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THE HYBRIDIZATION BETWEEN A PAIR OF SIBLING SPECIES, *DROSOPHILA IMMIGRANS* AND *DROSOPHILA FORMOSANA*

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ABSTRACT

The sibling species, *Drosophila immigrans* and *D. formosana* can only be distinguished by their fine morphological structures especially in males, by the differences in the tarsus of the foreleg and in the genitalia. As for cytological analyses, no significance between brain cell karyotypes was observed, although *D. formosana* shows longer total chromosome length (TCL). About 95% of the homology of the polytene chromosomes is existed in the whole X-chromosome, 2R-chromosome and 3-chromosome arms. As for the result of their sexual isolation experiments and hybridization tests, we found that complete sexual isolation between the two species and the phenomenon of non-backcrosses between F_2, F_3 and F_4 hybrids with their parental *formosana* although F_1 hybrid showed partial fertile. From the points mentioned above, we could be sure that both species have reached the full specific level in the process of their historical evolution. According to the zoogeographical distribution and living niches, we could further deduce that the populations of *D. immigrans* and *D. formosana* have diverged from the ancient population of *immigrans* stem having either unusual stasipatric speciation model or allopatric speciation 1b model, although they are sympatric now in Taiwan.

INTRODUCTION

Hybrid sterility is an important reproductive isolating mechanism which prevents the exchanges of genes between different incipient species, semispecies and sibling species (full species) (Mayr, 1963). Usually it inhibits or suppresses the reproductive capacity of F_1 hybrids or the later hybrid generations (Mayr, 1963; and elsewhere).

Drosophila immigrans and *D. formosana* were collected from Taiwan since 1967. They are sibling species which was defined by Mayr (1942, 1963, 1970) and Dobzhansky (1970) as morphologically similar or identical natural populations that are reproductively isolated. Iso-female lines were established and kept in our laboratory at Academia Sinica. The distribution of the two species in Taiwan is shown in Fig. 1. *D. immigrans* is one of the cosmopolitan species which can be collected from the higher mountane forests and the wildness down to cities in the plain and usually associated with human activities and orangeries. The fly distributes widely in Taiwan as *D. hydei, D. melanogaster, D. kikkawai* and *D. busckii* do. *D. formosana* rarely found from human association, neither from

Fig. 1. Map of Taiwan showing where collections were made. Solid circles showing the localities *Drosophila immigrans* was collected and open circles showing the localities *D. formosana* was collected.

scavenges or fruit markets, which mostly distributes in the wildness of central mountain ranges in Taiwan. The distribution of *D. formosana* is completely overlapped with *D. immigrans* but with a rather small distributional ranges than the later species (Fig. 1). Although they have a large area of same habitation, but rarely hybrid between the two species were observed in the nature. Certain degrees of genetical, ethological and seasonal isolations between these two sympatric species have been detected (Lin & Yeh, unpublished data). The data showed that the most abundant of *D. formosana* occurs in the June-July at Wulai, Taipei where *D. immigrans* showed that there are two populational peaks annually, one in the February-April period on the orange season and the other in the September-October period on the longana ripen season, which prevents the potential hybrid matings between the two species seasonally. For almost ten years observation, we

could not find out any hybrid individuals in the periods of November-January and May. It is said that they are seasonally isolated each other in the nature. One of the importance of sibling species in biology is that they are historical importance in the study of speciation. In order to test how much they are diverged genetically and how much they are speciated historically this experiment was designed.

MATERIALS AND METHODS

Three strains, *Drosophila immigrans* (Stock no. 0107.14), *D. formosana* (Stock no. 0107. 11) from Chi-tou, Nan-Tou and *D. formosana* (Stock no. 0125.2) from Wulai, Taipei were employed in the present experiment (Table 1). Stock nos. 0107.14 (*immigrans*) and 0107.11 (*formosana*) are sympatric, occupy the same food niche and habitat when collection was made at Chi-tou, Nan-Tou, the central part of Taiwan. Both species can be collected in a same sweeping, but rarely or almost none of their interspecific hybrid was seen. Similar phenomenon also observed at Wulai, Taipei, the northern part of Taiwan and San-ti-meng, Pintung, the southern part of Taiwan. Stocks were kept in vials with standard cornmeal medium. Milk bottles were replaced during the experiment was carried out for the mass production of the flies. They were kept in 24 ± 0.5 C of temperature, 85 ± 5% of relative humidity and 12–12 hours light-dark control throughout the experiment in growth chambers.

Abbreviations F_W, F_C and I_C were designated *Drosophila formosana* collected from Wulai, *D. formosana* from Chi-tou and *D. immigrans* from Chi-tou, respectively.

(1) Morphological distinction :

The females of *D. formosana* is indistinguishable from the females of *D. immigrans* in external morphology, except some abdominal banding patterns with a little differences but inconspicuous. Only minor differences can be detected from the male fore tarsi (Sturtevant, 1927) (Fig. 2), male genitalia and female egg guide (Fig. 3) using the sympatric collections from Chi-tou. We have found that there are two color forms of individuals in the two species. One is the dark form which has conspicuous distinguishable abdominal

Table 1
Strains used in this experiment

Stock no.	Species	Locality	Collectors & Date
0107.14	*Drosophila immigrans*	Chi-tou, Nan-Tou	Lin & Tseng, IX 18, 1972
0107.11	*Drosophila formosana*	Chi-tou, Nan-Tou	Lin & Tseng, IX 18, 1972
0125.2	*Drosophila formosana*	Wulai, Taipei	Lin et al., IV 6, 1974

Chi-tou — 1,250 m in elevation in the central Taiwan
Wulai — 300 m in elevation in the northern Taiwan

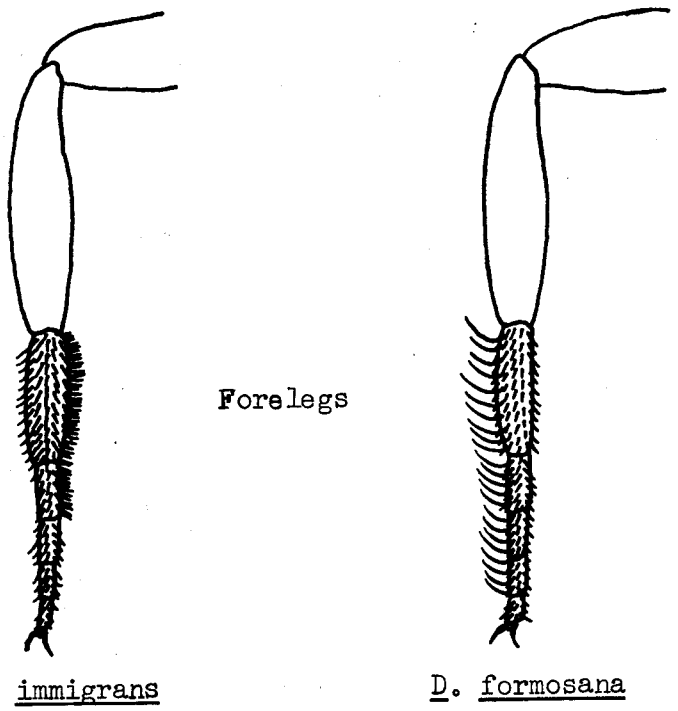

Fig. 2. The forelegs of *Drosophila immigrans* and *D. formosana* showing the differences in hairs rows and shapes of hairs on the tarsi.

bands on both sexes, and the other is the light form with inconspicuous abdominal apical bands. It is possibly controlled by polygenes (Ford, 1975). In fact, they are existed by a certain percentages in populations obviously and the dark form is a dominant one. It is interesting to note that we could easily to distinguish the two species by the percentages of the dark form, and the dark and light forms are fluctuated seasonally. *Drosophila formosana* seems having more percentages of the dark form throughout the year.

Wing-vein indices and pupal horn index of the three strains of flies were also compared. All male flies were used for the comparison (Table 2).

(2) Cytological comparison:

(i) Metaphase chromosomes: The brain metaphase chromosomes of the second instar larvae of the two species were compared with the arm ratio (AR), percentages of the total chromosome length (% TCL) and their karyograms (Boyes et al., 1971; Lin et al., 1974) (Table 3, data are taken from Lin et al., 1974).

(ii) Polytene chromosomes: The third instar larvae of the two species were dissected and the salivary chromosomes were then prepared by squash method as described elsewhere (Wilson et al., 1969). The banding patterns of the polytene chromosomes were compared and the homologies were photographed. Most of the homology were made from

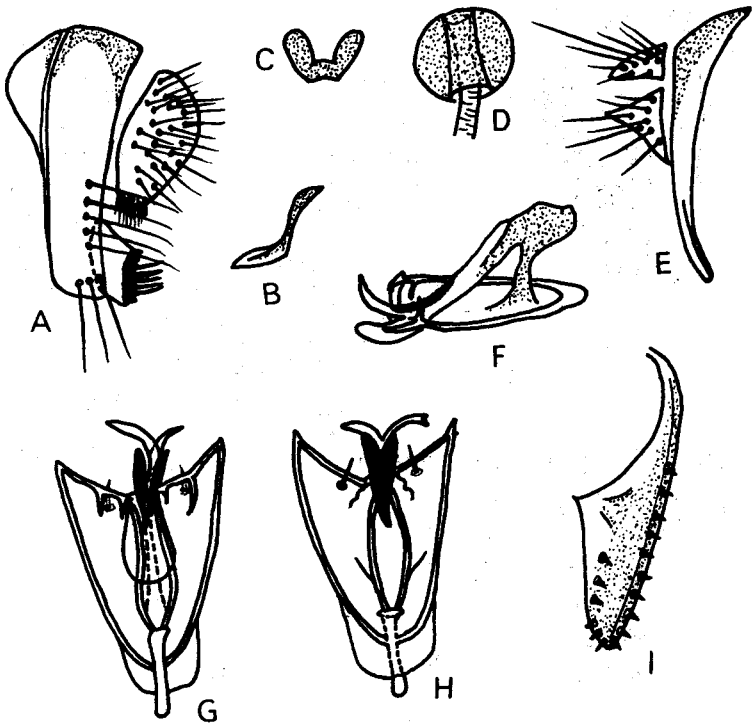

Fig. 3. *Drosophila immigrans.* A, Male genitalia; B, Ejaculatory apodeme; C, Bridge connected with claspers; D, Spermatheca; E, Female T–8 and anal plates; F, G, H, Lateral, ventral, dorsal views of copulatory apparatus; I, Egg guide.

the hybrids from the cross of *D. formosana* and *D. immigrans* to detect the pairing and unpairing of each homologous and heterogous segments of chromosomes as shown in Fig. 5.

(3) Sexual isolation:

The male choice experiment for the sexual isolation between the two species were performed. Sexual isolation index, chi-square were calculated (Stalker, 1942) as shown in the Table 4. The joint sexual isolation (Malogolowkin-Cohen et al., 1965; Ehrman & Parsons, 1976) from the data of Table 4 was made to show that whether they are strongly or weakly isolated among *D. immigrans* and the two strains of *D. formosana* (Table 5).

(4) Interspecific hybridization:

Nine parental cross tests were performed, which are F_w females x F_w males, Fc females x F_c males and I_c females x I_c males as control and F_w females x F_c males, F_w females x I_c males, F_c females x F_w males, F_c females x I_c males, I_c females x F_w males and I_c females x F_c males as test crossings (Table 6). Pair matings of five to eight days old virgin females and males were used for each test cross. When F_1 hybrids of the interspecific cross were produced, we keep on performing F_1 selfcrosses and F_1

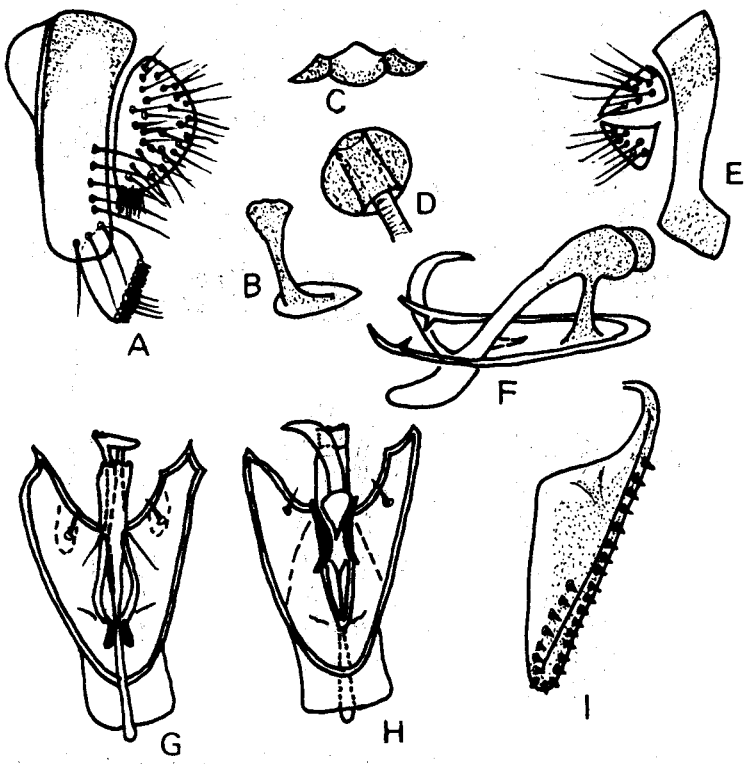

Fig. 4. *Drosophila formosana*. A, Male genitalia; B, Ejaculatory apodeme; C, Bridge connected with claspers; D, Spermatheca; E, Female T–8 and anal plates; F, G, H, Lateral, ventral, dorsal views of copulatory apparatus; I, Egg guide.

backcrosses with both sexes of their parental species. If F_2 hybrids from the F_1 selfcrosses were produced, then continue to perform selfcrosses and backcrosses as in F_1 hybrids do. In this experiment we have obtained the F_5 hybrids from the F_4 selfcrosses and the hybrids from the F_4 backcrosses with their parentals (Table 7).

Figure 6 shows that the schemic crosses performed in this study.

RESULTS AND DISCUSSION

(1) Morphological distinction:

The fore tarsi of *Drosophila immigrans* males have the short densed hairs on the rear row of the leg whereas *D. formosana* males have the long up-curved hairs on their frontal row of the leg as stated by Sturtevant (1927) (Fig. 2).

The long hairs on the male clasper of *D. immigrans* has 5 to 6 long hairs compared with 4 to 5 long hairs on the male clasper in *D. formosana* (Figs. 3A and 4A). The bridge connected with claspers (decasternum) are quite different in the two species as shown in Figs. 3C and 4C. The tip of aedeagus of the copulatory apparatus of *D. immigrans* is bifid and *D. formosana* is spade-like (Figs. 3G and 4G). The stout teeth on female egg guide (ovipositor) in *D. formosana* has 20 or more teeth on the margin and 5 to 6 teeth on the discal compare with *D. immigrans* has about 15 teeth on the margin and only 3 teeth on the discal of the egg guide.

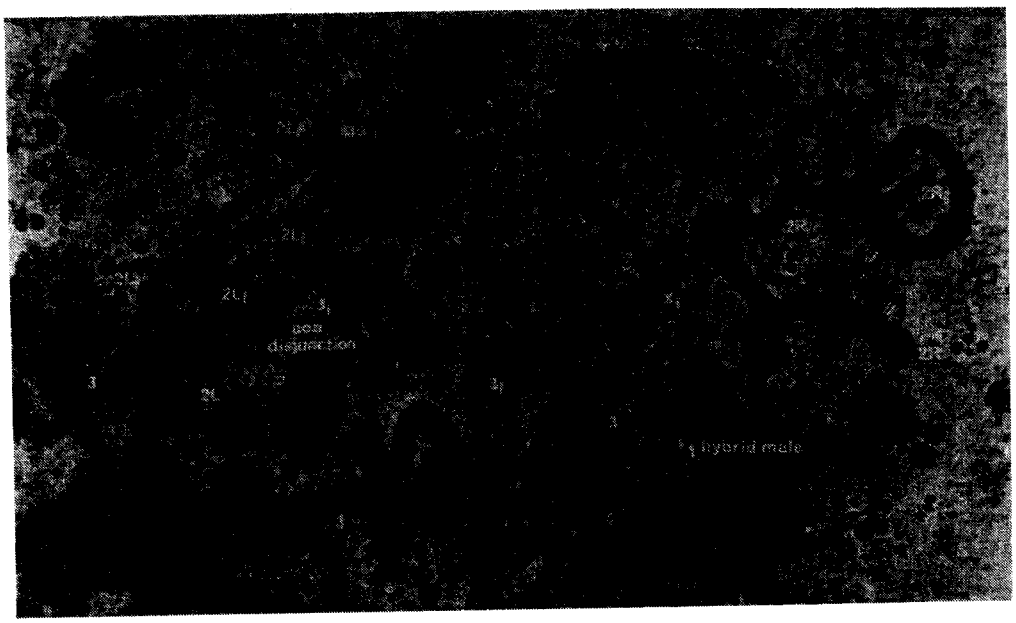

Fig. 5. Polytene chromosomes of F_1 hybrid male produced from the cross of Chi-tou's *Drosophila immigrans* female and Wulai's *D. formosana* male, showing the pairing and unpairing segments of chromosomes. Sub-letter *i* and *f* represent the chromosomes from *immigrans* and *formosana* respectively.

The comparison of wing-vein indices and pupal horn index showed that the three strains are significantly different although their wing length is the same, except C-index in the sympatric *D. immigrans* and *D. formosana* is not significantly different as calculated by the *t* value, and C-index, 4c-index and 5x-index between allopatric *D. formosana* also showed insignificantly different. Total of 20 male wings and 20 pupae were recorded for the calculations as shown in Table 2.

(2) Cytological comparison:

The total chromosome length (TCL) (Boyes et al., 1971) of *D. immigrans* is shorter than that of *D. formosana* which are 26.66 ± 2.72 microns in *immigrans* compared with 32.86 ± 6.81 in *formosana* (Lin et al., 1974), although they showed the same 1V3R in karyotype. The Y-chromosome of *D. immigrans* also shows shorter than that of *D. formosana,* 13.21 microns versus 20.33 microns. It seems to be that more genes are added to *D. formosana* which is assumed to be more derived due to the gene duplications (Ohno, 1970; Morescalchi, 1975) (Table 3).

The salivary chromosomes of *D. immigrans* showed less bands and shorter in length than that of *D. formosana*, we only show the hybrid male polytene chromosomes (Fig. 5) from the cross of female *immigrans* and male *formosana* to compare their banding patterns. Figure 5 shows the pairing of the chromosome segments of the two species. Almost 95% the chromosomes are identical and also shows that they share some homosequential segments of chromosomes (Carson et al., 1970). In Fig. 5, the X-chromosome is come from the parental *immigrans,* only shows hemichromosome. The 3-chromosome of the

Table 2

Wing indices and pupal horn index of Chi-tou's *D. immigrans* and *D. formosana* and Wulai's *D. formosana*, and their *t*-test

	Wing indices					
	C–index	Ac-index	4c-index	4V-index	5x-index	Horn index
D. immigrans (sympatric)	4.35 ± 0.196	1.43 ± 0.083	0.51 ± 0.016	1.32 ± 0.037	1.12 ± 0.037	0.337 ± 0.0145
	t = 1.300	t = 4.789*	t= 3.288*	t = 3.642*	t = 3.504*	t = 4.325*
D. formosana (sympatric)	4.28 ± 0.140	1.54 ± 0.062	0.53 ± 0.022	1.27 ±0.049	1.07 ± 0.052	0.356 ± 0.0183
	t = 1.726	t = 3.446*	t = 2.037	t = 5.324*	t = 1.773	t = 5.999*
D. formosana (allopatric)	4.18 ± 0.218	1.63 ± 0.090	0.55 ± 0.038	1.35 ± 0.046	1.04 ± 0.055	0.387 ± 0.0189

N = 20

$t\binom{19}{0.05} = 2.093$

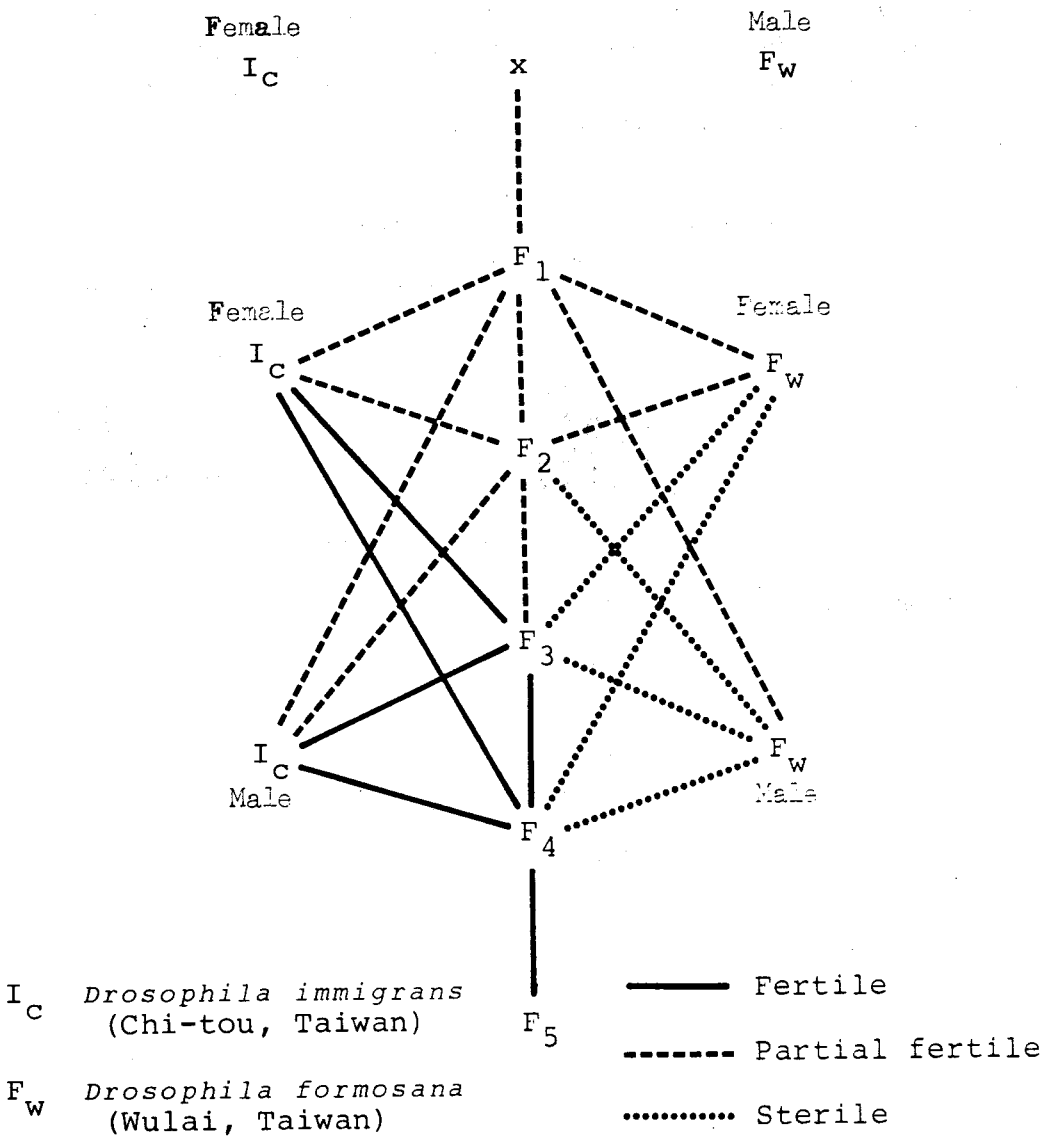

Fig. 6. The schemic figure represents the crosses and fertilities between hybrids selfcrosses and hybrids backcrosses in this experiment.

hybrid shows their bandings are homosequential entirely, although there is a segment of non-disjunction which is come from the parental *immigrans*, because there always has an inversion at this segment in Taiwanese *immigrans*. The 2L-chromosome shows that *formosana* has more bands at the center part of the chromosome but *immigrans* has 4 bands more than *formosana* at the basal part of the chromosome. The 2R-chromosome from the two species shows almost homosequence in their banding patterns except on the near free end of the chromosome. *immigrans* has 2 to 3 more bands than that of

formosana. The unpairing segment of the free end of the 2R-chromosomes are identical. Here we may conclude that *formosana* has a little more bands than that of *immigrans* which confirm the brain metaphse chromosome of the two species in which *formosana* shows longer total chromosome length (TCL) (Table 3).

Table 3
Karyograms and total chromosome length, and arm ratio
of *Drosophila immigrans* and *D. formosana*

Metapahse karyotypes

Chromosomes		*D. immigrans*	*D. formosana*
(Y)	%TCL	13.21	20.33 ± 2.06
	AR	∞	∞
X	%TCL	18.83 ± 0.22	23.47 ± 1.06
	AR	∞	∞
II	%TCL	34.04 ± 0.31	29.97 ± 1.34
	AR	1.31 ± 0.01	1.13 ± 0.00
III	%TCL	24.70 ± 0.38	24.58 ± 0.37
	AR	∞	∞
IV	%TCL	22.41 ± 0.17	22.21 ± 1.00
	AR	∞	∞
Average TCL in micra		26.66 ± 2.72	32.86 ± 6.81
No. cells analysed		14	10
No. larvae involved		4	7

TCL = Total chromosome length
AR (arm ratio) = length of long arm/length of short arm
AR = 1.00 – 1.20 —— metacentric, 1.20 – 2.00 —— submetacentric,
above 2.00 —— acrocentric, ∞ —— telocentric

Table 4
Male choice experiments showing sexual isolation between *Drosophila immigrans* and *D. formosana*

Males	Females	% Homogamic	% Heterogamic	Isolation index	X^2	No. pair matings
I_c, F_w	I_c	28.2	0.9	0.938±0.0038	57.72*	220
F_w, I_c	F_w	47.3	1.8	0.926±0.0018	46.61*	330
I_c, F_c	I_c	33.9	0.9	0.950±0.0024	53.40*	230
F_c, I_c	F_c	68.2	0	1	56.02*	390
F_w, F_c	F_w	40.6	47.6	−0.080±0.0066	1.88	340
F_c, F_w	F_c	59.4	48.8	0.098±0.0054	1.80	340

* $X^2 \left({}^{1}_{0.05} \right) = 3.841$, significantly isolated.

I_c —— *Drosophila immigrans* collected from Chi-tou, Taiwan.
F_c —— *Drosophila formosana* collected from Chi-tou, Taiwan.
F_w —— *Drosophila formosana* collected from Wulai, Taiwan.

(3) Sexual isolation:

Table 4 shows that the male choice experiments were employed in this study and the percentages of homogamic and heterogamic matings between these two species were shown. In which sympatric *immigrans* and *formosana* shows completely isolated reproductively due to the discrimination of behavior pattern habitating in the same niche and the mating using females of *immigrans* showed strong sexual isolation with males of *formosana* in this experiment. Interspecific crosses using allopatric species also showed strong sexual isolation that might be due to the courtship behavior and/or genetic incompatibility. Allopatric matings of the speices *formosana* showed negative sexual isolation (when F_W females x F_W and F_C males) and weak sexual isolation (when F_C females x F_C and F_W males). The results suggested that there is no sexual isolation between conspecific different populations and favors for heterogamic mating in order to get more genetic variations. The same results were observed in the crosses between *D. pseudoobscura* and *D. persimilis* (Dobzhansky & Epling, 1944; Mayr & Dobzhansky, 1945),and *D. paulistorum* species complex (Ehrman, 1964, 1965). The joint sexual isolation indices (Malogolowkin-Cohen et al., 1965; Ehrman & Parsons, 1976) are shown in Table 5, which show that the heterogamic matings are strongly isolated and the chi-squares being 6.5099 and 99.0294 respectively.

(4) Interspecific hybridization:

Nine combination test crosses were performed as mentioned before. Only one interspecific cross was successful, which is I_C females x F_W males, but shows partially sterile. The reciprocal cross of F_W females x $I_C$males, and the sympatric interspecific crosses of F_C females x I_C males and I_C females x F_C males get no offsprings at all table 6). This one way direction of mating success of the sibling species suggested that *D. immigrans* is more primitive one and *D. formosana* is the derived one (Watanabe & Kawanishi, 1979). We then use the hybrids produced from the cross of F_W females and I_C males to perform

Table 5

Joint sexual isolation index among *Drosophila immigrans* and two strains of *D. formosana*

A x B	% mating success				Sexual isolation index	x^2
	A x A	B x B	B x A	A x B		
I_C x F_W	28.2	0.9	1.8	47.3	0.929 ± 0.0348	6.5099*
I_C x F_C	33.9	0.9	0	68.2	0.988 ± 0.0117	99.0294*
F_W x F_C	40.6	47.6	48.8	59.4	0.089 ± 0.0054	0.0169

* $x^2 \left({}^{1}_{0.05} \right) = 3.841$, significantly isolated.

Table 6
Hybridization between the two sibling species,
Drosophila immigrans and *D. formosana*

females \ males	F_W	F_C	I_C
F_W	4,128[1] (70)[2] 59.3[3]	4,016 (70) 57.4	0 (110) –
F_C	5,973 (70) 82.8	6,976 (70) 91.1	0 (110) –
I_C	2,031[4] (110) 18.5	0 (110) –	5,971 (70) 85.3

1. F_1 progeny numbers
2. Pairs were used for crosses
3. Mean F_1 offsprings in each pair mating
4. Partially sterile and used for selfcrosses and backcrosses with parental *immigrans* and *formosana* subsequently

the subsequent selfcrosses and backcrosses with their parentals. The crosses were terminated till we got F_5 hybrids. The results are shown in the Table 7. The number in parenthesis represents the number of pair matings were used. The upper number on each row shows the offsprings have been obtained from the crosses and the lower row number shows the mean average of the offsprings produced from each single pair mating. Asterisk mark represents the significant level at 0.05. The selfcrosses from the F_3 subsequent generations showed completely fertile and so that we curtail the selfcross after F_4. F_1 hybrids backcrossed with their F_W parentals showed 32.5 and 25.9 flies per pair mating were gotten but showed that significantly reduce its fertility compared with the control crosses of $F_W \times F_W$ and $I_C \times I_C$ the parental crosses. Hybrids F_2, F_3 and F_4 backcrossed with parental *formosana* in both sexes showed completely sterile. Contrarily the backcrosses of F_1, F_2, F_3 and F_4 hybrids with parental *immigrans* in both sexes showed completely fertile. Which indicates that the hybrids' genetic components are more and more similar to *immigrans* and their genetic incompatibility did not happened. The banding patterns of F_5 polytene chromosomes are almost identical with that of *D. immigrans*. The external morphology of the hybrids are also similar to *D. immigrans*. This results could be explained that sympleisiomorphs are existed in the two species and apomorphs are appeared in *formosana*, such as the long up-curved hairs on the front of foreleg of males, more chromosomal bandings being added in the polyteny, longer total chromosome length, more teeth on the male clasper and more teeth on the female egg guide, these are presumely derived characters (apomorphs) (Hennig, 1965). The schemic

Table 7
Crosses of F_1, F_2, F_3 and F_4 selfcrosses and backcrosses with their parental species [1,2]

Females \ Males	F_1	F_2	F_3	F_4	F_w	I_c
F_1	2,185* / 33.6 (65)	–	–	–	1,037* / 25.9 (40)	1,304* / 37.3 (35)
F_2	–	1,487* / 25.2 (59)	–	–	0[4] / 0 (50)	1,197* / 23.9 (50)
F_3	–	–	6,425 / 80.3 (80)	–	0[4] / 0 (60)	3,923 / 65.4 (60)
F_4	–	–	–	4,985 / 71.2 (70)	0[4] / 0 (50)	4,254 / 85.1 (50)
F_w	1,139* / 32.5 (35)	124[3] / 2.5 (50)	0[4] / 0 (60)	0[4] / 0 (50)	–	–
I_c	1,532 / 43.8 (35)	2,245 / 44.9 (59)	2,905 / 48.4 (60)	4,515 / 90.3 (50)	–	–

1. Partially fertile of hybrids from the cross of F_w male and I_c female were used.
2. Reciprocal crosses of F_c x I_c (sympatric) produced no F_1 offsprings were omitted from this table.
3. Sterile, the fertility is only 4.2%.
4. Completely incompatible, get no offsprings.

* $X^2_{(0.05)}(1) = 3.841$, fertility has been reduced significantly compared with F_w x F_w and I_c x I_c the parental crosses.

figure of the crosses is presented in Figure 6, which shows the results of interspecific, selfcrosses of hybrids and backcrosses with their parentals and also shows the fertility (solid line), partial fertility (dashed line) and sterility (dotted line) of those crosses.

SUMMARY

1. Sibling species are very similar in their morphology, but one could distinguish them from the fine external structures with careful observation.
2. Genetically the sibling species is almost identical, their genealogical relationship are very close each other.
3. *Drosophila immigrans* is more primitive species than *D. formosana,* they share some pleisiomorphic characters (primitive characters), and *D. formosana* has some apomorphic characters (derived characters). We may concluded that *D. formosana* was

speciated from ancient *immigrans* stem in their historical evolution.

4. The interspecific crosses, only females of *immigrans* can accept the males of allopatric *formosana,* which may concluded that a) there is sexual discrimination existed in sympatric species which prevents hybridization and breakdown their reproductive isolation, b) *D. immigrans* is more primitive species and *D. formosana* is a derived species since the females of *immigrans* can accept the males of *formosana* in the crosses (Watanabe & Kawanishi, 1979).
5. Two models of speciation processes can be applied in the evolution of the two species, one is proposed by Bush (1975) called allopatric speciation model 1b and the other is proposed by White (1968, 1978) (Futuyma & Mayer, 1980) called stasipatric speciation process.

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同胞種大果蠅 (*Drosophila immigrans*) 與台灣大果蠅 (*D. formosana*) 之雜交

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大果蠅 (*Drosophila immigrans*) 與台灣大果蠅 (*D. formosana*) 係一對同胞種，在外表形態上不容易鑑別出來，只有從微小的性徵上我們可以把這兩種果蠅區別出來。本文從幾個外表上的性徵、細胞學 (包括腦細胞分裂中期之核型及唾液腺染色體)、性隔離程度及雜交試驗來證實這一對同胞種之差異，並且由這兩種果蠅之分布狀況、雜交及反交之不孕程度以及由外表形態上這兩種果蠅擁有共同祖先的形質而台灣大果蠅具有子孫的形質來探討這兩種果蠅之遺傳分化及種之形成 (Speciation) 證實台灣大果蠅係由於古時候的大果蠅分歧出來而形成了另一新種。