STUDIES ON *PERIPLANETA AMERICANA*

II. INTERCHANGE HETEROZYGOSITY IN ISOLATED POPULATIONS

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Received 28.xi.55

I. INTRODUCTION

INFORMATION concerning spontaneous structural changes in wild animal populations is extremely limited. This is particularly true of interchanges which appear to be rare in nature in the heterozygous condition. Of the recorded cases (*cf.* White, 1954) only Piza (1943 ; 1947*a, b* ; 1948*a, b*) and White (1940) have found established this type of structural hybridity.

Darlington and La Cour (1950) using interchanges as markers of ancestry have demonstrated the existence of a hybridity optimum and have also shown that a change from cross to self fertilisation favours the selective survival of ring forming progeny, that is of interchange heterozygotes. In the present account two isolated populations of the american cockroach (*P. americana*) are described in which imposed inbreeding has been accompanied by the establishment of interchange heterozygosity. *P. americana* has been introduced into this country by commercial traffic and populations of this organism have succeeded in establishing themselves only in a few restricted types of environment conditioned principally by temperature and humidity. The major habitat colonised by this species in South Wales has been the coal mine. These colliery populations all appear to have been established soon after the opening of the mines but within recent years the size of the populations has decreased.

2. MATERIAL AND TECHNIQUES

The investigation was made on male imagines obtained from three sources :—

- (i) A wild isolated population established in The Deep Navigation Colliery, Treharris, Glamorgan. This mine is over 2000 feet deep and was sunk in 1873. Individuals from this source are pre-fixed T.
- (ii) A mass laboratory culture set up and maintained from the wild Treharris population. This culture was started in 1946 by Mr G. T. Jefferson of the Zoology Department, Cardiff : since then additional specimens from the wild have been added to maintain its numbers. These specimens are pre-fixed NT or MT.
- (iii) A wild isolated population established in The Wyndham Colliery, Ogmores Vale, Glamorgan. This mine, sunk in 1868, is approximately 1000 feet deep. The pre-fix W has been used for specimens from this locality.

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The induction of diplotene-diakinesis facilitated complete nuclear analyses which were otherwise difficult due to the pre-metaphase stretch and the compact metaphase plate. For cytological examination aceto-carmin or acetic-orcein squash preparations were made following prior fixation in 1 : 3 acetic-alcohol.

3. OBSERVATIONS

All the male imagines examined from the three sources gave typical chromosome counts at mitosis or meiosis II. The observation of multiple associations at meiosis I, however, showed that the populations were carrying a series of structural changes in the heterozygous condition (table 1).

TABLE 1

*The incidence of interchange heterozygosity in
seventeen specimens of P. americana*

Population	Individual no.	No. of cells analysed	No. and type of multiple association
Treharris . . .	T. 11	7	{ 1 R.IV 1 R.IV+1 C.IV 2 R.IV 2 R.IV+1 C.IV 3 R.IV
	T. 16	15	
	T. 19	50	
	T. 9	15	
	T. 23	50	
	T. 15	100	
	T. 2	13	
	T. 1	100	
Laboratory . . .	NT. 1	20	{ None 1 R.VI+1 R.IV
	NT. 2	40	
	MT. 18	100	
	MT. 21	17	
	MT. 22	70	
Ogmore . . .	W. 2	8	{ 1 C.IV 2 R.IV+1 C.IV
	W. 3	25	
	W. 4	20	
	W. 1	11	

(1) Wild Treharris population

Twenty specimens have been examined from this locality and all have been heterozygous for at least one interchange. Three independent interchanges is the maximum number observed in any one individual and no multiple association higher than four has been recorded.

(i) *Degree and type of multiple association.* The interchanged chromosomes are frequently associated in multiples (table 2). In T. 19, heterozygous for one interchange, a multiple was observed in 96 per cent. of the spermatocytes. Both the interchanged chromosomes for which T. 23 is heterozygous were associated in multiples in 72 per cent.

of the cells. T. 15, although of the same chromosome formula, is exceptional: the maximum of two multiples per cell was observed in only 4 per cent. of the cases. Maximum multiple association occurred in 58 per cent. of the spermatocytes in T. 1 heterozygous for three interchanges. Unpaired chromosomes and associations of three were not recorded in any individual.

Ring formation is frequent but closed associations are not invariably formed (table 1). Three interchanges, the maximum recorded for

TABLE 2

The percentage frequency of associations of four in six wild specimens of P. americana

No. and type of IV association	Frequency of types observed per cent.					
	W. 3	W. 4	T. 19	T. 15	T. 23	T. 1
None	24	15	4	17	8	...
1 C	76	85	2	...	8	1
1 R	...	...	94	79	12	3
1 R+1 C	...	...	...	1	72	17
2 R	...	...	...	3	...	20
1 R+2 C	...	...	...	...	...	1
2 R+1 C	...	...	...	...	...	54
3 R	...	...	...	...	...	4
Total cells . . .	20	25	50	100	50	100
Chromosome formulae of individuals	1.IV			2.IV		3.IV

the population, were observed in closed associations in one individual (T. 1).

(ii) *Morphology of the multiples.* The three multiples observed in this population are of approximately equal size and similar morphology. In all cases:

- The pachytene crosses formed by associations of four chromosomes are roughly symmetrical (plate, fig. 1).
- The initial separation of homologous segments at late pachytene proceeds progressively from the centre of the cross: in bivalents it is initiated at the centromere.

All the interchanges are autosomal, the X chromosome of the male is invariably present as a univalent. Because of their similarity the multiples cannot be individually recognised with any certainty especially when they occur in different individuals.

(iii) *Orientation of the multiples.* Observations on the orientation of the multiples could be made only infrequently due to the closely packed metaphase plate. In the cells suitable for analysis both ring

TABLE 3
*Percentage frequency of multiple associations in three
laboratory bred specimens of P. americana*

No. and type of multiple association	Frequency of types observed per cent.		
	MT. 18	MT. 21	MT. 22
None	...	5.9	...
1 R.IV	4	...	1.4
1 R.IV+1 C.IV	1	...	...
1 R.VI	43	17.6	5.7
1 R.VI+1 C.IV	30	70.6	...
1 R.VI+1 R.IV	22	5.9	92.9
Total cells	100	17	70
Chromosome formulæ of individuals .	1.VI+1.IV+11.II+X		

TABLE 4
*Frequency of disjunctional orientation in six wild specimens of
P. americana*

No. of associations of IV	Orientation				Observed frequency per specimen					
	Rings		Chains		W. 1	W. 2	W. 3	W. 4	T. 6	T. 11
	Dis.	N-D.	Dis.	N-D.						
0	...	...	...	...	...	...	6	3	...	2
1	1	...	...	...	5	...	...	...	2	3
	...	1	...	...	2	...	...	...	...	...
	...	...	1	...	...	8	17	17	2	2
	...	...	...	1	...	...	2	...	...	...
2	1	...	1	...	1	...	...	...	7	...
3	1	1	1	...	1	...	...	...	...	...
	2	...	1	...	2	...	...	...	...	...
No. cells analysed					11	8	25	20	11	7
Chromosome formulæ					3.IV	1.IV				
Proportion disjunctional chains . . .					1.0	1.0	0.89	1.0	1.0	1.0
Proportion disjunctional rings					0.71	...	...	...	1.0	1.0

and chain multiples were invariably disjunctional (table 4). All the chromosomes at induced "diakinesis" and at metaphase lack interstitial associations. In bivalents homologues are associated terminally or rarely sub-terminally; in the multiples association is always terminal.

(2) *Laboratory population*

This population was started and has been maintained from the wild Treharris population. It is significant therefore that certain of the individuals from this culture are cytologically different from the wild specimens (table 1). Two individuals (NT.) were homozygous for all chromosomes (plate, fig. 3) while three (MT.) had a multiple association of six in addition to an association of four (plate, fig. 4).

(i) *Degree of multiple association.* The MT. individuals, although they are all of the same chromosome formula, vary appreciably in their degree of association (table 3). In all cases closed associations have been observed and in no instance have unpaired chromosomes or numerically uneven multiples been seen. In one individual (MT. 22) maximum multiple association was observed in 92.9 per cent. of the spermatocytes, the lowest recorded was 52 per cent. (MT. 18).

(ii) *Morphology of the association of six.* The pachytene configuration is star shaped and initial separation of homologous segments is located at the centre of the association (plate, figs. 5 and 6). Unfortunately, we do not yet have any information on the orientation of this multiple.

(3) *Wild Ogmire Vale population*

This population is considerably smaller than that at Treharris and only four individuals have been examined. All were structural heterozygotes (table 1). Three independent changes were observed in one individual (W. 1) and the highest multiple recorded was an association of four. As in the Treharris population only the autosomes are involved.

(i) *Degree and type of multiple association.* Multiples are formed less regularly than in the Treharris material. Nevertheless 76 and 85 per cent. multiple formation was recorded for W. 3 and W. 4 respectively, both of which are heterozygous for one translocation. In W. 1 only three of eleven cells analysed (*ca.* 27 per cent.) had maximum multiple formation. No ring formation was observed in the three individuals heterozygous for one translocation (W. 2, 3 and 4). In the fourth (W. 1) heterozygous for three changes, two of the multiples were observed in closed association.

(ii) *Morphology of the multiples.* Some of the multiples are morphologically similar to those described for Treharris (plate, figs. 7 and 8; text fig. 1a). One of the associations, however, is morphologically different. Here one of the chromosomes is much smaller than the others (plate, fig. 9; text fig. 1b).

(iii) *Orientation of the multiples.* The frequency of disjunctional

orientation is high but multiples do not invariably disjoin as they appear to do in the Treharris material. In W. 3 two of the nineteen chains of four were non-disjunctional and both of these were associated interstitially (plate, fig. 9; text fig. 1*b*). The three non-disjunctional ring multiples recorded for W. 1 were all observed at pre-metaphase and not after the organisation of a metaphase plate (plate, fig. 8; text fig. 1*a*).

FIG. 1.

- (a) Orientated pre-metaphase (2 R.IV+C.IV+10.II+X); one non-congressed discordant ring quadrivalent, one disjunctional chain quadrivalent and one disjunctional ring quadrivalent. Note asynchrony of congression (compare with plate, fig. 8).
- (b) Metaphase I (C.IV+14.II+X); one non-disjunctional chain quadrivalent with an interstitial association. Note one short chromosome in chain (compare with plate, fig. 9).

In both figs. the quadrivalent associations and the single X chromosomes are shown solid. $\times 1800$.

4. DISCUSSION

(1) *The nature of the structural changes*

Interchanges generally result in the production of closed multiple associations, there being few instances where they have occurred without subsequent ring formation (Burnham, 1932; Clarke and Anderson, 1935 and probably White, 1940). The cross-shaped pachytene configurations and the extensive formation of closed multiples in the Treharris material show that these structural hybrids are interchange heterozygotes. In the Ogmore material, however, three of the four individuals have only chain of four associations. The absence of rings cannot be due to any of the factors which would also limit the degree of multiple association because a high frequency was recorded in all three of these individuals. These chains of four include one very short chromosome. Therefore, while the loss of a fragment cannot be excluded, it seems more probable that this translocation is also reciprocal and that rings were not recorded because the interchange involved unequal segments.

(2) *The locus of breakage and reunion*

In all cases other than the asymmetrical chain of four, the basic chromosomes and their interchange derivatives are metacentric and approximately the same size. The pachytene crosses have approximately equal arms and separation of paired regions is initiated at the centre of the cross. It follows, therefore, that breakage and reunion have occurred near or at the centromere (*cf.* Morrison, 1953).

The slight inequality in arm length is more apparent in the pachytene association of six, three long arms alternating with three shorter ones. Since the chromosomes are approximately equal and metacentric the length of an interstitial segment is equal to only half the difference in length between adjacent arms and is therefore short. Further, the association of six is shaped like a star not a double obelisk ; consequently the interchanges in the common chromosome (*i.e.* the one involved in two interchanges) must have occurred close together and the differential segments are also short.

(3) *Fertility*

The absence and limitations of interchange heterozygosity in animals can be explained by the fact that interchange hybrids may, as a result of non-disjunction, be subject to semi-sterility and therefore to negative selection (Wright, 1941). Segregation in an interchange heterozygote will depend upon :

- (i) The degree of multiple association.
- (ii) The orientation of the multiples.
- (iii) The presence or absence of crossing over in the interstitial or differential segments.

In the interchanges under examination multiple associations are very frequently formed and no unpaired chromosomes or numerically uneven multiple associations have been found.

There is moreover a marked lack of randomness in the orientation of the multiples which is predominantly disjunctional. Disjunction in multiple associations depends essentially on the movement of adjacent centromeres to opposite poles. The probability of initial disjunction and its procession along a multiple is increased when the effective inter-centromeric distances are equal (Darlington, 1937 ; Östergren, 1951), a condition fulfilled when the chromosomes are equal-armed and associated only terminally (Darlington, 1937 ; Sax and Anderson, 1933). The present interchanged chromosomes tend to meet both these requirements ; the rare non-disjunction at metaphase occurred only when the chromosomes were associated interstitially.

These two factors will facilitate disjunction but they are hardly adequate to account for the almost complete absence of non-disjunction. The operation of a third factor, the pre-metaphase stretch, is therefore suggested. The utility of the stretch phase in a functional diploid is

not clear but it is significant that although this phase is absent in certain mantids with an XO/XX sex chromosome mechanism, it is invariably present where multiple sex chromosomes of the X_1X_2Y type are involved (Hughes-Schrader, 1950). Again in the marsupial *Potorous tridactylus* a pre-metaphase stretch has been described analogous to that in the *Orthoptera* and here too there is a sex-chromosome association of three, the orientation of which is invariably disjunctional (Sharman and Barber, 1952).

That the stretch phase probably does influence co-orientation is indicated by the fact that in *P. americana* terminally associated multivalents have only been observed in non-disjunctional orientation at pre-metaphase, never at metaphase. This applies also to the sex trivalent in mantids studied by Hughes-Schrader (1943a, 1950), who suggests that the centromeres are capable of re-orientation after the stretch phase. This stage not only results in the terminalisation of association but also increases and tends to equate the inter-centromeric distances, all of which will increase the pliability of the configuration, a factor of prime importance in determining disjunction (Darlington, 1937). Further, the precocious organisation of the spindle at late pachytene increases the time available for centromeric interaction.

In animals, unbalance of the gametes does not result in hybrid incapacity in the same way as in plants since balanced zygotes can be produced by the fusion of complementary gametes (Darlington and Mather, 1949). Thus even cases of non-disjunction need not result in the production of non-functional gametes. This does not improve fertility, on the contrary it is disastrous because balanced eggs will fail to develop if fertilised by unbalanced sperm. This condition makes disjunction even more necessary in animals than in plants.

Finally, chiasmata when they are formed are almost certainly localised near the chromosome ends. The possibility of crossing over in the short interstitial and differential segments is thus remote.

(4) Selection of hybridity

Ring and non-ring progeny from selfing a ring parent are sharply differentiated in genic as well as structural heterozygosity: a difference particularly pronounced with respect to the differential segments. Those from crossing with individuals with similar rings but dissimilar ancestry are not genically differentiated in anything like the same degree. In *Campanula*, artificially produced structural heterozygotes with ring formation show different degrees of true breeding in regard to ring formation according to the closeness of inbreeding. Structural homozygotes are less frequent in selfed progeny and more frequent in sister and non-sister progeny owing to the different degree of elimination of genic homozygotes (Darlington and La Cour, 1950). This principle of hybridity optimum, decisively demonstrated in *Campanula*, can account for the present position in *P. americana*.

The interstitial and differential segments of the present interchanges are very short. Genetically, however, a segment is also differential if it does not cross over and lies therefore between the centromere and the proximal chiasmata. Differential segments in this sense are a consequence of localised chiasmata and can occur in structural homozygotes. In *P. americana*, chiasmata, when they occur, are localised terminally and there are long proximal segments which do not cross over. Thus, although the interchanges have occurred near the centromere, the structural homozygotes and heterozygotes expected in the progeny of closely inbred interchange heterozygotes will be very different in their genic heterozygosity, those from cross breeding will not be.

The colliery populations must have arisen from small isolated units : they are therefore highly inbred. If there is an elimination of genic homozygotes, structural homozygotes will be few or absent from such populations. In fact they have not so far been found. The elimination of structural homozygotes from the progeny of wide crosses, however, is not expected. No controlled crosses have been made but the structure of the mass laboratory culture affords strong presumptive evidence that such structural homozygotes are not selected against.

The rings of six observed in the laboratory bred specimens have evidently been synthesised by the hybridisation of two interchange heterozygotes in which a common chromosome was affected : a synthesis similar to that described for *Pisum*, *Zea* and *Campanula* (Darlington, 1937). This method of origin can also account for the presence of structural homozygotes in the culture. The apparent absence of both these types in nature can then be explained on the assumption that the wild Treharris population consists of two spatially isolated mating groups : a suggestion supported by the distribution of roaches in the colliery. Representatives of both these mating groups have been brought together in culture and the cross may be represented as follows :

Thus the genic heterozygosity of the non-ring individuals need be little less than that of the ring progeny ; hence their persistence in the laboratory population. That their non-observation in the natural

population is due to insufficient sampling or to the different pressure of selection in nature as opposed to the laboratory culture cannot, however, be excluded (*cf.* Darlington, 1939).

Suomalainen (1946) recorded one individual heterozygous for a single interchange in a sample of twenty individuals from a surface population in Berlin. It is possible, therefore, that the interchanges now fixed in the heterozygous condition were previously floating in the species and their occurrence is not due to the intra-specific hybridisation of geographically isolated races.

The extreme localisation, and in some bivalents the possible absence, of crossing over in the male *P. americana* will tend to maintain gene sequences. And interchanges by extending the linkage group will operate in the same direction. In this way the rival needs of fitness and flexibility can be reconciled in an outbreeding species. If, however, unnatural inbreeding is imposed upon such a concatenated system there will be a rapid increase in the frequency of homozygotes produced at fertilisation. Such genotypes will depart from the characteristic products of the outbreeding system and will not have been subjected to adjustment by selection. They will tend to be eliminated and thus a transition from outbreeding to inbreeding will favour the survival of structural heterozygotes.

5. SUMMARY

1. Two inbreeding populations of wild *P. americana* exhibit interchange heterozygosity producing rings and/or chains of four at meiosis.

2. All the male imagines examined are heterozygous for at least one interchange indicating that hybridity is near fixation level.

3. Generally the interchanges have resulted from breakage and reunion near the centromeres of autosomes.

4. Where individuals are carrying fewer interchanges than are known to exist in the population it has not been possible to determine whether they were homozygous for the basic or interchanged chromosomes.

5. The orientation of the multiples is predominantly disjunctional. It is suggested that the pre-metaphase stretch facilitates disjunction.

6. In a laboratory culture from one of the wild populations ring-of-six heterozygotes have been recorded. It seems probable that they have arisen by the mating of two heterozygotes in which a common chromosome was involved in different interchanges.

7. Complete structural homozygotes were also recorded in the laboratory culture. Their persistence is ascribed to their genic heterozygosity.

8. It is suggested that these karyotypes have not been found in nature because the population consists of two spatially isolated mating groups.

Plate

Interchange heterozygosity in male *P. americana*. $\times 2250$.

- FIG. 1.—Early pachytene, cross of four showing complete pairing of diffuse arms (T.15 colchicine $4\frac{1}{2}$ hr.).
- FIG. 2.—Induced “diakinesis” (2 R.IV + C.IV + 10.II + X), X chromosome at 6 o'clock (T.1, α -bromonaphthalene 2 hr.).
- FIG. 3.—Induced “diakinesis” (16.II + X), chromosomes diffuse (NT. 1, colchicine 2 hr.).
- FIG. 4.—Induced “diakinesis” (R.VI + C.IV + 11.II + X), bivalents showing strong contraction (MT.18, colchicine $4\frac{1}{2}$ hr.).
- FIG. 5.—Mid pachytene, star of six chromosomes (MT.18, colchicine $4\frac{1}{2}$ hr.).
- FIG. 6.—Late pachytene, double cross of six chromosomes showing strong centromeric repulsion (MT. 18, colchicine $4\frac{1}{2}$ hr.).
- FIG. 7.—Late pachytene (2.IV + 12.II + X), chromosomes showing centromeric repulsion (W. 1, untreated).
- FIG. 8.—(2R.IV + 1C.IV + 10.II + X) Cell drawn in text fig. 1a (W. 1, untreated).
- FIG. 9.—(1C.IV + 14.II + X) Cell drawn in text fig. 1b (W. 3, α -bromonaphthalene 2 hr.).

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g. The establishment of interchange heterozygosity is correlated with a change from outbreeding to inbreeding.

Acknowledgments.—We are grateful to Professor C. D. Darlington for his counsel and constructive criticism during the preparation of these papers. We are also indebted to the South West Division N.C.B. for allowing us to visit Treharris and Ogmore Vale collieries and to the respective colliery managers for every assistance in collecting the material.

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