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THE BIONOMICS OF GRIBURIUS TRIANGULARIS SUFFR.

by

J. L. Gregory, B.Sc.(Hons.), Dip. Agric. Sci.

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Dissertation in part requirement for the Diploma
in Tropical Agriculture.

—— 1948-9 ——

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Introduction and Acknowledgements

As a preliminary to the biological control of Cordia macrostachya, a troublesome weed introduced into Mauritius from British Guiana about 1890, a survey of the insects living upon this plant in Trinidad was made by R.G. Donald and A.M. Adamson in 1944.

One of the insects noticed in this survey was Griburius triangularis Suffr., a Cryptocephalid (although Donald (1944) records it as a Hispid) feeding in the adult stage upon the inflorescences. This feeding habit would be useful from the point of view of biological control, but the insect is not common enough to be of any practical value in this respect in Trinidad.

The life cycle in the laboratory was studied by R.G. Fennah, who fed the larvae upon Cordia inflorescences. He noted a very high larval mortality, which he attributed to the planidia of Kapala furcata F. (Eucharidae) which appeared to pierce the skin of the larva and kill it.

This was thought to be peculiar as most Kapala species are parasitic upon ants, particularly upon those of the genus Odontomachus. Now Cryptocephalid larvae commonly feed upon decomposing vegetable matter, either on the ground or, more usually, in the nests of ants. It was thought that, in nature, the planidium of Kapala furcata might be carried into the ant's nest after attaching itself to the Griburius larva. This may happen in the case of Psilogaster sp. in Malaya which oviposits round the newly laid eggs of Selenothrips rubrocinctus (Clausen, 1940) and whose planidia attach themselves to the thrips nymph as it emerges. The rest of the life history is unknown but it is possible that the thrips nymph is in some way used to transport the Eucharid planidium to its host. It was with these ideas in mind that the investigation was started.

The object of the investigation then was twofold. Firstly to study the normal life history of the beetle to discover the reasons for its relative scarcity; and secondly to determine the relationship existing under natural conditions between the larva and Kapala furcata.

I would like at this point to express my thanks to Professor T.W. Kirkpatrick, who suggested this problem, for his interest and ready assistance and advice at all times; also to Dr. E.McC. Callan and Dr. F.J. Simmonds for their many helpful suggestions. Thanks are also due to other members of the College Staff for their ready assistance and co-operation.

PART I THE LIFE HISTORY OF GRIBURIUS TRIANGULARIS SUFFR.

(1) Description and General Habits of the Adult Beetle

The female is a small compact beetle, 4.5 to 5.0 mm. long by 2.5 to 3.0 mm. wide (Figures 1 and 2). The head is black but appears grey dorsally due to the presence of a fine white pubescence which covers the dorsal surface of the head and the dorsal third of the space between the eyes. These are reniform, and subtend, on the concave, mesial edge, the base of the antennae. The latter are slightly serrate and 11-jointed, of which the first and proximal half of the second joint are pitchy, the distal half of joint 2 and joints 3 to 6 are red and joints 7 to 11 are black.

The thorax is typically dark brown to black in colour with a slight purple or green metallic sheen, and diffusely punctured. The disc is black and glabrous but there is a fine white pubescence surrounding it which partially hides the lighter brown coloration of this area.

The scutellum is black, triangular in shape and diffusely punctured with a few white hairs upon it.

The elytra, which leave the pygidium exposed, are typically black, with a slight purple or green metallic sheen and a light brown spot at the base and apex of each elytron. The marking of both the elytra and the thorax varies considerably over the whole range from almost entirely black forms to those in which light brown predominates. In the elytra, the light brown spots may coalesce on the outer margin of the elytron but there is always a thin inner margin of black and a small semi-circular area of black on the mesial edge of each elytron.

The pygidium and ventral surface of the abdomen and thorax are dark brown to black in colour but are again rendered grey by the fine white pubescence. On the ventral surface of the thorax, are two cavities for the reception of the fore femora when the insect retracts its legs.

The coxae, trochanters and femora of the fore legs are dark red, the tibiae and first two tarsal joints are yellow and the last two tarsal joints are red. The middle and hind legs have tibiae and tarsi of the same colour as those of the fore legs. The coxae, trochanters and femora, however, are yellow, and the femora are much less highly developed than those of the fore legs.

The male is 3.5 to 4.0 mm. long by 2.0 mm. wide. It differs from the female in that the eyes are closer together and the size of the hairless disc of the thorax is relatively greater.

Griburius triangularis is observed most frequently on the surface of Cordia bushes, during bright calm weather. It shows a distinct preference for those bushes with plenty of young, green leaves and inflorescences.

It feeds upon the petals and flower buds of young Cordia inflorescences, usually eating half of the bud and then passing on to the next. Occasionally also the younger parts of the rachis, the undersides of the main leaf veins and even the edges of the leaves are eaten in the laboratory. The beetle feeds with a semi-circular movement, commencing in front of the head and moving posteriorly. The damaged surface later turns dark brown, a deeper shade than that caused by purely mechanical injury. Presumably this is due to the action of the salivary fluid.

When the beetle is disturbed, it may either fly away or retract its legs, the fore femora fitting into the cavities on the ventral surface of the thorax, and fall to the ground.

Two types of excretion were noted. The most common is in the form of an elongated, black, bead-like string. This is frequently noticed between copulating couples besides being the normal method of defaecation and is similar in colour and consistency to the material used to form the egg case. Occasionally also a yellow, semi-liquid droplet is exuded which later dries to form a dark brown stain on the surface on which it is deposited. The significance of the two types and the reasons for their production are not known.

In the laboratory, the beetles were kept and studied in inverted lamp glasses, over which were placed circular iron rings covered with gauze. Inside was a small tube of water containing a young Cordia shoot secured by a plug of cotton wool. The shoot was changed every 2 days and the beetles lived and laid eggs well under these conditions, an average life of 34 days and a maximum of 56 days being recorded for female beetles. The method has the disadvantage that the gauze covers tend to fall off in windy weather allowing the beetles to escape, but on the whole the method proved quite satisfactory.

(2) Mating

Mating takes place at frequent intervals throughout the life of the adult Griburius, sometimes more than once per day and pairs may remain in copulation for several hours, faeces being frequently noted between the two beetles. Beetles begin to copulate from 1 to 4 (usually 3) days after emergence, though a newly emerged male in the laboratory will often mount onto the females back and remain there for some time, rather to one side of the female, making no attempt to copulate. This was not observed in the field.

The male walks up to the female, and touches her head with his antennae. After doing this he climbs onto her back and, still facing the posterior end, walks along, turns round and lowers himself down and tries to insert his flat, spade shaped penis under her pygidium. The male takes up a position with the tarsi of the fore and mid legs resting upon the elytra of the female. The hind legs and tarsi are held close to, but not actually touching, the pygidium of the female, and seem to play no part at all in copulation.

(3) Egg laying

Egg laying commences normally about 3 days after mating. Eggs are occasionally laid in the laboratory if a female remains unmated for some time after emerging, but they are always infertile.

Before the egg is laid, the female balances herself upon the four front legs and raises the hind legs so that the hind tarsi are ready to hold the egg as it is laid. The pygidium makes one or two preparatory movements and then opens, and the egg is extruded. The hind tarsi move up to form a platform which supports the lower end of the egg and holds the other end against a slight depression in the centre of the last abdominal sternite.

While the egg is in this position, the tip of the anus is extruded through the pygidium, touches the posterior pole of the egg and extrudes a droplet of a viscous greenish fluid by a slight lowering of the tarsi and withdrawal of the anus. The droplet gradually turns to dark brown and is gently touched by the tip of the anus so as to slightly flatten the edges. After waiting for about 15 seconds, the egg is turned slightly in a clockwise direction, and another droplet is extruded which partially covers the edge of the first. This process continues with a spiral movement all the way round the egg. As more and more of it becomes covered in this way, the tarsi gradually move anteriorly, thus changing the position of the egg into a more vertical position. Instead of supporting the egg along its long axis, they now hold it at right angles to this.

When nearly all of the egg is covered, it is moved and held out behind the beetle. The egg case is completed by a single droplet being applied to the anterior end. As this is happening, the anus is retracted and the droplet is drawn out into the characteristic, curved prolongation on the anterior end of the egg case.

This process is completed in about 8 minutes, but the egg is retained by the female for a further period of 4 minutes or more to allow the egg case to harden still further. It is then dropped and falls to the ground, and no further interest in it is taken. A fallen egg is never picked up again, even if incompleted, as for example when the female is disturbed during egg laying and drops the egg, or when she has insufficient faeces to cover it.

The average female commencing to lay eggs does so at the comparatively low rate of 6 eggs per day for the first two or three days. This increases until at the end of the first week an average of 12 to 14 eggs per day is reached and maintained for approximately three weeks. Hereafter, the rate of egg laying slowly falls until the death of the insect.

The egg laying of 22 beetles was recorded for the whole of their life. They laid an average of 330 eggs each (range 14 to 630) over an average period of 26 days (range 3 to 49 days).

The continued formation of normal egg cases is dependent upon the availability of proper food. If the Cordia shoot upon which the beetles were fed was in poor condition, egg cases of a lighter brown colour were constructed. If the female is kept even longer without food , the egg may be laid without an egg case. For example, one female was kept without fresh food for 5 days, and at the end of this time, 50 eggs had been laid of which 19 were without egg cases.

(4) Description of the Egg and Egg case

The egg is 0.85 mm. long and 0.42 mm. broad. It is ellipsoidal in shape, light yellow in colour and enclosed by an unmarked hyaline membrane. It is usually covered by the egg case which is 1.5 mm. long by 0.76 mm. broad and is attached to the egg only at the posterior end, that which emerges first from the female. Between the egg and the case is an air space which is usually, though not invariably, continuous with the external atmosphere at the anterior apex.

Due to its method of formation, the egg case is warty in appearance, each individual 'wart' consisting of one of the original droplets whose edges had been spread out so as to serve as a base for the deposition of further droplets.

The egg case is constructed from the faeces of the female beetle. This may easily be seen by teasing a newly laid egg case in water, when pieces of undigested plant tissue become visible.

The probable function of the egg case is to protect the delicate egg from the external environment by enclosing it in a uniform environment of its own. Eggs laid without egg cases dry up within 2 days in the laboratory; whereas if they are kept moist, as may happen under natural conditions in the rainy season, they quickly succumb to fungal attack. The egg case may help to deter egg parasites, and certainly none have been discovered, but does not prevent attack by the ant pest of the laboratory, Tapinoma melanocephalum, which bites open the egg case to feed upon the egg inside.

(5) Development and Hatching of the Egg

Attempts were made to determine the best method for incubation in the laboratory. In all cases the eggs were kept in petri dishes while the substrata on which they lay were varied. The results, summarised in Table I, indicate that a greater proportion of eggs hatch on filter paper than on either soil or sand, and upon dry than upon wet substrata. This is due to the growth of a fungus which commences growing upon the egg case, and, in some cases, attacks and kills the egg. The fungus was noticed to be commonest on moist soil and least common upon dry blotting paper as the figures indicate. Moist blotting paper has the advantage of giving quicker hatching and so this has been used throughout the investigation for egg hatching, although 100 per cent hatching was not common later.

TABLE I

Comparison of Hatching on Various Substrata

Substratum	Number of eggs	Percentage hatching	Period of hatching
Moist blotting paper	14	100	12 days
Dry blotting paper	6	100	14 days
Moist Sand	15	87	12 - 15 days
Dry Sand	13	92	13 - 15 days
Moist Soil	18	50	14 - 17 days
Dry Soil	18	89	12 - 13 days

The difference in hatching period between eggs kept on dry and moist substrata is due to a different rate of development of eggs kept under these conditions. Eggs laid on a certain day were divided and half was kept on dry and half upon moist blotting paper. One egg from each was dissected daily to discover if it was a slower rate of development or difficulty in cutting through the dry egg cases which retarded the hatching of the larvae.

By the 3rd day after laying, the 'moist' egg has become more opaque in the centre with a transparent zone peripherally. There is also an anterior transparent region which is at first rather on one side, but which grows to take up the whole of the anterior third of the egg. In this anterior region, the appendages and head capsule are visible on the 7th day. Chitinisation begins on the 8th day on the cutting edges of the mandibles and the tarsi, and develops for some way before chitinisation of the head capsule and prothoracic dorsal plate begins on the 9th day. The ocelli are first visible on the 8th and are fully pigmented by the 9th day.

Movement may first be induced on the 10th day and the larva is fully developed and hatches from the chorion on the 11th day. After hatching, the larva seems to wait for a while before emerging on the 12th or 13th day.

In the 'dry' egg, development is rather slower and by the 10th day of development is one day behind those eggs developing on moist substrata. When on the 11th day, half of the 'dry' eggs were transferred to moist blotting paper, they developed as rapidly as the 'moist' eggs and hatched 1 day later than these. Those which were kept upon dry blotting paper the whole time developed more slowly after the 11th day and did not emerge until the 14th to 16th day.

Thus it is seen that the hatching of the larva is retarded because of the slower rate of development of eggs kept under dry conditions. The reason for this difference in the rate of development is not clear. It may be that the decreased humidity causes it, but Headlee (1917) stated that development of the eggs of Bruchus obtectus was retarded by increased, and not decreased, humidity.

Emergence from the egg case is commenced by the cutting of a small slit ventrally on the anterior end. This slit is lengthened laterally and widened dorsally to the base of the anterior protrusion, forming a roughly semi-circular opening. The circle is completed by cutting round the protrusion, which is pushed away by a few forward movements of the head. The larva then begins to enlarge the circular opening by scraping the cut edge with its mandibles until the whole of the anterior end of the case is cut away.

Altogether, the hatching of 3,530 eggs was recorded, of which 3,073 or 87.1 per cent emerged as larvae. The date of hatching was recorded for 1,736 of these, and the results are shown in Table II. As will be seen, the

TABLE II

The Incubation Period of Griburius Eggs

	Number of days after laying							
	12	13	14	15	16	17	18	Total
Number of eggs hatching	361	976	283	100	8	5	2	1736
Percentage eggs hatching	20.8	56.2	16.3	5.8	0.5	0.3	0.1	100.0

majority of the eggs (77 per cent) have hatched by the 13th and 99.1 per cent by the 15th day after laying.

Eggs were counted as not having hatched if the case was not cut 4 days after the last egg laid on the same day hatched. Some of these were dissected, and the results are shown in Table III. The most important reason was the inability of the larvae to emerge from the egg case after it had developed normally and emerged from the egg shell.

TABLE III

Reasons for Non-emergence of Larvae

	Number of eggs which did not hatch	Percentage of total
Larva dead in egg case	107	62.9
Eggs attacked by ants	22	12.9
Arrested development	18	10.6
Infertility of eggs	13	7.6
Fungal attack	10	5.9
Total	170	99.9

(6) Description of the Larva and Larval Case

The first instar larva is 0.83 mm. long and 0.62 mm. deep in the retracted position. The head is brown in colour and the abdomen, whose posterior end is turned underneath the posterior end of the thorax, is creamy white.

The head is 0.40 mm. dorso-ventrally and 0.35 mm. broad. It is very much compressed, being roughly circular when viewed anteriorly, and is highly chitinised. There are 6 laterally placed ocelli on each side, one group of 4 ocelli being dorsal, and another of 2, being posterior, to the antennae.

The latter are simple, 3-jointed structures, 0.08 mm. in length, on the inferior lateral border of the head.

On the anterior surface of the head, there are a number of peculiar hairs varying from 12 to 20. The basal half of these is smooth and narrow but distally they become twice as thick and covered with pointed projections. Their function is not known but they are possibly sensory.

The dorsum of the prothorax has a chitinous plate which extends half way down the sides of the segment. The rest of the thorax and abdomen is very little chitinised.

Spiracles, which are circular in shape, are present on the prothoracic segment and abdominal segments 1 to 8.

The legs are 5-jointed, ending in a claw-like, single-jointed tarsus, which is more highly chitinised than the rest of the legs.

The mature larva differs from the first instar larva only in size. It is 5 mm. long and 3.5 mm deep. The head is 1.8 mm. deep. A dark faecal mass shows through the white colour of the abdomen.

The length of larval life varies between 92 and 188 days, with an average of 115 days. In view of this variation, details as to the length of each stadium are rather meaningless. Fennah (private communication) records that moults 1 to 5 occur at 5 day intervals, and that succeeding stadia are 10, 13, 14, 20 and 27 days in length.

These are average figures but so much depends upon other factors that no attempt to give further details is made.

Before moulting, the larva seals up the anterior end of the case after attaching it to some object in the petri dish, such as a dry inflorescence stem or the muslin covers which were occasionally used, and remains enclosed for one to two days. Then the sealed end is cut away and the larva emerges, pulling with it the exuvium which is discarded.

Additions to the larval case are usually made after moulting. The larva partly emerges and lowers the head into the case. After a pause of a second or two, it raises its head, chewing faeces with the mandibles. The legs were not seen to assist in the transfer of the faeces from the anus to the mouth as they were always hidden by the larval case. Certainly the fore legs do not, as they rest on the anterior rim. The faeces~~,~~ appear~~s~~ to be quite wet, possibly owing to the admixture of saliva. After it has been chewed for several seconds, it is applied to the anterior end of the larval case and spread a little by the mandibles. It is allowed to harden for a short time, and then the larva pats and smooths the inside of the newly formed section with the outside of the mandibles. This process, which takes 1½ to 2 minutes, is then repeated until the case is large enough to hold the larva.

Larval cases are quickly repaired in the same way provided that a small cup is left to hold part of the abdomen. If, however, a larva becomes separated from its case, as occasionally happens due to some abnormality in moulting, it is unable to make a new one. Such larvae have been known to live for periods up to 12 days in length, and seem quite healthy, though they were not seen either to moult or pupate.

The larval case is at first identical with the egg case from which it originates, but the external markings are quickly changed. On adding to the case, 4 longitudinal ridges are formed, the two smaller of these being dorsal and the two larger dorso-lateral. The ridges correspond with 4 processes on the anterior end of the case which project over the opening, of which the 2 dorsal processes are longer than the dorso-lateral ones. There is an area of small irregularly placed ridges on the postero-dorsal surface. The ventral surface is usually without ridges.

The egg case does not remain separate from the newly formed larval case and later fall off as in Clythra quadripunctata (Donisthorpe 1902), but is incorporated into the larval case which is built round it.

As the larva increases in size, the lateral prolongations become relatively smaller and all projections except the 4 anterior processes, have disappeared by the time the larva is fully grown.

A fully grown female larval case is 5.9 mm. long and 3.5 mm. broad. No significant difference, was observed between the size of female and male fully grown larval cases.

The case made by larvae in the laboratory is wholly of faeces. Whilst testing methods of keeping the larvae, soil and medium-fine sand was put in petri dishes with newly hatched larvae. The latter were not observed to use either soil or sand in case construction, nor were soil particles seen in the larval cases themselves, and so the practise was discontinued.

On heating over a bunsen flame, the cases gave off a blue-white smoke, glowed and left on cooling a light fawn to grey-white replica of the original. When this was crushed, an amorphous grey-brown powder was formed which gave a violent effervescence on adding dilute hydrochloric acid.

A pupal case, produced by a larva living on soil in a plant pot, had a soiled appearance as though earth had been incorporated into it. It was washed gently with a camel hair brush but much soil still remained.

When it was heated over a bunsen flame, it gave off smoke and glowed with a duller red than the larval case mentioned above. The residual case was reddish-brown in colour, except for the sealed end of the pupal case which was greyish. On crushing, the resultant powder was found to contain numerous crystals of a quartz-like nature. The effervescence on adding hydrochloric acid was much less violent than previously, probably due to the adulteration of the basic constituent, presumably potassium carbonate, by the soil components.

Thus soil is seen to be present in cases formed by larvae living on soil. Whether it is actively incorporated by the larva, or sticks to the outside of the case when the latter is moist, is uncertain. Certainly the fact that the sealed end of the burned pupal case was grey instead of reddish-brown suggests that no soil is present in this part which would not come into contact with the soil. Unfortunately, this part of the pupal case was not investigated separately from the rest and so this cannot be more than a suggestion. It would suggest however that soil may be passively incorporated and is supported by the fact that larvae were not observed to use soil in case construction in the laboratory.

(7) Habits of the Larvae

Two methods were used for studying larval habits in the laboratory. In the first, larvae were transferred after hatching into petri dishes with a moist filter paper, and a Cordia inflorescence bearing several ripe berries was added as food. All flowers and flower buds had previously been removed from these inflorescences to obviate complications which might arise from the presence of Kapala planidia. As soil has been said to be used in the larval cases of Clythra quadripunctata (A. Chevrolat (1835) and J.H. Fabre (1879)) soil or medium-fine sand was added. However, inspection of the larval cases failed to show that any use was being made of this and the practise was discontinued.

Alternatively, larvae were kept on soil in plant pots in which Cordia, or a mixture of other herbaceous plants common under Cordia bushes, such as Mimosa, Railway Daisy (Bidens pilosa) and several species of grass, was growing. The larvae were enclosed by a inverted lamp glass and a gauze-covered iron ring. This method seemed to be better for survival of the larvae, but was largely abandoned in favour of the more convenient petri dish method.

The larval mortality under these conditions is very high. Of 523 larvae which were kept in the laboratory, only 18, or 3.4 per cent, finally pupated. The reasons for this high mortality could not be ascertained. Some, especially while they are young, drown themselves in drops of water which collect wherever the food touches the top of the petri dish. But drowning accounts for approximately 15 per cent of deaths only, and no reason could be found for the death of the other larvae. Some of them were attacked by white mould fungi, but this was invariably after death. The only reason which can be given is unsuitability of living conditions, the major factor of which may be the artificial food.

Originally, it was supposed that the Griburius larvae fed upon Cordia bushes as did the adult. But it was noticed that they live equally well in the pots containing a variety of plants as in that containing the Cordia plant alone; and that it is not the living plant, but the dead leaves and berries which have fallen onto the soil, upon which the larvae feed. In the petri dishes too, soft and decaying leaves and berries are preferred to the tougher, newly cut leaves.

Further, the larva does not climb well, being unable to surmount the edge of a petri dish ¼ inch. high. It seemed improbable therefore, that it would regularly climb the bush itself, although on one occasion a larva was noticed about 3 inches high biting the bark of a young Cordia stem when no other food was available.

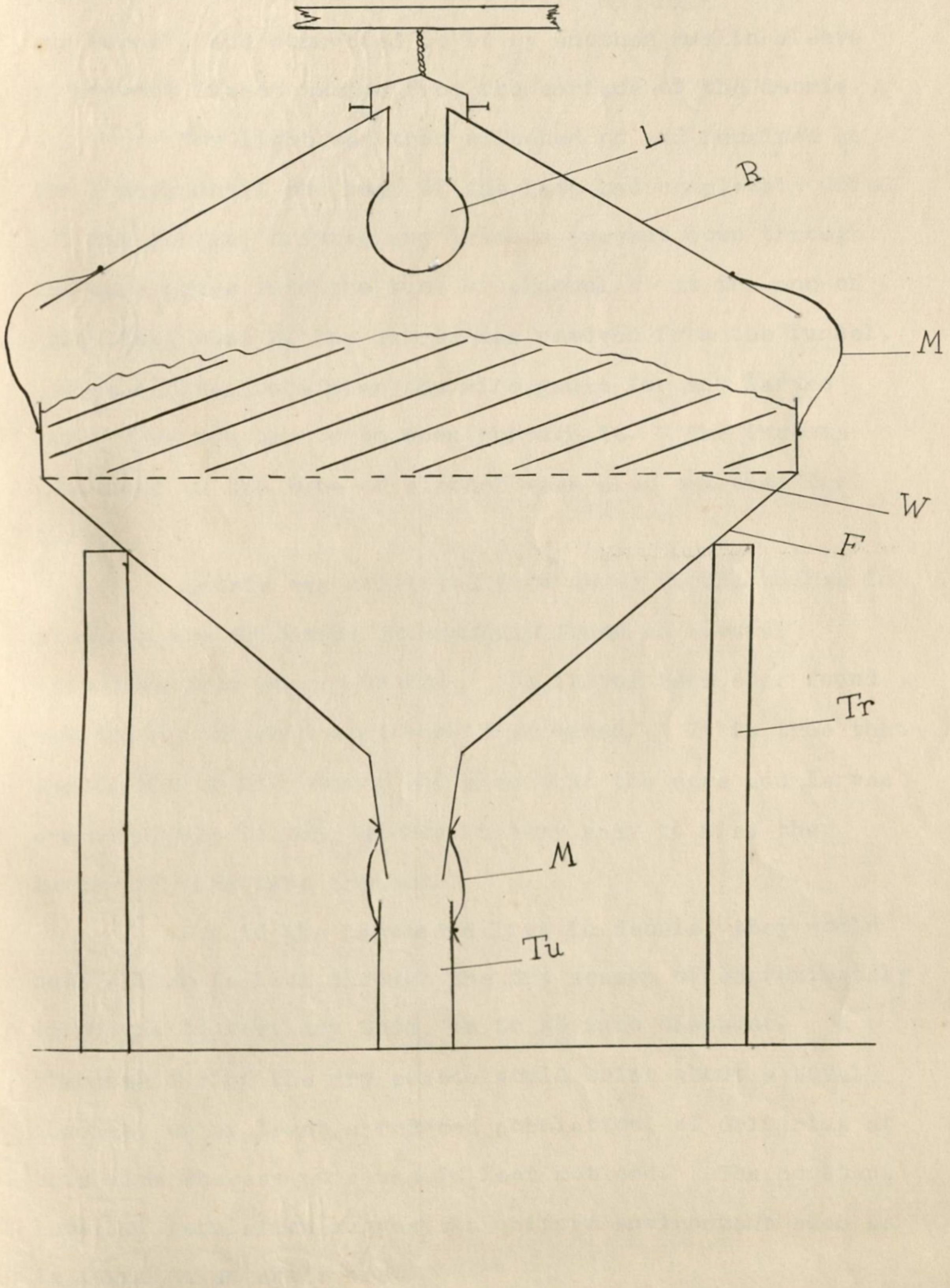
If the larva is frightened or disturbed in any way, it withdraws into the larval case, blocking the entrance with its hard, chitinous head. In this position, the larva cannot hold onto anything, and, if it lived on Cordia bushes, would immediately drop to the ground, and would have to climb a long way back to its food again.

All these factors suggest that the larva does not feed upon Cordia and indeedneither the writer, nor Dr. F.J. Simmonds, who has had considerable experience of Cordia insects, has ever seen Griburius larvae upon Cordia in the field.

The larva may then either live freely on the surface of the ground in the debris under the Cordia bush, or live in the nests of ants as many Cryptocephalids do. To test the former theory, some method of separating larvae from large quantities of leaves and other debris was required, and Berlese funnels (Text figure I) were used for this purpose.

The funnel (F) was of metal and was filled with the debris and put upon the tripod (Tr.). A tube was then held underneath the funnel and the whole shaken gently so

TEXT FIGURE I



as to allow excess soil to pass through the wire gauze (W). This was put aside, and later was searched for eggs and larvae. A tube of alcohol (Tu) was put underneath the funnel and insect escape prevented by the muslin sleeve (M) which was held fast to tube and funnel by rubber bands. A 100 Watt bulb (L) and a reflector (R) were placed above the funnel, and connected to it by another muslin sleeve to prevent insect escape from the surface of the debris.

The light was then switched on and remained so for 3 days until the heat of the lamp had completely dried all the debris, driving any insects present down through the wire gauze into the tube of alcohol. At the end of this time, most of the debris was removed from the funnel, and search was made near the wire gauze for any larvae which were too big to go down through it. The insects contained in the tube of alcohol were also searched for larvae.

Debris was collected from under Cordia bushes in places where Griburius is commonly found on several occasions near St. Augustine. No larvae were ever found but in one funnel 3 eggs were discovered. It is true that the beetle is not common and also that the eggs and larvae are difficult to see, making it very easy to miss the larvae if they were present.

But if the larvae did live in debris, they would have either to live through the dry season of approximately 4½ months on very dry food, or to go into diapause. A diapause during the dry season would bring about a total absence, or at least a reduced population, of Griburius at this time whereas none was in fact noticed. The constant level of population suggests a uniform environment such as is found in an ant's nest.

To test the possibility of larvae living throughout the dry season, groups of 20 larvae of different sizes were put into petri dishes containing old Cordia leaves and left without water. At the end of 3½ weeks, all the larvae were found to be dead, and it is probable that they had been dead for over a week as they had not been seen to move during this time. If larvae die in less than a month under these conditions, they cannot pass through the dry season on the surface of the ground.

For these reasons it is safe to say that the Griburius larva does not live free in the debris under Cordia bushes, and probably lives in the nest of an ant, presumably the one whose workers carry away the eggs, larvae and pupae of Griburius as described in the next section.

(8) The Relation between Griburius and the Ant

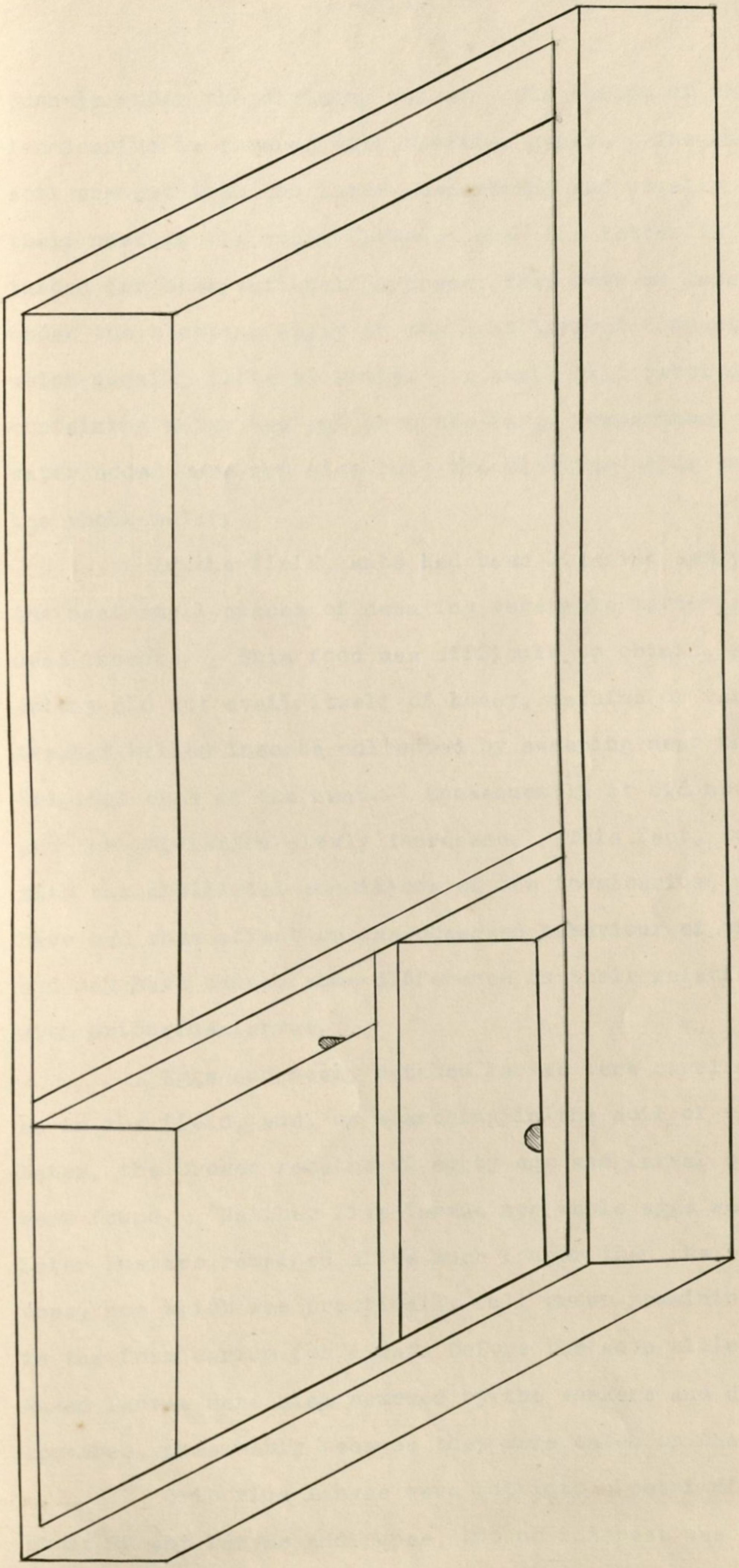
During the exposure of eggs and young larvae to possible parasites and predators, it was noticed that the former were being carried away to the nests of a certain ant (Pheidole fallax jelskii var. antillensis Forel) which are active from about 9.30 a.m. until 5.00 p.m. In the removal of an egg, the worker walk up to it, touch it several times with the antennae, turn and pick up the egg with the mandibles, and carry it straight back to the nest. The removal of eggs has been observed on many occasions, and seldom was there any hesitation.

When larvae are exposed to the ants however, much more apparent doubt is displayed as to whether they should be carried into the nest. When the worker touches the larva, the latter immediately withdraws into its case. The ant turns it round several times and then it may or may not pick it up as with the egg and take it to the nest. However all larvae are eventually removed, for example 20 larvae were taken from 2.00 p.m. to 4.30 p.m. by an ant colony on a bright day.

Pupae are also taken into the nest by ants in the field. One pupa was put close to the entrance of a nest at 10.45 a.m. A worker almost immediately came up to it and touched it all over with its antennae. Several more came, and two of them turned it round, one pulling at each end, so that the sealed end faced the entrance to the nest. One of the workers then pulled it to the entrance and turned it again, so that the rounded end went in first. The entrance hole was too small however, and so about 20 workers and soldiers began to enlarge the hole so that it could be taken in. This was still going on at 12.00 noon but the pupa had disappeared by 12.40 p.m. Again there seems to be little hesitation about carrying the pupae into the nest.

Having made these observations in the field, the next step was to set up a colony under controlled conditions in the laboratory. Unfortunately much time was lost in trying to find a method for keeping the ants alive in the laboratory. Consequently the observations made are not so full as they might have been had a suitable method been found earlier, and Griburius was not reared to the adult stage in the artificial formicaria. The method finally adopted was to dig up the nest, and put it, soil and all into a glass jar which was taken back to the laboratory. Here ants in all stages were picked out from the soil and put into the formicarium, adding only the minimum amount of soil necessary to avoid excessive handling of the delicate larvae and pupae.

The formicarium (Text figure II) is in the form of an open wooden box 15 inches long, 9 inches wide and 1¾ inches deep. It is subdivided into 3 compartments which are connected by 3 semi-circular



TEXT FIGURE II

tunnels under the dividing walls. The bottom of the formicarium is covered with blotting paper. The ants and soil are put into the large compartment and usually build their nest in the soil, although when the latter is disturbed for observational purposes, they move en masse under the blotting paper in the next largest compartment which usually lifts slightly. A small half petri dish containing water was put into the large compartment and water added here and also onto the blotting paper to keep the whole moist.

In the field, ants had been observed carrying to the nest small pieces of decaying vegetable matter and small dead insects. This food was difficult to obtain, and the colony did not avail itself of honey, raisins or various freshly killed insects collected by sweeping near the original site of the nest. Consequently it did not thrive, and the population slowly decreased. This fact, together with the artificial conditions of the formicarium, must have had some effect on the observed behaviour of the ants, and may have caused some difference in their relationship with Griburius larvae.

Eggs and newly hatched larvae were carried away as in the field, and, on searching in the soil of the nest later, the broken remains of empty egg and larval cases were found. Neither live larvae nor whole eggs were seen. Later instars remained alive much longer than the earlier ones, one which was practically full grown remaining alive in the formicarium for 4 days before the ants killed it. Naked larvae were also removed by the workers and disappeared, presumably because they were eaten by the ants.

Griburius larvae were put into a petri dish with about 20 ant larvae and pupae, but no interest was shown in the latter which are not eaten even if no other food is available.

Pupae put into the formicarium were carried onto the rubbish heap, and were not broken open by the ants. This seems to be at variance with the behaviour in the field, since it is hardly likely that a colony of ants would work for two hours to take a pupa into the nest, and then put it onto the rubbish heap.

The results shown above do not correspond with those of Donisthorpe (1902), who worked on Clythra quadripunctata, a commensal of Formica rufa. The eggs, larvae and pupae of this species are taken into the nest by the ants, and live by feeding on the decaying vegetable matter present in the nest. The larvae are often attacked, but escape by feigning death and holding onto twigs and other similar objects.

The difference between the observed habits of the hosts of Griburius and Clythra may be accounted for by the following hypothesis, which is suggested as the most reasonable explanation of the facts obtained. The ants carry eggs and larvae into the nest for use as food for themselves and their brood. If conditions outside the nest are such as to ensure an abundant food supply, the Griburius eggs and larvae may not be killed, owing to the preference of the host for some other food source. The larvae will then feed upon decaying vegetable matter in the nest, and subsequently pupate, after which they are safe from ant injury. If on the other hand, food becomes scarce, the ants will eat the Griburius larvae which thus serve as a reserve food supply.

Certainly it is difficult to imagine ants taking large numbers of eggs and larvae, (sometimes as many as 50 were removed by one colony in one day) if they are not going to use them. It is definitely the living part of the Griburius immature stages which are wanted and not the faeces of which the cases are made as the frass of Tettigonids, and of Griburius (the latter being of the same type as that of which the cases were made) were given to the ants together with normal eggs, and only the latter were removed.

It might be suggested that some other ant is the natural host, and that the one under consideration merely uses the young Griburius stages as food, and thus controls the population. But no other ant was observed to take away eggs or larvae in the field. Furthermore, this ant might act both as the natural host and as a controlling factor if the hypothesis put forward above is correct.

(9) Pupation and Emergence of the Adult

Before pupation, the larva seals up the case in a different fashion to that used for earlier ecdyses. A white substance is secreted by the larva, and is thinly plastered over the whole of the inside of the mouth of the larval case and the ventral surface of the 4 anterior processes. Then, using the white substance as a base, the larva gradually seals up the entrance, a process which may extend over 2 or 3 days. Concentric layers of faeces are applied so that, while decreasing in size, the opening is always roughly circular. The sealed end of the pupae is slightly concave, and is thinner at the centre than at the periphery. A ring of white remains visible anteriorly.

Movement and feeding may be continued after the larva has begun to close the larval case until the opening is too small to permit the head to be extruded. Thereafter, when not actually engaged in closing up the larval case, the larva blocks up the hole with its head.

After sealing up the case, the larva turns round so that the head is now at the posterior end of the case, and the ventral surface of the larva lies against the dorsal surface of the case. Pupation occurs in this position.

Pupae were kept in small corked tubes in the laboratory. Of 37 pupae obtained during the year, 29, or 78.4 per cent, emerged as adults. Those which did not emerge were dissected and, in every case, were found to have died before pupation.

The adult emerges by cutting away a neat, circular cap, approximately 1.2 mm. long at the posterior end of the original larval case. The cap is connected to the rest of the case along the mid ventral line, but is usually broken off by the beetle as it escapes from the pupal case.

The average pupal period for 25 individuals was 37.5 days with a maximum of 51 and a minimum of 23 days. That for 12 males was 35 days and for 13 females 39.8 days, but the difference is not significant.

(10) Length of the Life Cycle in the Laboratory

The maximum, minimum and average durations of the life cycle are shown in Table IV which shows that the average life cycle is 173 days, and varies between limits of 130 and 271 days.

(11) Natural Control

(a) Laboratory Observations

In the laboratory, several species of Chalcids and Braconids were found in the petri dishes in which the larvae were kept, but all were insects feeding upon the Cordia berries or their parasites, and none were true Griburius parasites.

A fungus with large, light brown, spherical sporangia was observed on dead larvae. One such larva was crushed in 1 to 2 c.c. of water and the fluid obtained was used to inoculate other larvae. Two methods were used. Firstly a fine needle was dipped in the liquid and thrust through the dorsal surface of the larval case. Alternatively the spore suspension was brushed onto the larval case using a fine camel hair brush. In each case, 20 larvae were treated but none of the larvae developed any fungal spores. Presumably, the fungus was not truly entomophagous, but had attacked the larva very soon after the death of the latter.

TABLE IV

Maximum, Minimum and Average Duration of the Life Cycle (in days)

	Maximum	Minimum	Average	Number of Individuals
Adult Maturation Period	5	2	4	5
Egg Maturation Period	9	1	3.5	7
Incubation Period	18	12	13	1736
Larval Period	188	92	115	19
Pupal Period	51	23	37.5	25
Total	271	130	173	

The action of the planidia of Kapala furcata upon Griburius larvae in the laboratory might also come under this section. However, it was thought advisable to refer to this in connection with the habits of the Kapala planidium, and the relationship is described in Part II.

(b) Parasites and Predators in the Field

In order to determine the presence and prevalence of parasites and predators in the field, eggs and newly hatched larvae were exposed in batches of 50 in petri dishes which were put under Cordia bushes. These were left out for varying periods up to 10 days and then brought into the laboratory and treated in the usual manner. No specific Griburius parasites were found, and the only predators noted were the ants mentioned above.

(12) Reasons for the Scarcity of the Beetle

If we consider the results obtained as to the mortality of Griburius in the laboratory, we find that mortality in the egg stage is 12.9 per cent, in the larval stage 96.6 per cent and in the pupal stage 21.6 per cent.

$$\text{Thus}\quad \frac{87.1}{100} \times \frac{3.4}{100} \times \frac{78.4}{100} \times 100 = 2.32 \text{ per cent}$$

of the eggs laid will reach maturity. Thus for every female (laying at the average rate of 330 per female),

$$330 \times \frac{2.32}{100} = 7.66 \text{ adults will reach maturity, i.e.}$$

each generation will be nearly 4 times as big as its predecessor. As the population in the field appears to be more or less static, these figures can not hold good under natural conditions.

Let us consider the causes of mortality in the laboratory and compare them with those to be expected in the field. Egg mortality (as in Table III) is of 5 kinds:-

(a) Larva dead in egg case	62.9 per cent
(b) Egg attacked by Tapinoma	12.9 per cent
(c) Arrested Development	10.6 per cent
(d) Infertility or Non Development ..	7.6 per cent
(e) Fungal attack	5.9 per cent

Of these (c) and (d) are caused by unknown factors and so must be assumed to be the same in the field as in the laboratory.

Death of the fully developed larva in the egg case (a) suggests that something has rendered the larva incapable of cutting open the case. If this is because of the hardness of the egg case, mortality may be increased by drought in the dry season and decreased in the wet season. If it is due to the weakness of the larva, no estimate of its prevalence in the field can be made.

Tapinoma has not been discovered to cut open egg cases in the field, and so this factor (b) may be disregarded. Fungal attack (e) will in all probability be even higher than in the laboratory as the eggs will be lying on the soil.

The reason for the death of the larvae in the pupal case is not known. The fungus which attacks the larvae probably does so after its death. Consequently it is not possible to say whether mortality in this stage will be greater or less than in the field, and we must therefore assume that it is the same.

The actual mortality which all these factors cause in the field is however, only speculative, and, for the rest of this discussion, the figures obtained in the laboratory will be used.

Assuming that the hypothesis suggested in Section 8 is correct, death in the larval stage may be effected in two ways. Firstly it may be due to adverse conditions above ground if they are not found by the ants. In the wet season, it is just possible that some larvae may complete their life cycle above the soil, feeding upon decaying vegetable matter, but in the dry season all must die. A very rough indication of the proportion of eggs which are found by the ants is given by the number of colonies found under 50 Cordia bushes spaced at 8 ft. by 8 ft. . During the year, eggs were noted to disappear under 6 bushes and the same number of nests were traced. Thus, since all eggs are laid in association with Cordia bushes, and one ant colony was never noted to forage under more than one bush, $\frac{6}{50} \times 100 = 12$ per cent of the eggs would be carried to the nests in this area.

If this were the only controlling factor, $\frac{87.1}{100} \times \frac{78.4}{100} \times \frac{12}{100} \times 100 = 8.21$ per cent of the eggs would reach maturity, and the population would increase $\frac{8.2}{100} \times \frac{330}{2} = 13.5$ times each generation. Obviously some other controlling factor must be involved and it could well be the number eaten in the ant nest. No idea can be gained of the numbers actually killed in this way but could be eaten and yet maintain a constant population. $\frac{12.5}{13.5} \times 100 = 92.6$ per cent.

Thus we see that there are two correlated factors which limit the population of Griburius triangularis in Trinidad. These are, firstly, the number of colonies of its ant host in any given area of land; and secondly, the amount of food present for those ants. As these two factors rise, so also will the Griburius population rise. Increases in the number of colonies are controlled by competition with other ants of similar feeding habits, and so a natural balance is set up between the number of colonies of ants and the food supply in the area. Any increase in the number of colonies will tend to increase the Griburius population since a greater area will be covered and more eggs found. But if the food supply is constant, a higher proportion of eggs and larvae will be eaten by each colony, thus lowering the Griburius population. The converse also applies. Thus a natural balance is set up which maintains the Griburius population at its present comparatively low level.

PART II THE BIONOMICS OF KAPALA FURCATA F.

(1) Description and General Habits of the Adult

The female is predominantly black with a bronze metallic sheen (Figure 3). It is normally 4.0 mm. long and 1.2 mm. wide, but this may be reduced considerably in the event of superparasitism.

The head is roughly triangular, and shiny black in colour save for the labrum which is yellow. It is finely pubescent and has 2 pairs of oblique striations on the dorsal surface. The eyes are at the dorso-lateral corners of the triangle, and between them, dorsally, lie 3 ocelli. The antennae are 11-jointed, of which the scape and funicle 1 are yellow, and funicle joints 2 to 10 are dark brown. The funicle joints are simple and densely setose. The scape is more than twice the length of funicle 1 which widens distally.

The thorax is black with a bronze metallic sheen, and is finely pubescent. The pronotum is coarsely cross-striated, and the scutum and scutellum are longitudinally striated and have a dorsal median groove. The arms of the scutellum, which arise posteriorly, are longitudinally striated and curve mesially. They are almost twice as long as the basal part of the scutellum. The parapsides are smooth.

The wings are evenly covered with bristles save in the anal region. There is a brown substigmal spot surrounded by an area which is faintly coloured brown. The coxae are black, and the trochanters, femora, tibiae and tarsi are yellow.

The petiole is black and finely pubescent. It is 0.6 mm. in length and roughly 3 times longer than broad. The second segment of the abdomen is black, smooth and glabrous anteriorly, with a light brown posterior margin.

The posterior segments of the abdomen are light yellow with 4 dorsal, chitinised segmental bands, but this posterior part becomes totally enclosed by the second segment when the female has completed egg-laying.

The male is 3.7 mm. long and 1.3 mm. wide. It differs from the female in the following respects.

The dorsal surface of the head has 2 pairs of longitudinal striations. The strongly serrate antennae (Figure 4) are 12-jointed, of which the scape and funicle joint 1 are yellow and funicle joints 2 to 11 are black, each bearing dorsally densely setose serrations, 1.6 mm. in length.

The arms of the scutellum curve more than in the female, and bear coarsely-toothed longitudinal striations. They are 3 times as long as the base of the scutellum. The parapsides are longitudinally striated. The wings have no faint brown colouration around the substigmal spot.

The petiole is 0.88 mm. long, roughly 6 times longer than it is broad, and is faintly longitudinally striated. The abdomen is similar in colour to that of an exhausted female, but is only half as long as the latter.

Kapala furcata is common throughout the year upon Cordia inflorescences which have a predominance of young unopened flower buds. It may also occasionally be seen upon Cousin Mahoe (Urena sinuata), Lantana sp., Crambe abyssinica and several unidentified weeds. Egg laying was not observed, and presumably the wasp is only a casual visitor to these plants.

The adult female was observed to feed upon several occasions. One was observed drinking at a small bead of fluid which had formed at a small semi-circular cut in a vein on the under surface of Cordia leaf. It was quite a fresh wound, and presumably had been made by the wasp itself although this was not observed. Presumably it was feeding upon sugary secretions from the phloem of the cut veins.

(2) Mating and Egg laying

Mating in the Eucharidae has only been recorded in Schizaspidia tennicornis (Clausen 1923) and Kapala terminalis. The males of these species swarm above the entrance to the nest of the host, and mating takes place as soon as the females settle upon nearby vegetation.

Swarming in Kapala furcata was only observed upon one occasion. At 11.15 a.m. on a bright, sunny day, about 20 males were observed flying around 3 Cordia bushes by the roadside. Mating was not observed although several females were present. The place was revisited several days later but the bushes had been cut down and the land cultivated.

Males could be found quite frequently resting upon the grass between Cordia bushes, and presumably they were waiting for females to appear. Again mating was not observed, and attempts to induce mating in captivity also failed.

Egg laying may be seen on any sunny day throughout the year, especially between 9.30 a.m. and 2.00 p.m., although occasionally females may be observed laying as late as 3.30 p.m. The female Kapala walks over the inflorescence, touching the sides of the flower buds with the tips of the antennae. When a suitable bud is found, the female walks forward over it and grasps it with the claws of the middle and hind legs. The abdomen moves ventrally, and the ovipositor is inserted into the bud and remains there for a period varying from 10 to 90 seconds, with an average of 45 seconds. At the end of this time, the antennae, which have been moving slightly up and down every 3 or 4 seconds, move downwards and outwards from the base of the scape, which has hitherto been motionless, and the ovipositor is retracted immediately afterwards.

The ovipositor is always inserted in the side of young buds between 1 and 2 mm. in diameter. It usually pierces the calyx and corolla, and the eggs lie free in the cavity of the bud although occasionally they may be found between the calyx and corolla.

Taking samples from Cordia bushes within a 1 mile radius of the College, irrespective of their proximity to the host nests, and dissecting 5 buds of various sizes from each inflorescence, 57 per cent of the inflorescences and 23 per cent of buds over 1 mm. in diameter were found to contain Kapala eggs. The number of eggs found in each bud varied from 7 to 156 with an average for 25 buds of 32 eggs. However of these 25 egg masses, 11 contained between 10 and 20 eggs and this may be the most usual basic number, very much higher numbers being due to several females depositing in 1 bud. Egg masses over 60 are very uncommon.

Each female contains a large number of eggs; e.g. 5,500 mature eggs in one case. Some eggs are mature on emergence from the pupa and egg laying can begin at once. Observations of the state of exhaustion of the abdomen in the field indicate that two or three days are necessary for the completion of egg laying.

The egg (Figure 5) is elongate oval in shape, with a long slightly curved stalk which widens out distally into a small bulb. It is 0.32 mm. long and 0.06 mm. wide, translucent white in colour with an unsculptured transparent chorion. The stalk begins to collapse soon after it is laid, and all the protoplasm is drawn into the main body of the egg.

(3) Description and Habits of the Planidium

Egg development is completed in 8 days, and the planidium emerges and remains inside the developing bud until it opens and allows the larva to escape.

The first stage larva of Kapala furcata is a planidium (Figure 6), 0.23 mm. long and 0.11 mm. broad. It is dark brown to black in colour, and has 12 segments exclusive of the head, the 12th being represented by the unchitinised caudal sucker.

The head is 0.072 mm. long and 0.065 mm. broad, dark brown in colour and rounded at the anterior end. It has two pairs of minute, semi-transparent round spots on the dorsal surface. The mandibles are sharply pointed and are enclosed in the buccal cavity.

The first body segment is as long as the next 2 combined. It has 1 pair of minute semi-transparent round spots dorsally and 1 minute bristle laterally on each side.

The second body segment has 1 spot as above on each side. Body segments 2 to 8 are slenderly produced at the postero-ventral corners to form curved processes. There are long, laterally placed spines which project posteriorly on body segments 5, 8 and 11.

When the Cordia flower bud opens, the planidium begins to move along in a looping fashion. It grips the surface with the oral sucker and slides the posterior end of the body along and takes hold with the caudal sucker. The head is then extended and the whole repeated. In this fashion, the young larva climbs up the petals, anthers or stigma until it reaches the mouth of the flower, where it takes up the waiting position.

In this position, the planidium is supported at an angle of approximately 60° to the surface. The body takes up an S-shape with the spines on segment 11 projecting almost horizontally backwards and those on segment 8 almost vertically. The caudal sucker is also serving to support the planidium. The head is constantly moving presumably to increase the chances of attaching itself to a host. If touched by a moving object, the planidium increases the vigour of these movements, and the head describes a wide, circular path in an attempt to touch the object again.

The planidium takes hold of any moving object that presents itself by means of the oral sucker and looses hold with the caudal sucker. If the object upon which it finds itself is unsuitable for food, particularly metallic objects, the larva reassumes the waiting position.

The length of life in the field is unknown, but in a tube in the laboratory planidia have lived for 6 days.

(4) The Normal Method of Transport to the Host

Planidia rapidly assume the waiting position upon the upper lip of the corolla. Their subsequent fate depends largely upon circumstances. As they grasp onto anything which touches them, many must attach themselves to the insects which visit the Cordia inflorescences. None of these will complete the life cycle unless their carrier is attacked and carried to the Odontomachus nest.

Odontomachus haematoda workers do not climb bushes. Consequently, if the planidium is to find its host, it must get down onto the ground. Clausen (1940, p.226) states:- "In the case of several species of Kapala . . . . this difficulty is overcome by the development of the jumping habit, wherein the planidia stand erect upon the caudal sucker and, by the use of the caudal cerci, project themselves into space. They thus reach the ground . . . " In Kapala furcata this was not observed although the planidia were watched upon many occasions. By using a sticky surface it was observed that a small proportion of the planidia did either jump or fall off the flower. There are two main methods whereby they reach the ground. Firstly, heavy rain washes planidia off the flowers onto the ground, and secondly when the corolla tube withers and falls, it carries with it many of the planidia waiting upon it.

As the Odontomachus workers pass by, they brush past the Kapala planidia which immediately cling on by means of the oral and caudal suckers. The chance of the two meeting is enhanced by the common habit which the ant has of nesting under an old Cordia stump.

Those parts of the worker which are most active are most likely to pick up planidia. When a worker is put into a tube containing a Kapala infested inflorescence, the fore tibiae, tarsi and the antennae pick up the parasite most frequently, the middle and hind legs and mandibles less frequently, and the rest of the body very seldom.

The ant seems to be irritated by the presence of the planidia and attempts to remove the irritation from the hind legs and antennae by drawing them through the V between the tibia and the tibial spur. The planidia are then removed from the fore legs by the use of the maxillae. It is less easy to free the mandibles and in this way the parasite may finally reach the host. The Odontomachus worker grips the thorax of its larva in the mandibles, and it is thus easy for the planidium to transfer itself onto the thorax of the larva.

Alternatively, planidia which are brushed off in the nest may wander around until they find a larva and attach themselves to it, although many will perish in the attempt.

This method of finding the host is very precarious, but this is counterbalanced by the large number of eggs laid, and as many as 3 Kapala larvae have been found in one Odontomachus cocoon. Out of 57 cocoonsfrom 4 colonies living in Cordia areas, 13 or 22.8 per cent were found to be parasitised.

(5) Development in the Odontomachus Cocoon

(a) The Planidium

When the planidium has attached itself to its host, it remains quiescent until the larva spins its cocoon. Then feeding commences almost immediately, as larvae have been noticed with swollen planidia before all faeces is cleared from the body which usually occurs on the second day completion of the cocoon.

The planidium is always to be found on the prothoracic segment when the host is in the larval or prepupal stages. Feeding is accompanied by a pulsation of the body wall and considerable distension. This is accomplished by virtue of the high elasticity of the intersegmental membranes which stretch until the planidium becomes many times its original size, and the head is completely hidden. The 6 anterior, chitinous plates become widely separated, and the seventh is just separated from plates 8 to 11 which remain undistended. The body becomes almost transparent save for the gut which is yellow.

When the planidium reaches this stage, a median dorsal slit appears in the thorax of the Odontomachus larva, the head of the pupa emerges, and the exuvium is forced backwards over the abdomen. As this ecdysis is taking place, the Kapala planidium moves forward and takes up a position just behind the posterior coxa. If two are present upon one host pupa, one takes up its position behind each coxa, and they develop symmetrically.

Soon after this, the parasite moults by means of a transverse slit between the head and the prothoracic segment, and the second stage larva emerges.

(b) The Second Stage Larva

This is also attached to the host behind the posterior coxa in the same position as the first stage larva. Segmentation is poorly shown and there is only one pair of spiracles visible, on the mesothorax. Pulsation of the body contents is still observable.

(c) The Third Stage Larva

The third stage larva is also attached to the host behind the posterior coxa. It attains 5.00 mm. in length, is translucent white in colour and has 10 visible body segments. Spiracles are present on thoracic segments 2 and 3 and abdominal segments 1 to 7. The body is covered all over by hundreds of small white papillae.

Feeding proceeds rapidly in this stage and is accompanied by a surging backwards and forwards of the body contents. The host pupa is soon exhausted, but the surging continues for 3 days after this. Pupation occurs on the fourth day.

The total length spent in this stage is not known. The maximum length noted was 5 days and the probable duration is about 7 days.

(d) Pupation and Emergence of the Adult

A median dorsal slit occurs in the thoracic region, and the exuvium is forced backwards over the body and comes to rest postero-ventrally between the abdomen and the remains of the host pupa. If there are two parasite pupae in one cocoon, both face in the same direction, and the host skin lies between them.

The pupa (Figure 7) faces anteriorly in the host cocoon. It varies considerably in size, according to the number of pupae present in the cocoon, from 6.24 to 3.3 mm. long and 2.40 to 1.3 mm. broad.

It corresponds in shape to the adult except in the following respects. There are two, blunt transparent processes on the head just mesial to the eyes which curve dorsally and mesially. Between them is a single process which projects anteriorly and slightly ventrally. These three processes cover the three ocelli.

The antennal sheaths lie along the ventral side of the head and thorax. Those of the male may be distinguished by being flatter, broader and longer than in the female.

There are four intersegmental welts which extend over the dorsal and lateral sides of the abdomen but which peter out ventrally. Each welt forms two blunt points, one dorsally and one laterally, on each side of the body.

At first, the pupa is white in colour. The prongs of the scutellum begin to darken on the third day, followed by the dorsal and ventral halves of the thorax respectively. At this stage, the eyes are light brown, and the abdomen opaque white in colour.

On the fifth day the head and the petiole are fully darkened. Four brown, chitinous bands appear segmentally on the dorsum of the abdomen on the sixth, and are fully coloured by the eighth day.

Emergence begins on the tenth day. A transverse split occurs in the head region so that the transparent process covering the median ocellus is included in the anterior, and the two lateral processes in the anterior portion of the cast pupal skin. The posterior part is worked backwards over the thorax but is left covering the abdomen for about a day. The anterior part similarly remains on the inferior half of the head for the same period.

The wasp emerges from the Odontomachus cocoon on the eleventh or twelfth day after pupation. A neat round slit is cut two thirds of the way round the cocoon, and the adult emerges by pushing aside the cap so formed.

Kapala adults are not attacked by the ants, and emerge from the nest between 9. a.m. and 11. a.m. Eggs in the female are fully mature, and are laid soon after mating.

The total length of life cycle was not determined as none of the larval stages was observed through the whole of each instar. The egg stage lasts 8 days, the pupal stage 11 or 12 days and the 3rd larval stage over 5 and probably about 7 days. The second stage larva of Schizaspidia tennicornis is 1 day long in a total larval period of 6 days, and is probably about 2 days long in Kapala furcata. The first stage larva moults soon after pupation of the host which is about 6 days after it has spun the cocoon. This will give an estimate of the length of the life cycle of about 35 days, omitting the period of arrested development between the liberation of the planidium and the spinning of the Odontomachus cocoon.

(6) The Relation Between Griburius and Kapala

When R.G. Fennah studied the life history of Griburius triangularis in the laboratory he found that large numbers of the larvae were dying. He fed them upon fresh Cordia inflorescences infested with Kapala planidia, and the latter found their way onto the bodies of the larvae.

Correlating these two factors, he assumed that the planidia were causing the high mortality by piercing the skin of the beetle larvae. The questions of interest were: firstly, does the Kapala planidium cause the higher mortality, and secondly, do Griburius larvae play any part in the natural life cycle of Kapala furcata?

In order totest the damage which may be attributed to the planidia, 8 batches of Griburius larvae were kept in petri dishes, half of which were fed upon Kapala infested inflorescences, and half upon food kept free from planidia. The bottoms of the petri dishes were covered with filter paper, at the outside edge of which two concentric semicircles were marked. Every day all the larvae in the petri dish were put into the outer of the two semicircles. Next day any which had not moved were put into the inner semicircle. Any of these which did not move by the third day were removed and put into another petri dish, free from planidia. If they did not move in a further 2 days they were assumed to be dead and dissected. The above method eliminates all possibility of moulting larvae being considered dead, as they never take longer than 2 days in the moulting process. Originally some of those in the inner semicircle which were thought to be dead were dissected and found to be alive, which explains why less larvae died than were present originally although no more were left in the petri dish.

The experiment was carried on for 40 days and the results shown in Table ~~IV~~ V. The mortality of larvae exposed to planidia is seen to be much higher than in those which were not. Of 57 of the former, 45 died, 28 of which had Kapala planidia present.

The effect of the planidia on the larvae was probably similar to the effect which ticks have upon cattle.

Their presence upon the delicate abdominal and thoracic skin of the larvae must be very irritating and causes some loss of condition, which causes the larvae to be more susceptible to the other factors which causes the high mortality present even in Kapala-free larvae. Certainly no direct loss is caused by feeding of the planidium on the larva. Planidia were never observed to undergo, even to the slightest degree, any of the swelling up which characterises their parasitisation of Odontomachus larvae.

TABLE V

The Effect of Kapala Planidia upon Griburius Larvae

Batch Number	1	2	3	4	5	6	7	8	Planidia	
									absent	exposed
Original No. of Larvae	15	15	14	14	14	15	13	14	57	57
No. dead on 30th day	8	11	5	11	7	10	4	13	24	45
No. dead on 40th day	9	11	8	12	10	11	4	13	31	47
Dead Larva infected by Kapala	-	3	-	9	1	6	-	10	1	28

If any part at all is played by Griburius in the life history of Kapala furcata, it must be purely accidental. Both Griburius eggs and Kapala planidia fall to the ground, and if the egg hatches there, the larva may quite easily pick up planidia. These then make their way inside the larval case and take up a position on the thorax or abdomen. An Odontomachus worker which picked up the larva and took it to its nest as food would carry the planidium with it and thus the Griburius larva would have played the part of a vehicle to carry the planidium to its host. But this relationship is purely accidental, and it is just as likely that any of the other insects which live in association with Cordia play the same role.

Under natural circumstances therefore, the relationship between Griburius and Kapala is, for all practical purposes, non-existant. Griburius larval may play a very small, but by no means essential, role in the transport of the planidium to its host. The Kapala planidia in their turn, may affect a few larvae developing from eggs which are not carried to the nest by their ant hosts. But these larvae would almost certainly die in any case, and so the planidium effects no control whatsoever upon the Griburius population. The relationship between the two is almost wholly confined to laboratory conditions brought about by the close proximity of the two insects under these conditions and by the habit of the planidium of attaching itself to any moving object with which it comes into contact.

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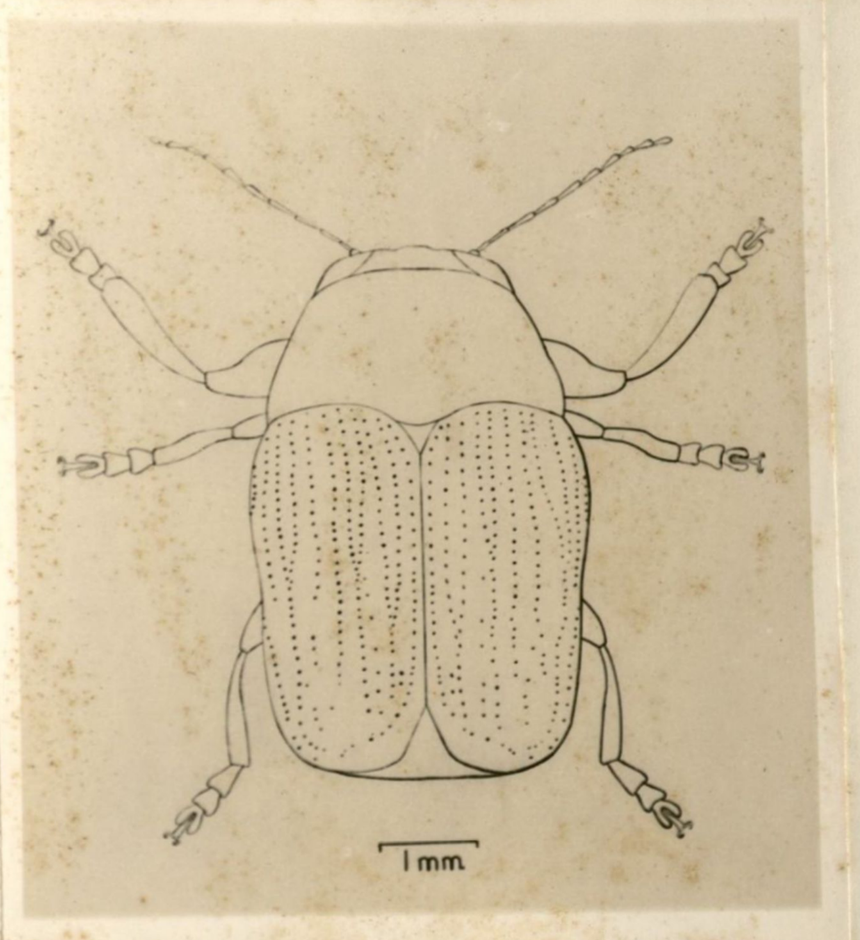

Figure 1. G. triangularis female (dorsal view).

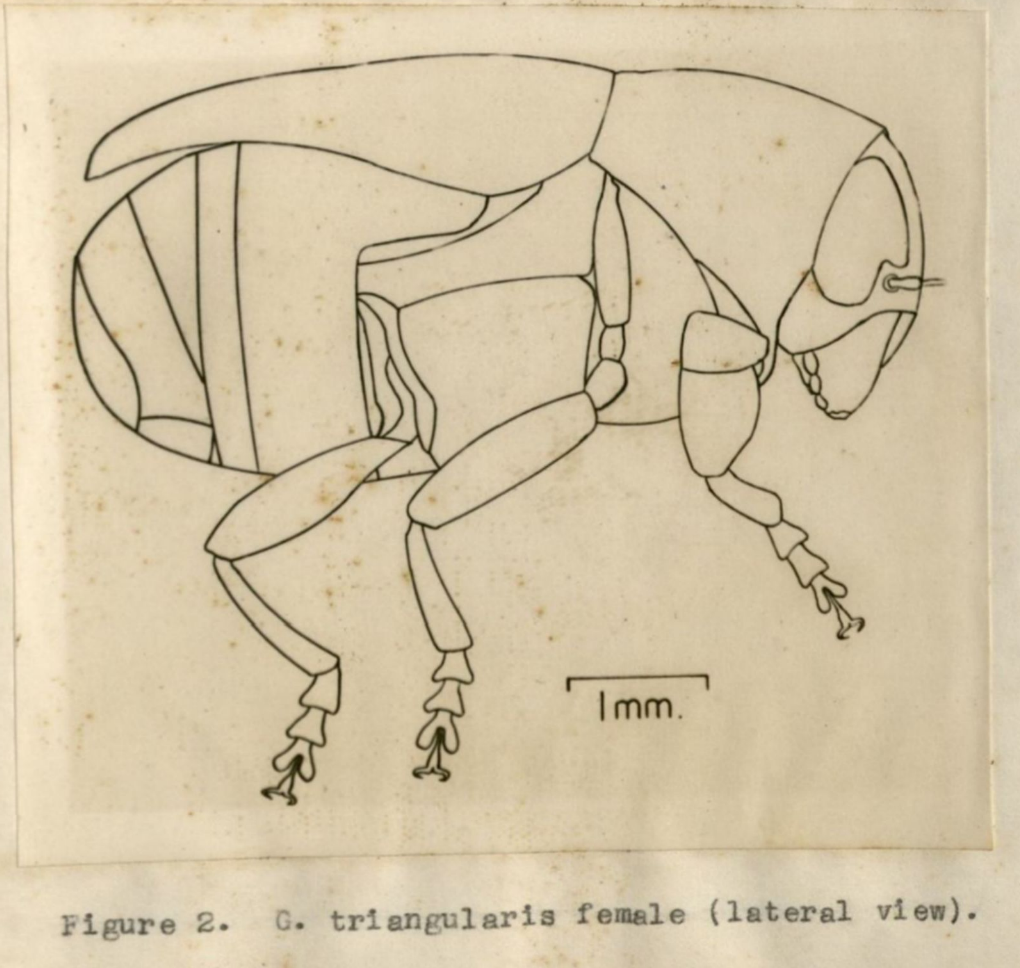

Figure 2. G. triangularis female (lateral view).

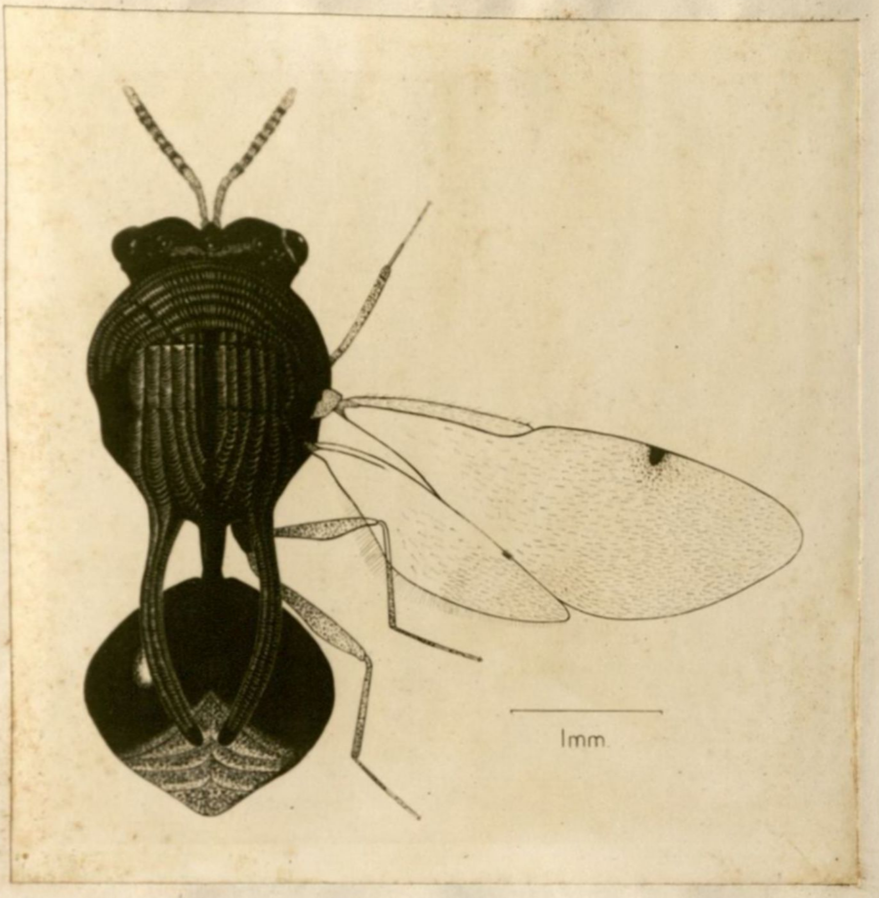

Figure 3. K. furcata female (dorsal view).

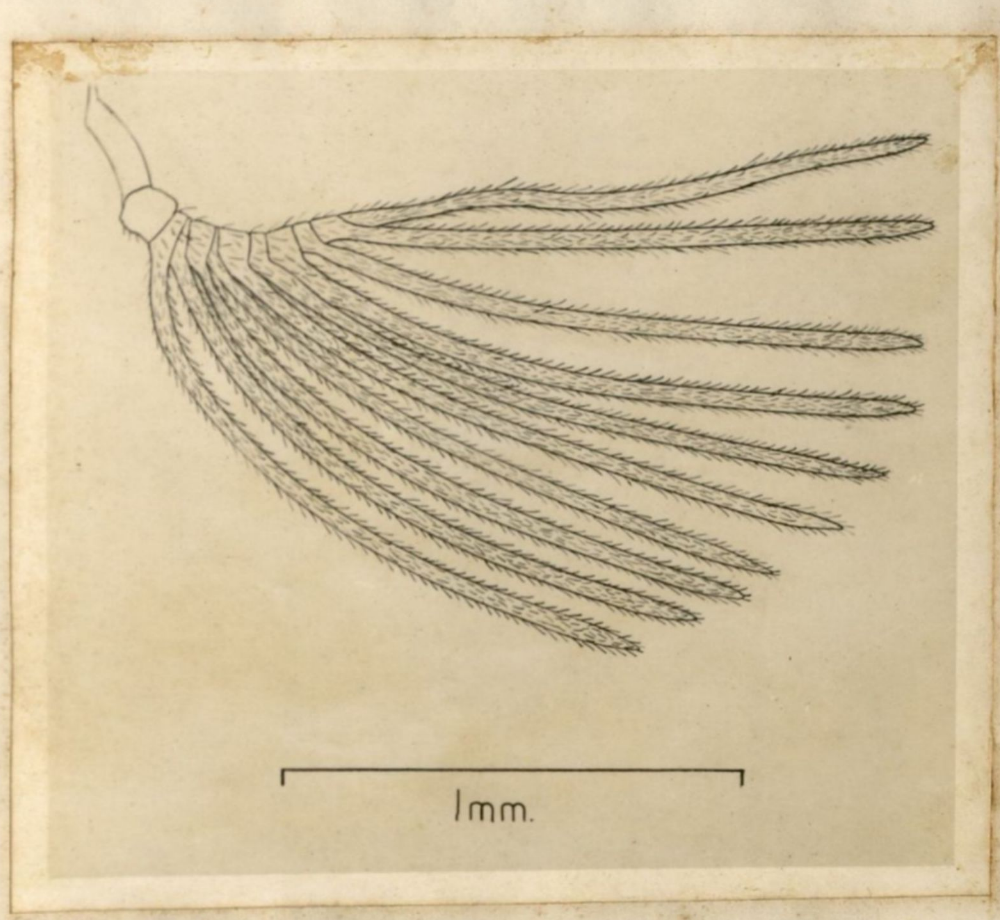

Figure 4. Antennae of male K. furcata

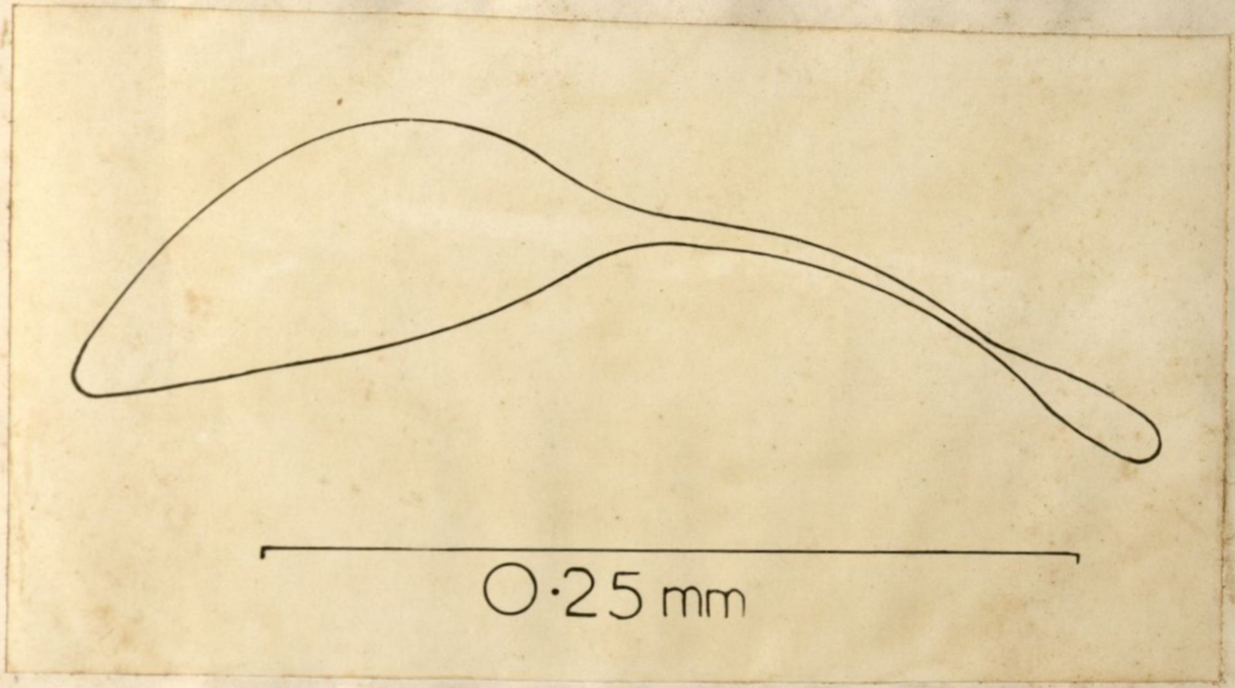

Figure 5. Egg of K. furcata.

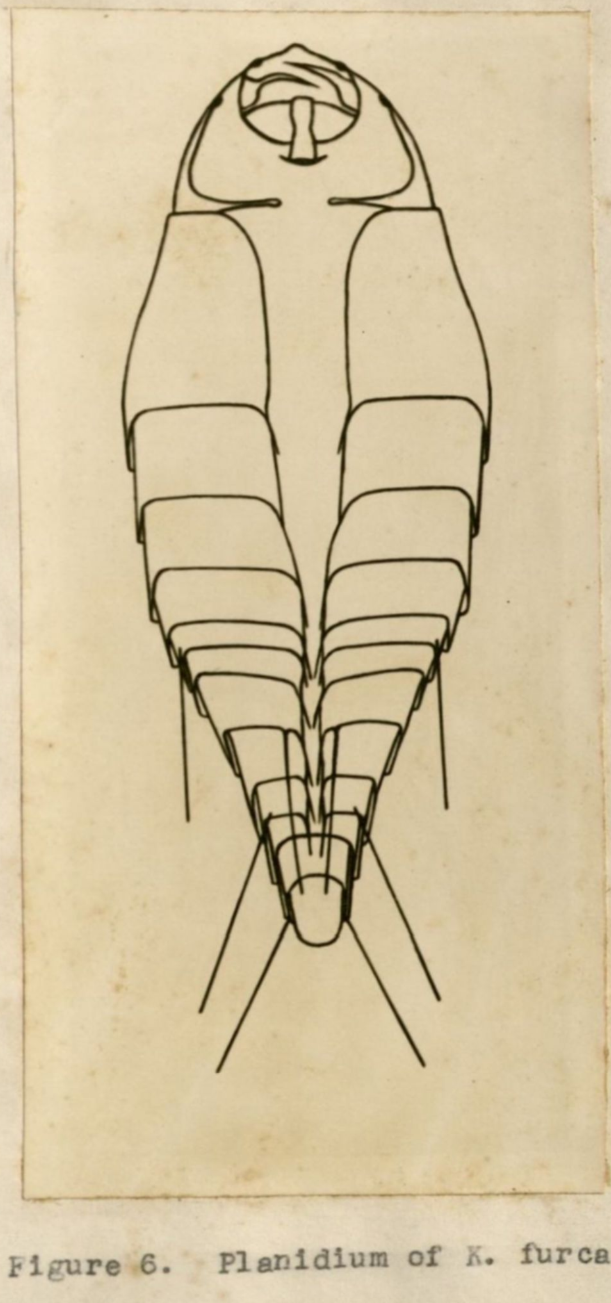

Figure 6. Planidium of K. furcata.

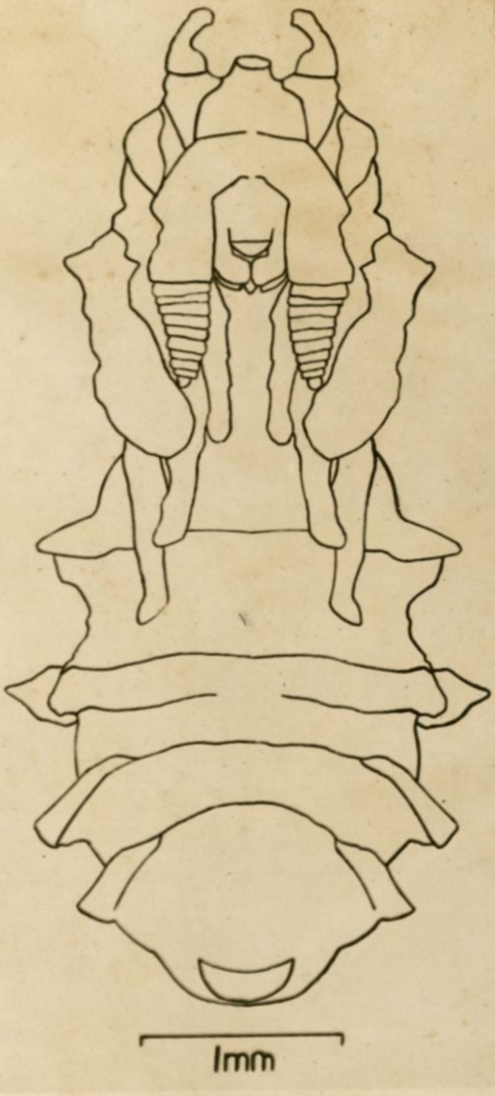

Figure 7. Pupa of K. furcata.