GONADAL HYBRID DYSGENESIS IN *DROSOPHILA STURTEVANTI* (DIPTERA, DROSOPHILIDAE)

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ABSTRACT

The occurrence of hybrid dysgenesis was investigated in *Drosophila sturtevanti* Duda, 1927 using diagnostic crosses similar to those used for induction of dysgenics traits in *D. melanogaster*. Reciprocal test crosses were made, at 27° C, between an old laboratory strain of *D. sturtevanti* (COL, from Colombia), assumed to be an M'-like strain, and eight freshly collected strains from several natural populations. The gonadal dysgenesis indices were under 10% in most of crosses, except in hybrids of COL with I_{27}, a strain from Minas Gerais (Brazil), in which the index values were moderate in both directions of crosses (25.71 and 12.87). The smallest productivity was also observed in hybrids of females COL mated to I_{27} males. No causal relationship between the observed gonadal dysgenesis and mobilization of *P* element or another transposable element could be effectively established.

KEYWORDS. Hybrid sterility, *P* element, *I* element, *hobo* element, transposable elements.

INTRODUCTION

Hybrid dysgenesis is a phenomena caused by mobilization of a family of transposable genetic elements, referred to as *P* elements (KIDWELL *et al.,* 1977). Dysgenesis syndrome can be observed in *D. melanogaster* Meigen, 1830 in germ line of F_1 offspring when males carrying autonomous *P* elements (P males) are crossed to females lacking *P* element sequences (M females), or carrying defective sequences (M' females) (KIDWELL *et al.*, 1977; BINGHAM *et al.*, 1982). Transposition occurs only in germ line of dysgenic hybrids and may lead to gonadal atrophy in both sexes, chromosomal rearrangements, male recombination, high mutability and embryonic lethality of F_2 eggs (GD sterility, ENGELS, 1983). Developmental temperature is critical for P-M dysgenesis syndrome manifestation. Dysgenesis can be also caused if males bearing active *I* elements (I males) are mated to females lacking it (R females); the *I* element transposes and the F_1 female may become sterile due to the death of their progeny at the embryonic stage (BUCHETON *et al.,* 1976, 1984, 1986). In both systems, the reciprocal crosses are nondysgenic. In addition to the P-M and I-R systems, other families of transposable elements are able to promote hybrid dysgenesis as *hobo* element in *D. melanogaster* (BLACKMAN *et al.,* 1987; YANNOPOULOS *et*

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al., 1987), and *Helena*, *Paris*, *Penelope* and *Ulysses* elements in *D. virilis* Sturtevant, 1916 (PETROV *et al*., 1995; VIEIRA *et al.*, 1998).

Populations can be characterized by two properties related to the phenotypic effect of their *P* elements: their capacity to mobilize *P* elements in a permissive background, called P-activity; and their potential to regulate or suppress P-activity, called P-susceptibility (KIDWELL, 1985; ENGELS, 1989). P-activity is measured by crossing males of a strain to be tested with females of a strain devoid of any *P* element (the A test). When developed at temperatures over 25ºC, the F_1 progeny exhibit a level of gonadal sterility (GD sterility) proportional to the *P* element activity of the tested males. P-susceptibility is measured by crossing females of a strain to be tested with males of a reference strain with high P-activity (the A* test). The F_1 progeny in that case exhibits GD sterility proportional to the capacity of the tested females to repress the P-activity of the males.

There are very few information on transposable elements distribution and their functional states in *D. sturtevanti* Duda, 1927. Among the transposable elements investigated, *P* element is the most studied (DANIELS & STRAUSBAUGH, 1986; DANIELS *et al.*, 1990; CLARK *et al*., 1995; CLARK & KIDWELL, 1997; SILVA & KIDWELL, 2000), but its functional state is not known.

The presence of *P* elements in all populations studied to date suggests that *D. sturtevanti* has not M strains anymore. However, observations of inactive sequences restrict to the heterochromatin in other species (SPRADLING & RUBIN, 1986; DEVLIN *et al*., 1990) supports the idea of *P* element mobilization in crosses between recently collected and old laboratory strains. The occurrence of hybrid dysgenesis in offspring of a recently captured strain of *D. sturtevanti* mated to a strain collected in Colombia in the 1950s (SENA & CARARETO, 1997; ALMEIDA, 2000) led us to search for phenotypic evidence of *P* element mobilization, through the analysis of gonadal dysgenesis in hybrids of wild derived strains of this species.

MATERIAL AND METHODS

The *D. sturtevanti* strains used in this study are described below according their geographical occurrence.

Material. MEXICO, **Veracruz**: Apazapan (APA), 19°11'N-96°10'W; **São Luis de Potosí**: Matlapa (MAT), 22°10'N-101°00'W, J.C. Silva col. (University of Arizona, Tucson, USA). COLOMBIA, Villavicencio (COL), 4°09'N-73°38'W, derived from stock "H193.3" (The Genetics Foundation University of Texas, Austin, USA). BRAZIL, **Minas Gerais**: Santana do Riacho (I_{27}), 19°00'S-44°00'W, C. R. Vilela col. (Universidade de São Paulo, São Paulo, SP); **São Paulo**: Mirassol (BRA), 20°47'S-49°28'W, W. J. Tadei col. (Universidade Estadual Paulista (UEP), São José do Rio Preto, SP); São José do Rio Preto (RP_1, RP_2), 20°50'S-49°20'W, L. M. Almeida col. (UEP); 20°60'S-49°18'W, F. R. Torres col. (UEP); Novo Horizonte (NHO), 21°29'S-49°18'W, F. R. Torres col. (UEP); **Rio Grande do Sul**: Maquiné (MAQ), 50°20'S-29°80'W, V. L. V. Gayeski col. (Universidade Federal do Rio Grande do Sul, Porto Alegre, RS).

A variation of the diagnostic A cross (SCHAEFER *et al.*, 1979) was used to evaluate gonadal dysgenesis in *D. sturtevanti*. Since it seems that there is no true M strain (devoid of *P* elements) in this species, we used COL as the reference strain assuming to be a M'-like strain, in which *P* elements apparently lack the ability to transpose and present low P-activity and high P-susceptibility. Diagnostic crosses were made between COL females and males of each strain (intercrosses I) in order to evaluate the P-activity and the reciprocal ones (intercrosses II) for evaluating P-susceptibility. Intra-population sterility was measured as a control.

Twenty virgin couples, four day old, were kept in bottles with fresh corn-wheat-arrowroot medium for seven days at an inducing gonadal dysgenesis temperature of 27ºC (ENGELS & PRESTON, 1979; KIDWELL & NOVY, 1979), and then discarded. The newly emerged flies were maintained at 25ºC for three days and after this period, 70 couples of each cross were individually put in vials at 25ºC for female oviposition. After seven days, these vials were observed for the presence or absence of larvae and each female and male

were dissected in order to investigate gonadal abnormalities. Gonadal dysgenesis indices (GD) of a cross were calculated as the proportion F_1 individuals with one or both dysgenic gonads divided to normal individuals. Two GD indices were calculated for females: GD1, a stricter index, considers as dysgenics only completely reduced ovaries, unilaterally or bilaterally, and GD2, which considers as dysgenic ovaries with dimensions reduced to at least 25% of normal (Schaefer *et al.*, 1979). After the emergence, productivity as the number of flies in F_2 generation was recorded.

Chi-square test (X^2) of heterogeneity was made to compare the strains according to the number of individuals with normal and dysgenic gonads. Analysis of variance was made to evaluate the homogeneity of the productivity means and test of Tukey for multiple comparisons was made to evaluate the differences among means (Zar, 1984).

RESULTS

The gonadal dysgenesis indices for females varied from zero (most of crosses) to 8.57% (males COL with females I_{27}) and from zero (several crosses) to 25.71% (males I_{27} with COL females), respectively GD1 and GD2. Males showed lower GD's than females, with values varying from zero to 2.85% in offspring of intracrosses of RP_1. The X^2 values showed significant differences only among F_1 females of intercrosses II (GD1) and irrespective of the direction of the crosses in the case of GD2 (tab. I).

In order to compare the mean number of offspring produced by each F_1 couple in intracrosses and its reciprocal intercrosses (tab. II), the means values were arranged in eight groups of comparisons in increasing order of four values to compare productivity of intra-crosses to the reciprocal intercrosses. The mean number of flies in intracrosses, mainly of COL, I_{27} and MAQ (12.37; 7.27 and 8.84 flies, respectively) were inferior to the respective intercrosses (35.99; 35.07 and 22.79 flies, respectively) as well as were significantly different the four means of each group of comparisons (test of Tukey, $p<0.01$). Hybrids originated from crosses between COL females and APA males and those originated from crosses between COL and MAT, BRA and RP_2 flies, irrespective of the direction of the crosses, produced one of the highest productivities ($p< 0.01$). However, the mean of COL females-I_{27} males hybrids presented smaller productivity ($p<0.01$) compared to their reciprocal crosses.

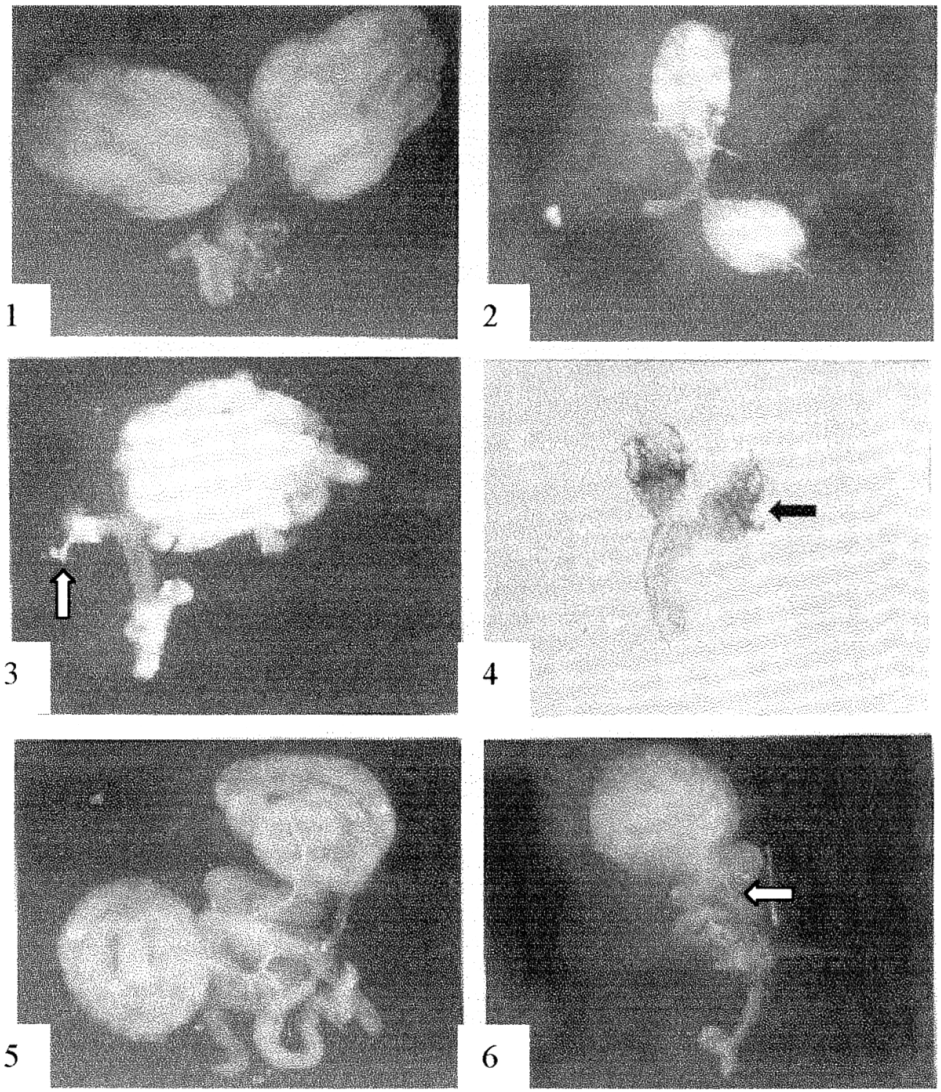
DISCUSSION

The phenomena of hybrid dysgenesis now analyzed, was previously observed in *D. sturtevanti* by Sena & Carareto (1997) and Almeida (2000). This study aimed to test the hypothesis that this phenomenon was due to *P* element mobilization. All the intra and interbreedings produced GD1 indices were inferior to 5% allowing classifying the strains as stable, as defined by Quenesville & Anxolabéhère (1997). The cross between males I_{27} and females COL was an exception; the hybrid dysgenesis index was higher than this value (8.57%). The GD2 indices were also low (< 6%) in all the crosses, excepting again the offspring of COL strain: GD2 was higher than that value in its intracross (7.85%), and in its hybrids with the strain I_{27} (intercrosses I 25.71% and II 12.87%).

P element transposition was a possible explanation for the phenomena of hybrid dysgenesis. The P-M system of hybrid dysgenesis is mostly asymmetric and the reciprocal crosses are non-dysgenic. This asymmetry is characteristic of crossings between a true M strains (devoid of P elements) and a strong *P* strains but have been also observed absence of any significant difference in regulatory ability in reciprocal crosses between the true M

Table I. Dysgenesis in offspring of intra and interstrain crosses of *Drosophila sturtevanti* raised at 27°C. Number of individuals with bilateral dysgenic ovaries and testis, Bi; normal ovaries and testis, N; rudimentary ovaries, RU; unilateral dysgenic ovaries and testis, UNI; index of dysgenesis, GD; without including rudimentary ovaries, GD1; including rudimentary ovaries, GD2; **, $p < 0.01$.

Crosses	Females				Males			Females(%)		Males(%)
	N	Uni	Bi	RU	N	Uni	Bi	GD 1	GD 2	GD
Intracrosses female male										
COL *vs* COL	70	0	0	5	70	0	0	0	7.85	0
APA *vs* APA	70	0	0	0	70	0	0	0	0	0
MAT *vs* MAT	70	0	0	1	70	0	0	0	1.42	0
I_{27} *vs* I_{27}	70	0	0	2	68	1	1	0	2.86	2.14
BRA *vs* BRA	70	0	0	2	68	2	0	0	2.86	1.42
RP_1 *vs* RP_1	68	0	2	0	68	0	2	2.85	2.86	2.85
NHO *vs* NHO	70	0	0	1	70	0	0	0	1.43	0
RP_2 *vs* RP_2	70	0	0	0	70	0	0	0	0	0
MAQ *vs* MAQ	70	0	0	2	68	2	0	0	2.86	1.42
X^2 (Uni *vs* Bi)			15.94				21.11			
X^2 (Uni *vs* Bi *vs* RU)			31.31							
Intercrosses I female male										
COL *vs* APA	70	0	0	0	69	1	0	0	0	0.71
COL *vs* MAT	70	0	0	0	69	1	0	0	0	0.71
COL *vs* I_{27}	70	0	0	18	70	0	0	0	25.71	0
COL *vs* BRA	70	0	0	0	70	0	0	0	0	0
COL *vs* RP_1	69	0	1	3	69	1	0	1.42	5.71	0.71
COL *vs* NHO	69	1	0	1	70	0	0	0.71	2.14	0
COL *vs* RP_2	70	0	0	1	70	0	0	0	1.42	0
COL *vs* MAQ	69	1	0	2	70	0	0	0.71	3.57	0
X^2 (Uni *vs* Bi)			13.03				5.27			
X^2 (Uni *vs* Bi *vs* RU)			100.33**							
Intercrosses II female male										
APA *vs* COL	70	0	0	0	70	0	0	0	0	0
MAT *vs* COL	70	0	0	0	70	0	0	0	0	0
I_{27} vs COL	61	6	3	3	70	0	0	8.57	12.87	0
BRA *vs* COL	70	0	0	0	70	0	0	0	0	0
RP_1 *vs* COL	70	0	0	0	70	0	0	0	2.86	0
NHO *vs* COL	70	0	0	0	69	1	0	0	2.86	0.71
RP_2 *vs* COL	70	0	0	0	69	0	1	0	0	1.42
MAQ *vs* COL	69	1	0	0	70	0	0	0.71	0.71	0
X^2 (Uni *vs* Bi)			57.30**				14.02			
X^2 (Uni *vs* Bi *vs* RU)			70.60**							



Figs. 1-6**.** Phenotypes suggestive of gonadal dysgenesis in *Drosophila sturtevanti*: 1, normal ovaries; 2, rudimentary ovaries; 3, unilaterally dysgenic ovaries; 4, bilaterally dysgenic ovaries; 5, normal testis; 6, unilaterally dysgenic testis. Arrows indicate abnormalities. Magnification 40X (figs.1,3,5,6); 63X (figs. 2, 4).

Table II. Mean productivity and comparisons of means in eight groups of *Drosophila sturtevanti* crosses. Groups of comparisons: intra and intercrosses between females (*f*) and males (*m*): COL and APA(1); COL and MAT (2); COL and I_{27} (3); COL and BRA (4); COL and RP_1 (5); COL and NHO (6); COL and RP_2 (7) and COL and MAQ (8). F for homogeneity of means; W for analysis of Tukey at p=0.05; **, p<0.01 (COL, Colômbia; APA, Apazapan; MAT, Matlapa; I_{27}, Santana do Riacho; BRA, Mirassol; RP_1, São José do Rio Preto; NHO, Novo Horizonte; RP_2, São José do Rio Preto; MAQ, Maquiné).

Groups	Crosses				$F_{3.276}$ $W_{0.05}$
1	*f*COL *vs m* COL	*f*APA *vs m* APA	*f*APA *vs m* COL	*f*COL *vs m* APA	$F_{3.276}$=30.95**
$\bar{x}$ ± SE	12.37 ± 13.22	23.89 ± 16.72	25.96 ± 14.23	35.99 ± 13.86	$W_{0.05}$= 6.32
2	*f*COL *vs m* COL	*f*MAT *vs m* COL	*f*COL *vs m* MAT	*f*MAT *vs m* MAT	$F_{3.276}$=17.68**
$\bar{x}$ ± SE	12.37 ± 13.22	28.86 ± 17.86	29.79 ± 19.22	33.06 ± 22.35	$W_{0.05}$= 8.01
3	*f*COL *vs m* I_{27}	*f*I_{27} *vs m* I_{27}	*f*COL *vs m* COL	*f*I_{27} *vs m* COL	$F_{3.276}$=58.13**
$\bar{x}$ ± SE	6.88 ± 8.34	7.27 ± 12.36	12.37 ± 13.22	35.07 ± 21.48	$W_{0.05}$= 6.36
4	*f*COL *vs m* COL	*f*BRA *vs m* BRA	*f*BRA *vs m* COL	*f*COL *vs m* BRA	$F_{3.276}$=26.94**
$\bar{x}$ ± SE	12.37 ± 13.22	16.0 ± 15.24	28.11 ± 17.02	31.37 ± 13.21	$W_{0.05}$= 6.40
5	*f*COL *vs m* COL	*f*COL *vs m* RP_1	*f*RP_1 *vs m* COL	*f*RP_1 *vs m* RP_1	$F_{3.276}$=16.37**
$\bar{x}$ ± SE	12.37 ± 13.22	14.54 ± 11.04	16.93 ± 12.96	27.03 ± 15.92	$W_{0.05}$= 5.82
6	*f*COL *vs m* COL	*f*NHO *vs m* COL	*f*NHO *vs m* NHO	*f*COL *vs m* NHO	$F_{3.276}$=15.65**
$\bar{x}$ ± SE	12.37 ± 13.22	15.77 ± 12.89	25.79 ± 17.27	25.83 ± 14.73	$W_{0.05}$= 6.35
7	*f*COL *vs m* COL	*f*RP_2 *vs m* COL	*f*COL *vs m* RP_2	*f*RP_2 *vs m* RP_2	$F_{3.276}$=15.76**
$\bar{x}$ ± SE	12.37 ± 13.22	18.76 ± 15.25	21.84 ± 15.72	27.44 ± 18.75	$W_{0.05}$= 6.87
8	*f*MAQ *vs m* MAQ	*f*COL *vs m* COL	*f*COL *vs m* MAQ	*f*MAQ *vs m* COL	$F_{3.276}$=13.67**
$\bar{x}$ ± SE	8.84 ± 16.19	12.37 ± 13.22	12.81 ± 8.66	22.79 ± 14.93	$W_{0.05}$= 5.88

and M' strains (KIDWELL, 1985) or incomplete asymmetry in intercrosses of moderate or weak P with M strains (BOUSSY, 1987; BOUSSY & KIDWELL, 1987; VETORAZZI *et al.*, 1999). *P* element transposition in species another than *D. melanogaster* is not completely unexpected. DANIELS *et al.* (1990) injected a *D. willistoni* Sturtevant, 1916 *P* element into *D. melanogaster* embryos and demonstrated that it was functional and capable of providing the trans-acting product necessary for mobilization of non-autonomous *P* elements.

In all hybrids, except those between the COL and I_{27} strains, the GD sterility was very low and we could exclude *P* element mobilization. To impute this gonadal dysgenesis to *P* elements transposition we have to assume the existence of at least one complete and functional *P* element in COL and I_{27} strains, but both with poorly regulatory cytotype.

The presence of a fragment of a 2.9 kb *P* element sequence was amplified by PCR in all nine strains analyzed in this study (L. M. Almeida, personal communication) suggesting that *D. sturtevanti* bears at least one copy of a putative complete *P* element. If *P* elements were transposing in these strains, also we would expect reduction of productivity in intercrosses of female COL, males of each strain when compared of their respective

intra and reciprocal intercrosses, but most of the intercrosses did not show it. Productivity of the F_1 hybrids was intermediate or even higher than productivity of one or both parental strains, as expected from the heterozygosys *per se*. But, productivity of hybrids from COL females - I_{27} males was the smallest one. However, the reciprocal cross showed one of the highest productivity.

Despite the existence of putative complete *P* elements in this species and moderate ovarian dysgenesis (GD2 indices) in COL - I_{27} no causal relationship between the observed gonadal dysgenesis and *P* element transposition might effectively be established because the phenotypes are not completely characteristic of the P-M system: the GD1 indices were very low and the GD2 were not asymmetric.

Since the strength of the phenomena occurs if we consider both the occurrence of rudimentary ovaries and low productivity, we could propose *I* transposable element as the causal agent. Dysgenic crosses between females lacking *I* elements (R females) with males bearing active *I* elements (I males) arisen females with reduced fertility and reciprocal cross normal (Busseau *et al.*, 1994). However, the progeny of male COL mated to I_{27} female presented the highest GD indices (1 or 2) but the second highest productivity. These results and the fact that all the symptoms in IR system occur only in females led us to exclude *I* element as the agent of hybrid dysgenesis.

Moderate and almost symmetric gonadal dysgenesis was also observed in both intercrosses involving an old laboratory stock and a freshly collected strain of *D. willistoni* (Regner *et al.*, 1999). Based on the absence of asymmetry, the authors concluded that the phenomena, in spite of presenting a morphology very similar to that found in *D. melanogaster*, could be due not to a *P* element transposition but to an unknown element harbored exclusively by some natural populations of *D. willistoni*, or to several unrelated transposable elements. The gonadal dysgenesis observed in *D. sturtevanti* and *D. willistoni* looks to be very similar and probably due to the same causes.

Other possibility is to impute to *hobo* element the occurrence of hybrid dysgenesis in *D. willistoni* and the *D. sturtevanti* since it induces high mutability and gonadal sterility in both reciprocal crosses between strains of *D. melanogaster* H (carrying *hobo*) and E (devoid of *hobo*). Although Daniels *et al*. (1990) reported the absence of *hobo* in the *saltans* group of *Drosophila*, its occurrence has been shown in *D. willistoni* (Loreto *et al.*, 1998). Although PCR amplification had suggested its occurrence also in *D. sturtevanti* and *D. prosaltans* Magalhães, 1956, sequencing analysis of these products did not confirm the occurrence of *hobo* in the *saltans* group of *Drosophila* (J. P. Castro, personal communication). As proposed by Regner *et al*. (1999) in *D. willistoni,* there are unknown transposable elements, or even symbiontic microorganisms such as *Wolbachia*, that cause hybrid sterility in *Drosophila* (Jiggin *et al*., 2001) and could be responsible for such a phenomena.

This is the first report of hybrid dysgenesis in natural populations of the *D. sturtevanti*. Despite no causal relationship between the observed gonadal dysgenesis and *P, I* and *hobo* elements element transposition might effectively be established, the abnormalities observed in hybrids of two strains COL I_{27} strains and indicates the occurrence of genomic stress that could be due to transposable elements mobilization.

The results here discussed show that additional studies are necessary to understand the hybrid dysgenesis observed in *D. sturtevanti* and *D. willistoni* species. Independent of the causal agent, hybrid dysgenesis is an important phenomenon to be observed in interpopulational hybrids since it might act as the first step of the reproductive isolation.

Different populations of a single species might accumulate different transposable element families, each having the potential for partial hybrid sterility in interpopulational hybrids (KIDWELL, 1983). On regaining sympatry, the combined effect of hybrid dysgenesis resulting of the destabilization of multiple transposable element families might, given the sufficient divergence time, result in reproductive isolation.

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