XV. *On the Histology of the Scent-organs in the Genus* Hydroptila, *Dal.* By H. Eltringham, M.A., D.Sc., F.Z.S.

[Read November 5th, 1919.]

Plate XXII.

My friend Mr. Martin E. Mosely has made a discovery of the first importance, which should prove of the greatest interest to entomologists. In a paper read before this Society on October 15th (p. 393), he described the external features of certain organs in the heads of various species of the Trichopterid genus *Hydroptila*.

Mistrusting his own skill as a microtomist with a lack of faith which, judging from some of his excellent preparations, I regard as unfounded, he has done me the honour to hand over to me a supply of material for the investigation of the minute structure of these organs. Just as Science generally is indebted to him for his discovery, I am personally under an obligation to him for enabling me to carry out an examination of unusual interest and fascination.

Some time ago I described and illustrated the scent-organs in certain male Danaine butterflies (Trans. Ent. Soc., 1913, p. 399; 1914, p. 152).

It will be remembered that these included certain eversible brushes located in the extremity of the abdomen. These brushes were formed of hairs of varying structure set on the inner surface of an eversible membranous bag, so that when the latter was everted, doubtless by fluid pressure, the hairs projected from its now outer surface. In some cases the scent material was obtained from glands in the wings, whilst in others the brushes themselves exhibited a glandular structure.

We know from the work of Dr. F. A. Dixey and others that certain special scales on the wings of butterflies act as scent-organs. In all these cases the scent-scales, brushes, glands, etc., are of comparatively considerable size, and occur on insects which, even in the case of Lycaenids, are large compared with *Hydroptila*. These little creatures

are themselves no larger than the brush of a Danaine butterfly, yet, as Mr. Mosely has shown, they possess eversible brushes, scent-scales, expanding membranes and tubercles, of a high degree of complication. Moreover, the organs in question are not located in the abdominal extremity, but in the back of the head.

It is a most interesting case of what may be termed the independent development of practically homologous structures in insects of different orders, since, however nearly related the Lepidoptera and Trichoptera may be, it cannot be urged that these scent-organs in the two orders had a common origin.

On Descriptive Terms.

Before describing the organs it may be well to define the terms applied to some of the structural details.

It has been suggested to me on more than one occasion that the term *hair* should be confined to mammalian hairs, and that insect hairs should be known by some other word. I referred to this matter in a note to my paper on the Danaine scent-organs (*l.c.*), and I am still unable to see the necessity for any alteration in terms.

The Oxford Dictionary defines a hair as "One of the cylindrical filaments that grow from the skin or integument of *animals*, especially of most mammals . . . ; applied also to similar looking filamentous outgrowths from the bodies of insects and other invertebrates, *although* these are generally of different structure."

Similarly, we speak of the *scales* on the wings of Lepidoptera and on other insects, without in any way implying that they are of the same nature as the homonymous structures in fish.

There is a greater difficulty which would not be removed by the invention of another word for insect hairs, namely, that of deciding the precise point at which an insect hair becomes an insect scale. Under a low power a Trichopterous insect such as *Hydroptila* may be regarded as covered with hairs on wings and body, but on examination with a higher magnification it is seen that the structures in question would be better described as elongated scales. Furthermore, we have in insects certain growths known as scent-scales or *androconia*. It is an unsatisfactory term, but as its signification is generally understood we may

retain it for the present. Is this term to be applied to any modification of insect scales or hairs characteristic of the male insect, or is it to be confined to those structures that have a direct connection with glandular tissue of a sexual character? If the former, the word becomes almost too vague to be useful, if the latter, then the brush hairs in *Hestia* are androconia, whilst those in *D. chrysippus* are not, and so before we can use the term at all, we must have a knowledge of the histology and perhaps even of the embryology of the structures to which we refer.

It would seem, then, that if we aim at greater precision in terms we merely arrive at the position of a person who cannot describe a landscape because he has not measured the elevations to see whether they are hills or mountains, and fears to mention a wood till he has identified the species of trees it contains.

In describing the organs in these small Trichoptera I propose, then, to use the word hairs when referring to the long, fine bristles which form brushes similar in form to the brushes described in the *Danainae*. In several species there are structures which, though of varying form, resemble more or less closely the scent-scales already known to occur in many Lepidoptera. Though the word is unsatisfactory I shall refer to them as androconia, for the reason already stated.

Finally, there are the elongated scales or hairs found so plentifully on the wings and body. As the order is known as "hairy winged" as distinguished from "scale winged" we will call them the cuticle hairs.

The organs to be described are, of course, only found in the male sex.

Descriptive.

Hydroptila sparsa Curtis.

Four eversible tubercles arise from a membrane lying across the back of the head, such tissue forming the lightest possible protection for the brain situated immediately beneath it. Towards the upper and anterior edge of this membrane there is on its underside a layer of moderately large cells which may be merely hypodermal, but probably also have a glandular function. Arising from this membrane on its upper portion and on either side of the centre line is found a small tuft of very remarkable androconia

(Plate XXII, figs. 1 and 2). They are pyriform with long delicate stalks, and the outer expanded portion is clothed with filaments apparently similar to those in the scent-scales of certain Pierine butterflies. Apart from their shape and position they possess a feature which I have been unable to find in any other species examined. Each has beneath its socket a large, granular, heavily nucleated cell, distinguishable by its size and structure from the other cells of the layer in which it lies. There are some twelve of these androconia on each side of the centre line. There is no trace of hairs or brushes. Structures somewhat resembling the "brush bags" in other species are present, but without hairs. These are the four eversible tubercles already referred to. There are two of these on each side, and when fully expanded they extend to a considerable length, as may be seen on reference to Mr. Mosely's photographs. The material of these tubercles is an extremely delicate chitin, not of the same nature throughout its entire length, since the proximal portion takes a different stain from that of the remainder.

A section through the partly everted tubercle (fig. 3) shows a few scattered cells on the inner side. These are probably hypodermal cells which have been displaced in the process of preparation. The whole tissue of the tubercle when not fully extended is thrown into a multiplicity of interlocking folds. When retracted it is inverted and not merely collapsed, and this remark applies to those eversible tubercles in other species, which are lined with hairs and form brush bags. A similar inversion takes place in the brush bags of the Danaine butterflies, but it can there be accounted for by the presence of a muscle attached to the apex of the bag, and acting as a retractor when the fluid pressure is released. It is a remarkable fact that no such muscle can be found in any of the species of *Hydroptila*. This is not due to any fault of the preparation. Muscle tissue is amongst the easiest of all to recognise in insect sections, and in my preparations other tiny muscles inside the head are easily observable.

So far I am unable to account for the inversion of the retracted tubercle, unless it is to be explained by some complicated condition of a variable coefficient of elasticity in different parts of the membrane. The fact of its differential staining already alluded to does not help us, as this occurs only in the present species.

The lobes which cover the eversible tubercles when retracted are somewhat of the shape and appearance of half an almond shell, but much thickened towards the base. Owing to the peculiar angle of view in fig. 1 their shape is not well shown. On the outer surface of the lobes the chitin is perforated by a multiplicity of openings, and in ordinary preserved material some of these perforations emit cuticle hairs of considerable length, whose stalks are deeply embedded in the hypodermal epithelium within. This epithelium may possibly be glandular, since it presents an active appearance (fig. 5). Mr. Mosely informs me that the lobes in this and some other species are densely covered with these cuticle hairs when the specimen is in fresh condition, but that they become detached with great facility, so that the lobes, even in life, are often found practically naked. We may therefore assume that in fresh examples each perforation carries a cuticle hair. We may further venture to speculate as to whether when detached they may not conceivably act in a manner analogous to that of the "dust particles" which are so marked a feature in some of the butterflies already referred to, and of which the use has, since their discovery, been actually observed and recorded by Carpenter (Proc. Ent. Soc., 1914, p. cxi).

Plate XXII, fig. 1 shows the head of this species with the lobes turned back and the tubercles in a condition of partial eversion. Fig. 2 shows two of the androconia with their special cells. Fig. 3 a highly magnified view of one of the tubercles partly everted. Fig. 4 a section through one of the lobes. Fig. 5 part of the same more highly magnified to show the cells lining the outer cuticle. Fig. 6 a vertical longitudinal section through the head and one of the tubercles incompletely everted.

H. simulans Mosely.

Each lobe in this species may be said to resemble externally half an acorn. The basal portion is thick and well rounded, and shows the same perforate structure as in *H. sparsa*. The upper part is smooth and rounded and of a somewhat darker colour, whilst the apical part is thin, flat, and subtriangular. On its inner surface each lobe has a deep oval concavity forming a receptacle for the retracted brush. No sign of androconia has been detected in this species, but the surface of the concavity of the lobe

has a peculiar structure as though formed of minute chitinous plates, giving it somewhat the appearance of a tessellated pavement. The thicker basal portion of the lobe shows in section a lining of hypodermal cells probably of a glandular nature. Beneath the lobes and directed upwards and centrally are two brushes formed of a mass of golden yellow hairs arising from small sockets in the lining of a brush bag, the whole presenting an arrangement and appearance closely resembling that in many Danaine butterflies. A section through the head in the plane of the long axes of the two brushes is shown at fig. 8. From this it will be seen that the hairs arise over nearly the whole length of the bag, and hence when the latter is everted the appearance is somewhat that of a test-tube brush or pipe cleaner. The hairs are slightly thickened towards their distal extremities. In the substance of the bag are two distinct layers, the inner one being thin chitin thrown into a multiplicity of folds and bearing the sockets of the hairs. These sockets are of peculiar formation, and resemble the structures known to botanists as bracts. Outside this membranous layer is a glandular epithelium consisting of granulated and heavily nucleated cells shown in fig. 10.

The hairs themselves are not smooth, but have an elaborate structure which I have endeavoured to represent in fig. 9. There are whorls of laminate projections having irregularly curved distal margins. Also the projections are not continuous round the hair, but the rings are intercepted at irregular intervals by more or less vertical fissures. The elaborate structure of the minute brush hairs in this and other species is one of the most notable features of the scent-organs.

The general arrangement in *H. simulans* seems to be analogous to that in the butterflies *Trepsichrois mulciber* and *Hestia lynceus*, in which the brush hairs themselves are the direct vehicles of a secretion produced by glands at the bases of their sockets. Fig. 7 is a view of the head with the lobes closed.

H. forcipata Eaton.

In this species the lobes are very small as is the whole area of the scent-organs. Fig. 15 is a view of the posterior surface of the head with the lobes turned back. Here we

find a new modification in the fact that the lobes are provided on their inner surface with a membrane which can be distended, probably by fluid pressure. On this membrane are a few androconia of not quite circular section, having long stalks and a very deeply ribbed surface. The androconia are probably porous or very absorbent, as they stain rapidly and intensely. The outer surface of the lobe is covered with extremely minute black setae having widened bases, like rose thorns. A section through the lobe, fig. 19, shows that the extensible membrane contains at its base a mass of granular, heavily nucleated cells which doubtless furnish a volatile secretion. The androconia are not provided in this species with special cells at the bases of their sockets. Indeed, this is a condition I have found only in those of *H. sparsa*. Fig. 16 shows a highly magnified view of the inner face of one of the lobes. The lobe itself is seen to the left, whilst the membrane extends all over it and some distance to the right. The androconia lie on, and arise from, the membrane in an irregular fashion. The small bunch of hairs here shown does not in reality arise from the membrane of the lobe, but from that on the back of the head between and beneath the lobes, though in this dissection they have come away with the lobe itself. They take the form of a mere tuft of bristles, and though the membrane from which they arise may be slightly extensible there is no eversible bag. The hairs are of the complicated structure shown in fig. 17 and in transverse section at fig. 18. There is a very slight development of glandular epithelium at the origin of these hairs. They have a very thin cuticle, and in section show a very large lumen.

H. maclachlani Klap.

The structure in this species bears a close general resemblance to that in *H. forcipata*. The lobes are smaller and very inconspicuous, but their extensible membranes seem to be more highly developed. Fig. 23 shows a section through one of the lobes and the neighbouring structures. The membrane has a dense mass of glandular tissue at its base, and bears a number of androconia, one of which is represented at fig. 20. These are very deeply ribbed and circular in section. On one lobe I have mounted there are twenty-one, and on another eighteen. The little pencil of

hairs is as in *H. forcipata*, but the hairs themselves appear to be longitudinally striated and without the dentate structure found in that species.

H. femoralis Eaton.

In this species the lobes, while distinctive in shape, resemble somewhat those of *H. simulans*, their perforate portion thickly clothed with cuticle hairs and containing a layer of epithelial cells into which the stalks of these cuticle hairs project. Attached to the inner face of the lobe there are numerous heavily ribbed androconia, the stalks of which pass through the chitin and communicate with an epithelial layer beneath. These androconia stain very deeply, have an oval section, and a small central lumen. The lobes cover two large eversible brushes provided with black hairs, the latter being considerably expanded at their distal extremities.

The brush bag appears to have much less glandular development than in *H. simulans*. The hairs are quite characteristic in structure, being very thick walled and covered on the outer surface with whorls of regularly arranged projections. Figs. 22 and 24. In many of the transverse sections of these hairs there is a slight staining of the central lumen indicating the presence of some structureless material in that position, probably a coagulated secretion.

Fig. 25 shows a section through the entire head of this species. At the lower side of the figure may be seen the lobes with part of the cellular material they contain, and their perforate external surface. Within the inner boundary are a few of the androconia cut across and portions of the brushes cut obliquely. Fig. 21 is a view of the entire head with brushes partly everted.

H. occulta Eaton.

The organs in this species are more remarkable than in any of the others examined. The lobes are narrow and somewhat conical. They bear on the inner surface a membrane, which towards the upper extremity contains a deep tubular pocket lined with long androconia. This pocket forms in fact a miniature eversible brush bag and can be extended so as to form a small secondary brush, the androconia then radiating from its surface. Besides this structure there are a few small androconia near the apex of the inner

surface of the lobe, and arising from a point near the base is a third mass of androconia still more elongated than those already referred to. Sections of the lobe show that this second mass of androconia also lies in a small pocket and can presumably be everted. Both androconia pencils are surrounded by glandular tissue. Text fig. 2 shows a section through part of a lobe. At this plane the section shows chitin on the inner surface of the lobe. Apparently the eversible membrane as a whole only covers a part of the surface.

Lying beneath the lobes and arising from a membrane on

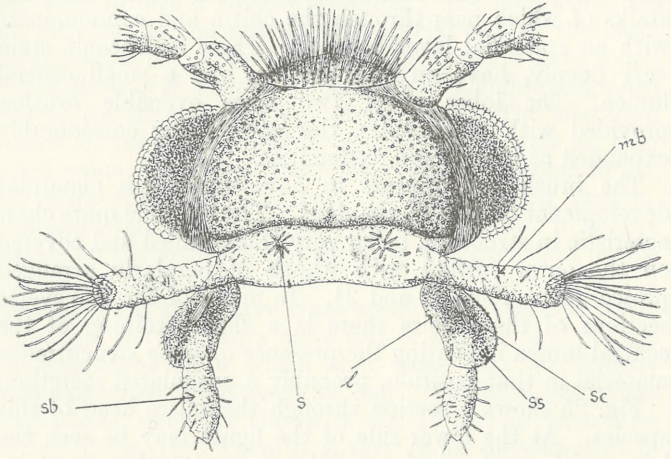


Fig. 1.—*Hydroptila occulta*. Head with scent-organs everted. *sb*. Secondary brush. *s*. Androconia. *l*. Lobe. *sc*. Patch of elongated androconia. *mb*. Main brush. *ss*. Small androconia. (Width across eyes ·64 mm.)

the back of the head are two small eversible brushes with yellow hairs resembling those in *H. simulans*, but their sockets are more concentrated towards the bottom of the bag. The hairs themselves appear to have a structure somewhat similar to that in *H. forcipata*. There are also two small tufts of androconia arising from the membrane between the main brushes and on either side of the centre line. The general arrangement of the head with expanded organs is shown in text fig. 1, herewith. Fig. 11 shows one of the brushes dissected out. Fig. 13 a view of the lobe, the secondary brush being in a retracted condition. Fig. 14 represents one of the androconia from the secondary brush.

It is hoped that in the course of time other species than those so far examined will be available. Mr. Mosely has in his collection two examples of *H. pulchricornis* Pict., but beyond the fact that this species has black brushes resembling those in *H. femoralis* he has not been able to examine them more critically. There are other British species and several not so far found in Britain, and doubtless many new forms still undiscovered. But few collectors are interested in these small and inconspicuous insects. Now that Mr. Mosely's discovery has revealed their curious

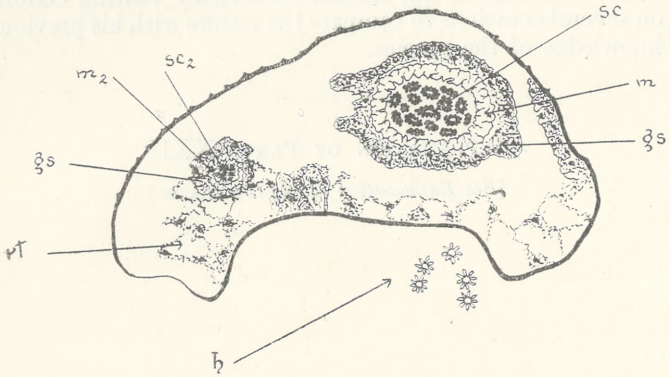


FIG. 2.—*Hydroptila occulta.* Section of lobe.

sc_2. Androconia of second tuft. m_2. Membrane of ditto. *rt.* Reticulated tissue. *sc.* Androconia of secondary brush. *m.* Membrane of ditto brush bag. *gs.* Glandular substance. *h.* Hairs of primary brush. (Length of section ·072 mm.)

and interesting features collectors will have a new incentive to secure examples.

In case this paper should be read by any one having facilities for securing further material, it should be noted that dry specimens are useless for observation. They should be dropped alive into a strong solution of bichloride of mercury in distilled water, to which has been added about half its bulk of 96 per cent. alcohol, and about 1 per cent. of acetic acid. After a few hours in this they should be transferred to clean 96 per cent. alcohol.

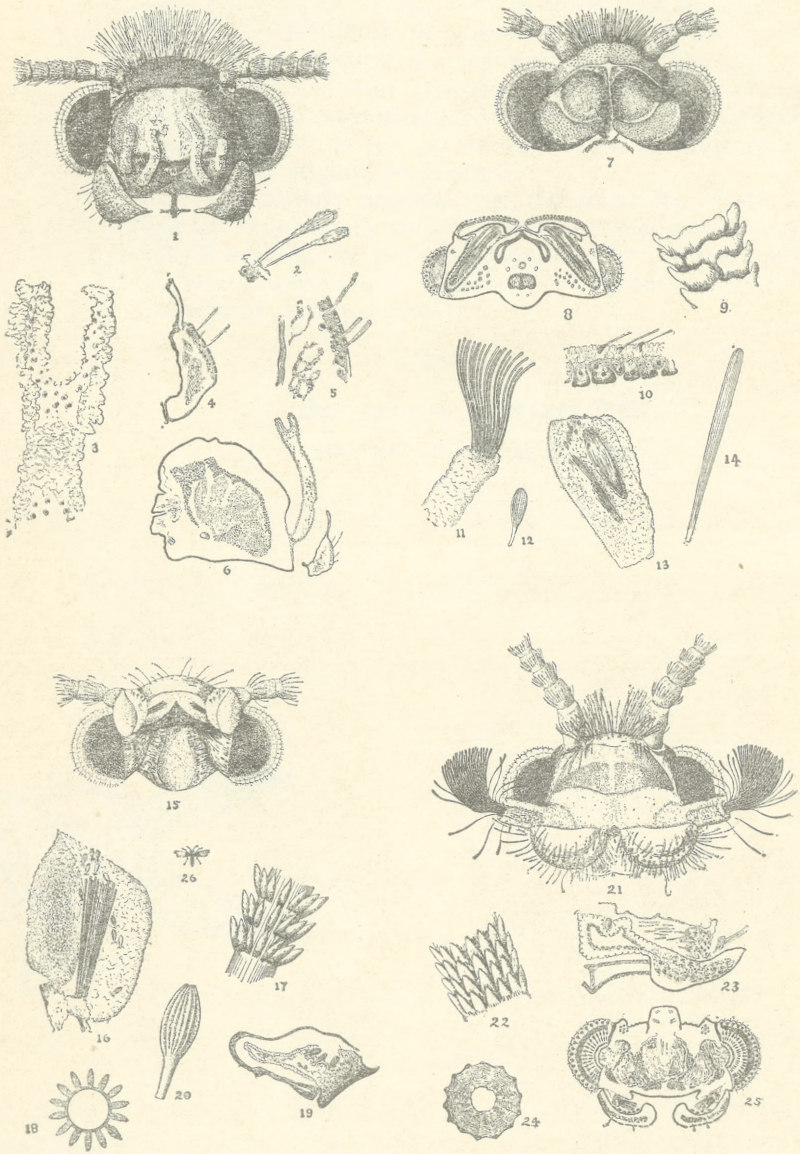
On the page facing the plate I have given the actual sizes of the various parts figured. A certain combination of objective and eyepiece may give a definite magnification, but when a figure has been drawn therefrom the size of the

figure may not really represent the true magnification, but a mere expansion of the view obtained with the objective used. A photograph of a section measuring two inches across may represent a magnification of a hundred diameters, but the same photograph projected on a six-foot screen is not a magnification of three thousand six hundred diameters, but merely an enlarged view of what can be seen in the original photograph.

I have already expressed my thanks to Mr. Mosely for having supplied the material for this investigation, and I would add that he has further assisted by visiting Oxford on several occasions to compare the results with his previous knowledge of the species.

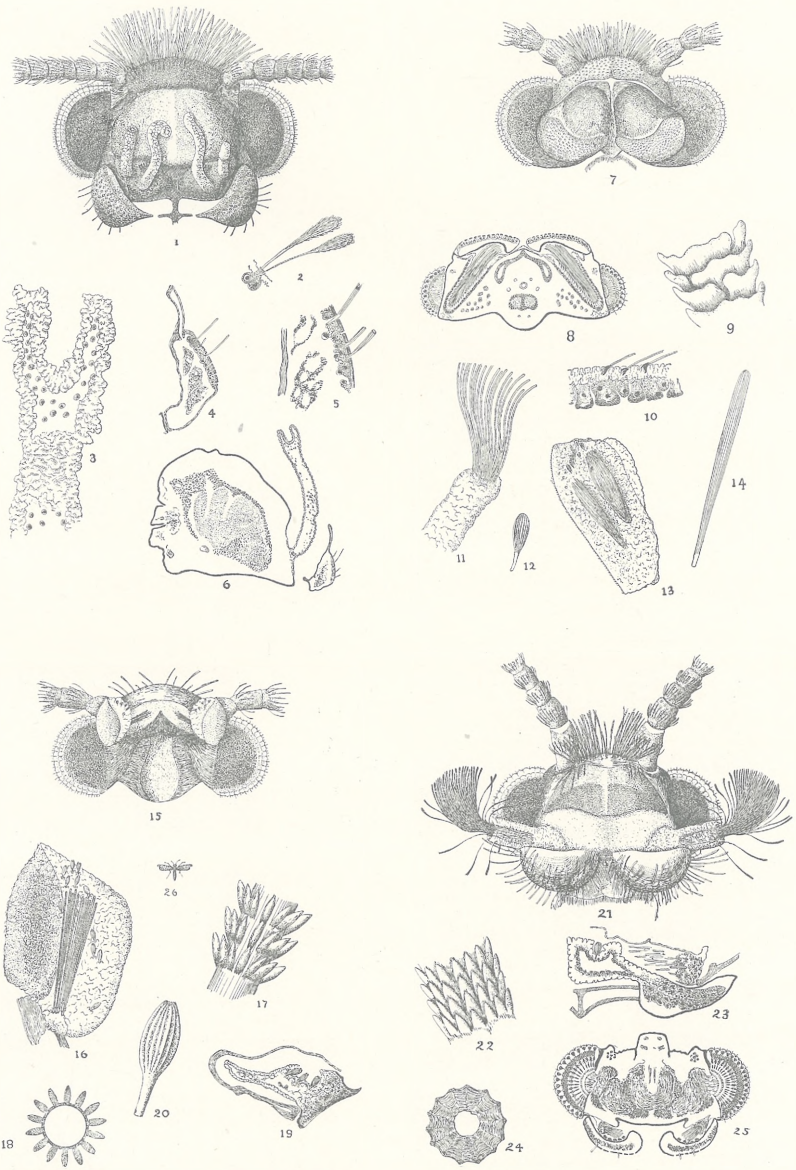
Explanation of Plate XXII.

[*See Explanation facing the* Plate.]



H. Eltringham del. *Half-Tone Eng. Co., Ltd.*

SCENT ORGANS IN *HYDROPTILA*.



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SCENT ORGANS IN *HYDROPTILA*.

Explanation of Plate XXII.

Fig. 1. *Hydroptila sparsa.* Head viewed from above showing four eversible tubercles partly expanded. Width across eyes ·6 mm.

2. Two of the androconia with their sockets and glands. Length from bottom of socket to apex of scale ·03 mm.

3. Enlarged view of one of the tubercles partly expanded. Width in narrowest part ·015 mm.

4. Section through one of the lobes. Length ·15 mm.

5. Part of ditto (not necessarily the same section) showing epithelium and parts of cuticle hairs. Greatest width ·03 mm.

6. Section through head showing one of the tubercles partly everted. Length of tubercle ·18 mm.

7. *Hydroptila simulans.* Head with lobes closed. Width across eyes ·77 mm.

8. Section through same in plane of brushes. Width across eyes ·6 mm.

9. Part of one of the brush hairs showing structure. Greatest width ·003 mm.

10. Enlarged view of brush bag showing hair sockets and epithelium. Greatest thickness ·015 mm.

11. *Hydroptila occulta.* Part of a brush. Length of hairs ·22 mm.

12. A small androconium from lobe of same. Length ·015 mm.

13. View of inner surface of lobe of same with secondary brush retracted, scent-scales, etc. Greatest length ·15 mm.

14. One of the scales of the secondary brush. Length ·06 mm.

15. *Hydroptila forcipata.* Back view of head with expanded lobe membranes and hair tufts. Width across eyes ·58 mm.

16. One of the lobes viewed from inner side. Length ·176 mm.

17. Part of one of the hairs. Diameter of main stalk ·003 mm.

18. Transverse section of same. Diameter over projections ·005 mm.

19. Section through one of the lobes showing gland cells at base. Length from end of membrane to upper corner of lobe ·09 mm.

Explanation of Plate.

FIG. 20. *Hydroptila maclachlani.* A scent-scale from lobe. Length ·015 mm.

21. *Hydroptila femoralis.* Head with brushes partly expanded. Width across eyes ·473 mm.

22. Part of a brush hair. Width across points ·003 mm.

23. *Hydroptila maclachlani.* Section through lobe, etc., showing glandular base. Length from point of membrane to point of lobe ·105 mm.

24. *Hydroptila femoralis.* Transverse section of hair. Diameter ·0015 mm. to ·0037 mm.

25. Section through head. Width across eyes ·55 mm.

26. Diagrammatic figure representing about the natural size of *H. femoralis.*