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January 17, 1969

Determination of bristle direction in Drosophila[1]

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INTRODUCTION

The pattern of bristles on the body surface of flies has been analyzed as a model for the localized differentiation of organs during development (review in Stern, 1968). In addition to their specific locations the different bristles are characterized by specific sizes and by the direction in which they point. Thus, in a wild type Drosophila melanogaster many bristles of the mesonotum point more or less closely, from their origin on the body surface, in a posterior direction, while the posterior supra-alars point posterior-medially. On the dorsal surface of the head the ocellar bristles are directed anterior-laterally, the vertical bristles medially, and the postverticals posterior-medially.

The determinants of bristle direction are not known in detail, although some relevant studies (cited later) have led to important insights. In a general way it may be asked whether the direction of a bristle depends on properties of the cell which secretes it (autonomy) or whether direction is imposed on it by outside agents (nonautonomy), or whether the organization of both the bristle cell and its surroundings plays a role. This question can be approached by the study of mutants which change the direction of bristles in comparison with the nonmutant state. One such mutant in D. melanogaster is the recessive autosomal allele aristaless (al, 2 - 0.01). Apart from effects elsewhere al singles out the posterior scutellar bristles of the mesonotum for a change in direction. Instead of lying close to the body surface and converging in a posterior-medial direction the posterior scutellars are erect and strongly divergent, thus pointing laterally (Fig. 1). The experiments to be reported here were devised to study the problem of autonomy or

nonautonomy of the action of al on the direction of the posterior scutellar bristles. Flies mosaic for al^+/al and al/al on their scutella were analyzed for the behavior of these bristles.

METHODS

Larvae heterozygous for al (al^+/al) were X-rayed at the ages 24 - 48 and 48 - 72 hours after egg deposition so as to induce somatic crossing-over, resulting in homozygous al/al cell patches (1300 r; 76 r/min; 140 kV, 4 mA, 1.5 mm Al inherent filtration plus 0.76 mm Al external filtration). Such patches were recognized by means of a marker, yellow (y, 1 - 0.0). Specifically the larvae carried y on each X chromosome and were heterozygous for the T (1;2) sc^{19} insertion into the left arm of the second chromosome about 1 - 2 crossover units to the right of dumpy (2 - 13.0). The insertion contains a y^+ gene. It was present in that second chromosome which carried the normal al^+ allele. The genotype of the larvae was therefore y or y/y; al^+y^+/al -. In addition the larvae were homozygous for the third chromosome mutant hairy (h, 3 - 26.5), which places microchaetae on the normally microchaetaeless scutellum. In mosaics the y^+ or y coloration of the microchaetae helped in delineating the area of the al/al spot.

Somatic crossing-over in the second chromosome of the irradiated larvae and appropriate segregation of the chromatids would have the following results: (a) Single crossing-over between the kinetochore and the y^+ locus of the sc^{19} chromosome would lead to two kinds of cells, (1) homozygous for al and without y^+, and (2) homozygous for al^+ and y^+. The first type, after growth into a cell patch, would develop into a yellow spot on the otherwise nonyellow heterozygous

background, whereas the second type, being nonyellow, would not be distinguishable from the background.

(b) Single crossing-over to the left of the $\underline{y}^+$ insertion would also result in (1) cells homozygous for al, but the spots developing from them would not be marked by a yellow phenotype; (2) cell types in this class of crossovers homozygous for $\underline{al}^+$ and containing $\underline{y}^+$, and having the same phenotype as the background.

(c) Double crossing-over to the left and right of the $\underline{y}^+$ insertion would lead to (1) cells heterozygous for $\underline{al}^+$ and without $\underline{y}^+$, and (2) cells heterozygous for $\underline{al}^+$ and homozygous for $\underline{y}^+$. The first type would form a yellow patch that is heterozygous for $\underline{al}^+$, as is the rest of the fly; the second type would be nonyellow and indistinguishable from the background.

After eclosion the irradiated individuals were fixed in 70 per cent alcohol and their scutella checked for the presence of a yellow patch. The mosaic scutella were then studied in detail.

THE EFFECT OF ARISTALESS IN NONMOSAIC SCUTELLA

It was first reported by Schultz and Curry (see Bridges and Brehme, 1944) that the scutellum of aristaless flies is shortened. In order to obtain more detailed information several measurements were made for a comparison of normal and aristaless scutella (Table 1). The two groups of flies were not isogenic, and some of the differences between them may be due to genetic or nongenetic variables. It is apparent from the data that certain distances vary little between the two groups--e.g., the distance between the posterior scutellars--while others vary considerably--e.g., the distance between the anterior scutellars. The greatest differences are found for the length of the

scutellum at the midline (M, Table 1) and the distance between the anterior and posterior scutellar bristles (AP). These differences are indicative of differential growth patterns of aristaless and nonaristaless scutella. The fact that the distance between the anterior scutellar bristle and the scutellar groove (SA) differs only slightly whereas the distance between the anterior and posterior scutellars (AP) differs greatly shows that in al/al scutella the posterior part grows (or expands) at a reduced rate. Thus, the abnormal direction of the posterior scutellars in al/al is only one of the mutant phenotypes of the posterior scutellar region. This fact is also seen in the direction in which the microchaetae that occur on the scutellum of hairy flies point. In nonaristaless flies the microchaetae of the posterior scutellar area usually point in a posterior direction. On the contrary, in aristaless flies the same microchaetae usually point forward.

Different directions are already shown during pupal life by the posterior scutellar bristles (Fig. 2). In nonaristaless late pupae the macro- and microchaetae on the scutellum in general point in a posterior direction, except for the posterior scutellars, which point anterior-laterally in such a way as to cross each other. In aristaless pupae the posterior scutellars point forward and thus do not cross, and the microchaetae in the posterior part of the scutella likewise often point in an anterior direction.

Taking into account all aspects of chaetal direction as described, one may visualize the difference of direction between nonaristaless and aristaless in the following way. In nonaristaless flies the scutellum grows or expands in a posterior direction to the greatest degree in its

posterior half. There the strongest effect is produced near the midline and the weakest near the posterior scutellar bristle. In aristaless flies this growth is decreased greatly, thus leaving the chaetae pointing in an anterior or lateral direction.

The view that the direction of the posterior scutellars is controlled by the specific growth of the scutellar region requires independent evidence. This can be provided by mosaics, and their analysis is presented below. First, however, some data on the posterior scutellars of heterozygous $\underline{al}^+/\underline{al}$ flies are given.

PENETRANCE AND EXPRESSIVITY OF HETEROZYGOUS ARISTALESS

Homozygous $\underline{al}/\underline{al}$ flies exhibit nearly always the strikingly abnormal direction of the posterior scutellar bristle. There is some variation, however, and a few flies show a lesser expressivity, including an almost normal direction. Heterozygous $\underline{al}^+/\underline{al}$ flies are more variable. Among the heterozygotes for aristaless, which carried the $T(1;2)\underline{sc}^{19}$ insertion as described under Methods, more than 10 per cent of scutellar halves showed slight or even strongly aristaless-like bristle direction. This heterozygous penetrance was found in nonirradiated controls as well as in the irradiated individuals that yielded the mosaics to be discussed below. Since all flies were homozygous for $\underline{h}$(hairy), a check was made to determine whether it was possibly the $\underline{h}$ gene that was responsible for abnormal bristle direction in a fraction of the $\underline{y}$ or $\underline{y}/\underline{y}$; $\underline{al}^+ \underline{y}^+/\underline{al}$ -; $\underline{h}$ flies. It was found that among 422 half scutellas of hairy flies none was typically aristaless-like in orientation, and in only three was the direction of the posterior scutellar bristle slightly abnormal. Among 760 yellow hairy half scutellas, no single posterior scutellar

was abnormal. This shows that the hairy gene by itself does not cause abnormal orientation of the posterior scutellars. The partial penetrance of aristaless in heterozygotes will be taken into account in the interpretation of the mosaics. (It is possible that some of the aristaless-like scutella have areas that are homozygous for al but nonyellow, due to crossing-over to the left of the y^+ insertion. This, however, would at most constitute a very small fraction of the cases with aristaless-like orientation of the posterior-scutellar bristles. The great majority, if not all, are based on penetrance of al^+/al heterozygotes.)

SCUTELLAR MOSAICS

Out of a total of 7743 flies that had developed from irradiated larvae, 47 were mosaics having a yellow area on their scutellum. Of these, 26 out of 4536 flies came from larvae irradiated at the age of 24 to 48 hours after egg deposition and 21 out of 4872 flies from larvae irradiated at the age of 48 to 72 hours. One of the mosaics from the latter group did not have a posterior scutellar bristle on the mosaic half of the scutellum and had to be excluded from further consideration.

Each mosaic scutellum was nonmosaic, i.e., nonyellow, on one half. The shape of the scutellum in 22 of the 46 mosaics was normal, but in 24 mosaics the posterior edge of the scutellum showed various degrees of depression. This was the result of the asymmetrical situation in which the nonmosaic half of the scutellum tended to be normal in length whereas the mosaic half tended to be shortened due to its homozygous aristaless genotype. The asymmetry of the scutellum was also expressed by the direction of the posterior scutellar bristle on the normal half of the scutellum. In consequence of the distortion of the

scutellum due to its being composed of two differently shaped halves the normal posterior scutellar often showed an abnormal direction, but usually unlike that of typical aristaless bristles.

For purposes of analysis the surface of each half scutellum was divided into three areas (Fig. 3). Area I lies posterior to a line drawn through the posterior scutellar bristle across the scutellum, vertically to the midline. Area I forms thus a posterior peripheral section. In hairy flies, as in these mosaic specimens, this area includes one or two microchaetae. The posterior scutellar bristle is regarded as separate from Area I. Area II constitutes the remaining peripheral region, which includes two microchaeta located between the sites of the anterior and posterior scutellars, and several microchaetae as well as sometimes a supernumerary macrochaeta neighboring the anterior scutellar bristle and usually located between the scutellar groove and the area lateral to the bristle. Area III forms the central part of the half scutellum. It contains scattered microchaetae. A further scutellar area consists of the underside of the scutellum. In hairy flies, it bears several microchaetae. Among the 46 mosaics no yellow spot was present on this underside, either by itself or as an extension of a yellow spot on the dorsal surface. This finding agrees with studies of cell lineage which have shown that the dorsal and ventral surfaces of the scutellum are not closely related to each other (Murphy and Tokunaga, unpubl.).

Table 3 lists the 46 mosaic scutella according to presence or absence of the depression of the posterior edge of the scutellum. The table also provides information on the mosaic or nonmosaic nature of the Areas I - III and on the coloration of the scutellar bristles. Finally, for each mosaic it states the direction of the posterior scutellar bristle.

Analysis of these data shows the following relations.

(1) When the depression at the posterior edge of the scutellum is present the direction of the posterior scutellar bristle is al-type regardless of its own genotype al/al or al^+/al (Fig. 4, a, b, c).

(2) When the posterior edge of the scutellum lacks a depression--i. e., is normal--the direction of the posterior scutellar bristle is al^+-type (Fig. 4, d). There are two exceptions to this role, Mosaics 17 and 103.

(3) When the depression along the posterior edge is present, Area I is a genetic mosaic. There is one exception to this rule, Mosaic 7.

(4) Scutella without the depression are nonmosaic normal in Area I.

The three exceptions to the rules, listed above, can be readily accounted for: (a) Mosaic 17 (Fig. 5a) has a yellow posterior scutellar bristle which points in a direction characteristic of al/al, but the scutellum has no recognizable edge depression and is not mosaic in Area I. This is in contrast to seven similar mosaics all of which have a posterior scutellar that points in the typical normal direction. Most likely, Mosaic 17 represents a case of heterozygote penetrance independent of any mosaicism. (It should be remembered that more than 10 per cent of al^+/al heterozygotes exhibit penetrance of al for the direction of the posterior scutellar. See Table 2. (b) Mosaic 103 (Fig. 5b) may also be explained by heterozygote penetrance. Here, the posterior scutellar bristle is nonyellow, and is located on a scutellum that has no depression and is mosaic in Area III only, covering four microchaeta. (c) Mosaic 7 (Fig. 5c) has a slight edge depression and a yellow posterior scutellar bristle that shows an al-type direction. The exceptional nature of this scutellum lies in the fact that Area I has no discernible mosaic make-up.

Possibly some tissue of Area I near the posterior dorsocentral is indeed mosaic but cannot be recognized by yellow coloration of either microchaeta (which are absent) or hypodermis. Another possibility is that the edge depression of Mosaic 7 was the result of a developmental accident occurring independently of the aristaless locus and that the depression was associated with the development of an aristaless-type direction of the posterior scutellar bristle.

Summarizing the findings on bristle direction, we conclude that yellow aristaless spots initiated at an early developmental stage in the prospective Area I of the scutellum lead to abnormal growth of the posterior part of the half scutellum involved. When the mosaic half scutellum joins with the half scutellum of the other side of the fly a depression of the posterior scutellar edge develops, which in its turn leads to the aristaless-type direction of the posterior scutellar bristle regardless of its own genotype. Thus, the direction of the posterior scutellar is imposed on it by the neighboring tissue. In this sense the direction is a nonautonomous trait. Since, however, in scutellar mosaics the bristle is sometimes nonyellow, $\underline{al}^+/\underline{al}$, and at other times yellow, $\underline{al}/\underline{al}$, the following paradoxical situation exists: a nonyellow $\underline{al}^+/\underline{al}$ bristle near a mosaic or wholly yellow Area I will nonautonomously show a direction not indicative of its genotype, but the same bristle associated with a nonyellow nonmosaic Area I will show a normal direction, seemingly in autonomous manner. Similarly, a yellow $\underline{al}/\underline{al}$ bristle near a mosaic or wholly yellow Area I will seemingly autonomously have a direction corresponding to its own genotype, but the same bristle associated with a nonyellow nonmosaic Area I will, nonautonomously,

have a normal direction. There is, then, autonomy of aristaless in the growth of Area I of the scutellum and, fundamentally, nonautonomy of aristaless in the direction of the posterior scutellar bristle.

DISCUSSION

In drosophila, genetic control of the direction of bristles has been reported for other than the posterior scutellars. A striking case involves the forelegs of males, where the teeth of the sex comb point more or less across the basitarsal segment, in contrast to females, where the bristles homologous to the teeth point in a proximal-distal direction (Tokunaga, 1962). Another case is that of the gene dumpy (2-13.0), which leads to a whorl-like arrangement of microchaetae on the thorax instead of the normal arrangement in which the chaetae all point posteriorly (King, 1964). A third case in which a polygenic system seems involved affects the microchaetae on the abdominal sternites. Normally, these bristles point in different directions, but a selection experiment was successful in increasing the tendency toward an antero-posterior orientation parallel to the longitudinal axis of the individual (Sondhi, 1965). In this last instance the problems of autonomy and nonautonomy were not investigated. For the first two cases, experiments using the mosaic method yielded results fundamentally similar to those obtained in the present study with aristaless; the direction of the sex comb teeth in the male genotype and that of the homologous bristles in the female genotype, and the vortex arrangement of bristles in dumpy, depend on the specific controlling pattern of the hypodermal tissue. The sexual and the dumpy genotypes express themselves primarily autonomously in the growth pattern of the region, and the

orientation of the bristles follows secondarily as either a nonautonomous or a seemingly autonomous process.

In insects other than Drosophila the nature of orientation of bristles or other epidermal structures has been studied by means of experimentally induced changes in direction of epidermal areas. Disturbances in the orientation of epidermal structures were observed when a piece of integument was excised and reimplanted after rotation by 90 or 180 degrees or when discontinuities in intersegmental membranes had occurred spontaneously or been induced experimentally, or in other essentially similar situations (Wigglesworth 1940, 1959 in Rhodnius; Piepho 1955, 1956 in Galleria; Locke 1959 in Rhodnius; Lawrence 1966 in Oncopeltus). These experiments have shown that a gradient exists in each segment which controls the polarity of the epidermal features.

Structures such as bristles which originate from single cells suggested to Wigglesworth the existence of a cytoskeleton within the cell which defines its orientation. This hypothesis fits well the orientation of structures in a uniformly growing epidermis. In addition, uneven growth of the epidermis is able to shift the direction of bristles and other epidermal structures. The orientation of the posterior scutellar bristle in aristaless individuals demonstrates anew the dual nature of the control of bristle direction.

SUMMARY

In Drosophila melanogaster the recessive mutant aristaless (al) leads to an abnormal orientation of the posterior scutellar bristles. The mutant also affects the shape of the dorsal scutellar surface. Heterozygous al^+/al flies show more than 10 per cent penetrance in causing

mutant-type bristle orientation. By means of genetic mosaics on the scutellum, caused by X-ray-induced somatic crossing over and marked by areas of yellow pigmentation on a nonyellow background, it is shown that al autonomously leads to abnormal scutellar growth. Secondarily, in cases of such abnormal growth, an aristaless-type direction is imposed on the posterior scutellar bristle, regardless of its own al/al or al^+/al genotype.

ACKNOWLEDGMENTS

We wish to thank Mrs. Cole P. Ulrichs for excellent technical help and Mrs. E. Reid for the preparation of the figures.

Table 1. Measurements on the scutellum of each of 20 y;h and y;al;h females and males. (1 unit = 0.01 mm.)

	AA	PP	M	AP		SA	
				left	right	left	right
y;h ♀♀	35.47±0.345	17.40±0.15	28.90±0.29	16.62±0.23	16.70±0.20	10.37±0.16	10.45±0.15
y;al;h ♀♀	31.92±0.38	17.03±0.37	23.37±0.33	11.43±0.36	12.10±0.32	9.93±0.11	10.23±0.18
y;h ♂♂	30.70±0.38	15.40±0.16	25.17±0.33	14.72±0.17	14.97±0.19	8.85±0.11	8.90±0.11
y;al;h ♂♂	27.22±0.35	14.42±0.24	19.35±0.32	10.47±0.26	10.60±0.27	8.52±0.17	8.62±0.16

AA = distance between the two anterior scutellar bristles.

PP = distance between the two posterior scutellar bristles.

AP = distance between the anterior and posterior scutellar bristles.

SA = distance between the anterior scutellar bristle and the scutellar groove.

M = length of the scutellum at the midline.

Table 2. Penetrance of abnormal bristle direction of the posterior scutellar bristle in flies heterozygous for al:y or y/y; al^+ y^+ /al -; h/h.

Treatment of larvae	Total number of disks	Direction of posterior scutellar bristle		
		normal	abnormal	% of abnormality
not irradiated	434	390	44	10.14
irradiated at				
24-48 hr	2056	1736	320	15.56
48-72 hr	1124	1001	123	10.94

Table 3. Details concerning the scutellas of the 46 mosaics.
psc - posterior scutellar bristle; asc = anterior scutellar bristle. For the delineation of Areas I, II, and III see Figure 3. The exceptional Mosaics 7, 17, and 103 are discussed in the text. (Flies homozygous for hairy, as those dealt with here, often have more than one anterior scutellar bristle on one or both sides of the scutellum. When these multiple anterior scutellar bristles are all nonyellow or all yellow they are jointly designated as + and y, respectively. When both yellow and nonyellow anterior scutellars are present they are designated as y/+).

Table 3

Scutellar depression	Mosaic pattern Area I	psc	Area II	asc	Area III	Direction of psc	Number of Mosaic Cases larvae irradiated at 24 - 48 hr	48 - 72 hr	Total
present	y	y	y	y	y	al-type	9	2	11
	y	y	y/+	y	y/+	al-type	1	2	3
	y	y	y/+	y/+	y/+	al-type	1	0	1
	y	y	y/+	+	y/+	al-type	1	0	1
	y	y	+	+	y/+	al-type	0	1	1
	+	y	y	+	y/+	al-type	1[a]	0	1
	y/+	+	y/+	+	y/+	al-type	1	0	1
	y	+	+	+	y/+	al-type	1	2	3
	y/+	+	+	+	y	al-type	1	0	1
	y/+	+	+	+	+	al-type	0	1	1
absent	+	y	y/+	y	y/+	al-type	1[b]	0	1
	+	y	y/+	y	y/+	+-type	1	0	1
	+	y	y	y	+	+-type	0	1	1
	+	y	y/+	y	+	+-type	0	2	2
	+	y	y/+	+	+	+-type	0	1	1
	+	+	y/+	y	+	+-type	0	1	1
	+	+	y/+	+	y/+	+-type	1	0	1
	+	+	+	y/+	y/+	+-type	1	0	1
	+	y	+	+	+	+-type	0	2	2
	+	+	+	y	+	+-type	0	1	1
	+	+	y/+	+	+	+-type	1	1	2
	+	+	+	+	y/+	+-type	5	2	7
	+	+	+	+	y/+	al-type	0	1[c]	1

[a] Mosaic 7

[b] Mosaic 17

[c] Mosaic 103

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LEGENDS

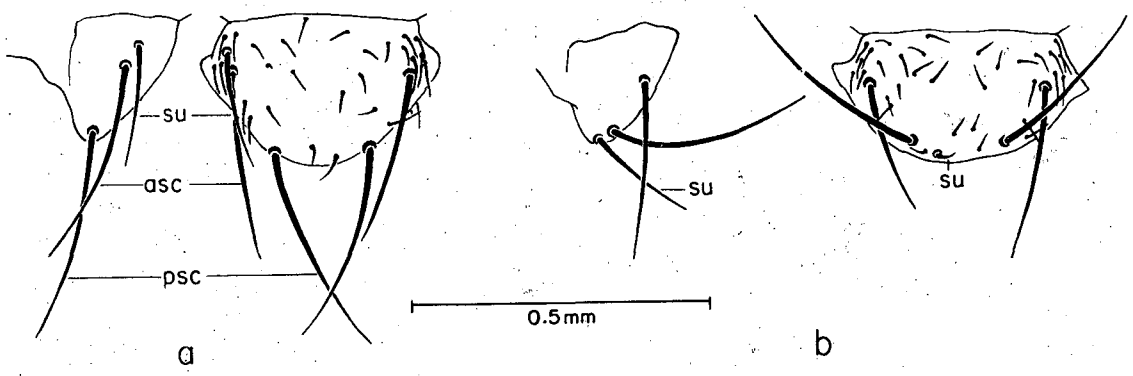
Fig. 1. Lateral and dorsal views of the scutellum of (a) a nonaristaless, yellow hairy male (y;al$^+$;h/h) and (b) an aristaless, yellow hairy male (y;al/al;h/h). Anterior and posterior scutellar bristles: asc and psc, respectively. Supernumerary scutellar bristle:su. (Supernumerary bristles are frequently found in h/h flies). The lateral views of Figs. 1, 4, and 5 show macrochaetae only.

Fig. 2. Dorsal view at a late pupal stage of the scutellum of (a) a y;al$^+$/al$^+$;h/h male and (b) a y;al/al;h/h male.

Fig. 3. Diagram of the scutellum of a nonaristaless fly. On the right half scutellum Areas I, II, and III are shown as well as the position of the anterior and posterior scutellar bristles.

Fig. 4. Lateral and dorsal views of four mosaic scutella. Solid chaetae: nonyellow. Chaetae in outline or shown as dotted lines: yellow. Note the depression of the posterior edge of the mosaic scutellar half in (a), (b), and (c) and the aristaless-like direction of the psc, as opposed to the lack of the depression in (d) and the normal direction of the psc. (a), (b) females; (c), (d) males.

Fig. 5. Lateral and dorsal views of the three exceptional mosaics discussed in the text. (a) Mosaic 17, no edge depression, aristaless-like direction of yellow psc. (b) Mosaic 103, no edge depression, aristaless-like direction of nonyellow psc. (c) Mosaic 7, edge depression, aristaless-like direction of yellow psc. (a), (b) females; (c) male.



DBL 691-4526

Fig. 1

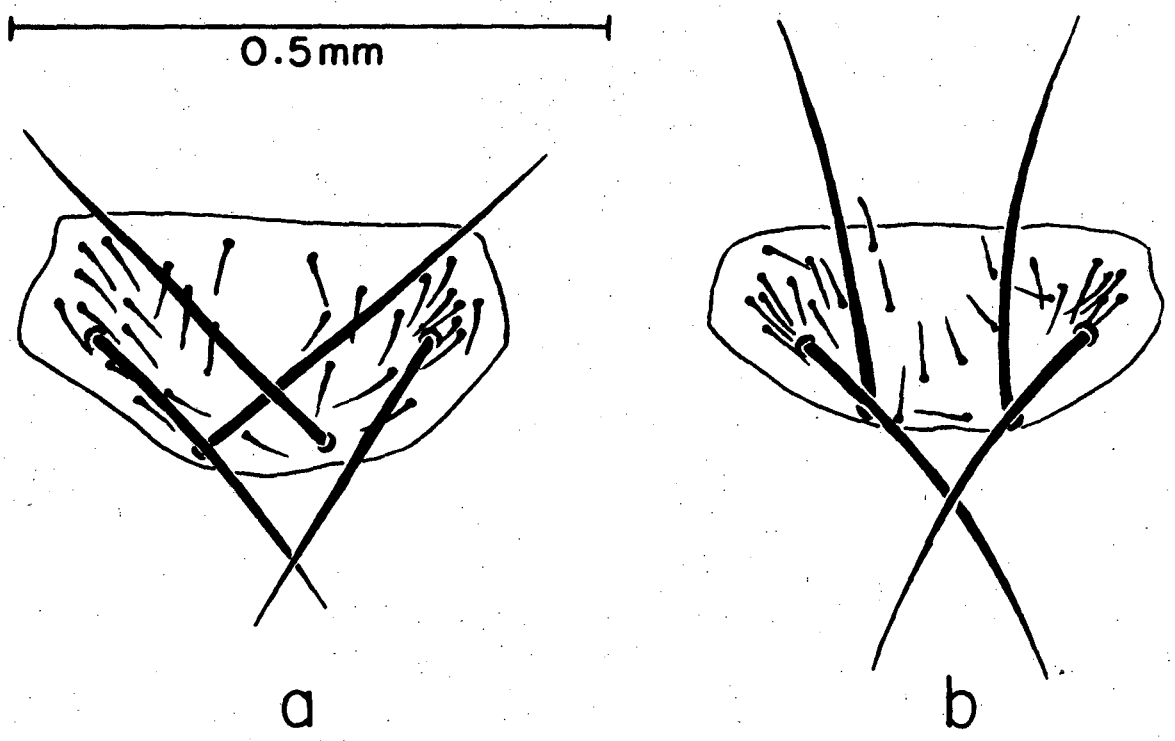


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Fig. 2

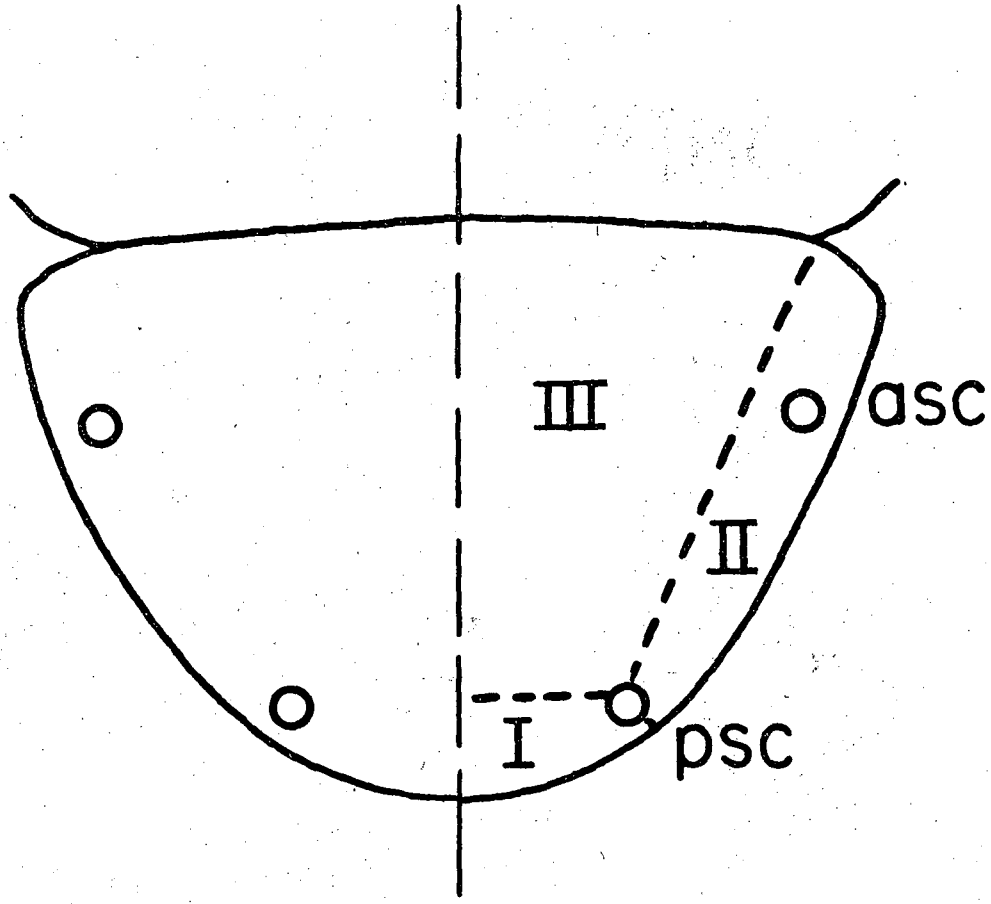

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Fig. 3

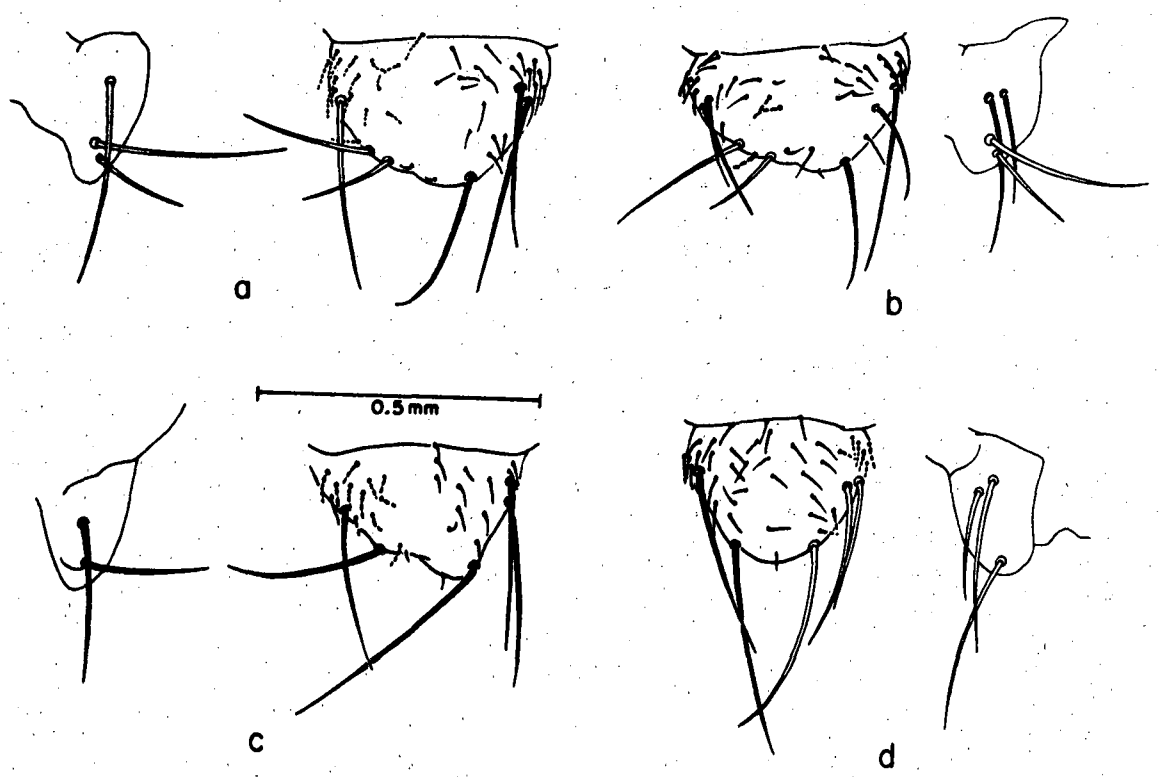

Fig. 4

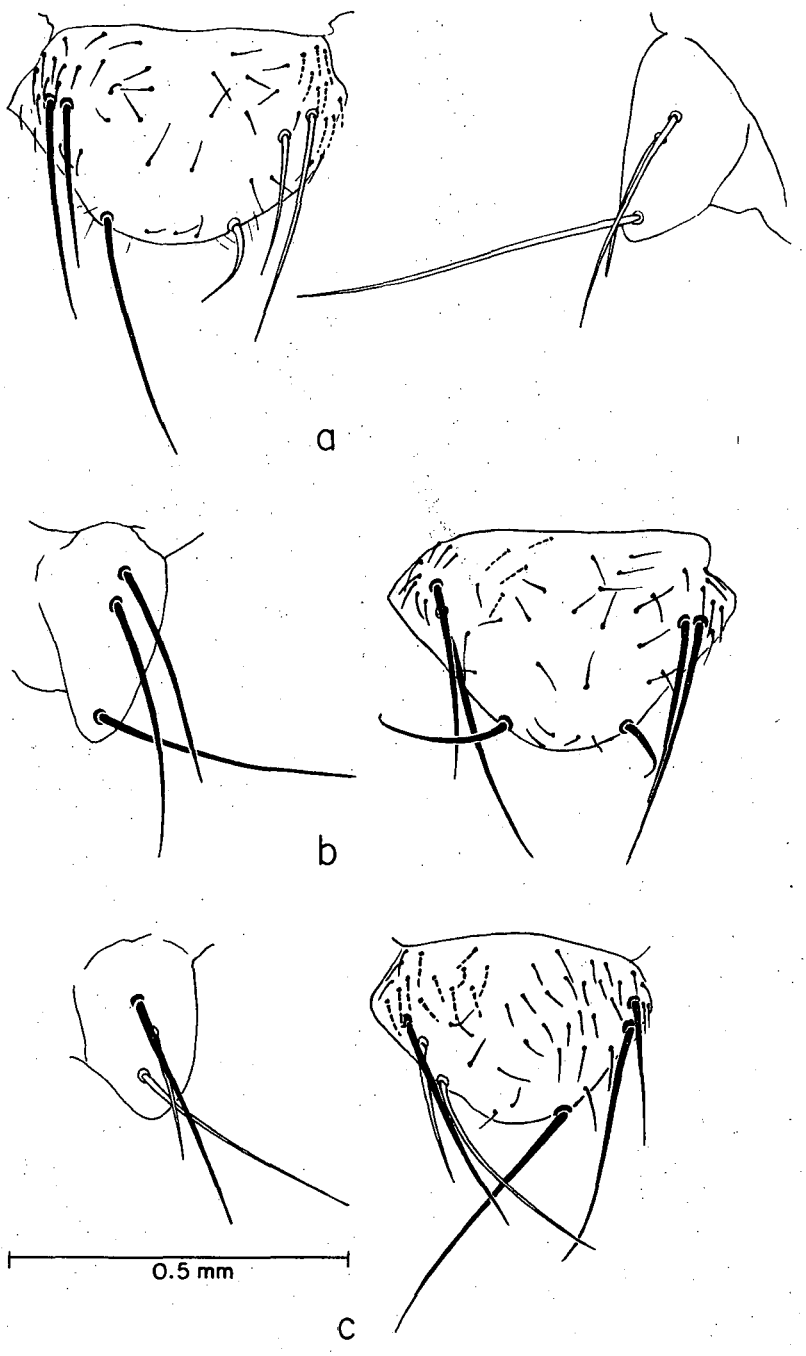

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Fig. 5

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