New results on the genetic characteristics of the Far East race of Drosophila melanogaster

By J. DAVID,* C. BOCQUET[†] AND E. PLA[†]

 * Laboratoire d'Entomologie expérimentale et de Génétique (associé au C.N.R.S.) Université Claude Bernard, 69621 Villeurbanne, France
 † Laboratoire de Génétique Evolutive du C.N.R.S., 91190 Gif-sur-Yvette, France

(Received 28 May 1976)

SUMMARY

Recently collected strains from Malay peninsula, Taiwan and Japan proved to be similar to previously studied Japanese strains kept for a long time under laboratory conditions. It is therefore possible to speak of a Far East race, characterized by slow growth, very high fresh weight and small ovariole number. High heterogeneity between laboratory strains founded from wild caught flies seems also typical. Among the three traits studied, a positive genetic correlation was observed only between duration of development and adult weight. No correlations were found between biometrical traits and the latitude of strain origin. The problem of the origin of the Far East race is discussed.

1. INTRODUCTION

Drosophila melanogaster is certainly the most studied species in laboratory conditions, while data concerning its wild populations are scarce (Parsons, 1973, 1975). This gap is, however, being progressively filled as significant geographic variations are discovered. Schematically, three extreme genetic types, or races, can be recognized in this species (Teissier, 1958; David & Bocquet, 1974, 1975*a*, *b*):

(1) a tropical and equatorial type found in Africa and America, characterized by light adult weight and a small number of ovarioles in females.

(2) a temperate 'type found' in 'Europe and North America of middle adult weight and a high ovariole number.

(3) a Japanese type with slower growth, high adult weight and small ovariole number. Laboratory strains from Japan are also characterized by a much bigger heterogeneity than are the two other types (Bocquet, David & de Scheemaeker-Louis 1973; David & Bocquet, 1974).

The temperate and tropical types are well defined. It is highly probable that they correspond to genetic adaptations to different environments because they are found at the ends of a regular latitudinal cline (David & Bocquet, 1975a,b). The status of the Japanese type, however, remained much less clear for two main reasons. The heterogeneity in that race was observed only in old laboratory strains and most likely reflected genetic drift in laboratory cultures and not a situation in wild populations (David & Bocquet, 1974). Moreover, it seemed very difficult to correlate genetic properties of these flies to climatic particularities of their countries of origin. New information was thus needed on strains recently collected in different countries of the Far East. Such data will be presented here and compared to previous studies.

2. MATERIAL AND METHODS

Fifteen strains recently collected and generally kept in laboratory cultures for less than a year were studied. Their geographic origins were as follows: Malay peninsula (two strains); Taïwan (five strains); Japan (eight strains). Conditions of study were the same as in previous work (David & Bocquet, 1974): 25 °C, killed yeast growth medium (David & Clavel, 1965) and low larval density. Three traits were measured: the duration of development from egg deposition to adult emergence; the adult fresh weight within 12 h after emergence; the ovariole number of females. These data were compared to those previously obtained on 55 Japanese old laboratory strains and also in some cases to results of French and tropical African strains.

3. RESULTS

(i) Data obtained on the 15 recently collected strains

Table 1 gives the values obtained on these strains for duration of development, fresh weight and ovariole number.

Average values of the three geographic groups are often quite different. However, the variability within each group is usually very great so that a variance analysis failed to show, except for ovariole number, significant differences between groups. Strains from the Malay Peninsula and Taïwan are therefore quite similar to Japanese strains and it is reasonable to calculate an overall mean for these new strains.

(ii) Comparison of the new strains with previously studied Japanese strains

Such a comparison can be made at two levels: the means and the variability between strains (variance and coefficients of variation). Results are given in Table 2. In all cases, the differences are not significant. The average values of the new strains are similar to those previously obtained on old laboratory strains. Moreover, the heterogeneity between strains is also of the same magnitude. All the data obtained up to now on strains of the Far East region can therefore be included in a single group.

(iii) Correlations between different traits

For any trait, a strong positive correlation is always found between male and female values. Such a result is not surprising nor very interesting since males and

	Ľ	lable 1	Biometrical chan	acterist	ics of the newly	collect	ed strains			
	Durati	on of de	velopment (h)		Adult fre	sh wei	ght (mg \times 100)			
Geographic origin of	Males		Females	1	Males		Females	1	Ovariole num	ber
strains	m	, u	m	e e	m	, u	m	, u	m	r
Malay peninsula Johore	<u> 227-74 + 1-32</u>	133	220-59 + 1-05	139	112.93 ± 1.32	30	150.93 ± 1.04	30	38.80 + 0.55	30
Singapore	219.22 ± 0.84	128	210.65 ± 0.68	129	85.87 ± 0.56	30	114.87 ± 0.81	30	41.30 ± 0.68	30
Average	$223 \cdot 48 \pm 4 \cdot 26$	61	215.62 ± 4.97	63	99.40 ± 13.5	63	132・55 土 17・7	61	40.05 ± 1.25	63
Taïwan										
Chi-Peng	$243 \cdot 21 \pm 1 \cdot 15$	114	242.63 ± 1.34	103	114.53 ± 1.23	30	161.76 ± 1.19	30	37·90±	30
Juei-Suei	227.55 ± 1.12	83	224.87 ± 0.98	93	104.43 ± 1.15	30	$144\cdot30\pm1\cdot65$	30	35.03 ± 0.56	30
Ma-Kong	$222 \cdot 26 \pm 0 \cdot 72$	121	216.91 ± 0.56	135	111.67 ± 0.60	30	$146 \cdot 43 \pm 1 \cdot 13$	30	35.30 ± 0.60	30
Taïchung	210.12 ± 0.94	143	205.38 ± 1.23	127	92.80 ± 0.81	30	127.03 ± 0.88	30	36-50 ±	30
Wulaï	231.35 ± 1.08	97	224.07 ± 0.96	112	105.77 ± 0.85	30	142.30 ± 1.43	30	33.37 ± 0.45	30
Average	226.90 ± 5.43	ũ	$222 \cdot 77 \pm 6 \cdot 07$	õ	105.84 ± 3.75	Ð	144.36 ± 5.35	5	35.62 ± 0.76	õ
Japan										
Katsunuma 74	220.69 ± 0.88	158	212.12 ± 0.29	51	91.90 ± 0.97	30	126.27 ± 1.03	30	42.50 ± 0.76	30
Katsunuma 75	$205 \cdot 18 \pm 0 \cdot 53$	132	200.85 ± 0.62	133	90.20 ± 0.83	30	130.93 ± 0.77	30	$43{\cdot}20\pm0{\cdot}68$	30
Matsue	$222 \cdot 65 \pm 0 \cdot 89$	62	213.36 ± 1.05	44	96.30 ± 1.36	30	131.03 ± 1.61	30	40.50 ± 0.67	30
Matsuyama	$211 \cdot 50 \pm 0 \cdot 89$	72	206.62 ± 0.64	104	103.77 ± 0.61	30	147.37 ± 0.73	30	38.70 ± 0.73	30
Naga	225.45 ± 0.64	116	$218 \cdot 12 \pm 0 \cdot 80$	66	96.99 ± 1.16	30	133.00 ± 1.80	30	$41 \cdot 20 \pm 0 \cdot 97$	30
Ogasawa	217.56 ± 0.53	129	210.16 ± 0.67	100	82.97 ± 0.65	30	120.43 ± 0.77	30	38.37 ± 0.80	30
Sapporo	205.68 ± 0.66	123	199.43 ± 0.69	125	98.87 ± 0.64	30	139.33 ± 0.76	30	$46 \cdot 40 \pm 0 \cdot 76$	30
Tokyo	206.34 ± 0.45	143	200.44 ± 0.44	123	96.97 ± 0.59	30	134.70 ± 0.71	30	$44 \cdot 23 \pm 0.93$	30
Average	214.38 ± 2.91	8	207.64 ± 2.45	80	94.74 ± 2.86	æ	133.13 ± 2.86	æ	$41{\cdot}89\pm0{\cdot}97$	œ

Far East race of Drosophila melanogaster

m: mean and standard deviation; n: number of flies or of strains

	Old	l strains		New strains			Comparisons	
Traits	m	v	c.v.	m	v	c.v.	\overline{m}	v
Duration of								
development	(h)							
ਹੱ	221.01 ± 1.34	99.023	4.50	219.77 ± 2.77	115.094	4 ·89	0.42	1.16
Ŷ	$215{\cdot}61 \pm 1{\cdot}38$	105.081	4.75	$213{\cdot}75\pm2{\cdot}96$	$131 \cdot 424$	5.36	0.61	1.25
Fresh weight								
$(mg \times 100)$								
đ.	99.58 ± 1.00	54 ·650	7.42	99.06 ± 2.49	93.002	9.75	0.23	1.70
Ŷ	$135{\cdot}02\pm1{\cdot}42$	111.149	7.81	136.67 ± 3.19	$152 \cdot 642$	9.05	0.52	1.37
Ovariole								
number	37.97 ± 0.63	21.844	12.31	$39{\cdot}55\pm0{\cdot}95$	13.538	9.29	1.21	1.62

 Table 2 Comparison of data obtained on the 15 recently collected strains

 on 55 old Japanese strains

m: mean; v: variance; c.v. coefficient of variation between strains. Comparisons made with Student's t parameter for means and Snedecor's F parameter for variances. None of the differences are statistically significant.



Fig. 1: Correlation between duration of development and fresh weight of females. Each point corresponds to a strain. \bullet Far East strains; \blacksquare French strains; \blacktriangle Equatorial African strains.

females of any strain have the same genotype and were also submitted to the same environmental fluctuations because they were reared in the same vials.

More interesting are the correlations between different traits since they can give us some information on their level of genetic relationship. No significant correlations exist between ovariole number and female weight (r = -0.23) or



Fig. 2: Correlation between duration of development of females and their ovariole number. Each point corresponds to a strain. \bigcirc Far East strains; \blacksquare French strains; \blacktriangle Equaorial African strains.

between ovariole number and duration of development (r = -0.13). A positive correlation is found, however, between duration of development and adult weight (r = 0.55 for each sex, P < 0.01). Regression slopes (weight as a function of growth duration) are 0.43 ± 0.08 in males and 0.58 ± 0.10 in females. An increase of 1 h in the duration of development results in an increase of about $5 \mu g$ in the adult weight.

Correlations are shown in Fig. 1, 2 and 3, for females only. On the same graphs, the points corresponding to French and to equatorial African strains are also given. The great dispersal observed for the Far East strains contrasts with the reduced surface occupied by the two other genetic types.

(iv) Correlation with latitudes of origin

The latitude of origin of the Far East strains ranged from 1° to 43° of North latitude. Correlation coefficients are given in Table 3. In no case was the coefficient significantly different from zero. Such results contrast with the high positive correlation with latitude for two of these traits (fresh weight and ovariole number) in European and African populations (David & Bocquet, 1975a).



Fig. 3: Correlation between ovariole number and fresh weight of females. Each point corresponds to a strain. \bullet Far East strains; \blacksquare French strains; \blacktriangle Equatorial African strains.

 Table 3 Correlation coefficients between latitude of origins of the

 Far East strains and different biometrical traits

Traits	Males	Females	Both sexes
Duration of development	-0.12	-0.10	-0.15
Fresh weight	0.00	+0.02	0.01
Ovariole number		-0.06	

4. DISCUSSION AND CONCLUSION

Data obtained for recently collected strains in three different Far East countries are similar to those previously obtained on Japanese strains kept for years under laboratory rearing conditions. It is thus possible to speak of a Far East genetic type or race in *D. melanogaster*. This type is characterized, when compared for example to the European type, by slower growth, higher fresh weight and smaller ovariole number. Another typical property is the high variability between strains founded from wild populations. This variability is at least 3 or 4 times higher than in European strains (David & Bocquet, 1974).

Although the characteristics of the Far East race are fairly well defined, their origin still remains a matter of speculation. In a previous paper (Bocquet *et al.* 1973), the variability between ovariole number of Japanese strains was attributed to laboratory genetic drift. Since the new strains studied here were more recently collected, laboratory drift appears less probable. Great genetic variability in the wild populations is more likely. The heterogeneity between laboratory strain may be attributed to founder effect (Hosgood & Parsons, 1967) since laboratory strains are always founded from a relatively small number of adult flies. However, the possibility also exists that natural populations are geographic mosaics, so that the average genotype could vary greatly between populations separated by short distances.

Two opposing hypotheses can be considered for explaining the genetic particularities of the Far East flies. It is possible that wild populations are adapted to particular environmental conditions which selected flies with a slow growth, a high weight and a low ovariole number. All the differences suggest that, compared to European flies, Far East strains might be more K than r strategists (McArthur & Wilson, 1967; David, 1970; David & Fouillet, 1971). However, this interpretation is not very likely because climatic conditions change considerably between the equator and 43° of latitude, while no indication of genetic modification with latitude has been detected.

Another interpretation is that the characteristics of the Far East flies are not particularly adaptive to a special environment and that they are mainly a consequence of the very long distance which separates them from Europe.

Biogeographical data now provide a strong argument that the melanogaster taxonomic subgroup originated in tropical Africa (Tsacas & Lachaise, 1974). However, when *melanogaster* reached its cosmopolitan and domestic status remains a matter of speculation. It is often assumed that D. melanogaster was introduced recently in most countries of the world, during historical times, by human transportations (Dobzhansky, 1965). This possibility is probably true for the American continent. However, for example in Europe, fly colonization could well be an old event which occurred long before the development of human civilizations. The establishment of the latitudinal cline between equatorial Africa and Europe possibly took many thousands of years. Colonization of the Far East may also have occurred during prehistorical times through the Nile valley, Middle East and asiatic countries around the Indian ocean. Such a natural extension should probably be very slow and the geographic progression would be permanently mediated by small marginal populations submitted to drift, increasing the probability of occurrence of genetic changes. Presently available data are insufficient for choosing between the two hypothesis and analysis of populations from other parts of the world are needed.

J. DAVID, C. BOCQUET AND E. PLA

The geographic variability of *D. melanogaster* wild populations demonstrates that long distance migrations, mostly by accidental human transportation, are not very frequent and, at least, are unable to standardize the genotype of this species all over the world. The great heterogeneity observed in the Far East populations could be, however, considered a consequence of a recent introduction of flies from other parts of the world, resulting in an increase of the overall genetic variance and perhaps a mosaic status of the wild populations.

We thank Dr V. Phang for providing the Malayan strains, Dr Fei-Jan Lin for providing the strains from Taïwan and Professors C. Petit and Kitagawa for giving us the Japanese strains. Dr Grantham kindly revised the manuscript.

REFERENCES

- BOCQUET, C., DAVID, J. & DE SCHEEMAEKER-LOUIS, M. (1973). Variabilité du nombre d'ovarioles des souches sauvages de *Drosophila melanogaster* conservées en laboratoire sans sélection volontaire. Archives de Zoologie expérimentale et générale 114, 475-489.
- DAVID, J. (1970). Le nombre d'ovarioles chez Drosophila melanogaster: relation avec la fécondité et valeur adaptative. Archives de Zoologie expérimentale et générale 111, 357-370.
- DAVID, J. & BOCQUET, C. (1974). Nouvelles particularités génétiques des souches japonaises de Drosophila melanogaster. Archives de Zoologie expérimentale et générale 115, 489-503.
- DAVID, J. & BOCQUET, C. (1975a). Evolution in a cosmopolitan species: genetic latitudinal clines in *Drosophila melanogaster* wild populations. *Experientia* **31**, 164–166.
- DAVID, J. & BOCQUET, C. (1975b). Similarities and differences in latitudinal adaptation of two Drosophila sibling species. Nature 257, 588-590.
- DAVID, J. & CLAVEL, M. F. (1965). Interaction entre le génotype et le milieu d'élevage. Conséquences sur les caractéristiques du développement de la Drosophile. Bulletin Biologique de la France et de la Belgique 99, 369-378.
- DAVID, J. & FOUILLET, P. (1971). Le taux intrinsèque d'accroissement naturel chez Drosophila melanogaster; intérêt de ce paramètre pour les études de dynamique des populations. La Terre et la Vie, 3, 378-394.
- DOBZHANSKY, TH. (1965). In 'The genetics of colonizing species'. (ed. by H. G. Baker and G. L. Stebbins), pp. 533. New York: Academic Press.
- HOSGOOD, S. M. V. & PARSONS, P. A. (1967). The exploitation of genetic heterogeneity among the founders of laboratory populations of *Drosophila* prior to directional selection. *Experien*tia 23, 1066-1067.
- MCARTHUR, R. H. & WILSON, E. O. (1967). The Theory of Island Biogeography. Princeton Univ. Press.
- PARSONS, P. A. (1973). Behavioural and Ecological Genetics; A Study in Drosophila. Oxford: Clarendon Press.
- PARSONS, P. A. (1975). The comparative evolutionary biology of the sibling species, Drosophila melanogaster and D. simulans. Quarterly Review of Biology 50, 151-169.
- **TEISSIER**, G. (1958). Distinction biométrique des Drosophila melanogaster francaises et japonaises. Annales de Génetique 1, 2-10.
- TSACAS, L. & LACHAISE, D. (1974). Quatre nouvelles espèces de la Côte d'Ivoire du genre Drosophila, groupe melanogaster, et discussion de l'origine du sous-groupe melanogaster (Diptera-Drosophilidae). Annales Université Abidjan, série E, 7, 193-211.

260