XI. On a new Structure in the Antennæ of Insects. By J. B. HICKS, Esq., M.D. Lond., F.L.S.

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THE object of this paper is to call attention to some peculiar structures to be found in the antennæ of insects, which have not been hitherto noticed. If we submit the antennæ to the bleaching process which I have before described (see pp. 141–2), these structures will be well brought into view; they vary somewhat in form in the different genera, but all, I believe, possess the same elements, and are formed on the same principle.

I shall first describe those of the Diptera.

The antenna of the common Blow-fly (*Musca vomitoria*) is usually described as consisting of three joints, the terminal one being dilated and elongate, having a plumose *seta* or *bristle* on one side. There are many genera of *Diptera* which possess a similar antenna, and it is on this third dilated joint that the structures about to be described are found. When the antenna is not so constructed, although many of the joints present similar appearances, yet I believe they will not be found on the first and second joints, but almost invariably, if not always, to commence on the third, as may be seen in the accompanying figures.

First, of the Blow-fly (*Musca vomitoria*) (Tab. XXIX. fig. 1). Over the whole surface of the elongated third joint may be noticed at first sight, a multitude of transparent dots, apparently vesicles, but on closer examination and in profile, they will be found to be level with, if not rather below the general surface (fig. 1, b 1). These dots after a careful investigation prove to be perforations of the inner coat of the wall of the antenna, closed in externally by a very thin membrane, which can be seen, when the antenna is crushed, on the lines of fracture.

Behind this closed perforation is a sac, rather larger than the perforation itself, which, when the antenna is broken up, may be found floating about in the balsam (fig. 1, d 1). The diameter of these perforations of the inner wall of the antenna is about $\frac{1}{5000}$ inch. They are placed very close together. The area on each half of the antenna covered by these structures, has a surface-measurement of $\frac{1}{90}$ inch by $\frac{1}{30}$ inch, and as each square of $\frac{1}{90}$ inch has within it 3025 (that is, a square having 55 on each of its sides), the total number embraced within the space occupied by them will be about 9075; and the total for both sides will therefore be about 18,150. But it will be proper to deduct from this number about 1000 for the space occupied by the apertures (presently to be described), and some possible irregularities in the disposition of these organs; we may therefore assign 17,000 for the whole surface of each antenna.

But besides this multitude of peculiar structures, there are numerous apertures leading into cavities, which may be either simple or composed of one to five chambers, all communicating with the common aperture. These apertures are protected slightly by hairs which arise from the edges, and also a little way within them (fig. 1, b 2, c, d 2). There are about eighty of these cavities on one side of the antenna, and probably about the same number on the other; their diameter varies from $\frac{1}{3000}$ to $\frac{1}{1420}$ inch. The largest sacculated chamber is about $\frac{1}{660}$ inch. By focusing down to the floor of this cavity, papillæ may be seen, each in the centre of an hexagonal area. On viewing these structures in profile, as at fig. 1, d, there may be seen beyond, and adherent on all sides to their walls, a firm granulated mass of considerable thickness, and which appears to be tubulated nearest the walls of the sac. This latter investigation is attended with some difficulty, and requires much care, but I think I am not far wrong in stating that the hexagonal areas correspond to the tubes which extend inwards from the walls of the chambers. This is shown at fig. 2, d 2.

In *Helophilus pendulus* (Tab. XXIX. fig. 2), the smaller organs first described are not so numerous as in *Musca vomitoria*, while the cavities are more frequent, though less chambered. Hairs also arise from the interior of the cavity, as is shown at fig. 2, d 2.

In many antennæ of this shape, there are one or two openings very much larger than the rest, in the lower part opposite the origin of the seta; these are well shown in *Mesembryum meridianum*. They possess the same structure as the cavities before described. These cavities, and their chambers or sacculi, will, I think, be found to consist of the same elements as the smaller organs; the chambers being compounded of groups of these, and seeming to be formed by the infolding of the external surface, as is shown by the presence of hairs inside them.

The above structures I have found in all antennæ of this form, varying in relative numbers in the different genera.

Before I take leave of this form of antenna, I would throw out a suggestion with regard to its true structure. The seta or bristle (Tab. XXIX. figs. 1 & 2) is 3-jointed, the last one plumose or not, as the case may be. Now it seems to me that these are the last three joints of a 6-jointed antenna, the third joint of which is more or less dilated on one side, thereby throwing aside the last three. This I think will be seen to be the true explanation of the seta, when it is considered what peculiar and important structures are developed on the third joint, which is probably dilated for their reception.

In *Tabanus* (Tab. XXIX. fig. 3) the third joint is much dilated, but unequally, so that the four other joints, although continued in the general direction of the antenna, are on one side of the axis. On all the five joints from the third to the apex, organs are found exactly like the smaller closed perforations in the Blow-fly, their diameter varying from $\frac{1}{7000}$ to $\frac{1}{3000}$ inch. Between each is a tooth-like projection of the cuticle, like a hair. The largest are scanty, and chiefly found on the lower part of the third joint.

In *Bombylius* the antenna is 5-jointed, the third joint only possessing these closed perforations, and being much elongated and slightly dilated; the diameter of the pores varies from $\frac{1}{8700}$ to $\frac{1}{3300}$ inch.

In *Hippobosca equina*, the antenna is 5-jointed; the third, fourth and fifth joints being devoted to the reception of the same structures. They are depressed beneath the general surface, in the form of a saucer, at the bottom of which is seen the thin membrane across

the perforation of the inner wall. The last joint is plumose, exactly resembling the third joint of the seta in *Musca*, *Mesembryum*, *Eristalis*, *Volucella*, and other similar forms.

In *Tipula* (Tab. XXIX. fig. 4) these organs (precisely like those in *Hippobosca*, *Bombylius*, &c.) are to be found on the third joint of the antenna, which is more elongated and dilated than the rest, as is seen in fig. 4, a. Their diameter is $\frac{1}{2400}$ inch.

In *Ctenophora* the third joint is much more dilated, as at fig. 4, b, c. In *Ctenophora* bimaculata (fig. 4, c) this dilatation is well marked on one side, and on this part these organs are readily observed, and the nerve distinctly seen to proceed to them, as in fig. 4, e 1.

In *Bibio Marci* the antenna is composed of nine joints; the first two are free from any of the above appearances; but the last seven all possess them on one side, and a nerve can be traced distinctly to them. But the most remarkable condition of this antenna is, that from the third to the eighth inclusive, on the outer aspect of each joint is a cavity of considerable size, similar to those described in *Mesembryum*, the appearance of the floor being the same. The aperture leading to this cavity is about $\frac{1}{370}$ inch diameter, and around its wall is a layer, apparently of tubuli, as around the chambered cavity of the Blow-fly, and to each of these a nerve can be very plainly seen to be given off from the antennal nerve as it passes by them.

In this insect the advantages of the use of chlorine are strongly shown, the whole of it being of a jet-black, which in a day or two becomes quite colourless.

The antenna of *Asilus cristatus* is very like that of *Bombylius* in shape and arrangement; the organs are, however, larger and more scanty.

The club-shaped antenna of the Butterfly approaches that of the Blow-fly very closely, in possessing both the small transparent dots as well as the chambered cavities. I have figured the antenna of Argynnis paphia (Tab. XXIX. fig. 5). Both the above structures extend nearly to the base of the antenna, but more sparingly towards the lower end. The small organs are surrounded by various cuticular markings, and vary from $\frac{1}{5000}$ to $\frac{1}{3000}$ inch (fig. 5, b 1). The openings into the chambers are in diameter from $\frac{1}{2300}$ to $\frac{1}{1500}$ inch (fig. 5, b 2, 2). The chambers of the cavity vary from two to six; in the centre of their base is a projection or papilla, and the floor viewed from above presents the same appearances as in the Blow-fly.

I may remark that the small organs can be in no way mistaken for the roots of the scales, their form being very dissimilar.

I have not carried out the examination in the antennæ of Moths, but have found these small organs in the dilated extremity of the divisions of the antenna of the Drinker Moth.

In the Hymenopterous group we find these organs very extensively spread over the antenna, the external form varying somewhat in aspect; that of the Hive-bee (*Apis mellifica*) being a beautiful illustration, showing as it does the structure on a larger scale than any I have as yet described; and as the antenna is very free from cuticular markings, the nerve is very distinctly seen to give off a branch to the groups, which in this insect only occupy one side of the antenna (Tab. XXX. fig. 6).

. Each structure consists (viewed from above) of round transparent spots, about $\frac{1}{1760}$ inch diameter, but on a side view they are seen to be depressions of the surface, the internal wall being perforated, with a very thin membrane closing in the perforation, which is

probably the external layer of the antennal wall continued over it; and this is perhaps' the condition in every variety of these structures (fig. 6, a 2).

In fig. 7 is represented the antenna of *Eucera longicornis*; the whole surface is occupied by a number of saucer-like depressions, which are arranged so close that they touch each other on all sides. In the centre of these is clearly seen the tubular perforation of the internal wall, closed in by the very thin membrane. The diameter of the perforation is about $\frac{1}{1700}$ inch; the whole saucer-like depression is $\frac{1}{1120}$ inch. If a fracture be made in the antenna, the above thin membrane will become detached and float about in the balsam. Beneath the perforation will be found, by very careful examination, a membranous sac (fig. 7, c). These sacs touch each other all round, the whole forming a thick layer on the internal surface of the wall of the antenna. The number of these structures in this insect is about 2000 for each of the ten joints furnished with them; the total will therefore be about 20,000.

In fig. 8 is shown the antenna of another Hymenopterous insect (Andrena fulva). It has the same construction as the last-mentioned, except that there are hairs between the saucer-like depressions; and each hair as well as the depressions being surrounded by a ring of very minute tubercles, the whole has a pretty appearance.

In the Ichneumons which I have examined, I find the appearance different, though the real structure is not so. The perforation remains the same, but the thin transparent membrane closing it in, is elevated above the general surface, and extends lengthwise beyond the perforation, while it is generally not so wide. The shape of this membrane is not unlike that of an inverted canoe, and a keel-like ridge extending longitudinally through its centre adds to the similitude. The perforation beneath it is oval. I have endeavoured to show this at fig. 9, a, b, c.

The extreme length of the external arched membrane I have found in one specimen to be $\frac{1}{640}$ inch; the longest diameter of the subjacent perforation is $\frac{1}{1360}$, the shortest $\frac{1}{2100}$ inch.

The antenna of *Vespa vulgaris* and of *V. crabro* is arranged on the same principle, but the organs are more numerous and not quite so regularly disposed. They are well shown in the pupa state.

In Nomada the appearance is much the same as in Apis mellifica.

But the most beautiful of all the structures I have as yet met with is that presented in the antenna of *Libellula depressa* (Tab. XXX. fig. 10). This antenna has six joints. The third, fourth and fifth have on one side the following organs. 1st, a simple, nearly round sac, formed in the internal membrane and projecting inwards; the external opening being closed in by the delicate thin membrane, as noticed in the other insects (fig. 10, a & b 2). 2nd, a sac as above, but opening inwardly into another convoluted membranous sac, which is shown at fig. 10, b 1. These are more simple towards the upper joints; and in some of the simpler sacs there seems to be a small cavity at the back. Whether there be any membrane separating the outer and inner sac, it is difficult to say; but I fancy there is no separation of the kind.

The nerve may be distinctly seen to pass to these structures, and as the cuticle has scarcely any marking, the whole is plainly visible, and forms a very interesting object.

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The diameter of the simple sacs is about $\frac{1}{2000}$ inch, that of the largest from $\frac{1}{2000}$ to $\frac{1}{1500}$ inch; the length of the longest sac $\frac{1}{640}$ inch.

In the Grasshoppers (*Tetrix*) (Tab. XXX. fig. 11) I find a structure very similar to that of the simple sacs of *Libellula*, and formed in the same manner; but there is a distinct papilla (of which there is some trace in *Libellula*) in the centre of the floor of the sac (probably where the nerve is connected with it), and from this papilla a small chain of minute bodies extends to the centre of the membrane which closes the aperture. This connexion is well seen in profile (fig. 11, c 1), and, when viewed from above, the point of contact with the external membrane is seen in the centre, as is indicated in fig. 11, B.

The diameter of those represented in fig. 15, is about $\frac{1}{1200}$ inch. There are about twenty-two joints in this antenna, the lower of which possess about twelve sacs; the number increases towards the apex, till about from the fourteenth to the last there are 100 on each, so that we may estimate the total number on each antenna to be at least 1000.

In *Gryllus*, *Gryllotalpa*, and *Blatta*, I have found these structures in each joint of the filiform antenna, generally from two to four in number, and commonly occupying the same position and aspect of the joint. I have drawn those of *Gryllus domesticus* at Tab. XXX. fig. 12.

In the Coleoptera, so far as I have examined, similar organs are to be met with.

In the attenuated antenna of the Longicorns, they are placed near the upper end of each joint, where they form groups of eight to ten, one group on each side.

In *Silpha clavicornis* they are scattered mostly on one side of the thickened joints, the membrane by which the aperture is closed projecting hemispherically.

In *Melolontha vulgaris* the whole surface of the lamella is thickly covered by organs which are apparently of similar structure; these are figured in Tab. XXX. fig. 12. They consist of an irregularly-round cup-like depression, the centre of which rises up nearly to the external surface of the antenna. From this projection a tube runs inwards quite through the internal layer of the wall of the antenna, while the external end which forms the central projection is closed by a delicate membrane.

The diameter of the cup is about $\frac{1}{1100}$, while that of the central projection is $\frac{1}{2700}$ inch. The external layer of the cuticle is marked by hexagonal lines so disposed that each of the cups occupies one of the areas considerably enlarged.

The nerve entering the antenna is large, and at the base of each lamella sends into it a branch, which dividing into four or five smaller branches, spreads out over the whole internal surface.

The number of these organs on each antenna is as follows. The area of one side of each lamella is about $\frac{1}{11}$ inch by $\frac{1}{44}$ inch; each square of $\frac{1}{44}$ inch has on each side 45 of these structures; the square would therefore hold 2025. As there are four of these areas in the entire side of the lamella, the number would be 8180. The sum for both sides will be 16,360, and as there are seven lamellæ on each antenna, the total number of these organs on the whole antenna will be 114,520. A deduction of 2000 or 3000 may be made for irregularities, difference of size, &c.; still, making the most liberal deduction, we may say there are at least 100,000 on each antenna.

As in some of the *Diptera* and *Lepidoptera*, so in this species, the antenna has cavities in which we can detect from three to ten organs similar to those on the outside.

With regard to the physiological relations of these organs, I think we may perceive in them a structure analogous to that of the reputed auditory organs at the base of the antennules in certain Crustacea; but whether the resemblance be sufficient to allow us to conclude that they have a similar function, it is perhaps premature to assume. Their essential parts seem to be, a cavity in the antenna-wall, filled with fluid, closed in from the outer air by a very delicate membrane, and to the back of which a nerve certainly proceeds. There seems to be some correspondence between the chain of minute bodies passing through the cavity in the Grasshoppers, and the otolithes in the Crustacea; but at present it is only in this tribe I have found such an arrangement, though subsequent observations may extend the number in which it exists. If these organs are connected with the auditory sense, the opinion, held by Carus, Straus-Dürckheim, Oken, Burmeister, and Rennie and Kirby, that the antennæ are organs of hearing, will not be without foundation. In considering the function of these structures, we must bear in mind that all the auditory organs hitherto discovered in the Invertebrata have been in aquatic animals, and consequently, when the elements of an auditory organ are found in an air-breathing animal, it will be necessary to consider the difference between the force with which sound is transmitted from water to water through a membrane, and through the same from air to water. If we assign an olfactory function to these organs, one difficulty presents itself, viz. that for the odorous particles to affect the nerve, they must reach it through a membrane and a stratum of fluid.

The careful anatomical examination of the antennæ in all the genera of Insects would be a work demanding much time and many labourers, but productive of a rich harvest. If the method of proceeding I have recommended be adopted, viz. the bleaching of the parts before they are placed in Canada balsam, I have no doubt many interesting varieties of these organs would be met with. The comparison of the habits of the insect with the structure of the antennal organs would afford a further confirmation of their nature. At the same time a comparison should be instituted between these organs and those I have before described in the base of the halteres and wings, especially with reference to their relation to the sense of smell.

I may add, that the magnifying powers required to show the structures in question best, are the $\frac{1}{4}$ th and $\frac{1}{8}$ th-inch objectives.

Note.—Since the reading of the above paper, I have seen (through the kindness of Mr. J. O. Westwood) a copy of the rare work of Erichson, "Dissertatio de Fabrica et Usu Antennarum in Insectis," 1847, in which he mentions the existence of "pores," which are shut by a thin membrane from the interior part of the antenna, and that their disposition varied in different insects; but their peculiar form in Ichneumons, Wasps, &c., also the sacs, cavities, and nerves proceeding to them, he has failed to notice.—J. B. H.

EXPLANATION OF THE PLATES.

(All the figures are magnified.)

TAB. XXIX.

- Fig. 1. Antenna of the Blowfly, Musca vomitoria:—a, antenna, showing both the smaller organs and the chambers; b 1, the smaller organs, having a diameter of ¹/₅₀₀₀ of an inch; b 2, the apertures to the chambers, having a diameter of ¹/₁₄₂₀ to ¹/₁₄₂₀ of an inch; c, aperture of chambers; c', ditto as seen focused lower down; d, section of wall of antenna, showing 1, the smaller organs, and 2, the chambers and their sacculi, the diameter of the largest being ¹/₆₆₀ of an inch.
- Fig. 2. Antenna of *Helophilus pendulus*:—*a*, antenna; *b* 1, the smaller organs, having a diameter of $\frac{1}{4700}$ of an inch; *c* 1, do. do.; *c* 2, apertures to chambers, diameter $\frac{1}{1500}$ of an inch; *c* 2^a, do. do. focused lower down; *c* 2^b, focused still lower; *d*, section showing the smaller organs at 1, and the chambers with their sacculi at 2.
- Fig. 3. Antenna of *Tabanus bovinus*:—a, antenna, with the third to the eighth joints furnished with the organs; b, enlarged view of the organs of various sizes.
- Fig. 4. a, Antenna of Tipula oleracea; b, antenna of Ctenophora ——?; c, antenna of Ctenophora bimaculata; d, section of organs; d, organs as seen from above, diameter ¹/₂₄₀₀ of an inch.
- Fig. 5. Antenna of Argynnis paphia :—a, antenna showing the position of the organs; b 1, small closed perforations of various sizes, the smallest $\frac{1}{5000}$, the largest $\frac{1}{3000}$ of an inch; b 2, openings to cavities, from $\frac{1}{2300}$ to $\frac{1}{1500}$ of an inch; c, last joint of the antenna, showing the openings to the cavities; d, section of chambered cavities, with a projection or papilla in the centre of each.

TAB. XXX.

- Fig. 6. *a*, Part of antenna of *Apis mellifica*; *a* 1, groups of organs; *a* 2, nerve giving off branches; *b*, view of organs, more highly magnified.
- Fig. 7. *a*, One joint of antenna of *Eucera longicornis*; *b*, saucer-shaped depressions, diameter from edge to edge $\frac{1}{1120}$ of an inch; *c*, section of wall of antenna, showing sacs or cells beneath; *c* 1, membrane closing in the openings in internal membrane, diameter $\frac{1}{17000}$ of an inch.
- Fig. 8. a, One joint of antenna of Andrena fulva; b 1, saucer-like depressions, with membrane in centre closing in the perforations; b 2, hairs; 1 and 2 are both surrounded by a ring of very minute tubercles; c, section of wall of antenna.
- Fig 9. a, One joint of antenna of a species of Ichneumon; b, section of wall of antenna, showing the transparent membrane overarching and extending beyond the perforation of the internal wall; c, enlarged view of organs; membrane as seen from above, very transparent, stretching over like an inverted canoe; the opening beneath is the perforation of the internal membrane.
- Fig. 10. a, Antenna of Libellula depressa, showing the 3rd to the 5th joints with organs placed on one side of the nerve; b, portion of wall of the 3rd joint; b 1, large sacs with plicated walls, closed externally by a delicate membrane; b 2, small simple sacs, also closed by membrane; b 3, nerve proceeding to sacs; c, sacs of 5th joint.

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- Fig. 11. *a*, Antenna of Tetrix —— ?, showing about 100 sacs to each joint; *b*, enlarged view of two organs from above; *b* 1, central spot where the connexion with papilla takes place; *c*, profile view of sacs, closed from the external air by a membrane, the centre of which is in connexion with the papilla by means of the delicate line *c* 1.
- Fig. 12. Antenna of *Melolontha vulgaris*:—*a*, enlarged view of surface from above; *b*, profile view of organs; *c*, a lamella showing the nerves. Diameter of cups about $\frac{1}{1100}$, of centre projection $\frac{1}{2700}$ of an inch.



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