

of the ring, from the ring synthesis are usually sterile or virtually so; moreover, those animals which are virtually sterile--at most 2 progeny--have sterile or nearly sterile progeny. R(3)S1, Df(3R)P47+ progeny from R(3)S1/Df(3R)P47 mothers also show this pattern of sterility. The few crossovers which are completely fertile show no indication of sterility in subsequent generations.

Because of this sterility problem and because of the lowered viability of R(3)S1+ due to hyperploidy, it is desirable to selectively recover ring-bearing progeny when inserting markers into the ring from a standard sequence chromosome. This can be accomplished by crossing R(3)S1, Df(3R)P47/marker females to Df(3R)P47/Dp(3;3)MRS, Sb--+ males to recover recombinant R(3)S1 chromosomes (with or without the marker) over Df(3R)P47 and later test for presence of the marker. To transfer markers from the ring to In(3R)C, it is convenient to recover an In(3LR)Ubx<sup>U</sup>L<sup>P88</sup>(3R)C, sbd<sup>2</sup> chromosome with the marker from R(3)S1, marker/In(3LR)Ubx<sup>U</sup>+(3R)C, sbd<sup>2</sup> ss Ubx<sup>U</sup> mothers: sbd<sup>2</sup> provides a marker for the inversion, and absence of the Ubx<sup>U</sup> phenotype identifies a crossover.

Stocks of (1) R(3)S1, Df(3R)P47, ca/In(3R)C, Sb cd Tb ca,  
 (2) Df(3R)P47/Dp(3;3)MRS, Sb--+,  
 and (3) In(3LR)Ubx<sup>U</sup>+(3R)C, sbd<sup>2</sup> ss Ubx<sup>U</sup> cd/T(2;3)ap<sup>Xa</sup> are available from the Pasadena stockcenter.

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 Transferring markers to or from autosomal inversions.

Markers can be transferred from a standard sequence chromosome into a large pericentric inversion by double crossing over. For inversions of moderate length--on the order of 10 numbered divisions--such double crossovers can be exceedingly rare and are prohibitively rare

for small inversions. It is, however, possible to transfer markers from one inversion to another through a sequence of selected single crossovers. InA/InB females are crossed to InB<sup>AR</sup>/InA<sup>LR</sup> males to selectively recover recombinant InA<sup>LR</sup> and InB<sup>AR</sup> chromosomes (it is assumed that InA<sup>LR</sup> and InB<sup>AR</sup> are lethally aneuploid genotypes). InA and InB are then reconstituted by crossing InA<sup>LR</sup>/InB<sup>AR</sup> females to structurally normal males. The reconstituted InA and InB chromosomes are frequently double crossover chromosomes, so that markers may be transferred from one inversion to the other via this sequence of crosses.

Transferring markers from a structurally normal chromosome to moderate length or smaller inversions is accomplished by first transferring the markers into a large inversion, then transferring the markers from the large inversion to the smaller one. As an example, the following sequence of crosses was used to insert se, h<sup>2</sup>, rs<sup>2</sup>, and th into In(3L)P:

P<sub>1</sub> C(1)M4, y<sup>2</sup>; In(3L)C90/se h<sup>2</sup> rs<sup>2</sup> th st cp in ri p<sup>P</sup> females were crossed to se h<sup>2</sup> rs<sup>2</sup> th st cp in ri p<sup>P</sup> males.

C(1)M4 is present in this cross to increase crossing over. In(3L)C90 is a large pericentric inversion with 62B and 80 breaks. In(3L)C90, se h<sup>2</sup> rs<sup>2</sup> th st was recovered in the P<sub>2</sub>. A balanced stock of C(1)M4, y<sup>2</sup>; In(3L)C90, se h<sup>2</sup> rs<sup>2</sup> th st/In(3L)P, Me h D<sup>3</sup> was then constructed.

P<sub>4</sub> C(1)M4, y<sup>2</sup>; In(3L)C90, se h<sup>2</sup> rs<sup>2</sup> th st/In(3L)P, Me h D<sup>3</sup> females were crossed to In(3L)C90<sup>L</sup>P<sup>R</sup>+(3R)P18, Ubx e<sup>4</sup>/In(3L)P<sup>L</sup>C90<sup>R</sup> males, to recover In(3L)C90<sup>L</sup>P<sup>R</sup>, se h<sup>2</sup> rs<sup>2</sup> th st/In(3L)P<sup>L</sup>C90<sup>R</sup> (recognizable as being Me<sup>+</sup> and Ubx<sup>+</sup>) and In(3L)P<sup>L</sup>C90<sup>R</sup>, se h<sup>2</sup> D<sup>3</sup>/In(3L)C90<sup>L</sup>P<sup>R</sup>+(3R)P18, Ubx e<sup>4</sup>. These two genotypes were crossed to each other to produce a

C(1)M4, y<sup>2</sup>; In(3L)C90<sup>L</sup>P<sup>R</sup>, se h<sup>2</sup> rs<sup>2</sup> th st/In(3L)P<sup>L</sup>C90<sup>R</sup>, se h<sup>2</sup> D<sup>3</sup> stock.

P<sub>6</sub> C(1)M4, y<sup>2</sup>; In(3L)C90<sup>L</sup>P<sup>R</sup>, se h<sup>2</sup> rs<sup>2</sup> th st/In(3L)P<sup>L</sup>C90<sup>R</sup> females were crossed to: th st cp in ri p<sup>P</sup> males.

A few th<sub>2</sub>st<sup>+</sup> offspring (In(3L)P, se h<sup>2</sup> rs<sup>2</sup> th) offspring were produced and a stock of In(3L)P, se h<sup>2</sup> rs<sup>2</sup> th was then established.

The In(3L)P, D<sup>3</sup> combination used in the above synthesis was derived in a somewhat similar manner; h was inserted into In(3L)P by a rare double crossover, and In(3L)P, Me h D<sup>3</sup> was constructed from these chromosomes and In(3L)P, Me.

Large paracentrics exist for all major autosomal arms--In(2L)DTD27 (21B; 40), In(2R)bw<sup>VDe1</sup> (41; 59), In(3L)C90, and In(3R)P110 (81F; 99). Stocks of In(2L)NS<sup>L</sup>DTD27<sup>R</sup>/In(2L)DTD27<sup>L</sup>NS<sup>R</sup> and In(2L)Cy<sup>L</sup>DTD27<sup>R</sup>/In(2L)DTD27<sup>L</sup>Cy<sup>R</sup> have been constructed in addition to the In(3L)C90<sup>L</sup>P<sup>R</sup>/In(3L)P<sup>L</sup>C90<sup>R</sup> complex. These stocks were derived by applying the methods which I have described for deriving crossover products of pericentric inversions (Genetics 99:75-77, 1981).

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Differential puffing activity in two E  
chromosomal arrangements of D.subobscura.

A comparison of the E chromosome puffing patterns of the different gene arrangements were carried out in order to investigate the possible effect of inversions on gene expression. Two strains of Drosophila subobscura were used: H271 which is homozygous for E<sub>st</sub> arrangement

and Ra121 which is homozygous for E<sub>1+2+9+12</sub> arrangement. The puffing patterns of late third instar larvae and different aged prepupae were analyzed. The prepupal samples were taken at 0, 4, 10 and 18 hrs after the eversion of the anterior spiracles. 20 individuals were analyzed per developmental stage and strain. Five nuclei were observed from each of the individuals analyzed. For the average degree of puffing activity two criteria were taken into account: (a) size of puffs, and (b) frequency of appearance of each puff at every stage analyzed. The puffs and breakpoints of E<sub>1+2+9+12</sub> inversion were located using the standard salivary gland chromosome map of Kunze-Mühl and Müller (1958). The breakpoints of E<sub>1+2+9+12</sub> arrangement are the following: E<sub>1</sub> 58D/59A-62D/63A, E<sub>2</sub> 58D/62D-64B/64C,

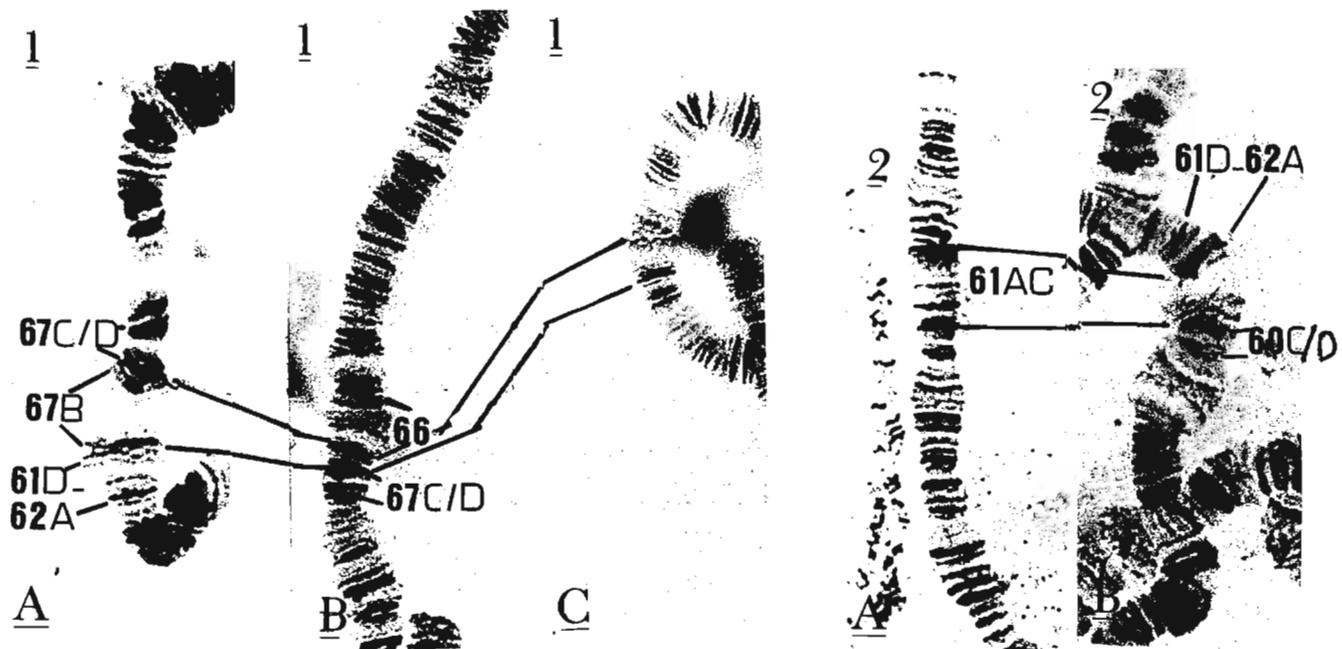


Figure. E chromosomes of D.subobscura: (1A) E<sub>1+2+9+12</sub> arrangement of Ra121 strain (18h prepupa). (1B) E<sub>st</sub> arrangement of H271 strain (4h prepupa). (1C) E<sub>st</sub> arrangement of H271 strain (0h prepupa). (2A) E<sub>1+2+9+12</sub> arrangement of Ra121 strain (0h prepupa). (2B) E<sub>st</sub> arrangement of H271 strain (18h prepupa).