

On the Bionomics and Development of *Lygocerus testaceimanus*, Kieffer, and *Lygocerus cameroni*, Kieffer (Proctotrypoidea-Ceraphronidae), parasites of *Aphidius* (Braconidae).

By

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With 18 Text-figures.

INTRODUCTION.

THE Proctotrypoidea have been less studied than most other groups of the Hymenoptera Parasitica. Ganin (1869) was the first to study the embryology of certain members of the group (8). In 1884, Ayers (2) described the development of the Scelionid, *Teleas*. In 1898, Kulagin (14) resumed the study of *Platygaster*; and in 1906, Marchal (18) published the results of his elaborate researches into the embryology and development of that family. In recent years much work has been done on this group from the systematic standpoint, notably in the monographs of Ashmead (1) in America, and of Kieffer (13) in Europe, but the life-histories of most of the families are comparatively little known.

The following is an account of the bionomics and post-embryonic development of two species of the genus *Lygocerus*, of the sub-family Ceraphroninae. These forms are parasites of the larvae and pupae of certain Braconidae, of the family Aphidiidae, which are themselves internal parasites of various plant-lice.¹

I would here express my sincere thanks to Professor Stanley

¹ A preliminary note on these observations by the writer appeared in the 'Proceedings of the Cambridge Philosophical Society', 1920, vol. xix, Pt. VI.

Gardiner, who gave me facilities to carry out the work in the Zoological Laboratory at Cambridge; and my obligations to Professor J. J. Kieffer, and to Mr. G. T. Lyle, who kindly determined the specimens of Proctotrypoidea and Braconidae submitted to them respectively.

BIOLOGICAL STATUS.

The genus *Lygocerus* was founded by Förster, and is included in the sub-family Ceraphroninae. Ashmead (1, p. 103) and Kieffer (13) state that the Ceraphroninae are almost exclusively parasitic upon Homoptera (Aphidae) and Diptera (Cecidomiidae, &c.). Riley is said to have reared a *Lygocerus* from a tortricid larva (Lepidoptera), but Ashmead considers the observation to be of doubtful accuracy. The genus contains a number of species obtained from aphides, but their bionomics have hitherto been in doubt, authorities disagreeing as to whether they are parasites or hyperparasites.

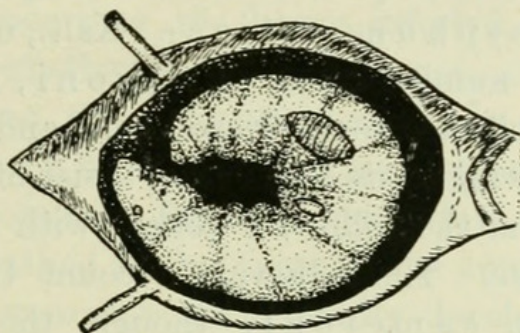
Curtis believed correctly that they were hyperparasites, and Buckton (4) agreed with him; but later writers have reverted to the view that these Proctotrypids are directly parasitic upon the aphides from which they are reared. Thus Ashmead (1, p. 21), who says that the larvae all feed upon the host internally, continues: '*Lygocerus* and allied genera living in the Aphidae, gnaw a hole through the ventral surface of the aphid, and after securely fastening the aphid by a silk-like secretion to the leaf or twig upon which it has been feeding, pupate within the body of their host, which, in lieu of a cocoon, affords ample protection to the larvae to undergo their transformations.' Gatenby (9) says, 'I am inclined to support the view that the Proctotrypid is a parasite and not a hyper-parasite'.

The subjects of this paper, *Lygocerus testaceimanus*, Kieff., and *L. cameroni*, Kieff., are both hyperparasites. The eggs are laid and the larva stages are passed outside the body of the host. The *Aphidius* larva, in the course of its development, devours the internal organs of the aphid in which

it is reared ; and when it is full-fed, it lines the empty skin with silk, and pupates within it. At this time, it is itself liable to parasitisation by the *Proctotrypids* (fig. 1).

Lygocerus does not confine itself to *Aphidiidae*. Twice I have observed its larvae upon newly-transformed and dead pupae of its own species. The aphidivorous *Braconidae* are known to be parasitised by certain *Chalcidae* and *Cynipidae*, some of which were reared from material collected in the field in the course of this work. *Lygocerus cameroni*

TEXT-FIG. 1.



Skin of *Macrosiphum urticae* cut open to show the full-grown larva of its parasite, *Aphidius ervi*, which has in turn been attacked by *Lygocerus cameroni*. An egg, and third stage larva of the hyperparasite are represented.

occurred occasionally upon the adult larvae of a Chalcid, probably *Asaphes vulgaris*, and also upon a second species, not yet determined, which is possibly a *Cynipid* (*Allotria* sp.). Apart from the two cases mentioned above, where the larva had been hyperparasitised by its own species, *Lygocerus* was never found to be attacked by another hymenopteron.

One remarkable instance of hyperparasitisation came under notice. An aphid (*Macrosiphum urticae*) had been parasitised by *Aphidius ervi*. The latter had been hyperparasitised by an undetermined species of Chalcid. This form, after metamorphosis, had been devoured except for the frass, the head, and part of the thorax, by a second hyperparasite, whose life-history is not yet worked out. This larva was full-grown when the cocoon was opened, but it had itself

been recently hyperparasitised by *Lygocer* *cameroni*. Hence, within certain limits, this species seems to be polyphagous.

MATERIAL.

The material used was obtained in Cambridge in the summer of 1919. At the end of June, a variety of *L. testaceimanus*, Kieff., was reared from the larvae of *Aphidius salicis*, Hal., parasitic in the sexuales of *Aphis saliceti*, Kalt., on the willow; and as the host material became scarce, I subsequently induced it to oviposit on larvae of *Aphidius ervi*, Hal., in *Macrosiphum urticae*, Kalt., on the nettle. In July, I reared a number of *L. cameroni*, Kieff., from the latter material collected round Newnham; and as the host was plentiful, and, owing to its larger size, easier of dissection than the parasites from the willow, I worked with it exclusively in July and August. The following account therefore applies especially to *L. cameroni*, though the life-history of *L. testaceimanus* is essentially the same.

Aphides parasitised by *A. ervi* were collected in the field, but a proportion of these were found to be already hyperparasitised by certain Chalcidae and Cynipidae. To ensure a 'pure culture' of *Lygocer*, nettles infested with *Macrosiphum urticae* were placed in water under bell-jars in the open air insectary, and exposed to *Aphidius ervi*. The aphides were kept under cover during the development of the parasite, and when the latter were about to transform, the leaf was cut off, and placed in a glass tube with a fertilized female of *Lygocer*. Thus the possibility of an infection by another hyperparasite was virtually eliminated.

I tried many times to cut open a flap on the dorsal side of the aphid skin, hoping by this means to follow the complete development of the hyperparasite from day to day, but the attempt always failed through the death of both the *Aphidius* and the Proctotrypid within a few hours.

PAIRING.

No parthenogenetic ovipositions were observed, and about 40 per cent. of the imagos reared were males. Pairing took place a few hours after emergence. It was noticed that the males paired only once. Thus *Lygocerus* differs from its Braconid host, in which a single male will fertilise two or three females successively.

OVIPOSITION.

The female *Lygocerus*, when about to oviposit, runs in an agitated manner over the leaves infested with plant-lice. Living aphides, whether parasitised or not, are ignored, and I have never seen the *Lygocerus* make the mistake of ovipositing on an *Aphidius* which had not begun to spin silk. The necessity is obvious, for until just before metamorphosis, the host is still bathed in the juices of the aphis, in which the egg of the hyperparasite could hardly develop. Sometimes a pupa is chosen instead of a full-grown larva; but these are never attacked in the later stages when the chitin is hardening.

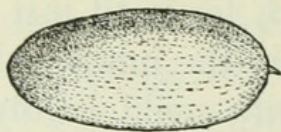
When a suitable host is found, the *Lygocerus* runs round and over it with much excitement, tapping it repeatedly with her antennae. The act of oviposition usually takes from 30-60 seconds. The Proctotrypid stands either on the thorax of the aphis skin, facing the head, or on the leaf behind it with the tip of her abdomen against its posterior part. Either way, the result is to bring the ovipositor, when exerted, into the curve formed by the body of the *Aphidius* as it lies, bent head to tail, in the cocoon. The ovipositor seems to penetrate the aphis skin with little effort. Sometimes it is partly withdrawn and inserted again, but only one egg is deposited on the host. Occasionally two females may be seen to oviposit simultaneously on the same *Aphidius*; and, later, it is not uncommon to find two or three young larvae, but only one of the latter reaches maturity, and two imagos were never reared from the same cocoon.

The number of eggs laid by a single *Lygocerus* is uncertain, but from observations made on females in captivity, and from dissections of mature ovaries, it does not appear to be more than fifteen or twenty, at most twenty-five. Calculation by the latter method is difficult, as the eggs do not all mature at the same time; and if the hosts be removed from the cage of a captive female, and restored two or three days later, she will recommence and complete oviposition.

THE EGG.

The egg of the hyperparasite, when newly laid, is elliptical, and measures $.25 \times .10$ mm. It is white and semi-translucent, with a minute protuberance at one end. Under the high power

TEXT-FIG. 2.



The egg immediately after oviposition. $\times 100$.

of the microscope, the chorion shows numerous longitudinal striae. Treatment with Aman's lacto-phenol and cotton-blue reveals the presence of bodies resembling the symbiotes of the 'pseudo-vitellus' of aphides. The egg is laid upon the upper surface of the host's body, and hatches in about twenty hours. As the development of the embryo proceeds, the egg becomes more spherical, and the jaws, gut, &c., of the future larva are visible through the chorion.

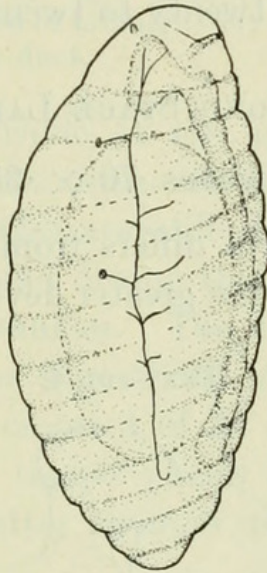
FIRST STAGE LARVA.

Dimensions $.45 \times .22$ mm.

The larva of the first instar is white and transparent, with a distinct head and thirteen body segments. The form is cylindrical, the greatest diameter being through the thorax, and the segments diminish regularly to the last which bears the anus. If removed to a slide, the larva can progress fairly actively by

a kind of peristaltic movement of the body, but under normal conditions it probably does not need to move from where it was hatched, provided that the host be a larva. If the latter be a pupa, the hyperparasite is generally found feeding on the posterior part of the abdomen, where the integument is still soft. As the egg, as previously described, is always deposited on the third or fourth segment of the *Aphidius*, the hyperparasite must needs seek the new situation for itself after hatching.

TEXT-FIG. 3.



The larva, newly hatched, showing tracheal and nervous systems.
× 200.

The internal anatomy, with the exception of the tracheal system, does not change essentially during development, so that an account of it is left to the description of the fourth instar. The mouth, which is very small and transversely oval, is furnished with two slender mandibles, set behind the hood-like labrum, and the labium (fig. 5). The head is furnished with two tactile papillae. The mid-gut, which at this stage, as with the other parasitic Hymenoptera, does not communicate with the proctodaeum, is large and globose, and its contents tinge the otherwise transparent larva pale yellow.

The tracheal system consists of a pair of lateral trunks, united by an anterior commissure passing above the oesophagus in

front, and a posterior commissure passing beneath the gut, in the eleventh segment, behind. Simple dorso-lateral, and ventro-lateral, branches are given off in segments 1, 3-8. When newly hatched there are only two pairs of open spiracles, the first between the first and second segments, and the second on the anterior part of the fourth, but the spiracles of the third and fifth segments open shortly afterwards. (See 'Moult's'.)

Seurat (26, p. 100) states that the young larva of the Chalcid, *Torymus propinquus*, has likewise four open spiracles, but situated on the first, fourth, fifth, and sixth segments.

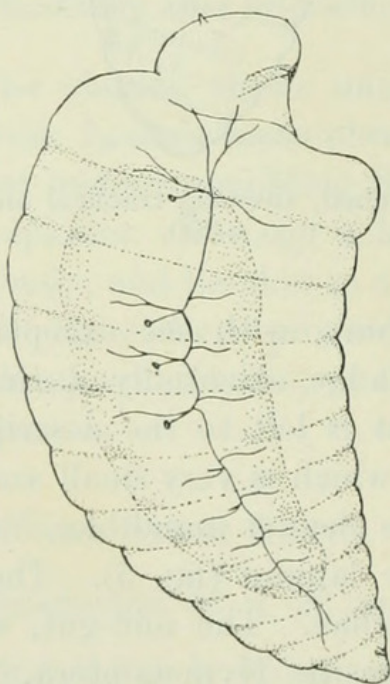
This stage lasts from twenty to twenty-four hours.

SECOND STAGE LARVA.

Dimensions $\cdot 70 \times \cdot 35$ mm.

The second stage larva differs from the first chiefly in the tracheal system, and in the greater development of the anterior

TEXT-FIG. 4.

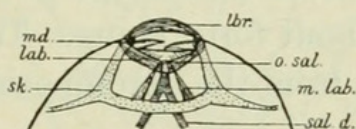


The larva of the second instar, showing tracheal system. $\times 200$.

part of the body in proportion to the head, so that the latter appears constricted off from the thorax, and the body resembles

a cone with the head projecting from the blunt end. The tracheal system is more complex: the ramifications of its branches are more numerous, and those of the second segment appear at this stage. The stigmatic trunks of segments six,

TEXT-FIG. 5.



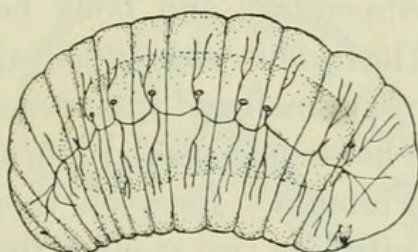
Mouthparts of second stage larva. $\times 400$. Ventral view. *o.sal.* = aperture of salivary duct. *sk.* = endoskeleton of head. *lab.* = labium. *m.lab.* = muscles of labium. *lbr.* = labrum. *md.* = mandibles. *sal.d.* = salivary duct.

seven, and eight are visible at the junction of the dorso-lateral branches with the main stem of the tracheae, but the corresponding spiracles are still closed. This stage lasts about thirty-six hours, and during this time the host dies and becomes black and shrunken. The hyperparasite seems to feed by suction, and the skin of the *Aphidius*, otherwise uninjured, is gradually emptied of its contents. As the fluid from the decomposing tissues passes into the mesenteron of the Proctotrypid, the latter changes in colour from yellow to brown.

THIRD STAGE LARVA.

Dimensions $1.00 \times .75$ mm.

TEXT-FIG. 6.



Larva of the third instar, showing tracheal system. $\times 49$.

In the third stage the body becomes globose, owing to the increased proportionate development of the first seven or eight segments to accommodate the distended mesenteron. The result

of this distension is to bend the head round ventrally to form an acute angle with the long axis of the body. The papillae on the head disappear. The branching of the tracheal system is more elaborate, and the spiracles of segments six, seven, and eight open in the order named, while the stigmatic trunk of the second segment appears. This stage is longer than the two preceding, and lasts about forty hours. The parasite is bathed in the fluid that oozes from the decomposing body of the host.

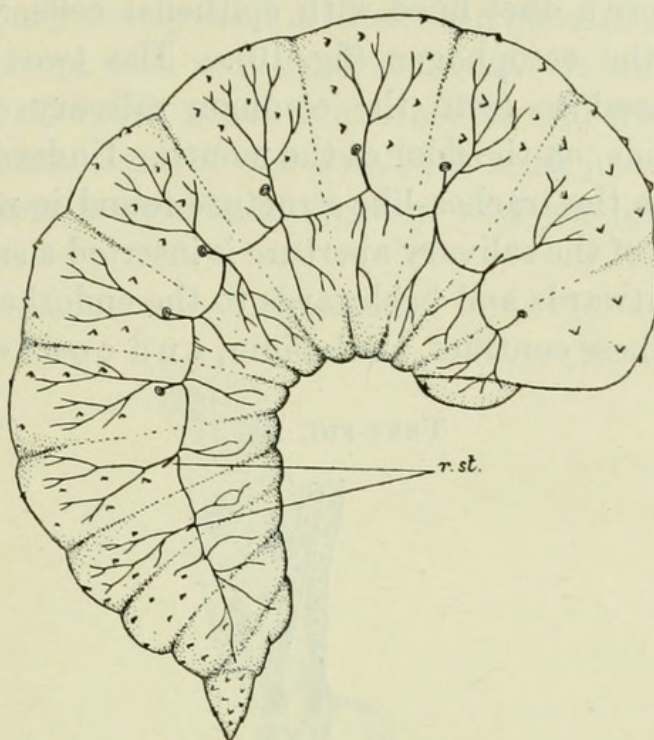
FOURTH STAGE LARVA.

The larva in the fourth instar differs considerably from that of the preceding stages in size and form. Immediately after ecdysis, the dimensions are not much greater than those of the third instar, and the body is transparent; but as the larva ingests the remainder of its host, it grows rapidly, and when fully fed, measures $1.67 \times .83$ mm. At the same time it becomes creamy white and opaque.

The first four body segments are greatly developed. The small head is bent completely round to the ventral side, and is almost hidden by the large prothorax. The abdominal segments diminish in diameter posteriorly, and the last bears dorsally a conical caudal appendage. The function of this is unknown, unless it is used as a lever by the larva which is able to turn round freely in the cocoon. Seurat (26, p. 99) has described a somewhat similar appendage in a Chalcid, *Encyrtus* sp., and supposes that its purpose is locomotion (fig. 9, *cd.*).

Both the caudal appendage and body bear short chitinous papillae or spines. The head is without larval antennae or palpi. The mouth, which is very small and transversely oval, is bounded anteriorly by a large horseshoe-shaped labrum, and posteriorly by a smaller square labium. Between these, and deeply set within the buccal cavity, are two stout little mandibles (fig. 8). The salivary glands extend from the dorsal part of the fourth segment forwards on either side of the mid-gut as two straight tubes with a considerable lumen. They are formed of polyhedral cells with large nuclei and granular cytoplasm, which stains deeply with haematoxylin. Each gland runs obliquely

TEXT-FIG. 7.



Larva of the fourth instar, showing tracheal system. $\times 49$. *r. st.* = rudimentary stigmatic trunks of segments 9 and 10.

TEXT-FIG. 8.



The mandibles of the full-grown larva. $\times 400$.

TEXT-FIG. 9.

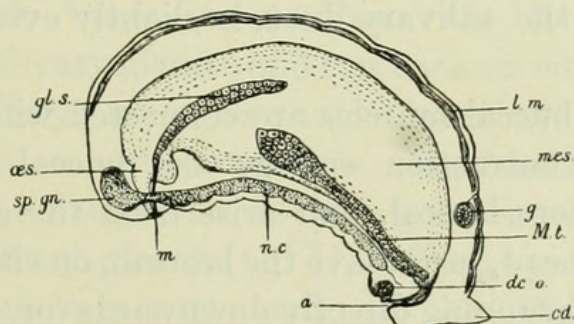
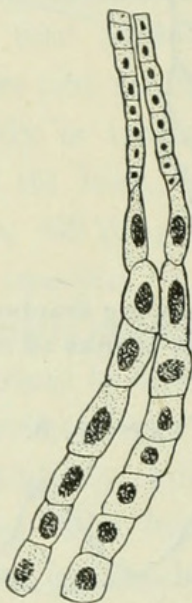


Diagram of the general structure of the fourth stage larva. *a.* = anus. *cd.* = cauda. *g.* = gonad. *dc. o.* = imaginal disk of ovipositor. *l. m.* = longitudinal muscles. *M. t.* = Malpighian tube. *mes.* = mesenteron. *m.* = mouth. *n. c.* = nerve cord. *oes.* = oesophagus. *gl. s.* = salivary gland. *sp. gn.* = supra-oesophageal ganglion.

forwards and downwards, and between the first and second segments enters a duct lined with epithelial cells, very similar to those of the oesophagus (fig. 10). The two ducts unite behind the head to form the common salivary duct, which opens just inside, on the floor of the mouth. Under high power, the ducts have the trachea-like structure found in most insects. On either side of the salivary aperture is inserted a small muscle, which runs outwards and backwards to the endoskeleton of the head. When these contract, the labium, and consequently

TEXT-FIG. 10.



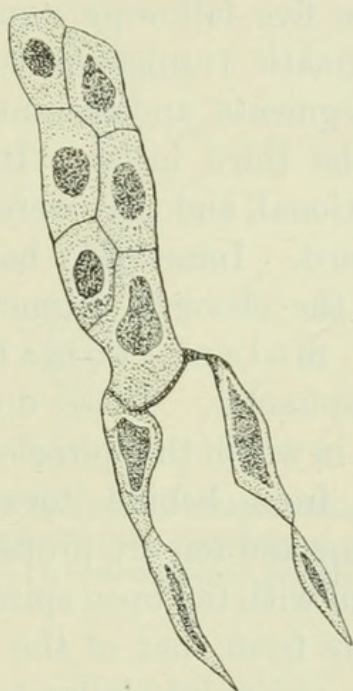
Longitudinal section through the salivary gland and duct of a larva of the fourth instar. $\times 300$.

the opening of the salivary duct, is slightly everted from the mouth (fig. 5).

Two pairs of buccal muscles are connected with the labrum, and by their contraction enlarge the buccal cavity. The anterior, and more lateral, pair arise from the exoskeleton of the front of the head, just above the labrum, on either side of the median line, and running directly downwards (or, having regard to the position of the head, backwards) are inserted on the roof of the mouth. The posterior and median pair arise together behind the last, and, running forwards obliquely between them, are inserted on the distal half of the labrum (fig. 13). The

short oesophagus opens into the mid-gut, which fills the greater part of the body cavity, and is lined with glandular cells, rather wider than deep, with well-marked nuclei. It contains a mass of fluid food material, which is churned to and fro by incessant muscular contractions of the body, but until just before metamorphosis there is no communication with the hind-gut. Two

TEXT-FIG. 11.



Longitudinal section through the Malpighian tube of a larva of the fourth instar, showing lumen. $\times 300$.

large Malpighian tubes extend from the fourth segment, ventral to the salivary glands, and run back on either side of the mesenteron. They are somewhat dilated at their anterior extremities, and in sections show a considerable lumen, surrounded by large flattened cells with great nuclei, resembling those of the salivary glands (fig. 11). In the posterior half of the tubes the lumen is very small and the cells are rounded. The tubes open into the ampulla of the proctodaeum, that is, the cup-like anterior end of the hind-gut, which abuts on the mid-gut in the eleventh segment (fig. 14).

The muscular system is well developed, especially the dorsal

longitudinal, and lateral muscles of the posterior segments (fig. 9).

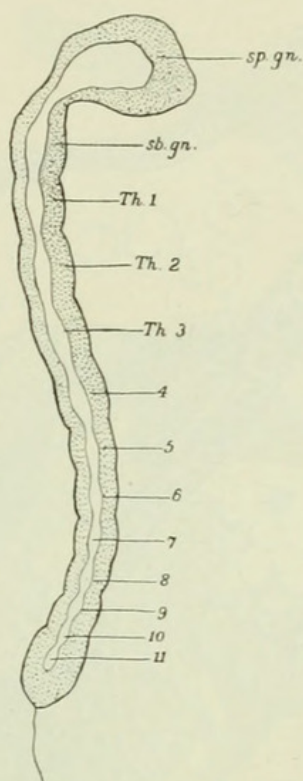
The circulatory system calls for no particular comment.

In the tracheal system of the fourth instar larva there are still seven pairs of open spiracles, for the eighth (mesothoracic) does not become functional until metamorphosis. The first spiracle is situated between the first and second segments, and the second on the posterior side of the third segment, while the remainder are on the five following segments. In addition, two rudimentary stigmatic trunks can sometimes be seen on the ninth and tenth segments, and the anterior one is occasionally visible during the third instar. It appears that these trunks are never functional, and they were not always apparent in the larvae examined. Imms (11) has described vestigial stigmatic trunks on the eleventh segment of the full-grown larva of *Aphycus melanostomatus*, which has nine pairs of functional spiracles. These do not appear in the *Lygocerus* larva, in which the spiracles have evidently been reduced in number from behind forwards. The aborted trunks of segments nine and ten are probably vestiges inherited from an ancestral form with ten open spiracles. The rest of the tracheal system differs from that of the preceding stage only in the greater calibre and more elaborate ramifications of the tubes. It should, however, be remarked that there is no anastomosis of the tracheal branches of the two sides of the body, such as Seurat (26) describes in certain *Ichneumonidae* and *Braconidae* (fig. 7).

The nervous system consists of two supra-oesophageal ganglia, united by a broad commissure, and connected with the sub-oesophageal ganglion by two short, thick circum-oesophageal commissures. The ventral nerve cord contains eleven ganglia. The four anterior are well marked; the five following are less distinct, and appear as a wide, slightly-segmented band. The cord terminates in a bulbous swelling, composed of two ganglia, that of the eleventh segment being fused with that of the tenth (fig. 12).

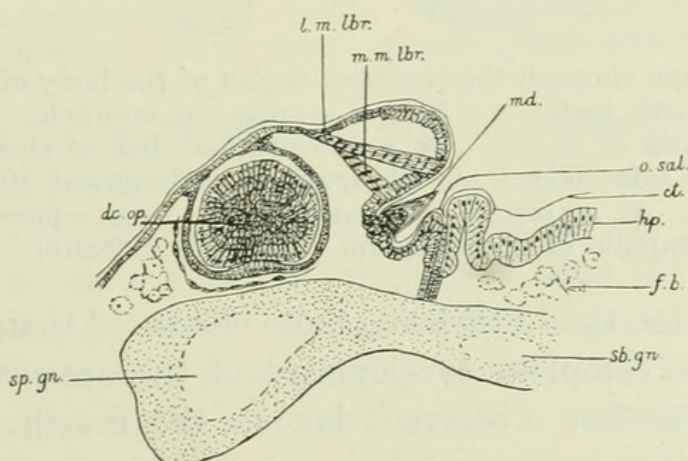
The genital organs lie above the mid-gut on either side as

TEXT-FIG. 12.



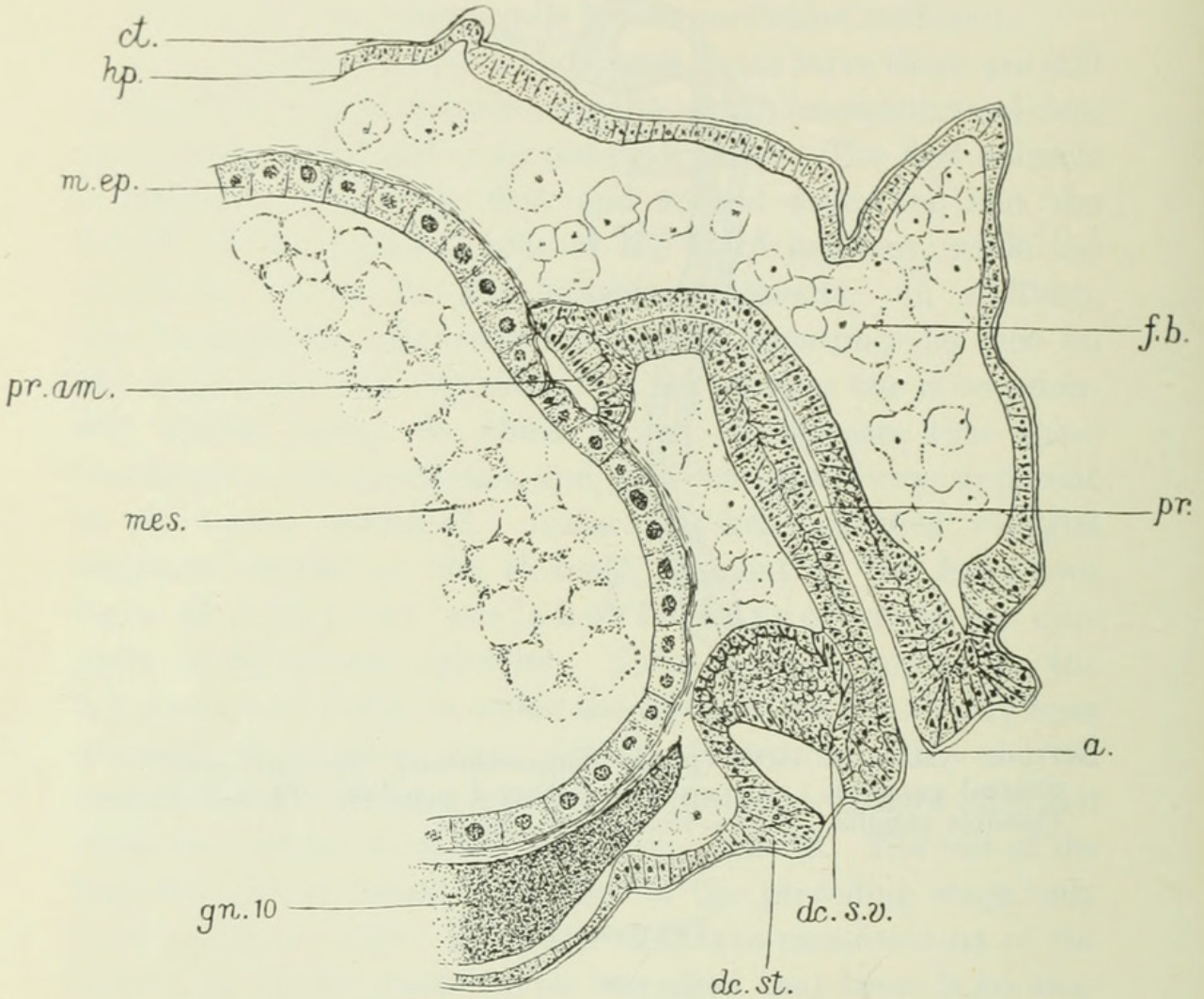
Nervous system of larva (partly diagrammatic). *sb.*=sub-oesophageal ganglion. *sp.*=supra-oesophageal ganglion. *Th.* 1-3 = Thoracic ganglia. 4-11.=abdominal ganglia.

TEXT-FIG. 13.



Vertical section through the head of a larva of the fourth instar. (The muscles of the labrum are shown somewhat diagrammatically.) $\times 200$. *cl.*=cuticle. *dc. op.*=imaginal disk of eye. *fb.*=fat body. *hp.*=hypoderm. *l. m. lbr.*=lateral muscles of labrum. *m. m. lbr.*=median muscles of labrum. *md.*=mandible. *o. sal.*=aperture of salivary duct. *sb. gn.*=sub-oesophageal ganglion. *sp. gn.*=supra-oesophageal ganglion.

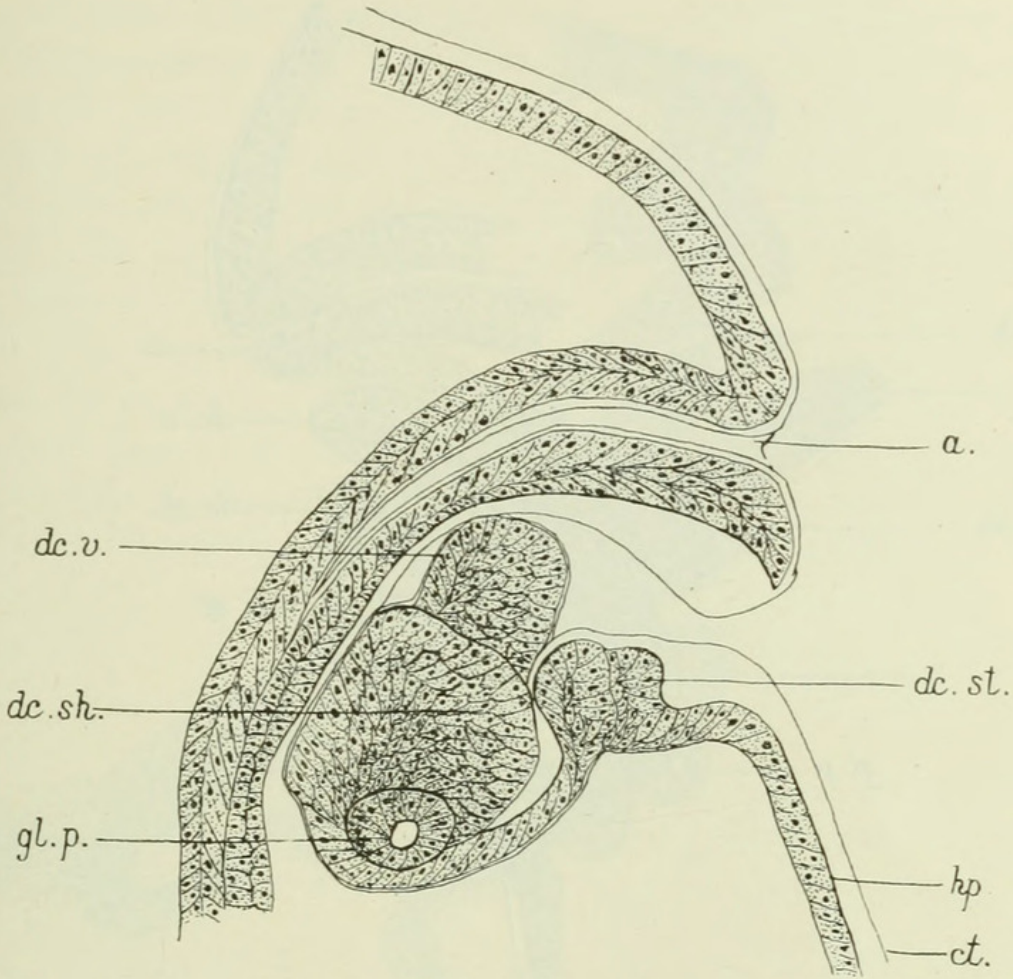
TEXT-FIG. 14.



Vertical section through the posterior region of the body of a larva of the fourth instar. $\times 350$. *a.*=anus. *ct.*=cuticle. *dc.st.*=imaginal disk of stylets. *dc.s.v.*=imaginal disk of sheath and valves. *fb.*=fat body. *gn. 10.*=ganglion of segment 10. *hp.*=hypoderm. *m.ep.*=wall of mesenteron. *mes.*=mesenteron. *pr.am.*=ampulla of proctodaeum. *pr.*=proctodaeum.

two oval bodies, the testis being more elongated than the ovary (fig. 9). The complete development of the accessory genital apparatus was not observed, but in the fourth instar the female armature exists as two imaginal disks on the eleventh and twelfth segments. In *Lygocerus* the relationship of the parts is somewhat obscured, owing to the curvature of the body and crowding together of the segments in the posterior ventral region, but my observations on the origin of the

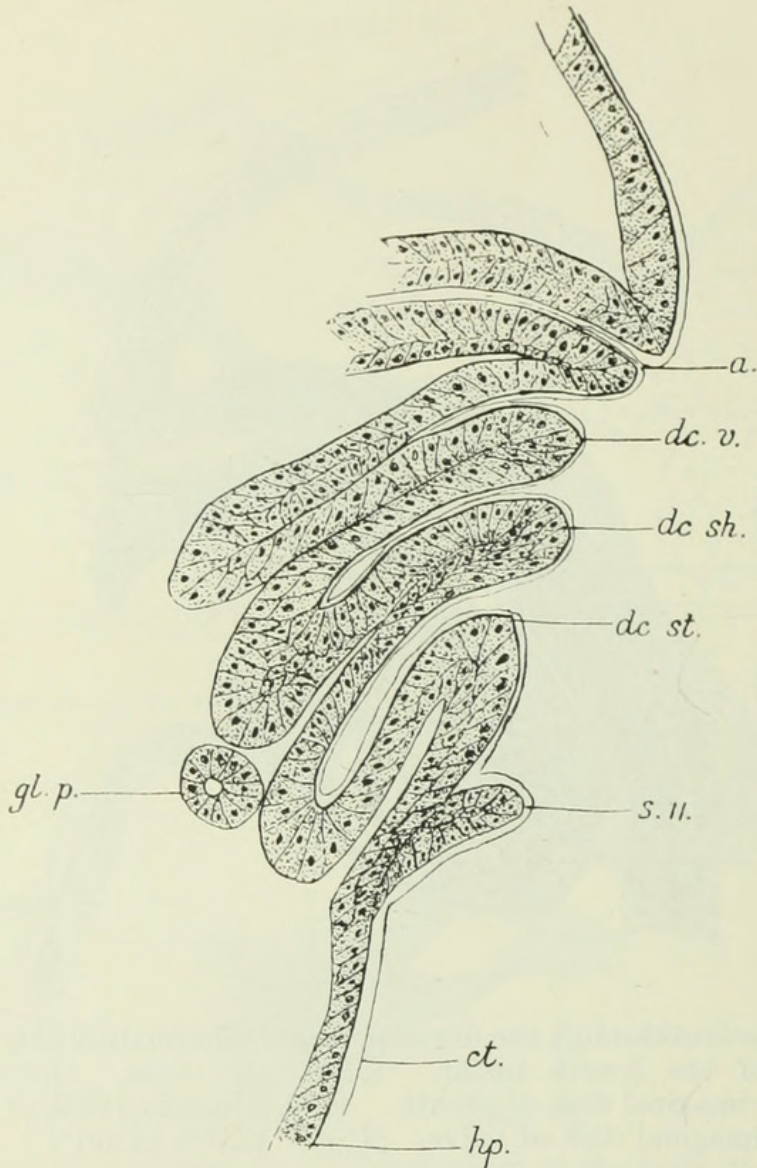
TEXT-FIG. 15.



Vertical section through the developing genital armature of a female larva of the fourth instar. $\times 350$. *a.* = anus. *ct.* = cuticle. *dc. sh.* = imaginal disk of sheath. *dc. st.* = imaginal disk of stylet. *dc. v.* = imaginal disk of valve. *gl. p.* = 'poison gland'.

ovipositor, as far as they go, are substantially in agreement with those of Seurat on *Doryctes gallicus*. The stylets arise from the posterior ventral wall of the eleventh segment, and the sheath and valves are derived from the reduplication of the imaginal disks of the twelfth segment. A tubular glandular structure is formed by constriction from the hypodermal cells at the base of the latter. In its origin and position it corresponds with that described by Seurat as 'la glande à venin'. Whether this organ is actually a poison gland in the Ceraphronidae I am unable to say. Saunders, quoted by Woodward (Ashmead, 1), records that he was stung by a female

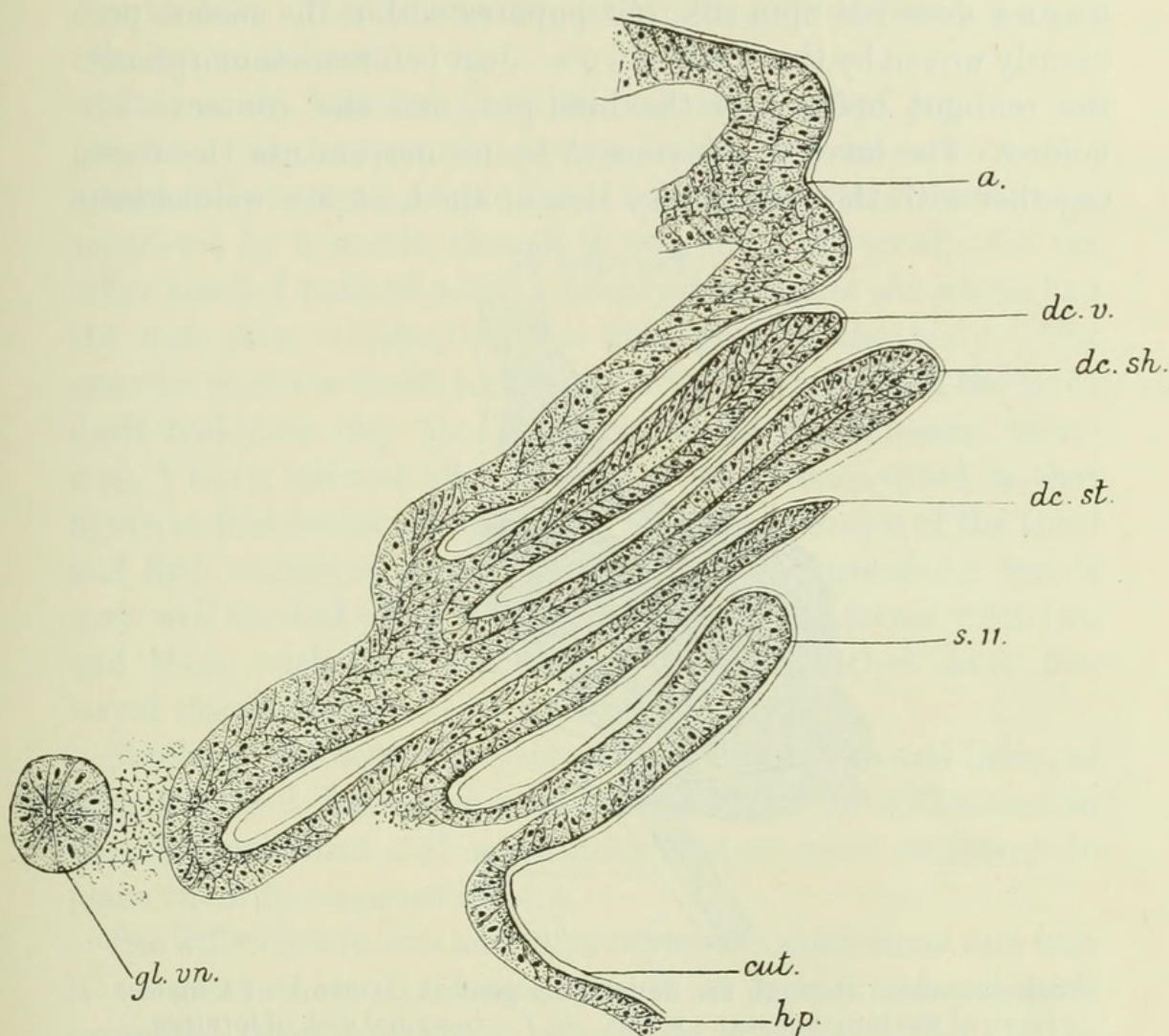
TEXT-FIG. 16.



The same as fig. 15, more advanced. $\times 350$. *a.* = anus. *ct.* = cuticle. *dc. sh.* = imaginal disk of sheath. *dc. st.* = imaginal disk of stylet. *dc. v.* = imaginal disk of valve. *gl. p.* = 'poison gland'. *hp.* = hypoderm. *s. 11.* = sternite of segment 11.

of *Scleroderma linearis*; and of other parasitic Hymenoptera, the female Ichneumonid, *Ophion*, will sometimes pierce with the ovipositor when handled. The pain is more severe and persistent than a mere mechanical stab would produce, so that presumably some secretion enters the wound. Bordas and others have described structures in various Terebrantia which appear to be homologous morphologically with the poison glands of the Aculeata, but their function is

TEXT-FIG. 17.



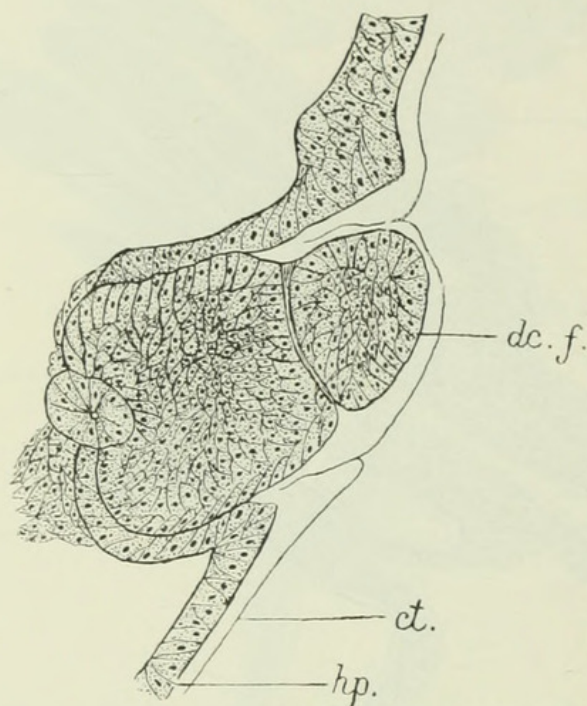
The same as in figs. 15 and 16, shortly before metamorphosis. $\times 350$. *a.* = anus. *ct.* = cuticle. *dc. sh.* = imaginal disk of sheath. *dc. st.* = imaginal disk of stylet. *dc. v.* = imaginal disk of valve. *gl. p.* = 'poison gland'. *hp.* = hypoderm. *s. 11.* = sternite of segment 11.

still uncertain. The tubular gland, 'glande tubuleuse', that Seurat describes in *Doryctes*, I have not traced in *Lygocerus* (figs. 14, 15, 16, 17).

Owing to lack of suitable material, the whole ontogeny of the male genital armature was not followed, but it appears to arise, as described by Seurat, from the imaginal disks of the twelfth segment only. In the fourth instar two terminal lateral processes appear at the end of the disks, and probably represent the future stipites (forcipies) (fig. 18).

The fourth instar lasts between two and three days. *Lygocerus* does not spin silk, but pupates within the cocoon previously woven by the *Aphidius*. Just before metamorphosis, the mid-gut opens into the hind-gut, and the contents are voided. The larva is active, and by its movements the frass, together with the now empty skin of the host, are welded into

TEXT-FIG. 18.



Vertical section through the developing genital armature of a male larva of the fourth instar. $\times 350$. *dc. f.* = imaginal disk of forecipes.
ct. = cuticle *hp.* = hypoderm.

a compact, moist pellet at the ventral side of the body. The frass of the Proctotrypid, Chalcid, and Cynipid parasites of *Aphidius* can readily be distinguished from one another, for that of *Lygocerus* is invariably a single black mass, whereas that of the Chalcidae and Cynipidae consists of several pieces of a different form and colour.

MOULTS.

The determination given of the number of moults, and the duration of the instars, is based on the examination of many individuals of different ages, and may be somewhat arbitrary; but it was the only practicable method to employ, since it

proved impossible to keep one larva alive for observation from day to day. The reasons for determining the different instars thus are as follows :

The newly hatched (first instar) larva of *Lygocerus* possesses only two pairs of open spiracles, but examples twelve hours old have four. At one time I believed that these forms were separated by a moult, though it was never observed. On the other hand, I noticed a larva twenty-four hours old which had the cast skin attached to the hind part of the body. The exuviae were too much torn to show the spiracles, but the larva itself had four (fig. 4). For purposes of convenience, therefore, I have referred all stages up to that represented in that figure to first instar, and assumed that the spiracles of the third and fifth segments opened as the stadium proceeded ; but it may well be that there is a moult between the forms with two and those with four spiracles. We should then have five larval stages, separated by four moults.

Similarly, the actual ecdysis between instars two and three, as here described, has never been observed, but the differences in the external form and respiratory system seem sufficient to place them in separate instars.

The difference in size and form between instars three and four is so great that, if a large number of larvae had not been examined, there would have been doubt in referring them to the same species. The fourth instar, immediately after the moult, is transparent, and half the size of that represented in fig. 7. But the caudal appendage and tracheal system are unmistakable, so that although the actual ecdysis has not been seen, this form has been described as the fourth instar.

PUPATION AND EMERGENCE.

The period of pupation is from fourteen to sixteen days. If disturbed, the pupa jerks its abdomen vigorously from side to side. It is possible that this habit, which is marked in both the larva and the pupa, and in which they differ from the *Aphidius* itself, and from its Chalcid and Cynipid parasites.

may in some degree protect them from ovipositions by the females of their own and other families.

When ready to emerge, the imago gnaws a hole somewhere on the dorsal side of the cocoon and creeps out. As Gatenby (9) has remarked, this hole differs from that made by *Aphidius* in having irregular edges, and is not necessarily placed in the dorso-posterior region of the aphid's skin.

The number of broods occurring in one year is not known, and probably depends on the number of species of *Aphidius* upon which the hyperparasites can live. Two broods were reared from *Aphidius ervi* in 1919; but the host did not appear in any numbers before July, and it is possible that earlier broods may have occurred with a different host. All the imagos of *Lygocerus* had emerged by the end of August, and there is no evidence to show whether the species over-winters as larva or pupa.

In captivity the imagos generally live five or six days, but sometimes as long as ten. They were observed to feed on sugar and water, on honey-dew from the aphides, and on sap oozing from cut leaves, but they seemed to live as long, and to remain as vigorous, when no food was supplied.

COMPARISON OF LARVAL CHARACTERS WITH THOSE OF OTHER SUB-FAMILIES.

The most complete comparative account of the larvae of entomophagous Hymenoptera is that of Seurat (26), who studied certain Ichneumonidae, Braconidae, and Chalcidae. Unfortunately he did not include the Proctotrypidae, and our knowledge of the larval morphology of this family, as already remarked, is very scanty. Seurat emphasized the importance of the tracheal system in determining the larvae of the different groups, but, as Lichtenstein and Picard have recently pointed out (15), increased knowledge has somewhat modified this view.

Some authorities have considered that the Proctotrypoidea are allied to the Chalcidoidea, but Ashmead (1) disputes this, and thinks them in every respect more nearly related to the Hymen-

optera Aculeata, and among Terebrantia, to the parasitic Cynipidae. The discussion of the affinities of the group is outside the scope of this paper, but it should be pointed out that the larval form of this particular genus of Ceraphroninae differs from the Chalcid larvae described by Seurat (26), Imms (11), Embleton (6), &c., in several respects. As regards the tracheal system, the late opening of the spiracle of the second segment is common to many larvae of the entomophagous Hymenoptera. On the other hand, the larva of *Lygocerus* is remarkable for the reduced number of abdominal spiracles, and the rudimentary nature of the stigmatic trunks of segments nine and ten, and differs from the Ichneumonidae and Braconidae studied by Seurat in the absence of anastomosis of the tracheal vessels of either side; though as Lichtenstein and Picard (15) have shown for the Braconid, *Sycosoter la vagnei*, this is not an invariable character of the external feeding Braconidae.

The reduction in the number of spiracles is carried still further in *Platygaster*. Marchal (18) figures four spiracles in *Platygaster ornatus*, the first between the first and second segments, and those succeeding on the third, fourth, and fifth. The spiracle of the fourth segment (the propodaeum of the imago) differs from the others in its larger size, and the greater proliferation of the hypoderm cells surrounding it. 'Il est pareil à une sorte d'histoblaste aux dépens duquel devra se former plus tard le grand stigmate du segment médiaire de l'adulte.' Further, in *Platygaster*, the main tracheal trunks are not joined posteriorly by a commissure. In *Lygocerus* a posterior commissure exists, and the spiracle of the fourth segment is indistinguishable from the rest.

Likewise M'Colloch (20) describes 'four or five pairs of well-developed spiracles' in the larva of the Scelionid, *Eumicrosoma benefica*; but Ganin (8) states that there are nine spiracles in the third stage larva of the form of *Platygaster* that he studied, and that spiracles are lacking only on the first, second, and three last segments.

Kulagin (14) for *Platygaster*, and Ayers (2) for

Teleas, do not describe the later stages of the larvae, and say nothing about the tracheal system. Keilin and Thompson (12) describe nine pairs of spiracles in a Dryinid larva, parasitic in *Typhlocyba* (Homoptera). The relative positions are not determined, but from the figure it seems as if the meso-, or possibly the metathorax, bears no spiracles.

I can find no other account of the tracheal system of the Proctotrypoidea, and until we have more knowledge of the hymenopterous larvae which live upon their hosts as external parasites, we cannot tell how far the characters observed indicate true phylogenetic relationships, or are merely secondary adaptations. Moreover, it is unwise to compare a highly modified internal parasite, such as *Platygaster*, with the more generalized external forms; though in this connexion it may be significant that the third stage larvae of *Platygaster* and *Eumicrosoma* have a certain resemblance to the early larva of *Lygocerus*.

The differences are not confined to the tracheal system. Marchal describes ten ganglia in the nerve cord, and three Malpighian tubes, in *Synopeas rhanis*. Keilin and Thompson observed thirteen ganglia, and no Malpighian tubes, in the Dryinid that they studied. This diversity of structure indicates either that little reliance can be placed on larval characters, which are often adaptive, or that the Proctotrypoidea as at present understood are, in some respects, an arbitrary group.

ECONOMIC STATUS.

From an economic standpoint *Lygocerus* must be regarded as an injurious insect. Parasitisation by Braconidae is an important natural check upon the increase of plant-lice; and this Proctotrypid, like the hyperparasitic Chalcidae and Cynipidae, is an enemy of the beneficial *Aphidius*. Unless, as seems improbable, it confines its attacks to a single species, it must destroy considerable numbers of Aphidiidae.¹ *Aphi-*

¹ Kieffer records that *L. testaceimanus* has been reared from a rose aphid (? *Macrosiphum rosae*) (13, p. 51).

dius ervi, and the nearly related species *A. avenae*, are parasites of such pests as *Macrosiphum granarium*, the grain aphid, and according to Marshall (19) are polyphagous, preying indiscriminately on various species of aphides. If their parasites follow them to other hosts, their efficiency as controls of plant-lice must be seriously impaired. For instance, two collections of *A. ervi* from *M. urticae*, made from different places round Cambridge in August, gave the following results :

	Number examined.	Parasitised by other families.	Parasitised by <i>Lygocerus</i> .	Total % parasitised.	% Para- sitised by <i>Lygocerus</i> .
I	50	12	16	56	32
II	38	6	17	60	44

Other collections, of which exact records were not kept, likewise showed a high percentage of hyperparasitisation by these Proctotrypids.

Aphidius is at least twice as prolific as its parasite, and each female destroyed by the latter means the loss of thirty or forty ovipositions, which would kill, or at least impair the fertility of, the same number of aphides. If this high rate of hyperparasitisation should occur in a grain crop infested by *Macrosiphum granarium*, attacked by *Aphidius*, the efficiency of this natural control might be lowered by 50 per cent.

SUMMARY.

1. *Lygocerus testaceimanus*, Kieff. is a hyper-parasite of *Aphis saliceti*, Kalt., through the primary parasite, *Aphidius salicis*, Hal.; and *L. cameroni*, Kieff. is similarly a hyperparasite of *Macrosiphum urticae*, Kalt., through the primary parasite, *Aphidius ervi*, Hal.

2. The *Aphidius* is attacked immediately before or after metamorphosis, when lying within the empty skin of the aphid within which it is reared.

3. The egg is laid, and post-embryonic development takes place, outside the body of the host.

4. The evidence points to the conclusion that there are four larval instars and three moults.

5. The larvae differ in several particulars from those of the families of Proctotrypoidea previously described, and there is considerable difference in form between the early and later instars.

6. During development, which lasts about six days, the larva devours its host, and then pupates within the skin of the aphid for a further period of two weeks.

7. Two, and possibly more, broods are reared in the season; and it is probable that the hyperparasite is a considerable check on the *Aphidius* in its control of plant-lice infestation.

8. *Lygocerus*, though occasionally attacked by its own species, was never found to be parasitised by another hymenopteron. This immunity is probably due to the active movements with which the larva and pupa in the cocoon respond to external stimuli.

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