PRODUCTION OF ALTERED Y CHROMOSOMES BEARING SPECIFIC SECTIONS OF THE X CHROMOSOME IN DROSOPHILA

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THE recovery and use of specifically marked Y chromosomes has greatly increased the versatility of the sex chromosome system of *Drosophila melanogaster* as a genetic tool. These Y's are marked by the normal alleles of a small heterologous segment of the genome. They have provided not only a simple means for following the Y chromosome through the meiotic divisions but also a useful tool for studying the segment of the genome for which the marked Y is duplicated. It is the second point that recommends the development of methods for accumulating a series of marked Y chromosomes.

For ease in referring to various marked Y chromosomes, we will establish the following conventions: (1) The long arm of the Y will be considered its left arm, so that when we write Y we infer $Y^L \cdot Y^S$, where the center point represents the centromere. (2) A marked Y will be symbolized by a combination of the symbol Y and the symbol of the marker commonly used; the marker symbol (e.g., m^+) will precede Y if it is located in Y^L, i.e., m^+Y, and follow Y if it is in Y^S, i.e., Ym^+. The symbol for the marked Y will not convey information about the origin or the relative positions of the genetic components of the chromosome. (3) The genetic constitution of a Y can be written *KL*·bb^+ *KS*, where *KL* and *KS* refer to the fertility complexes of Y^L and Y^S, respectively (BROSSEAU 1960). The constitution of a marker segment can be written a^+—b^+ where a^+ and b^+ are the extreme loci shown to be included in the segment. These two designations may be appropriately combined to describe a marked Y, e.g., *KL* a^+—b^+·bb^+ *KS* or *KL*(a^+—b^+)·bb^+ *KS* if the order of the a^+—b^+ segment is unknown.

Two marked Y's that have been widely available are the bw^+Y (DEMPSTER unpublished) and the y^+Y (=sc^s·Y of MULLER 1948). The bw^+Y is an X-ray-induced insertion of a subterminal section of 2R into the long arm of the Y chromosome probably proximal to the *KL* fertility complex. MULLER (1951) has shown that bw^+Y partially compensates for the Pale deficiency [*Df(2)P*] in that the combination +/*Df(2)P* does not survive whereas +/*Df(2)P*; bw^+Y does but produces a Minute phenotype. *Df(2)P* lacks a segment of 2R from the end of section 58E through 60D (BRIDGES 1937) or 60E1 (BRIDGES and BREHME 1944). GERSH (1956) has determined that the region of 2R inserted into the

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bw$^+$Y consists of at least the polytene bands 59E1·2 to 60E3. SLATIS (1955) has found that *bw* is situated between the bands 59D9 and 59E1·2; thus the region may be a few bands longer than the limits seen by GERSH. Since the right breaks in 2R for *bw*$^+$Y and *Df(2)P* practically coincide whereas the Pale deficiency extends much farther to the left than the *bw*$^+$Y duplication, the Minute phenotype characteristic of *+/Df(2)P; bw*$^+$Y is attributable to deficiency for a locus situated between the left breaks of these two rearrangements, i.e., *M(2)l*^{2}, (MULLER 1955). According to the cytological analysis of BRIDGES (1937), the region of 2R reported by GERSH to be inserted into *bw*$^+$Y carries, in addition to the brown locus, the loci of *mi, abb, pd, ll, mr, lx, l(2)NS, sp, bs, ba,* and possibly *M(2)33a.* We have tested *bw*$^+$Y in combination with *hv* (104.0) *bs, ba,* and *M(2)33a* and find that *bs* and *ba* are covered but *hv* and *M(2)33a* are not (see also MULLER 1955). Consequently, the segment of 2R inserted into Y^L extends from *bw*(104.5) to *ba*(107.4) inclusively, and the constitution of *bw*$^+$Y may be designated as *KL(bw*$^+$*—ba*$^+$*)·bb*$^+$*KS* (Table 1). The *bw*$^+$Y exhibits normal meiotic behavior and normal viability although two doses of *bw*$^+$Y are lethal.

The *y*$^+$Y (=*sc*^{s}·Y, MULLER 1948) arose as the consequence of an exchange between the distal inverted heterochromatic region of *In(1)sc*^{s} and the long arm of the Y chromosome distal to *KL.* Thus the distal uninverted euchromatic region of *In(1)sc*^{s}, bearing *l(1)J1*$^+$, *y*$^+$, and *ac*$^+$, was transposed to the terminus of Y^L. From detachment studies with the *y*$^+$Y, D. R. PARKER (personal communication) has determined that *bb*$^+$ from *In(1)sc*^{s} was not transposed to Y^L. An induced mutation from *y*$^+$ to *y* (=*y*^{53iY}) in the *y*$^+$Y was specifically sought and recovered by LÜNING (1953). Since this chromosome still covers deficiencies for *l(1)J1, y* and *ac* it is presumably *l(1)J1*$^+$ *y*^{53iY} *ac*$^+$ *KL·bb*$^+$ *KS* in constitution.

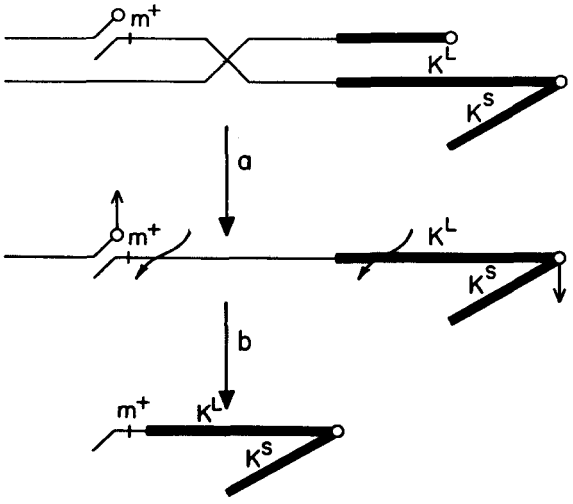

FIGURE 1.—The events required for the production of a Y chromosome marked with *m*+ from a T(1;4) broken just distal to *m*$^+$ and XY^L·Y^S. The straight arrows associated with the centromeres designate the distribution of elements at AI and the curved arrows the desired points of breakage for interstitial deletion.

TABLE 1

Tentative genetic constitutions of the existing marked Y chromosomes

Marked Y	Genetic constitution	Original designation and citation
Singly marked		
4Y	*((ci⁺–spa⁺)KL)·bb⁺ KS*	Tp4;Y MULLER and EDMONDSON 1957
B^SY	*B^S su^W-f⁺ KL·bb⁺ KS*	YB^S BROSSEAU and LINDSLEY 1958
*bw⁺*Y	*KL(bw⁺–ba⁺)·bb⁺ KS*	Y:*bw⁺* E. R. DEMPSTER, unpublished
*y⁺*Y	*l(1)J1⁺–ac⁺ KL·bb⁺ KS*	*sc^s*·Y MULLER 1948
Y*ma-l⁺*	*KL·su^W-f⁺–sw⁺ bb⁺ KS*	
Y*w⁺*	*KL·bb⁺ KS spl⁺–kz⁺*	
Doubly marked		
B^S*w⁺*Y	*B^S su^W-f⁺ kz⁺—dm⁺ KL·bb⁺ KS*	
B^SY*y⁺*	*B^S su^W-f⁺ KL·bb⁺ KS ac⁺—l(1)J1⁺*	BROSSEAU 1958
bw⁺Yy⁺	*KL(bw⁺—ba⁺)·bb⁺ KS ac⁺—l(1)J1⁺*	*sc^s*·Y:*bw⁺* COOPER 1952
y⁺YB^S	*l(1)J1⁺—ac⁺ KL·bb⁺ KS su^W-f⁺ B^S*	
y⁺Yw⁺	*l(1)J1⁺—ac⁺ KL·bb⁺ KS spl⁺—kz⁺*	
Triply marked		
y⁺Yw⁺B^S	*l(1)J1⁺—ac⁺ KL·bb⁺ KS spl⁺—kz⁺ su^W-f⁺ B^S*	

The marked ring Y of OSTER and IYENGAR (1955) is presumably of the same constitution as *bw⁺*Y. In general, the loci listed as being present have been accurately determined, but there may be additional loci that have not been detected, e.g., there may be *su^W-f⁺* as well as a mutant allele of *bb* between *ac⁺* and *KL* on *y⁺Yw⁺*. Furthermore, the order of elements may be in those derivatives that have an extensive history of irradiation.

The *y⁺*Y spontaneously mutated to produce the *y^{P59}*Y (MEYER 1959): the combination of *y^{P59}*Y with *y* in the X chromosome gives yellowish body and wings but dark bristles like *y^2*. The doubly marked recombinant *y⁺*Y/*bw⁺*Y (=*sc^s*·Y:*bw⁺*) was recovered by COOPER (1952) and subsequently shown by BAKER (1955, 1957), to be *KL(bw⁺—ba⁺)·bb⁺ KS ac⁺—l(1)J1⁺*. Apparently, the recombinant recovered by COOPER was between Y^L of the *y⁺*Y and Y^S of *bw⁺*Y. The *bw⁺Yy⁺* has been closed by OSTER and IYENGAR (1955) with the concommitant loss of *y⁺* to produce a ring Y still carrying the *bw⁺* segment.

A third marked Y, which to the best of our knowledge has not been widely used, is *Tp4*:Y described by MULLER and EDMONDSON (1957). This is an X-ray-induced transposition of all of chromosome 4 that is necessary for survival onto the Y chromosome. Two doses of this chromosome in the absence of any other Y- or 4-derived material produce viable and fertile individuals of both sexes. MULLER and EDMONDSON recovered a recombinant between this chromosome and $Y^SX{\cdot}Y^L$ that suggests that chromosome 4 is appended to or inserted into Y^L, and therefore in accordance with the conventions herein established this Y chromosome may be designated 4Y or *((ci⁺—spa⁺)KL)·bb⁺ KS* (STURTEVANT 1951; ABRAHAMSON, HERSKOWITZ and MULLER 1956, for chromosome 4 map data).

These marked Y's and their derivatives have been extremely useful, especially in studies of chromosome behavior and in radiation studies. This communication describes the production of several new marked Y chromosomes, one marked with B^S, one with *w⁺* and *N⁺*, and a third with *ma-l⁺*, by a method that theoretically may be used for production of Y's marked with any desired section of

the X chromosome. It must be emphasized that these marked Y's are derived by irradiation of complex rearrangements involving the X and the Y and cannot be considered to be normal Y's in any sense of the word. Their use must be tempered with the realization that the behavior of the Y itself is a variable that must be considered in any cross.

THE METHOD

This method requires the use of a reciprocal translocation that has a break in the X chromosome immediately distal to the region to be incorporated into the Y chromosome. One additional requirement of the translocation is that the second element must be broken sufficiently close to its tip that hyperploidy for this distal region will not adversely affect viability. Translocations with this second requirement represent an extremely restricted sample of T(X;2)'s and T(X;3)'s; furthermore, the male sterility that is commonly associated with T(X;2)'s and T(X;3)'s (SCHULTZ 1947; LINDSLEY, EDINGTON and VON HALLE 1960) drastically restricts their usefulness in the present scheme. For these reasons the method is nearly restricted to T(X;4)'s and T(X;Y)'s. It may seem that the restrictions placed on the chromosomal raw materials required for the production of marked Y's are so severe as to seriously limit the versatility of the method. However, a series of 86 T(X;Y)'s with X chromosome break points in every division of the polytene map has been produced and provides material for the production of a vast array of marked Y chromosomes (NICOLETTI and LINDSLEY 1960). We will describe the method, using as an example a T(X;4). The first step involves making the translocation heterozygous to $XY^{L.}Y^{S}$ (or $XY^{S.}Y^{L}$); these XY's were derived from detachment experiments by PARKER and MCCRONE (1958). An exchange proximal to the break point of the translocation replaces its proximal X heterochromatin with that of the XY (Figure 1a). The constitution of such recombinants may be designated as $X^{D}4^{P}$; $4^{D}X^{P}Y^{L.}Y^{S} = T(XY^{L.}Y^{S};4)$ (D = distal; P = proximal) and they may easily be balanced with attached-X's. Extra Y's are eliminated from the T(XY;4) stock by crossing males to XX/0 females. Consider for example a $T(XY^{L.}Y^{S};4)$ with the normal allele of a marker, m^{+}, just proximal to the break point in X. T(XY;4)/0 males produce four sperm types (1) $X^{D}4^{P}$; $4^{D}X^{P}Y^{L.}Y^{S}$, m^{+}; (2) 0 (3) $X^{D}4^{P}$ (4) $4^{D}X^{P}Y^{L.}Y^{S}$, m^{+}. Fertilization of X-bearing ova from *m* females will produce (1) X, $m/T(XY;4)$, $m^{+} = m^{+}$ daughters (2) X, $m/0$ = sterile *m* sons (3) X, $m/X^{D}4^{P} = m$ aneuploid (4) X, $m/4^{D}X^{P}Y^{L.}Y^{S}$, $m^{+} = m^{+}$ aneuploid; owing to lethality or sterility of the aneuploid classes, no fertile sons will result. The irradiation induced deletion majority of X^{P} from $4^{D}X^{P}Y^{L.}Y^{S}$ gametes can produce a derivative that approaches $4^{D}Y^{L.}Y^{S}$ in constitution, thus reducing the aneuploidy and consequently conferring viability or fertility or both upon $X/4^{D}Y^{L.}Y^{S}$ zygotes. The object of the present scheme is to recover such a deleted derivative that retains a distal remnant of X^{P} including m^{+} (Figure 1b). This product will be recognized as a fertile m^{+} son. With the exception of very rare patroclinous sons resulting from maternal primary nondisjunction, the only fertile sons of the above cross will carry a deleted $4^{D}X^{P}Y^{L.}Y^{S}$; if the parental flies are carefully discarded, their progeny may

simply be transferred to fresh medium and the production of larvae used to screen for those containing a fertile male. In a translocation where the X/$4^{D}X^{P}Y^{L}\cdot Y^{S}$ aneuploid is inviable, a fertile male with m^{+} may be recognized immediately in a fertile progeny. Where such aneuploids survive it is necessary to utilize the progeny of males carrying the deleted $4^{D}X^{P}Y^{L}\cdot Y^{S}$ to isolate this product.

The Bar Stone Y: We used $T(1;4)B^{S}$ to construct the $B^{S}Y$ chromosome according to the scheme described in the preceding section; $B^{S}Y$ has B^{S} appended to the terminus of Y^{L}. The marked Y's available before construction of $B^{S}Y$ are marked by normal alleles from some heterologous segment of the genome (except for the Hairy-wing effect of $y^{+}Y$), and their usefulness depends on rendering the remainder of the system homozygous for some recessive gene in the region homologous to the marker segment of the Y. Since this is often inconvenient, especially with $bw^{+}Y$, we decided to produce a Y marked with Bar (BROSSEAU and LINDSLEY 1958). $B^{S}Y$ can be readily scored in all combinations except those in which the X carries *B*.

$T(1;4)B^{S}$, B^{S} *car*/$XY^{L}\cdot Y^{S}$, y^{2} *su-w*^{a} *w*^{a} *KL·KS* females were crossed to $Y^{S}X\cdot Y^{L}$, *y cv v*/0 males; B^{S} *car*$^{+}$ sons were selected. They could have resulted from exchange between *w*^{a} and the translocation break point with primary nondisjunction of the XY from the proximal piece of $T(1;4)B^{S}$, i.e., $XY^{L}\cdot Y^{S}/4^{D}X^{P}$, B^{S} *car*, in which case they would have been sterile owing to hyperploidy for the proximal portion of the X. Alternatively, they could have been recombinants between B^{S} and *car*, i.e., $T(XY^{L}\cdot Y^{S};4)B^{S}$; in which case, they would have been of the desired genotype and fertile. All recovered B^{S} *car*$^{+}$ sons were crossed to attached-X, *y v bb*/0 females, and several of them proved to be fertile. The fertile crosses produced balanced stocks consisting of *y v bb* and *y v* B^{S} daughters and B^{S} sons. Males from such a stock were irradiated with 4000r and crossed to *y v* females. Before the F_1 began to emerge the parental flies were discarded, and the F_1 was subsequently transferred into fresh culture bottles which were later examined for evidence of fertile males. As described in the preceding section fertile males in the F_1 are either $T(XY;4)B^{S}/0$ resulting from maternal nondisjunction or $y\ v/4^{D}Y^{L}\cdot Y^{S}$, which are *y v B* males and result from deletion of a portion of X^{P} from $4^{D}X^{P}Y^{L}\cdot Y^{S}$. From this experiment one such deleted $4^{D}X^{P}Y^{L}\cdot Y^{S}$ chromosome was recovered (Figure 2a) that carries *KL* and *KS*, a remnant of X^{P} carrying B^{S} and *su*^{w}-*f*$^{+}$ (ZIMMERING 1959) but not *ma-l*$^{+}$ or *sw*$^{+}$, and a portion of the tip of chromosome 4 not including the locus of *spa*, which ABRAHAMSON *et al.* showed to be the distal-most marker on chromosome 4. According to LEWIS (1956), the fourth chromosome break in $T(1;4)B^{S}$ is in 102F. In T(X;Y)'s in which $B^{S}Y$ has been broken in Y^{L} (NICOLETTI and LINDSLEY 1960) the tip of the long arm of $B^{S}Y$ can be seen free of the chromocenter. It consists of three double bands; the distal-most has been seen to pair with the Bar region of the X and is probably 16A1; the proximal-most has been seen to pair with a band in region 20 (20A1-2 or 3) and is probably the *su*^{w}-*f* band. No bands of chromosome 4 are discernible. $B^{S}Y$ segregates regularly from a free X or attached-X's and is characterized by good viability in X/$B^{S}Y$ or X/$B^{S}Y$/$B^{S}Y$ males and in X/X/$B^{S}Y$ females.

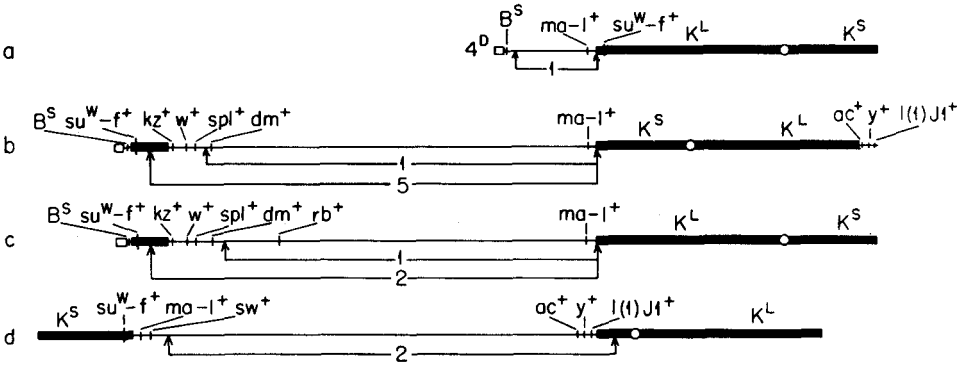

FIGURE 2.—The chromosomes irradiated to produce the marked Y chromosome recovered in the current experiments and the events proposed to account for their origin. The region bracketed between two arrows represents a deleted segment and the associated number indicates the number of such derivatives recovered. In each case only the half of the translocation in the irradiated sperm is figured. The thin line = X euchromatin; the open heavy line = autosomal euchromatin; the solid heavy line = Y or X heterochromatin.

BROSSEAU (1958) has recovered a recombinant between B^SY and bw^+Yy^+ that is B^SYy^+ (Table 1), and we have recovered a B^SYy^{31d} chromosome from an irradiated female that carried both the B^SYy^+ and a derivative of *In(1)sc*^{8} marked with y^{31d}. These chromosomes have great potential utility for studies of detachment and of translocation or recombination involving the Y.

The white$^+$ *Y:* A translocation between the X chromosome and the B^SY [T(X;Y)148 (NICOLETTI and LINDSLEY 1960)] was used in the construction of the w^+Y. T(X;Y)148 is a reciprocal translocation with the breaks in region 2D of the X and in Y^L proximal to B^S but distal to all members of the *KL* fertility complex. This was shown by demonstrating that males containing Y^{D}X^P from T(X;Y)148 and X^{D}4^P from T(1;4)w^{m5} are sterile in combination with Y chromosomes that are separately deficient for *kl-1*, *kl-2*, *kl-3*, *kl-4*, and *kl-5*, the five components of the *KL* fertility complex demonstrated by BROSSEAU (1960). The T(XY;Y) recombinants were recovered from T(X;Y)148, y B^S/XY^S·Y^L (129–16), y^2 *su-w*^{a} w^a *KS·KL* y^+ females crossed to Y^{S}X·Y^L, *Ins(1)EN*,dl-49, y *v f car*/0 males. The desired recombinants were recognizable as y^+ B^S males, and they were crossed to attached X y^2 *su-w*^{a} w^a *bb*/0 females; their progeny consisted exclusively of y^2 w^a females. In the absence of a free Y chromosome the two components of the translocation separate from each other with complete regularity; the y^2 w^a daughters were hyperploid for X^{D}Y^P, which carries the normal allele of *su-w*^{a}, and when backcrossed to their fathers they produced a balanced stock in which the males are X^{D}Y^P; Y^{D}X^{P}Y^S·Y^L/0 and the females are XX/X^{D}Y^P. Males from this stock were irradiated with 4000r and crossed to y w^a *spl rb* females. Owing to the regular segregation of the two halves of the translocation, the zygotes produced are y w^a *spl rb*/X^{D}Y^P, y *KL·KS* which survive and are y w^a *spl rb* males with hyperploid characteristics (including sterility), and y w^a *spl rb*/Y^{D}X^{P}Y^S·Y^L, B^S *KS·KL* y^+ which do not survive. Deletion of the ma-

jority of X^P leads to the production of sons that are y^+ and *B* and that may be w^+, depending on the break points (Figure 2b). A similar series of crosses were carried out with $XY^{L}\cdot Y^{S}$ (108–9), y^2 *su-w*^{a} *KL·KS* in place of $XY^{S}\cdot Y^{L}$ (129–16). Among ~ 12,000 progeny of irradiated sperm of the genotypes shown in Figures 2b and 2c, 11 fertile derivatives of $Y^{D}X^{P}Y^{L}\cdot Y^{S}$ and $Y^{D}X^{P}Y^{S}\cdot Y^{L}$ were recovered. One carried no markers other than fertility, one carried y^+ and fertility, and the remaining nine (which are explainable as interstitial deletions) are indicated in Figure 2b and c. The two derivatives marked with the normal allele of white, i.e., $y^+Yw^+B^S$ and B^Sw^+Y (Table 1), are characterized by normal meiotic behavior and normal viability. They show a dominant Confluens effect, and should be extremely useful in covering the lethal effect of Notch.

The triply marked $y^+Yw^+B^S$ has been irradiated, and a large number of fertile singly and doubly marked derivatives have been recovered. Among these are several y^+Yw^+ chromosomes. The y^+Y^L arm of one of these y^+Yw^+ chromosomes has been replaced with an unmarked Y^L by exchange in an $XX\cdot Y^{L}/y^+Yw^+$ female, where $XX\cdot Y^L$ is a reversed acrocentric compound X chromosome that carries an unmarked Y^L as a second arm. This recombinant, then, is Yw^+. Owing to the complex origin (through repeated irradiations) of these derivatives of the triply marked Y, their constitution as given in Table 1 is necessarily tentative. The order of elements is one that has been inferred from the events that are considered likely to have taken place.

*The Y*ma-l$^+$: This Y chromosome was recovered by a different method from the one described earlier in this communication. $Y^{S}X\cdot Y^{L}$, *In(1)EN, KS B y·KL*/0 males were irradiated and crossed to *ma-l* females. Two *ma-l*$^+$ sons were recovered and found to be fertile. Tests showed that the Y chromosomes carried by these sons contained normal alleles of *su*^{w}*-f*, *ma-l*, and *sw*, but not of *car* or *l(1)J1*. This Y presumably arose through deletion of a segment of the XY from the right of *sw*$^+$ (the left of *sw*$^+$ in a normal sequence) to the right of *l(1)J1;* its constitution is *KL·sw*$^+$—*su*^{w}*–f*$^+$ *bb*$^+$ *KS* (Figure 2d).

SUMMARY

A method for producing marked Y chromosomes by irradiating reciprocal translocations between an XY chromosome and some other element in the genome has been used and a series of marked Y's recovered. The most useful markers that have been appended to a Y are B^S, w^+ and N^+, and *ma-l*$^+$. In addition to these Y's, which carry single marker segments, a number of doubly marked Y's have been constructed. Table 1 lists the current best estimate of the constitutions of the known marked Y chromosomes.

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