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Author

Harris, William A.

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William A. Harris
DONNER LABORATORY

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THE FRUIT-FLY (DROSOPHILA MELANOGASTER): A SCANNING ELECTRON MICROSCOPIC STUDY

by William A. Harris
Donner Laboratory
Lawrence Berkeley Laboratory
University of California
Berkeley, California

To: Stephanie Sloan

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PREFACE

This brief monograph is intended for a wide audience. It is designed to introduce the fruit-fly Drosophila to scientists and students who are beginning to work with them as insects with a magnificently complex external morphology. It should also be useful to both geneticists and entomologists who wish to have a better idea of what the fine structure of the very microscopic external parts look like. Finally, it is aimed at the layman as a praise of one of nature's smaller animals (measuring about the size of this hyphen "-".)

The Scanning Electron Microscope is a powerful instrument for revealing the three dimensional structure of tiny biological objects, as this study shows. It gives, however, primarily morphological information. Morphology alone cannot say terribly much in the way of biological function, but it does sometimes hint. Therefore if this study offers many hypothetic functions for the various anatomical pecularities of the fly, the reader should understand that these hypotheses are not teleological fallacies but only tentative suggestions. Some of these suggestions are, perhaps, worth testing by more experimental techniques.

The layout of the study is straightforward. The first chapter is a general morphological introduction to the fly, and the chapters that follow deal with specific parts which represent longstanding interests.

I am deeply indebted to Professors Curt Stern, Collin Murphey, Chiyoko Tokunaga, Evert Schlinger, and Jack Citrin for their valuable

suggests on different portions of the text, and for their reassurance. I am especially thankful to Professor Rudolf Pipa for his thorough comments on the entire manuscript. But to Dr. Thomas Hayes who helped me tremendously in every aspect of this study, from beginning to end, I am most grateful of all.

This work was funded by the President's Undergraduate Research Fellowship of the University of California, and was also supported by the United States Atomic Energy Commission.

W. H.

A Note on Terminology

Entomologists and geneticists have different ideas on the naming of all the filamentous, tiny, external processes that arise over the entire surface of insects. It is not clear what we should call these hairs, bristles, setae, chaetae, spines, tichomes, or whatever.

In this book, an attempt has been made to consistently refer to the same types of processes in the same way. The name "mechanoreceptive spine" or just "spine" is usually used instead of "macrochaeta", "seta", or "bristle"; "sensilla trichodea" is used instead of "microchaeta"; and "hair" is used instead of "trichome" or "spinule". These terms were chosen because they are more indicative of function than classification, as a result, they are used more by entomologists than geneticists. On the other hand, one name is as good as another and whether one says "bristle" or "seta" or "spine" or "macrochaeta" makes no difference since they all refer to the same thing.

General Morphology and Chaetotaxy

God in His wisdom
Made the fly,
And then forgot
To tell us why.
Ogden Nash

It is wise to acquaint ourselves with the greater morphology of the fly before we focus our attention to the specific areas of interest. Yet since discussions of the general external morphology have been exhaustively handled by Snodgrass (1935), Crampton (1948), and Ferris (1950), I will not duplicate their efforts. Instead, to simplify matters, a series of diagrams will be presented in this short chapter.

These diagrams speak for themselves. So there will be no explanatory text. If the reader wants to hear something more of the head, the thorax, or the abdomen in general, he is referred the three aforementioned authors. Otherwise, let these figures serve to familiarize us with the nomenclature necessary to continue.

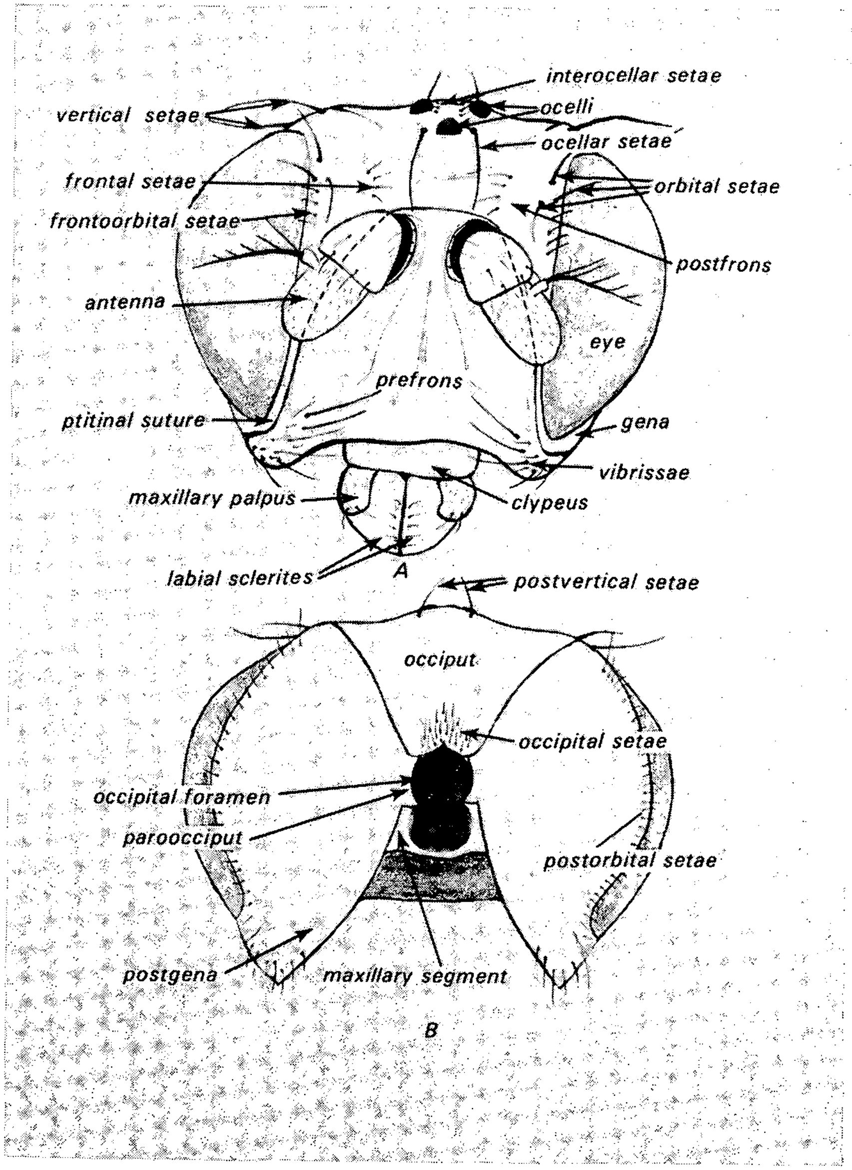
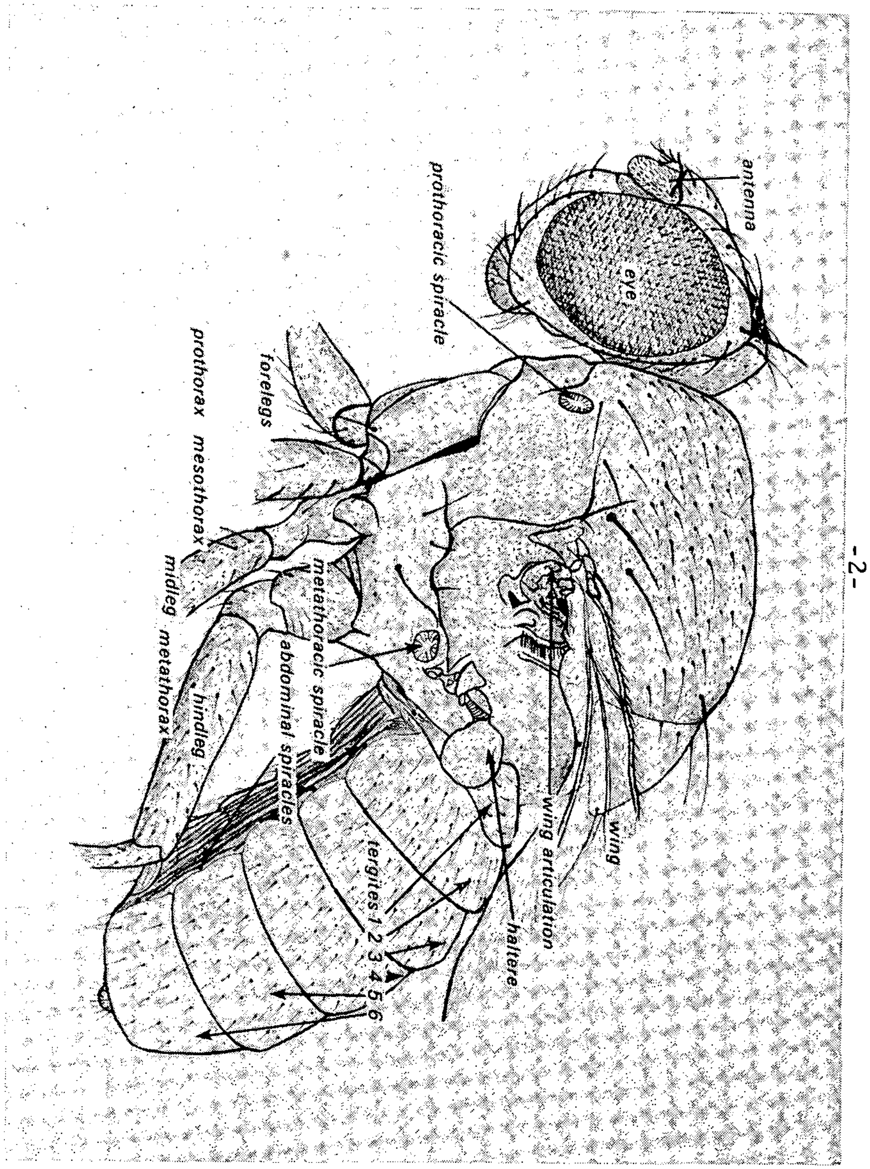
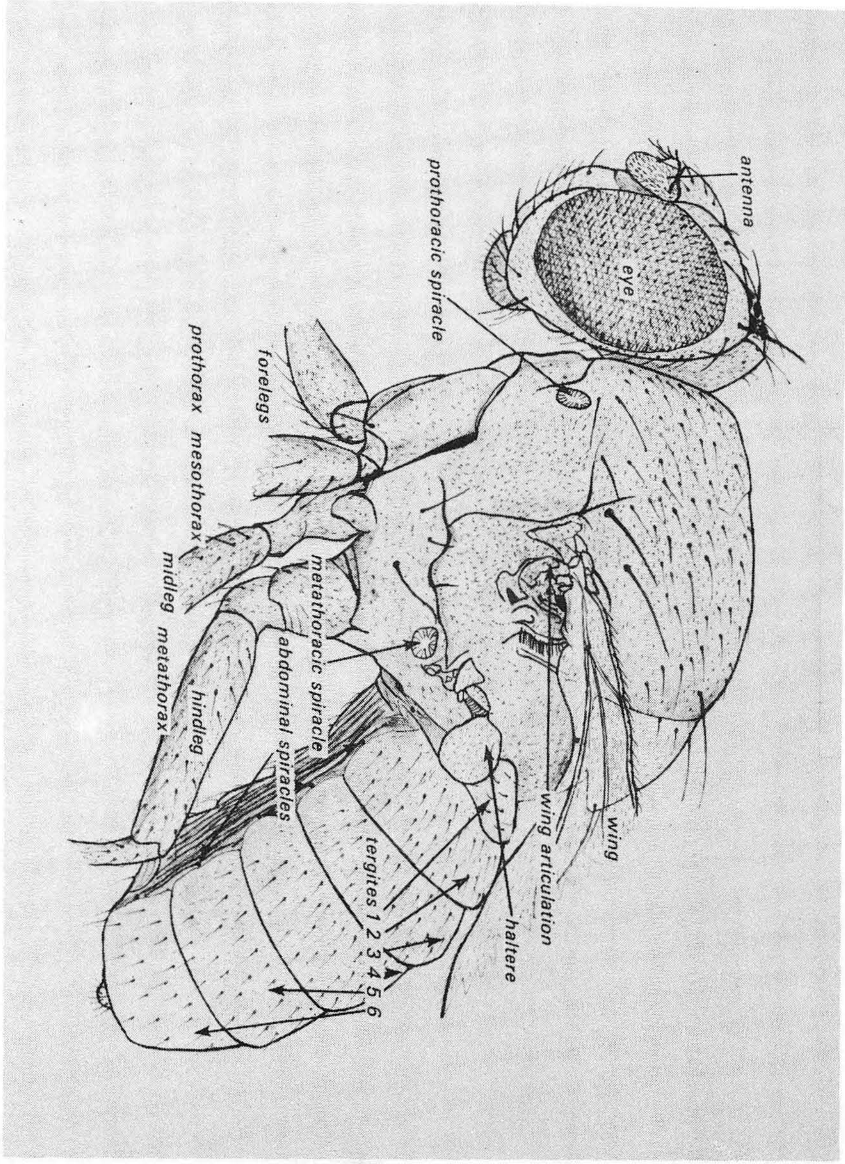


fig.2: Diagram of head; A, cephalic; B, caudal view.

fig.1: Diagram of whole Drosophila.





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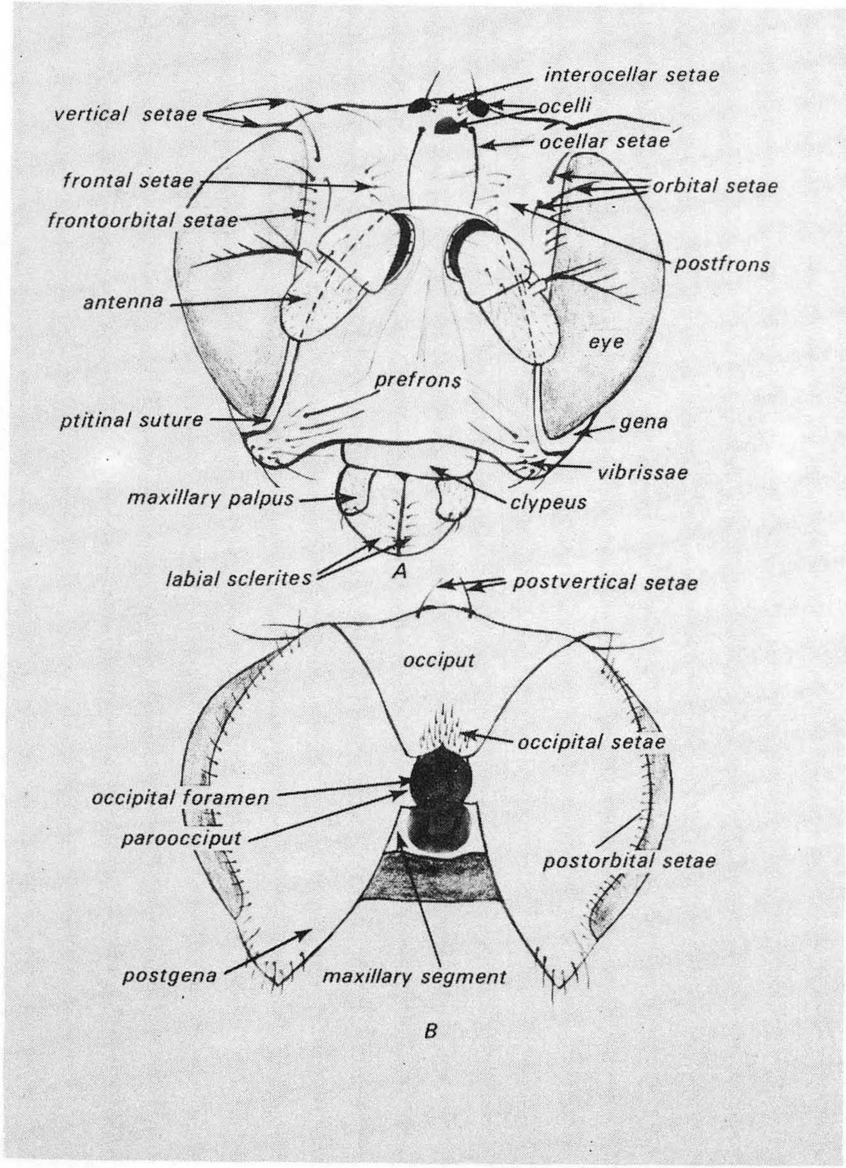


fig.2: Diagram of head; A, cephalic; B, caudal view.

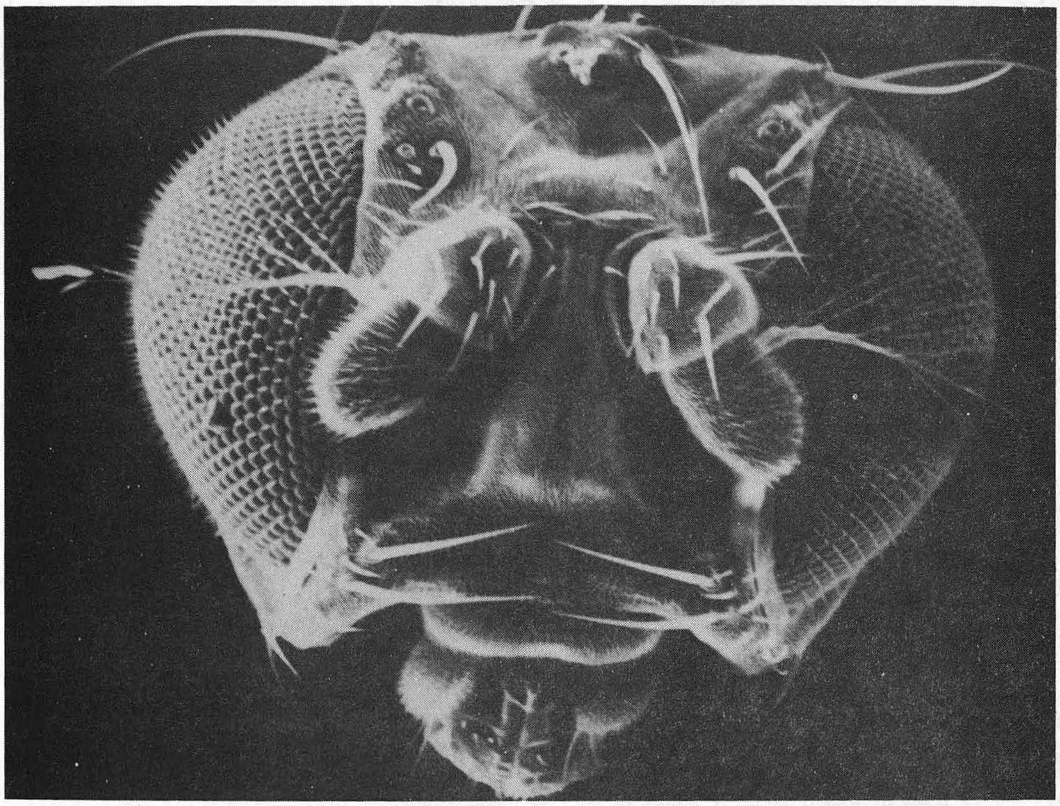


fig.3: Head, cephalic aspect.

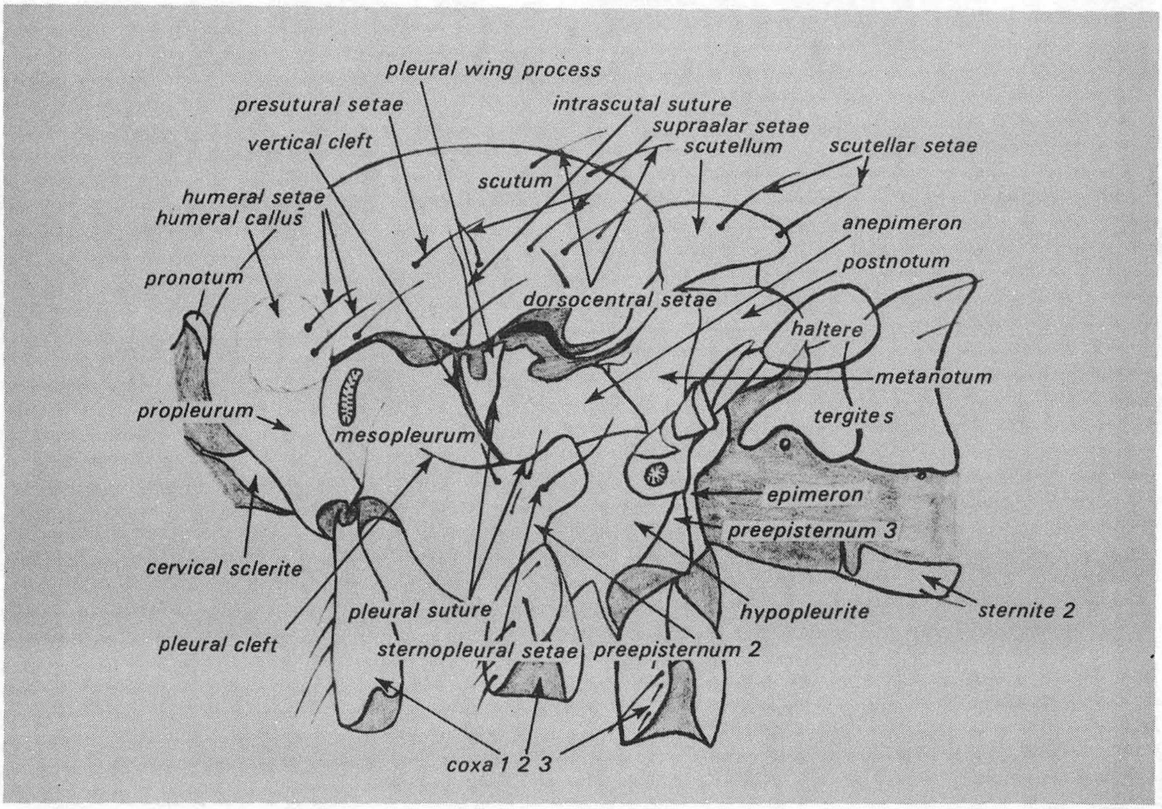


fig.4: Diagram of thorax, lateral view.

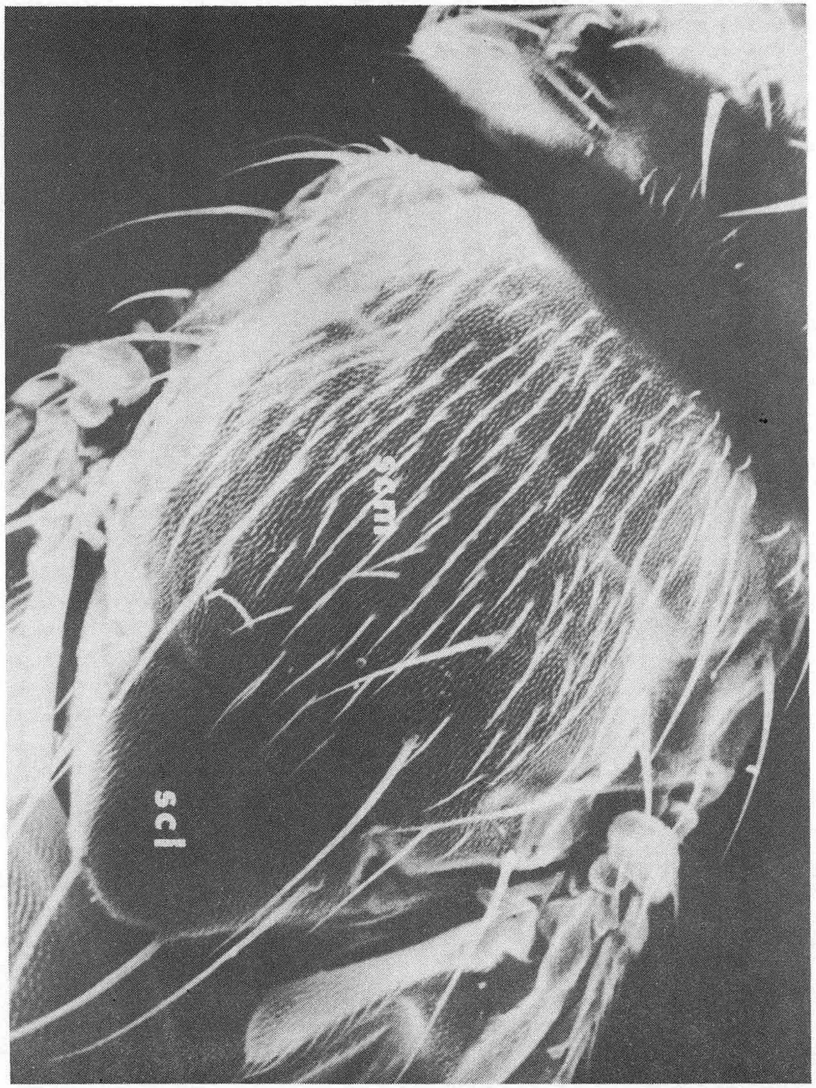


fig.6: Thorax, dorsal aspect; scm, scutum; scl, scutellum.

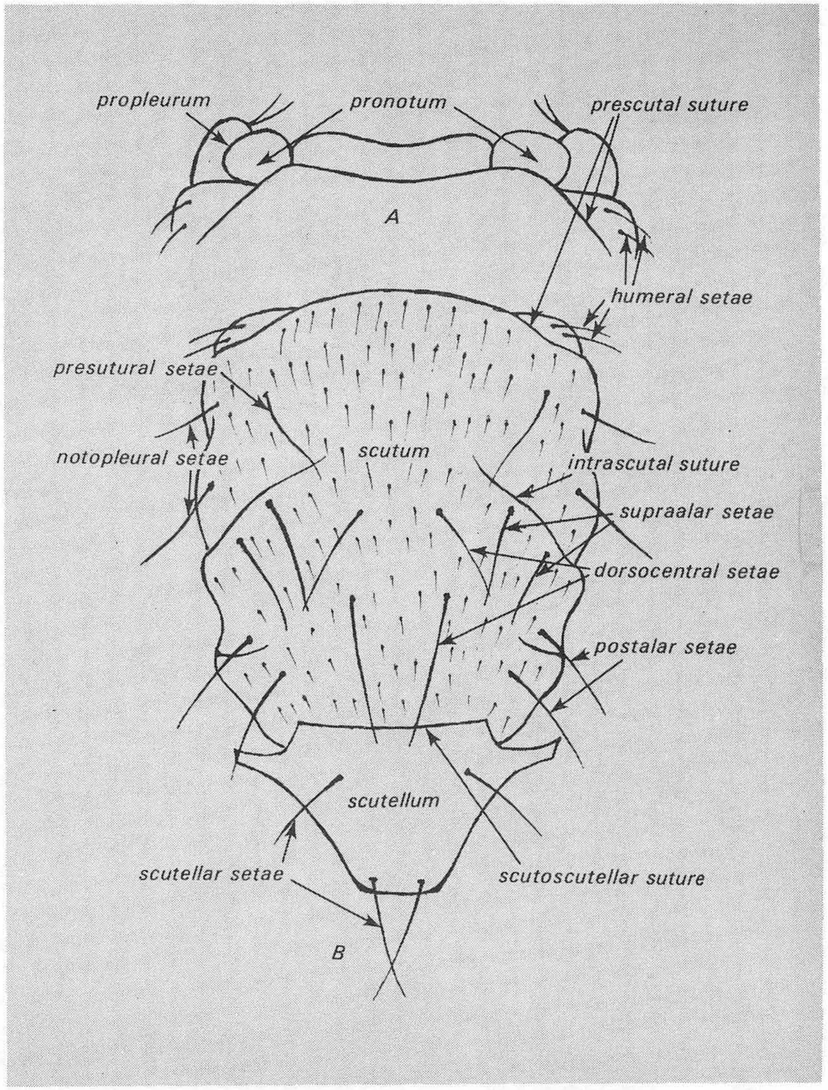


fig.5: Diagram of thorax, dorsal view; A, prothorax; B, pterothorax.

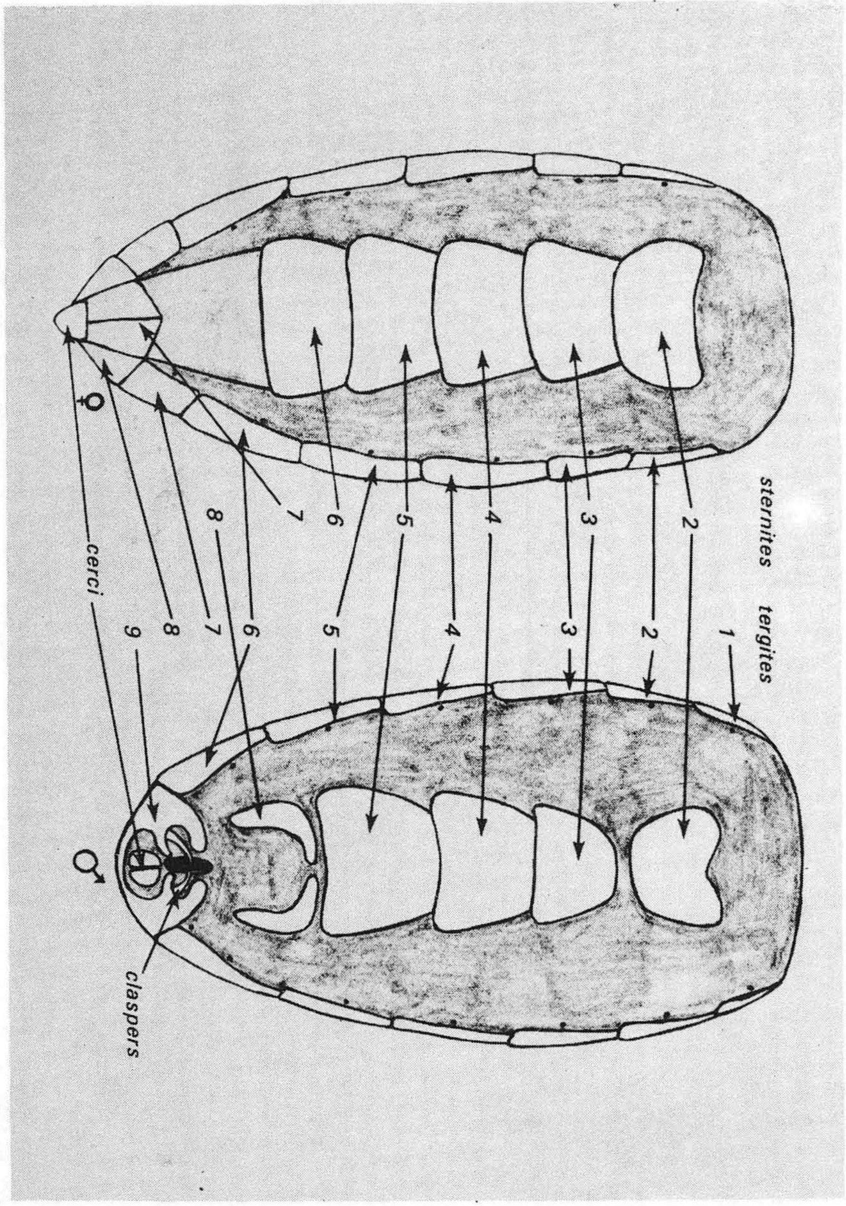


fig.8: Diagram of abdomen, ventral view, female (left), male (right).

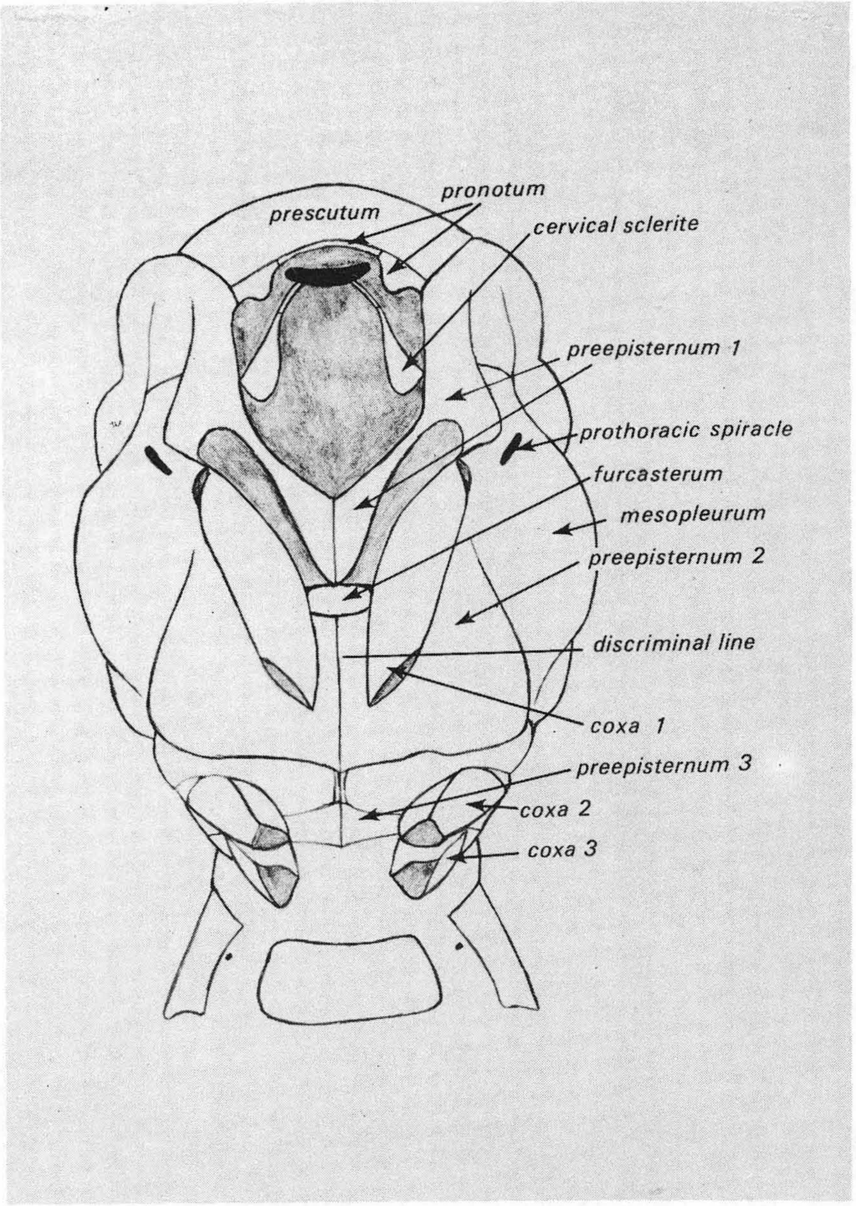


fig.7: Diagram of thorax, ventral view.

The Eyes

But eyes! Do not dispense with those!
Abandon ears; give up your nose.
But we most earnestly advise:
Hang on most firmly to your eyes.

Walter Brooks

The compound eyes, the immense visual organs that most insects and all true flies share, are particularly large in Drosophila (figure 1). To trace the exact origin of compound eyes in insects is extremely difficult, but we do know that similar organs of vision existed in trilobites as far back as the Paleozoic era five-hundred-and-seventy-million years ago, and are an ancient heritage of invertibrate arthropods, (Snodgrass, 1935).

Each element of the compound eye is called an ommatidium, and each ommatidium functions as a separate, individual, and simple eye. In the eye of the housefly there are about four-thousand of these ommatidia; there may be as many as twenty-eight-thousand ommatidia in a single one of the dragonfly's great globular eyes, (Wigglesworth, 1964). In Drosophila, each compound eye has between seven-hundred and eight-hundred ommatidia, (figure 2). Each eye is about 0.42 mm. high and 0.33 mm wide, and each ommatidium is about 0.017 mm. in diameter, (Miller, 1950). Using these numbers to calculate, one might expect that each eye should have only about five-hundred ommatidia. The actual number is greater, obviously, because of the curvature,

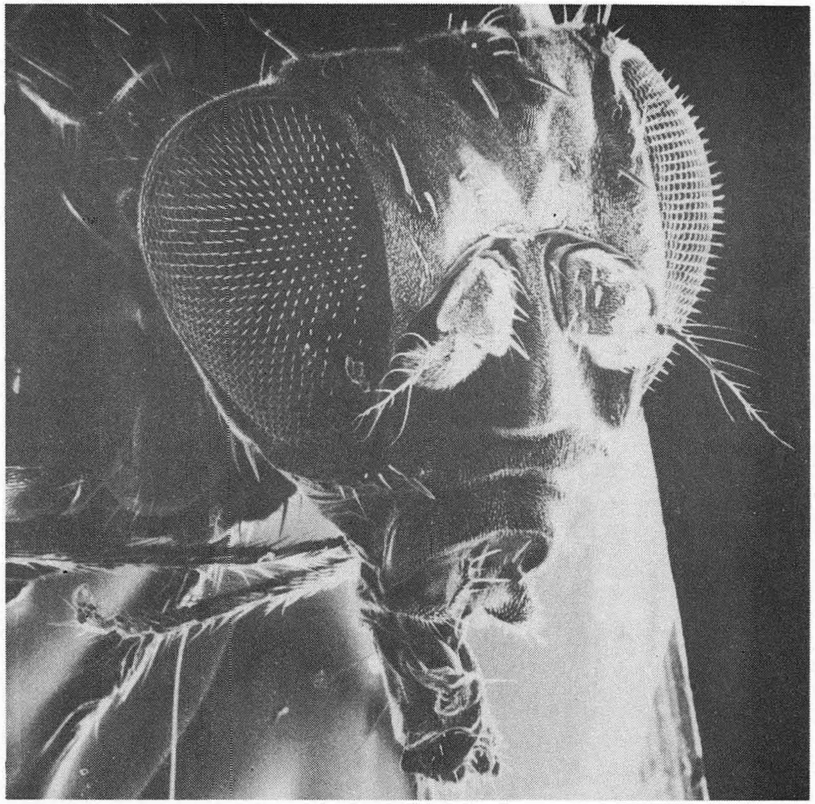


fig.1: Front view of head.

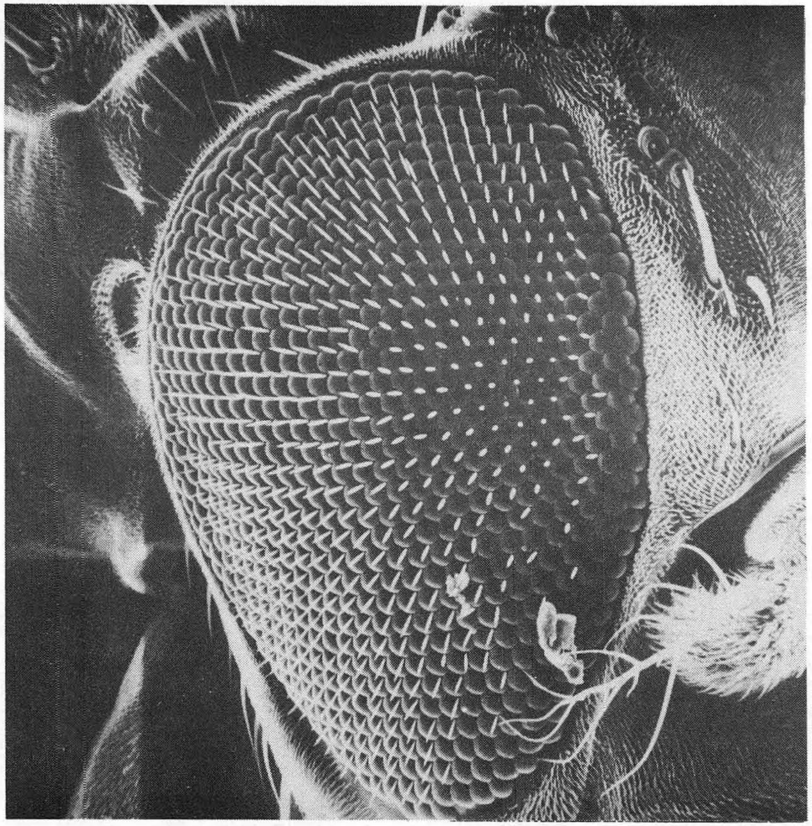


fig.2: The compound eye.

the bulging of the eye. Because of this great convexity of the compound eyes, the insect has visual access to approximately four-fifths of the sphere of solid angle which surrounds him. No two ommatidia on one eye look quite towards the same spot; thus there is no capacity for stereoscopic vision in a single eye.

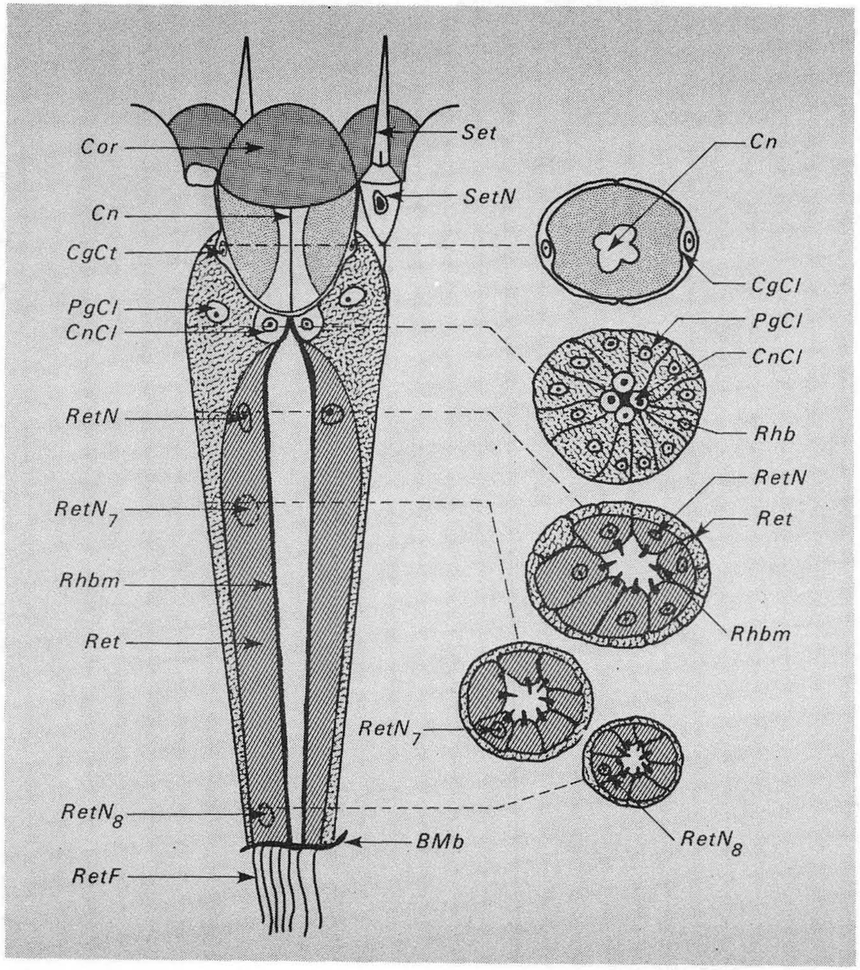
One of the ways in which we perceive the distance to an object is the extent to which our eyes converge as we look at it. But in an insect the eyes are immovable with respect to each other, so he must use a different means of distance perception. An insect can, for instance, face the object and gradually approach it; the visual images will move towards the inner part of the two eyes, thus telling him the distance by the rate of convergence of the images, (Wigglesworth, 1964). Of course, the fly may also be able to tell the distance to an object he is facing by standing still and judging the retinal positions of the two images, one in each eye, of that same object.

When one considers, however, how poor the acuity of vision is in the compound eye, (Burtt and Catton 1961), then it is clear that stereoscopic vision plays a minor role in the life of insects. Each ommatidium collects the light from a little patch of the outside world, and what the single ommatidium registers is the average intensity of light from that little patch, (Wigglesworth, 1964). Taken together, all of the ommatidia in the compound eye of a <u>Drosophila</u> pick up about eight hundred patches of light. The resolution in such a system is poor indeed, the fly can only resolve objects that are more than about one foot apart at a distance of about five feet; compared to human vision, the fly's picture of the world is very blurry.

The detail in figure 3 reveals that each ommatidial lens is covered by tiny bumps (diameter 265 mμ.). It has been suggested that these bumps tend reduce the reflection of incident light and thus serve to protect the fly by lowering the probability of a preditor detecting the fly by light scattered from the large eyes, (Beidler, 1969). But it may well be that these bumps serve some more physio-optical purpose.

The compound eyes of Drosophila are of an opposition type, which means that each ommatidium is separate and has its own retinal cells. Figure 4 is a diagram of a typical ommatidium. Each ommatidium has a surface corneal lens, and two corneagenous (pigment-bearing) cells which surround a crystalline cone used to focus the light. Four cone cells secrete the cone and lie immediately beneath it. The retinula consists of eight parallel sense cells round an axial rhabdom which has a receptive function and consists of a bundle of seven rhabdomeres (spread apart except at the upper end of the elongate retinular cells.) The eigth retinular cell, restricted to the base of the ommatidium is much smaller and has neither a rhabdomere nor a detectable optic fiber; its nucleus is near the basement membrane which underlies all the ommatidia and which is pierced by optic fibers from the retinular cells and by tracheae. Finally, a sheath of about twelve secondary pigment cells surrounds the retinular cells and shares these cells with adjacent ommatidia, (Miller, 1950).

The rhabdom is composed of highly refractile material so that light entering it is largely internally reflected from the inside walls;



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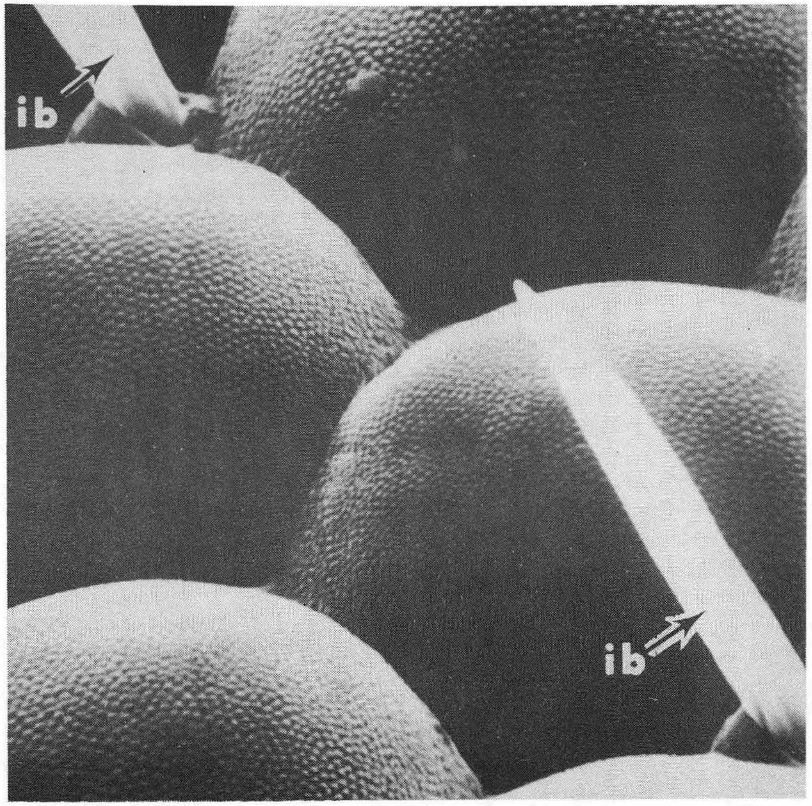

fig.3: A close-up of the ommatidial facets.

fig.4: Ommatidia of a compound eye, (after Hertweck). Longitudinal section and transverse sections at levels indicated. Bmb, basement membrane; CgCl, corneagenous cells; Cn, crystalline cone; CnCl, cone cells; Cor, corneal lens; PgCl, secondary pigment cells; Ret, retinular cells; RetF, optic nerve fiber; RetN, nuclei of retinular cells; $\text{RetN}_{7,8}$, nuclei of 7th, 8th retinular cells; Rhb, apex of rhabdom; Rhbm, rhabdomeres; Set, interommatidial bristle; SetN, neuron of bristle.

thus the rhabdom is a good conductor of light. In the basement membrane, the tracheal branches, in addition to their respiratory function, serve to reflect the light back so that the rays retraverse the rhabdom with the result that the sense cells are doubly stimulated, (Wigglesworth, 1939).

One can notice in figure 2 that the eye facets are packed hexagonally, and that at three of the six corners of each facet, there is a short spine called an interommatidial bristle, (figure 5). In eye mutant strains of Drosophila, however, the placing of these spines and the packing of the facets is often abnormal. In the eyeless-Russian mutant, (figures 6 and 7), the facets are tetragonally packed with a spin at each corner, (Hartman and Hayes, 1971). In the bubble-eyed mutant, (figures 8 and 9), there is irregular facet packing and interommatidial bristle array, (often two spines arise at one corner,) and there is an ingrowth of the integument into the eye, (Hartman and Hayes, 1971). The bar-eyed mutant, (figure 10), has few ommatidia and very few spines. The lozenge-eyed mutant, (figure 11), has an eyes with no facets at all, and only a very, very few spines, (Hartman and Hayes, 1971).

It has been noted with regard to visual—mutant flies, that the eye itself is always mutant. It does not matter if the whole rest of the fly is constructed of normal tissue. In other words the visual deficits of the fly and the causes of abnormal phototactic behavior lie within the eye, and not, as we might expect, in the brain, (Hotta and Benzer, 1970).

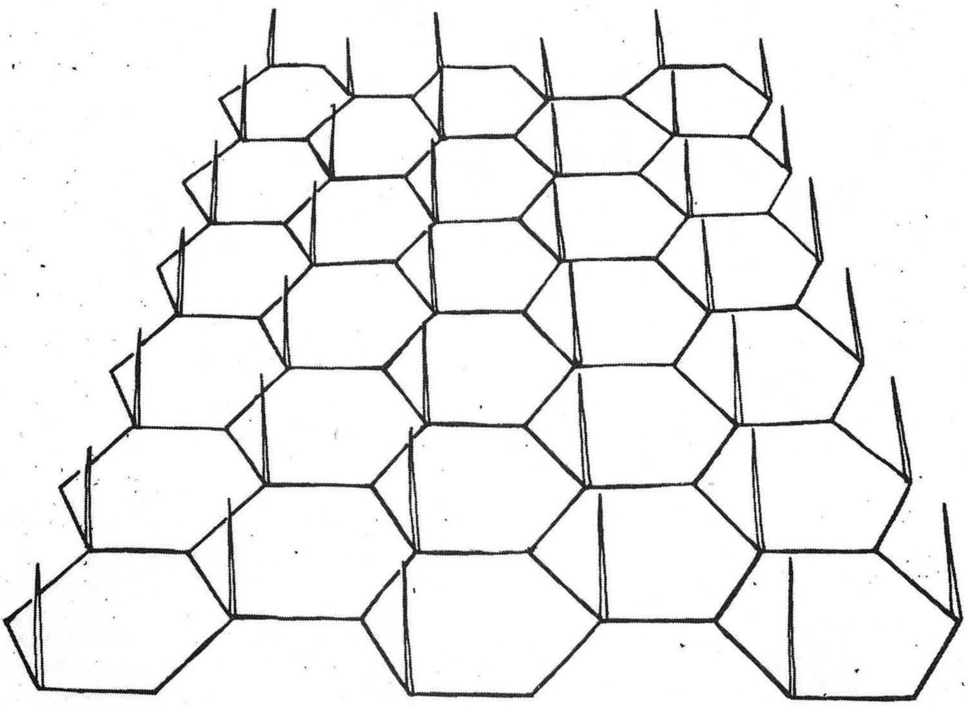

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fig.5: Schematic representation of facet packing and interommatidial bristle array in wild-type eye;(after Hartman and Hayes).

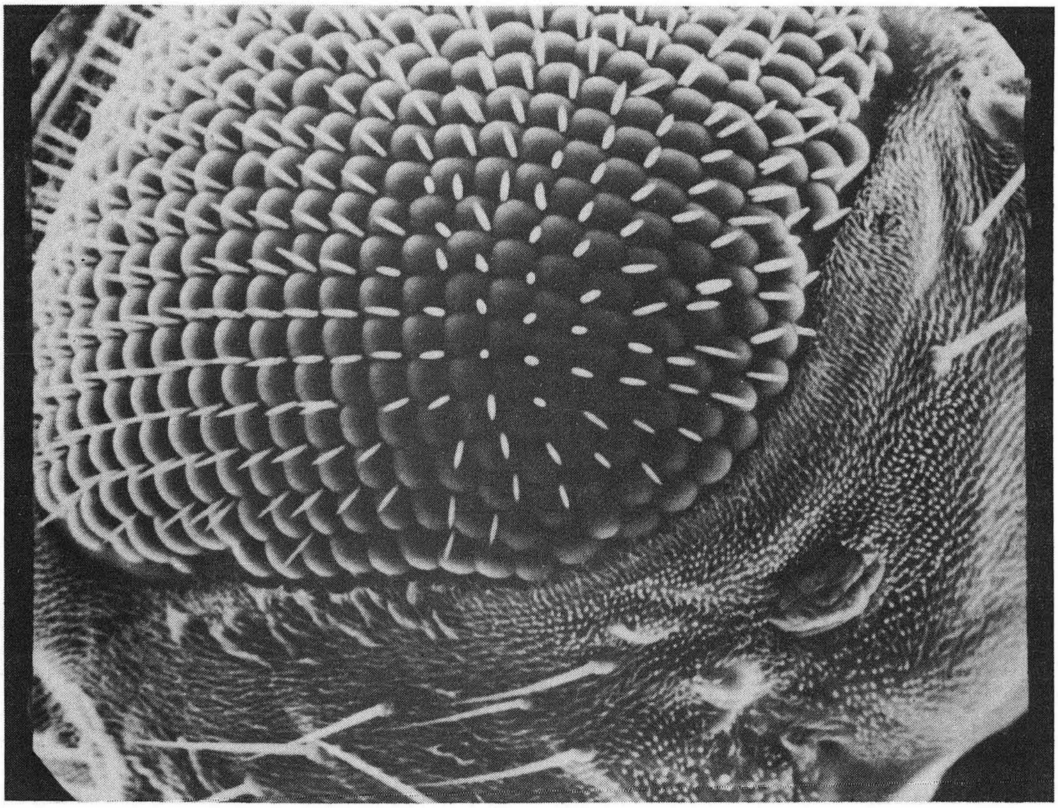

fig.6: The eye of an <u>eyeless-Russian</u> mutant.

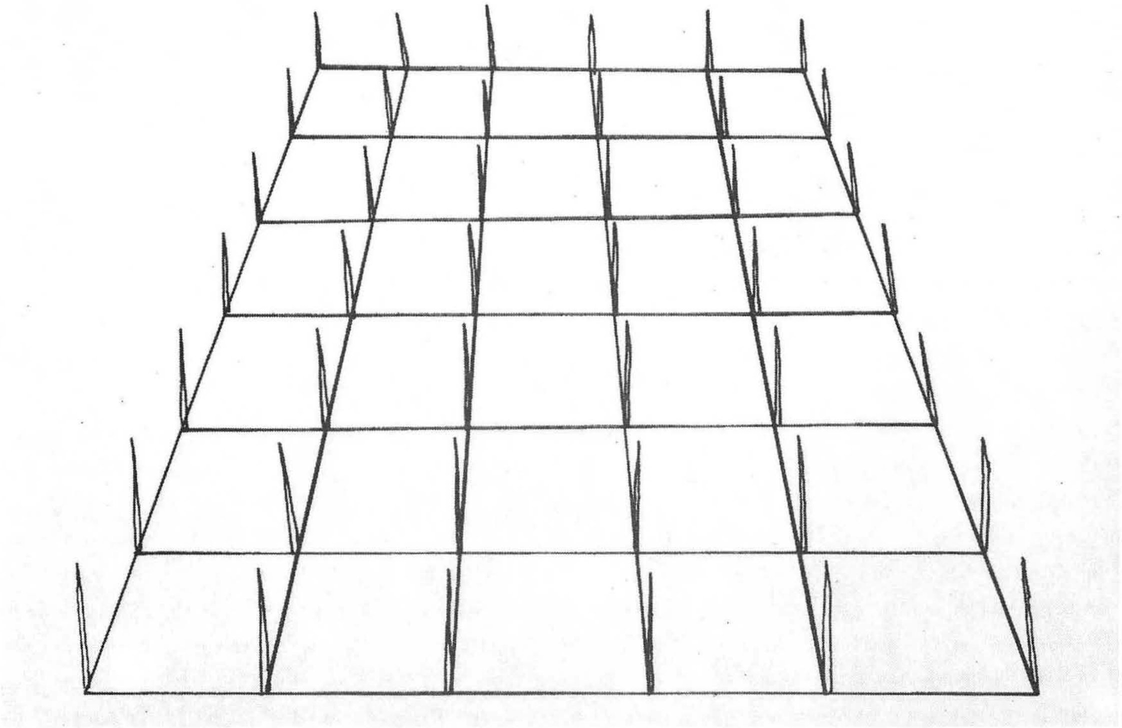

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fig.7: Schematic representation of facet packing and interommatidial bristle array in the eyeless-Russian eye;(after Hartman and Hayes).

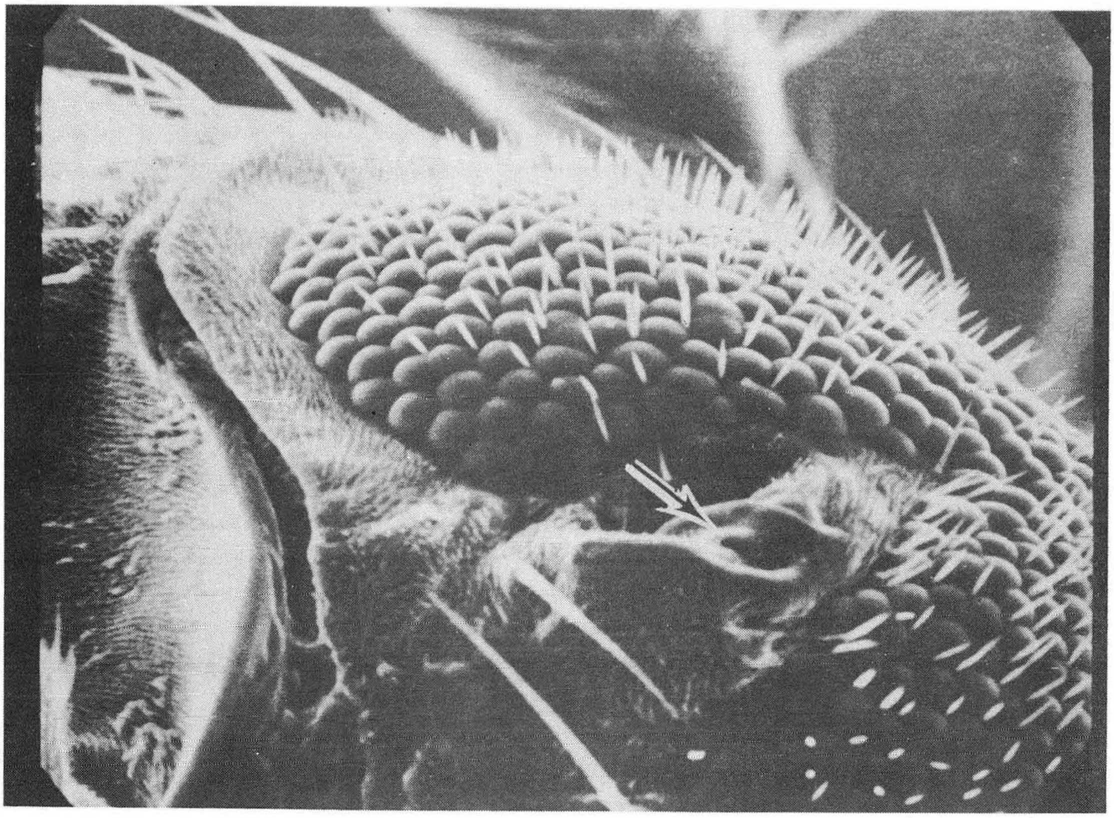

fig.8: The eye of a bubble-eyed mutant; arrow to the ingrowth of integument.

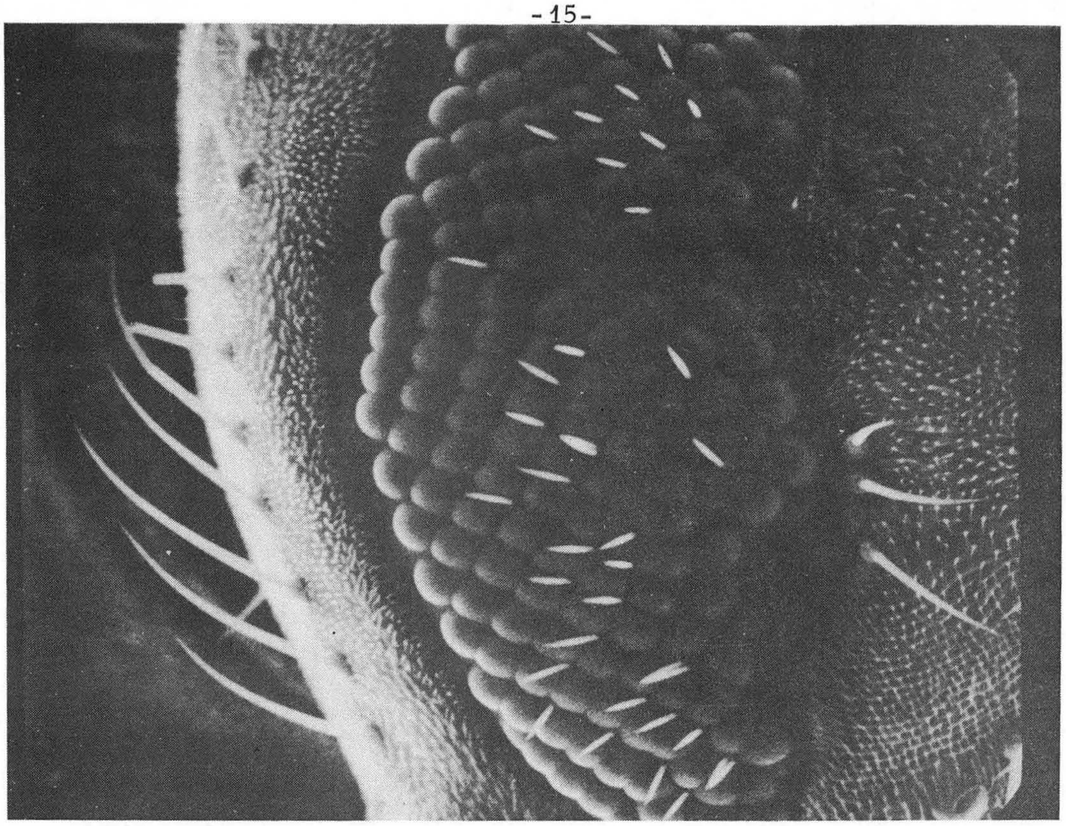

fig.10: The eye of a bar-eyed mutant.

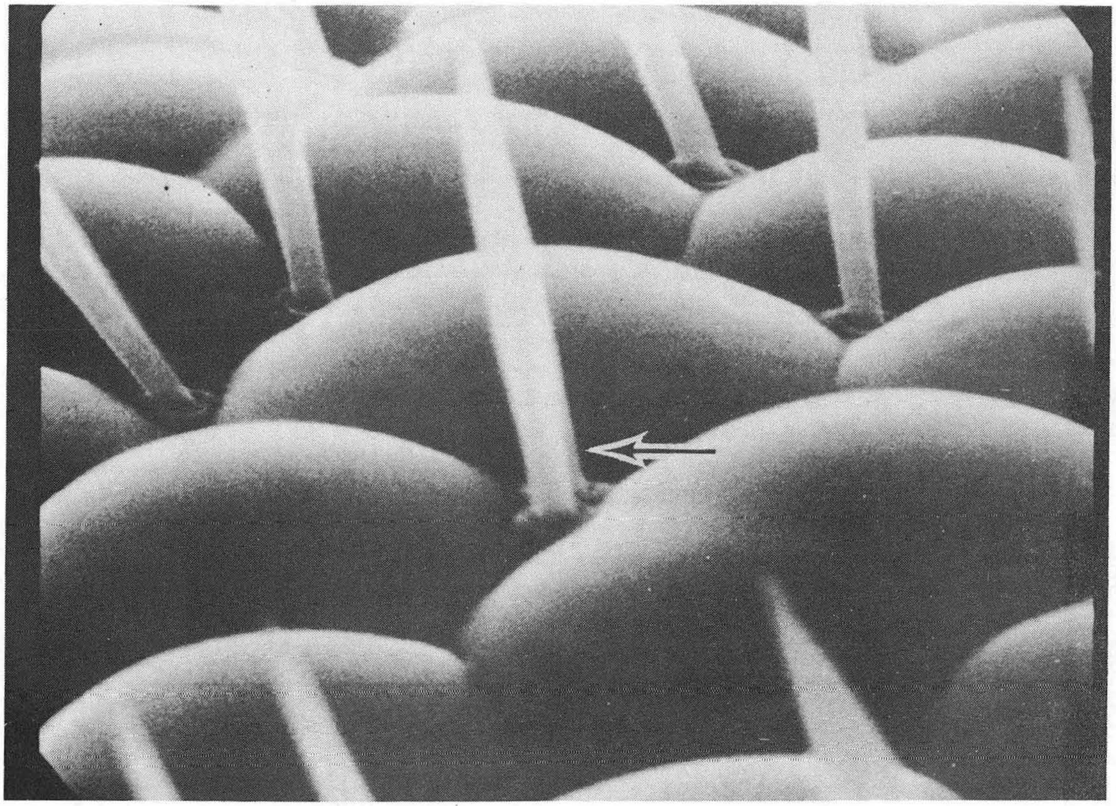

fig.9: A close-up of the eye of a <u>bubble-eyed</u> mutant; arrow to double bristle.

The furrows in the bottom of the interommatidial bristles are analogous to the furrows in mechano-receptive spines, (figure 3). Indeed, transmission electron microscopic studies reveal that the interommatidial bristles are like these spines in possessing a sense cells with complex terminal dendrites, (Perry, 1968). The interommatidial bristle, then, is most probably, a mechano-receptor. One hypothesis for the existance of such receptors on the eyes states that the fly can distinguish a speck of dust on his eye from a far object of he can feel it with an interommatidial bristle; of course, he can distinguish it without these spines if he turns his head slightly. A counter-hypothesis says that the interommatidial bristles may function as a protective barrier for the more delicate ommatidial lenses.

These micrographs do not show that the eye of Drosophila is a brilliant red. This red color results from the ommachromes which are pigments often associated with pterine which is also red. The ommachromes form granules in the secondary pigment cells, and in the eye they provide the screen that separates each ommatidium from its neighbor, (Wigglesworth, 1964). The granules can move up and down in the cell, and thus control the amount of light reaching the sensory portion of the ommatidium, (Ross, 1967). In a light adapted Drosophila eye the pigment cells completely isolate one ommatidium from another by spreading the granules over the cone and retinula. But in the dark adapted eye, the pigment is withdrawn, permitting light to pass from one ommatidium to the adjacent ommatidia, and thus allowing maximum photosensory stimulation, (Wolken, Mellon, and Contis, 1957).

In Drosophila, the eye pigments absorb light selectively, allowing only those wave-lengths which are most effective in stimulating the photo-receptors to pass. The major peak in sensitivity is at 366 mμ in the near ultra violet, (Wigglesworth, 1965), and there is a minor peak at about 487 mμ in the blue-green, (Dethier, 1963).

On the top of the fly's head sit three dorsal ocelli: one median, and two more lateral, (figure 12). They are amber in color and oval in form, measuring about 30 μ by 40 μ, (Miller, 1950). They are protected by large and small mechano-receptive spines which are arranged in a remarkable pattern. There is evidence that the median ocellus has been formed by the union of two primitive frontal ocelli, (Snodgrass, 1935).

Each ocellus, as diagrammed in figure 13, has a thick plano-convex lens or cornea, under which lies a layer of about fifty or more retinal cells which form a swelling called the ocular nerve. The upper ends of the sense cells form a hyaline zone where they group together in receptive rods or rhabdoms, (Miller, 1950).

The ocelli seem to be able to sense rapid changes in illumination, and they then stimulate or "wake-up" the nervous system and bring the fly into a state in which he can react quickly to what it sees through the compound eyes, (Wigglesworth, 1964). Thus the response of Drosophila to light is appreciably more rapid and persistent if the ocelli are intact than if they are blackened, (Wigglesworth, 1966).

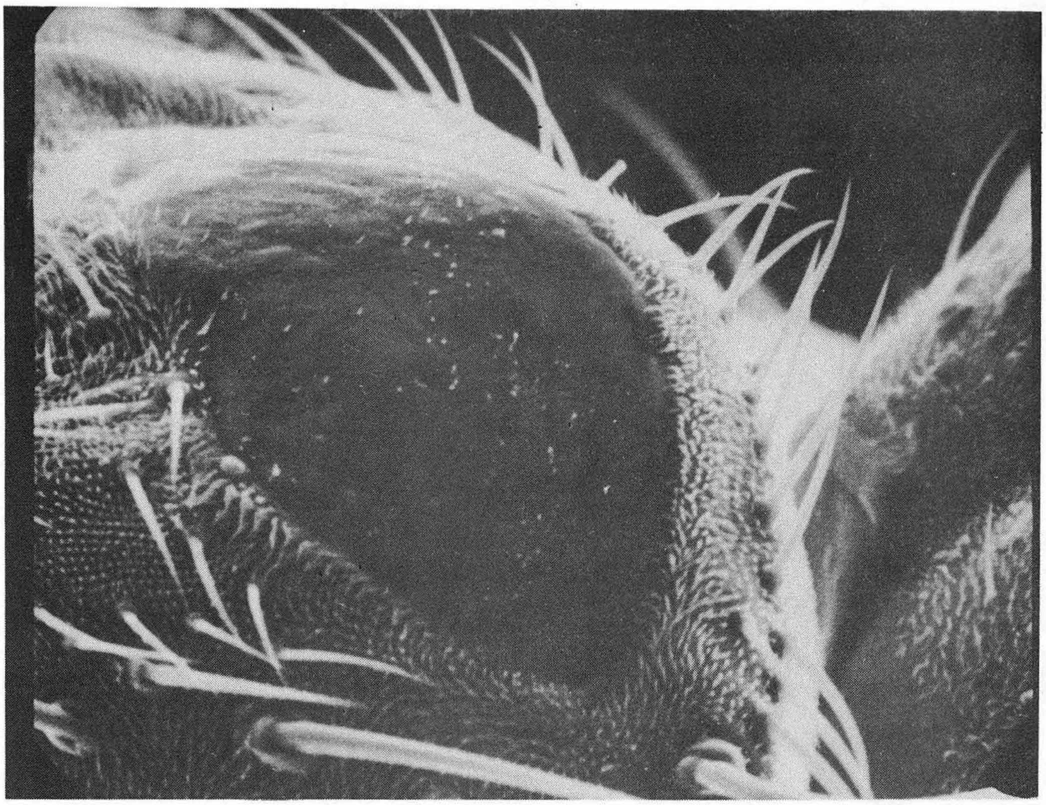

fig. 11: The eye of a lozenge-eyed mutant.

fig.12: Top view of head: the three ocelli and associated spines; mo, median ocellus; lo, lateral ocellus.

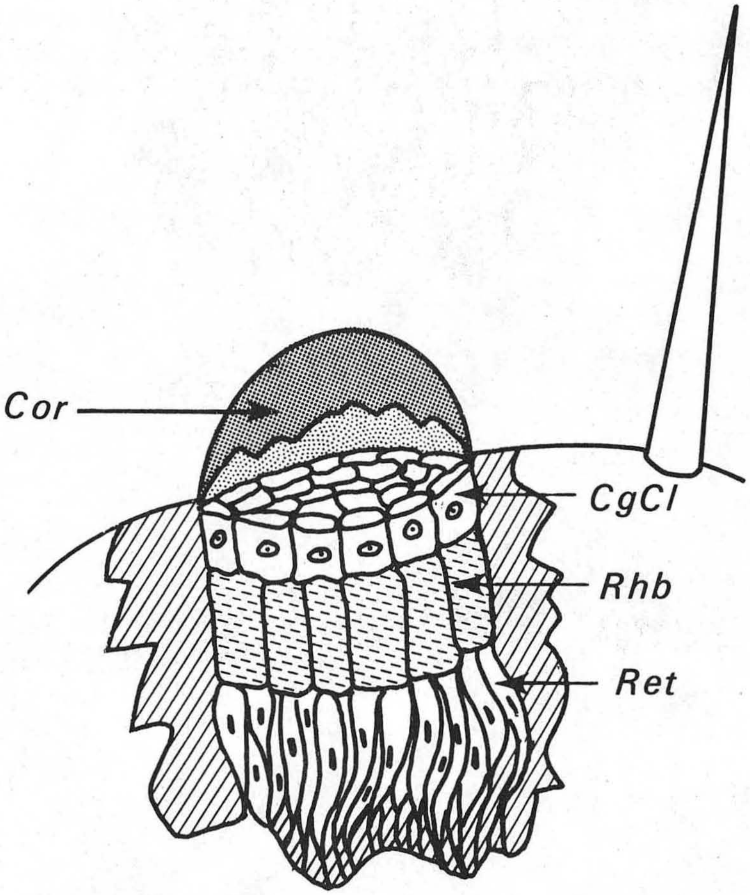

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fig.13: Diagram of an ocellus,(after Hertweck). Cor, cornea; CgCl, corneagenous cells; Rhb, rhabdom; Ret, retinal cells.

Anatomize they eye: survey its
structure and contrivance; and
tell me, from your own feeling
if the idea of a contriver does
not immediately flow in upon you
with a force like that of a
sensation.

David Hume

The Antennae

Thinks 'e's the world 'e does. . . My 'at!
These insec's all be'aves like that.
Ridic'lous creatures! Jest can't see
'Ow small they looks to you and me.

The brothers Čapek

The antennae of Drosophila are extremely complex; they hear, they touch, they smell, they taste, they judge wind pressure, and they sense temperature. And although some of these functions are in the first stages of investigation, we may soon prove them, and even find that the antennae perform tasks which we, as yet, do not know of.

The basic external morphology of an antenna is depicted in figures 1 and 2. The antenna is divided into six segments. The first, called the scape, is a small, narrow ring of cuticle that surrounds the base of the second segment, the pedicel. The pedicel is a large and somewhat conical structure into which the third segment fits. The third segment is large, bulbous, and exceedingly well covered with external sensilla. The fourth, fifth, and sixth segments are greatly reduced in diameter, with the fourth forming a minute ring. (In figures 1 and 2 the fourth segment is hidden in the roots of the sensilla of the third segment.) The fifth is longer and fatter, while the sixth is elongate, slender, and branched. Although the first and second segments are named specifically, the third, fourth, fifth, and sixth go collectively under the name flagellum. The branch-like sixth segment has earned its own name, the arista. Yet the third segment,

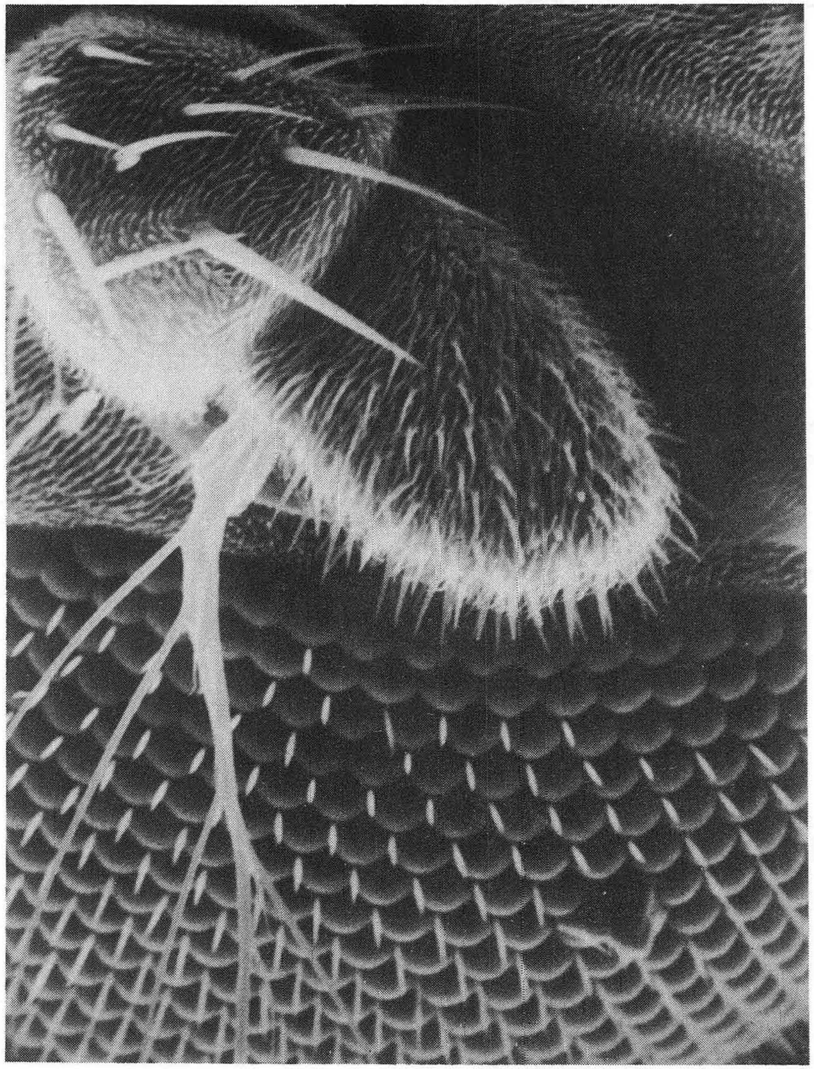

fig.2: Left antenna.

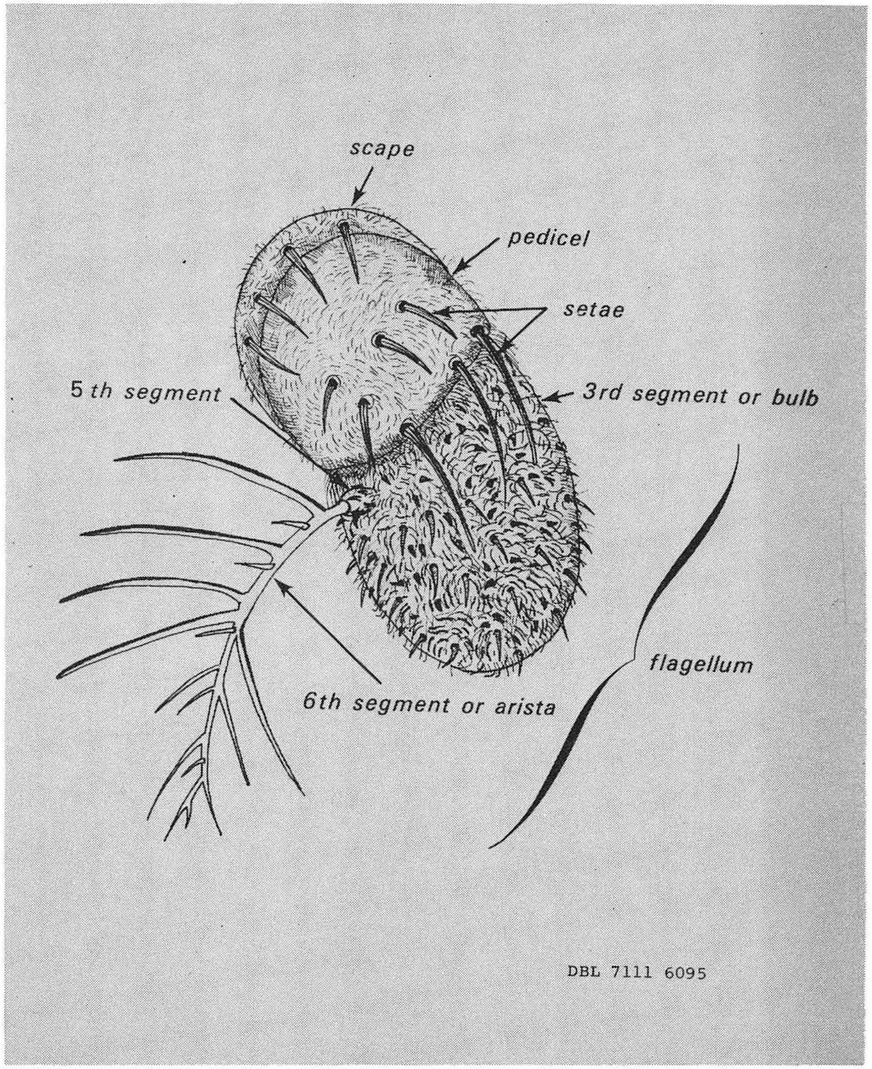

fig.1: Diagram of left antenna.

which performs so many sensory functions that it richly deserves a name, has none. I should like, therefore, to call it the bulb, which is, in many respects, a fitting name, and is easier and less confusing than the "third segment."

The antennae of Drosophila, (figure 3), are situated at the very front of the head. Since they inform the insect of environmental conditions, the antennae are conveniently placed so that they are the first parts of the body to contact the precincts that the fly is about to enter.

The scape articulates with the antennal sclerite, a tough piece of cuticle which surrounds the hole where the antennal nerves and vessels enter the head capsule. This hole is known as the antennal fossa, (Peterson, 1916). The scape, (figure 4), is an irregular ring, covered with tiny hairs; it also has four or five small mechano-receptive spines. These latter are usually found on the upper scape only, (Lowne, 1870). At the base of the scape the muscles that serve to move the flagellum take their origin, (Snodgrass, 1928).

The pedicel is a very important segment. It is shaped like an upside-down, rather rounded cone. A distinctive split, (figure 5) runs along the lateral surface only on one side, and does not slice the pedicel completely. The pedicellar cuticle is also covered with hairs, but it has numerous, about fifteen to twenty, mechano-receptive spines of various sizes. The larger of these spines, (figure 6), overhang the bulb and serve to protect it a little from being knocked about.

An inside view of the cup of the pedicel, (figure 7), which can be obtained if the bulb falls out, shows numerous folds or plicae made of

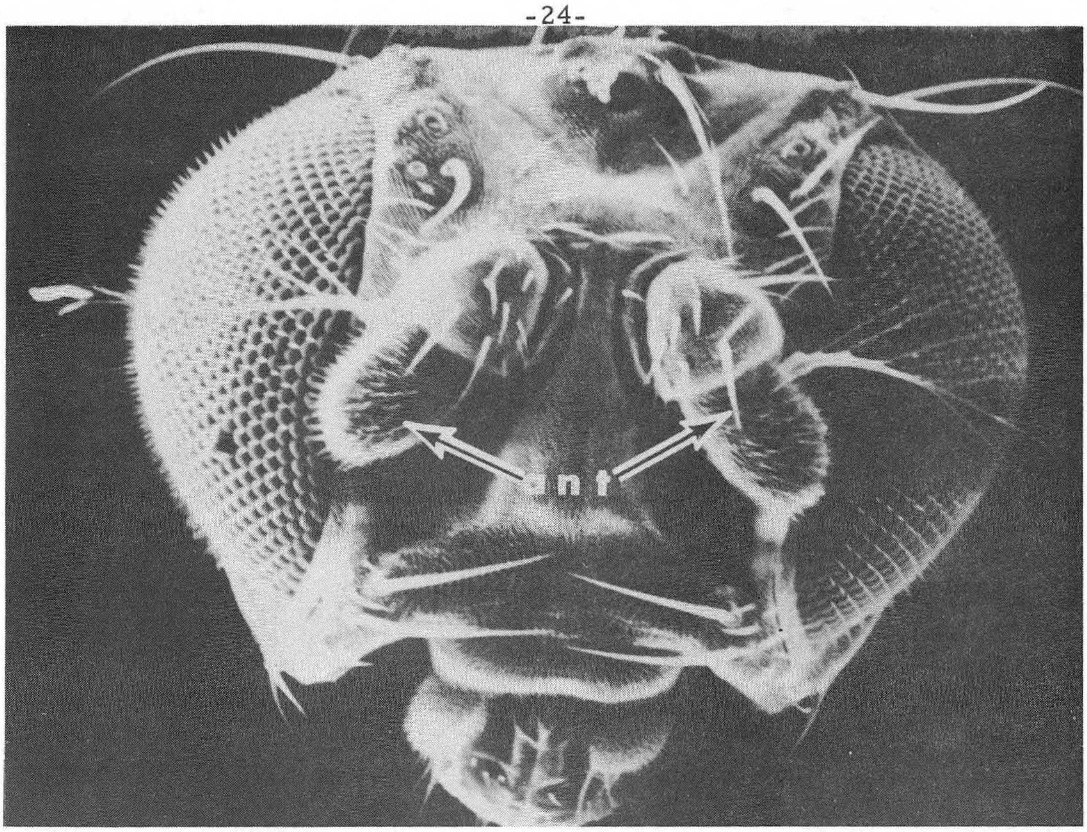

fig.3: Front view of face; ant, antenna.

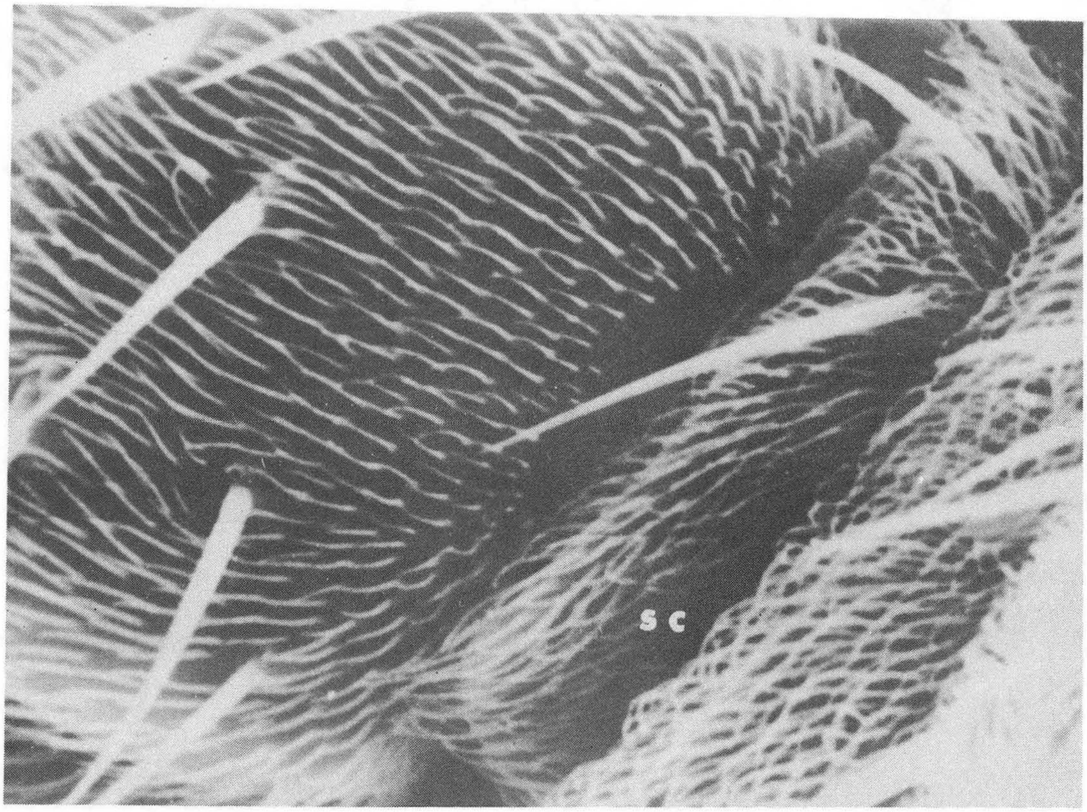

fig.4: The scape, sc.

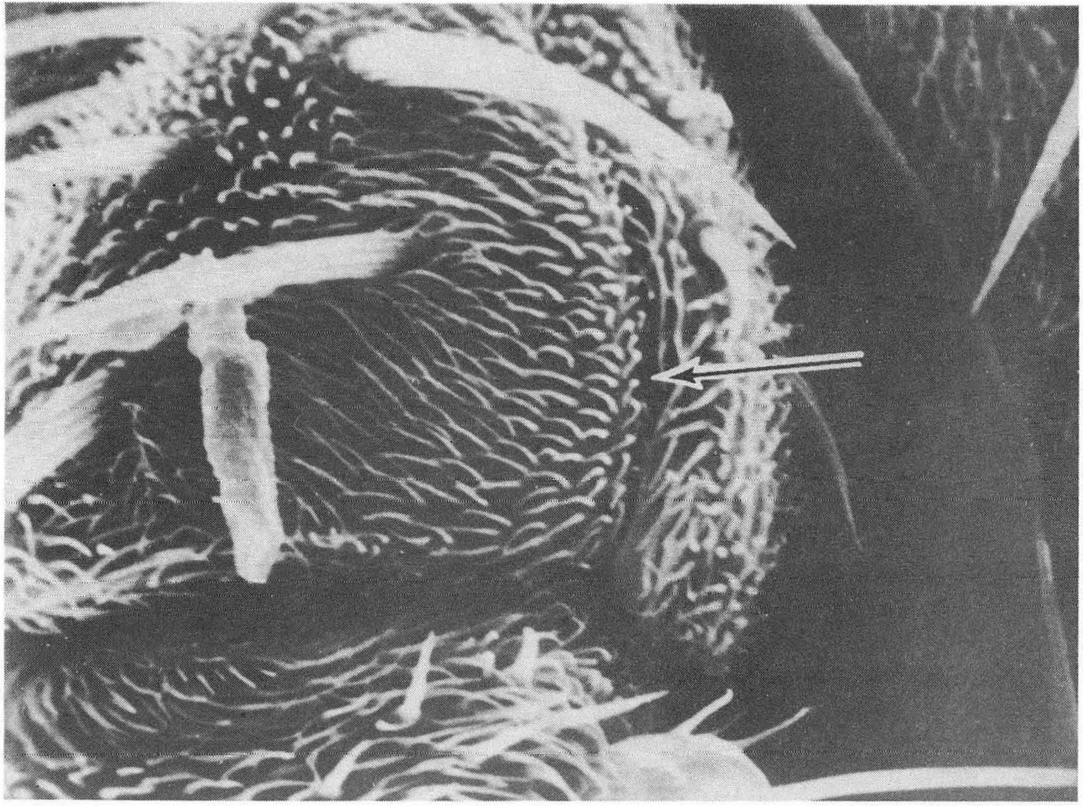

fig.5: The split in the pedicel, arrow.

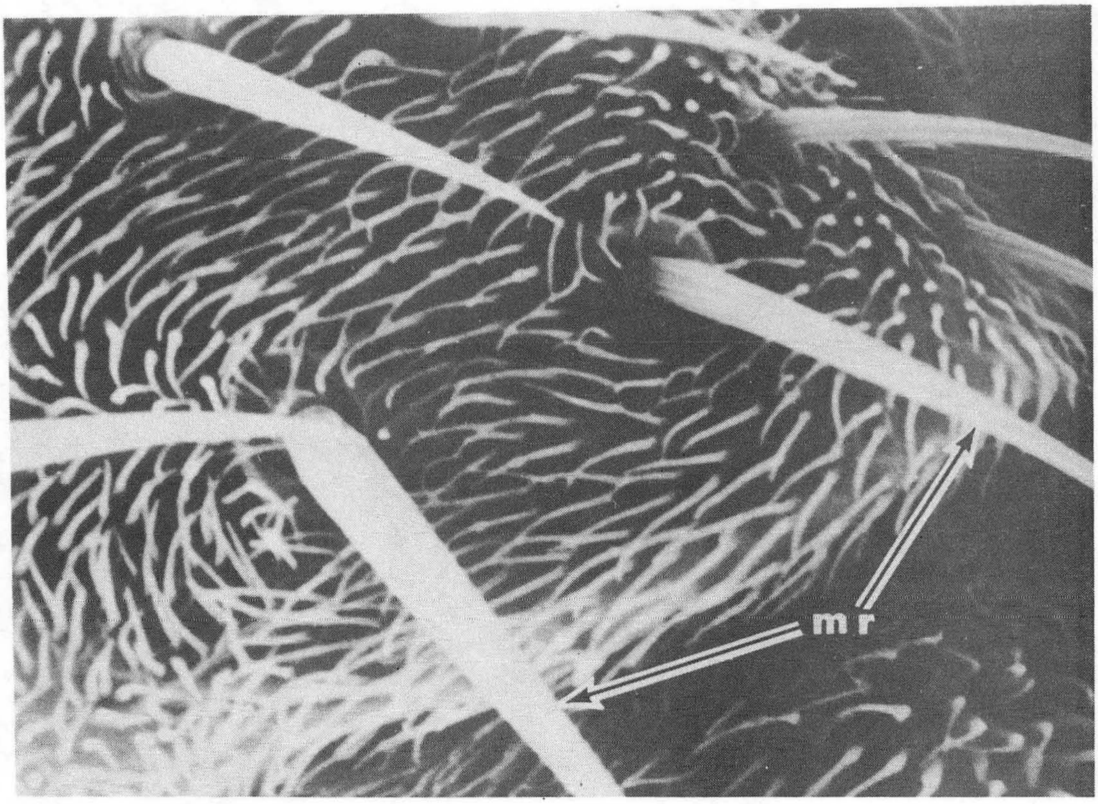

fig.6: The large mechano-receptive spines of the pedicel, mr.

schlerotized chitin and arranged in a roughly hexagonal pattern (Lowne, 1870). It is on these plicae that the bulb rests and turns. In figure 7 we can also see, on the right, the split in the pedicel that actually runs completely through the thickness of the segment at that point. In the center of the cone is a small opening into which the bulb articulates. Around this orifice the plicae are replaced with conventional hairs.

Most of the movements of the antenna take place beyond the pedicel, yet it is within the pedicel that the information about such movements is gathered, by a sense organ known as the organ of Johnston. Johnston's organ is sensitive not only to the movements of the antenna that are made by the fly itself, but also to movements brought about by external means, such as air currents. Thus we might suspect that Johnston's organ helps control flight. Aphids fly erratically when this organ has been immobilized, but normal flight returns when the restraint is removed, (Wigglesworth, 1964). Johnston's organ can also develop into an organ of hearing as in male mosquitos. The sound waves of certain notes set the whole flagellum vibrating, (Wigglesworth, 1964), which in turn stimulates the organ of Johnston. Finally Johnston's organ can also serve as a geo-receptive sensor. Since the flagellum, especially the arista, tends to hang down, a change in its orientation would result in a movement which would probably stimulate Johnston's organ.

The internal structure of the organ of Johnston consists of bundles of elongate sensilla within the pedicel, (shown very diagrammatically in

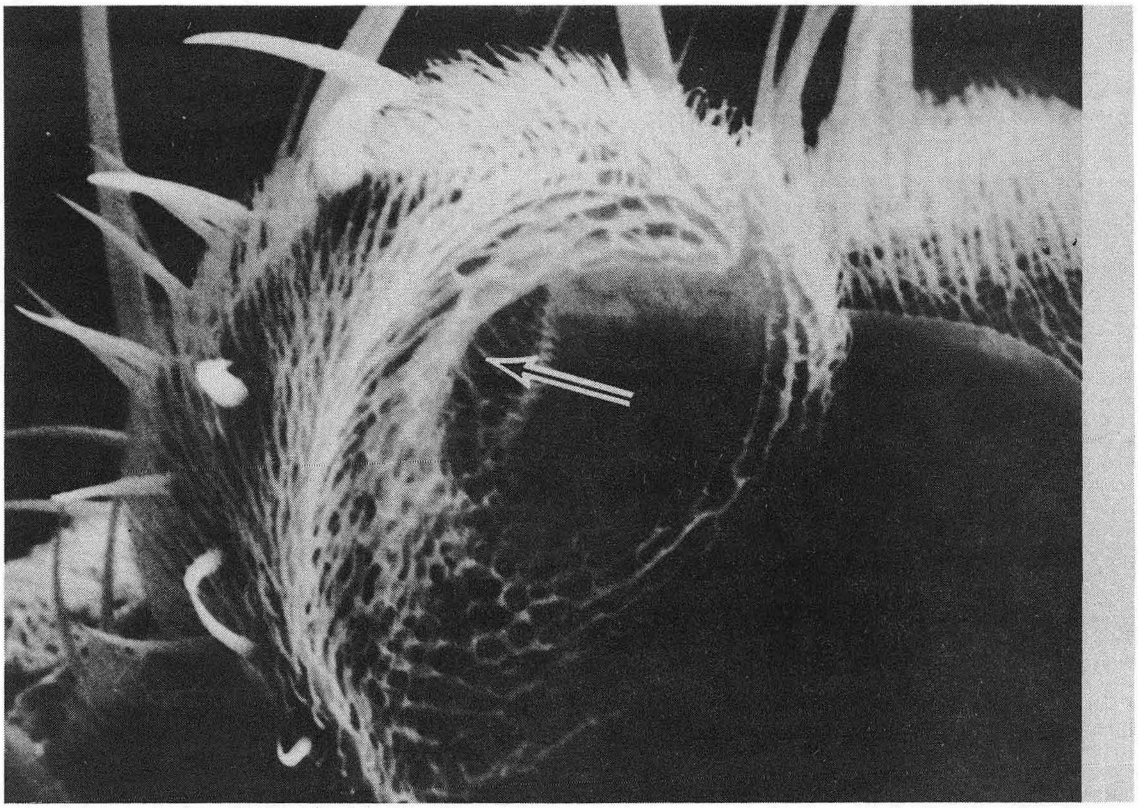

fig.7: Inside of the pedicellar cup; arrow to orifice for basal stalk.

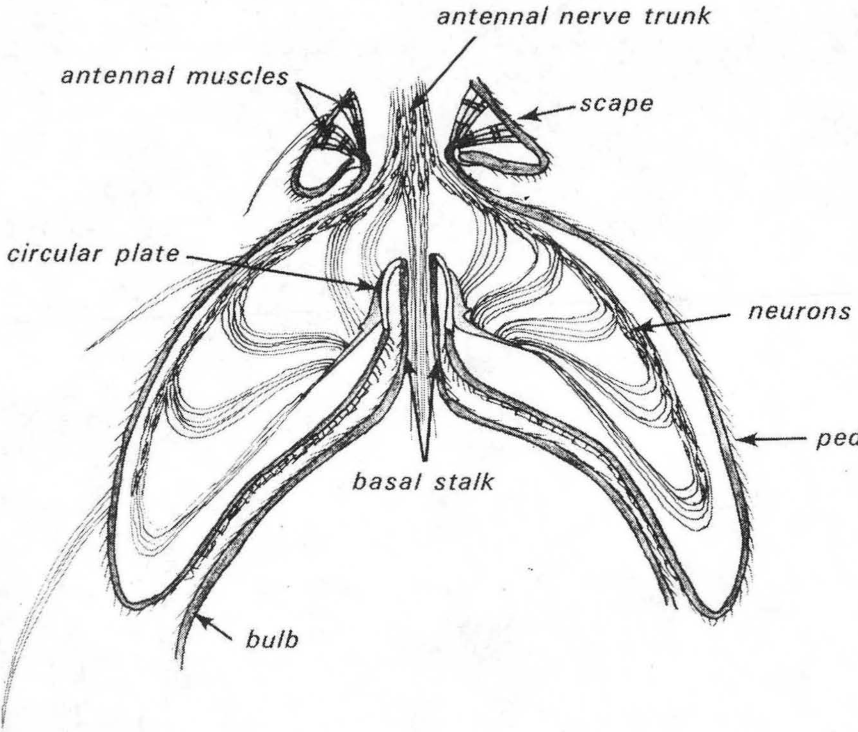

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fig.8: Johnston's organ.

figure 8). These groups of nerve cells are attached at one end to the prongs of a circular plate in the articular membrane between the pedicel and the bulb, and at the other end they join into the antennal nerve trunk, (Snodgrass, 1926). The articulation of the pedicel and the bulb is important for the sensitive functioning of the organ of Johnston. The bulb fits well into the cup of the pedicel and extends an narrow short stalk, called the basal stalk, (figure 9), into the orifice at the cup's top, (Miller, 1950). In this stalk is the trunk of all the nerve fibers that have their termination in the sensory structures of the bulb.

The bulb, (figure 9), is the largest and most important part of the antenna. It is covered with a vast number of sensilla of many different varieties, (figure 10): contact chemoreceptors or sensilla trichodea which appear in figure 10 as being rather thick and long, olfactory sensilla or sensilla basicona which are stubby and round-ended, and other, perhaps temperature sensitive sensilla, (Crampton, 1942), appear as small slender processes.

There are two types of sensilla basicona on the bulb, (figure 11), thick-walled and thin-walled. The thick-walled basicona are larger and sturdier looking than the thin-walled, and have an engraved surface architecture while the thin-walled basicona are smooth. Both the thin-walled and the thick-walled sensilla basicona, however, have pretty near the same internal structure, (Dethier, 1963), which is diagrammed in figure 12.

On the posterior surface of the bulb, (figure 9), we can find a minute pouch called the sacculus or olfactory pit, (figures 13 and 14).

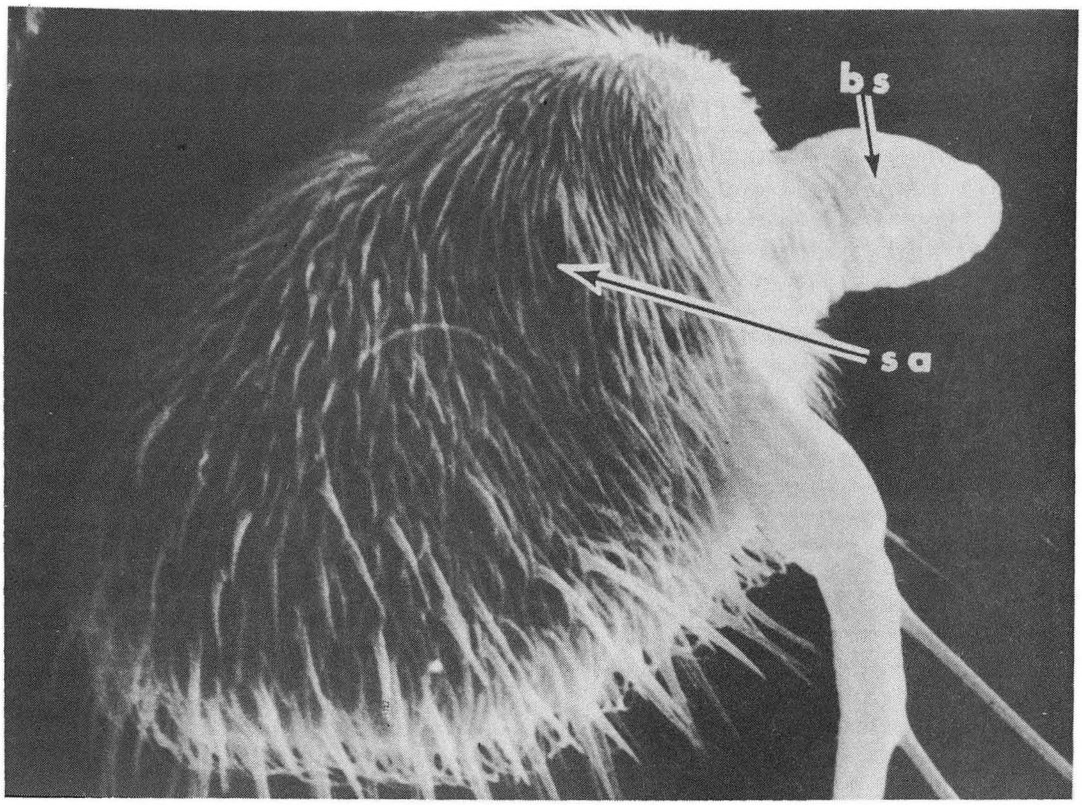

fig.9: Posterior surface of detached bulb; <u>bs</u>, basal stalk; <u>sa</u>, sacculus.

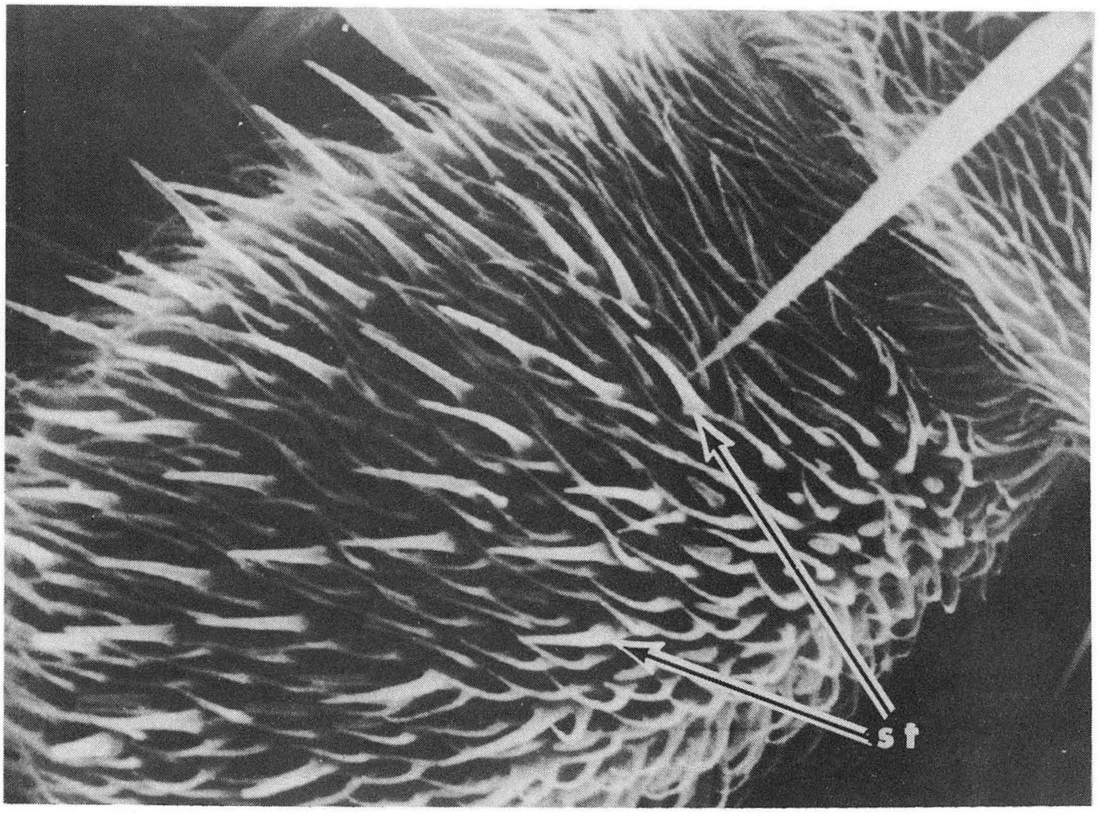

fig.10: Anterior surface of intact bulb; <u>st</u>, sensilla trichodea.

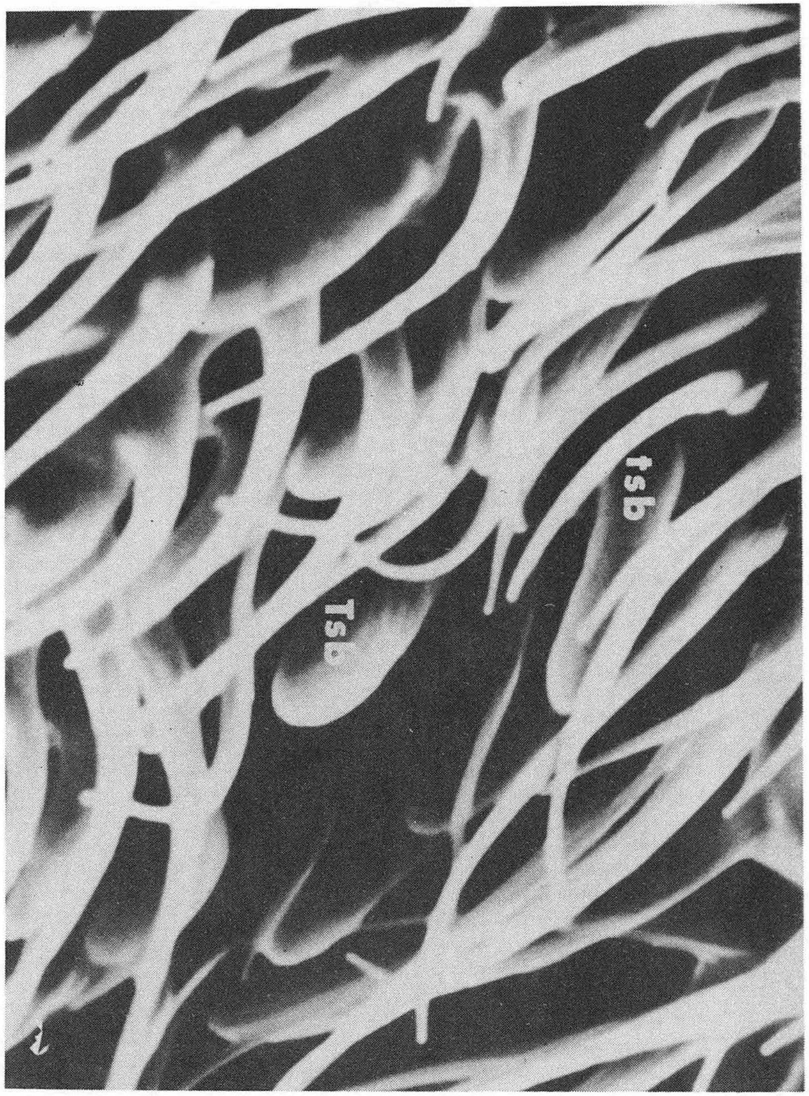

fig.11: Close-up of some sensilla; Tsb, tsb, thick, thin walled sensilla basicona.

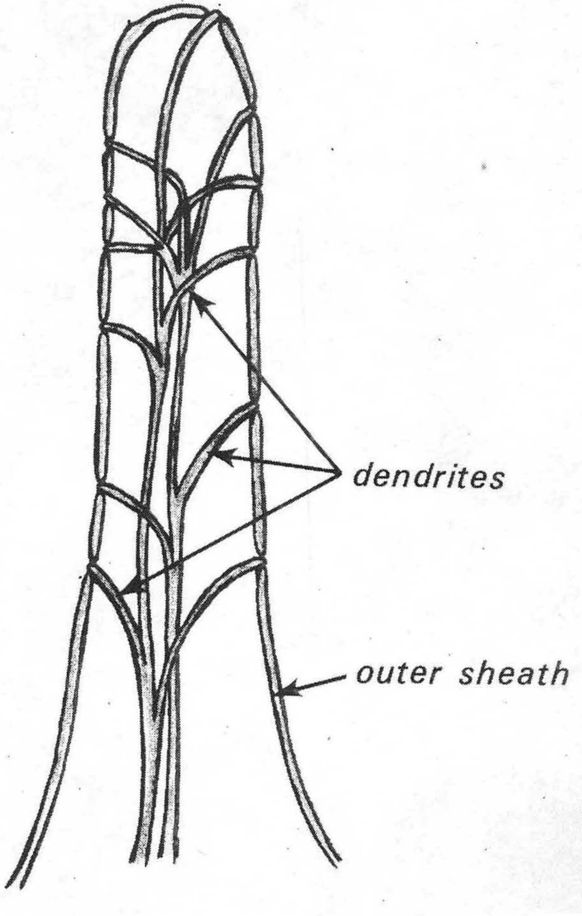

fig.12: Diagrammatic representation of a sensillum basiconum,(after Dethier).

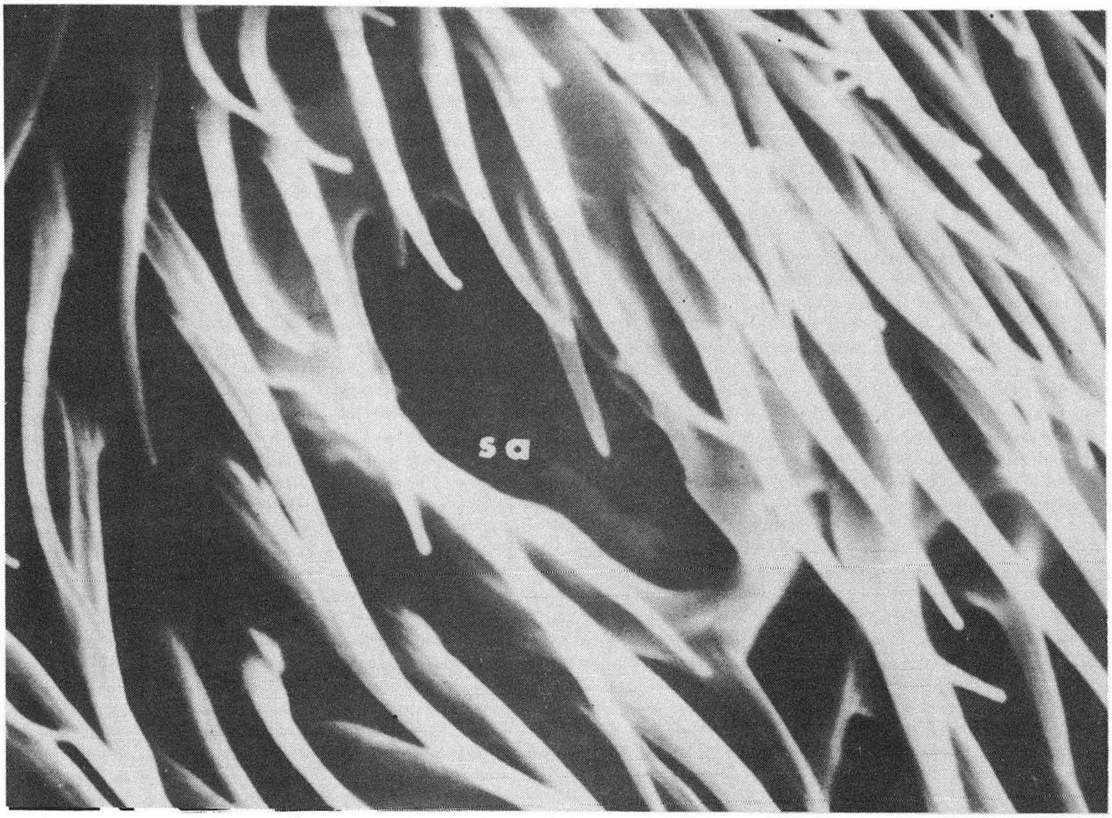

fig.13: Sacculus, <u>sa</u>.

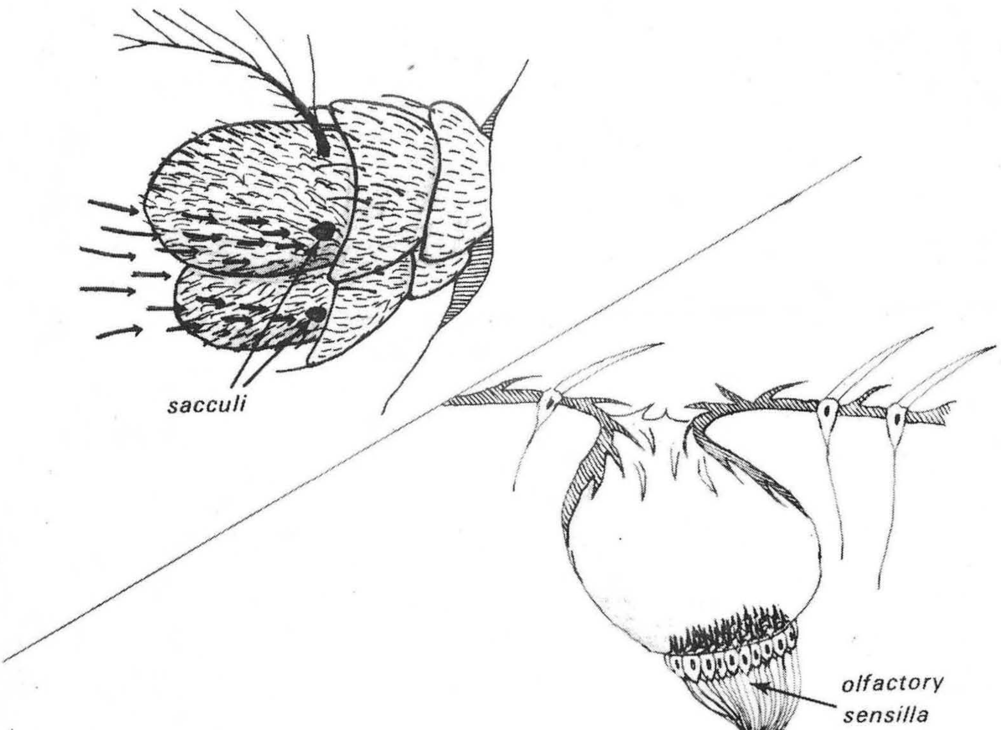

fig.14: Diagram of sacculus, (after Wigglesworth).

The sacculus is loaded with sensitive olfactory sensilla. When in flight a stream of air flows into the fly's sacculi providing him with chemical information about the different surroundings he enters, (Wigglesworth, 1939). It has been demonstrated, (Begg and Hogben, 1946), that Drosophila mutants, "antennaless" hardly respond at all to olfactory stimuli, although their other reactions seem quite normal.

The fourth segment is a very narrow ring on the outer side of the bulb. We can usually find it submerged under the sensilla of the bulb, (figure 15). The fifth segment is considerably longer and fatter with some thorny growths on it, (figure 15). The fifth segment acts as a rigid support for the plumose tapering arista which is solid throughout the greater part of its length in the mature fly, (Lowne, 1870). The arista, (figure 16), has branches of various sizes located on specific areas of its trunk. The longer ones are on the top, the shorter ones on the front, and on the back there are none.

When the insect flies, the wind pressure pushes on the arista which acts as a lever applying a torque to the bulb, which, being turned, stimulates the organ of Johnston in the pedicel. The fly can then correct for this displacement of the flagellum by use of the antennal muscles arising in the scape. The degree of correction is a measure of the wind pressure, or in other words, the flight speed. In this measurement we witness the interplay of all the antennal segments at once.

> But he no doubt reports to any
> With whom he crosses antennae,
> And they no doubt report
> To the higher up in the court.
> The word goes forth in Formic:
> "Death's come to Jerry McCormic."
>
> Robert Frost

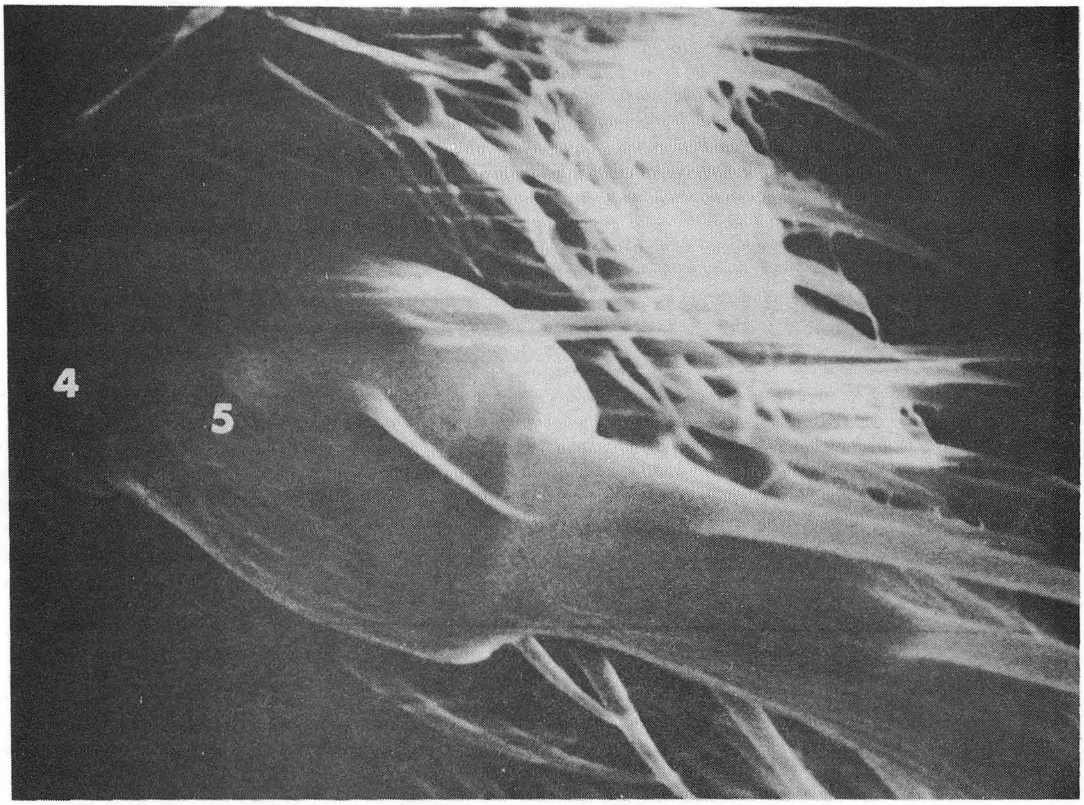

fig.15: 4th and 5th antennal segments, 4,5.

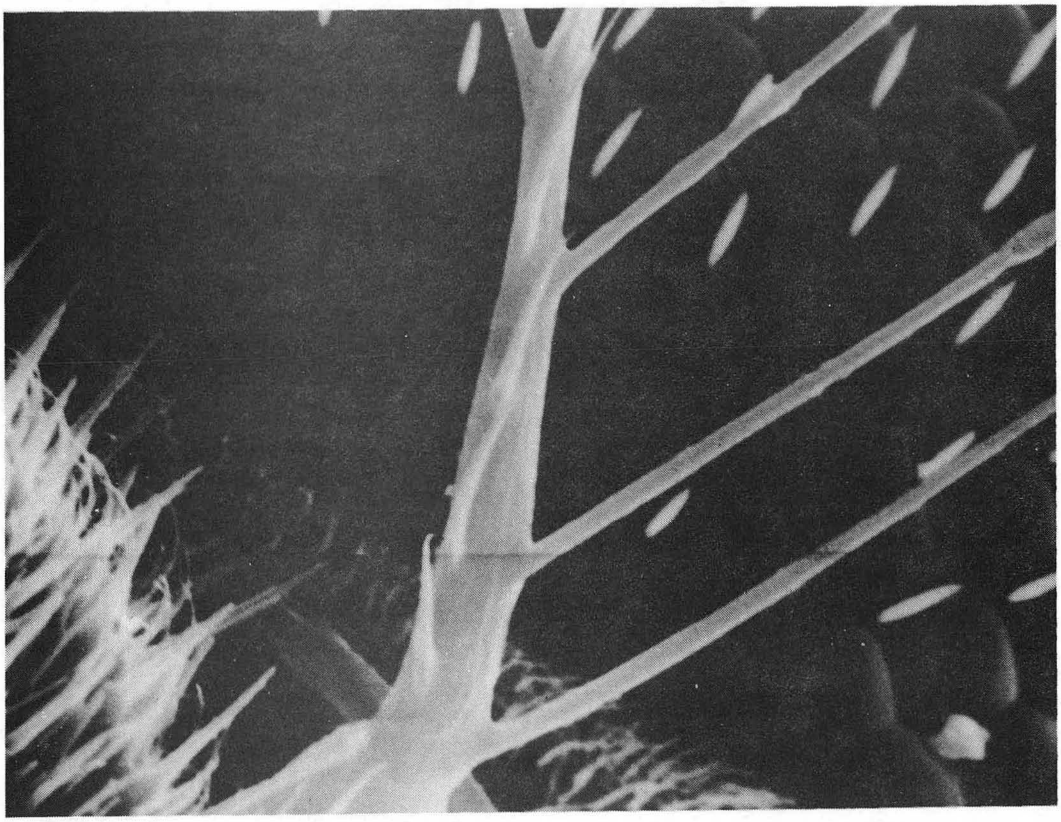

fig.16: Arista, anterior view.

The Proboscis or Mouth Parts

Busy, curious, thirsty fly!
Drink with me and drink as I:
Freely welcome to my cup,
Could'st thou sip and sip it up:
Make the most of life you may,
Life is short and wears away.

William Oldys

The organs of ingestion in Drosophila are extremely modified and specialized for the collection of food purely by sucking, (Lowne, 1870). Flies such as Drosophila, the housefly, and the blow-fly, that collect food in this way are called the "sponging type." Yet these flies can often be found feeding on solid food; for instance Drosophila are usually raised on banana, cornmeal, oatmeal, and wheat mediums, (Demerec and Kaufman, 1962). How can they do this? The answer is that the fly first extrudes a droplet of enzyme-rich saliva onto the food. The food dissolves in the saliva, and the solution is drawn up into the mouth as a liquid, (Ross, 1967).

The intricate morphology of the feeding organs will be more easily understood if a generalized morphology is first given. Thus figure 1 is a diagram of the entire structure. As a matter of convention, in speaking of the proboscis as a whole, we divide it into three regions: the basiproboscis which contains the clypeus, the submentum, the maxillary palpi, the maxillary lobes, and the labrum; the mediproboscis which contains the prementum; and the distiproboscis which contains the labial palpi and all their accouterments. The

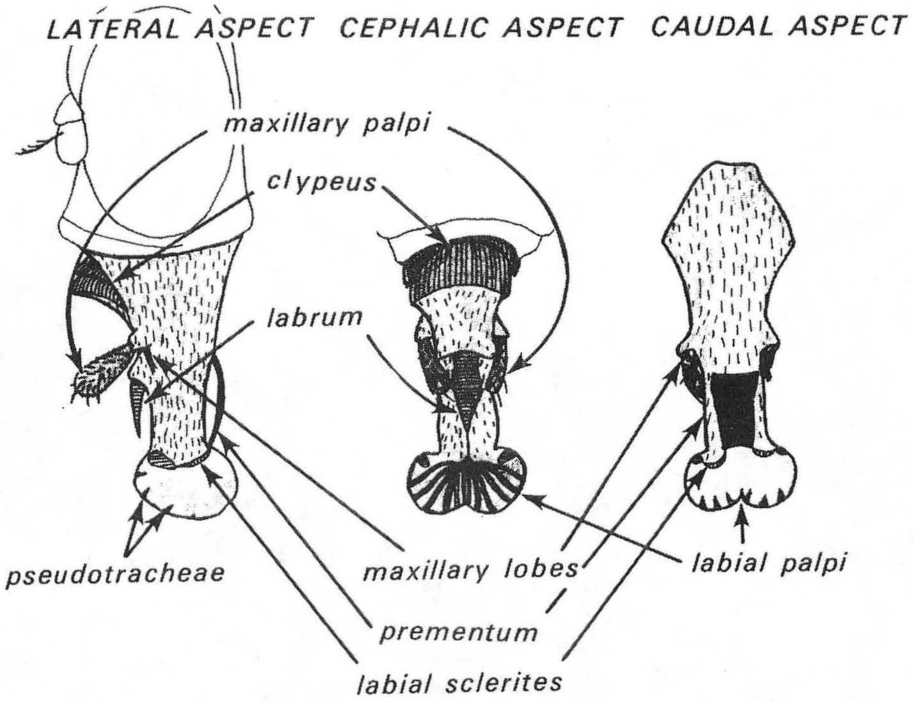

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fig.1: General structure of the proboscis,(after Ferris); lateral, cephalic, and caudal aspects.

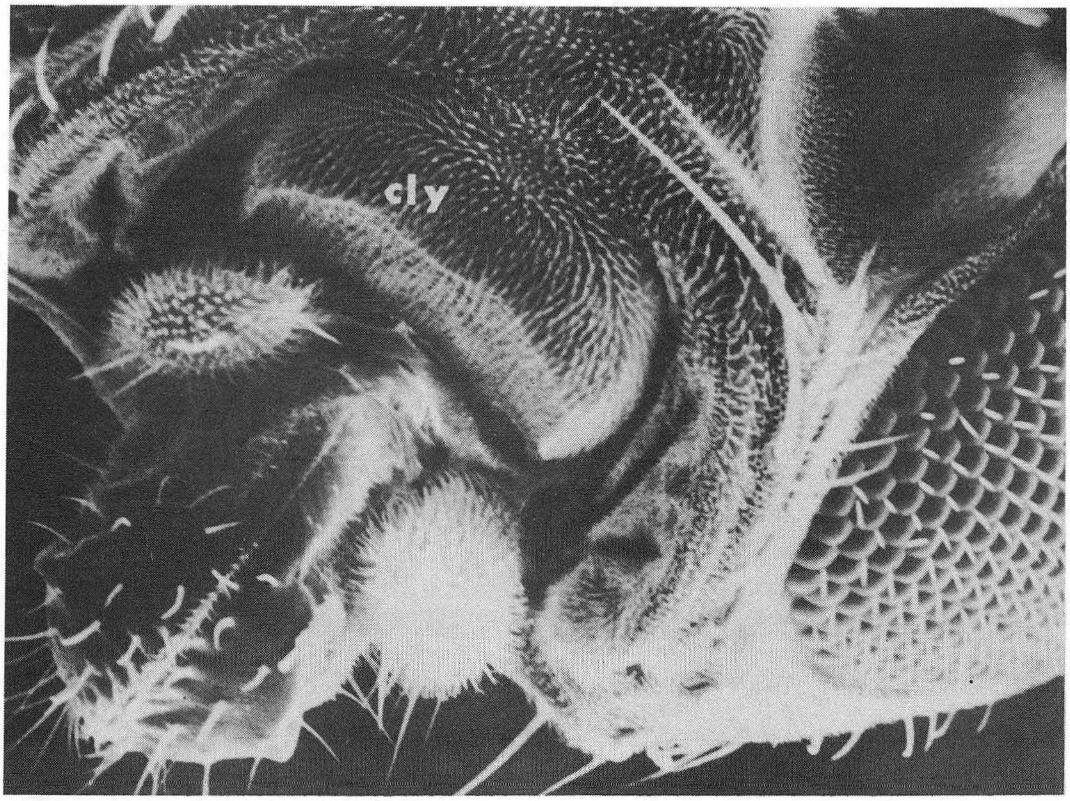

fig.2: The retracted proboscis; cly, clypeus.

mandibles which are the pinching parts of ants and most beetles have been lost altogether in Drosophila, (Ferris, 1950).

In the resting position, (figure 2), the proboscis is retracted into the head of the fly, and the lips of the fleshy labial palpi are folded against each other. In this position the fly can protect his more delicate mouth parts yet leave exposed the chemo-receptive maxillary palpi to the environment. Figure 3 shows the proboscis extended as it is during feeding.

Both figures 2 and 3 show distinctly the area known as the clypeus is one of the most conspicuous features of the proboscis: it is a rather large sclerotized plate somewhat in the form of an inverted "U", and it lies like an island in a sea of membrane. The plate is divided into two parts by a transverse fold, (Ferris, 1950). The upper portion of the plate, as seen in the micrographs, is called the postclypeus, and the lower part the anteclypeus, (Snodgrass, 1935). The postclypeus is often almost entirely hidden from view, (figure 2), but the anteclypeus is always clearly visible, even in a retracted proboscis. Originating on the clypeus are the muscles that operate the preoral pump which sucks up food solutions. Since the size of the clypeus is proportional to the amount of musculature originating on it, the sucking insects such as Drosophila, have much larger clypei than their nonsucking counterparts, such as ants, (Snodgrass, 1935).

Also conspicuous on the basiproboscis are the maxillary palpi. These, (figures 1, 2, and 3) are one segmented appendages. B. T. Lowne, in 1870, guessed, from the fact that the maxillary palpi of the

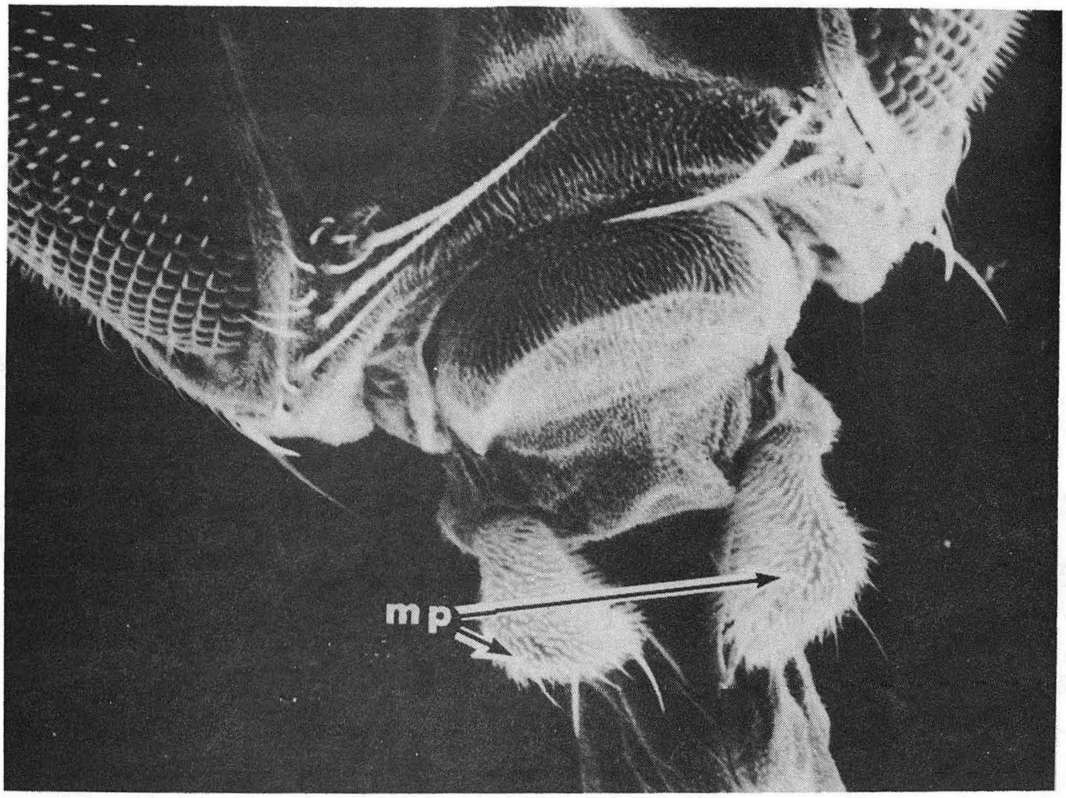

fig.3: The extended proboscis; mp, maxillary palpi.

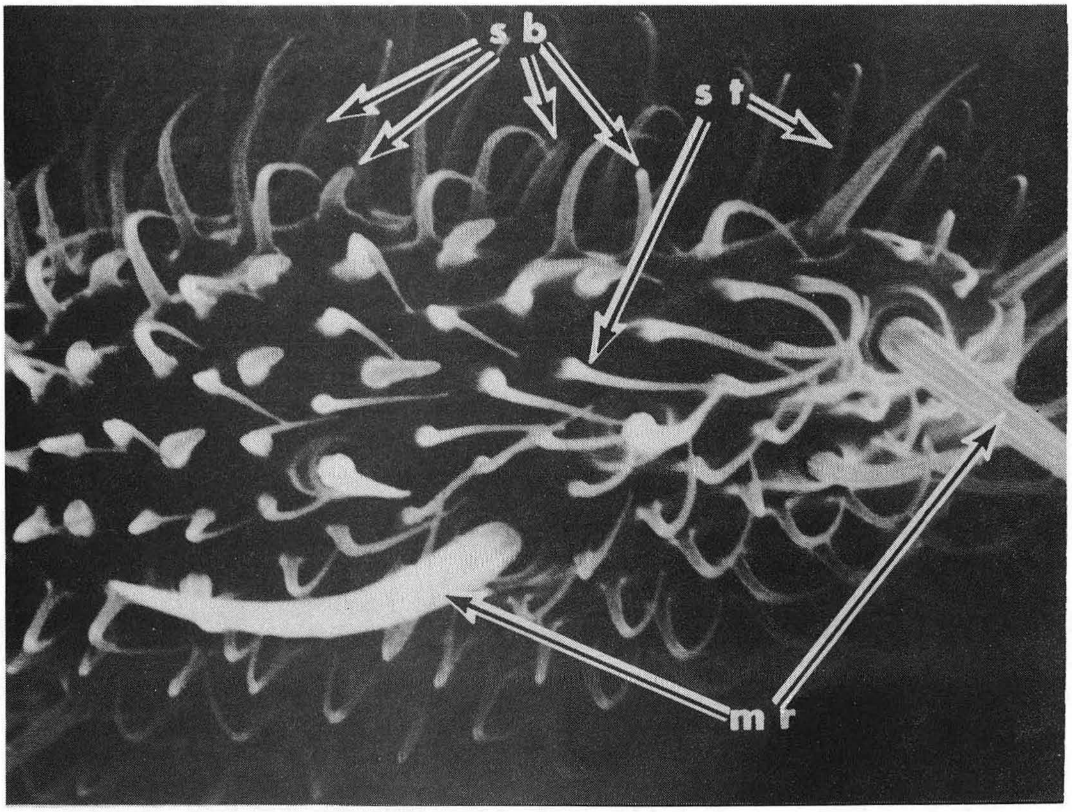

fig.4: Close-up of maxillary palpus; sb, sensilla basicona; st, sensilla trichodea; mr, mechano-receptive spine.

blowfly were always exposed to the environment, that these were probably organs connected with the sense of taste or smell, (Lowne, 1870). Figure 4 is a maxillary palpus at close range. It can be seen immediately that the palpi are covered with sensilla similar to those on the third segment of the antenna, (see chapter on antennae). One can also note, (figure 4), mechano-receptive spines of variable size which have no equivalent on the third antennal segment or bulb. On the upper surface we can see a very high concentration of peg-like sensilla basicona, the olfactory receptors. That the insect does much of its smelling on the maxillary palpi represents a case of convergent evolution. Although these palpi look nothing at all like the nostrils of a nose, it is also the case in vertebrates that olfactory stimulus receptors are located directly above the mouth. Advantage is obviously gained by being able to test the food by smell before eating it, (Bieri, 1964). We can also see a large number of sensilla trichodea or contact chemoreceptor all over the maxillary palpi, (Begg and Hogben, 1946; Frings and Frings, 1949), and especially pointing towards the preoral cavity.

In the angle formed by the maxillary palpus and the main trunk of the proboscis, there arises a very small pointed process which represents all that is left, in Drosophila, of the maxilla other than the palpus (Ferris, 1950). It is called the maxillary lobe, (figures 1 and 5). The maxillae in most insects more primitive than the higher diptera are used for handling food, in the horsefly the maxillae are part of the piercing apparatus, but what function they serve in Drosophila is not well known. Observations of their function is lacking most probably

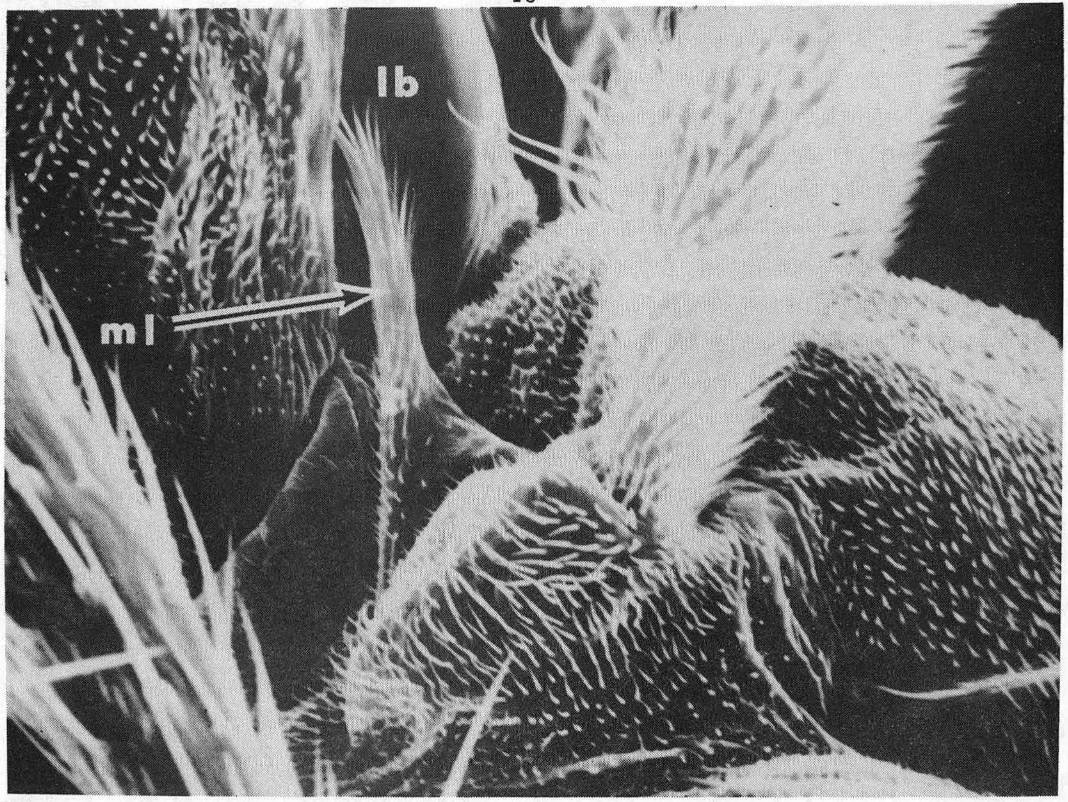

fig.5: Lateral view of area around base of labrum; lb, labrum; ml, maxillary lobe.

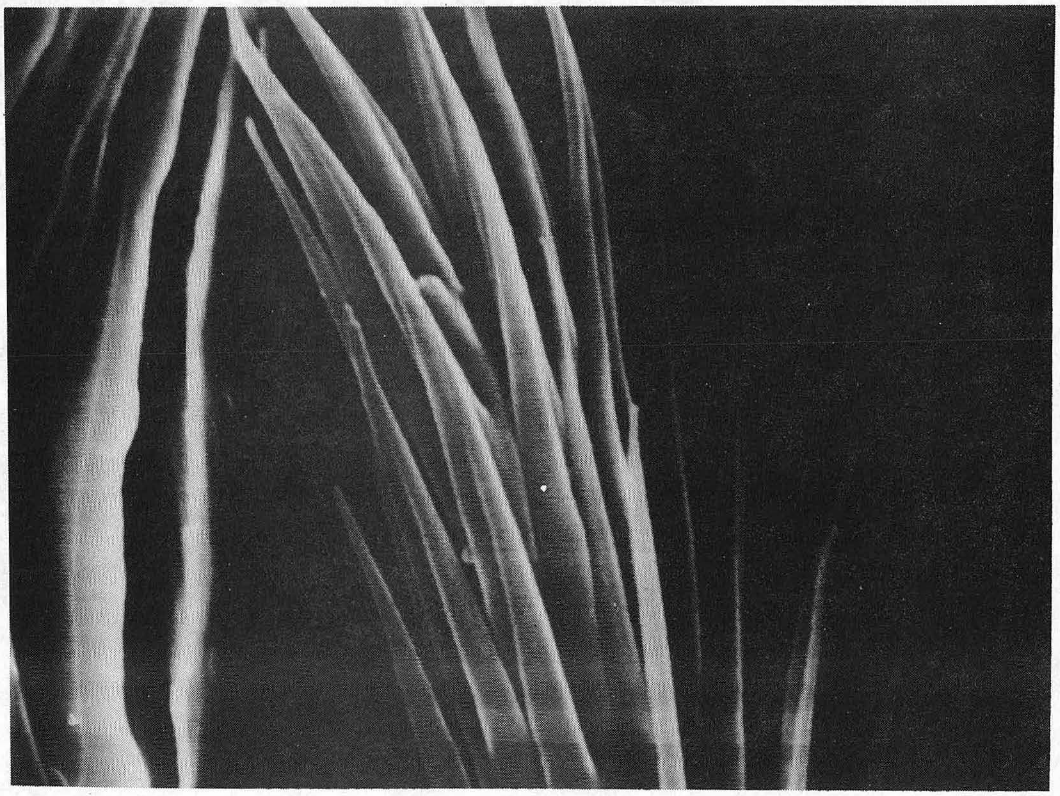

fig.6: Tip of maxillary lobe.

because these organs are so tiny. Figure 6 is a close-up of the tip of a maxillary lobe, which looks something like the bristles of a small paint brush. It is hypothesized that these little lobes help clean and brush the area of the preoral cavity directly under the base of the labrum, that is around the mouth opening and salivary stylet. The hypothetical movements of these lobes is diagrammatically illustrated in figure 7.

The labrum is the final structure of the basiproboscis we shall discuss. It is a schlerotized apically pointed flap, very smooth for the most part. It is, (figure 8), tucked into the preoral cavity at its apical end by two flaps of the mediproboscis. This tucking insures minimum leakage of food solution to the outside. If one looks closely at figure 8, he may be able to see the maxillary lobes between the maxillary palpi and the labrum. It is evident here that the maxillary lobes do swing into the preoral cavity underneath the labrum. Also visible in figure 8 are the tiny fans of microtubercles at the very base of the labrum. A closer inspection of these fans, (figure 9), shows these microtubercles to be quite unlike the ordinary hairs that cover much of the fly's body. These are much shorter and stubbier than the hairs. One can also see that they appear, for the most part, on the edges of the rills, and point in directions fanning out.

Underneath the labrum and at its base is the very small preoral opening, (figure 7). Under the preoral opening or mouth is a minute slender process which bears the opening of the salivary duct at its apex. This is simply a papilla formed about the opening of the salivary duct, and is called the salivary stylet, (Ferris, 1950). Saliva

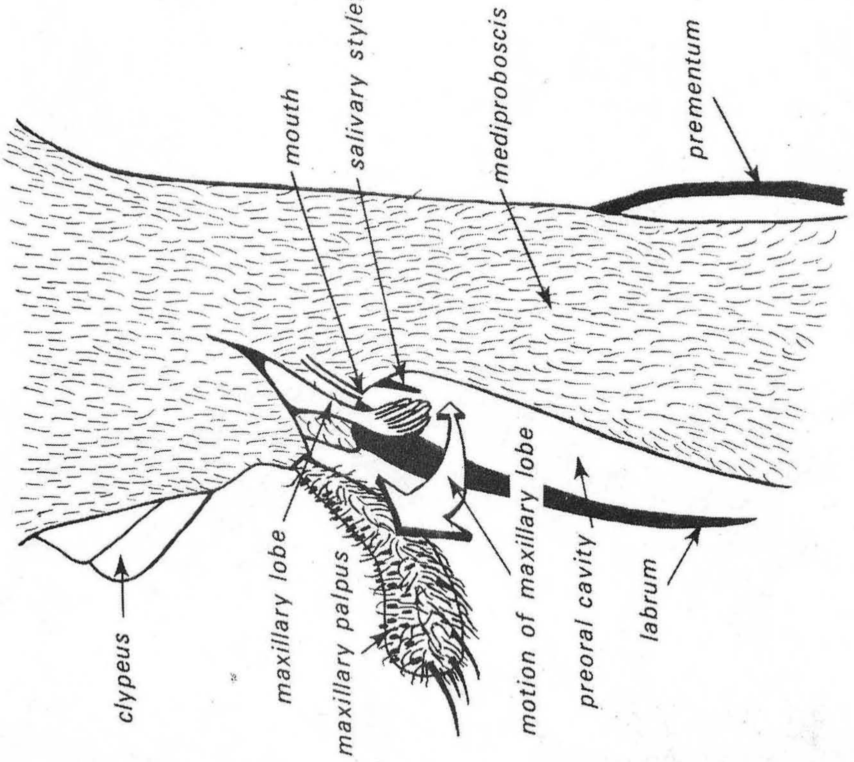

fig.7: Hypothetical function of maxillary lobes.

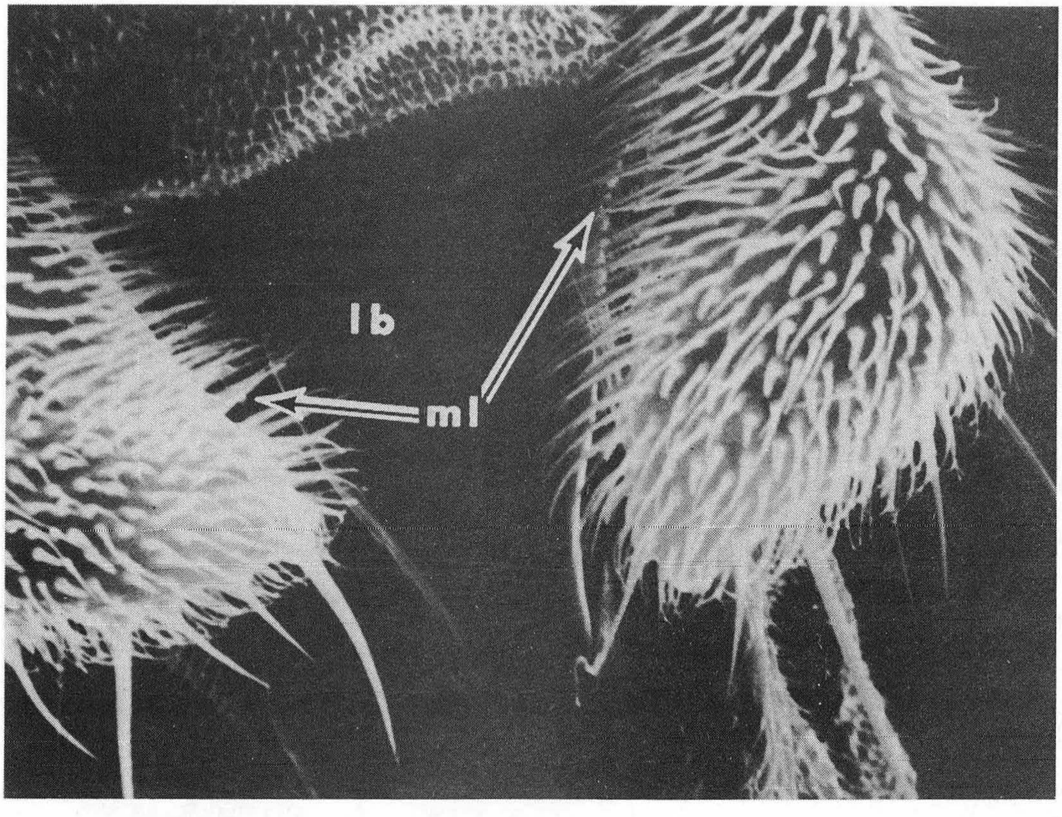

fig.8: The labrum, lb; ml, maxillary lobes.

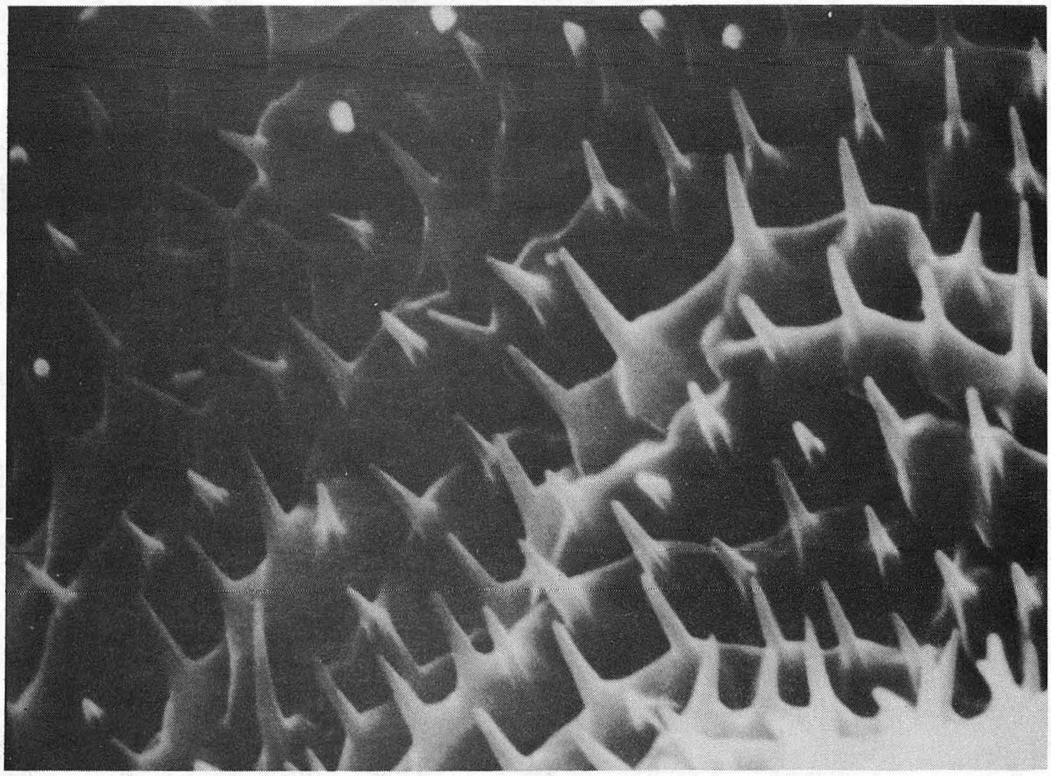

fig.9: The labral fans of microtubercles.

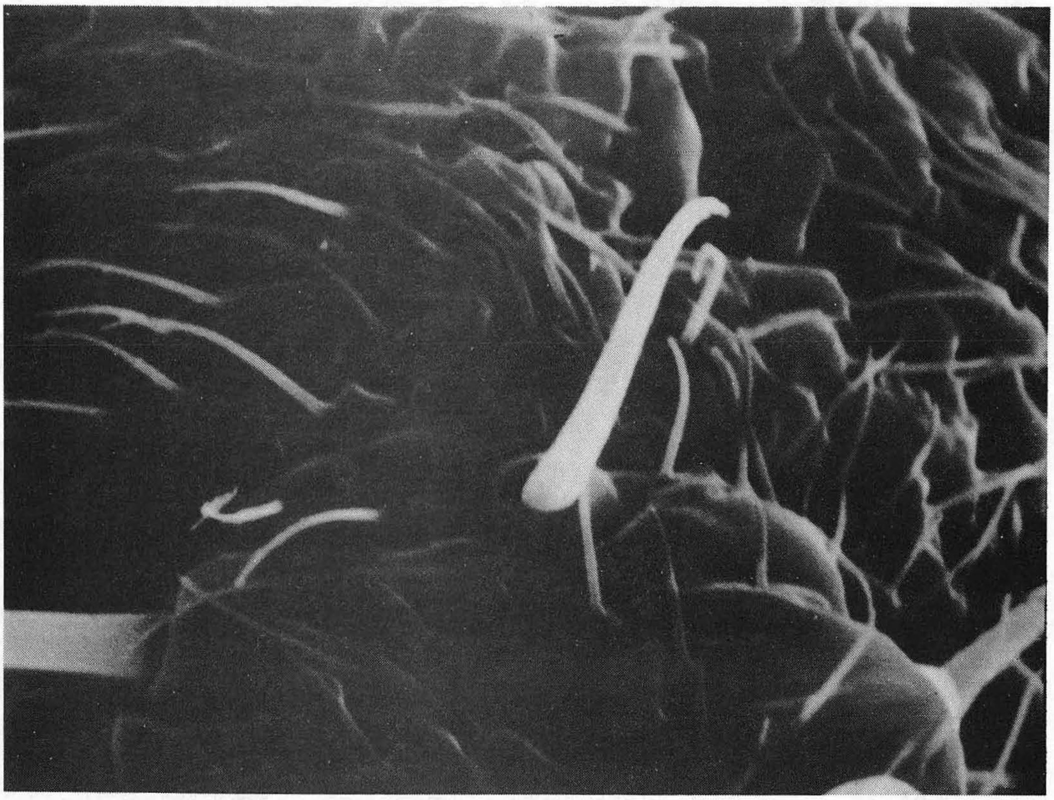

fig.10: Surface of prementum.

discharged at the tip of this stylet moistens and cleans the tube through which food solutions are sucked. The saliva also contains enzymes which begin to break down and digest some of the proteins and carbohydrates which Drosophila feeds upon, (Wigglesworth, 1966).

On the caudal aspect of the mediproboscis (figure 1), one can find a somewhat rectangular plate to which the labial palpi articulate. This is known as the prementum. Morphologically the prementum is formed by the fusion of the parts which in the maxillae of other insects are called the stipites, (Ferris, 1950). The prementum seems most functional as a brace for the soft and flexible proboscis, giving the main trunk extra support when extended. A micrograph of the prementum, (figure 10), shows that it is highly folded and convoluted. One can see a few small spines on the bumps, and a wealth of tiny hairs covering the plate.

Finally, our study brings us to the distiproboscis which is entirely devoted to the labial palpi. These, as we noted earlier, (figure 2), are folded against each other when at rest; but when they are open form large fleshy lobes. About two-thirds of their anterior surface is an oral sucker divided into two parts by the fissure between them, (Lowne, 1870). On the dorsal surface of the labial palpi, there are two minute sclerotized plates which articulate with the prementum, (Ferris, 1950). They are called the labial sclerites, (figure 1). When the palpi are folded these plates come together, the larger ones anteriorly, the smaller one posteriorly, and they seem to zipper the palpi closed. Figure 11 is a close-up of the pair of anterior labial sclerites in the "zippered" state. Let it be understood that these tiny plates do not actually function as a zipper does, but that they merely look like a zipper. This effect is caused by regularly placed spinules that match up in twos upon the closing of the palpi. A little farther away from the center, (figure 11), one can see opposing pairs of small mechanoreceptive spines.

The labella, as the fleshy parts of the labial palpi are called, are dilated by blood pressure and are operated by various small muscles attached to the labial sclerites, (Crampton, 1942). From the fissure between the lobes, known as the prestomum, there radiate six furrows in the derm, these are the pseudotracheae, (Ferris 1950). (See figure 12.)

An extensive and beautiful study of the pseudotracheae of the blowfly has been made by G. S. Graham-Smith, (Graham-Smith, 1911 and 1930). Most of his work, fortunately, is generalizable, and the difference in the pseudotracheae between the blowfly and Drosophila is minimal.

The channel of a pseudotrachea is an incomplete tube since a zig-zag, longitudinal cleft extends down its length. The fly in figure 13 has his labella partially open and this zig-zagging is visible. In figure 13, one can see all six pseudotracheae which appear a mountain ranges with deep zig-zagging crevices along their summits. A pseudotrachea is formed by a row of incomplete hoops which prevent the channel from closing. The hoops are forked or bifid at one end, (figure 14). The openings between the forked ends and the straight

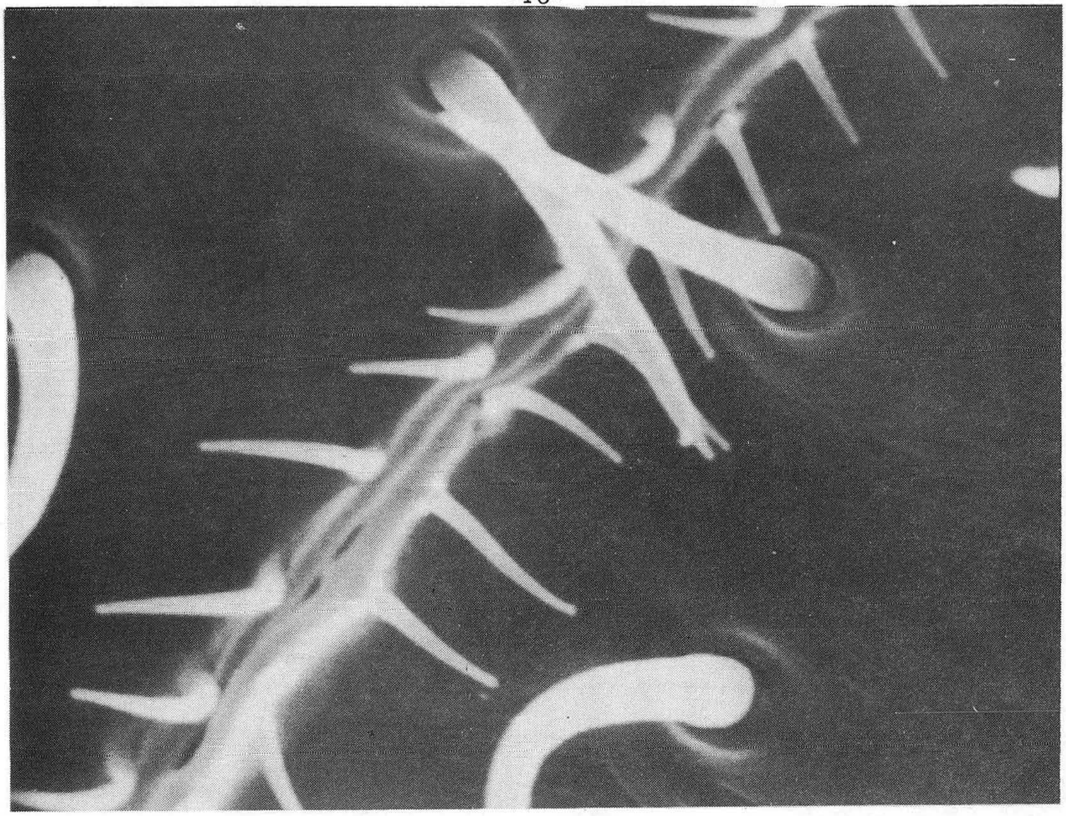

fig.11: Close-up of the labial sclerites in the "zippered" state.

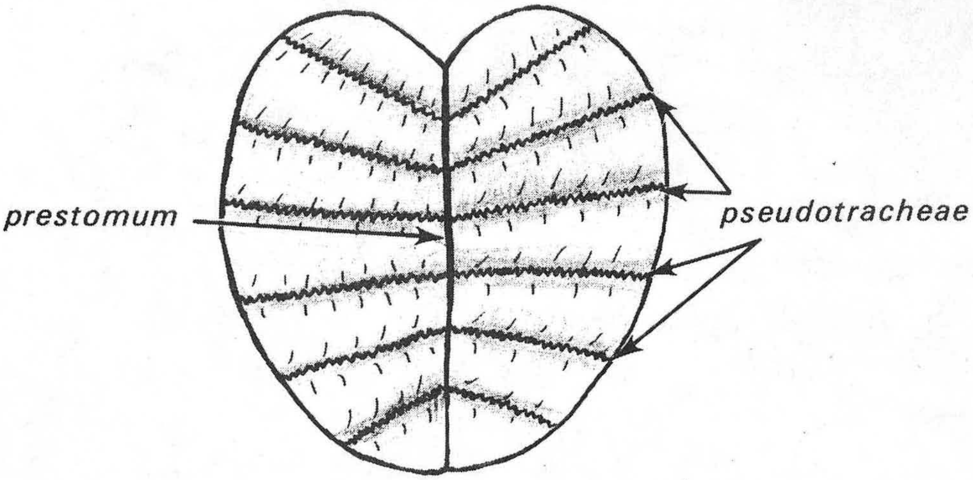

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fig.12: Labella, from underneath.

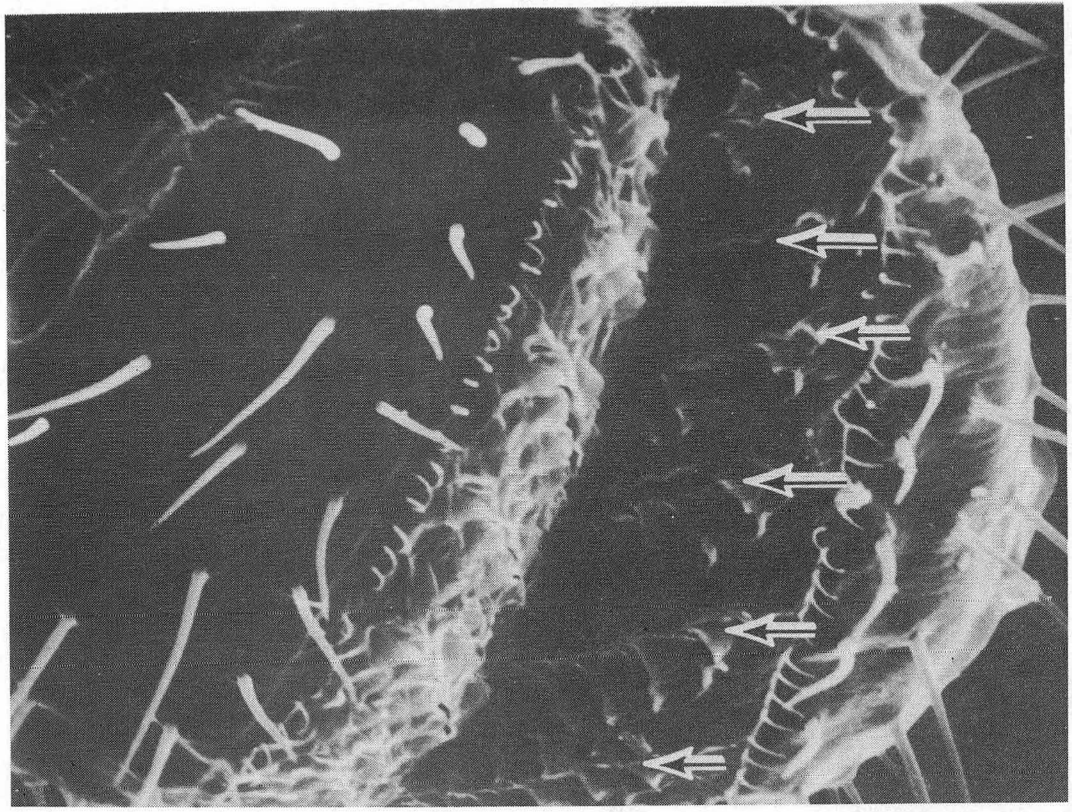

fig.13: Pseudotracheae, arrows.

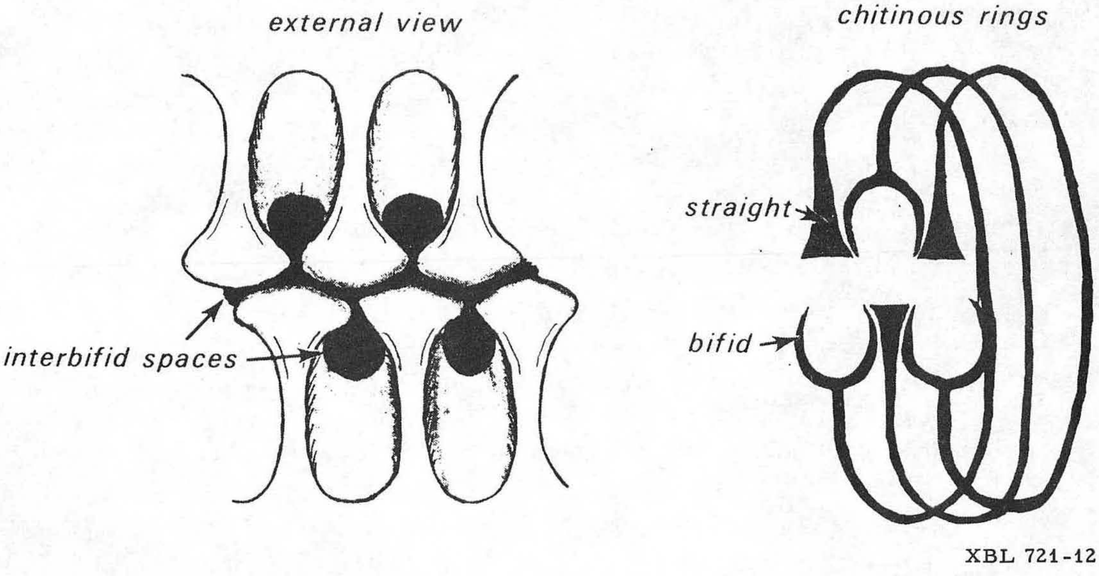

fig.14: A portion of a pseudotrachea, (after Graham-Smith).

ends are called the interbifid spaces, (Graham-Smith, 1911).

The pseudotracheae prvent particles larger than about 6 μ in diameter from entering the mouth, (Graham-Smith, 1911). If there were no such filter system, the preoral food cavity would probably become completely occluded.

> Mark but this flea, and mark in this
> How little that which thou denyst me is;
> It sucked me first, and now sucks thee,
> And in this flea our two bloods mingled be.
>
> John Donne

The Legs

> O mind your feet, O mind your feet,
> Keep dancing like a wave,
> And under every dancer
> A dead man in his grave.
>
> W. B. Yeats

Insects' legs are designed basically for walking or running, but many insects have a large number of extraordinary modifications which fit their legs to other uses. Grasshoppers have large and powerful hind-legs, for jumping; Praying Mantids have intermeshing spines on the femur and tibia of their fore-legs, for grasping prey; Water Boatmen have legs that resemble oars, for swimming; and Mole Crickets have strong, scraping, shoveling parts on their legs, for digging, (Ross, 1967). In fact many insects, including _Drosophila_, have a large assemblage of remarkable features on their legs, (figure 1).

The exoskeleton of insects is sclerotized, and gives strong support while being very light. The legs are heavily schlerotized and so manage the weight of body easily. The body hangs down from the legs, (figure 2), so that it almost touches the ground. This hanging down of the body gives the insect great stability by significantly lowering the center of gravity, (Hughes, 1965). Most insects don't easily fall over.

Each leg on a _Drosophila_ consists of ten different segments, (figure 3). The basal joint is the _coxa_ which is attached directly to the thorax of the fly; then there is a very short supporting segment, the _trochanter_; the _femur_, next, is large and mascular; the _tibia_ follows

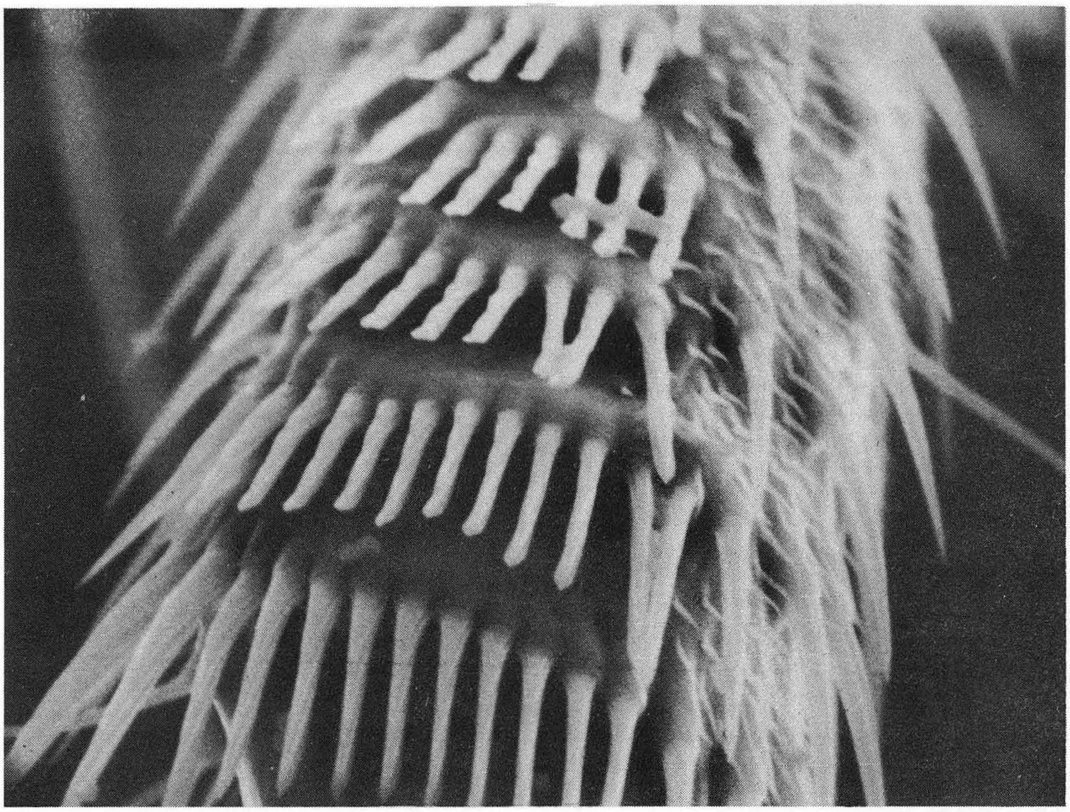

fig.1: Transverse tibial rows in a short-bristled mutant.

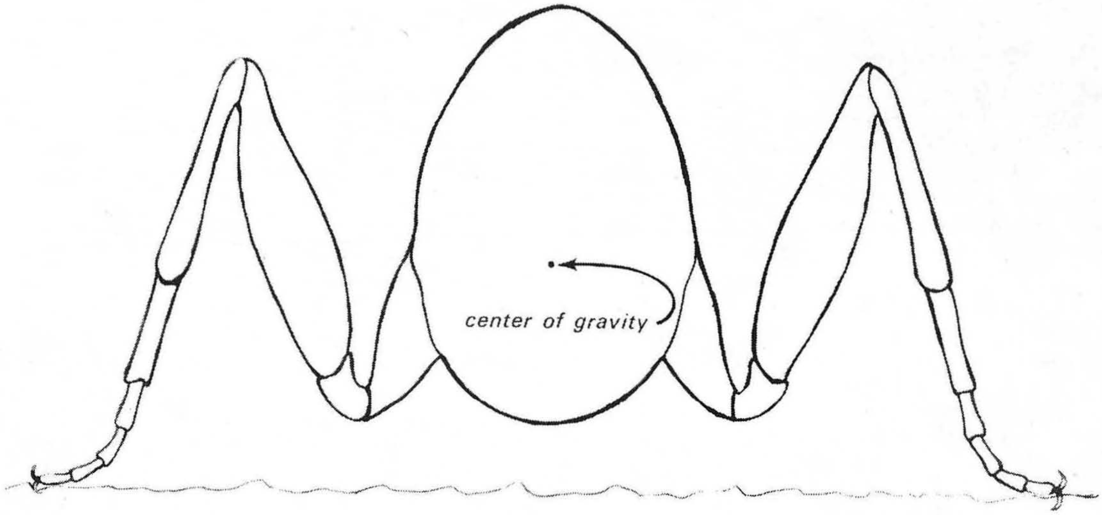

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fig.2: Diagram of how the body hangs, (after Hughes).

the femur and is strong and slender; after which five tarsomeres: the basitarsus or metatarsus, the second tarsomere, the third tarsomere, the fourth tarsomere, and the fifth tarsomere, articulate freely, and together with the pretarsus (which is the fly's foot) form the entire tarsus.

With this small bit of leg morphology we can consider, for a moment, the question of walking. How does an insect walk? More than a century ago, Johannes Müller showed that when an insect walks it uses three legs at a time. While being supported by the fore-leg and the hind-leg on one side, and the middle-leg on the other, the insect brings his other three legs forward. It has been said that the fore-leg acts as a tractor, the middle-leg as a support, and the hind-leg as a propulsor in the forward and sideward directions, (Wigglesworth, 1966). Slow motion film studies reveal that this mechanism is indeed used by insects in normal walking; yet when walking quickly or running the motions of the legs are terribly confusing. If an insect is caused to walk on smoked paper, it is found that each of the three legs on each side lie successfully on the same spot, (Wigglesworth, 1965). Insect walking, besides involving all these rather sophisticated mannerisms of leg placement, is characterized by a rapidity of forward progression, and an astonishing rate of directional change, (Hughes, 1965).

The complexity of the nervous control of walking is compounded to provide instantaneously for the loss of one or two legs. The insect does not have to relearn to walk if he meets with an accident that costs him, say, two legs; he immediately changes the sequence of leg movements to whatever will give the best results in the new circumstances,

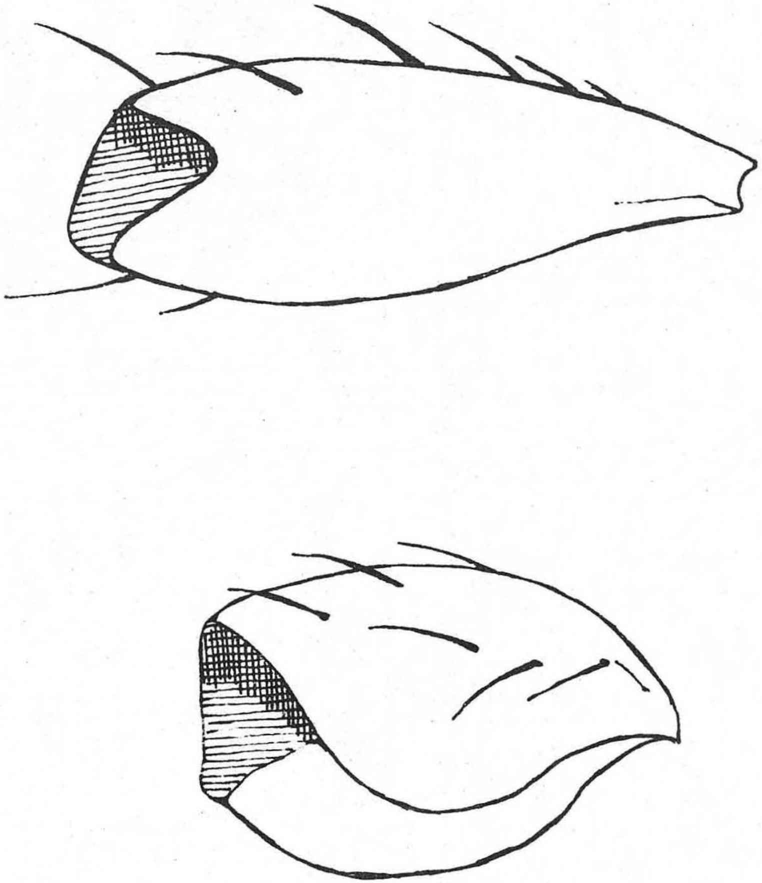

fig.4: Left: coxa of foreleg; Right: coxa of hindleg.

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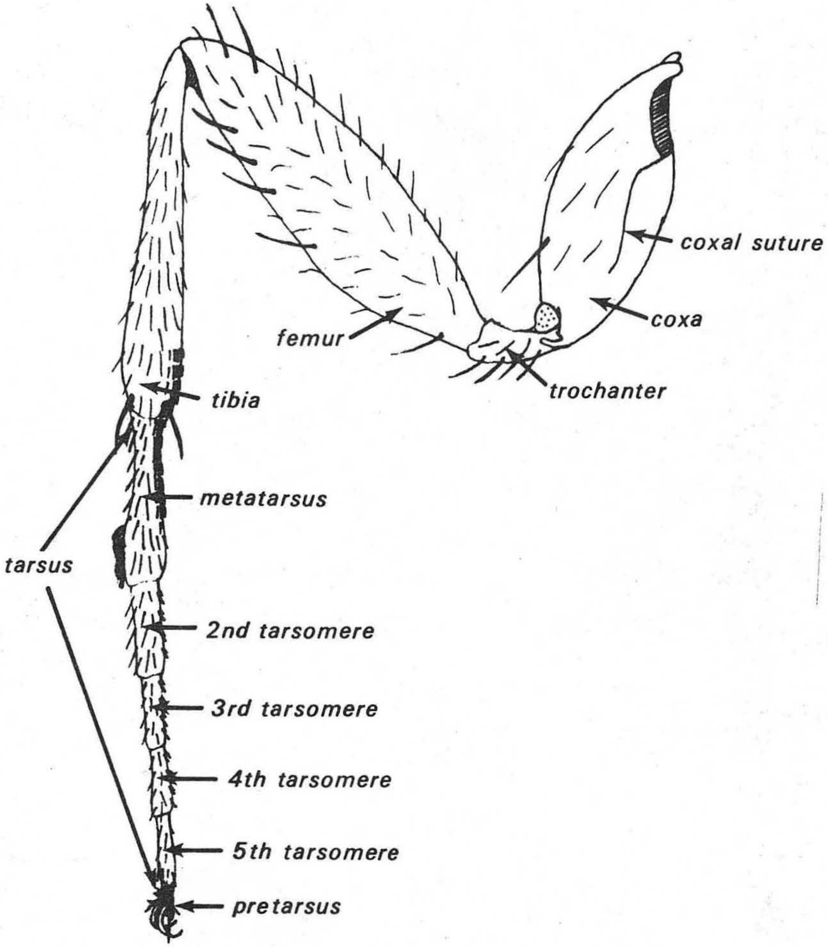

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fig.3: Diagram of right foreleg of the male, (after Ferris).

(Wigglesworth, 1964).

When at rest, the insect positions the coxae against the sides of the body, with the fore-legs directed anteriorty, the hind-legs stretched posteriorly, and the middle-legs taking whatever intermediate spot is most convenient, (Snodgrass, 1952). During flight, the legs of Drosophila serve no direct purpose, and are allowed to dangle, flop, and stream in the wind. The wings and not the legs, steer the flight of the fly.

Often we see Drosophila clean themselves by using their legs as brushes. When an antenna or an eye needs cleaning, the fly will reach up and slide his hairy fore-leg over it. When the wings need cleaning the fly twists his hind-leg so that the tibia and tarsus lie on the top surface of the wing, then slides them off, and repeats the action until the wing is deemed clean.

Let us return to the morphology of the Drosophila leg. The coxa, as we have said, is the basal joint of the leg. In Drosophila it is attached to the body by a membrane and a single point of articulation, the pleural articular socket, and thus the coxa can be moved quite freely. The coxae of the first thoracic segment, or prothorax, are longer and more cylindrical than those of the middle and hind legs, (Sturtevant, 1921), presumably because the fly gains most of his directional control in walking from the accurate movement of the fore-leg. The coxae of the mesothorax and metathorax are short, sturdy, truncate, and have a more definite coxal groove (often called coxal suture), all of which provides extra support for the attachment of muscles, (Snodgrass, 1935). Thus, the fact that the fore-legs appear to determine the course of the insect when walking, while the hind-legs serve as the chief organs of propulsion, is reflected in the morphology of the coxae, (figure 4).

Proceeding towards the foot, we find a hinged joint at the bottom of the coxa. Hinged joints are called monocondylic if they have one hinge, dicondylic if they have two. The joint between the coxa and the trochanter is dicondylic with anterio-posterial hinges so the fly can swing the trochanter only in the dorso-ventral plane. If one examines figure 5, he will see that the coxa extends a gripping protrusion into a groove in the trochanter. This is the anterior hinge. One can also see that the joint works on a ball and socket mechanism, and that the ball looks "furry."

The trochanter itself, a very small segment, is bent about forty-five degrees from linearity. Under the ball of the ball and socket, it projects its tip well into the coxa, providing a strong process for the attachment of muscles, (Snodgrass, 1927). The trochanter while moveable at one end, is more or less fixed to the femur. Lastly, with regard to figure 4, one may note the slender mechanoreceptive spines on the ventral side of the trochanter.

The coxo-trochanteral joint possesses a hair plate, (figure 6). Hairs plates are concentrations of minute sensilla trichodea, and are a common feature in the joints of insects. In all cases the sensilla are stimulated by folds of the intersegmental membrane or by contact with adjoining surface as the joints are moved, (Dethier, 1963). In the case

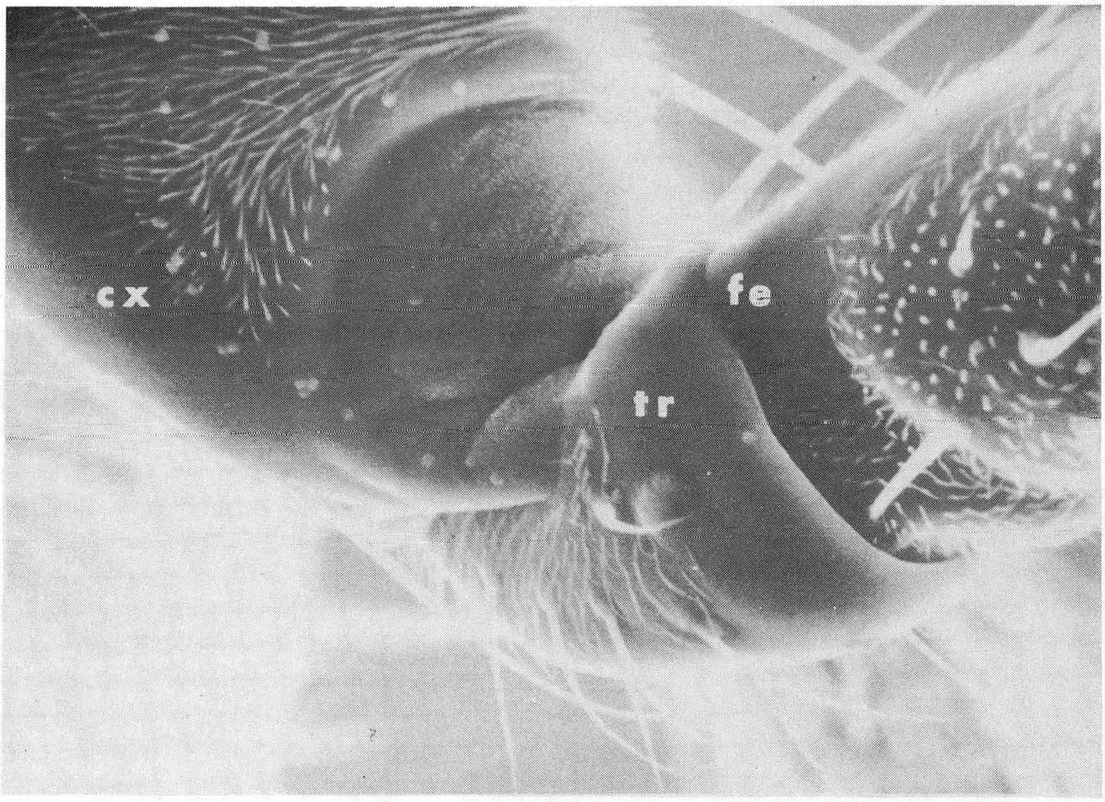

fig.5: Trochanter of hindleg; cx, coxa; tr, trochanter; fe, femur.

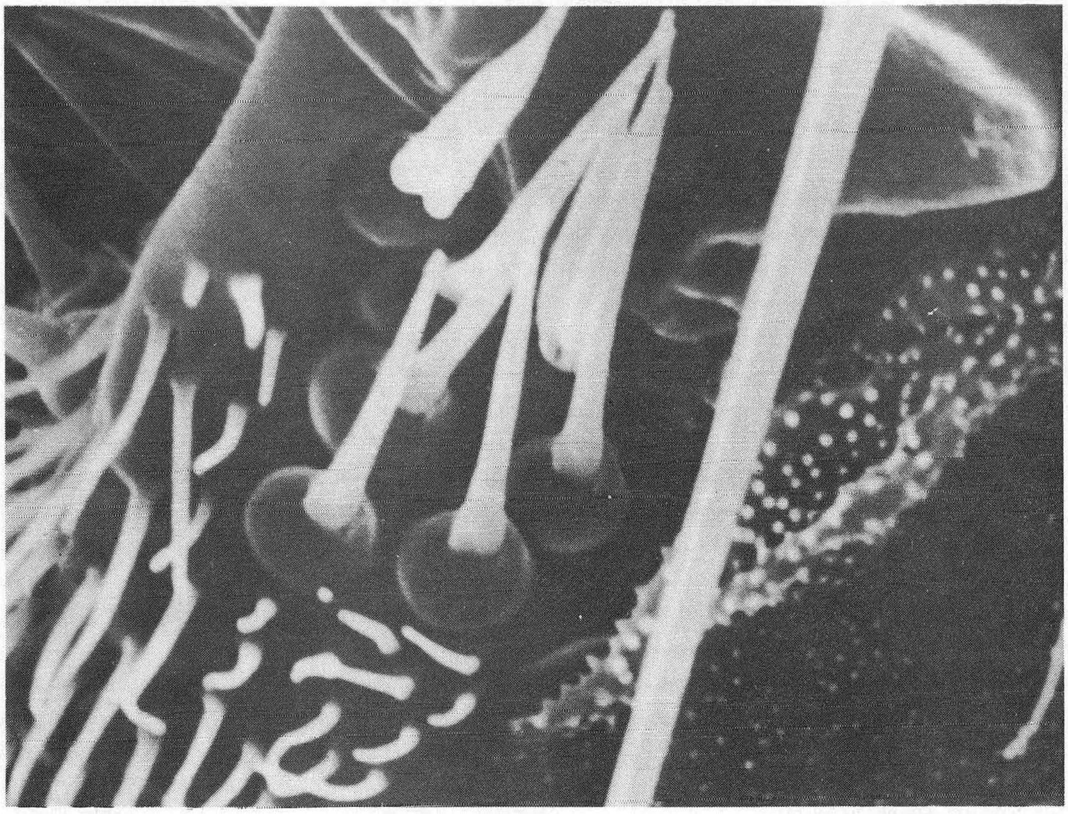

fig.6: Hair plate in the coxo-trochanteral joint.

of figure 6, there is a special "contact plate" that pushes the sensilla and stimulates them.

The femur is the longest and strongest segment of the Drosophila limb. The volume of the femur is generally correlated with the amount of muscle contained within it. In figure 5, one can see that the femur actually bulges with muscle.

The femora-tibial joint is also dicondylic, with anterio-posterial hinges. Figure 7 describes this joint well. Besides hair plates as a means of proprio-reception, insects also use campaniform sensilla which are dome shaped stress receptors. When the surrounding cuticle is strained the campaniform dome is deformed causing an excitation of the associated neurons. Figure 8, a ventral view of the femora-tibial joint shows two campaniform sensilla on the femur just above the tibia.

The tibia, as we have said, is a slender segment, a little shorter than the femur where the muscles that control it originate. At the distal end of tibia, on the ventral side there arise about eight rows of sensilla trichodea. Figure 1 shows some of these rows of slightly twisted chemoreceptive sensilla, in a mutant fly. In a wild-type fly the sensilla are much longer and more slender, (figure 9).

At the distal end of the tibia, there are two very large mechanoreceptive spines, called the tibial spurs, (figure 10). They are thick, strong, heavily corrugated, and electrophysiological work has proven them to be slow adapting tactile sense organs, (Dethier, 1963). One can see, (figure 11), how the spurs would be disturbed by the extreme flexion or extension of the joint, and they should, therefore, serve to register momentarily such events, (Pringle, 1938).

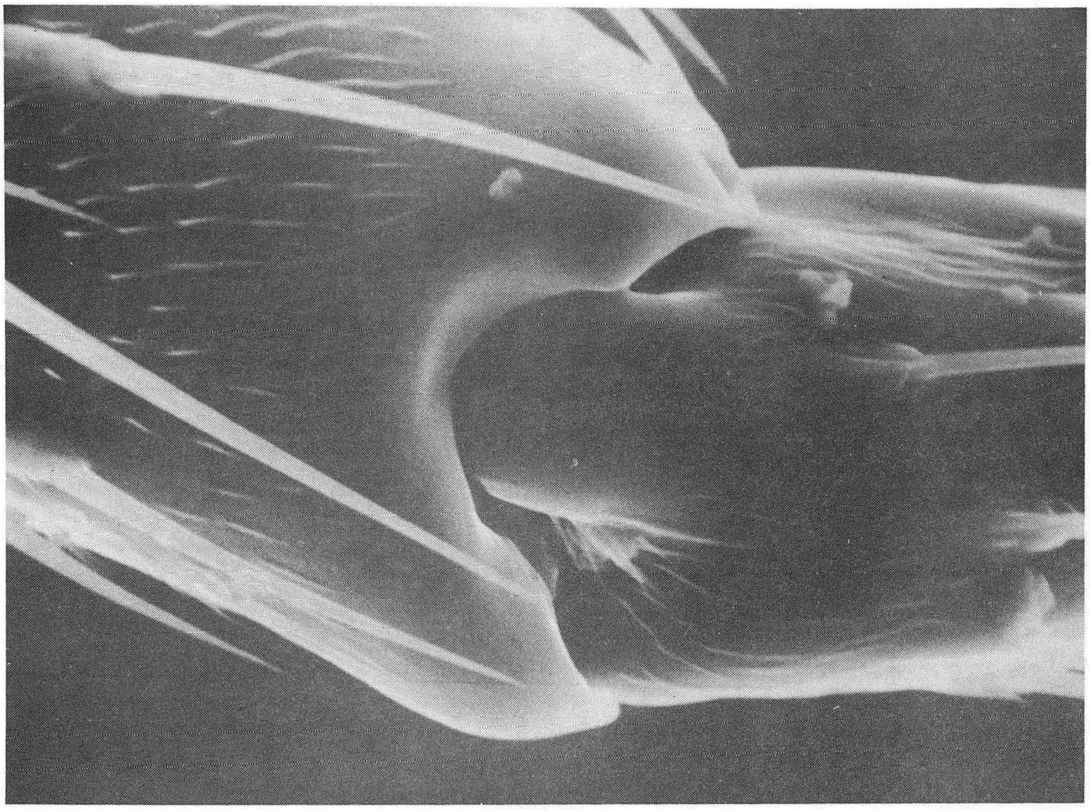

fig.7: Midleg, femuro-tibial joint.

fig.8: Campaniform sensilla at femuro-tibial joint, <u>cs</u>.

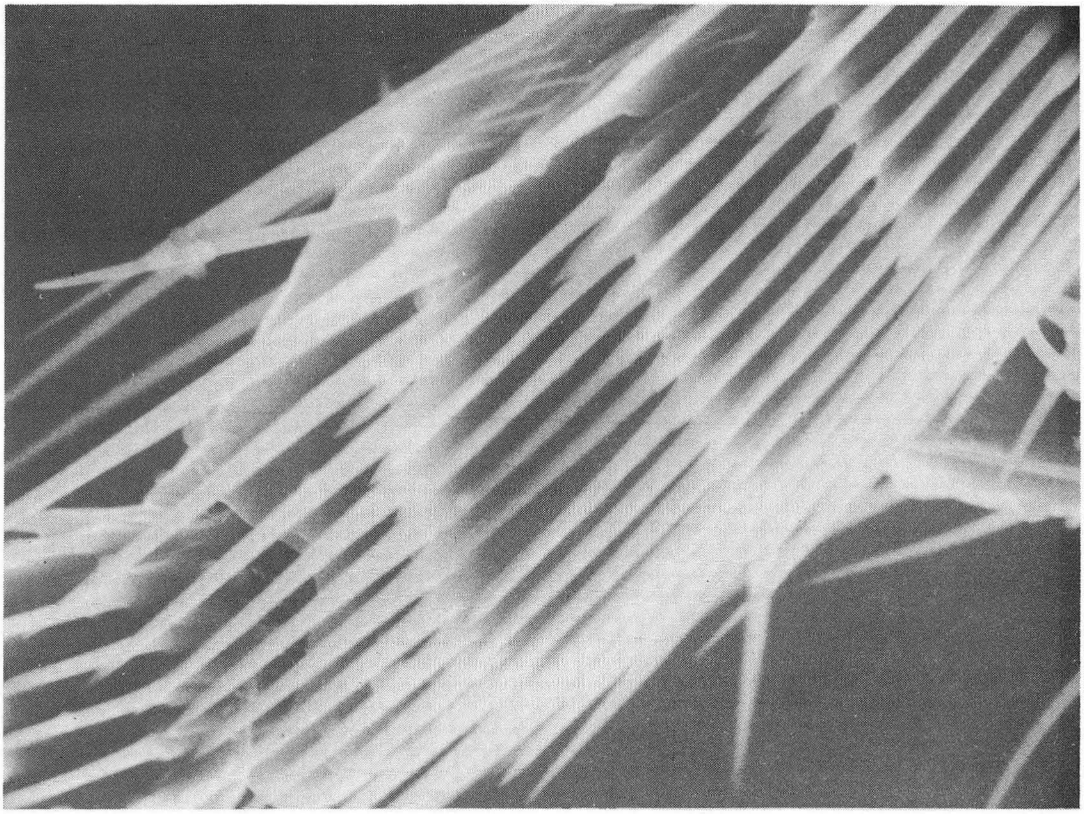

fig.9: Transverse rows of sensilla trichodea on the tibia of a female wild-type fly.

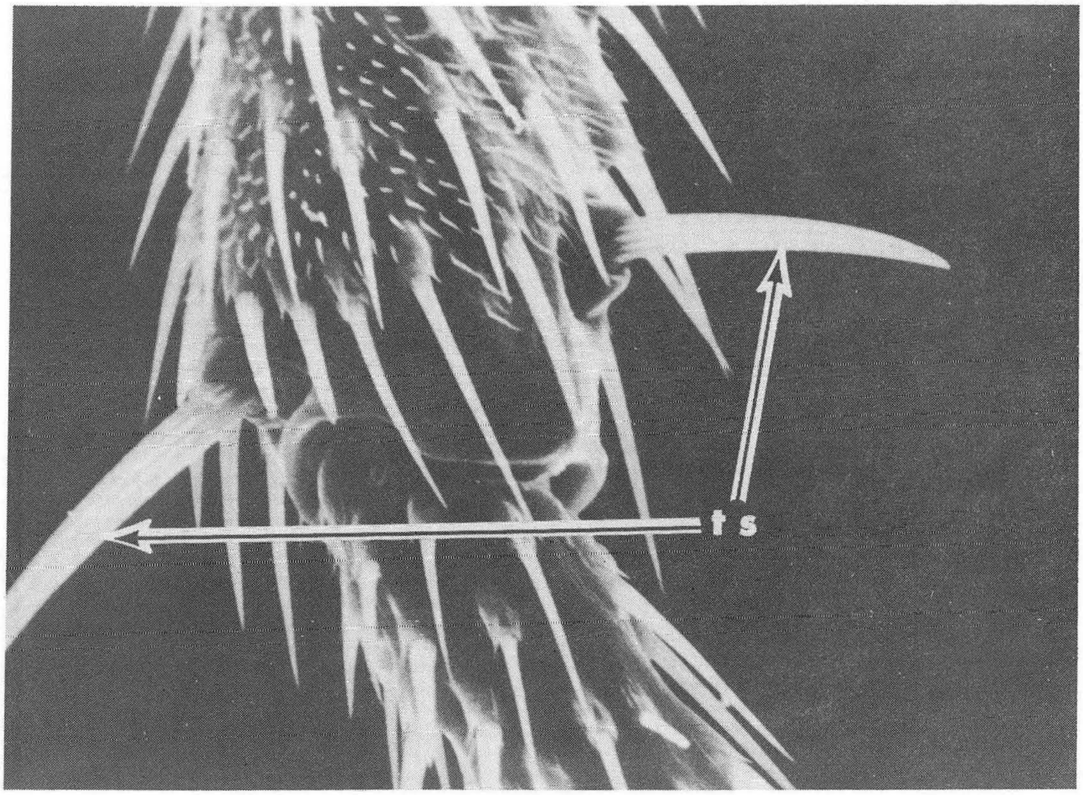

fig.10: Tibio-tarsal joint, midleg; ts, tibial spur.

One can see in figures 10 and 11 that there are many smaller but basically similar mechano-receptive spines on the femur and the tibia. In fact they exist on all the leg segments. But unlike the tibial spurs, each of these smaller spines has associated with it a small hair-like process, called a bract, that overlaps the base of the spine, (figure 12). Such spines are called by geneticists bract-bristles.

The tibio-tarsal joint, (figures 10 and 11), is dicondylic, having dorso-ventral hinges. Thus in principle, the basitarsus can move only anterio-posteriorly on the tibia; but actually, if one watches a live fly under a dissecting microscope, he will notice that the movement is considerably more free than he would expect, (Snodgrass, 1952).

Proceeding further along the leg we find ourselves at the basitarsus—the first tarsomere. The ventral side of this segment is covered with rows of sensilla trichodea much like the rows on the tibia only shorter, (figure 13). One can see they have bracts and that in this female fly there are eight rows on the foreleg. Also visible are two sensilla trichodea that jut out at a large angle from the dorsal side of the basitarsus. When the insect walks, the rows of sensilla trichodea are placed flat on the ground so that the fly can taste whatever it is that he is standing on, (a capability that would prove disastrous in humans). In figure 13 one can see numerous small balls stuck to the sensilla. These balls are yeast cells that are part of the medium on which the fly was raised.

Also on the metatarsus is an important sexual dimorphism due to the presence in the male alone of a peculiar organ, the sex comb, (figure 14). In the male there are two or three fewer transverse rows

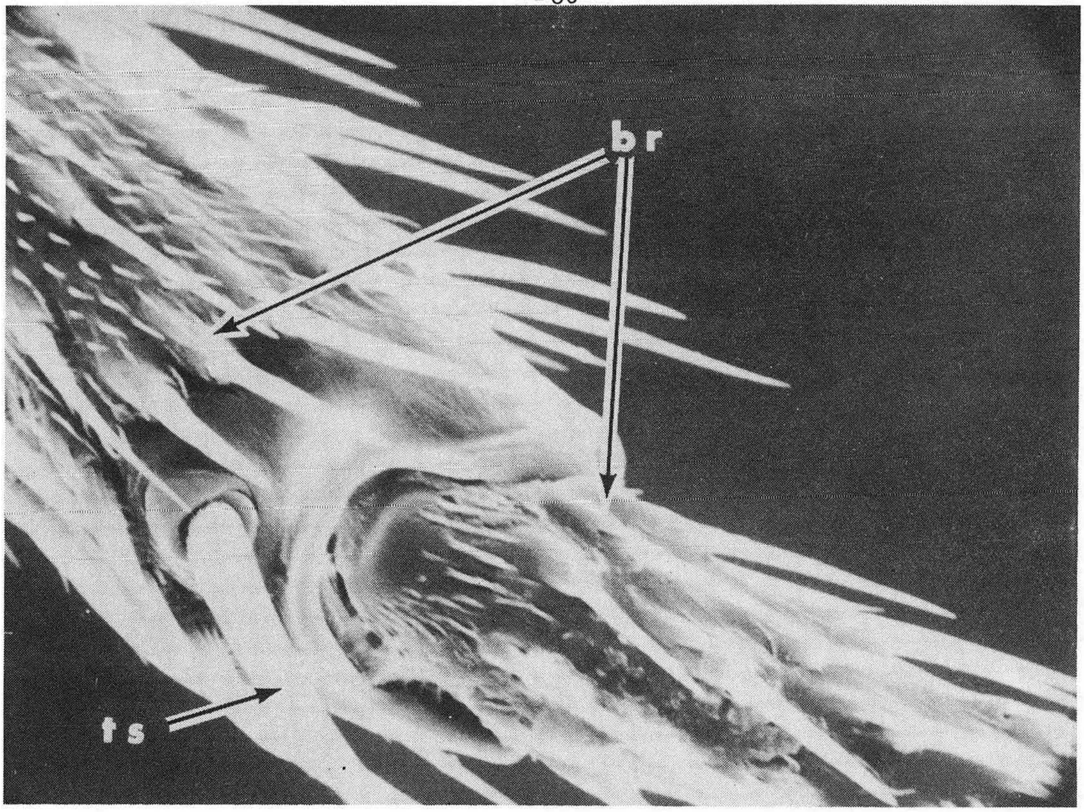

fig.11: Tibio-tarsal joint, hindleg; ts, tibial spur; br, bract.

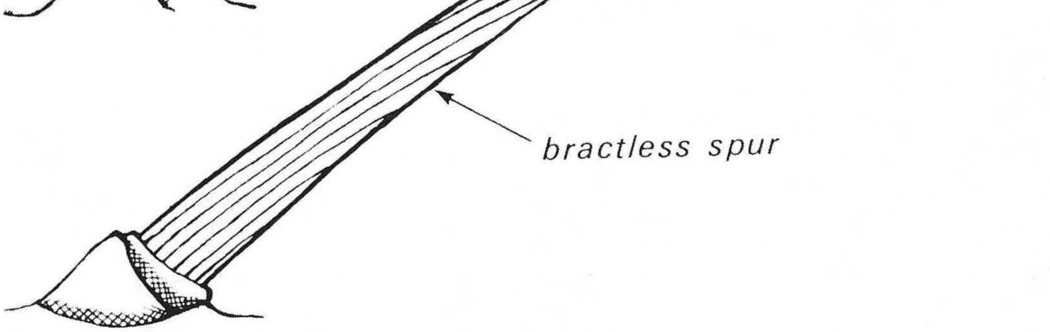

fig.12: Diagram of tibial spur and bract-bristle.

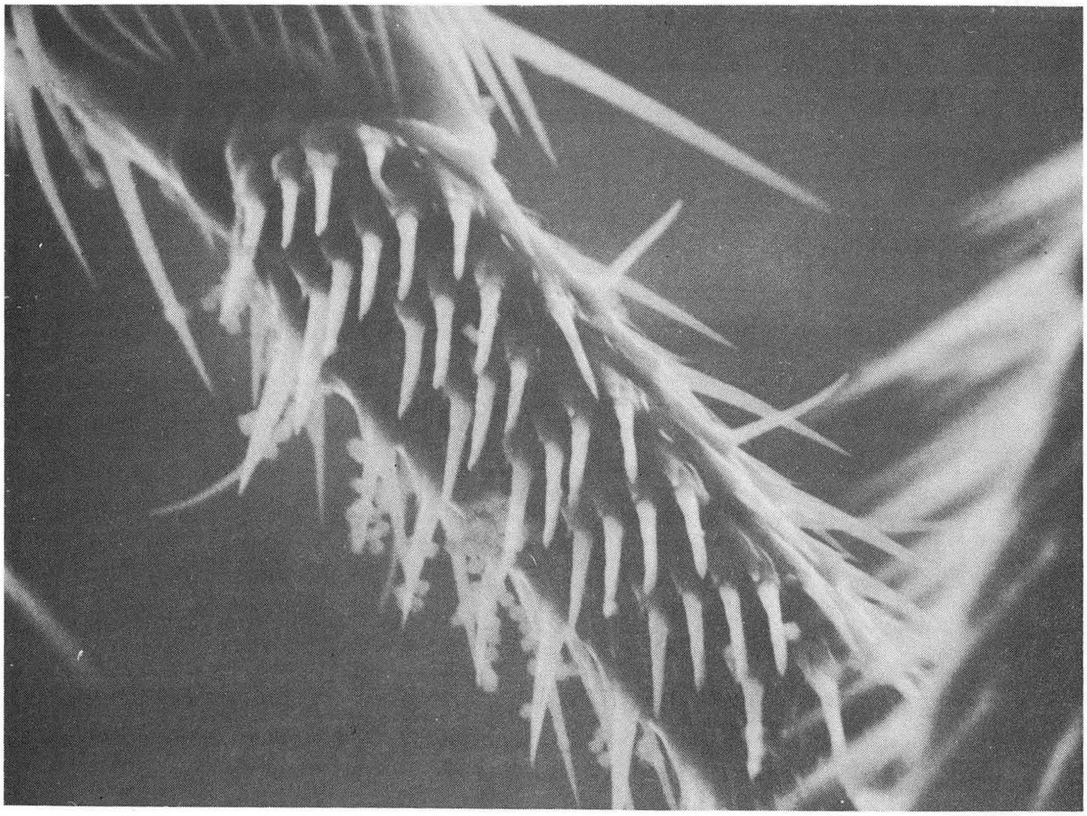

fig.13: Basitarsal rows of sensilla on female foreleg

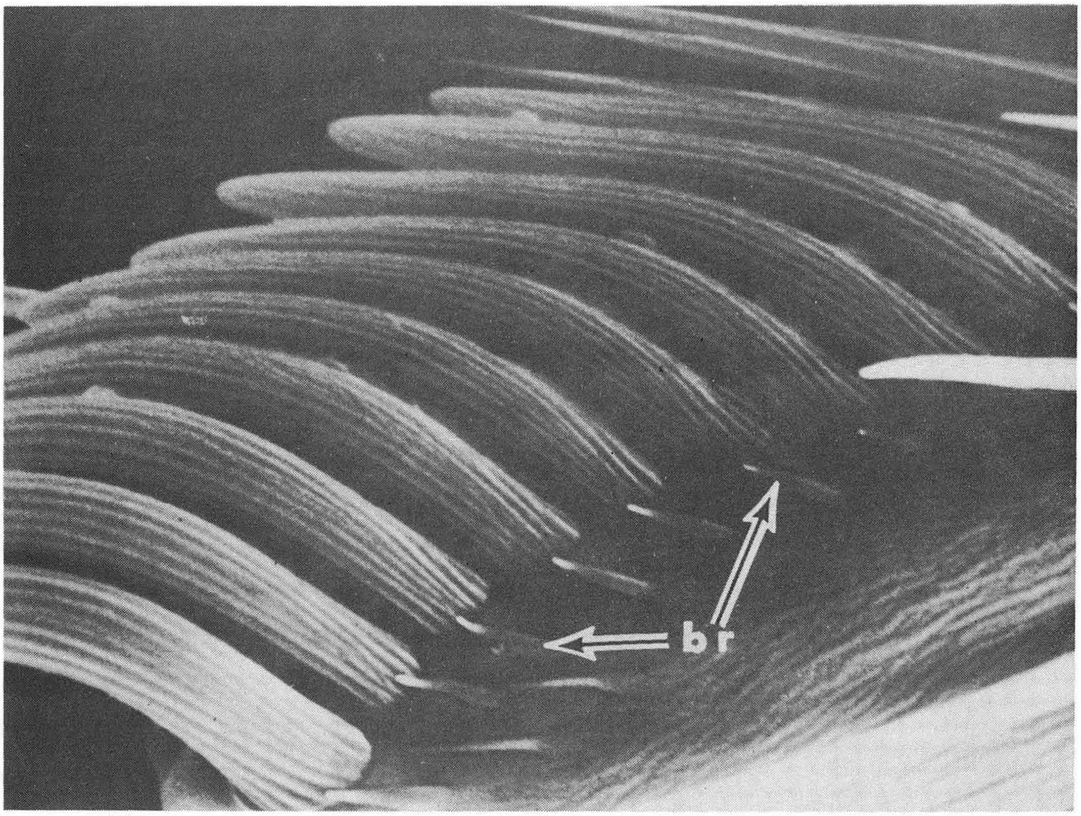

fig.14: The sex comb; br, bract.

of sensilla trichodea. In the more apical region the rows stop and there is a sex comb which consists of enlarged cylindrial spines that look very similar to about ten closely spaced slightly bent, teeth of a comb, (Stern, 1954). These teeth have bracts and are very finely corrugated. There seems to be a strong homology between the sex comb and the traverse rows of sensilla. It is not known what function the sex comb serves, whether the teeth are mechano-receptors, chemo-receptors, or neither; but because no such apparatus is found in the female it is thought that the sex comb might play some grasping rôle during mating.

One can also locate on the basitarsus, (figure 15), occasional sensilla basicona, or smell receptors. Sensilla basicona look like small blunt pegs, much shorter than sensilla trichodea. In figure 15 there are two such pegs on the basitarsus, one about one-fifth of the way down the segment clearly in view, the other about five-sixths of the way down rather more obscure and quite sharply bent.

The four other tarsomers are regularly shaped, short cylinders, covered with bract-dressed spines and sensilla trichodea, (figure 16). The tapered base of each tarsomere fits into the hollow, cone-like cavity in the tarsomere proximal to it, (Lowne, 1870). Thus, although the intratarsal joints, (figure 17), limit the extent of certain movements they do limit the direction of movement.

At the end of the fifth tarsomere is the last segment, the pretarsus. The pretarsus is an amazing piece of apparatus, (figure 18). Two large claws known as <u>ungues</u> are used for holding on to rough surfaces. The claws can be flexed by muscles originating in the femur

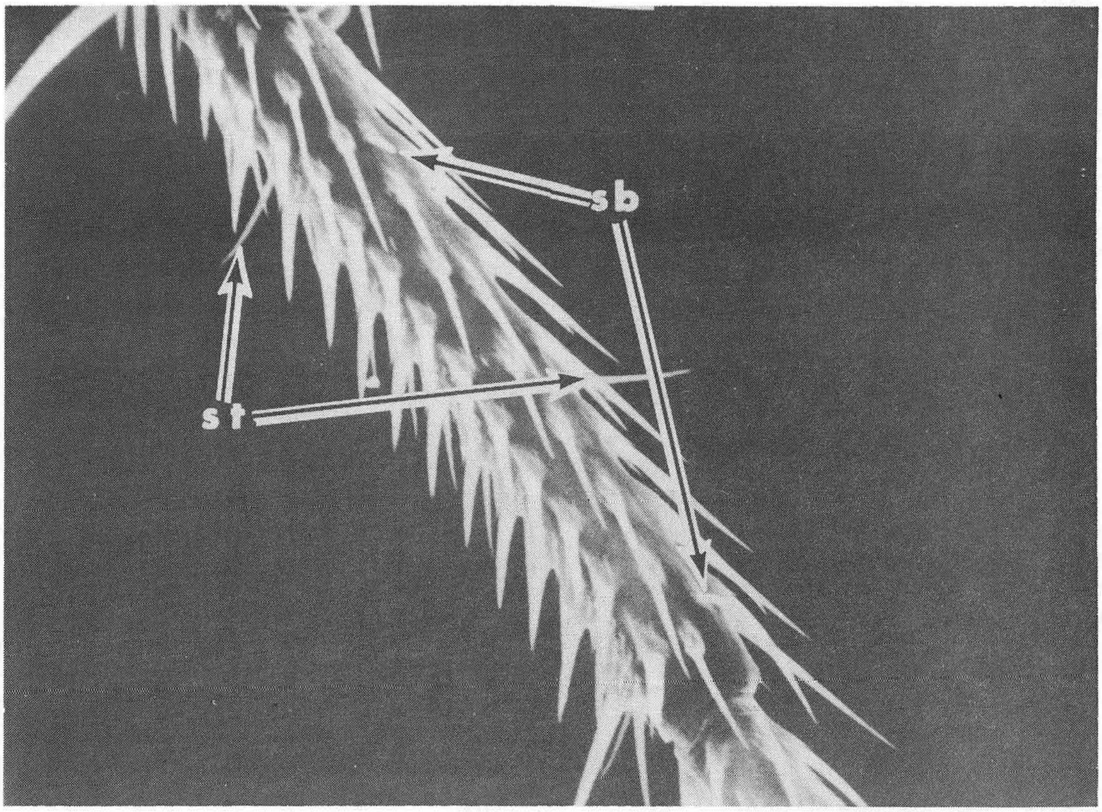

fig.15: Dorsal surface of basitarsus. st, sensillatrichodea; sb, sensilla basicona.

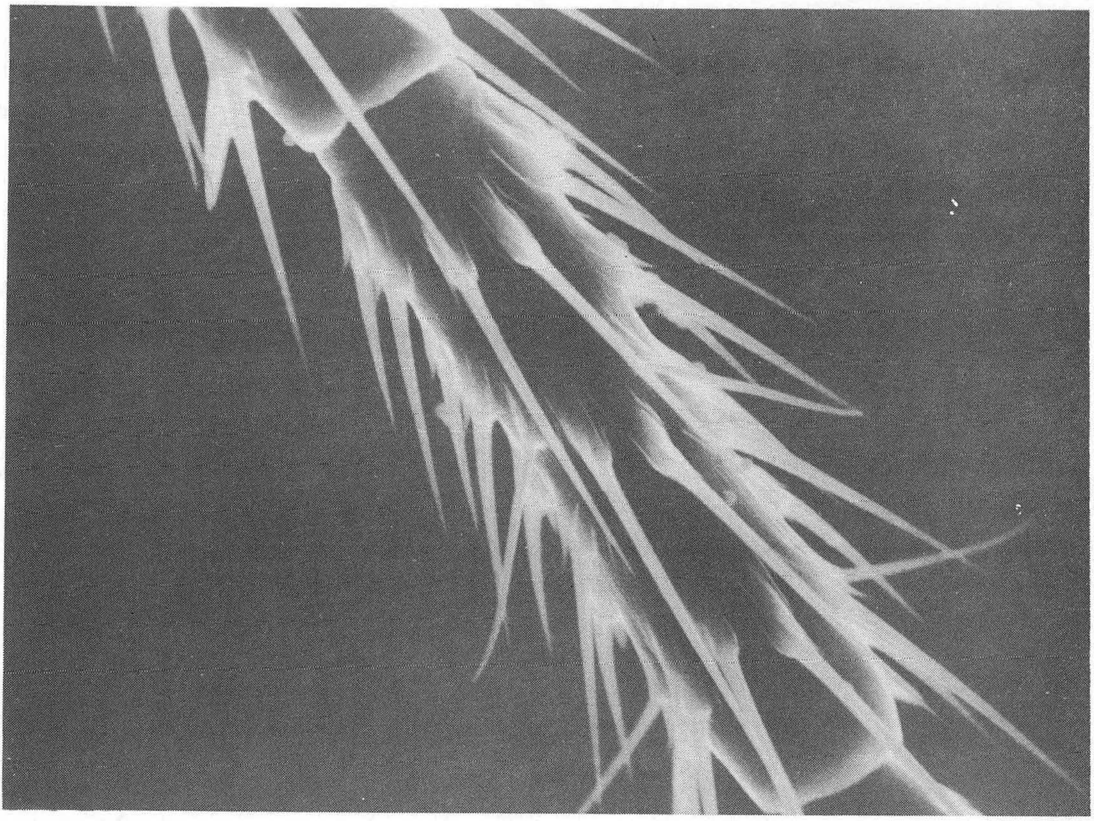

fig.16: Third tarsomere, dorsal aspect, midleg.

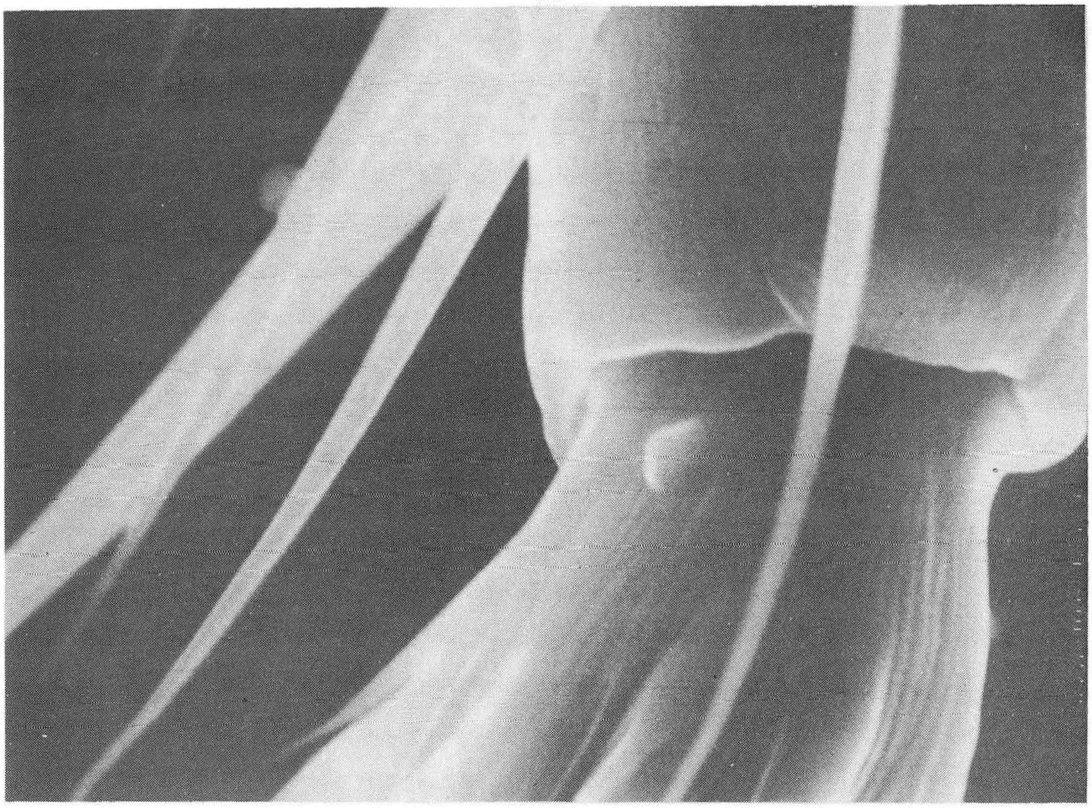

fig.17: Intratarsal joint, (third to fourth tarsomere), midleg.

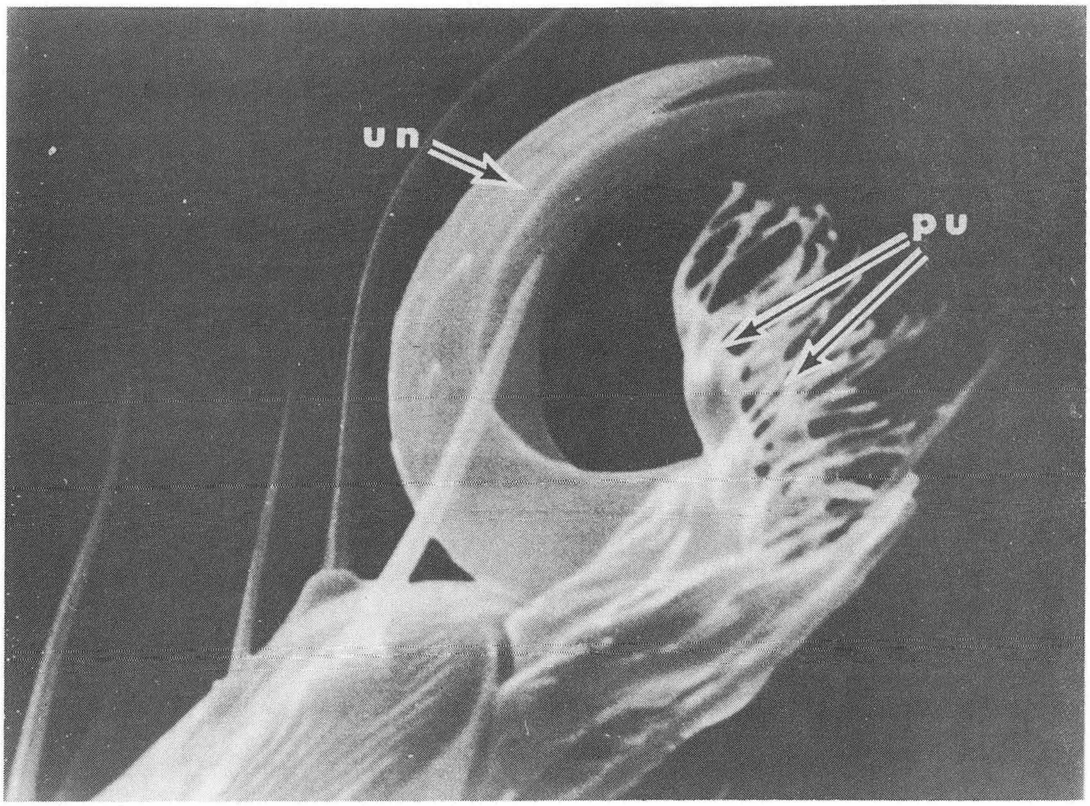

fig.18: Pretarsus, lateral aspect; <u>un</u>, unguis; <u>pu</u>, pulvilli.

and reaching down to the unguitractor plate, (figure 19), on the ventral side of the pretarsus. At the distal end of the unguitractor plate sits a median process called the empodium, (Snodgrass, 1935). What its function is, no one knows. Underneath the claws are the foot pads or pulvilli. The pulvilli enable the fly to walk upon smooth surfaces upside down, apparently in defiance of the laws of gravity. How is this done? On the pads we find a viscous fluid that glues them to any flat surface on which the insect walks. Upon dissection we can find a closed sack full of this fluid that extends through the four distal tarsomeres. The sack secretes the fluid by exuding it into the pulvilli as well as into the hollow trumpet-flared hairs, (figures 18 and 19). The hairs are always kept full of fluid, (Lowne, 1870). The insect can readily release these pads by rolling them inward from the margins, (Crampton, 1942).

A non-living, tough, and most often rigid cuticle effectively insulates tissues from all but the grossest disturbances from the external environment. That is why we see so many sensilla on the legs: the mechano-receptive spines, the hair-plates, the campaniform sensilla, the sensilla trichodea, and the sensilla basicona; to provide the surface sensitivity denied by the exocuticle, (Dethier, 1963). It is because the legs so frequently come into direct contact with the environment that these sensilla are so numerous there.

Am not I
A fly like thee?
Or art not thou
A man like me?

For I dance
And drink, and sing,
Till some blind hand,
Shall brush my wing?

William Blake

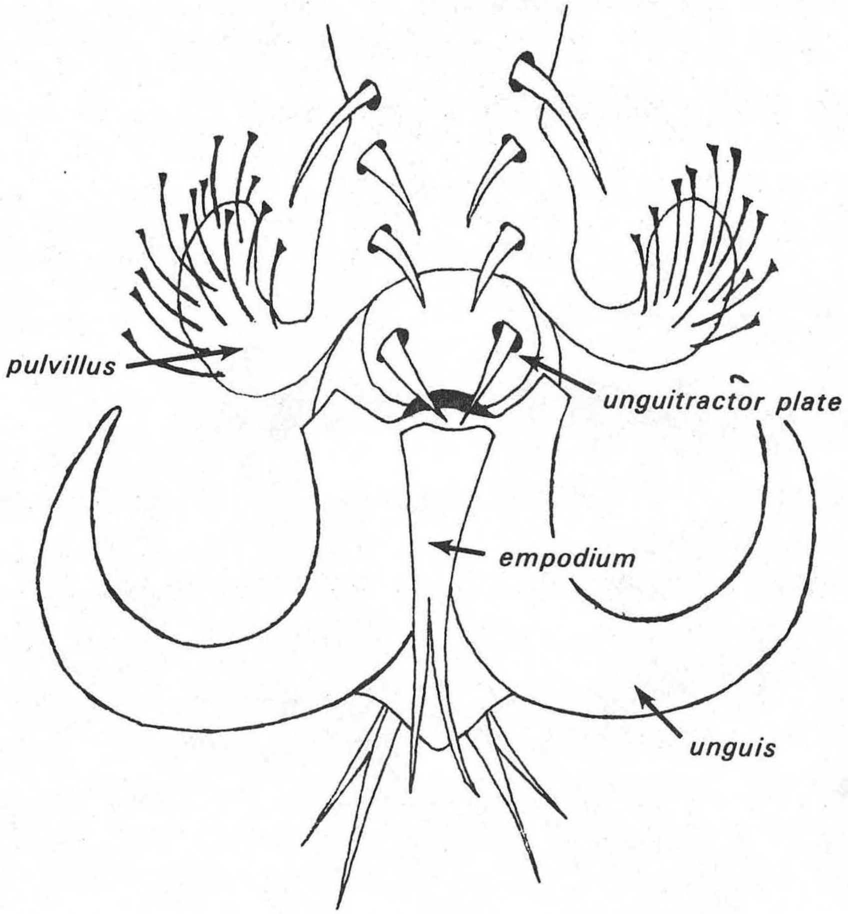

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fig.19: Diagram of pretarsus, ventral aspect.

The Wings

I heard a fly buzz when I died;
And the stillness round my form
Was like the stillness in the air
Between the heaves of storm.

Emily Dickinson

The evolutionary development of wings in insects is a topic of interesting hypotheses. In bats and birds the wings developed as modifications of the anterior legs; but in insects wings arose de novo as outgrowths of the body wall, and as a result there are no muscles attached inside the insect wing, (Ross, 1967). Paleontological evidence shows that the oldest known insects, from the Carboniferous era, had two pairs of fully developed wings, (Snodgrass, 1935). Furthermore, studies of the patterns of venation in the wings of insects suggest that all winged insects stem from a common ancestor, (Wesché, 1906).

It is thought that insect wings began to develop as sideways expansions of the dorsal part of the thorax. Initially, these may have been used as gliders. Large jumping insects and arboreal insects would have been stabilized by these gliders when they launched into the air; and it is not hard to conceive how the insects with the better gliders would have a slight selective advantage over the others. Eventually these gliding wings grew large, their articulation with the thorax evolved, and the muscles of the thorax began to have some control over them, which resulted in modern beating wings, (Snodgrass, 1935).

This development in winged insects means that a new neuromuscular as well as a new skeletal system contained in the same body segments are superimposed on that required for walking. Over the millenia, the wings of insects have become highly specialized and individualized in different species. In the diptera there has been a reduction of the number of wing viens by a process called coalescence. In coalescence the point of branching between two viens evolves nearer and nearer the margin of the wing, until finally the two become one, a point which is reflected in the morphological nomenclature, (Comstock and Needham, 1898). This process is largely responsible for the present morphology of the wings of Drosophilia.

The wing is essentially a hollow extension of the body wall, the dorsal surface being directly continuous with the scutum or mesonotum, and the ventral surface merging into the lateral body wall or pleural area, (Snodgrass, 1935). In fact, the half-mesonotum, half-scutellum, wing proper, and pleural structures all arise from the same so-called "wing" disc. The wall of the wing consists of the same elements as the body wall, namely cuticula, epidermis, and basement membrane. Its lumen contains nerves, tracheae, and hemolymph or blood. The cuticle is lightly sclerotized which helps to stiffen and protect the wings, and thick rod-like veins that run from the wing base to the margins further rigidity the wings. Each vien has a morphological name which will be given in figure 2. Figure 1 is a micrograph of a small section of one of the rod-like veins.

The thin spaces of the wings which are bounded by veins are called cells. When a cell is completely surrounded by viens, it is said

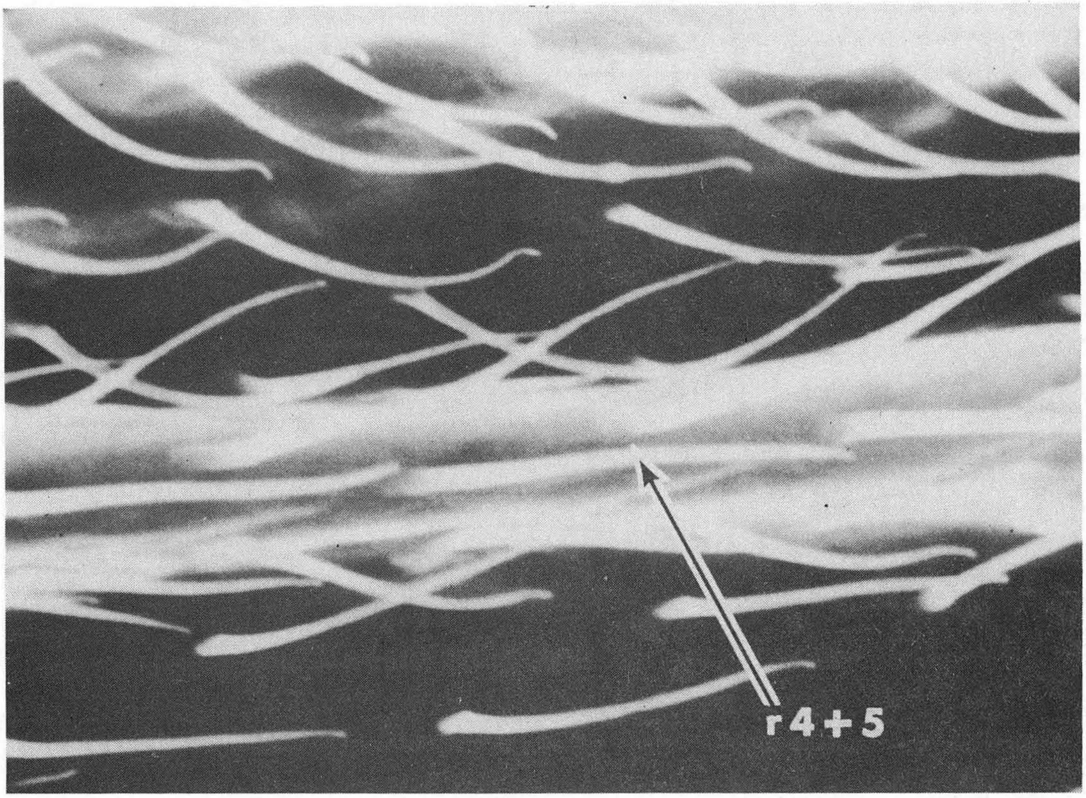

fig.1: Radius$_{4+5}$, dorsal view, r4+5.

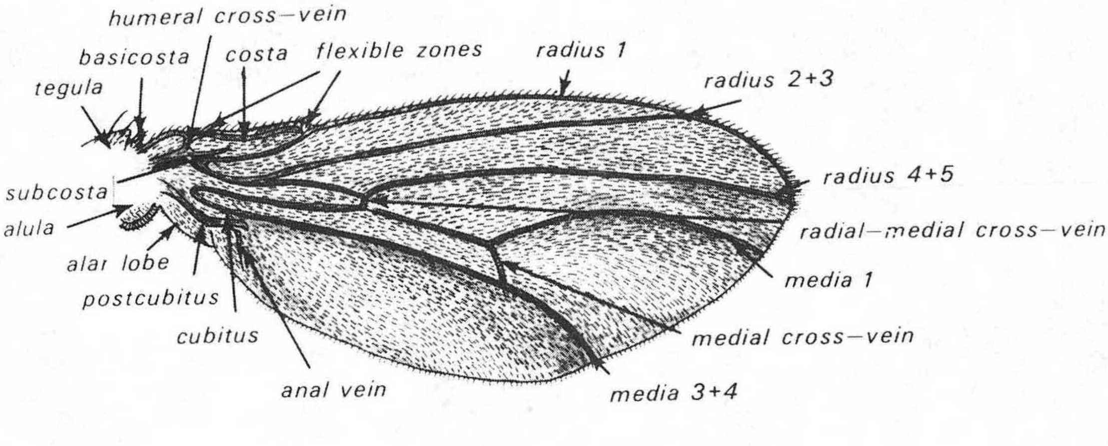

fig.2: Diagram of dorsal surface of right wing,(after Ferris).

to be closed; when it extends to the wing margin, it is said to be open, (Comstock, 1918). Figure 2 is a diagram of the dorsal surface of the right wing of a Drosophila in which the veins have been given their morphological names rather than their systematic names. Compare this diagram with the micrograph of the ventral surface of the wing, (figure 3). There is a forward crowding of the veins which stiffens the anterior parts of the wings and improves the aerodynamics.

At the point where the costal vein ends and radius 1 begins on the anterior edge, there is a flexible zone, (figure 4). The function of this area may be to prevent the insufficient elasticity of the large anterior veins from being injurious to the wing. This more delicate zone is itself protected by two large mechano-receptive spines which branch out over it, (figure 4). In the costa, a little distal to the humeral cross vein there is a thinning of the vein, what we might call a secondary flexible zone, (figure 5). This is also served by a large mechanoreceptive spine.

The entire surface of the wing is covered with small hairs which probably heighten the mechanical effect of the wing on the air, (Ritter, 1911). Figure 6 is a micrograph of some hairs arising out the wing. The fact that they are arranged in rows will be made clear later.

Near the base of the wing there are reported to be a number of sensilla campaniformia, (Dethier 1963). In this study with the scanning electron microscope they were not seen, a fact which suggests that they are not really there on Drosophila.

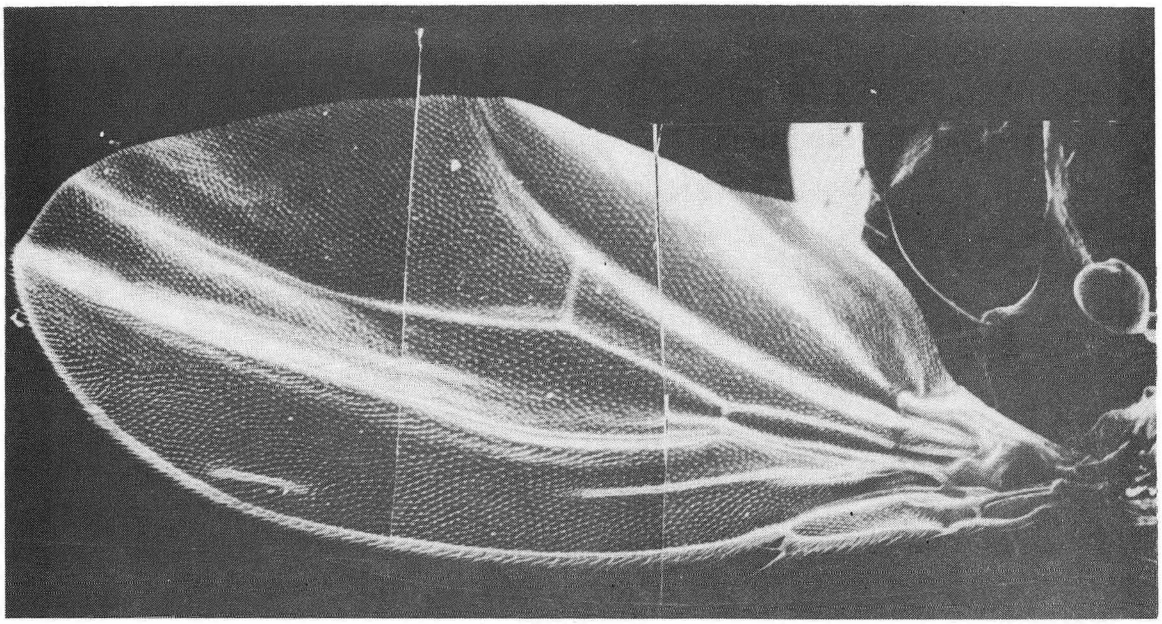

fig.3: Ventral aspect of left wing.

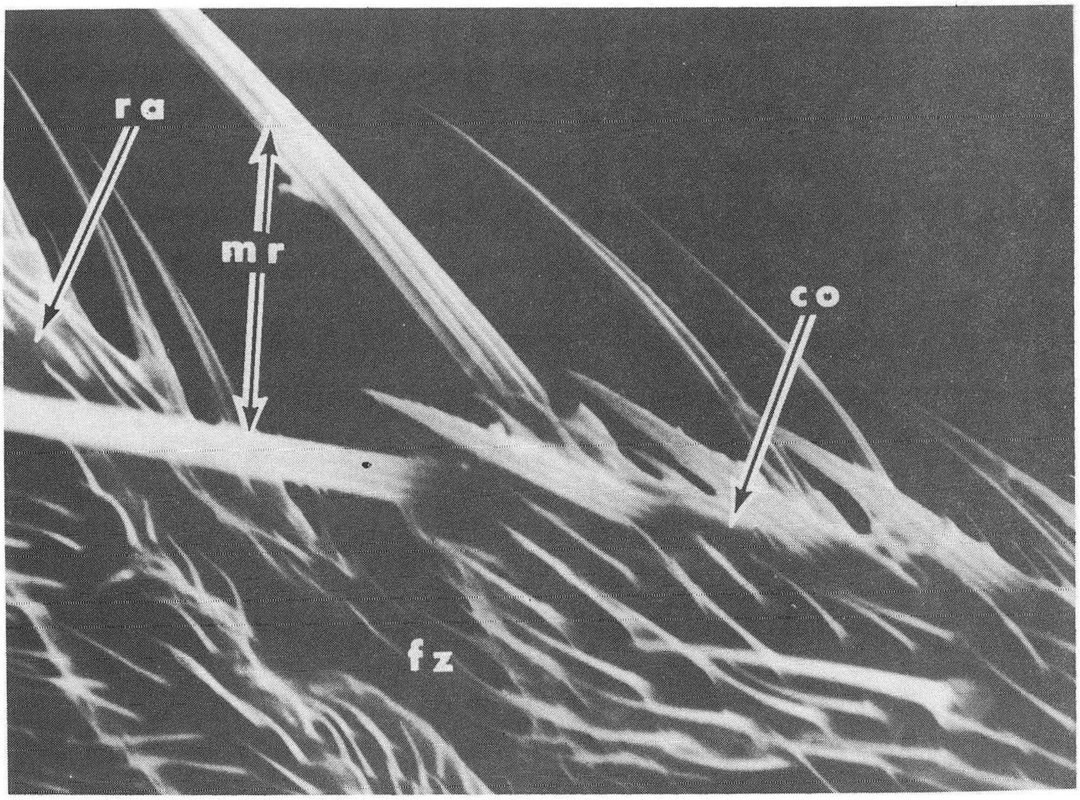

fig.4: Flexible zone, fz; mr, mechano-receptive spine; ra, radius; co, costa.

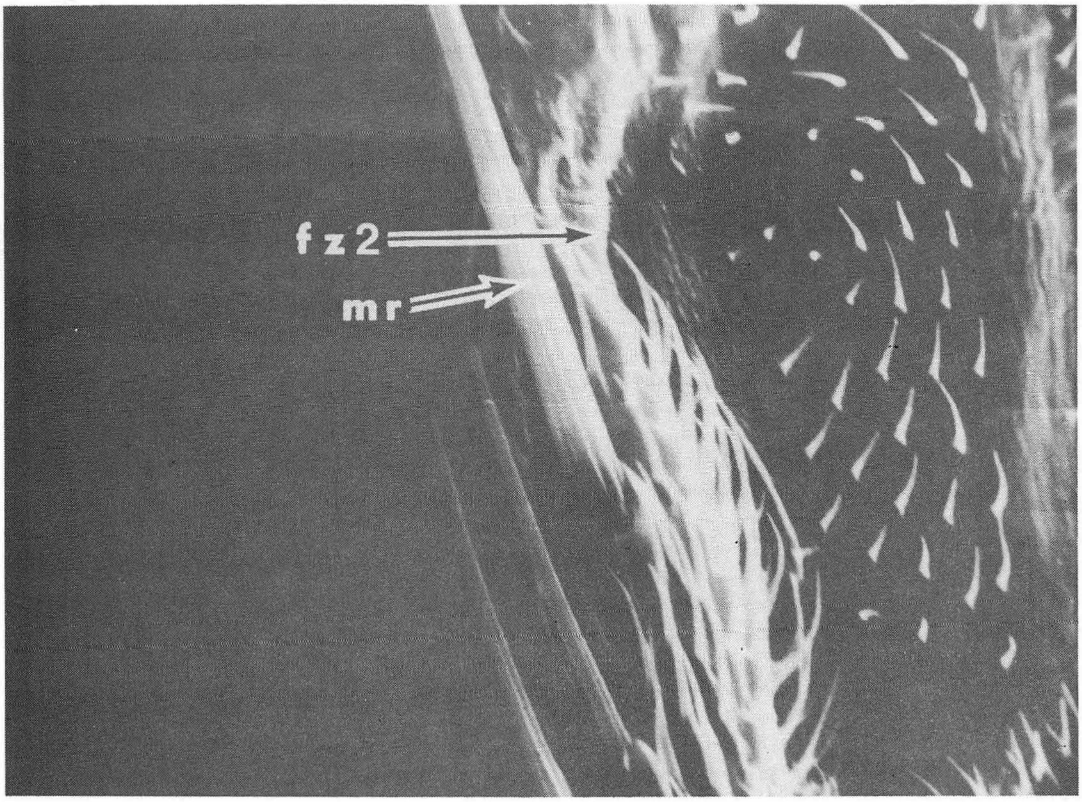

fig.5: Secondary flexible zone on costa,<u>fz2</u>; <u>mr</u>, spine.

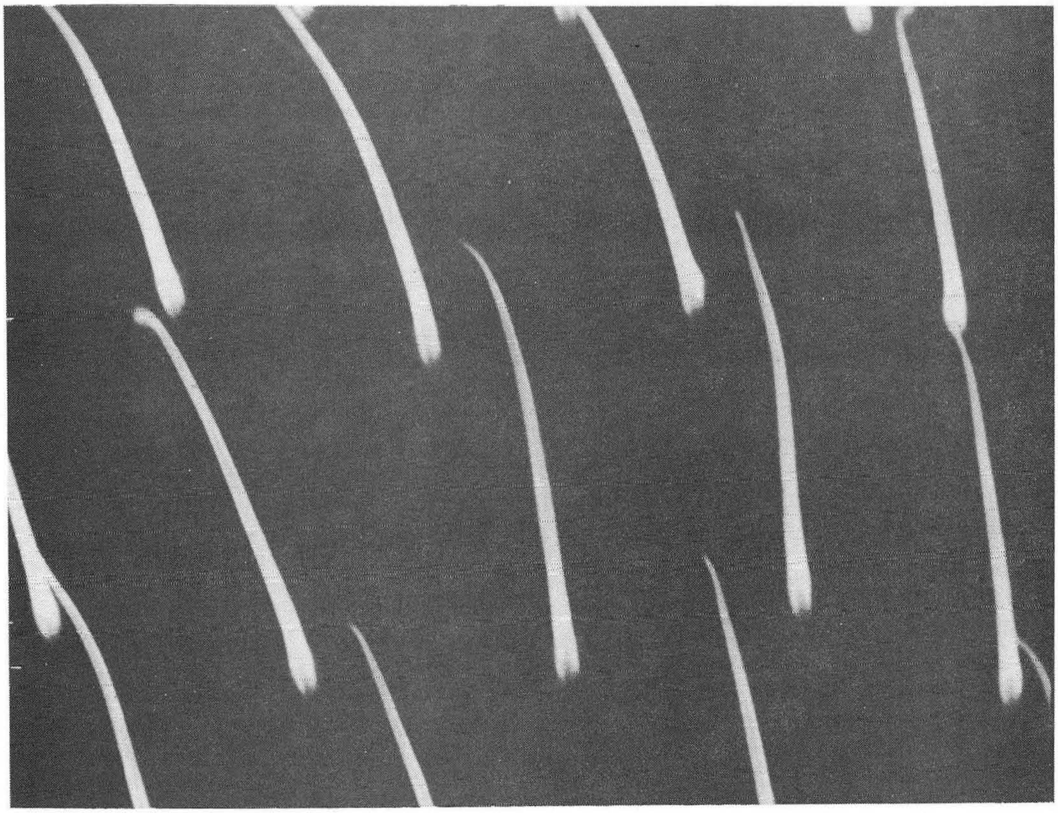

fig.6: Hairs on wing cell.

The edges of the wings are worthy of some special attention. As mentioned earlier, the anterior portion of the wing is thick and strong. Figure 7 is a micrograph of radius 1 which runs along the anterior margin of the wing. This is a very large vein with three sets of mechano-receptive spines arising on it, (two sets are shown.) The primary set, which points along the plane of the wing, consists of large but stubby spines. The function of these may be to shield the wing by deflecting objects that would otherwise hit the vein itself. Of the two other sets of spines, one points dorsally, the other ventrally. These spines are longer but much more slender than those of the primary set. It is likely that these secondary sets of spines are stimulated by the air currents during flight.

The apical edge of the wing has no primary set of stubby spines, (figure 8). The two secondary sets of spines, however, are present, and are rotated towards the plane of the wing. Finally on the posterior edge of the wing, where there is no vein to arise from, there are no mechano-receptive spines, (figure 9). Instead we find long hairs on the extreme edge pointing out along the plane of the wing.

Ridges occur on the wing surface, (figure 9), within the cells. The hairs arise at the summit of these ridges and so are arranged in rows. On the other sides of the ridges in figure 9, small white dots are visible which mark the spots where the hairs arise on the other surface of the wing. A cross-sectional portion of a wing cell is represented in figure 10.

The various movements of the wings, especially in insects like <u>Drosophila</u> which flex their wings horizontally over their backs when a

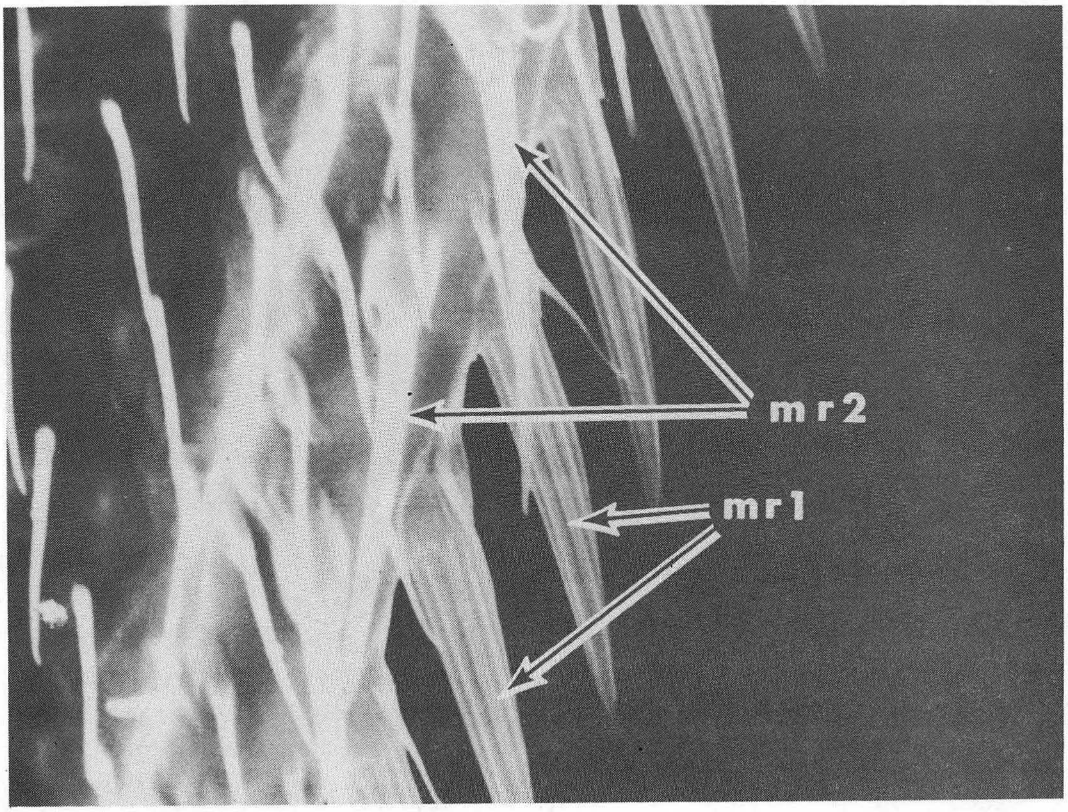

fig.7: Anterior wing edge; mr1, mr2, primary and secondary set of mechano-receptive spines.

fig.8: Apical wing edge; mr, mechano-receptive spines.

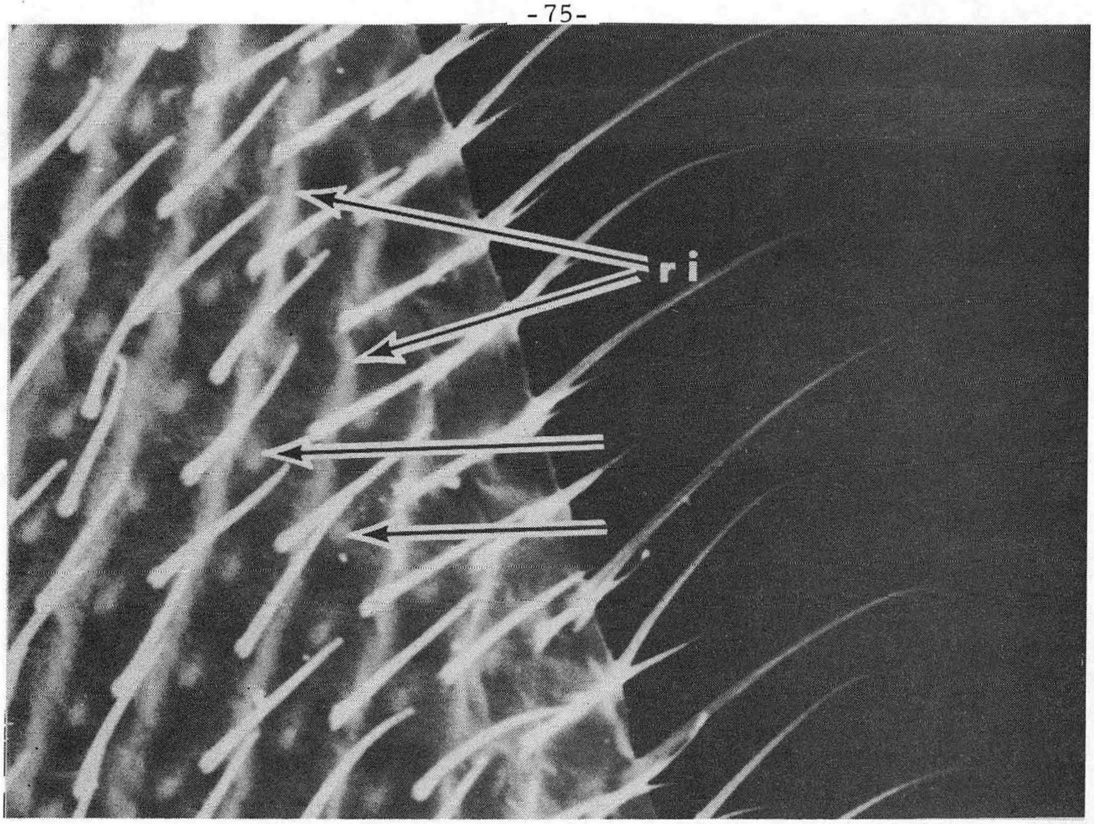

fig.9: Posterior wing edge; ri, ridges; arrows to white dots.

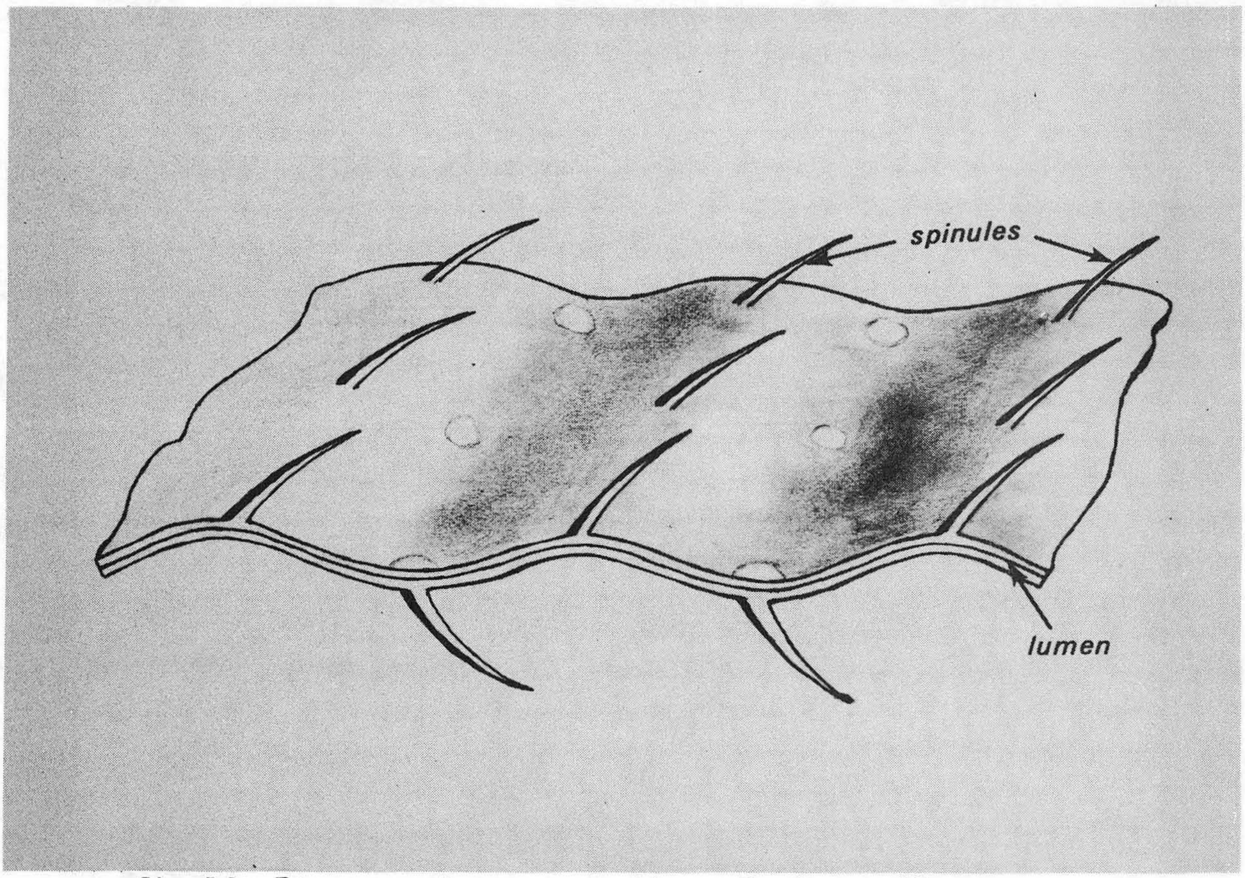

fig.10: Diagram of cross-section of wing cell.

rest, demand a more complicated articulation at the wing base than a mere hinge to the body, (Snodgrass, 1935). In fact the wing articulates at two points on its dorsal fold and at one point on its ventral fold. At these points the cuticle of the wing is thickened and convoluted in a complex manner creating a number of axillary sclerites called pteralia, (Pringle, 1965). The pteralia, in addition to allowing flexion of the wing, are involved in some of the more subtle wing movements during flight, (Crampton, 1942). In Drosophila the pteralia are in a pattern that is quite close to the typical form, and a great deal like that of the house-fly, (Zalokar, 1947).

The ventral articulation, (figure 11), is extremely complex, and not really well understood. Figure 12 is a micrograph of a portion of the ventral articulation, in which the base of the radius, the humeral plate sometimes called the basicosta, and axillary sclerite 1 are all visible. Figure 13 is a micrograph of the dorsal articulation, in which the tegula, a spiny pad that overlaps the basicosta, (Shannon, 1924), axillary sclerite 2, and the basalare appear. Finally there is a lobe or flap known as the alula, (figure 14), which has a thick vein running along its margin, and pairs of slender probably mechano-receptive spines pointing outwards similar to those at the apical end of the wing.

> The wanton boy that kill the fly
> Shall feel the spider's enmity.
>
> William Blake

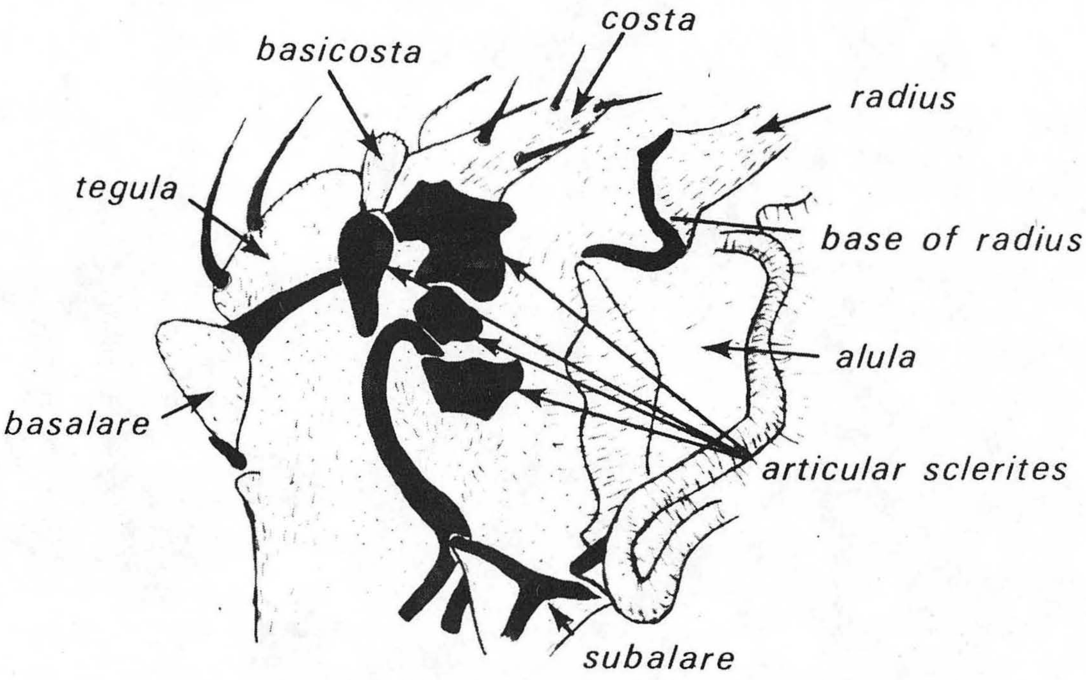

fig.11: Diagram of ventral articulation of wing,(after Zalokar).

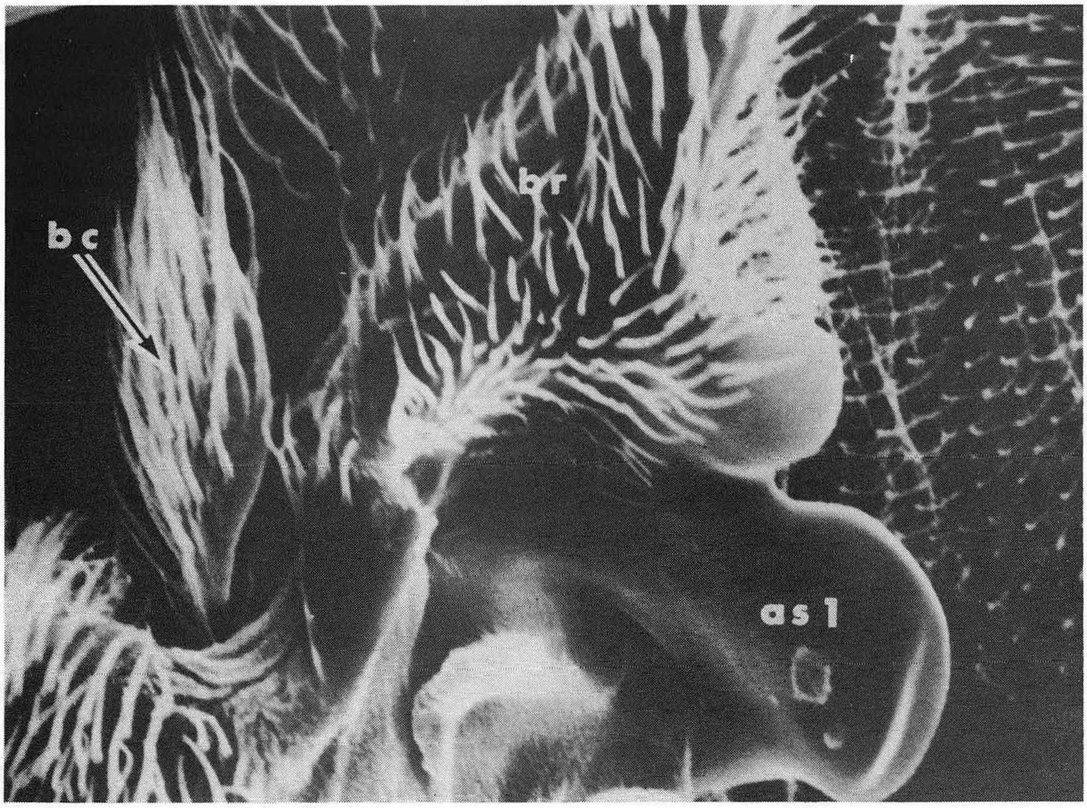

fig.12: A portion of the ventral articulation; <u>bc</u>, basicosta; <u>as1</u>, axillary sclerite 1.

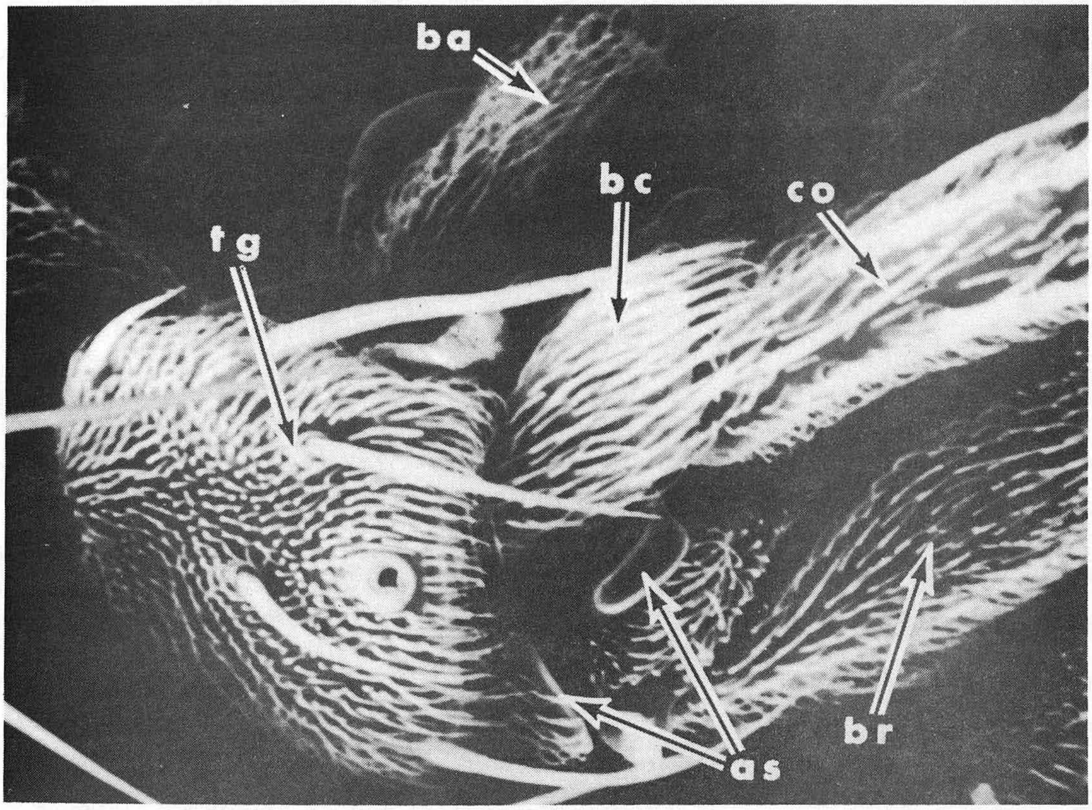

fig.13: Dorsal articulation; ba, basalare; tg, tegula; bc, basicosta; as, axillary sclerites; br, base of radius; co, costa.

fig.14: The alula; ps, paired spines; av, alular vein.

The Halteres

Only the flies which buzz and whirl, and the flies
in the air, on the wall, in the room by the stairwell
they whirl with their buzzing.
Only the insects fly with their buzzing and buzzing buzzing.
Wheeling and whirling and turning,
and then turning they stop and alight.

Anonymous

The order of insects called Diptera, of which *Drosophila* is a member, have only one pair of wings, while other orders of flying insects, the Lepidoptera, the Hymenoptera, the Odonata etc. have two pairs. It is quite clear that the halteres located on the metathorax of Diptera represent the missing metathoracic wings. Although at first glance, (figure 1), the halteres look nothing at all like wings, the evidence for their alar ancestry is compelling.

At the base of the haltere, (figure 2), we find minute axillary sclerites and epipleurites which, though unnamed, can be clearly homologized with those at the base of the wing, (Buddenbrock, 1919). Further proof of their origin comes from the mutant *Drosophila* called bithorax in which the halteres are actually replaced by small hind wings with clearly recognizable venation, (Imms, 1964). Examination of these *bithorax* specimens indicates that the three segments of the haltere, (which we shall soon discuss), correspond to areas separated by the proximal and distal costal breaks in the wing, (Sturtevant, 1921).

So, without any question, the halteres are the morphological equivalents of the metathoracic wings although they have come far from

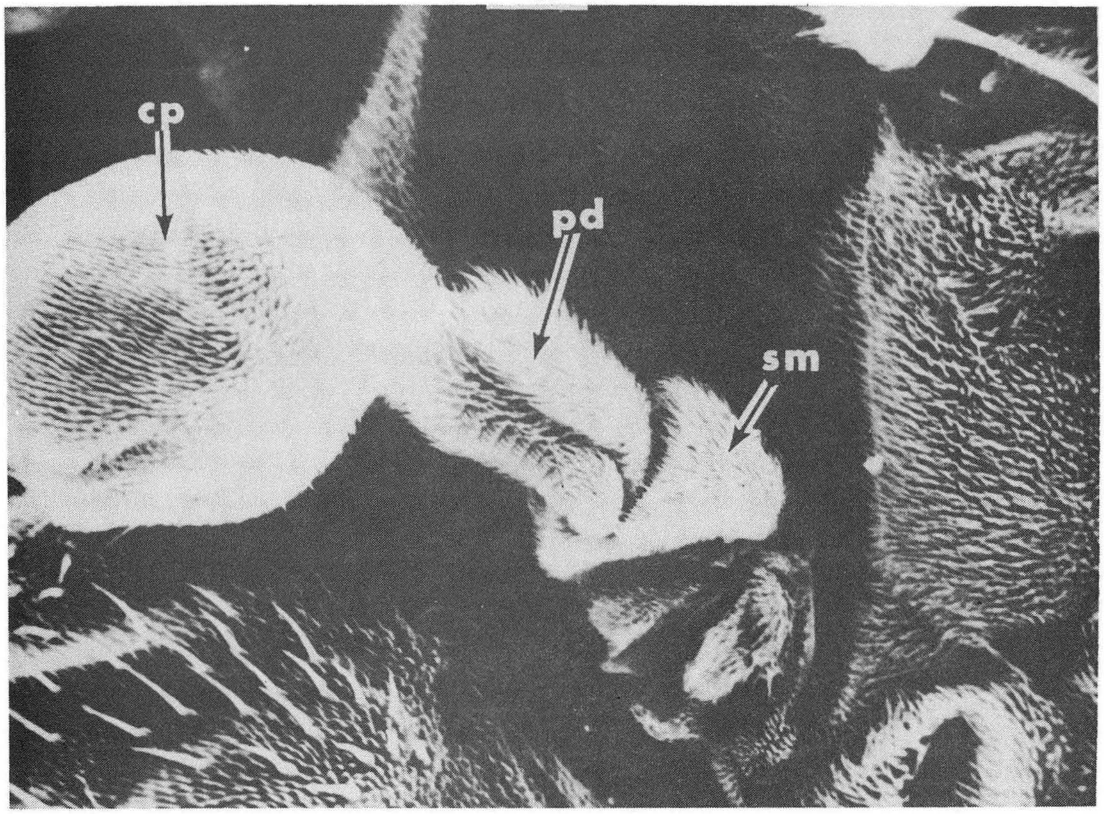

fig.1: Right haltere; cp, capitellum; pd, pedicel; sm, scabellum.

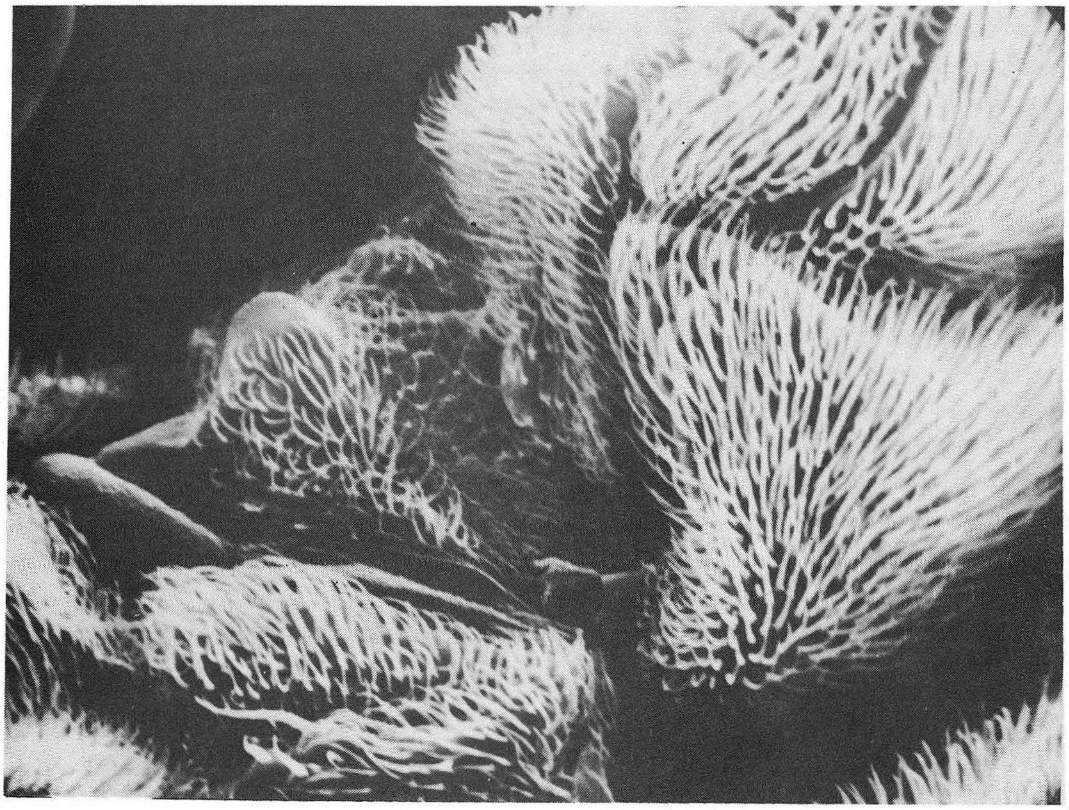

fig.2: Ventral articulation of haltere to thorax.

their antecedents, (Ferris, 1950). It is often said that the halteres are "rudimentary" wings, but this overlooks their great complexity. That they are highly modified wings is true, but that they are rudimentary organs is in no sense true, (Lowne, 1895). As we shall see, the halteres have become highly specialized organs which act as oscillating gyroscopes during flight informing the fly of changes in direction, much as the gyroscope on a ship informs the navigator of any chnage in the ship's course.

The haltere is divided into three parts: a basal segment or scabellum which bears numerous special mechano-receptive organs arranged in rows, (Lowne, 1870); a median segment or pedicel which is slender and stalk-like; and a swollen, globular, apical segment or capitellum, (Ferris, 1950). Figure 3 is a diagram of the dorsal and ventral views of a Drosophila haltere.

The scabellum is a ring-like segment. On its dorsal surface are found about seven columns of stress receptors called Hick's papillae. Figure 4 is a micrograph of the ventral view of the scabellum, and figure 5 is a micrograph of the Hick's papillae. The papillae, probably sensilla campaniformia, are semi-spherical bulges in the integument and between each row there arise a number of evenly spaced hairs which curve over the papillae. Moreover, four small muscles taking their origin in the thorax are inserted into the scabellum. These muscles move the whole organ and are responsible for generating the gyroscopic oscillations, (Crampton, 1942).

The pedicel, (figure 6), is composed of three elongate parts, a median cylinder and two lobes, one on each side. On the median

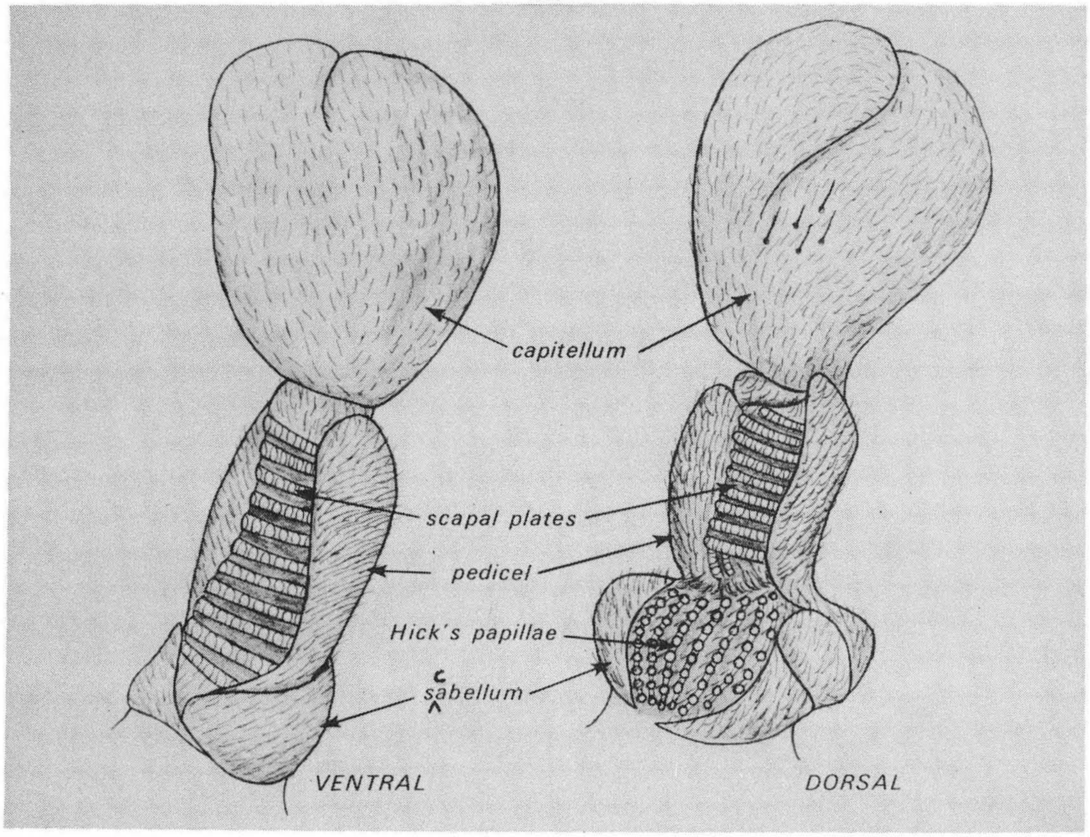

fig.3: Diagram of haltere, ventral and dorsal views.

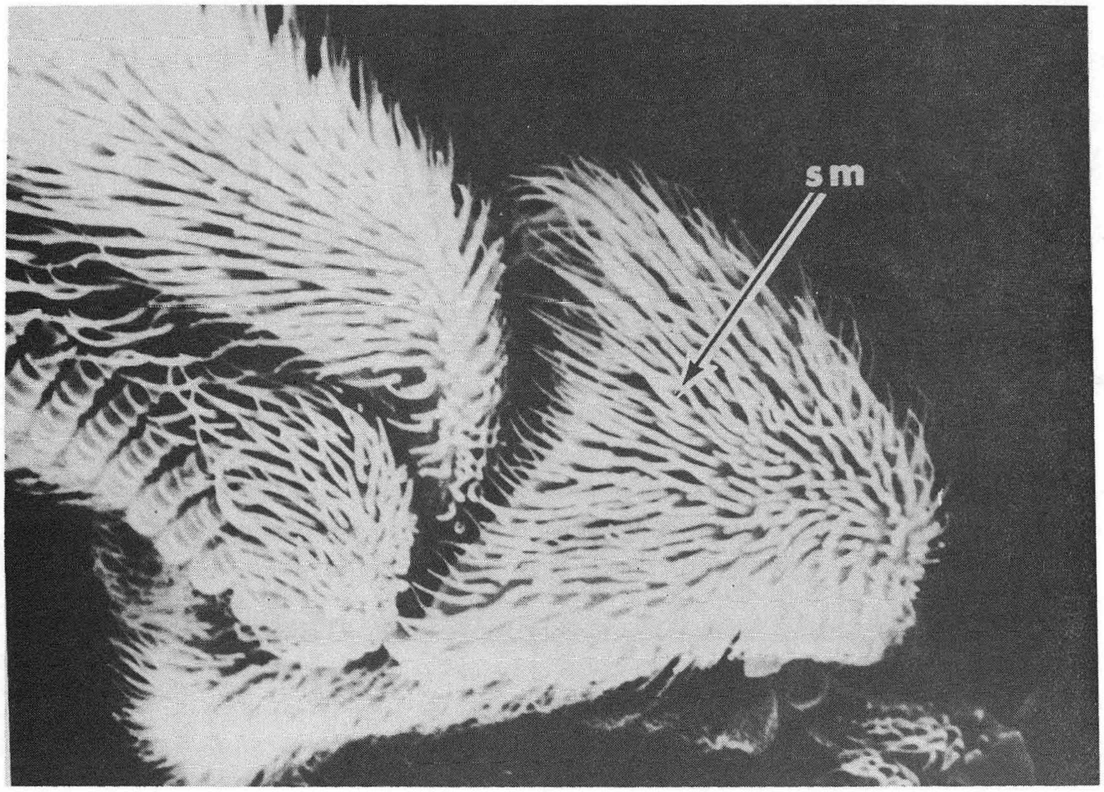

fig.4: Scabellum, <u>sm</u>.

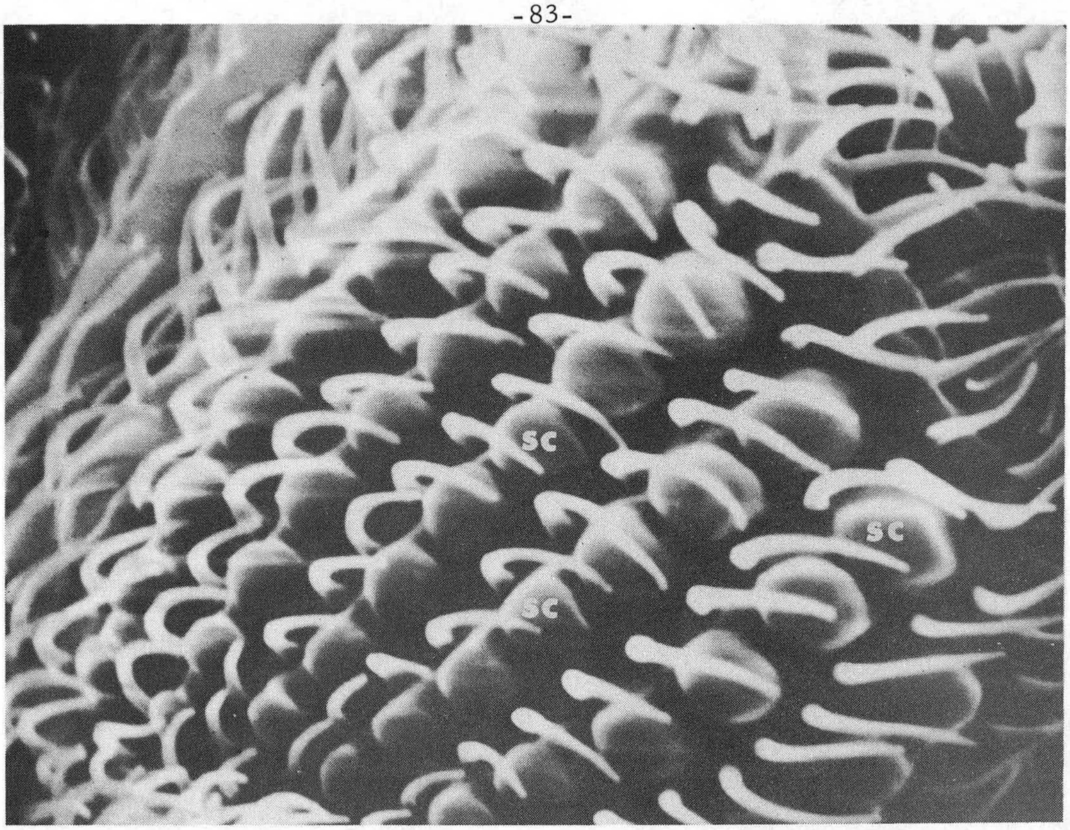

fig.5: Hick's papilla; sc, sensilla campaniformia.

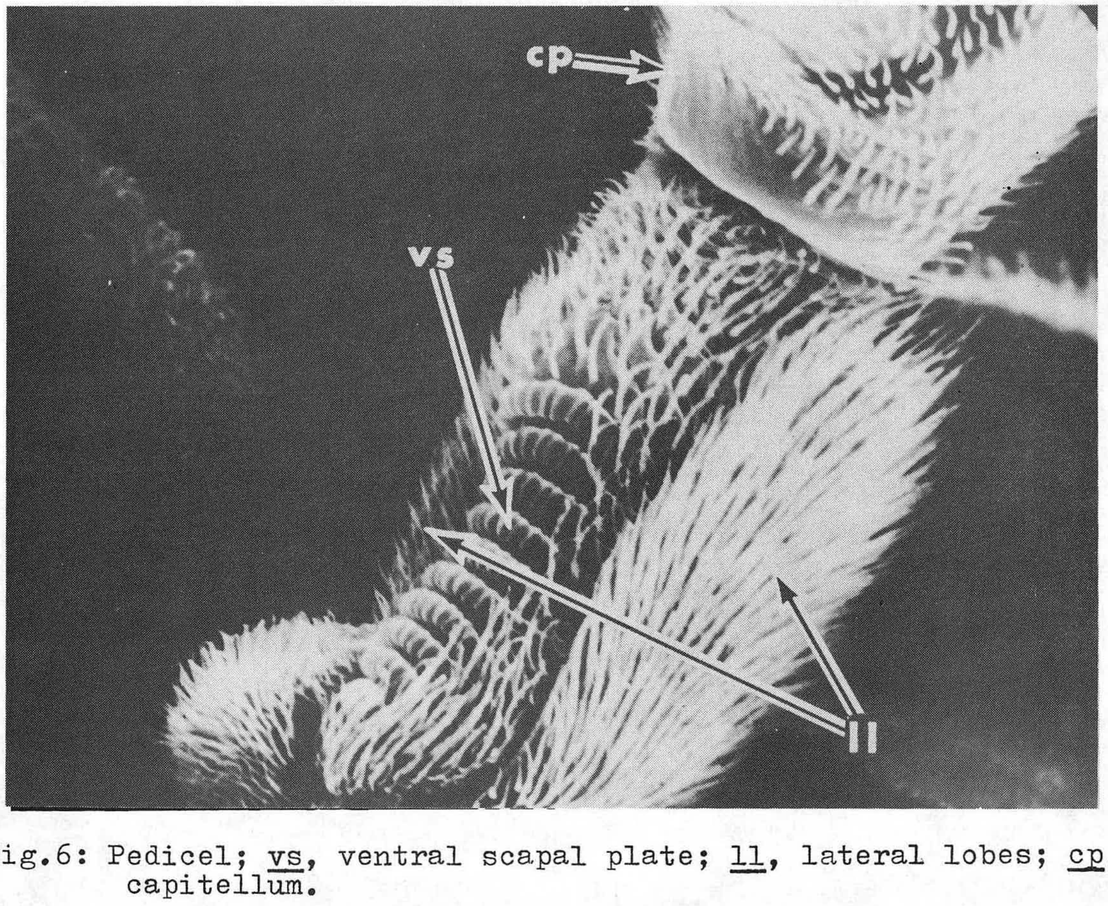

fig.6: Pedicel; vs, ventral scapal plate; ll, lateral lobes; cp, capitellum.

portion there are two scapal plates, the ventral scapal plate, and the dorsal scapal plate, (figure 3). Each plate has about ten rows of sensoria. Figure 7 is a micrograph of a portion of the ventral scalpal plate. Each row of sensoria seems to be a chain of sensilla campaniformia-like bulges with overlapping flaps of cuticle. On the dorsal surface of the pedical, just at its junction with the scabellum we find more, (usually two), of these chains running parallel with the pedicel, (figure 3). The fine structure of the lobes is also of some morphological interest. Figure 8 is a micrograph of a portion of the outside or distal lobe. The processes arising on these lobes look very much like sensilla trichodea. What chemo-receptors would be doing on the halteres is hard to imagine, but it known that sensilla trichodea can sometimes function as mechano-receptors, (as in the hair plates on the legs.) Perhaps that is there function here.

The pedicel terminates in the capitellum, (figure 9). The capitellum is a membranous, fleshy sac; it is the weighted mass of the gyroscope. The integument of the capitellum is extremely delicate and transparent. Figure 10 is a micrograph of a small segment of the membrane. The hairs that arise on it are short, have flattened bases, and attach broadly to the integument. On the dorsal surface of the capitellum one can find a few small mechano-receptive spines.

Let us now discuss the function of some of the various parts of the halteres and consider how this complicated and heavily innervated gyroscope actually functions for the fly. The first thing to note is that the mass of the halteres is only about 0.04% the mass of the fly, so a direct gyro-stabilizing effect is out of the question, (Pringle, 1957).

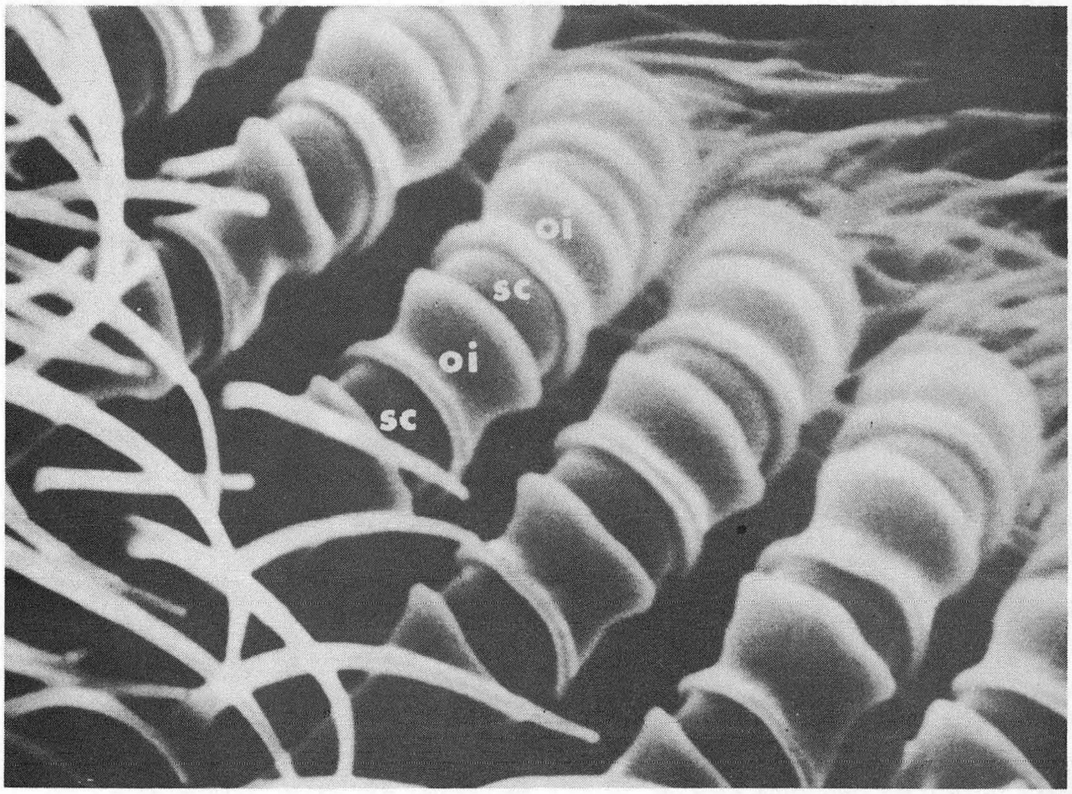

fig.7: Sensoria of scapal plate; <u>sc</u>, sensilla campaniformia; <u>oi</u>, overfolding integument.

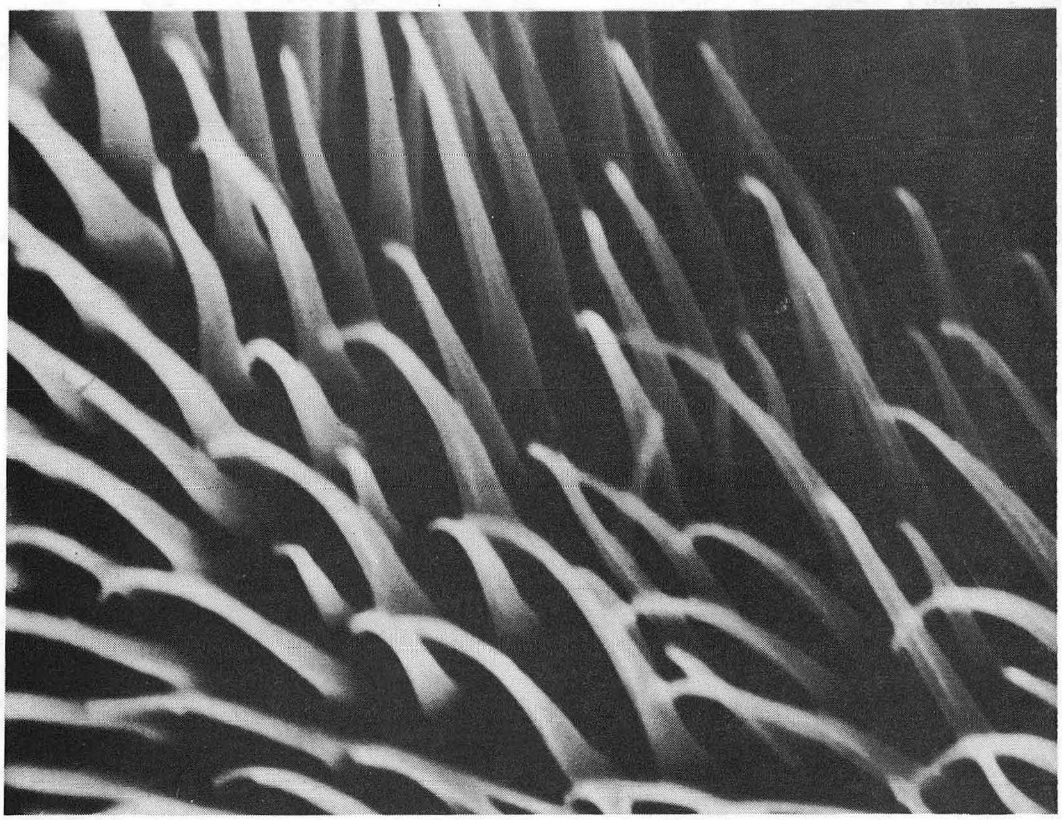

fig.8: Close-up of pedicellar lateral lobe.

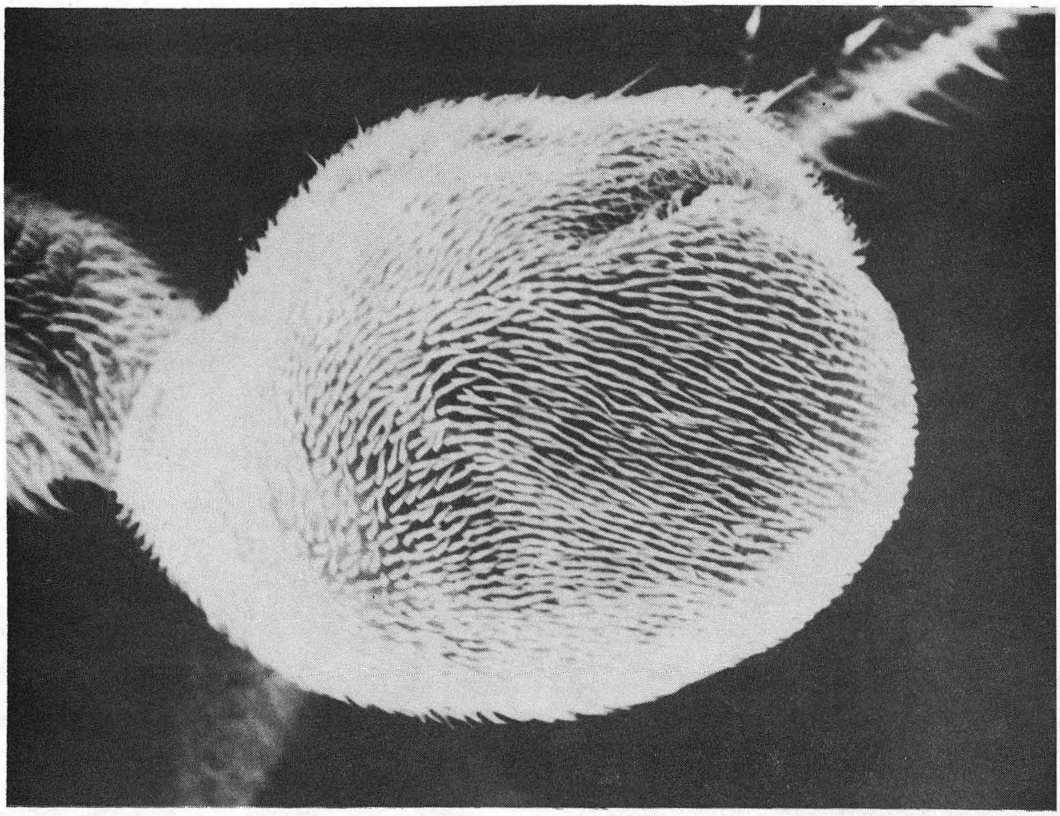

fig.9: Capitellum, ventral aspect.

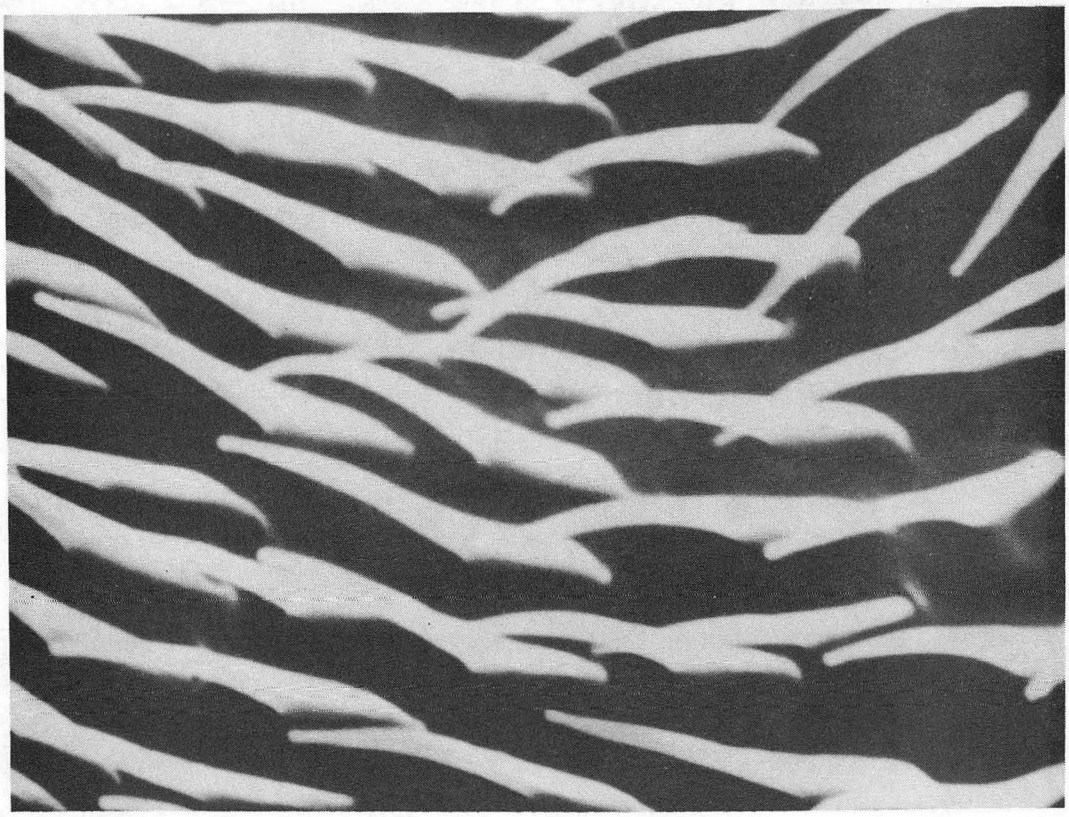

fig.10: Capitellar hairs.

We have seen that the halteres are lavishly equipped with mechanoreceptors, but essentially each haltere is a heavy mass of tissue on the end of thin stalk. During flight the halteres are vibrated rapidly through an arc of about 90° in the vertical plane. The frequency of the oscillation is synchronized closely with that of the wings, (Fraenkel and Pringle 1938).

Electrical recordings from the scapal plates suggest that the impulses from these plates serve to reflect the amplitude of haltere oscillation, and, by reflexy, inhibit the contractions of the haltere muscles, thus preserving a constant amplitude of oscillation, (Pringle, 1948).

The Hick's papillae, (figure 5), are oriented in such a way as to suggest that when a fly changes directions during flight in the horizontal or yawing plane, the lateral shearing forces that would be set up in response would strain the cuticle at the base of the haltere and stimulate these sensitive papillae, (West, 1951). These signals act as feedback to the flight muscles for controlled flight.

These dynamical considerations lead to predictions about the flight of flies without halteres. Such predictions can be tested by experiment. Flash photography of a fly with halteres amputated shows that it flies in spiral paths, unable to go in a straight line, (Wigglesworth '65). The same is true with the mutant <u>bithorax,</u> (Fraenkel, 1939). Finally, another experiment which indicates the stabilizing function of halteres is this: the loss of equilibrium in a fly without halteres can almost be eliminated by fixing a piece of cotton thread to the tip of the abdomen. This stabilizes the flight, much as the tail on a kite, and largely compensates for the loss of halteres, (Fraenkel and Pringle, 1938).

They that crawl and they that fly
Shall end where they began.

Thomas Grey

The Spiracles

A closed mouth
catches no flies.

Cervantes

The cuticle of insects is usually thick and intricately architectured, (figure 1). It is waterproofed, a condition that is vital to the emancipated life of insects. But impermeability to water entails a very serious disability; the cuticle is also impermeable to oxygen, (Wigglesworth, 1964). To meet this disability insects have developed a respiratory system quite unlike that of any other class of animals. Insects breathe through small holes or involutions in the protoderm. Where these holes meet the surface of the integument, they form spiracles, (Lowne, 1870).

Spiracles were first discovered in 1669 by Marcello Malpighi who found a series of these holes along each side of the body of a silk worm. He followed the spiracles to air filled tubes or tracheae. The tracheae are the breathing tubes which branch out quickly and frequently, thus becoming smaller and smaller until the finest branches are resolvable only with a high powered microscope. Finally, the tubes end by either surrounding or indenting the living cells, (Wigglesworh, 1964), and in that way deliver oxygen to and remove carbon dioxide from them. That is, by diffusion.

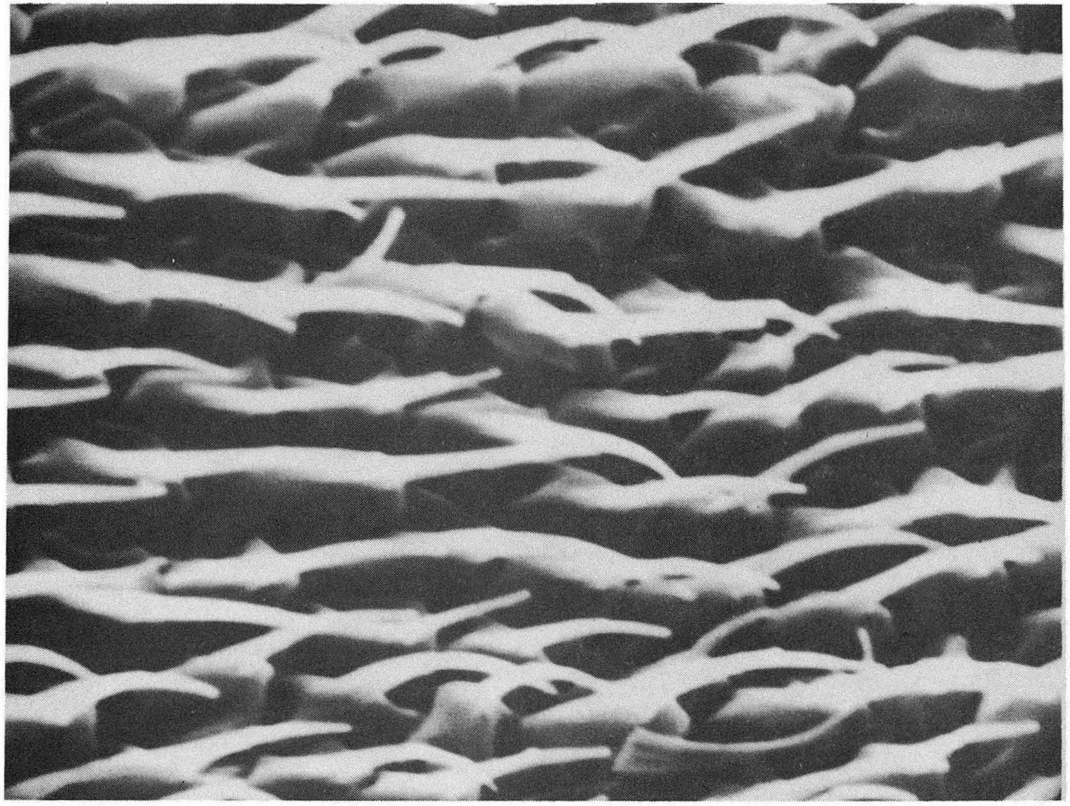

fig.1: Cuticular architecture.

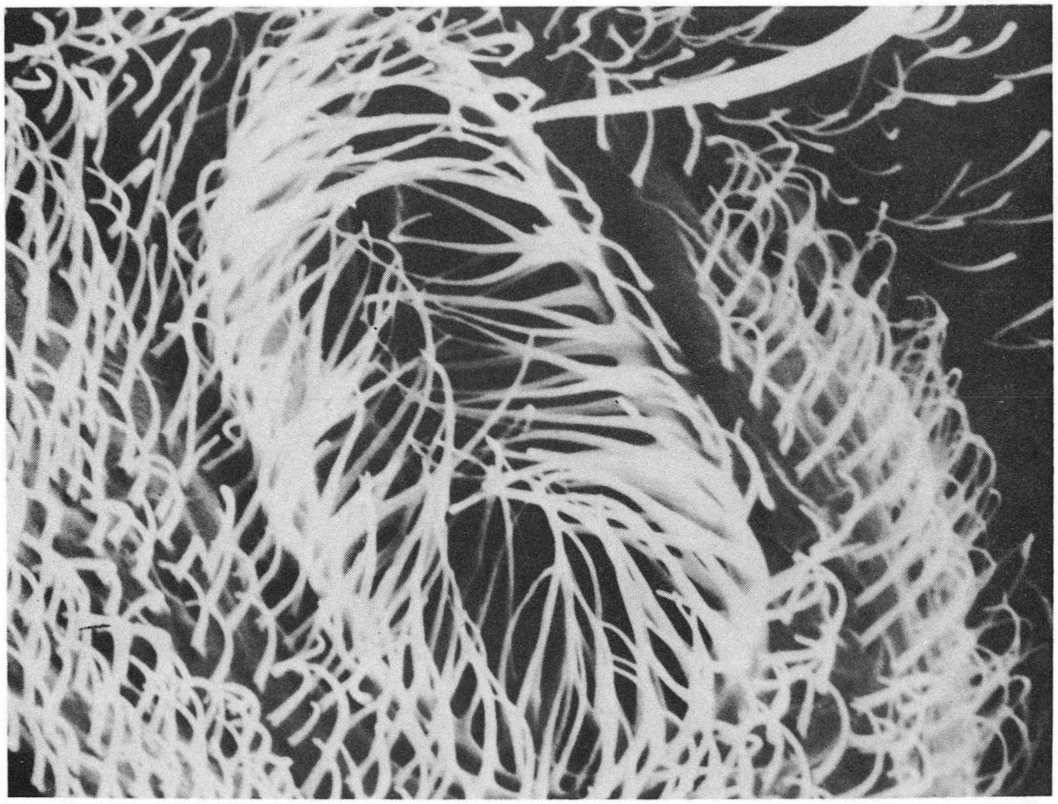

fig.2: Anterior thoracic spiracle.

In their simplest form, the spiracles are merely openings in the integument leading into the tracheae. In general, however, and this is the case in *Drosophila*, the primary tracheal apertures are sunken into secondary depression in the integument. The external part of each spiracle thus becomes a tubular chamber which is called the *spiracular atrium*, (Snodgrass, 1935).

The location and number of spiracles is often an important guide in distinguishing different species of flies, (Crampton, 1942). *Drosophila* have two pairs of large thoracic spiracles and seven pairs of small abdominal spiracles.

Of the two pairs of thoracic spiracles, the more anterior is located on the prothorax just above the forelegs, the more posterior on the metathorax just under the halteres. The anterior pair, (figure 2), are larger and more elliptical than the posterior pair, (figure 3). Each anterior spiracle measures about 60 μ × 30 μ while each posterior spiracle measures about 40 μ × 30 μ. Otherwise, the two thoracic pairs of spiracles are identical in structure and function, (Hassan, 1944).

Each thoracic spiracle has an internal closing apparatus, a valve, which can be held tightly shut. The valve is located at the dividing point between the atrium and the trachea. It consists, as diagramed in figure 4, of two membranous flaps covering the tracheal entrance. Their inner rims are thickened to form an elastic ring. At one end of the ring is attached a small fan-like closing muscle which has its broad base on a "Y"-shaped apodemal ridge. Muscle contraction brings the flaps together (Hassan, 1944). The fly normally keeps his spiracles closed as much as possible and opens them only just

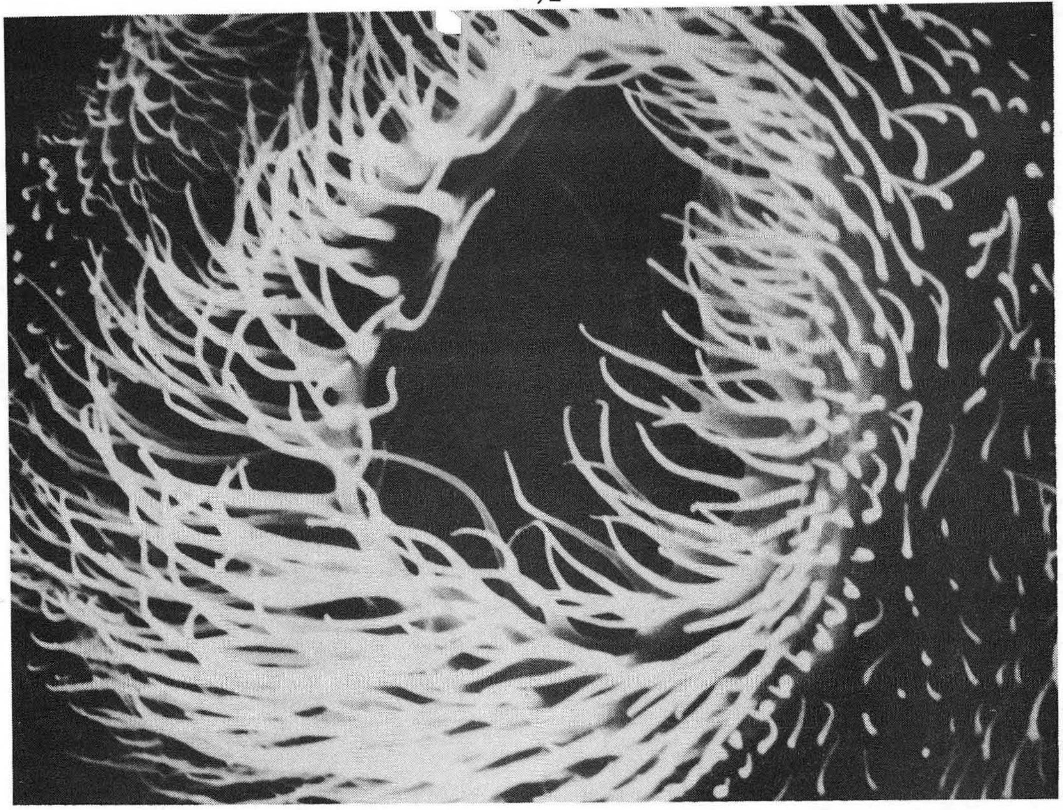

fig.3: Posterior thoracic spiracle.

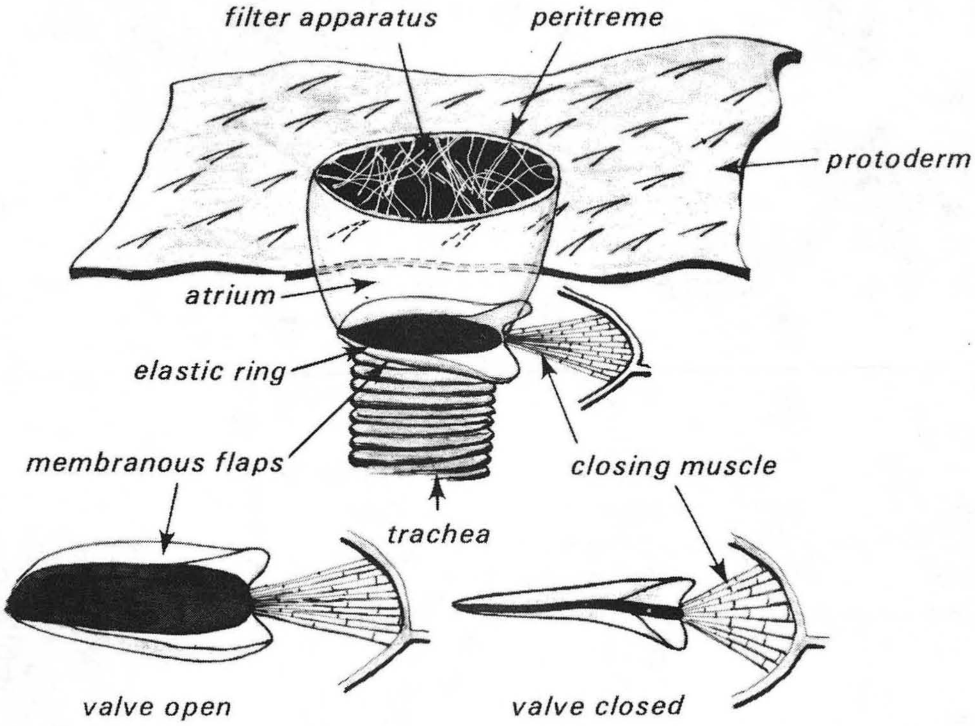

fig.4: Internal thoracic spiracle and closing apparatus, (after Hassan).

frequently enough to let in the oxygen it needs and to allow the carbon dioxide to escape, (Ségny, 1950).

Accessory structures are often present in the outer part of the atrium in a spiracle which has an internal closing apparatus. They are well developed in Drosophila and take the form of a complex of thick interlacing hairs, known as a filter apparatus, (Snodgrass, 1935). High magnification micrographs, (figures 5 and 6), of these hairs on the anterior and posterior thoracic spiracles respectively, show them to be unlike any other type of hair, spine, or sensillum on the fly's body. They are sclerotized, multi-branched, tree-like processes that arise on the rim or peritreme of the spiracle and spread out over the atrial opening.

There are, as has been noted, seven pairs of abdominal spiracles. All of these lie in the pleural membrane just under the ventral edges of the tergites. Figure 7 shows the fifth abdominal spiracle of a male Drosophila and the way in which the tergite overhangs the small opening. The abdominal spiracles are all of a single type; they have very small openings, about 8 μ in diameter, and they have no hairy filter apparatus. The openings are rigidified by a thick sclerotized ring of cuticle, the peritreme. The heavy peritreme is evident in figure 8, a micrograph of the first abdominal spiracle of a female Drosophila. It looks as though a filament of dust became stuck in this spiracle.

There is a well developed atrium in each abdominal spiracle, the membranous walls of which are supported by spiral thickenings or irregular rings of sclerotized cuticle continuous with the body wall.

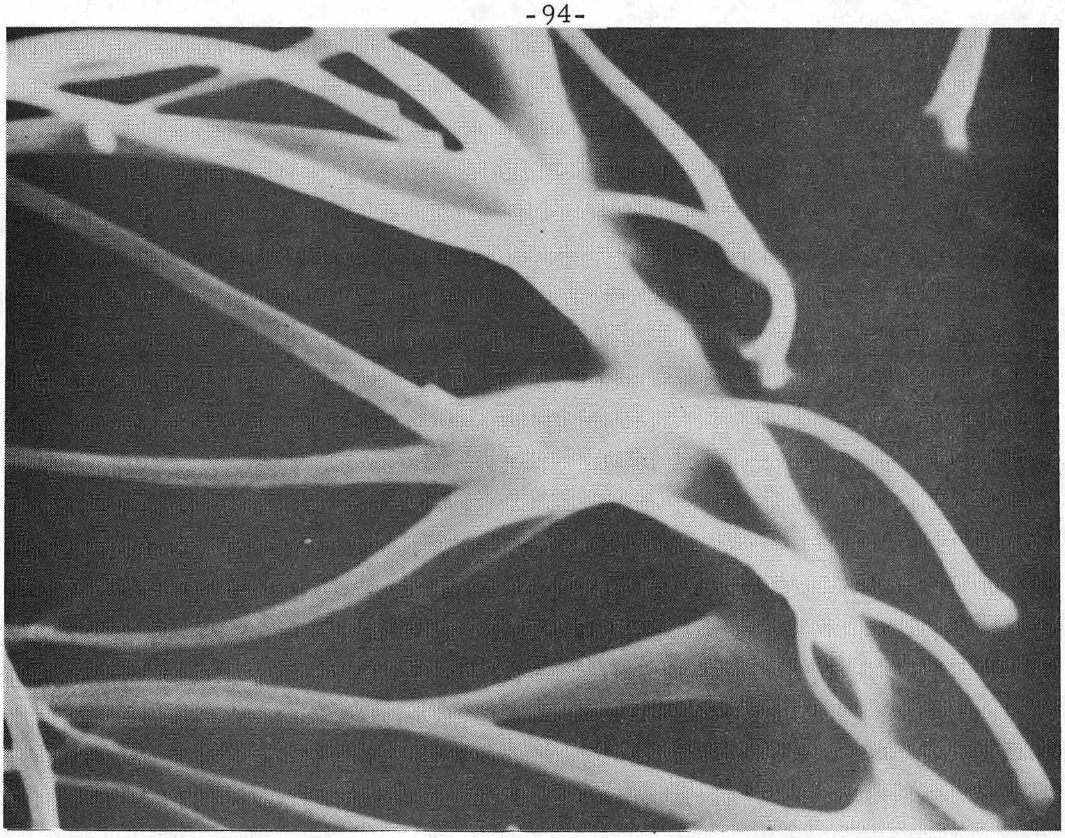

fig.5: Filter hairs of anterior thoracic spiracle.

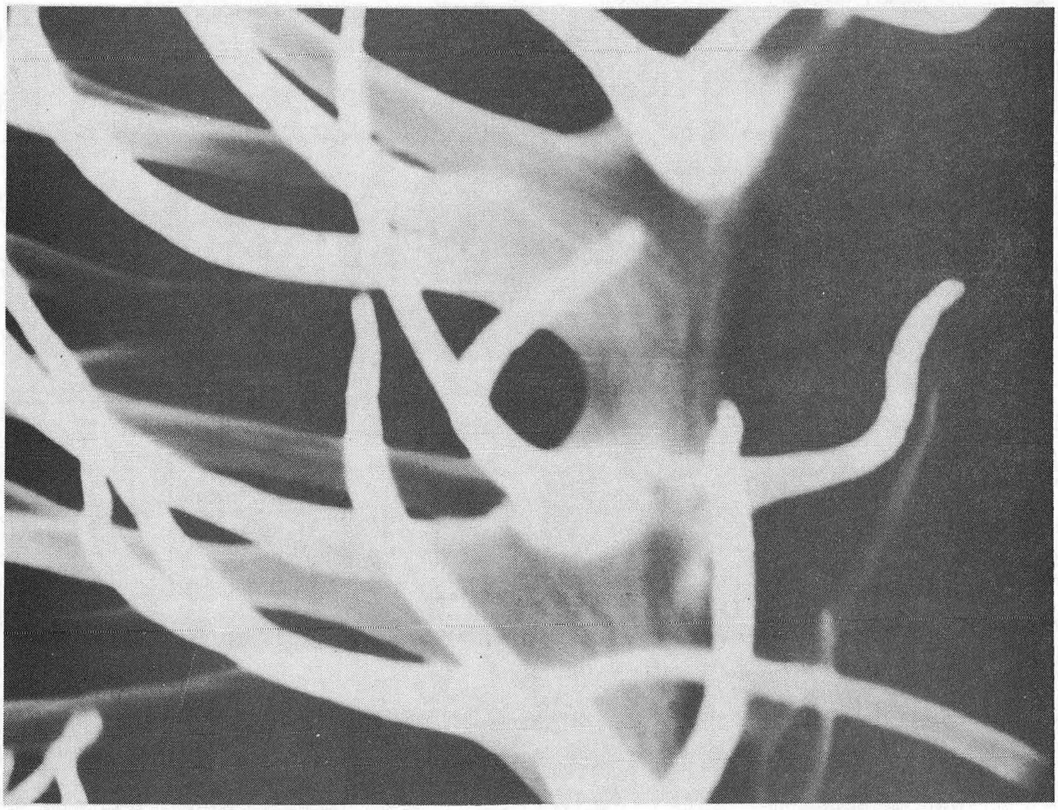

fig.6: Filter hairs of posterior thoracic spiracle.

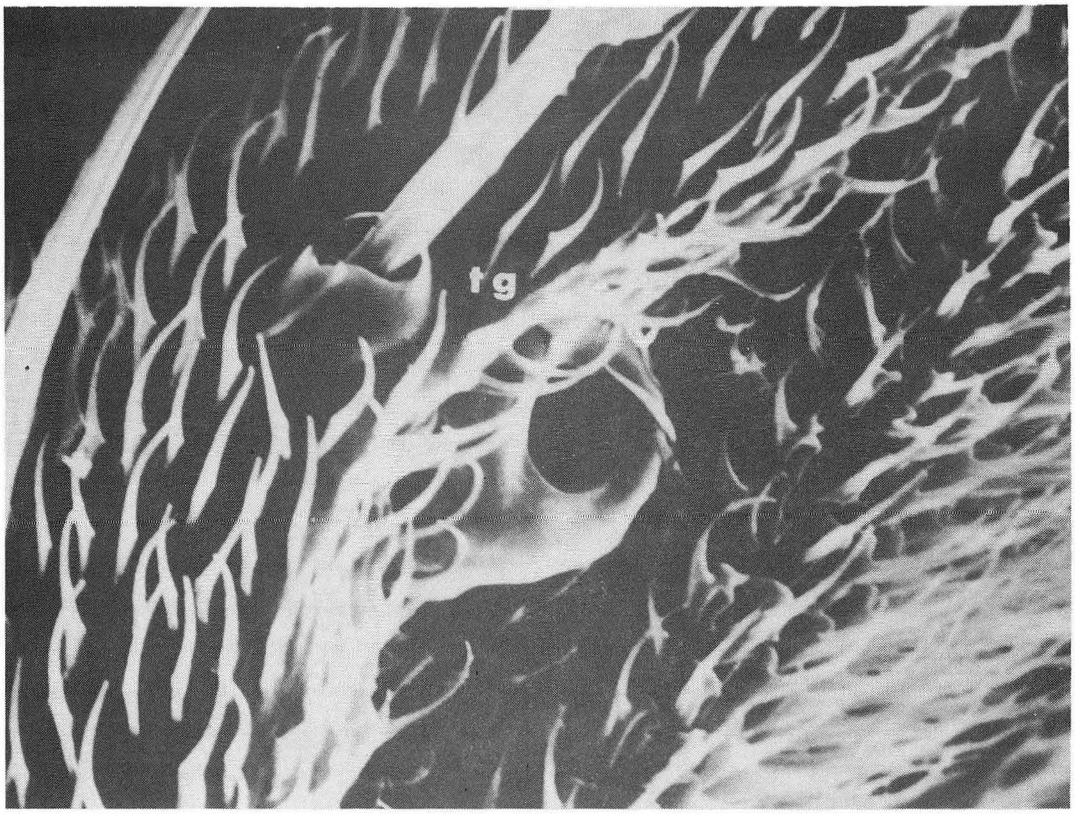

fig.7: Fifth abdominal spiracle of a male; <u>tg</u>, tergite.

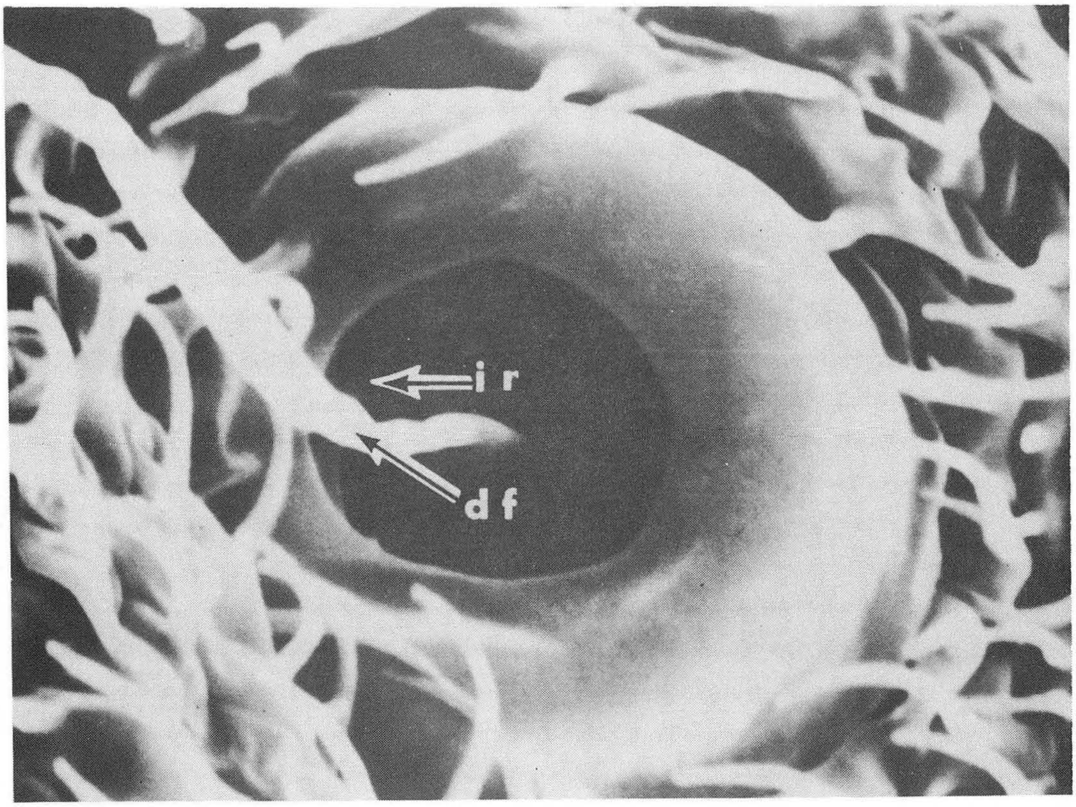

fig.8: First abdominal spiracle of a female; <u>ir</u>, inner ring; <u>df</u>, dust filament.

The first of these rings can be seen in figure 8. At the end of this series of rings there is an internal closing apparatus diagramed in figure 9. Two bands pass along the proximal part of the atrial wall and are situated just above the very narrow tracheal entrance. The spiracle is closed when the muscle that connects the apodemal ridge to one of the bands contracts. A lever mechanism pushes one band against the other, (Hassan, 1944).

As we noted, the spiracles are usually kept closed except when oxygen is needed. When in flight, however, the Drosophila respires at approximately eleven times the basal rate, (Chadwick, 1947). The fly cannot, in such a high state of activity, get enough oxygen by diffusion alone. If one looks closely at a Drosophila who has just stopped flying, he can see the fly actually pumping air in and out much as we pump air in and out of the lungs. The abdomen is alternatively expanded and compressed.

A King there was once reigning
Who had a goodly flea,
He loved him without feigning
As his own son were he.

Goethe

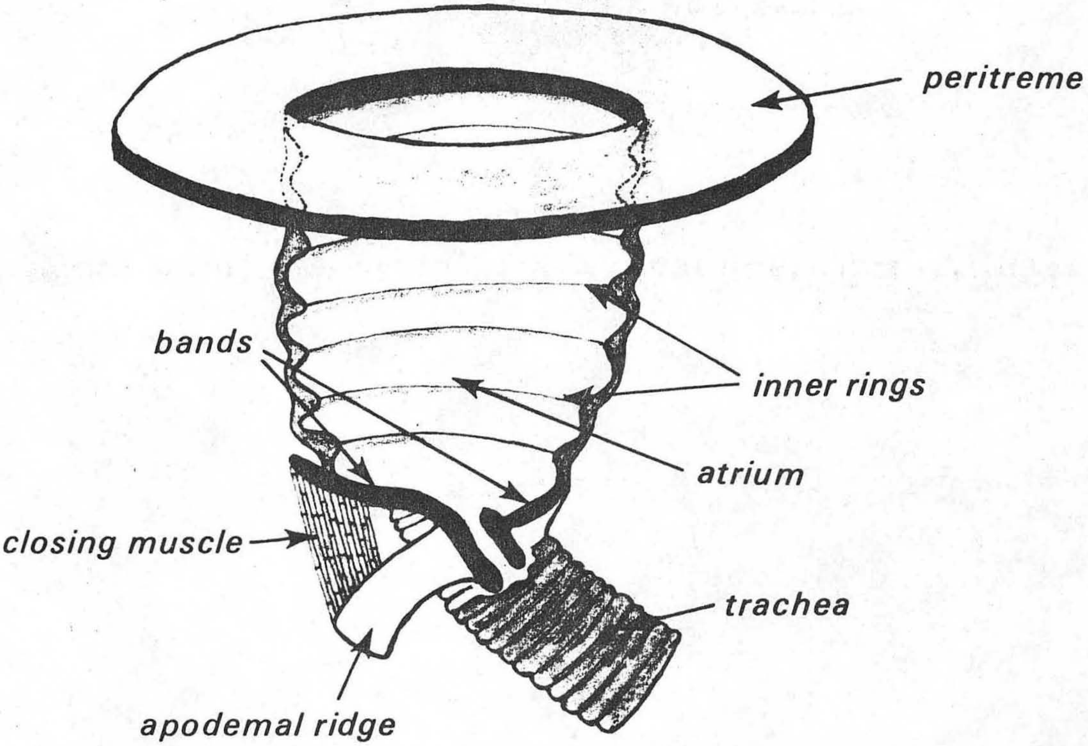

fig.9: Internal abdominal spiracle and closing apparatus,(after Hassan).

The Terminalia

And the small guilded fly
Does lecher in my sight,
Let copulation thrive !
Shakespeare

The reproductive organs differ from all the other organs of the body in that their functions do not contribute primarily to the welfare of the individual of which they are a part; their chief concern lies with the succeeding generation, (Snodgrass 1935). In this chapter we shall look at and discuss the external form of the genital and anal parts of *Drosophila*, both male and female. These structures are borne on the terminal portion of the abdomen and are referred to collectively as the *terminalia*, (Freeborn, 1924). The terminala cause substantial modification in the posterior abdominal segments rendering the latter almost unrecognizable. We shall discuss the male first, and then the female.

The Male

Modification of the abdomen begins with the sixth segment. The spiracles of the seventh segment have moved forward to become associated with the posterior margin of the sixth tergite. The sixth sternite is divided medially into two elongate plates which bear no spines, (Ferris, 1950).

The seventh segment is entirely membranous, having possibly merged with the sixth in the course of evolution. It is represented externally by its migrant spirale alone. The eighth segment is represented merely by a small, tergal plate on each side of the body, (Ferris, 1950). This is all diagramed figure 1.

The ninth segment bears the male genetalia and is highly modified. It is alternatively called the genital segment or andrium. Most conspicuous externally is the large and elaborately shaped tergal plate which runs downward on each side past ventral margins of the body. Viewed from the side, (figure 1), this plate shows a prominent lobe on its posterior border, and below this it continues into a rounded point, on which a number of slender, presumably mechano-receptive spines arise. Figure 3 is a diagram of the male terminalia as viewed from the rear, illustrating many of the same features.

In both figures 2 and 3, one can see a pair of curved finger-like lobes that arise from a narrow band which is a continuation of the ninth tergite running beneath the anus. These lobes have their mesal margins set with stout spines, (figure 4), which remind one a great deal of the sex comb. Perhaps there is some functional correlation between these bristles and those of the sex comb. At their base, the lobes are weakly sclerotized, (Séguy, 1950), so they are movable. It is likely that these structures are adapted for grasping the female during intercourse, (Snodgrass, 1935). Because of this presumed function, they are called claspers, (Snodgrass, 1931). In the chapter on the legs we mentioned the speculation that the sex combs may perform a similar "clasping" function.

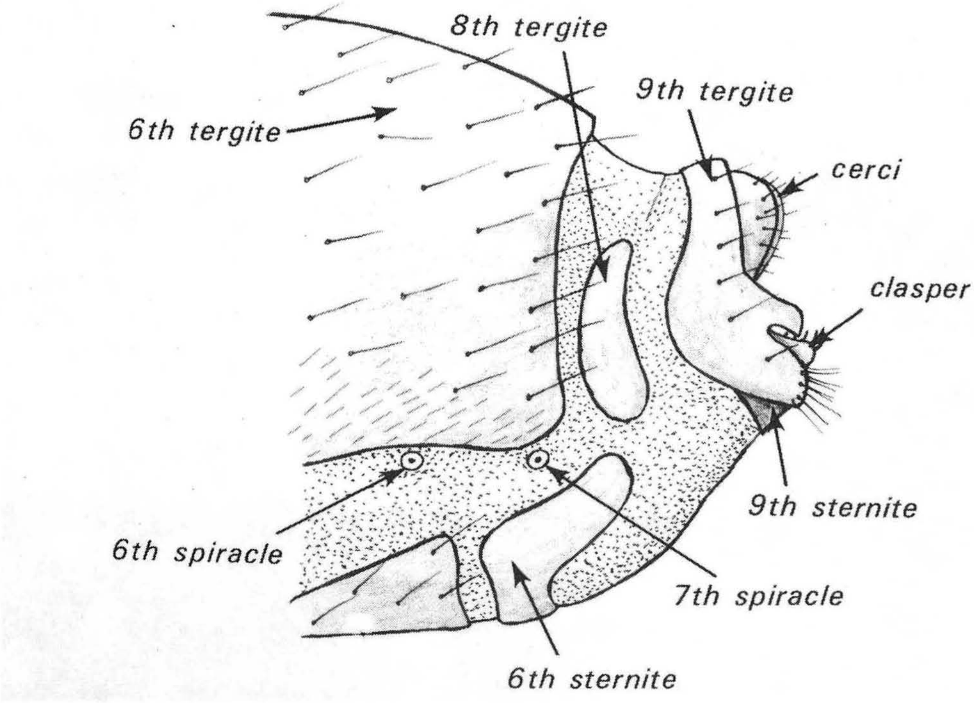

fig.1: Diagram of rear abdomen in the male, lateral view.

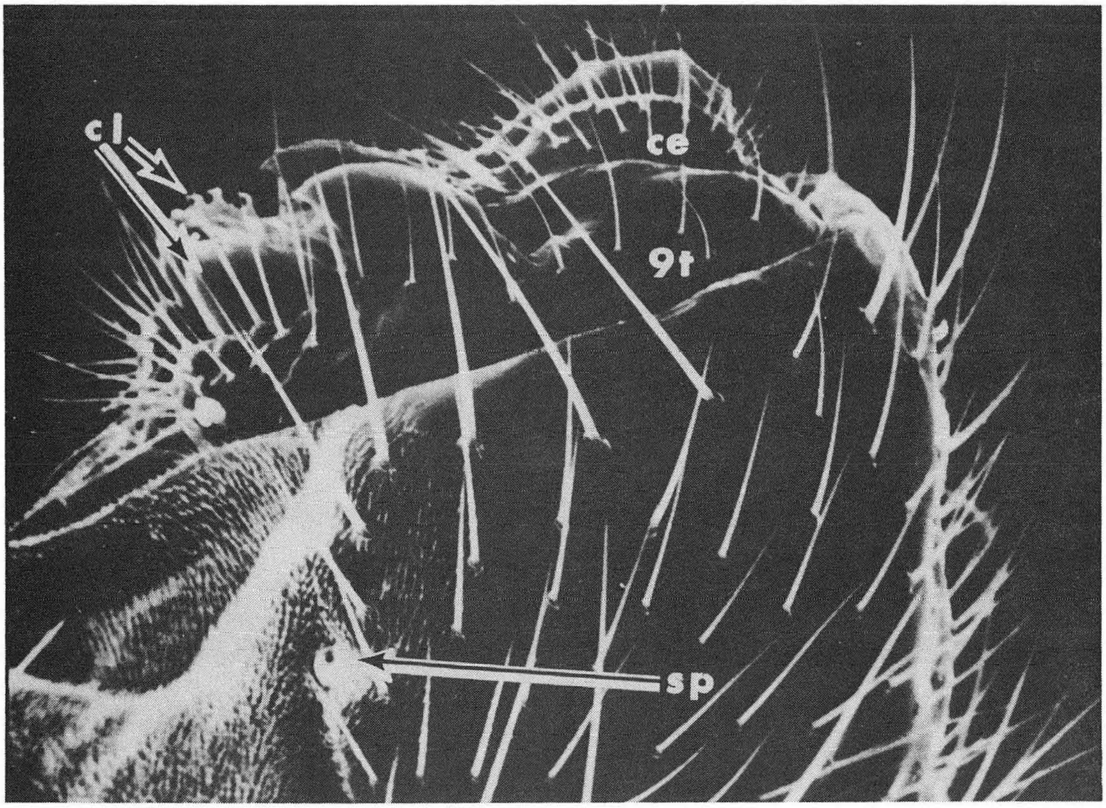

fig.2: **Lateral** aspect of the rear abdomen in a male; sp, spiracle; 9t, 9th tergite; ce, cerci; cl, claspers.

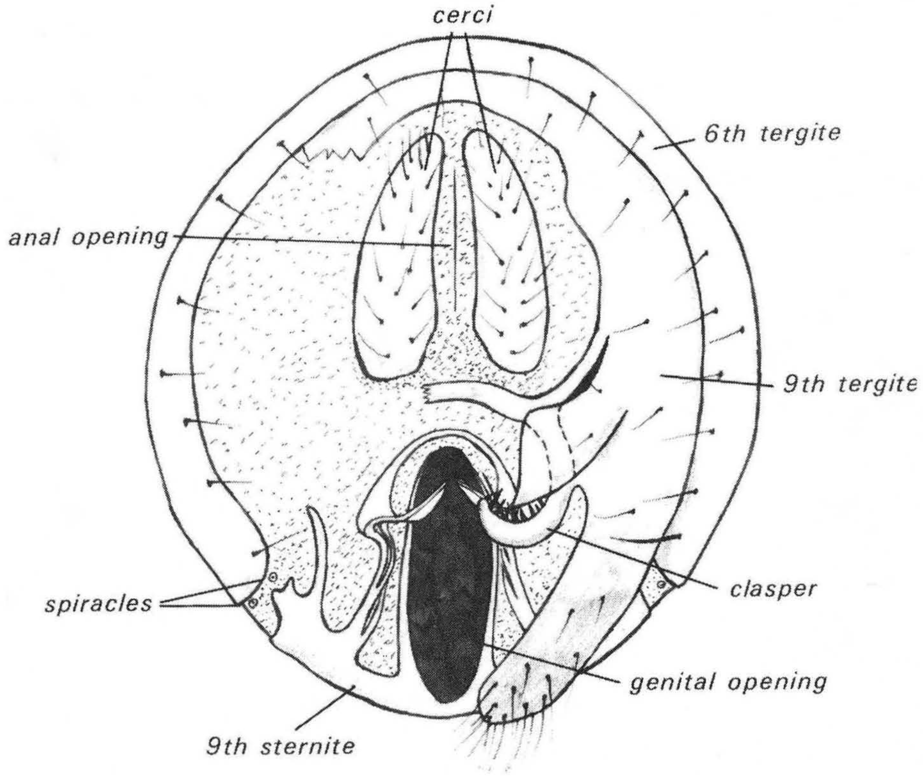

fig.3: Diagram of caudal view of the male terminalia.

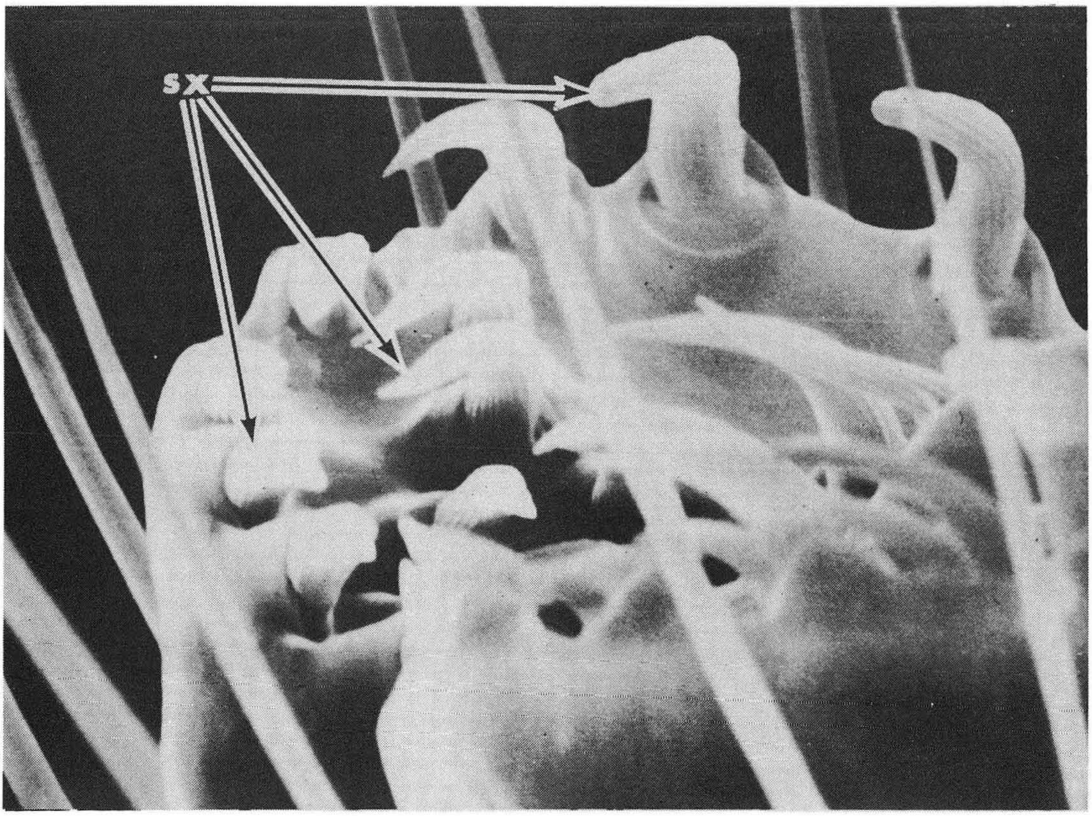

fig.4: Claspers; <u>sx</u>, sex bristles.

The ninth sternite is also an elaborate structure. Its base is continued into the body as a large flat phragma. Its posterior margin, however, is formed into several narrow processes, the mesal pair of which encloses the genital opening. The ninth sternite is shown in figure 3.

Although the ninth sternite is the genital segment, the genital opening of the male is between the ninth and the tenth segment, figure 5). One can also see, here, the ninth tergite with the claspers curving in front of the genital opening, and part of the ninth sternite.

The copulatory apparatus of the male includes, besides the claspers, an organ for conveying the spermatozoa into the sperm receptacle of the female. Thus organ is called the aedeagus. Figure 6 shows the external portion of the apical end of the aedeagus resting in the genital opening. Thus, the genital opening of the male is sometimes called the foramen of the aedeagus. Many stubby spines or sensilla which may well be sensilla basicona jet out in all directions on the tip of the aedeagus. Actually, the aedeagus is a comparatively long process and is permanently attached at some place well inside the body, (Cole, 1927).

The tenth segment, (figure 3 and figure 5) bears a pair of upright sclerotized plates flanking the anus, (Ferris, 1950). These plates are sometimes called anal plates, sometimes cerci. In any case, they have a wealth of slender spines on sensilla. The eleventh segment is entirely membranous, (Ferris, 1950).

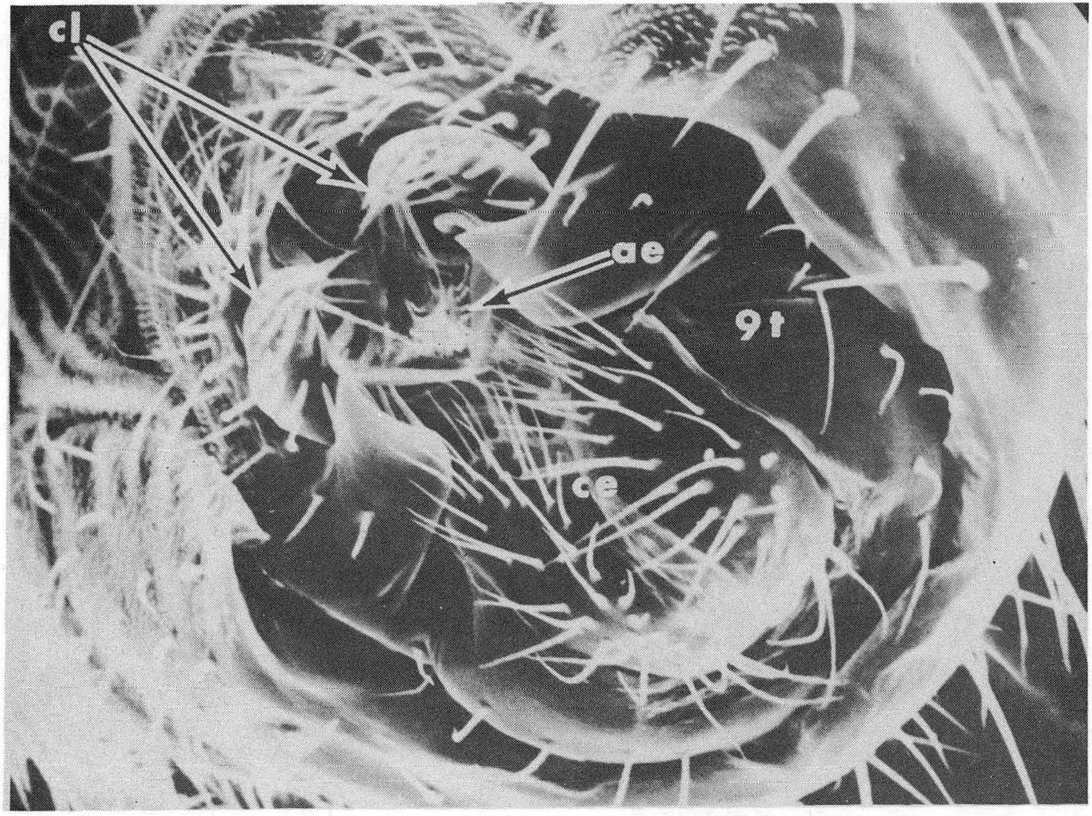

fig.5: Caudal aspect of male terminalia; cl, claspers; ce, cerci; 9t, 9th tergite; ae, aedeagus; go, genital opening.

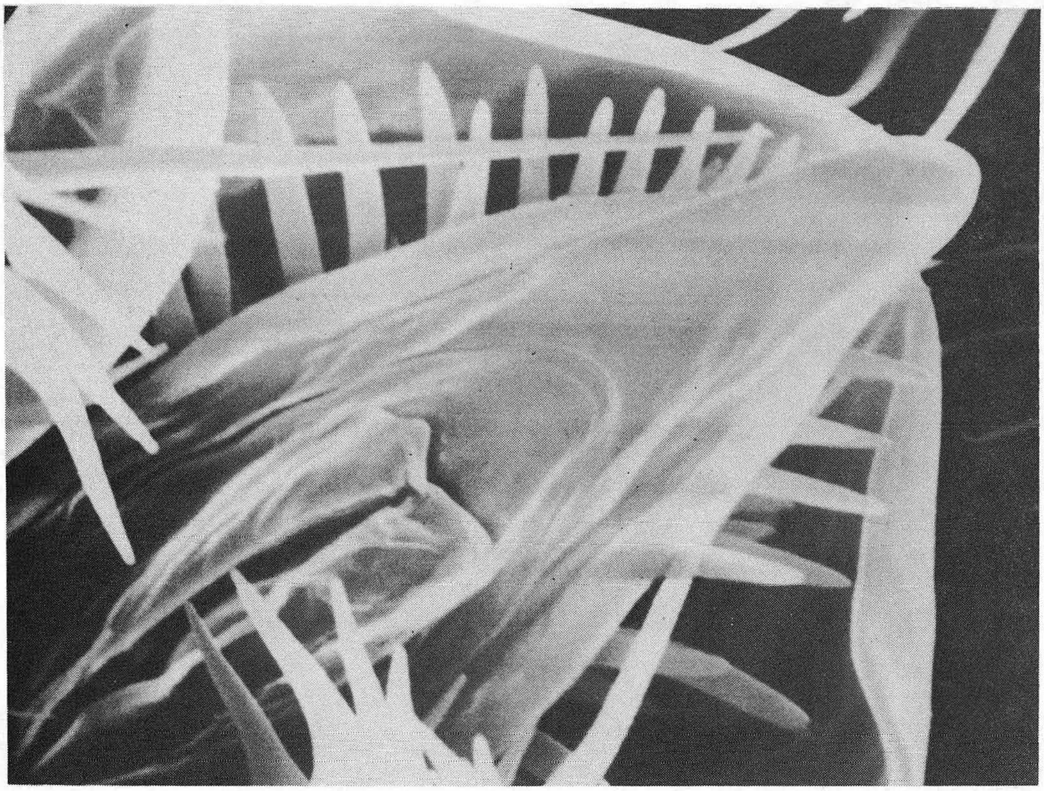

fig.6: Apical end of the aedeagus.

The Female

The eighth segment of the female Drosophila lacks spiracles and a sternite. Ventrally, this segment bears two elongate plates which are connected by a narrow, heavily sclerotized bar. These plates represent the gonopods of the eighth segment, and are all that remains of the ovipositor. The vulva lies between these gonopods, (Ferris, 1950). Figure 7 is a diagram of the lateral and candal aspects of the female terminalia. Figure 8 is a ventro-lateral view of the same region.

In figure 8, one can see a row of small peg-like processes arising from the heavily sclerotized gonopods. A closer view of these processes, (figure 9), shows them to be sex bristles.* Also visible in figure 8 is a longer, more slendor process, probably a sensillum trichodeum, that is found inside the row of sex bristles and just ventral of the posterior apex of each gonopod.

A postero-ventral view of the female terminalia, shows that the eighth tergite, (like the ninth tergite of the male), possesses a slender arm which passes beneath the anal plates and separates the genital and anal openings. In the female the anal plates, which represent the ninth tergite and ninth sternite, are just as hairy as those of the male. In the male, however, the anal plates flank the anal opening from each lateral side, and in the female from above and below, (Séguy, 1950).

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*"Sex bristles" denotes bristles analogous to those of the sex comb. The bristles of the claspers are sex-bristles.

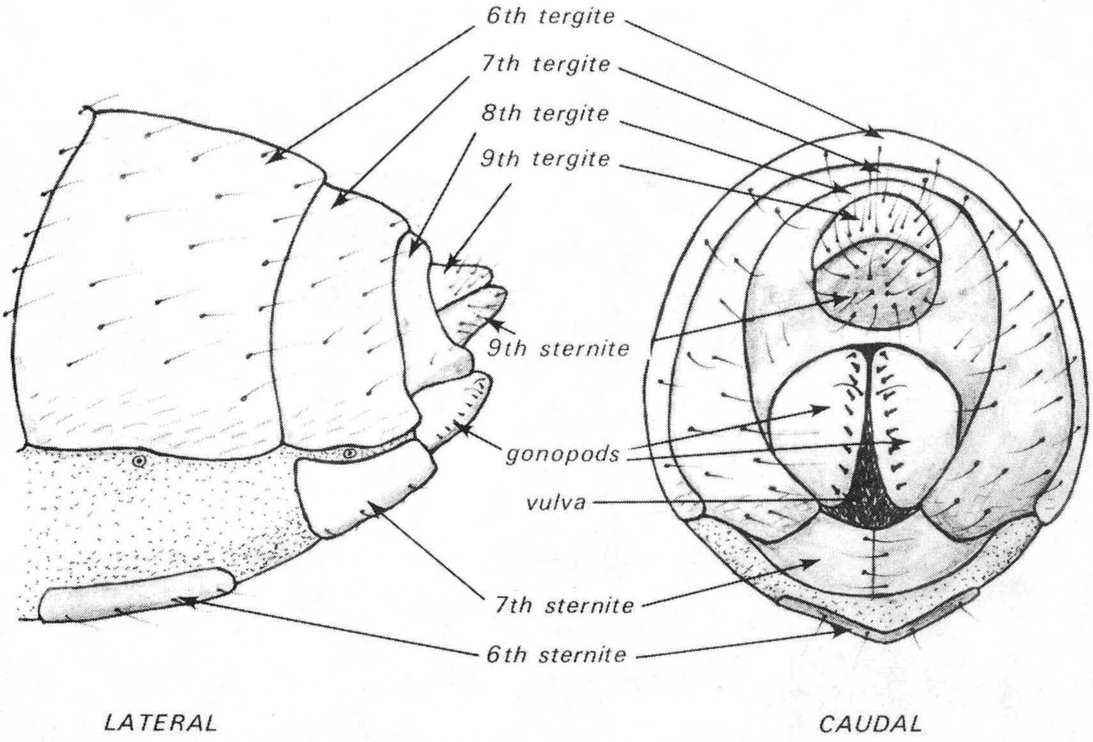

fig.7: Diagram of the female terminalia.

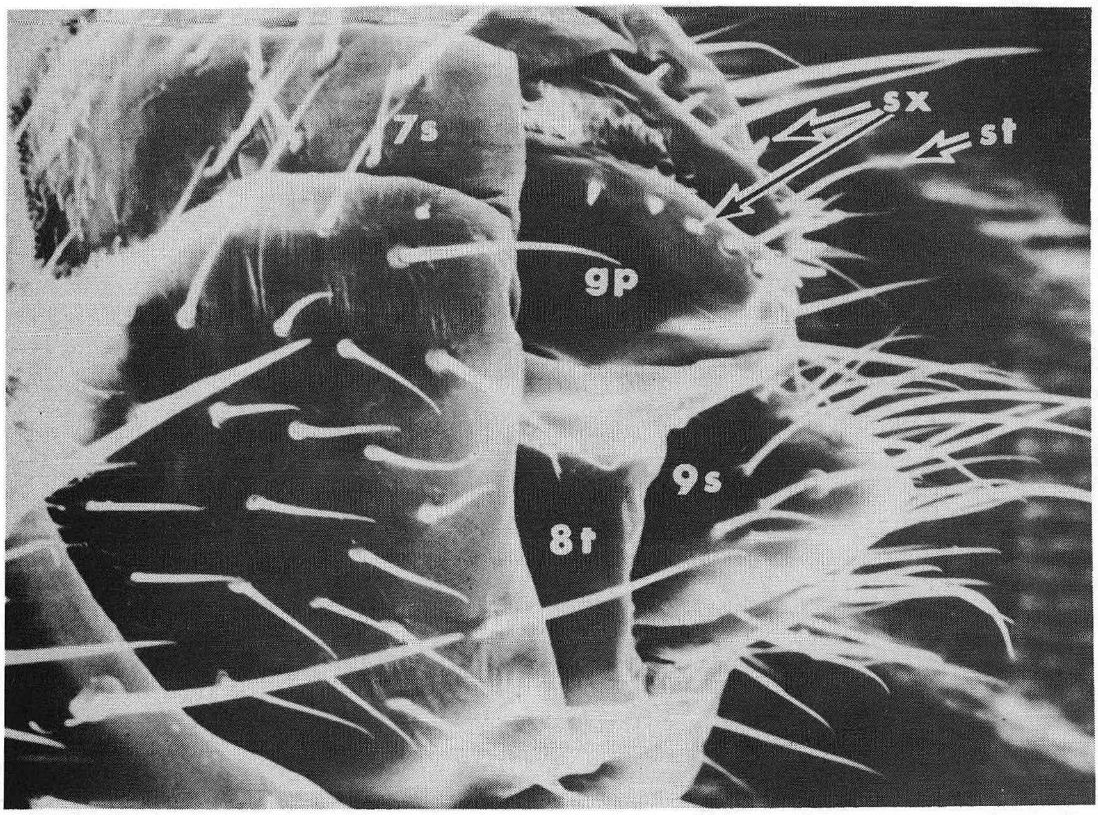

fig.8: Lateral aspect of female terminalia; gp, gonopods; 9s, 9th sternite; 8t, 8th tergite; 7s, 7th sternite; sx, sex bristles; st, sensilla trichodea.

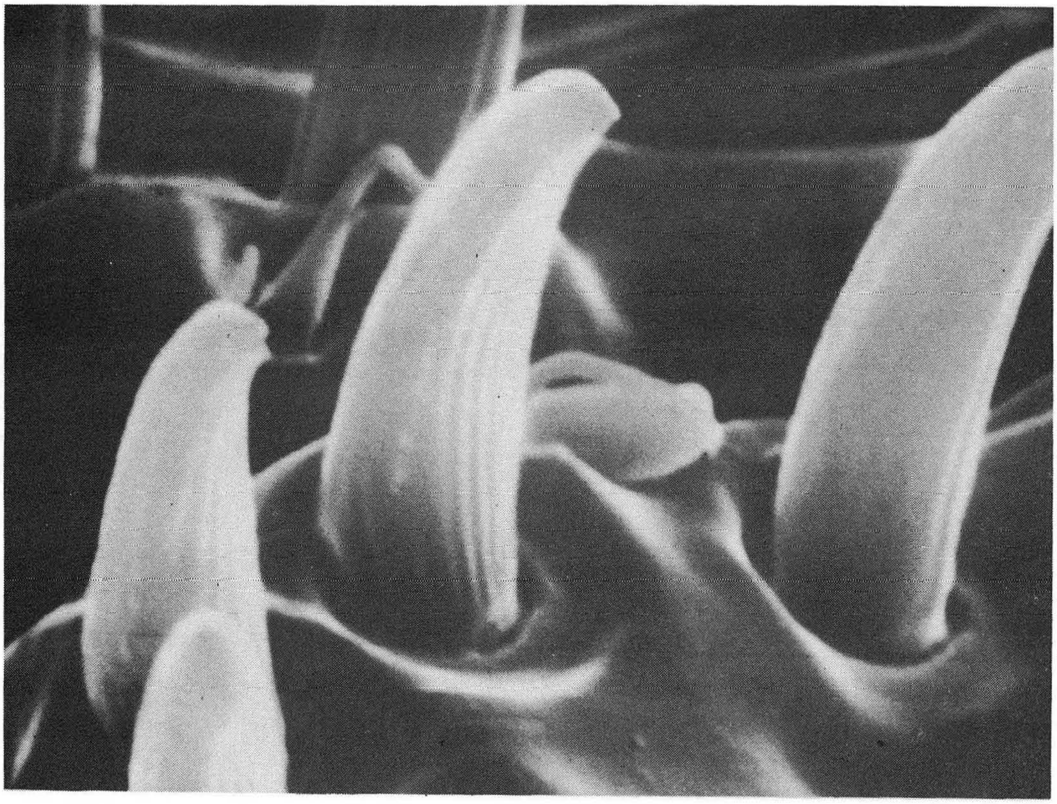

fig.9: Sex bristles on gonopod.

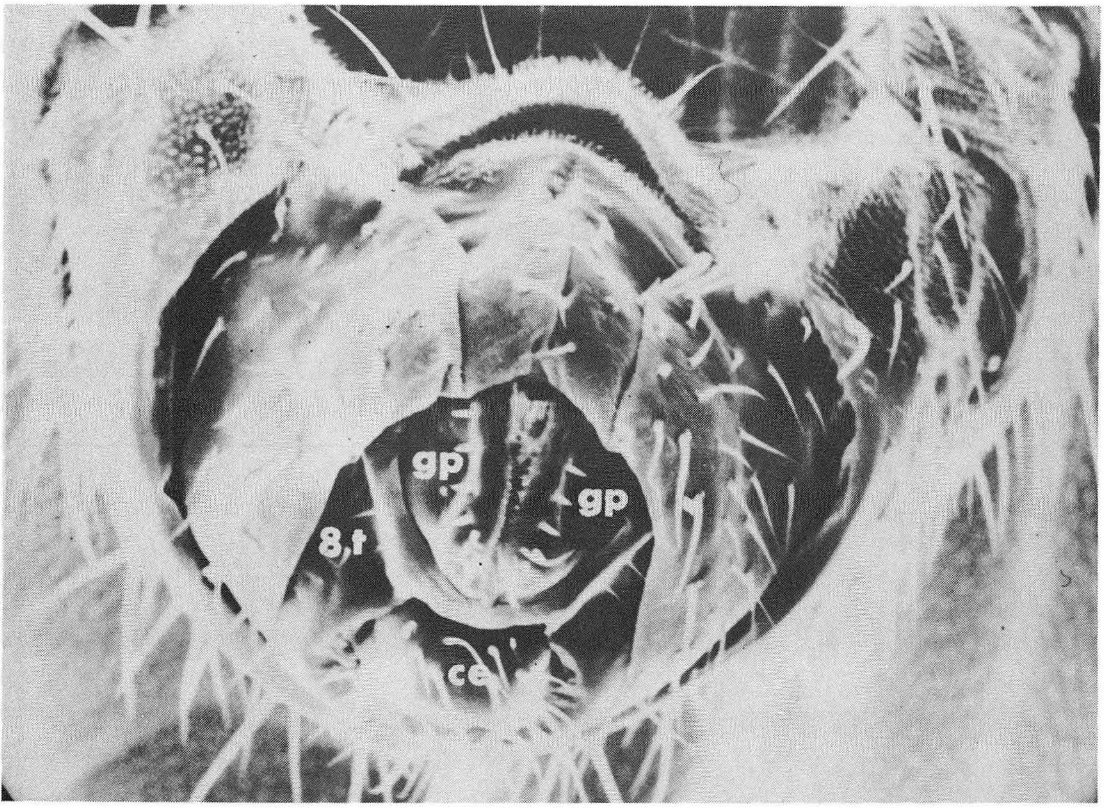

fig.10: Female terminalia, posterio ventral view; <u>8t</u>, 8th tergite; <u>ce</u>, cerci; <u>gp</u>, gonopods.

The vulva, (copulatory pouch, or spermathecal diverticulum), receives the aedeagus during copulation, and bears the recepticle of spermatozoa. Figure 11 shows this area in a female fly that has her gonopods slightly separated. One can see in the vulva a rather prominent process of which figure 12 is a close-up. The process seems to consist of a number of flexible plates lying together in a cone shaped clump. It is not clear what this process is, but perhaps it is an outpouching of the vagina specially adapted for collecting sperm.

Kill a fly in July,
You've killed just one fly.
Kill a fly in June,
They'll be scarce soon.
Kill a fly in May
You've kept thousands away.

Old English Rhyme

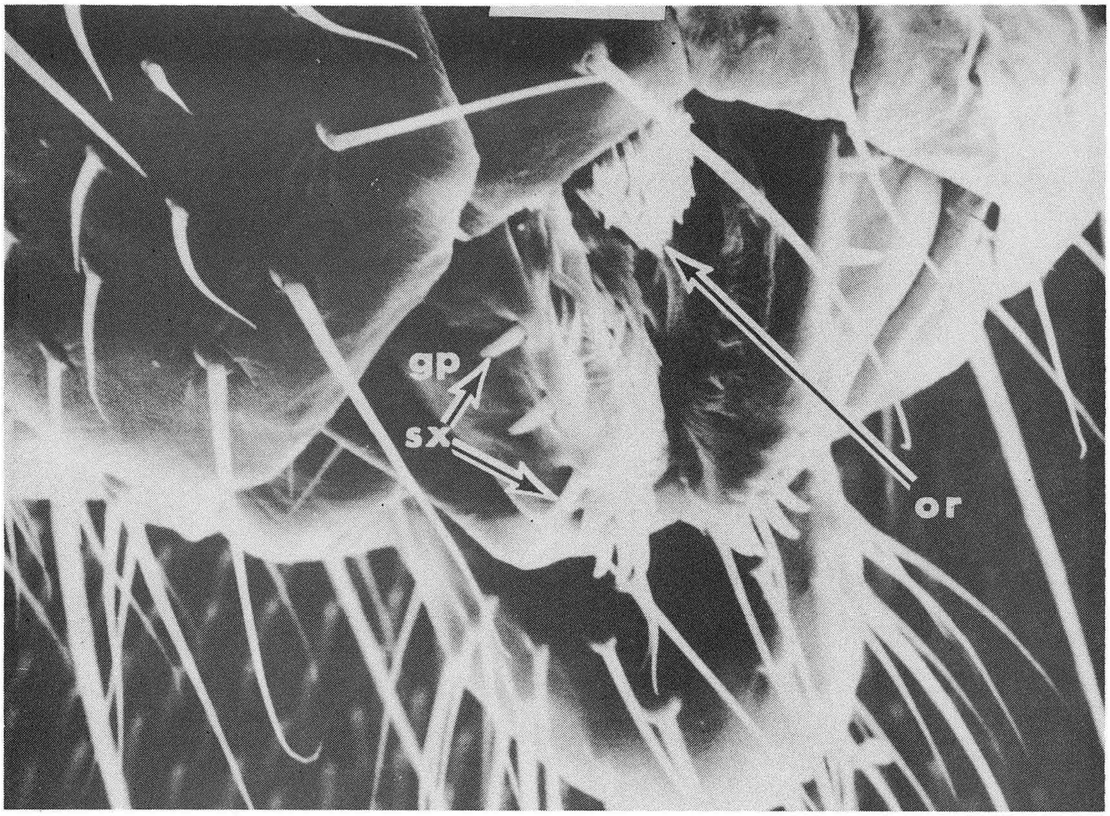

fig.11: The vulva; <u>gp</u>, gonopods; <u>sx</u>, sex bristles; <u>or</u>, outpouching recepticle.

fig.12: Outpouching recepticle.

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