This divergence has occurred since 1949, with all strains being derived from the one sent to the University of Utah from the University of Texas in 1946.

Modifiers influencing penetrance have been detected in laboratory and natural populations by GARDNER, STOTT and DEARDEN (1952). Further evidence for second chromosome modifiers increasing penetrance was obtained by WOOLF, KNOWLES and JARVIS (1964). When heterogeneity is present for these modifiers in a strain, penetrance can be quickly increased or decreased by selection; the penetrance will decrease if the strain is kept unselected for many generations.

The tu-h (ASU) strain has been maintained at Arizona State University either at room temperature or at 18°C. Selection has usually been made each generation for 20 to 40 flies (non-virgin females) showing an expression of the tumorous-head trait.

DR. E. J. GARDNER (personal communication) states that in 1957 two sublimes were established of the tumorous-head strain at Utah State University. One subline was the general laboratory stock which was kept routinely with other laboratory stocks at room temperature. It showed a penetrance of about 60%; hence the name tu-h(60). The other subline, which was being used in experimental work, was highly selected for abnormal head growths and kept in a constant temperature chamber at 25°C. The penetrance was over 90%. This subline was symbolized by tu-h(90). When the initial work with the tu-h(90) subline was completed, it was placed on the laboratory shelf with the other laboratory stocks. Selection was usually made for an expression of the trait each time a culture was changed. At the present time, as shown in the present study, little difference in penetrance exists between tu-h(60) and tu-h(90); at least in the stocks received at Arizona State University.

DR. E. B. LEWIS (personal communication) states that the tu-h(CT) strain maintained at the California Institute of Technology has been kept as a mass culture, unselected, at 18°C since July, 1949, when it was received. This method of propagation accounts for the low penetrance.

Little information can be obtained on the history of the tu-h(JH) stock. According to DR. HENRY L. PLAINE (personal communication) it was requested in order to study the possible relationship between the tumorous-head and erupt (er) traits. The erupt phenotype is somewhat similar to that found in the tumorous-head strain. A tumor suppressor (*su*^{DIS28}) was incorporated in the stock of Johns Hopkins University, which has no effect on the tumorous-head phenotype. DR. E. J. GARDNER (personal communication) reports that when he sent the strain to Johns Hopkins University, he also included a sample of the Stephenville wild-type strain which contains an isoallele of *tu-1*. This isoallele, symbolized by *tu-1*^S, gives a higher penetrance than *tu-1* (GARDNER and STOTT 1950). It may be that during the synthesis of the tu-h(JH) strain with the suppressor, *tu-1*^S was also incorporated in the stock, but this cannot be confirmed.

The origin of the genetic systems giving a high frequency of aspermia and

reduced productivity of female homokaryotypes is an enigma. The systems are independent and likely polygenic in nature. Possible hypotheses for their origin have been proposed (WOOLF, KNOWLES and JARVIS 1964), including chance fixation, inbreeding degeneration, pleiotropism of the genes increasing penetrance, and selective advantage in the presence of the deleterious genetic mechanisms (*tu-1*, *tu-3* and modifiers increasing penetrance) giving rise to the amorphous head growths. The last hypothesis implies that these systems have a pleiotropic action. For example, an increased productivity or viability of heterokaryotypes because of one or the other system could overcompensate for the deleterious effects of the system. No definite conclusions can be reached at the present time concerning the origin of these genetic systems in the various strains.

It is noteworthy that two strains from the same institution, namely *tu-h*(60) and *tu-h*(90), with about the same penetrance value, differ remarkably in the level of productivity of the female homokaryotypes. These females from the *tu-h*(90) strain are similar in productivity to female homokaryotypes from the *tu-h*(CT) strain. The *tu-h*(90) and *tu-h*(CT) strains differ greatly in penetrance; the former being highly selected while the latter has been mass-dumped. The *tu-h*(CT) strain is a further enigma. This was first received at Arizona State University in the spring of 1962 (WOOLF, KNOWLES and JARVIS 1964). At that time, female homokaryotypes showed very low productivity; in fact, in the early studies with this strain, they did not produce any offspring. The recessive gene *hairy* (*h*) was placed in the left arm of chromosome 3A (position: 26.5) in order that homokaryotypes could be distinguished phenotypically in the *tu-h*(CT) strain. This derived strain has been kept in the laboratory for a two-year period and the female homokaryotypes are practically sterile. Yet, female homokaryotypes received in later shipments from the California Institute of Technology showed relatively high productivity. Dr. E. B. LEWIS (personal communication) recently stated that two sublines of the tumorous-head strain are kept at this institution: a white-label strain and a yellow-label strain. Both have now been tested. Female homokaryotypes from the white-label strain show relatively high productivity while those from the yellow-label strain show low productivity; however, not quite as low as those derived from the shipment received in 1962, nor those from the strain with *hairy* now maintained at Arizona State University. It seems highly probable that the first shipment received at Arizona State University was from the yellow-label strain and the later shipments were from the white-label strain. The difference between the white- and yellow-label strains is further evidence for genetic divergence for a fitness character in sublines of the same strain kept at the same institution. The *tu-h*(CT) strain received in 1962 was observed to diverge while kept at Arizona State University. During the autumn and winter of 1963, it was noticed that the productivity of the female homokaryotypes in some stock bottles increased. It was for this reason that new shipments were requested from the California Institute of Technology.

Experimental evidence has suggested that the polygenes increasing penetrance are at least partially similar to those causing aspermia (WOOLF, KNOWLES and JARVIS 1964). This conclusion is supported by the observation that strains with the highest penetrance [*tu-h*(ASU), *tu-h*(90) and *tu-h*(60)] also have the highest frequency of aspermia. The low frequency of aspermia in the *tu-h*(JH) strain even though the penetrance is relatively high is understandable if this strain contains *tu-1^s*. Homozygosity for this isoallele results in a high penetrance even in the absence of modifiers (GARDNER and STOTT 1950). Outcrossing to synthesize a strain with *tu-1^s* and *su^{DIS28}* would have introduced genetic variability. Natural selection would have favored the incorporation of wild-type second chromosomes as well as the substitution of wild-type segments, by crossing over, in

the left arm of chromosome 3A. The consequence would be a strain with a high penetrance, low frequency of aspermia and female homokaryotypes that show relatively high productivity.

An interesting phenomenon is the absence of heterokaryotypes in the tu-h (Phil) strain, as indicated by the absence of scarlet offspring in outcrosses to *bw;st* flies. DR. I. I. OSTER states (personal communication) that when the tu-h (Phil) strain was received at The Institute for Cancer Research it was maintained in vials as a mass culture, unselected, at 16° to 18°C. For the past 3 years selection has been made every 6 to 8 months for approximately ten pairs of flies (non-virgin females) showing an abnormal head growth. Although the absence of scarlet offspring is also compatible with the absence of *st*, or the presence of a *st* suppressor, in the tu-h(Phil) strain, evidence that *In(3L)P* is missing in this strain came from testing for a mechanism suppressing the appearance of cross-over products in the left arm of the third chromosome. Such a mechanism was not found for 100 third chromosomes selected at random. The 3B chromosome could have been lost through random chromosome segregation (genetic drift) because of the small number of parents used to propagate the stock at The Institute for Cancer Research, or it might have been absent, by chance, in the original small sample sent to the Institute (founder principle). Three sublines of this strain are kept at The Institute for Cancer Research. All three sublines lack chromosome 3B.

The female homokaryotypes in the tu-h(Phil) strain show relatively high productivity; indeed, when the 3B chromosome was lost, natural selection would have favored any mechanism increasing the productivity of these types. An attempt to maintain a tu-h(ASU) strain free of chromosome 3B was unsuccessful (WOOLF and CHURCH 1963). Because of the low number of offspring produced, mold and bacteria soon took over the culture and the bottles had to be discarded. It seems evident that such an attempt would be successful for the tu-h(60), tu-h(JH), or white-label tu-h(CT) strain, but not for the tu-h(90) or yellow-label tu-h(CT) strain.

An experiment was designed to determine the effect on productivity if a 3B chromosome from tu-h(ASU) strains was inserted into the tu-h(Phil) strain. This was accomplished by mating males from the stock M5; *Cy/Pm; ru h D³ st ri InRC e Be/3B* with tu-h(Phil) females. Selection was made for Muller-5 (M5), Curly (*Cy*), and non-Dichaete (*D³*) F₁ females, and Curly, non-Dichaete F₁ males. These flies were then mated. Selection was made in the following generation for flies lacking the M5 and *Cy* chromosomes. These flies were used to initiate a new strain symbolized by tu-h(Phil-3B). After mass-mating for two generations, virgin females were selected from this strain, aged for 3 to 5 days, and mated singly with three *bw;st* males, also aged 3 to 5 days. The test for productivity was carried out as in the previous experiments. As expected, female heterokaryotypes were more productive than female homokaryotypes. The difference between medians (50 vs. 64), based on 447 matings, is highly significant. Thirty-nine percent of the females producing offspring were homokaryotypes. Sixteen percent of the matings were sterile. The frequency of aspermia ($n = 120$) was 0.83%.

Half-pint bottles of the tu-h(Phil) and tu-h(Phil-3B) strains were kept on the same laboratory shelf. It became apparent that more flies were being produced in bottles of the latter strain than the former. To test this observation objectively 40 males and 40 females from each strain were placed in half-pint bottles. The bottles were placed in incubators set at 18, 22, 25, and 28°C. After 7 days the parental flies were removed. The number of flies eclosing was determined each day

TABLE 4

Comparison of the productivity of tu-h(Phil) and tu-h(Phil-3B) strains at 18°, 22°, 25°, and 28°C

Day	18°C		22°C		25°C		28°C	
	tu-h(Phil)	tu-h(Phil-3B)	tu-h(Phil)	tu-h(Phil-3B)	tu-h(Phil)	tu-h(Phil-3B)	tu-h(Phil)	tu-h(Phil-3B)
1	11.3	52.4	0	5.8	99.0	233.0	111.4	122.8
2	15.3	38.8	6.3	38.8	70.0	120.8	131.2	128.8
3	...	...	26.7	108.8	70.3	98.0	81.2	95.7
4	76.0	131.6	...	...	73.0	99.0	45.4	55.2
5	13.3	41.8	179.7	251.8	...	...	52.0	67.5
6	22.6	51.8	40.3	65.2	98.7	122.0	35.0	61.8
7	18.3	40.2	58.3	76.8	12.3	35.2	30.0	58.2
8	14.7	39.2	54.0	72.6	4.3	32.0	20.2	46.8
9	10.0	51.6	53.0	88.2	0.6	30.8	8.6	29.5
10	1.7	17.2	25.0	46.4	...	23.0	...	...
11	1.7	14.0	21.7	95.8	...	9.6	...	...
12	1.3	6.2	...	...	...	...	...	...
Mean number eclosing each day	16.9	44.1	46.5	85.0	53.5	80.3	57.2	74.0
Mean number per bottle	186.6	487.8	467.6	884.8	428.3	854.0	515.0	666.3

Forty male and 40 female parental flies were left in half-pint milk bottles for 7 days. The measurement is the average number eclosing each day among five bottles of tu-h(Phil) and tu-h(Phil-3B) flies for 18°, 22°, and 25°C. At 28° six bottles of Phil-3B and five bottles of Phil were used. (The blanks within the table represent days when flies were not counted).

for 12 days. After 11 days all flies had eclosed in each bottle except for those kept at 18°C because of the slower life cycle at lower temperatures. The results are summarized in Table 4. Using as the criterion of productivity the mean number of flies eclosing each day, or the total number of offspring produced in each bottle, it is clear that flies from the tu-h(Phil-3B) strain are more productive than those from the tu-h(Phil) strain. A marked difference existed at each of the four different temperatures. Even though chromosome 4 is not controlled, the difference between strains is undoubtedly due to the presence of the 3B chromosome. This serves as experimental evidence for the situation where the fitness of a population, as measured by productivity, can be increased by the addition of a chromosome which is homozygous lethal. The heterotic advantage of the heterokaryotypes overcompensates for the deleterious nature of the homokaryotypes.

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SUMMARY

Tumorous-head strains are maintained in various laboratories in the United States: Arizona State University [tu-h(ASU)], California Institute of Technology [tu-h(CT)], Johns Hopkins University [tu-h(JH)], The Institute for Cancer Research [tu-h(Phil)] and Utah State University [tu-h(60) and tu-h(90)]. All are descended from the strain kept at the University at Utah before 1949. Two different types of third chromosomes (3A and 3B) are segregating in all these strains except tu-h(Phil), which has lost the 3B chromosome containing the Payne inversion and the recessive gene for scarlet eyes, apparently by random chromosome segregation. The 3B chromosome is homozygous lethal. When both

the 3A and 3B chromosomes are present in a strain, female heterokaryotypes (3A/3B) produce more offspring than female homokaryotypes (3A/3A). Furthermore, heterokaryotypes of both sexes are more viable than homokaryotypes. The reduced productivity of the female homokaryotypes is under polygenic control. Genetic divergence has occurred among the various strains for this fitness character. In some of the strains [tu-h(CT) and tu-h(90)], the female homokaryotypes show low productivity, in another [tu-h(ASU)] the productivity is moderate, while in others [tu-h(60) and tu-h(JH)] it is relatively high—A 3B chromosome from the tu-h(ASU) strain was inserted into the tu-h(Phil) strain, creating a new strain symbolized tu-h(Phil-3B). Female heterokaryotypes from the tu-h(Phil-3B) strain are more productive than female homokaryotypes. Furthermore, the fitness of the tu-h(Phil-3B) strain is increased over that of the tu-h(Phil) strain, using as a criterion of fitness the mean number of offspring produced each day or the total number of offspring produced in half-pint milk bottles.—Genetic divergence has also occurred among the strains for a polygenic system affecting the frequency of aspermia. Three of the strains [tu-h(ASU), tu-h(60) and tu-h(90)] show a relatively high frequency of aspermia (>17%). The frequency is low in the other strains (<2.5%).—These results serve as evidence for the genetic divergence that can occur among laboratory stocks of *D. melanogaster* for polygenic systems, even those affecting important fitness characters.

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