

The Morphology and Biology  
of *Anomala vetula* Wied.

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AN ARTHROPOD PEST OF TURF  
IN SOUTH AFRICA

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## INTRODUCTION.

For the past eight years, the Zoology Department of Rhodes University College, in co-operation with African Explosives & Chemical Industries Ltd., has been studying certain entomological problems relating to turf on the golf courses along the coastal belt of the Eastern Cape Province. The position is briefly as follows:- On the golf courses at Mossel Bay, Hunewood (Port Elizabeth), Port Alfred and East London, vast damage has been done to the greens and fairways by "white grubs", the larval stages of Scarabaeidae. It would appear that these beetles had been present in the environs of the courses for many years, but it was only when large areas of the natural veld were converted into fairways, with a more or less uniform cover of grass, with Cynodon dactylon Pers. predominating, that conditions were inadvertently created which favoured the development of the beetles. It was not long after the establishment of these golf courses, that the beetles assumed the proportions of a pest, and the larvae began destroying the root system of the grasses covering the greens and fairways (Omer-Cooper, Whitnall, and Fenwick, 1940).

Fenwick, 1948, has dealt briefly with the position at the respective golf courses, in her work on "Some Arthropod Pests of Turf in South Africa". In view of this

- potential -

potential danger to turf along the coastal belt of the Eastern Cape, it was felt that the Department of Defence should keep a watch on their aerodromes in this part of the country. When beetles have built up a big population of grubs in the turf, these grubs can do much damage in a very short time. The experiences of the golf courses mentioned above are adequate proof of this.

On 25.11.43 Dr. Hall and Mr. Whitnall visited the aerodrome at 42 Air School, Port Elizabeth. The aerodrome had a good covering of "kweekgras" (Cynodon dactylon Pers.), and on the surface all appeared well. There was, however, much evidence of the activities of insectivorous moles, and experience had shown that this was generally indicative of the presence of insects, beneficial or otherwise, in the soil. Excavations were made at the aerodrome, and under an area of turf 2 ft. x 3 ft., forty-eight "white grubs" were found. This dense population compared with that found in the devastated areas on the Humewood golf course, situated about three miles distant from the aerodrome.

It was felt that the "white grub" population on this aerodrome could not be overlooked. The identity of the grubs was not known, but they were not Macrophylla pubens Perring., the pest at Humewood.

In the literature Anomala orientalis Waterh.

and the closely allied Popillia japonica Newm. were recorded as serious pests of turf in America. In view of the limited knowledge of "white grubs" which we have in South Africa, it was decided that a detailed study should be made of this beetle, Anomala vetula Wied., in order that its relation to turf might be better understood.

MORPHOLOGY.

1. THE EGG.

The newly laid eggs are fairly uniform in appearance and size. They are white and have a smooth surface, which is sticky, owing to a secretion from the colleterial glands of the female, which cause sand particles to adhere to the egg. The shape of the egg is oval; only a few eggs vary from this form. Fenwick, 1942, p.154, states that difficulty was experienced in measuring eggs of Macrophylla n. sp. (= pubens Péring.) because, as they increased in size, they became more fragile. In Anomala vetula Wied. the chorion remained strong throughout development.

It is characteristic of the eggs of Lamellicornia, that the shape and size change during growth after deposition. (Inns, 1934, p.538). In the subfamily Rutelinae (Hayes, 1929, p.74-76), this has been recorded in Anomala binotata Gyll. (Hayes, 1918, p.141), Anomala kansana H. and McC. (Hayes and McCulloch, 1925, p.592), Popillia japonica Newm. (Smith and Hadley, 1926, p.14), Phyllopertha horticola L. and Anomala seneca Geer. (Rittershaus, 1927, pp. 389-390, and p. 403), and Anomala orientalis Waterh. (Friend, 1927, p.362). The increase

in size is dependent on the absorption of moisture from the soil.

Measurements of twenty-five eggs of Anomala vetula Wied. that were five days old, had a mean length of 1.9 mm. a mean diameter of 1.4 mm. The appearance of the egg undergoes striking changes five days after deposition. It becomes pearly white in colour. After seven days the mean length had increased to 2.3 mm., and the mean diameter to 1.6 mm. After this stage the increase in width is greater in proportion to the increase in length, so that the egg loses its elliptical shape, and becomes rounded. Sand particles do not adhere after twelve days. The maximum size was reached twelve days after deposition, when the mean length was 2.6 mm., and the mean diameter 2.2 mm. The largest egg was 2.7 mm. long and 2.3 mm. broad.

## II. THE THIRD LARVAL INSTAR.

### 1. External features. (Fig. 1.)

The larva of Anomala vetula Wied. is cruciform. This type is common among Lamellicornia. (Dms, 1934, pp. 192-193, and p. 490). The three larval instars are similar in shape, in the relative length and width of the appendages, and in the general arrangement of setae. They can be distinguished most easily on the proportional increase in size of the head-capsule of succeeding instars. They differ in features of minor importance, relating to the number of setae, and degree of chitinisation of body areas, which will be dealt with in the following chapter.

When the larva is at rest, the body is bent ventrally in the form of a "U". The curvature becomes increasingly pronounced in successive instars, until in the third instar the mouthparts and the raster, on the ventral surface of the last abdominal segment, lie close together.

The body is subcylindrical. The head-capsule remains constant in size during an instar, but the size of the body varies considerably, according to the age of the grub and the amount of feeding, as in the larvae of Phyllopertha horticola L. and Anomala aenea Geer. (Ritterhaus, 1927, pp. 339-340).

Measurements of the size of the body are not therefore of great value, and hence they are not included here. The

ratio of the size of the head-capsule to the body size is greatest in newly hatched or freshly moulted specimens, and decreases as development proceeds within the instar.

The body segments are subdivided into annulets, which obscure the primary segmentation. They overlap one another, and allow for the bending and straightening of the body, in its alternation from a stationary to a crawling attitude.

The head-capsule is attached directly to the prothorax, without an intervening neck membrane. The three thoracic segments are slightly dorso-ventrally flattened. This is especially pronounced in the third instar, so that in a lateral view, the thorax appears almost concave, in comparison with the rounded abdomen.

Each thoracic segment bears a pair of legs. They are light brown in colour, and increase in size from the first to the third pair. In the first instar they are relatively conspicuous, in comparison with the small size of the body. In later instars, active feeding causes the body to increase in size, and the legs become comparatively small.

The first six abdominal segments are almost equal in size. The remaining segments become enlarged, owing to the distension of the posterior region of the alimentary canal during feeding. The last segment is tapering, and terminates

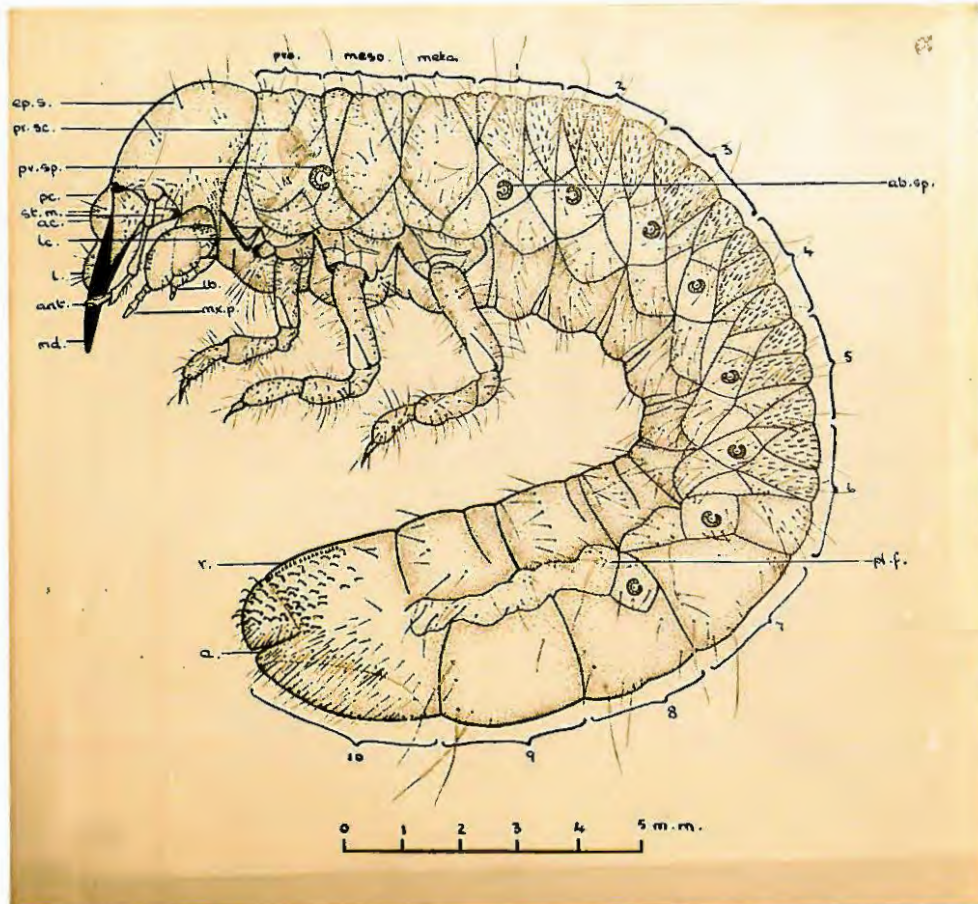


Fig. 1. = Third Instar Larva. : ANOMALA VETULA WIED.

- 1 - 10 = abdominal segments.
- ac. = anteclypeus.
- ant. = antenna.
- a. = anus.
- ep. s. = epicranial suture.
- ab. sp. = first abdominal spiracle.
- lb. = labium.
- l. = labrum.
- lc. = laterocervicalia.
- md. = mandible.
- mx. p. = maxillary palp.
- meso. = mesothorax.
- meta. = metathorax.
- pl. f. = pleural fold.
- pc. = postclypeus.
- pro. = prothorax.
- pr. sc. = prothoracic sclerite.
- pr. sp. = prothoracic spiracle.
- r. = raster.
- st. m. = stridulating area of mandible.

in a transverse anus.

The head-capsule is strongly chitinised, and dull ochre in colour. The mouthparts are attached to the ventro-lateral margin. The body is soft, and covered by a thin, though firm, transparent integument, with a vestiture of scattered hairs and bristles. The creamy white colour of the body is due to the accumulation of fat deposits beneath the integument. The last 2-3 abdominal segments are a greyish-blue colour. This is due to the presence of food in the posterior parts of the alimentary canal of the actively feeding larva, and the absence of fat deposits in this region. Here the fine silver trachea are particularly clear. The closely set asperites on the terga of abdominal segments 1-6, give these segments a superficial light brown appearance.

The first thoracic segment bears a roughly triangular shaped prothoracic sclerite, and a smaller chitinised area ventral to it, above the pleural fold.

The sieve plates of the spiracles are conspicuous light brown structures on the sides of the body. The thoracic spiracle is large; the concavity of its sieve plate is directed posteriorly. The remaining eight pairs of spiracles, situated on abdominal segments 1-8, are smaller, and have the concavity of their sieve plates directed anteriorly.

The third instar larva has been chosen for

- description -

description, as here the degree of chitinisation, and the arrangement and number of setae is complete.

(a) The Head.

The Head-capsule. (Figs. 1 and 2).

The head-capsule, or cranium, consists of those immovable parts of the head situated above the frontoclypeal, or epistomal suture. It is the most strongly chitinised part of the body.

The head is hypognathous, the facial aspect being directed forwards, and the mouthparts suspended from the ventro-lateral margins of the head-capsule. This condition is seen when the larva is at rest. In the active larva, however, the mouthparts are directed forwards, so that the long axis of the head is antero-posterior. In this prognathous attitude the mouthparts assist in burrowing through the soil, and rasp off grass roots.

The head-capsule is narrower than the pro-thorax. The width below the bases of the antennae varies from 3.8 mm.-5.0 mm., with a mean 4.41 mm. for thirty specimens. The cranium is broader than long. The length from posterior margin to the frontoclypeal suture, varies from 2.5 mm.-3.4 mm., with an average of 2.71 mm. for thirty specimens.

It is hemispherical in shape. Dorsally the anterior margin is straight, but the posterior margin is semi-circular. It is dorso-ventrally flattened, the dorsal

- surface -

surface being convex, and the lateral and posterior margins broadly rounded. It is dull ochre in colour, shading into dark brown at the dorsal and ventral articulation parts of the mandibles. The "Y"-shaped epicranial suture is incomplete. The epicranial arms, or frontal sutures, do not reach the subgenal ridge, but terminate slightly posterior to it, between the point of attachment of the antenna, and the dorsal articulation point of the mandible. They are fine and colourless and are not impressed. Anteriorly the sutures are slightly concave to the inside, posteriorly they straighten. They meet behind the centre of the dorsal surface of the cranium, at an angle of approximately  $90^{\circ}$ . The epicranial stem or coronal suture, extends from the junction of the frontal sutures to the middle of the posterior margin of the head-capsule. It is slightly impressed, and more distinct than the frontal sutures. It is approximately one-third of the length of a frontal suture. The posterior two-thirds of the coronal suture form a darkly coloured internal keel, or endophragma, for the attachment of muscle (Subklew, 1938, p. 274). The head-capsule splits along the epicranial suture at the time of moulting. The median triangular facial region, between and anterior to the frontal sutures is the frons. Distally it is bounded by the frontoclypeal suture, which connects the

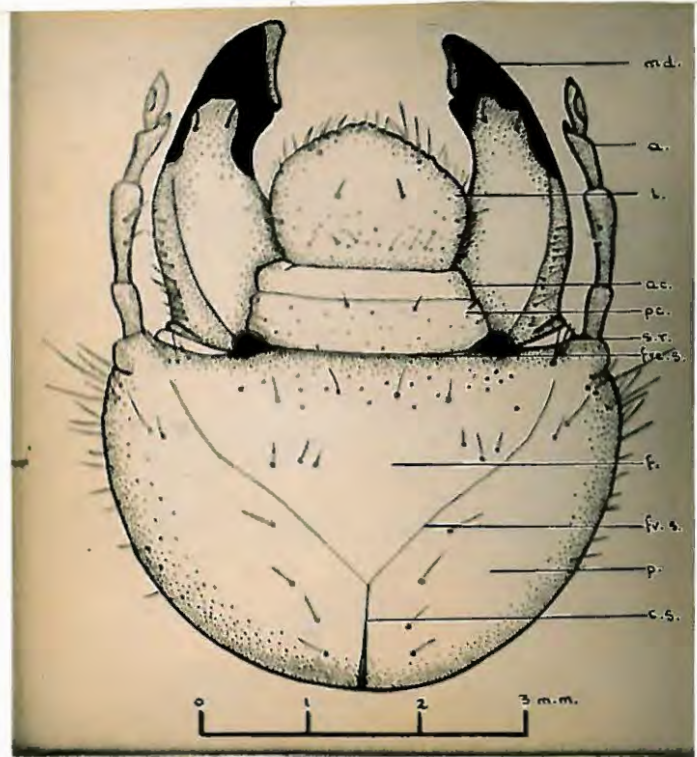


Fig. 2. = Dorsal view of Head-capsule of  
Third Instar Larva.  
ANOMALA VETULA WIED.

- ac. = anteclypeus.  
a. = antenna.  
f. = frons.  
c. s. = coronal suture.  
fr. s. = frontal suture.  
fr. s. = frontoclypeal suture.  
l. = labrum.  
md. = mandible.  
p. = parietal.  
pc. = postclypeus.  
s. r. = subgenal ridge.

dorsal articulation points of the mandibles.

The ventral and lateral margins of the head-capsule form the thickened subgenal ridges. The epistomal suture, with its corresponding epistomal ridge, separating the clypeus from the frons, is well developed. It unites the anterior ends of the subgenal ridge.

Each antero-lateral angle of the frons near the condyle, bears a group of 2-5 setae; usually two of these are long and the remainder short. The anterior margin has two moderately long setae on either side of the median line. Between these, and the condyle, is one short seta. There is a transverse row of 2-4 setae on either side, anterior to the straight portion of the lateral outline of the frons. The anterior half, behind the entire frontoclypeal suture, bears scattered, small, round sense pits.

The areas posterior to, and on either side of, the frontal sutures, are the parietals. (Crampton, 1921, p. 71).

They are separated dorsally by the coronal suture. They extend posteriorly to the occipital suture, and laterally are continuous with the genae. Each parietal bears an oblique series of four hairs, one opposite the fork of the epicranial suture, one anterior to this, and two posterior. There are a few setae round the antennal base. Posterior to these are two setae, the anterior longer than the posterior. The lateral margin of the

head-capsule bears two long setae, and a number of smaller ones. The posterior lateral margin bears a few small setae. The anterior ventral surface of the gena is clothed in moderately long setae. Ocelli are absent.

The occipital foramen occupies a large part of the posterior surface of the head-capsule. It is narrower and more rounded ventrally than dorsally. A narrow postocciput surrounds the occipital foramen, and to it is attached the first thoracic segment. It is marked off from the rest of the cranium by a postoccipital suture, which follows the outline of the foramen laterally and dorsally, but ends anteriorly, on either side, in the posterior tentorial pits. The post-occipital suture forms an internal ridge. Lateral to the post-occiput is the wide occiput, marked off from the gena, by the occipital suture, which runs parallel to the post-occipital suture. Ventral to the occiput, is a small, triangular postgena, separated from the occiput by an occipito-postgenal suture. The postgena bears the ventral articulation points of the maxillae. The occipital suture ends ventrally in a darkly sclerotised patch, above the ventral articulation point of the mandible. It disappears dorsally so that here the postgena and occiput are continuous.

The tentorium.

The tentorium is the very delicate endoskeleton of the head. It is composed of three pairs of apodemes.

The hypostomal portion of the subgenal ridge, between the ventral articulation points of the mandibles, is produced internally to form a bridge. On it the posterior tentorial arms arise, from the posterior tentorial pits, situated at the ends of the post-occipital sutures. The bases of these arms are expanded, and lie close together in the middle line. As the posterior arms extend forwards they diverge slightly.

The anterior tentorial arms arise from the anterior tentorial pits, which are situated slightly lateral to the dorsal articulation points of the mandibles. They run posteriorly into the head cavity and unite with the posterior arms.

The dorsal tentorial arms originate from the anterior arms. They are attached to small maculae, situated to the outside of, and halfway along the frontal sutures, on the external surface of the head-capsule. Similar depressions are present lateral to the frontal sutures in Melolontha hippocastani Fabr. (Subkiew, 1933, p. 274), but to the inside of the frontal sutures in Canthon laevis Drury and Euphoria inda L. (Hoyes, 1939, p. 13). They are presumed to be the points of attachment of the dorsal tentorial arms.

The Antennae. (Figs. 1, 2 and 3).

The antennae are a pair of slender jointed appendages, situated lateral to the extremities of the frontoclypeal suture, midway between the dorsal and ventral articulation points of the mandibles. When extended they are as long as the mandibles. In the active larva they are directed laterally, with the two terminal segments turned forwards. At rest they point ventrally, the ultimate and penultimate segments projecting slightly inwards and upwards.

The proximal segment, between the shaft of the antenna and the head-capsule, is immovable; the four remaining segments are freely movable. Two opinions are held as to the morphological value of the basal segment, and the consequent number of segments comprising the antenna.

According to the interpretation of Hayes, 1929, p. 119, and Fidler, 1936, p. 119, the antenna is five-segmented. Schiodte, 1874, p. 511, Crampton, 1921, p. 73, Grandi, 1925, p. 160, Ritterhaus, 1927, p. 354, Böving, 1935, p. 170, Subklew, 1938, p. 277, and Viado, 1939, p. 349, regard the antenna as four-segment, the basal segment not being regarded as a true segment. I consider the antenna as four segmented, the immovable basal segment as a projection of the head-capsule.

- 14a -

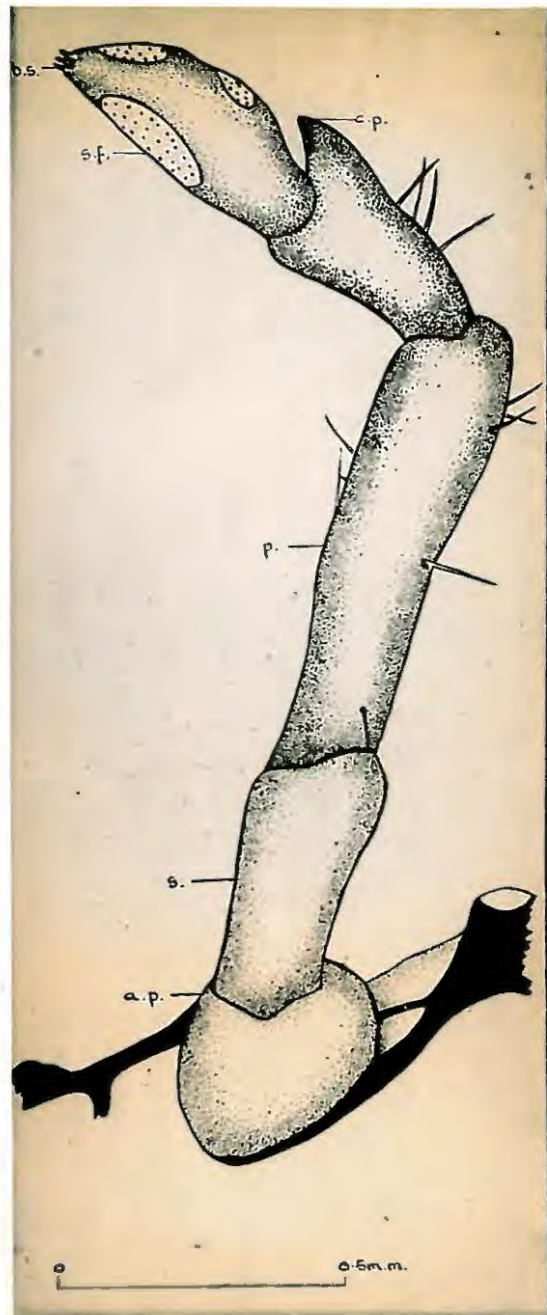


Fig. 3 - Antenna of Third Instar Larva.  
ANOMALA VETULA WIED.

- a.p. = antennal prominence.
- b.s. = basiconic sensilla.
- c.p. = conical process of third segment.
- p. = pedicel.
- s. = scape.
- s.f. = sense field.

A narrow chitinous ring extends ventrally, from the dorsal surface of the base of the antenna, to the chitinous border of the triangular membranous area, at the base of the mandible.

The immovable antennal prominence is short and conical. The first segment, or scape of the antennal shaft, is nearly twice the length of the antennal prominence. The length is twice the breadth; it expands distally. The second segment or pedicel is the longest; it is three times the length of the antennal prominence. It widens gradually, from about one-third of the distance from the base, to the distal end. The third segment is equal in length to the scape, and is produced distally, on the inner ventral surface, into a conical process, which extends about one-third of the length of the terminal segment. The fourth segment is equal in length to the third segment. It is widest slightly distal to the level to which the conical process of the third segment extends; it tapers distally. It is asymmetrical, the inner side being more convex than the outer.

On the fourth segment there are three well developed sense fields, or sensilla placodes (Böving, 1936, p. 170). The largest of these is oval, and extends lengthwise

along the inner surface. There are two smaller sense fields, running round the outer surface. The smallest field is on the inner surface of the ventral process of the third segment. These fields are convex, semitransparent plates, perforated with pores.

The antennal prominence, and the four antennal segments, bear scattered sense pits. The antennal prominence and the scape are without hairs. The pedicel has 4 - 5 hairs, along the inner ventral surface, and 2 - 3 hairs dorsally. The third segment bears one to four hairs in a ventral longitudinal row, behind the conical process. The terminal segment is without hairs.

The tip of the fourth segment is a sense receptor, with 7 - 8 basiconic sensilla, arranged in an irregular circle. Eight small pegs are described in this position in Malolontha hippocastani Fabr. (Subklew, 1938, p. 277), and twelve in Macrophylla pubans Péring. (Fenwick, 1942, p. 93). There are one, or occasionally two basiconic sensilla distal to the sense field of the third segment, but not quite at the tip of the conical process. There are three chitinous pegs on the tip of this segment, and two, more proximal, in Phyllopertha horticola L. (Ritterhaus, 1927, p. 354).

The levator and depressor muscles which move the antennal shaft, arise from inside the head-capsule and

are attached to the proximal end of the first segment.

The Clypeus. (Figs. 1, 2 and 4).

It is trapezoidal in outline, with anterior and posterior margins subparallel. The shorter anterior margin is attached to the labrum, which it overlaps.

The anterior angles are rounded. At the widest point it is two and a half times broader than long.

The clypeus is divided transversely into a distal anteclypeus, and a proximal postclypeus.

The anteclypeus is membranous and white, without hairs or sense pits. The postclypeus is more strongly sclerotized, especially along the lateral and posterior margins. The setation is sparse and symmetrical. There are 2 - 3 lateral setae, situated one behind the other. Between the anterior lateral seta and the middle line, there is one seta on either side.

The Mouth-parts.

The larva has typical biting mouth-parts, arranged in an ellipse round the ventral margin of the head-capsule.

The clypeus is attached to the frons.

The labrum is hinged to the distal margin of the anteclypeus. The membranous ventral wall of the labrum and clypeus forms the epipharyngeal surface of the preoral cavity, and is continuous with the dorsal wall

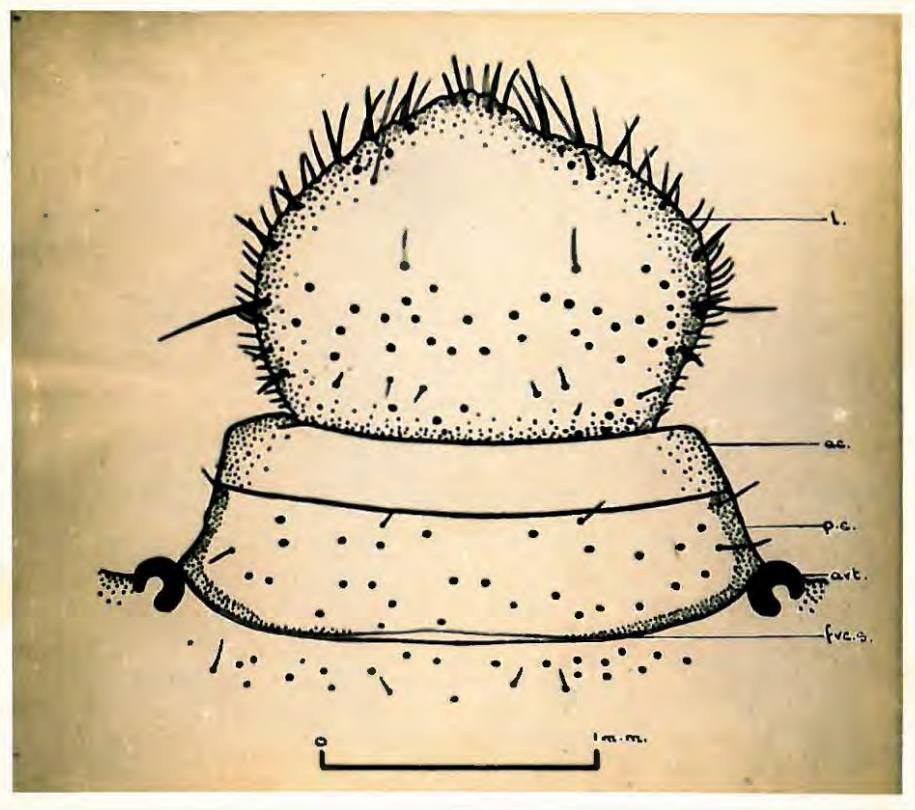


Fig. 4. = Clypeus and Labrum of  
Third Instar Larva.  
ANOMALA VETULA WIED.

- ac. = anteclypeus.  
art. = dorsal articulation point of mandible.  
frc.s. = frontoclypeal suture.  
l. = labrum.  
p.c. = postclypeus.

of the pharynx. The mandibles bound the mouth cavity laterally. In an anterior view the mandibles and labrum obscure the maxillae and labium. The floor of the mouth cavity is formed by the membranous extension of the hypopharynx. The dorsal surface of the mandibles is connected with the membranous epipharynx, the ventral surface with the maxillae. These membranes are continuous with one from the inner angle of the base of the mandible, and they close up round the opening of the pharynx.

The membranous ventral surface of the maxillae is attached to the lateral margin of the postmentum of the labium.

(1) The Labrum and Epipharynx (Figs. 1, 2, 4 and 5).

The labrum is an unpaired lightly sclerotised plate, capable of limited up and down movement.

It is one and a half times wider than long. The length is one and a half times that of the clypeus; it is mitriform, somewhat asymmetrical, the anterior projection being displaced to the left of the median line, and the right antero-lateral margin being slightly depressed. The apex is crenulate, and the antero-lateral margins have three obtuse dilations. The surface is rugose, as in Anomala kansana H. and McC. (Hayes, 1927, p. 176), with scattered sense pits and a characteristic

arrangement of hairs.

The apical projection has four moderately long stiff setae. Posterior and lateral to these, there is a single seta on either side. Near the centre and further back, is a pair of shorter hairs; all these hairs are directed anteriorly. On either side, and slightly posterior, is a single seta, directed outwards. There is a transverse row of delicate setae at the base of the labrum. The majority of the sense pits are situated between this row, and the median pair of hairs, but a few scattered sense pits occur posterior to them. Anteriorly there are 2 - 3 sense pits, at the base of the obtuse lateral dilations. Submarginally a row of short hairs extends posteriorly from these dilations, to the base of the labrum.

The epipharynx forms the ventral surface of the labrum and clypeus.

It is attached to the free margin of the labrum, and thus, is somewhat asymmetrical, with the anterior projection displaced to the right of the median line. The junction between the labrum and clypeus is marked by the tommae, situated laterally in the angle of the labrum and clypeus, and extending towards the middle line. Posteriorly, the boundary of the epipharynx is marked by the transverse, anteriorly concave crepis.

Earlier workers on the epipharynx include Schiödte, 1874, who figured the epipharynx of Geotrupes. Böving, 1931, figured and briefly described the epipharynx of Popillia japonica Newm. Rittershaus, 1927, pp. 342-344, and p. 368, described and carefully figured the epipharynx of Phyllopertha horticola L. and Anomala aenea Geer., and was the first to name some of the various parts. Hayes, 1927, p. 197, described the epipharynx of Anomala kansana H. and Mc.C. and demonstrated the taxonomic importance of the structural details of the epipharynx in larval Lamellicornia. Sim, 1934, distinguished Scarabaeid larva with the aid of detailed epipharyngeal structure. Böving, 1936, p. 176-181, assigned new names to special parts of the epipharynx which he applied in a study of larvae of Popillia japonica Newm. (Böving, 1939, pp. 184-185), and the genus Phyllophaga (Böving, 1943).

The terms used here in referring to special parts of the epipharynx are those proposed by Böving, 1936, pp. 176-181. A table for comparison of terms used by various authors appears at the end of the description of the epipharynx of Anomala vetula Wied. Throughout the description "right" refers to the left-hand-side of the figure, and vice versa.

The epipharynx of Anomala vetula Wied. is similar to that described for other species of the Tribe Anomalini. The main differences occur in the number and arrangement of hali on the hapternum, the form of the epixygam and xygam, the number of sensilla of the hapternum and the number of marginal spines. The Tribe Anomalini shows affinities to the Melolonthinae, in the presence of plegmatia and in the structure of the sensory areas, including the hali, which, however, are fewer in number than in the Melolonthinae. In the absence of plegmatia the Tribe Rutelini shows a relationship to the Dynastinae.

The clythrum is absent, so that corypha and acroparia are united into a large apical region bearing spinelike setae inserted in basal rings. These setae are nearly vertical to the plane of the epipharynx. This subtriangular region has free antero-lateral margins, following the outline of the labrum, with three obtuse dilations on either side, each bearing a large seta. The anterior irregular emargination bears four spine-like setae; two setae are inserted ventral and towards the inside of these. The posterior limits of this region may be determined as being situated in front of the plegmatia and xygam.

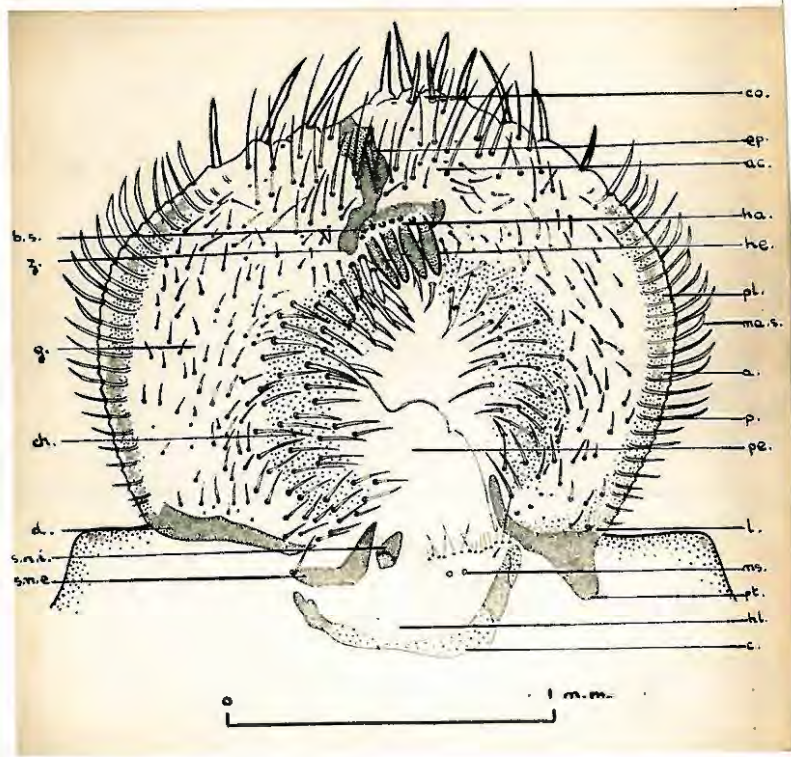


Fig. 5. = Epipharynx of Third Instar Larva.  
ANOMALA VETULA WIED.

- |        |   |                           |
|--------|---|---------------------------|
| a.     | = | acanthoparia.             |
| ac.    | = | acroparia.                |
| b.s.   | = | basiconic sensilla.       |
| ch.    | = | chaetoparia.              |
| co.    | = | corypha.                  |
| c.     | = | crepis.                   |
| d.     | = | dextotoma.                |
| ep.    | = | epizygum.                 |
| g.     | = | gymnoparia.               |
| hl.    | = | heptolachus.              |
| ha.    | = | haptomerum.               |
| he.    | = | helus.                    |
| l.     | = | lacotor_ma.               |
| ms.    | = | macrosensilla.            |
| ma.s.  | = | marginal spines.          |
| pe.    | = | pedium.                   |
| p.     | = | plegna.                   |
| pl.    | = | plegnatium.               |
| pt.    | = | ptemotoma.                |
| s.n.e. | = | sclerome nesium externum. |
| s.n.i. | = | sclerome nesium internum. |
| z.     | = | zygum.                    |

The epizygum is connected with the right arm of the zygum; the left arm of the zygum is incomplete, being represented by a small sclerotized area, not connected with the epizygum. Along the inside of this discontinuous zygum is a row of 6 - 10 large, approximately equidistant, basiconic sensilla. The heli vary from 3 - 5 and are strong, dark, immovable spines, arranged in a single row, directed posteriorly. There are 3 - 4, usually three heli, in Phyllonertha horticola L. (Rittershaus, 1927, p. 343). According to Hayes, 1939, p. 75, in a key to genera of the subfamily Rutelinae, in the genus Anomala, two spines of the distal sensory area of the epipharynx are fused at the base to form a bifid cone. This was not found to be a constant feature in the larvae of Anomala vetula Wied. These sensilla and heli together form the prominent overhanging heptomeres or distal sensory area (Hayes, 1936, p. 205). The labrum is thickest at this part.

The proplegmatia are absent. The acanthopariae carry 21 - 27 marginal articulated spines, inserted in strong basal rings.

The anterior 12 - 15 spines are broad and ooltrifera, curving forwards. The remainder are

- straight -

straight, decreasing in length posteriorly, the setae at the base of the epipharynx being small and weak. From the base of each marginal spine, a short transverse chitinous carina extends inwards. These plegma decrease in length posteriorly, corresponding to the decrease in length of the marginal spines. The anterior 2 - 3 plegma may not reach the lateral margin. According to Heyes, 1938, p. 285, these lateral striae are characteristic of Melolonthinae and the Tribe Anomalini, and occur only in these two groups. The absence of lateral striae in the Tribe Rutelini distinguishes it from the Anomalini.

The central pedium is depressed, and free of hairs. It is longer than broad, asymmetrical, and bordered laterally by the curved articulated setae of the chaetoparia. These setae are directed towards the centre of the pedium, and become more widely separated, and smaller, towards the plegmatia. They are more numerous on the right than on the left side of the pedium. The setae of the gymnopariae are poorly developed. The distal 2 - 3 setae of the right chaetoparia are stronger than the rest, but may be distinguished from the heli by their basal rings. The pedium is traversed by a diagonal fold

- extending -

extending from the distal region of the right chaetoparia to the inner end of the left torma.

The right and left tormae are asymmetrical chitinised sclerites. The laetorma is provided with a posterior pternotornal process, but the anterior branch is entire, not being divided into epitornal and apotornal prolongations. The dextorma is straight and simple without processes.

The semicircular proximal sensory area (Hayes, 1928, p. 235), or heptolachus, extends posteriorly from the inner ends of the tormae to the crepis. Most of this field lies ventral to the anteclypeus. The crepis is a continuous, asymmetrical, anteriorly, concave bar, more heavily chitinised laterally than medially. A transverse row of about fifteen delicate hairs extends towards the middle from the left end of the crepis. At the inner end of the dextorma is a "V"-shaped chitinous plate (Hayes, 1928, p. 235), or sclerome nesium externum, attached basally along one arm of the "V", with the other arm directed anteriorly. 1-3 long hairs are attached to the right end of the base. The conical sense cone (Rittershaus, 1927, p. 343), or nesium internum, is smaller than the right nesium and situated in the median longitudinal line. The inner surface of the nesium internum bears two sensilla. There are two

macrosetae situated posterior to the transverse series of delicate hairs, to the left of the haptolachus.

The haptomerus projects into the space between the curved inner edges of the mandibles, the heli probably assisting in tearing roots apart. The complicated arrangement of sense structures on the surface of the epipharynx is presumably for the perception of taste stimuli. The labral muscles are attached to the inner surface of the frons and are inserted on the inner ends of the tormae.

	Böving 1936	Rittershaus 1927	Hayes 1929	Sim 1934
acanthoparia	-	-	-	-
acroparia	-	-	-	-
apertoma	-	-	-	-
chaetoparia	-	-	-	-
clithrum	-	-	-	-
corypha	-	median lobe	(apical or (median lobe	
crepis	{ ring-shaped { chitinous { thickening	{ transverse { strongly { bowed bar	-	
dextertoma	{ chitinous { strip	right toma	right toma	
epitoma	-	-	-	
epizygum	-	-	-	
gymoparia	-	-	-	
haptolachus	-	(proximal (sensory area	epigusta	
haptomerum	-	(distal (sensory area	(sensory (eminence	
heli	{ chitinous { pegs	{ chitinous { spines	{ fixed spines { or teeth	
laetoma	{ chitinous { strip	left toma	left toma	
marginal spines	bristles	{ lateral { setae	{ articulated { lateral spines	
nesium(right)	{ chitinous { plate	{ chitinous { plate	{ clypeal { sclerotised plate	
nesium(left)	sense cone	sense cone	sense cone	
paria	-	{ rounded { lateral { margin or { lobe	-	

Böving 1936	Rittershaus 1927	Hayes 1929	Sim 1934
pedium	{ furrow free of { bristles	{ clear non- { setose { central area	{ central bare { area
phoba	{ delicate { bristles	{ cluster or { group of { delicate { slender fixed { spines	sensory hairs
plegma	-	-	-
plegnatium	striae	lateral striae	marginal striae
proplegmatium	-	{ submarginal { striae	-
pternotoma	-	-	-
sensillum	sensillum	sensillum	sensilla
zygus	-	-	{ distal { sclerotised { plate

(2) The Mandibles. (Figs. 1, 2, 6 and 7).

These are the largest and most heavily chitinised of the mouthparts.

They are situated on either side of the clypeus and labrum. They are longer than broad, the distal darkly sclerotised tips projecting beyond the anterior margin of the labrum, when they are closed. They are the chief organs of mastication, and are particularly well developed, on account of the burrowing habit of the larva.

The base is triangular, the basal angles forming the dorsal and ventral articulation points of the mandible with the anterior margin of the head-capsule.

The dorsal ginglymus fits onto a projection at the base of the lateral margins of the clypeus. The ventral condyle fits into a socket at the lower edge of the gena. Between the two articulation points the base is convex, and between it and the point of insertion of the antenna, is a membranous triangular area, attaching the mandible to the head-capsule. It is probably homologous with the basimandibula (Crampton, 1917).

The inner angle of the triangle forms the molar region.

In a dorsal or ventral view the mandibles are sickle

- shaped -

shaped. Looked at from the inner margin, the proximal molar region is slightly oblique, the anterior portion being inclined ventrally, the posterior dorsally. The incisor edge follows an oblique inclination in the same direction as that of the molar region, but it is more exaggerated. It thus appears as though the proximal portion of the incisor edge had been turned dorsally. Hence, the outside lateral surface decreases only slightly towards the apex, due to this turning of the incisor edge. This forms a slight spoon-shaped cavity, suitable for scraping away earth.

The distal half of the ventral surface of the mandible is concave; the proximal half is almost straight. The outside and dorsal surfaces are convex.

The centre of the dorsal surface and the scrobis are yellow. A longitudinal reddish-brown strip, running anteriorly from the dorsal acetabulum, separates these two parts. The ventral stridulating area is yellow, becoming reddish-brown towards the incisor and molar regions, which are black. The distal heavily chitinised incisor area has a sharp cutting edge, the Pars incisiva (Subkiew, 1958, p. 232), limited posteriorly by a small notch. Proximal to the notch, the edge is produced into a small tooth. The Pars incisiva of the left mandible is concave, and longer than the right; the right is "S"-shaped.

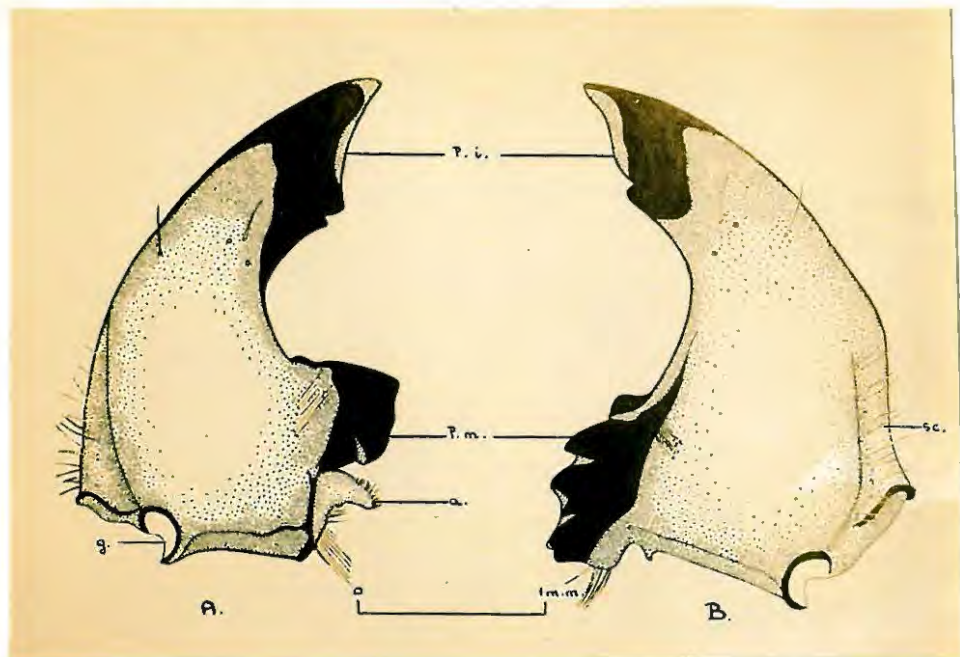


Fig. 6. = Dorsal view of Mandibles of Third Instar Larva.

ANOMALA VETULA WIED.

A. Left Mandible.

B. Right Mandible.

a. = acia.

P.i. = Pars incisiva.

c. = condyle.

P.m. = Pars molaris.

g. = ginglymus.

P.a. = Processus accessorius.

h. = heel.

st.a. = stridulating area.

sc. = Scrobis.

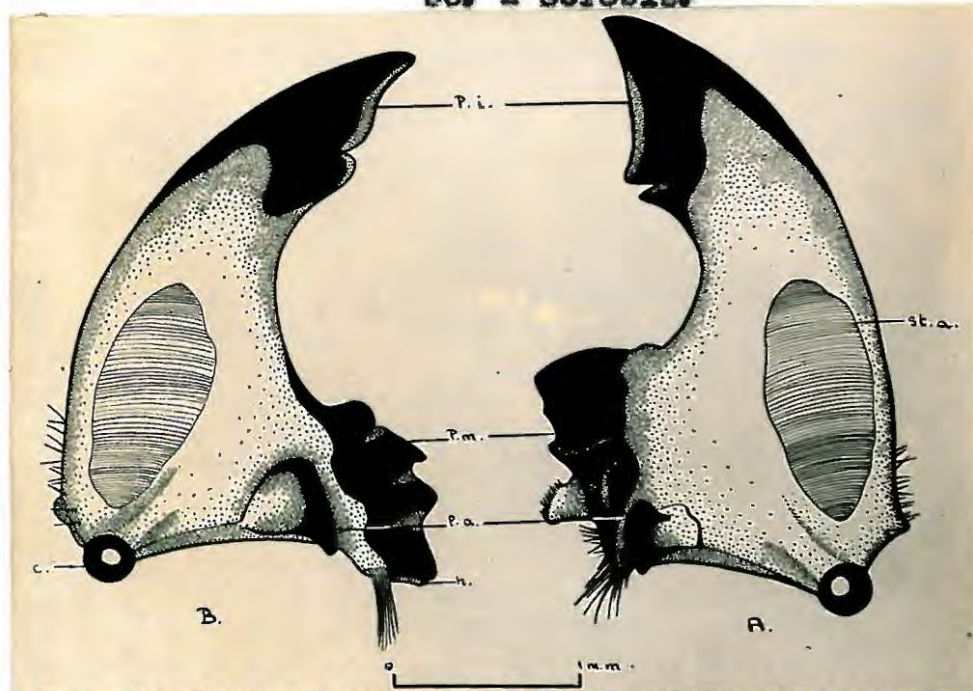


Fig. 7. = Ventral view of Mandibles of Third Instar Larva. : ANOMALA VETULA WIED.

The tooth of the left mandible is sharper than that of the right. The posterior limits of the incisor area are not sharply defined. The concavity between the incisor and molar regions is deeper and shorter in the left than in the right mandible.

The Pars molaris bears the masticating molar teeth, which are different and asymmetrical in the left and right mandibles. These teeth fit into each other when opposed, and also move against the projections of the hypopharyngeal sclerite, thus forming an efficient masticating mechanism.

The molar structure of the right mandible is tri-lobed, with the lobes increasing in size towards the heel or calx at the base. These lobes are directed ventrally. The heel has a flat surface and is a little longer than broad. The base is slightly emarginate to the right of the middle line.

The molar structure of the left mandible projects anteriorly, and recedes posteriorly. It is bilobed. The anterior lobe is large, and overhangs the posterior lobe obliquely. This is elongated, slightly concave and has two transverse carinae. The heel is distinct. The dorsal surface is characterized by a thin chitinous piliferous projection, the acia or uncus. It is attached between the anterior tooth of the second molar lobe and the base. The projecting

arm has a number of short closely set hairs, pointing forwards. The inner surface of the base bears a row of hairs; they are directed inwards.

A similar piliferous projection is described by Rittershaus, 1927, p. 347, in Phyllopertha horticola L.

There is a well developed brush of about fifty long hairs at the base of the molar structure of both mandibles. On the left mandible they are spread out in a semi-circle, but form a cluster on the right mandible.

On the ventral surface of both mandibles there is a well developed heavily chitinised projection, between the molar region and the condyle. It is directed towards the molar region, and is larger in the right mandible, where it reaches to the middle molar tooth. It is the *Processus accessorius* (Grandi, 1925, p. 164). The *Processi accessori* fit into the lateral accessory condyles of the hypopharyngeal sclerite of the labium, when the mandibles are closed.

In *Lamellicorn* larvae, stridulating organs of the mouth parts are confined to Scarabaeidae. According to Hayes, 1929, p. 44, they were first described by Schiödte, 1874, though the mandibular striae were figured earlier by De Ham, 1836. In *Anomala vetula* Wied. the stridulating area is an oval field, displaced

slightly towards the outside of the centre of the ventral surface, of both left and right mandibles. It consists of a transverse series of fine ridges, which decrease in length anteriorly and posteriorly. The ridges in the centre are placed closer together than those at the ends of the field. Each ridge is transversely serrated. Opposed to this stridulating area there are 5 - 7 stridulating teeth, on the dorsal surface of the stipes of the maxillae.

The lateral and external outline of the mandibles is elongate and subtriangular. A dorsal carina from the ginglymus, and a ventral carina from the condyle, converge apically to the posterior end of the incisor area, but they do not meet. Distally, there is one long seta at the end of the scrobia, and 15 - 17 setae at the base, with sensory punctures interspersed. There is a longitudinal series of about fifteen setae along the ventro-lateral carina.

On the dorsal surface of both mandibles, the incisor area has one large sense pit. Anterior to this is one long seta, with another sense pit next to it. There is a longitudinal row of 6 - 8 setae near the anterior molar teeth, in both left and right mandibles.

The mandibles are moved by two powerful muscles,

- which -

which are attached by means of tendons to chitinous projections at the base of the mandibles. The abductor tendon arises between the dorsal and lateral articulation points, the adductor between the molar region and the Processus accessorius. The muscles spread out fanwise, and are attached by their broad ends to the dorsal wall of the cranium.

(3) The maxillae. (Figs. 1, 8, 9 and 10).

The maxillae are situated immediately ventral to the mandibles, so that the dorsal surfaces are pressed against them. They are symmetrical, and lie on either side of the labium. The cardo articulates with the ventral edge of the head-capsule, halfway between the condyle and Processus accessorius of the mandible. The attachment of the maxillae allows for considerable movement, and in the living grub they are in constant motion. They assist in holding the food.

The cardo forms an angle of approximately  $45^{\circ}$  with the ventral margin of the head-capsule, and  $90^{\circ}$  with the proximal parts of the maxilla. It is large and subquadrato, and can be distinguished into an outer sclerotised region and an inner membranous region. Fidler, 1956, p. 128, and Hayes, 1959, p. 37, recognised these parts as the cardo and labacoria respectively.

Rittershaus, 1927, p. 348, and Subklew, 1938, p. 285, regard these two regions as part of the cardo, and do not give them separate names.

There is a lightly sclerotised field on the inner margin of the labacoria, which bears a number of hairs. Between this region and the cardo, is a circular slightly sclerotised region without hairs. The remainder of the labacoria is without hairs, except for a group at the distal region of the dorsal surface towards the inside of the stridulating teeth.

The cardo is divided into<sup>a</sup> small triangular proximal region, which bears the articulating point, and a larger distal region. The dividing sclerotised strip runs in a posterior direction from the ventral to the dorsal surface. Hayes, 1929, p. 37, and Fidler, 1936, p. 123, recognised these two regions as the subcardo and alacardo respectively. The subcardo bears several hairs laterally. There are hairs on the lateral and dorsal surfaces of the alacardo.

The stipes is attached to the distal margin of the alacardo and labacoria. It is quadrilateral in outline, and is separated from them by a sclerotised strip. Distally it is limited by a sclerotised strip, which is continued in a posterior direction on to the dorsal surface. These two strips do not quite reach

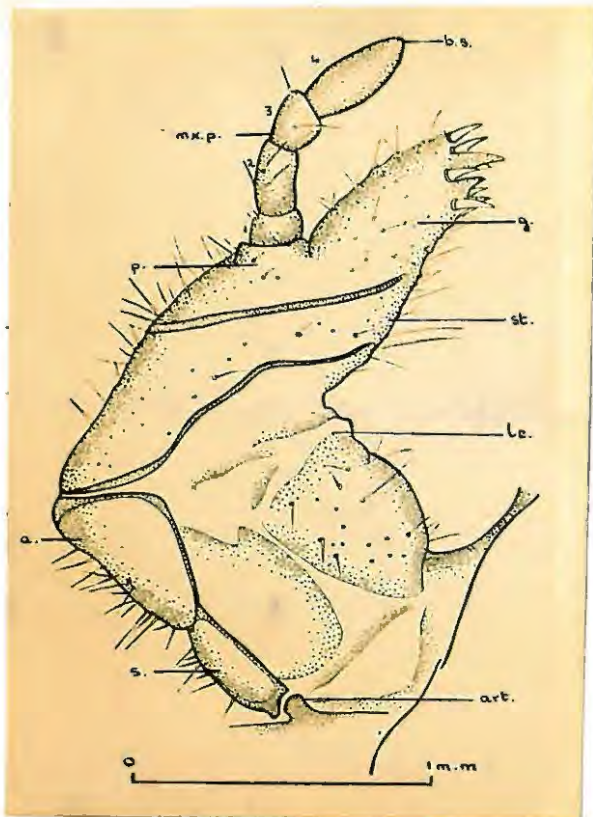


Fig. 8. = Ventral view of Maxilla of Third Instar Larva.

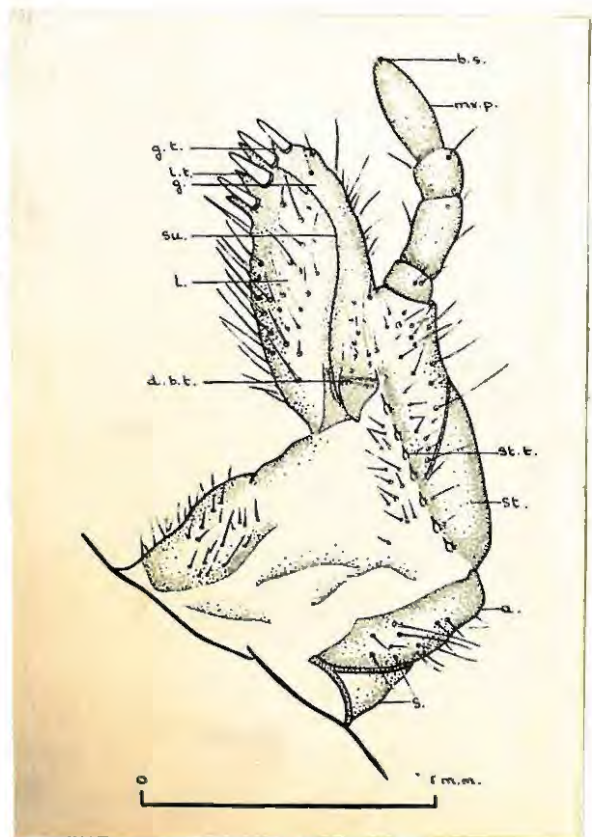
ANOMALA VETULA WIED.

- a. = alacardo.
- art. = articulation with head-capsule.
- b. s. = basiconic sensilla.
- g. = galea.
- lc. = labacoria.
- mx. p. = maxillary palp.
- p. = palpifer.
- st. = stipes.
- s. = subcardo.

Fig. 9. = Dorsal view of Maxilla of Third Instar Larva.

ANOMALA VETULA WIED.

- a. = alacardo.
- b. s. = basiconic sensilla.
- d. b. t. = dorso-basal tooth.
- g. = galea.
- g. t. = galeal tooth.
- l. = lacinia.
- l. t. = lacinial teeth.
- mx. p. = maxillary palp.
- st. = stipes.
- st. t. = stridulating teeth.
- s. = subcardo.
- su. = sulcus.



the inner ventral margin. Distally the stipes bears the palpifer outwardly and the lacinia and galea inwardly. They are immovably attached to the stipes. The ventral and outer surface of the stipes bears a few scattered hairs.

The palpifer bears a four-segmented maxillary palp, which projects beyond the lacinia and galea. Ventrally the palpifer bears 1 - 3 hairs, and dorsally a number of scattered hairs. The separate segments of the maxillary palp are attached by means of a weak chitinous membrane, and are freely movable. The basal segment is the shortest, and is nearly half the length of the second segment. The third segment is slightly larger than the first. The fourth segment is truncated; it is the longest, being nearly 1.5 times the length of the second segment. The basal segment bears four hairs, two dorsally and two ventrally. The second segment bears three hairs and one sense pit. The third segment has three hairs. The fourth segment has no hairs, but apically there is a circle of ten basiconic sensilla.

According to Ims, 1934, p. 491, the majority of Coleopterous larvae have a single maxillary lobe or mala, though the component galea and lacinia are

evident in Lamellicornia. Hayes, 1929, p. 37, states that in many larvae of coprophagous Scarabaeidae the lacinia and galea are distinctly separate and show no traces of fusion. He suggests the condition may be correlated with food habits. Hayes, 1928, p. 297, divides the Lamellicornia into the Pleurosticti, consisting of larvae with fused galea and lacinia, and Leparosticti, in which the galea and lacinia are separate. The Rutelinae belong to the former group. Fusion of galea and lacinia is complete in Anomala retula Wied. though on the dorsal surface an "S"-shaped longitudinal sulcus indicates the line of fusion. As in Phyllopertha horticola L. and Anomala senae Geer., this sulcus is not very distinct. (Rittershaus, 1927, p. 350).

The ventral surface of the mala is formed almost exclusively by the galea. By comparison with Electris alisma Chapin, (Böving, 1936, p. 171), and Macrophylla rubens Péring. (Newick, 1942, Fig. 44), it would appear that the sclerotized strip delimiting the stipes distally, indicates the proximal boundary of the galea, the lacinia only being apparent on the dorsal surface. The ventral surface of the galea bears a few scattered hairs. The inner margin bears a number of short, and long, thin bristles. Except for a few fine hairs proximally and 1 - 3 distally,

- the -

the dorsal surface of the galea is without hairs. Apically the galea bears a large immovable galeal tooth or uncus, with a broad base, and is surrounded to the outside, by a half circle of five strong articulated bristles, two ventral and three dorsal.

The arrangement of bristles on the lacinia is very definite. Three parallel rows of bristles run from the inner ventral margin, dorsally towards the apex of the lacinia. The basal row consists of fine hairs. The terminal 3 - 4 hairs of the middle row are well developed bristles. The three terminal chitinous structures of the top row, are the immovable lacinial teeth (Eöving, 1936, p. 171), similar to the uncus of the galea. The inner tooth is often small, similar to the small accessory protuberance of the galeal tooth mentioned by Rittershaus, 1927, p. 369, in third instar larvae of Anomala aenea Geer. The uncus of the galea, and the lacinial teeth are separated by a well developed chitinous bar. Rittershaus, 1927, p. 361, suggests that this may represent the division between the galea and lacinia. The remainder of the lacinia bears fine scattered hairs. There is a triangular chitinous area at the base of the lacinia, with the apex directed distally.

The arrangement of bristles and teeth of the galea and lacinia is similar to that of Phyllopertha horticola L. and Anomala senes Geer. (Rittershaus, 1927, pp. 350-351, and p. 369), except that in Anomala vetula Wied. there are three lacinial teeth, compared with two in the above-mentioned species. An accessory protuberance to the galeal uncus, as occasionally found in third instar larvae of Anomala senes Geer. (Rittershaus, 1927, p. 369), does not occur in Anomala vetula Wied.

At the base of the dorsal surface of the galea, immediately in front, and to the side of the stridulating teeth, there is a transverse dorso-basal tooth (Böving, 1943, p. 20). It forms the base of a sclerotised triangle, whose apex is directed posteriorly. A similar tooth is described in Phyllopertha horticola L. (Rittershaus, 1927, p. 349), and in Melolontha melolontha L. (Fidler, 1936, p. 123).

The dorsal surface of both maxillae is characterised by the possession of a longitudinal single series of stridulating teeth, which form the plectrum. They are situated on the distal margin of the labacoria. They vary from 6 - 8, and may differ in number in the left and right maxillae of a pair. The basal 1 - 2 teeth may be very small. According

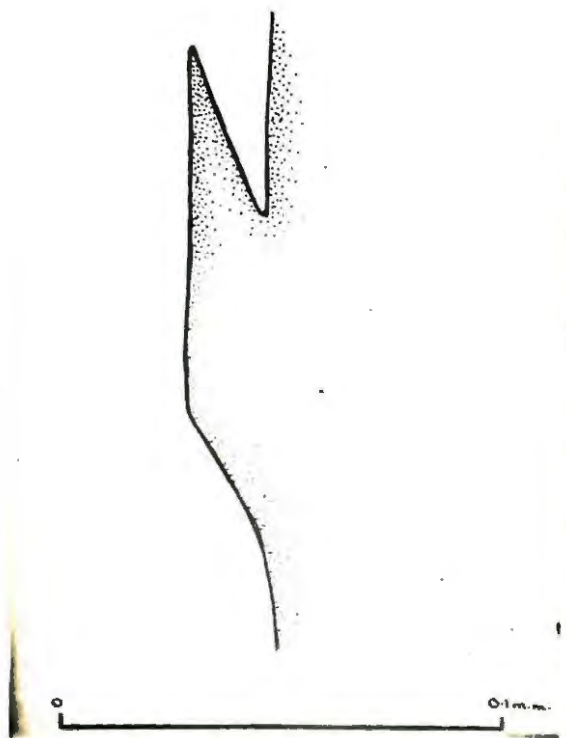


Fig. 10. = Stridulating tooth of Maxilla  
of the Third Instar Larva.

ANOMALA VETULA WIED.

to Rittershaus, 1927, p. 348 and p. 369, the stridulating teeth vary from 5 - 7 in third instar larvae of Phyllonertia horticola L. and 7 - 8 in Anomala seneca Geer. Hayes, 1927, p. 199, describes and figures six teeth on the right maxilla, and one on the left of Anomala kanasana H. and McC. The teeth are pointed and directed forwards, and may overlap one another. According to Gardner, 1936, p. 10, the stridulating teeth of Rutelinae curve acutely forwards, a character which he uses in a key to larvae of the subfamily Scarabaeidae.

During continual motion of the maxillae, the stridulating teeth scrape against the oval stridulating area on the ventral surface of the mandibles. Rittershaus, 1927, p. 348, quotes van Lengerken, 1921, as stating that the plectrum forms the active part of the stridulating organ, and rubs against the passive Pars stridens of the mandible.

The adductor muscles of the maxilla arise from the tentorium and are attached to the inside of the cardo and base of the stipes. The abductor muscle arises from the epicranium and is attached to the cardo. The maxillary palp is moved by muscles which arise on the stipes, and insert on the inner and outer sides of the base of the palp.

(4). The labium. (Figs. 1, 11 and 12).

The labium lies between the maxillae; it is small, thinly sclerotised, and partly concealed by them.

The structure of the labium does not differ greatly from that of other Scarabaeidae. It is similar to that of Ochriside villosa Burm. (Anderson, 1936, p. 21).

Ventrally a chitinous labral suture divides the labium into a proximal trapezoidal postmentum, and a distal prementum. A membranous area divides the prementum into a proximal rectangular second prementum, and a distal semicircular first prementum, which bears the two-segmented labial palps.

The postmentum is large, and is continuous proximally with the prothorax. There is no gular region. From the lateral articulation points of the maxillae, a chitinous triangle extends forwards along the postmentum. Midway along the lateral margin of this chitinous triangle, there is one hair, and a few sensilla on either side. There are a few hairs along the distal outer angles.

The second prementum is short antero-posteriorly. Laterally it is continued onto the ventral surface of the hypopharyngeal sclerome, to a greater extent on the right, than on the left side. Thus ventrally

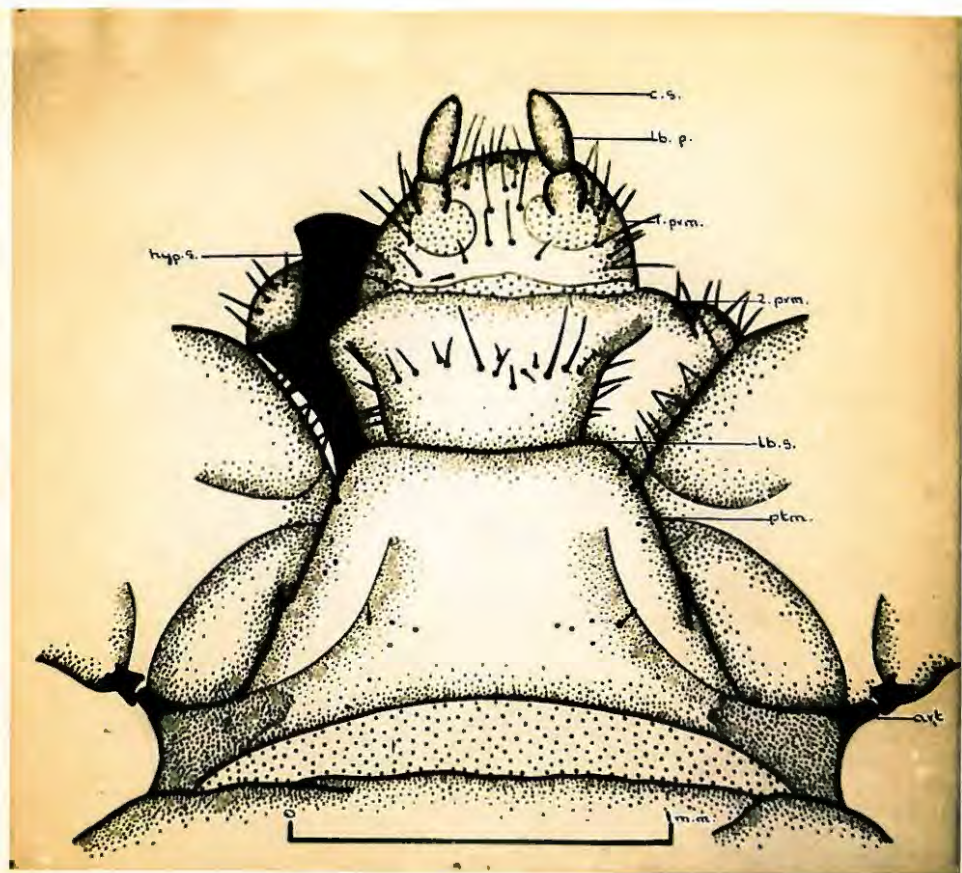


Fig. 11. = Ventral view of Labium of Third  
Instar Larva.

ANOMALA VETULA WIED.

- art. = articulation with maxilla.
- c. s. = conical sensilla.
- 1. prm. = first prementum.
- hyp. s. = hypopharyngeal sclerome.
- lb. p. = labial palps.
- ptm. = postmentum.
- 2. prm. = second prementum.
- lb. s. = labial suture.

more of the hypopharyngeal sclerose is visible on the right than on the left side. The posterior half of the second prementum is chitinous; the anterior half is membranous. On this border there is a transverse row of hairs. Two of these, one on either side of the middle line, are longer than the remainder. The anterior margins of the lateral continuations onto the hypopharyngeal sclerose, bear a number of hairs.

The first prementum, or stipula, (Hayes, 1927, p. 199), is rounded transversely, and antero-posteriorly. It is slightly asymmetrical. Glosseae and paraglosseae are not differentiated. A membranous area encircles the base of each labial palp. The first prementum is strongly setose. The anterior margin bears a number of hairs which are directed towards the middle. A number of fine hairs surrounds the membranous area at the base of the palp. On either side of the median line there are two especially long setae.

The labial palps are directed antero-ventrally, and are situated posterior to the apex of the first prementum. The basal segment is short and conical. The second segment is truncated, and bears, at its tip, a circle of about eight conical sensilla. As in Phyllopertha horticola L. (Rittershaus, 1927, p. 352), the labial palps are without hairs.

) The -

The hypopharynx forms the dorsal surface of the labium. It has been described in Phyllopertha and Geotrupes by Carpenter and MacDowell, 1918, pp. 389-393. Anteriorly it consists of a densely setaceous area, which is fused distally with the first prementum. Posterior to this is the strong hypopharyngeal sclerite (Böving, 1936, p. 178). The basilar membrane forms the ventral surface of the mouth cavity, and is pierced posteriorly by the opening of the alimentary canal.

The area distal to the chitinous sclerite is composed of fairly thin chitin, and bears a group of short stout setae on either side of the median line. They are directed anteriorly and inwards. These setae do not extend posteriorly to the chitinous sclerite, so that a non-setose area remains in the concavity of the anterior margin of the sclerite. The lateral margins bear a number of hairs directed laterally.

The hypopharyngeal sclerite is very strongly chitinised. It is asymmetrical, and obliquely transverse. The anterior margin is deeply concave. The right side forms a strong dorsally directed "toothed projection" (Carpenter and MacDowell, 1918, p. 392). As in Phyllopertha horticola L. (Rittershaus,

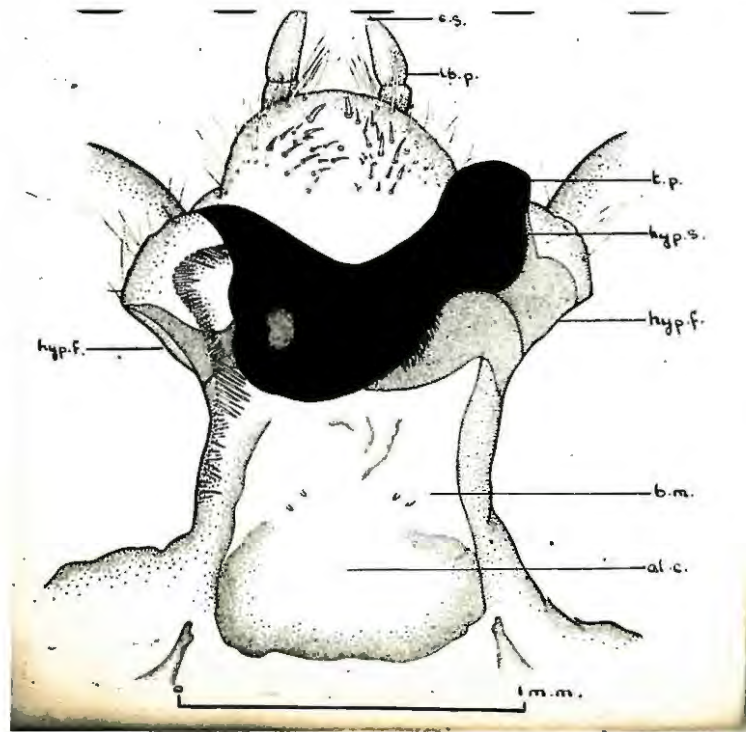


Fig. 12. = Dorsal view of Labium of Third Instar Larva.

ANOMALA VETULA WIED.

- b.m. = basilar membrane.
- c.s. = conical sensilla.
- hyp.f. = hypopharyngeal fossa.
- hyp.s. = hypopharyngeal sclerome.
- lb.p. = labial palp.
- al.c. = opening of alimentary canal.
- t.p. = "toothed projection".

1937, p. 353), the inner margin has two small sharp teeth. The left side has a flattened laterally directed process. The antero-posterior length is greatest on the left side, owing to the concavity on the right hand side of the posterior margin.

The area on either side of the hypopharyngeal sclerome is membranous. It obscures the hypopharyngeal fossae (Böving, 1936, p. 172), which are strongly chitinised lateral sclerites. The Processus accessorii of the mandibles, fit into the concavities of these sclerites, and form an accessory masticating surface. The hypopharyngeal fossae are asymmetrical. As in Phyllonerta horticola L. (Ritterhaus, 1937, p. 353), the right fossa is larger than the left, to accommodate the greater Processus accessorius of the right mandible.

A row of well developed setae occurs on the posterior margin of the hypopharyngeal sclerome, to the right of the middle line. On the membranous area, to the left of the transverse sclerome, there is a single longitudinal row of setae. Anteriorly this row is concave to the inside, posteriorly it almost reaches to the commencement of the alimentary canal.

Posterior to the hypopharyngeal sclerome, the basilar membrane is continuous with the ventral wall

of the pharynx. It bears several small bosses lateral to the opening of the pharynx are two strong tendons, inserted at the base of the hypopharynx.

A pair of ventral adductor muscles arises from the posterior tentorial arms, and inserts on the base of the prementum. The retractor muscles are attached to the postmentum, and insert on the base of the second prementum. According to Anderson, 1936, pp. 4-6, these muscles determine the morphological relations and divisions of the labium.

(b) The thorax. (Fig. 1).

Larvae were etherised for an examination of the thorax and abdomen, as suggested by Rittershaus, 1927, p. 354. It was found that the annulations were more distinct under this condition than in preserved material.

The thorax is clearly distinguishable into pro- meso- and metathorax, each of which bears a pair of legs. It differs from the abdomen in being slightly dorso-ventrally flattened, compared with the cylindrical form of the abdomen. The setation of the thoracic terga is very sparse in contrast to that of the abdominal terga.

The body segments are subdivided into annulets, which obscure the primary segmentation. A lateral pleural region overhangs the sternal region of each  
- segment -

segment, and separates it from the dorsal tergal region. The body wall is not sclerotised to form definite plates, as in the adult.

The interpretation of the number of segments, and relationship of the annulations to these segments, is based mainly on comparison of the position, number and arrangement of the hairs. The pupa which develops within the larval skin of the prepupa is very contracted.

This prevents correlation between the annulots of the larval integument and the underlying segments of the developing pupa. Thus Böving, 1936, pp. 172-173, and Böving, 1942, fig. 13, interprets an annulation recognised by Hayes, 1927, p. 200, Rittershaus, 1927, pp. 354-355, and Fidler, 1936, p. 124, as the metatergite of the metathorax, as the protergite of the first abdominal segment in Plectris aliena Chapin and Popillia japonica Newm.

I consider the thoracic segmentation in Anomala vetula Wied. to be similar to that described by Rittershaus, 1927, pp. 354-355, and p. 369, in Phyllopertha horticola L. and Anomala senes Geer.

The prothorax is slightly wider than the posterior region of the head-capsule, which it overlaps dorsally and laterally. Ventrally it is continuous with the

submentum; laterally and dorsally it is attached to the post-occipital suture. Dorsally two tergites can be clearly distinguished. Depending on the degree of extension of the head, an anterior fold may be recognised, overlapping the posterior margin of the head-capsule. Subkiew, 1938, p. 291, interprets this as the acrotergite. It is figured in the larva of Oryctes by Berlese, 1909, p. 166.

On either side of the prothorax there is a shiny sclerotised area, with a "V"-shaped depression, whose apex is directed posteriorly. Ventral to this prothoracic sclerite, a similar sclerotised plate is conspicuous in third instar larvae.

By comparison with the setation of succeeding thoracic segments, it is probable that the prothoracic tergum consists of four annulations. The most anterior is the acrotergite, which has a dorso-ventral row of hairs. Dorsally there is a long seta on either side of the middle line, suggesting the protergite. The centre of the segment bears a number of small hairs, scattered ventral to, and on the prothoracic sclerite. These resemble those of the following thoracic mesotergites. The posterior tergite bears a row of stout hairs similar to those of the meso- and metathoracic tergites.

There is one pair of thoracic spiracles, situated on either side of the prothorax, posterior to the prothoracic sclerite, and dorsal to the pleural fold. It is larger than the abdominal spiracles, and in contrast to them, has the concavity of its sieve plate directed posteriorly. The structure of the thoracic spiracle is similar to that of the abdominal spiracles, which will be described later.

The meso- and metathoracic terga are each divided into three annulets. Dorsally the tergites are about the same width. The pro- and metatergites overlap the mesotergite. They decrease in size laterally, and extend approximately half-way down the sides of the body. The mesotergites are the largest and increase in width to the point where the pro- and metatergites terminate, and then narrow to a point dorsal to the pleural fold. The acrotergites are not visible. According to Borlase, 1909, p. 106, they tend to become endoskeletal phragma in the thorax. The protergites of the meso- and metathorax each bear a long hair on either side of the mid-dorsal line, and a few small hairs. The mesotergites bear a long hair on either side. It is more lateral than that on the prothorax and not as long; laterally the mesotergites bear scattered hairs. The metatergites are traversed

by a transverse row of short hairs.

The first instar larva of Anomala vetula Wied. differs from succeeding instars by the possession of a small hatching spine. (Hayes, 1929, p. 48), or mucronate process (Söving, 1939, p. 137), on the mesotergite of the metathorax. This will be described later in a comparison of the three larval instars.

A pleural region separates the tergal and sternal regions. It is divided into an anterior and a posterior fold in each thoracic segment. They bear a number of scattered hairs.

The sterna are divided into pro- meso- and metasternites, but the divisions are not as clear as in the tergum. The pro- and metasternites are small folds, and are without hairs. The mesosternite is well developed and bears a number of hairs directed towards the middle line. They are especially well developed on the mesosternite of the prothorax. The subcoxal elements, for the insertion of the legs, are situated on either side of the mesosternite.

The ventro-lateral margin of the prothorax in front of the subcoxae of the first pair of legs, is strengthened on either side by two chitinous strips. These are the Jugulare (Berlese, 1909, p. 371) or

-laterocervicalia -

laterocervicalia (Subklew, 1938, p. 292). The anterior strip runs longitudinally, the posterior one transversely.

The legs. (Figs 1 and 13).

A pair of legs is attached to each thoracic segment, between the pleural fold and the mesosternite. When walking, the legs move in an anterior - posterior direction on either side of the body. They also assist in burrowing through the soil. They are without stridulating organs.

The legs increase in size from the first to the third pair. The mesothoracic pair is intermediate in length and width between the prothoracic and mesothoracic legs. This is due mainly to an increase in size of the coxa. This is shown in tables of the measurements of individual segments of the legs of Phyllopertha horticola L. (Rittershaus, 1927, p. 362), and Anomala humeralis Burm. (Viado, 1939, p. 350).

Each leg arises from a strong truncated cone, or subcoxal element (Subklew, 1938, p. 293). According to Hansen, 1930, pp. 32-33, the coxa of the larva of Limnophilus is articulated on the end of a thick obtuse cone. He considers it to be a well developed trochantin. In Lyda the trochantin is a protruding,

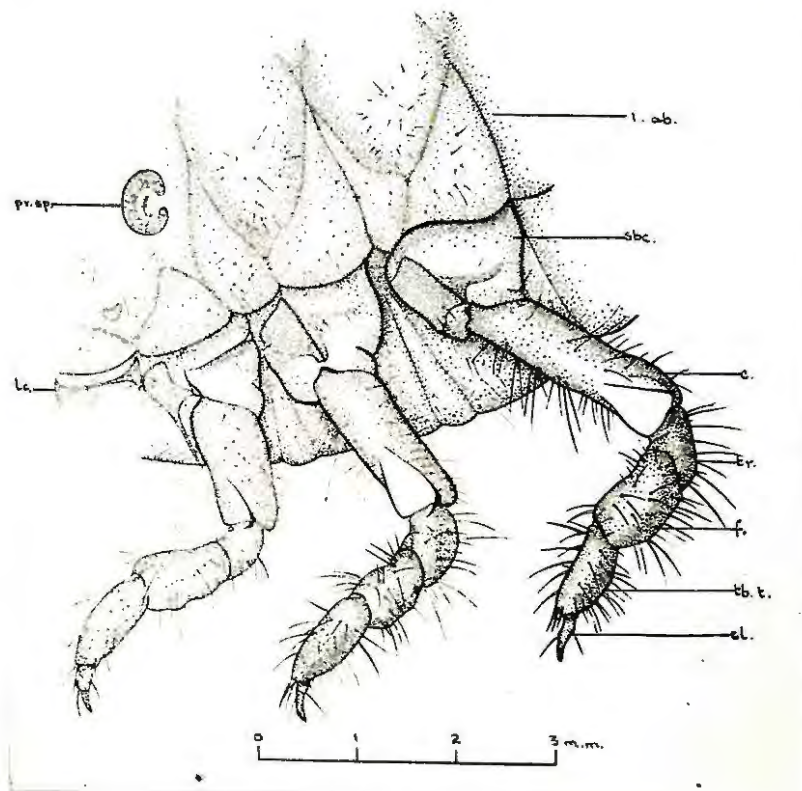


Fig. 13. = Legs of Third Instar Larva.

ANOMALA VETULA WIED.

- l. ab. = abdominal segment, 1.
- c. = coxa.
- cl. = claw.
- f. = femur.
- lc. = laterocervicalia.
- pr. sp. = prothoracic spiracle.
- sbc. = subcoxal element.
- tb. t. = tibio-tarsus.
- tr. = trochanter.

thick, conical joint; the remainder of the leg is slender (Hansen, 1930, p. 85). These trochantine resemble the subcoxal elements of Anomala vetula Wied.

The outside of the meso- and metathoracic subcoxae is divided into two unequal parts, by a longitudinal suture, which extends distally to the articulation point of the coxa. The smaller anterior parts are strengthened by rectangular chitinisations, which extend forwards from the suture. An "L"-shaped chitinous strip extends posteriorly from the suture. The distal half of the prothoracic subcoxae is divided by a longitudinal suture. Extending posteriorly from the base of this suture is a transverse suture, with a chitinised ventral border. The posterior laterocervicalia abut on the prothoracic subcoxae. 6 - 10 moderately long hairs arise from the chitinised areas of the subcoxae.

The coxa is the longest joint of the leg. It is cylindrical and slightly swollen at the distal end. On the antero-exterior face a triangular membranous area, whose apex is directed posteriorly, separates the coxa from the trochanter. This hinge joint allows the trochanter to be brought forward against the anterior face of the coxa, and only  
- permits -



permits movement through  $180^{\circ}$ . The articulation is dicondylic. According to Snodgrass, 1935, p. 194, monocondylic hinges are usual in legs of larvae, a condition found in the remaining articulation points of the leg. The anterior face of the coxa, bears numerous long hairs; the hairs on the posterior surface are not as dense. Distal to the triangular membranous region, the coxa is without hairs. The inside of the coxa bears a few short hairs.

The trochanter is twice the length of the coxa, and placed at right angles to it. It is trapezoidal in shape. The proximal end of the trochanter extends into the cavity of the coxa, as a heavily sclerotised projection, on which the depressor muscles of the trochanter insert. The posterior surface bears a number of long hairs.

The femur and trochanter move as one unit. The distal end of the femur is clavate. It bears a number of long scattered hairs. Together they are about 1.2 times the length of the coxa.

The following segment has been interpreted as the tibia by Fidler, 1936, p. 125, and Viado, 1939, p. 350, the tarsus being represented by the terminal claw. Snodgrass, 1927, p. 81, states that the tibia and tarsus frequently fuse. Rittershaus, 1927, p. 362, Hayes, 1927,

p. 200, and Böving, 1936, p. 173, consider the tibia and tarsus to have fused to form a tibio-tarsus, an interpretation with which I agree. The coxa is 1.4 times the length of the tibio-tarsus in the first pair of legs, 1.8 times in the second pair of legs, and 2.1 times in the third pair of legs. The tibio-tarsus is narrowed at either end, and bears numerous hairs. A circle of strong hairs surrounds the base of the claw. Anterior to it, three hairs arise close together, and are particularly well developed.

Each leg terminates in a single claw, which has a conical base, and a sharp, darkly sclerotized point. The metathoracic claw is more slender and shorter, than the pro- or mesothoracic claws. The base of each claw bears an inner and an outer bristle. The inner bristle is inserted distally, and extends beyond the tip of the claw. The outer one is inserted more proximally, and does not reach the tip of the claw. In Phyllopertha horticola L. (Rittershaus, 1927, p. 362), the claw of the metathoracic pair of legs is considerably shorter than the two bristles on its side.

(c) The Abdomen. (Fig. 1).

The abdomen is divided into ten segments, the number generally accepted for Lamellicorn larvae.

- (Rittershaus -

(Rittershaus, 1927, p. 354). Ten segments are distinguishable in the abdomen of the larvae of Anomala aenea Geer. and Phyllopertha horticola L. (Rittershaus, 1927, p. 354), Anomala kansana H. and McC. (Hayes, 1927, p. 200), Plectris aliena Chapin (Böving, 1936, p. 173), and Macrophylla pubens Péring. (Fenwick, 1942, p. 114). Berlese, 1909, p. 267, figures a small fourteenth segment, consisting of a triangular tergum and a divided sternum surrounding the anus of the larva of Oryctes, but I can find no trace of this in Anomala vetula Wied.

The segments are divided into annulets, as in the thorax. The annulation and setation is similar to that described for Phyllopertha horticola L. and Anomala aenea Geer. (Rittershaus, 1927, pp. 355-359). Terga 1 - 6 inclusive, each consist of a pre-, meso- and metatergite. Dorsally they are approximately equal in length. The pre- and metatergites are wedge-shaped, and often overlap the mesotergite. The protergite extends along the shorter anterior margin of the trapezoidal mesotergite. Ventrally the meso- and metatergites extend to about the same level.

In front of the ventral angle point of the protergite is the acrotergite (Rittershaus, 1927, p. 355). There are eight pairs of spiracles; each is situated on a rectangular field separated off from the ventral  
- margin -

margin of the mesotergite, of the first eight abdominal segments (Rittershaus, 1927, p. 355). A small triangular region is inserted posterior to the first six pairs of abdominal spiracles. A narrow fold is divided off from the anterior margin of the metatergite in the first six abdominal segments, by the sutura meso-meta-tergales (Rittershaus, 1927, p. 355). This corresponds in position and setation to the postscutellum of Plectris aliena Chapin (Böving, 1936, p. 173). As explained earlier the interpretation of the annulation of the body by Böving, differs from that used here.

The terga of abdominal segments 7 - 10 inclusive are undivided. The acrotergite is absent. According to Berlese, 1909, p. 166, in all the abdominal segments after the first, the acrotergite tends to become incorporated into the protergite. The spiracular folds of segments seven and eight are approximately the same size as those of the preceding abdominal segments.

The last or tenth abdominal segment is the largest. This is due to the distension of the thin body wall by food in the large colon. On the dorsal surface a subcircular field is present, which extends

almost from the anal slit to near the anterior margin of the tenth segment. Posteriorly it is slightly narrowed and elongated. The border is chitinised and is clearly visible against the fatty deposits in the abdomen of a prepupa. Posteriorly it is interrupted in the middle line. A similar field is present in Anomala aenea Geer. (van Emben, 1941, p. 125).

A ventro-lateral pleural fold on either side of the body, separates the terga and sterna of each segment except the tenth. The pleural fold enlarges in the anterior region of segment ten, where it terminates. It consists of an undivided ventrally directed fold, except in abdominal segments 7 - 9 inclusive, where it is irregularly elongated.

Most of the body is covered with setae. These are of two kinds, long and short hairs, and asperities, which are found on the dorsal surface of the first six abdominal segments. The anterior and posterior margins of each annulation are bare, as described in Anomala aenea Geer. and Phyllopertha horticola L. (Rittershaus, 1927, p. 356), and in Macrophylla pubens Pering. (Fenwick, 1942, p. 115). This is not always apparent, depending on the degree of contraction of the larva.

The first abdominal segment is intermediate in

its form of setation, between the sparsely bristled thoracic segments, and the following abdominal segments. As in the thorax, the protergite bears a large hair on either side of the middle line, and a number of small hairs, but no asperities. Latero-dorsally the mesotergite bears a long hair as on the mesotergite of the meso- and metathoracic segments. A transverse row of short hairs extends along the posterior margin. A number of asperities are scattered irregularly over the mesotergite. The anterior margin of the basal rings of both hairs and asperities is strengthened, to prevent bending, as in Melolontha hippocastani Fabr. (Subkiew, 1938, p. 296). In the density of asperities the metatergite is similar to the following segments. The posterior margin bears a transverse row of short setae.

All the terga of abdominal segments 2 - 5 inclusive are covered with short brown asperities; these point dorsally. In addition, the protergites bear a large hair on either side of the mid-dorsal line; the mesotergites bear one long latero-dorsal hair, and a transverse row of short hairs along the posterior margin; the metatergite is traversed by a row of short hairs along the posterior margin. Subkiew, 1938, p. 296, states that the long hairs have a probable tactile function.

The sixth abdominal segment is intermediate in its form of setation between abdominal segments 2 - 5, and abdominal segments 7 - 9. The pro- and mesotergites are similar to those of abdominal segments 2 - 5. The metatergite bears scattered short hairs and a few asperities. No asperities are found posterior to this segment. The acrotergite is without hair or asperities. The spiracular fold bears 6 - 9 short hairs. The spiracle in Phylloxera horticola L. is surrounded by 3 - 5 short hairs, and in Anomala senae Geor. by 10 - 15 hairs (Ritterhaus, 1927, p. 356). The small triangular fold posterior to spiracles 1 - 6 is bare. The strip separated off from the metatergite bears a transverse row of short hairs, near the posterior margin.

The anterior half of segment seven bears a group of short hairs. They are less in number in this position on segment eight. The posterior half of these two segments, bears a number of short scattered hairs, and a few very long wavy hairs. This arrangement of setae into an anterior and a posterior region suggests that these two segments were originally each divided into two annulets, as in Serica brunnea L. (Fidler, 1936, p. 124), and

Macrophylla pubens Péring. (Fenwick, 1942, p. 114).

Segment nine has 1 - 4 short hairs in the anterior half. The centre is bare, and is followed by short hairs, and a few very long wavy hairs on the posterior margin. These hairs are the longest on the body of the larva.

The subcircular field on the dorsal surface of the tenth abdominal segment bears a number of uniformly spaced very short, or short hairs. Two longer hairs stand on either side of the middle line, slightly posterior to the break in the chitinised border, at the anal end of the field. All these hairs are directed posteriorly. The lateral and posterior margins, and the posterior one third of the median line, are without hairs. The area between the subcircular field and the anus, bears a number of very short, dorsally directed hairs. Lateral to this subcircular field the posterior two-thirds of the dorsal surface of the tenth segment is covered with moderately long hairs, which point postero-medianly. Anterior to the subcircular field, the tenth segment has only a few, very short hairs.

The pleural folds bear 8 - 10 moderately long

- hairs -

hairs in each segment. In the anterior six abdominal segments they are directed ventrally. In the last four abdominal segments they point posteriorly or postero-dorsally.

The sterna are not as distinctly subdivided as the terga. Those of the anterior eight abdominal segments are divided into pro- meso- and metasternites. The mesosternite is the most conspicuous subdivision; the pro- and metasternites are narrow folds. On either side of the mesosternites of segments 1 - 8 inclusive, there are small triangular elevations. In their position they resemble the subaxal elements. The ninth segment is indistinctly divided into a narrow anterior, and a wider posterior sternite. The tenth sternum is undivided.

Only the mesosternites of segments 1 - 8 inclusive and the larger posterior region of the ninth sternum bear hairs. The hairs of the first abdominal sternum are more numerous than on succeeding segments. They are short, and form a transverse row across the segment. The lateral triangular elevations of the mesosternites bear a few short hairs.

The Raster (Figs. 1, 14 and 15).

In Lamellicorn larvae, the ventral surface of the tenth abdominal segment, in front of the anus, has a definite arrangement of hairs, spines and bare areas. This complex was first termed the radula (Hayes, 1927, p. 201), and later the raster (Böving, 1936, p. 179). It consists of the septula, a pair of palidia, and a pair of tegilla.

The septula is a narrow median non-setose area, between a pair of longitudinal palidia, which diverge slightly posteriorly. It extends from the middle of the transverse base of the lower anal lip, to about three quarters of the length of the venter of the tenth abdominal segment.

Each palidium is monostituous and consists of 16 - 23 pali.

The pali are dagger shaped, about two and a half times longer than broad, measured at their widest point. The pali are separated from one another by a distance approximately equal to the width of their bases. Anteriorly the width of the septula is equal to about the length of two pali, posteriorly to the length of five pali. The pali are recumbent, with their apices directed towards the middle line. Each

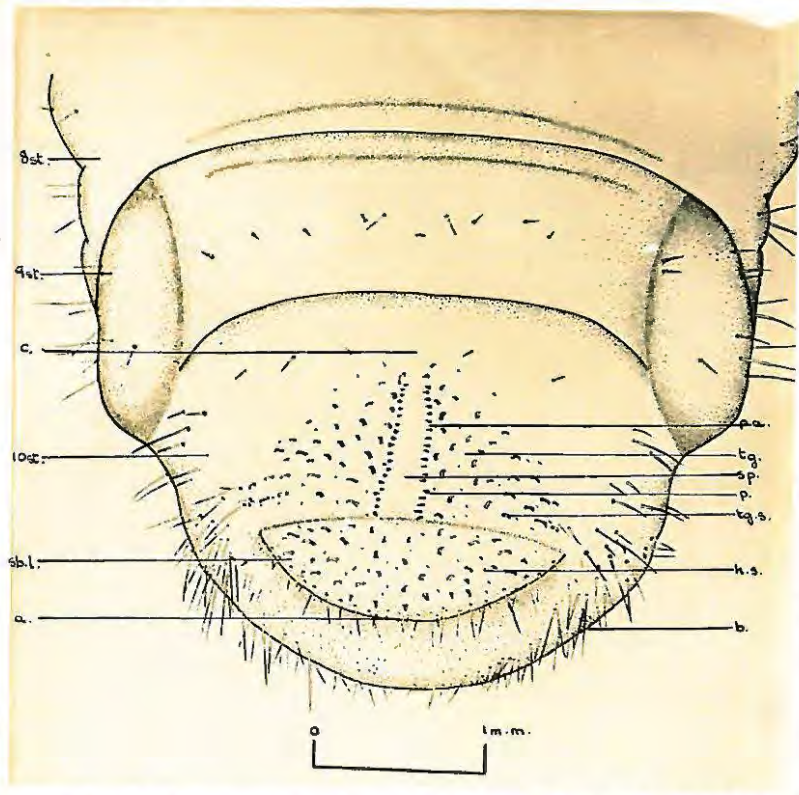


Fig. 14. = Raster of Second Instar Larva.  
ANOMALA VETULA WIED.

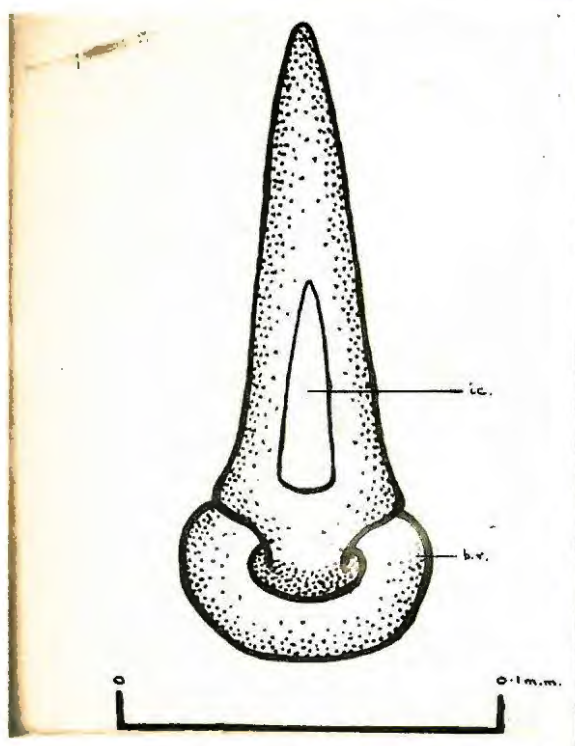


Fig. 15. = Palus of Left Palidium  
of Raster of Third Instar Larva.  
ANOMALA VETULA WIED.

- a. = anus.
- b. = barbula.
- c. = campus.
- h. s. = hamate setae.
- pa. = palidia.
- p. = palus.
- sp. = septula.
- 8st- = sterna 8 - 10.
- sb. l. = subanal lip.
- tg. s. = tegillar setae.
- tg. = tegillum.

- ic. = inner cavity.
- b. r. = strong basal ring.

has a triangular inner cavity. They are inserted in strong basal rings, which are strongly chitinised towards the outside, to prevent bending.

Each tegillum consists of a triangular area of erect hamate setae, on either side of the palidia. At the base of the lower anal lip, the tegillar setae extend from the palidia to the corresponding barbula, but anteriorly they consist of a few setae adjacent to the palidia. They do not unite anterior to the palidia, and are irregularly distributed. They decrease in size anteriorly and laterally, and have small hamate setae interspersed.

The tegillar setae are flat and each has a long inner cavity. The lateral margins are thin; they converge slightly towards the tip. The setae have strong basal rings, which are strengthened on the posterior margin, to prevent the setae from bending forwards.

There are no presuptular setae. The region in front of the paired tegilla, termed the campus (Böving, 1936, p. 176), is bare, except for three short hairs, on either side of the median line.

Hayes, 1927, p. 201, assigned to the raster, the function of raking debris off the mouthparts. This is probably the case, for when not crawling, the

larvae lie curled up, with the mouthparts and raster close together.

The importance of the raster in systematic determination is obvious from the work of previous writers, such as Fidler, 1936, p. 126, Subklev, 1938, p. 22, Viado, 1939, pp. 349-350, and Fenwick, 1942, pp. 117-118. Böving, 1936, pp. 176-181, assigned new terms to the taxonomically important parts of the raster, and applied them to a study of larvae of Plectric aliens Chapin (Böving, 1936, p. 173), Popillia japonica Newm. (Böving, 1939, p. 185), and the genus Phyllophaga (Böving, 1943, pp. 11-13).

In all descriptions of species of the subfamily Eutelinae which I have been able to obtain, the pali form two longitudinal rows, either parallel to each other or diverging posteriorly. The number of pali to each palidium varies. In Phyllopertha horticola L. there are 13 - 18 pali in each palidium (Rittershaus, 1927, p. 359), in Anomala kansana H. and McC. 10 - 12. (Hayes, 1927, p. 201), in Anomala orientalis Waterh. about fourteen, (Sim, 1934, p. 4), in Anomala humeralis Burm. 9 - 10 (Viado, 1939, p. 350), and in Popillia japonica Newm. 6 - 7 (Böving, 1939, p. 185).

The pali of opposing palidia may be separated from one another by varying distances. In Phyllopertha horticola L. they never overlap, and

very seldom touch (Rittershaus, 1927, p. 360). In Anomala seneca Geer. the points of the pali reach to the place of attachment of the opposite pali (Rittershaus, 1927, p. 370). The shape of the pali and tegillar setae varies in different species.

The sides of the tenth segment bear a number of fairly long, thin hairs, termed the barbula. (Böving, 1936, p. 176). They are directed posteriorly.

The anus is terminal and transverse, as in most of the larvae of Scarabaeidae (Hayes, 1929, p. 44). The subanal lip is convex, and bears numerous irregularly arranged hamate setae, similar to the tegillar setae of the raster. Small hamate setae are scattered among them. The hairs on the posterior margin of the subanal lip are moderately long, and arch over the anus.

#### The Spiracles. (Figs. 1 and 16).

There is one pair of thoracic spiracles; one spiracle is situated on either side of the prothorax. According to Snodgrass, 1935, p. 427, prothoracic spiracles are present in some insects in the embryonic stage, but disappear before hatching. The thoracic spiracles often migrate

forwards during development. The mesothoracic spiracles, in particular, are subject to the forward migration, and often occur in larval stages of insect on the sides of the prothorax. Thus it is apparent that the spiracles on either side of the prothorax in Anomala vetula Wied. are mesothoracic in origin, but are often termed "prothoracic", because of their position in the larval stages. Steinke, 1919, p. 5, and Böving, 1939, p. 187, recognise this pair of spiracles as mesothoracic. Hayes, 1927, p. 200, Hayes, 1929, p. 43, and Fenwick, 1942, p. 119, term the spiracle prothoracic.

There are eight pairs of abdominal spiracles, the maximum number of abdominal spiracles found in postembryonic stages of all insects (Snodgrass, 1935, p. 429). They are situated on rectangular fields, separated off from the ventral margin of the mesotergite of the first eight abdominal segments. (Rittershaus, 1927, p. 355). The last two abdominal segments are without spiracles.

The mesothoracic spiracle is larger than the abdominal spiracles, which are approximately equal in size. In Anomala kansana H. and McC. (Hayes, 1927, p. 200), the thoracic spiracles are nearly twice as

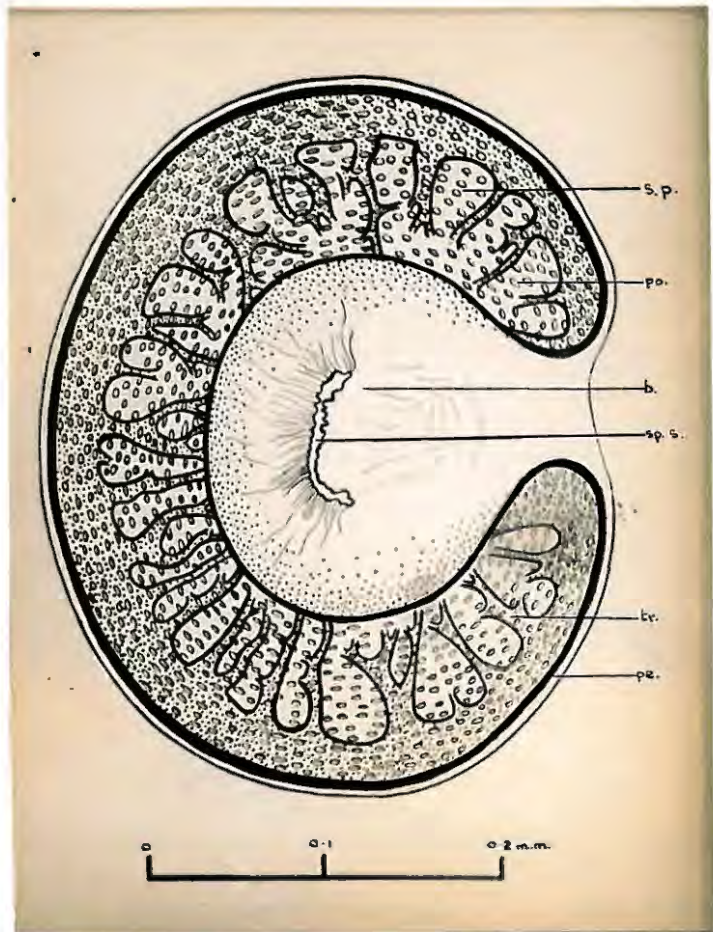


Fig. 16. = Second Abdominal Spiracle of  
Third Instar Larva.  
ANOMALA VETULA WIED.

- b. = bulla.
- pe. = peritreme.
- po. = pores.
- s.p. = sieve plate.
- sp. s. = spiracular slit.
- tr. = trabecula.

large as the others.

The shape of the spiracles is oval, the long axis being dorso-ventral. They become rounded in the posterior abdominal segments. The actual respiratory structure is a crescentic sieve plate, which is well developed in second and third instar larvae. The concavity of the sieve plate in first instar larvae is only slightly indicated. The structure of the spiracles of the first instar larva will be dealt with in a comparative study of the three instars. The concavity of the thoracic respiratory plate faces posteriorly, that of the abdominal sieve plates anteriorly, as in most Scarabaeid larvae (Hayes, 1929, p. 43).

The sieve plate is yellow-brown in colour, and is perforated by numerous elongated pores which are irregularly distributed. The concavity of the respiratory plate is occupied by the bulla, which has a curved spiracular slit. The bulla is a specially strengthened part of the integument which projects into the atrium. Folds of the surface of the bulla radiate from the convex side of the spiracular slit. The outer margin of the sieve plate is surrounded by a heavily sclerotised peritreme.

The sieve plate is supported by underlying

- trabeculae, -

trabeculae, which extend from the peritreme towards the bulla. The outside of the trabeculae forms a band, which breaks up into numerous moderately strong branches.

The sieve plate covers the external opening of the underlying atrium. The walls of the atrium lack taenidia. The atrium is short, and the main tracheal branches arise from its inner end. The occlusor muscle consists of delicate strands which extend from the wall of the atrium to the bulla.

Boas, 1898, p. 590, states that in Melolontha vulgaris Fabr. during moulting, there is an opening at the exterior, between the concave margin of the sieve plate and the bulla. The trachea are shed through this aperture at ecdysis. After moulting the opening closes. A similar aperture has been observed in Melolontha hippocastani Fabr. by Subklew, 1938, p. 298. It corresponds to the spiracular slit in Anomala vetula Wied.

2. INTERNAL ANATOMY.

For an examination of the internal anatomy of the larva of Anomala vetula Wied., grubs were given an anaesthetic of chloroform. The freshly killed specimens were then dissected under water, with the aid of a binocular microscope. Third instar larvae were used, except in investigations for comparative purposes.

The body was opened by making a median dorsal incision through the body-wall, from behind the head-capsule to the anus. On making the incision, a colourless watery fluid exuded from the haemocoel. The incision was continued laterally behind the head-capsule, and the body-wall was pinned out. The dorsal wall of the head-capsule was removed, by two dorso-lateral incisions, from the posterior margin, to the frontoclypeal suture.

The viscera are obscured by abundant deposits of fat, which are in the form of small white globules supported by connective tissue. The fat deposits are situated mainly in the anterior half of the body, where they surround the gut, but are particularly abundant laterally. It is the fat-body that imparts to the grub the characteristic white colour of the anterior region. The white colour of the prepupa is due to the accumulation of fat deposits. Dorsally

the connective tissue supporting the fat deposits, extends across the gut. Fat globules are only found on either side of the heart and pericardial-haemocoel, which form a median longitudinal line, dorsal to the alimentary canal.

The posterior half of the body is dark, owing to the absence of fat. Here the colon, which is greatly distended with food, can be seen through the transparent body-wall.

Careful removal of the fat-body reveals the viscera.

(a) The Respiratory System. (Fig. 17).

There is one pair of thoracic spiracles, situated laterally, one on either side of the prothorax, and there are eight pairs of abdominal spiracles, on the lateral extensions of the mesotergites of the abdominal segments 1 - 8 inclusive. Each spiracle opens into an atrium, which lacks taenidia. It soon gives rise to a short stem, which divides into a dorsal and a ventral trunk. The dorsal trunk is shorter than the ventral one.

The dorsal trunk gives rise at its base to a fine trachea, which divides profusely between the sheet of fat deposits and the body-wall. The main trunk gives origin to a small anterior and posterior trachea,

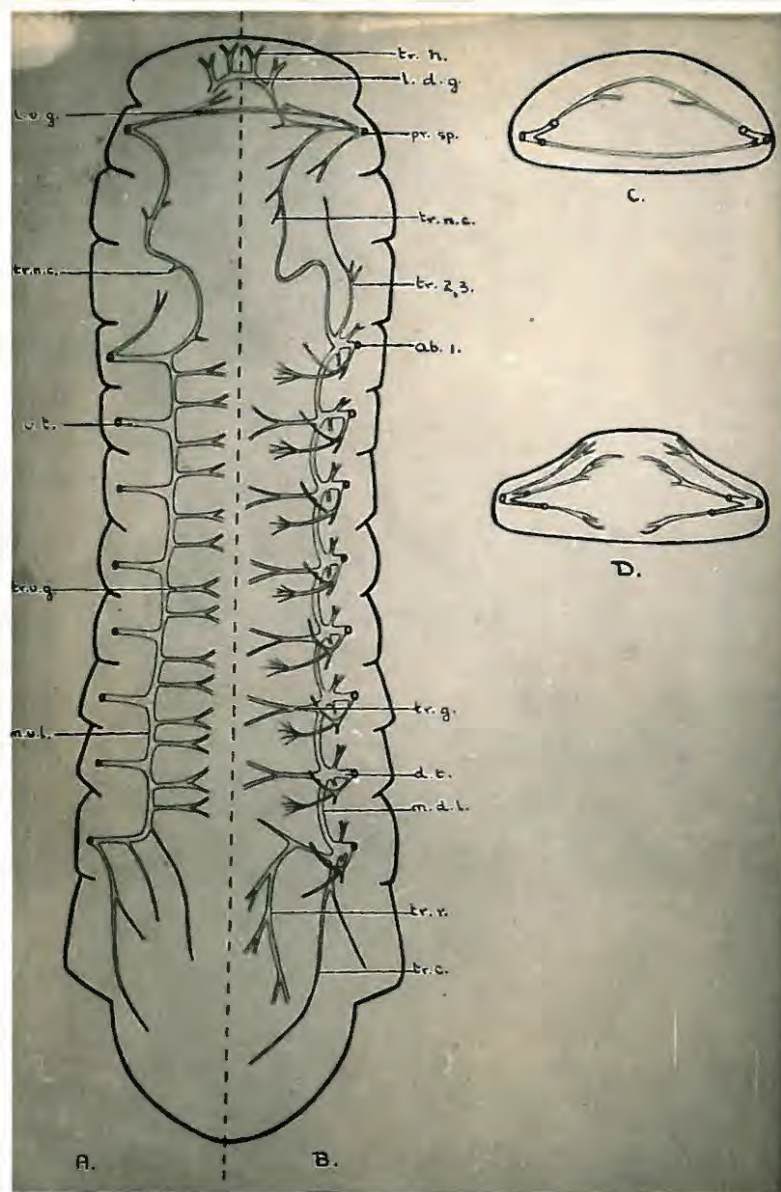


Fig.17. = Diagrammatic Representation of Respiratory System of Third Instar Larva.

ANOMALA VETULA WIED.

A. Ventral.

B. Dorsal.

C: T.S. Prothoracic Spiracle.

D: T.S. Abdominal Spiracle.

d. t. = dorsal trunk.  
 ab. l. = 1st. abdominal spiracle.  
 l. d. g. = loop dorsal to gut.  
 l. v. g. = loop ventral to gut.  
 m. d. l. = main dorsal loop.  
 m. v. l. = main ventral loop.  
 pr. sp. = prothoracic spiracle.  
 tr. c. = trachea to colon.

tr. g. = trachea to gut.  
 tr. h. = trachea to head.  
 tr. n. c. = trachea to nerve cord.  
 tr. r. = trachea to rectum.  
 tr. 2, 3. = trachea to 2nd. and  
 3rd. thoracic segments.  
 tr. v. g. = trachea to ventral  
 surface of gut.  
 v. t. = ventral trunk.

before dividing into the main anterior and posterior branches. The anterior branches, except for the prothoracic, join the posterior branches from the preceding trunk. From these dorsal loops conspicuous secondary branches arise, which divide, and supply the dorsal surface of the gut. The ventral nerve cord is richly supplied with trachea from the loop between the prothoracic and first abdominal trunks. The main trunk from the first abdominal spiracle sends a trachea forwards into the second and third thoracic segments. A conspicuous branch from the thoracic spiracle joins the corresponding branch from the opposite side of the body, forming a loop dorsal to the gut. Anteriorly this loop gives off four conspicuous branches, which divide to supply the head. The last abdominal spiracle supplies the hind-gut by means of two posteriorly directed trachea; the inner one branches on the colon, and the lateral one supplies the rectum.

The ventral trunks likewise divide into anterior and posterior branches, which unite to form a ventral series of loops between adjacent spiracles. Trachea are given off from these loops to supply the ventral surface of the gut, and in the thorax, trachea are given off to supply the ventral nerve cord. An

anterior branch from the thoracic spiracle unites with that from the corresponding spiracle of the opposite side, to form a loop ventral to the gut. From this loop anterior branches arise to supply the head. From the trunk of the posterior spiracle three conspicuous branches arise to supply the posterior part of the body.

(b) The Heart.

The heart is a transparent, narrow tube, situated immediately dorsal to the alimentary canal; it does not appear to be divided into chambers. It was only found in third instar larvae, and was most easily seen in the middle section of the mid-gut.

(c) The Alimentary Canal. (Figs. 18 and 19).

As the larvae of Anomala vetula Wied. are voracious feeders, the alimentary canal is, as would be expected, the most conspicuous of the internal organs. This is particularly evident posteriorly, where the gut is almost invariably distended with food, which shows as a dark mass through the thin wall of the alimentary canal.

In gross structure the alimentary canal is similar to that of Oryctes nasicornis L. (Orlov, 1924, p. 427), and Macrophylla pubens Péring. (Fenwick,

1942, p. 129). In points of finer detail it agrees closely with the description of Phyllopertha horticola L. and Anomala aenea Geer. (Rittershaus, 1927, p. 372).

The fore-gut extends from the mouth to the end of the mesothorax. The mouth leads into the pharynx, which narrows distally to form the thin walled oesophagus. The crop is the dilated posterior end of the oesophagus. The anterior region of the mid-gut overlaps the fore-gut, which is continued into the mid-gut as a trumpet-shaped cup. There are no salivary glands.

The mid-gut follows on the fore-gut. It has a larger lumen, and extends from the mesothorax to about the seventh abdominal segment. It can be <sup>divided</sup> distinguished into three sections.

(1) The anterior section occupies one-third to one-half of the entire mid-gut, and has a wrinkled surface, due to the folding of the wall. The anterior and posterior limits of this section bear blind ending coeca.

The first series of coeca in the first instar larva consists of six pouches on the left side, and five pouches on the right side, each of which shows slight lobulation. There is a faint indication of an inner group of pouches, corresponding in number

and position, to the outer ring of pouches, thus a double ring of pouches surrounds the first part of the mid-gut. The two medio-ventral pouches are directed posteriorly; the remainder point anteriorly.

In the second instar larva, the first series of coeca consists of six pouches, as in the first instar, but here the pouches are more clearly subdivided. The medio-ventral pair is the largest being 4 - 5 lobed, and posteriorly directed; the remainder point forwards. The three pouches on either side of the mid-dorsal line are 3 - 5 lobed, and the remaining two lateral pouches on each side are smaller, consisting of 2 - 4 lobes. The inner ring of pouches is better developed than in the first series of coeca of the first instar larva, but is smaller than the outer ring.

In the third instar larva, the first series of coeca comprises an irregular double row of small white diverticula dorsally and laterally. This row is broken mid-dorsally, and mid-laterally. The dorso-lateral group consists of about twenty diverticula, the latero-ventral group of about twelve diverticula. The diverticula may arise separately, or in small groups. They are larger than

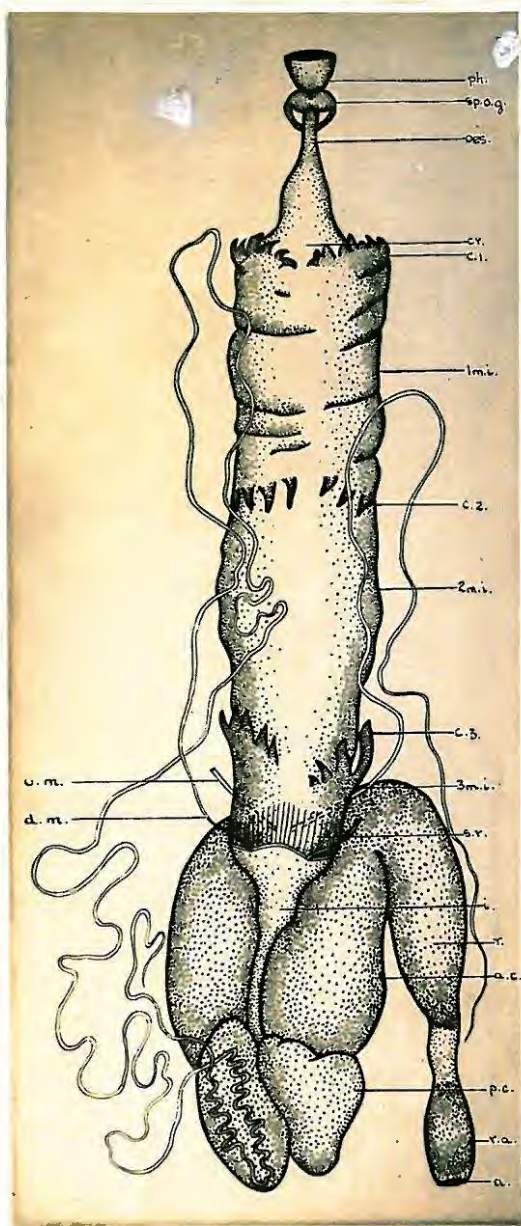
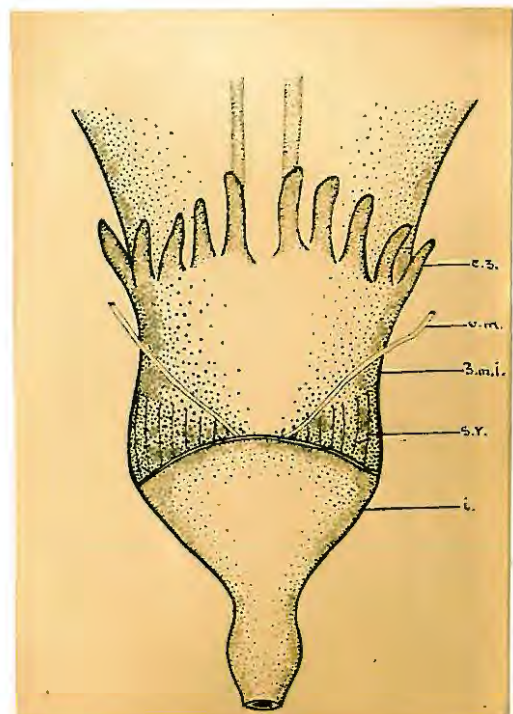


Fig. 18 = Alimentary Canal of  
Third Instar Larva.  
ANOMALA VETULA WIED.

- a. c. = anterior sacs of colon.  
a. = anus.  
c. 1. =  
c. 3. = coeca, series 1-3.  
cr. = crop.  
d. m. = dorsal Malpighian  
tubes.  
i. = ileum.  
1m. i. =  
3m. i. = mid-intestine, sections  
1-3.  
oes. = oesophagus.  
ph. = pharynx.  
p. c. = posterior sacs of colon.  
s. r. = striated region.  
sp. o. g. = supra-oesophageal  
ganglion.  
r. a. = rectal ampulla.  
r. = rectum.  
v. m. = ventral Malpighian  
tubes.

Fig. 19 = Junction between Mid-  
gut and Hind-gut of  
Third Instar Larva.  
Enlarged.  
ANOMALA VETULA WIED.

- c. 3. = coeca, series 1.  
i. = ileum.  
3m. i. = mid-intestine,  
section 3.  
s. r. = striated region.  
v. m. = ventral Malpighian  
tubes.



those of the second instar, and overlap each other more strongly. Ventrally there is a group of diverticula on either side of the median line. They are in a single row, in the form of a hand, with five "fingers", the second and third from the mid-ventral line being the largest. All the coeca of this first series are directed anteriorly, except for the two ventral "hands", which point anteriorly. The "fingers" are the largest of this series of coeca. It is thus apparent that the anterior ring of blind coeca is different in all three larval instars. There is a progressive increase in the number and degree of overlapping of coeca in the three larval instars. There is also a much stronger wrinkling of the anterior one-third of the mid-gut.

The second series of coeca, which forms the posterior limits of the anterior one-third of the mid-gut, arises at the level of the third abdominal segment. In the first instar larva, there are usually sixteen pouches, but two additional undeveloped pouches have been found in one specimen. The second instar has 17 - 18 blind pouches. In the third instar larva, the series consists of eighteen coeca. It is interrupted in the mid-dorsal

and mid-ventral lines. The coeca are longer than those of the first series, and increase in size ventrally. They are directed posteriorly.

(ii) The second one third of the mid-gut has a smooth, unwrinkled surface, without pouches. It extends from the third to about the sixth abdominal segment. On the ventral surface there is a median longitudinal fold.

(iii) The last one third of the mid-gut extends from the sixth to the seventh abdominal segment. The third series of coeca surrounds the commencement. In all three instars this series consists of eighteen coeca. It is divided into lateral groups, with a narrow mid-dorsal and mid-ventral interval. There is a progressive increase in size of these coeca from the first to the third instar larvae. In the third instar this series consists of the largest diverticula of the three series. They are finger-shaped, with swollen bases, and increase in size ventrally. There is no forwardly directed pouch of the stomach into which these coeca open, as there is in Macrophylla pubens Péring. (Fenwick, 1948, p. 131). The ventral coeca of this series arise anterior to the dorsal ones.

Dorsal and ventral pouches are smallest; the lateral ones are usually longer, but undeveloped single pouches may occur, in between the long lateral ones, as in Phyllopertha horticola L. (Rittershaus, 1927, p. 372).

Posterior to this ring of coeca there is a smooth area, followed by a longitudinally striated region. This field is broadest dorsally, where it is approximately half the length of the area between the third series of coeca and the end of the mid-gut. It decreases in size ventrally, so that the two sides meet in a narrow strip. Posteriorly this region is surrounded by a small swelling, which marks the junction of the mid- and hind-guts. The Malpighian tubes are inserted here; the dorsal pair arises laterally on either side of the median line; the ventral pair arises close together in the mid-ventral line.

The hind-gut is divisible into three distinct regions, which are folded on each other in the form of an "S", each fold being situated ventral to the preceding one. When stretched out it forms approximately half the length of the gut.

The ileum forms the first region, which is cup-shaped, and narrows posteriorly, to form an

elongated stem. It extends from the seventh to the beginning of the tenth segment. It is white in colour, and is in striking contrast to the dark underlying pair of anterior colon sacs.

The colon is clearly distinguishable from the ileum, as it is almost invariably distended with food. It fills the greatly enlarged posterior region of the larva. It thus obscures the underlying rectum, and forms the most conspicuous part of the alimentary canal. It is continued forwards from the tenth to the sixth abdominal segment. It has four parts, two anterior and two posterior sacs. The posterior sacs are heart-shaped, and lie behind the termination of the ileum. It is on these sacs that the dorsal pair of Malpighian tubes winds in a characteristic wavy "U"-shape. The anterior pair of sacs is approximately twice as large as the posterior sacs, and is furrowed longitudinally to accommodate the ileum.

The rectum is narrower than the greatly enlarged anterior colon sacs, with which it is continuous. It curves sharply, and passes to the anus. The posterior region of the rectum forms a conspicuous rectal ampulla.

The arrangement of the three series of coeca

of the mid-gut in the three instars of Anomala vetula Wied., bears striking resemblance to that of Phyllopertha horticola L. and Anomala aenea Geer. (Rittershaus, 1927, pp. 374-375).

The third series of coeca retains a constant number of diverticula in all three instars of these three species. There are eighteen diverticula in Anomala vetula Wied. and in Anomala aenea Geer., and sixteen in Phyllopertha horticola L. (Rittershaus, 1927, p. 375).

The second series of coeca shows a regular increase in the number of diverticula from the first to the third instar larva in all three species:-

	<u>Anomala vetula</u> <u>Wied.</u>	<u>Phyllopertha</u> <u>horticola</u> L.	<u>Anomala aenea</u> <u>Geer.</u>
First instar	16 -18	16	15 - 16
Second instar	17 -18	16 - 18	16 - 18
Third instar	18	16 - 17	18

The first series of coeca is different in all three instars of these three species. There is, however, a striking similarity of development of this anterior coecal ring from first to third instar, in the three species. In the first instar of Phyllopertha horticola L., there are five pouches on either side of the middle line, but six pouches in

Anomala vetula Wied. In both species there is an indication of faint individual lobulation of the pouches, all of which point to the head, except the two medio-ventral lobes, which point posteriorly. In Anomala vetula Wied. there is an indication of the sprouting of an inner ring of coeca in the first instar. According to Rittershaus, 1927, p. 375, this is only apparent in the third instar of Anomala senea Geer. and Phyllopertha horticola L. Thus a regular increase in number of the diverticula is only found in the first series of coeca in the three species.

It is stated by Rittershaus, 1927, p. 376, that food never penetrated into these pouches but that they function as glandular crypts.

(d) The Excretory System. (Figs. 18 and 19).

The principal excretory organs are two pairs of Malpighian tubules. An accessory excretory function is performed by the fat body described above.

The origin of the Malpighian tubes is similar to that described for Phyllopertha horticola L. (Rittershaus, 1927, p. 373). The dorsal pair of Malpighian tubes opens dorso-laterally into the gut, at the level of the circular swelling surrounding the junction between the mid-gut and the ileum. The members of the ventral pair of

Malpighian tubes, enter the gut close together, in the mid-ventral line, anterior to the dorsal tubes, but on the same circular swelling. Thus the mid-gut commences slightly more anterior on the ventral surface than on the dorsal surface. Both pairs of tubes are unbranched, and end blindly in the haemocoel.

The proximal ends of the dorsal tubes wind anteriorly, on either side of the gut, to the level of the first row of enteric coeca. They then turn and pursue a winding course to the posterior part of the body cavity. They continue on to the surface of the posterior coecal sacs, of the corresponding side, and wind in a characteristic wavy "U"-shape. Although closely applied to the walls of these sacs, they do not open into these chambers. The dorsal tubes become very delicate towards their distal ends, and after a number of coils, they end ventral to the anterior coecal sacs.

The ventral Malpighian tubes are thinner than the dorsal tubes, and do not extend as far forwards. Distally they wind in the folding of the posterior part of the alimentary canal, and end close to the rectum.

In the posterior region of the body cavity the larger trachea keep the Malpighian tubes in position. Anteriorly, they are bound closely to the mid-gut by numerous fine trachea.

(e) The Nervous System. (Fig.20).

The brain lies dorsal to the alimentary canal, at the level of the anterior region of the oesophagus. The remainder of the central nervous system is obscured by the overlying alimentary canal. Removal of the gut reveals the stout ventral cord, which lies wholly within the pro- and meso-thorax.

The brain consists of a pair of supra-oesophageal ganglia, closely united in the middle line. They are oval, white structures, clearly visible after separating the muscles in the head. There is no visible division into protocerebrum, deutocerebrum or tritocerebrum. Two nerves arise close together from the anterior margin. The inner antennary nerve passes over the outer nerve, which is continued forwards along the pharynx.

The brain is connected with the suboesophageal ganglion by means of a pair of circumoesophageal

- connectives,-

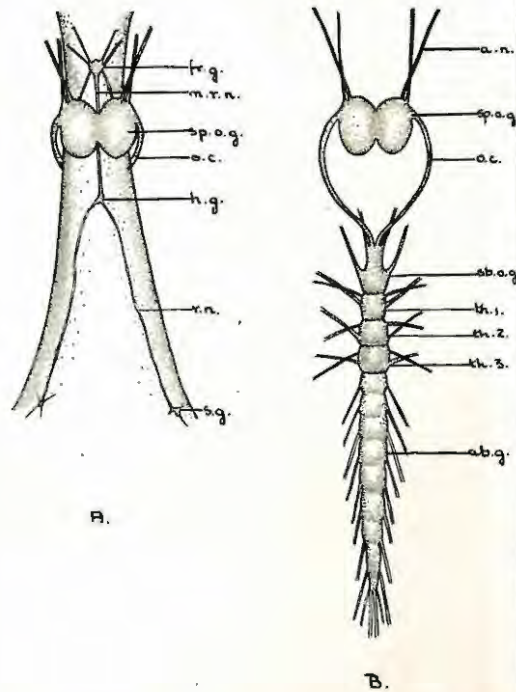


Fig. 20. = Nervous System of Third Instar Larva.  
ANOMALA VETULA WIED.

A. Oesophageal Sympathetic Nervous System.

- c. c. = circumoesophageal connectives.
- fr. g. = frontal ganglion.
- h. g. = hypocerebral ganglion.
- m. r. n. = median recurrent nerve.
- r. n. = recurrent nerve.
- st. g. = stomachic ganglion.
- sp. o. g. = supra-oesophageal ganglion.

B. Central Nervous System.

- ab. g. = abdominal ganglia.
- a. n. = antennary nerve.
- c. c. = circumoesophageal connectives.
- sb. o. g. = sub-oesophageal ganglion.
- sp. o. g. = supra-oesophageal ganglion.
- th. 1. - th. 3. = thoracic ganglia 1-3.

connectives, which arises from the antero-lateral margins of the brain. The sub-oesophageal ganglion is elongated, and gives rise anteriorly to two pairs of nerves, which supply the mouthparts.

The ventral nerve cord consists of three thoracic ganglia, situated in the prothorax, and eight abdominal ganglia in the mesothorax. The ganglia, however, are so concentrated that they appear as a single undivided ventral cord, with the absence of commissures and connectives.

The thoracic ganglia are more readily distinguishable than the abdominal, as they are larger and broader. Each gives rise to two pairs of nerves, which run laterally, to supply the leg muscles and general musculature of the corresponding segments.

The limits of the individual abdominal ganglia are not easily determined. Each gives rise to a pair of nerves, which runs posteriorly, almost parallel with the ventral nerve cord, but diverges to supply the general musculature of the corresponding segments. Three pairs of nerves arise close together from the eighth abdominal ganglia, indicating a fusion of ganglia.

The oesophageal sympathetic nervous system lies dorsal to the oesophagus. A median white frontal ganglion lies a short distance in front of the brain. Anteriorly it sends branches over the surface of the oesophagus. It is connected to the brain on either side.

Posteriorly the frontal ganglion gives off a median recurrent nerve, which runs along the mid-dorsal line of the oesophagus. It passes under the brain, and a short distance behind it, it forms a hypocerebral ganglion. This ganglion innervates the adjacent region of the oesophagus. Posteriorly, the hypocerebral ganglion gives off two recurrent nerves, which extend to the posterior end of the fore-gut, and each terminates in a stomachic ganglion. The stomachic ganglia give off small branches to the surrounding oesophageal regions.

There were no traces of the reproductive system in any of the larvae studied.

III. COMPARISON OF THE EXTERNAL FEATURES OF  
THE THREE LARVAL INSTARS.

The published descriptions of Scarabaeid larvae usually apply to the third instar only. With the notable exception of Böving, 1939, and 1942, little attention has been paid to the comparison of the larval instars, to show whether the characters of the third instar which distinguish the species, are present in earlier instars, or by what characters the three instars can be separated from one another.

Anomala vetula Wied. passes through three instars in its larval development. The most useful criterion for distinguishing between the instars is the proportional increase in size of the head-capsule of succeeding instars. The head-capsule, being chitinous, is unable to increase in size, except at, and immediately after, ecdysis. The size of the body of the grub changes considerably during each instar.

The fact that the width of the head-capsule of an insect larva is more or less constant for any instar of a species, was first shown by Dyar, 1890. He observed that the width of the head of Lepidopterous larvae followed a regular geometric progression in

successive instars (Inns, 1934, p. 195). Dyar's Law has been shown by Ritterhaus, 1927, p. 340, to be applicable to the larvae of Phyllopertha horticola L. and by Ludwig and Abererombic, 1940, to apply to larvae of Popillia japonica Newm. The number of instars in Melolontha melolontha L., Amphimallus solstitialis L., and Serica brunnea L. were determined with the aid of Dyar's Law by Fidler, 1936, p. 419, and in Macrophylla pubens Péring., by Fenwick, 1942, pp. 127). By dividing the width of the head-capsule of one instar by that which precedes it, a ratio of increase in each instar is obtained. It is thus possible to determine whether an ecdysis has been overlooked or not during a study of the life-cycle.

The length and width of the head-capsule of larvae of Anomala vetula Wied. were taken. The length was measured from the frontoclypeal suture to the posterior margin of the cranium. The width was measured across the head-capsule, posterior to the bases of the antennae, at the widest point.

First instar.

<u>Length</u>	largest	1.1 mm.
	smallest	.7 mm.
<u>Width</u>	largest	1.8 mm.
	smallest	1.5 mm.

Mean for 17 specimens:-

Length	0.96 mm.
Width	1.65 mm.

Standard deviation for 17 specimens:-

Length	0.118 mm.
Width	0.077 mm.

Second instar.

<u>Length</u>	largest	1.9 mm.
	smallest	1.2 mm.
<u>Width</u>	largest	2.8 mm.
	smallest	2.4 mm.

Mean for 36 specimens:-

Length	1.55 mm.
Width	2.66 mm.

Standard deviation for 36 specimens:-

Length	0.192 mm.
Width	0.109 mm.

Third instar.

<u>Length</u>	largest	3.4 mm.
	smallest	2.3 mm.
<u>Width</u>	largest	5.0 mm.
	smallest	3.8 mm.

Mean for 30 specimens:-

Length	3.71 mm.
Width	4.41 mm.

Standard deviation for 30 specimens:-

Length	0.313 mm.
Width	0.243 mm.

The length of the head-capsule in the second instar is 1.59 times the length in the first instar, and in the third instar it is 1.77 times the length in the second instar. The ratio of the width of the head-capsule of the second instar larvae, to that of the first instar larvae was 1.6 1; the ratio of the width of the head-capsule of the third instar larvae, to that of the second instar larvae, was 1.65.

The measurements show that the larvae fall into three well defined groups, each characteristic of a larval instar. There is no overlapping of measurements of larvae of successive instars. The differences in size are sufficiently obvious to enable one instar to be recognised from the other in a superficial examination. The ratio for the increase in length of the head-capsule in successive instars is not the same as the ratio for the increase in width.

The increase in width of the head-capsule is directly proportional to its increase in length. This also occurs in Popillia japonica Newm. (Ludwig and Abercrombie, 1940, p. 389). Ludwig and Abercrombie, 1940, p. 390, found that the growth ratios for both length and width of the head-capsule of Popillia japonica Newm. diminish with successive instars. This

does not apply to larvae of Anomala vetula Wied. van Enden, 1941, p. 187, calculated the ratio of the increase in width of the head-capsule of successive instars of Phyllopertha horticola L. as 1.5.

The following is a comparison of the more important points in the external morphology of the three larval instars of Anomala vetula Wied.

(a) The Head.

The Head-capsule.

In the newly hatched grub this is white in colour; the dorsal and ventral articulation points of the mandibles with the head-capsule are the only regions of dark sclerotisation. In second instar larvae the head-capsule is light ochre, becoming darker in fully grown larvae.

In all three larval instars the epicranial suture is fine but distinct. The arrangement of hairs on the head-capsule is identical in the three instars.

The Antennae.

The length of the antenna of the second and third instar larvae is slightly more than one and a half times that of the preceding instar. The basal segment becomes increasingly larger, and more heavily chitinised in successive instars. There is an increase in length of all the segments from one

instar to the next, but the proportions remain constant. The most conspicuous elongation occurs in the second antennal segment. The sense fields on the penultimate and terminal segments are relatively smaller in second and third instar larvae. The number and arrangement of the hairs on the antennal segments is identical in the three instars. There are 7 - 8 basiconic sensilla at the tip of the fourth segment in all three instars; there are 1 - 3 sensilla situated near the tip of the penultimate segment.

#### The Clypeus.

The shape of the clypeus, and the number and arrangement of setae on the surface, are the same in all three instars.

The distal ante-clypeus is membranous, whitish, and without hairs or sense pits in all three instars. In the first instar larva the surface of the post-clypeus is wrinkled, but is smooth in succeeding instars. It is not as conspicuous as in second and third instar larvae, owing to the slight degree of sclerotisation. The absence of strong sclerotisation of the lateral and posterior margins of the post-clypeus in the newly hatched grub is conspicuous.

1. The Labrum and Epipharynx.

The mitriform shape of the labrum is common to all three instars. In the first instar the anterior projection is not as pronounced as in the two succeeding instars, with a corresponding reduction in the depression of the antero-lateral margins, so that the labrum appears more rounded anteriorly. Measurements of the average length and width of twenty specimens in each instar are proportionally as follows:-

1:1.45 in the first instar,  
1:1.52 in the second instar, and  
1:1.52 in the third instar.

The length was taken from the margin of the anterior projection, to the frontoclypeal suture, and the width, across the widest part of the labrum.

The setae are identically arranged in all the three larval instars.

There are 15 - 20 sense pits between the transverse row of delicate hairs at the base of the labrum, and the median pair of hairs in first instar larvae. The number varies from 20 - 26 in the second instar, and 25 - 30 in the third instar.

The form and arrangement of structures on the surface of the epipharynx is identical in all three instars. As has been stated already, much

attention has been paid to the structure of the epipharynx by earlier workers, with a view to its possible use in specific determination of Scarabaeid larvae. The similarity of the epipharynx in all three instars of Phyllopertha horticola L. and Anomala aenea Geer. (Rittershaus, 1927, pp. 342-344), Popillia japonica Newm. (Böving, 1939, p. 187), Macrophylla pubens Péring. (Fenwick, 1942, p. 123), species of the genus Phyllophaga (Böving, 1942, p. 8), and Anomala vetula Wied, further accentuates this possibility.

As stated in a description of the clypeus, the anterior emargination is less pronounced in first instar larvae than in the second or third instars. The degree of chitinisation, and the length of the setae increase in succeeding instars. In the first instar the epixygam is not well developed, so that the unconnected left and right zyga appear as an incomplete half circle anterior to the heli. The acanthopariae bear 18 - 25 marginal articulated spines in the first instar, 20 - 26 in the second instar and 21 - 27 in the third instar. Rittershaus, 1927, p. 342, and p. 369, states that there are 17 - 19 marginal spines in all three larval instar of Phyllopertha horticola L. and 19 - 23 in Anomala aenea

Geer. The setae of the chaetoparia are not as strong as in the other two instars; laterally they are small and inconspicuous. The laetorma, dextorma, nesium externum and nesium internum are present, but they are not as heavily chitinised as in the second and third instars.

## 2. The Mandibles.

The mandibles of the first instar larva are more truncate than in the two succeeding instars. The concavity between the incisor and molar regions becomes increasingly deeper from first to third instar. As the incisor region is not worn down greatly in first instar larvae, the notch at the base of the incisor region appears deeper than in second or third instar larvae. In freshly moulted second and third instar larvae however, the incisor and molar regions are sharply developed.

In the newly hatched grub the tips of the mandibles, the individual molar teeth and the dorsal and ventral articulation points, show up as dark brown or black heavily chitinised regions, in contrast to the colourless head-capsule. As development proceeds the mandibles become yellow, shading into reddish-brown and black at the incisor and molar regions. In the second instar larva, the centre of the dorsal

surface of the mandible is yellow, becoming more dull towards the margins. Ventrally the stridulating area is yellow; the remainder is a chestnut brown. The molar regions, like the tips, are almost black.

The Processus accessorius is not heavily chitinised in the newly hatched grub, but becomes darker towards the end of the instar. It is conspicuous in second and third instar grub.

The form of the mandibles is the same in all three instars. The arrangement of the hairs of the acia is the same throughout larval development.

There are 11 - 15 hairs at the base of the scrobis in first instar larvae; 11 - 16 in the second instar, and 15 - 17 in the third instar. The setae of the ventro-lateral carina of first and second instar larvae are very small. On the dorsal surface, anteriorly, the one long seta and the two sense pits are common to the three instars, as also are the 6 - 8 setae near the anterior molar tooth.

### 3. The Maxillae.

The sclerotisation of the maxilla increases from first to third instar. In the first instar larva the labacoria is membranous and is

without the sclerotised areas, which are present in the two succeeding instars.

The number and arrangement of the hairs are identical in all three instars; the lacinial and galeal teeth are well developed.

The plectrum consists of 6 - 8 stridulating teeth throughout larval development. In Phyllopertha horticola L. there are 4 - 6 stridulating teeth in the first instar, and 5 - 7 in second and third instar larvae. (Rittershaus, 1927, p. 348).

#### 4. The Labium.

The chitinisation of the labium increases in successive instars. The number and arrangement of the hairs and sense pits remain constant. The terminal sensilla of the labial palps are conspicuous in all three instars; there are approximately eight in each instar.

The form of the hypopharynx and the position and number of setae are constant during larval development. The sclerotisation of the hypopharyngeal sclerome becomes increasingly greater as development proceeds. In the first instar larva the two small teeth on the anterior margin of the hypopharyngeal sclerome are very conspicuous. During larval development they become  
- worn -

worn down by feeding.

The row of hairs which follows the outline of the right hand side of the posterior margin of the hypopharyngeal sclerose, is conspicuous in first instar larvae: owing to the strong chitinisation of succeeding instars, it is not as obvious.

(b) The Thorax.

The hairs on the thorax of first instar larvae are small; they become increasingly longer in succeeding instars. In the three instars the annulations of each thoracic segment may be recognised by the length and position of certain hairs. The protergites of the three thoracic segments can be recognised by the possession of one long hair on either side of the middle line, and a few small hairs. The mesotergites bear short scattered hairs, and one long lateral hair on either side. The metatergites have a transverse row of short hairs. The pleural folds bear scattered hairs. The transverse row of hairs on the mesosternites are well developed, and are directed towards the middle line.

The thoracic spiracle is the largest in all three instars; the concavity of the sieve

plate faces posteriorly. The prothoracic sclerite is not distinguishable in first instar larvae; it is only faintly indicated in the second instar. The sclerotisation of the laterocervicalia increases with succeeding moults.

In first instar larvae there is a small sharp chitinous spine, on either side of the dorso-lateral surface of the mesotergite of the metathorax. Each spine is a roughly triangular, smooth margined mucronate process, situated near the posterior margin of a lighter coloured chitinous area. It bears a stiff seta, which is about twice the length of the spine.

These processes can be seen through the chorion of the egg, towards the end of embryonic development. They are present throughout the first instar, but are shed at the first ecdysis; they are not present in second or third instar grubs. As will be explained later, they are important in initiating the rupture of the chorion during eclosion.

They are variously known as hatching spines, raptor ovi or egg bursters (Hayes, 1929, p. 48). They are present in a number of insects (Imms, 1934, p. 188). Similar structures have been described in Anomala

amea Geer. and Phyllopertha horticola L. (Rittershaus, 1927, p. 391), and in Popillia japonica Newm. (Böving, 1937, p. 189). In the first two species mentioned above the form of the hatching spine is similar to that in Anomala vetula Wied.; there is also a long bristle about twice the length of the spine. The mucronate process in Popillia japonica Newm. is figured by Böving, 1939, p. 189, as having small sharp rigid points; the accompanying hair is short.

The legs.

In the newly hatched larva the legs are almost white, but as development proceeds, the chitin assumes a yellow-brown colour and the hairs become reddish-brown.

Comparative measurements of the segments of the three pairs of legs in the three larval instars, show similar changes during development, as in the larvae of Phyllopertha horticola L. (Rittershaus, 1927, pp. 352-363).

The coxa is shortest in the prothoracic pair of legs, and longest in the metathoracic pair of legs in all three instars. In the second instar the coxa is about twice the length of the coxa of the first instar larva; the ratio of the length of

the coxa of second and third instar larvae is slightly less.

The femur of the prothoracic pair of legs is shorter than that of the meso- and metathorax, which are approximately equal in length. The length of the femur is doubled from first to second instar; the difference between the length of the femur in second and third instar larvae is not as great.

The tibio-tarsus is approximately the same length in the three pairs of legs. In the second instar the length is approximately twice that of the first instar, but the difference is not as great between second and third instar larvae.

The claws of the metathoracic pair of legs are the shortest in each instar; those of the pro- and mesothoracic pair of legs are approximately the same length.

(c) The Abdomen.

The number of hairs is approximately the same in the three larval instars. They are most conspicuous in the third instar, as they are longer and more heavily chitinised. The asperities appear to be more dense in the first instar, owing to the small area of the surface of the abdomen

compared with third instar larvae.

The distribution of hairs and asperities is the same as in the third instar.

The rounded field on the dorsal surface of the tenth abdominal segment is not as distinct as in the two succeeding instars; the chitinisation of the margin is only faintly indicated.

The Raster.

The form and arrangement of the setae of the raster, including both pali and tegillar setae are similar in all three instars. The number of pali may vary from 17 - 22 in any one instar. They increase in size from first to third instar, but the length is about two and a half times the width in each instar. The distance between adjacent pali is slightly greater in first and second instar grubs, than in the third instar. The tegillar setae number from 39 - 43 in the third instar. Typically they are well developed, but increase in size gradually towards the anus. In the second instar the tegillar setae vary from 33 - 38. Approximately twenty-four of these are well developed, but the remainder are small and inconspicuous. There are about twenty-six tegillar setae in the first instar; 7 - 8 of these are

- usually -

usually very small.

Böving, 1939, p. 186, states that in Popillia japonica Newm. the form and arrangement of the setae of the raster are identical in all instars; their length and thickness, however, vary according to the instar. There are 6 - 7 pali in all three instars, but the number of tegillar setae is considerably smaller in the first instar, than in succeeding instars. According to Fidler, 1936, p. 177, the number of pali increases in each succeeding instar in Melolontha melolontha L., Amphimallus solstitialis L., and in Serica brunnea L.

The setae of the barbula are more delicate in first instar larvae than in succeeding instars.

#### The Spiracles.

The one pair of thoracic and the eight pairs of abdominal spiracles are conspicuous in all three instars. The thoracic spiracle is the largest. The concavity of the sieve plate is directed posteriorly, that of the abdominal spiracles anteriorly.

During larval development the size of the bulla increases relative to the sieve plate. In first instar larvae the sieve plate is reniform; the bulla is small, so that the concavity of the respiratory plate is only slightly indicated. The

peritreme is not well defined and there is no spiracular slit. In second and third instar larvae the sieve plate is crescentic, the bulla is large, and has a curved spiracular slit. In Popillia japonica Newm., the spiracles in the first instar larvae have a rounded respiratory plate; there is no bulla and no spiracular slit. In second and third instar larvae the respiratory plate is "C"-shaped, and surrounds a large bulla, with a curved spiracular slit (Böving, 1939, p. 187).

The following are the chief distinguishing features of the three larval instars:-

The first instar larvae are separable from both second and third instar larvae, by the presence of a small hatching spine on the mesotergite of the metathorax. The respiratory plate is large, compared with the small size of the bulla; it lacks a well defined peritreme. Second and third instar larvae are inseparable by any structural character.

1. The average width of the head-capsule is 1.65 mm. in first instar larvae, 2.66 mm. in second instar larvae, and 4.41 mm. in third instar larvae.

2. There is increasing sclerotisation from first to third instar, particularly of the

- head-capsule -

head-capsule, prothoracic sclerite,  
laterocervicalia, legs and spiracles.

3. The ratio of length to breadth of the labrum is 1: 1.43 in the first instar, 1: 1.52 in second and third instars. The sense pits towards the base of the labrum vary from 15 - 20 in the first instar, 20 - 26 in the second instar, and 25 - 30 in the third instar.
4. The lateral spines of the scanthoparia of the epipharynx vary from 18 - 25 in the first instar, 20 - 26 in the second instar, and 21 - 27 in the third instar.
5. There are 11 - 15 hairs at the base of the scrobis in the first instar, 11 - 16 in the second instar, and 13 - 17 in the third instar.

IV. THE EXTERNAL FEATURES OF THE PUPA.

As in all Coleoptera, the pupa is of the exarate or free type, in which the wings and legs are not secondarily attached to the body. During this stage, it is unable to feed, and lies motionless in the pupal cell, constructed from the surrounding soil. The abdomen alone is capable of limited movement in a dorso-ventral plane.

The Pupa (Figs. 21 and 22).

The dorsal surface of the pupa is convex, the pronotum and last five abdominal segments curving ventrally. The head is thus not visible in a dorsal view, and the mouthparts are directed caudo-ventrally. The body increases in width gradually from the prothorax to the third abdominal segment. From this point it narrows gradually to the sixth abdominal segment, and more sharply to the posterior end.

The integument is creamy-brown in colour; the dorsal arc-shaped ridges of the abdomen and the spiracles, are very noticeable, being the only strong chitinisations of the soft pupal skin. It is thin, so that the colouration of the developing imago can be followed clearly. The first

- pigmentation -

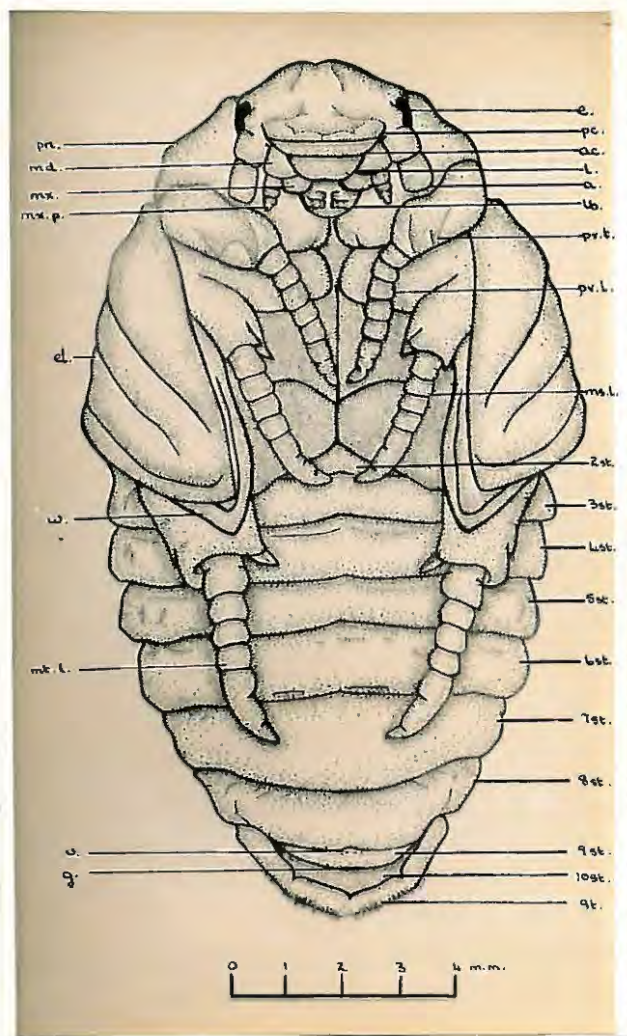


Fig. 21 - Ventral view of Female Pupa.  
ANOMALA VETULA WIED.

- |                                   |                             |
|-----------------------------------|-----------------------------|
| ac. = anteclypeus.                | pr. l. = prothoracic leg.   |
| a. = antenna.                     | pr. t. = prothoracic tibia. |
| v. = closed orifice of<br>vagina. | 2st. =                      |
| e. = compound eye.                | 10st. = sterna 2-10.        |
| el. = elytron.                    | 9t. = tergum 9.             |
| g. = gonopore.                    | w. = wing.                  |
| lb. = labium.                     |                             |
| l. = labrum.                      |                             |
| md. = mandible.                   |                             |
| mx. = maxilla.                    |                             |
| mx. p. = maxillary palp.          |                             |
| ms. l. = mesothoracic leg.        |                             |
| mt. l. = metathoracic leg.        |                             |
| pc. = postclypeus.                |                             |
| pn. = pronotum.                   |                             |

pigmentation appears in the eyes, which are large and black. In later development, the bi-dentate form of the anterior tibiae can be seen. Further development of adult structures within the pupa will be dealt with in the biology of the adult.

The entire surface is covered with very small regularly arranged spines, which are only visible under high magnification. The ninth tergum has a well developed fringe of hairs on the posterior margin.

The lateral margins of sterna 2 - 8 inclusive are finely rugose and slightly raised. Distinct lateral elevations are described in Phyllopertha horticola L. and Anomala aenea Geor. (Rittershaus, 1927, p. 276). The eighth tergum is rugose, the wrinkles running obliquely from the antero-lateral angle to the back of the tergum. There is an elevation on either side of the median line of the dorsal surface of the ninth tergum. The remainder of the integument is smooth. The posterior end is bluntly rounded.

The sexes can be readily distinguished on the structure of the ventral surface of the posterior end of the abdomen. This will be described later.

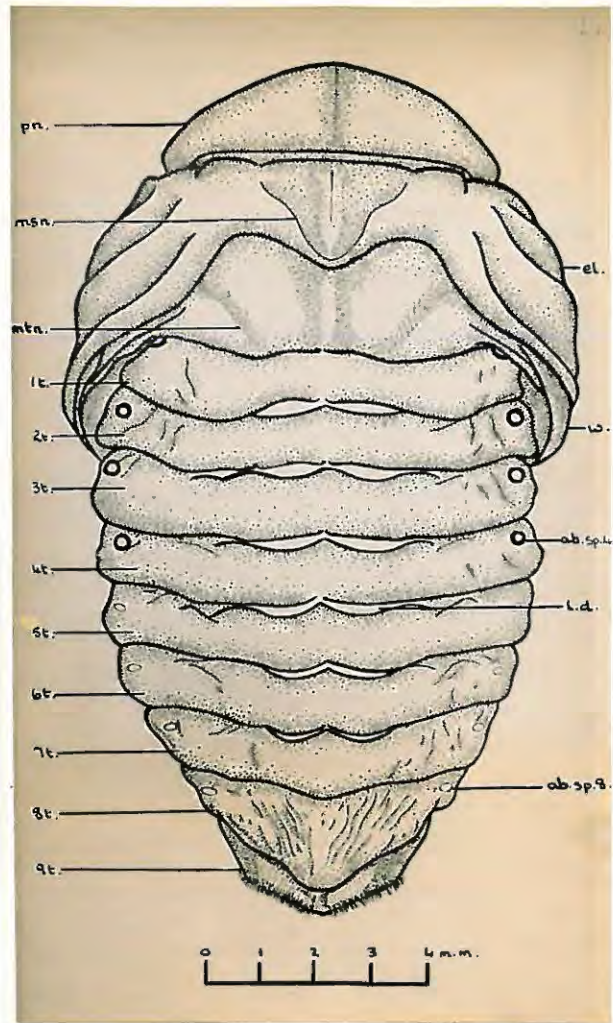


Fig. 22 - Dorsal view of Female Pupa.  
ANOMALA VETULA WIED.

- ab. sp. 4. = abdominal spiracle 4.
- ab. sp. 8. = abdominal spiracle 8.
- el. = elytron.
- l. d. = lenticular depression.
- msn. = mesonotum.
- mtn. = metanotum.
- pn. = pronotum.
- l. t. -
- 9t. = terga 1-9.
- w. = wing.

(a) The head. (Figs. 21 and 23).

The posterior margin of the head is obscured by the pronotum, and through the curvature of the body, is directed caudo-ventrally. The mouth-parts are easily recognised, and are similar to those of the imago.

The epicranial suture is distinct, but it is not as obvious as in the larvae. The frontal sutures diverge to the posterior angle of the clypeus. Laterally the darkly pigmented compound eyes of the imago are a prominent feature. They are partially divided by the developing canthus.

The clypeus is separated from the frons by the frontoclypeal suture, which is obliterated medianly. It shows signs of the developing concavity on the dorsal surface of the adult clypeus. As in the imago, the post-clypeus is at right angles to the ante-clypeus. The labrum is attached distally, and has a median notch on the posterior margin. The mandibles are visible between the antennae, and the lateral margins of the ante-clypeus and labrum. Distal to them, the maxillae and four-segmented maxillary palps can be seen. The labium is situated anterior to the maxillae, with the developing three-segmented labial palps.

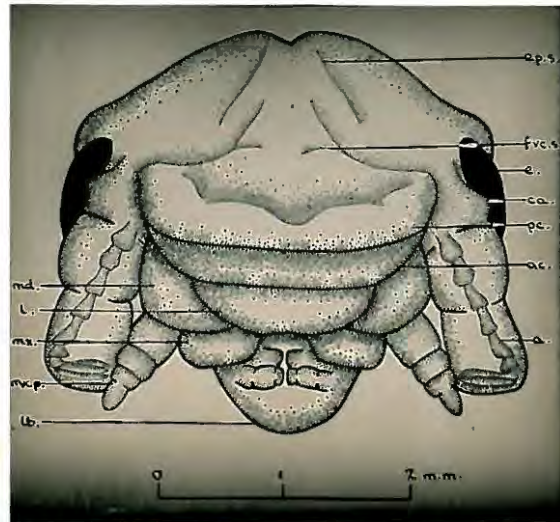


Fig. 23 - Head of Female Pupa.  
ANOMALA VETULA WIED.

- ac. = anteclypeus.
- a. = antenna.
- ca. = canthus.
- e. = compound eye.
- ep. s. = epistomal suture.
- fro. s. = frontoclypeal suture.
- lb. = labium.
- l. = labrum.
- md. = mandible.
- mx. = maxilla.
- mx. p. = maxillary palp.
- pc. = postclypeus.

The antennae arise between the posterior angle of the post-clypeus and the eye. They are directed ventrally and lateral to the mouth-parts. In the late pupal stage the form of the adult antenna can be recognised within the pupal integument. Here it is seen that the antennal shaft extends from the inner proximal region of the pupal covering to the outer distal region. The three-lamellate club lies at the distal extremity of the pupal covering, at right angles to the long axis of the antennal shaft. The lamellae fit into each other, so that the first segment of the club, or seventh antennal segment is directed inwardly, and is the most proximal segment of the club. The antennae of the male and female are similar.

(b) The thorax (Figs. 21 and 22).

The pronotum is large, and is similar to that of the imago. In a dorsal view it forms the anterior region of the pupa, and slopes ventrally. It overlaps the hind-part of the head-capsule. It is divided medianly by a longitudinal dorsal suture. The prothoracic legs reach almost to the end of the

metasternum, where they nearly meet in the middle line. The two teeth on the outer surface of the developing adult tibia can be seen clearly. In all three pairs of legs the segmentation of the tarsi is visible, but there is no claw, the distal extremity being rounded. The last segment is longer than the preceding segments, to accommodate the developing fifth tarsal segment and claw of the imago.

The mesonotum is continuous laterally with the first pair of wings. A short while before the emergence of the imago, the triangular mesonotum of the adult can be seen through the thin pupal integument. Anteriorly it is divided by a median dorsal longitudinal suture, which is bounded by a depression on either side. The mesothoracic wings may be described as flattened sacs, which fold round the body of the pupa onto the ventral side. The posterior margin is thickened, and two distinct striae on the surface of the wing, run parallel to this thickened ridge. The ventral angle of the wing is slightly rounded. The mesothoracic legs are similar to the prothoracic, but lack the toothed lateral process of the anterior tibiae. The sternum is visible as a small sclerite between the second

pair of legs.

The metanotum has a median longitudinal depression, and is continuous laterally with the hind pair of wings. These are more delicate than the mesothoracic wings, under which they are folded, so that only the tips are visible. The metathoracic legs are the largest, and reach to the seventh abdominal sternum. The distal extremity of the tibia bears a small protuberance on the inner side, to accommodate the developing spines of the tibia of the imago. The metasternum is large, and bi-emarginate anteriorly and posteriorly, to enclose the meso- and metathoracic coxal cavities.

There are two pairs of thoracic spiracles, as in the adult. The first pair is situated ventrally in the membrane between the prothorax and mesosternum. They are more readily found than in the adult, as they are not covered by the epimeral process of the prothorax. They are similar to the first four pairs of abdominal spiracles, being large and round, and produced externally into short tubes. The second pair is smaller, and is situated in the membrane between the meso- and

- metathorax -

metathorax, at the base of the wings.

(c) The abdomen. (Figs. 21, 22, 24 and 25).

In the larva, the abdomen consists of ten segments. The abdomen of the pupa consists of ten terga and nine sterna, the first abdominal sternum having disappeared. The terga thus represent segments 1 - 10, the sterna segments 2 - 10. The first visible sternum is small. The tenth tergum is not visible externally, as it is turned in on the ventral surface, under the rounded caudal elevation of the ninth tergum.

Rittershaus, 1927, p. 276, did not commit herself in the numbering of the divisions between the eighth sternum and the ninth tergum in Phyllopertha horticola L., although she describes its division into an anterior and a posterior region. It is obvious that the anterior of these two regions represents the ninth sternum, as it is bordered posteriorly by the genital aperture, and the posterior region represents the tenth sternum, as the anus is between it and the infolded tenth tergum.

Terga 1 - 7 are similar in form, their antero-posterior length being almost equal

- throughout -

throughout. The lateral margin of the eighth tergum is approximately equal in length to that of the preceding terga, but it increases in length medianly, so that it is triangular in shape. The ninth tergum is concave anteriorly to accommodate the apex of the eighth tergum. Posteriorly it is slightly angular, and is continued on to the ventral surface, where it appears as a rounded elevation surrounding the tenth segment.

Between succeeding terga 1 - 7 there is a lenticular depression on either side of the median line. An anteriorly directed cone is formed between the two arc-shaped ridges of the posterior terga. It fits into an opening in the chitinous margin of the preceding segment. When the pupa curves, so that the ventral surface becomes concave, these chitinisations move apart. When it curves dorsally they come together. The intersegmental membrane, which is folded in, has an arrangement of spines similar to that of the remainder of the integument. Gardner, 1935, p. 26, mentions the occurrence of similar structures in the Tribe Anomalini, and they have been described in detail in Phyllopertha horticola L. (Rittershaus, 1927,

1927, pp. 364-365). In the Melolonthinae they have been observed between segments four and five, and five and six, in Amphimallus solstitialis L. and Melolontha melolontha L. (Fidler, 1936, p. 130), and in Macrophylla pubens Péring. (Fenwick, 1942, p. 137).

The Female Genitalia. (Figs. 31 and 34).

The ninth sternum is narrow, and has a transverse depression on its posterior margin in the middle line. There is no opening here, and the developing vagina ends internally beneath this depression. In all Coleoptera the female gonopore is situated in this position. (Metcalf, 1932, p. 90, Snodgrass, 1933, p. 21). In late pupal development two lateral elevations can be seen beneath the ninth sternum. These are the vaginal palps, which become invaginated in the imago, and lie on either side of the gonopore. They represent the reduced ninth and tenth sterna of the imago.

The tenth sternum is overlapped laterally and posteriorly by the rounded caudal elevation of the ninth tergum; it is flat.

According to Rittershaus, 1927, p. 276, it is flat in Phyllopertha horticola L., but has two

lateral elevations in Anomala aenea Geer.

In the prepupa of Sitrodrepa panicea L. (Metcalfe, 1932, pp. 94-97), the vagina opens to the exterior, between sterna eight and nine. The spermatheca forms a separate invagination between the ninth and tenth sterna. During the early part of pupation, the two ducts unite with each other for most of their length, the intervening walls disappear, and the opening of the anterior vaginal duct, situated behind the eighth sternum, closes. The gonopore thus is the external opening of the original spermathecal duct. In the pupa of Anomala vetula Wied., the original external opening of the vagina is marked by a scar between the eighth and ninth sterna. On each side of the scar there is a small elongated chitinous apodeme of the ninth sternum. An ovipositor is not present; this is the usual condition when the gonopore is situated behind the ninth sternum (Snodgrass, 1935, p. 607). The eggs are simply laid from the apex of the abdomen.

The invagination of the posterior segments of the body in late pupal development, results in the formation of a space between the last externally visible eighth segment of the imago, and the posterior end of the pupa.

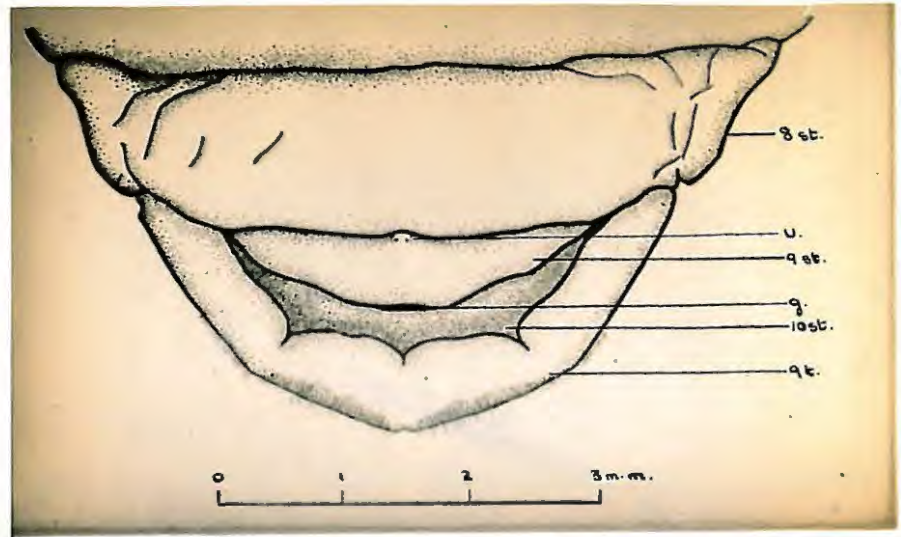


Fig. 24 - Ventral view of posterior end of  
Abdomen of Female Pupa.  
ANOMALA VETULA WIED.

v. = closed orifice of vagina.  
g. = gonopore.  
8st., -10st. = sterna 8-10.  
9t. = tergum 9.

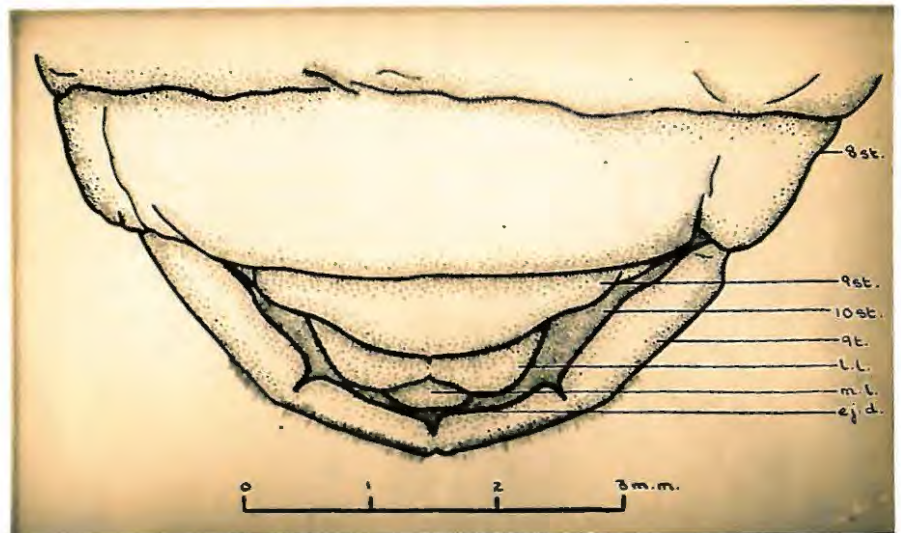


Fig. 25 - Ventral view of posterior end of  
Abdomen of Male Pupa.  
ANOMALA VETULA WIED.

l.l. = developing lateral lobe.  
m.l. = developing median lobe.  
ej.d. = position of orifice of ejaculatory duct.  
8st., -10st. = sterna 8-10.  
9t. = tergum 9.

The Male Genitalia. (Fig. 25).

The eighth sternum in the male is narrow, similar to that of the female. Posterior to it, the median and two lateral prominences of the developing male genitalia are conspicuous, enabling the sexes of the pupae to be readily distinguished. Their arrangement is similar to that of Phyllopertha horticola L. (Ritterhaus, 1927, pp. 278-279).

The two lateral protuberances lie adjacent to the posterior margin of the ninth sternum. They are bluntly rounded, and though united together, are distinguishable by a notch in the posterior middle line. They form the lateral lobes of the developing aedeagus. Between them lies the median protuberance, which is traversed by the developing ejaculatory duct. It represents the median lobe of the aedeagus, the concavity on the posterior margin marking the position of the future external opening of the male genital duct.

In the late pupal stages, if the ventral integument be removed, the arrangement of the posterior sterna can be seen. The narrow arms of the ninth sternum, or spiculum gastrale, lie behind

the eighth sternum. The median and lateral lobes of the aedeagus lie under the corresponding prominences of the pupal integument. Here it is seen that the lateral lobes develop on the ventral aspect, a fact which will be dealt with in the description of the aedeagus of the imago.

It is thus apparent, that the aedeagus is formed as an outgrowth of the ninth abdominal sternum. During development it is invaginated, together with the ninth sternum, and comes to lie within the body cavity.

The Spiracles. (Fig. 22).

There are eight pairs of abdominal spiracles, situated on the sides of the terga 1 - 8. The anterior pair is obscured by the wings. The first four pairs are large and are the most prominent. They are circular, and have raised margins, which form short darkly pigmented tubes. They are similar to the first three pairs of spiracles of Lepidoderma albehirtum Waterh., described by Jarvis, 1927, p. 339. The fifth and sixth pairs of spiracles are less conspicuous, and are transversely elongated. They have pigmented folds radiating from the centre. The seventh and eighth pairs of spiracles are the smallest.

Abdominal spiracles 1 - 7 inclusive, are retained

in the imago. The eighth abdominal spiracle of the pupa is rudimentary in the imago. Shortly before the adult emerges from the pupal skin, a fine chitinous strand connects the eighth abdominal spiracle of the pupa with the rudimentary eighth abdominal spiracle of the imago. In the imago, the point of attachment of this strand can be seen in the lateral angle of the reflexed margin of the eighth tergum.

V. THE IMAGO.

I. External Features.

(a) The Head.

The Head-capsule (Figs. 26, 27, 28, 29 and 30).

The head-capsule is small in comparison with the rest of the body. Normally the posterior region of the cranium is withdrawn into the prothorax by a telescoping of the neck-membrane, so that little of the head is visible dorsally.

The head is prognathous, the mouth-parts are attached to its anterior margin, and are directed forwards. This condition is apparent when the head-capsule is extended. The change from hypognathism in the larva, to prognathism in the imago, has resulted in the elongation of the ventral surface of the head-capsule; the occipital foramen retaining its vertical position.

The head is dorso-ventrally flattened. Dorsally the posterior region of the cranium is rounded; it slopes gradually to its distal margin, and more steeply to the occipital foramen. The ventral surface is flattened, except for the raised median submentum. The sides of the cranium are broadly rounded, and slope gradually to the occipital foramen. The colour of the head-capsule is lighter than that of the

- thorax -

thorax or elytra. It is ferruginous; the clypeus is fuscous, and the eyes are black.

A uniform strong sclerotisation of the head-capsule is typical of Coleoptera (Stickney, 1923, p. 16). The sclerites are closely united, with a tendency to obliteration of sutures in Anomala vetula Wied. Straus-Durckheim (1828), regarded the epicranium of Melolontha vulgaris Fab. as a single piece, the epicranial arms being obsolete (Stickney, 1923, p. 34).

The epicranial suture is absent in the imago of Anomala vetula Wied., although it is present in the larva and the pupa.

According to Stickney, 1923, p. 24, and Imms, 1934, p. 478, the frons is fused with the post-clypeus, the dividing frontoclypeal or epistomal suture being absent. They state that the epicranial suture is in the process of disappearing in Coleoptera, but is generally represented by a line, formed by the forward migration of the epicranial arms, demarcating the fused frontoclypeus from the vertex. I consider in Anomala vetula Wied., that the epicranial suture has disappeared, and that the frons and vertex have fused, the frontoclypeal suture separating the fused frons and vertex from the clypeus. A similar

- interpretation -

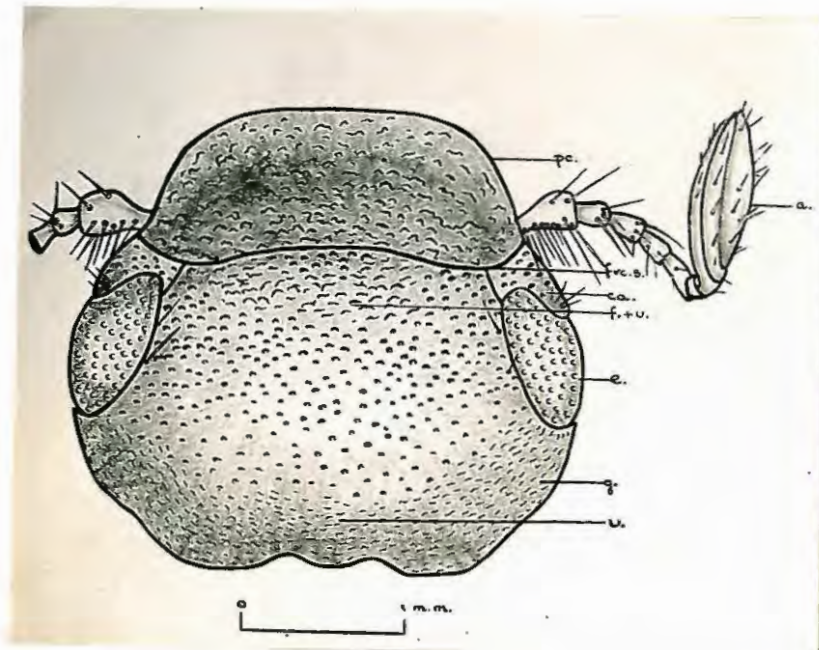


Fig. 26 - Dorsal view of Head of Imago.  
ANOMALA VETULA WIED.

- ca. = antenna.
- ca. = canthus.
- e. = compound eye.
- f. + v. = frons + vertex.
- fr. s. = frontoclypeal suture.
- g. = gena.
- pc. = postclypeus.
- v. = vertex.

interpretation is given to the head-capsule of Lachnosterna crassissima Blanch. by Hayes, 1922, p. 5. Evidence is obtained from the position of the labral muscles, which in the larva are attached to the inside of the frons and in the imago are attached just posterior to the suture separating the clypeus from the remainder of the head-capsule. Snodgrass, 1928, p. 42, states that the labral muscles always extend from the base of the labrum to the frons.

As in the larva, the epistomal suture extends between the ventral condyles for the articulation of the mandibles. In the imago, however, the ventral position of the mandibles has resulted in the extension of the frontoclypeal suture onto the ventral surface of the head-capsule. According to Snodgrass, 1928, pp. 36-37, the typical position of the frontoclypeal suture is on a line between the mandible bases, and passes through the anterior tentorial pits .

The subgenal ridge is the ventral continuation of the epistomal ridge, and is especially thickened to give strength to the articulation of the mouth-parts. According to Snodgrass, 1935, p. 110, when the epistomal suture is present, the anterior tentorial

pits are usually in this suture, but when the epistomal suture is absent, the pits lie in the anterior ends of the subgenal sutures. Stickney, 1923, p.20, states that the anterior tentorial pits are situated on the epicranial suture. In the larva of Anomala vetula Wied., both epicranial and frontoclypeal sutures are well defined and the anterior tentorial pits occur on the frontoclypeal suture. In the adult they also occur on the frontoclypeal suture, lateral to the ventral articulation points of the mandibles.

The area surrounding the compound eye posteriorly and ventrally is the gena. A short subocular suture extends from the frontoclypeal suture to the anterior margin of the compound eye. The canthus is a posteriorly directed process of the lateral margin of the subocular region of the epicranium. The compound eyes are divided for about one-third of their length by the canthus. This condition is nearly universal in the Lamellicornia. (Hatch, 1926, p. 344-345).

The occipital foramen occupies the main part of the posterior region of the head-capsule; the dorso-lateral angles are rounded. It decreases in size ventrally where it is bounded by the median

- submentum. -

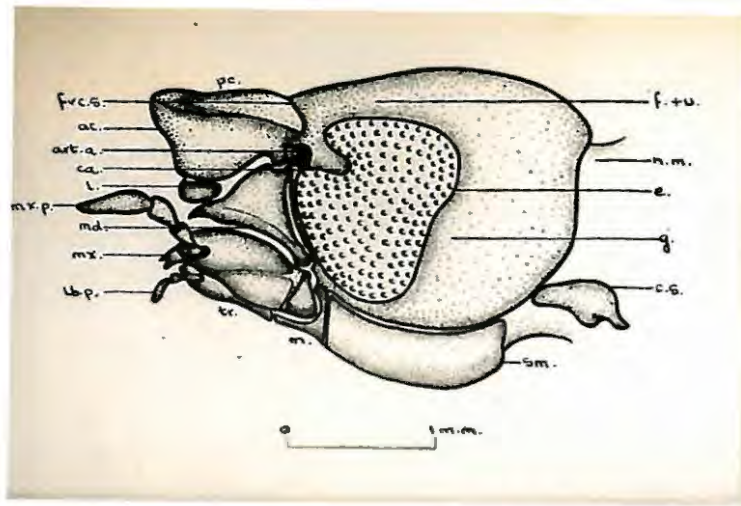


Fig. 27 - Lateral view of Head of Imago.  
ANOMALA VETULA WIED.

- |                                 |  |
|---------------------------------|--|
| ac. = anteclypeus.              | md. = mandible.                                |
| ca. = callus.                   | mx. = maxilla.                                 |
| c. s. = cervical sclerites.     | mx. p. = maxillary palp.                       |
| e. = compound eye.              | m. = mentum.                                   |
| f. + v. = frens + vertex.       | n. m. = neck membrane.                         |
| frc. s. = frontoclypeal suture. | pc. = postclypeus.                             |
| g. = gena.                      | art. a. = process for articulation of antenna. |
| lb. p. = labial palp.           | sm. = submentum.                               |
| l. = labrum.                    | tm. = transmentum.                             |

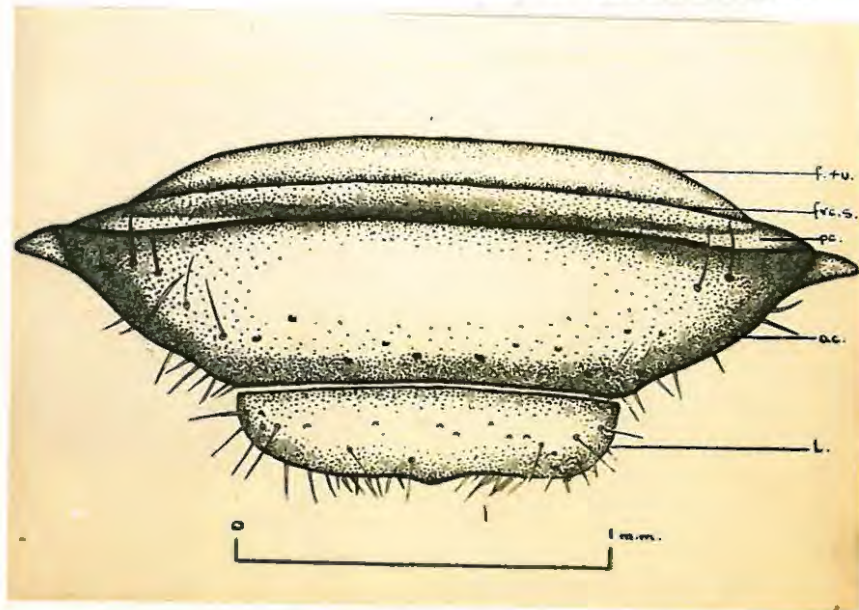


Fig. 28 - Anterior view of Head of Imago.  
ANOMALA VETULA WIED.

- |                           |                                 |
|---------------------------|---------------------------------|
| ac. = anteclypeus.        | frc. s. = frontoclypeal suture. |
| f. + v. = frens + vertex. | l. = labrum.                    |
|                           | pc. = postclypeus.              |

submentum.

The postoccipital suture runs parallel to the dorsal and lateral margins of the occipital foramen, and ends ventrally in the posterior tentorial pits. It is the most constant suture of the epicranium, according to Snodgrass, 1928, p. 36; the neck-membrane is attached to it. Internally it forms a postoccipital ridge, surrounding the occipital foramen. The occipital suture is absent.

The ventral surface of the head-capsule is lengthened by an expansion of the postgenal regions.

A transverse ridge, which extends from the posterior articulation point of the mandible to the compound eye, separates an anterior pleurostomal region from a posterior hypostomal region of the subgenae (Snodgrass, 1935, p. 183). The pleurostomal area extends anteriorly to the epistomal suture, and contains the articulation points of the mandibles.

The eyes are large and black, and are situated laterally, on either side of the head-capsule, towards the anterior margin, posterior to the insertion of the antennae. The surface of the eye is convex. Dorsally the eyes are more prominent in the male than in the female. In both sexes more of

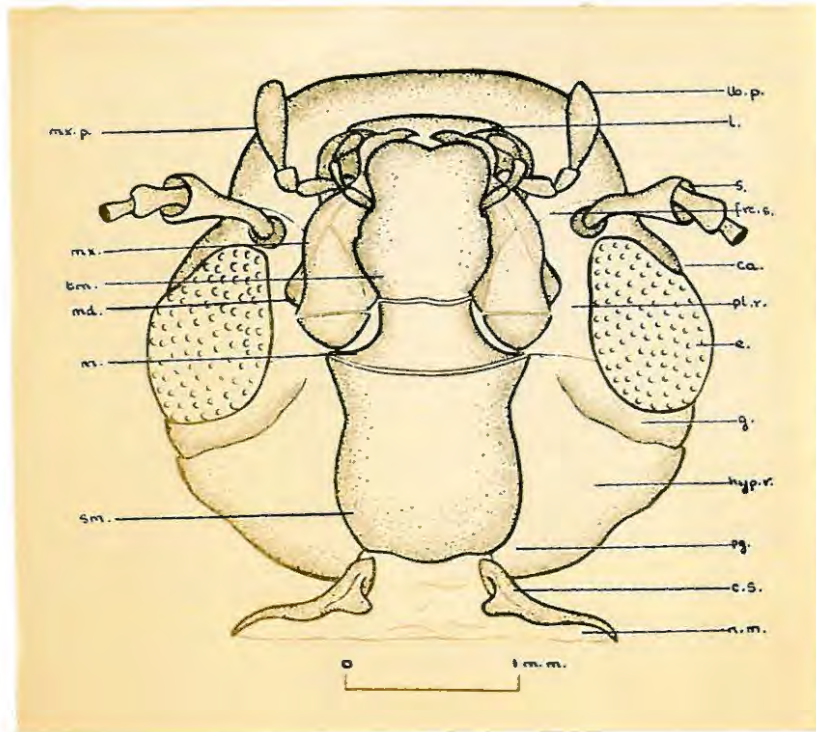


Fig. 29 - Ventral view of Head of Imago.  
ANOMALA VETULA WIED.

- ca. = canthus.
- c. s. = cervical sclerites.
- e. = compound eye.
- fr. c. s. = frontoclypeal suture.
- g. = gena.
- hyp. r. = hypostomal region.
- lb. p. = labial palp.
- l. = labrum.
- md. = mandible.
- mx. = maxilla.
- mx. p. = maxillary palp.
- m. = mentum.
- n. m. = neck membrane.
- pl. r. = pleurostomal region.
- pg. = postgena.
- s. = scape of antenna.
- sm. = submentum.
- tm. = transmentum.

the eye is visible ventrally than dorsally. The eye is surrounded by an inflection of the epicranium, which forms a ridge, corresponding to an ocular sclerite. Ocelli are absent, as in most Coleoptera.

The antennae are inserted on the ventral surface of the cranium, between the ventral extension of the epistomal suture and the compound eye. They are attached to the head-capsule by means of a membranous ring, which is strengthened towards the outside by an annular sclerite, the antennal sclerite. The anterior margin of the antennal sclerite forms a pivot-like process, for the articulation of the basal segment of the antenna.

The region of the head--capsule between the compound eyes, forming the vertex, is finely and closely punctured anteriorly, but less densely posteriorly. The posterior region of the epicranium is minutely wrinkled. A transverse strip, posterior to the frontoclypeal suture, is transversely rugose. The surface of the canthus is punctured; it bears 3 - 4 short hairs, laterally directed. Two longer hairs are inserted on the inner margin of the compound eye.

The Tentorium. (Fig. 30).

The anterior tentorial arms arise from the anterior tentorial pits, which are situated in the ventral extension of the epistomal suture, lateral to the condyles for the articulation of the mandibles. Each arm extends posteriorly and towards the centre of the head cavity. The anterior one-third is well developed, and bears a laterally directed process. The posterior portion is a thin chitinous strand.

The posterior tentorial arms originate from the posterior tentorial pits, which are situated at the ends of the postoccipital suture. They are short and broad. The posterior tentorial arms of each side coalesce, and unite with the anterior tentorial arms to form the body of the tentorium.

The body of the tentorium forms a narrow bridge. Ventrally two chitinous processes, which are directed anteriorly, and towards the centre, give support to the bridge. Two well developed muscles are attached to them. The circumoesophageal connectives pass below the bridge, before entering the thorax, the alimentary canal above it.

The dorsal tentorial arms arise from the broad anterior region of the anterior tentorial arms. They extend dorsally, and are attached to the dorsal

Fig. 30 -Dorsal surface  
of Head-capsule removed  
to show Tentorium.

ANOMALA VETULA WIED.

- a. t. a. =anterior tentorial  
arms.
- a. t. p. =anterior tentorial  
pits.
- art. m. =articulation point  
of mandible.
- b. t. =body of tentorium.
- ca. =canthus.
- c. p. =chitinous process.
- e. =compound eye.
- d. t. a. =dorsal tentorial  
arms.
- fr. s. =frontoclypeal  
suture.
- g. =gena.
- lb. =labium.
- pc. =postclypeus.
- p. t. a. =posterior  
tentorial arms.
- s. a. =socket of antenna.

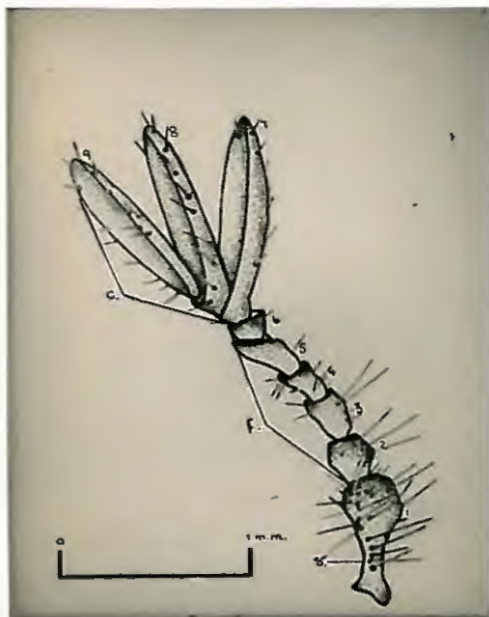
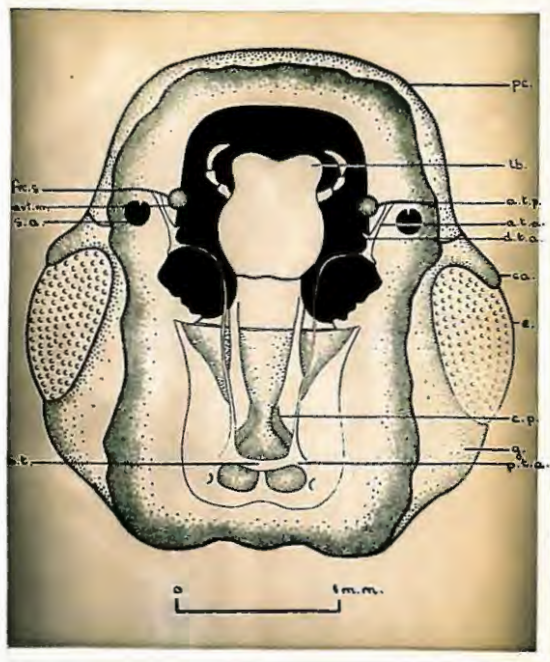


Fig. 31 - Antenna of Male  
Imago.

ANOMALA VETULA WIED.

- c. = club.
- f. = funicle.
- 1-9. = segments 1-9.
- s. = scape.

surface of the head-capsule.

The Antennae. (Figs. 26 and 31).

The antennae are attached to the head-capsule ventral to the canthus, between the anterior margin of the compound eye and the ventral extension of the epistomal suture. The pivotlike process on the anterior margin of the antennal sclerite fits into a socket at the base of the scape. It forms an articular point for the base of the antenna, allowing it to move freely in all directions.

The form of the segments and the arrangement of setae are similar in both sexes. The antenna is composed of nine segments including a well differentiated lamellate club, characteristic of *Lamellicornis* (Inns, 1934, p. 531). Inns, 1934, p. 478, states that there are usually eleven segments in the antennae of Coleoptera.

The club-shaped scape is the longest segment. It bears a number of short hairs basally. A longitudinal row of hairs extends along the posterior margin. Distally the posterior surface bears several moderately long hairs. Basiconic sensilla are scattered over the surface of the segment.

Segments 2 - 6 inclusive form the funicle.

- Segment -

Segment two is short and clavate; distally it bears 2 - 3 moderately long hairs on the posterior surface. Segments three and four are elongated, and bear several moderately long, and some short hairs on the posterior surface. The posterior margin of segment five is elongated. It forms a saucer-shaped depression into which the short sixth segment fits. This causes the sixth segment and the club to be inclined to the remainder of the segments at an angle of approximately  $90^{\circ}$  when the imago is at rest. Segments five and six bear a few short delicate hairs. The five segments of the funicle have basiconic sensilla scattered over the surface.

Segments 7 - 9 inclusive form the club. The anterior margin of each is drawn out into a long lamella, with the obliteration of the cup-shaped basal portion in segments eight and nine. The outer surfaces of segments seven and nine are convex; the remaining surfaces of the lamellae are flat, so that when the antenna is at rest they fit closely together to form an ovoid structure. During sensory perception the lamellae are divaricated.

The ventral surface of the first lamella bears a number of very short apically directed hairs. The dorsal surface of the last lamella bears a median

longitudinal row of three or four short hairs distally. The margins of the lamellae, except for the inner margin of the middle lamella, bear short hairs. These are longer on the outer than on the inner margin.

The surface of each lamella is covered with coeloconic sensilla, except for the basal portion. They impart a honeycombed appearance to the lamellae.

The antenna is moved as a whole by means of levator and depressor muscles, which extend from the inner surface of the cranium to the base of the scape.

The antennae of the male and female differ only in the size of the individual segments. It is shorter in the female than in the male, as in *Apocrita gambosicola* Peringuey, 1902, p. 836.

The following are the average lengths of the segments of the antennae of the male and female of Anomala vetula Wied.:

		The Female	The Male
Scape		0.53 mm.	0.71 mm.
Segment	2	0.30 mm.	0.30 mm.
	3	0.24 mm.	0.25 mm.
	4	0.22 mm.	0.24 mm.
	5	0.32 mm.	0.26 mm.
	6	0.13 mm.	0.13 mm.
Labella Seg. 7		0.98 mm.	1.15 mm.
	8	0.69 mm.	1.07 mm.
	9	0.80 mm.	0.98 mm.

The Clypeus. (Figs. 26, 27, 28 and 29).

The frontoclypeal suture is slightly arcuate anteriorly, between the subocular sutures. On either side of the head-capsule it curves anteriorly, and extends onto the ventral surface to terminate in the condyles for the articulation of the mandibles.

The clypeus lies anterior to the frontoclypeal suture. From a study of the pupa it appears that in the development from larva to adult, the lateral margins of the post-clypeus become reflexed ventrally carrying with them the condyles for the articulation of the mandibles. The ante-clypeus and labrum are turned ventrally, down the anterior surface of the head. Thus in the adult, the post-clypeus occupies the dorsal and ventral surfaces of the clypeus, the ante-clypeus the anterior surface. Stickney, 1923, p. 26, considers the membrane between the anterior margin of the labrum and the head-capsule to represent the ante-clypeus.

The dorsal surface of the post-clypeus is trapezoidal. The anterior angles are broadly rounded, and the anterior margin slightly arcuate. The antero-posterior length is less than half the width, which is approximately equal to the distance between the frontoclypeal and postoccipital sutures. It is distinctly hollowed, so that the anterior and antero-lateral margins are curved dorsally. The posterior region is more densely rugose than the cranium; anteriorly the punctures are more dispersed. Hairs are absent.

The ante-clypeus forms a right angle with the post-clypeus, so that it is invisible dorsally. It is trapezoidal, the dorso-ventral length being about one quarter of the width. The lateral margin bears several short hairs. Sense pits are scattered along the basal region.

The Mouth-parts.

The imago has typical biting mouth-parts, but they are not as well developed as in the larva. Their arrangement is similar to that in the larva. Owing to the change from the hypognathous to the prognathous condition, they form an ellipse round the anterior instead of the ventral margin of the head-capsule.

(1) The Labrum and Epipharynx. (Figs. 27, 28, 29 and 32).

The labrum is attached to the distal margin of the ante-clypeus, and thus is invisible dorsally. It lies in the rectangular cavity formed between the ventrally reflexed walls of the clypeus. It forms the anterior wall of the preoral cavity, enclosed by the mouth-parts.

The labrum is a small unpaired sclerite, anteriorly it is slightly emarginate, and the lateral

angles are broadly rounded.

The dorsal surface is a narrow transverse sclerotised strip, which is without hairs. The anterior surface forms a right-angle with the dorsal surface. It is a flattened triangle, with the apex directed ventrally. Laterally it bears a number of moderately long erect hairs. These decrease in size towards the middle, and curve inwards.

The ventral surface is membranous, and is attached to the clypeus laterally. Posteriorly it is continuous with the dorsal wall of the pharynx. Two sclerotised strips extend posteriorly from the anterior lateral angles to the median line, where they unite. These are the tormae. Each gives off a short median, and a lateral branch.

The most prominent feature of the epipharynx is a "V"-shaped elevation whose margins follow the course of the tormae. The setaceous area between the incisor and molar regions of the mandible fits into the concave margins of this epipharyngeal elevation. The apex is provided with a dense covering of posteriorly directed sensory hairs. These are continued antero-laterally as a row of delicate hairs. Anteriorly the sense field consists of a group of short setae on either side of the median

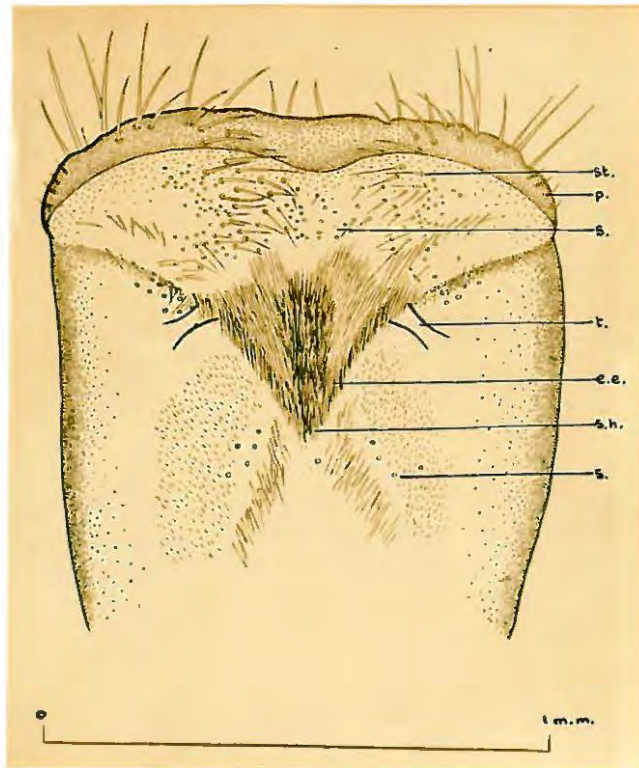


Fig. 32 - Epipharynx of *Drago*.  
*ANOMALA VETULA* WIED.

- e. e. = epipharyngeal elevation.
- p. = plegna.
- s. = sensilla.
- s. h. = sensory hairs.
- st. = setae.
- t. = torma.

line, and numerous sensilla. The setae are inserted in basal rings, and are directed inwards. The sensilla occur mainly between, and lateral to, the groups of setae. Short chitinous carinae extend inwards from the lateral margins of the anterior surface. They correspond to the plegmatia of the larva, but are not as regular or as distinct. Posterior and lateral to the epipharyngeal elevation the membranous wall bears several sensilla. Posteriorly on either side of the median line, there is a postero-laterally directed group of short hairs.

The labrum is moved by a pair of labral muscles which are inserted on the antero-lateral margin of the labrum, and are attached to the frons, immediately posterior to the epistomal suture.

(2) The Mandibles. (Figs. 27, 29, 33 and 34).

The mandibles are small, compared with the other mouthparts and with the conspicuous mandibles of the larva. They are situated on either side of the mouth cavity, ventral to the labrum. When closed the tips fit into the lateral concavities of the anterior surface of the labrum and do not project beyond it, as they do in the larva. They are heavily chitinised, and have typical incisor and molar areas.

The mandibles of the male and female are similar. The right mandible is slightly larger than the left.

The base is triangular, as in the larva. It articulates with the head-capsule by means of a dorsal ginglymus, which fits onto a rounded condyle at the end of the epistomal suture, and a ventral condyle, which fits into a concavity in the subgenal ridge, anterior to the articulation of the maxilla. The base of the outer surface is convex.

The molar regions of each mandible are asymmetrical. In the left mandible the grinding surface is rectangular and concave. It consists of a series of transverse ridges; the middle ones generally branch towards the ventral margin. The right molar area is a flattened heart-shape, and fits into the concavity of the left molar area. It consists of a series of transverse ridges. The basal one is well developed, and gives off a series of short unbranched posteriorly directed ridges. The areas between the ridges are hollowed. The centre of both molar areas bears numerous small teeth, which arise from the ridges.

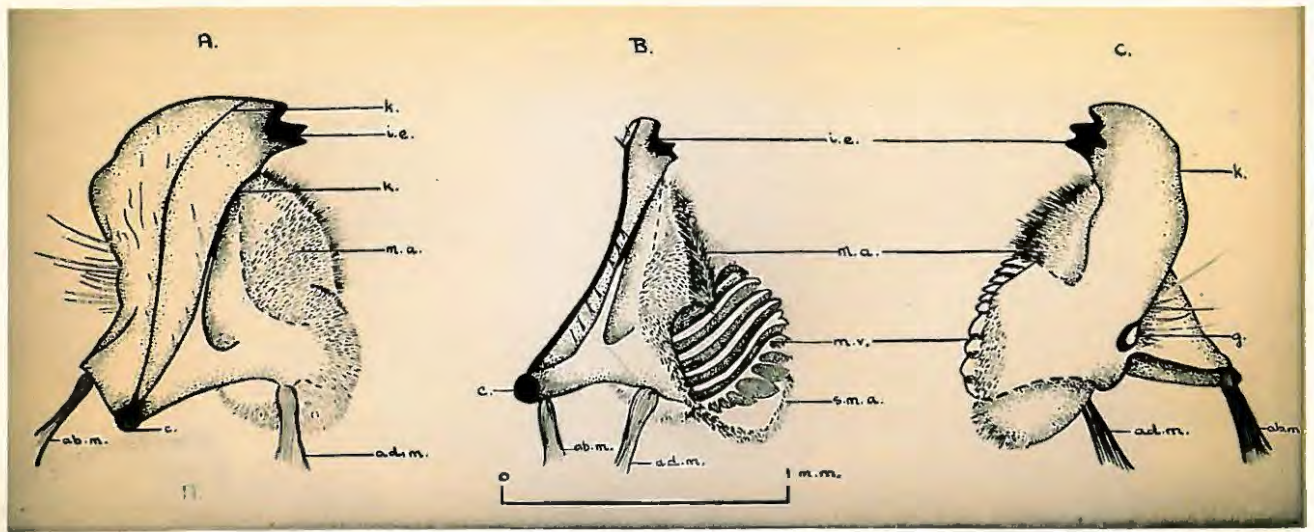


Fig. 33 - Right Mandible of Imago.  
ANOMALA VETULA WIED.

A: Ventral view.      B: Lateral view.      C: Dorsal view.

ab.m. = abductor muscle.  
ad.m. = adductor muscle.  
c. = condyle.  
g. = ginglymus.  
m.a. = hairs on membranous  
area.  
i.e. = incisor edge.

k. = keel.  
m.v. = molar region.  
s.m.a. = semicircular  
membranous area

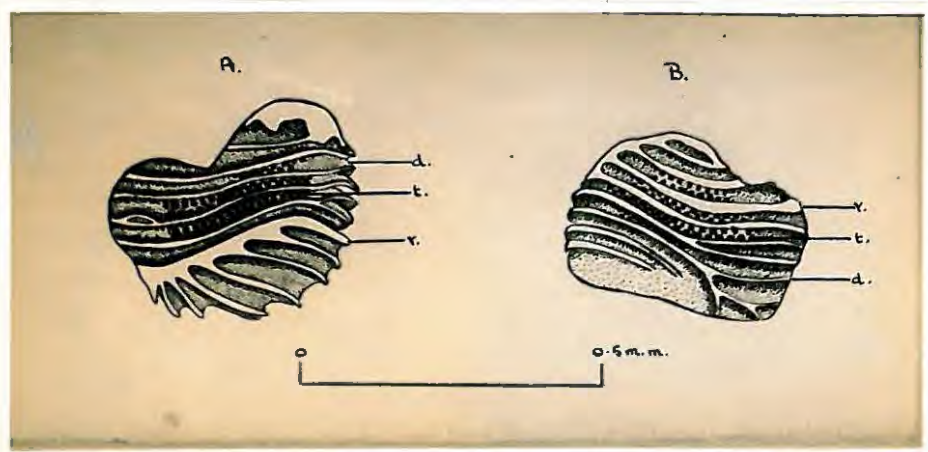


Fig. 34 - Molar Regions of the Mandibles of  
the Imago.

ANOMALA VETULA WIED.

A: Right Mandible.      B: Left Mandible.

d. = depression.      r. = ridge.      t. = teeth.

The incisor tips of both mandibles are three-toothed. The concavity between the distal and middle teeth of the right mandible is deeper than that of the left mandible. The incisor edges meet medianly, when the mandibles are closed.

A sharp sinuate keel extends from the ginglymus to the tip of the incisor region. Two diverging keels run from the condyle towards the incisor edge. The outer surface of the mandible between the sinuate keel and the outer keel from the condyle, is concave. It bears several short scattered hairs, and a row of longer hairs dorsal to the condyle. The latter are more numerous and larger in the right than in the left mandible. The inner keel from the condyle bears a few short hairs. The ventral surface is without hairs.

The concavity between the molar and incisor regions is occupied by a membranous area, which is covered with very short inwardly directed hairs. A median longitudinal fringe consists of longer and more densely arranged hairs. The hairs are continued as a narrow band round the ventral surface of both molar areas. They connect up with a fringe of delicate hairs surrounding a semicircular

membranous area at the base of both mandibles. The membranous area is continuous with the sides of the pharynx.

The abductor muscle is inserted by means of a tendon on the outer side of the mandible base, dorsal to the condyle. The tendon of the adductor muscle is inserted on the ventral margin, close to the molar region. Both muscles arise on the inner surface of the gena.

(5) The Maxillae. (Figs. 27, 29, 35 and 36).

The maxillae are attached to the subgenal ridge, between the ventral articulation points of the mandibles and the labium. They are well chitinised. The inner surfaces are closely applied to the lateral margins of the labium.

The cardo is moderately large. The proximal part is bifid, and projects into the head-capsule. The inner process is acute, the outer process articulates with the head-capsule. The distal triangular region is the only part of the cardo that is visible externally. The lateral margins are fringed with several short hairs.

The stipes is attached to the anterior margin of the cardo. It is similar to that of

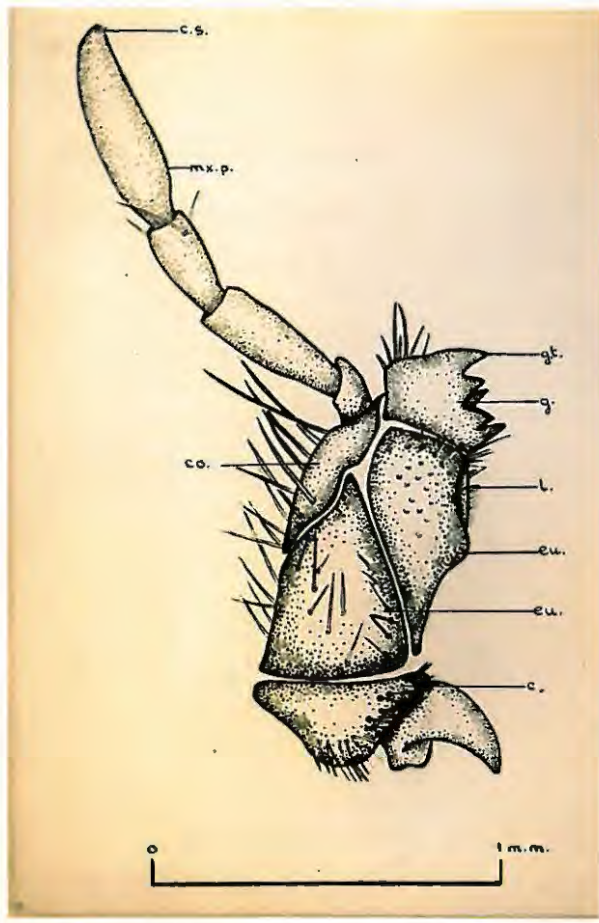
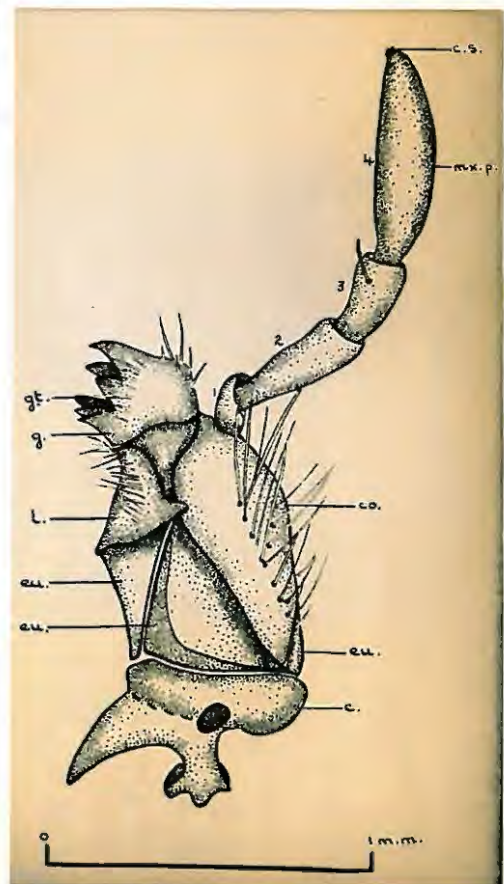


Fig. 35 - Ventral view of  
Left Maxilla of Imago.  
ANOMALA VETULA WIED.

- c. = cardo.
- c. s. = conical sensilla.
- co. = costipes.
- eu. = eustipes.
- g. = galea.
- g. t. = galeal teeth.
- l. = lacinia.
- mx. p. = maxillary palp.

Fig. 36 - Dorsal view of  
Left Maxilla of Imago.  
ANOMALA VETULA WIED.

- c. = cardo.
- c. s. = conical sensilla.
- co. = costipes.
- eu. = eustipes.
- g. = galea.
- g. t. = galeal teeth.
- l. = lacinia.
- mx. p. = maxillary palp.



Melolontha described by Hanson, 1930, p.170.

It is secondarily divided into two sclerites, the eustipes and the costipes. The eustipes is divided by an oblique suture, which runs from the proximal inner angle towards the distal outer angle. The proximal triangular sclerite so formed is mainly ventral in position; the distal sclerite is only visible ventrally. The costipes is an elongated shield-shape, and is mainly dorsal. The maxillary palp is attached to it. The proximal sclerite of the eustipes bears several moderately long hairs. The distal sclerite of the eustipes has a few short hairs. The dorsal surface of the costipes bears a number of very long anteriorly directed hairs.

The lacinia is attached to the inner anterior margin of the distal sclerite of the eustipes. It is triangular, the apical angle being acute. It is dorsally reflexed. It bears a median longitudinal row of short hairs.

The base of the gales lies along the anterior margin of the distal sclerite of the eustipes. Proximally it articulates with the terminal angle of the co-stipes. Anteriorly it is

armed with three powerful teeth, the two lower ones of which are bifid, but connate basally. The outer half of the anterior margin bears several moderately long hairs. Dorsally there is a row of hairs along the base of the teeth.

The maxillary palp is four-segmented. It is attached to the outer distal surface of the coxites. The first segment is the shortest. The second segment is about three times the length of the first. It increases gradually in size towards the distal end. The third segment is approximately twice the length of the first. It is swollen distally. The fourth segment is almost equal in length to the two preceding segments. It is sub-fusiform, and bears a number of conical sensilla at the tip. Segments one and two have a few very short hairs. Segment three bears 3 - 4 hairs distally. Segment four is without hairs, but has an oval sense field on the outer surface. Sense pits are scattered over all four segments.

The adductor and abductor muscles are inserted into the cardo; the former arises from the anterior tentorial axis, the latter from the

posterior region of the head-capsule. The anterior tentorial arm also gives origin to the adductor of the stipes. The galea is moved by a muscle, which is inserted at its base and arises from the inner surface of the eustipes. Flexor and extensor muscles are attached to the inner and outer sides respectively of the base of the palp, and originate inside the eustipes.

(4) The Labium. (Figs. 27, 29, 30 and 37).

The prognathous condition has resulted in an elongation of the ventral surface of the head-capsule, in order to retain the vertical plane of the occipital foramen. In many Coleoptera the postoccipital sutures extend anteriorly along the ventral surface of the head-capsule, due to the forward migration of the posterior tentorial pits. The sclerite formed between the posterior tentorial pits and the occipital foramen, and bounded laterally by the postoccipital sutures, is the gula (Stickney, 1923, p. 33, Inms, 1934, p. 17, and Snodgrass, 1935, p. 293). In Anomala vetula Wied. the posterior tentorial pits have not migrated forwards; a gula does not exist. The submentum is large, and

extends from the mentum to the occipital foramen. A similar condition is described in Melolontha by Hansen, 1930, p. 233.

The structure of the labium is similar to that of Melolontha described by Hansen, 1930, pp. 170-171. The position of the muscles is important in determining the homology of the component parts.

The submentum is large, and slightly longer than broad. It curves ventrally, and is thus raised above the surrounding region of the head-capsule. The lateral margins are immovably attached to the postgenae, but are marked off from them by well defined sinuate sutures, which are produced internally as prominent ridges. It is narrowest medianly, and widens anteriorly and posteriorly to approximately the same width. The anterior margin is concave, and is reflexed to form a strong ridge. The median retractor muscles of the prementum arise on this ridge, and insert on the base of the distal sclerite. There is a semicircular row of very short hairs anteriorly, on either side of the median line of the submentum.

The mentum lies proximal to the insertion of

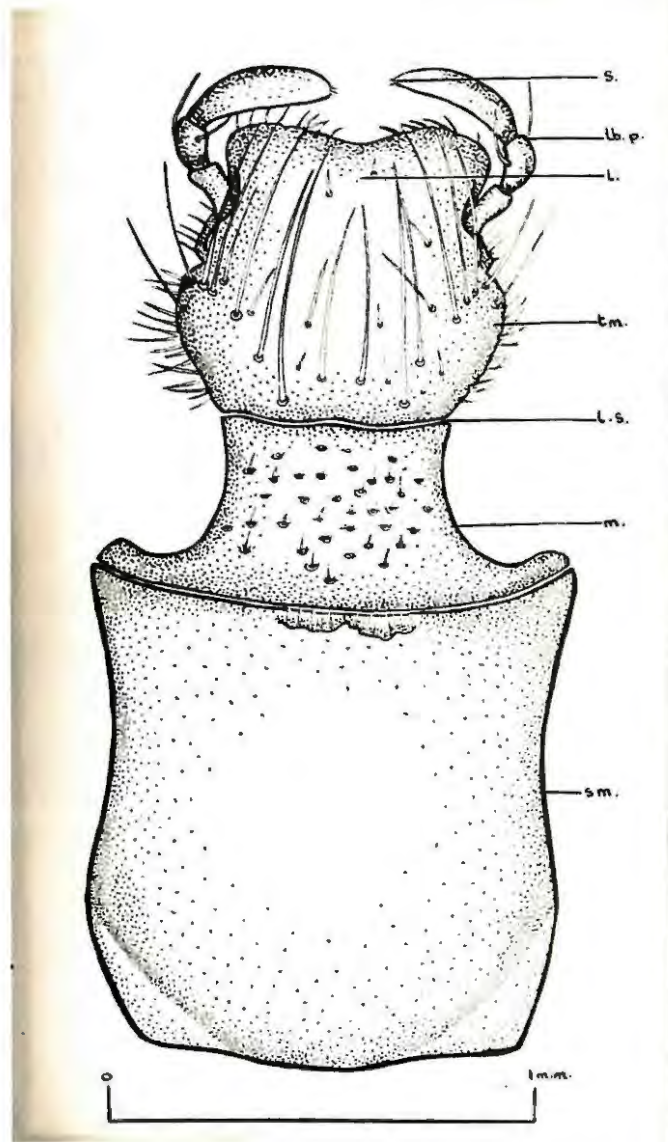


Fig. 37 - Ventral view of Labium of Imago.  
ANOMALA VETULA WIED.

- lb. p. = labial palp.
- l. s. = labial suture.
- l. = ligula.
- m. = mentum.
- s. = sensilla.
- sm. = submentum.
- tm. = transmentum.

all labial muscles (Snodgrass, 1935, p. 295). It is without muscle attachments. It extends forward from the distal margin of the submentum to the labial suture. Inns, 1934, p. 21, recognises the mentum and submentum as subdivisions of the postmentum. The posterior region of the mentum is the same width as the anterior margin of the submentum. It narrows abruptly to form two deeply concave lateral margins. The anterior margin is slightly bi-emarginate. The anterior and lateral margins are folded over onto the dorsal surface. Several short anteriorly directed hairs are scattered over the surface.

The transmentum is identified by the median retractor muscles which insert on its proximal margin. It also bears the origin of the levator and depressor muscles of the palps. It is somewhat ovate from the base to the point of insertion of the palpi. The anterior angles are broadly rounded, and the anterior margin is emarginate medianly. Proximally the lateral margins are deeply reflexed onto the dorsal surface; anterior to the lateral palps they are folded in to a lesser degree. The broad terminal area, anterior to the insertion of the labial palps represents the fused glossae and paraglossae of other

Hexapoda. It is termed the ligula, and is similar to that of Phyllophaga, figured by Snodgrass, 1935, p. 392. The anterior median surface has a cordiform impression, reaching from the anterior margin to beyond the median part. The non-impressed part is covered with dense and very long fulvous setae ventrally or slightly anteriorly directed. The apical margin has a few short setae pointing inwards. The short setae of the lateral margin point antero-laterally.

The labial palpi are three-jointed. They are attached to the lateral margin and curve round the anterior angles of the labium. The first segment arises from within a deep depression. It is cylindrical, and approximately equal in length to the second segment. The outer anterior margin bears one long hair. The second segment is broader than the first. The outer surface is longer than the inner, so that it curves inwards. A long hair is situated on either side, and there are three shorter hairs near the distal margin of the ventral surface. Segment three is as long as the two preceding segments. It is slightly curved and truncated apically. The tip bears a number of sensilla, and sense pits are

scattered over the surface. It is without hairs.

The dorsal surface of the labium is membranous. Anteriorly and laterally it is attached to the reflexed walls of the transmentum; posteriorly it is continuous with the ventral wall of the pharynx.

The hypopharynx is a "V"-shaped densely setaceous ridge, situated on the dorsal surface of the transmentum. Anteriorly, on either side of the ridge, there are a number of sensilla. Half-way along its length, it is bridged by a transverse row of setae. Anterior to this there is a transverse row of approximately six sense points. The apex of the ridge projects posteriorly as a median lobe; ventrally it is supported by a narrow transverse basal plate (Snodgrass, 1935, p. 114). On each side there is a narrow elongated sclerite, which articulates anteriorly with the lateral margin of the basal plate. They extend postero-laterally, to support the ventral wall of the pharynx. Posteriorly they give insertion to the retractor muscles, which arise on the frons. These sclerites are termed the *fulcrum hypopharyngeum* by Hayes, 1922, p. 8, or *fulturac* by Snodgrass, 1935, p. 115.

Near the posterior end of these sclerites, are two small transverse pharyngeal sclerites.

The Neck Region. (Figs. 27 and 29).

The head is attached to the anterior margin of the prothorax by a short neck-membrane. Anteriorly the membrane is attached to the submentum ventrally, and to the postoccipital suture dorsally and laterally; posteriorly it is attached to the reflexed dorsal and lateral margins of the prothorax, and ventrally to the anterior margin of the prothoracic sternum.

The neck-membrane is supported by a pair of lateral cervical sclerites, on either side of the ventral surface. The anterior sclerite is large. It is broad and curved, and is directed posterolaterally. The ends are rounded, and more heavily sclerotised than the middle region. Anteriorly it articulates with the basal angle of the submentum, and posteriorly with the anterior end of the second cervical sclerite. The posterior sclerite is quadrate. It is approximately one third of the size of the anterior sclerite, and lies in a transverse plane, at the base of this sclerite. Posteriorly it articulates with the anterior lateral margin of the prothoracic sternum. The distal region of the anterior cervical sclerite bears a number

- of -

of hairs.

The sclerites are connected to the cranium and to the prothorax by muscles. Cephalic muscles arise on the postoccipital ridge, and are inserted on the first and second cervical sclerites. The protergal muscles arise from the prothoracic tergum, and are inserted on the first cervical sclerite. By the action of these muscles the head may be extended or retracted into the prothorax.

The morphological value of the neck and cervical sclerites is uncertain. Carpenter, 1903, p. 325, says, "... in the more generalised Insects at least, the labial segment is incompletely fused with the head-capsule, part of its skeleton forming the cervical sclerites". Martin, 1916, p. 74, and Shodgrass, 1927, p. 8, suggest that the head and prothorax enter into the formation of the neck. It appears possible that the cervical sclerites are formed as chitinisations of the neck-membrane, and have no significance from a segmental standpoint.

(b) The Thorax.

The prothorax is the largest and most conspicuous of the thoracic segments. It is clearly

- distinguishable -

distinguishable from the head and pterothorax. It is freely movable. According to Imms, 1934, p. 180, this is a characteristic feature of the prothorax of Coleoptera. It is similar to that of Hydrophilus piceus L., figured by Berlese, 1909, p. 180.

The meso- and metathorax bear the elytra and wings respectively. They are closely united laterally and ventrally to form the pterothorax, which gives firm support in flying. The mesothorax is smaller than the metathorax, as the elytra are used less in flying than the wings. The mesonotum is visible externally as a small cordate sclerite, overlapped by the posterior margin of the pronotum. During rest the elytra cover the lateral margins of the mesonotum, and the entire metanotum. They overlap the pleural regions dorsally, but the sterna of the meso- and metathorax are visible externally.

The thorax is similar to that of Hydrophilus piceus L., (Berlese, 1909, p. 180, p. 197, and plate IV). The ventral aspect of the thorax of Melolontha resembles that of Anomala vetula Wied. (Berlese, 1909, p. 195, after Straus - Durckheim, 1828).

The Prothorax (Figs. 38 and 43).

The prothorax is similar to that of Hydrophilus (Berlese, 1909, p. 180, and p. 197), and Melolontha (Berlese, 1909, p. 195, after Straus - Durckheim, 1888).

The pronotum is undivided, and is entirely visible from above. It is about one and a quarter times broader than long. It slopes downwards from the mesothorax to the head. Anteriorly, it overlaps the posterior region of the head-capsule; posteriorly it overlaps the mesothorax. The pronotum is convex, transversely and longitudinally. The transverse convexity is greater than the longitudinal, and it extends laterally to the level of the sternum.

The lateral margins of the pronotum are plainly attenuate from the middle to the anterior margin. They are subparallel from the middle to the base, which is slightly broader than across the middle. The basal angles are rounded but well defined. The base is bi-sinuate.

The pronotum has a narrow rufescent marginal fold all round. In the male it is reddish-brown in the middle; in the female the middle is

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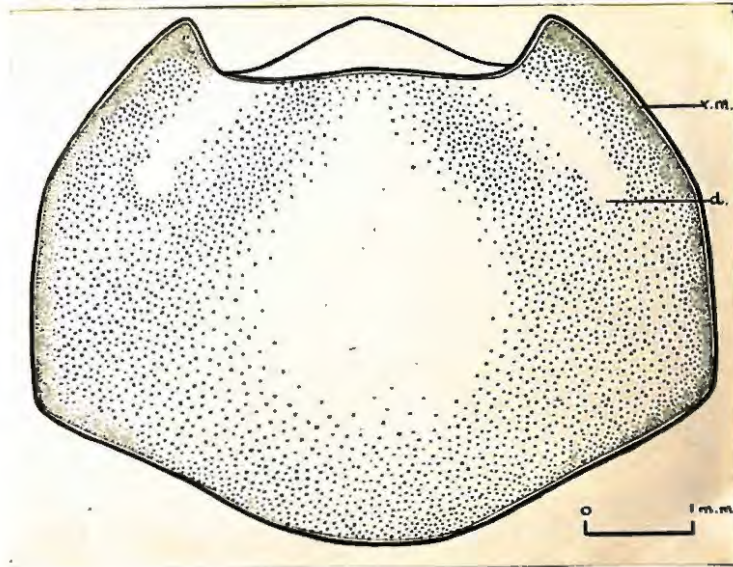


Fig. 38 - Promotum of Imago. ANOMALA VETULA WIED.

d. = depression marking position of  
articulation of prothoracic coxa.  
r.m. = rufescent margin.

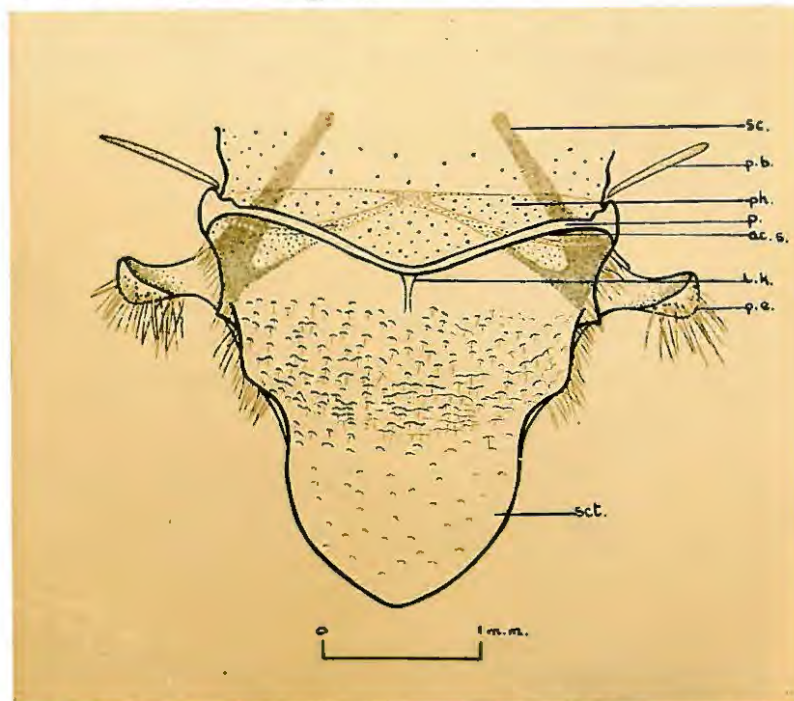


Fig. 39 - Mesonotum of Imago. ANOMALA VETULA WIED.

ac. s. = antecostal suture.	p. = precosta.
l. k. = longitudinal keel.	p. e. = projection on which elytron rests.
ph. = phragma.	sct. = scutellum.
p. b. = prealar bridge.	sc. = scutum.

light brown, with reddish-brown patches on either side. Antero-laterally on either side there is a small round reddish depression; this marks the position of the internal process with which the prothoracic coxa articulates.

The surface of the pronotum is faintly punctured. The lateral margins bear 7 - 8 setigerous punctures, often asymmetrically placed. A fringe of short, closely set hairs arises from the anterior margin.

The sides of the pronotum turn sharply inwards in the horizontal plane. The line of reflexion represents the division between tergal and pleural regions, though a suture is not present. This condition often occurs in Coleoptera, so that a single shield covers the dorsal and lateral regions of the prothorax (Imms, 1934, p. 490).

The pleural region lies on either side of the sternum, and bounds the coxal cavities outwardly. The pleural suture and its corresponding internal ridge are absent, so that the episternum and epimeron are not separated by a suture. The episternal region is separated from the sternum by a pleuro-sternal suture, which extends anteriorly, from the

outer margin of the coxal cavity to the lateral margin of the head cavity. This suture is present in Macrophylla pubens Pering. (Fenwick, 1942, p.40). According to Hayes, 1922, p.9., it is present in Melolontha vulgaris Fab. but absent in Lachnosterna crassissima Blanch.

A postcoxal bridge from the epimeral region extends posterior to the coxal cavity and inserts in a slot on the side of the furcisternum. These processes lie outside the membrane between the coxae and the mesosternum. The coxal cavities are therefore not closed posteriorly.

A pleural coxal process on the outer margin of the prothoracic coxal cavity is absent. The inner wall of the pleural region is reflexed on itself, and strengthens the outer wall of the coxal cavity. At the level of the outer margin of the coxal cavity it becomes membranous, and is continued onto the inner surface of the pronotum. A coxal process is formed at this point for the articulation of the prothoracic leg.

The pleural region is clothed with moderately long fine hairs. A fringe of closely set hairs bounds the coxal cavities laterally. A fringe

of larger hairs arises from the posterior margin of the epimeral arms.

A well sclerotised "T"-shaped sternum separates the coxal cavities. The anterior arms close the coxal cavities, and are separated from the episternal regions of the pleuron by the pleurosternal sutures. The anterior margin is reflexed, and gives attachment to the neck membrane. The posterior margin also forms an internal keel. Between the coxal cavities, the sternum forms a rectangular plate. It is excavated on either side, to accommodate the distal region of the coxa of the prothoracic leg. A transverse division on this plate, with a corresponding internal bridge, divides the sternum into an anterior basisternum and a posterior furcisternum. (Snodgrass, 1927, p. 11). The furcisternum forms the slots for the insertion of the postcoxal processes of the epimeral region. On either side of the furcisternum, an entosternal arm projects dorso-laterally, into the cavity of the prothorax.

The anterior margin bears a fringe of hairs, which decrease in length towards the middle; they overlap the posterior region of the head-capsule. A continuous transverse fringe of shorter hairs runs

anterior to the coxal cavities. The posterior region of the sternum bears two parallel rows of transverse hairs, one on the margin, the other anterior to the slot for the insertion of the epimeral arm.

The antecosta, internal phragma, and the precosta are absent. According to Snodgrass, 1927, p.9, a true antecosta and precosta are never found in the pronotum, these parts presumably having been lost in the neck region. The longitudinal dorsal muscles of the prothorax that arise on the phragma of the mesothorax, thus become inserted inside the head-capsule, and serve to move the head. The ventral longitudinal muscles arise from the entosternal arms, and are inserted on the posterior region of the head-capsule.

The Mesothorax. (Figs. 39, 40 and 43).

The mesothorax is the smallest of the three segments of the thorax. After removal of the pronotum and the elytra, the mesonotum is visible. It is not divided into sclerites.

The scutellum is ogival, and transversely impressed. The anterior region is lightly sclerotised. Anteriorly there is a short median longitudinal keel.

The posterior region, which is normally exposed, is heavily sclerotised. Both regions are slightly longitudinally convex. The posterior margin is reduplicated, so that the prescutum of the metathorax is completely obscured. A membrane is attached to this reduplication, and connects the mesothoracic tergum to the prephragma of the metathorax.

At the level of the transverse impression there is a longitudinal ridge on either side, but no suture. The antero-lateral margin on each side is produced as a linear arm, which lies along the metathoracic prescutum, and is closely united to its anterior angles. These arms represent the divided scutum. On either side they form an outwardly directed projection, upon which the edge of the clytron rests.

The mesonotum is marked anteriorly by an arcuate antecostal suture, which separates off a narrow precosta from the rest of the mesonotum. The antecostal suture forms a corresponding ridge, which is produced internally to form a transverse phragma, which extends for some distance into the mesothorax to give increased surface for the

attachment of the dorsal longitudinal muscles. The phragma is strengthened by a chitinous strip, which extends forwards and inwards, from the bases of the linear scutellar arms.

A small linear sclerite anterior to the articulation point of the elytron, forms a prealar bridge, between the anterior angle of the mesonotum and the episternum.

The anterior region of the scutellum is transversely rugose, and bears a number of very short posteriorly directed hairs. The posterior region is without hairs dorsally, and is sparsely punctured. The reduplicated posterior margin, and the lateral margins, have a vestiture of moderately long hairs. The lateral processes of the scutellar arms are densely setaceous.

The pleural region is divided into an episternum and an epimeron. The episternum is sub-rectangular; a triangular area is marked off at the base. Anteriorly the dorsal angle is rounded, the basal angle is acute. The ventral margin is concave and borders the sternum. The epimeron is larger and trapezoidal; the dorsal region is at right angles to the rest. The posterior margin is broadly reflexed, and overlaps the membranous

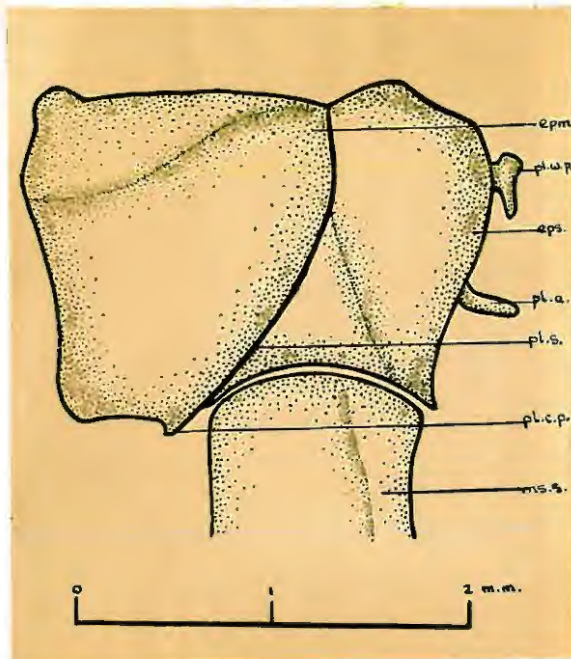


Fig. 40- Pleural sclerites of Mesothorax of Imago.  
ANOMALA VETULA WIED.

epm. = epimeron.  
eps. = episternum.  
ms. s. = mesothoracic sternum.  
pl. a. = pleural arm.  
pl. c. p. = pleural coxal process.  
pl. s. = pleural suture.  
pl. w. p. = pleural wing process.

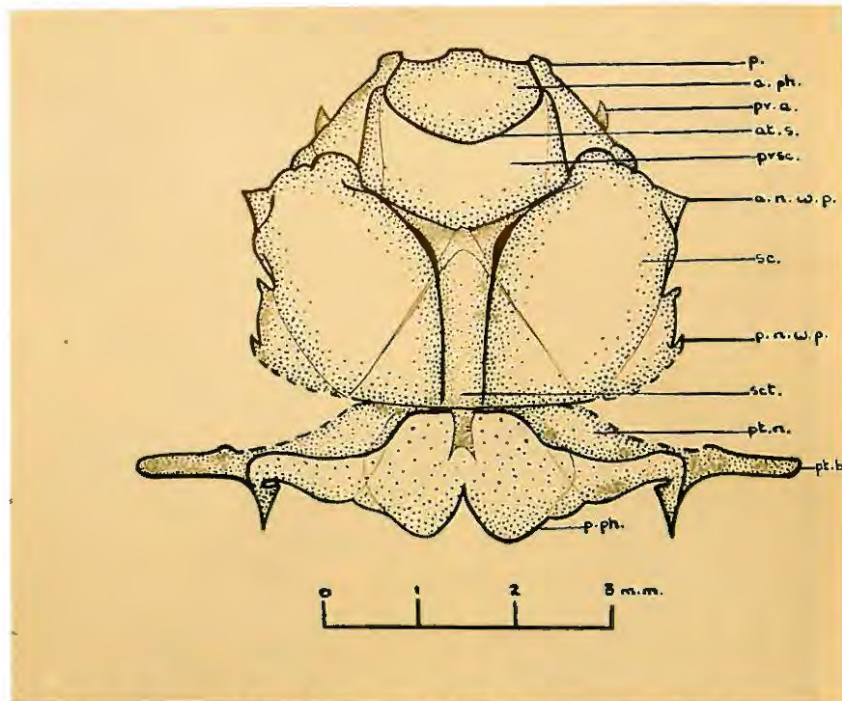


Fig. 41 - Dorsal view of Metathorax of Imago.  
ANOMALA VETULA WIED.

at. s. = antecostal suture.	pr. a. = prealar bridge.
a. n. w. p. = anterior notal wing process.	prsc. = prescutum.
a. ph. = anterior phragma.	p. = projection closely united to scutum of mesothorax.
p. n. w. p. = posterior notal wing process.	sct. = scutellum.
p. ph. = posterior phragma.	sc. = scutum.
pt. n. = postnotum.	
pt. b. = postalar bridge.	

connection between the meso- and metathorax.

The base of the epimeron bounds the coxal cavity laterally. The pleural suture is arcuate; internally it forms a pleural ridge. It extends dorsally from the anterior margin of the mesothoracic coxal cavity. The lower edge of the pleural ridge forms the pleural coxal process for the articulation of the mesothoracic coxa. The pleural arm is situated approximately half-way along the pleural ridge. It projects inwards and forwards, and gives attachment to muscles of the elytron. The pleural wing process is formed from the upper region of the pleural ridge. It serves as a support for the elytron.

There is a small subalare sclerite lying in the pleural membrane, dorsal to the epimeron. It is connected to the second axillary sclerite at the base of the elytron, by a long thin tendon. Sclerites lying in the membrane dorsal to the pleuron are termed epipleurites collectively, by Snodgrass, 1935, p. 184. He identifies the anterior ones as basalares, the posterior ones as subalares. Basalares are absent in Anomala vetula Wied.

Dorsally the episternum bears a number of hairs. The surface, except for the triangular area,

- bears -

bears short hairs in shallow depressions. The upper surface of the epimeron is clothed in delicate hairs; the sides bear numerous long posteriorly directed hairs.

The sternum is "T"-shaped. The arms bound the mesothoracic coxal cavities anteriorly, and meet the episternum on either side. The median region separates the coxal cavities. It is extended on either side to form a broad concave shelf to accommodate the mesothoracic coxae.

A median inflection of the sternum forms a "Y"-shaped endoskeletal structure. It is attached to the sternum posteriorly by a "V"-shaped base, and anteriorly by a transverse arm on either side. The furcal arms extend forward into the mesothoracic cavity. Externally the sternum is undivided. It bears a number of delicate posteriorly directed hairs.

The dorsal longitudinal muscles extend from the prephragm of the metathorax to the phragma of the mesothorax. The ventral longitudinal muscles connect the entosternal arms of the mesothorax with those of the prothorax.

#### The Metathorax. (Figs. 41, 42 and 43).

The metathorax is large in correlation with the development of the wings as the chief organs of

flight. The metanotum has been modified to serve the function of the wings, by reduction of the intersegmental membranes between the mesothorax and the precosta of the first abdominal segments, to form a firm pterothorax, the development of internal ridges for muscle attachment and lateral processes for articulation of the wings.

The metanotum is divided into the three sclerites of a typical thoracic segment, the prescutum, scutum, and scutellum (Duns, 1934, p. 481).

A postnotum consists of a greatly enlarged precosta, antecosta and phragma of the first abdominal segment (Snodgrass, 1927, p. 48). It is closely applied to the metanotum, as in the wing bearing segments of most Pterygota (Duns, 1934, p. 27). It is functionally part of the metanotum. According to Snodgrass, 1927, p. 51, a phragma is formed at either end of the segment that contains the largest wing muscles, to give increased surface to the tergum for muscle attachment.

The antecostal suture is semicircular and has a corresponding internal antecostal ridge. It separates off a narrow precosta from the anterior margin of the tergum. A phragma is developed from the antecostal ridge, and projects into the

metathoracic cavity, to give increased surface for attachment of the dorsal longitudinal muscles.

The prescutum surrounds the antecostal suture laterally and posteriorly. The median region, which is covered by the mesonotum normally, is membranous, except for a narrow lightly sclerotised posterior strip. The lateral regions are more heavily chitinised. The anterior margin, adjacent to the prephragma, forms a ventral projection on either side, which is closely united to the scutellar arms of the mesothorax. The prealar bridge is a small triangular sclerite between the prescutum of the metathorax and the episternum of the mesothorax. Snodgrass, 1927, p. 52, states that the prescutum reaches its greatest development in the metathorax of Coleoptera. The intersegmental membrane between the meso- and metanotum is attached to the antecosta.

The scutellum is a median sclerite, posterior to the prescutum. It is bounded on each side by a longitudinal suture, which separates it from the scutum.

According to Imms, 1934, p. 481, the scutellum of Coleoptera is median, and divides the scutum into two separate plates. The scutum is large and convex. The inner surface of both scutum and scutellum is

divided up by ridges for muscle attachment. The most prominent is an inverted "V"-shaped ridge, with the apex attached to the distal end of the scutellum and the arms to the base of the scutum.

The anterior margin of the scutum at the level of the basal angle of the proscutum is produced forwards as a rounded prominence. The lateral margins are produced to form an anterior notal wing process, and a posterior notal wing process; the former projects laterally, the latter anteriorly. Between the two processes there is a lateral emargination of the scutum. They form supports for the articular sclerites of the wing. The posterior margin of the tergum is reflexed ventrally.

The postnotum projects ventrally. It is a large transverse sclerite, produced laterally to form the postalar bridge, which extends to the dorsal surface of the katopimeron.

The intersegmental membrane, between the metathorax and the abdomen is attached to the posterior margin of the postnotum.

The pleural suture follows a sinuate course from the outer anterior angle of the metathoracic coxal cavity to the pleural wing process. Internally

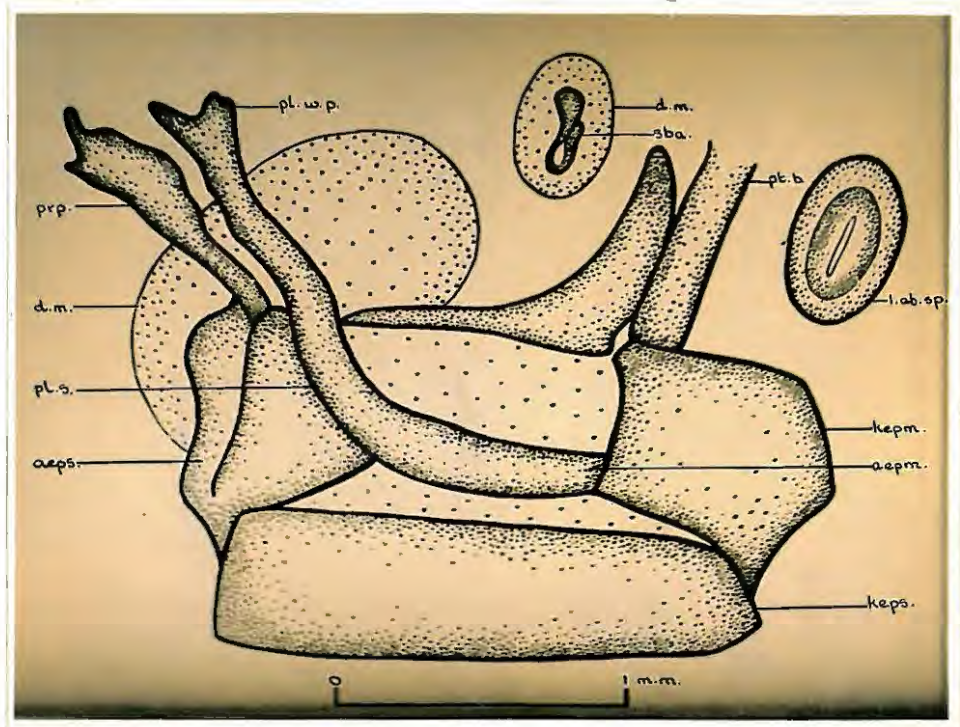


Fig.42 - Pleural Sclerites of Metathorax of Imago.

ANOMALA VETULA WIED.

- aepr. = anepimeron.
- aepr. = anepisternum.
- d.m. = disc for muscle attachment.
- l.ab.sp. = first abdominal spiracle.
- kepm. = katepimeron.
- keps. = katepisternum.
- pl.s. = pleural suture.
- pl.w.p. = pleural wing process.
- pt.b. = postalar bridge.
- prp. = preparapterum.
- sba. = subalare.

it forms a pleural ridge. Ventrally the pleural coxal process forms the articulation of the coxa with the pleural region. It divides the pleural region into an antero-ventral episternum and a postero-dorsal epimeron. The episternum is divided into a ventral katepisternum and a dorsal anepisternum, the epimeron into a posterior katepimeron and an anterior anepimeron. (Crampton, 1909.)

The katepimeron is an elongated strongly chitinised sclerite, which is attached to the sternum along its ventral length. The triangular anepisternum is attached to the antero-dorsal angle of the katepisternum, and to the anterior margin of the katepimeron. The preparaplerum arises from between a median fold of the anepisternum, and extends to the articulation point of the wing. Internally it forms a large disc, on which the anterior pleural wing muscles are attached. The epimeron is a rectangular sclerite attached to the posterior dorsal angle of the katepisternum. The postalar bridge is attached to its anterior dorsal surface. The anepimeron extends forwards from the lower region of the anterior margin of the katepimeron. It is a narrow irregular sclerite, continuous distally with the pleural wing process. It is bounded dorsally and ventrally by membranous

areas. A sclerite lying between the anepisternum and the antero-dorsal angle of the anepimeron is possibly part of the epimeron. The subalare, or postparapteron, is a small sclerite situated in the pleural membrane posterior to the pleural wing process. Snodgrass, 1927, p. 57, states that the subalare is always an independent sclerite in adult insects. Internally it bears a disc for attachment of the posterior pleural wing muscles.

The katopisternum has a vestiture of long hairs, those of the anepisternum are shorter and more numerous.

The surface of the katepimeron is covered with moderately long hairs; those on the anepimeron are shorter.

The sternum is large. It is divided into two symmetrical halves by a median sternal groove, which marks the point of attachment of the metendosternite. Crowson, 1938, p. 398, states that the development of this longitudinal suture is a variable character in Coleoptera. Anteriorly the sternum is bi-emarginate, and bounds the mesothoracic coxal cavities posteriorly. The sternum closes the metathoracic coxal cavities anteriorly. The anterior

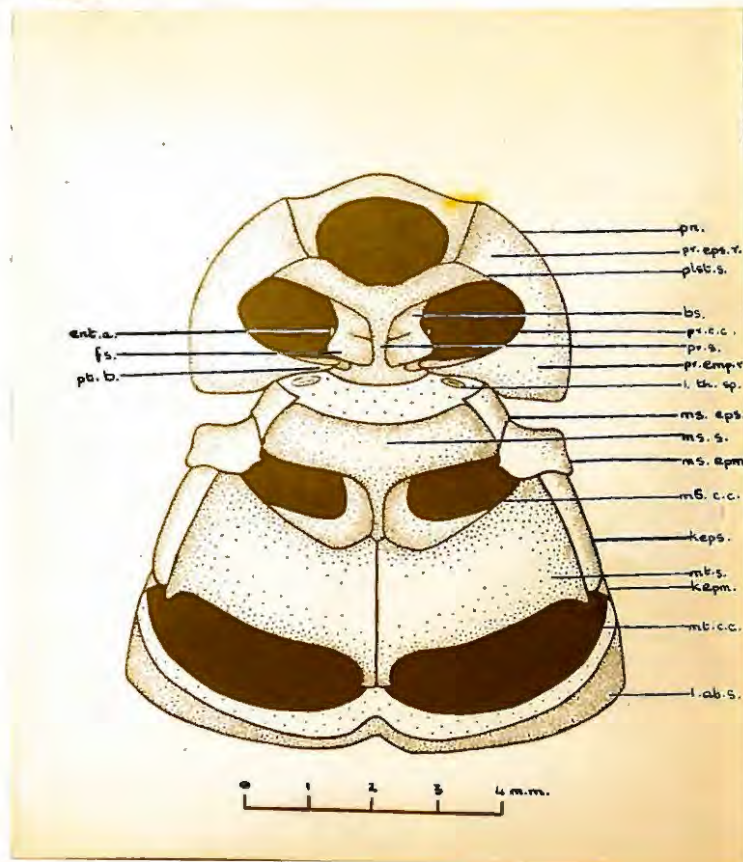


Fig. 43 - Ventral view of Thorax.  
ANOMALA VENTULA WIED.

- bs. = basisternum.
- ent. a. = entosternal arm.
- l. th. sp. = first pair thoracic spiracles.
- l. ab. s. = first abdominal sternum.
- fs. = furcisternum.
- kepi. = katepimeron.
- keps. = katepisternum.
- ms. c. c. = mesothoracic coxal cavity.
- ms. epi. = mesothoracic epimeron.
- ms. eps. = mesothoracic episternum.
- ms. s. = mesothoracic sternum.
- mt. c. c. = metathoracic coxal cavity.
- mt. s. = metathoracic sternum.
- plst. s. = pleurosternal suture.
- pt. b. = postcoxal bridge.
- pn. = pronotum.
- pr. c. c. = prothoracic coxal cavity.
- pr. epi. r. = prothoracic epimeral region.
- pr. eps. r. = prothoracic episternal region.
- pr. s. = prothoracic sternum.

margin of these coxal cavities is sinuate. The inner margin forms an articulation point for the distal end of the metathoracic coxa.

The metendosternite is formed of a high median keel, expanded internally to form a triangle. The anterior projection gives attachment to the tendons of the metafurca. The lateral processes are directed posteriorly, and form the furcal arms.

In a comparative study of the metendosternite in Coleoptera, Crossen, 1938, p. 406, states that the furca is heavily thickened in all Lamellicornia.

The metanotum has an anterior and a posterior phragma, so that the dorsal longitudinal muscles of the metathorax are segmental instead of intersegmental. This condition is characteristic of Coleoptera (Snodgrass, 1927, p. 49). The ventral longitudinal muscles connecting the entosternal arms of the metathorax with those of the mesothorax, are short, owing to the close union of meso- and metathorax. A pair of tendons arise close together from the median projection of the metafurca, and are connected to the mesofurcal arms by short muscles. A band of muscle extends from the first abdominal segment to the metafurcal arms. It allows the abdomen to move on the thorax. The dorso-ventral muscles

are large, and almost fill the metathoracic cavity. They extend from the tergum to the sternum, lateral to the entosternal structure. Powerful sternopleural muscles fill the metathoracic cavity ventrally.

The Spiracles. (Figs. 42 and 43).

There are two pairs of thoracic spiracles, the number that is typical of the thorax in Hexapoda (Snodgrass, 1927, p. 39). The first pair is ventral. It lies in the membrane between the posterior margin of the prothoracic coxae and the anterior margin of the mesosternum. It is obscured by the epimeral arm of the prothorax. The second pair is lateral. It is situated in the membrane between the epimeron of the mesothorax and the katapimeron of the metathorax. It is entirely covered by the former. According to Snodgrass, 1935, p. 40, the second pair of spiracles of adult Coleoptera is formed from the small chitinous discs situated between the meso- and metathoracic folds on either side of the larva. Snodgrass, 1935, p. 427, states that the thoracic spiracles migrate forward during development. He therefore maintains that the origin of the two pairs of spiracles are mesothoracic and metathoracic, respectively.

Both pairs of spiracles are transversely elongated, and are approximately the same length. They are surrounded by a chitinous peritreme. The lips of the first spiracle are raised above the surface of the surrounding membrane. The external part of each spiracle therefore becomes a shallow spiracular atrium, opening to the exterior by the secondary atrial orifice. The primary atrial orifice is a short slit to one side of a chitinised strip, which extends the length of the membrane at the base of this atrium. The aperture leads into a chamber which has a narrow distal opening, into the main tracheal trunk. At the junction of these two, the lateral margin projects inwards to give attachment to the occluder muscle. The tracheal trunk arises from the distal end of the second chamber.

The lips of the second pair of spiracles are closely approximated, and are flush with the surrounding membrane. They open directly into the tracheal trunk. There is no mechanism for regulating the size of the aperture.

#### The Appendages of the Thorax.

##### (1) The Legs. (Figs. 44 - 51 ).

They are well developed, and project beyond

the body from the distal end of the femora. The broad flattened surface of the prothoracic tibia is well suited to burrowing. The metathoracic legs are strongly developed. They are the longest pair of legs.

The legs become increasingly stronger from pro- to mesothorax. They are more darkly sclerotised in the male than in the female. The prothoracic femur and tibia are a light reddish-yellow; the articulation points and the teeth at the distal end of the tibia are a dark reddish-brown. The tibiae are very conspicuous in the male, being the lightest part of the beetle that is visible dorsally. The mesothoracic legs are uniformly darker. They are ferruginous, with darker hairs and spines. In the male, the metathoracic legs are a dark reddish-brown, and resemble the dorsal surface of the pronotum in colour. In the female they are a lighter colour.

The trochantin is the basal segment in the pro- and mesothoracic legs. It is absent in the metathoracic legs. Hansen, 1930, p. 51, states that trochantins have been observed in very different families of Coleoptera in the pro- and mesothoracic pairs of legs, but that they are seldom, or generally, not distinguishable in the metathoracic leg.

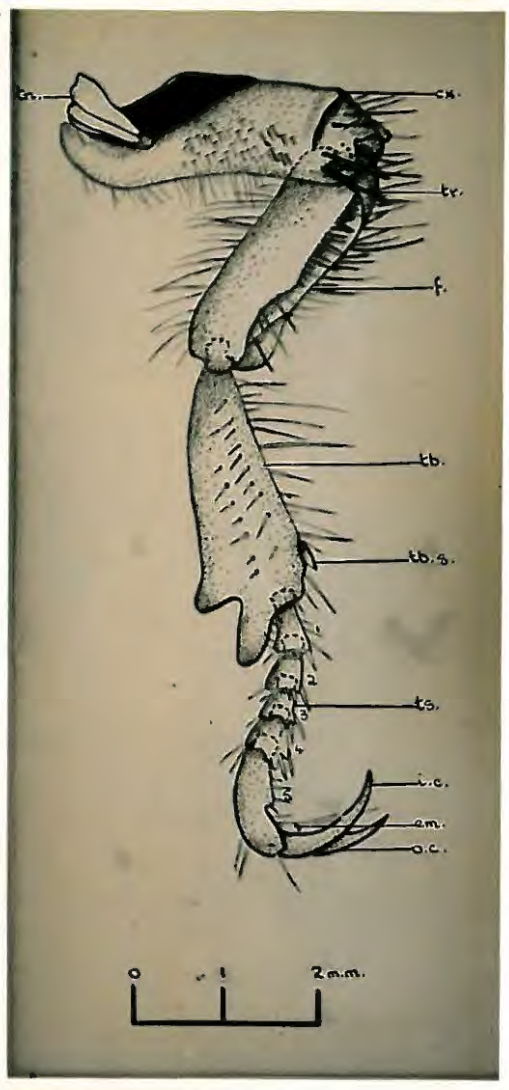
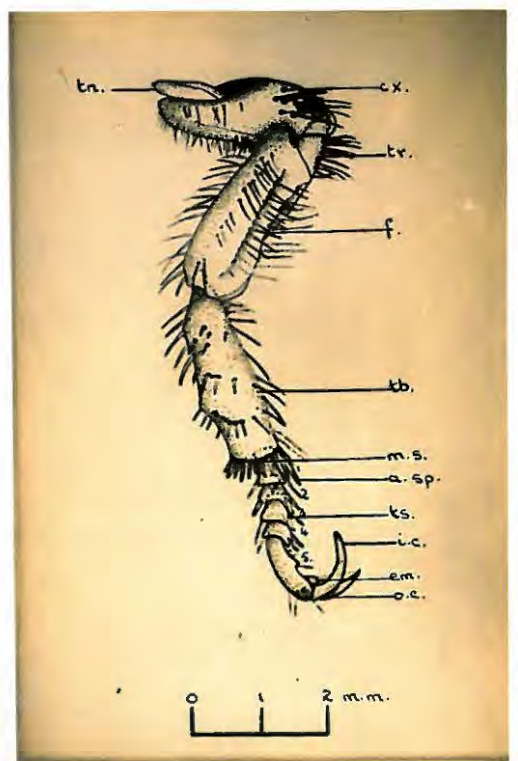


Fig. 44- Prothoracic Leg of Male Imago.  
ANOMALA VETULA WIED.

tb. = bidentate tibia.  
cx. = coxa.  
em. = empodium.  
f. = femur.  
i. c. = inner claw.  
o. c. = outer claw.  
ts. = tarsus.  
tb. s. = tibial spur.  
tr. = trochanter.  
tn. = trochantin.

Fig. 45- Mesothoracic Leg of Male Imago.  
ANOMALA VETULA WIED.

a. sp. = articulated spurs.  
cx. = coxa.  
em. = empodium.  
f. = femur.  
i. c. = inner claw.  
m. s. = marginal spines.  
o. c. = outer claw.  
ts. = tarsus.  
tb. = tibia.  
tr. = trochanter.  
tn. = trochantin.



The coxa is the segment by which all three pairs of legs articulate with the body. The prothoracic coxa extends through the coxal cavity, and articulates with a process on the inner surface of the prothorax, as already described. The mesothoracic coxa articulates with the coxal process at the ventral extremity of the pleural ridge. The anterior margin of the metathoracic coxa is attached to the coxal process proximally and to the sternum distally. The coxae are large and fit into the coxal cavities. They are connected to the margins of the coxal cavities by membrane. The proximal margins are reflexed to form the basicosta. They are well developed in the pro- and mesothoracic legs. The firm attachment of the coxae to the margins of the coxal cavities allows only limited movement in an antero-posterior direction. This movement is very slight in the metathoracic leg. According to Snodgrass, 1927, p. 73, immovable metathoracic coxae are usual in adult Coleoptera.

In the prothoracic leg the forward movement is effected by means of a promoter muscle, attached to the tergum and inserted on the trochantin. Backward movement is effected by large remotor muscles, which arise on the tergum, and are inserted

on the posterior margin of the cavity of the coxa. The promotor muscles of the mesothoracic leg arise on the tergum, and are attached to the anterior margin of the cavity of the coxa, and to the trochantin. The remotor muscles arise on the entosternal area and are inserted on the posterior margin of the cavity of the coxa. Promotor and remotor muscles of the metathoracic leg arise at the furca and tergum; the former is inserted on the anterior margin, the latter on the posterior margin of the cavity of the coxa.

The coxo-trochanteral hinge is dicondylic, with anterior and posterior articulation points; movement is therefore restricted to a dorso-ventral direction.

The trochanter is the basal segment of the telopodite. It is small, as is always the case in the insect leg. (Snodgrass, 1935, p. 197). The proximal end projects into the coxa as a rounded process for muscle attachment. It bears a few hairs distally and more delicate ones proximally. It increases in size from pro- to metathoracic leg. The telopodite is moved by levator and depressor muscles. The former arises in the coxa, and is inserted dorsally on the proximal margin of the trochanter; the latter

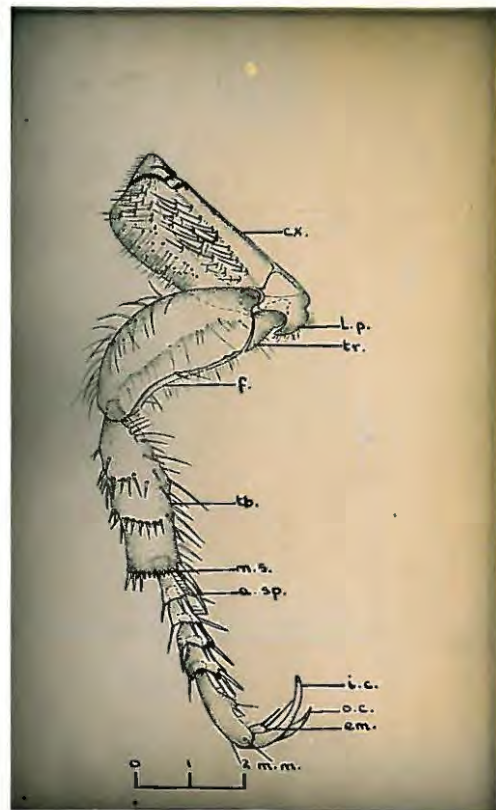


Fig. 46. - Metathoracic Leg of Male Imago.  
ANOMALA VETULA WIED.

- a. sp. = articulated spurs.
- cx. = coxa.
- em. = empodium.
- f. = femur.
- i. c. = inner claw.
- l. p. = lobate process of coxa.
- m. s. = marginal spines.
- o. c. = outer claw.
- tb. = tibia.
- tr. = trochanter.

originates on the coxa, and on the tergum, and is attached ventrally, on the base of the trochanter.

The femur has a dorsal and ventral articulation point with the trochanter. They move as one unit. The dividing suture extends obliquely towards the upper margin. The surface of the femur which moves across the coxa is flattened and smooth.

Distally the femur articulates with the tibia by means of an anterior and a posterior articulation point. The distal end of the tibia forms a rounded head, which projects into the femur, and allows the tibia to be flexed against the under surface of the femur.

The tibia of the prothoracic legs is flattened, and strikingly different from those of the meso- and metathoracic legs, which are rounded. The levator and depressor muscles of the tibia arise on the femur, and are attached to the base of the tibia.

The tibio-tarsal hinge is dicondylic, with anterior and posterior articulation points.

The tarsus has five segments, the number characteristic of *Lamellicornis* (Dunn, 1934, p. 481). The first four segments are robust and subtriangular. Distally two bristles are borne on the outer margin;

the inner margin forms three spinelike projections. A strong seta is formed on either side of the median projection, and on the outside of the lateral projections. The lateral setae are not as robust as the inner two. The fifth segment has a different shape to the preceding four tarsal segments. It is the longest segment of the tarsus and is flattened. The outer margin is curved. The inner margin has a small rounded toothlike projection, approximately half-way along its length. Distal to the projection the segment is excavated to accommodate the pretarsus. The distal margins are rounded. The inner margin bears a few short hairs proximally, two hairs on the projection, and several longer hairs distally. There is one long hair on either side of the segment, and one on the posterior margin.

The segments of the tarsus are connected by membrane. They do not have individual muscles. Movement of the tarsus as a whole is effected by levator and depressor muscles, arising on the tibia.

The base of the pretarsus is sunk into the terminal portion of the fourth tarsal segment. It is composed of an inner and an outer claw, a median flexor plate, an empodium, and a pair of pulvilli. It is similar to that of Melolontha vulgaris Fab.,

figured by Packard, 1898, p. 101. The Rutelinae differ from the Melolonthinae in having claws of unequal size. The claws are parallel; the inner claw is longer than the outer. They are curved. The inner claw of the pro- and mesothoracic legs is cleft in the female, and simple in the male. The claws of the metathoracic legs in both female and male are simple. The flexor plate is situated between, and posterior to, the claws. A pulvillus is formed on either side of the anterior margin of the flexor plate; each is attached to the base of a claw. The empodium is a process of the distal margin of the flexor plate; it lies between the bases of the claws. It is laterally compressed. Distally it bears one long and one short seta.

The Prothoracic Legs of the Male and Female.  
(Figs. 44, 47, 50 and 51).

The trochantin is a small triangular sclerite, approximately one quarter of the length of the coxa. The anterior basal angle is attached to the inner surface of the prothorax, anterior to the articulation point of the coxa. The posterior angle articulates with a condyle at the anterior margin of the cavity of the coxa. It is attached by membrane to the anterior proximal margin of the cavity of the coxa, with which the apex of the trochantin  
- articulates. -

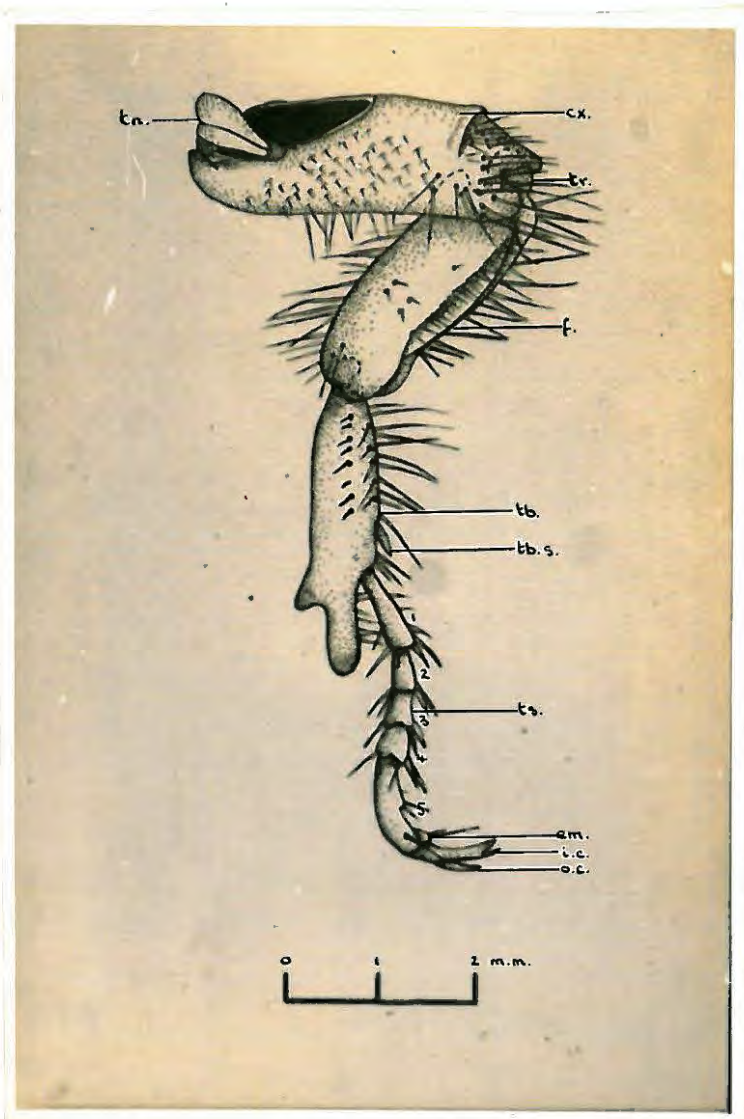


FIG. 47 - Prothoracic Leg of Female Imago.  
ANOMALA VETULA WIED.

- tb. = bidentate tibia.
- i. c. = cleft inner claw.
- cx. = coxa.
- am. = ampodium.
- f. = femur.
- o. c. = outer claw.
- ts. = tarsus.
- tb. s. = tibial spur.
- tr. = trochanter.
- tn. = trochantin.

articulates. Outwardly it is raised to form a median longitudinal ridge, which thus divides the sclerite into two approximately equal halves.

The coxa is the longest segment of the leg in the female. In the male it is approximately equal in length to the tibia; they are longer than the other segments of the leg. It is cylindrical. The cavity at the base extends from the proximal end to approximately half-way along the dorsal surface. The distal margin is excavated dorsally and ventrally to accommodate the trochanter. Distally the dorsal surface has a conspicuous darkly sclerotised transverse ridge. Distal to the ridge the coxa bears a number of long, proximally directed hairs. There is a longitudinal row of delicate hairs along the ventro-lateral margin. The lateral surfaces are rugose.

The trochanter is approximately the same length as the trochantin.

The femur is approximately three-quarters of the length of the coxa in the female. In the male the ratio is greater. The side adjacent to the tibia is longitudinally ridged on either side, thus forming a concavity to accommodate the tibia when it is flexed. The ridges bear hairs, those of the upper row are shortest. The upper surface is clothed with hairs

which increase in length distally.

The tibia is approximately equal in length to the coxa in the male. In the female it is intermediate in length between the coxa and femur. It is bi-dentate outwardly in both sexes. The apical tooth is the longest; it extends approximately half-way along the second tarsal segment. It is rounded distally, and slightly outwardly directed. The basal tooth is more broadly rounded, and laterally directed. The inner margin of the apical tooth bears several strong bristles. The tibia increases in width distally; the inner margin is approximately straight, the outer margin is curved. Distally the ventral surface is concave, to assist in burrowing. At the base of the cavity for the insertion of the first tarsal segment, there is a short movable tibial spur. It projects beyond the inner margin of the tibia. There are two longitudinal rows of short hairs on the upper and lower surfaces. The inner margin bears a few short hairs.

The tarsus is shorter in comparison with the tibia in the female than in the male. In the female the basal segment is approximately twice the length of the three following segments, which are

- approximately -

approximately the same length; it is a little shorter than the fifth segment. In the male the basal segment is slightly longer than the three following segments, but approximately one-third of the length of the fifth segment. The spines on either side of the median projection on the inner margin of segments three and four are more strongly developed than those on the preceding segments.

The inner claw in the female is approximately the same length as the first tarsal segment; in the male it is almost three times the length of the first tarsal segment.

The Mesothoracic Legs of the Male and Female.  
(Figs. 45 and 48).

The trochantin is a small elliptical sclerite. It is closely applied to the anterior proximal margin of the cavity at the base of the coxa, and the posterior margin of the mesothoracic sternum. Proximally it extends beyond the end of the coxa; distally it articulates with the coxa. The longitudinal median ridge is not as distinct as in the prothoracic trochantin. It is slightly longer than the prothoracic trochantin. The relative size of the trochantin of the pro-

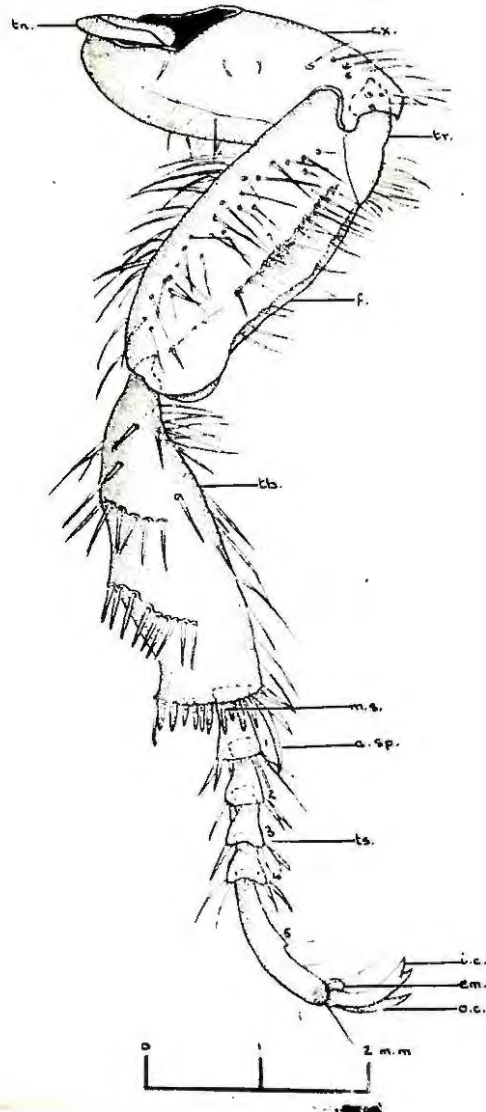


Fig. 48 - Mesothoracic leg of Female Imago.  
ANOMALA VERTULA, WIED.

- a. sp. = articulated spurs.
- i. c. = cleft inner claw.
- cx. = coxa.
- tr. = trochanter.
- f. = femur.
- m. s. = marginal spines.
- o. c. = outer claw.
- ts. = tarsus.
- tb. = tibia.
- tn. = trochantin.

and mesothoracic legs is similar to that of Geotrupes. (Hansen, 1930, p. 68).

The coxa is approximately two and a half times the length of the trochantin. It is proportionately broader than long compared with the prothoracic coxa. As in the prothoracic leg, the cavity at the base extends for approximately half the length of the dorsal surface. The coxa is excavated anteriorly and posteriorly to accommodate the trochanter. The distribution of hairs is similar to that on the prothoracic coxa.

The femur is the longest segment of the leg. Distally and laterally it has a vestiture of long hairs.

The tibia is approximately the same length as the coxa in the female, but intermediate in length between the coxa and femur in the female. The meso- and metathoracic coxae are cylindrical, but slightly antero-posteriorly flattened in both sexes. The proximal end is narrow; the width increases medianly; distally the outer margin is excavated. The distal end is truncated, and is slightly narrower than the median part. The anterior face of the tibia in both pairs of legs has two rows

of strong spines running obliquely distally, towards the inner margin of the tibia. The meso- and metathoracic tibiae of both sexes have a fringe of short well developed spines on the anterior and lateral margins. Internal to these there are two strong articulated spurs; the posterior one is the larger. They extend beyond the first tarsal segment.

The inner margin bears a number of strong bristles; those of the ventral surface are more numerous and more delicate.

The tarsus is shorter than the tibia, and shorter than that of the prothoracic leg. The first four segments decrease in length slightly, towards the distal end. The spines and projections of the inner margin are stronger than in the prothoracic leg. The fifth segment is about three and a half times longer than the basal segment in the male, and two and a half times longer in the female.

The claws are approximately the same length as the corresponding claws in the prothoracic leg in both sexes.

The Metathoracic Legs of the Male and Female.  
(Figs. 46 and 49).

The coxa is the longest segment, and is

- larger -

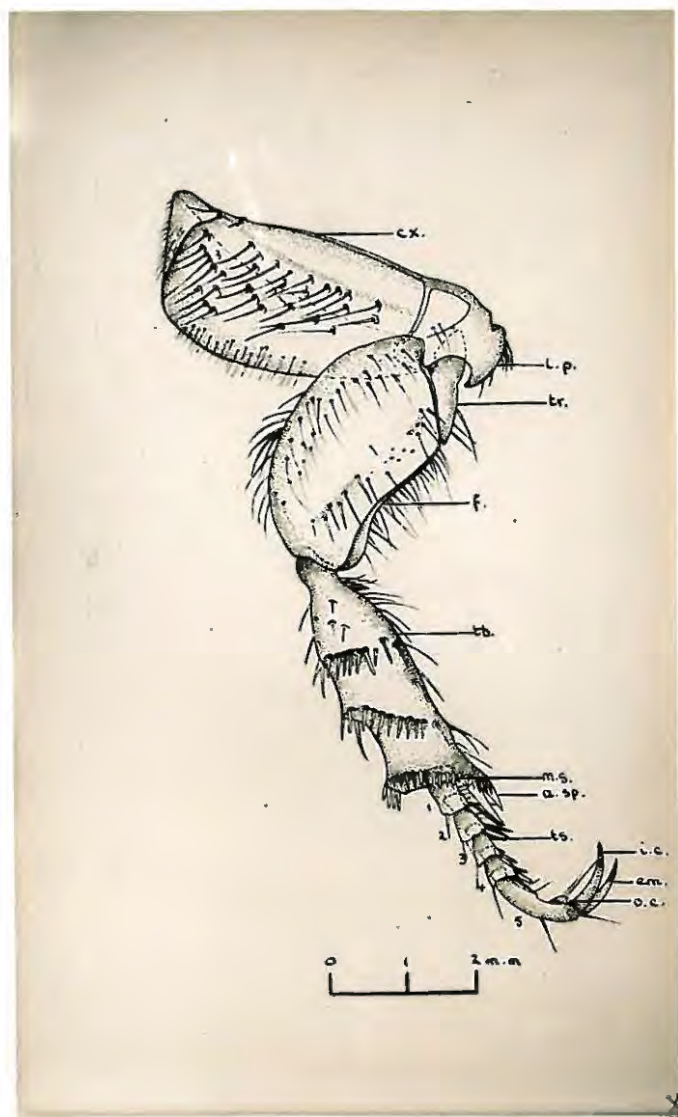


Fig. 49 - Metathoracic Leg of Female Imago.  
ANOMALA VERTULA WIED.

- a. sp. = articulated spurs.
- cx. = coxa.
- om. = empodium.
- f. = femur.
- i. c. = inner claw.
- l. p. = lobate process of coxa.
- m. s. = marginal spines.
- o. c. = outer claw.
- ta. = tarsus.
- tb. = tibia.
- tr. = trochanter.

larger than that of the meso- or metathorax. Proximally the width is approximately equal to that of the femur at its widest point. It is flat and decreases in width distally. The cavity of the coxa extends the length of the ventral margin. As in the mesothoracic leg, the cavities for accommodation of the trochanter are on the anterior and posterior faces. Distally, a posteriorly curved lobate process extends beyond the trochanter. Peringuey, 1902, p. 587, states that this process arises from the trochanter. The processes are contiguous medially. The anterior region of the outer surface of the coxa is without hairs; the lobate process, and the posterior region bear a number of hairs.

The femur is shorter than the coxa. It is robust, but more compressed than in the pro- or mesothoracic legs. The outer margin is sigmoid, the inner curved. The dorsal surface bears moderately long hairs.

The tibia is shorter than the femur. It is antero-posteriorly flattened. It is longer and more robust than the mesothoracic tibia. The spines of the oblique rows and the marginal fringe are more numerous than on the mesothoracic tibia. The spurs

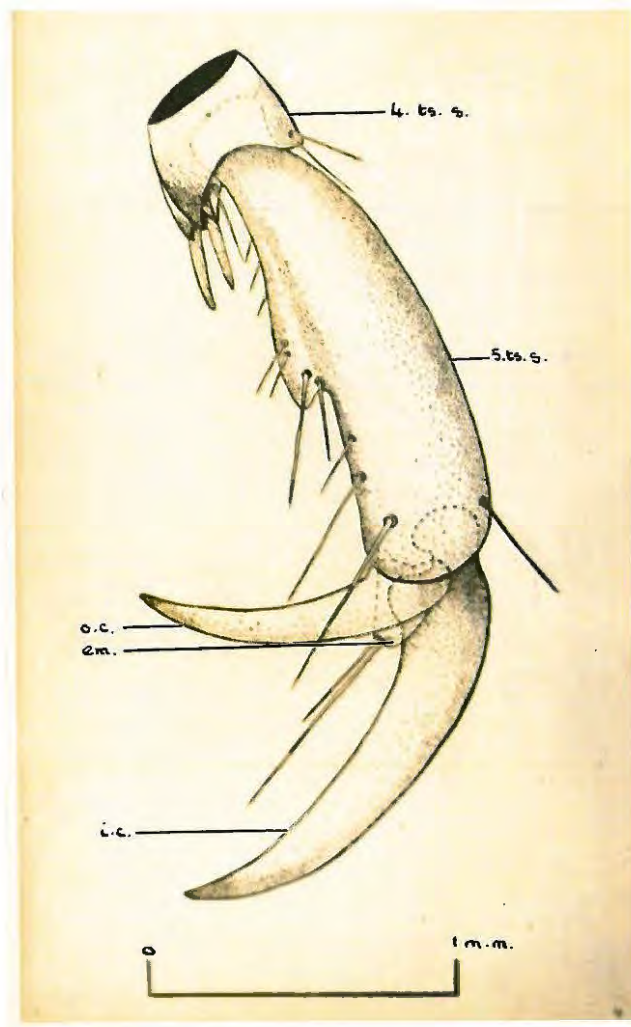


Fig. 50 - Fifth Tarsal Segment and Pretarsus  
of Prothoracic Leg of Male Imago.  
ANOMALA VERULA WIED.

- i. c. = cleft inner claw.
- em. = empodium.
- o. c. = outer claw.
- 4 - 5 ts. s. = tarsal segments 4 and 5.

are well developed, the posterior one extends almost to the end of the second tarsal segment. The setation is similar to that of the mesothoracic tibiae.

The tarsus is longer than the tibia. In the male it is longer than that of the prothoracic leg; in the female it is approximately the same length. The first four segments decrease in length distally. The fifth segment is approximately two and a half times the length of the basal segment.

The claws in both sexes are longer and stronger than in the pro- or mesothoracic legs.

The legs of the male and female differ in the following points:-

Prothoracic leg.

- (1) The femur is larger in the male than in the female, but approximately the same width.
- (2) The tibia is strikingly narrower in the female than in the male.
- (3) The basal segment of the tarsus is conspicuously elongated in the female, and almost twice as long as the corresponding segment in the male.

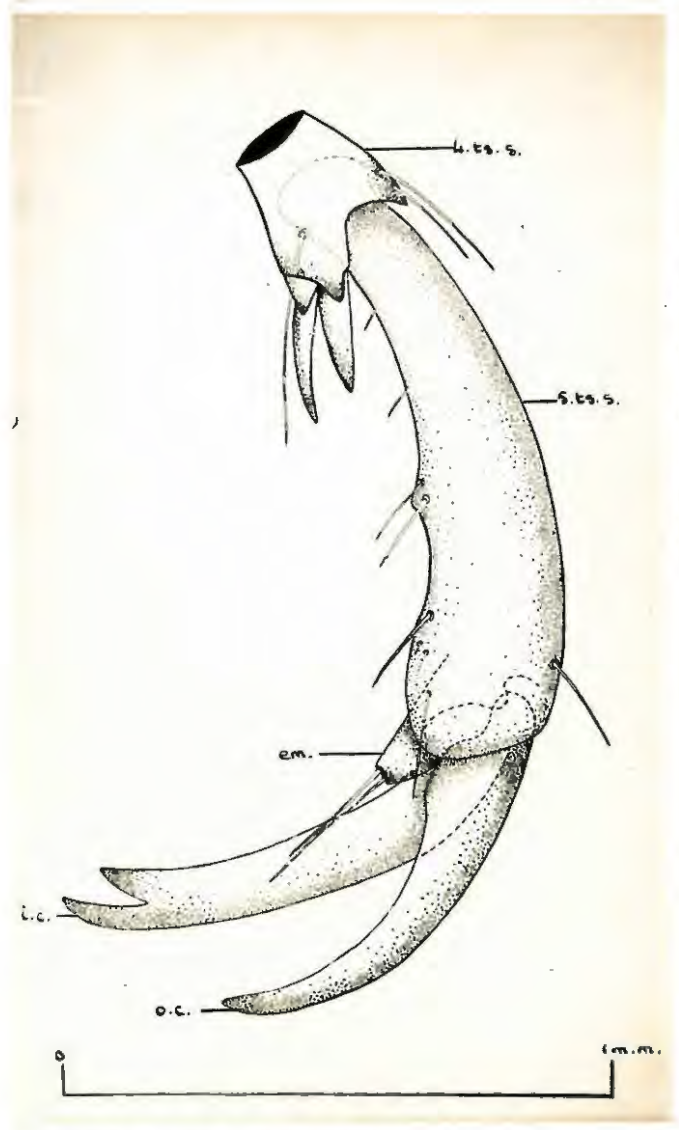


Fig. 51 - Fifth Tarsal Segment and Pretarsus  
of Prothoracic Leg of Female Imago.  
ANOMALA VETULA WIED.

- em. = empodium.
- i.c. = inner claw.
- o.c. = outer claw.
- 4-5 ts.s. = tarsal segments 4 and 5.

- (4) The fourth tarsal segment is longer in the male than in the female.
- (5) The claws are shorter in the female than in the male. The inner claw in the male is approximately equal in length to the outer claw in the female.
- (6) The outer claw in the female is cleft, that in the male is simple.

Mesothoracic leg.

- (1) As in the prothoracic leg, the length of the femur is shorter in the female than in the male, but is approximately the same width.
- (2) The femur is shorter and narrower in the female than in the male.
- (3) The fourth tarsal segment is longer in the male than in the female.
- (4) The size relationship of the claws in the female and male is similar to that in the prothoracic leg.
- (5) The outer claw in the female is cleft, that in the male is simple.

- Metathoracic... -

Metathoracic leg.

- (1) The coxa is longer in the male, but not as broad.
- (2) The femur is longer in the male than in the female, and approximately the same width.
- (3) The tibia is more robust in the male than in the female, being both longer and broader.
- (4) The tarsal segments are longer in the male than the female, particularly the fourth segment.
- (5) The claws are larger and stronger in the male than in the female.

II. The Elytra. (Fig. 52).

When at rest the elytra cover the dorsal and lateral surfaces of the metathorax and abdomen; the mesoscutellum is exposed. The level to which the elytra extend, depends on the degree of extension of the abdomen; normally the pygidium is exposed. In the male they usually reach to the posterior margin of the penultimate segment; in the female the posterior half of the propygidium and the pygidium are usually

- exposed. -

exposed.

The following measurements were taken, using a travelling microscope. The length was measured between two parallel lines, the one through the anterior margin of the scutellum, and the other through the elytron tip. The width was measured across the widest point, from the sutural to the lateral margin.

MALE:

<u>Length:</u>	Longest	9.6 mm.
	Shortest	8.3 mm.
<u>Width:</u>	Broadest	4.6 mm.
	Narrowest	3.4 mm.

Mean for 30 specimens:

Length	8.81 mm.
Width	3.86 mm.

Standard deviation for 30 specimens:

Length	0.324 mm.
Width	0.276 mm.

FEMALE:

<u>Length:</u>	Longest	10.1 mm.
	Shortest	8.0 mm.
<u>Width:</u>	Broadest	4.6 mm.
	Narrowest	3.5 mm.

Mean for 17 specimens:

Length	9.18 mm.
Width	4.02 mm.

Standard deviation for 17 specimens:

Length	0.545 mm.
Width	0.303 mm.

The elytra are a shiny dark brown or reddish brown. They are large, sub-rectangular, and coriaceous. Anteriorly they are approximately the same width as the base of the prothorax. The outer margin of each elytron is slightly amplified from the humeral angle to about three-quarters of its length. The posterior outer angle is broadly rounded, and the tip is truncated. There is a distinct callus in both humeral and apical regions. The margin of the scutellar area is obliquely truncated; it is overlapped by the edges of the mesonotum. The upper surface slopes gradually towards the lateral margins; the posterior region is more abruptly declivous.

The upper surfaces of the elytra have deeply punctured striae. Twelve series can be recognised in each elytron in both sexes. The interval between

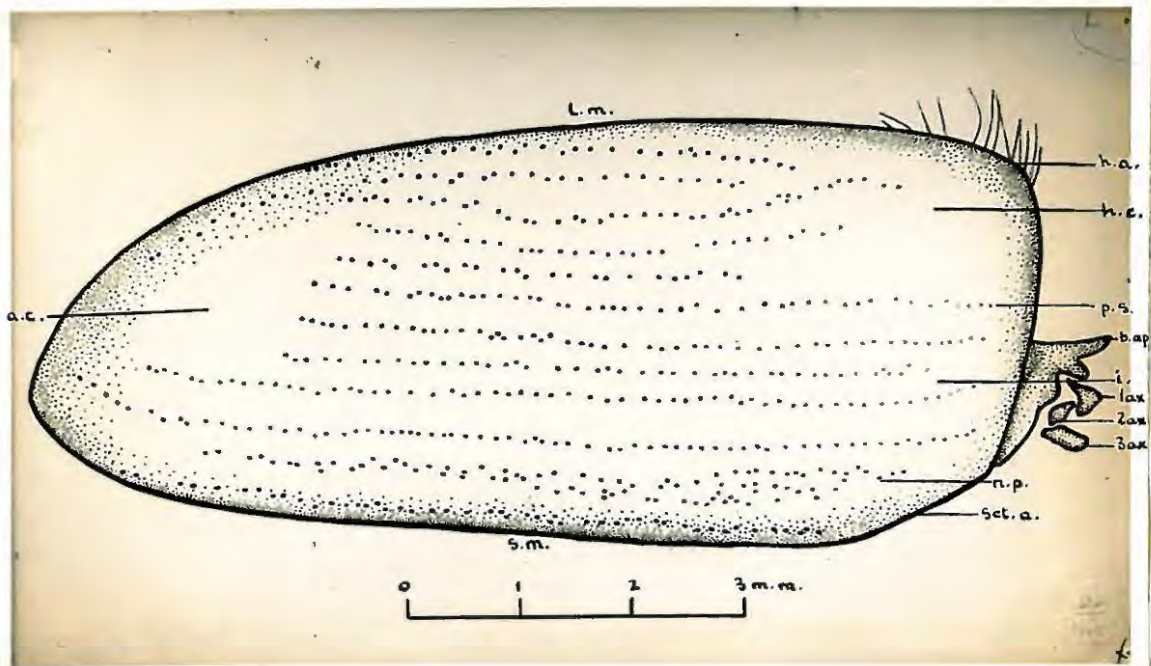


Fig. 52a - Left Elytron of Male Imago.  
ANOMALA VETULA WIED.

- a. c. = apical callus.
- 1. ax. - 3ax. = axillary sclerites 1-3.
- b. ap. = bifurcated apophysis.
- h. a. = humeral angle.
- h. c. = humeral callus.
- i. = interval.
- l. m. = lateral margin.
- n. p. = non-seriate punctures.
- p. s. = punctate striae.
- sct. a. = scutellar area.
- s. m. = sutural margin.

each series is costulate, but more distinctly so in the male than in the female. The interval between the costa adjacent to the middle line and the second costa, is filled in the anterior three-quarters with irregular non-seriate punctures; posteriorly these resolve themselves into a line. In the female the interval between the tenth and eleventh series is filled with numerous irregularly arranged punctures; this area is non-punctate in the male. The striae are interrupted on the humeral callus and the apical callus; those in the middle of the elytron do not extend to the apex. The outer margin bears about thirty-five hairs in both sexes; the anterior fifteen are close together, the remainder arise at regular intervals.

The elytra are inserted on the mesothorax, between the mesoscutellum and the episternum. There is a strongbifurcated apophysis approximately midway along the basal margin of each elytron; it articulates with the pleural wing process of the mesothorax. There are three axillary sclerites, situated in the membrane between the base of the elytron and the mesonotum. The first sclerite usually lies next to the apophysis, while the second and third sclerites are folded underneath. The first axillary sclerite

articulates with a small process on the anterior lateral margin of the mesonotum. The second axillary sclerite is small. It lies posterior to the first axillary sclerite, and between it and the third sclerite. It is attached to the subalar sclerite by a ligament. The third axillary sclerite is larger; it is the most posterior of the three sclerites, and lies parallel to the apophysis.

The interlocking mechanism of the elytra resembles that of Lachnosterna fusca described by Breed and Ball, 1908, p. 291, (Hayes, 1922, p. 12). They describe four devices; the first three are present in Anomala vetula Wied.

1. Co-adaptation of the elytra along the middle line.
2. The inner anterior margin of the elytron fits into a groove on the dorsal surface of the metathorax.
3. The inner anterior angles of the elytra are slipped under the mesonotum.

The outer anterior angles of the elytra curve sharply ventrally, but there is no corresponding groove or ridge on the metathorax for hooking the elytra, as in Lachnosterna fusca.

III. The Wings. (Fig. 53).

The wings are membranous structures, supported by chitinous veins. They are approximately three times longer than broad, and one and a half times longer than the elytra.

In Anomala vetula Wied., the veins do not follow the course of the trachea. Observations made by Comstock, 1918, p. 300, suggest that the venation precedes the tracheation in Coleoptera. Two groups of three longitudinal unbranched trachea enter the base of the hind wing of the pupa of Anomala vetula Wied. They correspond to the costo-radial and cubito-anal groups of Comstock, 1918, p. 300. The cubitus vein, which usually follows the course of the cubital trachea, should therefore occur towards the anal end of the wing. In the adult the two principal convex veins, which, according to Needham, 1935, p. 118, are the radius and cubitus, are found near the anterior margin.

The arrangement of the veins conforms to the description of the venation of the hind-wings of Coleoptera given by Tillyard, 1926, p. 180.

The costa ( $c^+$ ) and subcosta ( $Sc^-$ ) can be distinguished as separate veins at the base of the

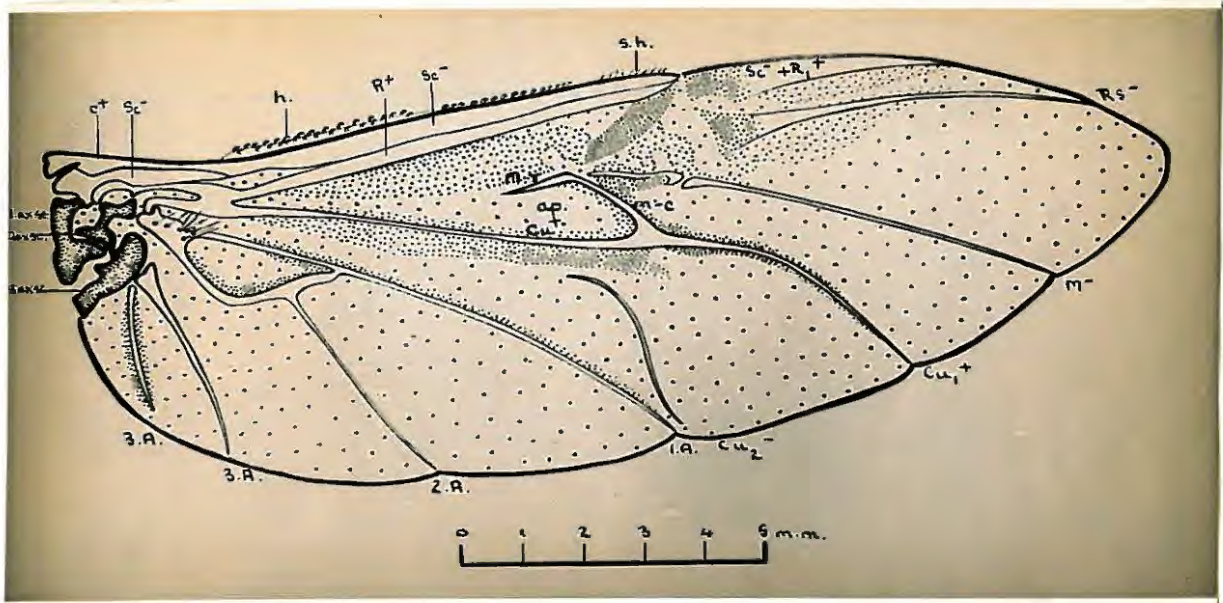


Fig. 52b - Right wing of *Image*.  
ANOMALA VETULA WIED.

- 1-3 ax. sc. = axillary sclerites.
- 1.A. - 3.A. = anals.
- ap. = apertum.
- C+ = costa.
- Cu<sub>1</sub> - Cu<sub>2</sub> = cubitus.
- h. = hamuli.
- M- = media.
- M. r. = medial recurrent.
- m-c. = medio-cubital.
- RS- = radial sector.
- R+ = radius.
- s. h. = stiff hairs.
- Sc- = subcosta.

costal margin of the wing. After a short distance they fuse. The subcosta is continued to the apex of the wing. It is interrupted at the hinge, about two-thirds along its length; beyond that it fuses with  $R_1^+$ .

The radius ( $R^+$ ) is the most anterior of the two principal convex veins. It runs parallel to  $Sc^-$  to the hinge. Distally it divides into  $R_1^+$ , which fuses with  $Sc^-$ , and  $Rs^-$ , which extends to the apex of the wing. The division of  $R^+$  is affected by the folding of the apical area; the base of  $Rs^-$  is represented by a diffuse chitinous area.

The media ( $M^-$ ) is not heavily chitinised. It is incomplete basally, and is termed the "medial recurrent" (Forbes, 1922, p. 333), or "returning vein" (Tillyard, 1926, p. 180). Near the centre of the wing there is a roughly triangular cell, the apertum, characteristic of Polyphaga (Tillyard, 1926, p. 180). It is open basally, bounded anteriorly by  $M^-$ , posteriorly by  $Cu^+$ , and distally by the medio-cubital cross-vein (Comstock, 1918, p. 78).

The base of the cubitus ( $Cu^+$ ) is fused with  $R^+$ . It is the second principal convex vein. Distally it divides into  $Cu_1^+$  and  $Cu_2^-$ .  $Cu_1^+$  is well chitinised

and extends to the wing margin.  $Cu_2^-$  is a short vein, whose connection with the main stem has been lost; it does not quite reach the margin of the wing.

The anal area is strengthened by four veins, which extend to the margin of the wing. The main stem of the anal vein is closely associated with the base of  $Cu^+$ . It soon divides into 1.A. and 2.A. 2.A. is bent at right angles, about one-third of its length from the base. At this point 1.A. and 2.A. are connected by a transverse vein. 3.A. divides into two small veins in the posterior region of the wing.

During rest the apical one-third of the wing is folded at right angles at the hinge, under the basal two-thirds. In addition, the apertum is folded over the small rectangular chitinous field, which projects obliquely backwards from the hinge. The base of the wing, posterior to 2.A., is folded under the wing.

The anterior margin of the wing bears a series of hamuli, whose hooks are directed apically. They extend from the point of fusion of  $C^+$  and  $Sc^-$  almost to the hinge. Just before the hinge they are replaced by small stiff hairs. The base of the anal

vein bears a tuft of hairs.

The wings are articulated to the body by three axillary sclerites:-

1. The first axillary or notopterale, is a large heavily chitinised "C"-shaped sclerite. The inner margin is hinged to the tergum. Anteriorly it is supported by the anterior notal wing process; it articulates with the second axillary by its inner margin. The anterior extremity is associated with the subcostal vein.
2. The second axillary or intra-alare, is a small sclerite situated to the inside of the first axillary, with which it articulates. The ventral surface is convex, and rests upon the pleural wing process, when the wing is expanded. It is attached to the subalare sclerite by a tendon-like connection.
3. The third axillary or basenale, is a large rectangular sclerite, which lies at the base of the anal veins. The principal flexor muscle of the wing is inserted on this sclerite, and is attached posterior to the mesothoracic pleural ridge. It articulates with the posterior

notal wing process.

A small "y"-shaped sclerite lies between the first and third axillaries. This is not a true axillary sclerite, because the third axillary does not articulate with the posterior notal wing process when a fourth axillary is present (Snodgrass, 1927, p. 62). A median plate is situated at the base of the wing to the outside of the three axillary sclerites.

#### IV. The Abdomen. (Fig. 53)

The length of the abdomen is approximately equal to that of the combined head and thorax. It is shorter and broader in the female than in the male. The base of the abdomen is broad, being about the same size as the posterior region of the metathorax. It increases in width gradually to the level of the third segment, and narrows more abruptly to the apex. Dorsally it is convex; the ventral surface is flat.

The elytra cover tergites 1 - 6, and the anterior half of the propygidium; laterally they extend over the pleural region; these areas are more thinly sclerotised than the exposed regions.

The abdomen of the larva consists of ten complete segments. In the pupa the first sternum has become

membranous, the visible terga representing segments 1 - 10, while the sterna represent segments 2 - 10 inclusive. Each of the first eight abdominal segments in the larva and the pupa, has a pair of spiracles. In the adult terga 1 - 8 and sterna 2 - 8 are visible externally; the first sternum is membranous. The posterior end of the abdomen is invaginated and bears the reduced ninth and tenth segments. The first seven segments have spiracles. Just before emergence the rudiment of the eighth abdominal spiracle of the imago is connected with the eighth abdominal spiracle in the pupa by a fine chitinous strand. In the imago, the place of attachment of the strand is marked by a small scar on the lateral extremities of the reflexed margin of the eighth tergum. Consequently the last visible tergum and this reflexed margin, represent the eighth segment, or pygidium. Beflese, 1909, p. 319, interprets the reflexed margin as a separate segment in Oryctes nasicornis. The arrangement of abdominal segments 1 - 8 inclusive is identical in the male and female. The ninth and tenth abdominal segments differ in the two sexes.

A similar interpretation of the numbering of the segments is given by Rittershaus, 1927, p. 273,

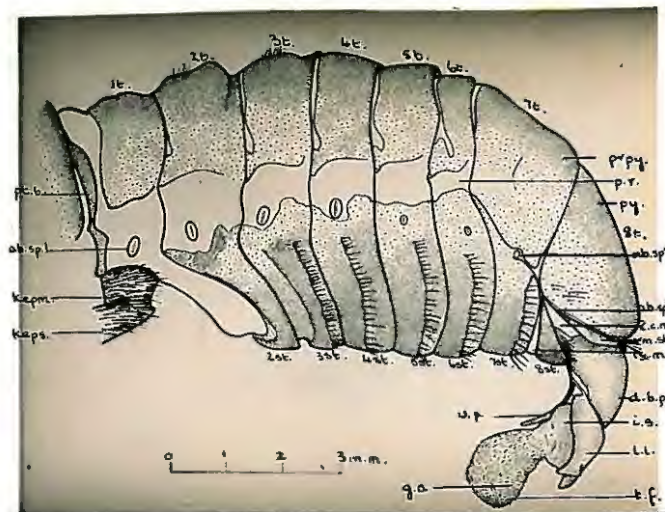


Fig. 53 - Lateral view of Abdomen of  
Male Imago.  
ANOMALA VETULA WIED.

- ab. sp. 1. = abdominal spiracle 1.  
 ab. sp. 7. = abdominal spiracle 7.  
 ab. sp. 8. = attachment point of abdominal  
                   spiracle 8.  
 d. b. p. = distal basal piece.  
 i. s. = internal sac.  
 is. m. = intersegmental membrane.  
 kepm. = katepimeron.  
 keps. = katepisternum.  
 l. l. = lateral lobe.  
 p. r. = pleural region.  
 g. o. = position of male genital opening.  
 prpy. = propygidium.  
 pt. b. = postalar bridge.  
 py. = pygidium.  
 r. m. 8t. = reflexed margin of tergum 8.  
 2 c. m. = second connecting membrane.  
 2st.-8st. = sterna 2-8  
 1. t.-8t. = terga 1-8.  
 t. f. = thorn field.  
 v. p. = ventral plate.

in Phyllopertha horticola L. and Snodgrass, 1935, p. 596, in Phyllophaga chiriquiana. In Coleoptera the first abdominal sternum at least is absent. (Irons, 1934, p. 483). Rittershaus, 1927, p. 274, states that in several specimens of Phyllopertha horticola L. and Anomala senae Geer. remains of the first abdominal sternum were found on either side of the middle line, in the membrane connecting the second abdominal sternum to the metathorax. I have been unable to find any indication of chitinous remains of the first abdominal sternum in Anomala vetula Wied.

The abdominal segments are similar in form, and are less modified than the preceding thoracic segments. Each segment is annular, and is divided into a dorsal and a ventral sclerotised plate. The anterior five sterna curve up round the sides. They are separated from the corresponding terga by membranous pleura. The tergum and sternum of the seventh segment are separated by a suture. The membranous pleural region allows an increase in size of the anterior region of the abdomen.

A narrow precosta is separated off from the anterior margin of each abdominal segment by an inconspicuous antecostal suture. The precosta,

antecosta and phragma of the tergum of the first abdominal segment form the postnotum of the metathorax. A lateral phragma is developed on either side of the anterior margin of the second abdominal tergum. Phragmata are not present on succeeding segments. The first six sterna decrease in size posteriorly. The intersegmental membranes between the first six abdominal terga and the following terga are well developed. They permit extension of the dorsal surface of the abdomen. Normally the posterior margin of the first six terga overlaps the anterior margin of the following terga.

The centre of the second and third terga bears a number of delicate hairs. The propygidium and pygidium are declivous; the propygidium is inclined at an angle of approximately  $45^{\circ}$ , and the pygidium is almost vertical. The antero-posterior length of the propygidium is almost twice that of the preceding segment.

The lateral region and posterior half, which are not covered by the elytra are transversely rugose; the concealed area is minutely punctured. The division between these two regions is marked on either side by a conspicuous narrow strip, which is very lightly sclerotised; it is concave towards the

apex of the abdomen. The propygidium is without hairs. The dorsal surface of the pygidium is triangular. It is more truncate in the female than in the male. It is more gibbose in the male than in the female. The reflexed margin decreases in width towards the apex. It is covered with round equidistant punctures, which are fairly closely set. The posterior margin bears a fringe of moderately long fulvous hairs, which are directed backwards.

The posterior margin of the metathoracic coxa extends to approximately half-way along the third segment. The third sternum is mainly visible laterally and between the metathoracic coxae. The remaining sterna 4 - 8 inclusive are visible externally. The first sternum is narrow. The antero-posterior length increases laterally. The anterior margin is bi-emarginate; it has a small raised median process, which projects between the metathoracic coxae. The process is covered with a number of short hairs. The lateral margins extend forwards, ventral to the second abdominal spiracle. They bear a number of short posteriorly directed hairs. The second sternum is divided into weakly chitinised anterior and posterior regions, by a transverse chitinous ridge.

The ridge bears a number of short regularly spaced hairs, which increase in size laterally. The third sternum is slightly bi-emarginate. It is divided into an anterior lightly sclerotised region, and a posterior well sclerotised area by a transverse ridge. Laterally, the latter extends to the posterior margin of the second sternum. The hairs on the transverse ridge are longer than those on the ridge of the second sternum. The third sternum is raised into a median process as in the second sternum, but it is not as conspicuous.

Sterna 4 - 8 inclusive are heavily chitinised. Each bears scattered punctures, and has a transverse median row of setigerous punctures, which extend across the ventral surface of the sterna, but not along the up-curved lateral regions. The hairs become progressively longer in succeeding segments. They are shorter and more delicate in the female than in the male. The eighth sternum is broadly rounded, the hairs are long, delicate, and closely arranged; they arise close to the posterior margin of the segment, and are directed posteriorly.

The intersegmental membrane between sterna 2 - 7 inclusive is not visible externally. The membrane between the seventh and eighth sterna is

- wide. -

wide. It is visible under the pupal skin as a light strip, a few days before ecdysis. It permits extension of the posterior region of the abdomen.

The rectum and vagina open into a wide cloaca, formed by the invagination of the apex of the abdomen. The dorsal wall of the cloaca is formed by a membranous continuation of the reflexed margin of the pygidium; ventrally it is bounded by the membrane connecting the eighth sternum to the reduced ninth sternum. The anus is situated between the eighth sternum and the eighth tergum, and is directed ventrally, owing to the slope of the pygidium.

The Posterior Abdominal Segments of the Female. (Fig. 54).

The female genital aperture is situated posterior to the ninth sternum. This position of the female gonopore is characteristic of Coleoptera. (Metcalf, 1932, p. 90, Snodgrass, 1953, p. 21). In the description of the genitalia of the female pupa it was explained that the gonopore is the original opening of the spermatheca, the primary vaginal aperture between eighth and ninth sternum having been closed over during development.

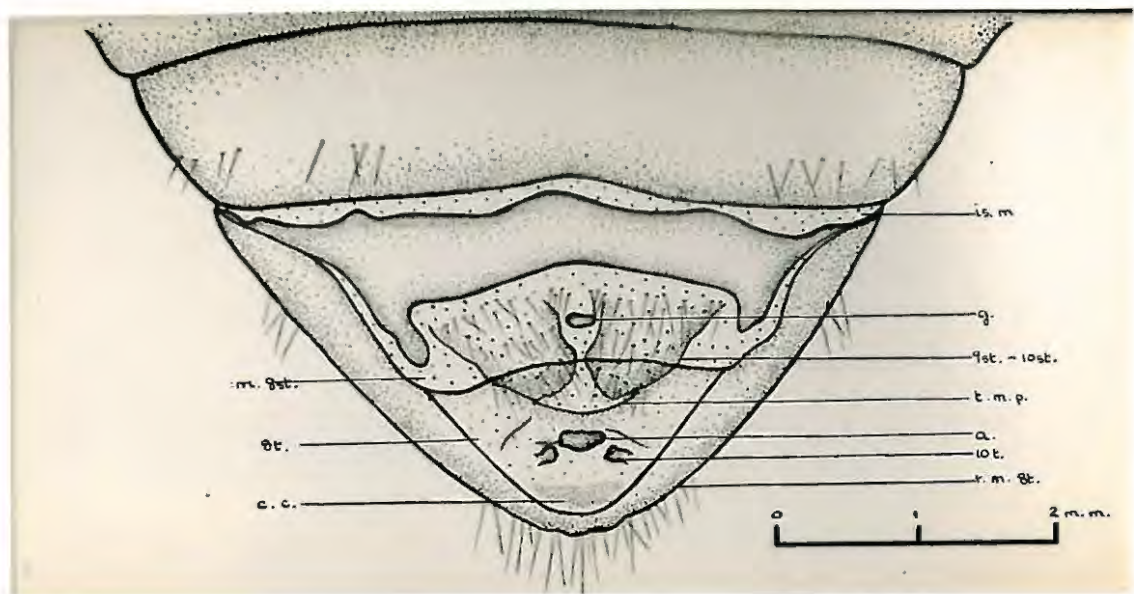


Fig. 54 - Ventral view of Posterior End of Abdomen of Female Imago with eighth sternum removed.

ANOMALA VETULA WIED.

- a. = anus.
- c. c. = chitinous area on dorsal wall of cloaca.
- g. = genopore.
- is. m. = intersegmental membrane between sterna 7 and 8.
- m. 8st. = membrane attached to distal end of sternum 8.
- r. m. 8t. = reflexed margin of tergum 8.
- 9st. - 10st. = sterna 9-10.
- 8t, 10t. = terga 8 and 10.
- t. m. p. = triangular membranous projection.

The ninth and tenth sterna are fused, and comprise the vaginal palps (Rittershaus, 1927, p. 276). They are placed close together on either side of the gonopore. The ninth sternum is the larger sclerite; it is triangular, and has numerous long hairs. The tenth sternum is a small chitinous plate attached to the outer margin of the base of the ninth sternum. It is separated from it by a distinct suture, and is without hairs. The vaginal palps of Phyllopertha horticola L. and Anomala aenea Geer., are similarly interpreted by Rittershaus, 1927, pp. 277-278.

The anus is situated dorsal to the gonopore; a triangular membranous projection is placed between the anus and gonopore. A pair of dorsal sclerites is situated between the anus and the reflexed margin of the eighth tergum. They lie close to the anus, on either side of the middle line. They represent the tenth tergum. The ninth tergum is absent. According to Hilger, 1894, p. 335, it is rarely present in Coleoptera. The distal region of the cloacal wall adjacent to the reflexed margin of the pygidium is lightly sclerotised.

The Posterior Abdominal Segments of the Male.  
(Figs. 53 and 55).

The invaginated cavity within the eighth segment contains the reduced ninth and tenth segments. The ninth segment is represented by a "Y"-shaped sternum, which bounds the mouth of the genital chamber ventrally. A complete annulus, representing the ninth segment, surrounds the opening in Carabidae, but in Amosia vetula Wied., the ninth tergum is absent as in Phyllopertha chircuiana (Snodgrass, 1935, pp. 595-597). The genital aperture thus lies posterior to the ninth sternum, as is characteristic of male Coleoptera (Snodgrass, 1931, p. 17, Metcalfe, 1938, p. 90).

The ninth sternum corresponds to the spiculum gastrale of Metcalfe, 1938, p. 54. The unpaired stem of this "Y"-shaped sclerite is inclined anteriorly. The dorsal arms are strongly divergent, and almost at right angles to the stem. Towards the distal end of each arm, a short inner branch is given off. A pair of chitinous plates, with numerous long hairs, is situated between the arms. They resemble the vaginal palps of the female, but are smaller. According to Rittershaus, 1927, p. 280, the "Y"-shaped spiculum and the setaceous sclerites are considered

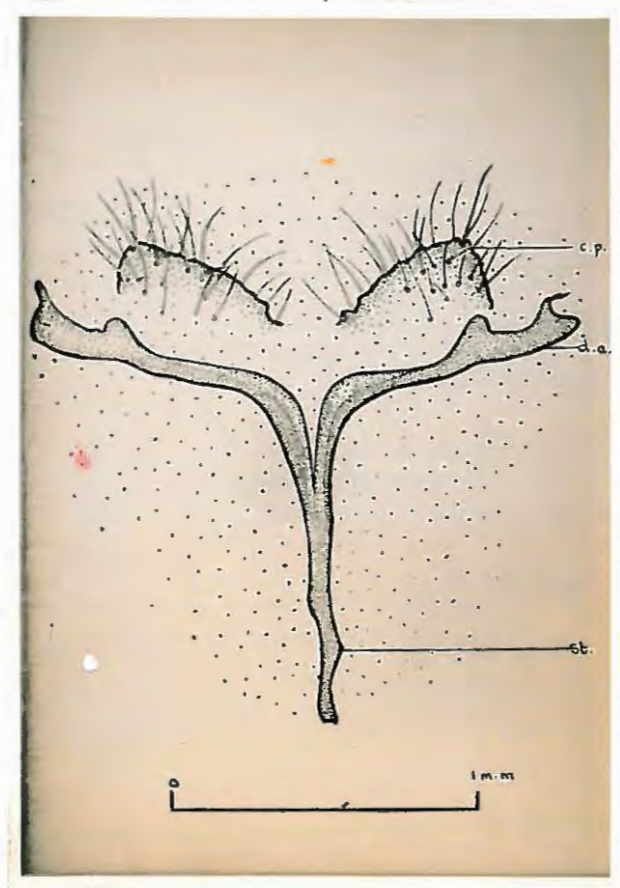


Fig. 55 - Spiculum Gastrale or 9th. Sternum  
of Male Imago.

ANOMALA VETULA WIED.

c.p. = chitinous plate.  
d.a. = dorsal arms.  
st. = stem.

by Verhoeff, 1893, to represent the ninth sternum.

The genital chamber containing the aedeagus and the end sac will be dealt with later.

The tenth sternum, which would be situated between the gonopore and the anus, is absent.

According to Hilger, 1894, p. 386, it is never present in the male. According to Rittershaus, 1927, p. 280, it is considered by Verhoeff to be absent in *Lamellicornia*. The tenth tergum is represented by a pair of small sclerites, which lie between the anus and the reflexed margin of the eighth tergum. They lie on either side of the middle line, and resemble the paired sclerites of the tenth tergum of the female. The dorsal wall of the cloaca, adjacent to the reflexed margin of the pygidium is not chitinised as it is in the female.

The Aed. sacus. (Figs. 53, 56, 57 and 61).

The male copulatory apparatus is situated between the ninth and tenth abdominal sternae. The structure is comparable to a pair of tubes, placed one within the other, the walls of the two tubes being continuous at their distal apertures. The outer tube represents the aedeagus, and consists of a number of closely set sclerites; it is continuous with the body wall. The distal portion of the inner

- tube -

tube is ectodermal, and forms the inner sac; proximally it represents the mesodermal ejaculatory duct. The genital tube is thus without a true orifice.

Normally the aedeagus is retracted within the abdomen; it is turned to the right so that the tegmen lies at right angles to the long axis of the body. The aperture of the genital duct is thus proximal to the opening of the genital pocket between the eighth tergum and the eighth sternum. During copulation the aedeagus projects from the posterior end of the abdomen. The basal piece is directed vertically downwards, and the lateral lobes forward, for insertion into the vagina of the female. The internal sac is evaginated and protrudes between the tips of the lateral lobes of the aedeagus.

The terminology used in the following description is that employed by Sharp and Muir, 1912, pp. 477-542, in a study of the male genital tube in Coleoptera. The male genital tube of Anomala retula Wied. is similar to that of Anomala assimilis, described by Sharp and Muir, 1912, p. 590.

The aedeagus comprises a proximal tegmen, composed of a basal piece and a pair of lateral lobes, and a distal median lobe.

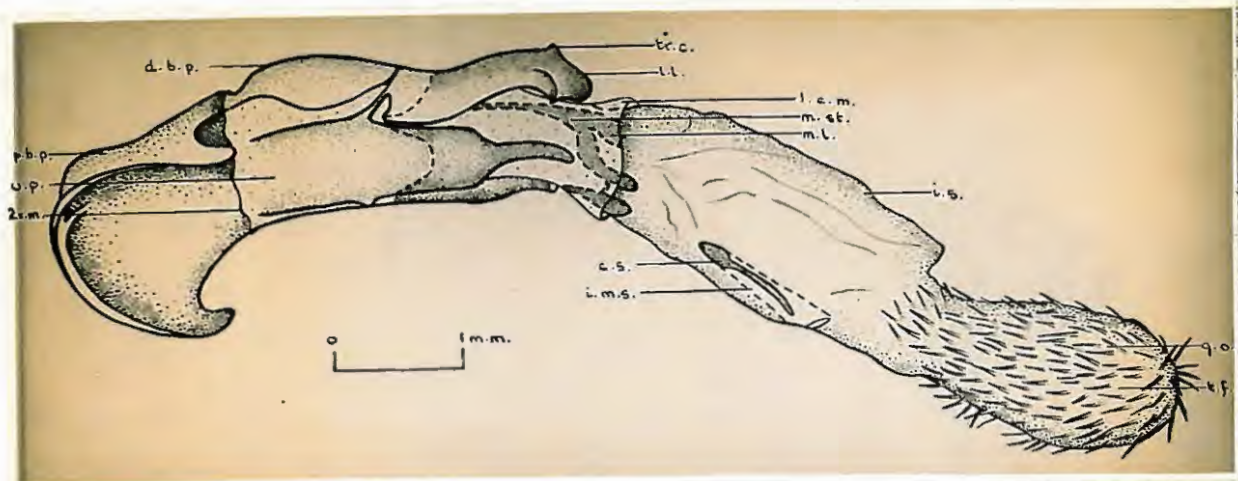


Fig. 56 = Ventro-lateral view of Aedeagus of  
Imago, with Internal Sac evaginated.  
ANOMALA VETULA WIED.

- c. s. = chitinous spine.
- d. b. p. = distal basal piece.
- l. c. m. = first connecting membrane.
- g. o. = genital opening.
- i. s. = internal sac.
- i. m. s. = invaginated membranous sac.
- l. l. = lateral lobe.
- m. l. = median lobe.
- m. st. = median strut.
- p. b. p. = proximal basal piece.
- 2. c. m. = second connecting membrane.
- t. f. = thorn field.
- tr. c. = transverse carina.
- v. p. = ventral plate.

The basal piece is a very large sclerite, termed the "tambour" by Straus - Durekheim, 1828. It is divided into a proximal part and a distal part. The proximal part is the smaller; it is slightly curved, and less strongly chitinised. It does not extend on to the ventral surface, thus leaving a wide opening for the ejaculatory duct. The base is rounded, and forms a well developed rim. The distal part is tubular and more strongly chitinised. The distal margin is rounded. The joint between the two regions is constricted; it marks the point of attachment of the second connecting membrane, which attaches the tergum to the body-wall. It is wide, to allow for the protrusion of the aedeagus. The ventral plate forms a closed tube with the distal part of the basal piece, to which it is attached by membrane. It is connected to the base of the lateral lobes by a thin chitinous strand. It is an undivided strongly chitinised sclerite, the distal region of which is double. Distally it narrows fairly abruptly, and forms a narrow elongated process, which curves ventrally. It extends slightly beyond the tips of the lateral lobes.

The lateral lobes are paired, and attached to the apical margin of the distal basal piece.

They are short and broad. The bases meet distally, or may overlap slightly, but are not consolidated together; ventrally they are widely separated. The tips curve ventrally. There is a short transverse carina on the distal region of the dorsal surface. The lateral lobes are broadly reflexed. The first connecting membrane is attached at one end to the reflexed margins of the lateral lobes and the ventral plate, and at the other end to the median lobe. It is well developed, and allows the median lobe to be extruded during copulation. At rest the median lobe is retracted into the tegmen, so that it is concealed, and lies next to the proximal part of the basal piece.

As in all Scarabaeidae, the chitinisation of the median lobe is reduced (Sharp and Muir, 1912, p. 628). In Anomala vetula Wied. the median lobe consists of a pair of small arc-shaped plates in the ventral wall of the genital tube. The boundary between the chitinous plates and the surrounding membranous region is not distinct. Each sclerite is produced into a long anteriorly directed strut. They lie close together, on either side of the mid-dorsal line, but outside the thick muscular sheath of the ejaculatory duct. They are not as strongly

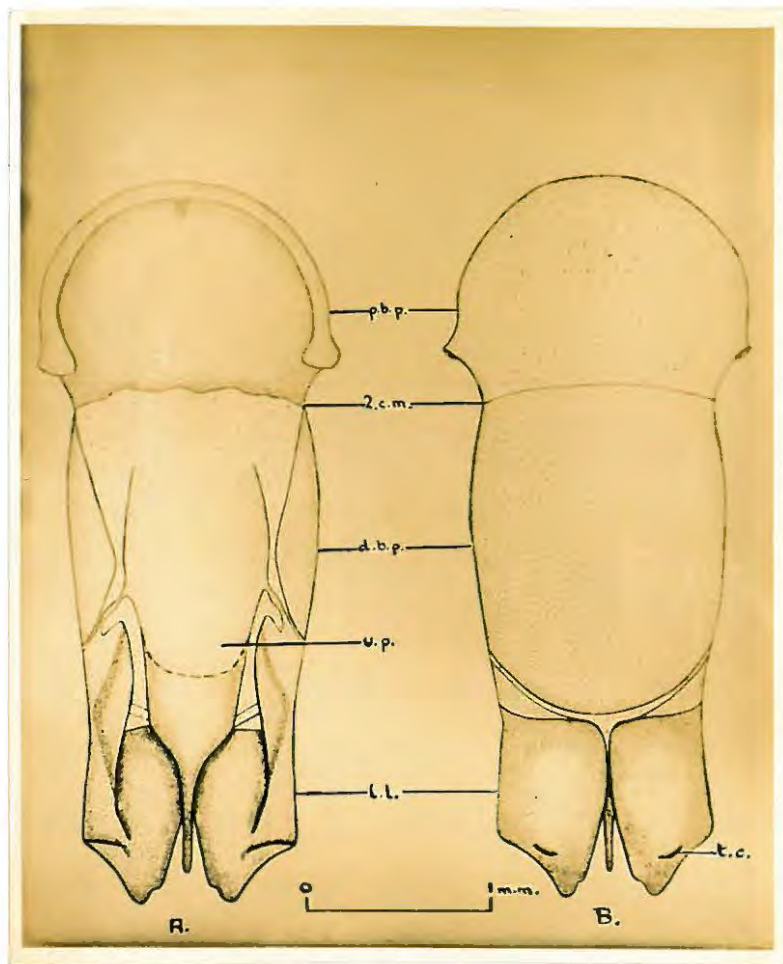


Fig. 57 - Aedeagus of Imago.  
ANOMALA VETULA WIED.

A: Ventral view.                      B: Dorsal view.

- d.b.p. = distal basal piece.
- l.l. = lateral lobes.
- 2<sup>d</sup>c.m. = point of attachment of second connecting membrane.
- p.b.p. = proximal basal piece.
- t.c. = transverse carina.
- v.p. = ventral plate.

chitinised as the median lobe, and they follow the curvature of the tegmen. In the possession of a pair of lateral lobes and a median lobe, the aedeagus of Anomala vetula Wied. is of the "generalised trilobe type". (Metcalf, 1932, p. 53).

The internal sac is very large, as is usually the condition in Scarabaeidae (Sharp and Muir, 1912, p. 607). When it is ovaginated it is longer than the aedeagus. Distally the sac is abruptly narrowed on the dorsal surface. The apex is rounded, and covered with numerous short posteriorly directed spines, which prevent the internal sac being withdrawn from the vagina of the female during copulation. The genital aperture is situated on the dorsal surface, slightly proximal to the apex; as in Anomala orientalis it is without any transfer apparatus (Muir, 1919, p. 406). On the ventral surface there is a conspicuous chitinous spine, attached to the base of an invaginated membranous sac.

The lateral lobes develop from the lateral protuberances, which lie adjacent to the posterior margin of the ninth sternum in the pupa. The median lobe forms from the median protuberance which lies between the lateral lobes of the pupa. The concavity

on the margin of the median protuberance marks the position of the aperture of the ejaculatory duct, near the apex of the inner sac in the adult. Thus in the pupa the genital structures are external, but in the imago they become wholly invaginated. Moreover in the pupa, the lateral lobes develop on the ventral aspect and are revolved through 180° during development. This confirms a similar observation made by Muir (Sharp and Muir, 1912, p. 582), on a species of Anomala. The orientation adopted in the above description of the adult is based on the position of the sclerites as they occur in the evaginated condition of the aedeagus in the imago.

The Abdominal Spiracles. (Fig. 53).

There are seven pairs of spiracles. The eighth pair of spiracles which is present in the pupa, is marked in the imago by a scar on the lateral extremities of the reflexed margin of the pygidium.

The first pair of spiracles is situated in the membrane ventral to the tergum of the first abdominal segment, and posterior to the postalar bridge of the metathorax. The following three pairs of spiracles occur in the ventral region of the

membranous pleura of the second, third and fourth abdominal segments. The first four pairs of spiracles are large and elliptical.

The fifth and sixth pairs of spiracles are placed in the dorsal regions of the sclerotised sterna of the corresponding segments. The seventh pair of spiracles is situated in the suture separating the tergum and the sternum of the propygidium. The last three pairs of spiracles are round, and smaller than the first four pairs. The atria into which they open however, are not reduced.

The secondary atrial orifice of each pair of spiracles is flush with the surface. The primary atrial orifice extends almost the whole length of the membrane at the base of the atrium. The second chamber has an inwardly directed diverticulum from the posterior wall of the chamber to which the occlusor muscle is attached.

2. Internal Anatomy.

After removal of the elytra and the wings, the body was opened by making an incision on either side, dorsal to the spiracles, from the apex of the abdomen to the anterior margin of the thorax. The terga and dorsal surface of the head-capsule were removed.

In the abdomen the heart lies in the middle line, immediately ventral to the terga. The viscera are obscured by numerous air-sacs, between which are fat deposits. The amount of fat present in the body decreases during the life of the imago. The large wing and leg muscles occupy most of the thorax.

(a) The Respiratory System.

The respiratory system of the imago is highly developed. It is similar to that of the larva, except for the presence of air-sacs, which have developed to act as reservoirs of air when the imago is flying. It resembles that of the imago of Melolontha vulgaris Fab. figured by Berlese, 1909, p. 816, after Straus-Durckheim, 1828.

There are two pairs of thoracic and seven pairs of abdominal spiracles. Each leads into an atrium, the walls of which lack taenidia. Each atrium

is continuous with an inner chamber, from the distal end of which the main tracheal trunk arises. This is very short, and soon divides into a dorsal and a ventral trunk. Each of these divides into an anterior and a posterior branch. The anterior branches unite with the corresponding posterior branches from the preceding spiracle, thus forming a series of dorsal and ventral loops along either side of the body, as in the larva. The anterior branches from the prothoracic spiracles penetrate into the head. The posterior branches from the seventh abdominal spiracle, branch into fine tracheoles in the seventh and eighth abdominal segments.

As in the larva, secondary branches arise from the dorsal and ventral loops. They divide into numerous small branches which terminate in air-sacs. These are present in the head, thorax and abdomen. They lack taenidia. As is general in Coleoptera, they are not very large (Imms, 1934, p. 487), but they are very numerous.

(b) The Circulatory System.

The dorsal blood vessel is the only part of the haemocoel enclosed by definite walls; elsewhere the blood circulates in the body.

The dorsal blood vessel extends from the

posterior end of the abdomen through the thorax, and ends immediately behind the brain. It is differentiated into a heart, which lies in the abdomen, and an aorta, which is confined to the thorax and head.

In the abdomen the dorsal blood vessel lies immediately ventral to the terga. At the anterior end of the abdomen it dips down between the two halves of the postnotum of the metathorax, so that the aorta lies immediately dorsal to the alimentary canal.

The heart is divided into seven chambers, which are dilated in the middle, and narrow towards the ends. The first chamber is the largest. Each chamber has a slit-like ostium on either side, situated posterior to the middle of the chamber. The blood enters the heart through these ostia. Posteriorly the heart is very narrow, and it was not possible to determine a division into chambers.

The aorta is very narrow; it is not divided into chambers. It widens anteriorly before dividing into two short terminal branches, immediately posterior to the brain.

The alary muscles spread out in a fan-shape, from the points of attachment on the terga, to each chamber

of the heart. They occur in the abdomen only.

(c) The Alimentary Canal. (Fig. 53).

The alimentary canal is not as conspicuous as in the larva, in correlation with the reduced amount of feeding in the imago.

It is similar to that of other Scarabaeidae, as illustrated by Popillia japonica Newm. (Swingle, 1930, pp. 181-185), Phyllophaga gracilis Burm. (Fletcher, 1930, pp. 109-111), Melolontha vulgaris Fab. (Emms, 1934, p. 485), Melolontha melolontha L. (Lison, 1936, pp. 196-200), and Macrophylla pubens Péring. (Fonwick, 1942, pp. 76-78).

It is approximately twice the length of the body. Morphologically it is divisible into a fore-intestine, a mid-intestine and a hind-intestine.

The fore-intestine or stomodeum, is a short straight tube, which extends from the mouth to approximately the middle of the prothorax. There are no salivary glands. The pharynx is the enlarged anterior region; it reaches to the brain. The oesophagus is continuous with the pharynx. It is narrow and extends into the prothorax. The crop is a dilation of the posterior region of the oesophagus, but it is not well developed. There is no sharp

- demarcation -

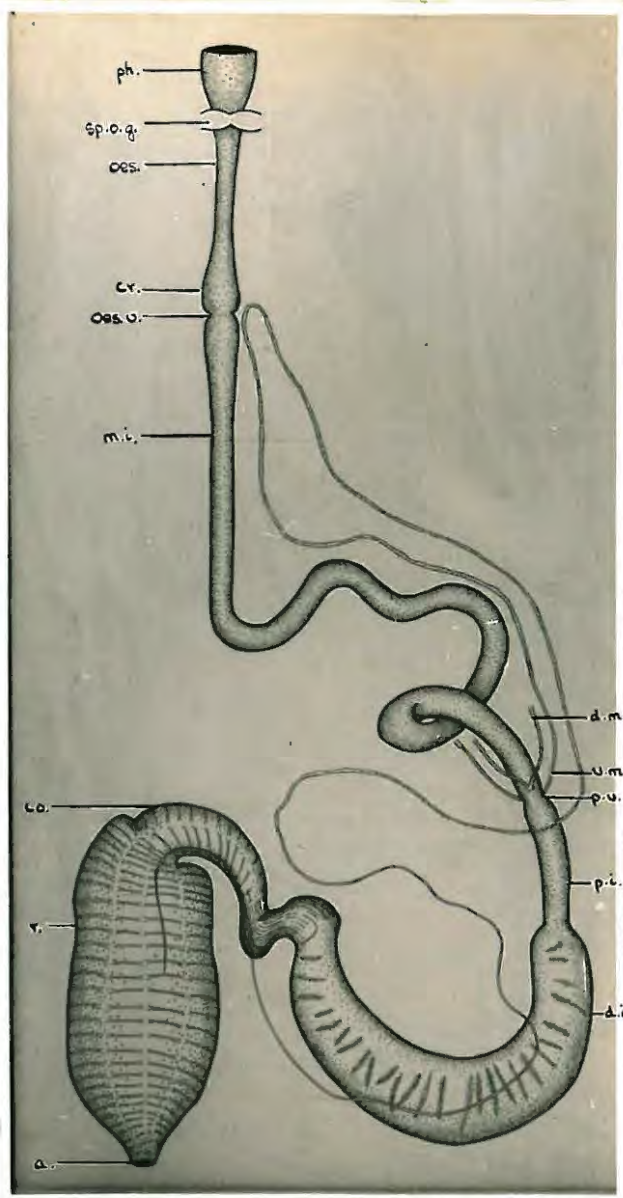


Fig. 58 - Alimentary Canal of Imago.  
ANOMALA VETULA WIED.

- a. = anus.
- co. = colon.
- cr. = crop.
- d.i. = distal ileum.
- d.m. = dorsal Malpighian tubules.
- m.i. = mid-intestine.
- oes. = oesophagus.
- oes.v. = oesophageal valve.
- ph. = pharynx.
- p.i. = proximal ileum.
- p.v. = pyloric valve.
- r. = rectum.
- sp.o.g. = supra-oesophageal ganglion.
- v.m. = ventral Malpighian tubules.

demarcation between the regions of the fore-intestine.

The oesophageal valve forms a constriction between the fore-gut and the mid-gut.

The mid-intestine, or stomach, is approximately one-third of the total length of the gut. It is a narrow cylindrical tube, uniform in diameter, except for a slight swelling at the junction with the fore-intestine. It extends as a straight tube to the fourth abdominal segment. It then curves slightly to the left of the abdomen, and continues to the fifth abdominal segment. It then makes a complete loop, and continues posteriorly to the sixth abdominal segment. The walls of the mid-intestine are thin; they lack the coeca which are present in the larva.

The commencement of the mid-gut is marked by two pairs of Malpighian tubes. The pyloric valve forms a constriction posterior to the insertion of the Malpighian tubes; it is well developed. In Phyllonhaga gracilis Burm. (Fletcher, 1930, p. 111), and Melelonthe melelontha L. (Lison, 1938, p. 196), the Malpighian tubes are attached to the hind-intestine, posterior to the pyloric valve. The condition in Anomala vatula Wied. is similar to that in Popillia japonica Newm. (Swingle, 1930, p. 185).

The hind-gut is a little more than half the length of the whole gut. It is clearly differentiated into four regions, as in Phyllophaga arcuella Burm. (Fletcher, 1930, p. 111), Melolontha melolontha L. (Lieson, 1933, pp. 290-301), Melolontha vulgaris Fab. (Jansa, 1934, p. 453), and Macrophylla rubens Péring (Fenwick, 1943, pp. 77-79).

The proximal ileum is a short cylindrical tube, similar to the mid-intestine. It extends into the seventh abdominal segment. The distal ileum is the most conspicuous region of the hind-intestine. It is clearly differentiated anteriorly from the proximal ileum, and distally from the colon. It is wider than the proximal ileum and about five times longer. It decreases in size posteriorly. In situ it is "S"-shaped and lies dorsal to the anterior part of the rectum. The anterior end lies nearer the apex of the abdomen than the posterior end. When untwisted the distal ileum resembles a mammalian stomach. The walls are thick, opaque and yellow. The inner surface is covered with parallel longitudinal rows of papillae.

The colon is a narrow tube, connecting the distal ileum to the rectum. It is directed anteriorly.

The rectum extends posteriorly from the

seventh abdominal segment to the anus. It is transparent, large and capable of great distension. Both circular and longitudinal muscles are visible on the surface. Posteriorly it narrows, before opening to the exterior at the anus.

(d) The Excretory System. (Fig. 58).

There are two pairs of Malpighian tubes, as in the larva. According to Lison, 1938, p. 201, there are usually four Malpighian tubes in Scarabaeidae. The dorsal pair of tubes unite before opening into the gut; the common aperture is situated in the middle line, a short distance in front of the pyloric valve. The ventral pair of tubes arise separately, on either side of the gut, and posterior to the dorsal tubes. This condition is similar to that in Phyllophaga gracilis Burm. (Fletcher, 1930, p. 111), Ponillia japonica Newm. (Swingle, 1930, p. 185), and Melolontha melolontha L. (Lison, 1938, pp. 201-202), except that in the first two, the Malpighian tubes arise behind the pyloric valve, as already mentioned.

The Malpighian tubes are white and unbranched. The dorsal tubes are longer than the ventral tubes, but both pairs are longer than the gut.

The dorsal tubes are cylindrical, for a short distance near their insertion, where they lie free in

the haemocoel, between the coils of the mid-intestine. Soon they become closely applied to the mid-gut by tracheoles. At this point they assume a characteristic bi-pectinate appearance, similar to that illustrated by Swingle, 1930, p. 188, in Popillia japonica Newm. They travel along the mid-gut to the level of the oesophageal valve. Here they turn back, and follow a parallel descending course to the end of the mid-gut. Here they lie free in the haemocoel, between the mid-gut and the rectum. They lose their bi-pectinate appearance, and become cylindrical again. They coil on the surface of the distal ileum and rectum, and end blindly near the hind end of the rectum.

The ventral tubes are also cylindrical at their point of insertion, and assume a similar bi-pectinate appearance after a short distance. They follow the loop of the mid-gut, and pursue a meandering course over the distal ileum and rectum. They become cylindrical, closely applied to the rectum, and terminate blindly, near its posterior end.

There are two closely coiled tubes situated in the anterior region of the prothorax, on either side of the alimentary canal; they may be responsible for emitting the pungent odour characteristic of the species.

(c) The Nervous System. (Fig. 59).

The central nervous system is concentrated into the head and thorax. A similar condition is figured by Packard, 1896, p. 225, for Lachnosterna fusca.

The protocerebrum is represented by a pair of protocerebral lobes, and a pair of optic lobes. The protocerebral lobes are united in the middle line to form a bilobed ganglion, which constitutes the greater part of the brain. They are continuous laterally with the optic lobes. These are well developed in correlation with the large compound eyes. The optic nerves arise from the outer margin of the optic lobes.

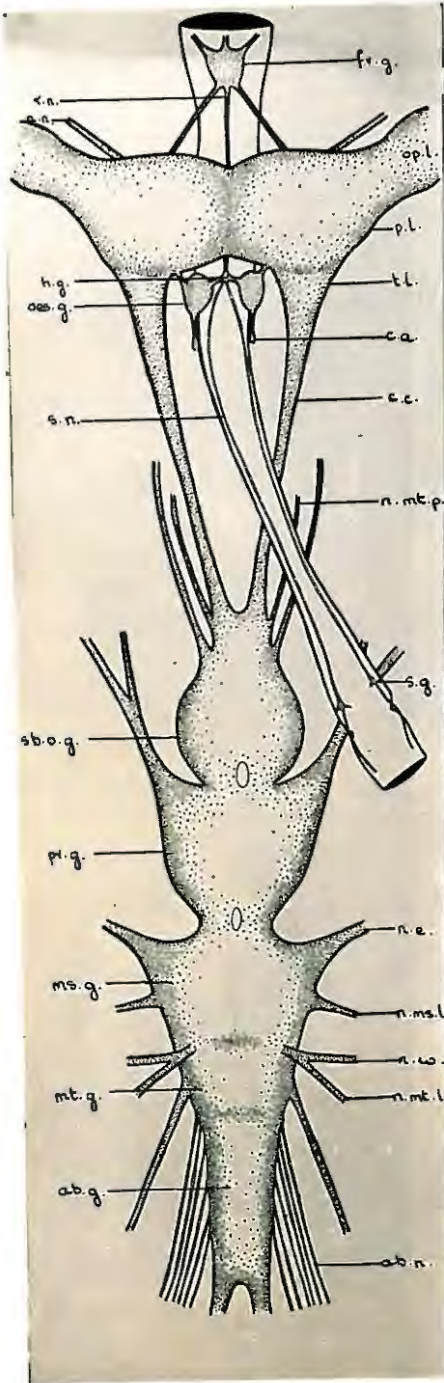
The deutocerebrum is composed of a pair of antennary lobes, situated on the antero-ventral surface of the brain. They give rise to a pair of anteriorly directed antennary nerves.

The tritocerebrum consists of two small lobes on the posterior surface of the protocerebral lobes. It gives rise to the circum-oesophageal connectives. These pass in a posterior direction round the oesophagus, to unite the brain and suboesophageal ganglion.

The suboesophageal ganglion is situated in the centre of the prothorax. It gives rise ventrally to nerves which innervate the mouth-parts.

The prothoracic ganglion lies in the posterior

Fig. 59 - Nervous System of  
 Imago.  
ANOMALA VETULA WIED.



- ab. g. = abdominal ganglion.
- ab. n. = abdominal nerves.
- a. n. = antennary nerve.
- c. c. = circumoesophageal connectives.
- c. a. = corpora allata.
- fr. g. = frontal ganglion.
- h. g. = hypocerebral ganglion.
- ms. g. = mesothoracic ganglion.
- mt. g. = metathoracic ganglion.
- n. e. = nerve to elytron.
- n. ms. l. = nerve to mesothoracic leg.
- n. mt. l. = nerve to metathoracic leg.
- n. mt. p. = nerves to mouth-parts.
- n. w. = nerve to wing.
- oes. g. = oesophageal ganglion.
- op. l. = optic lobes.
- pr. g. = prothoracic ganglion.
- p. l. = protocerebral lobe.
- r. n. = recurrent nerve.
- s. g. = stomacic ganglion.
- s. n. = stomatogastric nerve.
- sb. o. g. = sub-oesophageal ganglion.
- t. l. = tritocerebral lobe.

part of the prothorax. It is united with the suboesophageal ganglion by short parallel connectives. The ganglion gives rise anteriorly to a large nerve, which divides into a small nerve, which supplies the general musculature of the segment, and a larger branch which innervates the muscles of the prothoracic leg.

The mesothoracic, metathoracic and abdominal ganglia are closely united owing to the disappearance of connectives. The condition is characteristic of a number of Lamellicornia including Melolontha Lachnosterna and Phyllopertha (Inns, 1934, p. 487). The fused ganglia extend from the anterior region of the mesothorax to the anterior region of the metathorax. The three centres are separated from one another by slight concavities. The prothoracic ganglion is connected to the mesothoracic nerve centre by short connectives. The meso- and metathoracic nerve masses each give rise anteriorly, on either side, to a nerve, which supplies the elytra and wings respectively, and posteriorly to a nerve which innervates the legs, and musculature of the corresponding segments.

Separate abdominal ganglia cannot be distinguished. A number of slender nerves arise on either side of the abdominal nerve mass and supply the abdominal segments.

The oesophageal sympathetic nervous system lies on the dorsal surface of the alimentary canal, and extends from the pharynx to the oesophageal valve. The median frontal ganglion lies on the dorsal surface of the pharynx a short distance in front of the brain. It is connected to the tritocerebral lobes of the brain by a pair of frontal ganglion connectives. Posteriorly it gives off a median recurrent nerve which passes beneath the brain, along the dorsal surface of the oesophagus. A short distance behind the brain it forms the hypocerebral ganglion. Posteriorly the hypocerebral ganglion gives rise to two stomatogastric nerves. These extend along the sides of the oesophagus and each terminates in a separate stomachic ganglion, situated a short distance in front of the oesophageal valve. A pair of oesophageal ganglia lie just behind the brain. They are connected to the brain and to the hypocerebral ganglion.

The corpora allata are two small white bodies situated a short distance behind the oesophageal ganglia. Each is supplied by a nerve from the oesophageal ganglion. Previously they were considered as posterior sympathetic ganglia. According to Imms, 1934, p. 137, they have a glandular structure, and Wigglesworth, 1934, p. 202,

suggests that they are responsible for secreting a hormone, which in Rhodnius prolixus induces moulting.

(f) The Female Reproductive System. (Fig. 60).

The structure of the female reproductive system is similar to that of Melolontha melolontha L. (Schwerdtfeger, 1927, pp. 263-270), Phyllonerta horticola L. and Anomala aenea Geer. (Rittershaus, 1927, pp. 300-303), and Macrophylla pubens Péring. (Fenwick, 1942, pp. 83-85).

There are two ovaries situated in the abdomen, one on either side of the alimentary canal. Each consists of six ovarioles. Normally the ovaries of the above-mentioned species are composed of six ovarioles, except that of Anomala aenea Geer. which has twelve ovarioles. The ovaries are acrotrophic, which according to Gross, 1903, is the normal condition in Lamellicornia. (Rittershaus, 1927, p. 300).

The anterior region of each ovariole consists of a slender terminal filament. The length of the filaments varies according to the degree of development of the eggs. In the pupa, and in the freshly emerged beetle, in which the eggs are not fully developed, the filaments are closely applied to each other. Just before egg laying, the filaments are only bound together

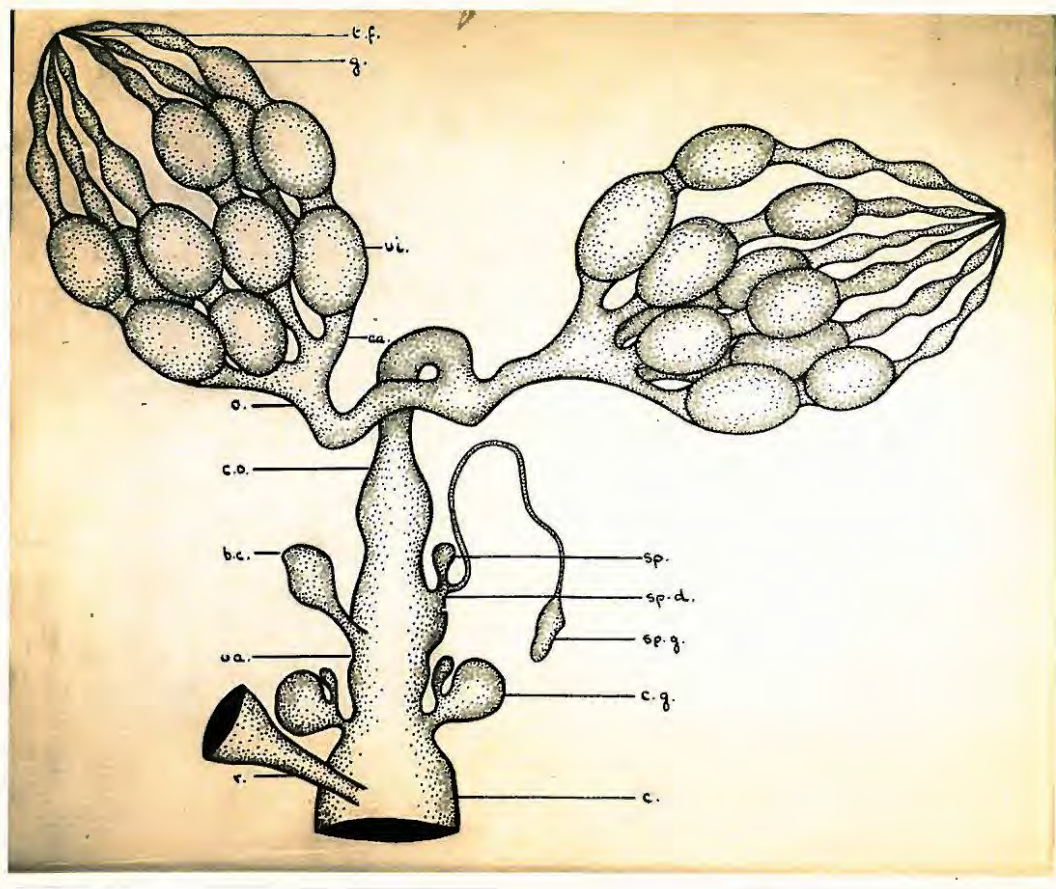


Fig. 60 - Female Reproductive Organs of Imago.  
ANOMALA VETULA WIED.

- b. c. = bursa copulatrix.
- ca. = calyx.
- c. = cloaca.
- c. g. = colleterial gland.
- c. o. = common oviduct.
- g. = germarium.
- o. = oviduct.
- r. = rectum.
- sp. = spermatheca.
- sp. g. = spermathecal gland
- sp. d. = spermathecal duct.
- t. f. = terminal filament.
- va. = vagina.
- vi. = vitellarium.

for a short distance anteriorly. According to Gross, 1903, (Rittershaus, 1927, p. 302), all Lamellicornia have "ovaria fasciculata". The gonarium is the enlarged region of the ovariole, posterior to the filament. It enlarges to form the vitellarium, which is the most conspicuous part of the ovariole, as it contains the developing eggs. In Anomala vetula Wied. developing eggs may be present in all twelve ovarioles at the same time, but seldom more than three eggs ripen in one ovariole at a time. The maximum number of developing eggs found in a female was thirty-one, which corresponds roughly to the number of eggs laid by one female. The eggs become successively larger towards the base of the ovariole. The tube is constricted between consecutive eggs, to give it a beaded appearance. The pedicels at the base of each ovariole unite to form the calyx, which is continued as a short wide oviduct.

The oviducts from each side unite in the middle line to form the common oviduct. As in Popillia japonica Newm. (Rittershaus, 1927, p. 302), the anterior region of the common oviduct turns forwards, and then ventrally. Posteriorly it enlarges to form the vagina, which enters the cloaca ventral to the anus.

The short common duct, formed from the union of the spermatheca and the spermathecal glands opens

into the anterior region of the vagina. The bladder-like spermatheca is short. The spermathecal gland is elongated, and has a large narrow duct, similar to that of Phyllopertha horticola L. and Anomala aenea Geer., figured by Rittershaus, 1927, pp. 301-302.

The bursa copulatrix discharges into the vagina to the right, and slightly posterior to the entrance of the common spermathecal duct. It is a pouch for the reception of seminal fluid before it passes to the spermatheca. It is similar to that in Anomala aenea Geer., with a narrow stem, and an enlarged distal region, but it lacks the paired evaginations present in that species.

Large rounded collateral glands, with a smaller gland attached to them, discharge into the posterior end of the vagina on either side, close to its entrance into the cloaca. According to Rittershaus, 1927, p. 303, they are termed the "akzessorische Scheidendrüsen" by Stein, 1847; Schwerdtfeger, 1927, p. 269, refers to them as cement glands.

(g) The Male Reproductive System. (Fig. 61).

This is similar to the male reproductive organs of Phyllopertha horticola L. and Anomala aenea Geer. (Rittershaus, 1927, pp. 281-283).

There are two testes, situated ventrally on either

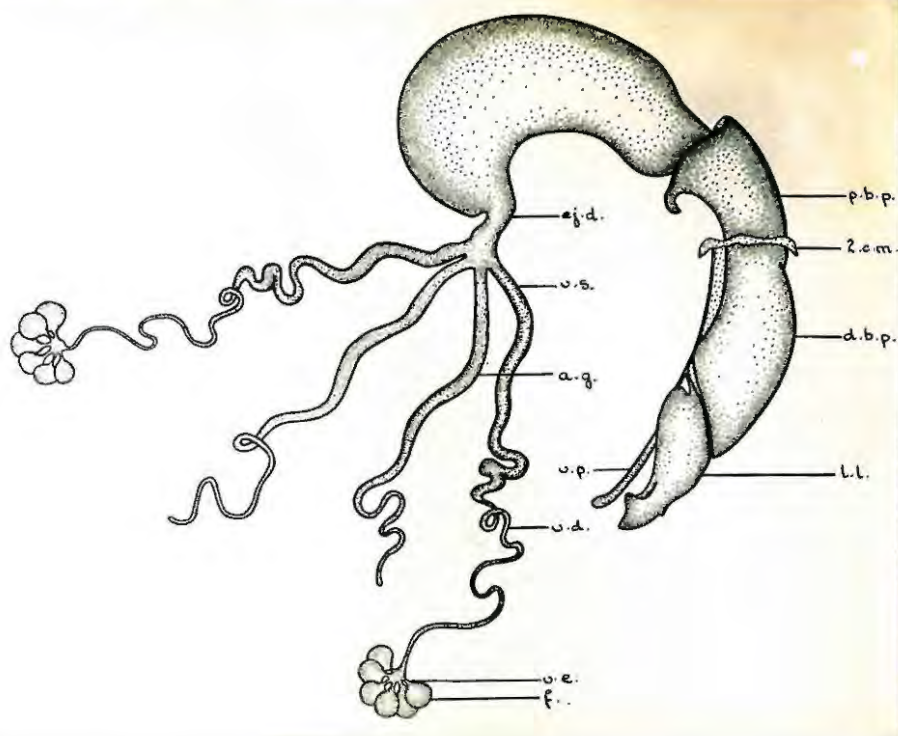


Fig. 61 - Male Reproductive Organs of Imago.  
ANOMALA VETULA WIED.

- a. g. = accessory gland.
- d. b. p. = distal basal piece of aedeagus.
- ej. d. = ejaculatory duct.
- f. = follicle of testis.
- l. l. = lateral lobe of aedeagus.
- p. b. p. = proximal basal piece of aedeagus.
- 2. c. m. = second connecting membrane.
- v. d. = vas deferens.
- v. e. = vas efferens.
- v. p. = ventral plate of aedeagus.
- v. s. = vesicula seminalis.

side of the seventh abdominal segment. In Phyllopertha horticola L. they lie close together in the ventral middle line. In Anomala aenea Geer. they lie apart on either side of the abdomen. They are kept in position by numerous tracheae and fat deposits.

Rittershaus, 1927, p. 261, states that according to Bordas, 1899, the Scarabaeidae have paired compound "buschelige Hoden". In Anomala vetula Wied. each testis is composed of six follicles, as in Phyllopertha horticola L. Twelve follicles are present in Anomala aenea Geer. (Rittershaus, 1927, p. 261). In the pupa the follicles are narrow and elongated; in the imago they are spherical. Each follicle has a short slender vas efferens connecting it to the distal end of the vas deferens. They pass dorsally, and to the left of the abdomen, and then curve over the basal piece of the copulatory apparatus, which, as has been explained already, is turned towards the left of the abdomen when retracted. They increase in size proximally, the basal region forming the vesicula seminalis. They unite posterior to the lateral margin of the basal piece of the copulatory apparatus, to form the ejaculatory duct.

There are two accessory glands, which follow closely the course of the vas deferens of the

corresponding side. They lie to the inside of the vas deferentia. They increase in size gradually towards the base. The vas deferentia and the accessory glands are connected to the distal end of the ejaculatory duct.

The ejaculatory duct curves round to enter the aperture at the base of the copulatory apparatus. Immediately after the union of vas deferentia and accessory glands, the ejaculatory duct is very narrow. After a short distance it increases in size greatly, due to the presence of a thick muscular sheath. Within the copulatory apparatus the ejaculatory duct coils a great deal. It is through this that it possesses the necessary length for evagination of the inner sac during copulation.

- BIOLOGY. -

1. THE EGG. (Figs. 62 and 63).

The eggs are laid about six inches below the surface of the ground. In very hard dry soil eggs have been found two inches below the surface. In the laboratory if the soil in which the eggs were laid was allowed to become dry, they failed to increase in size, became wrinkled, and did not hatch. Thomas, 1925, p. 359, and Smith and Hadley, 1926, p. 14, state that the length of the egg stage in Popillia japonica Newm. is determined by temperature and moisture of the soil.

The eggs are simply deposited in the soil, and are not laid in a "nest" as in the genus Phyllophaga, described by Ritter, 1940, p. 17. They are laid singly, as in Phyllopertha horticola L. and Anomala senae Geer. (Ritterhaus, 1927, p. 330). They are not enclosed in a ball of earth. A similar condition occurs in Popillia japonica Newm. (Thomas, 1925, p. 359), and in Anomala currea Hope. (Yasuda and Endo, 1936). In American June beetles, genus Phyllophaga Harris, named Lachnosterna Hope until 1916, according to Langston, 1927, p. 7, (Fenwick, 1942, p. 146), each egg is enclosed in a ball of earth, formed by a glutinous secretion from the female. (Davis, 1915, p. 137, and 1916, p. 263; Hayes, 1920, p. 309; Luginbill, 1938, p. 7;

Fig. 62 - Eggs of  
ANOMALA VETULA WIED.  
(Natural Size).

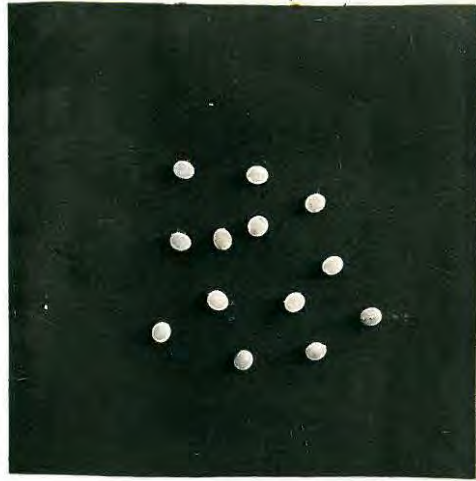
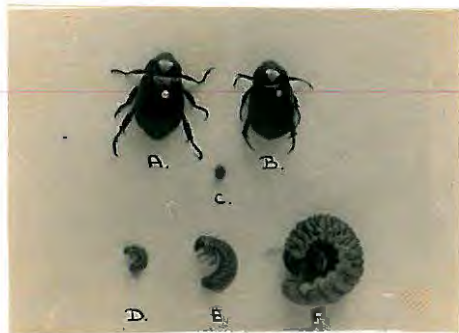


Fig. 63 - ANOMALA VETULA  
WIED.



- A. = Male Imago.
- B. = Female Imago.
- C. = Egg.
- D. = First Instar Larva.
- E. = Second Instar Larva.
- F. = Third Instar Larva.

(Natural Size).

Hammond, 1940, p. 5 and Ritcher, 1940, p. 118). The secretion from the colleterial glands of the female of Anomala vetula Wied. makes the surface of the eggs sticky, so that sand particles adhere to the eggs, but it is not sufficient to cause a ball of earth to form round them.

1. Embryonic Development.

As in other Scarabaeidae the form of the developing embryo can be seen through the chorion (Hayes, 1939, p. 48). By comparison with descriptions of the embryo in other species, the chorion in Anomala vetula Wied. appears to be less transparent. In Macrophylla pubens Péring. the shape of the embryo could be seen after seven days, but it was indistinct (Fenwick, 1948, p. 154). In Anomala vetula Wied. the eggs retained their homogeneous appearance for twelve days.

After twelve days the position of the grub is indicated by a cloudy white appearance along one side, and at either end of the egg. The remainder of the egg is clear and transparent. At this stage the chorion is strong; if the egg is dropped it bounces, and is not damaged. By the nineteenth day the shape of the embryo is more distinct; the mandibles can be seen faintly, as small sclerotised areas on the ventral side. They do not appear to lie immediately beneath

the chorion, but are situated deeper down. The outline of the mandibles is more distinct by the twenty-second day. They are directed towards each other; in most larvae they are crossed, and situated one in front of the other. By the twenty-third day the mandibles can be seen clearly through the chorion; they can be observed to move apart and to come together. The legs appear as sclerotised regions at the side, and show slight movement. The curvature of the body has changed; the anterior part is only slightly ventrally inclined, the posterior part is curved forwards, so that the embryo is "V"-shaped.

By the twenty-fifth day the hatching spines can be seen as very small faint brown areas, situated on either side of the mid-dorsal line. They are pushed against the chorion by the alternate expansion and contraction of the grub. A faint brown coloration on the dorsal surface indicates the presence of the asperities on the terga. The position of the labrum is marked by a faint brown area between the mandibles.

### 3. Hatching.

Just before hatching the thorax and posterior end of the larva swell. The chorion is stretched tightly round the body of the larva, so that the egg assumes an irregular shape. The mouth-parts,

- particularly -

particularly the mandibles, the legs, hatching spine and hairs on the body, can be detected, owing to their darker sclerotisation.

Careful observation reveals continuous movement of the body, which can be seen by the changing position of the hairs and hatching spines on the dorsal surface of the larva. Slight motion of the legs occurs occasionally. Movement of the mandibles is more distinct and more rapid than previously.

Muscular contraction of the larva with the aid of the hatching spines causes the chorion to rupture. The importance of hatching spines in the splitting of the egg-membrane is dealt with by Rittershaus, 1927, p. 391, in Phylloxera horticola L. and Anomala senae Geer. In Anomala vatala Wied. the first rupture of the egg shell occurred almost invariably in the position of the hatching spines, and was always transverse. Usually the movements of the larva cause the curvature of the dorsal surface to become more pronounced; this results in the rupture of the chorion. The split is small at first, but further muscular activity of the larva causes the split to continue down the sides of the body, until the embryo is able to emerge.

The dorsal surface of the middle of the body usually protrudes first, the head and anal segments

remaining within the egg. Waves of movement continue to pass along the embryo, almost unceasingly. This movement is assisted by pressure of the head and posterior segments against the inside of the egg shell; the legs do not appear to assist in the hatching process.

The mandibles and lower region of the head appear occasionally; eventually the anterior region of the body is extricated. Towards the end of the hatching the grub becomes quiescent, and only movement of the mandibles and maxillae occurs. Pieces of the chorion may adhere to the posterior region of the grub for several days. Eventually they are removed by the legs, by the rubbing together of the posterior segments and the mouth-parts, or by movement in the soil.

The hatching process extends over a period of approximately three hours. This is undoubtedly longer than is normally required when the grub is surrounded by earth.

## II. THE LARVAL INSTARS.

### 1. The First Instar Larva. (Fig. 63).

The newly hatched grub is delicate and pale in colour. The thorax and abdomen are white, the reddish-brown asperities and hairs give it a superficial ferruginous appearance. The hatching spines are conspicuous. The spiracles appear as light brown areas. The head-capsule is soft and rugose. It is large in comparison with the small body. The tips of the mandibles and their articulation points with the head-capsule are a dark reddish-brown. The tip of the galea and lacinia, and the terminal segment of the antenna is lightly sclerotised. The hypopharyngeal sclerome is almost black. The legs have a transparent appearance; the coxal joint is slightly ringed.

After twenty-four hours the grub is still white, feeding not having commenced. The head-capsule is light brown; the tips of the mandibles and the hypopharyngeal sclerome are still the most conspicuous features. The thoracic segments are wider than the head-capsule, and the body tapers to the anal segment. The claws are colourless.

The grub soon becomes more active, and assumes a darker colour. Feeding usually starts 1-2 days after eclosion. This causes the posterior region

of the abdomen to become a light blue-grey. As feeding continues the gut is distended, and the last segments become a dark grey; the colour decreases anteriorly.

First instar grubs are active crawlers. They do not appear to travel far, but radiate out a short distance from the focal point where the eggs are laid. They feed on small roots and humus, which is sufficient nourishment during this instar.

At the end of each larval instar ecdysis is accompanied by a splitting of the head-capsule along the epicranial suture. The split is continued along the dorsal surface of the body to the end of the abdomen. The thorax, head, and finally the abdomen are extricated.

### 2. The Second Instar Larva. (Fig. 33).

Freshly moulted grubs in the second instar can be distinguished from first instar larvae by the larger size of the head-capsule, and the longer and stouter legs. Until feeding is resumed the size of the body is similar to that of the first instar grub just before moulting.

Second instar grubs are the most active of the three instars. They have carnivorous tendencies, and if confined in a small area they bite each other; they were therefore kept in separate jars. They have

not been observed to eat each other, but they inflict wounds. Carnivorous tendencies have been described in larvae of Anomala orientalis Waterh. (Britton, 1926, p. 541).

In Anomala vetula Wied. most of the feeding is done in the second instar. In Macrochylia pubans Péring (Fenwick, 1942, p. 163), it is the second instar larvae that cause most of the damage to turf. The grubs of Anomala vetula Wied. are usually found in the field 6-9 inches below the surface of the ground in the grass roots, where they are surrounded by an abundant food supply. In the laboratory, if placed on top of the soil, they burrowed down rapidly, with the aid of the mandibles and first two pairs of legs. Unlike third instar larvae, they were seldom found inactive in cells at the bottom of the jar, unless the soil was very dry.

The larvae construct earthen cells in the soil. In the glass breeding jars, the movements of the larvae could be clearly observed, when these cells were constructed near the glass. The cells are large enough to allow the larvae to turn in them. The walls are made smooth by pressure exerted by movements of the body. They usually lie on the dorsal surface, with the head and last abdominal segments close together, so that the legs grip round the last abdominal segments.

When the larva advances the mandibles and the

first pair of legs, scrape away the earth in front of the larva. The loosened earth is pushed backwards and towards the ventral surface of the grub. This is accompanied by continuous waves of contraction, which pass along the dorsal surface of the grub. In this way no passages are left as the larva moves through the soil.

Larvae of Popillia japonica Newm. form similar cells in the soil. They feed on fine rootlets at the top and bottom of the cell, following the course of the rootlets before attacking others. The result is that damage is not severe, unless the infestation is heavy, as then only, are plants found in which all roots have been destroyed. (Smith and Hadley, 1926, p. 19).

### 3. The Third Instar Larva. (Fig. 65).

In the third instar, the size of the head-capsule and the legs is greater than in the preceding instar. Feeding causes the body to increase in size, so that it can readily be distinguished from that of a second instar larva.

Feeding, however, does not occur throughout the this instar. It usually ceases after 3-4 months. During the remaining months they usually lie inactive in earthen cells. These may be constructed anywhere

in the soil, but were usually found next to the glass at the bottom of the breeding jar. During this period fat accumulation commences. According to Smith, 1923, p. 307, larvae of Popillia japonica Newm. are positively thigmotropic to living roots. If these were not available the larvae were attracted to stones, sticks, or sides and bottom of the breeding cages.

The grubs of all three instars of Anomala vetula Wied. are able to crawl actively on a flat surface. This also occurs in larvae of Phyllopertha horticola L. and Anomala senae Geor. (Ritterhaus, 1927, p. 383). Fidler, 1936, p. 117, states that grubs of Melolontha melolontha L. are unable to crawl on a flat surface, as they cannot straighten the body sufficiently.

#### 4. The Prepupa.

When third instar larvae have completed their development, each constructs an oval earthen cell. These are slightly larger than the grubs, and have smooth firm walls. In these the grubs pass through an inactive prepupal stage, in preparation for pupation. The grub ceases to feed; it usually lies on its lateral surface. An ecdysis does not occur between the third larval and the prepupal stages. Inms, 1934, p. 198, states that the prepupa represents a greatly abbreviated instar, during which an ecdysis has been suppressed.

The prepupal stage is recognised by the white appearance of the body, due to the contents of the alimentary canal being voided, and the deposition of a subdermal layer of fat. During the prepupal stage the gradual change from larva to pupa occurs. These changes are particularly obvious in the last abdominal segment. The abdomen becomes shorter and wrinkled. The last 1-2 segments of the larval integument become folded under the ventral surface of the contracted prepupa. It is during this stage that the first abdominal sternum is lost. The wings and elytra become everted, and lie outside the body, but beneath the larval integument. The legs become smaller, and only extend as far as the trochanter of the larval integument.

As development proceeds, the darker colour of the pupa can be seen through the tightly stretched larval integument. The genitalia appear on the ventral surface, at the apex of the abdomen.

When the pupa is ready to emerge it becomes increasingly restless. There are however, long intervals of quiescence, during which it lies on its ventral surface. Immediately before ecdysis waves of contraction pass along the pupa; they exert pressure on the larval integument, and cause it to split. The first rupture occurs in the mid-dorsal line, in the  
- region -

region of the first abdominal segment. It is continued anteriorly along the epicranial suture, and posteriorly as far as the seventh abdominal segment. The abdomen is extricated before the head-capsule.

5. Food Habits.

The larvae of Anomala vetula Wied. are similar to many other Scarabaeidae in that the larvae are root feeders. They have only been collected from turf, where they feed on roots; larvae have not been observed to damage crops. A number of species of the subfamily Rutelinae are injurious to turf and crops, in the larval stage. The following table includes the more important crops attacked by these larvae in different parts of the world.

Crop.	Species	Locality	Reference.	
Tea roots	<i>Anomala superflua</i>	Ceylon	Hutson, 1920.	
Maize Roots	<i>A. plebeja</i> Ol.	Italian Somaliland	Chiaromonte, 1933.	
	<i>A. egregia</i> Bab.	Italian Somaliland	Chiaromonte, 1933.	
	<i>A. antiqua</i> Gyll.	Java.	Franssen 1936,	
Potatoes	<i>Phyllopertha horticola</i> L.	Denmark	Blunck 1934,	
Vine	<i>A. vitis</i> F.	France	Feytaud 1916,	
Sugar Cane	<i>A. bengalensis</i>	India	Fletcher 1919,	
	<i>A. gussumeri</i>	India	Fletcher 1920,	
	<i>A. antiqua</i> Gyll.	Burma	Ghosh 1923,	
	<i>A. humeralis</i>	Burm.	Philippines	Vichanco 1928,
	<i>A. calceata</i> Cher.	Cuba	Bruner 1928,	
	<i>A. australasiae</i> Blkb.	Queensland	Burns 1928,	

Crop.	Species.	Locality	Reference.
Sugar cane (Contd.)	<i>A. orientalis</i> Waterh.	Hawaii	Pemberton, 1932.
Grass	<i>A. marginata</i> F.	U. S. A.	Britton, 1924,
	<i>Popillia japonica</i> Newm.	Eastern U. S. A.	Fleming, 1938,
	<i>A. orientalis</i> Waterh.	U. S. A.	Fleming, 1938,
	<i>Phyllopertha horticola</i> L.	Scotland	Meikle and MacFarlane, 1938,
	<i>A. kansana</i> H. and McC.	U. S. A.	Hayes and McCulloch, 1925,
	<i>A. aenea</i> Geor.	Germany	Rittershaus, 1927,
	<i>Phyllopertha horticola</i> L.	Germany	Rittershaus, 1927,
	<i>A. aureola</i> Hope	Malaya	Corbett, 1935,
Rice roots	<i>A. rufocuprea</i> Motsch.	Italy	Sawa, 1931,
Wheat	<i>A. aenea</i> Geor.	Germany	Rittershaus, 1927,
	<i>Phyllopertha horticola</i> L.	Germany	Rittershaus, 1927,
	<i>A. binotata</i> Cyll.	U. S. A.	Hayes, 1929,
	<i>A. kansana</i> H. and McC.	U. S. A.	Hayes, 1929,
Oats	<i>Phyllopertha horticola</i> L.	Germany	Rittershaus, 1927,
	<i>A. aenea</i> Geor.	Germany	Rittershaus, 1927.

The nature of the feeding habits of larvae of Anomala vetula Wied. is similar to that of other Scarabaeidae. The degree of destruction however is not as severe as that caused by infestations of larvae of Popillia japonica Newm. and Anomala orientalis Waterh.

(Fleming, 1938, pp. 3-4), Phyllopertha horticola L. and Anomala aenea Geer. (Rittershaus, 1927, p. 388 and p. 402). Smith, 1922, p. 306, reports that injury to grass by larvae of Popillia japonica Newm. was so extensive that it could be rolled up like a carpet. The larvae of these species are voracious feeders. When present in large numbers they may destroy the entire root system by eating through the grass roots a few inches below the surface of the ground. Turf which has been attacked in this manner can be rolled back, and usually reveals numerous larvae. According to Davis, 1916, p. 365, all observations on larvae of Anomala indicated that they fed on living rootlets, but apparently they were never sufficiently abundant to noticeably damage crops. He stated, however, that at any time they might prove important pests of crops.

The presence of forty-eight larvae of Anomala vetula Wied. within an area of 2ft. x 3ft., on the aerodrome at 48 Air School, Port Elizabeth, on 25.11.43, suggested that this species might be a serious pest of turf. Observations made in this area, however, do not indicate that the larvae have caused serious damage to the turf. A possible reason for this is that larvae of Anomala vetula Wied. confine their attacks to small roots and rootlets, a small amount of feeding extending through the long larval period.

In Macrophylla pubens Pöring (Fenwick, 1942, p. 163) feeding during the second instar causes most of the damage to the turf; the grass covering is completely severed from the roots. The presence of larvae of Anomala vetula Wied. in the turf is indicated by soft spongy areas, caused by the burrowing of the grubs a few inches below the surface of the ground. In dry seasons these patches can be recognised by the brown colour of the grass.

6. Depths at which the Instars are found.

The entire life-history of Anomala vetula Wied. except for the adult stage, is passed within one foot of the surface of the ground. The adults appear above ground for approximately two months of the twenty-four months which are normally required for the completion of the life-cycle.

The females burrow into the soil to a depth of six inches, where the eggs are laid. First and second instar larvae are found in the root system of the grass, within 6-9 inches of the surface of the ground. Towards the end of the second instar, the grubs descend a few inches, the third instar, including the prepupal stage, and the pupae occurring 9-12 inches deep. The imagines remain in the pupal skin for a few days before emerging. They make their way to within 4-6 inches of

the surface, where they pass most of their lives, except for a short period at twilight each night.

The principle of temperature "turnover", as developed by McColloch and Hayes, 1923, in which the temperatures near the surface become higher than those at lower levels in summer, the reverse condition occurring in winter, is applicable to movements of many species of Scarabaeid larvae. Larvae of species of June beetles feed on grass roots from June-September of the first year. In winter they descend deeper down, and hibernate in a special cell. In April or May of the following year they ascend to the surface, and feed until September or October, when they descend for a second time to hibernate. In the Spring of the third year, they return to the surface until June, when they descend to pupate. (Davis, 1916, pp. 263-264, Luginbill, 1938, pp. 5-6, Hammond, 1940, pp. 5-7).

In New Jersey, adults of Popillia japonica Newm. (Thomas, 1925, pp. 357-360), lay eggs in June-July, two inches below the surface of the ground. The larvae feed on grass roots until late November, when the cold weather causes them to move slowly downwards to 8-12 inches, where they hibernate. In Spring of the next year, with increase in the temperature of the soil, the larvae become active, and upward movement occurs.

In May, most of the larvae are four inches below the surface, and here they pupate. According to Friend, 1927, p. 363, eggs of Anomala orientalis Waterh., are laid singly at a depth of 3-9 inches in July-September in Connecticut. First instar larvae ascend to the roots of the grass, and continue to feed until the end of the second instar, when the larvae travel down to 10-15 inches, and hibernate in the third instar. Towards the end of April they return to the surface, and resume feeding at approximately 3-9 inches below the surface, where they pupate. In the neighbourhood of Tokyo, eggs of Anomala cuprea Hope (Yuasa and Endo, 1938), are laid about six inches below the surface. The larvae feed close to the surface of the soil, but descend to 12-20 inches to hibernate. In April the larvae resume feeding, and then descend a second time to 8-10 inches to pupate.

In the winter of the first year of the life-cycle Anomala vetula Wied. occurs in the field as second instar larvae 6-9 inches deep. In the second winter third instar larvae descend to 9-12 inches, but they do not return to the surface in summer to resume feeding, but pupate at the depth to which they descended as third instar larvae. The fact that larvae of Anomala vetula Wied. do not descend and ascend according to the seasons of the year, is

probably due to the more equable climate experienced in Port Elizabeth compared with that in New Jersey, New York and Tokyo.

The depth to which larvae descend in the soil varies greatly in different species of Scarabaeidae. Pupation usually occurs at the deepest level to which a species descends, unless after hibernation the larvae return to the surface to resume feeding before pupating, in which case pupation occurs a few inches below the surface. Pupation occurs in Macronhylla pubens Péring (Fenwick, 1942, p. 165), at 3 feet 6 inches. The pupation depths of nine species of Phyllophaga in Kentucky range from a minimum of two inches in Phyllophaga ophilida (Say.) to a maximum of twenty-three inches in Phyllophaga hirticula (Knoch.) (Ritcher, 1940, p. 135). Species of the tribe Anomalini do not appear to descend deep into the soil. Hibernation occurs in Popillia japonica Newm. at 8-12 inches in New Jersey (Thomas, 1925, p. 360), in Anomala orientalis Waterh. at 10-15 inches in Connecticut (Friend, 1927, p. 363), in Anomala cuprea Hope at 12-20 inches in Tokyo (Yusa and Endo, 1938). The greatest depth to which Anomala vetula Wied. descends is 9-12 inches, where pupation occurs.

Larvae kept in dry soil did not reach the

same size as those reared in soil moistened each week with a small quantity of water. Ludwig, 1934, p. 44, conducted experiments on desiccation and survival of Popillia japonica Newm. He records that at the rate at which various instars become desiccated decreased in the following order:- first, second, third instar larvae, late prepupae, early prepupae and pupae. In his experiment, larvae were able to survive desiccation until their weight was 50% of its original value.

III. THE PUPA. (Fig. 64).

The freshly emerged pupa lies on its ventral surface, enveloped in the integument of the third larval instar, and thus does not come into contact with the soil. A similar condition is reported in Anomala binotata Gyll. (Hayes, 1918, p. 139), Phyllopertha horticola L. (Rittershaus, 1927, p. 398), Popillia japonica Newm. and Anomala orientalis Waterh. (Hallock, 1930, p. 284). When the integument of the pupa has hardened, the pupa turns on to its dorsal surface, and rests on the chitinous arc-shaped ridges of the terga. It is generally motionless; if disturbed, movements of the abdomen may cause the pupa to wriggle out of the larval skin. It then lies next to it in the pupal cell.

Immediately after emergence, the pupa is a dull yellow colour; later it becomes darker. Details of the pigmentation have been described in the chapter on the external features of the pupa.



Fig. 64 - Pupae.

ANOMALA VETULA WIED.

- A. = Ventral view of Male.
- B. = Ventral view of Female.
- C. = Dorsal view of Male.
- D. = Dorsal view of Female.

(Natural size).

IV. THE IMAGO. (Fig. 63).

1. Emergence.

Shortly before emergence the form of the adult can be seen clearly through the pupal integument. The dark colour of the head, in particular that of the eyes and clypeus, the anterior tibiae and pro- and metathorax are prominent features. The abdomen of the adult is shorter than that of the pupa, so that there is a space at the end of the pupa before emergence.

The pupal integument is not shed as a whole, but in fragments. The first split usually occurs along the mid-dorsal line of the thorax. The integument often splits across at the base of the head and legs, due to their jerking movement, and remains of the pupal integument adhere to them for several days. They are eventually freed by rubbing against the surrounding soil. By a series of movements the elytra and wings are extricated; the integument covering these does not usually split. In the freshly emerged pupa the wings are stretched out, and only when they have hardened are they withdrawn under the elytra. The abdomen is extricated by alternate contraction and expansion assisted by movement of the legs.

In the laboratory adults of Anomala vetula Wied. remain in the pupal cells for a few days until

the chitin has hardened and the beetle has attained the normal colour.

Adults of Anomala binotata Gyll. remain in the pupal cells during winter (Hayes, 1918, p. 142).

The number of males collected at one time in one locality is greatly in excess of the number of females collected, as illustrated in the following table:

Date.	Locality.	No. of Males Collected.	No. of Females collected.
19.1.44.	42 Air School, Port Elizabeth.	54	3
Jan. 1945.	Kleinemonde.	37	1
8.1.45.	Golf Course, East London.	200	-
17.1.45	Grahamstown	77	4
19.1.45	Golf Course, Port Alfred.	23	1

In the laboratory the sexes emerged in equal numbers. The same condition is recorded in Phyllonotus horticola L. (Ritterhaus, 1927, p. 380); in the evening, however, males are more numerous than the females on the bushes. In Anomala vetula Wied. the females burrow back into the soil after copulation. This accounts for the greater number of females

collected in the field.

## 2. Habits.

Adults of Anomala vetula Wied. are crepuscular in their habits. During the day they remain approximately six inches below the surface of the ground, and only appear above ground shortly after sunset, for approximately two hours. Males and females have been observed emerging from the soil between 6.30 p.m. and 7.30 p.m. By 9 p.m. most males and females have returned to the ground. In the laboratory, beetles emerged at approximately the same hour as those in the field. They showed great activity in walking and attempting to fly. Both males and females returned to the soil several times during the evening. Occasionally some remained on the surface until the following morning. If adults were put in a jar without soil they continued to be active all night, but became quieter during the day. Meunier, 1928, p. 111, states that the swarming instinct in Lamellicornia is awakened by twilight, and that swarming occurs at a certain degree of darkness.

Adults of Anomala binotata Gyll. fly by day, often at dusk, but infrequently at night (Hayes, 1918, p. 142). Adults of Popillia japonica Newm. are active during the day. (Thomas, 1925, p. 359). A considerable

part of the life of the imago of Anomala orientalis Waterh. is spent in the ground. Most of the flying occurs between 7.30 a.m.-10 a.m., and 1.30 p.m. - 4.30 p.m., but there is some evidence of night flying (Friend, 1927, p. 363).

Both males and females of Anomala vetula Wied. have been observed to fly. The flights however are of short duration, as in Anomala orientalis Waterh. (Friend, 1927, p. 333). They are not attracted to lights. Adults of Anomala binotata Gyll. (Hayes, 1916, p. 142), and Anomala orientalis Waterh. (Friend, 1927, p. 363), are attracted to lights.

Adults of Anomala vetula Wied. have not been observed to feed.

Destruction caused by other adult Rutelinae, particularly those of Popillia japonica Newm. and Phyllonerta horticola L. has been very severe, and has resulted in the enforcement of scouting and quarantine regulations. Popillia japonica Newm. attacks more than 200 species of plants; 273 beetles have been removed from one apple (Smith and Hadley, 1926, p. 25 and p. 27).

The following is a list of the more important species of Rutelinae that cause destruction in the adult stage:-

- Plant etc.....

Plant.	Species.	Locality	Reference.
Mango.	<i>Anomala undulata</i> Hels.	Florida	Mozette 1920
Oil palms	<i>A. dorsalis</i> F.	Malaya	Gater 1925
Fruit trees	<i>A. binotata</i> Gyll.	Kansas	Hayes 1918
	<i>A. aenea</i> Geer.	Germany	Rittershaus 1927
	<i>Phyllopertha</i> <i>horticola</i> L.	Germany	Rittershaus 1927
Apple foliage and blossom	<i>A. orientalis</i> Waterh.	Connecticut	Friend 1927
Vines	<i>A. vitis</i>	France	Feytaud 1916
Cocoa	<i>A. demuda</i> Arr.	Belgian Congo	Maynes 1917
Willow	<i>A. frischei</i>	France	Clément 1916
	<i>A. aenea</i> Geer.	Germany	Rittershaus 1927
Peaches, apples, plums.	<i>Popillia</i> <i>japonica</i> Newm.	New Jersey	Smith & Hadley 1926
	<i>A. aenea</i> Geer.	Germany	Rittershaus 1927
Rose blossoms	<i>Strigoderma</i> <i>arboricola</i> Fab.	Kansas	Hayes 1927
	<i>Phyllopertha</i> <i>horticola</i> L.	Germany	Rittershaus 1927
Cherry trees.	<i>A. aenea</i> Geer.	Germany	Rittershaus 1927

### 3. Copulation.

When the females emerge from the pupal cells they contain a number of large eggs, but these are not fertile. Males are able to copulate immediately they emerge from the pupal cell. Hayes, 1917, p. 259, reports that in the Dynastid Ligyris gibbosus DeG. mating occurs underground. This has not been observed in Anomala vetula Wied.

Almost immediately after the female emerges from the ground it is surrounded by a number of males. As many as fifteen males have been observed round one female. In Anomala binotata Gyll. the main copulatory time occurs during the day (Hayes, 1918, p. 140). In Anomala kansana H. and McC. mating was only observed in the laboratory; it occurred in the late afternoon (Hayes and McCulloch, 1925, p. 592). The main copulatory time in Phyllopertha horticola L. is from 10 am. - 12 a.m. (Rittershaus, 1927, p. 379). In Anomala orientalis Waterh., copulation occurs at night (Halleck, 1930, p. 285).

Anomala vetula Wied. has a characteristic pungent odour, which is stronger during the period of activity during the evening than during the day. Presumably the male is attracted to the female by a special scent as in a number of other Lamellicornia (Rittershaus, 1927, p. 378). Males which are not

successful in finding a female, crawl up long grass blades, or stems of flowers. They may remain motionless on these or crawl actively up and down. In the latter case they usually fly off after a short while, in search of a female. This may be repeated several times. Rittershaus, 1927, p. 378 and p. 400, describes a similar habit in Phyllopertha horticola L. and Anomala nemosa Geer.

The female usually tries to escape from the numerous males which collect round her. They endeavour to climb on to the back of the female. The successful male attempts to copulate almost immediately. At first the male lies almost directly above the female; maintaining that position by grasping the body of the female with the two front pairs of legs. In this position the female usually crawls around with the male on her back. In order to take up the position for copulation, the male moves further back and erects the anterior portion of the body. The first pair of legs grasps the female between the prothorax and elytra, the second pair round the abdomen, while the third pair of legs trails on the ground. Copulation lasts for several minutes. Males have been observed to attempt to copulate with each other.

A number of males may copulate with one female.

In the laboratory a male has been observed to copulate with four different females in one evening. Repeated fertilization does not appear to be necessary. One female which was isolated laid a total of twenty-six eggs in six batches over a period of fourteen days.

#### 4. Oviposition.

After copulation the female returns to the soil. During the time of maximum emergence, holes in the ground, from which the beetles emerged, are very numerous. Sometimes these holes are used again when the beetles return to the soil. The female is frequently followed by the male, but this does not always occur. The beetles burrow into the ground using the strong front tibiae, and with the aid of up-and-down movement of the head.

In the laboratory the period between copulation and oviposition varied from 3-8 days, but eggs were usually laid five days after copulation. Females which have not copulated were observed to lay sterile eggs 24-31 days after emergence. The preoviposition period is short, but is similar to that in Anomala kansana H. and McC. (Hayes and McColloch, 1925, p. 592), where egg laying occurs 3-6 days after copulation.

The maximum number of eggs laid in captivity

by one female was 35, extending over a period of twenty days; one egg was found on 16.1.45; six more were laid by 30.1.45; twenty-three more were laid by 34.1.45; three more were laid by 29.1.45 and two more by 5.2.45. This is the longest time over which egg-laying occurred. In other cases egg-laying extended over periods of varying length. In one instance thirty-four eggs were laid by one female over a period of sixteen days. According to Schwerdtfeger, 1927, pp. 278-279, egg laying in Melolontha takes the form of repeated ovipositions occurring over a period of several days. Smith and Hadley, 1926, p. 18, state that in Popillia japonica Newm. eggs are laid every third or fourth night, egg laying extending over 3-4 weeks. Rittershaus, 1927, p. 361, recorded thirty-seven eggs laid by one female of Phyllonarthra horticola L. over a period of nineteen days. In Anomala orientalis Waterh., (Friend, 1927, p. 363), the largest number of eggs laid by one female was thirty-two extending over a period of seven days, a few eggs being laid at frequent intervals. The average number of eggs laid by Anomala cuprea Hope is 98 (Yuasa and Endo, 1938).

After the last egg-laying in Anomala vetula Wied. the females do not usually return above ground, but die next to the last batch of eggs that was laid.

The same phenomenon is recorded in Phyllopertha horticola L. (Rittershaus, 1927, p. 382).

V. DURATION OF THE LIFE-CYCLE. (Fig 65).

Anomala vetula Wied. normally requires two years for the completion of the life-cycle. It extends into three calendar years, as eggs which are laid at the beginning of one year, transform into adults at the beginning of the next year but one. The two life-cycles run concurrently, so that there is an emergence of beetles towards the end and at the beginning of each year. A small percentage of the larvae may fail to transform into pupae towards the end of the second year of the life-cycle. They continue through the following year as prepupae, pupate about November, and emerge as adults at the beginning of the next year, thus completing a three year life-cycle.

Adults of Anomala vetula Wied. which were collected on the aerodrome of 42 Air School, Port Elisabeth, on 19.1.44 were mated in the laboratory, and laid eggs in captivity on 2.2.44. First instar larvae hatched from these eggs on 13.2.44, and changed into second instar larvae on 29.3.44. These grubs were kept in the laboratory until December of the same year, when they died. Second instar larvae collected in the

field on 21.3.44, were reared through to imagines, which emerged in February of the following year, thus completing the second year of the life-cycle. No specimen completed the entire life-cycle in the laboratory. By means of field and laboratory observations, the length of each stage in the life-cycle was ascertained.

Oviposition extends over a period of almost two months. In 1945 in the laboratory, egg-laying commenced on 4th. January, and continued until 26th. March. The number of eggs present reached a maximum from 29th. January to 4th. February. Although egg-laying continued after this date, the number of eggs present decreased, as first instar grubs, which commenced to hatch from these eggs on 4th. February, were in excess of the number of eggs laid. Excavations were made at the aerodrome at 42 Air School, Port Elizabeth, on 5.2.44. At a depth of six inches, forty first instar larvae and three eggs of Anomala vetula Wied. were collected. These hatched on 13.2.44.

During January and February 1944, 127 eggs laid in the laboratory changed into first instar larvae. The duration of the egg stage varied from 16-47 days with an average of 26 days. The incubation period in Strigoderma arboricola Fab. varies from 10-14 days

(Hayes, 1921). In Popillia japonica Newm. it ranges from 9-27 days (average 14 days), according to Smith and Hadley, 1926, p. 14, in Anomala orientalis Waterh. from 10-41 days (average 23 days), according to Friend, 1927, p. 364, and from 15-30 days in Phyllopertha horticola L. and 25-35 days in Anomala senoa Geer. (Ritterhaus, 1927, p. 389, and p. 403). It varies from 9-19 days (average 12.2 days), in Anomala kansana H. and McC., 11-19 days (average 14.6 days), in Anomala inuba, 7-11 days in Anomala binotata Gyll., 8-26 days (average 14.9 days) in Pelidnota punctata L. and 18-27 days (average 20.9 days) in Cotalpa lanigera (L.). (Hayes, 1929, p. 49). The duration of the egg stage is thus similar to that of Anomala orientalis Waterh. and Anomala senoa Geer., but longer than that recorded for the other species. The length of the egg stage does not appear to vary with the length of the life-cycle; in Anomala orientalis Waterh., which usually has a one year life-cycle in Connecticut, the average incubation period is 23 days, which except for Phyllopertha horticola L., is longer than that recorded for any species which has a two year life-cycle.

The first instar lasts for about two months. Grubs commenced to hatch out in the laboratory on 4.2.45, and continued to do so until 2.4.45; the majority however

THIRD YEAR

SECOND YEAR

FIRST YEAR

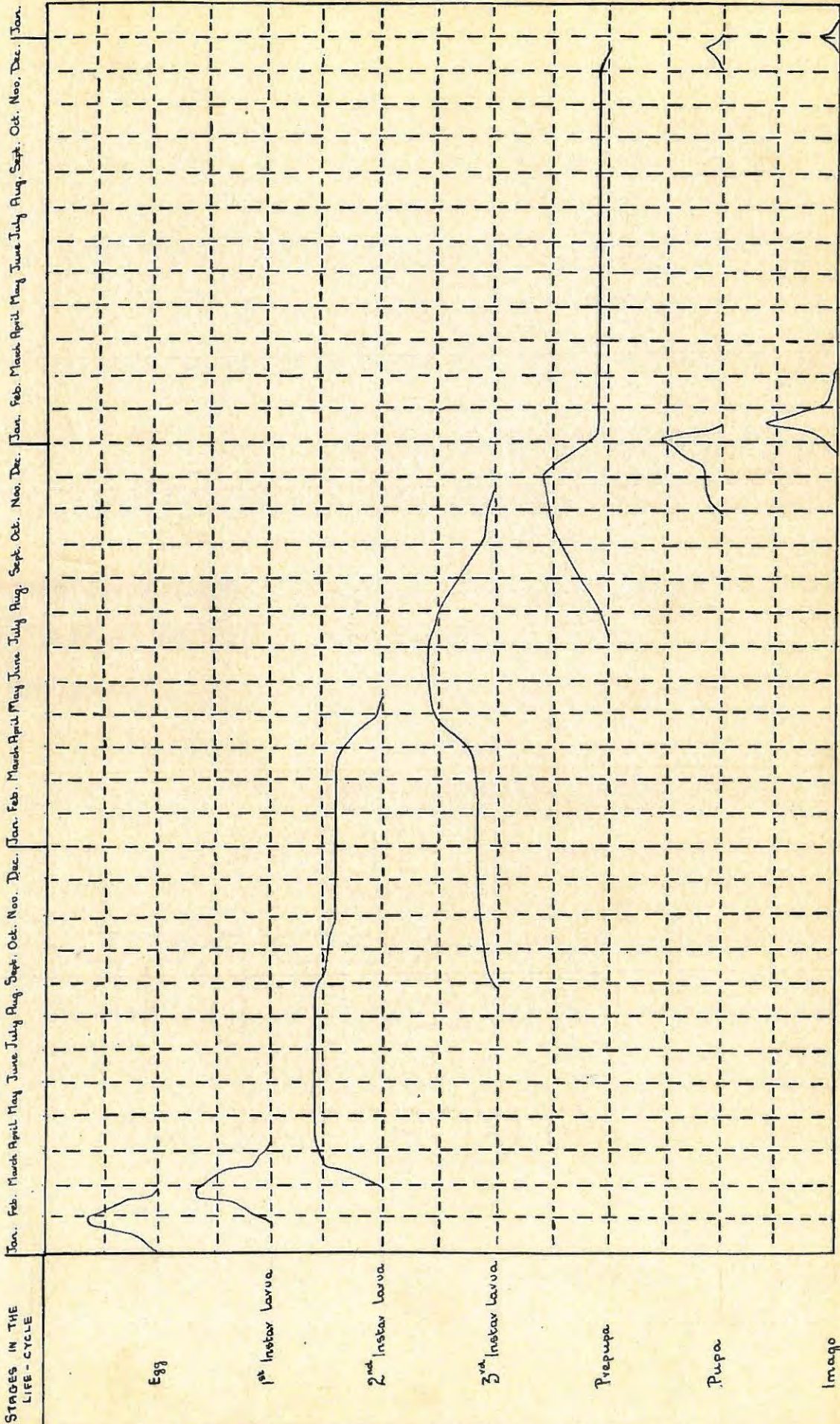


Fig. 65 - DIAGRAMMATIC REPRESENTATION OF THE EXPERIMENTAL EVIDENCE OF THE LENGTH OF THE STAGES IN THE LIFE-CYCLE OF ANOMALA VETULA WIED.

STAGES IN THE LIFE-CYCLE

Egg

1st Instar larva

2nd Instar larva

3rd Instar larva

Prepupa

Pupa

Imago

had hatched out by 25.2.45. The maximum number of first instar larvae were present between 23rd. February and 4th. March. From the latter date the number of first instar larvae decreased, owing to the increasing number of grubs transforming into the second instar. The length of life of a first instar larva ranged from 20-40 days, with an average of 29 days for 24 grubs.

On 21.3.44 five first instar grubs were found approximately nine inches below the surface of the aerodrome at 42 Air School, Port Elizabeth. By 23.3.44 these had all transformed into second instar larvae, except for one, which remained in the first instar until 3.4.45. The length of the first instar varies from 7-10 days in Popillia japonica Newm. in New Jersey. (Smith and Hadley, 1926, p. 14), in Anomala kanasana H. & McC. from 13-36 days with an average of 20.5 days (Hayes, 1927, p. 195), in Phyllonarthra horticola L. from 14-25 days and in Anomala senae Geer. for approximately nine months (Rittershaus, 1927, p. 394, and p. 404), and in Cotalpa lanigera (L.) it averages 23.6 days (Hayes, 1929, p. 51). The length of the first instar in Anomala vetula Wied. is similar to that in Cotalpa lanigera (L.), which also has a two or three year life-cycle.

The second instar is of comparatively long duration, second instar grubs of one life-cycle being

present in the soil for approximately fourteen and a half months. In the majority of the larvae of Anomala vetula Wied., the second instar is the longest in the life-cycle. The first larval ecdysis occurs during March, the second instar being completed by May of the following year. Holes excavated on the aerodrome at 42, Air School, Port Elizabeth, on 21st. March, revealed that 12% of the grubs collected were in the first instar, 76% in the second instar, and 12% in the third instar. These grubs were bred in the laboratory. 30% of the second instar grubs proved to be in the second year of the life-cycle, transforming into the third instar in March-May of the same year. The remainder of the second instar grubs were in the first year of the life-cycle, presumably having turned into second instar grubs approximately one month previously.

A small percentage of larvae changed into the third instar between September and November. The remainder lived through that year as second instar larvae, but died before changing into the third instar. Excavations on the aerodrome of 42 Air School, Port Elizabeth, revealed that second instar grubs were present in the soil on 19.4.44., 3.6.44., and 13.9.44. Only one grub completed the entire second instar in the laboratory; it spent 217 days as a second instar larva.

One grub however spent 265 days in the second instar, but died before transforming into a third instar larva.

The second instar lasts for 17-33 days in Phyllonetha horticola L. and about two months in Anomala asnea Geer. (Ritterhaus, 1927, p. 394 and p. 404). In Cotalpa lanigera (L.) the duration of the second instar ranged from 26-326 days with an average of 232.8 days. Those with a short second instar moult twice during the season in which they hatch, the remainder delay the second moult until the following season (Hayes, 1929, p. 51).

The duration of the third instar of Anomala vetula Wied. is usually eight months, extending from April to December. A few larvae, as already stated, may transform into the third instar between September and November, and continue as third instar larvae into the second year of the life-cycle.

Third instar larvae were collected at the aerodrome at 42 Air School, Port Elizabeth, on 21.3.44., 19.4.44., 3.6.44., 13.9.44., and 21.11.44. Only one grub completed the third instar in the laboratory; this lasted for 278 days. One grub, however, spent 307 days as a third instar larva in the laboratory, but died before becoming a prepupa.

In Phyllonetha horticola L. the length of the third instar, including the prepupal stage, is about seven and a half months, and in Anomala asnea Geer.

about twelve months (Rittershaus, 1927, p. 394 and p. 404).

The duration of the prepupal stage is usually 70-80 days, and extends over a period of approximately six months from July-January, in the second year of the life-cycle. In one instance however, the prepupal stage was only nine days long. The exact date on which the prepupal stage commences is not easy to determine, as defaecation in preparation for the prepupal stage is a gradual process. On 21.3.44 four prepupae were collected on the aerodrome at 42 Air School, Port Elizabeth. Two of these transformed into pupae in November, 1945. It is presumed that adverse conditions towards the end of 1943 prevented these larvae pupating at the end of that year. Prepupae were also collected in the field on 13.9.44 and 21.11.44.

In Anomala vetula Wied. the length of the larval instars is approximately twenty months. In Anomala viti it lasts for eighteen months, (Feytaud, 1913), in Palidnota punctata L. for 698 days and in Cotalpa lanigera (L.) for 604.6 days (Hayes, 1929, p. 67), and in Anomala curvae Hope for eleven months (Yunasa and Endo, 1933).

Pupae were present at the aerodrome of 42 Air School, over a period of two and a half months, from the beginning of November to the middle of January.

Three pupae were collected at 42 Air School, on 21.9.45 in an area of one square yard. The maximum number of pupae occurred during the first week in January. In the laboratory the first pupa was found on 13.11.45.

The duration of the pupal stage is comparatively short. It varies from 24-54 days with an average of 30 days for 15 specimens. The duration of the pupal stage is similar to that of Phyllopertha horticola L. and Anomala aenea Geer. but it is longer than that recorded for other species of Anomalini. In Anomala binotata Gyll. it lasts for 13-22 days, average 16 days (Hayes, 1918, p. 142), in Strigoderma arboricola Fab. 10-14 days (Hayes, 1921), in Anomala antiqua 13-14 days (Ghosh, 1923), in Anomala kansana H. and McC. 8-20 days (Hayes and McCulloch, 1925, p. 594), in Popillia japonica Newm. 9-20 days (Smith and Hadley, 1926, p. 16), in Anomala orientalis Waterh. 15 days (Friend, 1927, p. 363), in Phyllopertha horticola L. 25-39 days and in Anomala aenea Geer. 26-41 days (Rittershaus, 1927, p. 394 and p. 404), and in Anomala cuprea Hope 10-21 days (Yuasa and Endo, 1933).

Beetles are found on the wing towards the end of December; they are usually present until the end of February or the beginning of March. The maximum period

of emergence is towards the end of January. On 19.1.44 adults of Anomala vetula Wied. were very numerous at 42 Air School, Port Elizabeth. In 1945 adults were collected from the aerodrome on 3rd. January and 11th. January. Large numbers of beetles were collected from the golf course at East London on 3rd. January and 8th. January, from the Port Alfred golf course on 19th. January, and in Grahamstown on 17th., 23rd. and 29th. January. In America all species of Anomala mature in June-August.

In the laboratory in 1944, the first beetle emerged on 11th. December. Sixteen beetles emerged in the laboratory, the sexes being in equal number. By 12th. January seven females and one male had emerged; by 22nd. January all the males, and the eighth female had emerged. It is not known if the females emerge before the males in the field. Thomas, 1925, p. 358, states that in Popillia japonica Newm. the males usually emerge a few days before the females.

In captivity the length of life of the imago of Anomala vetula Wied. is thirty days in both sexes. In Popillia japonica Newm., the males live for 54.25 days in captivity and 46 days in the field; the females live for 37.94 days in captivity and 44 days in the field (Smith and Hadley, 1926, p. 17).

There is a considerable variation in the length of the life-cycle in the sub-family Rutelinae. This difference is due to variation in the length of larval development. Not only does it vary from one species to another, but it may differ in the same species in different localities, or a difference of one year may occur in the life-cycle of a species in one locality. It has been observed by Ritcher, 1940, p. 96, that the duration of the life-cycle of a given species of Phyllophaga apparently varied in different localities.

According to Hayes, 1925, species of the Tribe Rutelini require two or three years for the completion of the life-cycle. Pelidnota punctata L. has a two year life-cycle; Cotalpa lanigera (L.) has a life-history requiring two or three years for completion. In the Tribe Anomalini the following are the more important species, because of their destructive habits, which have a one year life-cycle:-

Anomala binotata Fab. in Kansas (Hayes, 1921),  
Anomala antica in Burma (Ghosh, 1923), Anomala inania  
F. in the United States of America (Hayes, 1925),  
Anomala kansana H. and McC. in Kansas (Hayes and  
McColloch, 1925, p. 594), and Phyllopertha horticola L.  
in Germany (Rittershaus, 1927, p. 394). Anomala vitis  
in the south of France (Feytaud, 1916), and Anomala aenea

Geer. in Germany (Rittershaus, 1927, p. 408), have two year life-cycles. Anomala currea Hope. requires one or two years for its life-cycle in Japan, one year being more usual in Tokyo. Those with a two year life-cycle hibernate twice (Yuasa and Endo, 1933). Anomala orientalis Waterh. usually has a one year life-cycle in Connecticut, but a small percentage require two years to complete the life-history. Hibernation usually occurs in the third instar, but if they hibernate during the first instar they do not complete the development the following season, but hibernate during the second winter in the third instar and pupate a year later. (Friend, 1927, p. 364). According to Kwayama, 1940, Anomala rufocurra Motsch. has a three year life-cycle in Hokkaido, but only requires one year near Tokyo. Popillia japonica Newm. is indigenous to Japan. The length of the life-cycle increases from one to two years as it extends northwards from Yokohama to Sapporo. A similar phenomenon occurs in Lechnosterna; the further north a species occurs, the longer is the life-cycle (Davis, 1916, p. 262). Popillia japonica Newm. was introduced into the United States. Here the life history extends over one year, but under exceptional conditions larvae may require two seasons to complete the life-cycle. (King, 1931, p. 454).

VI. DISTRIBUTION.

I have collected specimens of Anomala vetula Wied. from the coastal area of the Eastern Cape Province, between East London and Port Elizabeth, and as far inland as Grahamstown. Péringuey, 1903, p. 592, includes Mossel Bay in its distribution.

Adults were collected from the golf course at East London in large numbers on 2.1.45 and 8.1.45. I received specimens collected from the natural vegetation at Kleinmond in January, 1942. At Port Alfred adults were collected on the wing on 11.2.39, 25.1.44, and 19.1.45. A large number of specimens were collected in the precincts of Grahamstown on 13.2.44, and in the following year on 17th. and 29th. January. Specimens were received from the Hill Course, Port Elizabeth, on 4.12.40 and 13.2.42.

In order to study the life history of Anomala vetula Wied., excavations were made at intervals from 25.11.43 to 21.11.44, on the aerodrome of 43 Air School, Port Elizabeth. The behaviour of adults above ground was also observed. The study of the life-history is confined to specimens collected in this locality.

Excavations were continued throughout the

period, in order to compare the development of the various stages of Anomala vetula Wied. in the laboratory with those in the field.

TECHNIQUE.

1. Breeding.

Excavations were made on the aerodrome at 42 Air School, Port Elizabeth, at intervals from 25.11.43 to 21.11.44.

During this period all stages of Anomala vetula Wied. were collected. They were obtained by digging up a sod of grass with a sharp edged spade and examining it, if necessary breaking it apart. They were reared in the laboratory in soil obtained from their natural habitat. Excavations were continued throughout the year, in order to compare the stages found in the field with those bred in the laboratory. Adults collected from the golf courses at East London and Port Alfred, were mated in the laboratory, and laid eggs which were reared to second instar grubs.

Two types of breeding cages were used. The first consisted of two pieces of glass 9 inches square, which were laid in a parallel position approximately one inch apart, by means of a metal frame. This was filled with moist sand to a depth of approximately seven inches, and covered with a loosely fitting metal lid. The purpose of this breeding cage is to enable grubs to be observed in

the soil as the glass plates are close together. This was not possible with larvae of Anomala vetula Wied. as they are small, and furthermore, difficulty was experienced in placing the food supply in the cages.

Grubs were reared successfully in a second type of breeding case which was used. This was a wide mouthed glass jar, approximately  $3\frac{1}{2}$  inches in diameter and 4 inches deep. This was filled with moist sand to a depth of about 2 inches, in which grass was planted. During larval and pupal development the jars were covered by fine organdi, secured by a rubber ring. During the adult stage the organdi was replaced by a lid to prevent the beetles from tearing the organdi and escaping. All breeding jars were kept in the laboratory.

Various types of breeding cages have been used in experiments on "white grubs". Davis, 1915, pp. 135-139, used several types of cages in life-history studies. The most successful was a standard size flower pot, filled with soil, and seeded with grass. These pots were buried in the soil, and covered with cylinder-shaped tops. Grubs were kept in one ounce tin salve boxes to study the habits. Rittershaus, 1937, p. 272, bred imagines in covered wooden boxes, filled with moist earth. Glass vessels 50-60 cms. high were found to be the most

suitable for the larvae. One ounce metal salve boxes were used in breeding experiments on larvae of Popillia isapanica Newm. (Ludwig, 1932, p. 451). Lacquered gallon tin cans, half packed with moist sifted soil, were used by Ritcher, 1940, p. 145, to confine adults of Phyllorhaga.

Eggs laid in the laboratory and those collected in the field were each placed in small depressions made in moist soil in the jars. This prevented the newly hatched grubs from coming into contact and injuring each other. The grubs which hatched from these eggs were placed in separate jars.

Two types of food were supplied to the larvae. The first type consisted of fresh grass roots obtained from 42 Air School, Port Elizabeth, or from Grahamstown, when grass roots from the former area were not available. These were planted in the jars of soil. The second type consisted of "Taystee Nuts". Finely ground granules of these were placed in small cells made in the soil. Newly hatched grubs were placed directly on these, and covered with soil. First and early second instar larvae were reared successfully on a diet consisting of "Taystee Nuts" only. During later development it was necessary to supplement the food supply with grass roots. Reinhard, 1944, p. 53,

- successfully -

successfully reared larvae of a number of different species of Phyllonhaga through the entire larval development on a sole diet of "Grapenuts". Adults from these were normal; they fed, mated and laid eggs during the usual period. In some instances however, in the third instar, carrot was supplied to supplement the "Grapenut" diet.

In Anomala vetula Wied. as the prepupal stage approached, the grass roots were removed and the soil was well moistened. Pupal cells were almost invariably made at the bottom of the glass jar. In order to observe the development of the pupa it was put into a cell constructed artificially in the soil, approximately one inch below the surface of the soil, next to the glass. After transformation into imagines, they were left undisturbed until ~~until~~ the chitin had hardened and assumed its normal colouration. They were then put in pairs into jars of fresh moist soil. Mating occurred in the laboratory, and the soil was examined at intervals for eggs.

Throughout the breeding, observations were made at weekly intervals. At these times fresh grass roots were supplied if necessary, and the soil was moistened.

2. Preservation of Material.

Larvae of Angonala vetula Wied. were preserved in a number of different solutions, including 70% formalin, neutral formalin, 70% ethyl alcohol, Carnoy's fluid and Bouins solution. The most successful method was that described by Viado, 1939, p. 345, for "white grubs". The larvae were fixed in hot water at 90°C. for 30 minutes. They were then placed on ice for 30 minutes, and finally transferred to 80% alcohol. It was necessary to puncture third instar larvae to admit the alcohol.

Neutral formalin was the best preservative for the pupae and adults. 70% alcohol, Bouins solution and Carnoy's fluid were tried, but they were not good. An incision was made in each case to admit the preservative.

3. Preparation of Material for Microscopic Examination.

Parts of larvae which were required for microscopic examination were cleared in 10% potassium hydroxide for 12-24 hours. The soft internal parts were then removed. The chitinous remains were rinsed in water, to which a little acetic acid had been added, to neutralise the potassium hydroxide. The material was washed in distilled water, and dehydrated in

- increasing -

increasing strengths of alcohol. Clove oil or toluene were used as clearing agents, and mounting was done in "clarite". Fluid mounts in neutral formalin were made of soft tissue, such as spiracles and surfaces of the body-wall with their setation, to prevent distortion from pressure of the cover glass.

First instar larvae and delicate parts of second and third instar larvae were stained in a variety of media including aqueous and alcoholic eosin, erythrosin, Delafield's haematoxylin, Iron alum haematoxylin, azo black and Kern-schwarz.

Imagines were treated in 5% potassium hydroxide for 18-24 hours. It was sometimes necessary to warm the solution. They were then rinsed, dehydrated and mounted as in the larvae. Delafield's haematoxylin was the best stain for the spiracles. The structure of the tentorium showed clearly when stained with a saturated solution of iodine in 70% alcohol. Staining was unnecessary for the remaining parts of the imago.

SUMMARY.

A detailed morphological study of the external features of the eggs, larvae, pupae, and adults of Anomala vetula Wied. is given, and compared with that of other Rutelinae. Special reference is made to the form and arrangement of hairs, setae and sensilla on the epipharynx and raster of the larva, with a view to their possible taxonomic importance. The three larval instars are distinguishable by the proportional increase in size of the head-capsule in succeeding instars. A hatching spine is present on the metathorax of first instar larvae, but is absent in succeeding instars. The sexes of the pupae are distinguishable by the form of the developing genitalia on the ventral surface of the rounded posterior end of the abdomen. The female imago is distinguishable from the male by the lighter colour of the prothorax, the presence of irregularly arranged punctures between the tenth and eleventh punctate striae of the elytra, and a cleft inner claw of the pro- and mesothoracic legs. The enumeration of the abdominal segments is based on the observation that the

- corresponding -

corresponding spiracles in the pupa and imago are connected by a chitinous strand immediately before ecdysis.

The internal anatomy of the larvae and adults is described. Special reference is made to the development of the three series of coeca of the alimentary canal of the three larval instars.

The life-cycle is completed in two or three years, depending on the length of the prepupal stage. The larval period extends over approximately twenty months. Except for the adult stage, the entire life-cycle is passed within one foot of the surface of the ground. Imagines are present for approximately two months; they have a characteristic pungent odour. Both sexes fly; they are not attracted to light.

The larvae feed on grass roots, and are a potential danger to turf; the imagines have not been observed to feed.

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