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Surface Structure of the Compound Eye of Various Drosophila Species and Eye Mutants of *Drosophila melanogaster*

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Summary. The surface structure of the compound eyes of 6 Drosophila species and 12 eye mutants of *D. melanogaster* were compared by scanning electron microscopy.

D. melanogaster, D. simulans, D. hydei, D. funebris and *D. virilis* displayed hexagonal facets and differed only slightly in the distribution of bristles. *D. lebanonensis* displayed tetragonal facets.

No obvious differences in surface structure of the eyes of colour mutants of *D. melanogaster* were found. Mutants with structural modifications of the eyes revealed irregular patterns of bristles, variations in bristle number and variations in facet shape, size and organization. The mutant spa^{pol} does not display clear-cut delineated facets.

Introduction

Scanning electronmicroscopy has become a useful technique in studies on surface structures at high resolution. The scanning electron microscope may reveal details of surface structures as well as their organizational patterns which so far have been unresolved by the use of light microscope and conventional electron microscope techniques.

Because the morphogenesis of surface structures is generally thought to be among the phenotypic characters which are genetically controlled, a comparative study of the surface of compound eyes of various Drosophila species and eye mutants was undertaken. The results of such a comparative study should not only provide a better insight into the constancy of patterns of surface structures among various Drosophila wild-type species, but also could contribute to a better characterization of the complex phenotypic changes produced by mutations affecting the form and structure of the eye.

Materials and Methods

All observations were made with a JSM-U3 Scanning Electron Microscope operated at 15 kV. Mature flies were etherized and attached to a 14 mm ⌀ brass mount with conductive paint. Conductive coating was performed with gold while the specimen was rotated and titled so as to obtain a relatively uniform gold coating of about 300 Å thickness.

The compound eyes of the following Drosophila species were studied: *D. melanogaster, D. simulans, D. hydei, D. funebris, D. virilis* and *D. lebanonensis*. The flies were derived from laboratory stocks.

In addition, the surface structure of the eyes of the *D. melanogaster* eye colour mutants (white (w), vermilion (v), cinnabar (cn), brown (bw), Plum (Pm) and brown-cinnabar (bw/cn)), as well as mutants displaying structural modifications of the eye (Bar (B), rough (ro), roughoid (ru), eyeless Dominant (ey^D), echinus (ec) and sparkling-poliert (spa^{pol})), were investigated. Some observations were also made on the heterozygotes wild/spa^{pol} and wild/Bar.

Results

As described previously (Hartman and Hayes, 1971), the surface of the wild-type eye of *D. melanogaster* displayed hexagonal packing of the facets and bristles at three of the corners of each facet (Fig. 1, 5). An essentially similar pattern of eye surface structure was observed in *D. simulans, D. hydei, D. funebris* and *D. virilis*. The eyes of each of these species, as well as those of *D. melanogaster*, displayed a distal peripheral zone, 5–6 facets wide, in which no bristles were present between the facets (Fig. 2, 3, 4). Occasionally, patches of facets at other locations were also devoid of bristles.

In contrast to the regularly observed hexagonal packing of the facets (Fig. 5), the eyes of *D. lebanonensis* clearly revealed a tetragonal packing with bristles present at each of the corners (Fig. 6). This character can be seen most distinctly in the strain "Utah". In the strains "Arizona" and "Leiden" the regular localisation of bristles does not always exist (Fig. 7).

In all species irregularities in the occurrence of bristles could be observed occasionally (Fig. 8). Sometimes the length of the bristles also differed, some bristles remaining extremely short compared with the normal bristle length observed.

A comparison of the eye surfaces of various eye colour mutants of *D. melanogaster* (see under material and methods) did not reveal obvious differences in the surface structures compared with the surface of the wild-type eye (Fig. 9).

The Bar-mutant eye showed irregular packing of the reduced number of facets and sometimes the presence of extremely long bristles in homozygotes as well as heterozygotes (see also: Hartman and Hayes, 1971) (Fig. 10, 11). A similar aberrant packing of the facets was observed in the echinus mutant (Fig. 12), which also displayed an obvious reduction in the

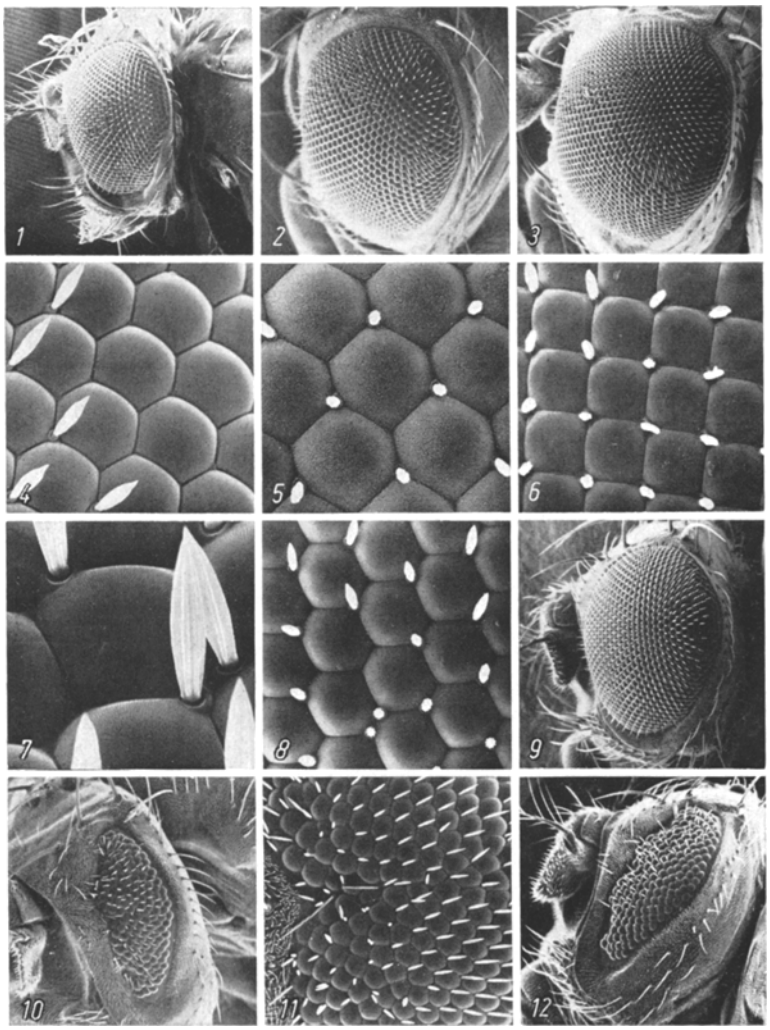

Fig. 1. *D. melanogaster*, Wild-type (50×)

Fig. 2. Eye of *D. funebris*, note: missing bristles in different areas of the eye (50×)

Fig. 3. Eye of *D. hydei* showing at its periphery a zone 5 facets in breadth devoid of bristles (50×)

Fig. 4. Detail of a region lacking bristles in an eye of *D. virilis* (500×)

Fig. 5. Hexagonal packing of facets in the eye of *D. melanogaster* (660×)

Fig. 6. Tetragonal packing of facets in the eye of *D. lebanonensis*, "Utah" (500×)

Fig. 7. Irregular localisation of bristles in the strain "Arizona" of *D. lebanonensis* (1,200×)

Fig. 8. Irregularities in the implantation of bristles at the surface of the eyes of *D. simulans* (500×)

Fig. 9. The eye colour mutant cinnabar of *D. melanogaster* (50×)

Fig. 10. Homozygote Bar, *D. melanogaster* (50×)

Fig. 11. The occurrence of long bristles in the eye of a heterozygote wild/Bar of *D. melanogaster* (150×)

Fig. 12. The eye of the mutant echinus of *D. melanogaster* (50×)

number of bristles and great variation in bristle size (Fig. 13).

The mutant eyeless-Dominant showed irregularly shaped facets, a reduced number of facets and variation in bristle size (Fig. 14). The eye shape seems to be equal to that of the female of the F_1-generation of the cross B × wild.

The most obvious differences, when compared with the surface structure of the wild-type eye of *D. melanogaster*, however, were seen in the eyes of the mutants, rough, roughoid, and sparkling-poliert (Fig. 15, 16, 17). The mutant rough displayed irregular implantation of the bristles, variations in bristle size and irregularly shaped facets. Sometimes, groups of bristles were closely packed (Fig. 18). The mutant roughoid displayed essentially the same features as the mutant rough. Incomplete separation of ommatides was very often seen in this mutant (Fig. 19, 20). In contrast to the structural mutants, B, ec and ey^D (Fig. 10, 12, 14), the eye shape of ro and ru (Fig. 15, 16) is round, though the surface corresponds to that of the above mentioned mutants.

Like the mutant lozenge (Hartman and Hayes, 1971), the mutant sparkling-poliert has no clear-cut facets on the eye (Fig. 17, 21, 22). The eyes of heterozygotes (+/spa^{pol}) are identical to those of the wild type. This is not the case for heterozygotes of Bar and eyeless-Dominant. These heterozygotes displayed structural characteristics on the eye surface which are identical to those found in the homozygous mutants. However, the extent to which these characteristics were present is intermediate between the wild type and the homozygous mutant type (Fig. 10, 23, 24).

Discussion

As to the gross morphology of the eyes of mutants of *Drosophila melanogaster*, this investigation confirmed earlier descriptions which formed the basis for identification of the mutant phenotype (see for *Bar*: Tice, 1914; Morgan and Bridges, 1916; Krafka, 1924,

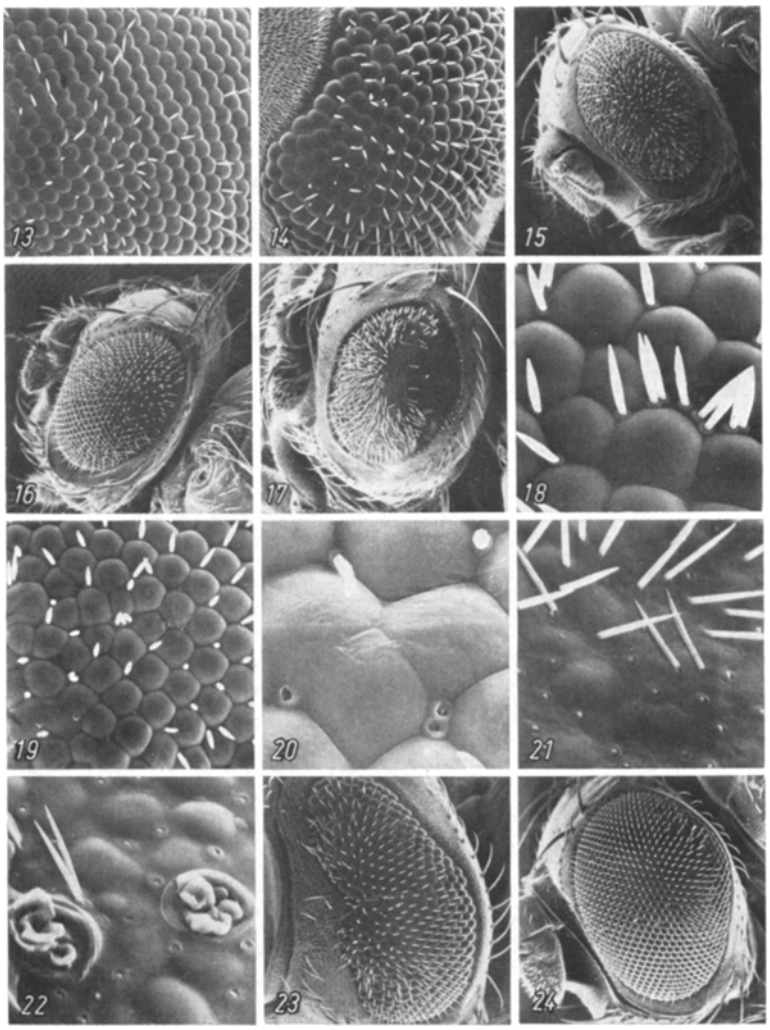

Fig. 13. Small bristle number and variation in bristle size in the eye of the mutant echinus of *D. melanogaster* (150×)

Fig. 14. The mutant eyeless Dominant (ey^D) of *D. melanogaster* (150×)

Fig. 15. The irregular structure of the eye in the mutant rough of *D. melanogaster* (50×)

Fig. 16. Surface structure of the eye in the mutant roughoid of *D. melanogaster* (50×)

Fig. 17. Surface structure of the eye of the mutant spa^{pol} in *D. melanogaster* (50×)

Fig. 18. Group of eight bristles implanted closely together in the eye of the mutant rough of *D. melanogaster*. Note the irregular shapes of the facets (660×)

Fig. 19. Detail of the eye surface in the mutant roughoid of *D. melanogaster* with variable length and irregular distribution of the bristles and the shape of the facets (330×)

Fig. 20. Incomplete separation of three ommatidia in the eye of the mutant roughoid of *D. melanogaster* (1,000×)

Fig. 21. Detail showing the absence of a clearly delineated facet structure in the mutant spa^{pol} of *D. melanogaster* (500×)

Fig. 22. Modified facets in the eye of spa^{pol} in *D. melanogaster* (660×)

Fig. 23. Heterozygote Bar/wild in *D. melanogaster* (70×)

Fig. 24. Heterozygote spa^{pol}/wild in *D. melanogaster* (50×)

for *eyeless-Dominant*: Chen, 1929; for *rough* and *roughoid*: Bridges and Morgan, 1923; for *echinus*: Morgan, Bridges and Sturtevant, 1925; for sparkling-poliert: Rickenbacher, 1954). The present investigation adds, essentially, only details to those previous descriptions. This is also clear from the comparison of the eyes of eye colour mutants with the wild-type eye, which were, according to Johannsen (1924), identical in their surface structure. Eye colour mutants only differ from wild-type flies in the amount and distribution of the two colour pigments.

The eye of the eyeless mutant ey^D has the normal hexagonal facet pattern but the mutant eyeless-Russian (Hartman and Hayes, 1971) shows tetragonal packing of the facets. We observed tetragonal facet packing in *Drosophila lebanonensis* also, but the three strains investigated ("Arizona", "Leiden" and "Utah") differ in the degree of this special character.

The mutant rough is distinguished by facets which are different in size or are fused together, and for the random distribution of the bristles. Muller (in Bridges and Morgan, 1923) has described this mutant as one displaying ommatidia and in which the facets are variable in size and shape and are crowded in irregular rows.

Eye structure similar to rough is found in the mutant roughoid. This mutant was detected by Sturtevant (Bridges and Morgan, 1923) and differs from rough by having a number of large black ommatidia which are scattered over the surface of the eye though more frequent in the central part.

The mutant spa^{pol}, spontaneously originated in Zürich in 1952 and described by Rickenbacher (1954) under the name poliert = pol, has an eye without any facets. In contrast to lozenge, it has more bristles, which are irregularly arranged, especially in the periphery of the eye, while the centre lacks bristles entirely. The craterlike structures visible on the eye surface may be identical with the tormogen-trichogen cell complex, described by Lees and Waddington (1942), which normally becomes visible 15h after pupation. Perhaps in the spa^{pol} mutant the physiolo-

gical state of the eye is functionally arrested at the pupal phase.

Since the scanning electron microscope combines high resolution and a large depth of field, it could be applied to the detailed investigation of modifications of wild-type and mutant surface structures under the influence of different genetic backgrounds. Because a great variety of mutants of *D. melanogaster* with structural modifications have been described, and some of them, as shown here, display clearly distinguishable patterns of structures which differ from the wild-type, these could be used for studies on the influence of different genotypes upon the morphogenesis of such patterns. The details resolved by the scanning electron microscope should not only provide an opportunity to use many structures in such studies but also to map their positions.

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