# STUDIES IN RELATION TO MALARIA.

## II.

### THE STRUCTURE AND BIOLOGY OF ANOPHELES

(*Anopheles maculipennis*).

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(*Continued from page* 276.)

BEFORE proceeding to describe the imago of *Anopheles*, we wish to record some observations regarding the hibernation of the larvae of various Culicidae. Grassi (1900, p. 47)[1] considered that *A. bifurcatus* hibernated chiefly in the larval form, for he found the larvae of this species in midwinter in Southern and Central Italy, the imagines being rarely encountered. It was quite different with *A. maculipennis*. In this case the imagines congregated in houses, huts, caverns, etc., whereas no larvae could be found during the winter. Though he assumed that it was so, his finding the larvae in midwinter in the first instance did not prove that they hibernated, for they might well have been derived from late-laid eggs. Ficalbi (1901, p. 66) says he has only seen the larvae of *A. bifurcatus* hibernate in Italy, but that during the past winter, which set in late, *A. maculipennis* was found later than usual

[1] See Bibliography, p. 75, this *Journal*, as also at the end of this paper.

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along the Adriatic slopes. He thinks the larvae of this species may possibly live through the winter in warm countries like Sicily.

Of the larvae collected in various parts of England in the summer of 1900, only three lots hibernated in the laboratory. Whereas with the advance of winter all the larvae of *A. maculipennis* died off, those of *A. bifurcatus*, which were by no means as numerous, remained alive. One of us reported this observation in a preliminary note in June. As *A. bifurcatus* has likewise been proved to transmit the malarial parasite, it seems in place to make a note regarding its biology, especially as we have found that it may live for *seven to eight months* in the larval stage.

*Observations on the Hibernation of A. bifurcatus larvae.*

I. Larvae caught 12 Aug., 1900, at Gainsborough. Some lived until 12 April, 1901, *i.e.* eight months. The larvae were kept in tanks in a room which was used. None of the larvae pupated.

II. Larvae caught 10 Sept., 1900, on the river Ure. A number died during the winter. The first pupae appeared on 12 April, 1901, the imago appearing four days later. These larvae had lived seven months and eight days in the laboratory. Two others subsequently underwent successful metamorphosis.

III. Larvae caught 14 Sept., 1900, near Garstang. Of these one survived, pupating 19 March, 1901, the imago appearing eleven days later. In this case the larval stage had lasted seven months.

These observations prove conclusively that the larvae of this species are able to hibernate. Whether those of *A. maculipennis* are capable of hibernating or not cannot be positively stated, although it would appear unlikely judging from our observations and those of Grassi.

That the larvae of other species of Culicidae are capable of resisting a considerable degree of cold is proved by a number of independent observers. Gorham (15 Jan., 1901, p. 330) in the United States writes, "though ice of considerable thickness had formed above them, and they could breathe only the air collected beneath," larvae were found living in natural waters in December, 1900. Gorham does not state whether the larvae were those of *Culex* or *Anopheles.* Wright (13 April, 1901) states that he found *Anopheles* larvae (species not stated) hibernating beneath the ice at Torphins in Scotland. Annett and Dutton (27 April, 1901) in a preliminary note, state that *Anopheles* larvae (again species not stated) collected at Wye in December, had lived through the winter, but had not undergone metamorphosis when they published. Brakeley and Smith (June, 1901, cited by Howard, pp. 7 and 83—90)

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of New Jersey, U.S., have made the interesting observation that the larvae of *Culex pungens* may hibernate in the water which is contained in the tubular leaves of *Sarracenia*. The larvae were found in January within the solid ice which was contained in the leaves, the temperature for some time having been 2 to 2·5° F. below zero (– 19 to 20° C.). The larvae could be seen lying curled up in the ice. When the ice was thawed the larvae became active and fed, and on being transported to a room they slowly grew in size, the imago appearing in March. Smith suggests that the swarms of mosquitoes observable in Alaska and other northern countries may perhaps hibernate as larvae, maturing rapidly with the melting of the ice. The suggestion seems very reasonable.

Galli-Valerio and Narbel (27 June, 1901) have found the larvae of *Anopheles bifurcatus* in the vicinity of Lausanne in Switzerland, hibernating beneath the ice in January, February and March. The larvae which they collected, were placed in tubes, and the first imago was seen to appear in the end of March. The mean temperatures (Centigrade) during the three months were as follows:

| | | | | | | |
|---|---|---|---|---|---|---|
| January: | Mean | – 0·5° | Minimum | – 12·8° | Maximum | 7·1° |
| February: | „ | – 2·84° | „ | – 14·6° | „ | 1·4° |
| March: | „ | – 2·73° | „ | – 6·7° | „ | 5·2°. |

These observations regarding the resistance of culicid larvae to frost possess a considerable degree of interest: it is however essential that the species should be accurately determined in each case if the observation is to possess scientific value.

### *Observations on "stranded" Pupae.*

When pupae are placed in shallow water or wriggle to the side of a saucer containing little water, they lie on one side breathing through but one respiratory trumpet. Five pupae of *A. maculipennis* were removed from the tanks within 3 to 48 hours of the time when they had issued from the larval skin, the pupae being carefully placed upon moistened filter-paper by means of a pipette and within test-tubes loosely plugged with cotton. All of these insects underwent successful metamorphosis within 48 to 72 hours, the temperature ranging between 20 and 23° C. Whenever the tubes containing the pupae were handled, the insects wriggled about vigorously, at times making a "long jump" to a distance of 1 to 2 cm. over the surface of the paper. Pupae of

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various ages were next placed on dry filter-paper within tubes, but it was found that the majority shrivelled up and died. A few made unsuccessful efforts at extricating themselves, only succeeding in protruding the thorax; one fly extricated itself from the pupal-skin, but lost a leg in the operation, but in this case a little water had been allowed to flow on the filter-paper before the fly began to appear. It is evident then that the pupa cannot resist desiccation except to a moderate degree, metamorphosis not being impeded however by their simply being stranded on a moist surface. Experiments made with the pupae of *Culex pipiens* gave similar results.

*Conditions which hasten Pupation and the Appearance of the Imago.*

Howard (1901, p. 12) observed that when he placed creosote-oil on the water in breeding-jars containing *Culex stimulans* and *C. perturbans* larvae which were nearly full grown, their metamorphosis into pupae was hastened. The larvae struggled violently when the creosote was added, and, as they were about to transform, "the violent struggling evidently assisted in the breaking of the larval skin, leaving the pupa bare." Still more interesting was the observation that the pupal stage only lasted 15 hours instead of 48 hours. One of us was very much struck (26 July, 1901) by the effect of a showery afternoon on mature *Culex* larvae in a water-butt. The weather had been relatively dry for a couple of days before the downpour. After the rain had ceased a vast number of larvae were found to have become converted into pupae. The hastened metamorphosis was doubtless caused through the disturbance of the surface of the water.

*The Emergence of the Perfect Fly.*

When transformation is about to take place the pupa remains quietly at the surface of the water. Fine streaks due to the contained air appear upon the dorsum, extending antero-posteriorly between the respiratory trumpets, anteriorly as far as the base of the head. The air at first only extends a short distance posteriorly to the trumpets, but it gradually accumulates along the dorsal surface until it reaches to about the anterior margin of the seventh abdominal segment. Suddenly the pupa, which has become more buoyant, alters its position by extending its abdomen so that it comes to float parallel to the surface of the water, immediately beneath the surface-film to which it becomes attached. This usually lasts two minutes. Usually a minute later the dorsal

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surface of the thorax protrudes through the dorsal slit in the pupa-skin and projects above the water. The insect's body seems to "grow" without visible effort out of the pupal covering, although a forward bend in the abdomen, near the thorax, indicates that the insect pushes itself out by pressing the abdomen against the pupa-skin. As the abdomen is protruded, the abdominal portion of the pupa-skin gradually fills with air. The head is pulled backward and then upward, and with the mouth-parts, palps and antennae, is then gradually pushed upward and forward, the appendages of the head remaining at first bent backward beneath the body of the insect. The base of the wings and the abdomen are gradually extruded, the wings are soon freed and immediately straighten out and harden. All this time the legs are still retained by their soft, folded ends which lie within the pupal covering, which also contains the posterior extremity of the abdomen. The insect now projects far beyond the anterior extremity of the pupa-skin, like the exaggerated figure-head of a vessel. If it were not for the air-filled pupa-skin which lies extended posteriorly, and is fixed to the surface-film, the fly would certainly fall forward into the water, for, taking the anterior extremity of the pupa-skin as the centre, the insect's head projects about as far anteriorly over the water as the pupal tail-flaps do posteriorly beneath the surface-film. We see in this straightening and filling of the abdominal portion of the pupa-skin with air, a very wise adaptation against the possible disaster of the tipping over of the fly into the water whilst issuing. We are not aware that the process has hitherto been closely watched or described. At this stage, then, the bunched legs all project backward and downward in a straight line until they enter the pupal covering. The front legs are first freed, the femoro-tibial articulation projecting forward and upward after the manner of a bent knee, the tarsal extremities still remaining in the pupa-skin. The posterior pairs of legs next bend backward and upward at the femoro-tibial joint. The tarsal extremities of the anterior legs are now withdrawn and all the tarsal joints rest flat upon the surface of the water. The appendages of the head now quickly assume their normal position. With the posterior extremity of the abdomen resting against the posterior margin of the slit in the pupa-skin, the fly now pulls the tarsal extremities of the posterior pair of legs forward, whereby the tibio-tarsal articulation is bent forward. The pupa-skin has now become quite filled with air. The abdomen is quite free, the tarsal joints of the second and third pair of legs are now withdrawn in rapid succession by short jerky pulls and the insect rests upon the surface



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of the water, or partly upon the surrounding vegetation, or proceeds immediately to climb up the walls of the vessel in which it is contained. As stated above the insect seems to "grow" out of the pupa-skin, there being no visible effort until shortly after the wings have straightened, when a slightly forward and backward rocking of the body may be observed, followed subsequently by jerky movements when the extremities of the legs become freed. The straightening of the abdomen naturally facilitates its withdrawal. It is difficult to understand the mechanism whereby the insect leaves the pupa-skin unless it be by the pushing of the abdomen, but it is reasonable to suppose that the entrance of air into the pupa-skin plays no unimportant part in helping the insect to free itself.

In one case, the imago was seen to leave the pupa-skin in an exceptional manner, the pupa having floated into the corner of the rectangular aquarium. As the pupa straightened, its body was drawn by capillary attraction into contact with the walls of the vessel, so that it assumed a vertical position, which it maintained throughout the process of extrusion. As the pupa-skin filled with air, it was drawn more closely against the walls of the vessel, and the imago issued protruding backward over the surface of the water. As soon as its legs were freed it clambered up the sides of the aquarium.

If we study the empty pupa-skin we find it exceedingly buoyant, it being almost impossible to force it beneath the surface, owing to its containing air and offering a large surface for attachment to the surface-film. The dorsal slit, through which the insect issued, runs antero-posteriorly and is seen to be gaping, fusiform, and wider anteriorly at a point corresponding to that through which the bulk of the insect passed. The slit extends from a point corresponding to the anterior central margin of the imago's thorax, to a point corresponding to about the two hairs situated posteriorly to the respiratory trumpets as shown in Fig. 10, Plate II. Apparently the chitinous sack is in a state of tension just prior to the exit of the fly, so that the slightest exertion on the part of the insect causes the rupture of the pupa-skin, the slit widening of itself.

Wishing to preserve specimens of the insects in various stages of metamorphosis, we observed that they made violent efforts to extricate themselves when disturbed even during the first stage, when only the dorsal surface of the thorax protruded. Thus it was that some of them succeeded in a few moments in freeing themselves in a manner that otherwise took some minutes. It is essential that the surface of the

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water shall not be disturbed whilst the fly issues from the pupa-skin, as even the slightest disturbance may be fatal. If the fly falls upon its back the dorsal surfaces of the wings adhere to the water and the insect is usually incapable of freeing itself. This exit of the fly is a very critical period in its life-history, and a number fail to free themselves. Reckoned from the moment when the thorax appeared, the fly usually freed itself completely, if left undisturbed, within 5 to 10 minutes. We cannot agree with some authors who state that the whole process takes but a few moments. A number of insects perish in the act of issuing from the pupa-skin: some die in the first stage, the head not being freed; and they may die, being unable to free themselves, at any stage following. Sometimes they make vain efforts to escape, only the tarsal extremities which remain within the skin keeping them back. We have seen them tear themselves loose at times, the violence of the effort resulting in the loss of one, two, or even, once, in the loss of three legs, which remained attached within the pupa-skin.

When the fly is left undisturbed, it remains resting until its limbs and wings have sufficiently hardened for it to fly and walk about with ease. It may take flight directly from the pupa-skin, or crawl to a safe place, where it remains quietly until the chitin hardens. The young imago is pale in colour, the thorax being pinkish-brown, the abdomen generally translucent and green, the legs pale brown, the wings only faintly showing the characteristic spots on their dorsal surface. The abdomen is at first very long: it may project 1 mm. beyond the wing-tips. Almost immediately after the insect has issued the abdomen begins to retract, this being accompanied by the expulsion of five or more very minute clear glistening greenish drops from the anus. The abdomen usually contracts to its normal size within about 5 minutes. When disturbed, the young insects were seen to fly perfectly in from 5 to 10 minutes after they issued. It was difficult to get them to fly sooner: if disturbed, they only moved away by means of their legs, or made unsuccessful efforts to fly, which ended in their falling into the water. The young imago begins to darken almost immediately, so that its colour changes within a few minutes. After 2 hours or more they acquire their normal coloration. It is difficult to say when complete hardening of the parts takes place. One insect was observed to rest in the characteristic position with the tips of the hind legs turned upward, 20 minutes after it had undergone metamorphosis. It was noticed that when the wings of the newly-hatched imago were cut off these did not become darkened.



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It was repeatedly noticed that if anything prevented the insect from properly extending its limbs during metamorphosis or immediately after it had issued from the pupa-skin, the parts hardened and remained distorted throughout life.

## Anatomy of the Imago of *Anopheles maculipennis* Meigen.

### External Structures.

### I. The Head.

The head of both sexes of *Anopheles* is shaped like a circular cushion, slightly flattened on its posterior surface, from the centre of which a membranous neck arises which unites it to the thorax. The surface of the head consists largely of two enormous, somewhat kidney-shaped eyes. These consist of several hundred ommatidia with their corresponding cuticular lenses very regularly arranged, with a beautiful greenish-black hue like so many emeralds set on a black ground. Dorsally the two eyes are almost in contact but are separated by a narrow area bearing a number of small grayish-black hairs which are directed forward and upward like a cock's comb. Ventrally the eyes are all but continuous, being separated only by a fine line (Fig. 16, Pl. IX.). In a transverse section passing near the posterior border of the eye the head seems to be almost completely surrounded by ommatidia and lenses. The posterior border of the eye is almost straight, but bends forward above to leave a triangular space, the vertex, which is gray in colour and bears numerous hairs and scales. The hairs are simple, black in colour, and a row of them is borne parallel to the posterior border of the eye and bending forward and overhanging the eye. These black hairs are also numerous at the sides of the head, but on the vertex they are replaced by certain flattened white scales, spatulate in shape. These latter, like the hairs, bend forward and overhang the head, giving the appearance of a rather ruffled, untidy head of hair. The anterior limits of the eyes are so shaped that they leave a triangular area on the front face of the head, one angle of which is ventral and two are latero-dorsal. From the former arises the clypeus overhanging the proboscis and from each of the latter an antenna.

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*Appendages of the Head.*

In describing the appendages of the head we have adopted the nomenclature of Dimmock (1881). The appendages are as follows:—

1. A pair of antennae or feelers, markedly different in the male and female.

2. A pair of mandibles, absent in the male. These are the cultelli of some anatomists.

3. A pair of 1st maxillae each bearing a jointed palp. These are the scapella of some anatomists.

4. A pair of 2nd maxillae. These have fused together to form a median piece called the labium. They have no palp.

Besides these paired appendages there are three unpaired appendages connected with the mouth, (i) the median anterior labrum, with which according to Dimmock is united (ii) the epipharynx, and lastly (iii) the hypopharynx or tongue, a median style arising behind the mouth. In the following description we use the word proboscis to include the whole of the mouth-parts, viz. the mandibles, the 1st maxillae, the 2nd maxillae or labium, and the unpaired processes, the labrum, the epipharynx and the hypopharynx, with the exception of the maxillary palps, which take no part in biting. All these structures enter the skin except the labium, which acts as a sheath and guide to the other parts.

The antennae of the female *Anopheles maculipennis* consist of fifteen segments, the first two of which differ markedly from the succeeding ones. The first is an extremely short segment, just a ring of chitin (Fig. 13, Pl. IX.). The second segment is a flattened sphere in shape, attached at one side to the head and on the opposite side deeply pitted. From the centre of this pit the third segment takes its origin. The large swollen second segment lodges a special and highly remarkable auditory ganglion which will be described in connection with the brain. From it a nerve arises which traverses the antennae.

The third segment is markedly longer than any other, the fourth is the shortest: after the fourth the segments increase regularly in length, but the last six differ little if at all in that respect. The proximal end of each segment is colourless and transparent, and this colourless band comprises about a seventh of the total length of each segment, the rest of which is light brown. The transparent part bears in the female six fairly

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long hairs set in a symmetrical manner with an angle of 60° between each, these curve forward like the ribs of an umbrella which has been turned inside out. The longest of these hairs measures about ·325 mm., but they vary much in length (Fig. 5, Pl. IX.). Terminally each segment bears two short hairs also turned towards the tip, and the last segment, which ends in a blunt point, is protected by five such hairs. Other small hairs are borne on the segments, especially on those nearest the base, but they are not so definitely arranged nor so conspicuous as those mentioned above.

The antennae of the male differ markedly from those of the female, and their bushy nature is the most conspicuous naked-eye character by which the sexes may be determined. It is probable, as we shall see later, that it is by means of the sensory, probably auditory, function of these organs, that the male seeks out the female: at any rate the ganglion in the second segment or basal bulb is more highly developed and twice as large in the male as in the female, in correspondence with the increase in number and complexity of the antennal hairs.

There are sixteen segments, one more than in the female. The first is a mere chitinous ring, the second is similar to though larger than the corresponding part in the female. The third segment bears a few irregularly scattered hairs, the fourth to the fifteenth segment bear the long conspicuous hairs so characteristic of the male (Fig. 16, Pl. IX.). These hairs attain a length of 0·8 or 0·9 mm. Each whorl of hairs (there are twelve of them) is carried by two semicircular chitinous bars which clasp the segment of the antennae at an angle, each bar bears 25—30 hairs which spread out in a fan-like manner. The hairs of each half are not however in contact, so that two lines devoid of hairs, *i.e.* between the fans, run along each antenna. The hairs of the proximal segments are shorter than those of the distal, whilst those of each edge of each fan are usually shorter than the central hairs (Fig. 16). The hairs seem capable of considerable movement and at times the antennae seem spirally beset with hairs, but a closer inspection shows that in reality the hairs are arranged in half rings. The captive males, during the daytime, usually carried the hairs closely applied to the shafts of the antennae, the hairs being extended (as in Plate I.) when they began to fly about in the evening. On one occasion three males extended their antennal hairs after being fed on sugar and water, this being in the evening when they were active. One of them, on coming to rest, flattened down the hairs again with his fore-legs. The fifteenth segment is a very long one, four times as long as any of the others;

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besides its proper ring it is covered with minute hairs pointing forward. The sixteenth and last segment is almost half the length of the penultimate, and covered with similar hairs: near its base it bears six long hairs like those of the female antennae, and it ends in a blunt point. The basal part of each segment is not transparent and thus the beaded appearance of the female antennae is not present.

Mouth appendages. The other appendages of the head are grouped together as mouth appendages.

Taking now the various mouth-parts in their morphological order, the mandibles are in the female extremely delicate, finer in fact than any other part of the apparatus. Each has the shape of a very long and narrow chitinous blade curved so that in cross-section it looks like a segment of a circle of some 60—70° (Fig. 9, Pl. IX.). Each is of a bright yellow colour and is solid chitin. At the base the mandible is slightly swollen, it has its origin from the sides of the labrum and we have detected no special muscle attached to its proximal end. The mandibles are moved by the complex of muscles which move the labrum. When the labrum is being pressed into the skin they also enter, being impelled by the same elastic force which induces the sharpened end of a piece of whalebone to pierce a soft body if the other end be pushed towards the surface. The distal end of the mandible is flattened and formed into a very fine knife-blade, something like a butcher's knife but rather broader (Fig. 3, Pl. IX.). The cutting edge of this is provided with 31 extremely fine teeth, very much finer than those of the maxillae and too fine to be completely shown in Fig. 1, Pl. IX. In the male the mandibles are absent.

The first maxillae are slightly longer than the mandibles, and although they also are extremely fine stylets they are considerably stouter than the mandibles. Each consists of a chitinous rod which on its outer surface passes into a very thin flange, so that in transverse section the maxilla has the outline of a razor hollowed on one side (Fig. 9, Pl. IX.). The flange is extremely fine and has the sharpest possible edge. With a very high power fine lines can be seen running obliquely across the flange and dividing it into polygonal areas which are longer than broad (Fig. 2, Pl. IX.).

At the tip of each maxilla the chitinous rod is produced into 13 minute teeth, though in comparison with the fine serrations of the mandibles they are coarse and blunt (Fig. 4, Pl. IX.). The maxillae arise at the side of the base of the labium (Fig. 12, Pl. IX.), and each bears on the outer angle of its point of origin a palp which is but very

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slightly shorter than the labium and the other organs which form the proboscis. In life these palps are usually carried slightly above and external to the proboscis, and the three form as it were an almost equal limbed tripod. In diameter the maxillary palp is slightly, but only slightly, less than the whole complex which we here call the proboscis. When biting the palps are generally carried at right angles to the axis of the proboscis, well out of the way. In the female each palp is five-jointed, and as Figs. 1 and 11 show the relative length of the joints is not always constant. The first joint is very small, about as long as broad. The third joint is always the longest, then comes the second, then the fourth, and finally the last, which terminates in a simple rounded end. The whole palp is beset with scales, some finer, some coarser, those of the two basal joints are of the flattened, ribbed, scale-like variety, pointing towards the free end and overlapping one another.

In the male the maxillary palps differ from those of the female just described. The distal end of the third joint is enlarged and broadened, and the fourth and fifth joints are much broadened, flattened and spatulate (Fig. 16, Pl. IX.). Their inner surface and edges are provided with numerous stout and long hairs, and the flattened ribbed scales are more widely distributed along the outer surface of the organ than is the case in the female. These enlarged ends to the maxillary palps are visible to normal eyesight, and together with the antennae form a ready criterion of sex. In some males the spatulate extremity of the palp is turned outward so that it roughly resembles a hoe. When viewed from above the outwardly turned extremities are seen to bend off at about a right angle, the proboscis projecting between the diverging ends.

Attached to the base of the maxillae just at the point where the maxillary palps emerge between the clypeus and the base of the proboscis, and on the inside of the head, is a chitinous bar which runs backward towards the posterior ventral aspect of the head, to the chitinous covering of which it is attached by numerous muscles. This endoskeletal rod or apodeme is well shown in Figs. 11, 12 and 13. The rods from each side converge so that together they form a V whose apex is directed posteriorly. It is obvious that this rod and the muscles attached to it play a considerable part in the protrusion and retraction of the maxillae. The retractor muscles are the more considerable, but there are certain fibres which from their disposition would obviously serve to protract the maxillae and help them in piercing the skin.

It is perhaps worth while to recall here that the palps of the female

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*Culex* are very short three- or four-jointed structures, in the male *Culex* they are however five-jointed and at least as long as in *Anopheles*, but in those we have examined the last joints are curved upward, and have not the strongly spatulate, flattened, and terminal joints of *Anopheles*. In *Aedes* the palps are short in both sexes.

The second maxillae are united to form a soft, dorsally grooved labium, the median and most ventral of all the mouth-parts. The labium is of fairly uniform diameter and has two joints only. The proximal is very long and covered with small scales which are replaced by hairs on the distal segment. This consists of two halves termed the labellae slightly separated in the middle line (Fig. 6, Pl. IX.). The complex of stylets which form the piercing organ of the mosquito are guided and directed between these two labellae much in the same way as a billiard-cue is guided between the first and second fingers of a player. The labium is covered by a thin coat of cuticle: its cavity is largely hollow but is traversed by nerves, two tracheae, and a certain number of muscle fibres. Within this space in those mosquitoes which are infested with the embryos of *Filaria bancrofti* and *F. immitis*[1] the nematodes, after leaving the muscles of the thorax or the Malpighian tubules, come for a time to rest. Two parasites are generally present at one time, and it would be interesting to know if these are male and female. How the nematodes leave the labium of the mosquito and enter the body of man is still a matter of conjecture. The labium certainly does not enter the skin.

All along the upper surface of this organ is the deep groove in which the piercing stylets are concealed; their relative position when at rest will be described after the consideration of two median structures which play a large part in the mosquito's bite. These are (i) the labrum, with which is combined according to Dimmock (ii) the epipharynx, and finally, (iii) the hypopharynx. The labrum-epipharynx is in cross section something like an $\Omega$, the slit-like opening of the otherwise complete tube being ventrally placed (Figs. 9 and 10, Pl. IX.). The organ consists of a double layer of chitin with, except at the angles, practically no space between. At the base of the labrum-epipharynx these two cylinders which form its walls do however part company and a space appears between them. The more dorsal portion is continuous with the chitinous covering of the clypeus—that dorsal swelling at the root of the proboscis—the ventral unites along its edges and passes

[1] Noè. *Rend. Acc. Lincei*, Ser. v. x. 1900, p. 357; *v.* also Bancroft in *Nature*, LXIV. 1901, p. 416.

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uninterruptedly into the chitinous lining of the stomodaeum (Figs. 8 and 11, Pl. IX.). In the space thus formed in the clypeus, numerous paired muscles pass from above downwards and from behind forwards. These raise the proboscis and doubtless help in the movements which insert and retract the stylets when the insect bites.

At its distal end the labrum is shaved down into a sharp point, which in the female runs smoothly to the tip, but in the male is truncated and rather like the tip of an Indian elephant's proboscis (Figs. 1 and 16, Pl. IX.). It is a characteristic criterion of sex. The slit between the incurved edges of the labrum is very narrow, so narrow as to almost form a closed tube. This is especially the case in the male. In the female the slit is closed by the apposition of the last stylet to be described, the hypopharynx.

In the female *Anopheles* the hypopharynx is like a two-edged sword. It has its origin just above the base of the labium and stretches down the labial groove, closing ventrally the slit-like aperture of the labrum-epipharynx. At its base the hypopharynx has its origin in a wedge-shaped chitinous mass pierced by the common salivary duct, and this basal piece is attached by two powerful muscles which run longitudinally along the ventral surface of the oral cavity to be inserted in a half-saucer shaped flange which projects laterally and ventrally from the chitinous stomodaeum (Fig. 20, Pl. IX.). These muscles doubtless serve to retract the hypopharynx.

We have compared the hypopharynx to a two-edged sword, but the thickened median portion of the sword lying between the two edges is more pronounced on the ventral surface. The dorsal surface which lies close against the labrum is flat or even very slightly curved. Along this ventral thickening runs the salivary duct to open at the pointed free end of the hypopharynx. It is a chitin-lined tube of extreme fineness, somewhere between ·035 and ·036 mm. in diameter, yet along it passes the cause of death and disease, ruining great cities and devastating large districts. Few ducts have played so large a part in the history of the world, or in the spread of civilization, for it is through this duct that the malarial parasites are expelled with the saliva of the insect in which they have undergone their development.

In the male the hypopharynx is fused with the labium (Fig. 10, Pl. IX.). As in the female it is traversed by the salivary duct, but it is no piercing organ, and for this reason the male cannot pierce the skin and bite.

We have termed the apparatus the component parts of which have

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been just described the proboscis. The proboscis then is the biting organ, and consists of all the mouth-parts, labrum, mandibles, 1st maxillae, 2nd maxillae (labium), epipharynx united with labrum and the hypopharynx. The maxillary palps lie free from the proboscis, and although they doubtless play some part in selecting the spot to be bitten they take no actual part in the biting.

The arrangement when at rest of the various parts here enumerated is as follows. The labrum, which is soft and almost fleshy, is grooved along its upper surface, and in this groove lie the other organs of the proboscis (Figs. 9 and 10, Pl. IX.). Most dorsal of all is the labrum-epipharynx, forming a second groove whose opening is very narrow and faces downward. Immediately ventrally to this slit is the hypopharynx. Either by the approximation of the edges of the slit or by the pressing of the hypopharynx against this groove the labrum-epipharynx is converted into a tube which is continuous with the cavity of the mouth (Fig. 20, Pl. IX.); and along it, drawn up by the action of the suctorial pharynx in the head, the liquid food, whether vegetable sap or animal blood, is drawn. At the angles of the labrum lie the two mandibles: the inner end of them is between the labrum and the hypopharynx, and in this respect they differ in position from those of *Culex*, where according to Dimmock the mandibles lie ventral to the hypopharynx between it and the 1st maxillae. Below the hypopharynx lie the maxillae, very neatly fitting in each side against the thickening formed by the salivary duct (Fig. 9, Pl. IX.). In the male the mandibles are absent: the 1st maxillae lie at the angle of the labrum; and the hypopharynx is as described above fused with the labium.

## *Method of feeding.*

The newly-hatched insect is unable to perforate the skin until the mouth-parts have hardened, a process which requires a variable length of time. Gray (1900, p. 583) of St Lucia has seen Culicidae suck blood six hours after transformation. We have seen *A. maculipennis* feed readily after 24 hours, so that the statement made by Creagh (1899, *Brit. Med. Journ.*, I. p. 1062) that the insects will not feed until after 6—8 days is wrong. Kerschbaumer (1901) thinks he has observed the imago drinking water whilst issuing from the pupal skin, and that the insect's abdomen became thicker. We feel sure that he is in error. To begin with, the insect has all it can do to free itself. We

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have repeatedly observed the insect issuing, watching the process from the side with a magnifying-glass, through an aquarium made of thin glass. We do not doubt but that Kerschbaumer was deceived through watching the process from above. When watched from the side, the insect is seen to keep its mouth-parts away from the surface of the water, and although it may occasionally occur that they come in gentle contact with the surface-film, this does not mean that the imago is drinking, but that it has overbalanced itself. The abdomen as we have already described shortens rapidly and therefore may appear somewhat thicker after completed transformation.

When about to feed, both sexes move their antennae and palps out of the way, that is upwards, so that they form nearly a right angle to the axis of the mouth-parts which are inserted into the skin (Pl. X.).

When feeding on fluids or the moist surface of fruit, the insects feel about with the two-lobed extremity of the labium, and having found a suitable spot proceed to use their suctorial apparatus.

The males feed more slowly than females and take up very much less nutriment. When five males and five females were allowed to feed on milk and sugar, the females had gorged themselves on an average within 5 minutes, whereas the males took an average of 8 minutes to complete a very frugal meal, only the anterior two-thirds of their abdomen being slightly distended. And it was moreover noticed that the males evidently exerted themselves more in feeding, the sucking being accompanied by rapid to and fro movements of the palps and antennae, an appearance not observable when the female was feeding. When, as in blood-sucking, the skin has to be pierced, the female proceeds to use her stylets, which are worked to and fro with a visible effort which is made evident through slight forward and backward and lateral movements of the head. If it does not succeed in obtaining blood from the puncture, it gradually withdraws the stylets and tries again elsewhere. In one case one of us observed a fly try four times before it succeeded in obtaining blood. The blood is drawn up in the hollow of the labrum-epipharynx, a toxic saliva being injected through the delicate tubular, sharply pointed hypopharynx. The labium does not penetrate the skin. Its lobes rest upon the surface at the point where the stylets enter, and serve to steady and direct them. In sucking blood, the labrum-epipharynx, mandibles, maxillae and hypopharynx penetrate the skin to a greater or less depth until blood is obtained. They may penetrate almost to their entire length. As these organs penetrate the labium becomes bent backwards like a bow. If the

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mouth-parts penetrate deeply, the labium becomes bent at an angle, the upper portion, which is shortest, being directed backward, the lower forward, forming two sides of a triangle which is closed by the stylets, which penetrate the skin at the point where the two lobes of the labium are resting. When the parts have penetrated, saliva immediately issues from the aperture of the hypopharynx. It has been assumed that the saliva is injected with the object of preventing the coagulation of the blood whilst it ascends through the groove of the labrum-epipharynx. That the saliva injection precedes and accompanies the act of blood-sucking was made very evident in the observation above referred to where an insect penetrated the skin at several places. Ross, Annett and Austin (1900, p. 24) have made the same observation. All the points of puncture reacted by becoming swollen and itching; the one from which blood was obtained reacted most, consequent upon the insect injecting more saliva than at the other points. Where the skin is thick and resistant the stylets are held almost at a right-angle to the long axis of the body, otherwise they project slightly forward. A detailed description of the internal mechanism by which the insect sucks blood is reserved for a future communication, in which the internal anatomy of the fly will be duly considered.

When the female has filled herself, the process when undisturbed lasting 2 to 3½ minutes by the watch, she withdraws her mouth-parts by bracing the legs against the skin and raising the body.

### *Tubular Tunnels.*

A curious feature of the head of *Anopheles* is that it is pierced in an antero-posterior direction by two tubes (Fig. 13, Pl. IX.). These tubes open in front by a slit-like trumpet-shaped orifice situated between the anterior limit of the eye and the side of the clypeus: then converging slightly they pass backward and open by two trumpet-shaped apertures into a slight depression at the back of the head, near the ventral edge, below the neck. The tubes thus form a complete passage through the head, through which a bristle could be passed if it were fine enough, and through which air doubtless streams as the insect flies about. The tubes are lined by a well-marked layer of chitin which shows none of the spiral thickening associated with the tracheae. In its course through the head each tube is not of uniform diameter, and half-way along it bears a sharp, dorsally projecting spine, and near the posterior end it sends off another dorsally placed process which fuses with the

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chitinous back of the head. This acts as a stay. The tubes lie in the angle formed by the great optic ganglion with the brain: they undoubtedly serve as a kind of strut to strengthen the chitinous exoskeleton of the head and to prevent its exoskeleton from collapsing. They also serve for the attachment of muscles, the chief of which are loose aggregates of more or less isolated muscle fibres—rather like those of a leech—which run to the maxillary palp. Other muscles run to the first sucking pharynx and several to the antennae.

Mr D. Sharp tells us that he has observed somewhat similar tubes piercing the head of the Sialid, *Corydalis*, and very similar tunnels are described by Miall and Hammond (1900, pp. 89—90) in the head of *Chironomus dorsalis*. The last named authors also mention and figure (Fig. 62) their occurrence in *Anopheles maculipennis*. Their suggestion that the tunnels are of the nature of apodemes which remain hollow seems probable.

### *The Neck.*

The greater part of the wall of the neck is soft and only very thinly chitinised, thus allowing considerable mobility to the head. It is however strengthened by two lateral chitinous plates which approach one another dorsally but do not fuse (Fig. 15, Pl. IX.). Underneath, these two halves approximate, but do not unite, by means of a strap of chitin which extends across the neck like the two ends of a stand-up collar. The whole forms a skeleton roughly resembling an **H** broken in the middle. From the anterior inner angles of this sclerite two stout chitinous bars run forward towards the head. Posteriorly these are jointed on to the **H** shaped piece. They serve for the attachment of muscles. The remaining integument of the neck is delicately papillated and is transparent, as is shown by the red spot which appears there in the insect when sucking blood (Fig. A and Plate X.).

## II. The Thorax.

Of the three divisions into which the body of an insect is primarily divided, the head, the thorax, and the abdomen, in *Anopheles* the thorax is by far the largest. It is perhaps some 12—15 times as big as the head and 4—6 times as big as the abdomen. The latter is however very extensile and when distended with eggs or by a heavy meal these proportions are altered.

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The thorax is, roughly speaking, the shape of a four-sided pyramid whose lateral sides are twice as long as the anterior and posterior sides are broad. The apex, which looks ventralwards, is cut short, and here the three pair of legs emerge. The base of the pyramid, which is the dorsal surface, is strongly arched both from before backward and from side to side. Looked at from above, the angles of the base of the elongated pyramid are seen to be slightly shaved off so that the dorsal surface seems eight-sided; but of these sides the lateral are by far the largest. Anteriorly the thorax protrudes over the retracted head, posteriorly over the anterior limit of the abdomen.

The homologies and the limits of the sclerites which make up the skeleton of the thorax are very difficult to determine. Wherever possible the nomenclature of Brauer has been followed.

The dorsal surface is then a broad, slightly arched plane corresponding with the praescutum and scutum of Brauer. This is of a grayish-brown colour and hairy. Besides the smaller hairs there are a number of longer bristles symmetrically placed, and these are especially prominent towards the sides.

Near the posterior limit of the dorsal surface, between and just behind the insertion of the wings, is a curved thickening of the integument which arches over the back and serves to strengthen the exoskeleton in this important region of the body: this is the scutellum. It bears very conspicuous rows of hairs. Behind comes a rounded, vaulted, triangular sclerite, the post-scutellum, which reaches almost to the first abdominal segment.

The portion which we have here, following Brauer, described as post-scutellum is by Theobald (1901) called the metathorax. It is an important region, as the presence or absence of hairs and scales on it is a matter of generic importance. In *Anopheles maculipennis* it is, as Theobald says, nude.

According to Brauer all these dorsal pieces are part of the mesothorax; the prothorax is confined to the anterior surface of the thoracic pyramid and does not appear on the upper surface at all (Figs. A and 15, Pl. IX.). The metathorax is similarly almost squeezed out dorsally between the post-scutellum and the first abdominal segment, and appears only laterally and ventrally. There appears to be a trace of the metanotum or dorsal portion of the metathorax, forming a very narrow band between the post-scutellum and the first abdominal tergum.

Ventrally the neck passes into the thorax, and its transparent integument is extended on to the median area of the prothorax. This

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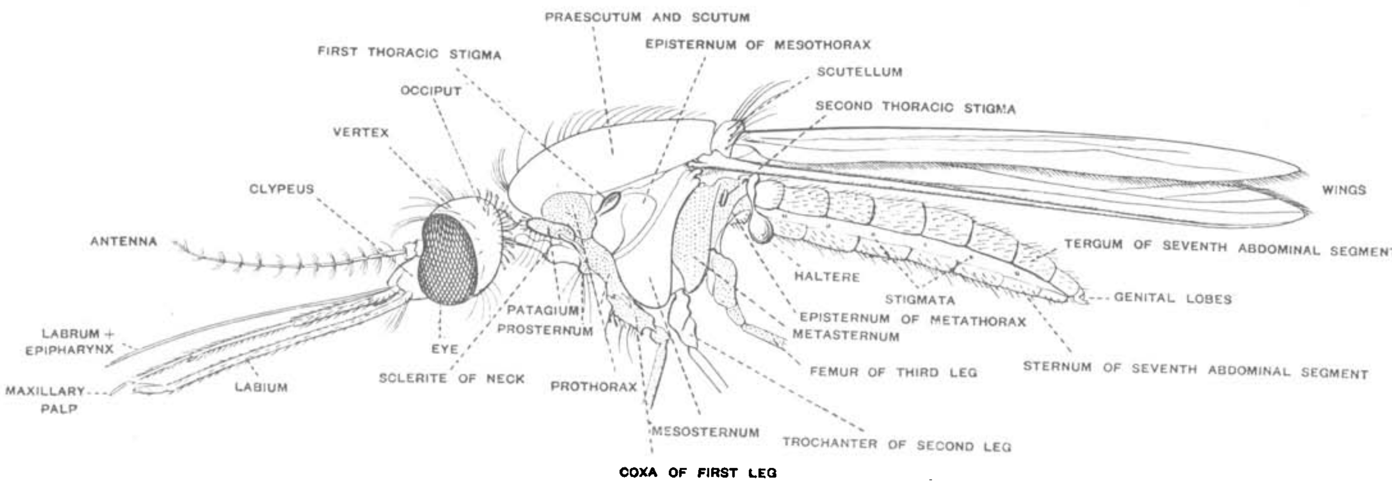


FIG. A. Side view of a female *Anopheles maculipennis* Meigen × about 22 to show the various parts of the body. The prothorax and metathorax with their respective legs are dotted.

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is very manifest when the female mosquito is sucking blood, a bright red bead appearing here and contrasting with the otherwise sombre hue of the thorax. This area is bounded posteriorly by the origin of the prothoracic or first pair of legs, and laterally by a pair of plates bearing a pair of sausage-shaped organs called the patagia (*v.* p. 477). Between each patagium and the origin of the leg is a small prominence bearing particularly large hairs. The same plate of exoskeleton which bears the patagium extends along the side of the body almost as far as the anterior border of the first or mesothoracic spiracle. This together with another piece is figured and described by Christophers (March, 1901, plate I.) as the pleuron of the mesothorax. We regard it as prothoracic and have so shaded it. Sharp (1895, p. 446) indeed regards the first spiracle of the Diptera as prothoracic. Whichever segment it really belongs to it is the largest spiracle in the body and opens by a wide-mouthed cavernous-looking orifice. This prothoracic portion of the lateral walls of the body is slightly hollowed out like a sunken cheek.

The sides of the mesothorax form a large part of the side of the thorax. Above in the region of the spiracle is an area which appears to correspond with Brauer's episternum, and below, not very clearly marked off from the episternum, is the mesosternum. This portion is greatly enlarged and stretches ventrally to form the apex of the pyramidal thorax. Dorsally it runs up to the insertion of the wing, where it is raised above the surface into a tri-lobed knob. It looks as if this knob fitted into a socket at the base of the wing when the wings are extended at right angles to the body.

The metasternum of the third or post-thoracic segment is similarly enlarged, like that of the second segment, in connection with the attachment of muscles: between the two the second pair of legs emerge: close behind the last arise the third pair of legs. Above and slightly behind this is a region, the episternum (?) of the metathorax, which bears the second thoracic spiracle and from which the halteres arise.

Behind and between the last pair of legs and the anterior abdominal segment is a somewhat triangular patch of soft and rather transparent integument.

On the ventral surface the following sclerites occur. Behind the neck, like a collar of a coat, two prosterna (Fig. 15, Pl. IX.). In the middle line these meet in a straight suture. Laterally these prosterna bear the knob of hairs already mentioned. The cords from the patagia, to be mentioned hereafter, run into the lateral angles of the prosterna.



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Between the two prosterna and the coxa of the first leg is a region of soft integument which permits the movement of the coxa as the leather joints permit movement in plate-armour.

Owing to the great bulk of the mesosterna the interval between the first and second pair of legs is greater than between the second and third pair: in fact the rounded lobes of the mesosterna almost meet in the middle, and the two are strongly 'tied' together by a transverse bar or bridge of thick chitin, which forms a very conspicuous and striking structure when the legs are removed (Fig. 17, Pl. IX.). The swollen lobes of the metasterna do not approach each other so closely, but end external to the insertion of the last two pair of legs. The mesothoracic legs emerge from a plate which has a line or groove in the median line: this plate must belong to the mesosternum (Fig. 17, Pl. IX.).

## *The Legs.*

The six legs are each composed of the typical Insect parts, viz., the coxa, trochanter, femur, tibia, tarsus, the last of which is built of five segments and ends in a pair of claws. The six coxae or basal joints of the three pairs of legs converge about the apex of the pyramidal thorax: they all slope inwards and downwards. The coxa of the first leg obviously arises from the prothorax. It is closely adpressed against the anterior surface of the mesothorax. The coxa of the mesothoracic leg is wedged in between the mesothoracic and metathoracic mesosterna, to the posterior surface of which the coxae of the hind or metathoracic legs are applied. The right and left coxae of these last-named limbs touch each other, and are even for a short distance on their hinder aspect fused together. All three pairs of coxae are short, cylindrical pieces bearing many hairs: particularly is this the case on the anterior face of the first pair. Distally each bears the second joint or trochanter, a piece shaped like a signet-ring, broader on one side than the other. The measurement of the coxa is difficult, as it is of irregular shape, but roughly speaking it is ·5 mm.; the trochanter is from ·1 to ·2 mm.

The remaining segments of the leg are the femur, the tibia and the five-jointed tarsus. The length of these various segments is far from constant in different specimens.

Each segment of the leg is covered with numbers of the flattened,

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longitudinally striated scales which have been described in many parts of the body. They vary somewhat in shape, but as a rule are something like old-fashioned cricket-bats in outline. Towards the distal end each segment swells out, and here there are longish hairs as well as scales that overhang the joint. The metatarsus, as the first segment of the tarsus is called, bears a double row of little black spines unlike anything on the other segments of the legs.

In the male the terminal segment of the first pair of tarsi is hollowed out on one side like a spoon: this area bears a number of curved short hairs with enlarged bases which encircle three-quarters of the hair like a collar and permit movement in one plane only (Fig. 18, Pl. IX.). The anterior leg in this sex terminates in a peculiar claw, which at its base bears two short, curved, lateral stumps of unequal size and is then continued into a long hook which forks into two in a plane at right angles to that in which the two stump-like processes lie. Both the hind legs bear two simple hooks, adjacent or fused at their bases, and divaricating at their tips. In these limbs the terminal segment is not hollowed but is cylindrical throughout (Fig. 19, Pl. IX.). Some authors write as though the front legs bore—like the others—two hooks. We have only observed one, though in some cases there seems to be a slight suture between the main hook and the lateral stump-like processes. Theobald (1901) states that the "fore and middle" claws are "always unequal" in the male, but in our specimens of the *A. maculipennis* it was with one exception the anterior claws only that departed from the ordinary structure of the other legs and of those of the female. In one specimen we noticed that it was the second pair of legs which had the hollow terminal tarsal segment and the forked hook, and in this case the hooks of the first pair of legs resembled those of the third. In the female all the tarsi terminate in the double hook, and the terminal joint is not hollowed out in the manner of the terminal tarsal segment of the prothoracic leg of the male.

The single muscle which bends the hooks is attached to a short chitinous piece, the "Streckplatte" of de Meijere (1901) and the extensor-plate of Packard (1898), which in its turn is attached to the hook. The hook bends on a joint which seems to be borne by a chitinous thickening of the rim of the end of the last tarsal segment. It straightens itself by elasticity. The empodium, a median process, which in many insects projects between the hooks, is possibly here represented by a short process bearing a tuft of hairs (Fig. 18, Pl. IX.).



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## *The Wings.*

The wings arise from high up on the sides of the mesothorax between the scutum and the episternum of that region. Their point of origin is a longitudinal slit, the posterior limit of which is at the level of the scutellum. The base of each wing is overhung by a series of stout hairs which arise from the scutum.

The anterior margin of the wing is straight and there are no lobes or indentations, but near the base of the wing the posterior edge is indented twice, and two lobes are thus produced which we may follow Sharp (1895) and call the squama and alula (Fig. 21, Pl. IX.). The squama is the most proximal portion; when the wing is extended the squama forms as it were a hollow vault or armpit, and the large hairs which project backward from its posterior edge form with certain hairs which arise from the metasterna a hollow dome. It is the squama which, when the wing is at rest, is thrown into a kind of fold, such as is made if the end of a strip of paper being fixed the paper be twisted through a right angle.

The alula is hardly so much a lobe as a depression: it lies as it were sunk within the margin: the depressions which limit it are deep, and its edge is but slightly rounded. This edge bears a sparse fringe of small hairs which are continued on to the anal or basal angle of the wing. These hairs continue along the edge of the wing but are soon replaced by the characteristic scales which fringe the posterior margin.

The area of the wing which is bounded behind by the squama and alula is broken up by a series of thickenings and ridges, from some of which the nervures take their origin. These ridges are not constant, they differ markedly in different specimens, those figured (Fig. 21, Pl. IX.) have perhaps the average arrangement. The ridges on this portion are probably formed when the wing loses its moisture and dries up, and the variety in its pattern is doubtless due to the varying activities of the many factors which play a part in this process.

Amongst these irregularities on the under surface of the base of the wing, in the axilla as it were, is a small socket which very accurately fits on to a knob borne by the episternum of the mesothorax. When the wing is in use this arrangement doubtless serves to maintain the forward position of the wings.

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*Nervuration of Wing.*

In mapping out the nervures of the wing we have followed the scheme of Comstock and Needham (1898), in whose recent attempt to reduce the nervuration of insects to a system there is an account of the various views held by other entomologists. The accompanying figure (B) shows that the nervures of *Anopheles* correspond essentially with those figured by Comstock and Needham for *Dixa*, the chief differences being the much greater extension of the subcosta in *Anopheles*, the failure of the second radius and combined fourth and fifth radii to be connected with the first, and the presence of the cross-nervure *O*.

From the diagram it will be seen that each nervure is named after the main branch from which it arises, and the different branches are distinguished by the numerals 1, 2, 3, etc. beginning with that lying next to the anterior edge of the wing. When two nervures have coalesced the resulting nervure is indicated by such a symbol as $R_{4+5}$ which indicates that the fourth and fifth radii have fused. The various cells or areas into which the wing is divided are in this scheme named after the chief nervure which takes part in forming its anterior limit.

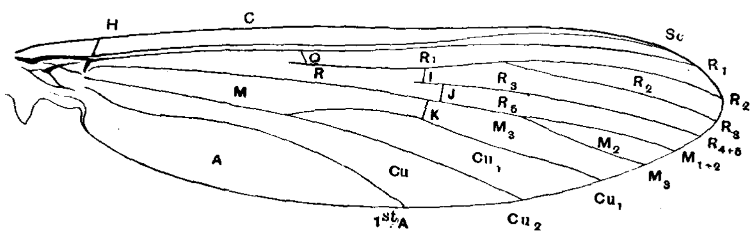


FIG. B. The right wing of a male *Anopheles maculipennis* Meigen × about 14. The scales have been removed to show the nervuration.

*A*. Anal area. *1st A*. Anal nervure. *C*. Costa. *Cu*. Cubitus. *H*. Humeral cross-nervure. *I*. Cross-nervure between $R_1$ and $R_{4+5}$. *J*. Cross-nervure between radial and medial systems. *K*. Cross-nervure between medial and cubital systems. *M*. Media. *O*. Cross-nervure between $R_1$ and $R_2$. *R*. Radius. *Sc*. Subcosta.

The cross-nervures connecting the longitudinal ones still remain to be mentioned. These are the humeral (*H*, Fig. B) running from the costa to the subcosta, a very constant cross-nervure; the radio-medial (*J*, Fig. B) connecting the system of the radius with that of the medius, and the medio-cubital (*K*, Fig. B) uniting the medial system with that of the cubitus. These three are very generally met with, but there is

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in *Anopheles* a fourth cross-nervure uniting $R_1$ with $R_{4+5}$ ($I$, Fig. B), this exists also, but is much smaller in *Dixa,* and a cross-nervure ($O$, Fig. B) which unites $R_1$ with $R_2$. This last seems hitherto to have escaped notice.

As a rule the wing of a dipterous insect is divided into two areas of nervures by an interval which is traversed but by one short transverse bar. This bar in the case of *Anopheles* appears to be the radio-medial.

All the veins are covered with scales, those on the upper surface being of a pointed feather shape, and those on the under surface more usually truncated. Along each nervure these scales are arranged in a feathered series, all pointing to the outer edge of the wing. The spots or maculations on the wings are caused by an unusual aggregation of these scales in certain places (Fig. 21, Pl. IX.). These are four in number in *A. maculipennis,* (i) at the point of origin of the radius nervure, which as is just stated arises suddenly in the middle of the wing; (ii) at the point of origin of the $R_{4+5}$, which has a similar origin; this spot can with the aid of a single lens be resolved into three because the aggregation of scales on the $R_{4+5}$ seems to have set up by sympathy an aggregation at the same level on the adjacent medius and cubitus; (iii) at the point where the $R_1$ forks into $R_2$ and $R_3$; and (iv) at the point where the $M_3$ forks into $M_{1+2}$ and $M_3$.

Along each nervure there is usually a double, sometimes a treble row of the striated scales which spread out right and left.

One of the most beautiful structures in a mosquito is the posterior edge of the wing. Along its upper edge it bears a row of scales which attain their greatest length in the region next the alula. These lie side by side or even slightly overlapping. They stand out from the edge like a regular row of cypress-trees (Fig. 14, Pl. IX.). Alternating with these and arising from the other or under side of the wing is a second series of pointed scales about half the size of the others. Along the upper edge of the wing close to its margin is a definite ridge, and this ridge bears opposite every alternate big scale a small, somewhat battledore-shaped scale which hangs obliquely over the point of insertion of the big scale. The whole forms a structure of singular regularity and beauty. It tends to disappear along the outermost edge of the wing, and there passes with no abrupt change into the anterior border, where the scales are massed together and overhang one another in a matted and irregular way.

The greater part of the tissue of the wings is transparent. It bears, as is shown in Figs. 14 and 21, Pl. IX., a number of small spines like the

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skin of a shark, but these diminish but little the transparency of the membrane. They however seem to break up the light, as it is this part which gives rise to the beautiful iridescence of the mosquito's wing.

The size of the wings varies considerably in different females. Out of a series of five the largest measured from the external tip of the wing to the groove between the alula and the squama 6 mm. in length and 1·5 mm. in breadth at its greatest. The smallest wing of the same series measuring the same area was 4·8 mm. × 1·3 mm. In each case the measurements do not include the scales. The male wings are smaller. Of a similar series of five the largest measured 5 mm. × 1·1 mm. and the smallest 4·3 mm. × ·9 mm. It is thus evident that the male wing is more slender than that of the female.

### *The Halteres.*

The Halteres or Balancers arise from the metathorax close to the junction of the metathoracic episternum with the post scutellum. They are usually regarded as the representatives of the metathoracic or second pair of wings, which are always absent in the Diptera but are found in nearly all other insects. The halteres arise from a broad base which quickly narrows, forming a small cone, from the apex of which a short rod arises. This chitinous rod is not circular in section but slightly irregular: proximally it is jointed and is capable of a certain amount of movement, twitching up and down when flying. At the outer end the chitinous rod expands into a rounded knob. The basal half of the knob has a thicker chitinous covering than the distal, which is enclosed by a very thin membrane: around the equator of the knob lie a number of small scales which overhang the thinner portion to a slight extent. The distal hemisphere is itself studded with small brown bodies probably of a sensory nature. In the majority of preserved specimens this outer half does not bulge out, forming a club-shaped end to the haltere, as it should in life, but is sunk in or invaginated.

The whole organ is about ·4 mm. in length. When the wings are folded the halteres usually lie backward, overhanging the first abdominal segment, and their tip reaches to the posterior edge of this tergum. When the wings are in a position of flight the halteres usually project out from the body, not quite at right angles but pointing backwards.

### *The Patagia.*

On the anterior face of each side of the prothorax, in front of the first pair of spiracles, is a sausage-shaped body, termed by Christophers

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the patagium, resting on the shoulders of the mosquito like a pair of epaulettes. It corresponds in position very fairly with the patagium of the Lepidoptera and of some other insects (Cholodkovsky, 1896 and 1897). The structure in *Anopheles* resembles very much the shape of a short sausage, applied to the prothorax. It is separated by a deep groove from the body on the outer side and at each end. The groove is less apparent on the median aspect. The whole is covered with hairs of various lengths.

From an external view there is little to suggest any function for these peculiar organs. At times when the head is retracted it rests upon these bodies much as one's head rests against the curved supports at the back of a dentist's chair; but the patagia can hardly be there to support the head. A thinning of the cuticle over a small area near the lower, inner end affords some clue to the problem. Continuous with this thinning is a strand or ridge which runs downwards and inwards towards the base of the first thoracic legs (Fig. 15, Pl. IX.). From the inner surface of each patagium a very large number of muscle fibres arise, which come together into something like a tendon which passes along this ridge. It will probably be necessary to return again to this point in the description of the muscles, but at present we are inclined to regard the patagia as arrangements for increasing the surface of attachment of a powerful muscle which runs to the coxae of the first or prothoracic legs.

## III. The Abdomen.

The abdomen of *Anopheles* consists of eight segments, each composed of a dorsal chitinous plate, the tergum, and a ventral chitinous plate, the sternum. Between the edge of the terga and sterna is a soft membrane, the pleuron (Fig. A). In the imago which has just appeared from the pupa the abdomen is very much longer than it is later. It stretches far beyond the wings, the ends of which only just reach the eighth tergum. In the older female imagines the abdomen is much contracted, and about a third, sometimes more, of the wing projects beyond the posterior limit of the body. In the male imago the wing-tips do not project beyond the last abdominal segment. The newly appeared imago also shows very clearly the pleura, which in fact project as a roll on each side of the abdomen, and in this state it is possible to see the minute abdominal stigmata, one on each side of the 2nd, 3rd, 4th, 5th, 6th and 7th segments, in each case a little in front of the centre of the segment. The number of abdominal stigmata is a

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rather debatable point. Christophers says there is "one in each segment," and he draws in one figure seven and in another eight. The most careful search has only revealed six pairs to us and we do not believe there are more. They are however very difficult to see. When the imago is older the terga and sterna approach and overlap, and the pleuron and stigmata are hidden: the segments are also telescoped into one another for a considerable extent. In the imago which has just escaped from the pupa-skin the junction of the abdomen and the thorax is in a plane at right angles to the longitudinal axis of the mosquito, but as the thorax consolidates the pyramidal shape becomes emphasized and the plane of union is drawn forward and downwards. This drags the sterna forwards and produces what geologists would term a "fault" between the anterior terga and the anterior sterna. The first sternum is so pressed under the sloping metathorax that it lies almost entirely in front of the first tergum, and the limits of sterna and terga are not found in one plane until the fourth or fifth segment is reached; the sterna of the first three or four segments lie all somewhat in front of their corresponding terga.

From the surface of the terga and sterna numerous hairs project arranged in more or less transverse rows. These are more conspicuous on the dorsal than on the ventral surface, and most conspicuous in newly emerged imagines. The absence of scales on this part of the body is as Theobald (1901) points out a feature of generic importance. Projecting from the posterior end of the last segment in the male is a pair of stout basal lobes covered with hairs. In the imago as it appears when quitting the pupa these basal lobes seem to arise from the sternum, but in imagines of an older birth they seem to be borne by the terga. Each terminates in a long, yellow, chitinous claw—the clasper—tipped with black. The size and shape of these claws is of some systematic importance. The two claspers are usually folded over one another as a man's arms are crossed in the traditional attitude of resignation. This crossing is usually ventral, but it may in rare instances be dorsal, and this usually is the case in newly emerged imagines. On the inner side of the basal part, which is packed with muscles, there is a stout spur or spine which prevents the base being bent inwards beyond a certain point. During life the claspers are capable of a good deal of movement and are doubtless essential organs of copulation. In one male which lay a-dying the basal lobes were periodically thrown out till they lay almost at right angles to one another. The basal lobes then twitched four or five times per second and then the claspers were divaricated. It appeared as if the muscular effort was that of opening

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not of closing the hooks. Miall and Hammond (1900) draw attention to the fact that such claspers as are here described do not occur in those insects where the female is provided with an ovipositor. In between the bases of these organs there is another set of very minute hooks and a very complex internal skeleton which supports part of the reproductive apparatus. The rectum is sometimes prolapsed for a short distance between the claspers. In the female the claspers are absent but their place is taken by two lateral flaps which probably play some part in oviposition.

### *Hairs and Scales.*

The body of *Anopheles maculipennis* is scattered over with hairs and scales. In some places, *e.g.* the legs and labium, the scales are so thickly placed that they conceal the structure which bears them, in other places, *e.g.* the head and wings, the scales are comparatively sparsely scattered and overlap but slightly or not at all.

The hairs are usually scattered, sometimes in rows. The longest are those of the male antennae, the stoutest those of the scutellum. Each hair arises from a thin, circular area in the chitin, which, when the hair is knocked off, remains conspicuous. The hairs are in all cases simple and show none of the complex beauty of the branched or palmate hairs of the larva.

The scales have their origin in a similar thin spot, but a much smaller and less conspicuous one. The scales have two or three varieties in their shape, and since Theobald has shown their great systematic importance it is worth saying a few words about them.

The scale of the wing is almost invariably lanceolate-shaped: a few however broaden out towards the free end, which, however, remains rounded. This latter shape is the common one for the scales of the legs, the palps and the labium. The scales of the head stand upright, well separated one from another and slightly arching forward so as to overhang the eyes. They have straight sides, and the end of the scale is either cut off straight or shows a reentrant angle which is intensified by a slight groove in the scale. All the scales are striated, and the thickenings which form the striae seem to project beyond the level of the end of these scales like a ragged fringe. In *A. maculipennis* we saw none of the minute scales which Theobald figures at the base of these cephalic scales, nor did we find any on the scutellum. In fact on the thorax proper and on the abdomen we saw no true scales, though hairs are abundant.

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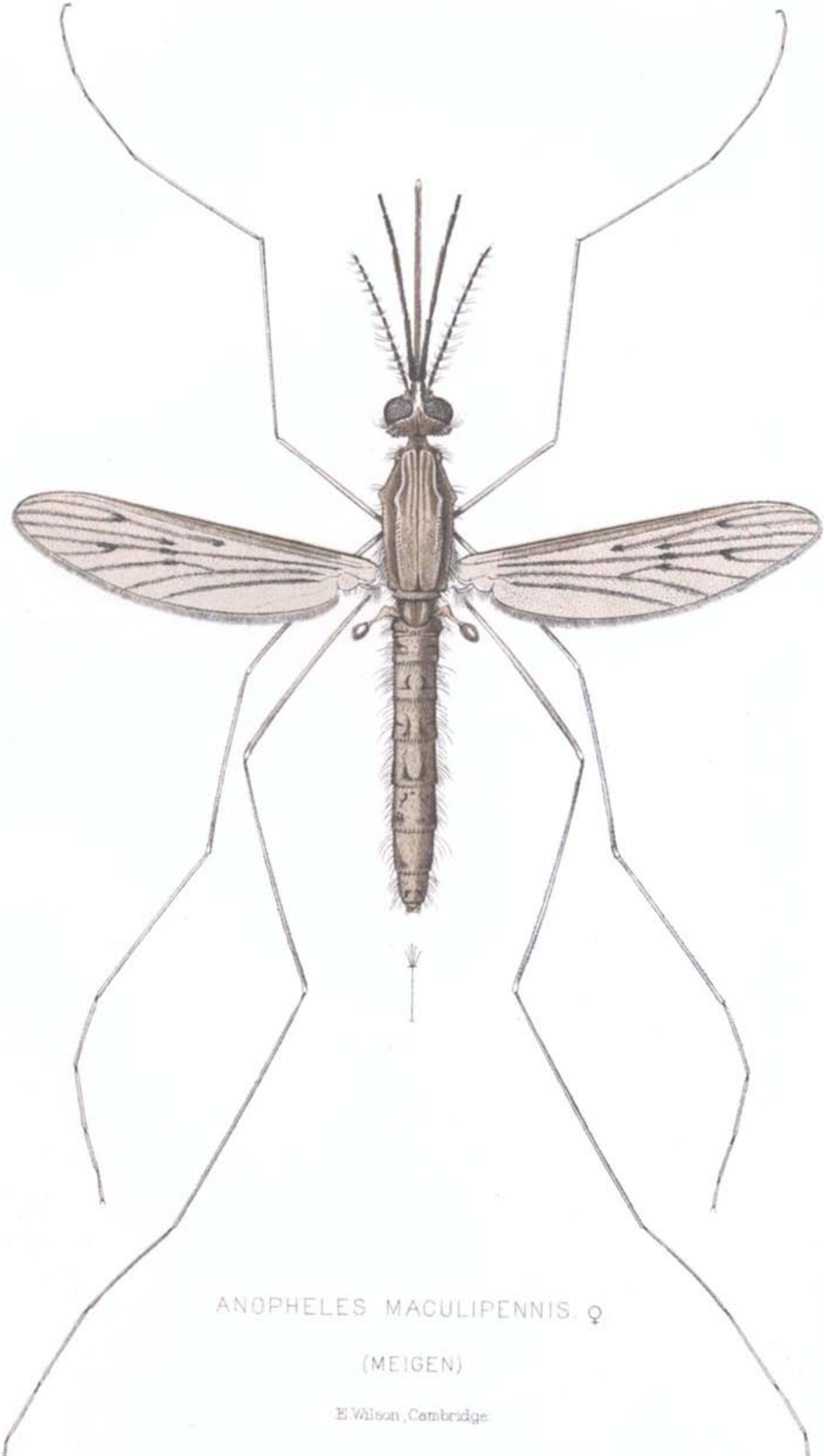

ANOPHELES MACULIPENNIS ♀

(MEIGEN)

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# EXPLANATION OF PLATES.

Illustrating the Paper of G. H. F. Nuttall and A. E. Shipley on "The Structure and Biology of *Anopheles maculipennis*," Part III.

## EXPLANATION OF THE ABBREVIATIONS USED ON PLATE IX.

*a.* Antennae.
*al.* Alula.
*ao.* Anterior opening of the tubular passage through the head.
*ap.* Apodeme of 1st maxilla.
*b. a.* 1st segment of antenna.
*b. l.* 2nd segment of antenna containing auditory apparatus.
*cl.* Clypeus.
*co.* Coxa.
*c. s.* Cephalic scales.
*e.* Epipharynx.
*em.* Empodium.
*e. p.* Extensor plate on foot.
*f.* Femur.
*fl.* Flange round pharynx from which the muscle to the hypopharynx arises.
*h.* Hairs with collared sockets on foot of male.
*ho.* Hooks on feet.
*hp.* Hypopharynx.
*l.* Labrum.
*lxe.* Labrum + epipharynx.
*la.* Labellae.
*li.* Labium.
*mn.* Mandible.
*m. p.* Maxillary palps.
*ms.* Mesosternum.
*mt.* Metasternum.
*mus.* Muscles.
*mx.* 1st maxilla.
*p.* Patagium.
*po.* Posterior opening of the tubular passage through the head.
*pr.* Proboscis.
*Pr.* Prosterna.
*ps.* Prosternum.
*r.* Ridge connecting right and left mesosterna.
*s.* Strut of tubular passage through the head.
*sal.* Salivary duct.
*sc.* Sclerite of neck.
*sp.* Triradiate sucking pharynx.
*sq.* Squama.
*t.* Trochanter.
*tr.* Trachea.
*tu.* Tubular passages through the head.
*x.* Space between clypeus and base of proboscis.

## PLATE VIII.

*Anopheles maculipennis*, dorsal view of female × 9.

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## PLATE IX.

Fig. 1. Side view of the head of a female *Anopheles maculipennis* × about 40, with the various mouth parts separated but in the relative position in which they lie when enclosed in the groove of the labium. This figure shows the characteristic cephalic scales.

Fig. 2. A small portion of the maxilla very highly magnified to show the blade with its characteristic areas.

Fig. 3. The very finely toothed, sawing tip of the mandibles, very highly magnified.

Fig. 4. The much more coarsely tooth tip of the maxillae, very highly magnified.

Fig. 5. A segment of the antenna of a female *Anopheles maculipennis* showing the area free from pigment which bears the circlet of hairs.

Fig. 6. A side view of the labellae and piercing organs of the proboscis of a female *Anopheles maculipennis* dissected out to show the tips of the mandibles, maxillae and labrum + epipharynx. The hypopharynx is not shown.

Fig. 7. Side view of the head of a female *Anopheles maculipennis* × about 26, showing the mechanism of biting. The labium is being curved and the labrum + epipharynx and the mandibles are appearing between the labellae at the tip of the labium.

Fig. 8. Transverse section through the base of the proboscis and maxillary palps close to the anterior end of the clypeus and through the point of origin of the maxillary palps of a female *Anopheles maculipennis*. Muscles are shown running from the dorsal part of the clypeus to the ventral part and to the epipharynx. The labium has not yet become grooved. The space marked $x$ is outside the body and represents the section of the chink between the lower anterior part of the clypeus and the origin of the labrum + epipharynx.

Fig. 9. Transverse section through about the middle of the proboscis of a female *Anopheles maculipennis* showing the relative position of the parts when at rest. Two tracheae and two pairs of extensor and flexor muscles are seen in the labium.

Fig. 10. Transverse section through about the middle of the proboscis of a male *Anopheles maculipennis*. The hypopharynx is fused with the labium and there are no mandibles.

Fig. 11. Left first maxilla and its palp dissected out to show the connection of the two and the stout apodeme for the attachment of muscles, which traverses the head.

Fig. 12. A horizontal section through the ventral portion of the head of *Anopheles maculipennis* showing the origin of the first maxilla and its palp and the strong apodeme. This traverses the head and has numerous muscles which arise from the skeleton of the head inserted along its course. It moves the maxilla.

Fig. 13. A side view of the head of a female *Anopheles maculipennis*, which has been boiled in potash so that only the chitinous parts are left, to show the tubular passages and their openings, the apodemes of the maxillae and the triradiate sucking pharynx.

Fig. 14. A portion of the hinder margin of the wing of *Anopheles maculipennis* highly magnified to show the arrangement of the fringing scales. The tissue of the wing is shown above. The large scales arise from the upper side of the edge, the medium sized scales which alternate with them from the under surface of the edge, and the

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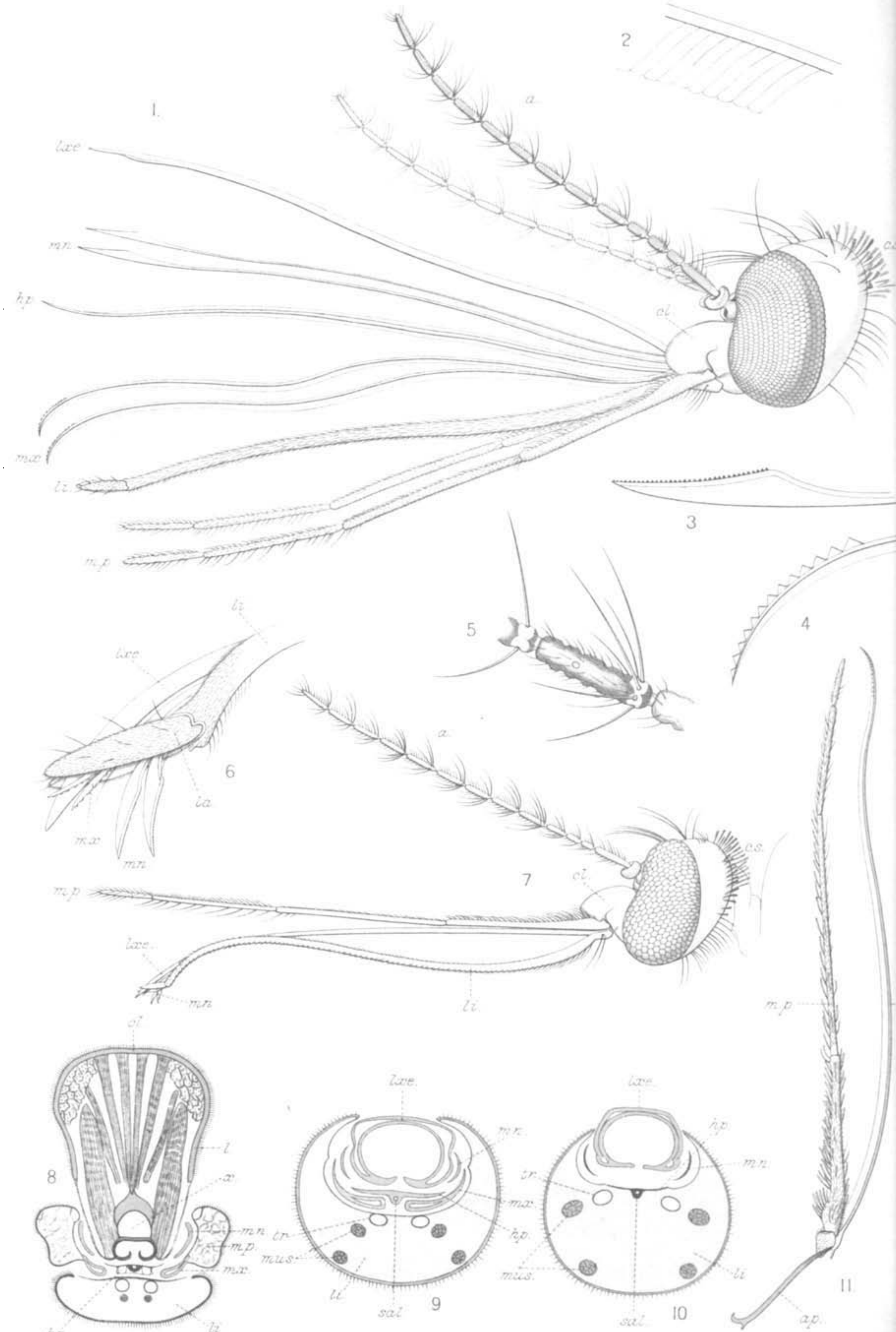


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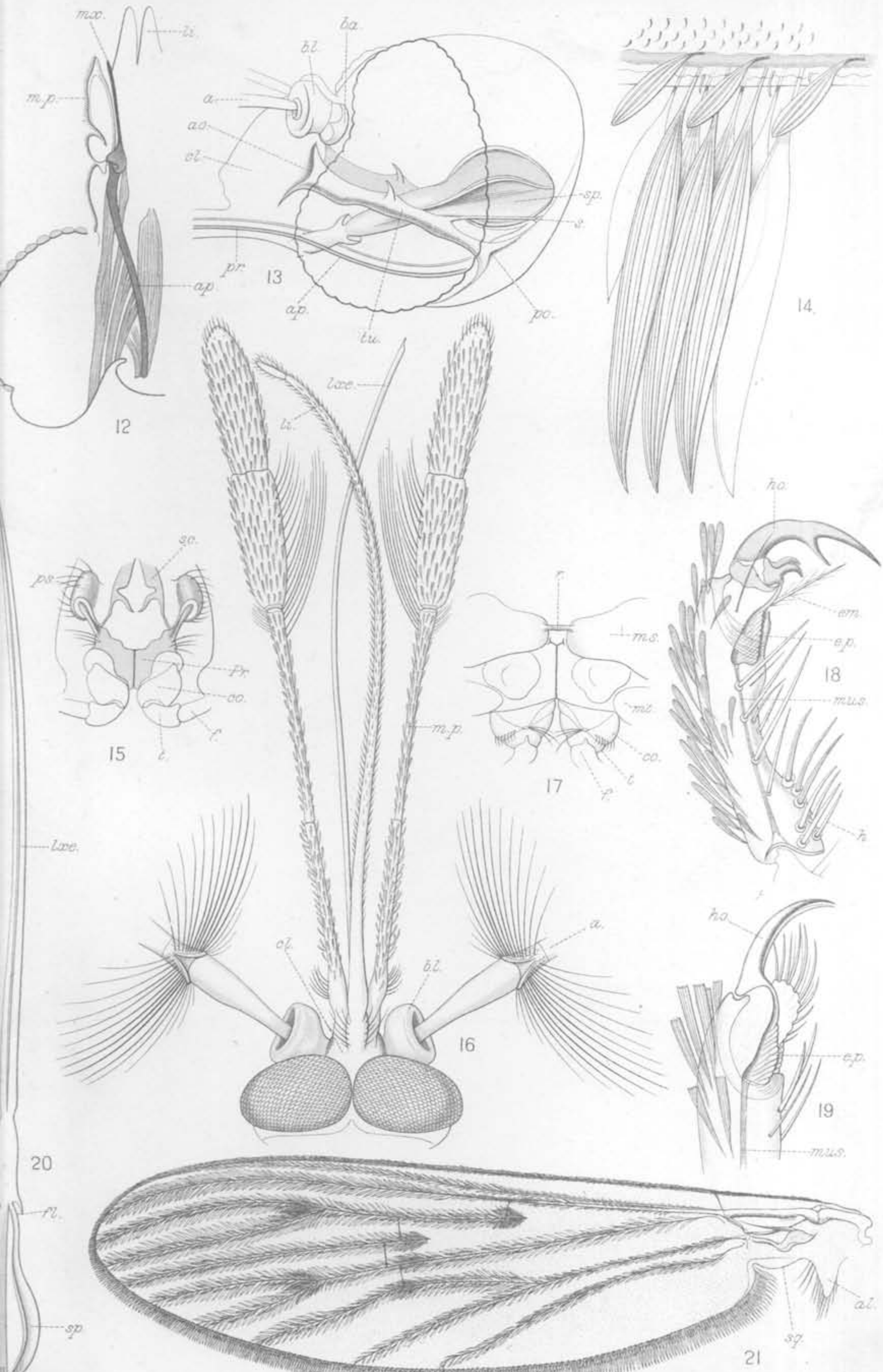


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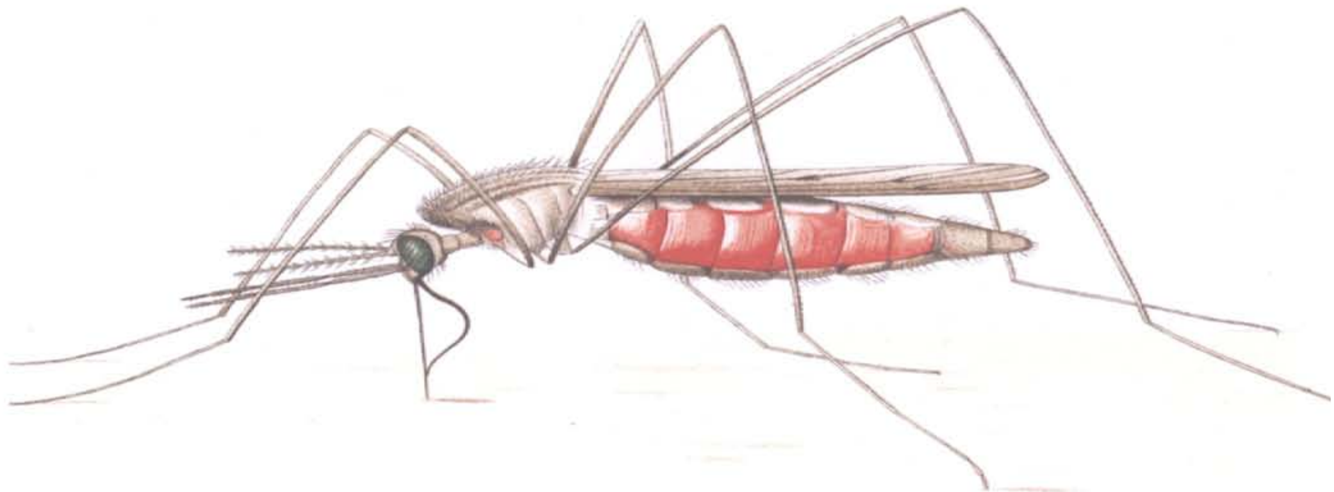

ANOPHELES MACULIPENNIS. ♀

SUCKING BLOOD

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small scales which overhang the bases of the large scales from a ridge on the upper surface.

Fig. 15. The under surface of the neck and prothorax of *Anopheles maculipennis* to show the patagia and the processes running down from them towards the coxae of the anterior pair of legs. The thin skin of the neck which permits the red of the blood to be seen when the insect is biting lies in front of the prosterna.

Fig. 16. Ventral view of head of male *Anopheles maculipennis* showing the approximation of the eyes and the under surface of the clypeus, the mouth organs and the arrangement of the auditory hairs on the antennae.

Fig. 17. A ventral view of the mesothorax and base of the metathoracic legs, showing the bridge clamping the mesosterna together. The second pair of legs have been removed.

Fig. 18. A side view of the terminal tarsal segment of the first legs of a male *Anopheles maculipennis*, showing the hollow, the peculiar collared hairs, the 'extensor plate,' the retractor muscle and the complex hook.

Fig. 19. A side of one of the legs of a female *Anopheles maculipennis* showing the double hooks, 'extensor plate' and muscle.

Fig. 20. Labrum + epipharynx and pharynx and sucking pharynx. The groove of the labrum + epipharynx is shown here to pass into the tube of the mouth and pharynx.

Fig. 21. View of wing of female *Anopheles maculipennis* showing the arrangement of the scales.

## PLATE X.

*Anopheles maculipennis*, side view of a female × 7, in the act of feeding on a human arm.

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