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Research Article

Genetically Masked of Dorsocentral Bristle Expression by a Single Dominant Gene *DCm* in Melon Fly, *Zeugodacus cucurbitae* (Coquilett)

Yun Cheng[1], Dong-Hong Wu[2], Zu-Hsien Wang[3], Yu-Bing Huang[4,*], Ming-Yao Chiang[5],
Hsiu-Ying Lu[6], and Chung-Min Yang[3]

Abstract

Cheng, Y., D. H. Wu, Z. H. Wang, Y. B. Huang, M. Y. Chiang, H. Y. Lu, and C. M. Yang. 2020. Genetically masked of dorsocentral bristle expression by a single dominant gene *DCm* in melon fly, *Zeugodacus cucurbitae* (Coquilett). J. Taiwan Agric. Res. 69(2):113–121.

The melon fly, *Zeugodacus cucurbitae* (Coquilett), does not possess the dorsocentral (DC) bristles. In a selected DC (+)-line, two rows of 4–6 median size macrochaetes appeared in the dorsocentral domain of scutum and it is interesting to explore its morphological identity and genetic origin. In morphology, these DC (+) bristles fit into the dorsocentral domains of Diptera chaetotaxy ground plan and those of model insect species, *Drosophila melanogaster* and *Ceratitis capitata*. In genetics, by crossing wild type to DC (+)-line, the majority of F_1 progeny were DC (–) phenotype or wild type. Segregation pattern of DC (+) and DC (–) phenotypes in the F_2 progeny fit a 1 : 3 inheritance pattern, with DC (–) phenotype being dominant. The backcross of F_1 to the DC (+)-line produced a 1 : 1 ratio in respect to DC (+) and DC (–) phenotypes, while F_1 backcross to wild type produced most DC (–) progeny, confirming that DC (+) bristle was suppressed by a single dominant gene. The gene was given the symbol *DCm* for *DorsoCentral bristles masked*. The DC (+) bristle was stereotype patterned instead of randomly expressed, hence the atavistic origin is preferred.

Key words: Dorsocentral bristles, Melon fly, Atavistic origin.

INTRODUCTION

The location and the arrangement of bristles, particularly on thorax, are defined characters (chaetotaxy) in the taxonomy of Diptera (McAlpine 1981; White & Elson-Harris 1992; Drew & Hancock 1994). There are many species of Diptera have different but equally stereotyped bristle patterns. The question arises as to how all of these different patterns are made from the basic genetic mechanisms (Simpson *et al*. 1999; Simpson & Marcellini 2006). A schematic representation of the ground plan of bristles (macrochaetes) on the scutum of Muscomorpha (McAlpine 1981)

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[*] Corresponding author, e-mail: ybhuang@tari.gov.tw

[1] Former Research Fellow, Applied Zoology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.

[2] Associate Research Fellow, Crop Science Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.

[3] Technicians, Applied Zoology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.

[4] Associate Research Fellow, Applied Zoology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.

[5] Assistant Research Fellow, Applied Zoology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.

[6] Director, Miaoli District Agricultural Research and Extension Station, Miaoli County, Taiwan, ROC.

consisted of four rows of bristles: acrostichal (AC), dorsocentral (DC), intra-alar (IA) and supra-alar (SA). *Drosophila melanogaster* has been a model insect for the investigation into the genetic control of the arrangement of sensory bristles (Ghysen & Dambly-Chaudiere 1988).

The dorsocentral bristles are lacking in the melon fly, *Zeugodacus cucurbitae* (Coquilett) (White & Elson-Harris 1992), and so are in most Dacinae (Drew & Hancock 1994). In the study of genetics of acrostichal prescutellar bristles (prsc) (Cheng *et al*. 2014), a multiple prsc (MB) strain which deprives the genetic modification of wild type and preserves only the quantitative genetic characters of prsc trait, was selected. In MB strain, some individuals developed two rows of median size stereotype patterned macrochaetes in the dorsocentral domain. The variant was isolated and designated as "DC (+)-line".

The macrochaetes patterns of Diptera were varied in the progress of evolution (Simpson & Marcellini 2006). By investigating the DC (+) variant, the inheritance information obtained may improve our knowledge in the development, the expression and the evolution of macrochaetes in Diptera (Simpson & Marcellini 2006), and the present study is going to focus on performance location and genetic analysis of DC (+) bristles.

MATERIALS AND METHODS

Insect materials

The parental materials used in this study constituted two melon fly strains. First, the wild strain, which has no dorsocentral bristles and was reared from the field collected specimens (Cheng *et al*. 2014). Second, the dorsocentral positive-strain [or DC (+)-line], the DC (+) phenotype, was isolated and cultured from the MB strain (Cheng *et al*. 2014).

Methods

Evaluation of DC (+) bristles. The expression of DC (+) bristles is scored into two classes in melon fly: the wild type does not exhibit DC (+) bristles and is designated as DC-free or DC (–) phenotype. The individual display DC (+) bristles is designated as DC-positive or DC (+) phenotype.

Performance location of DC (+) bristles and related chaetotaxy. The DC (+) bristles were positioned by their relative distance, from the notum midline (ML) to the intra-alar bristles, in a range of 100%. Two hypothetic chaetotaxy schemes and two model insects, which possess DC bristles, were chosen for the comparison.

(1) The ground plan of thorax macrochaetes of the Muscomorpha [Fig. 1A, adapted from Simpson *et al*. (1999) and McAlpine (1981)].
(2) The dorsal view of Dacinae thorax [Fig. 1B, from Drew & Hancock (1994)], showing the nomenclature and the location of bristles and a DC-free chaetotaxy model belonging to the taxonomic family of melon fly.
(3) *D. melanogaster* (Fig. 1C), an universal model insect in the chaetotaxy study (Simpson *et al*. 1999).
(4) *Ceratitis capitata* (Fig. 1D), a tephirite fly with DC bristles [from Wülbeck & Simposon (2000), Calleja *et al*. (2002), and Pistillo *et al*. (2002)].

Nota of wild type and MB-strain were presented in Fig. 2A–2B.

Genetic trials. Genetic trails were conducted between DC (+)-line and wild type. The target trait of inheritance analysis was evaluated in the F_1, F_2, and two backcross populations (BC_1 and BC_{1r}) derived from each parent involved three reciprocal crosses. The experiment was arranged in a randomized complete block design with 3–6 replications. Data were collected for goodness-of-fit to theoretical ratios using the Chi-square test (Kozik & Wehner 2008; da Cruz *et al*. 2010) for each of F_1, F_{1r}, F_1 (pooled), F_2, BC_1, and BC_{1r} families (Russell 2005; Griffiths *et al*. 2008).

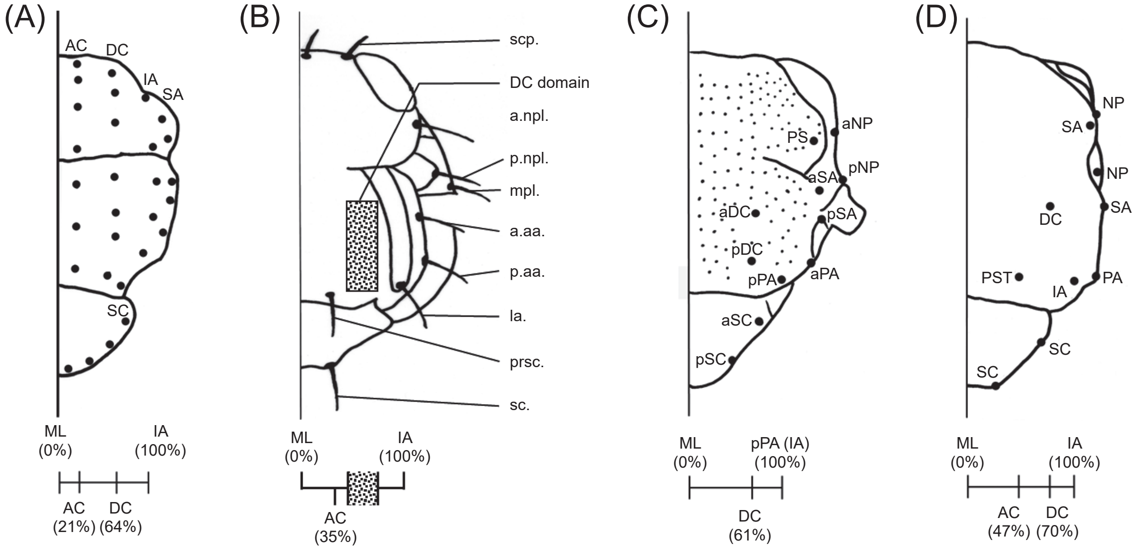

Fig. 1. The relative distances among bristle domains of chaetotaxy. (A) Diptern from McAlpine (1981) and Simpson *et al*. (1999); (B) Dacinae modified from Drew & Hancock (1994) to show the DC domain; (C) *Drosophila melanogaster* from Calleja *et al*. (2002); (D) *Ceratitis capitata* from Wülbeck & Simpson (2000). All bristle abbreviations corresponded to their original reports.

Statistical analysis

All data analysis was performed in the R 3.3.3 (R Development Core Team 2008) environment. Except F_1 and BC_1 families with recurrent parent "wild type", the families of F_2 and BC_1 population derived from recurrent parent "DC (+) type" were evaluated by counting the number of expression and non-expression of DC (+) bristles. The data was subjected to the Chi-square test to verify adjustment to the theoretical proportions expected the inheritance patterns for one gene, two duplicate genes and two complementary genes. The Chi-square values were obtained through the following formula:

$$\chi^2 = \sum (F_o - F_e)^2/F_e$$

Where F_o = observed frequency for each class; and F_e = expected frequency for each class, based on the Mendelian proportion.

RESULTS

The chaetotaxy comparison of DC (+)-line to two hypothetic schemes and two model insects were presented in Table 1 and Figs. 1–2. The AC bristles are located closer to the thorax midline than the DC bristles. The prsc usually is the only postsutural AC bristle in Acalypterata (Simpson *et al.* 1999), in a 100% range from ML to IA, the AC domain is 21–47% from the ML, while the DC domain is 60–70% from the ML. Two rows of 4 DC (+) bristles located at 65% from ML to IA, and fit into the DC domain (Fig. 2C–2D).

In genetic study, F_1 hybrids of 6 families were developed by the three reciprocal crosses between DC (+)-line and wild type. The segregation patterns of each family were presented in Table 2, the progenies with DC (+) bristles were very few (37 flies) in 541 pooled F_1 flies and the segregation patterns were similar in the three reciprocal crosses. The results suggested that the sex-linkage effect was not involved in the inheritance of DC (+) bristles. The segregation pattern of each F_1 family was close to the ratio of 1.0 for DC (+) phenotype and the other type. The six full-sib families of F_2 progenies were developed from the three re-

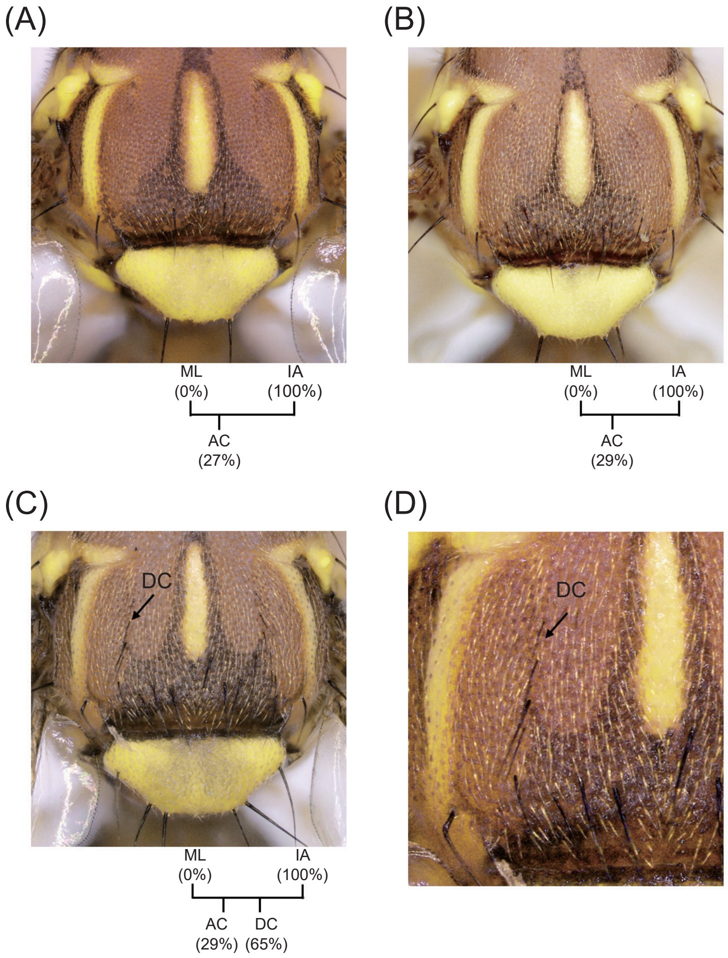

Fig. 2. The relative distances among bristle domains of (A) wild type; (B) MB strain; and (C) DC (+)-line of *Zeugodacus cucurbitae*. (D) Enlarged view of plate C to show DC bristles.

Table 1. Relative distance of acrostichal (AC) and dorsocentral (DC) from midline (ML) of scutum to intra-alar (IA) in the chaetotaxy of models and fruit fly species.

	Relative distance from ML (100% to IA)		
Model or fruit fly	AC	DC	Fig.
Ground plan of Diptern[z]	21	64	1A
Ground plan of Dacinae[y]	35	-	1B
Drosophila melanogaster[x]	-	61	1C
Ceratitis capitata[w]	47	70	1D
Zeugodacus cucurbitae	27	-	2A
Z. cucurbitae, the MB strain	29	-	2B
Z. cucurbitae, the DC (+)-line	28	65	2C

[z] Adapted from McAlpine (1981) and Simpson *et al*. (1999).
[y] Adapted from Drew & Hancock (1994).
[x] Adapted from Calleja *et al*. (2002).
[w] Adapted from Wülbeck & Simpson (2000).

Table 2. Number of DC (+) phenotype, DC (–) phenotype, total progeny and adjustment of Chi-square test for 6 F_1 families of melon flies evaluated for dorsocentral bristle expression.

Family	Cross^z	DC (–)	DC (+)	Total	Chi-square test 1 : 0
F_1N_1	W × D	87	13	100	-
F_1N_2	W × D	97	2	99	-
F_1N_3	W × D	60	2	62	-
F_1R_1	D × W	82	18	100	-
F_1R_2	D × W	82	2	84	-
F_1R_3	D × W	96	0	96	-
Pooled		504	37	541	-

^{z} D and W indicate DC (+) phenotype and wild type [DC (–) phenotype], respectively.

ciprocal crosses between DC (+)-line and wild type strain. The fly number of DC (+) progenies was up to 651 in the pooled F_2 population (2,835 flies) and the ratio of DC (+) was closed to 23% (Table 3). In advance, the segregation ratio of each F_2 family was determined in Chi-square goodness-of-fit tests for the pattern of one gene (3 : 1), two duplicate genes (15 : 1) or two complementary genes (9 : 7). The results showed that the inheritance pattern of DC (+) bristles was very significantly different with two gene model. The segregation ratios of four mating population were good to fit the one dominant gene pattern and DC (+) phenotype was the recessive trait compared with wild type.

In backcross families, there were two backcross populations developed with two recurrent parents (RP), respectively. In the backcross population derived from the RP "wild type", the segregation pattern of three reciprocal crosses was close the ratio of 1 : 0 for DC (–) and DC (+) phenotype (Table 4). The DC (+) type were only ten flies in the 541 pooled backcross progenies. In the other backcross population, the DC (+) type strain was used as the recurrent parent. The inheritance pattern of six BC_{1r} backcross families (pooled 560 flies) was determined to fit the ratio of 1 : 1 for DC (–) and DC (+) phenotypes (Table 5), suggesting that the one dominant gene controls the expression of DC (+) bristles and DC (+) phenotype belongs to the recessive trait compared with wild fly.

Table 3. Number of DC (+) phenotype, DC (–) phenotype, total progeny and adjustment of Chi-square test for 6 F_2 families of melon flies evaluated for dorsocentral bristle expression.

Family	Cross^z	DC (–)	DC (+)	Total	Chi-square test^y 3 : 1	15 : 1	9 : 7
F_2N_1	W × D	532	150	682	3.29	288.52***	131.17***
F_2N_2	W × D	322	96	418	0.92	199.35***	73.37***
F_2N_3	W × D	351	104	455	1.11	214.17***	80.70***
F_2R_1	D × W	158	86	244	13.66***	350.12***	7.17**
F_2R_2	D × W	390	83	473	14.01***	103.03***	131.96***
F_2R_3	D × W	431	132	563	0.73	284.12***	94.31***
Pooled		2,184	651	2,835	6.27*	1,351.50***	497.78***

^{z} D and W indicate DC (+) phenotype and wild type [DC (–) phenotype], respectively.
^{y} $\chi^2_{.05(1)} = 3.84$, $\chi^2_{.01(1)} = 6.63$, $\chi^2_{.001(1)} = 10.83$.
*, **, ***Significant at 5%, 1% and 0.1% levels, respectively.

Table 4. Number of DC (+) phenotype, DC (–) phenotype, total progeny and adjustment of Chi-square test for 6 BC_1 families with recurrent parent "wild type" of melon fly evaluated for dorsocentral bristle expression.

Family	Cross[z]	DC (–)	DC (+)	Total	Chi-square test 1 : 0
BC_1N_1	F_1 × W	41	0	41	-
BC_1N_2	F_1 × W	73	1	74	-
BC_1N_3	F_1 × W	27	5	32	-
BC_1R_1	W × F_1	157	1	158	-
BC_1R_2	W × F_1	107	2	109	-
BC_1R_3	W × F_1	126	1	127	-
Pooled		531	10	541	-

[z] W stands for wild type or the DC (–) phenotype.

Table 5. Number of DC (+) phenotype, DC (–) phenotype, total progeny and adjustment of Chi-square test for 6 BC_{1r} families with recurrent parent "DC (+) type" of melon fly evaluated for dorsocentral bristle expression.

Family	Cross[z]	DC (–)	DC (+)	Total	Chi-square test[y] 1 : 1
$BC_{1r}N_1$	F_1 × D	26	14	40	3.600
$BC_{1r}N_2$	F_1 × D	44	29	73	3.080
$BC_{1r}N_3$	F_1 × D	16	11	27	0.930
$BC_{1r}R_1$	D × F_1	95	96	191	0.005*
$BC_{1r}R_2$	D × F_1	65	59	124	0.290
$BC_{1r}R_3$	D × F_1	50	55	105	0.230
Pooled		296	264	560	1.830

[Z] D stands for DC (+) phenotype.
[y] $\chi^2_{.05(1)} = 3.84$.
*Significant at 5% level.

The symbol *DCm* for *DorsoCentral bristle masked* is proposed to designate this single completely dominant gene.

DISCUSSION

In morphology, DC (+) bristles is located in the dorsocentral domain of the scutum. The monohybrid cross confirmed that wild type melon fly hosted *DCm*. The genetic analysis fits the Mendel's general conclusions (Russell 2005) as followings: (1) The results of reciprocal crosses were always the same. (2) All F_1 progeny resembled one of the parental strains. (3) In F_2 generation, the parental trait that had disappeared in F_1 generation reappeared at 1 : 3 ratios. The results of two backcrosses confirmed the single dominant gene action in wild type can prevent the expression of DC (+) bristles in melon fly.

The melon fly did not have the dorsocentral bristles, and so there is an issue about the identity of newly emerged DC (+) bristles. The observation is that DC (+)-line only emerged in the MB strain naturally and frequently. One thing we know so far about the MB strain is that it deprives the genetic input of wild type; hence, conserves the quantitative genetic nature in prsc trait. The results showed that the *DCm* exists in wild type, but not in the MB strain. The DC (+) bristles are expressed in the MB strain only. Similarly, it has been concluded in the prsc study that the MB strain is wild type free (Cheng *et al*. 2018).

How about the origin of DC (+) bristles? It has been mentioned in genetics that, if a trait acted as a recessive allele and can be hidden in the population as heterozygotes, once the suppression factor was lifted, the recessive allele has the chance to form homozygotes in population and the trait reappeared (Hartl 1999). Deja Vu, the DC (+) bristles may serve as a perfect example. The wild type, the MB strain, the DC (+)-line, the DC (+) phenotype and the *DCm* are all parts of the story. Therefore, DC trait reappeared in the atavistic pattern at the original DC domain (Simpson *et al*. 1999). The probability of DC (+) phenotype to be a mutant is also possible, but the probability is low. Instead of randomly expressed, DC (+) bristles emerged stereotype pattern in a fixed domain and can be considered as highly organized complex in developmental biology (Carroll 2005).

Although DC (+) bristle emerged in the MB strain, but it has not related to the prsc bristle because the dorsocentral and acrostichal clusters have different developmental origins (Wülbeck & Simpson 2000).

It has been speculated that DC bristles were long lost in most species of Dacinae in evolution, while the *DCm* and DC (+) bristles proved that it is not the case in melon fly. Whether the *DCm* is a common gene shared in other DC-free Dacinae species need to be further studied.

CONCLUSION

By comparing the chaetotaxy of *D. melanogaster*, *C. capitata* and Diptern model, two rows of 4–6 medium sized macrochaetes in the dorsocentral domain of DC (+) phenotype are identified to be DC bristles. The genetic study confirmed that DC bristles are a recessive character, coming out from the suppression of a single dominant gene *DCm*. The emerged DC (+) bristles were stereotype patterned at fixed location of dorsocentral domain, implying that DC (+) bristles are highly organized and specialized. Thus, the atavistic origin is possible. In other words, the dorsocentral bristle of melon fly may not be lost in evolution, rather simply being masked by a dominant gene, *DCm*.

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瓜實蠅 [*Zeugodacus cucurbitae* (Coquillett)]「背中區剛毛」受單一顯性基因 *DCm* 抑制表現之研究

鄭允[1] 吳東鴻[2] 王志賢[3] 黃毓斌[4,*] 江明耀[5] 呂秀英[6] 楊崇民[3]

摘要

鄭允、吳東鴻、王志賢、黃毓斌、江明耀、呂秀英、楊崇民。2020。瓜實蠅 [*Zeugodacus cucurbitae* (Coquillett)]「背中區剛毛」受單一顯性基因 *DCm* 抑制表現之研究。台灣農業研究 69(2):113–121。

雙翅目「中胸背板」上剛毛之數量分布及排列模式是分類的重要依據，其中「背中區剛毛」在瓜實蠅所屬的 Dacinae 亞科中已因演化而消失。行政院農業委員會農業試驗所飼育之瓜實蠅中，有一「中胸背板多剛毛」品系中頻頻出現具兩列整齊排列「背中區剛毛」的個體。此等個體上「背中區剛毛」之來源及發生原因，具有剛毛發生及遺傳上之研究價值。本研究特將具此特徵之瓜實蠅另行育成 DC (+)-line 品系，以供研究之用。出現於 DC (+)-line 之「背中區剛毛」為縱向整齊排列 4–6 隻中型大小之剛毛，分列中胸背板兩側之「背中區」，經測定位於自背板中線 (midline) 起，至「翅內剛毛」(intra-alar) 止之 60–70% 處；也落於「雙翅目中胸背板剛毛模式圖」 (groand plan of chaetotoxy; McAlpine 1981) 背中區內，此與兩種具「背中區剛毛」模式 (model) 蠅種 *Drosophila melanogaster* 及 *Ceratitis capitata* 之位置相當。以「野生型」與「背中型」進行遺傳試驗時，用處女 (雄) 蠅配對，兩品系雌雄交互配對各 3 對，並觀察子代之表現型及數量。發現 F_1 子代中「背中型」出現的機率趨近於零 (37/541)，而 F_2 子代中「背中型」出現且可達 23% (651/2,835)，6 組配對中有 4 組合乎 3 : 1 之單一顯性因子理論推論，並與雙因子 (15 : 1) 及雙互補因子 (9 : 7) 遺傳之推論全數不符合，且無性聯遺傳現象 (sex-linkage)。而在回交的測試，與「野生型」之回交中產生的「背中型」在全數 531 隻子代中僅有 10 隻，而趨近於零。與「背中型」回交之子代 560 隻中產生近半數之「背中型」，數值為 264 隻，經 Chi-square 分析，驗證與 1 : 1 之理論推值相符。本研究結論為瓜實蠅之「背中剛毛」之表現與否，係由單一顯性基因控制，存在於「野生型」中，由其抑制「背中剛毛」之表現，而「背中剛毛」表現屬隱性特徵，因此將此一基因定名為 *DCm* (*DorsoCentral bristle masked*)。由於「背中剛毛」之出現是在無「野生型」介入之「多剛毛」品系中，且完整地以兩列整齊方式出現，而非以逢機或突發性方式出現，因此推論為「返祖」現象而非突變。因隱性基因可長期以 heterozygotes 方式隱藏於族群中，當顯性抑制基因消退時，逐漸形成 homozygotes 而重現。此外，是否 *DCm* 為現今雙翅目中抑制「背中區剛毛」之共同因子，亦為未來值得探討的方向。

關鍵詞：背中區剛毛、瓜實蠅、返祖。

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[*] 通訊作者：ybhuang@tari.gov.tw

[1] 農業委員會農業試驗所應用動物組退休研究員。台灣 台中市。

[2] 農業委員會農業試驗所作物組副研究員。台灣 台中市。

[3] 農業委員會農業試驗所應用動物組技工及技術工。台灣 台中市。

[4] 農業委員會農業試驗所應用動物組副研究員。台灣 台中市。

[5] 農業委員會農業試驗所應用動物組助理研究員。台灣 台中市

[6] 農業委員會苗栗區改良場場長。台灣 苗栗縣。