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ON THE LIFE HISTORY OF "WIREWORMS" OF  
THE GENUS *AGRIOTES*, ESCH., WITH SOME NOTES  
ON THAT OF *ATHOUS HAEMORROIDALIS*, F.<sup>1</sup>

PART II.

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(With 4 Text-figures and Plate IV.)

EXTERNAL STRUCTURE OF *AGRIOTES OBSCURUS*, L.

THE first part of this paper contained an account of the biology and life-history of *Agriotes*. This part contains descriptions of *Agriotes obscurus*, L. in the oval, early and late larval stages, together with observations on the pupa. The stages are taken in their natural order, but since an acquaintance with the later stages for the sake of brevity has been presumed in describing the early ones, it may perhaps be necessary to refer to the general description of the final instar in some cases. In addition, it has been considered desirable to describe the mouth parts and spiracles of the larva in greater detail than was possible in a general description. Separate sections for each of these have therefore been added.

In the third part of the paper it is hoped to give some description of the larva of *Agriotes sputator*, L. with some notes on the early stages of *A. sobrinus*, Kies. = *acuminatus*, Steph. and *Athous haemorrhoidalis*, F.

I must again express my gratitude to Dr Russell and the Committee of the Lawes Agricultural Trust for the facilities given me at Rothamsted for carrying on the earlier stages of this part of the investigation, as well as for the figures reproduced in the plate. The later stages have been completed at Cambridge through the kindness of Prof. Stanley Gardiner, to whom my thanks are also due. I wish further to express my indebtedness to Mr C. Forster Cooper and Dr Hugh Scott for kindly allowing me during the last six months to work in the Cambridge Zoological Museum and to make use of the books and collections there.

<sup>1</sup> A grant in aid of publication has been received for this communication.

## THE EGG.

Generally broadly ovoid, but irregular in both shape and size. Average dimensions of four ova .59 mm. × .47 mm. A fifth measured after fixation .64 × .40. Shell transparent, exhibiting the milky-white yolk and embryo within. The germinal band of the embryo appears as a yellowish-green stripe. The surface of the shell is almost smooth, though a few irregular shallow punctures are visible under the microscope.

## FIRST LARVAL INSTAR.

The young larva on hatching is about 2.5 mm. in length and less than 4 mm. in breadth across the prothorax. It is milky white in colour, shining, but when examined under the microscope is found to be minutely punctured and wrinkled. It has the general appearance of being broader and more stumpy than the later stages. Only the mouth parts are yellow, the mandibles being darker still and quite brown at their apices. The 9th abdominal segment is pointed and somewhat constricted at about two-thirds of its length. All the setae are colourless, the eye spots black. The head and all the body segments, with the exception of the 9th and 10th abdominal segments are broadest in the middle and somewhat rounded at the sides. The cauda and margins of the sensory pits of the 9th abdominal segment are colourless, so that the latter are difficult to make out in life. The marginal striae at the base of the body segments, though present, are also only to be made out with difficulty.

Throughout the first instar the larva remains pale and semitransparent, though at the end its general colour has become faintly yellow. The margins of the sensory pits on the 9th abdominal segment are then visibly brown, the constriction near the end of the same segment has been lost and the anterior half of the segment has its sides subparallel, while the posterior tapers to a point at the cauda, which is still colourless or almost so. Five larvae taken from the pots at this age measured 3.25-3.5 mm. in length.

The following points may also be noted in which the young larva of the first instar differs in greater or less degree from the full-fed larva.

Sides of the head subparallel. It is broader than long, measuring the breadth across the middle and the length from the insertion of the mandibles to the base of the head.

Instead of the three-pronged nasale or clypeal process, the latter is represented by a single-toothed process, twice as broad as long and blunt at the apex (Fig. 2e).

In the antenna the 3rd or supplementary segment is proportionally longer than the same segment in full-fed larvae, being two-thirds the length of the 1st and 2nd segments combined.

The mandibles are broader in proportion to their length than those of the full-fed larva, the width at the base being rather more than two-thirds of their length. The apex is finely pointed and considerably incurved. The eye spot is pitchy, situated somewhat further from the base of the antenna than in the full-fed larva and is more conspicuous.

The nervous ganglia, which are plainly visible through the integument in stained preparations, are in proportion to its size very large in the young larva. The two lobes of the supra-oesophageal ganglion, situated in the prothorax and extending backwards into the mesothorax are especially noticeable. There are thirteen ganglia in all, as is common in coleopterous larvae. The spiracle itself is rather more rounded in the young larva, the breadth across the two orifices being greater in proportion to the length than in older larvae. The teeth on either side of the stigmatic orifices are few in number, being about seven or eight in the thoracic and six in the abdominal spiracles.

At first the peritreme is almost colourless, but later it becomes yellow, though it is less strongly chitinised than in older larvae. Each orifice is bordered separately by its own peritreme, so that the two orifices have the appearance of separate spiracles with a small interval between them. At the anterior end of each the peritreme disappears and the boundary to the orifice is merely the unthickened cuticle.

The hairs situated on the tergites between the mesothoracic and 8th abdominal segments are pale, the posterior row slightly longer than the length of the segments to which they belong, the anterior short. In the prothorax, however, where the segment itself is longer than the other segments, the hairs in both rows are considerably shorter than the segments and are about equal to one another. On the 9th segment the hairs surrounding the apex are noticeably long and the posterior hairs of the head are also long, being longer than the anterior hairs and as long as those on any other part of the body.

## SECOND INSTAR.

As already stated (Pt. I, p. 126) the first ecdysis takes place in June. The larva is then of about 3.5 mm. in length. In the second instar its growth is much more rapid and at the end it has attained a length of 5.5-6.5 mm. and breadth of about .5 mm. The colour of the larva is now pale yellow and the body is quite opaque. The tergites are nearly smooth,

but under the microscope can be seen to bear numerous short irregularly shaped striations. The sternites are smoother.

The segments of the body are cylindrical or nearly so, but the head is flattened dorso-ventrally and is somewhat darker in colour than the remaining segments.

The setae are slightly yellowish and all are shorter than the segments to which they belong. The setae of the posterior row are longer than those of the anterior, as in older larvae.

The marginal striae at the base of the 2nd and 3rd thoracic and of the abdominal segments are very fine, but are visible under the microscope. Similarly, those forming the anterior and posterior margins of the prothorax.

The nasale, or clypeal process, is now trifold, with a stout median dens and a smaller lateral dens on either side of the median one, scarcely half as long and little more than half as broad as the median one. Ventral to the nasale the semi-lunar process over the mouth, described in the older larva, can now be identified. In the specimen in which it was found four or more teeth could be seen, the remainder being represented by the sinuate margin of the process. The proportion of length to breadth of the mandible now nearly corresponds to that of the full-fed larva. In the antenna the dorsal process at the apex is still proportionately longer than in the late stages, being about one and a half times the length of the 2nd segment.

The spiracles are now distinctly margined by a brown peritreme, which however is pale and very narrow on the anterior margin of each respiratory orifice. The posterior margin is also narrow but more distinct. The lateral margin and also the central septum are broader than those of the first instar and furnished with pittings or corrugations corresponding to the number of teeth which project from the sides of each orifice. These number eight or nine in the abdominal and eleven in the thoracic spiracles.

The stigmatic scar is visible as a colourless strand in the chitin placed at an obtuse angle to the axis of the spiracle and dorsal to it. The inner end is attached to the atrium, while the outer terminates in a slightly divaricate fork in the cuticle.

The 9th abdominal segment is subparallel at the sides for nearly two-thirds of its length. It then tapers sharply to the apex, from which the cauda is produced. The latter is distinct, sharply pointed and in colour tinged with yellow.

The sensory pits are bordered by an ochraceous rim which is elevated

above the surrounding area chiefly at the sides. Behind, it is less raised and paler in colour.

#### THIRD INSTAR.

The second ecdysis occurs at the end of July or in August and the larva passes its second winter in the third instar. At the beginning it is about 6-8 mm. in length and  $\frac{1}{2}$  mm. in breadth. In colour it is distinctly yellow and in other respects also except size closely resembles the full-fed larva.

The tergites are sparsely punctate but bear numerous irregular striations, which may be seen under a low magnification.

The sternites are smoother. Setae distinctly yellow. Nasale trifold, with median dens the stoutest. Dorsal process of antenna about equal to the second segment.

Spiracles are now distinctly different from those of *A. sputator* at the same age, being shorter and proportionally wider.

The teeth or corrugations at the sides of the orifices number eight to ten in the abdominal and fourteen in the thoracic segments.

The stigmatic scar is thicker than in the previous instar.

The 9th abdominal segment is broadest just posterior to the sensory pits and from that point gradually tapers to the distinctly pointed cauda. Sensory pits margined on all sides with brown.

The following table gives some idea of the actual increase in length of the larva during the early instars. All the larvae hatched in 1916 (or 1918) and were afterwards kept in pots under normal conditions as far as possible.

| Instar          | Date of observation | Average length mm. | No. of specimens | Range of length mm. |
|-----------------|---------------------|--------------------|------------------|---------------------|
| First (1st day) | Aug. 1916 (1918)    | 2.5                | 5                | 2.0 — 3.0           |
| " (9 months)    | May 1917            | 3.35               | 5                | 3.25— 3.5           |
| Second          | End July 1917       | 5.75               | 6                | 4.5 — 6.5           |
| Third           | Mid Sept. 1917      | 6.82               | 7                | 5.75— 8.5           |
| Fourth          | End July 1918       | 9.25               | 2                | 8.5 —10.0           |
| Fifth           | End Aug. 1918       | 10.46              | 14               | 8.25—13.0           |
| Eighth          | Early July 1920     | 17.0               | 3                | 16.0—18.5           |

If this table of records is compared with the estimate made in Part I of this paper (p. 127) it will be seen that the larvae were about a year behind the estimate in 1920. It seems likely, therefore, that the length of life in the larval stage is, or at least may be, of six years' duration<sup>1</sup>.

<sup>1</sup> Some confirmation of this forecast has been obtained since the above was written. Of three larvae of the 1916 brood, on August 22nd, 1921, one was found to have developed into an imago (♀), a second remained a larva (of length 22 mm.), the third was not found, possibly having attained maturity and so having been overlooked in the soil.

## GENERAL DESCRIPTION OF THE LARVA IN FINAL INSTAR.

Length 22-26 mm.; breadth 1.75-2.0 mm.

Apart from the head and 9th abdominal segment nearly cylindrical; yellow, usually rather pale.

*Head* quadrangular, slightly broader than long, flattened above and beneath; somewhat darker in colour than the remaining segments. Wider behind than in front, bearing a long seta near each of the four angles, besides several shorter ones situated chiefly anteriorly; punctures sparse and irregular.

Upper surface with an elongate-oval plate (the cephalic plate), which is expanded anteriorly over the base of each mandible. Anterior margin of the plate, over the entrance to the mouth, with a strongly chitinised brown process, which divides into three sharply pronged denticles, the middle one being the longest. Anterior angles of the head slightly rounded.

*Antennae* situated close to the base of the mandibles, short, consisting of two segments and two processes borne separately at the apex of the 2nd segment. Ventral process shorter, conical and nearly colourless; dorsal process darker and more strongly chitinised, linear and about equal in length to the preceding segment. Probably the latter should be regarded as the 3rd segment.

*Eye spot* dark brown or black, situated laterally, a little below the base of the antenna.

*Mandibles* rather small, stout, yellowish brown, with sharply pointed, pitchy black apices; each bearing two denticles on the inner margin and a brush-like process, the penicillus, at the base.

Ventral surface of the head with a pair of somewhat oblique furrows, brown, nearly straight and reaching from the base of the mandibles to points beyond the base of the hypostome, also with two ridges of darker brown chitin, somewhat bowed, situated in the cavity between the epicranial plates (genae) and the maxillae and nearly reaching the posterior apices of the cardines.

*Maxillae* (Fig. 1) each with a very short cardo, articulating with the tentorium at its second branch. Stipites somewhat rounded on their outer margins and straight within. Palps yellowish-brown, composed of four segments and borne on white membranous palpifers at the apices of the maxillae. Galeae composed of two segments, with a small thimble-shaped process at the apex. Laciniae small, triangular, sharply pointed and densely margined with wavy hairs on their inner margins. Terminal

lobe of the *labium* approximately pentagonal, wider in front than behind, bearing two long yellow setae. Labial palps two-jointed, the first segment with several setae near its apex. Between the bases of the palps, the margin of the labium is usually somewhat produced and probably represents the ligula. Mentum transverse, broader than the submentum, almost membranous. Submentum almost tongue-shaped, usually strongly

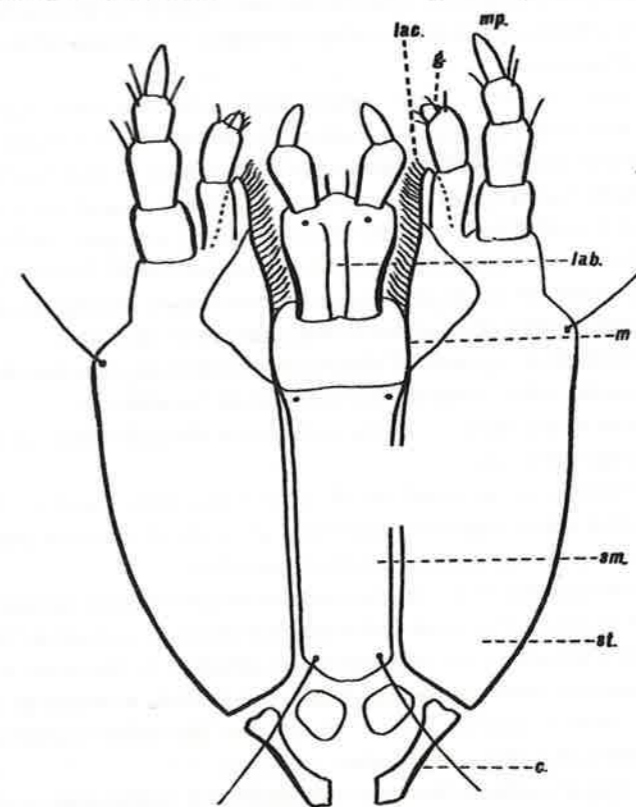


Fig. 1. Hypostome of larva (*R. Green del.*). *c*=cardo; *st.*=stipes; *sm.*=submentum; *m*=mentum; *lab.*=apical portion of labium; *mp.*=maxillary palp; *g.*=galea; *lac.*=lacinia.

chitinised, with the anterior and lateral margins nearly straight, terminating in a blunt point posteriorly. A long seta is borne at each of the four lateral angles.

*Prothorax* nearly as long as the meso- and meta-thorax taken together. Both anterior and posterior margins of the pronotum have a border of fine longitudinal striations, the anterior extending somewhat further than

the posterior margin. The edge of the border is defined by a transverse brown line and a transverse series of minute pores, which are almost equidistant from each other. The meso- and meta-notum, as also abdominal segments 1-8, have the border only on the posterior margin.

The pronotum, like the tergite of each succeeding segment up to the 8th abdominal segment, is separated from the pleura by a narrow suture, running from one marginal border to the next. The pleura of the prothorax is, however, nearly triangular in shape instead of being parallel-sided as in the other segments.

Prothoracic sternum large, pentagonal, with its apex extending almost to the anterior coxae. Sterna of the meso- and meta-thorax narrow, nearly parallel-sided but somewhat broader in the middle. All coxae are surrounded by striations, concentrically arranged around their bases, except on the inside. They are rather long and pale and bear on their anterior and posterior faces a number of short, stiff, brown bristles. Each is approximate to its pair. A small brown spot, having the appearance of a pore, is placed near the lateral margin of the coxa.

Each succeeding segment of the leg is considerably shorter than the coxa and the broadest little more than half its breadth.

*Trochanter* much longer on the inner than the outer side, *femur* on the outer than the inner.

*Tibia* about equal in length to the femur but more slender. *Tarsus* consisting of a single segment, narrowed at a short distance from the base into a long, sharp, almost sickle-shaped claw.

The inner margins of the trochanter, femur and tibia bear short stiff bristles like those of the coxa, evidently of use in progressing through the soil. There are also two long fine setae attached to the inner margin of the trochanter, and one to the femur, as well as a whorl of rather shorter fine hairs round the base of the tarsus. The outer margin of the leg bears only a few fine, short hairs.

On the upper surface the *cuticle* is shallowly sculptured with fine punctures and irregular sutures, its general appearance being much smoother than in that of *A. sputator* (Plate IV, figs. *b* and *c*). The area anterior to the spiracles is smooth, or almost so. There is a fine medio-dorsal suture running from the anterior margin of the prothorax to the posterior margin of the 8th abdominal segment interrupted in its course only by the marginal striations already mentioned.

The tergite of each segment from prothorax to 8th abdominal segment bears two transverse rows of six rather long yellow hairs near the anterior and posterior margins respectively, the posterior hairs being

about twice the length of the anterior. The prothorax has a further row of short hairs rather variable in number close to the anterior marginal border. The ventral surface of the thorax is bare save for three pairs of short hairs on the prosternum. On the abdominal sternites 1-8 three rows are present bearing four, two, four hairs respectively.

The single pair of thoracic *spiracles* is situated in the pleurae of the mesothorax; those of the first eight abdominal segments near the lateral margin of the tergites a little behind the anterior margin (Plate IV, fig. *a*).

The abdominal segments gradually increase in size from the 1st, which is the smallest, to the 9th.

The *muscular impressions*, present on the abdominal segments of most Elaterid larvae, can hardly be made out in this genus; the longitudinal branch can, however, sometimes be seen behind and somewhat dorsal to the spiracle, running nearly parallel to the lateral suture.

The 9th abdominal segment is considerably longer than the preceding one, conically paraboloid (as Beiling<sup>(2)</sup> aptly describes it), with a pair of large open pits, margined with brown, situated one on either side near the anterior margin of the tergite (Plate IV, fig. *a*). In life they are nearly round, but contract at the sides to an elongate oval shape when preserved in spirit. Their margin of stout brown chitin is somewhat raised above the general area of the tergite on either side. Within, the pits are lined with pale membrane, which bears numberless minute dark hairs arranged over the entire surface. Similar fine hairs are also found on the inner surface of the chitinous rim just mentioned. In consequence of the presence of these hairs situated within the pits, the latter are presumed to have a sensory function, though what it may be has not yet been ascertained. Formerly, they were wrongly supposed to be spiracles, but more recently they have been referred to as muscular impressions by Henriksen<sup>(7)</sup> and Schiödte<sup>(12)</sup>.

From the posterior margin of each of these pits an almost straight suture runs backward, terminating beyond the middle of the segment, slightly more dorsal than the sensory pit. Situated between these two sutures is another pair of parallel sutures, arising and terminating at corresponding points of the tergite (seen in Plate IV, fig. *b*).

The apex of the segment is brown and is slightly produced into a stumpy cauda.

The 9th tergite (Plate IV, fig. *a*) is continued uninterruptedly on the ventral surface for about half its length posteriorly, while the 9th sternite, which is an arch-shaped area and contains the pseudopodium near its apex, is separated from the tergite by a deep and brownish

suture. Within the suture is a belt of strong yellow chitin, marked transversely with striae similar to those forming the border to the other segments. The remainder of the sternite is a semi-ovoid area strongly chitinised and almost smooth. This encloses near its apex, posteriorly, the cylindrical pseudopodium, which is by some considered to represent the 10th segment. Surrounding the pseudopodium the 9th sternite is convex and margined with a concentric border of fine striae in a somewhat darker yellow area. The *pseudopodium* itself is white, fleshy and tubular and bears around its base a whorl of eight short, tapering, incurving hairs. It is situated somewhat anterior to the middle of the 9th abdominal segment. The anal aperture is linear and extends across the pseudopodium in the longitudinal axis.

The 9th tergite both above and beneath bears numerous rather long yellow-brown hairs, which are more numerous towards the apex. The 9th sternite, anterior to the pseudopodium, has a transverse row of six hairs, the two median ones of which are shorter and slightly anterior to the rest. A single short hair is also usually present on either side of the pseudopodium.

#### HEAD AND MOUTH-PARTS OF LARVA.

On the dorsal surface of the head there is a *cephalic plate*, expanded anteriorly over the base of each mandible, tapering posteriorly and ending in a point in the occipital region (Fig. 2a). Doubtless it is composed of several fused sclerites, probably the frons, clypeus and labrum. Laterally it is separated from the epicranial plates by a deep suture. In *Agriotes*, and apparently also in *Cardiophorus*, the *epicranial plates* meet for a short distance at the base of the head (vertex) behind the cephalic plate, though in most Elaterid larvae the apex of the cephalic plate extends backwards to the posterior margin of the head and the epicranial plates are dorsally entirely separated by it. On the ventral surface the cephalic plates are fused together posterior to the base of the hypostome and though there is little sign of a suture in the median line, there is a distinctly darker line ventral to the tentorium which probably represents the line of junction. There appears to be no true gula.

In its general plan the structure of the *tentorium* is simple. On the floor of the head at the base two arms extend for a short distance on either side, almost parallel to the thickened margin of the occiput. From the occiput the main longitudinal trunk is carried forward by two beams, closely approximate, on the floor of the head to the base of the maxillae. At this point two small plates of thickened brown chitin are developed

on the tentorium and with these plates the cardines of the maxillae articulate at their posterior apices. From this point one pair of arms extend, diverging somewhat, beneath the margins of the hypopharynx to the inner margin of the mandibles. A second pair, more dorsal, extend forwards, diverging outwardly towards the large flexor tendons of the mandibles, but terminating abruptly with a number of short ligaments before reaching them.

The *antennae* are short and are situated at the anterior angles of the head, close to the base of the mandibles. They consist of (1) a stout basal segment, nearly twice as long as broad, rounded on the outer but almost straight on the inner side, and bearing a rather long tapering seta not far from the apex on the outer margin; (2) a second segment about two-thirds the length of the first and more slender, widest near the apex and bearing a short seta on the inner side of the apex; (3) two processes at the apex of the second segment, borne separately, the ventral and shorter one conical, very thinly chitinised and nearly colourless, the dorsal and longer one more slender, yellow and strongly chitinised, about equal in length to the second segment, though not more than half as broad. The apex of the dorsal process bears a long stiff seta and also three minute ones, all projecting forward, the first-named being longer than the process itself. In Carabid and Staphylinid larvae, where somewhat similar processes are found on the antennae, Kemner<sup>(8)</sup> regards the longer process as the terminal segment and calls the shorter ventral one "supplementärglied." Gahan<sup>(9)</sup> has suggested that the latter is a sensory organ.

Three pores, which appear to have a sensory function, are present in the basal segment. In the second segment a pore bearing a short spine is present on the outer margin near the distal end, while another similar pore may be found near the middle of the anterior margin.

The *eye* is small, dark brown or black, situated laterally, a little below the base of the antenna. The chitin of the head is continued uninterruptedly over it and is not raised.

The *mandibles* are curved inwards and bear on their inner surface two denticles. The first of these, situated near the apex, is flattened dorsi-ventrally and overlaps the mandible of the opposite side when the two are brought together, that of the right mandible usually, but not invariably, overlapping the left. The presence of this denticle is characteristic of the genus *Agriotes* amongst Elaterid larvae, though it is present in certain other groups of coleopterous larvae. It is somewhat rounded in outline, though its anterior margin forms almost a right

angle with the inner edge of the mandible at the point of junction, and projects in the horizontal plane.

The second denticle, also on the inner face of the mandible, is situated nearer to the base. It is much sharper than the first and is on a plane nearer to the ventral surface of the mandible, arising from a point a little within the actual margin. This denticle is called by Schiödte the *retinaculum* and is common to all the Elaterid larvae known with the exception of the section *Agripnini* (of which *Brachylacon murinus*, L. is our only British species) and the genus *Cardiophorus*.

At the base of the inner edge of the mandible there arises a small process of brush-like structure called by Schiödte and Henriksen the *penicillus*. Ford, who gives a figure of the mandible (5), has called this process the "lacinia mobilis," but it is certainly not homologous with the lacinia mobilis of some of the Malacostraca, to which the term was first applied. In them, as Mr L. Borradaile has kindly pointed out to me, the process is independently moveable, whereas the process in *Agriotes* is fixed. Its function seems to be to cooperate with the rest of the dense mass of hairs at the entrance to the mouth in preventing the entrance of unwholesome matter to the mouth. Schiödte, however, refers to it as assisting in the absorption of blood. Several hair follicles are visible on an examination of the dorsal surface of the mandible, of which one is situated about in a line with the *retinaculum* and almost on the outer margin of the mandible: two others are situated nearly in the median line, more basally. The first of these bears a seta of considerable length, which extends obliquely forwards and doubtless has a tactile function.

The mandible itself is of considerable thickness and somewhat excavate on its outer side, but is narrowed on the inner side to form the cutting margin. In transverse section it is therefore almost triangular. Much variation appears to exist in the mandibles of this species, but some of the apparent variation is caused by erosion, mandibles which should normally be sharp-pointed and somewhat long presenting an appearance of stumpy bluntness.

The principal condyle is ventral and articulates with the thickened anterior margin of the epicranial plate, ventral to the base of the antenna.

Between the mandibles, at the anterior margin of the compound structure which has been called the cephalic plate, there is a thickening of the chitin into a tridental process, of which the middle denticle is the longest (Fig. 2 b). This process is situated immediately above the entrance to the mouth and was referred to by the older writers as the clypeus, but

as it probably only represents a portion of the clypeus it is perhaps better to adopt Henriksen's term of *nasale*. This also, like the mandibles, is much subject to erosion and though the three denticles are visible as a sharply pronged trident in some specimens, in others they are worn down to a level with the base. Variation appears to take place to some extent in regard to this organ, one specimen having been found bearing four denticles.

Ventral to the "nasale," nearly apposed to it, and also extending outwardly, is another chitinous process, semi-lunar in shape and bearing

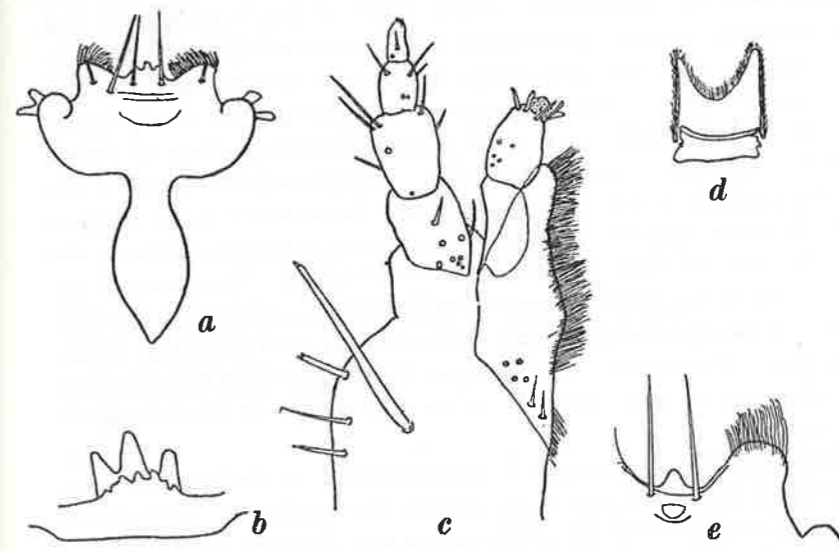


Fig. 2 a. Cephalic plate of larva.  
b. Nasale and subnasal process from beneath.  
c. Anterior portion of maxilla.  
d. Hypopharynx.  
e. Nasale of larva in first instar.

some seven teeth (Fig. 2 b). It does not extend so far as the nasale, the points of the teeth reaching little beyond the base of the nasale. The teeth are asymmetrically disposed and of unequal length. They may also, with the nasale, be supposed to provide a gripping surface in apposition to the mandibles. No suture has been found between the nasale and this process to indicate that it is a separate sclerite, though so much fusion appears to have taken place between the sclerites on the dorsal surface of the head, that it may possibly represent the labrum of other insects. A similar process has been found in the larva of *Dichiro-*



*trichus placidus*, Gyll., a Carabid, by Kemner<sup>(8)</sup>. From the base of this process the chitin is continued in a fairly thick band on the palate of the mouth.

On either side of the nasale the anterior margin of the cephalic plate bears a tuft of fine yellow hairs, screening the opening of the mouth. The aperture itself is small and of a contracted oval shape. Within the mouth, on its lower surface, the *hypopharynx* is situated (Text-fig. 2 d). It is composed of a basal bar of stronger chitin, followed by an anterior portion, less strongly chitinised. This latter is yellow and almost quadrate in form, save for the anterior margin, which is deeply excavated in a semicircular form, leaving a slightly projecting horn at the entrance to the mouth on either side. Its surface, both dorsal and ventral, is covered with minute hairs in transverse rows. The main portion of the hypopharynx is strengthened by a rim of thicker chitin supporting its lateral margins. Its anterior margin and sides, but especially the apices of the projecting horns, bear a mass of fine yellow hairs, which doubtless perform the same function as do those constituting the penicillus of the mandible and the tufts on either side of the nasale. The apices of the horns fit up to the basal portion of the laciniae on either side, the base of the hypopharynx being slightly anterior to the base of the mandibles, but considerably posterior to the nasale. The length of the hypopharynx in a full-grown larva, measured from the exuvia, was .28 mm., the width .26 mm.<sup>1</sup>

Ventral to the hypopharynx but attached to it at the base is a semi-membranous plate, the floor of the mouth. In length it is about double that of the basal plate of the hypopharynx and therefore is considerably less than the hypopharynx itself. In breadth it extends considerably beyond the margins of the hypopharynx and near its antero-lateral margin bears a small tuft of bristles on either side in juxtaposition to those of the anterior margin of the cephalic plate just referred to. The anterior margin is somewhat bowed inwards and is bordered by minute hairs. Ventrally and almost on a level with the side margins of the hypopharynx on either side is a brownish semicircular mark, with five or six alveoli, which may be sensoria, situated in two rows on its anterior border.

<sup>1</sup> Miss A. M. Evans in a recent paper on the hypopharynx and maxillulae (*Journ. Linn. Soc.* 34 (1921), 429-456) figures the hypopharynx of the larva of *Campylus linearis* as representative of Elaterid larvae. She considers the anterior portions which I have called "horns of the hypopharynx" to be vestigial maxillulae. In the absence of more evidence than is at present available, I have some doubt in accepting this homology and therefore use the term used above.

On the ventral surface of the head, bounded on either side by the epicranial plates, the oval *hypostome* is found (Text-fig. 1). It projects forward much beyond the opening of the mouth and is composed of the sclerites of the first and second maxillae. Around its margin, forming the boundary of the maxillary stipites, there is a rim of stouter chitin, corresponding to a similar but even stouter rim at the margin of the epicranial plates. The latter originates close to the point of articulation of the maxillary cardo with the tentorium and reaches almost to the base of the mandibles on either side, gradually becoming more slender as it extends forwards.

Between the two rims of thickened chitin there is a considerable flap of membrane which is ordinarily tucked in between them. At the base of the hypostome, posterior to the submentum and maxillary stipites, there is a considerable field which, save for the two pairs of small sclerites which constitute the cardines, is also membranous. The hypostome is thus capable of considerable extension either in the dorsi-ventral plane or simply forwards, the membranous margin causing it to function as a kind of pouch.

On either side of the hypostome, within the margins of the epicranial plates, there is a long oblique suture of a brownish colour, extending backwards from the base of the mandibles.

The two pairs of small sclerites mentioned above are situated near the base of the maxillary stipites. Each one of the outer pair, which is nearly apposed to the stipes, is of an irregular elongate form with its apex pointing obliquely backwards. Posteriorly it is attached to the tentorium at the second branch of the latter. The innermost pair of sclerites, each of which is nearly circular, is situated near the median line and sometimes overlaps the outer pair, the latter being somewhat beneath the general surface of the cuticle. Henriksen (p. 280) considers these small sclerites to have no importance and says that the outer one is not attached to the tentorium. As I have found it to be so attached, it must be considered to represent the maxillary *cardo*, as Ford has described it. No attempt can be made here to homologise the round sclerite. The outer margin of the *stipes* is rounded, the inner (bordering on the submentum) straight. It is yellow in colour, strongly chitinised and bears at its exterior angle, near the base of the palpiger, two longer and two shorter setae (Fig. 2 c).

The *maxillary palps* are composed of four segments, which gradually contract in width from the basal to the apical segment. They are brownish-yellow in colour and are borne on a whitish palpiger which generally

protrudes considerably from the anterior margin of the stipes. The second segment is longer than any of the others, though not so broad as the first. Two short setae are borne on the first segment, a whorl of four around the apex and two at the outer margin of the second, a similar whorl of four near the apex of the third, and two very short ones near the middle of the fourth. At the apex a series of ten or more exceedingly minute short bristles are present, which must make the palps extremely efficient tactile organs. In addition to the setae a number of pores are present on the palps, of about the same size as the follicles of the setae. These have presumably a sensory function and occur as follows:

Segment 1; a single pore at the base, in the median line of the ventral surface, also a cluster of six pores of varying size near the inner margin: segment 2; one large pore somewhat beyond the middle of the segment and one very small one at its base, both on the ventral surface: segment 3; two pores placed side by side on the ventral surface near the middle of the segment: segment 4; one pore on the outer margin of the segment near its base.

The *galeae* are two-jointed, the first segment being slightly longer than the second. Its outer margin is almost straight, while the inner margin is bowed outwards, almost elbowed. It is without setae and sensory pits. The second segment is rounded at the margin on either side, but the outer is longer than the inner side and the galea inclined inwards by reason of the manner of the articulation of the first with the second segment. A large sensorium is borne near the middle of the segment on the ventral surface, while four or five smaller ones are borne on the outer margin between the middle and the base. The apex of the segment is surrounded by a whorl of six short thick setae and within the whorl a colourless thimble-shaped process is enclosed. This process is inclined inwards and is barely one quarter the length of the preceding segment. It is covered with rounded, colourless scales.

The *lacinia* lies somewhat dorsal to the galea and is partially overlapped by it. It is flattened, composed of a single segment with the apex bluntly pointed, almost triangular and reaching a little beyond the first segment of the galea. On its outer margin it articulates behind (*i.e.* dorsally to) the base of the galea, while its inner margin is continued posteriorly to a level with the opening of the mouth, at the base of the terminal lobe of the labium. The whole inner margin and apex is almost concealed by a dense mass of wavy yellow hairs, which arise for the most part near the outer margin of the organ and protrude into the space before the mouth. At the base, near the angle of the inner margin two

short setae are situated and above them eight or nine pores of varying size.

The *submentum*, which constitutes the basal piece of the labium, is strongly chitinised, elongate with parallel sides and the base bluntly pointed. It extends from a point level with the bases of the maxillary stipites to the point of insertion of the lacinia. Its anterior margin is almost straight and it bears four long tapered setae in pairs at its anterior and posterior angles. Many small pores are found on the surface.

The *mentum* is membranous, nearly colourless, transverse and joined at its sides for about half the length to the inner margins of the laciniae. The anterior half is free. It is joined to the submentum just posterior to the level of the insertion of the laciniae and is produced forwards nearly to the level of the insertion of the galeae. The mentum is broader than the base of the *terminal lobe* of the *labium* which succeeds it but the angles are rounded off.

The terminal lobe itself, composed of the fused palpigers and ligula, is nearly pentagonal in shape. The labial palps are situated one on either side of the anterior margin, while between them the margin protrudes forwards a little in a pale rounded projection, which is evidently the ligula. Further back the palpigers may generally be roughly traced by the darker colour of the cuticle on either side, that overlying the ligula being pale and extending almost to the base of the apical lobe.

A pair of setae are situated dorsally near the apex of the ligula, projecting forwards and a second pair occur ventrally a little posterior to the first. The longest pair are placed one on each palpiger at some distance from the base of the palp, while a fourth pair of quite short spines are found not far from the base of each palpiger.

In addition to the setae there are a number of pores on the ventral surface of palpigers and ligula, as follows: a row of three between the two long setae of the palpigers, a single unpaired one on the left side just behind them, and a pair behind the setae, followed by a single unpaired median pore, while yet another pair occur almost in a line with the short basal spines, one on the outer side of each. All these pores appear to have a rather wide rounded margin with only a very minute aperture (or perhaps a sensory pin) in the middle.

The *labial palps* are each composed of two segments. The basal segment is stout and considerably rounded at the sides, especially on the inner side. It is yellowish like the general surface of the cuticle, but is paler at the apex. The apical segment is only about half the breadth of the basal segment, brownish yellow, slightly turned inwards and gradually

narrowed to the bluntly pointed apex. A pore, probably sensory, is situated near the base of the segment, while a second, bearing a short spine is present near the middle. The apex, like that of the maxillary palp, has an exceedingly minute tuft of short spines, which just break the surface of the cuticle and are visible only under the microscope.

In the basal segment there is a whorl of four moderately long setae near the apex, two of these being ventral, the others dorsal. Two pores are situated near the inner margin of the segment, one behind the other, a third in the median line near the base, and a group of two or three pores near the base of the outer margin.

The pores found on the palps appear to be more open than those on the body of the labium.

#### SPIRACLES OF LARVA.

The two thoracic spiracles are situated in the pleurae of the mesothorax. They are larger than those of the abdominal segments but are otherwise similar in structure. They lie almost, if not quite, parallel to the longitudinal axis of the larva.

The abdominal spiracles, which are present in each of the abdominal segments 1 to 8, are placed in the anterior third of the dorsal scutum on either side, just above the longitudinal groove separating the tergite from the epipleura. In their case the long axis of the spiracle does not lie parallel to that of the long axis of the larva but is raised anteriorly so as to form an angle of some 45 degrees.

The shape of the complete spiracle is elongate oval (Plate IV, fig. *d*) and it is broader in proportion to its length in *A. obscurus* than in *A. sputator*. Each spiracle is provided with two slit-like orifices, between which there is a wide septum, widest at the surface (Figs. 3 *a*, 3 *b*). The septum divides the spiracle completely into two chambers and is continued anteriorly beneath the cuticle. In this portion of the spiracle, which I have named the antechamber, there are a number of pale coloured processes or trabeculae, sometimes branched, which extend far across the lumen of each antechamber. Internally another chamber called the atrium (see Böving<sup>(3)</sup>) comes into apposition with the antechambers and receives the air from them (Fig. 3 *b*). It is not, however, so wide as the width of the two antechambers and the latter are continued a little beyond the opening of the atrium, leaving a slight *cul-de-sac* in each case. From the antechambers the atrium extends inwards (*i.e.* away from the cuticle) for a distance of about double its width to meet the trachea which carries the air thence to the main longitudinal trachea

on either side of the body of the larva. At the point of contact of the atrium and the trachea there is a slight thickening around the latter.

There are no taenidia lining the atrium, but its epithelium is composed of irregular pentagonal cells, which are plainly visible in a stained preparation, even of an exuvia. Miall and Denny<sup>(10)</sup> have described a very similar chamber with polygonal epithelial cells as existing just within the stigmatic orifices of cockroaches and Böving<sup>(3)</sup> has described it in the larvae of *Donacia*, *Hister* and an Elaterid from Java.

The margins of the two stigmatic orifices are thickened into a peritreme of stout brown chitin, the surface of which, as well as the sides and

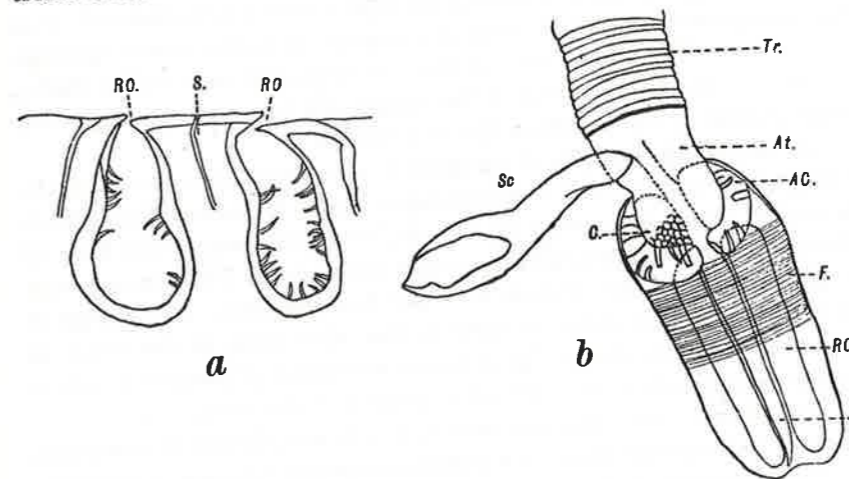


Fig. 3 *a*. Transverse section of larval spiracle.  
*b*. Larval spiracle as seen from beneath.

Sc. = Scar; S. = Septum; RO. = Respiratory orifice; F. = Floor of spiracle; AC. = Antechamber; At. = atrium; Tr. = Trachea; C. = polygonal cells of atrium (a few only shown).

floor of the orifice itself, is transversely corrugated. A fine, somewhat irregular, suture separates the peritreme of each orifice on the surface of the septum. At the anterior and posterior ends of the orifice, the peritreme is narrower, especially at the posterior end. In young larvae of the first and second instars the peritreme is invisible at the anterior end, though present as a narrow ridge of chitin at the posterior end.

The corrugations already mentioned which project as small teeth on either side of the stigmatic orifices, vary in number according to the instar. In the final instar they number some 47 in the thoracic and 40-43 in the abdominal spiracles. In the young larva of the first instar they

number only about seven to eight in the thoracic and five to six in the abdominal spiracles.

Towards the anterior end of the atrium there is attached an apparent strut, connecting the atrium with the outer cuticle near the anterior end of the spiracle but a little more dorsal and running at right angles to the axis of the spiracle. This "strut" is moulted with the exuvia. It is not present in the first larval instar, although present in the second and subsequent ones. Evidently it is the scar left by the withdrawal of the trachea at the last preceding ecdysis, as was pointed out by Schiödte (12, at p. 493). At the point where the trachea has been withdrawn through the cuticle there is an oval scar of a brownish colour at the margin and sometimes bearing a septum of similar colour through its long axis. The central area of this scar is covered with yellow chitin, similar to the general colour of the cuticle and was evidently deposited subsequently to the withdrawal of the trachea.

At ecdysis the position of the spiracle is moved back a little and the lining of the atrium, with a considerable length of tracheal lining from beyond it, comes away with the exuvia, leaving the scar in the body of the newly moulted larva anterior to the new spiracle. This moving back of the spiracle at each ecdysis does not however imply any change in its position in each instar relative to the other parts of the body, as measurements have shown. The extent of the change of position therefore merely corresponds to the increase in growth of the larva.

The necessity for some provision to avoid the difficulty of extracting whole a tracheal tube through a biforous stigmatic opening is manifest. This phenomenon of the growth of a completely new spiracle, alongside the old, appears to resolve the difficulty.

De Meijere (9) found somewhat similar remnants of spiracles in the case of amphipneustic dipterous larvae, although in the cases dealt with by him the cause was apparently the covering of the stigmatic orifice by a membrane, usually complicated, which could scarcely be renewed after ecdysis had taken place.

Böving (3) deals with the anatomy and functions of biforous spiracles in coleopterous larvae and speaks of a "spiracular slit" near the spiracle in *Hister*, which he figures, as well as sections of the spiracles of a larval Elaterid from Java. In neither of these cases do his sections show the "spiracular slit" completely closed, but probably in both cases it represents the scar of the trachea just described.

Scott (13) found biforous spiracles of very similar structure in the larva of *Epuraea depressa*, but he does not describe any scar.

Not infrequently larvae are found having one or more "blind"

spiracles with no opening to the exterior but merely a brown spot of hardened chitin indicating the position of the atrophied spiracle. Probably a functional spiracle would reappear after the next ecdysis, but no investigations into this subject have been made.

#### PUPA.

The pupa has been described by Curtis (4), Beling (2), Ford (5) and others. A few notes on certain points which require amplification are therefore all that it seems necessary to add.

At the base of the pronotum on either side of the median suture a small papilla is placed. These do not bear spines. Nine abdominal segments are visible, the external genitalia being seen in their pupal sheaths in apposition to the ventral surface of the ninth.

In the male, close to the margin of the 8th sternite, there is a rounded and slightly notched flap, which probably represents the 8th sternite of the adult. Posterior to this flap and arising from beneath it are three rounded lobes, the median one not extending so far posteriorly as those on either side of it. Probably these represent the median and lateral lobes of the male external genital organs (Fig. 4a).

In the female (which was the sex described by Ford) the 8th sternite is slightly produced into a blunt point behind and bears two small punctures side by side near the apex. From beneath the 8th sternite the pupal sheath of the ovipositor arises. This is elongate, subparallel and has a deep suture in the median line. At each of the posterior angles there is a small pointed papilla, which is the sheath of the tactile process at the apex of the ovipositor.

The apex of the ovipositor is almost co-terminous with that of the 9th tergite (Fig. 4b). The small spurs observed by Ford (p. 108) at the base of each posterior spine, though frequently present, are not constant and are sometimes present on one side only. Ancillary unpaired spines may also occur on the cerci or even on the median posterior portion of the segment.

In both sexes the sternite of the 7th abdominal segment is produced posteriorly, so as partly to cover the next segment. In the adult the 7th is the last visible segment and the sternite is similarly produced to a blunt point posteriorly. The preceding sternites (2-6) of the pupa have their anterior and posterior margins subparallel as in sternites 3-6 of the beetle. The 1st sternite is very narrow and is represented by a mere fold of the integument. Both tergites and sternites of the 2nd to the 8th abdominal segments are produced laterally a little at the posterior margin, but not so much as to conceal the spiracles.

*Life History of Wireworms*

The apex of the elytral sheath is slightly hooked but less so than in some allied species (e.g. *Athous haemorrhoidalis*). The number of spiracles is the same in the pupa as in the larva. The single thoracic pair is situated ventrally in the membrane between the pro- and meso-thoracic segments, anterior to the intermediate coxae. The abdominal spiracles are situated laterally in the pleurae between the folds of the tergite and sternite, but are not concealed as in *A. sputator*. Those of the first segment are almost in the middle of each pleura, the remainder, on segments 2 to 8, are near the anterior margin of the pleura.

The spiracles are uni-forous, almost circular and bear on their

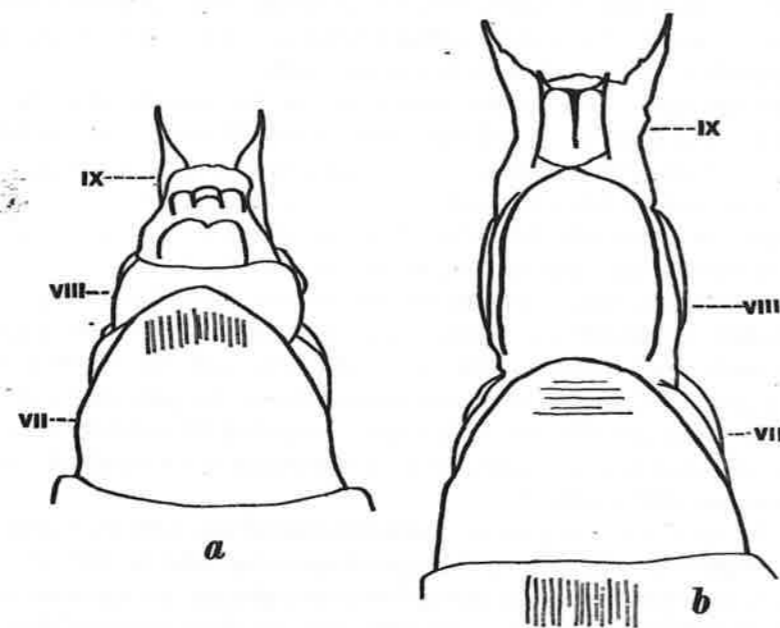
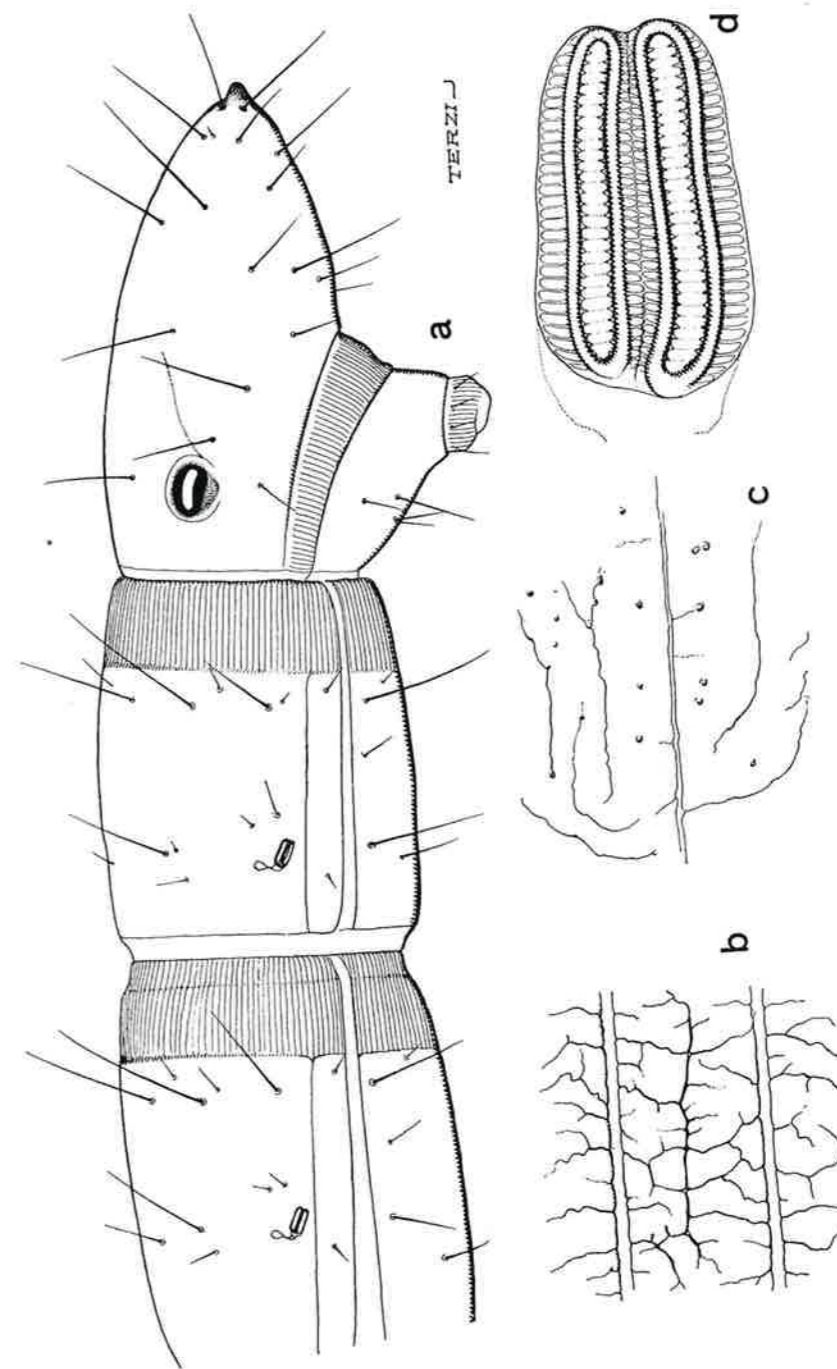


Fig. 4. Terminal segments (a) of ♂ pupa, (b) of ♀ pupa, from ventral surface.

posterior margin somewhat dorsally a small round scar with a fine linear cicatrix in the middle. There is no appearance of any atrium and the taenidia extend to the aperture.

It is interesting to compare the segments and spiracles of the pupa with those of the adult. In the latter there is one pair of spiracles more than in the pupa or larva. There are the same number (eight) in the abdomen, but two pairs in the thorax, situated (1) ventrally, in the membrane between the pro- and meso-thoracic sternites, on either side of the prosternal process and (2) dorsally, in the pleurae of the meta-thorax, beneath the insertion of the wings.



Again, in the abdomen of the adult beetle there are normally visible seven tergites dorsally and but five sternites ventrally, the first two sternites being suppressed beneath the third. Within the 7th segment the 8th is concealed for the greater part of its length. In the female the ovipositor arises from this segment and in the male there are evidences of two rudimentary segments beyond it, as Verhoeff found<sup>(15)</sup>, making ten in all. Stein<sup>(14)</sup> made out nine abdominal segments in the female, considering the ovipositor to be formed of the 9th tergite and 8th and 9th sternites. The eighth, however, is the last segment bearing a pair of spiracles in both sexes, so that the remaining two segments, if true segments, must constitute parts of the ovipositor. The "Vaginal palpe," or tactile process on either side of the aperture of the oviduct, is the terminal one according to Stein.

Therefore though there is considerable similarity between the form of the first seven abdominal segments in the pupa and the adult, the segments posterior to the 7th are entirely different, continuing to taper gently to the apex of the 9th in the pupa, while in the adult they are much narrowed and normally contracted within the body of the beetle.

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## EXPLANATION OF PLATE IV

*Agriotes obscurus*, L. larva in late stage.

- a. Last three segments.
- b. Cuticle of 9th abdominal segment, between the sensory pits (much enlarged).
- c. Cuticle of 8th abdominal segment along the medio-dorsal suture (much enlarged).
- d. Spiracle.

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