Incipient type of polymorphic inversions in *Drosophila melanogaster* natural populations.

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Usually chromosomal abberations observed in *Drosophila* natural populations are most commonly paracentric inversions. Most of them are detected only once in a particular population, but some inversions are found nearly always in most populations. Mettler *et al.* (1977) categorized naturally occurring inversions of *D. melanogaster* populations into 4 classes considering their frequency and geographical distribution, *Common cosmopolitans*, *Rare cosmopolitans*, *Recurrent endemics* and *Unique endemics*. Seventeen years later Inoue and Igarashi (1994) reformed their classification through compilation of more data from the world-wide investigations into 5 classes, *Common cosmopolitans*, *Rare cosmopolitans*, *Quasi-cosmopolitans*, *Endemics* and *Uniques*. Modifications were the following three points: (1) Rare cosmopolitans were limited to 3 inversions, *In(3L)M*, *In(3R)C* and *In(3R)Mo*, instead of 8 inversions originally included, (2) a new class of *Quasi-cosmopolitans* was added to distinguish between *Rare cosmopolitans* and *Recurrent endemics* of Mettler *et al.* (1977), (3) *Recurrent endemics* was replaced with two classes, *Endemics* and *Uniques*. Definition of each class and included inversions are as follows:

(a) *Common cosmopolitan* inversions are present in many populations all over the world with high frequencies. Occasionally they are more frequent than standard chromosomes. Four inversions are included, each of which exists in the right and left arms of two major autosomes, respectively, *In(2L)t*, *In(2R)NS*, *In(3L)P* and *In(3R)P*. The character of this class is the geographical north-south cline in frequency, higher toward the equator in both hemispheres, as noted by Mettler *et al.* (1977), Knibb *et al.* (1981) and Inoue *et al.* (1984). Other classes of inversions absolutely do not show such a geographical cline.

(b) *Rare cosmopolitan* inversions are also distributed throughout the species range, but their frequencies are usually low, being absent in some populations, not enough to show the geographical frequency cline.

(c) *Quasi-cosmopolitan* inversions are also widespread in the world but just not enough to say "cosmopolitan" in their distribution. Their frequencies are usually in the same or lower level in comparison with Rare cosmopolitans. A total of 7 inversions of *In(2L)A*, *In(2L)Cy*, *In(2L)NS*, *In(2R)Cy*, *In(3L)Y*, *In(3R)K* and *In(3R)M* are included in this class. In Japan *In(2L)A*, *In(3L)Y* and *In(3R)K* have been detected.

(d) *Endemic* inversions appear repeatedly but in a geographically region-specific manner. In a given local population they show a low frequency level of polymorphism even if just for temporal appearance. The inversion members of this class and their frequencies may thus change from survey to survey. They are distinguished from *Unique* inversions mentioned next by appearance more than two times in the single population survey.

(e) *Unique* inversions are all individually different from one another and usually recorded only once each. They are probably selected out soon after they were formed and dismissed by a stochastic process. The records of *Uniques* accumulate as more surveys are conducted, and these inversions occupy the majority of inversions found in nature.

Here are two inversions which were first found in the Japanese natural population and have been settled since then. *In(2L)W 28C;32C* is a relatively short inversion existing in the middle of the left arm on the second chromosome (Figure 1-a). It was first found in a single fly of the central

Table 1. Frequencies of In(2L)W and In (3L)Y per autosome arm.*

Localities		Year	N**	2LW	3LY
Eastern Japan					
	Hokkaido	1977	240	0.033	0.004
		1982	68	0	0
	Yamagata	1977	240	0	0.008
		1982	200	0	0
Middle Japan					
	Yamanashi	1975	203	0.030	0.005
		1976	200	0.030	0.030
		1977	240	0.029	0.029
		1990	200	0.010	0
		1997	204	0.005	0
	Nagano	1977	240	0.046	0.013
		1982	200	0	0
	Tochigi	1983	530	0.006	0
West Japan					
	Wakayama	1982	78	0.013	0
	Ehime	1982	680	0.001	0
	Oita	1982	96	0	0.010
South-west Islands					
	Amami-oshima	1974	332	0	0
		1983	260	0.004	0.004

*Data from Inoue and Watanabe (1979), Inoue and Igarashi (1994) and the present study. ** Number of chromosomes tested.

Japanese population at Katsunuma, Yamanashi prefecture, in 1972 (Inoue and Watanabe, 1979), and the "W " is derived from Dr. T.K. Watanabe. This inversion has not been found in areas other than Japan. *In(3L)Y 68F;75C* is a relatively long inversion existing in the middle of the left arm of the third chromosome (Figure 1-b). It was also first found in the same locality as *In(2L)W* in 1975 (Inoue, 1979), and the "Y " was named from Yutaka Inoue. This inversion was recorded in regions other than Japan, in Spain with a frequency of 3/238 (Roca *et al.*, 1982) and North Carolina, U.S.A., in 1974-1975 with 1/172 (Inoue and Igarashi, 1994). The Katsunuma population has been surveyed by Oshima *et al.* (1964), Watanabe (1967) and Watanabe *et al.* (1976), and there were no *In(2L)W* and *In(3L)Y* in the 1960's. So these two inversions probably arose or invaded Japan in the 1970's. The distributions of these two inversions in Japan are shown in Table 1. Populations having only *In(2L)W* or *In(3L)Y* are listed here with each frequency per autosome arm. Although frequencies are at a low level of at most 0.046 and there were many other populations without these two inversions, they both have already spread all over Japan. In the South-west Islands they were found in only the Amami-oshima sample. A total of 656 chromosomes from Ishigaki-jima surveyed in the period of 1973-1982 and a total of 1726 chromosomes from Okonawa-hontoh in 1975-1999 proved not to have these two inversions. Also a total of 1100 chromosomes from eight other small South-west Islands were surveyed in 1971-1999 to be without these two inversions.

When a population is surveyed repeatedly in a short period, not the usual one-time survey, some *Unique* inversions are possibly sampled more than two times, being then classified as *Endemic* inversions. Some stable *Endemics* such a *In(2L)W* possibly spread its distribution through migration and adaptive process to become the *Quasi-cosmopolitan* inversion. And some stable *Quasi-cosmopolitans* such as *In(3L)Y* possibly get wider distributions to become the *Rare cosmopolitan* inversion. Thus the boundaries among these four inversion classes are continuous and can not be clear-cut. Although their range of distribution is different, their frequencies are all similarly at a low level. Their frequencies have not been at as high a level as the four *Common cosmopolitan* inversions. *Common cosmopolitans* somehow obtain the special characteristics necessary to display polymorphisms of stable and high frequency. Only their breakpoints of both sides might have happened to occur in the DNA site which has no negative effect on adaptability compared with the standard chromosomes.

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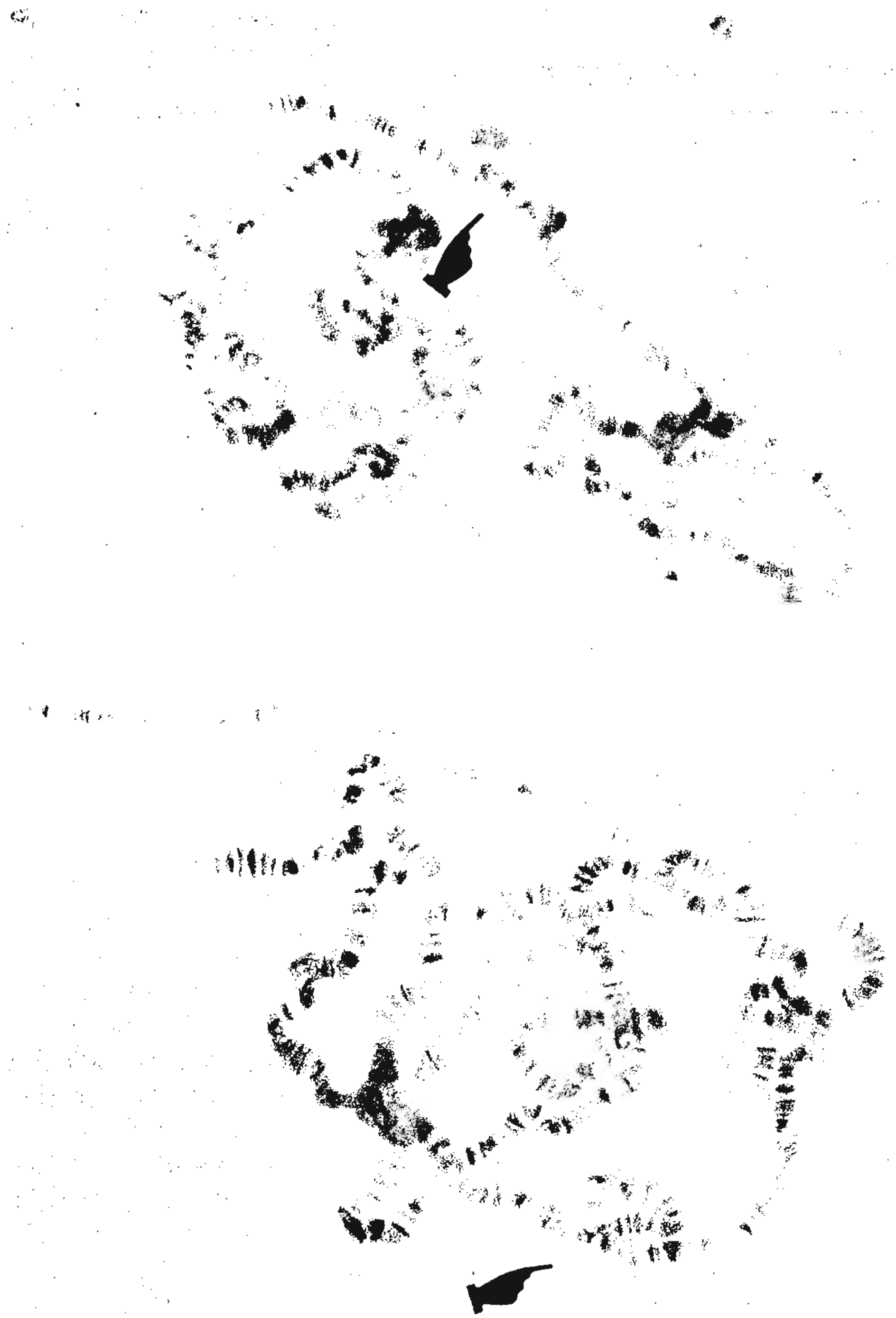

Figure 1. (a) Polytene chromosomes from heterokaryotype of *In(2L)W*. (b) Polytene chromosomes from heterokaryotype of *In(3L)Y*.

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