Studies of the Genetics and Expression of Prowing (Pw): A Primitive Homeotic Mutant of the German Cockroach, Blattella germanica

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Studies of the Genetics and Expression of Prowing (*Pw*): A Primitive Homeotic Mutant of the German Cockroach, *Blattella germanica*

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ABSTRACT—The prowing, T (9; 10)/9; 10 *Pw*, is a homeotic mutant of the German cockroach, *Blattella germanica*. Adults are characterized by winglike extensions from the pronotum. This trait is associated with a reciprocal translocation of chromosomes 9 and 10. Translocation heterozygotes express the trait and homozygotes are lethal. The expression of *Pw* is variable in adults. Individuals with excellent expression show that the pronotal extension is undoubtedly a primitive wing, judging from its venation. We crossed adults with different degrees of expression and found that crosses between parents with excellent expression tended to produced F_1 with excellent expression and those with poor expression produced F_1 with poor the expression. This suggests that more than one factor is involved in the expression of the trait, and that the different expressions cannot be due to different "expressivity". We also found that the expression *Pw* was greatly reduced when prowings were crossed with the Nara wild strain, although this did not happen when they were crossed with individuals with wild-type expression from the *Pw* strain. This suggests that at least one more factor participates in the expression of *Pw*. We observed meiosis clearly even in the adult stage. We examined many male adults and confirmed that the reciprocal translocation cause *Pw* expression without an exception. We also observed the frequencies and stages of embryonic death of F_1 from both *Pw* and *Pw* × wild type parents. The results agreed well with the ratio between alternate and adjacent disjunction at metaphase I. *Pw* individuals tended to be delay in nymphal development compared with the wild type.

INTRODUCTION

The *Pw* was first described by Ross (1964), and has been maintained in the Genetic Stock Center for the German Cockroach in the Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA., USA. Genetic studies showed that *Pw* is inherited as an autosomal, semi-dominant lethal trait (Ross and Cochran, 1965). Subsequently, it was discovered that *Pw* is associated with a reciprocal translocation between chromosomes 9 and 10, T(9; 10)/9; 10 *Pw* (Cochran and Ross, 1969). Because pronotal winglets also characterize a deficiency of chromosome 9, it is thought that the trait is associated with the breakage of chromosome 9, (Ross and Cochran, 1971). *Pw* is characterized by winglike-expansion of the pronotum in the adult stage and a trancheal pattern like that of the meso- and metathoracic wing buds in nymphs. The prowing resembles the paranotal lobes of ancestral insects. Fossil evidence indicates that extinct pterygotes had wing on every thoracic and abdominal segment (Kukalova-Peck, 1978; Carroll *et al.*, 1995). This mutant of the German cockroach is very interesting, since it is a rare case of extant insects bearing a pair of prothoracic wings. It is known that the expressivity of *Pw* is variable; some individuals have large protrusions that look like wings but others bear only tiny protuberances. However, this expressivity has not been studied quantitativively. Studies of the expressivity may reveal the factors that are involved in the expression of the trait. The purpose of the present study was to examine the combinations of crosses of individual cockroaches with different expressions of *Pw* and to investigate the meiocytes of the translocation heterozygotes. These date will serve as a foundation for future studies using this variable mutant.

MATERIALS AND METHODS

Maintenance of stock

Translocation heterozygotes T(9; 10)/9; 10 *Pw* are characterized by pronotal winglets. The homozygote is lethal. Thus, both crosses (*Pw*/+ × *Pw*/+ and *Pw*/+ × +/+) can be used for maintenance of the stock. The former cross results in *Pw*/+ : +/+ $\fallingdotseq$ 2:1 in the ratio of offspring, but embryonic trapping caused by neighboring dead embryos due to lethal *Pw*/*Pw* and adjacent disjunction increases the frequency of embryonic death. The latter cross results in a high percentage of viable offsprings, but the ratio of +/+ increases. Therefore, we used both crosses to maintain the stock. Newly molted adult males with +/+ expression were eliminated twice a week, because males can copulate about 4 days after adult ecdysis. This means that

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both crosses (*Pw*/+ male × *Pw*/+ female) and (*Pw*/+ male × +/+ female) take place in the stock container. The simple energy-saving method may be the best way to maintain the *Pw* stain.

Crosses

Newly molted adults were used for crosses in most cases. All females used were newly molted adults of the males, newly molted adults were preferably used as parents. However, a few males with degrees of *Pw*1 and *Pw*2 (see below) in *Pw* expression were used from the stock container, because these degrees were relatively rare and it is sometimes difficult to achieve good timing for mating only newly molted males were to be used. The *Pw* expression of the parents was categorized into 4 grades: poor (*Pw*1), intermediate (*Pw*2), good (*Pw*3) and excellent (*Pw*4). Individuals with completely wild type expression from the *Pw* strain were also used (*Pw*+). Nara wild individuals (Nara) were also mated with every expression (*Pw*+ - *Pw*4) of the *Pw* strain. For the judgment of F_1 expression, degrees were classified into 7 grades: *Pw* 0, 1⁻,1, 2, 3, 4 and 4⁺; in addition to the grades used in the parents, the two grades of marginally poor (1⁻) and exceptional (4⁺) were added. In the calculation of the average, the degrees of Pw expression 1⁻, 1, 2, 3, 4, and 4⁺ were given the values 0.5, 1, 2, 3, 4, and 4.5, respectively. To identify the stage of embryonic death, the developmental table of the German cockroach was used (Tanaka, 1976).

Chromosome observation

The testes of the fourth to the last instars and adults were observed. The testes were dissected and then immersed in water for 5 min. to make them swell. The left and right testes were placed separately in droplets of 15% acetic acid on a glass slide, and excess fat body was removed from the testes forceps. The testes were stained with acetic orcein less than 5 min, covered with a cover glass, and pushed gently with the head of a forceps; the excess orcein was thus soaked up. Each testis was then wrapped with tissue paper, put upside down and, pushed forcefully by the examiner's thumb from behind the slide to flatten the testis. Fingernail polish was then spread along the edge of the cover glass. The specimen was observed with a phase contrast microscope.

RESULTS

The expressivity of *Pw* in adults was variable. Expression was often similar between the left and right sides, as shown in Fig. 1, but sometimes differed between the sides. Individuals without the translocation (+/+) in the *Pw* stock showed wild type expression, as in Fig. 1a. The translocation heterozygotes showed a large variety of *Pw* expression (Fig. 1b-f). A few *Pw* individuals in the *Pw* stock showed still poorer expression, designated as (1⁻), which was often encountered in the heterozygotes outcrossed to the Nara wild strain. Close examination confirmed the finding of Ross (1964) that postero-lateral protrusions of the pronotum are serially homologous with wings and similar to structures in early fossil insects, although sometimes this seemed doubtful in gross examinations, especially when the degree of expression was poor. Figure 2 shows that veins occur in pronotal winglets like those of the wing (also see Ross 1964, Fig. 5c-d).

Table 1 shows the percentages of *Pw* expression in F_1 individuals between parents with various expression of *Pw*. Crosses between phenotypical wild type siblings of *Pw* resulted in no F_1 with *Pw* expression. Reciprocal crosses between Nara wild strain and *Pw*+ also resulted in no *Pw* expression in the

F_1. The percentages of *Pw* individuals from crosses between the Nara wild and *Pw* strain with *Pw* expression fluctuated in the range from 41.0% to 53.3% by the degrees of *Pw* expression. The average of these was 46.6%, nearly equal to the expected 50%. The percentages of *Pw* from crosses within the *Pw* strain between wild type siblings and *Pw* (*Pw* 1~4) ranged from 46.5% to 57.6%. The average was 52.3%, also nearly equal to the expected 50%. The percentages of *Pw* from crosses between parents with *Pw* expression fluctuated from 59.4% to 83.3% by the degrees of expression. The average of 16 combinations was 72.1% *Pw*, close to the expected value, 69% (see Discussion).

In order to study the *Pw* expressivity between P_1 and F_1, crosses of various degrees of expression were carried out. Individuals showing the typical degrees +~4 (Fig. 1) were selected as parents. The Nara wild strain was also used as a control of the outcross. In the observation of F_1, besides the typical degrees 1~4, very poor expression (*Pw*1⁻) and exceptional (*Pw*4⁺) were encountered. Therefore, in the calculation of the average expression, *Pw*1⁻ and *Pw*4⁺ were given the values 0.5 and 4.5, and *Pw*1 to *Pw*4 were assigned the values 1 to 4, respectively. Table 2 summarizes the results of these crosses. In the experiment with parents both with *Pw* expression, *Pw*4 × *Pw*4 resulted in the highest average value (3.53), but less than the parental value of 4. Likewise, *Pw*4 × *Pw*3 resulted in the value 3.26, the reciprocal average of 101 offspring (61 from *Pw*3 male × *Pw*4 female and 40 from *Pw*3 female × *Pw*4 male). The value from the *Pw*3 × *Pw*3 cross (2.85) was nearly equal to that of the reciprocal averages of *Pw*4 × *Pw*2 (3.01). The next highest values appeared in the reciprocal averages of *Pw*3 × *Pw*2 (2.85) and *Pw*4 × *Pw*1 (2.55). These values were almost equal to the average of the parents. The value of *Pw*2 × *Pw*2 was 2.28, and the reciprocal average of *Pw*3 × *Pw*1 was 2.38; both values were slightly higher than the values of the parental average. The next lowest value was found in the *Pw*2 × *Pw*1; the reciprocal average was 1.78, also somewhat higher than that of the parents. The lowest average (1.50) was from the *Pw*1 × *Pw*1 cross; this value was higher than that of the parents. In the crosses between *Pw* and wild type siblings (*Pw*+), the reciprocal averages of *Pw*+ × *Pw*1, *Pw*+ × *Pw*2, *Pw*+ × *Pw*3, and *Pw*+ × *Pw*4 were 1.88, 2.42, 2.29, and 3.01, respectively. These values did not suggest any inhibitory factors of *Pw* expression from *Pw*+ parents, especially in the crosses of *Pw*+ × *Pw*1, and *Pw*+ × *Pw*2. In contrast, when *Pw*1, *Pw*2, *Pw*3, and *Pw*4 were outcrossed to the Nara wild strain, the reciprocal averages much lower, i.e., 0.92, 1.18, 1.24, and 1.08, respectively, suggesting that the Nara wild strain has inhibitory factor(s) on *Pw* expression. The F_1 of Nara wild × *Pw*+, and *Pw*+ × *Pw*+ all showed wild type expression, as expected.

Table 3 shows the percentages of hatching and deaths at various embryonic stages. Both crosses of Nara wild × *Pw*+ and *Pw*+ × *Pw*+ resulted in high percentages of hatching. The former showed the normal percentage of the Nara wild standard. In the latter, a few embryos (3.42%) died before stage 12; the reason for this unknown. There were no
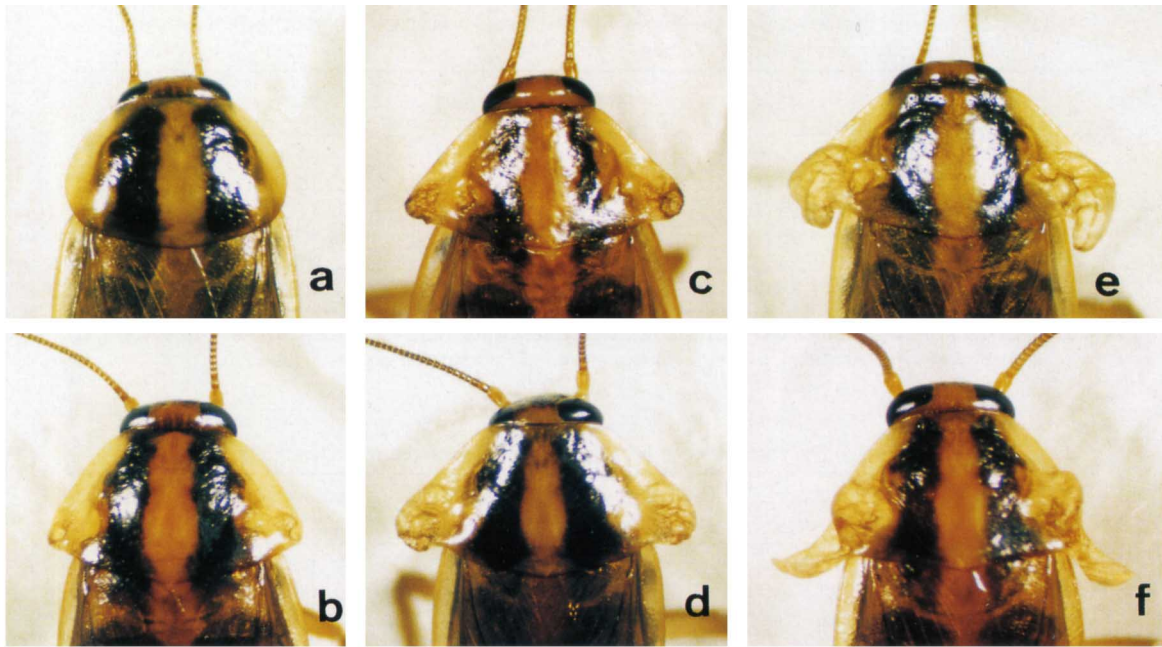
Fig. 1. Wild type (**a**) and various expressions of *Pw*. Degrees of 1~4⁺ (**b**)~(**f**), respectively. 1, poor; 2, intermediate; 3, good; 4, excellent; 4⁺, exceptional.
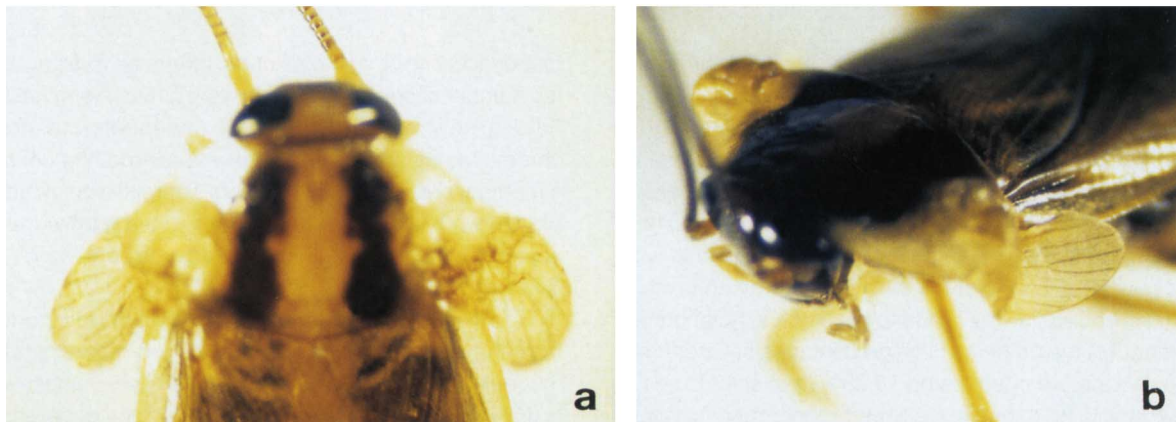

Fig. 2. Evidence that a pronotal protrusion is actually a small wing, judging from its venation.

Table 1. The percentages of *Pw* individuals in F_1 from crosses with various degrees of *Pw* expression, including outcrosses to Nara wild strain

♂＼♀	Nara	Pw+	Pw1	Pw2	Pw3	Pw4
Nara	——	0.0 (277)	41.9 (160)	48.4 (128)	49.7 (173)	53.3 (122)
Pw+	0.0 (290)	0.0 (247)	57.6 (118)	51.8 (193)	48.0 (148)	46.5 (157)
Pw1	44.4 (216)	57.1 (119)	83.3 (54)	65.3 (72)	69.7 (109)	75.0 (68)
Pw2	41.0 (173)	48.8 (160)	59.4 (69)	72.7 (66)	75.6 (90)	77.6 (67)
Pw3	44.3 (183)	56.7 (171)	71.2 (52)	80.9 (68)	71.6 (102)	77.2 (79)
Pw4	51.1 (219)	54.1 (146)	67.0 (94)	69.9 (73)	72.7 (55)	68.7 (67)

Numbers of F_1 that reached adulthood are shown in parentheses. Nara, Nara wild strain; *Pw+*, wild-type expression of *Pw* stock; *Pw1*, *Pw2*, *Pw3* and *Pw4*, degrees 1-4 expression of *Pw* stock, respectively (see Fig. 1).

Table 2. Average degrees of *Pw* expression in F_1 from crosses with various degrees of *Pw* expression, including outcrosses to Nara wild strain

♂ \ ♀	Nara	Pw+	Pw1	Pw2	Pw3	Pw4
Nara	–	– (0)	0.84 (67)	1.05 (62)	1.24 (86)	1.25 (65)
Pw+	– (0)	– (0)	1.46 (68)	2.79 (100)	2.16 (71)	3.18 (73)
Pw1	0.98 (96)	2.29 (68)	1.50 (45)	1.81 (47)	2.17 (76)	2.64 (51)
Pw2	1.30 (71)	1.95 (78)	1.74 (41)	2.28 (48)	2.46 (68)	3.19 (52)
Pw3	1.25 (81)	2.39 (97)	2.82 (37)	2.73 (55)	2.85 (73)	3.15 (61)
Pw4	0.98 (112)	2.85 (79)	2.48 (63)	2.82 (51)	3.43 (40)	3.53 (46)

Numbers of F_1 with *Pw* expression are shown in parentheses. Nara, Nara wild strain, *Pw+*, wild-type siblings of *Pw*; *Pw1*, *Pw2*, *Pw3* and *Pw4*, degrees 1-4 expression of *Pw* stock, respectively (see Fig. 1).

Table 3. The percentages of embryos hatched or died at various stages

cross	Total number of embryos	died before or at st. 12[a] (%)	died at st. 13 to st. 17[b] (%)	embryonic trapping[c] (%)	hatched (%)
Nara × Pw+	575	0.52	0.35	0	99.13
Pw+ × Pw+	263	3.42	0	0	96.58
Nara × Pw1-4	2039	29.08	0.59	1.37	68.96
Pw+ × Pw1-4	1862	29.05	1.34	1.24	68.37
Pw1-4 × Pw1-4	4086	48.21	10.33	11.04	30.42

Data of reciprocal crosses of both sexes were combined, because no significant differences were found.
[a] eyes are not observable through the surface of ootheca.
[b] eyes observable through the surface of ootheca (Tanaka, 1976).
[c] embryos trapped by oothecae at hatching.

significant differences between Nara wild × *Pw* (1~4) and *Pw+* × *Pw* (1~4) in the percentages of hatching and embryonic death, in spite of great differences in *Pw* expression (Table 2). Both crosses showed about 68% hatching, very close to the theoretical value, 67% (see Table 4). The embryonic death rate before stage 17 was about 30%, also close to the theoretical value (33%). In the crosses between parents with *Pw* expression (1~4), 11% of the embryos died by embryonic trapping (Keil and Ross, 1977) due to the death in neighboring compartments of the ootheca. High percentages of embryonic death, 48.21% before or at 12 and 10.33% from st.13 to st.17, caused siblings to fail to hatch due to embryonic trapping within the ootheca. The percentage of hatching including those of embryonic trapping reached about 41%, close to the theoretical value, 36% (see Discussion). The total death rate by stage 17 was about 59%, also close to the theoretical value (64%).

The diploid number of chromosomes of *Blattella germanica* females is 2n = 24, XO type (Suomalainen, 1946). We found that meiosis is easily observable, even in the adult stage. We examined many testes of adult males with or without *Pw* expression, and found that all translocation heterozygotes show *Pw* expression and all wild type zygotes have wild type pronota. Figures 3 and 4 show some comparisons between translocated and wild type meiocytes. There was a clear difference at the diplotene stage. Eleven paired chromosomes and an X chromosome were always found in the wild type (Fig. 3a), whereas configurations typical of reciprocal translocations were always found in the *Pw* males (Fig. 3b). At diakinesis in the wild type, 12 groups of chromosomes were

found including X, some as rings, others as rods, according to the number of chiasmata which were already terminalized (Fig. 3c). In contrast, in the *Pw* at diakinesis, 11 groups of chromosomes were found; one was a large ring consisting of 4 member chromosomes (Fig. 3d). The wild type at metaphase I is shown in Fig. 4a. The *Pw* meiocytes showed either the adjacent type of disjunction (Fig. 4b) or the alternate type (Fig. 4c), as described by Cochran (1977).

Table 4 shows all possible combinations of chromosomes from the matings between translocation heterozygotes. The theoretical average percentage of such undeveloped embryos is 64% (both parents are *Pw/+*) or 33% (one of parents is +/+) if the alternate:adjacent ratio is 2:1, the same ratio as in the testis and ovary. Dead embryos were easily distinguished from normal ones. Figure 5 shows some examples of oothecae including such embryos together with normal ootheca. Figure 5a is a normal wild type ootheca. An advanced- stage embryo can be seen in each compartment. When one of the parents was *Pw*, about 1/3 of the embryos died during embryonic development (Fig. 5b). About 2/3 of the embryos died when both parents were *Pw* (Fig. 5c).

We compared the period of nymphal development between individuals with various degrees of *Pw* expression and wild type expression (Table 5). The total period from hatching to adult ecdysis was recovered in all individuals. Siblings from the same ootheca were divided into groups: reaching adulthood in the first half period among the siblings, and reaching adulthood in the last half period. The date of the individuals from all oothecae in each type of cross are
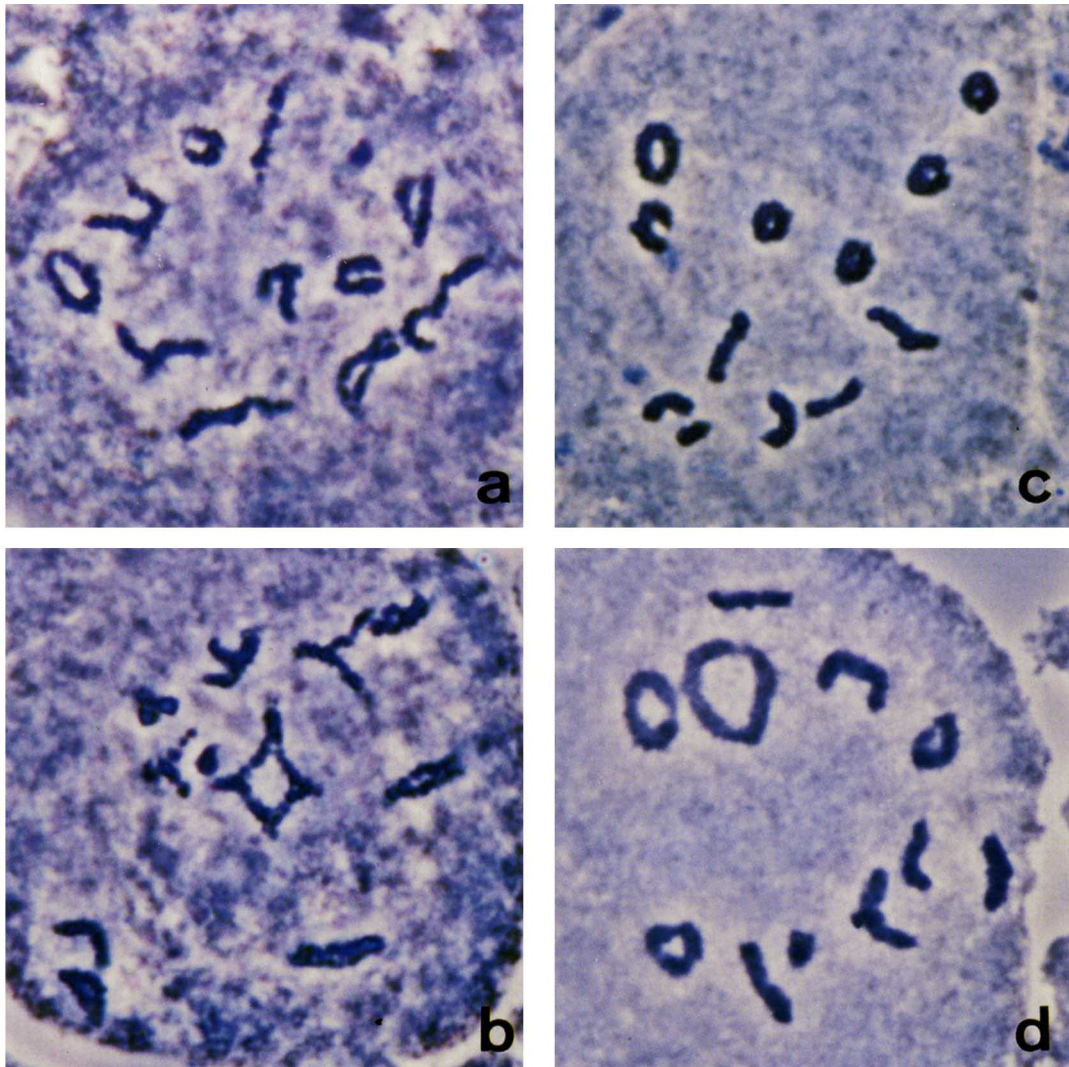
Fig. 3. Meiosis I of *Blattella germanica* (n=12). (**a**) and (**b**), diplotene~early diakinesis; (**c**) and (**d**), diakinesis; (**a**) and (**c**), wild type; (**b**) and (**d**), prowing. A diamond shape (**b**) and a large ring (**d**) show reciprocal translocation.
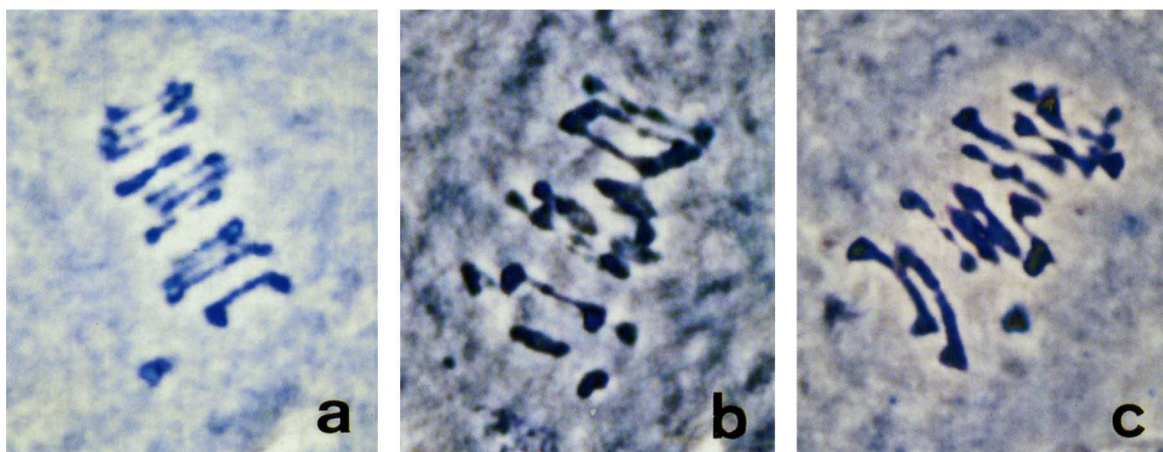

Fig. 4. Metaphase I of *Blattella germanica*. (**a**) wild type; (**b**) prowing, adjacent disjunction (rectangle-shaped); (**c**) prowing, alternate disjunction (Z-shaped in the center of the photo).

Table 4.   Zygotic combination from every disjunction type of gamete in the crosses between translocation heterozygotes, T(9; 10)/9: 10 Pw

sperm egg	Alternate		Adjacent			
	ab 4	t_1t_2 4	at_1 1	bt_2 1	at_2 1	bt_1 1
ab 4	aabb 16+/+	abt_1t_2 16 Pw/+	$aabt_1$ 4	$abbt_2$ 4	$aabt_2$ 4	$abbt_1$ 4
t_1t_2 4	abt_1t_2 16 Pw/+	$t_1t_1t_2t_2$ 16 Pw/Pw	$at_1t_1t_2$ 4	$bt_1t_2t_2$ 4	$at_1t_2t_2$ 4	$bt_1t_1t_2$ 4
at_1 1	$aabt_1$ 4	$at_1t_1t_2$ 4	aat_1t_1 1	abt_1t_2 1 Pw/+	aat_1t_2 1	abt_1t_1 1
bt_2 1	$abbt_2$ 4	$bt_1t_2t_2$ 4	abt_1t_2 1 Pw/+	bbt_2t_2 1	abt_2t_2 1	bbt_1t_2 1
at_2 1	$aabt_2$ 4	$at_1t_2t_2$ 4	aat_1t_2 1	abt_2t_2 1	aat_2t_2 1	abt_1t_2 1 Pw/+
bt_1 1	$abbt_1$ 4	$bt_1t_1t_2$ 4	abt_1t_1 1	bbt_1t_2 1	abt_1t_2 1 Pw/+	bbt_1t_1 1

a and b indicate chromosome 9 and 10, respectively, in case of T(9; 10)/9: 10 Pw.
t_1 and t_2; two different types of translocated chromosomes.
+/+, wild type; Pw/+, phenotypical Pw; Pw/Pw, homozygotic lethal.
Other combinations are lethal due to an incomplete set of chromosomes.
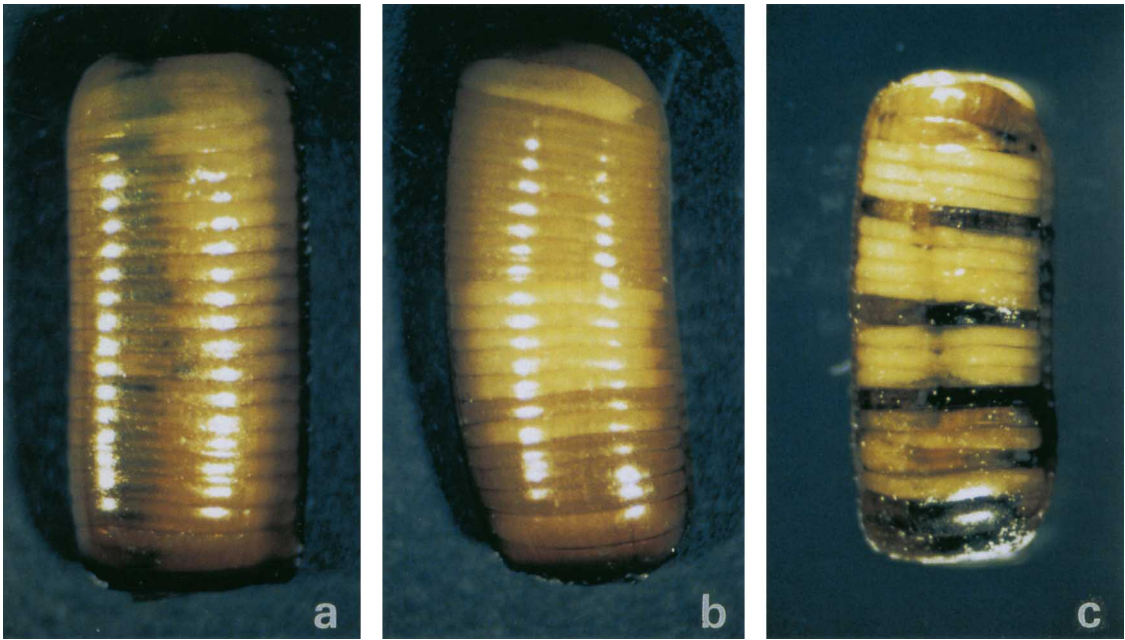Numbers indicate ratios in supposition that alternate: adjacent=2: 1

Fig. 5.   Comparison of oothecae. (**a**) wild type (living); embryos of advanced stage can be seen through the surface of the ootheca in all compartments. (**b**) $Pw \times$ wild type (living); dead embryos (white appearance) are often found (theoretically 33% dead). (**c**) $Pw \times Pw$ (specimen in 80% ethanol); live embryos are dark, dead embryos are light-colored (theoretically 64% dead).

summarized in Table 5. In every type of cross, the wild type individuals tended to grow faster than those with Pw expression. In the cross of Nara wild to Pw, many F_1 with extremely poor expression (1⁻) appeared, and some were delayed in nymphal growth.

DISCUSSION

It was found that the expression of Pw is more or less inheritable (Table 2). Therefore, differences in the expression of Pw cannot be thought of as differences of the expressivity of genetically identical individuals. The date in Table 2 suggests that Pw expression may be related to three or more factors. Since Pw is associated with the breakage of chromosome 9

Table 5. Comparison of nymphal period of F_1 between wild-type and *PW* expression

Cross	No. hatched	No. died before adulthood	No. reached adulthood		+	Pw	(1⁻	1	2	3	4	4⁺)	(Average)*
Nara × Pw 1-4	1406	32	1374	F	422	288	83	116	78	11	–	–	(1.20)
				L	312	352	153	126	62	11	–	–	(1.02)
Pw+ × Pw 1-4	1273	61	1212	F	366	364	8	40	88	88	38	2	(2.44)
				L	212	370	14	54	135	118	42	7	(2.39)
Pw 1-4 × Pw 1-4	1243	58	1185	F	222	425	11	50	123	139	92	10	(2.66)
				L	109	429	8	64	122	166	63	6	(2.54)

F and L, individuals reached adulthood during the first half period, or the last half period, respectively, of the total period of adult molts.
*1⁻, 1, 2, 3, 4 and 4⁺ were given value 0.5, 1, 2, 3, 4 and 4.5, respectively, in calculation.

(Ross and Keil, 1978), the site of chromosome breakage may include one or more inhibitory factor(s) of pronotal wings, because normal gene(s) in the site act as inhibitor(s) to completely suppress the primitive trait. The expression of the F_1 showed a gradient according to that of their parents in the crosses between two parents with *Pw* expression. This finding suggests that more than one factor is involved in *Pw* expression. Some factor(s) might not be in the translocation site. Another factor may exist because the average expression tended to be much less in the outcrosses to Nara wild strain than in the crosses to the +/+ of the *Pw* strain.

It has been believed that the meiosis of cockroaches is rarely encountered in adult testes and should thus be observed during the nymphal stage. We found here that many meiocytes can be frequently observed in the adult testes. The occurrence of early-stage meiocytes in adult males is possibly a reserve for later matings, since the males copulate several times during their life span. We confirmed the findings on *Pw* nymphs (Cochran and Ross, 1969) that individuals with *Pw* expression have translocated chromosomes and those with wild type expression have wild type chromosomes. The penetrance is thus 100%.

The ratios between alternate and adjacent disjunction differ among mutants of translocation heterozygotes. It is known that the frequency of alternate disjunction in the prowing mutant is 63~64% in male nymphs (Cochran and Ross, 1974; Cochran, 1977). Table 4 shows all zygotic combinations with the ratio in supposition that the alternate:adjacent ratio is about 2:1, close to the previous finding in the testes (Cochran and Ross, 1974). The observation of meiocytes in ovaries is almost impossible due to the large amount of yolk. Therefore, the same ratio was assumed in the ovary to make this table. The ratio of +/+:*Pw*/+:*Pw*/*Pw* (lethal):deficiencies (lethal) is 16:36:16:76 under the supposition of alt.:adj.=2:1 in both male and female meiocytes. The percentages are theoretically 11%, 25%, 11%, and 53%, respectively. The average *Pw* expression of F_1 from the *Pw*/+ × *Pw*/+ crosses shown in Table 1 was 72.1%, which agrees well with the theoretical estimates of 69% and 67.1% from an earlier study (Ross and Cochran, 1965). *Pw*/*Pw* may correspond to late embryonic death, and chromosomal deficiency may cause early embryonic death. This supposition also explains the results shown in Table 3

that the incidence of late embryonic death was 10.33% and that of early embryonic death was 48.21%. The first column of Table 4 shows the results that would be expected from matings between *Pw*/+ and +/+. The ratio of offspring of +/+, *Pw*/+, and deficiencies (lethal) are 33% each. Thus, the expected ratio of viable offspring between +/+ and *Pw*/+ is 1:1. This explains the results of Tables 1 and 5 that the frequency of *Pw* was 46.6% in Nara wild × *Pw*/+ and 52.3% in *Pw*/+ × *Pw*/+. Both were close to 50% and agree with the data of Ross and Cochran (1965). The percentages of embryonic death as of stage 17, about 30% in both Nara wild × *Pw*/+ and +/+ × *Pw*/+ (Table 3), are also explained by the date in the first column of Table 4.

From the viewpoint that *Pw* expresses a primitive developmental pathway, it is of interest that the loci of other primitive traits such as notched sternite (*st*) (Ross, 1966), miniature-wing (*min*) (Ross and Keil, 1978), stumpy (*sty*) (Ross, 1975; Tanaka and Ross, 1989), and maxillary-palp-elongate (*mpe*) (Ross and Tanaka, 1988; Tanaka and Ross, 1990) are on the same chromosome. Concerning the origin of insect wings, the pronotal wings of the German cockroach seems to favor the paranotal hypothesis (Hinton, 1963; Rasnitsyn, 1981), although other evidence seems to support the pleural hypothesis (Wigglesworth, 1963; Kukalova-Peck, 1983).

ACKNOWLEDGMENTS

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