On the so-called 'Olfactory Pores' in the Honey-bee.

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With Plates 38-9 and 5 Text-figures.

I. INTRODUCTION

Distributed over various regions of the body in insects of many orders are peculiar sensory organs commonly termed campaniform sensillae. MacIndoo, in recent years, has published a number of papers dealing with these structures in Coleoptera, Diptera, Lepidoptera, and Hymenoptera. He has, however, studied them more particularly in the honey-bee, Apis mellifica L., and, in his lengthy paper published in 1916, he described them as olfactory organs. He bases this conclusion upon varied experimental evidence and claims that, histologically also, they are adapted for the reception of olfactory stimuli. MacIndoo states that the nerve-endings, in relation with these organs, end where there are minute cuticular pores
and are consequently freely exposed to the outside air. It is for this reason that he gives the name of olfactory pores to these campaniform sensillae. A number of competent investigators, notably Sihler (1924), Lehr (1923), Hochreuter (1923), and others, have studied similar organs among other insects, but none has been able to detect the peculiar histological features described by MacIndoo. So far as the present writer is aware, no studies have been made on the so-called olfactory pores of the honey-bee since MacIndoo's paper. It therefore appeared desirable to reinvestigate these organs in that same insect, using MacIndoo's and other methods of technique. The work was carried out at the Rothamsted Experimental Station at the suggestion of Dr. A. D. Imms, F.R.S., whose unfailing interest and advice I wish to acknowledge.

According to MacIndoo the structure of an olfactory pore from the base of the wing is as follows (vide Text-fig. 1 A).

A typical olfactory pore of the honey-bee is an inverted flask in which the bottom of the flask forms the external covering or chitinous layer of the pore (Text-fig. 1 A, cl). This layer contains
the pore aperture, \( p \). The chitinous cone, \( co \), is not separated from the pore-wall, \( pw \), but it is evidently somewhat different in composition from the surrounding chitin, since it stains less deeply with iron haematoxylin and eosin or in safranin and gentian violet. The sense-cell, \( s \), is bipolar, long, slender, and comparatively large. The sense-fibre, \( f \), of this cell runs into the hollow of the cone, pierces the bottom of the cone, and enters the lowest portion of the transparent pore aperture. The figure accompanying the above description is actually from the leg of the bee. It is also the most complete that is given and, although those figured by MacIndoo from the wing (Text-fig. 1 b), are less detailed and more schematic, the structure is the same. MacIndoo adds that, since the pore apertures are so small, only occasionally does the microtome knife pass through the lowest part of the aperture. On account of this it is difficult to find a sense-fibre running into the aperture, but when several sections are critically studied it is possible to see several such connexions. He does not deal with the accompanying hypodermal cells.

The distribution and number of the 'pores' are fully described in all three types of bees. For example, he described 21 groups on the worker bee—the first 5 on the wing-bases, 6–18 on the legs, and 3 on the sting—totalling on the average 2,268 'pores' for each worker. On the queen he found 1,860, on the drone 2,604. The pores on the legs present a rather different appearance in surface view from those of the wing.

II. METHODS AND TECHNIQUE.

For the purposes of this investigation the so-called olfactory pores of the wing-bases were selected for study. Both adult and pupal wings were used, the latter being derived from pupae about sixteen and more days old: all were those of worker bees.

In order to investigate the purely cuticular parts of these organs, bases of the wings were detached from the body and placed in a 10 per cent. solution of potassium hydroxide. After washing in distilled water they were stained with carbol fuchsin. Corresponding portions of the wings of other specimens were merely decolorized by treatment with chlorine gas. These were
either left unstained and mounted in 15 per cent. potassium acetate, as recommended by MacIndoo, or stained in toto and mounted in euparal or in Canada balsam.

For the purpose of studying the complete structure of these organs it is obviously necessary to resort to section cutting. Various methods were tried, including the complicated paraffin wax and celloidin technique described by MacIndoo (1926). Simple embedding in paraffin wax of 60° C. melting-point for adult material, and of 54–6° C. for the pupal wings, gave adequate and more certain results.

A number of fixatives were used, including the Carnoy-Lebrun mixture, Sansom's modification of Carnoy's fluid, Gilson's fluid, Worcester's fluid, Bouin's fluid, Schwabe's formula as given by Sihler (1924), and Henning's fixative for chitinous objects. Of these the first two and the last were found most suitable. Good sections were obtained of material fixed in Henning's fluid, the cutting being notably facilitated, and there was no evidence of poor preservation, as mentioned by Hochreuter.

For purposes of staining the usual haematoxylins were all used, including Heidenhain's iron-haematoxylin, Erhlich's, and Delafield's. Among other stains used were gentian violet and safranin, Mann's methyl-blue-eosin, Mallory's phosphotungstic haematoxylin, and Mallory's phosphomolybdic haematoxylin. In the latter case the formula used was that given by Bolles Lee, and it was applied both with and without mordanting in copper sulphate. From among these various methods the best general results were obtained with Mann's methyl-blue-eosin. For the finer details of structure iron haematoxylin and the two stains of Mallory gave the best differentiation.

Several types of silver impregnation were tried, but the only method that gave moderately successful results was Boeke's modification of Bielchowsky's silver and silver oxide impregnations. A few trials were made with methylene blue both in intra vitam and post mortem, but, owing to the fact that the stain has to penetrate between the two layers of wing membrane, and because it is not possible to watch its progress through the brown chitin, neither method gave good results.
III. The Structure of the 'Olfactory Pores'.

(a) The Cuticular Parts.

Text-fig. 2 shows the arrangement and position of these organs on the wing-bases. On the dorsal surface of the front wing there is a single group; on the ventral surface there is one large group and two groups of smaller size; one of the smaller groups lies in a plane at right angles to the others. The hind wing possesses a single group on each surface. It will be seen from Text-fig. 3 that there is a variation in the diameter of the individual organs.

Little of their structure can be made out from surface examination alone. When the ventral sensillae of a wing, which has been bleached and stained, are examined in surface view under a high power, all that is visible is a small central circular spot surrounded by a ring, which is differentiated from the surrounding chitin by its deeper staining properties (Text-fig. 3 A, a). The central spot is presumably the 'pore aperture' of
MacIndoo, but in order to understand its significance reference must be made to fig. 8, Pl. 39, which shows the sensillae in section. The cuticle in this region is excavated to form a some-

what flask-shaped cavity, which is lined with material staining more deeply than the surrounding chitin. This lining substance (tc) is the 'Polstermasse' of many German writers and the 'chitinous cone' of MacIndoo; it is here named the terminal cap. It embraces the highly refractive scolopala (sa) or termination of the sense-fibre. It is probable, therefore, that the so-called 'pore aperture' of MacIndoo is nothing more than the

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**Text-fig. 3.**

Surface view of a group of campaniform sensillae from A the ventral and B the dorsal surface of front wing. a-a before, b-b after treatment in caustic potash.
refractive apex of the scolopala. The surrounding ring is merely an optical section of the inner lining of the cavity mentioned.

This opinion is confirmed when a specimen (Text-fig. 3 B, b), after treatment with potash and stained in carbol fuchsin, is examined in surface view. The small central spot is no longer visible. By gradually focusing downwards a single ring, which gradually increases to a maximum size, is evident; it then contracts to a smaller diameter, and gradually enlarges again to form the internal opening of the cavity. When microtome sections of material acted on by potash are made (Text-fig. 4) the reason for this difference is apparent. It will be seen that

![Text-FIG. 4.](image)

Section through ventral sensillae of fore wing after treatment with potash. For explanation of lettering $x$, $y$, $z$ see accompanying text.

c1, c2, outer and inner layers of cuticula.

the scolopala and the terminal cap are dissolved away and the series of optical sections observed in surface view above correspond with the sections represented at $x$, $y$, and $z$.

The implication here is that the so-called olfactory pore of MacIndoo is merely the apex of a highly refractive sense-rod; when specimens are suitably treated with potash this is dissolved away and with it the pore-like appearance.

The word suitably is here used advisedly for, if the potash treatment is not too prolonged, it appears from some of the preparations that the scolopala is unaffected, and remains in situ. This would indicate that it has an attachment of some kind to the external layer of the cuticula. If so, then conditions would seem to be similar to those observed by Sihler, in the Acridian, *Gomphocerus rufus*, where he found that the sense-rods of the tactile hairs of the cerci are shed at ecdysis.

The appearance of the dorsal group of sensillae is essentially
similar except that each sensilla appears to lie at the base of a small depression in the chitin (fig. 9, Pl. 39).

(b) Cellular Structure.

Fig. 1, Pl. 38, is a reconstruction of the general appearance, in section, of the dorsal group of sense-organs on the hind wing. It was taken from an adult but incompletely pigmented bee, which had not yet left the pupal cell.

The sense-cell (s) appears to be binucleate and bipolar. It narrows proximally into a fibrous strand the identity of which is finally lost in the nerve-bundle, nb, which can be traced for some distance towards the thorax. Distally, the cell ends in the sense-fibre, sf, ending in a slight swelling, sa, which lies centrally within the terminal cap (tc) of the cuticular cavity. The apex of this fibre is a highly refractive body and is presumably chitinoid in nature. It completely pierces the terminal cap and lies directly against the very thin cuticular layer that separates it from the outer air. The sense-fibre can be traced proximally as far as the first nucleus, where it appears to be lost in the cytoplasm of the sense-cell. The two nuclei, separated from one another by the median constriction of the cell, present the usual ovoid shape and contain scattered chromatin. The question of the binuclear structure will be referred to again later.

The hypodermis, h, appears as a narrow layer surrounding the bases of the sense-cells. In older specimens (fig. 9, Pl. 39) it becomes very attenuated in the parts more remote from the sense-organs. No accessory cells can be definitely associated with the sense-cell but, as is evident from fig. 9, Pl. 39, there are traces of cytoplasmic extensions from the periphery of the sense-cell extending to the terminal cap (tc). This figure is from a preparation fixed in Henning's fluid and similar evidence can be found in sections fixed by other methods.

IV. Developmental Phases.

In order to get further evidence as to the nature of the elements forming the sensory complex, late pupal stages were examined. The earliest of these (wherein the eyes begin to show a reddish pigmentation) are shown in fig. 2, Pl. 38, and
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fig. 4, Pl. 39 (taken from the dorsal and ventral groups respectively), fig. 2, Pl. 38, being an attempt to reconstruct a number of sections. It will be seen that, although the sense-cell itself is advanced some way in its formation, the actual structure of the cuticular part is in an early stage. The cuticula is, as yet, relatively thin and there is no cavity enclosing the termination of the sense-cell. The latter is short, and comparatively stout, and covered with a dome of deeply staining material (rtc) which is the rudiment of the future terminal cap. The rudiment of the sensory fibre is seen at rf. Unmodified interstitial hypodermal cells are very evident at this stage. Proximally the sense-cells already appear as binucleate cells gradually tapering off into definitely fibrous processes. These latter are finally collected together into a bundle of nerve-fibres running towards the thorax. In the figure the basement membrane is shown surrounding the whole group of cells but, farther back in the series of sections, it appears to be broken through by the collected strand of fibres. The condition shown in the figure is due to a change in direction of the fibres at the basement membrane; they run parallel to it, i.e. at right angles to their original direction, before collecting together to emerge finally as indicated above. This also accounts for the way in which the fibrous ends of the sense-cells are cut through proximally.

The initial growth stages of the ventral group of sensillae (fig. 4, Pl. 39) are essentially similar, though the cuticle is here very much thinner. Owing to the fact that the sense-cells make their right-angle bend, to run parallel to the flattened plane of the wing, rather sooner (i.e. at the region of the first constriction) than in the case of the dorsal group, they can be followed longitudinally for only a short distance.

A rather later stage of development of the dorsal group of sensillae is shown in fig. 3, Pl. 38. The sense-cells have elongated somewhat, and a certain amount of differentiation has occurred at their distal ends. The lining layer (tc) appears as a cap-like termination of the sense-cell, but is actually in contact with the cuticle at only one point. In association with the termination of the sense-cell the following elements may be made out. Firstly, a median fibre-like structure (f, in figs. 3
and 6, Pl. 38–9), which can be traced back some distance towards the first nucleus, nl, and which is presumably the sense-fibre in course of development. Secondly, surrounding this fibre is differentiated a tract of cytoplasm, s1, which itself is flanked on either side by strands of cytoplasm, s2, the latter being at least optically distinct from it. These strands stain rather more deeply and are fibrous in appearance. Distally they terminate on the side-walls of the terminal cap—proximally their identity cannot be definitely determined. There are two possibilities: (a) that they are hypodermal cells such as are shown in fig. 3, Pl. 38, as occurring on either side of the region under discussion; or (b) that, as is believed to be the case, they are a result of differentiation within the sense-cell itself. The former theory, involving homologues of the trichogen and hair-membrane cells, would of course be the orthodox one, but it can be scarcely upheld on the evidence here presented and no nuclei can be detected.

A slightly later stage is shown in figs. 5 and 6, Pl. 39. The terminal caps, tc, which stain much deeper, are now embedded in the cuticular layer, c2, which has been laid down around them. In favourable examples the apex of each cap can be seen to be in contact with the surface layer, c1, of the cuticle (fig. 6, Pl. 39). It is evident that the cap forms the future 'lining' of the cavity of the sense-organ, while the rest of the cuticula is laid down by the hypodermal cells. No sign of any pore is to be seen. The triangular process terminating the sense-cell has assumed at its tip a highly refractive appearance, sa, which appears to be an early stage in the development of the future scolopala. The surrounding cytoplasm shows the usual deeply staining fibrous nature. The basement membrane, b, is shown enclosing, in part, the elongated sense-cells.

From the foregoing evidence it is now possible to come to some conclusion as to the existence of a pore aperture in relation to these sensillae.

MacIndoo, in his summary, says, 'Judging from the structure of these organs it is observed that the cytoplasm in the end of the sense-fibre just beneath the pore aperture is constantly in touch with the outer air'. It is obvious from the foregoing
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remarks that if, as it appears to be, the end of the sense-fibre (i.e. the scolopala) is of a refractive chitinoid nature, its cytoplasm cannot be exposed to the outside air. Further, it appears from sections made from material after treatment with potash, that, after the terminal caps have been dissolved away, there is still a thin layer of cuticle separating the cavity of the organ from the outside air. Lastly, no definite evidence of the existence of a pore aperture was found in the surface examinations made. With regard, however, to the identification of the cells forming the sensory complex it is more difficult to reach a decision and the matter is briefly discussed in another section.

V. WING-BASE Sense-organs in other Insects.

It appears that the sense-organs herein described fall into that class grouped together under the name campaniform sensilla. These have each a single sense-cell and are classified structurally among the tactile organs of the hair-and-peg variety. They have been described from practically all regions of the cuticle in various insects of most orders and have been found in some larvae. The shape of their cuticular parts varies a good deal, as does also the nature of the elements composing the cellular complex.

The most satisfactory information concerning the cellular elements of campaniform organs is given in the paper of Sihler (1924) and includes some very clear figures. The organs are described from cerci of Orthoptera. Their cuticular parts appear to be laid down by a large, well-defined, 'dome forming' or trichogenous cell which is pierced at one side by the sense-fibre from a bipolar nerve-cell. Such a condition seems to differ rather fundamentally from what is apparently the case with the sense-organs figured in the bee, so that the question as to whether the campaniform organs form an homologous group at once arises. It will, therefore, be to the point to review briefly the structure, as described by other observers, of the wing-base organs in other insects.

In the Lepidoptera such work has been done by Freiling and more notably by Vogel (1911). The latter author figures the large elongate sense-cell as the central structure of the sense-
organ, but no dome-forming cells at all comparable with those figured by Sihler are shown. From the presence of two small subhypodermal nuclei, on either side of the sense-fibre at the inner opening of the cuticular cavity, however, he postulates the existence of two auxiliary cells. These he calls the 'Hüllzelle' and the 'Kuppel-' or 'Kappenzelle', but admits there are no cell-boundaries visible. The nerve-cell has a sheathing layer or neurilemma containing a nucleus.

The sense-cells in the bases of the wings and elytra of Dytiscus marginalis have been studied by Lehr (1928). This observer also finds supernumary nuclei and associates them with the presence of the 'Kappenzelle' and 'Hüllzelle' of Vogel. His figures (Text-fig. 5 A) of the proximal subcostal group seem to indicate a general structural similarity between these organs and those of the honey-bee.

A free translation of Lehr's description is as follows: Each sense-cell is enclosed by a fairly thick sheet of sheathing cells (Nebenzellen). There can be differentiated therein nuclei of three kinds ... indicative of three types of cells. First of all there are nuclei of a more elongate shape, with a good deal of scattered chromatin, reminiscent of the neurilemma nuclei of the nerve, but not to be confused with them on account of their considerable size and sharp-pointed ends. They have a constant position and are the most distal of all the nuclei. Perhaps here is seen the ('Kappen-' or 'Kuppelzelle') cap-cell of Vogel . . . Nearby and more proximal to the sense-cell nucleus are nuclei which differ in their more rounded shape. Some of these resemble the hypodermal nuclei; they lie somewhat distal to the sense-cell nucleus and may perhaps be compared with the 'Hüllzellkern' of Vogel. Others, and these lie proximally, must be recognized as similar to the neurilemma nuclei and must be identified with the neurilemma cells of Vogel.

From Text-fig. 5 A it will be seen that, since no cell-boundaries are apparent, each sense-cell is a single elongate multinucleate structure. It is traversed throughout its length by a median fibre which ends distally in the scolopala, divides proximally to enclose the large sense-cell nucleus, and unites again behind it. In the honey-bee this central fibre could not be traced back
farther than the nucleus and, in this respect, agrees with a figure given by Erhardt (1916) from the wing of *Agrion pueella*. Only one supernumary nucleus is figured in this sense-cell which she calls the 'Hüllzellkern'. In *Chrysopa*
The sense-cell is enveloped in a sheath containing two 'Hüllzellen' and structurally, therefore, she says, it is essentially similar to those described by Freiling, Günther, and Vogel in Lepidoptera. In her figure of an organ from the hind wing of *Locust*(a) *cantans* but one accessory nucleus is shown and this lies just beneath the terminal cap itself—actually at the distal end of the cuticular cavity. In the Hymenoptera she gives a single figure from the wing-base of a wasp, *Vespa rufa*. No accessory cells are shown. The letterpress reads, 'In axial section is seen a rounded surface-pit in whose neighbourhood the chitin is slightly raised. Across the pit projects a small cap (Kuppel) through which a fine canal nearly reaches the outside. It stains deeply ... The attached sense-cells do not differ essentially from those described above; their long spindle shape is particularly emphasized. They are closely packed together and between them are found numerous supporting cells (Stützzellen)'.

A single figure given by her, of the wing-base organs of *Eristalis tenax*, agrees with that from *Vespa rufa*; here, apparently, no sheathing cells and no accessory nuclei occur in association with the sense-cell.

VI. THE CELL ELEMENTS COMPOSING THE SENSE-ORGANS.

The question here raised concerns the number and identity of the cellular components of each sensory unit.

It is generally supposed that the different types of insect sense-organs, with the tactile hairs (*sensilla trichodea*) at one extreme and becoming modified in various ways through the *sensilla chaetica*, *sensilla basiconica*, &c., to the simple campaniform organs at the other extreme, represent a continuous evolutionary series. The tactile hair is presumably the more primitive type and the others must be derived from it. This being so, it follows that evidence of the presence of cells composing the sensory hair complex should be forthcoming throughout the series.

Theoretically three cells are involved.

1. The hair-membrane cell, also called the distal enveloping cell or cap-cell.
2. The trichogenous cell, also termed the basal enveloping cell or the envelope cell.

3. The nerve-cell.

Such cells are indeed described by Schneider (1923) in the hair sense-organs of the cabbage caterpillar (P. brassicae). The innervation here, it should be noted, is by a sub-hypodermal nerve-cell whose distal process penetrates the basement membrane and trichogen cell.

Essentially the same structure occurs in the tactile organs of adult insects. As an example, the sensory hairs described by Sihler from the cerci of Orthoptera may be mentioned. Each hair has at its base a large, well-defined, trichogenous cell, which is innervated from the side by the sensory process of an intra-hypodermal nerve-cell.

This condition is obviously different from that occurring in the honey-bee. In the latter insect the main central element of each sensilla is the sense-cell which itself appears to secrete non-cellular parts of the sense-organ and also to give rise to the sensory fibre. There are two possible explanations of these differences. Either there is no homology between these campaniform sensillae and other sensory organs of the tactile hair type, or else the nerve-cell has usurped in some measure the function of, or become intimately fused with, the two accessory cells which, in their turn, have lost their separate identity. Such is presumably the opinion of Vogel and of Lehr. The latter author regards the sensory cell as being surrounded by a syncitial sheath of cytoplasm in whose nuclei he recognizes membrane cell nucleus and trichogen cell nucleus (Kuppelzellkern and Hüllzellkern, Text-figs. 5 A, B, c). Some of Lehr’s figures, it may be said, do resemble to some extent those given here (fixed with Henning’s fluid), but unfortunately he has not studied developmental stages. In fact the writer is not aware of the existence of any adequate figures of the development of these wing-base sense-organs. It is reasonable to suppose that in the earlier stages, if anywhere, definite evidence of the separate component parts of the sensillae might be obtained. In the earliest pupal stage of the bee examined, however, there appears to be little or no evidence of accessory cells being
involved. It appears, in fact, that a single cell lays down the sensilla and becomes differentiated within itself and that this differentiation, in the case of the sensory fibre, takes place from before backwards—i.e. distally—proximally. It is considered that, in this case, such optical differentiation as is apparent is not sufficient evidence of a sheath of accessory hypodermal cells as has been described by Lehr, for Dytiscus (see Text-fig. 5 c). The accessory nuclei occurring in the honey-bee are judged to be those of the ordinary hypodermal cells laying down the cuticula.

As is pointed out in the previous section, Erhardt's figures from the wing-base of Vespa rufa show neither cap nor trichogen cells, and a similar absence of these structures appears to occur in the sense-organs of the halteres of some Diptera. The figure given in 'Gli Insetti', p. 684, for example, of a section through the haltere sense-organs of Tabanus, is very similar to those figured here from the honey-bee. In both cases, incidentally, the sense-cell is uninucleate, and this raises the question of the binuclearity of the sense-cells in the honey-bee. It may be said at once that this feature is concluded to occur largely as a deduction from the following considerations. At the region of their first constriction the majority of the cells turn through a right angle to run parallel with the basement membrane. They are, therefore, usually cut off short at this region in sections; but, proximally to these cut-off ends, there lie cells beginning distally with a constriction and widening out into a typical cell of the bipolar form. Although these two sets of cells lie in different planes it is believed that one is a continuation of the other. This conclusion is supported by more direct evidence where occasionally, in favourable cases, the continuity is more apparent. It may be added that binuclear sense-cells are figured in 'Gli Insetti', p. 624, from the dorsal region of the antenna of Sphinx convolvuli.

VII. ON THE ORIGIN OF THE SENSORY NERVE-FIBRES.

It is the case that a notable difference between the sensory nervous system of vertebrates and invertebrates consists in the position of the sensory neurons. 'In the earthworm we have a
primary sensory neurone with its cell body in the skin and its nerve process ending in ramifications of the neuropile of the segmental ganglia.' This is typical of invertebrates. 'In the vertebrates . . . the primary sensory neurones instead of having their cell bodies in or near the surface have undergone a change in situation . . . so that the cell body is placed . . . close to the central nervous system' (Bayliss, p. 464 et seq.).

It is to be expected, therefore, that the sensory neurons of insects would lie in the hypodermal layer, but this has never been demonstrated. At the same time no one has so far been able to prove their existence in the central ganglia. The position has been well summed up by Snodgrass (1926) and is recapitulated here. He points out that since no sensory neurons have been found in the central ganglia or anywhere associated with them, general opinion follows that of von Rath in insisting that the generative cells of the sensory system must be found in the periphery, i.e. in the ectodermal tissue of the body-wall. Now the only cells so far found in the course of the sensory nerves are the peripheral sense-cells themselves.

The sensory nerve-fibres, when traced outwards, are found to end in cells, which may be multipolar or bipolar and are placed by Zawarzin (1912) into two categories. The first of these is made up of bipolar cells whose distal processes go direct to specific ectodermal sense-organs. The second includes bipolar, or more usually multipolar cells, which give off terminal processes ending in fine branches on the inner surface of the hypodermis. They may also supply the skeletal and abdominal wall-muscles. The cells described in this paper belong to Zawarzin’s type 1, and such cells (and indeed those of type 2 as well) are the only ones that occur in the whole course of the sensory nerves. This fact has given rise to the idea that they are the neurons of the sensory fibres. The developmental origin of the sensory cells of type 1 has been studied by many investigators and all agree that they are specialized hypodermal cells, but no one has demonstrated the growth of a nerve axon from these cells. On the other hand, several observers have claimed that a nerve-fibre grows outwards and unites with the sense-cell. The base of the sense-cell, Vogel says, may elongate slightly
towards the nerve, but the connexion with the latter is made in the immediate neighbourhood of the cell. He claims that the innervated cell of an insect sense-organ becomes secondarily a sense-cell by union with a nerve-fibre. On the other hand, his conclusion that there must be found in the deutocerebrum a ganglionic nerve-centre from which antennal sensory cells take origin has never been substantiated.

It is suggested that the neuron of the sensory system connected with the organs herein described is situated in the hypodermis and is in fact the sensory cell itself. The evidence for this is as follows:

1. The proximal elongation of the sense-cells and the consequential pushing-back of the basement membrane by them.
2. The nature of the proximal ends of the sense-cells which narrow down to form fibrous processes which collect together and apparently form the bundle of fibres which can be traced back towards the thorax.
3. The formation of the distal sense-fibre (the fibre of the sense-organ itself) which appears to be differentiated from before, backwards, i.e. distally—proximally.

Against this suggestion it may be urged that a connexion with the sensory nerves from the central nervous system may occur much more proximally. It is conceivable that fibres from an outgrowing nerve may meet and fuse with inward prolongations of the peripheral sense-cells. This is considered to be unlikely in the present case, but only by examination of earlier pupal material than that studied here could the matter be definitely settled.

VIII. On the Function of the 'Olfactory Pores'.

Hicks, in 1857, was the first to describe examples of these peculiar organs from the legs and wing-bases of insects, and thought that they might have an olfactory function. Since then many workers have studied them, but none except MacIndoo has been able to uphold this view. It is generally considered that they are tactile organs of some kind though, in the case of those occurring on the wing-bases, it is not clear what tactile
function they could perform. Especially is this so when they are almost walled in by folds of chitin so that they cannot be seen in surface view. Lehr describes such conditions from the wing of *Dytiscus*. With regard to wing-base organs themselves, Erhardt points out that they are most numerous on the strong flyers and, occurring as they do on both wings, it would seem reasonable to suppose that they are in some way connected with flight. Presumably some mechanism is necessary to correlate wing vibration with varying air conditions and pressures, but it is difficult to speculate with so little basis of experimental knowledge. Such experimental knowledge, so far as the writer is aware, is limited to the experiments of MacIndoo (for those of Sihler were concerned only with the cercal campaniform organs of Orthoptera) and his results conflict with those of von Frisch (1919). Von Frisch has definitely shown that the olfactory sense resides in the antennae of honey-bees. Two main lines of experiment indicate this. He has shown that, firstly, bees trained to recognize colours still continue to do so after amputation of the antennae; secondly, bees trained to an odour entirely fail to distinguish it after amputation of the antennae. These experiments seem to indicate that the second result is not due to shock following amputation but is caused by the loss of the olfactory organs themselves.

Further, the eight distal segments of the flagellum of the bee’s antenna differ from the three proximal segments and the scape, in being supplied with the so-called ‘pore plates’. If all of these eight distal joints are cut off then the bee is incapable of recognizing the odour to which it has been trained. If, on the other hand, only one of these distal segments on either antenna is left intact then the bee is still able to respond. When this remaining segment is amputated the bee finally loses this ability. As von Frisch remarks, with reference to the question of shock induced by such experiments, it is difficult to believe that the physiological processes of the bee should be so much more deranged by the loss of all eight distal segments of both antennae than from the loss of eight on one side and seven on the other.

MacIndoo found, however, that the resultant shock invalidated results from experiments involving antennal amputation. The
criterion he used for measuring response was the amount of time taken by the bees to react in some visible way (for example, by vibrating the antennae) to certain essential oils which were placed in close proximity to them. For normal bees the reaction time was found to be on an average 2-3 seconds; when one antenna was cut off this reaction time was doubled; when distal segments 2-8 of the remaining flagellum were removed, the reaction was increased to from 15 to 88 seconds, pari passu. This could be taken as direct evidence in favour of the antennae being the organs of olfactory sense—indeed MacIndoo says that at a first glance it does so appear. He disregards it apparently because the behaviour of antennaless bees is generally abnormal and because of the positive reaction (2-9 secs.) and more normal behaviour in the presence of the same stimuli of at least a proportion of those bees which have their antennae intact but coated over with glue.

On the other hand, when the 'olfactory pores' on the wings were removed the reaction time was increased to 27 seconds; when, in addition, the pores on the legs were coated over with certain substances the average reaction time was 40 seconds. This is presumably the chief argument for supposing the olfactory pores to be the main receptors of olfactory stimuli, for the bees in these last experiments had their antennae intact and uncoated.

While one is led to conclude, therefore, from von Frisch's experiments, that the olfactory sense in the honey-bee mainly resides in the antennae, a certain capacity for odour perception is also betrayed by the campaniform organs, according to MacIndoo.

Two points may be mentioned here. The first is that, having regard to MacIndoo's observations with antennaeless bees, the difference possibly lies in the interpretation of the results rather than in the results themselves. The second, as has been pointed out by Snodgrass, is that, whereas von Frisch used the milder floral odours under open-air conditions, MacIndoo used powerful smelling and possibly irritant substances under confined conditions. Hence it may well be that, while the antennae are the organs enabling the bee to respond to the normal odour
stimuli encountered during foraging flights, it is capable of detecting the presence of strong smells at close quarters by other means.

IX. Summary.

1. The structure of the campaniform sensillae occurring on the wing-bases of the adult worker bee is described.

2. The essential features in their later developmental phases in the pupa have been followed.

3. The observations described lend no support to those of MacIndoo, that the actual termination of the nerve-fibre is exposed to the outside air.

4. The wing-base organs, as described by other workers in different insects, are discussed, with special reference to the identity of the cellular elements composing these structures.

5. The paper concludes with a short discussion of the position of the sensory neuron and a brief review of the supposed function of the campaniform sensillae.

X. Literature.


Hochreuter, R. (1923).—“Der Hautesinnesorgane”, in Korschelt’s ‘Der Gelbrand, Dytiscus marginalis L.’ (Leipzig), pp. 253 et seq.

Lehr, H. (1923).—“Die Sinnesorgane der beiden Flügelpaare”, ibid, pp. 311–71.


Weinland, E. (1891).—“Über die Schwinger (Halteren) der Dipteren”, ibid., 51, pp. 55–166.

XI. EXPLANATION OF PLATES 38 AND 39.

REFERENCE LETTERING.

b, basement membrane; c1, c2, outer and inner layers of the cuticula; cc, cuticular cavity; f, sensory fibre; h, hypodermis; n, nucleus of sense-cell; nb, nerve-bundle; nf, nerve-fibre; nn, nucleus of neurilemma; rlc, rudiment of terminal cap; rf, rudiment of sensory fibre; s, sense-cell; sa, scolopala; tc, terminal cap.

PLATE 38.

Fig. 1.—Section through dorsal group of sensillae of hind wing of un-pigmented adult bee (extracted from cell). Fixed with Henning’s fluid; stained in iron haematoxylin. × 760.

Fig. 2.—Section through dorsal group of front wing. Early pupal stage (eyes showing pigmentation). Fixed in Carnoy-Sansom; stained in iron haematoxylin. × 760.

Fig. 3.—Section through dorsal group of front wing; stage slightly later than fig. 2. Fixed in Carnoy-Lebrun; stained in gentian violet and safranin.

PLATE 39.

Fig. 4.—Section through ventral group of front wing; same stage and treatment as fig. 2. × 790.

Fig. 5.—Section through dorsal group of fore-wing; later pupal stage. Fixed in Henning’s fluid; stained in iron haematoxylin. × 730.

Fig. 6.—Distal part of sense-cell from fig. 5. × 1030.

Fig. 7.—Section through ventral group of front wing, later pupal stage than in fig. 4. Fixed in Carnoy-Sansom, stained in iron haematoxylin-eosin. × 760.

Fig. 8.—Section through ventral group of front wing, late pupal stage. Fixed in Carnoy-Lebrun; stained in phosphotungstic haematoxylin. × 730.

Fig. 9.—Section through dorsal group, hind wing, of adult bee. Fixed in Henning’s fluid; stained in Ehrlich’s haematoxylin. × 2380.