SOME ASPECTS OF THE BIOLOGY, ECOLOGY AND CONTROL OF THE PINE BROWN TAIL MOTH, Euproctis terminalis, Walk.

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I N D E X.

CHAPTER I.

I N T R O D U C T I O N.

The subject of this thesis is an indigenous Lepidopteron species Euproctis terminalis, Walk, which has for some years shown up as a serious pest of exotic pines in South Africa. In 1929 it was reported that an unknown insect has completely defoliated approximately 60 acres of Pinus patula, Schl. et Cham. and Pinus leiophylla, Schl. et Cham. in plantations of the Department of Forestry at Jessievale in the Eastern Transvaal. Upon investigation, it was found that the insect responsible for the damage was the Lymantriad, E. terminalis. There was no record which would suggest that this insect was of the slightest economic importance in its natural habitat. Once it had adapted itself to feeding on pines, it apparently could become a very serious pest. To the family Lymantriadae belong some of the most serious forest pests in the world. The species Euproctis chryssorhoea L. (Nygmia phaerhoea Don.) and Lymantria dispar. L. are very serious pests in pines in Europe and America, while in the last mentioned country another species of major economic importance, Lymantria monacha L., occurs

During 1930, the infestation of E. terminalis at Jessievale recurred, and on a much larger scale, 350 acres of pine being completely defoliated. In the same year a severe outbreak of the pest occurred in pine plantations at Harrismith in the Eastern Orange Free State, where 100 acres of trees were defoliated. A great number of trees in the last mentioned area were so weakened by the attack, that they failed to survive the summer drought of 1930.

Since then, outbreaks have periodically been reported from various pine plantations situated in the Eastern portions of South Africa, some of these being

extensive/.....

extensive, while others were of limited scope. Only in the Jessievale plantations, where this pest was first discovered attacking pines, however, has severe infestation remained as a permanent endemic feature. In all other areas the initial outbreaks appear to have been controlled by natural factors, since there has been no recurrence of striking infestation.

During the years 1932 to 1934, the amount of damage brought about by E. terminalis at Jessievale, decreased considerably, but by 1935 the infestation commenced expanding rapidly. By 1934 no less than 2,000 acres carried such heavy larval populations, that a very real threat existed of complete defoliation of all trees of the susceptible species in the area.

At this stage it appeared that immediate and drastic steps would have to be taken to control the pest if the plantations were to be saved, and chemical control was the only answer. Calcium arsenate, the cheapest and most promising insecticide available at the time, was applied to the plantations by aircraft, as a dust, with the excellent results reported by Tooke (1938). Subsequently calcium arsenate applications were persevered with, using land-based apparatus to effect treatment, but owing to the difficult terrain, and constantly mounting cost, the policy of attempting to control the insect by chemical means, had perforce to be abandoned.

In general it is most inadvisable to practice the general application of insecticides, especially the modern contact poisons which hit the parasite populations as readily as they do the host insect, without prior and comprehensive understanding of the whole biological background of an insect problem. In many cases it has been found that after contact poisons have been applied, the parasite complex recovers much more slowly than the host insect and more severe outbreaks occur, if the insecticidal applications are not

continued indefinitely/...

continued indefinitely. In the case of plantations, where many years must elapse before felling is possible, the cost of repeated applications of insecticides soon becomes prohibitive.

To improve the efficiency of biological control at Jessievale, the Tachinid parasite Compsilura concinnata Meig., which attacks Lymantriid species in Europe and America, was introduced into South Africa during 1942. That this parasite has adopted itself to local conditions, is proved by the fact that the writer has recovered it on numerous occasions subsequent to 1950 from the Jessievale and other plantations. However, it is clear that the introduction of this Tachinid has not had the desired effect as E. terminalis continues to reach epidemic proportions at Jessievale.

At this stage it was decided to carry out a thorough study of the bionomics of E. terminalis. The results of this study are given in this thesis and the following aspects are dealt with:-

A detailed morphological description of the adult Euproctis terminalis, and of all its immature stages from egg to pupa. The known distribution of the species, and by means of an analysis of the climate of these localities, the delineation of the probably distribution area in South Africa. A detailed study of the life history and habits of the insect, as well as of its host plants, both indigenous and exotics. A study of the influence of indigenous host plants on infestation in contiguous plantations. Assessment of the degree of larval infestation in the plantation

by a study/.....

by a study of needle and faecal pellet drop counts; and study of the factors influencing population density of the insect, including food supplies, fungal and insect parasites. The description and life history of the most important species of parasites affecting the egg, larval and pupal stages. A study of the effect of climate on these controlling factors. Finally, in order to be prepared for the contingency at any time in the future to control E. terminalis in plantations by chemical means, a series of tests were carried out by the writer to determine which of the modern insecticides would be most effective. These experiments bring up to date the work done by Petty (1948), who evaluated the insecticides available for testing at that time for the control of this species.

CHAPTER II.

D I S T R I B U T I O N.

There is a natural tendency for any insect species to spread over as wide an area as possible. From the regions where optimum conditions for its existence are to be found, it will normally extend into the marginal zones, beyond which it cannot survive owing to environmental resistance.

Of the various factors which together constitute environmental resistance and prevent the wider spread of an insect species, undoubtedly the most important are precipitation and temperature (Uvarov 1931).

As E. terminalis is an indigenous insect, it may safely be assumed that the species is already as widely spread in the Union as the limiting factors will permit. To establish its distribution area, records of localities from which this species has been collected were obtained from the British Museum, the S.A. museum, the Transvaal

museum, the Albany museum, the Natal museum and the collection of the Division of Entomology, Pretoria. These localities are listed below, the collector's name, when available, being given in parenthesis in each case. It is of interest to note that the species is not as yet represented in the insect collections of the Museums in Southern Rhodesia and Mozambique.

TRANSVAAL:-

Barberton (Randall).
Belfast (F.G.C. Tooke).
Berlin (J.H. Grobler).
Bultfontein (J.H. Grobler).
Elandshoek (? Tvl. Museum)
Entabeni (F.G.C. Tooke).
Haenertsburg (Janse).
Hendriksdal (J.H. Grobler)
Jessievale (F.G.C. Tooke)
Makubalaan (J.H. Grobler)
Ceylon (J.H. Grobler).
Chilovane (? Tvl. Mus.)
Coetzeestroom (J.H. Grobler).
Driekop : Pilgrimsrest (J.H. Grobler).
Malto : Puntberg (van Son).
Piet Retief (E.E. Plat).
Spitzkop : Sabie (F.G.C. Tooke).
Tweefontein : Sabie (J.H. Grobler)
Witklip : White River (J.H. Grobler).
Woodbush (Janse.)

ORANGE FREE STATE:-

Harrismith (F.G.C. Tooke)
Mons : Memel (J.H. Grobler)

NATAL:-

Durban (Leigh)
Eshowe (E.L. Clark)
Estcourt (? Natal Mus.)
Giants Castle (? Tvl. Mus.)
Greytown (J.H. Grobler)
Karkloof (Leigh. Marshall).
Krantzkop (? Natal Museum).
Natal National Park (J.G. Ogivie).
Wartburg (? Tvl. Mus.)
Weza (J.H. Grobler)

CAPE PROVINCE:-

Bashi River (Bowker)
East London (Clark)
George (B.W. Dumbleton)
Grahamstown (G. Hampson)
Inziswa (F.G.C. Tooke)
Kowie River (Irwing)
Knysna (R. Lightfoot)
Libodi (? Br. Museum).
Mvenyana (J.H. Grobler).
Ngqeleni (H.H. Swinny)
Port Elizabeth (Clark)
Port St. Johns (H.H. Swinny).
Stutterheim (Clark)
Transkei (Barrat).

In fig. 1/.....

In figure 1 these localities have been plotted on a map of South Africa. It is clear apparent that the species is distributed throughout the Eastern and South Eastern zones of the Union, where precipitation is highest.

Temperatures prevailing in the known distribution area of E. terminalis are generally encountered in other and adjoining regions in which this species has not hitherto been found. The main factor limiting the wide spread of the species in S.A. would thus apparently not be temperature as such, but humidity (rainfall).

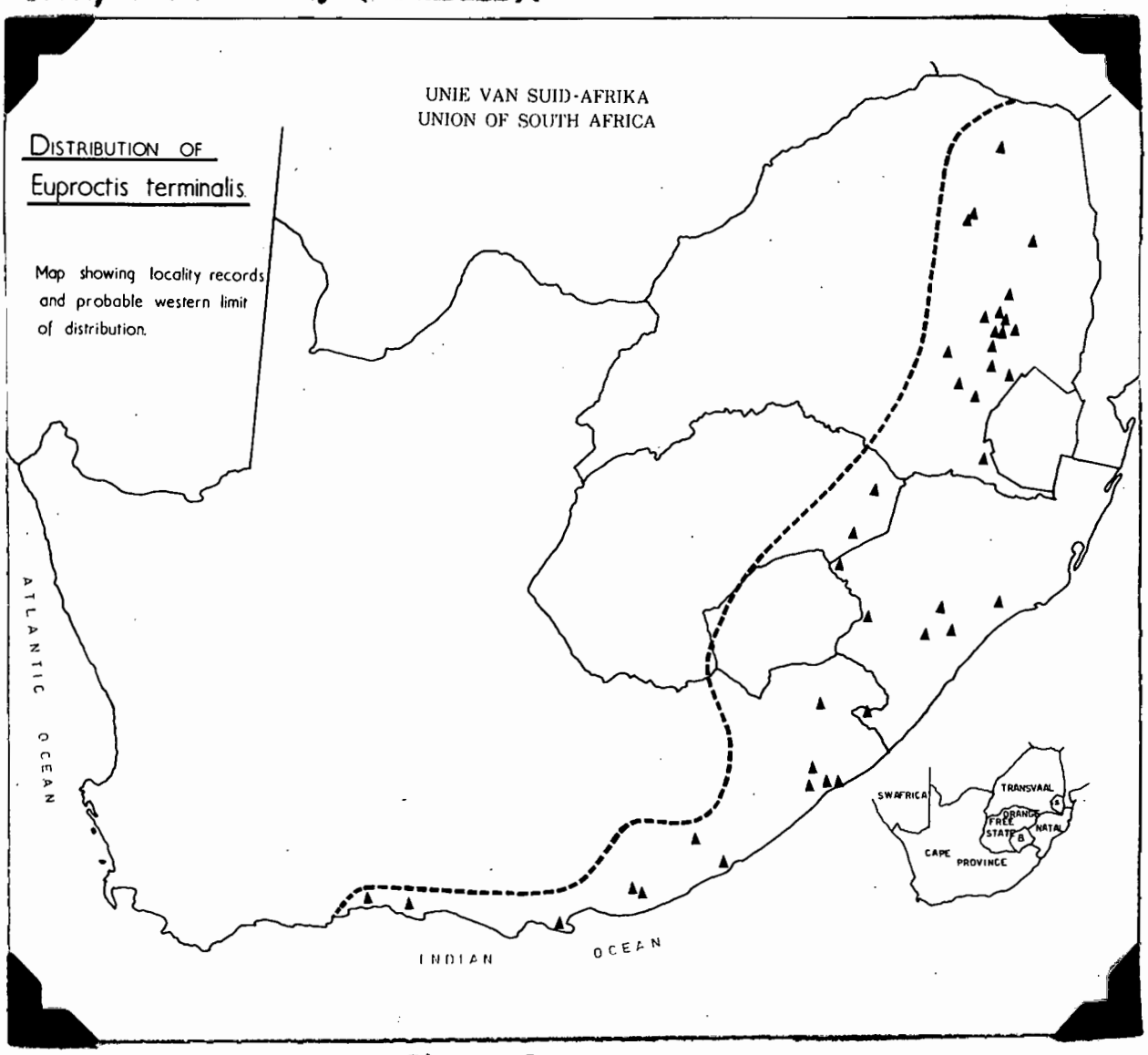


Figure 1.

Known distribution of E. terminalis, Walk., and probable western limit of distribution.

The S.A. Weather Bureau has produced a map showing the distribution of rainfall in the Union, and the details

reflected /.....

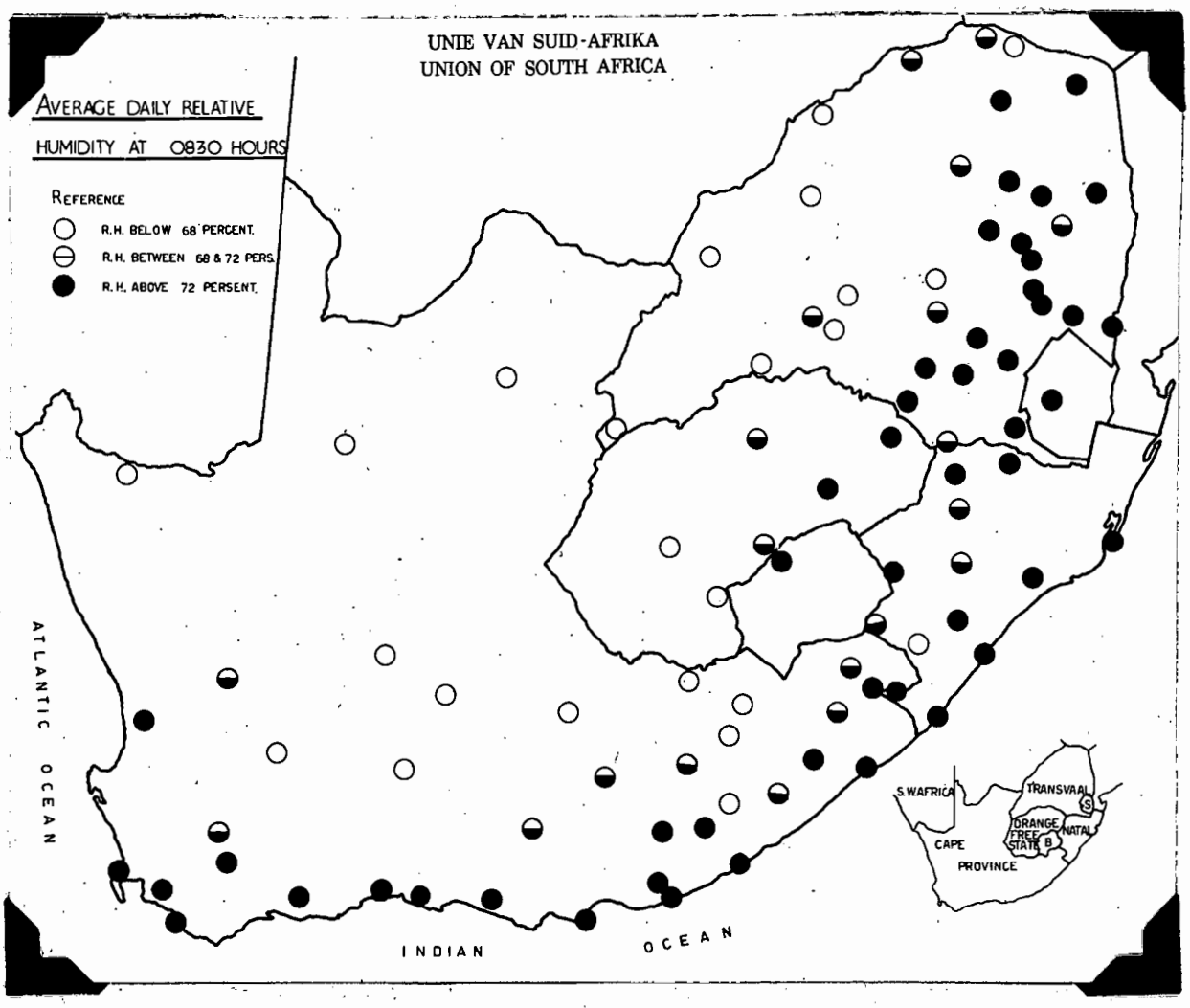


Fig. 2.

Distribution of E.terminalis superimposed on the average daily relative humidity.

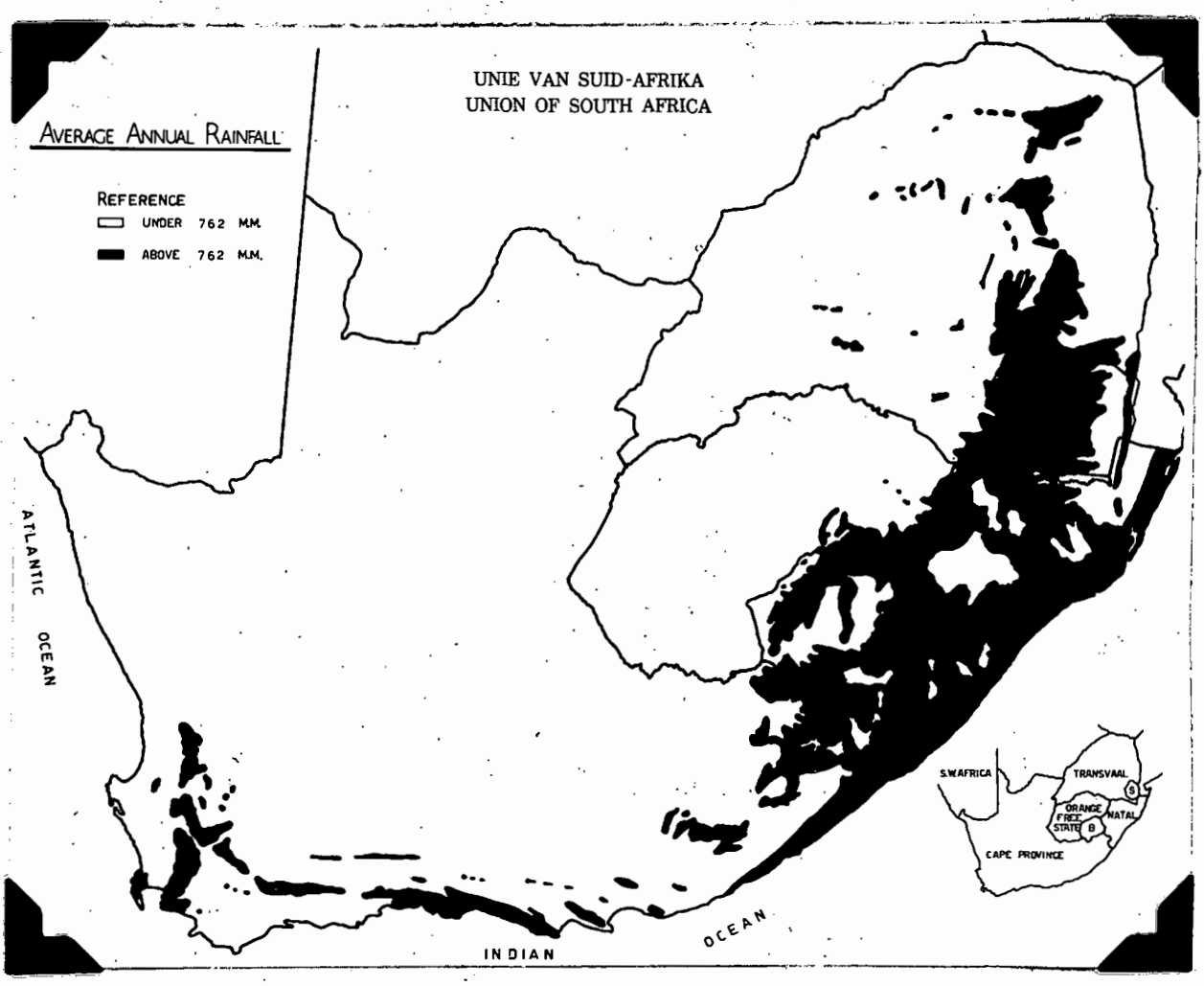


Fig. 3.

Distribution of E.terminalis superimposed on the zone with a precipitation of 762m.m. or more.

reflected in Figure 2 have been obtained from this source. Unfortunately there is no official chart reflecting the average relative humidity of the air of South Africa. The details in this respect, reflected in figure 3, have been plotted by the writer using figures contained in the Annual Reports of the South African Weather Bureau.

When the distribution chart of E. terminalis is superimposed on figure 3, it is clearly apparent that there is a close correlation with the precipitation. Of the 46 localities from which the insect is recorded, practically all fall in the zone with a precipitation of 762 m.m. or more per annum. By superimposing figure 1 on figures 2 and 3, it will be noted that the few exceptions fall in areas where the average relative humidity of the air equals or exceeds 72%.

It therefore seems that E. terminalis can exist only in areas where tha average relative humidity of the air (or the rainfall) reaches or exceeds the abovementioned critical levels. It is interesting, however, that the species has not been collected from the South-Western Cape Province, where rainfall (humidity) exceeds the critical level. It is hardly likely that this species would have been missed by collectors, since the South-Western Cape Province, and its fauna has been closely studied for a very long period. It is thus clear that other limiting factors must prevent its survival in this area.

In Australia the distribution of the "lucern Flea" (Smythurus virides Linn) is very closely correlated with precipitation, - of 49 locality records for the species, only 2 fall in an area with an annual rainfall of less than 15" p.a. (Holdaway 1929).

In order to/.....

In order to understand the absence of E. terminalis in the Western Province, climatographs were prepared
(a) of the Stellenbosch, Jonkershoek and Elgin areas, a representative of the South-Western Cape province where E. terminalis is not found, despite apparently suitable conditions of humidity (rainfall) and
(b) of Knysna, Stutterheim, Weza, Cedara, Jessievale and Pilgrimsrest areas, 6 localities selected at random from South to North in the known distribution area of the species. (Fig. 4).

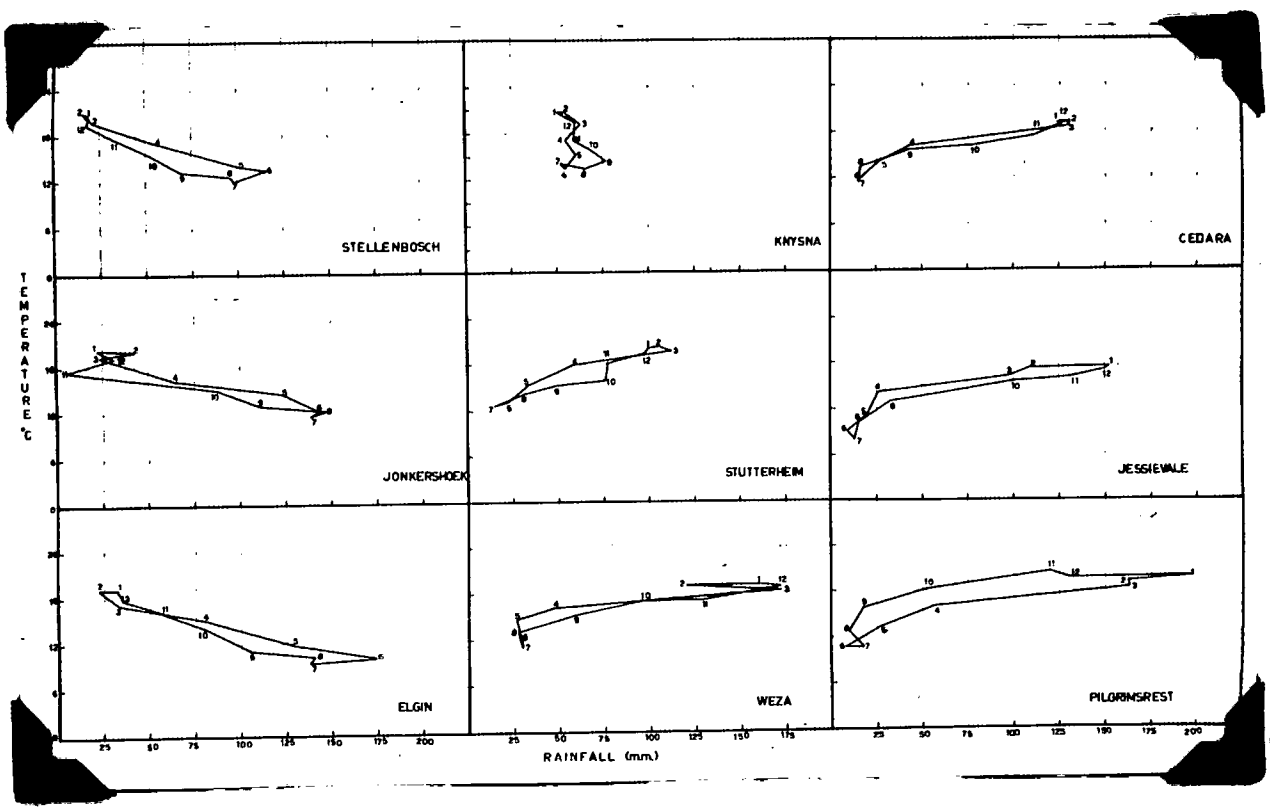


Figure 4.

Climatographs of rainfall and temperature in and out of the known E. terminalis distributional area.

In laboratory tests on E. terminalis (Chapter V) it was found that relatively low humidities are not necessarily lethal to the insect, provided the temperatures are low as well, but if the temperature is increased and humidity remains low, the insect perished in all cases.

Ir the limiting/.....

If the limiting effect of relatively low humidity combined with high temperature is borne in mind when studying the climatographs in figure 4, it can readily be explained why E. terminalis cannot exist in the South-Western Cape Province.

The South-Western Cape Province has its rainfall during the winter months, when temperatures drop to their lowest levels; during the summer months when temperatures are highest, there is very little precipitation and humidity is at its lowest level. In the distribution area of E. terminalis, the reverse is the case - rain falls in summer when temperatures reach their highest levels, while the meagre precipitation of the winter months is accompanied by low temperatures.

In figure 1, a line has been drawn, which represents the probable limit to the West of the distribution area of E. terminalis. Enclosed by it are areas where the average relative humidity of the air is 72% and higher, and those, where the annual rainfall reaches or exceeds 762 m.m. The areas of winter rainfall to the South, where maximum temperatures occur when humidity is lowest, have, however, been excluded. The boundary could be expected to fluctuate somewhat, since weather conditions vary from year to year.

Up to the present there is no evidence to show that E. terminalis occurs beyond the boundaries of the Union of South Africa. However, should there be other regions, e.g. in Swaziland and Mozambique, where the above mentioned climatic conditions exist, collectors will without doubt, reveal its presence there in the future.

CHAPTER III./.....

CHAPTER III.

T H E M O T H.

1. RELATIONSHIP AND PUBLISHED DESCRIPTION

Euproctis terminalis is a Lepidopteron belonging to the family Lymantriadae.

The genus Euproctis was described by Hübner (1819) using Bombyx chrysorrhoea as the genotype.

The following, although brief, is the full German description as given by him.

> "Die Flügel sehr sparsam bezeichnet; bei Streichler und der After färbig". L A.

The species terminalis was described thirtysix years later in Latin by Walker (1855).

The following is his full description:-

> "Mass. Pallide aurantiaca; palpi testacei; antennae ramis fuscis; pectus testaceum; abdomen apice nigro pilosum". L ? a ?

The specimen was collected by Dr. Kraus at Port Natal (Durban).

In 1905 Hampson published keys to the genera and species of the Lymantriadae occuring in South Africa, the one dealing with Euproctis containing only thirteen species.

In 1915 Janse published a new key to the genera and species of South African Lymantriadae, and in this he noted seventeen Euproctis species.

The following is Janse's description of the genus Euproctis, in which he used E. fasciata as the genotype.

> "Euproctis Hübn.
>
> Male: Proboscis absent or very rudimentary; palpi porrect, just reaching frons; first joint conical with the point curved upwards, nearly 2 times longer than thick; second joint cylindrical, as thick as first joint, but 3 times longer than thick; third joint a little

shorter than/.....

shorter than first joint, thin and bluntly pointed, hidden in hair; all joint with a little hair above and much long hair on under side (in female the palpi are a little ascending; second joint longer and thinner, about 3 times first joint; third joint as long as ½ second joint and thinner; the whole palpus less hairy); eyes rather large, over width of frons, rounded; frons rounded and with short hair; antennae nearly ½ of costa (in female only ¼ of costa), curved, bipectinate; in male the pecten are 6 to 8 times shaft, ending in a long bristle; in female only 3 times shaft; vertex and thorax covered with moderately long hair; abdomen longer than hind wings covered dorsally with short hairs and ventrally longer hairs, ending in a long hairy tuft in male and becoming truncate in female; on dorsum a tuft of hair on first and second segments; legs very hairy on femora, tibiae, and tarsi; forelegs with a process as long or a little longer than tibiae, curved somewhat like a S terminally, and pointed; in female a little shorter and thicker; mid tibiae with 2 spurs; hind tibiae with 4 spurs.

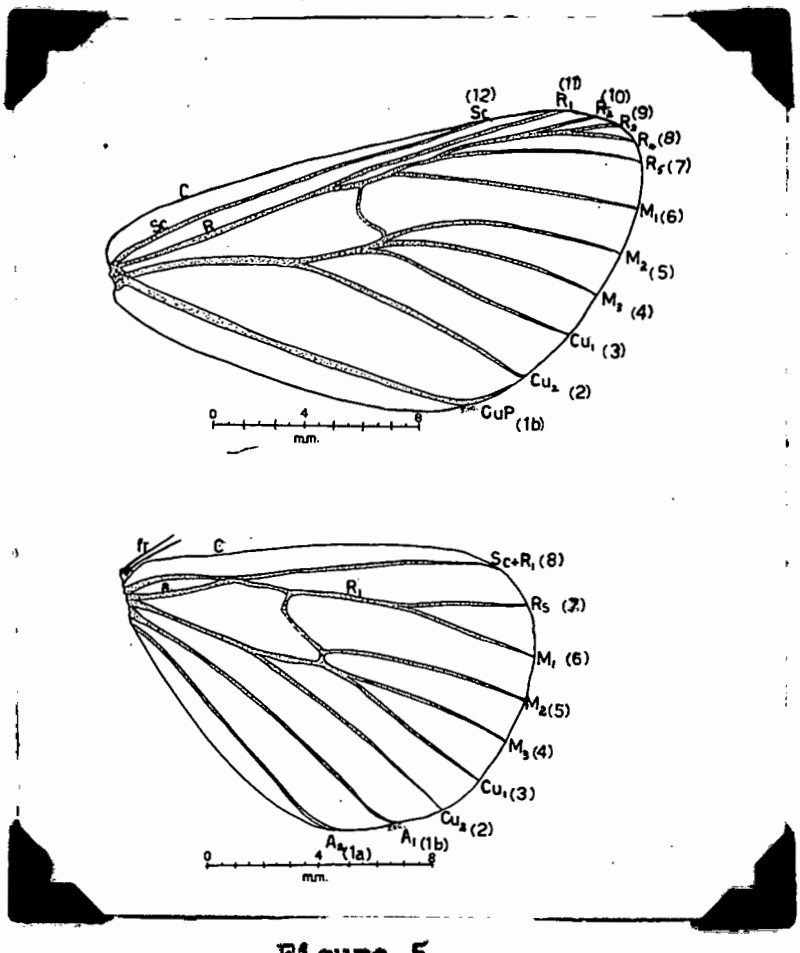


Figure 5.

Fore and hind wing of E. terminalis.

Forewing/....

Forewing long, (figure 5) sub-triangular; costa and outer margin somewhat rounded; inner margin well rounded; apex and tornus rounded; 1b simple at base; 2 from beyond $\frac{2}{3}$ lower median; 3 from well before angle; 4 and 5 from lower median; 6 from just beyond upper angle; stalk of 7, 8, 9, 10 from upper angle; 7 from beyond $\frac{1}{4}$ of 8; 9 from $\frac{2}{3}$ of 8; 10 from $\frac{1}{2}$ of vein 8; 11 from $\frac{4}{5}$ upper median; 12 somewhat parallel to upper median. Hind wing triangular; costa, outer and inner margin somewhat rounded; 1a long, straight; 1b nearly straight; 2 from $\frac{2}{3}$ lower median; 3 and 4 on a short stalk from lower angle; 5 from above this angle; 6 and 7 on a stalk of $\frac{1}{6}$ of vein 6 and from upper angle; 8 bent to beyond $\frac{1}{2}$ upper median, where that vein is angled upwards, so as just to touch it, but not anastomosing with it, then curved at end".

Under the short description of Euproctis terminalis, Janse states as follows:-

"In this species the palpi have the second joint only 2 times as long as the first joint and the process is more slender and a little longer than in E. fasciata."

2. REDESCRIPTION:

The following is a detailed morphological description of Euproctis terminalis:

(a) The head. (Fig. 6).

The head capsule is densely covered with scales and setae, except for the region near the two compound eyes which are large and sparsely covered by tiny setae. No ocelli are present.

Mouthparts. The labrum is very rudimentary and consists only of a narrow band. Maxillary palpi are absent. The labial palpi are well defined and are made up of three

segments/.....

segments, which are densely covered by scales. The proboscis is extremely rudimentary, and no mandibles are present.

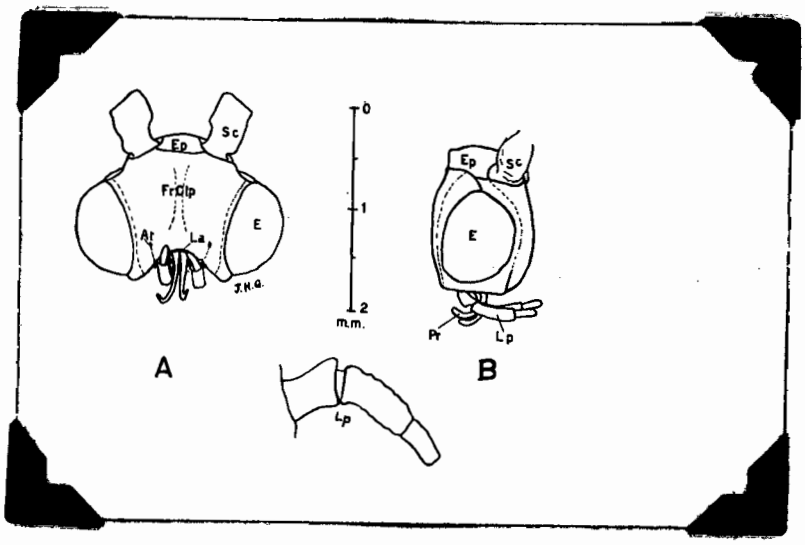


Fig. 6.

Anterior (A) and lateral (B) view of the head.
Lp - enlargement of the labial pulpus.

At - Anterior tentorial pit.
Ep - Epicranium
La - labrum
E - Compound eye.
FrClp - Frontal clypeus
Lp - labial palpus.
Pr - Proboscis.

The mouthparts are vestigial and they are not, therefore, suited for feeding.

Antennae. The antennae of the moth are bipectinate, but those of the male differ markedly from those of the female by virtue of the fact that they are plumose whereas those of the female are not.

Male Antennae. (Fig. 7). The basal stalk or scape, fig.7b., of the antenna, which is about 1½ times as wide as it is long, has a swollen appearance and is considerably longer than the other segments.

The median segment, the pedicel, which is short, and only about half the length of the scape is slightly wider than the first segment of the flagellum which is made up of 31 segments. These segments gradually become longer and thinner towards the distal end of the flagellum.

The distal segment/.....

The distal segment, however, is as much as twice the length of the preceeding segment. Every segment has two long pectinae which are densely covered with slender setae. On the tip of every pectina there are, in addition to the slender setae, two which are much larger and more prominent than the others.

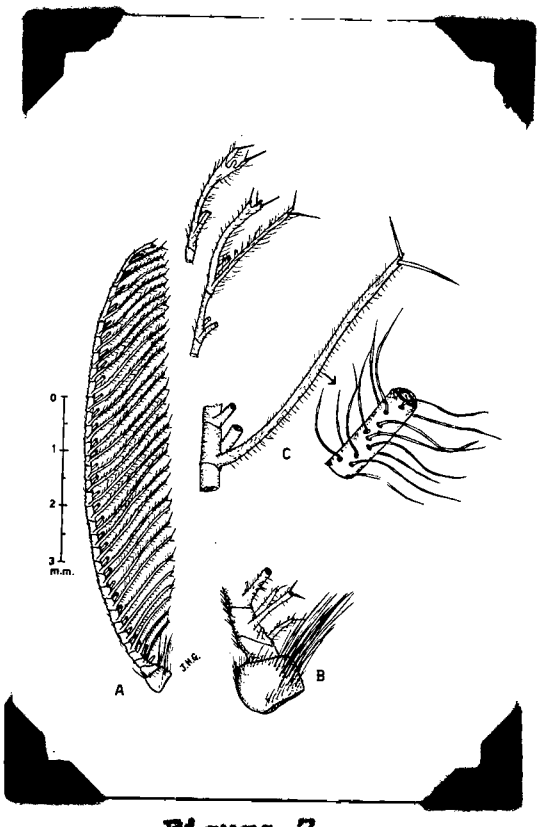


Figure 7.

A. Plumose antenna of male.

B. Scape of antenna.

C. Enlargement of the pectinae and two variations found in the terminal segment of the flagellum.

The feathery appearance of the antennae is due to the long pectinae, figure 7 C., the longest of which are six times the length of the segment on which they are situated.

The last segment varies markedly in shape and as an illustration of this variation, two forms in which it may occur are shown in figure 7.

Female antennae (Fig. 8).

In the female the scape differs markedly from that of the male, being twice as long as it is broad, while the

pedicel which/.....

pedicel which is slightly wider than the first segment of the flagellum is only $\frac{2}{5}$ as long as the scape, figure 8 E.

In general the flaggelum consists of 27 segments, but in 3 of the cases examined the number of segments was found to be only 26.

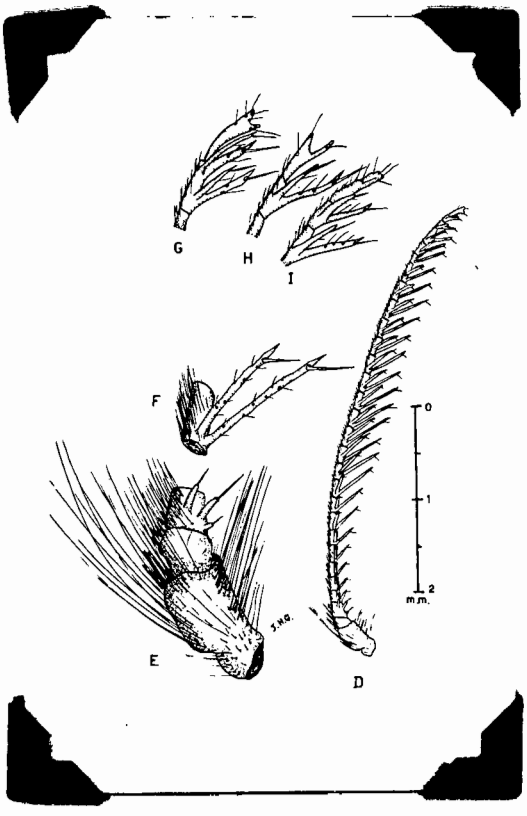


Fig. 8.

D. Antenna of the female moth.

E. Scape of antenna.

F. Enlargement of the pectinae.

G. - I. Variations found in the terminal segment of the antenna.

The main difference in the flagella of the two sexes is the length of the pectinae. In the case of the female, they are much shorter than those of the male, the longest being only twice instead of six times, the length of the segment on which they are situated.

The pectinae are comparatively sparsely covered with setae, and have only one prominent seta instead of two near the distal end.

As in the male/.....

As in the male, the last segment of the flagellum may exhibit marked shape variations as is illustrated by the three examples given in figure 8, G.H.I.

(b) Thorax. (Figure 9).

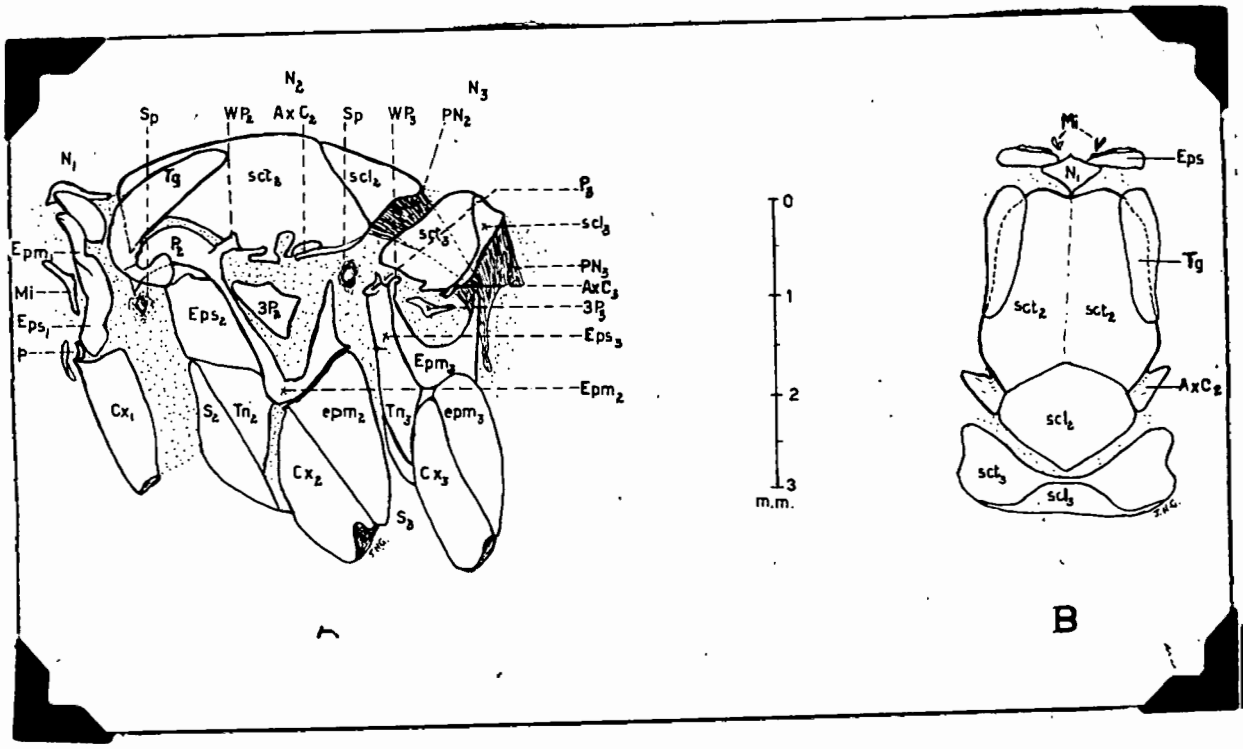


Fig. 9.

Lateral and dorsal aspect of the thorax.

Protharax.

Epm_1 - Epimerum
Mi - Microthorax
p - Articulating plate of coxa
Eps_1 - Episternum
N_1 - Notum
Cx_1 - Coxa

Mesothorax.

AxC_2 - Axillary cord
Epm_2 - Epimerum
N_2 - Notum
$3P_2$ - Post Parapterum
S_2 - Sternum
sct_2 - scutum
Tg - Tegula
Cx_2 - Coxa
Eps_2 - Episternum
P - Parapterum
PN_2 - Post notum
scl_2 - scutellum
Sp - speracle
WP_2 - Wing process of pleuron

Metathorax.

AxC_3 - Axillary cord
Cx_3 - Coxa
epm_3 - subdivision of epimerum
P_3 - parapterum
PN_3 - Postneulum
sct - scutum
WP_3 - Wing process of pleuron
S_3 - sternum
Epm_3 - Epimerum
N_3 - Notum
$3P_3$ - post parapterum
scl_3 - scutellum
Tn_3 - Trochantin

(Terminology based on that used by Snodgrass (1909).)

Microthorax/.....

Microthorax.

The microthorax which forms the neck segment, is not a true thoracic segment, and consists of only two sclerites which are situated on each side of the neck.

Thorax.

The thorax is composed of three well defined segments, the pro-, meso- and metathorax. The meso- and metathorax which bear the wings are less clearly separated from each other than are the pro- and mesothorax.

The prothorax is elongate and depressed and is only about a quarter the length of the mesothorax which, in turn, is approximately three times as long as the metathorax.

The aggregate length of the three segments equals their height and is twice their width.

The sclerites of the thorax, whose relative position is shown in figure 9, differs only slightly from those of the higher Lepidoptera.

Legs. (Fig. 10).

The legs of E. terminalis moths, which are densely covered with setae and have a fluffy appearance, do not differ in the two sexes, as is commonly the case with other Lepidoptera.

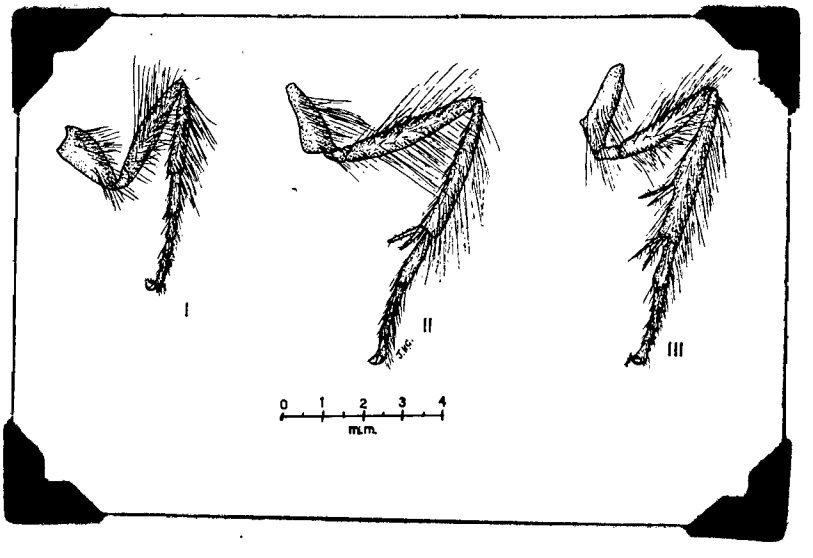


Fig. 10.

Front, Middle and hind leg of E. terminalis moth.

No spurs are present on the tibia of the fore legs while those of the mid-legs have a terminal pair, and those of the hind legs, have, in addition to these, a pair of

mid-tibial spurs/....

mid-tibial spurs.

The fore legs are much shorter than the mid or hind legs. The femur of the mid-legs is longer than that of the hind legs while the tibia, on the other hand is shorter.

The tarsus consists of 5 segments, the first segment being much longer than any of the other four. The terminal segment bears two claws and the pulvilli.

(c) Abdomen. (Fig. 11).

The abdomen of E. terminalis is made up of ten segments. In each segment, the tergite dorsally and the sternite ventrally are strongly chitinised.

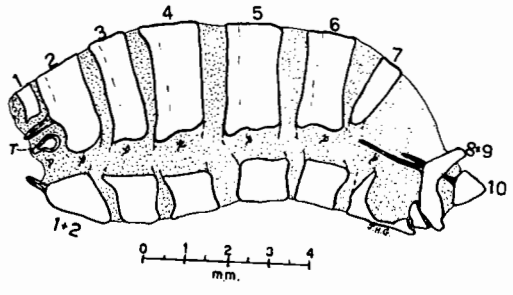


Fig. 11.

The abdomen of the female moth.

T - tympanium 1 - 10 - segments.

The sternites of the first and second segments are fused, and the eighth, ninth and tenth segments are modified into the genitalia.

The tympanium is situated in the first segment.

Segments one to seven carry a pair of stigmata each, which are situated laterally one on each side, on the less chitinised section between the tergite and sternite.

The only /.....

The only difference between the abdomens of the female and male, apart from the genitalia, is their shape, that of the female being cylindrical whereas that of the male is conical in shape.

Internal reproductive organs of the moth.

Janse (1932) considers that no description of a moth species is complete unless the genitalia have been taken into consideration. As the genitalia of E. terminalis have never been described, I include them in this study.

Male. (Fig. 12).

The pale yellow-green testes (t) are fused to form a single median ball - shaped testis, but in exceptional cases (Fig. 12 D.) it is still possible to discern the individual testes.

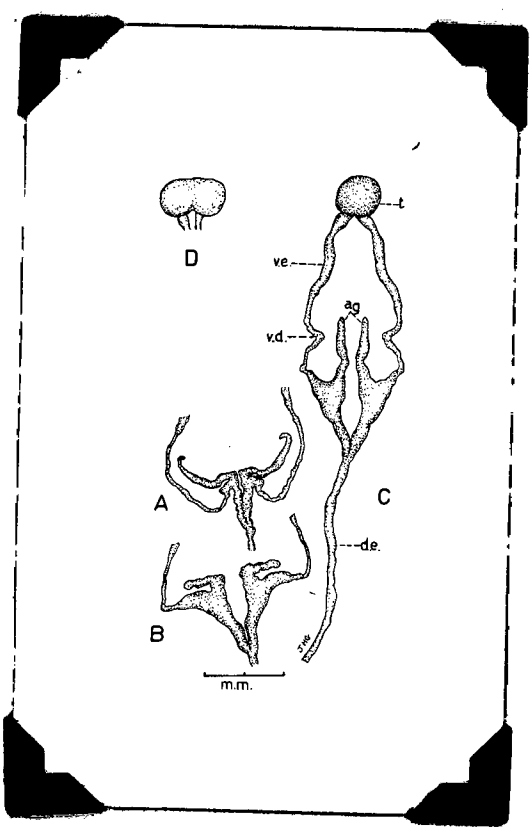


Fig. 12.

Male reproductive organs.

a.g. - accessory glands. d.e. - ductus ejaculatoris.

t - testes v.e. - vesicula seminalis

v.d. - vas deferens.

The vasa deferentia (v.d.) which emerge separately from the testis and which are slightly constricted after emergence, ~~widen out~~ enlarge to form the vesiculae seminalis (v.e.).

Thereafter/.....

Thereafter the vasa deferentia again gradually become narrower only to ~~widen out~~ broaden once more to form a swollen portion, - into which the accessory glands open, - before they unite to form the ductus ejaculatoris (d.e.)

Female. (Fig. 13.)

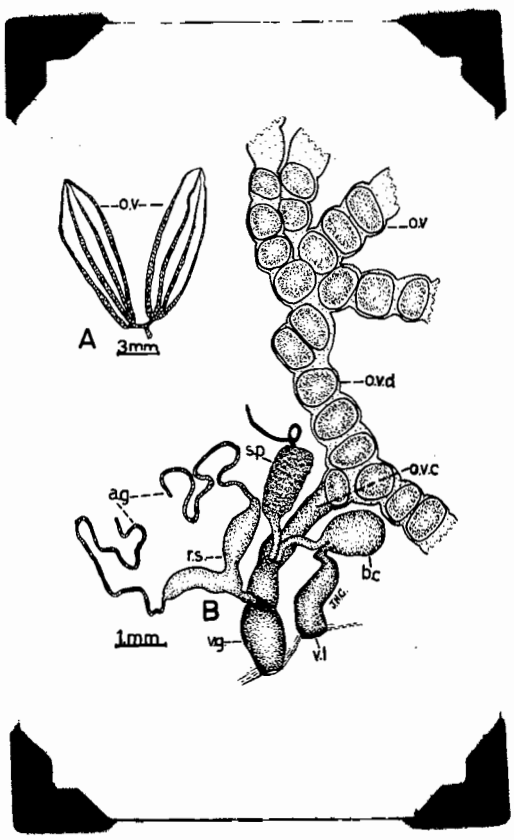


Fig. 13.

Female reproductive organs.

a.g. - accessory gland.
o.v. - ovariole.
o.v.d. - oviductus lateralus.
s.p. - Spermathéca.
b.c. - bursa copulatrix.
o.v.c. Oviductus communis.
r.s. - receptaculum seminalis.
v.g. - vagina.
v.l.-vulva.

The internal genitalia of the female moth consist of two oviducts (o.v.d.), each of which is made up of four ovarioles (o.v.) The two oviducts fuse to form the oviductus communis (o.v.c.) into which open firstly, the spermatheca (s.p.), and the narrow duct from the bursa copulatrix (b.c.) and secondly lower down near the external aperture, the fused tube of the two accessory glands (a.g.)

Each of the two/.....

Each of the two accessory glands opens into a receptaculum seminalis (r.s.), which opens into the oviductus communis.

The bursa copulatrix (b.c.) is connected to the exterior by a widened vulva (v.l.).

There is a narrow constriction at the point where the spermatheca and the bursa copulatrix opens into the oviductus communis and also lower down where the common duct of the accessory glands opens into it.

External genitalia of the moth.

Male. (Fig. 14).

The tenth segment of the abdomen of the male is modified into special clasping organs to assist it in holding the female during copulation. The tergite or uncus (Un.) is strongly sclerotised with two well developed lateral projections. The sternite or valva (Va.) consists of two hammer shaped valvae, and in the figure the right valva has been removed to expose the organs lying between the two valvae.

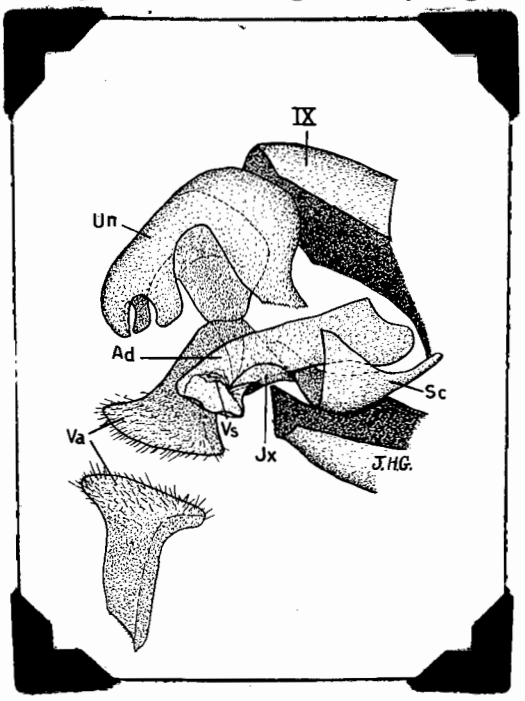


Fig. 14.

The external male genitalia.

IX - ninth abdominal segment.
Jx - juxta.
Va.- valva.
Ad. - aedeoagus.
Sc. - saccus.
Un. - uncus.
Vs. - vesica.

The sclerotised/.....

The sclerotised saccus (S.c.), which is bluntly pointed anteriorly, originates from an inward projection of the ninth segment. The juxta (Jx) has two lateral jointed projections.

The aedeoagus (Ad.) whose length is about four times its width, and which contains a membrane, the vesica (Vs.), is strongly sclerotised and ~~is~~ slightly widens at the apex.

In certain Lepidoptera the vesica may be covered with spines and hooks, the cornutae, but in E. terminalis, these are absent.

During copulation this membrane in which the ductus ejaculatorus is situated, extend into the bursa of the female, and the seminal fluid is thus passed into it.

Female. (Fig. 15.)

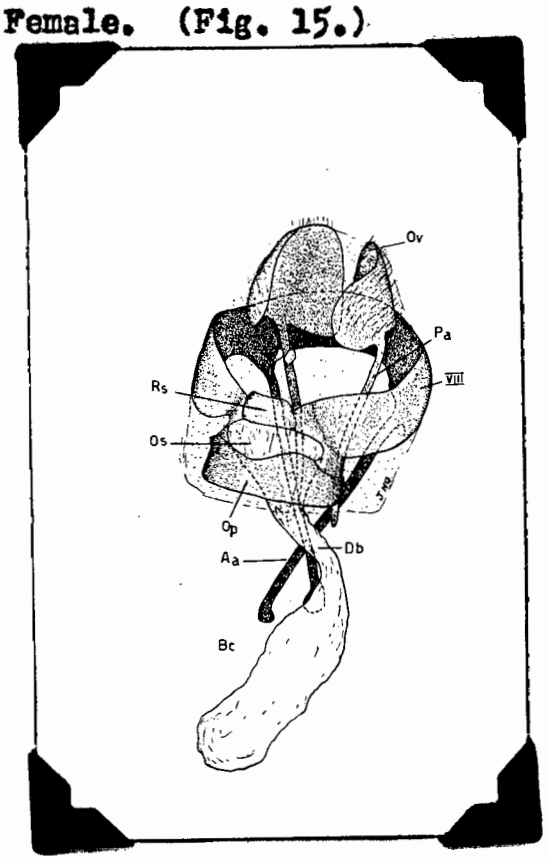


Fig. 15.

The external female genitalia.

VIII - eighth abdominal segment.
Aa. - anterior apophyses.
Db. - ductus Bursa.
Os. - ostium.
Pa. - posterior apophyses.
Bc. - bursa copulatrix.
Op. - ostium plate.
Ov. - ovipositor lobes.
Rs. - reduced 8th sternite.

The lobes of/.....

The lobes of the ovipositor are rounded at their posterior ends, and the posterior apophyses (Pa.) which are attached to the anterior ends of these lobes are slender, long and gently curved. The anterior apophyses (Aa.) which are attached to the anterior section of the eighth segment (VIII), are straight and slightly spatulated at their tips.

Copulation takes place through the opening in the eighth sternite, the ostium bursa. The ostium (Os.) is strongly sclerotised and the ostium plate (Op.) has two lateral rounded projection at its posterior end.

The ductus bursee (Db.) and bursa copulatrix (Bc.) are weakly sclerotised and have no signa.

3. HABITS.

Immediately after the moth emerges from the cocoon it makes its way through the covering layer of debris on the forest floor to reach the surface where it sits while its wings are drying. If a trunk or branch is in the vicinity, the insect will crawl up against it and come to rest in a vertical position. A period of approximately an hour elapses between the time of emergence and the moment the insect commences flying. As soon as the wings are sufficiently dry for flight, the moth takes off, initially flying low over the surface but gradually circling higher and higher until finally it disappears in the crowns of the trees.

The female moth, being heavily laden with eggs, flies more slowly and straighter than the male. The matter is a strong and fast flier, and always moves in zig-zag fashion, rather erratic, never to any set objective. The flying habits of the two sexes differ so radically that they may be distinguished with ease in the field on this basis.

Matting may/.....

Mating may take place at any time after the emergence of the female from the cocoon, but frequently she will repel the male initially, and mating usually takes place about half an hour after emergence. The males mate only after they have commenced flying. If a male with wings not yet fully unfolded be placed next to females, no attempt is made by it to commence mating.

In Table 1 the maximum, minimum and average times taken by 18 pairs of moths to complete copulation are reflected.

On occasions it has been observed that a female, immediately after copulating with one male for about 20 minutes, repeats the process for an equally long period with another male without hardly any time lapse between the two matings. Mating normally takes place in the crowns of the trees in which the moths congregate as soon as they are able to fly.

Moths emerging from the forest floor and unfolding their wings on the surface are most frequently seen during the early hours of the morning. After sunrise, as the temperature rises, these newly emerged moths mill around in flight below the trees and later ascend to the tree crowns. By midday relatively few moths will be found below the crowns of the trees. By observing from a tree taller than the average in a compartment of Pinus patula it was observed that the ascending moths first of all fly around above the tree crowns and then descend to settle in the crowns. If the moths which have settled in the trees are disturbed, they take off, fly about for a very short period, and then settle once more.

Time taken to complete copulation.	Maximum	Minimum	Average
	95 mins.	6 mins.	65 mins.

Table 1.

Duration of copulation of moths of E. terminalis.

If one/.....

If one examines the crowns of trees in which moths have settled some time after the peak of the flight period, many dead moths will be found adhering to the pine needles. When they settle in the crowns of Pinus trees, the moths fold their legs around the needles in such a manner that even after their death many of them adhere firmly to the foliage.

A very small proportion of moths deposit their eggs on tree trunks and branches but the vast majority oviposit in the crowns of the trees where the young larvae will be in direct contact with food supplies.

An attempt was made to determine the frequency distribution of egg packets at various levels of Pinus patula trees in an infested compartment in the Jessievale plantation. The trees were all from 35 to 40 feet high in this section. The first branches bearing foliage were situated on an average 17 feet above the forest floor, the crowns averaging 18 to 23 feet in height and 9 feet in diameter. Three sample trees were selected, and the crowns were surveyed meticulously for egg packets. Subsequently those parts of the trees below the crowns, i.e. the trunks and dead branches, were equally thoroughly examined. The results of this survey are compiled in Table 2. From this it is clear that most of the oviposition takes place in the upper 10 feet of the crown, and very little below the crowns.

Tree.	No. of egg packets.		
	Ground trunk and lower dead branches.	Bottom 8-13 feet of crown.	Uppermost 10 feet of crown.
No. 1.	1	5	29
No. 2.	0	7	26
No. 3.	1	5	34
Total	2	17	89
%	1.85	15.74	82.41

Table 2.

Distribution of egg packets of E. terminalis in Pinus patula.

The difference/....

The difference between the number of egg masses deposited at different heights in the tree is significant (χ^2 - 5.991 D.F. 2), especially when it is borne in mind that the upper level of the crown of the tree offers the smallest area on which oviposition can take place.

The number of eggs laid by one female varies between 58 and 287, the average number being 185. These figures were obtained by counting the eggs deposited by 57 mated females kept in captivity. Occasionally females have been observed to start laying an egg packet, stop and abandon it, and then to commence ovipositing elsewhere.

Just before the female commences ovipositing, there is a rapid movement of the lobes of her ovipositer, and as a result a dense mat of setae present on the anal tip of her abdomen becomes detached. The first eggs are deposited against this small ball of loose setae, and those laid subsequently are in turn covered with more setae also derived from the anal tuft. When oviposition ceases, the whole egg packet is covered with setae, all orientated along the long axis of the packet.

Usually ovipositing takes place 24 to 72 hours after emergence, but occasional exceptions in which ovipositing only started after 96 hours, have been observed. A healthy female completes oviposition in from 60 to 100 minutes provided the eggs are laid in one packet. In those exceptional cases where the eggs are deposited in more than one egg packet, a longer time is taken to complete the process.

Temperature has very little effect on the longevity of the moth, although it distinctly influences activity. A series of experiments was carried out to determine the influence of various combinations of temperature and relative humidity on the longevity and oviposition of the female

moths. The/.....

moths. The results are compiled in Table 3. At each combination of temperature and relative humidity 10 moths were used as test insects.

When Table 3 is studied, it is clear that low relative humidity does play a part in decreasing the life span of the moth. However, bearing in mind the fact that at a relative humidity as low as 36.8%, the moth is still able to live an average of 6 days at temperatures ranging from 15.5 - 32.5°C. it is clear that low relative humidities would not normally shorten the life span of the moth sufficiently to have a limiting effect on subsequent larval populations. Given a life of 6 days, the female moth would complete normal oviposition.

Migration of the moths.

If a study is made of the areas defoliated each year over a period of years in the Jessievale plantation, it is clearly ~~apparent~~ that severe infestations of E. terminalis occur at new sites each year, the same area never being heavily infested for two successive years. This phenomenon has given rise to the post hoc theory that the moths migrate from a defoliated to an undefoliated compartment. Superficially this theory is supported by the fact that of the thousands of moths visible during the early morning in an infested section, very few can be seen in the afternoon. Further support to the migration theory was thought to be found in the fact that few egg packets were noticed on the trees in infested sections while moths were ovipositing. This evidence, however, is ~~valueless~~ misleading since, as has been stated above, the bulk of the eggs are laid in the crowns where they would not be visible from the ground.

The writer's obsevations do not support the migration theory. Moths in defoliated sections were seen to move straight up into the tree crowns and deposit their eggs there.

Additional/.....

	% Relative Humidity.	Longevity of Moths in days. Mean	Standard error	Significant different from:
			15.5°C	
1	36.8	6	± 0.3333	2 to 6
2	56.8	8	± 0.3649	1, 3 to 6
3	66.8	10	± 0.4345	1, 2
4	82.9	10	± 0.6325	-
5	92.1	10	± 0.3650	-
6	96.1	10	± 0.7745	-
			21.0°C	
1	36.8	6	± 0.3463	2 to 6
2	56.8	8	± 0.6834	1, 3 to 6
3	66.8	10	± 0.0349	1, 2
4	82.9	10	± 0.4216	-
5	92.1	10	± 0.5961	-
6	96.1	10	± 1.6195	-
			26.5°C	
1	36.8	6	± 0.0332	2 to 6
2	56.8	8	± 0.0943	1, 3 to 6
3	66.8	10	± 0.4216	1, 2
4	82.9	10	± 0.4216	-
5	92.1	10	± 0.5775	-
6	96.1	10	± 1.0595	-
			32.5°C	
1	36.8	6	± 0.6496	1 to 6
2	56.8	8	± 0.6667	1, 3 to 6
3	66.8	10	± 0.6667	1, 2
4	82.9	10	± 0.3333	-
5	92.1	10	± 0.4472	-
6	96.1	10	± 0.6992	-

Table 3.

Combined effect of temperature and relative humidity on longevity of the moth. The standard error of the difference between two means :

$$\sqrt{(\text{Standard error of Mean}_1)^2 + (\text{Standard error of Mean}_2)^2}$$

The minimum significant difference was calculated from:-

M.S.D. = Standard error of the two means x t, where t = a value found from t tables at the desired probability level, which in this case is 19:1 odds.

Additional tests to prove or disprove the theory of moth migration were carried out by marking moths.

Various workers, (Fletcher (1936), Queri (1936), Williams et. al. (1942) and Skaife (1953)) have described techniques to mark insects in order to study their movements. Although these methods are excellent, the marking process is too laborious and time-consuming to be applied in cases where large numbers of insects are to be dealt with. The method described by Collins and Potts (1932) appeared to be the most practical one in this case. Aniline dye is dissolved in 70% alcohol and painted on the wings of the moth, using for this purpose a camel-hair brush. This method has decided advantages in that it can be speedily applied, the solution dries almost immediately, and also in that sticky substances which could glue the wings together, are not used.

As described above, the newly emerged moths of E. terminalis sit inactive on the forest floor during the mornings while awaiting the unfolding of their wings, and fly off later when the temperature rises. By selecting a compartment heavily infested at Jessievale at a period when moths were emerging, ample numbers of moths could be marked with ease within a small area during the early morning. The best time for marking was found to be at sunrise when temperatures were still ~~too~~ low ~~readily to permit~~ and the moths with wings already unfolded ~~to fly~~ inactive. Using the technique of Collins and Potts, it was possible to mark 5,000 moths in an area only 60 x 120 feet in extent during the time of 4 hours one early morning. By using a very dark blue solution, which showed up extremely well on the normally yellow wings, the marked moths could be very clearly differentiated even when in flight.

The area/.....

The area in which the moths were marked, and undefoliated sections of the plantation adjoining it, were kept under continous and meticulous observation for a period of ten days. During this extended period of observation, a total of 310 marked moths were recovered, every single one of which was found within a radius of 600 feet of the area in which marking was carried out. Although the whole of the surrounding area of the plantation was kept under very close observation, not a single marked moth was seen there.

The observation shows that although a small number of moths in a defoliated section may perhaps fly over into adjoining undefoliated sections and thus spread the infestation, the numbers involved if this does occur are so limited that this movement can in no way be described as a migration. It is quite clear that the bulk of the moths emerging in a defoliated compartment oviposit in that area without migration.

It may thus safely be accepted that the peak infestations developing in new areas from year to year in the Jessievale plantation build up progressively from small nuclei until epidemic proportions are reached, and not as a result of mass migration of moths from heavily infested into adjoining uninfested compartments.

The bulk of the moths emerging in a defoliated compartment lay their eggs in that compartment without migration. The resulting larval population, as will be shown later, is so large that it becomes highly susceptible to other controlling factors which then reduce it to a minimum level. Many years elapse before this surviving nucleus has once more built up sufficiently to give rise to another outbreak.

CHAPTER IV/.....

CHAPTER IV.

T H E E G G.

1. MORPHOLOGY:

From the dorsal aspect the globular egg has an even circular outline, but viewed from the side it is oval in shape. The ventral surface, on which the micropyle is situated, is flattened in the newly laid egg, but with increasing age it becomes concavely indented.

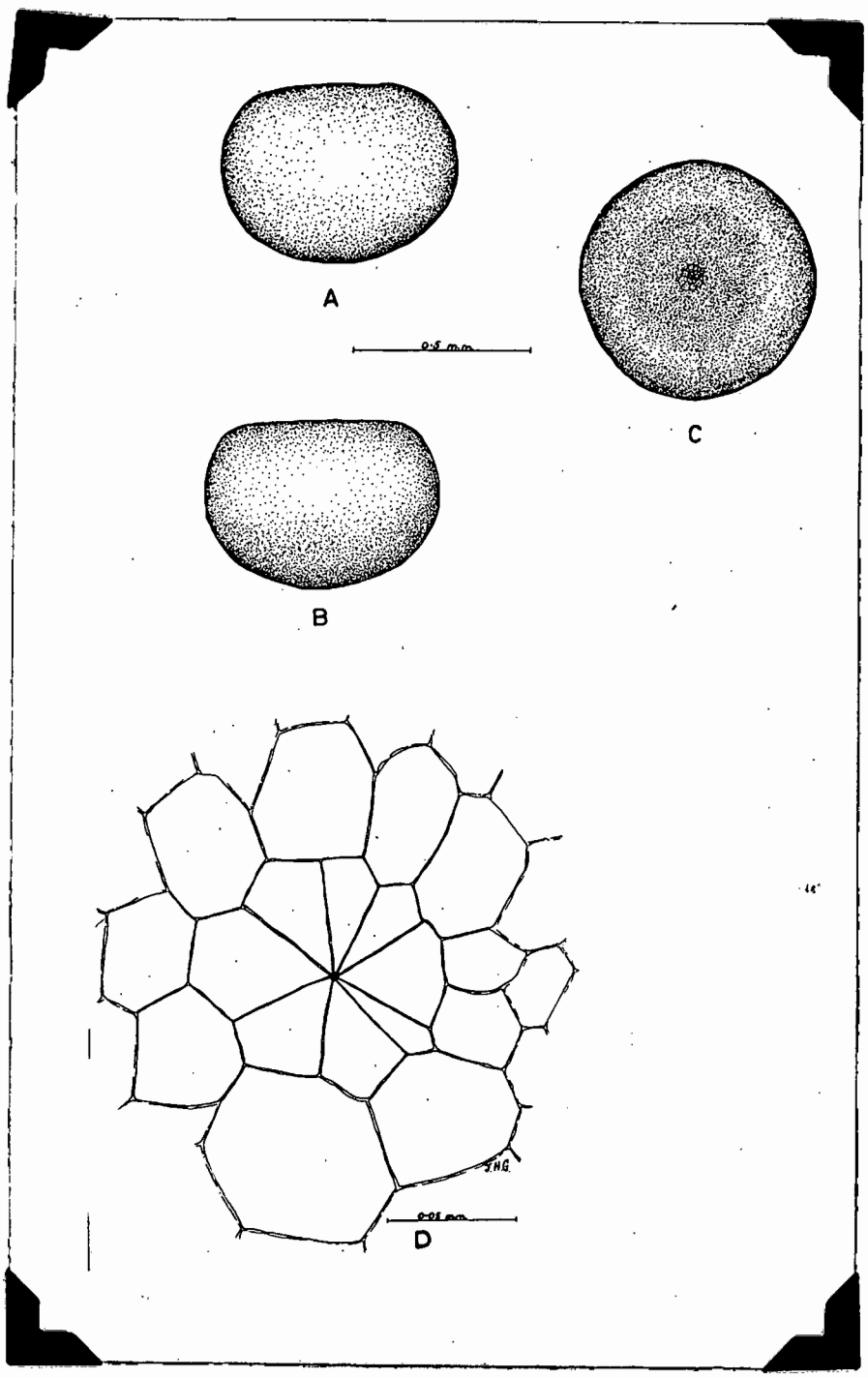


Fig. 16.

A. Lateral aspect of a newly laid egg. B. Same of an older egg. C. Ventral aspect of the egg, showing micropyle. D. Micropyle area.

Fig. 17./.....

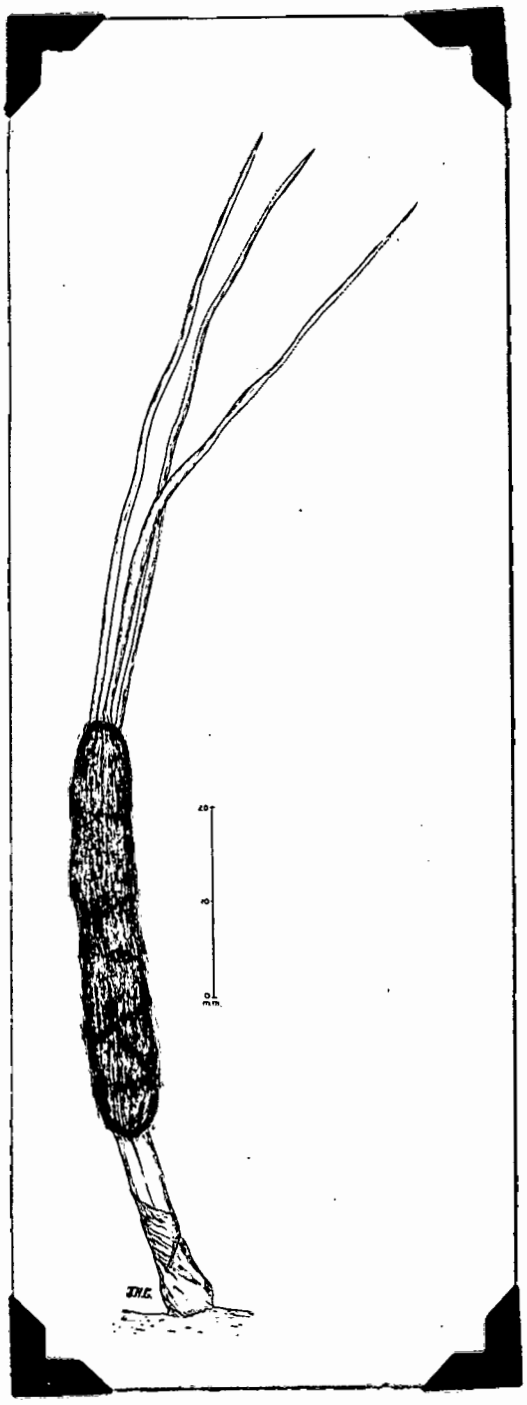


Fig. 17.

Egg mass covered with setae on a needle facet.

In Table 4 the average dimensions and size variation of 30ø eggs are given.

	Average.	Standard Deviation.
Diameter, dorsal aspect	0.66	± 0.00003
Height, lateral aspect:		
Newly laid	0.49	± 0.01634
10 days old	0.46	± 0.00002

Table 4.

Egg dimensions in millimetres.

The unsculptured, glistening, whitish chorion is somewhat translucent and allows the contents to show through, hence the newly laid egg is tinged pale pastel green, while the more mature egg appears to be coloured

a pastel shade/.....

a pastel shade of brown. The chorion is unmarked except in the immediate vicinity of the micropyle in the middle of the ventral surface, where there is a reticulated area extending to a radius of 0.08 m.m. from the micropyle.

The eggs are deposited in elongated, irregularly shaped masses (Fig. 17) which are covered with pale brown hairs derived from the tip of the abdomen of the female moth. Each egg in a mass touches but never overlaps its neighbour.

(a) Biology.

(i) Method of controlling relative humidity.

In view of the fact that the habitat of E. terminalis includes areas where there are wide fluctuations in temperature and relative humidity, a series of experiments was performed to determine the influence of variations in these factors on the egg, larval and moth stages of this insect.

Various research workers have employed different techniques by means of which test insects could be kept constantly at any particular humidity desired. Since the experiments to be carried out by the writer were to be conducted under varying conditions of temperature, it was decided to use sulphuric acid to control humidity. The humidity of an atmosphere above any given concentration of this acid varies extremely little with changes in temperature. This fact is very clearly illustrated in the graph prepared by Wilson (1921), (Fig. 18) especially when it is considered that the temperature range of the writer's experiments extended only from 10°C to 32.5°C.

When alkalis are used instead of sulphuric acid to control humidities, these chemicals have the decided advantage only in that they absorb excess carbon dioxide which may be formed. To eliminate the difficulty of excess CO_2 when using the acid method, it was decided to adopt a system of maintaining a slow, moving air stream by bubbling

air through/.....

air through the acid in each container. Solomon (1931) also considered that $H_2 SO_4$ was the best humidity controlling agent to use in experiments of this nature since "the physical data for sulphuric acid solutions are probably more accurately determined than the data for any other compounds".

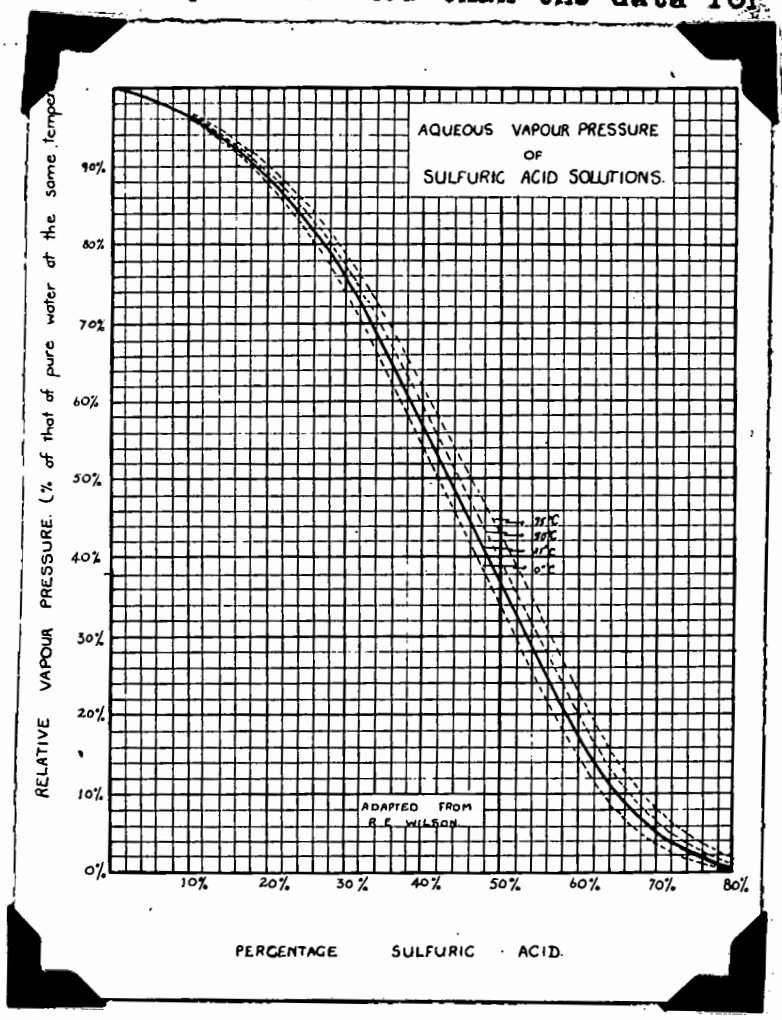


Fig. 18.

Graph adopted from R.E. Wilson (1921) indicating the aqueous vapour pressure of sulphuric acid solutions, showing the extremely little change with fluctuations in temperature.

The technique employed by the writer is based on the same principle as that proposed by Wilson (1921) and Buxton (1931), namely, to pump a stream of air through sulphuric acid of varying strengths in different bottles, the air in each case then being led over the test insects. (Fig. 19).

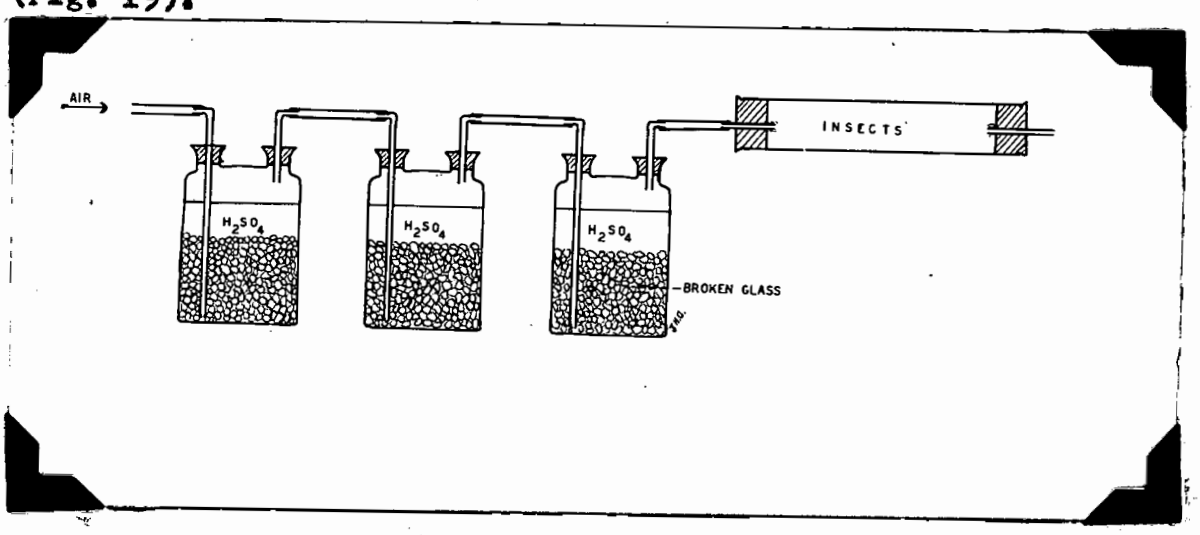


Fig. 19.

Bottles containing sulphuric acid and broken glass through which air is pumped.

The point/.....

The point of the glass tube through which the air is led into the acid solution in each container, is narrow to decrease the size of the air bubbles. In addition, the bottles containing the acid, hold broken glass to break up the air into still smaller bubbles, and to slow down their passage through the acid solution. To ensure that the air passing through the acid solution attains the desired humidity, it is pumped through the system at a speed range of only 80 - 100 c.c. per minute.

The eggs, larvae or adults ~~are contained~~ were contained in glass cylinders, of a diameter of 15 m.m. in the case of the eggs, and 30 m.m. in the case of the larvae and moths. The cylinder was corked at each end, and through the corks air was introduced via a glass tube at one end and led out by another at the other end. The full details concerning the connection of the glass cylinder in the air circuit producing the desired relative humidity, are shown in the illustration given herewith.

Buxton (1931) considered that this type of apparatus was not ideally suitable for experiments in which larvae, to be fed on fresh moist foliage, serve as test insects. His grounds for this statement, are the fact that the larvae are in contact with the transpiring leaves, which automatically create a higher humidity in the air immediately surrounding them, and secondly, the moist air arising from the leaf actually flows over to the test insect. The theoretical relative humidities to which the test insects are exposed, thus do not correspond with the actual humidity of the air surrounding them, and the results obtained will thus not give a true reflection.

In the case of the larvae of E. terminalis, only a few needles of Pinus patula were provided as food in each cylinder. The surface of the leaves, from which transpiration can take place, is relatively small, and the effect

of such transpiration/..

of such transpiration on the humidity in the cylinder, through which a slow air stream is passing, would be negligible. By limiting the number of needles, and renewing the food supply at more frequent intervals as replacement became necessary, the need for using plenty of leaves in the cylinder, which would in turn affect the humidity, did not arise.

In any case, seeing that the insects used in such tests are in nature confined to transpiring leaves, the relative effect of varying atmospheric humidities on the insects would be more or less ~~constant~~ the same in the laboratory as out of doors.

b. <u>The combined influence of temperature and humidity on the hatching of E. terminalis eggs</u>.

To determine the combined influence of temperature and relative humidity on the incubation of <u>E. terminalis</u> eggs, the eggs were maintained at various constant humidities as previously described and at constant temperatures of 16.6°C, 21.0°C and 26.0°C. At every combination of temperature and humidity, 100 eggs were used. The results of the experiment are compiled in Table 5, and the data are reflected as smoothed curves in Fig. 22.

The results indicate that at 26°C relative humidity does not affect the incubation of the eggs to the same extent as at temperatures of 16.6°C and 21.0°C. Secondly, it is quite clear that at relative humidities of approximately 85% and higher, temperature is the main factor which determines the length of incubation, while the various relative humidities tested have no influence on it.

Relative humidities from 46.8% and lower seem to be fatal at the three temperatures the eggs were exposed to.

Fig. 20/.....

In experiments carried out at the Jessievale plantation to determine how long fourteen E. terminalis egg masses, containing an average of 180 eggs per mass, took to hatch, it was found that at an average temperature of 15.5°C, the first larvae appeared 18 days, and the last larvae 21 days after the eggs were oviposited.

The egg masses were not removed from the needles on the branches where they were deposited, but were only covered with the celluloid - organdi cages (Chapter V.2) to prevent parasites from attacking them.

CHAPTER V./.....

CHAPTER V.

T H E L A R V A.

1. MORPHOLOGY.

In the description given below, colour classification is based on the system proposed by Ridgeway (1912.)

(a) General description.

There are eight larval stages of E. terminalis. The newly hatched larva is on an average 1.68 m.m. long. By the time it has reached the last stage, and is fully grown, the length averages 30 m.m.

As the differences between the various instars are so slight, only the first and last instar has been described fully. In the key to the larval instars, the difference between all the different stages are mentioned.

All larval instars of E. terminalis bear a large and constant number of verrucae (Fracker 1915.) on their bodies, on which setae of variable length and type are abundantly present. The result is that the larvae have an extremely hairy appearance. This effect is added to by the fact that shorter setae, placed between the dorsal verrucae are found in the later instars, and especially in the case of the fullgrown larva. Even the head appears hairy due to its being covered with fine primary and secondary setae.

In the full grown larva the head is flame-scarlet in colour, blotched irregularly with darkbrown. The three pairs of thoracic legs, and four pairs of prolegs situated on the third to sixth and the last abdominal segments, are all well developed and of an orange-chrome colour. On each of the sixth and seventh abdominal segments a gland opening is to be found, placed medially between the dorsal verrucae - in the later instars these openings are practically completely obscured by the secondary setae found in this area.

Fig. 23/.....

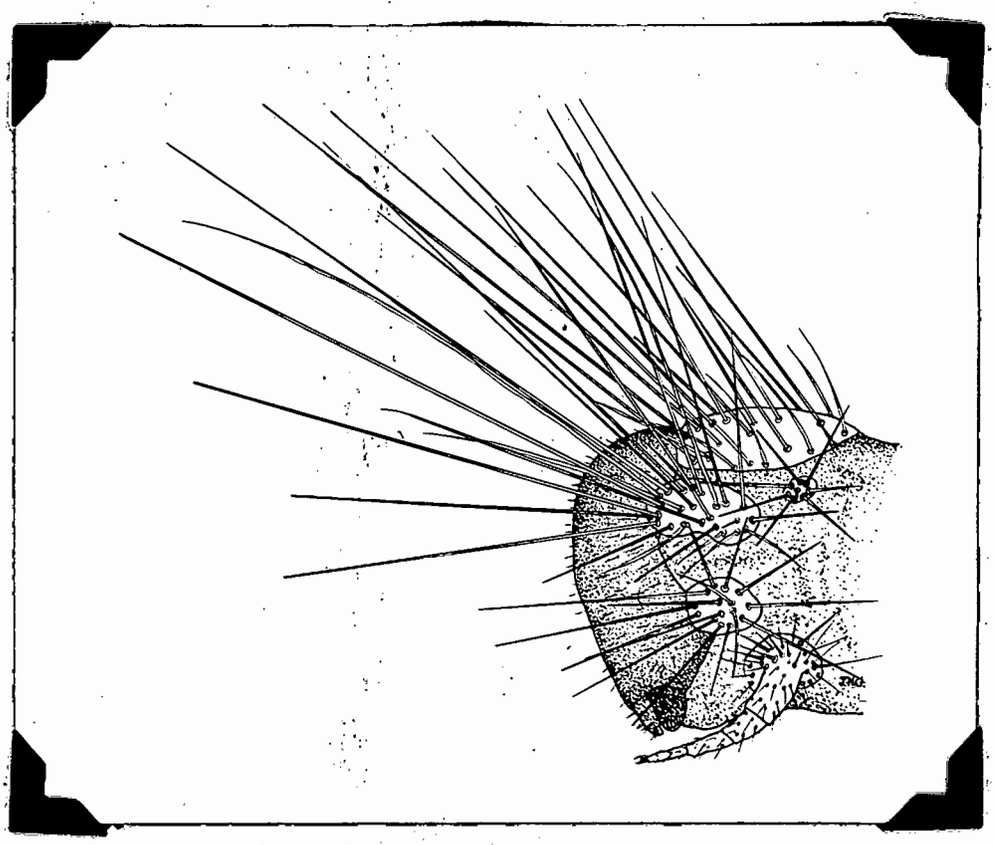


Fig. 21.

Lateral aspect of the first thoracic segment showing relative length of setae on the verrucae.

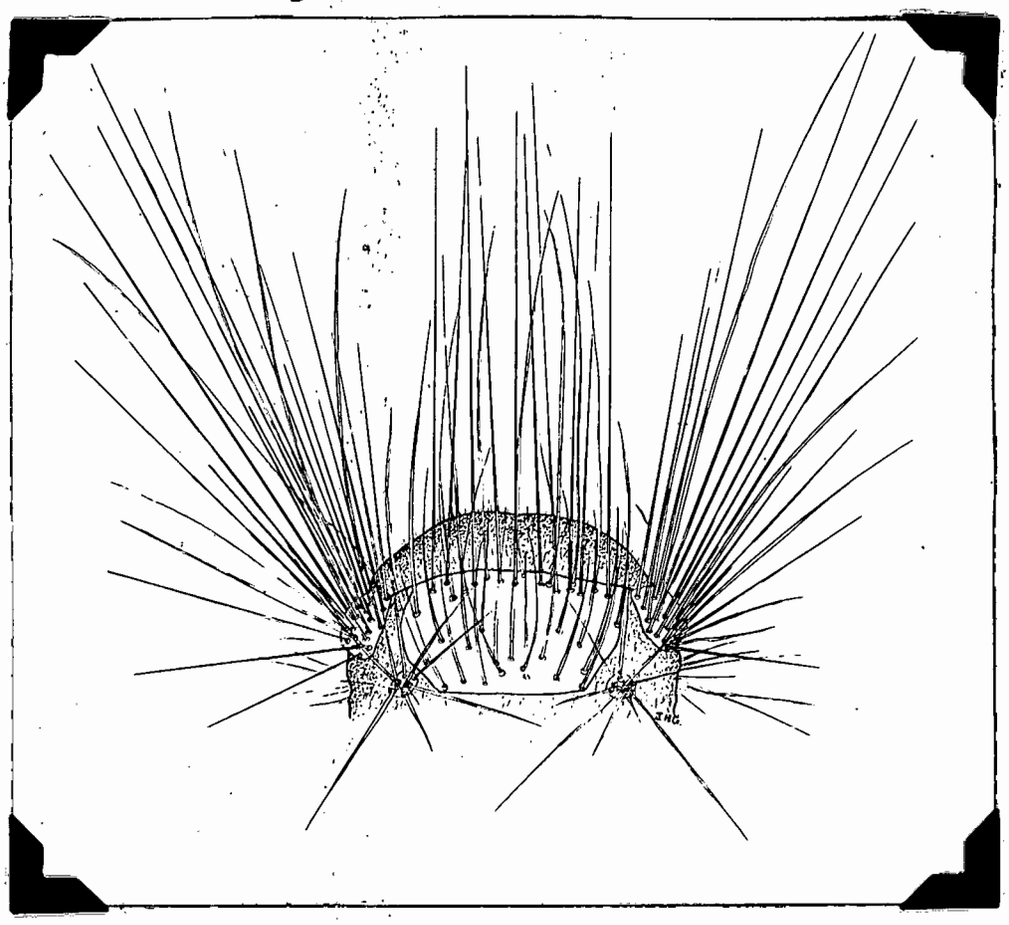


Fig. 22.

Dorsal aspect of the first thoracic segment.

Black and yellow-orange/....

Black and yellow-orange form the ground colours of the integument. The proportion of the skin area occupied by each of these colours is not constant, and varies according to climatic conditions. This aspect is dealt with in detail elsewhere in this paper and need not be considered here.

The surface of the larval skin is covered by a dense mass of small projections. By sectioning and microscopic examination, these projections will be found to be non-cellular, purely cuticular structures, spread evenly over the whole body surface, each of which has its origin in a polygonal area of the skin. (Fig. 23).

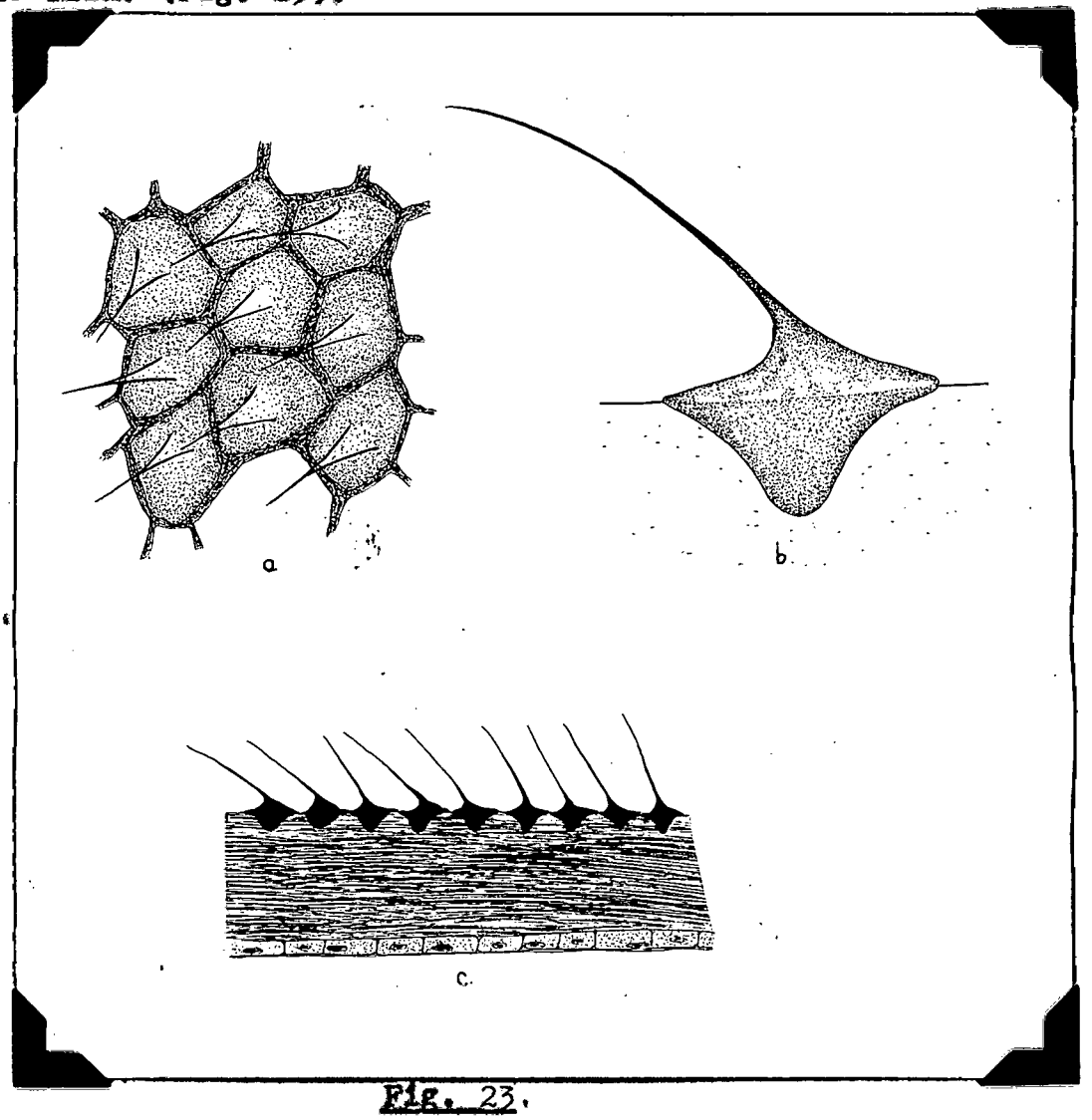


Fig. 23.

Noncellular projections on the surface of the larval skin.

a. Dorsal aspect.

b. Enlarged projection.

c. Section of the skin, showing the position of the projections.

b. Chaetotaxy of the first and last larval instars.

i. Technique: Various research workers, amongst others Dayer (1894) Fracker (1915) Garman (1921), and Gerasimov (1935) have studied the chaetotaxy of the Lepidopteran larvae, but unfortunately no uniform nomenclature was adopted and a state of utter confusion in this field resulted.

Hinton (1946) proposed a completely new nomenclature. He adopted this procedure after realising that the generally accepted views on the homology of many setae were wrong, and after he had discovered that certain workers had not taken into consideration all the small microscopic setae, with the result that their work was even yet more inaccurate.

Workers such as Williams (1951, 1953) and Singh (1953) have applied the nomenclature of Hinton with success. In this study the writer has also followed Hinton, although the application of his nomenclature is rendered extremely difficult by the large numbers of secondary setae present on the larvae of E. terminalis.

In this study the positions of the long setae only are charted in view of the fact that the detail of a setal map would be entirely obscured if all the secondary setae, present in this type of larva, are included. (Figs. 21 and 22).

The setal maps of the three thoracic segments, also of the first, second, and sixth to ninth abdominal segments, are given in full. The third to the fifth abdominal segments correspond with the sixth segment in setal pattern, hence setal maps for these segments are not given. In the case of the tenth abdominal segment no map is given, since its setae are not considered to be of any taxonomic importance.

The setae missed by earlier workers and brought to light by Hinton, are in many cases extremely small.

Those present/.....

Those present on the prosternum of E. terminalis are only 0.008 m.m. long. These are classified by Hinton as microsetae or proprioceptors. He gives no details concerning the technique employed by him when studying these setae, except for mentioning that in many cases he made use of blown larvae.

The following technique adopted by the writer greatly facilitated studies in this field on E. terminalis and ensured that very small setae would not pass unnoticed.

Very small larvae:-

(a) Boil the larva for 30 minutes in a 5% solution of KOH. Thereafter wash well in distilled water to eliminate most of the KOH.

(b) Sever the head from the body under water by carefully cutting it away, using a small sharp scalpel for the purpose.

(c) The body of the larva is once again boiled in KOH, as a result of which the skin becomes very clear. Washing with distilled water to remove all the KOH is then applied.

(d) The next step involves cutting the skin along the ventro-median line and pinning it open, whereafter the skin is mounted on a slide. In view of the difficulty of such dissection in the case of the very small larva, the writer adopted the following procedure:- A glass rod of a diameter slightly exceeding that of the larva, is heated in a flame and drawn out to taper off into a sharp point. The pointed end is now inserted into the body of the larva from the end where the head was removed. By manipulation with a fine pair of forceps the body of the larva is drawn upwards along the tapering end of the rod, the point being passed through the anal opening, until eventually the skin at the anterior end is tightly drawn around the rod. The skin can now readily be cut along the ventro-median line at the anterior end where it is tightly drawn over

the rod. After each cut the body of the larva is moved up the rod, thus tightening the next section of the skin, which may in turn be neatly cut. In this way the opening of the skin along the ventro-median line from the head end to the anus is neatly and efficiently accomplished.

(e) When skinning is complete, the skin is flattened out between two slides, and in this position is passed through increasing strenghts of alcohol to dehydrate it, and finally through Xylol for clearing. Unless the skin is kept between two slides during this process, it tends to curl up and assume its normal position, and it cannot then be flattened out for mounting. When the dehydration and clearing processes have been completed, the skin is mounted in Canada Balsam on a slide under a cover slip. Owing to its shape, the tenth abdominal segment does not readily flatten out for mounting. This difficulty may be overcome by making a short incision into this segment along the dorso-median line.

Larger larvae:- To mount the skins of the later larval instars, the same technique as described above may be used except for the fact that it is no longer necessary to use a glass rod. The cut along the ventro-median line can be made directly using a small pair of sharp scissors. However, modifications of technique are necessary if the colour pattern of the skin is to be permanently maintained for study in addition to the chaetotaxy.

The following technique was found to be most satisfactory when both chaetotaxy and colour pattern of the larger larva were to be studied:-

(a) The larva is placed in a Petri dish on the bottom of which a layer of Paraffin wax ½ inch deep is provided. It is mounted therein on its back by fixing the two anal prolegs to the wax layer, using minutchen pins for the purpose; a third pin is now passed through the head, the

body is/.....

body is drawn forward until fully extended, and the pin is stuck into the wax layer. Water is now added to the Petri dish until the body of the larva is completely submerged.

(b) Using a small pair of sharp scissors, the body of the larva is ~~new~~ opened along the ventro-median line. The skin is then pinned flat on the bottom of the Petri dish, the mimutchen pins used being passed through the legs into the underlying wax layer.

(c) With a sharp scalpel the head of the larva is ~~new~~ removed from the body, and the internal organs of the body are carefully eliminated. To remove adhering muscles from the skin, the internal surface is gently scraped ~~by means of~~ with a needle with a bent tip, the water in the dish at this stage being replaced by 35% alcohol (stronger alcohol should not be used since this would harden the skin and thus create difficulty in evening out folds and wrinkles when the specimen has subsequently to be mounted). When the skin has been cleared in this way of all adhering tissue, it is mounted between two slides, dehydrated in alcohol and cleared in Xylol, and mounted permanently on a slide in the way described above for small larvae.

The great advantage of this skinning technique lies in the fact that it enables the research worker to study the chaetotaxy and colour pattern of the skin by means of transmitted light, thus permitting the use of a much higher magnification than would be the case if reflected light is used.

The setae present on the thoracic and abdominal segments of a Lepidopterous larva are divided into 3 classes. The division was ~~instituted~~ worked out by Fracker (1915) and adopted by Hinton (1946). The classes delimited are as follows:-

(a) Primary setae:- Setae found on generalised larvae in all instars.

(b) Subprimary setae:/...

(b) Subprimary setae:- Setae having a definite position in certain larvae, but not present on the first instar of generalised groups.

(c) Secondary setae:- Numerous setae having a general distribution and not limited to verrucae and other forms of tubercle. In addition, a group of primary setae which are extremely small, have been named microscopic setae or proprioceptors by Hinton (1946). Excepting one on the prothorax (MXD1), all the last-mentioned setae are found on the anterior section of a segment.

In the setal maps of the first and last larval instars of E. terminalis (Figs. 24, 25, 26 and 27), the details are plotted of only one side of each segment studied.

ii. Microscopic or Proprioceptor setae.

(a) The thorax.

Prothorax: Three proprioceptor setae are found on the prothorax. These are placed as follows:-

(i) MXD1. This seta is the only one of the proprioceptor setae to be found on the anterior section of a segment, and is placed on the caudo-dorsal margin of the sclerotized thoracic shield near the dorso-median line of the segment. In the case of the last larval instar this seta is identified with difficulty owing to the fact that numerous secondary setae obscure it.

(ii) MV_2 and MV_3. These two proprioceptor setae are placed on the prosternum of the segment, MV_2 being situated more dorsally than MV_3.

Mesothorax: Six proprioceptor setae are found on this segment, and these are situated as follows:-

Fig. 24./.....

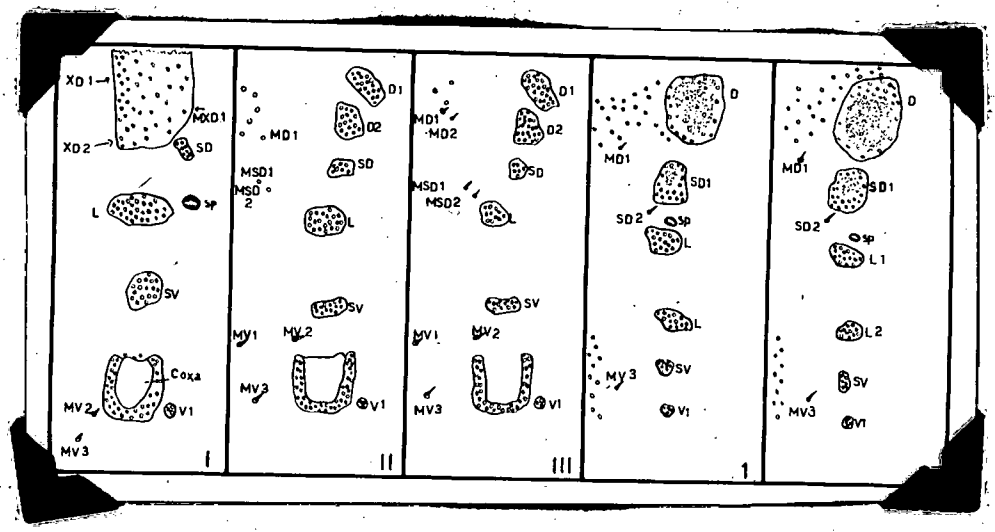


Fig. 24.

Setal map, last instar, thoracic and first two abdominal segments.

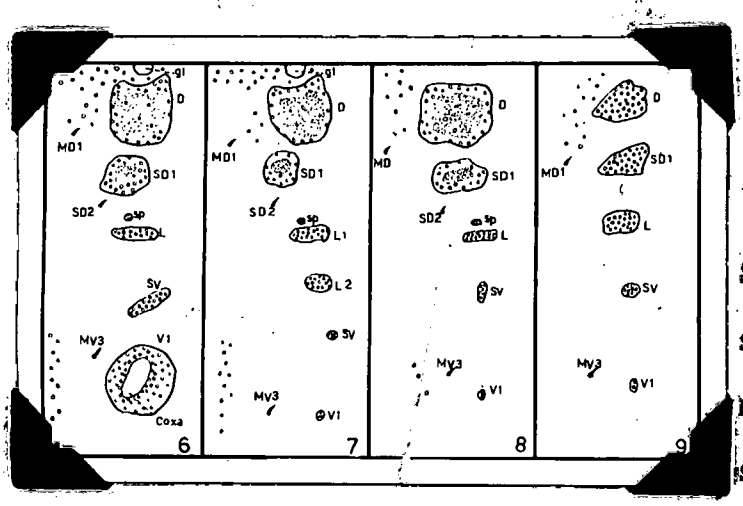


Fig. 25.

Setal map, last instar, ~~seventh~~ sixth to ninth abdominal segments.

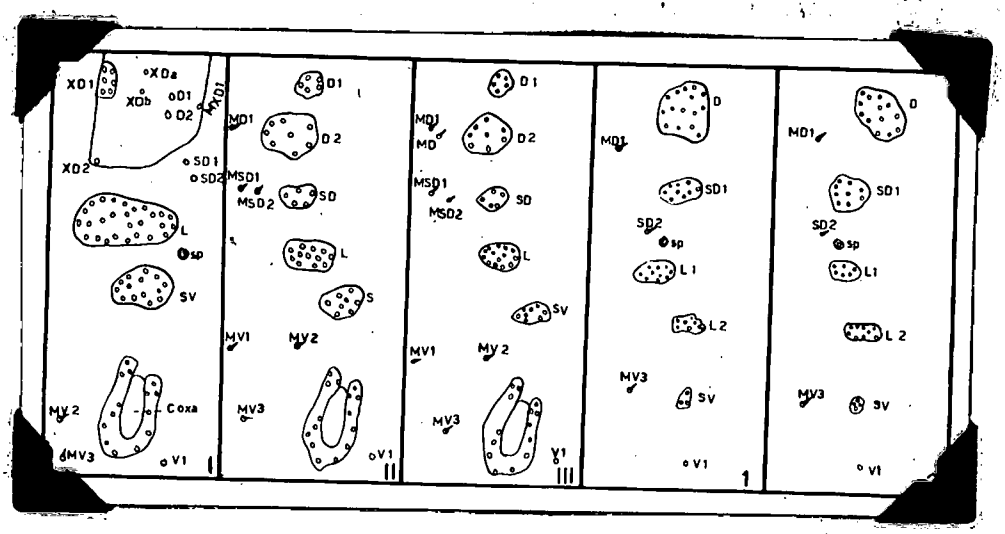


Fig. 26.

Setal map, first instar, thoracic and first two abdominal segments.

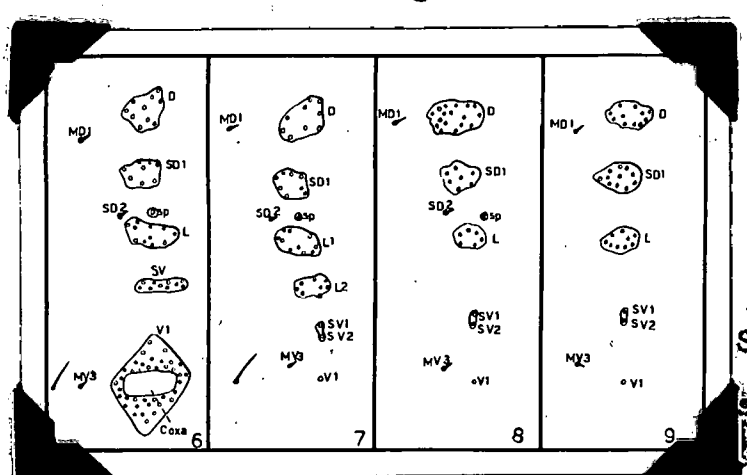


Fig. 27.

Setal map, first instar, ~~seventh~~ sixth to ninth abdominal segments.

(i) MD_1. Situated on the dorso-anterior area of the segment immediately anterior to D_2.

(ii) MSD_1 and MSD_2. These two setae are ventral to MD_1 and immediately anterior to SD, MSD_2 being the most caudal of the two.

(iii) MV_1, MV_2 and MV_3. These three proprioceptor setae are found on the prosternum of the segment. According to Hinton (1946) the most anterior and dorsally situated of these is MV_1, but in this case the anterior most of the three setae is set in line with the caudal seta. The writer has accordingly numbered the anterior most seta MV_1, the most vertral one MV_3, and the most caudal seta MV_2.

Metathorax: The proprioceptor setae on the metathorax correspond with those on the mesothorax excepting for the fact that there is an additional MD seta, MD_2, which is situated just caudo-ventral to MD_1.

(b) Body segments 1 - 9.

Only two proprioceptor setae, MD_1 and MV_3, occur on each of the abdominal segments.

(i) MD_1. Situated more ventrally in relation to D than is the case with the meso-and metathorax, where MD_1 is situated immediately anterior to D_2.

(ii) MV_3. On segments 1, 2, 7, 8 and 9, MV_3 is placed antero-dorsally in relation to the SV group. On segments 3 - 6, which bear prolegs, MV_3 is placed anterior to the coxa.

iii. The long or tactile setae.

XD Group. This group, confined exclusively to the prothorax, consists of two setae only. In the first larval instar of E. terminalis only XD_2 is clearly apparent since XD_1 occurs on a verruca together with secondary setae which obscure it. In the last instar there are so many

secondary setae/.....

secondary setae, that neither of the XD setae can be clearly differentiated.

Both XD setae are situated on the anterior margin of the thoracic shield, XD_2 being the one placed in the ventro-anterior corner thereof. On the thoracic shield there are two punctures, XDa and XDb, situated caudally to the verruca on which XD_1 is found. These punctures, which may readily be differentiated only in the first instar larvae, where they are not obscured by secondary setae, are placed vertically between the XD_1 seta and the D_1 seta. XDb is placed on the line drawn between the verruca of XD_1 and the D_1 seta, while XDa is situated somewhat more dorsally.

Dorsal group.

This group consists of two primary setae only, namely D_1 and D_2. In the first instar larva it can clearly be seen that these two setae are placed on the thoracic shield of the prothorax. In the last instar it is difficult to determine which of the setae are D_1 and D_2 since there are so many secondary setae to obscure the issue.

On the meso- and metathorax of the first as well as the second instar larvae, these setae are borne on two verrucae, but they cannot be differentiated owing to the large number of secondary setae also present on the verrucae. The same conditions exist on the abdominal segments, except that the D setae, together with a large number of secondary setae, are found on a single verruca. In this case the verruca together with its setae is denoted by the letter D.

Subdorsal Group.

Only two primary setae, SD_1 and SD_2, compose this group. They can be clearly differentiated only on the prothorax of the first instar larva, being found close together adjacent to the postero-ventral corner of the thoracic shield. On the meso- and metathorax of the first, and all three thoracic segments of the last instar, these setae, together with large numbers of secondary setae, are placed on one

verruca. On the/.....

verruca. On the first to the eighth abdominal segments, however, these primary setae are separated and distinct. SD1, together with secondary setae, is placed on one verruca, and just ventral to this, SD2 can be clearly seen as a small, isolated seta. On the ninth abdominal segment, as in the case of the meso- and metathorax of the first instar larva, there is only one verruca, denoted by the letters SD, on which the presence of the primary setae is completely obscured by numerous secondary setae.

Lateral Group.

The lateral group is composed of 3 setae numbered L1, L2 and L3. Hinton (1946) states that L1 and L2 are primary setae on the prothorax, while on the meso- and metathorax only L1 is primary, L2 and L3 being subprimary setae; on the abdomen he holds that L1 and L2 are primary on segments 1 - 8, L3 being subprimary, while on the ninth segment all three are primary.

In the case of E. terminalis this group of setae is represented on the thoracic segments, and the abdominal segments 3 to 6 as well as 8 and 9, by one verruca bearing many secondary setae, which is denoted by the letter L. In the abdominal segments 2, 3 and 7, however, the group is represented by two verrucae which are shown as L1 and L2 respectively.

Subventral Group.

According to Hinton (1946), two setae, numbered SV1 and SV2, are universally present on the prothorax. The larva of E. terminalis has only one verruca on the prothorax representing this group, denoted as SV. Owing to the numerous secondary setae borne by this verruca, it is not possible to distinguish the two primary setae. In this respect the meso- and metathorax correspond.

In the first instar larva, this group is represented as follows in the abdominal segments:- SV on segment one is a verruca bearing either two or occasionally

three setae; on segment two, the verruca SV may bear either three or occasionally four setae; on segments 3 to 6, the SV verruca bears a large number of secondary setae which confuse the issue; on segments 7, 8 and 9 the group is represented by only two setae which are dnoted as SV1 and SV2. In the case of the last larval instar, the SV group is represented on each segment by one verruca which bears a large number of secondary setae.

Ventral group.

In the first larval instar, this group is represented on the thoracic segments by a single seta, V1, which is situated ventro-posteriorly in relation to the coxa. In the first, second, seventh, eighth and ninth abdominal segments, it also consists of a single seta, V1, which is situated ventrally to the SV group. In the third to the sixth abdominal segments, which bear prolegs, the setae belonging to the V group are completely obscured by the secondary setae present on the coxae of the prolegs.

In the last instar, V1 appears in the thoracic segments on a verruca bearing two secondary setae. In the first and second abdominal segments the verruca bearing the V1 seta has also 3 secondary setae, while in segments seven and eight, it has 2 secondary setae with V1. The ninth abdominal segment possesses a verruca bearing V1 plus one secondary seta.

Additional secondary setae, which are not situated on verrucae, occur in both first and last instar larvae, and are also charted in the setal maps. In the first place these occur in both instars on the anterior section of abdominal segments 3 to 7, anterior to the MV3 seta. Secondly they are to be found in the area between the dorsal verrucae on the second and third thoracic segments and all the abdominal segments of the last instar larva.

c. Setal types/.....

c. Setal types and colouration.

(a) First instar larvae.

Only two types of setae occur on the first instar larva, both of which are of variable length.

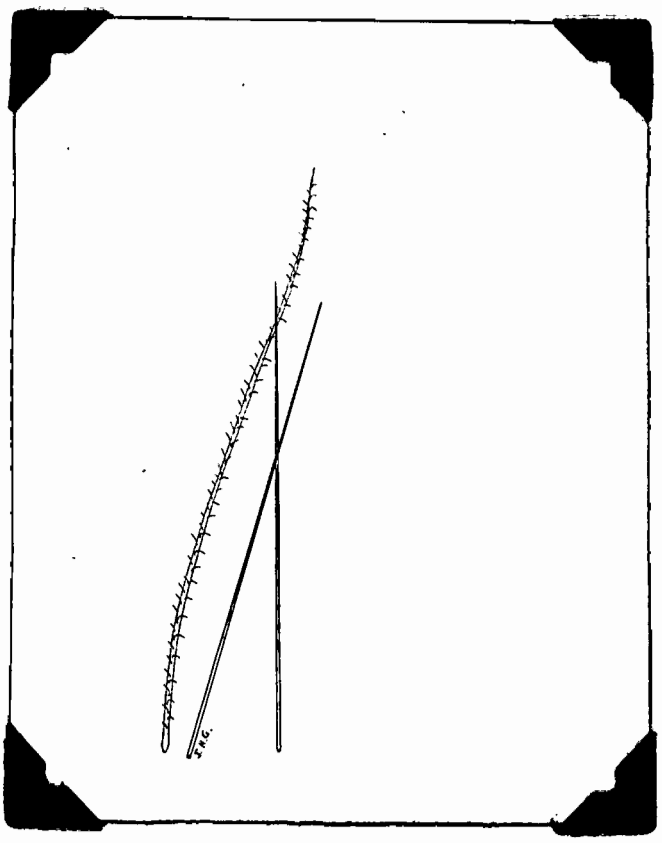


Fig. 28.
Setae from the first instar larva.

The first type, which includes all the proprioceptor setae, is typically spiculiform (Fig. 28), and occurs both on and off the verrucae. The second type is spiniferous spiculiform in structure (Fig. 28) and is found only on the verrucae themselves, mixed with the spiculiform type.

The setae of the first instar larvae are of a general drab brown-grey colour.

(b) Last instar larvae.

Six differing types of unicellular setae may be differentiated in the case of the last instar larva of E. terminalis. These are as follows:-

(i) Poisonous setae (Fig. 33).

These occur on the dorsal and subdorsal verrucae of abdominal segments 2 to 8 of the eighth instar larva. On the dorsal verruca they are placed evenly and closely together but on the subdorsal verruca are found only on a sickle-shaped patch, constituting approximately from a third to a half of the total area of the verruca, situated along its dorsal edge.

In instars/.....

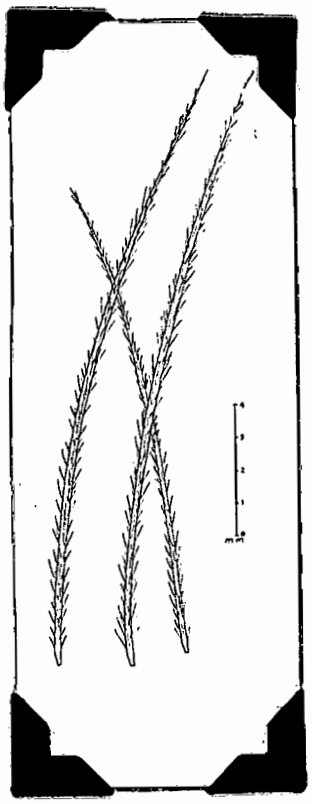


Fig. 29.

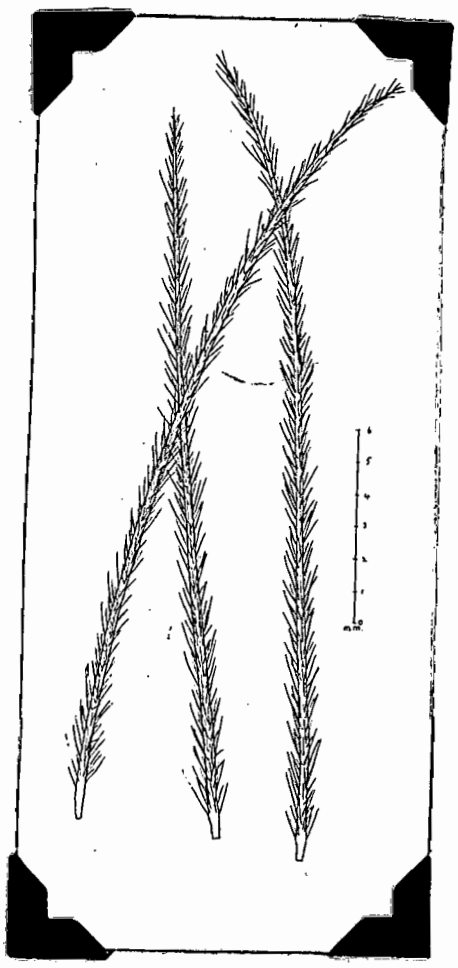


Fig. 30.

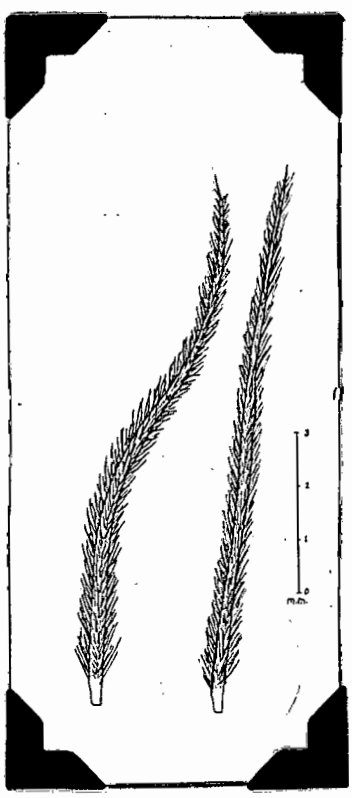


Fig. 31.

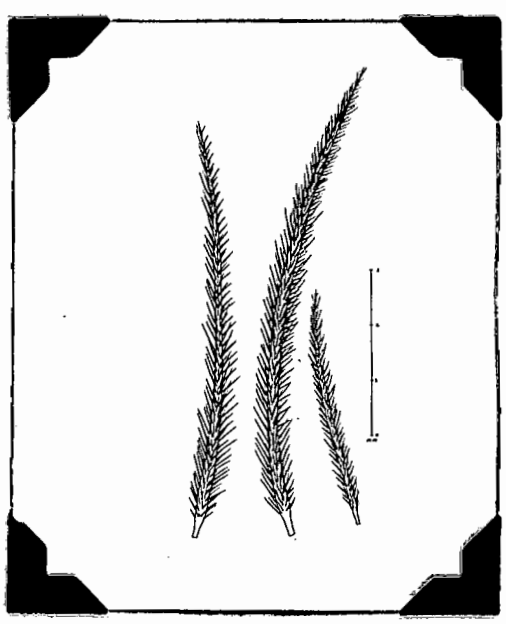


Fig. 32.

Various types of setae found on the last instar Euproctis terminalis.

In instars 2 - 7 poisonous setae are found only on the dorsal verrucae of the first abdominal segment. None are present on the first instar, except for loose ones carried away from the egg masses.

In colour the poisonous setae are dark olive buff when viewed individually; when closely packed together on the verruca, they give it a dark, blackish, velvety appearance. The integument between the dorsal verrucae along the dorso-median line, is coloured yellow-orange, but that section lying between the dorsal verruca of one segment and that of the next, is coloured black. In view of the fact that the poisonous setae blacken the dorsal verrucae themselves, the larva in consequence appears to have a dorso-median stripe of orange, bordered on either side by a black stripe, along the full length of the body.

The properties of the poisonous setae are dealt with in detail later.

(ii) Normal spiculiform setae.

Spiculiform setae of variable length, such as described over the whole body of the last instar.

(iii) Spiniferous spiculiform setae.

In the eighth instar four types of spiniferous spiculiform setae may be differentiated, the main differences between these being colour and the density of spines on the setae.

Type (1) is formed by white setae carrying the least number of spines. This type occurs on all the verrucae of the second and third thoracic segments, and on the dorsal, subdorsal and lateral verrucae of abdominal segments 1 to 9. In a low percentage of larvae this type of seta may be pale brown in colour instead of white. (Fig. 29).

Type (2) setae are coloured mousegrey, carry more spines on them than do Type (1), and occur on all the verrucae of the first thoracic segment, between the dorsal verrucae of the eighth abdominal segment, and on the dorsal and subdorsal/.....

sal and subdorsal verrucae of the ninth abdominal segment. (Fig. 30).

The setae belonging to Types (1) and (2) together constitute the long setae of the larva, while the two types to be described below are much shorter.

Type (3) setae are orange in colour and bear more numerous spines than do Types (1) and (2). They occur only on the dorsal side of the dorsal verrucae of the second abdominal segment (Fig. 31).

Type (4) setae are all short, all have a squat appearance owing to the dense mass of spines they bear, and in colour may be either orange or white. They are found on the lateral edges of the dorsal verrucae (D1 and D2) of the third thoracic segment, and also on and between those dorsal verrucae of the abdominal segments on which poisonous setae are present. (Fig. 32).

d. The poison hair of Euproctis terminalis.

By virtue of the toxic nature of its hair, the larva of E. terminalis is probably the most obnoxious larval pest in South Africa, since it occurs in cultivated plantations where it constitutes a continous hazard to those working in these infested areas.

The first symptom of contact with E. terminalis is a severe itch on the neck or other exposed parts, where clothes rub against the skin. This itch is followed by swelling of the infected areas.

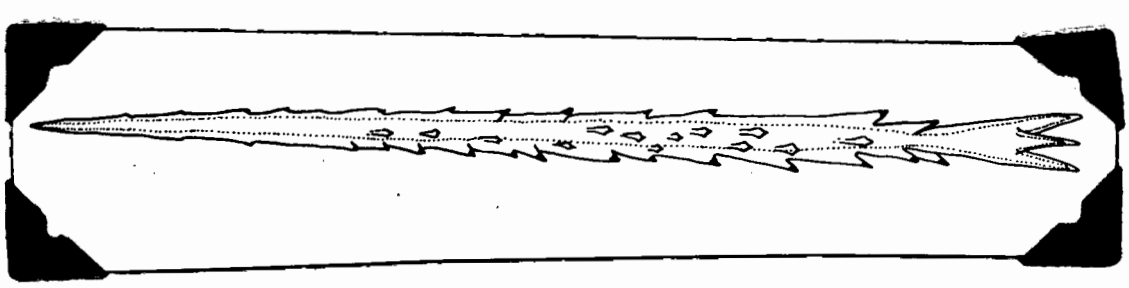


Fig. 33.

Poison hair from E. terminalis.

The urtication is caused by minute, sharply pointed, barbed hairs, (Fig. 33) which vary in length from

0.07 m.m./.....

0.07 m.m. to 0.2 m.m. with an average length of 0.16 m.m. The hair, which tapers from the distal to the proximal end, is covered with barbs, two or three at the distal end being slightly longer than the others. The hairs which are light brown in colour and somewhat transparent, are capable of penetrating clothing and causing dermatitis. They may be carried by the wind for a distance of as much as three miles. This method of distribution was clearly demonstrated in 1936 during the aerial application of insecticides to the Jessievale plantation. On this occasion the personnel in charge of the landing strip, which was situated three miles from the nearest E. terminalis infestation, ~~started itching~~ was affected even before operations began, although they had not been near the plantation. The only way to account for this was that there was a strong wind blowing at the time from the direction of the infested area, which carried the hairs to the landing strip.

In the 2nd to 7th instar the hairs grow from the two subdorsal verrucae, situated on the fourth segment. In the last instar, however, they occur on the 4th to 11th segment on the two subdorsal verrucae and also on the two lateral verrucae located on each side, adjacent and just lateral to the subdorsal ones. (Figs. 29-32).

These hairs are very loosely attached and cover the verrucae so thickly that they give them a velvety appearance. On the adult larva as many as 709,300 poisonous hairs have been found clustered together on the verrucae.

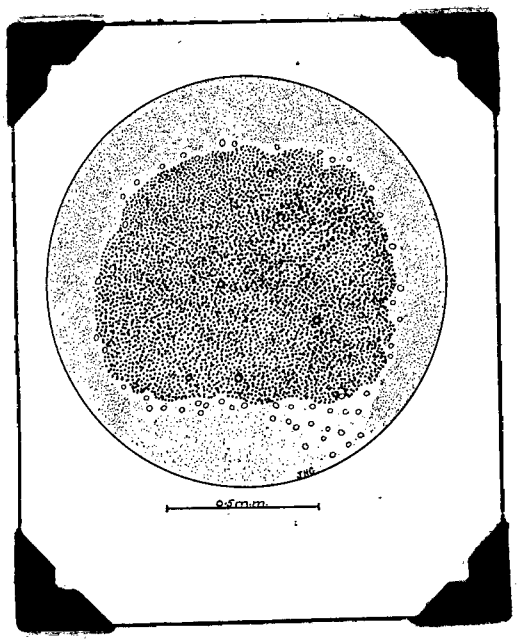


Fig. 34.

Enlarged subdorsal verruca.

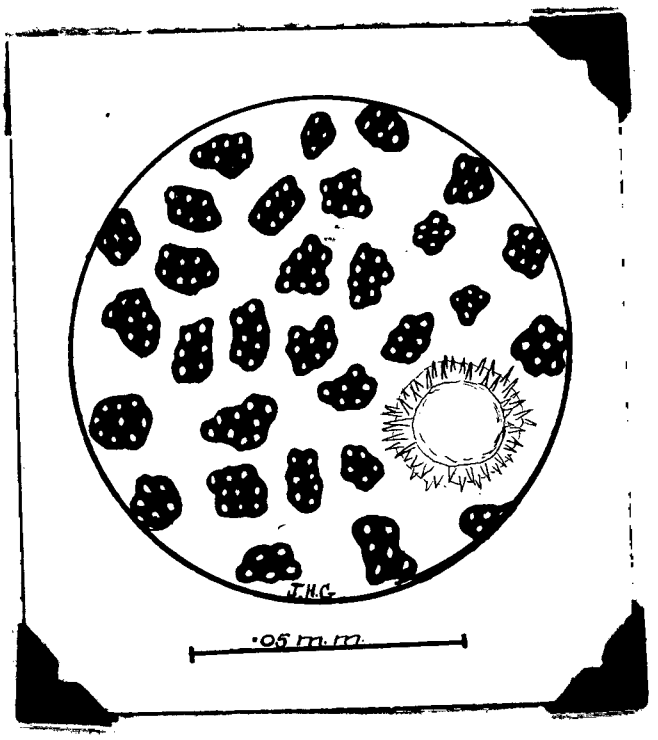


Fig. 35.

Portion of verruca showing the minute papillae.

Each verruca consists of minute cupshaped papillae, (Figs. 36 & 37B) which are formed by the exocuticula, and are slightly darker than the surrounding cuticula, thus giving the verrucae a speckled appearance. (Fig. 34).

In each papilla there are an average of 7.6 openings (maximum 14, minimum 2) in which the hairs are situated, and just under each cuplike papilla there is a much widened pore canal which connects it with the poison gland. (Fig. 37B). In this connection it is of interest to record that detailed studies on larval glands and their attachment to poison hairs were carried out by Kephart (1914) and Gilmer (1925).

Gilmer (1923 and 1925) made an intensive study of the various types of poison hairs found on Lepidoptera. He states that the reason why this type of hair remains poisonous for long periods, even after ecdysis, is due, largely, to the fact that the venom is not a true secretion, but that the cytoplasm of the gland functions directly as the toxic agent, and that the dried remnant within the

hair/.....

hair lumen may retain its efficacy for a long period.

In the case of E. terminalis the writer has found that the hair remains poisonous for up to three years and possibly longer.

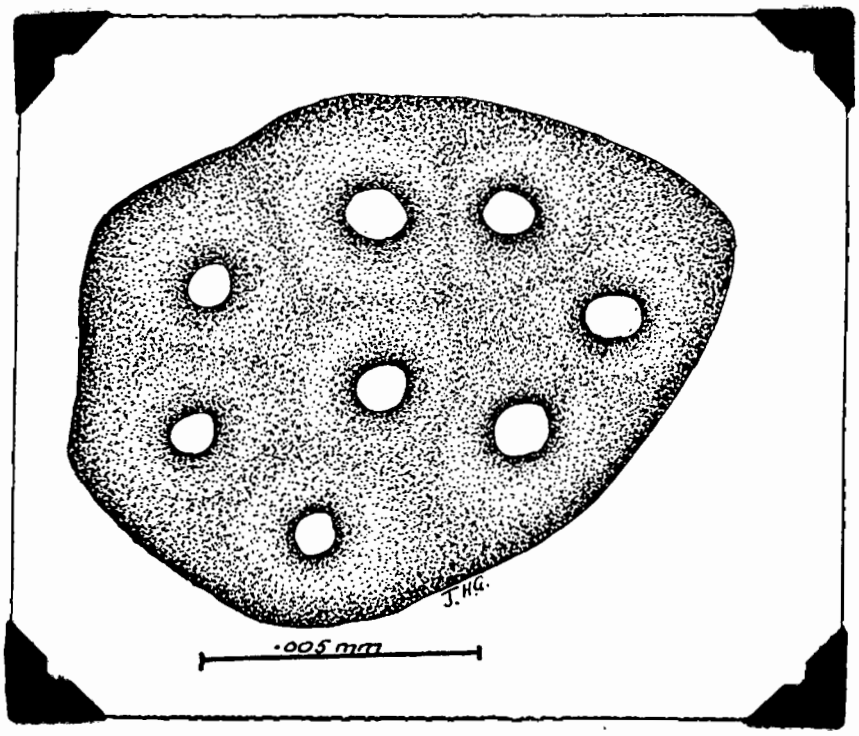


Fig. 36.

Dorsal aspect of the cuplike papilla.

Hase (1939) found that the hairs from Thaumetopoea were still able to cause irritation after 12 years. As a result of his experiments he came to the conclusion that there was no poison in the hair, but that the irritation caused was purely mechanical. However, judging from the work done by Gilmer (1923), Hase's technique would not have destroyed the poison in the hair, and it is thus doubtful whether Hase's conclusions about the poison being destroyed were correct.

Tyzzer (1907) was the first worker to point out that the poison from the hairs of Lepidopterous larvae has a definite effect on blood. If the hairs are brought into contact with blood, they have a strange effect on the red corpuscles. The rouleaux are broken up, (Fig. 38) and the red corpuscles become coarsely crenated. Subsequently the corpuscles decrease in size and the coarse crenations

are transformed/.....

are transformed into slender spines, which thereafter rapidly disappear, leaving the corpuscles in the form of spheres.

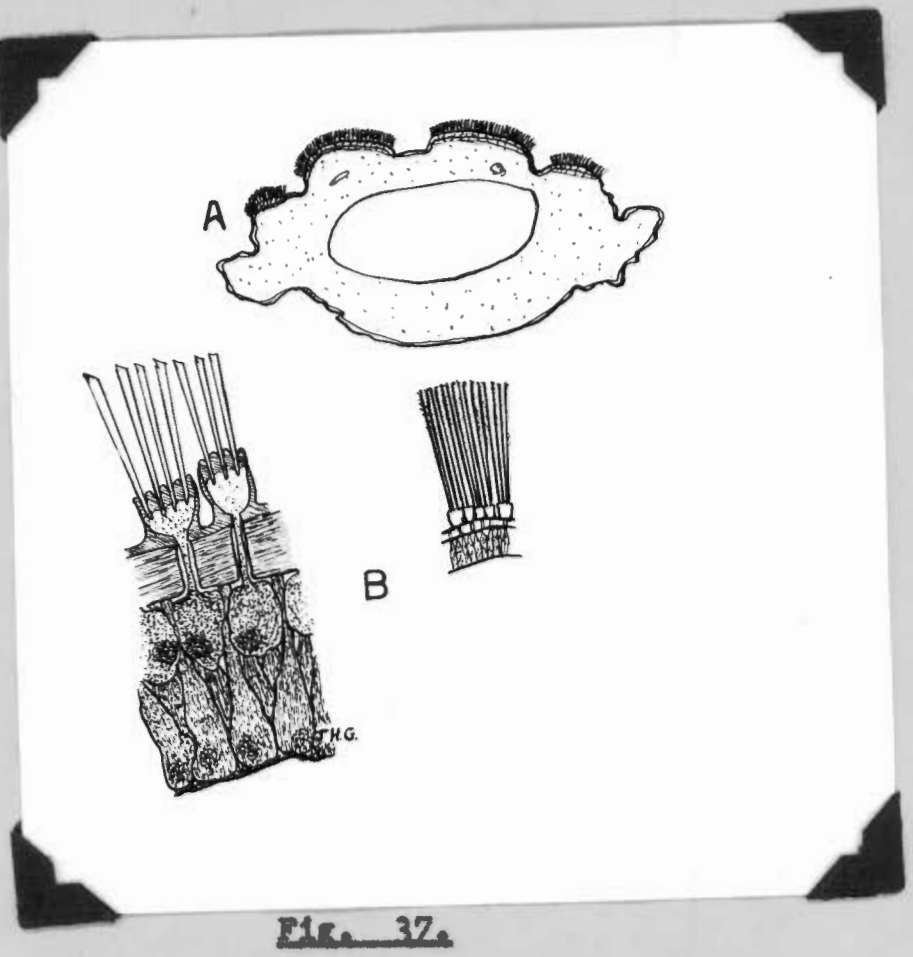


Fig. 37.

A. Section through the sub-dorsal tubercles and the lateral tubercles.

B. Section of the tubercle, enlarged, to show the cuplike shape of the papilla and the poison glands.

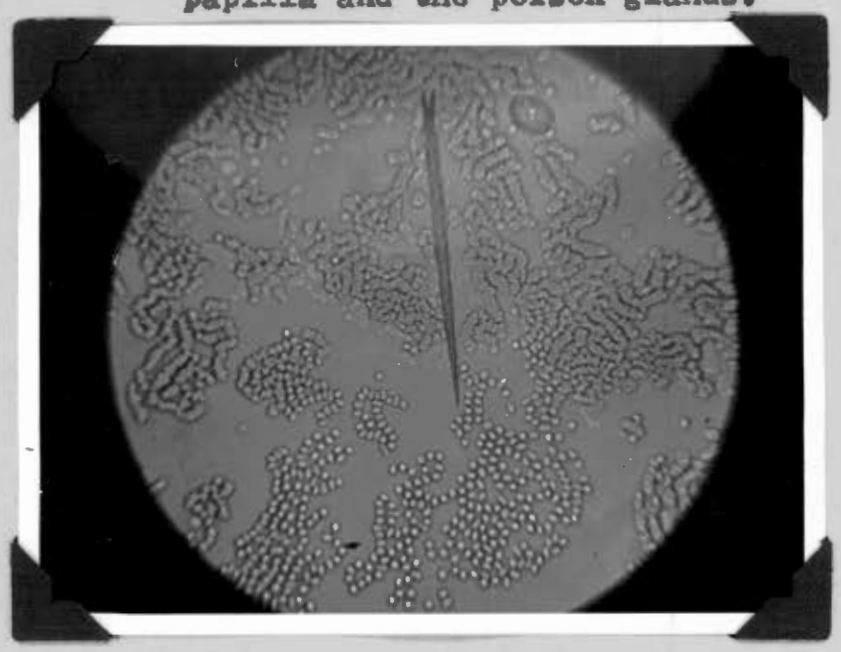


Fig. 38.

An E. terminalis (poison seta) in human blood, it is clearly shown how the rouleaux are broken up.

The writer studied the effects of introducing E. terminalis hairs into blood of various persons, and found/.....

found that in some cases the rouleaux broke up instantaneously, where as in others, up to 60 seconds elapsed before the same effect was produced. When the writer commenced these studies 5 years ago it took 60 seconds for his blood to react, but at present it takes only about 10 seconds. This agrees with the findings of Caffrey (1918) and Gilmer (1923) in their study of the "range" caterpillar, Hemileuca olivia. They found that the susceptibility to the poison increases from year to year in those who are constantly exposed to it.

With E. terminalis the reaction always begins at the sharp basal point of the hollow hair (Fig. 38). In one instance, when an air bubble was accidentally formed round the sharp basal point of a hair in a blood slide, the writer observed no reaction on the blood corpuscles. After removing the air bubble, however, the reaction commenced as usual.

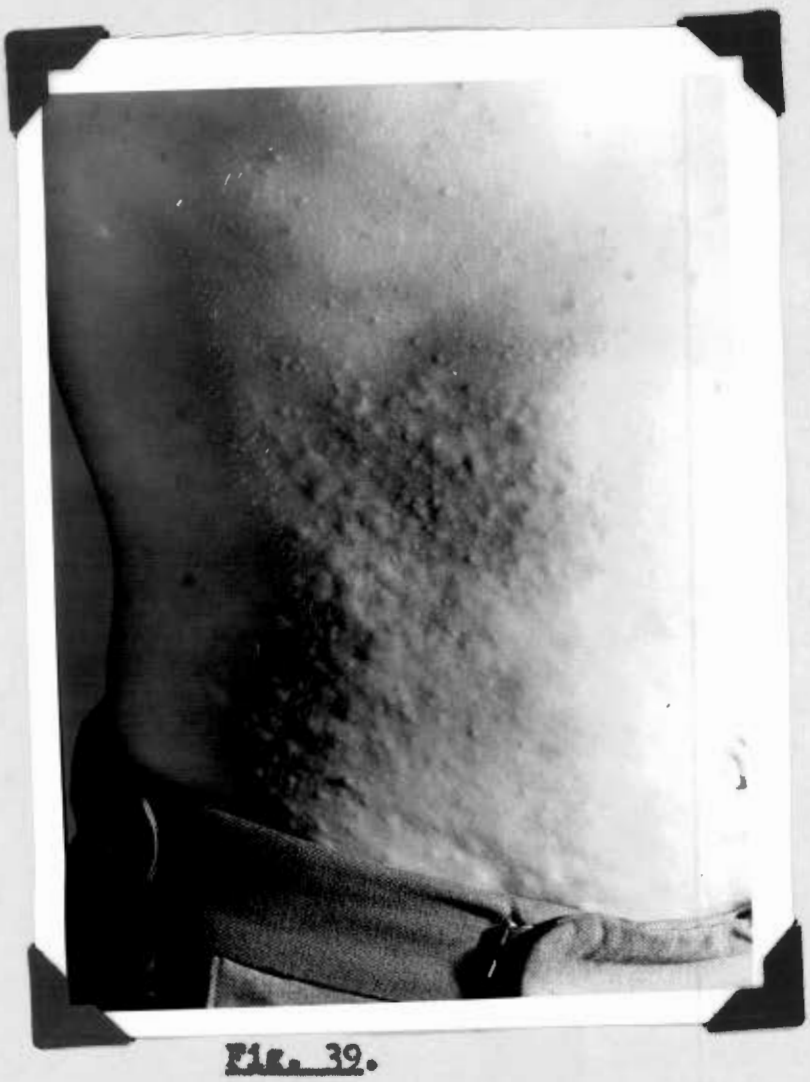


Fig. 39.

Distinct swelling on the skin caused by the poison hairs.

If/.....

If some of the poisonous hairs are rubbed on the skin, an itching and burning sensation is experienced within six minutes and this is soon followed by a distinct swelling. (Fig. 39). This swelling remains painful for about seven hours, after which it may subside; the itching, however, may continue for 24 hours or longer. Of the numerous cases the writer has studied the reactions varied in each case, some individuals showing practically no symptoms at all.

Many remedies have been tried to soothe the itching caused by the hairs, but ~~the writer has found that~~ a strong solution of ammonium hydroxide applied externally appears to be the only one to have any effect. This agrees with the findings of Gilmer (1925), namely that a strong alkali dissolves the dried protoplasmic hair contents, after which the hairs were found to be non-irritant.

Although the poison hairs are found growing only on 2nd to last instar larvae, the pupae and moths are covered with detached hairs derived from the larval stages.

In spinning it's cocoon the larva rubs the hair off its body and these are interwoven into the loosely spun cocoon, thus making this stage the most dangerous one to handle, from the point of view of skin irritation.

When emerging from the cocoon, the moth becomes covered with detached poison hair, large numbers of them adhering to the long hairs of the anal tuft, thus also rendering the egg stage obnoxious to handle.

When the larvae hatch, they crawl through the hairs covering the egg mass, and thus they in their turn become contaminated.

It is only when they moult for the first time that they shed these old hairs with their skin, but at this stage they develop their own poison hairs.

From the/.....

From the foregoing it will be apparent that at no stage of development is E. terminalis free of poison hairs. In view of this, the study of this insect is an extremely difficult one, since the utmost care must be taken and due precautions observed when handling any of the stages from egg to adult.

e. Colour variation in the larvae of Euproctis terminalis.

A comparison of E. terminalis larvae collected from different plantations in S.A. showed that larvae from different localities exhibited distinct colour variations, and it was at first thought that more than one species might be responsible for the damage. Microscopic examination of the skins of these larvae, mounted on slides, indicated, however, that this was not the case and that the difference in the colour pattern was in no way correlated with any morphological differences.

It is well known that variations in the colour pattern occur in some insect species, and many theories have been advanced to account for them. For example Faure (1932, 1943) has shown that with locusts and army worms, the increased density of population per unit area causes typical colour changes due to increased activity of the closely crowded individuals.

In the case of E. terminalis, however, no colour changes attributable to population density could be observed. Gloger's rule (George 1953) demonstrates that in the warm and humid parts of the range of a species, individuals contain relatively more melanin. Reddish melanins prevail in arid regions and the blackish ones are diminished; in very cold areas the black ones also are reduced. Thus from the tropics to the Arctic, members of a given species would be expected to vary from predominantly yellowish or reddish, through black to white.

Dobzhansky (1933)/...

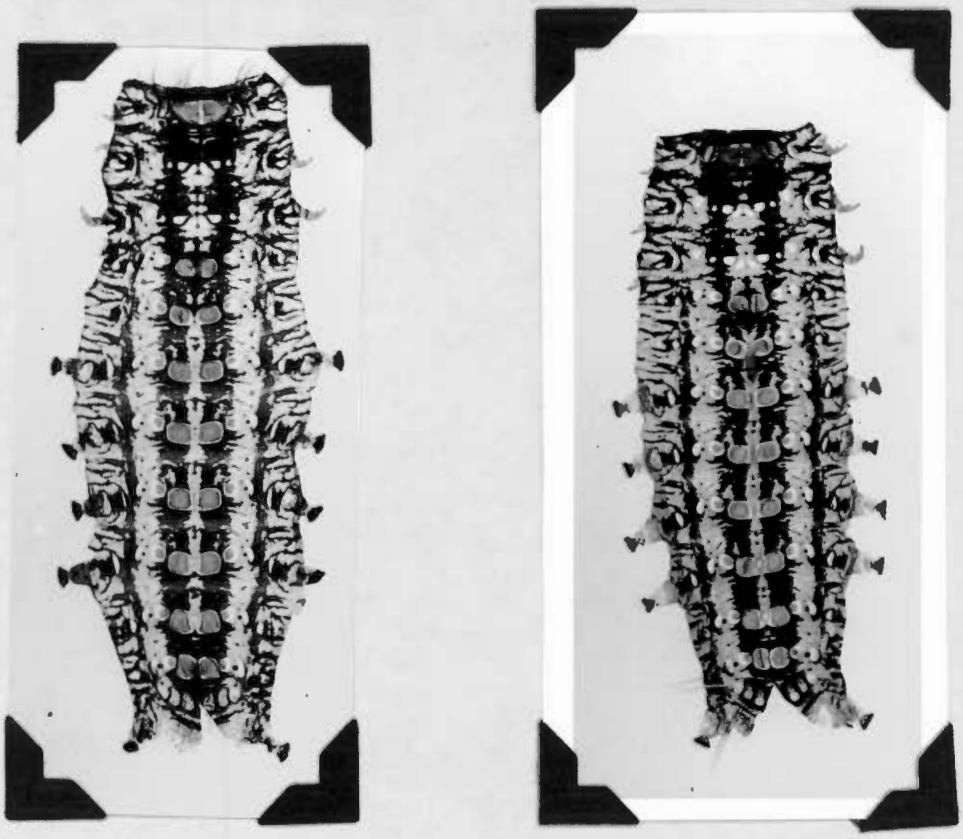


Fig. 40.

Larvae from Mons Plantation.

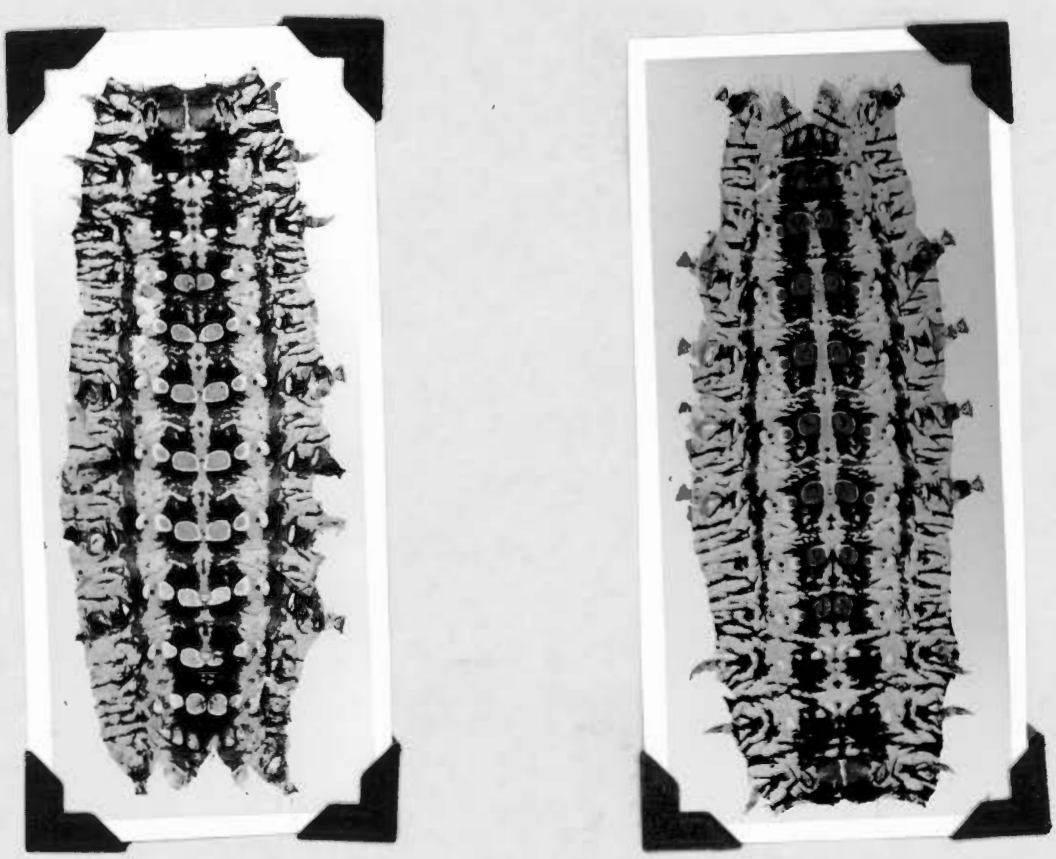


Fig. 41.

Larvae from Belfast Plantation.

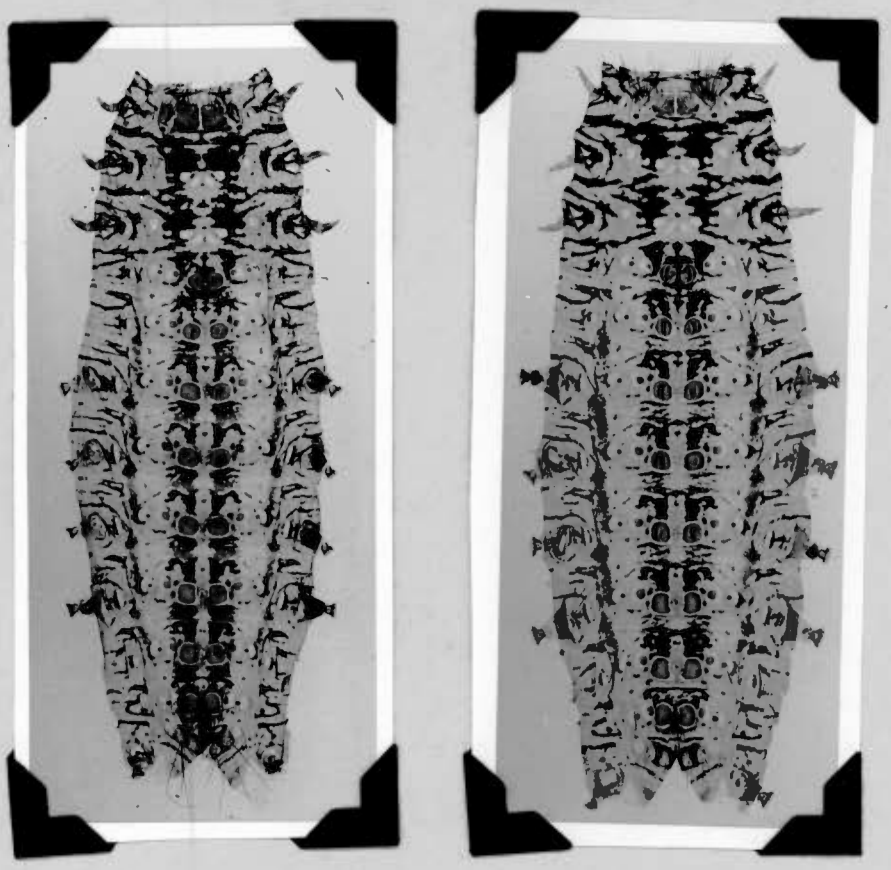


Fig. 42.

Larvae from Jessievale Plantation.

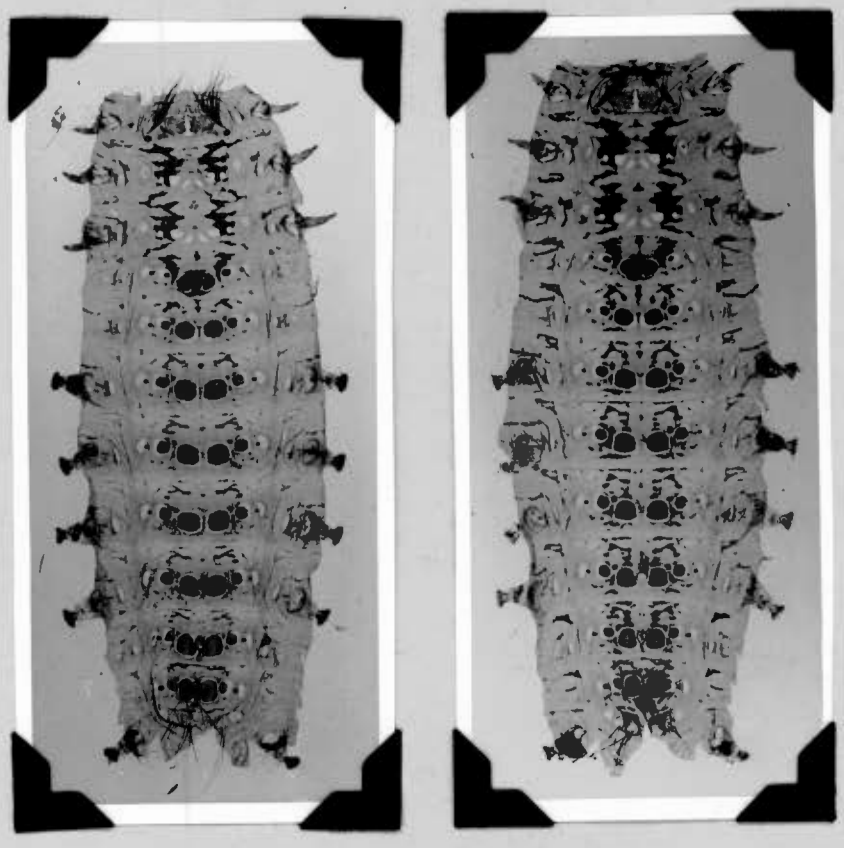
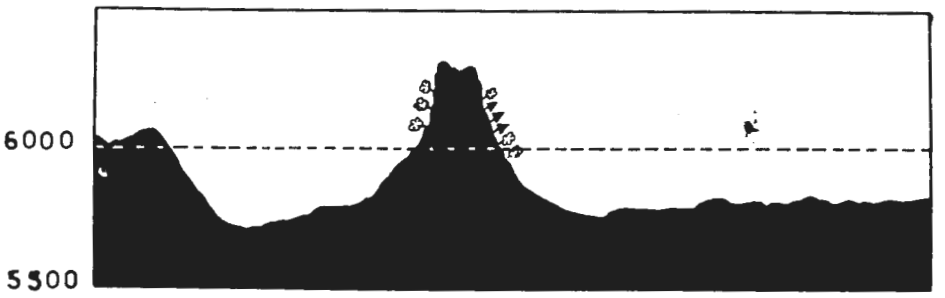
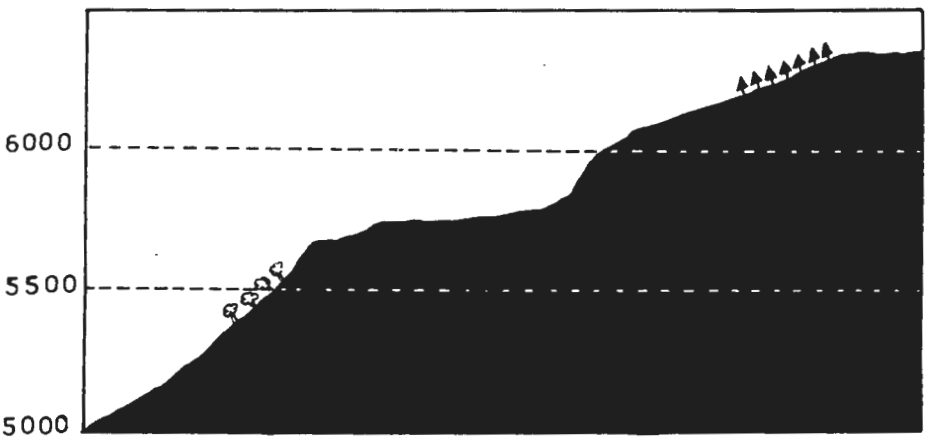


Fig. 43.

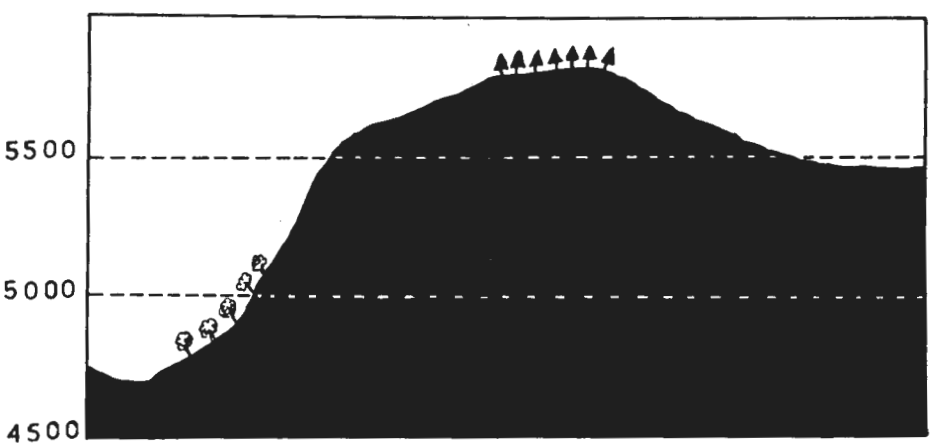
Larvae from Spitzkop Plantation.



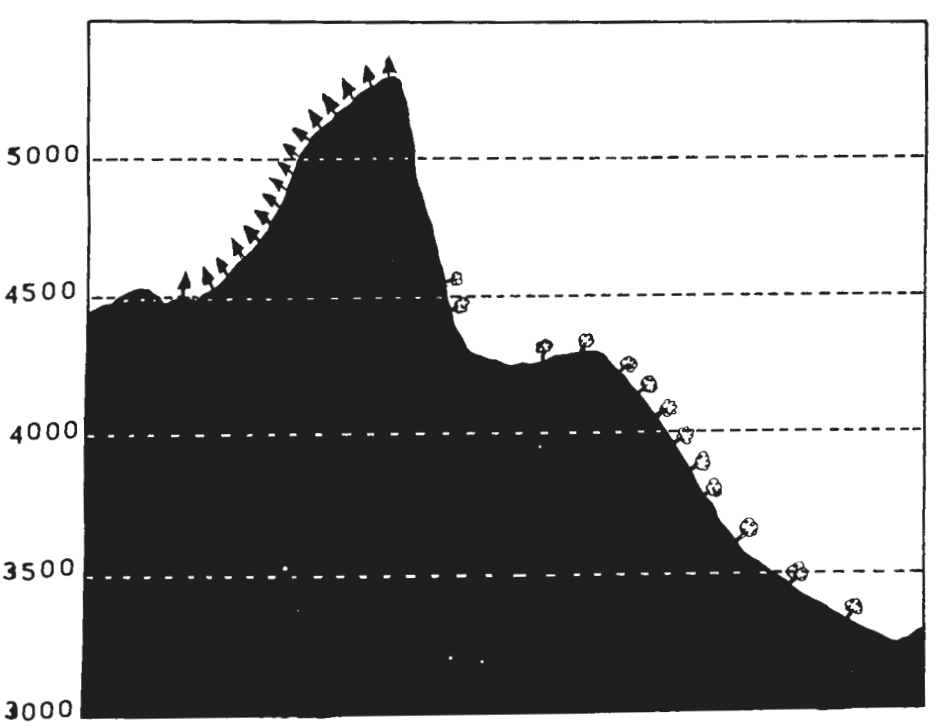
E-W CROSS SECTION THROUGH
MONS PLANTATION



N-W CROSS SECTION THROUGH
BELFAST PLANTATION



N-S CROSS SECTION THROUGH
JESSIEVALE PLANTATION



E-W CROSS SECTION THROUGH
SPITSKOP PLANTATION

♠ – PINE TREES

♀ – INDIGENOUS TREES AND SHRUBS

MILES

Fig 44.

Dqbzhansky (1933) found that in the lady beetle, Adonia variegata, there is a definite colour variation between the beetles from the different geographical areas. It was found that the colour pattern on the elytra varied according to the temperature and humidity variations. As the temperature and humidity decreased, so more and more black spotted individuals with more and more black spots were found.

In the case of the Lepidopteron Arachnia levana and the wasp Habrobracon it was ~~seen~~ found that only temperature had an influence on the colour pattern, whereas in the Lepidopteron, Hestina assimilis, humidity was the main factor in determining the colour pattern. (Wigglesworth 1939).

A study of the climatic differences between the various geographical areas in which E. terminalis occur, indicate clearly that temperature is the main factor in determining the colour variation in this insect.

An examination of the specimens collected from Mons, Belfast, Jessievale and Spitzkop plantations (figs. 40-43) reveals the fact that black melanin is more prevalent in the caterpillars from the Mons plantation where the coldest conditions prevail. As the temperature rises in the Belfast and Jessievale areas, there is an increase in the orange-yellow colouration until in specimens from Spitzkop, where the temperature is highest, the orange-yellow melanin predominates.

Correlating the colour variation of E. terminalis with temperature differences, it may lead to confusion if only the temperatures of the plantations, in which this insect is at present found, are considered. It is necessary to go deeper into the matter than this and take into consideration the temperature in the nearest indigenous shrubs and forests from which E. terminalis originally/.....

originally migrated into the cultivated plantations.

If ~~we look at~~ is studied the cross-section map of the various areas (Fig. 44), the picture becomes much clearer.

(1) Mons Plantation.

Here the cultivated plantation and indigenous host plants are both found at the same altitude and on the same slopes of the mountain range. There is, therefore, no temperature difference between the areas occupied by the host plants and that occupied by the plantation, where black melanin is found to be the prevailing colour.

(2) Belfast Plantation.

This plantation is situated on the open high-veld at about the same altitude as the Mons plantation, although the average temperature in this plantation is slightly lower than that of the Mons plantation. In spite of this however, the larvae exhibit a lesser amount of black melanin. This can be explained by the fact that the nearest indigenous host plants from which E. terminalis could have migrated to the plantation are situated about 1,000 feet lower in the sheltered valleys where the average temperature is higher than that prevailing in the plantation.

(3) Jessievale Plantation.

This plantation is situated at a lower altitude than the Belfast Plantation, and with a higher average temperature. The area from which E. terminalis must have migrated from the natural host plants to the plantation is also approximately 1,000 feet lower than the plantation itself, and forms a portion of the escarpment between the warmer low veld and the colder high veld. Here the larvae exhibit less black melanin than those in the Belfast plantation.

(4) Spitzkop Plantation/....

(4) Spitzkop Plantation.

This plantation is situated at nearly as high an altitude as the Jessievale plantation and the average temperature is slightly higher. It borders the true escarpment between the highveld and the hot lowveld. The indigenous host plants are found all along the escarpment and extend down into the hot lowveld. In the larvae from this plantation, the orange-yellow melanin predominates over the black.

A study of table 6 indicates why it would be misleading to take only the temperature conditions prevailing in the plantations into consideration without reference to those areas from which the insect migrated, to the cultivated plantations. It will be seen that the average temperature at Mons is higher than that at Belfast, the larvae from the last named area, however, contain less black melanin than those from Mons.

Plantation	Mons	Belfast	Jessievale	Spitzkop
Mean average Temperature °C.	13.33	12.44	13.88	15.06
Maximum average Temperature °C.....	19.94	20.44	20.06	20.72
Minimum average Temperature °C.....	6.72	4.50	7.72	9.38
% Rel. Hum. taken at 8 a.m. ..	73.5	77.0	74.2	77.0

Table 6.

Temperatures prevailing in the various plantations.

The colour is probably an inherited factor which has been acquired through generations and is influenced mainly by temperature. In the case of E. terminalis it is not

considered/.....

considered that humidity is the leading role in determining the colour pattern. In this connection, however, it is worthy of mentioning that Allee et. al. (1949), stated that in their opinion, humidity is, in most cases, the factor governing colour variations.

f. Key to the larval instars.

This key has been worked out to enable differentiation between the various larval instars of E. terminalis.

A.	(i)	Larvae very small (± 2 mm.) and of a uniform colour	First instar (Fig. 45)
	(ii)	Larvae larger (2-30 mm.) and not of a uniform colour	B
B	(i)	The dorsal verrucae bear poisonous setae only on the first abdominal segment, the resulting effect being that of a single, velvety black elevation of this segment.	C
	(ii)	The dorsal verrucae on each of the first to eighth abdominal segments carry poisonous setae, the resulting effect being that of two distinct, velvety black elevations on each of these segments	Eighth instar (Fig. 48)
C.	(i)	The setae, except for the poisonous type on the dorsal verrucae of the first abdominal segment, of a uniform colour ..	D
	(ii)	Distinct colour variations in setae visible	E
D.	(i)	Colour of abdominal integument uniform dark olive buff	Second instar. (Figs. 46 & 47).
	(ii)	Colour of abdominal integument not uniform, there being a contrasting sordid white stripe along the dorso-median line, between the dorsal verrucae, which runs from the first to the ninth abdominal segment	Third instar.

E. (i) At/.....

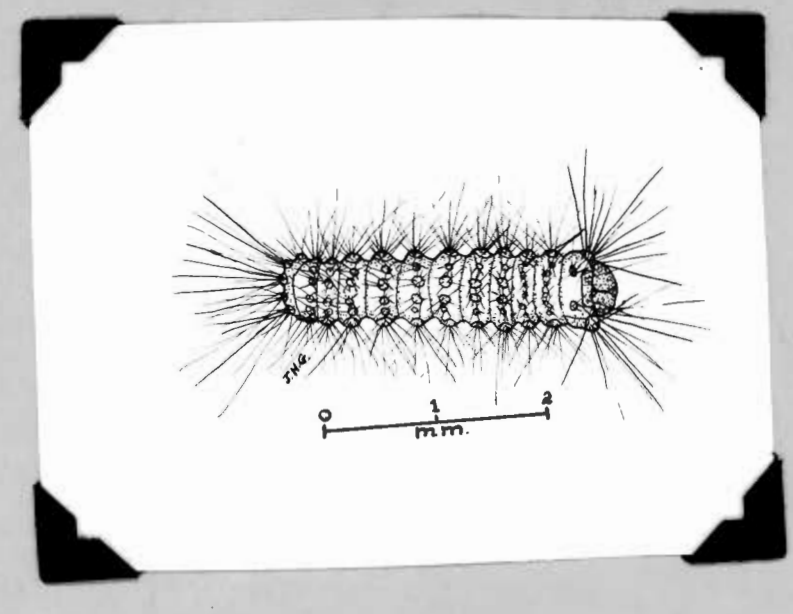


Fig. 45.

Dorsal aspect of first instar larva.

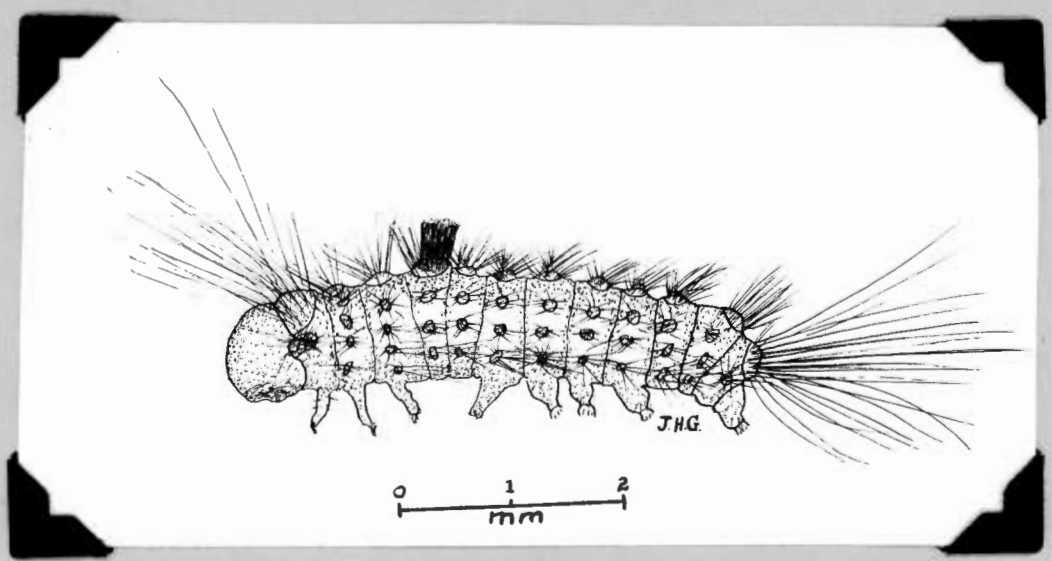


Fig. 46.

Lateral aspect of second instar larva.

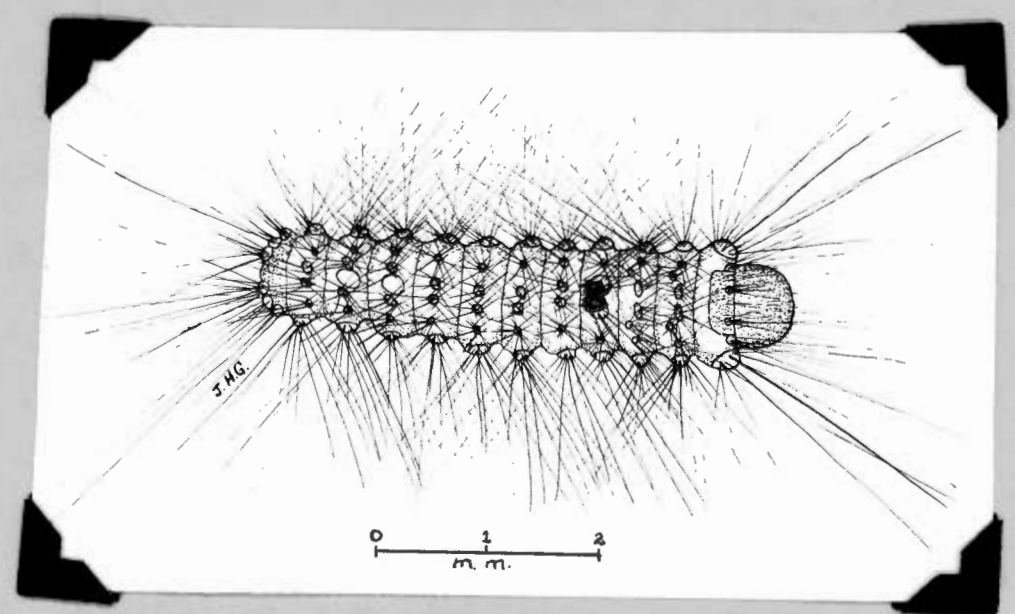


Fig. 47.

Dorsal aspect of second instar larva.

E. (i) At the posterior end of each of the two dorsal verrucae on the first abdominal segment a bunch of erect, orange coloured setae is present..... Fourth instar.

(ii) Additional colour differentiation of setae apparent..... F

F. (i) Situated dorsally on the ninth abdominal segment a tuft of erect black setae is present. Fifth instar.

(ii) Additional colour differentiation of setae apparent ... G

G. (i) The horizontal setae borne on the sides of the larva are white (or in a limited number of cases pale brown)..... Sixth instar.

(ii) Additional colour differentiation of setae apparent ..... H

H. (i) On and between the dorsal verrucae of the abdominal segments short, squat orange and white coloured setae bearing large numbers of spines are present ..... Seventh instar.

Fig. 48.

Last instar larvae of E. terminalis.

~~The writer has~~ It was found that if the larvae, which are first distended in the paraffin, 95% alcohol, dioxan and glacial acetic acid formulation of Petersen(1951), are preserved in 95% alcohol, their characteristics are clearly visible.

2. BIOLOGY OF THE LARVA.

(a) Rearing Methods.

When the studies on this insect were originally commenced, the larvae were confined in cages on foliated branches of P. patula. In spite of all precautions taken, it was impossible to keep the larvae on the foliage. Invariably they climbed down and crawled away from their only food supply to die of starvation. Attempts were made to confine the larvae on the foliage by banding the branches with tangle foot, but they merely crawled into the bands and died there. The use of electricity and channels of water to prevent such migration proved to be equally abortive.

It was then realised that the larvae would have to be confined on foliage on living trees, the cages to be of such a type that the insects could continually be kept under observation. After various types of cages had been tested experimentally, the following two, to be described below, were found to be the most satisfactory.

Type I:- A cage developed in which large numbers of larvae could be reared in isolation from their parasites for various studies in figured in Figure 49. It consists of a rectangular framework, the top and three sides of which are covered over with organdie. The one side is covered with a sheet of "Perspex" to serve as a window through which observations can be taken. The base is als covered with "Perspex", and in the middle an opening is cut, through which the small tree used may be inserted into the cage. A sleeve of organdie, projecting downwards from the opening in the base, surrounds the tree trunk to which it is tightly tied at the distal end to ensure that there is no access to and from the cage.

Fig. 49/.....

Fig. 49.

Perspex cage.

The top facet of the cage, which is of organdie as stated above, is provided with an opening sealed by a zip through which the larvae can be placed in or removed from the cage. The whole cage is supported by three "Perspex" legs attached to the base and resting on the soil surface.

Type 2 :- The second type of cage is suitable for use when smaller numbers of larvae are being kept under observation. (Fig. 50) The sides take the form of a cylinder of celluloid, four inches long with a diameter of four inches. At either end the cylinder is extended by a sleeve of organdie of a corresponding diameter.

Fig. 50.

Celluloid cylinder cage.

The/.....

The cage is drawn over the tip of a branch, the lower organdie sleeve is tightly tied to the stem of the branch to seal off the bottom, the requisite number of larvae are placed on the foliage in the cage, whereafter the top sleeve is tied tightly to seal off the upper end. The cage is kept upright in a rigid position by binding it to a stake inserted in the soil.

A third type of cage (Fig. 102), used mainly for studies on the Meteorus larval parasite of E. terminalis, is described in chapter VIII. It consists of a celluloid cylinder fitting exactly at either end into the upper or lower halves of Petri dishes. Only in the case of early instar larvae was this type of cage used. As soon as the larvae were larger, they were placed in the Type 2 cage described above.

(b) Larval Movements.

As soon as the larval development in the egg has been completed, the caterpillar emerges through an irregular shaped opening which it eats through the shell. The newly hatched larvae do not leave the egg mass from which they emerge until their first moult. They remain on it, feeding on the egg shells. During this period they are continuously in contact with the hairs covering the egg mass, with the result that their bodies become covered therewith and have, in consequence, a grey, woolly appearance. (Fig. 51)

If newly hatched larvae are immediately removed from the egg mass and are placed on green leaves, they do not feed at all. Only after their first moult, when the second instar has been reached, do the larvae commence feeding on green foliage. (Fig. 52).

Lammerst (Wigglesworth 1939) states that the young larvae of Euproctus chrysorhoea are markedly positively phototactic before they commence feeding.

Fig. 51/.....

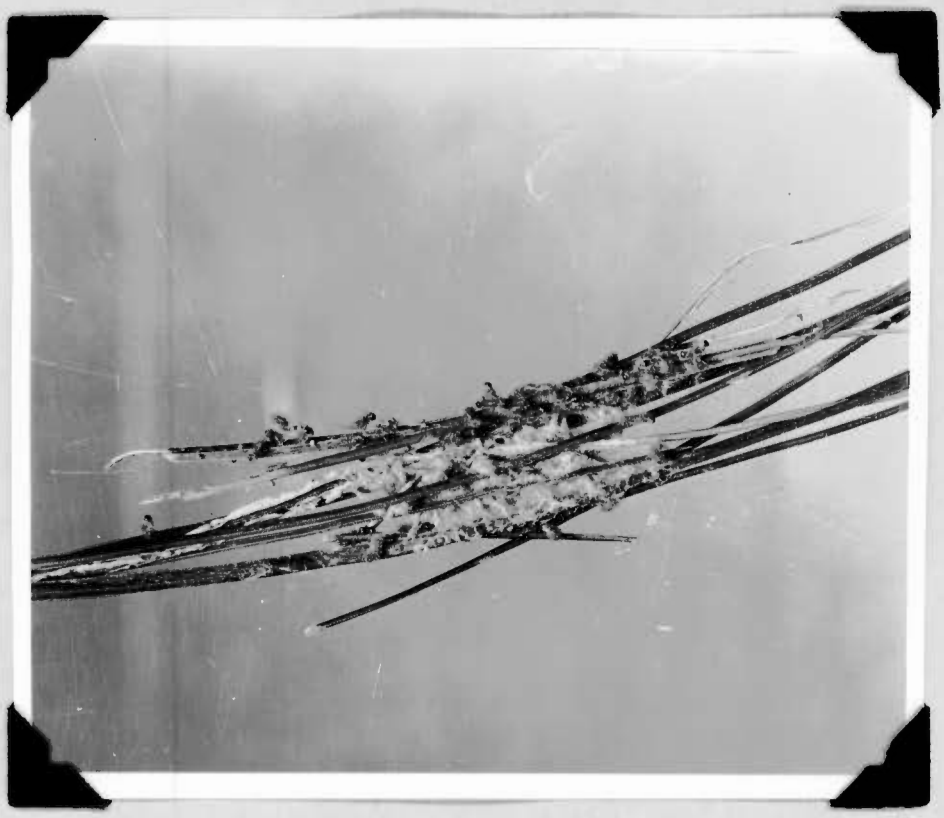


Fig. 51.

Skins of the moulted first instar larvae on an old egg mass.

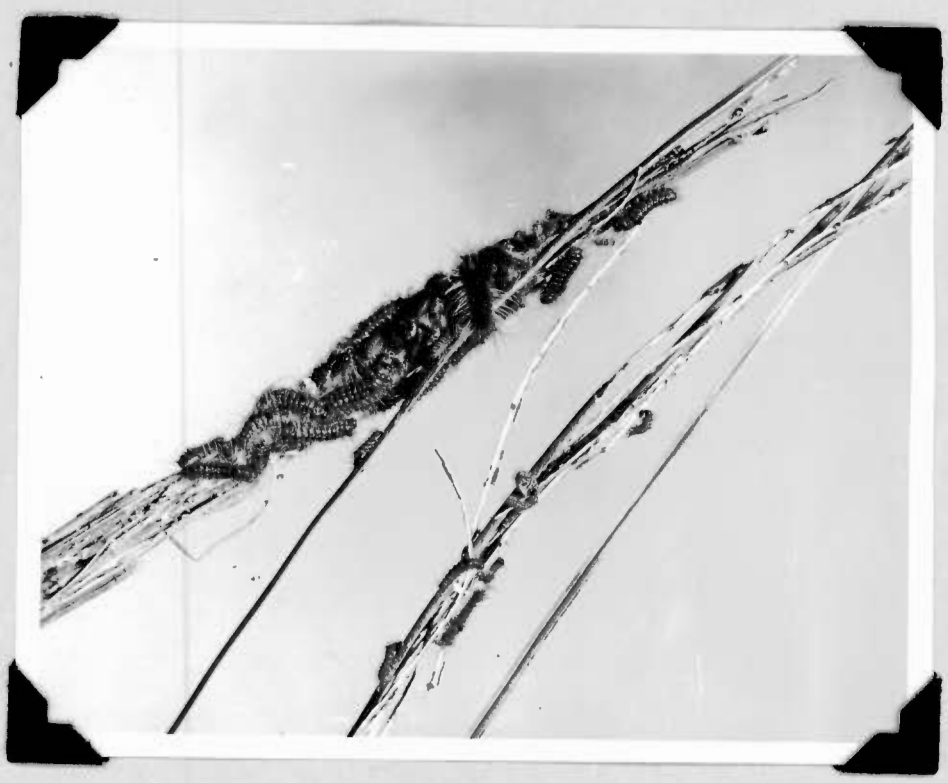


Fig. 52.

Mainly second instar larvae feeding on the foliage of P. patula.

In the case of E. terminalis, however, light has no attraction for the first instar larvae. ~~Only in~~ The second instar, however, show ~~is~~ positive this/.....

~~this trait in evidence~~ positive phototropism. Immediately after their first moult the larvae move in the direction of the most intense light, with the result that they normally converge on the tips of branches in amongst the youngest leaves. (Fig. 53). Here they feed and grow until the second moult takes place.

In cases where the female moth deposits its eggs on the trunk of the tree, the survival of the larvae will depend on the distance between the egg mass from which they hatch, and the nearest foliage. After hatching, the larvae remain on the egg mass until their first moult, whereafter they crawl up the trunk. Should the trunk of a Pinus tree be covered with very rough bark, the larvae are unable to move very far; on the old Pinus patula trees, however, the bark is comparatively smooth, and in such cases it has been established by banding the trunk with "tanglefoot" that the larvae can climb 20 feet before they succumb from starvation. In the section on the habits of the moth, it was shown that most of the eggs are deposited in the crowns of the trees, and the majority of the larvae have not to move far in their second instar to reach foliage.

Immediately after the second instar larvaehave moulted, they lose their gregarious habits, and each one moves, feeds and developes as an individual.

The young larvae are frequently observed to hang suspended from branches by means of silken threads. By doing so, they ~~are enabled to~~ can contact branches at lower levels, or the wind could possibly swing them across to adjoining branches where food is available. This way of moving from branch to branch is different from that in which young larvae on a long silken thread are dispersed by wind, as for instance in Acanthopsyche junodi. (Hardenberg 1918).

The older larvae of E. terminalis also frequently make use of silken threads to move to new feeding sites, when the branch on which they are situated is completely

defoliated./....

defoliated. In cases where they are descending from the lowest branches, they lower themselves for considerable distances and then remain suspended, thus making it possible for the wind to swing them in pendulum fashion across to adjoining trees.

After the larvae has been suspended on its thread for some time without finding new food supplies, it will once more climb up the thread to the branch from which it is suspended. This it accomplishes by working the thread into a ball between its thoracic legs. When the ball becomes too unwieldy, it is shifted towards the rear, and a new one is accumulated. In this manner the larva has been observed to climb up the thread at a rate of one foot in twenty minutes.

Many larvae have been observed to loose their foothold in the trees, most frequently when they sever a pine needle at a point proximal to their position on it. In some such cases, the caterpillar will remain suspended in the air on a thread and regain the branch in the manner described above. If it falls to the forest floor, it will crawl until it encounters a tree trunk, and then try to reach the foliage.

(c) Moulting.

As soon as a larva is ready to moult, it spins a silken platform on which it takes up its position with the crochets of the prolegs hooked in the silk. The skin then splits open after a time along the dorsomedian line of the thorax, and the next instar emerges. If a larva which is due to moult, is removed from its silken platform, it experiences great difficulty in shedding the old skin. This is an error readily made in the laboratory, especially when dealing with early instar larvae, which are then unable to get rid of the posterior section of the cast skin, and eventually die.

(d) Host plants and feeding habits of E. terminalis.

Although E. terminalis is indigenous to South

Africa/...

Fig. 53.

Second instar E. terminalis amongst the youngest foliage in the tips of a branch.

Africa, prior to 1950 there were no data available concerning the natural indigenous host plants on which the larvae subsisted. The main reason for this was the fact that the insect only recently has been recognised as a pest.

By covering vast areas in the distribution area of E. terminalis and examining meticulously the flora found therein for the presence of E. terminalis the writer succeeded in discovering eleven indigenous species of plants on which the larvae feed in uncultivated areas. (Fig. 54)

These are:-

A. Gymnosporia albata (N.E. Br.) Srm.
B. Acacia caffra (Thumb.) Wild.
C. Ziziphus mucronata. Wild.
D. Dombeya pulchra. N.E.Br.
E. Solanum giganteum. Jacq
F. Tricalysia lanceolata (Sond.) Burt Davy
G. Rhus rehmanniana. Engl.
H. R. pyroides. Burch
I. R. dura. Schonl.
J. Gymnosporia undata. (Thb.) Szyz.
K. Brachylaena transvaalensis. Phill. and Schweik.

Although these plants are widely distributed over vast areas of South Africa, even in some areas from which E. terminalis has not hitherto been recorded, they make up a very small portion of the flora found in the distribution area of E. terminalis. (Acocks 1953).

In most cases the larvae attack their natural host plants from the under surfaces of the leaves, where they are sheltered from direct exposure to the sun. During the survey it was not possible to spot the insects from above only; to spot infestation, it was frequently necessary to bend the branches so as to expose the lower surfaces of the leaves.

Fig. 54./.....

Fig. 54.

Indigenous host plants of E. terminalia, indicating the damage done to them by the larva.

A. Gymnosporia albata (N.E.Br.)Sim.
B. Acacia caffra (Thumb.) Willd.
C. Ziziphus mucronata Willd.
D. Dombeya pulchra N.E.Brown
E. Solanum giganteum Jacq.
F. Tricalysia lanceolata (Sond.) Burt-Davy.
G. Rhus rehmanniana Engl.
H. R. Pyroides Burch.
I. R. dura Schonl.
J. Gymnosporia undata (Thb.) Szyz.
K. Brachylaena transvaalensis Phill and Schweick.

Fig. 55./.....

Fig. 55.

Typical area where E. terminalis was found on its indigenous host plants.

As can be noted in figure 54 F & G, the young larva feed only on the epidermis of the leaves, whereas the older larvae chew through the whole leaves of various points. The damage to the leaf is never such that it drops. The Emspean monacha L. consumes the leaves of the host plant at the base, with the result that they drop off. (Wellenstein et al 1942).

It is not clear what factors caused E. terminalis to switch over from its natural host plants to plantations of exotic trees. Scent without doubt attracts the moths to plantations of P. patula, as the following observations show: When a person enters a compartment of P. patula, the moths flying around the trees pay no attention to him. If, however, the person has climbed in and out a few trees, and in doing so has collected resin on his skin and clothing, the moths will circle around and actually fly against him. This phenomenon has been observed and frequently tested using different persons acting as guinea pigs. This attraction of moths by humans causes extreme discomfort to the latter, as the moths are covered with loose toxic hairs, which irritate the skin.

Fig. 56./.....

Fig. 56.

The Rhus dura plant on which E. terminalis was found, in its natural surroundings.

Fig. 57.

A close-up view of figure 56 showing the E. terminalis larvae on the Rhus dura leaf.

The exotic trees planted in South Africa on which E. terminalis larva have been recorded to feed are the following:-

A. Species on which E. terminalis occurs in large numbers and which are on occasions completely defoliated.

1. Pinus patula. Schl. and Cham.
2. P. leiophylla. Schl. and Cham.
3. P. radiata. D. Don.

B. Species/.....

B. Species on which E. terminalis occurs but not in large numbers.

1.	Pinus pinaster.	Sol.
2.	P. longifolia.	Roxb.
3.	P. taeda.	Linn.
4.	P. montezumae	Lamb.
5.	P. pseudostrobus	Lind.
6.	Cupressus benthami	Endl.
7.	Acacia mollisima	Willd.
8.	Quercus spp.	
9.	Eucalyptus maideni	F.v.M.
10.	Acacia melanoxylon	Willd.

The manner in which the larvae attack the broad-leafed species in the list given above, corresponds with that observed in the case of the indigenous host plants, but the mode of attack on the needle shaped leaves of the Pinus spp. differs considerably.

Owing to the fact that the pine needles are so thin, the leaf is severed at the first bites of the older larvae, and the terminal section drops to the forest floor. The result is, that in an infested compartment the ground below the trees is carpeted with green pine needles. This forms an easy indication to determine whether larvae are actively feeding in a tree. A second instar larva is too small to sever a pine needle completely and cleanly, but takes deep bites out of it. (Fig. 52) - many needles so treated will sooner or later drop as well.

The larvae are ~~in consequence~~ therefore extremely wasteful feeders in pine plantations, and in the case of some Pinus spp. severe infestation results in complete defoliation. The average length of the terminal sections of 2,707 pine needles which dropped to the forest floor as a result of larval feeding in a tree over a period of 24 hours, was found to be 71 mm. To this wastage must be added the basal sections of the needles remaining on the tree which are consumed

by/....

by the larvae.

According to Loock (1950), the average length of the needle of *P. patula* is 190.5 mm. (7.5 inches). Accepting this figure as a basis for calculation, it would appear that the larvae, when feeding, consume 62.7% of the foliage attacked, while 37.3% drops to the ground and is wasted.

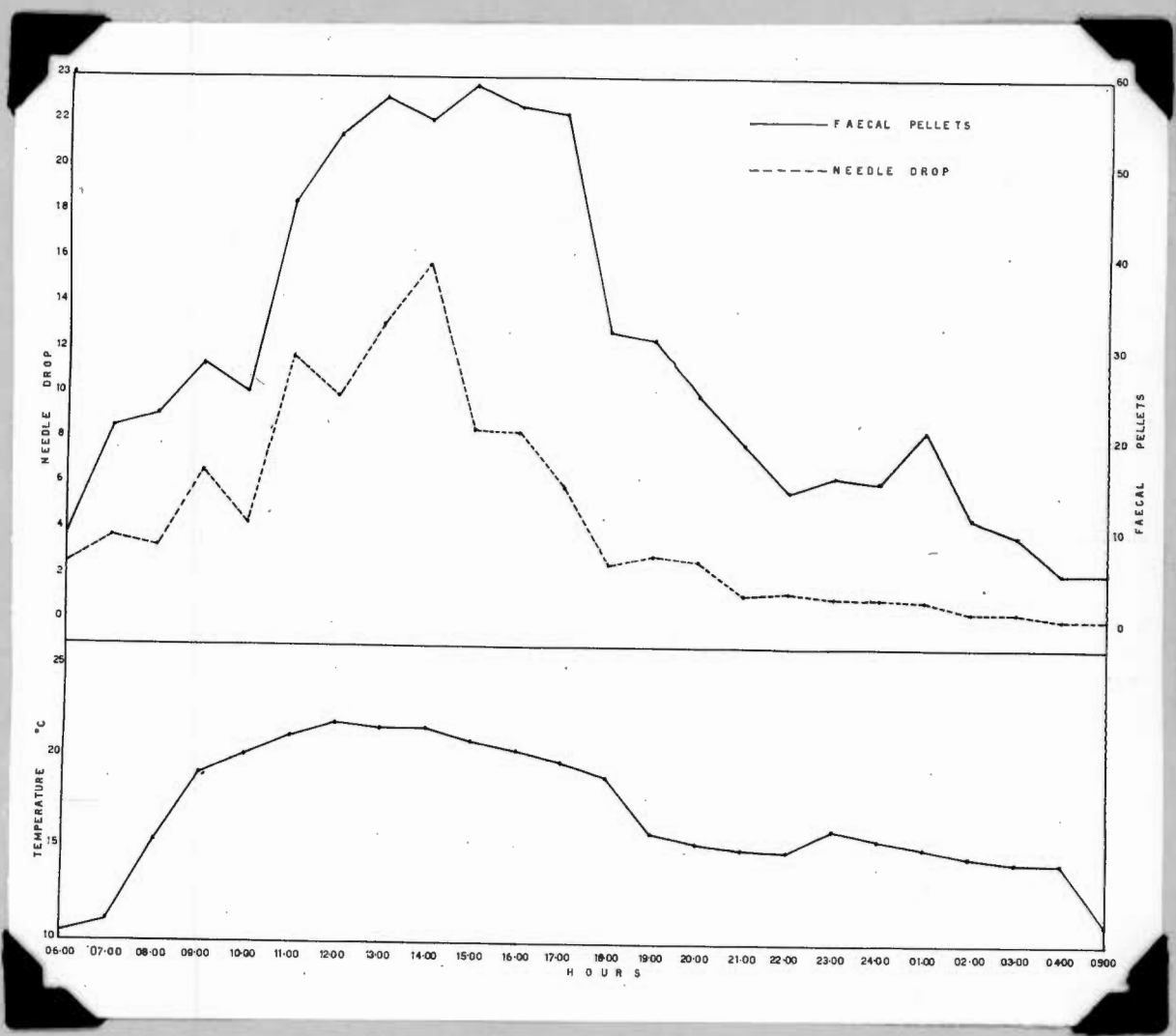


Fig. 58.

Hourly counts of faecal pellet and needle drop.

At Jessievale it is fortunate that the most severe damage to the plantation trees occurs towards the end of October, during a period when rains normally fall and foliage flushes. During normal seasons the trees would thus replace lost foliage fairly quickly; should drought conditions occur during this period, the trees affected die very readily. In preliminary experiments it was found that larvae kept in

the/.....

Temperature °C	One Sq. ft.	Faecal pellets dropped on 62 sq. ft.	One sq. ft.	Needles dropped on 62 sq. ft.	Time.
11.0	9.76	605	2.58	160	06.00
12.25	21.50	1333	3.79	235	07.00
16.0	22.88	1419	3.36	208	08.00
18.5	28.60	1773	6.71	416	09.00
20.5	25.39	1574	4.40	273	10.00
22.5	43.75	2713	11.66	723	11.00
24.0	48.60	3013	9.95	617	12.00
23.5	52.90	3280	13.23	820	13.00
23.5	50.16	3110	15.83	982	14.00
22.0	58.06	3600	8.52	528	15.00
21.0	52.76	3271	8.35	518	16.00
19.75	52.13	3232	6.11	379	17.00
18.25	32.24	1339	2.58	160	18.00
17.0	31.31	1491	2.95	183	19.00
16.0	25.19	1562	2.79	173	20.00
15.25	19.90	1234	1.29	80	21.00
15.0	14.55	902	1.36	84	22.00
17.5	16.31	1011	1.23	76	23.00
16.5	15.81	980	1.19	74	24.00
15.5	21.47	1331	1.13	70	01.00
14.8	11.90	738	0.57	35	02.00
14.0	9.95	617	0.58	36	03.00
14.0	5.87	364	0.34	21	04.00
12.5	5.79	359	0.32	20	05.00

Table 7.A

Hourly counts of needle and faecal pellet drop on 62 sq. ft. over a period of 24 hours.

the laboratory at a constant temperature of 22°C, fed at a more or less constant rate by day and night. This would indicate that light and darkness do not affect feeding. Within the normal plantation range of humidity, laboratory observations also indicate that varying humidities do not affect the rate of feeding activity.

In Table 7Ahourly counts of needle and faecal pellet drop to the forest floor below infested trees over an area of 62 sq. feet are compiled. These counts are shown graphically in fig. 58, and the rise and fall of temperature is also reflected. It may be deduced from the graph that the main factor influencing the rate of larval feeding is temperature. It will be seen that, as the temperature rises, feeding increases, and vice versa.

(e) <u>The influence of the combined action of temperature and relative humidity on the larvae of E. terminalis.</u>

To determine in detail the combined influence of temperature and relative humidity on the larvae of <u>E. terminalis</u>, third and seventh instar larvae were maintained under various combinations of these two factors. In the case of the third instar larvae, they were exposed for ten days while the seventh instar larvae were exposed for 15 days to the various constant combinations of temperature and humidity. The technique to maintain the desired relative humidity is fully described in chapter IV. At each combination of temperature and relative humidity tested, 20 test insects were used and this series of experiments ~~were~~ was twice replicated.

The results of the test expressed as averages are compiled in tables 7Band 8, and reflected in the smoothed graphs of fig. 59 and 60.

From the data regression lines were then calculated by using the Y axis to reflect the percentage of larvae surviving after the predetermined period of exposure and the x axis to reflect the logarithm of the relative humidity.

The results of these calculations are shown in Table 59 and in Figs. 61 and 62.

From figures 61 and 62 it is now possible to determine what percentage of larvae can be expected to survive in any area where temperatures and relative humidity data are available. It is clear that the larval stage of E. terminalis especially the younger instar are extremely sensitive to low relative humidity especially when the temperature is comparatively high.

The column in table 9 in which percentage relative humidity is indicated represents the zone in which the percentage relative humidity may be regarded as optimum for the instar involved at the given temperatures.

As indicated in table 10 the period taken by the larval stage to reach maturity is greatly influenced by temperature. The duration of the larval stage in the plantation at Jessievale is significantly longer than that in the laboratory where the larvae were maintained at constant temperature and humidity.

% Rel. Humidity	Percentage larvae alive after 15 days.		
	10°C	16.5°C	30.0°C
9.8	0	0	0
17.2	0	0	0
26.8	11.0	0	0
36.8	15.0	0	0
46.8	50.0	5.5	2.5
59.8	74.9	60.0	48.0
66.8	96.0	92.0	70.5
75.6	100.0	100.0	91.9
82.9	100.0	94.2	88.5
88.8	98.5	84.0	75.0
92.9	90.1	60.8	60.0
96.1	76.0	45.9	42.0
100	56.0	25.0	18.0

Table 7.B

Influence of temperature and relative humidity on third instar larvae.

Table 8/....

% Rel. Humidity	Percentage larvae alive after 10 days.			
	10°C	16.5°C	25.5°C	30.0°C
9.8	30	4	0	0
17.2	60	25	0	0
26.8	85	65	10	0
36.8	100	80	40	0
46.8	100	85	61	10
59.8	100	95	80	58
66.8	100	100	90	75
75.6	100	100	100	100
82.9	100	100	96	90
88.8	100	100	90	85
92.9	100	90	86	80
96.1	98	87	80	45
100.0	97	80	70	35

Table 8.

Influence of temperature and relative humidity on seventh instar larvae.

(f) Preparation for pupation.

As soon as the eighth instar larva is fully grown, it drops from the tree to the forest floor where it immediately commences crawling about in search of a suitable spot in which to pupate. The related species E. chryssorhoea of Europe and America pupates in the host trees, (Doane et al 1936), but E. terminalis never pupates in the trees, not even in the forks where accumulations of old leaves frequently collect. The pupation site is invariably a spot providing suitable shelter on the forest floor. (Fig. 63).

In a plantation of P. patula, the forest floor is covered by a dense mat of fallen pine needles, and in certain rows there will be heaps of dead branches removed from the trees during pruning. (Fig. 63).

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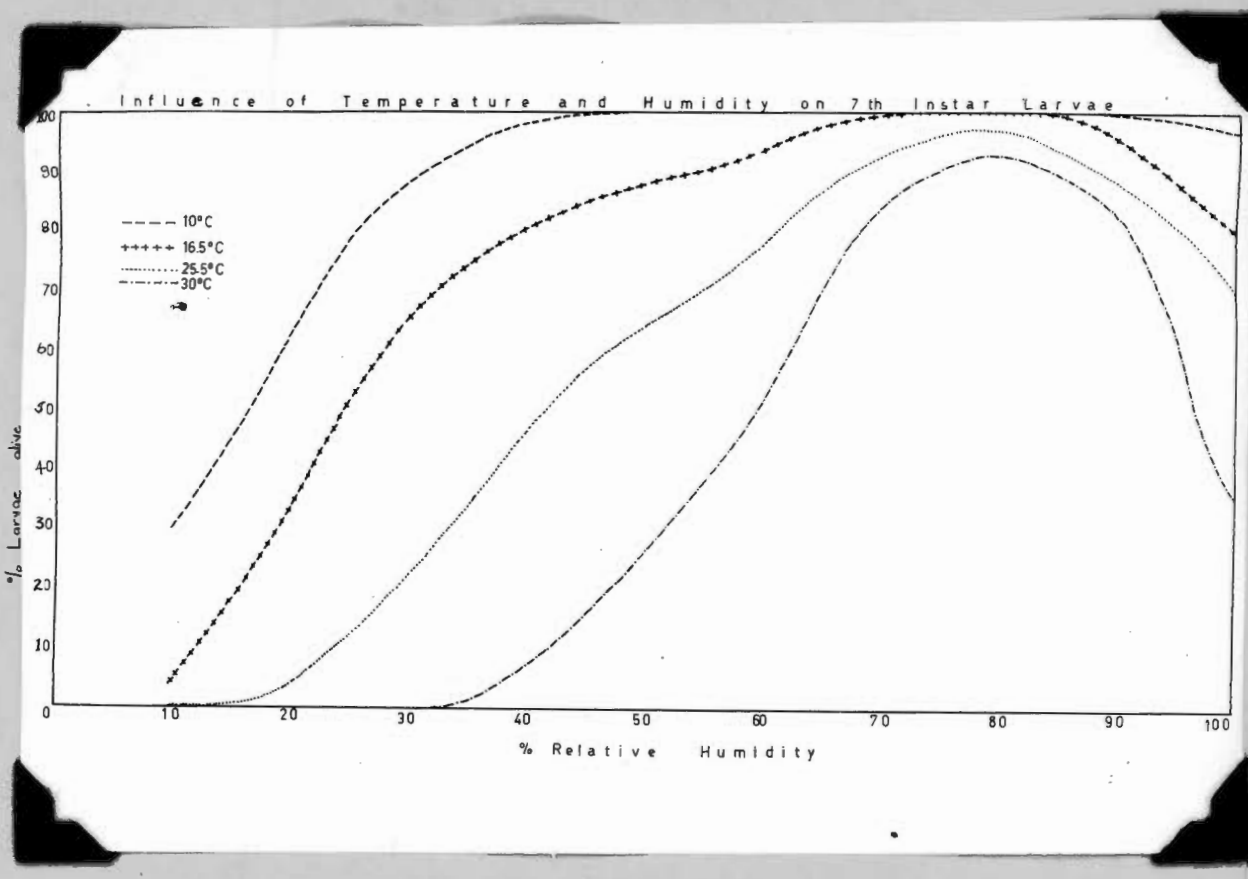

Fig. 59.

Influence of temperature and humidity on 7th instar larvae.

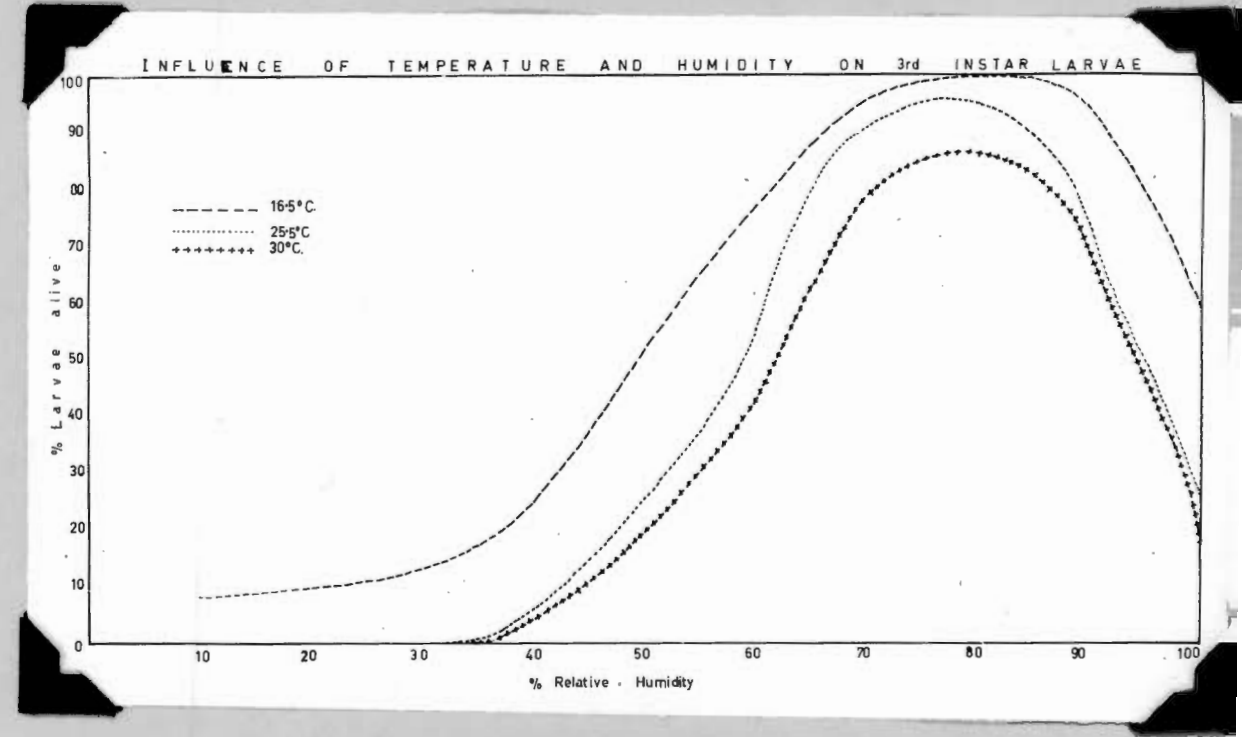

Fig. 60.

Influence of temperature and humidity on 3rd instar larvae.

Instar	Temperature.	Y		Value of X		Corresponds to a relative humidity of:
				Up to:	Beyond.	
3rd Instar	16.5° C.	i. Y = -453.8246 + 299.990	x	1.824		66.6 %
		ii. Y = 116.8702 - 525.963	x		1.936	86.30%
	25.5° C.	i. Y = -779.666 + 472.190	x	1.86		72.44%
		ii. Y = 1278.893 - 620.936	x		1.90	79.43%
	30° C.	i. Y = -713.2745 + 428.781	x	1.89		77.62%
		ii. Y = 1222.3499 - 594.880	x		1.89	77.62%
7th Instar	10° C.	i. Y = -90.74 + 121.98	x	1.56		36.31%
		ii. Y = 829.192 - 374.692	x		1.97	93.33%
	16.5° C.	i. Y = -117.46 + 121.55	x	1.79		61.66%
		ii. Y = 829.192 - 374.692	x		1.95	89.13%
	25.5° C.	i. Y = -272.231 + 198.45	x	1.875		74.99%
		ii. Y = 682.6089 - 304.664	x		1.915	82.22%
	30° C.	i. Y = -70.6599 + 42.928	x	1.88		75.86%
		ii. Y = 1093.069 - 523.476	x		1.90	79.43%

TABLE 9.

Regression line values calculated from Tables 7 & 8.

Series No.	Temperature larvae were kept at:-	Duration of larval development in days.										
		Instars.								Mean	Standard error	Significant different from:
		1	2	3	4	5	6	7	8			
1	Jessievale	15	29	41	45	48	32	29	30 269	260	± 8.7286	No. 3
2	21°C and 70% R.H.	14	22	34	38	40	27	28	28 281	227	± 11.6967	No. 3
3	26°C and 70° R.H.	12	16	22	35	25	24	24	25 183	178	± 13.9408	Nos. 1 and 2

TABLE 10.

The difference in duration of the larval period at Jessievale and under controlled laboratory condition.

The method used to calculate the standard error and significant differences is the same as that employed in Table 3.

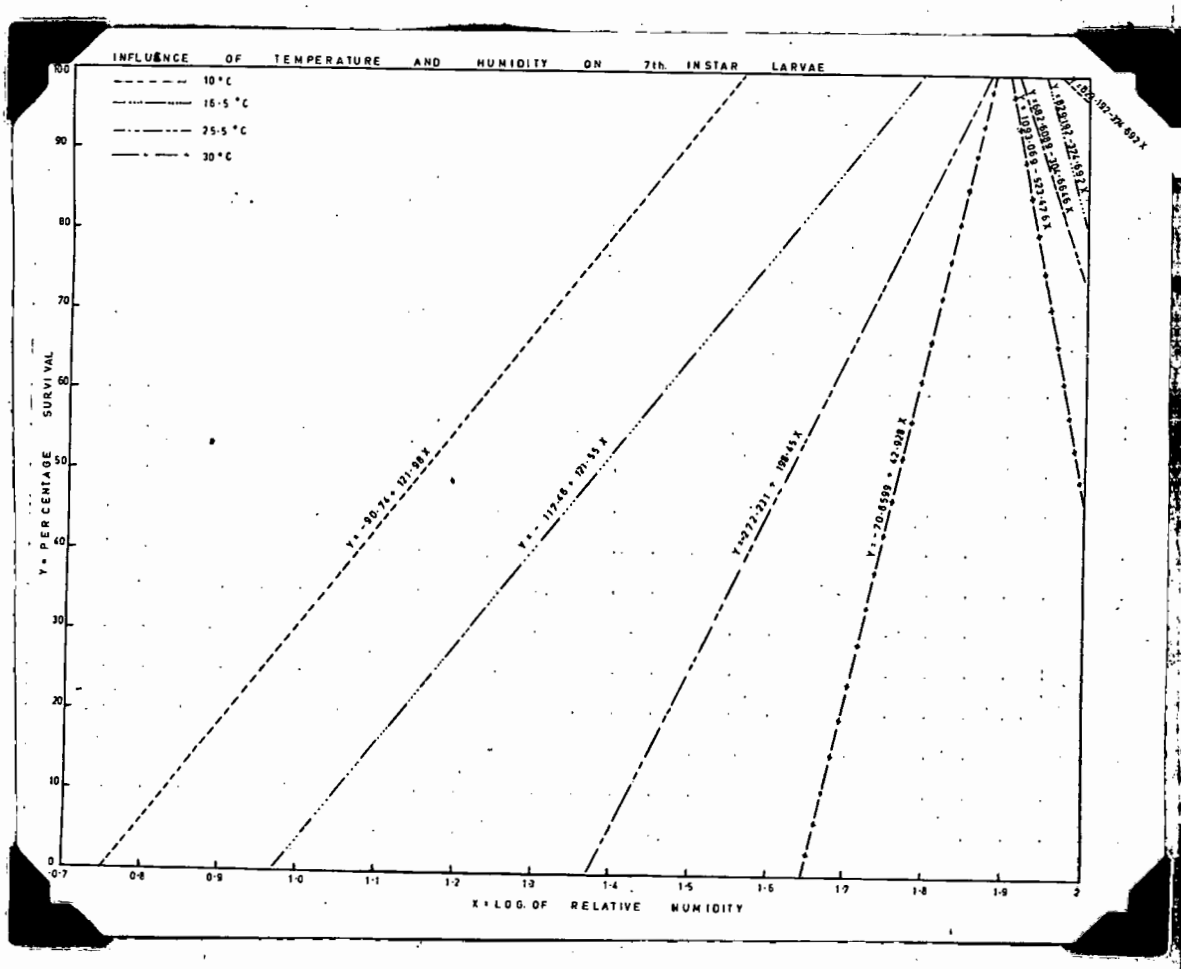

Fig. 61.

Regression lines for 7th instar larvae

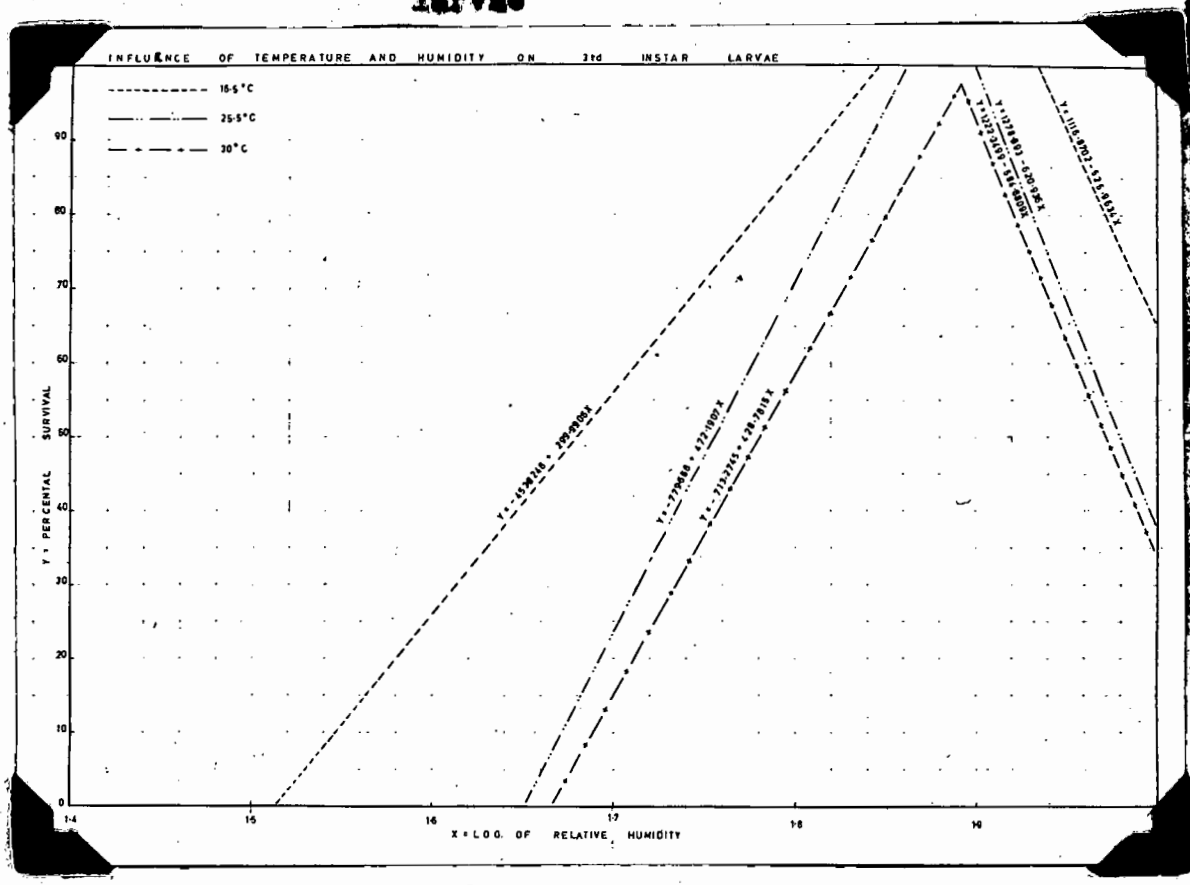

Fig. 62.

Regression lines for 3rd instar larvae.

Fig. 63.

Collecting pupae in a P. patula plantation.

These sheltered sites are ideal for the pupation of E. terminalis. On the forest floor the larvae crawl over the needle mat till they encounter a tree trunk, and then work their way down the trunk through the mat to the soil surface where pupation occurs, or they follow a similar procedure in the piles of dead branches. Entry into the needle mat where it lies level between the trees is rarely observed. Almost invariably the larvae enter the mat at a point where they can work downwards against a trunk or a dead branch lying on the floor.

The cocoon (Fig. 64) is irregular in shape, spun of a sordid brown silk, and to the exterior are attached dead leaves and refuse from the forest floor, which camouflage it very successfully.

Fig. 64.

The cocoon of E. terminalis.

3./....

3. ASSESSMENT OF POPULATION DENSITY.

Various methods have been used to assess the density of an insect population in a given area, the most generally applied one being to count all insects in randomised sample plots of known area, and from the data obtained to calculate the population density of the area as a whole.

It is not always possible to reach the insects for counting, and in many cases sampling of the type mentioned above is virtually impossible. Especially is this the case with the larval stage of E. terminalis, which inhabits the crowns of pinetrees. A further difficulty lies in the fact that poisonous setae cover the bodies of all the larval instars, which renders large-scale handling of this insect a physical impossibility. To determine population densities of the larval stage of this insect, methods other than direct handling had in consequence to be developed.

In view of the fact that the larvae sever the needles during the process of feeding in P. patula plantations, there is a continuous rain of freshly severed needles to the forest floor below infested trees. There is also a continuous drop of faecal pellets below such trees. An attempt was thus made by the writer to correlate needle with faecal pellet drop, and both of these with larval populations in the trees above.

Various factors would of course affect the rate of faecal pellet and needle drop, the most important of these being the size of the larvae and air temperatures.

The amount of food consumed by a larva would obviously be influenced by its size and instar. The larger the larva, the higher would be its rate of food consumption and the rate of faecal pellet drop. In addition, the faecal pellets themselves progressively increase in size as the larvae becomes more mature. In

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the case of a population consisting of larvae of mixed instars, the correlation between needledrop, faecal drop and population would vary so widely that the figures obtained would be of negligible value. It was determined by observations in the field that fortunately a very high percentage of all larvae in the Jessievale plantations hatch within a concentrated period of two weeks. At the beginning of October, i.e. 9 months later, practically all of these have reached the 7th instar and are of equal size. It was at this stage that experiments were carried out to correlate density with needle and faecal pellet drops.

The influence of temperature on feeding activity, and consequently on both needle and faecal pellet drop, is considerable, as shown in figures 66 and 67.

It was thought at first to be possible to determine in the laboratory the correlations between larval density, needle and faecal pellet drop. However, when the larvae are excessively handled and confined in cages, the many artificial factors introduced might have an appreciable effect on the results obtained . For this reason it was decided to obtain the desired information by means of large-scale field tests under normal plantation conditions.

The experimental site at Jessievale consisted of a uniform 200 acre stand of *P. patula* of one age group, the crowns of the trees forming an even canopy overhead. The trees were at the time (October) infested mainly by 7th instar larvae, occasional sixth and eighth instar specimens also being present.

In this stand of trees six points were selected as test sites. At each point a tarpaulin was spread on the forest floor below the infested canopy to catch up the needles and faecal pellets dropped by the larvae immediately above them. After an exposure of 24 hours, all needles

and/.....

and faecal pellets on each of the tarpaulins were collected and bottled for subsequent counting. Immediately after the 24 hour period had elapsed, the tree canopy above each tarpaulin was thoroughly dusted with a knock-down insecticide. This resulted in the larvae responsible for the faecal and needle drop on the tarpaulin also to drop down. These could then be counted.

A count of the needle and faecal drop on each of the 6 selected test sites was carried out on different days. This procedure was adopted for two reasons. Firstly, in order that detailed observations could be made during each experiment - if all six experiments would be carried out simultaneously, such individual attention could not be given. In the second place, by carrying out each experiment on a different day, a wider range of temperature variation was introduced into the investigation. Continuous recordings of temperature and relative humidity during the 24 hour duration of each experiment were provided by thermo-hydrographs situated in the crowns of the trees on the site.

After the tarpaulin had been spread on the forest floor at a test site, its sides were raised somewhat to ensure that needles and faecal pellets dropping on it remained there. Thereafter the total catchment area of the tarpaulin in square feet was accurately determined. In the sixth and last experiment, the experimental area was much larger than in the five preceding ones, since more tarpaulin was then available. The size of the tarpaulin used would not affect the results, provided its area in square feet had been accurately determined.

The insecticide used to bring the larvae down from the canopy on to the tarpaulin below at the conclusion of each experiment was 5% Malathion dust. To make absolutely sure that all the larvae involved were taken, the dust was applied at an extremely high dosage. Two hours

after/.....

after application of the insecticide practically all the larvae had dropped from the trees. Those which fell during the first half hour crawled about on the tarpaulin for a short while before perishing, but those dropping later, showed no sign of mobility. To ensure that all the larvae were recovered, however, the tarpaulins were left on the site for 24 hours after dusting, and checks were made by climbing the trees and look for larvae.

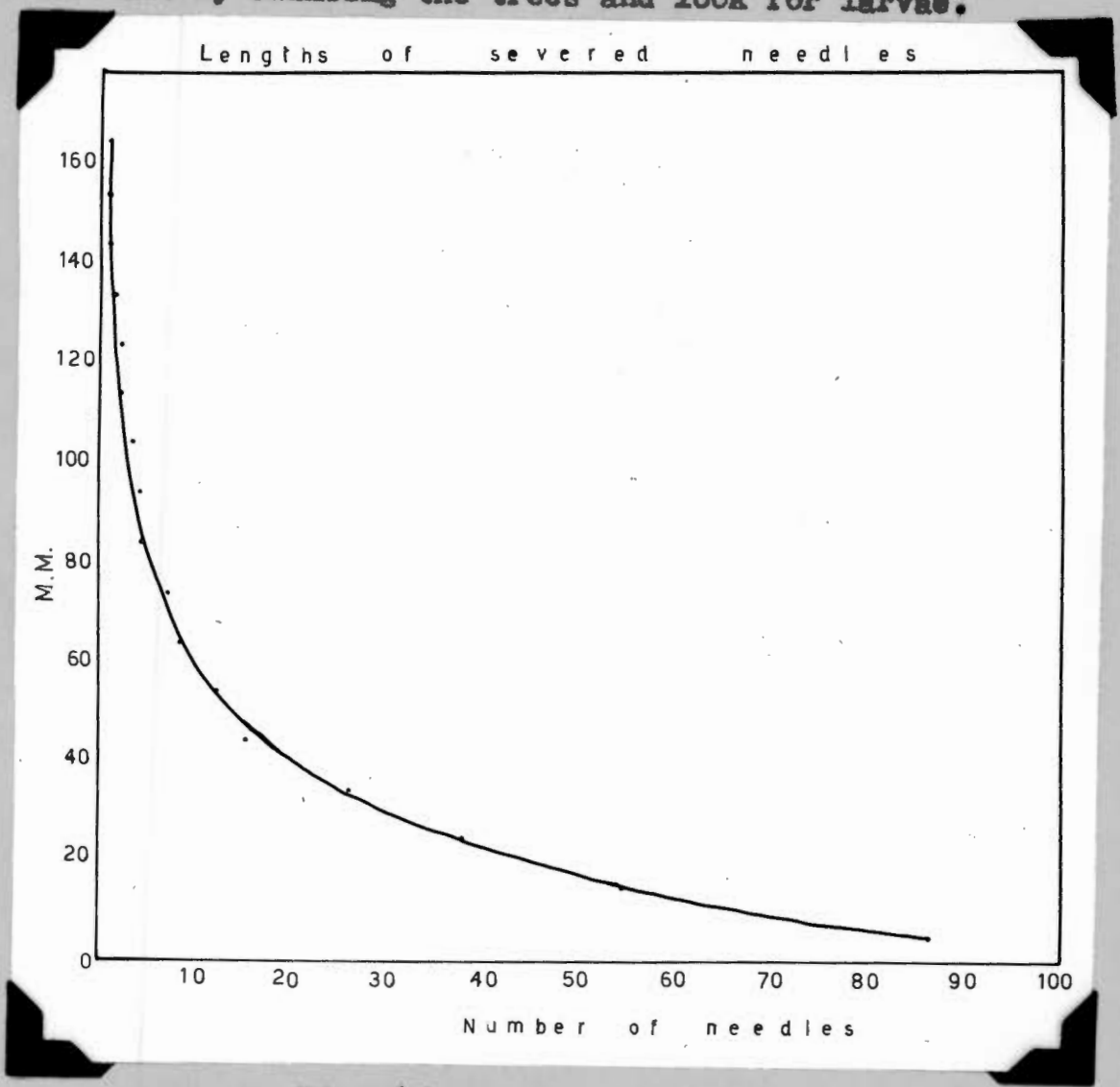

Fig. 65.

Lengths of severed needles.

The data obtained from this series of experiments are compiled in Table 11. The larvae and needles recovered from each experiment were counted individually. The faecal pellets were all of approximately the same size, and it was determined that on an average one cubic centimetre holds 202 pellets. The number of faecal pellets recovered in each experiment could thus be determined on a volumetric basis with a high degree of accuracy.

Faecal/.....

	Exp. 1.	Exp. 2.	Exp. 3.	Exp. 4.	Exp. 5.	Exp. 6.
Larvae	10,397	6,108	8,143	7,083	6,885	15,504
Needles	43,693	18,056	27,198	30,440	27,540	48,372
Faec. pellets.	293,133	116,655	200,049	213,142	188,924	343,925
Temp. °C	17.3°C	13.4°C	15.5°C	19.8°C	18.1°C	13.8°C
Ratio.						
Larvae: Needles.	4.20	2.95	3.34	4.30	4.00	3.12
Larvae: Faec. pellets	28.19	19.10	24.56	30.10	27.44	22.18
Needles: Faec. pellets	6.71	6.46	7.36	6.99	6.86	7.11
Larvae per sq. ft.	36.10	32.84	43.78	38.08	37.02	19.14
Needles per sq. ft.	151.71	97.07	146.81	163.66	148.07	59.72
Faec. pel. per sq. ft.	1017.82	627.18	1075.53	1145.93	1015.72	424.59
Tot. sq. ft. for experiment	288	186	186	186	186	810
No. of trees on experimental area.	3	2	2	2	2	8

TABLE 11.

Observations from which graphs in figs. 66 and 67 were calculated.

Faecal pellets as a gauge of larval population density can effectively be used only during periods of fair weather. When rain falls, they disintegrate, and accurate counts cannot be made. It is for this reason that population assessment by counts of needle drop was investigated as a possible and more stable method.

As will be seen in Fig. 65, the lengths of the needles dropped by the larvae vary considerably, and for this reason it was felt initially that they would not prove to be a reliable indicator. However, from Table 11, it will be seen that the correlation between a single needle or portion thereof and the number of faecal pellets is far higher in all 6 experiments than could have been expected. It is for this reason that needle counts have been included in the graph as well, where they serve as a reliable check on population density assessments based on faecal pellet counts.

By collecting the faecal pellets and dropped pine needles on a measured area over a period of 24 hours, during which the average air temperature has been determined, a fairly accurate estimate of the density of larval populations in the trees above may be arrived at by referring to the graphs in Figs. 66 and 67.

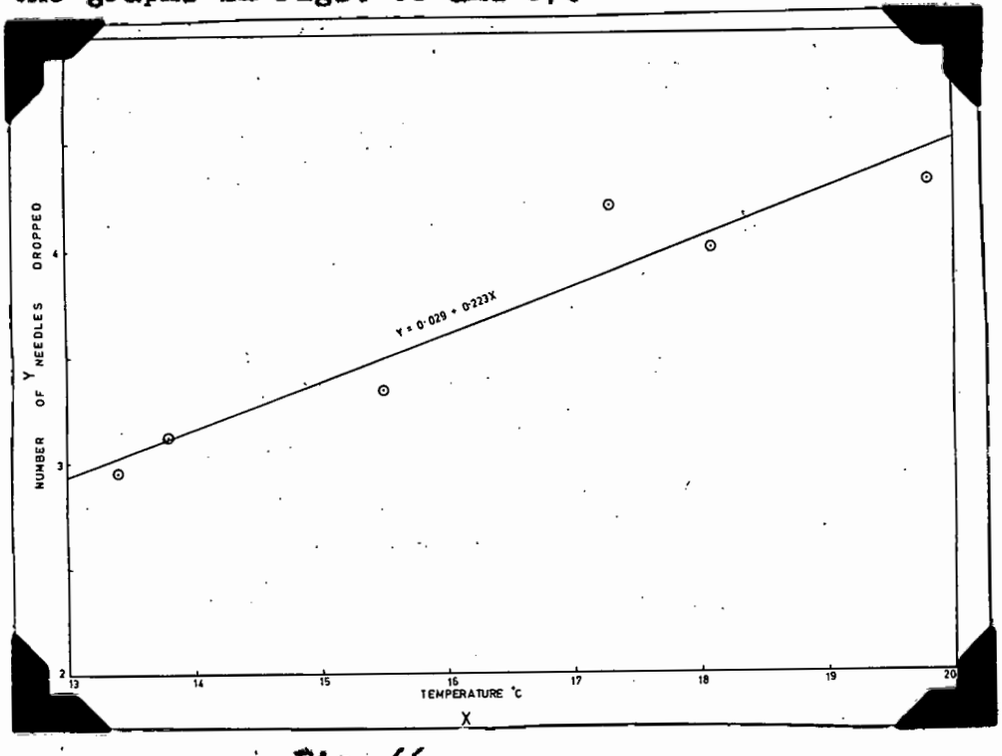

Fig. 66.

Needle drop as influenced by temperature.

Fig. 67/....

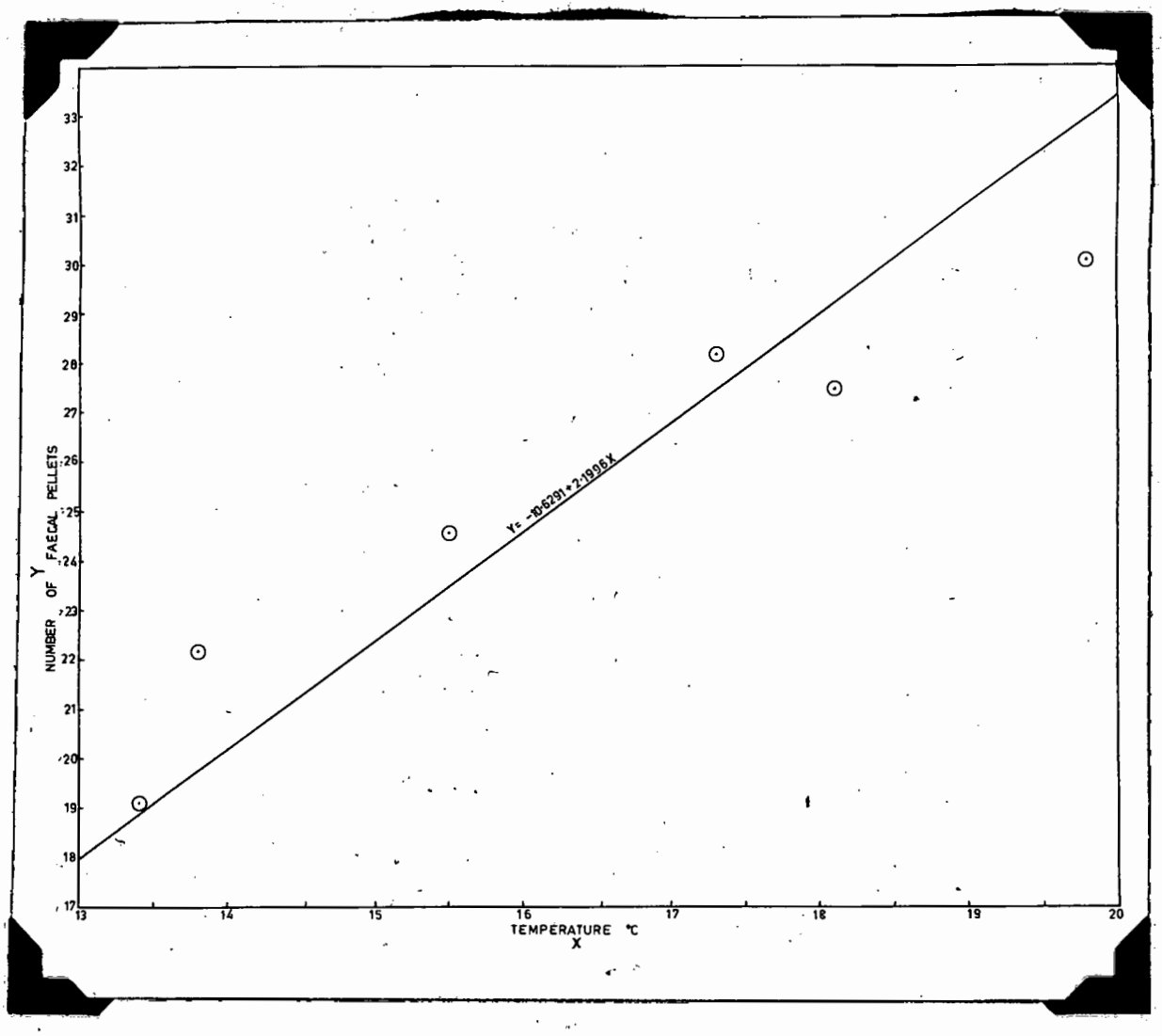

Fig. 67.

Faecal pellet drop, as influenced by temperature.

The standard deviation of the regression lines were calculated from the formula:

$$Sy.x = \sqrt{\frac{\text{Sum (deviations)}^2}{N-2}}$$

Where deviations = the difference between observed and calculated number of needles, and was found to be $\pm$ 0.1905 in figure 66 and $\pm$ 2.177 in figure 67.

The coefficient of variation was calculated from the formula

$$\frac{Sy.x \times 100}{\text{Mean}}$$

The value found for the graph in figure 66 was 5.2163% and for that in figure 67 8.6178%.

It/.....

It is realised that the straight lines given in the figures mentioned above are only part of a curvilinear regression line, and that a linear regression, such as that indicated in the figures will only hold good for temperatures ranging from about 13°C to 20°C. It can be logically expected that at lower temperatures feeding and excretion will increase as temperatures increase, at first slowly, and then gradually more rapidly. Conversely at higher temperatures than those indicating on the graphs, feeding and excretion will start decreasing, at first gradually and then more rapidly as the temperature increases above a certain level.

CHAPTER VI.

THE PUPAL STAGE.

1. MORPHOLOGY.

Euproctis terminalis has a typically obtect pupa, the wings and other head and thoracic appendages, pressed tightly against the body being clearly visible (Fig. 68). The abdominal segments do not move very freely. When the pupa is disturbed, only slight movements of the abdomen can be discerned.

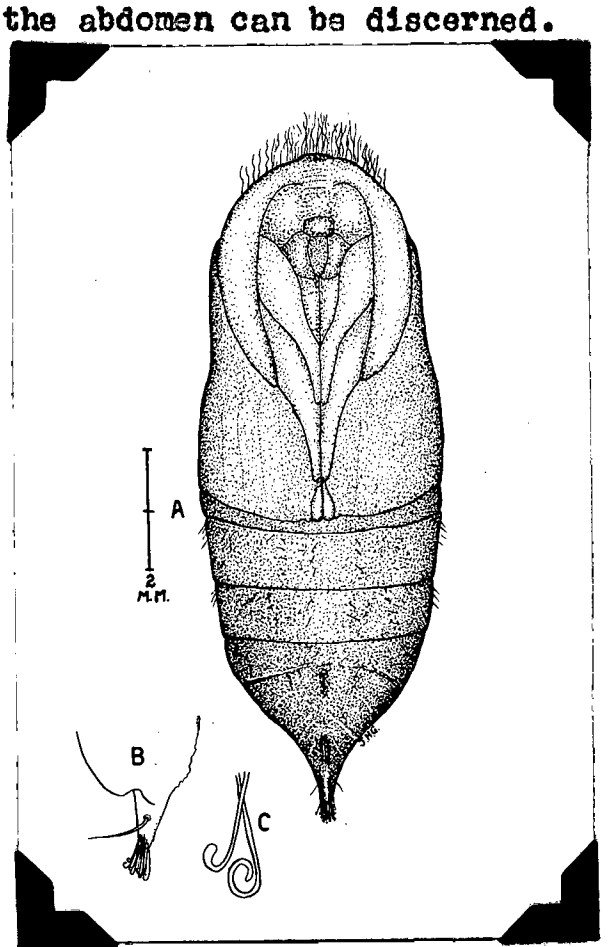

Fig. 68.

A. Pupa of E. terminalis.

B. Enlargment of the cremaster.

C. Setae on the cremaster.

As the pupa ages, its colour becomes progressively darker until finally, its colour varies from English red to Mahogany red. In the older pupa the eyes are darker than, and contrast in colour with that of the rest of the body.

The dimensions in Table 12 are based on 50 measured pupae.

2./....

2. HABITAT.

In view of the fact that the pupae are found in the forest floor of plantations, beneath a mat of needles and other type of refuse, which may vary in depth from 3 - 10 inches, it is clear that they are not exposed to any marked variation in temperature and humidity.

	Average.	Standard deviation.
Length	10.88 m.m.	± 0.04947
Width	4.44 m.m.	± 0.02199

Table 12.
Dimensions of E. terminalis pupae.

The soil and pine needles in the immediate vicinity of the pupa is always moist, even at times during the winter months at the Jessievale plantation, when the rainfall is at its lowest level. As a result the pupa is always exposed to humidities nearly equivalent to that of moisture saturated air. Temperature variations to which the pupa is exposed would also be negligible compared to those prevailing between the tree canopy and the forest floor.

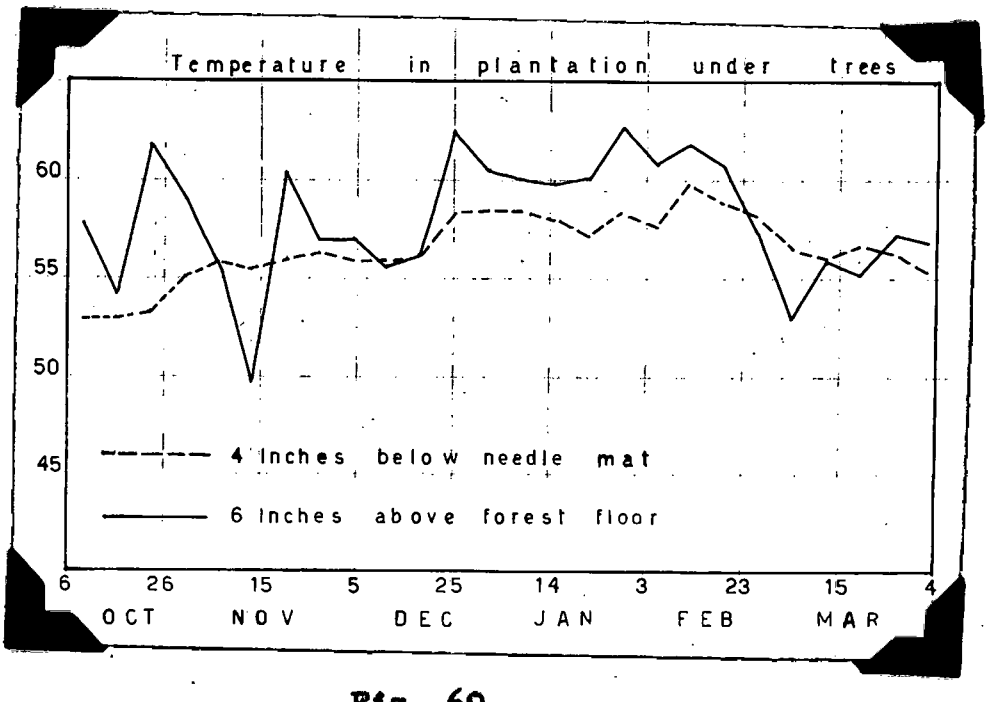

Fig. 69.

Temperature in degrees Fahrenheit 4 inches below and 6 inches above the forest floor in the Jessievale plantation.

The/.....

The temperatures 6 inches above the forest floor and 4 inches below the needle mat prevailing at Jessievale during the period 6.10.51 to 2.3.52 are expressed in figure 69. During this period, when pupation occurs at Jessievale, the temperature under the needle mat is much more constant than that of the air above it, the range between the maximum and minimum being approximately half that of the air temperature (Table 13).

	Maximum	Minimum	Variation
Temperature in the forest floor	59.8°F	53.0°F	6.8°F
Temperature above the forest floor	62.5°F	49.9°F	12.6°F

Table 13.

Comparison of temperatures above and below forest floor.

3. DURATION OF THE PUPAL STAGE.

In order to determine how long it takes for the pupal stage to be completed under natural conditions, 50 pupae were kept below the needlemat on the forest floor in the Jessievale plantation during the period 31.10.1951 onwards, and records were kept of moth emergences. The last moth emerged on 7.1.52, the average duration of the pupal stage at an average temperature of 56.8°F being 57 days (~~Table 15~~ Fig. 69).

CHAPTER VII.

HABITATS AND ENVIRONMENTAL RESISTANCE.

1. ANALYSIS OF OUTBREAKS IN PLANTATIONS.

In spite of the fact that E. terminalis was discovered in South Africa as early as 1855 it was only in 1929, after Pinus spp. had been planted on an extensive scale, that the attention of the economic entomologist was focussed on this insect owing to outbreaks which then occurred in certain plantations.

This insect has switched over gradually from indigenous vegetation to exotic trees, especially Pinus patula, and to a lesser degree P. leiophylla and P. radiata and permanently established itself in plantations of this species. In most cases the factors responsible for controlling the rate of multiplication of the insect accompanied it to the new habitat, but in certain plantations these factors took longer to become fully established there, with the result that a number of outbreaks occurred in the plantations before a state of equilibrium, such as prevails in the natural habitat, was established. In one plantation however, namely the Jessievale State Plantation, this adaptation to the state of equilibrium has not taken place.

In an attempt to explain why the state of equilibrium prevailing in the natural habitat of E. terminalis, where no outbreaks of this insect have hitherto been recorded, has not developed in the Jessievale Plantations, a study ~~has been~~ was made of all the known factors which constitute the environmental resistance of this insect.

It is necessary first of all to examine the early history of the insect during the period when it was first observed in the plantations. It is not clear what caused the insect to adopt the exotic Pinus spp. as additional host plants, but during the period before the insect

was noticed in the plantations there must have been a gradual and progressive increase of the populations which originally migrated there from indigenous host plants.

In spite of the fact that, according to Lotka (1925) the reproductive potential of an insect has no influence on the average population density, it will certainly exert an influence on the rate of increase of an insect which moves from one habitat to another and where all the environmental resistance factors do not immediately operate at the full strength prevailing in the previous habitat.

According to the formula of Thompson as adapted by Chapman (Graham 1952), $P(zy)^n$, where P represents the original number of the population, z the products of the number of eggs laid by one female and the sex ratio, y the number of descendants per egg, and n the number of generations in a given time, the reproductive potential for E. terminalis (if the formula is expressed in figures), appears as follows for on year: $1(185 \times 1)$, = 185.

This reproductive potential of 185 per year is relatively low for an insect, and it would thus have taken considerable time from the moment the insect occurred in Pinus plantations, until the population had reached a heavy density which caused noticeable defoliation.

The first plantations where E. terminalis became of economic importance, were those at Jessievale where the insect defoliated an area of 110 acres of P. patula and P. leiophylla in 1929. During the next year, 1931, according to Tooke (1938), the insect "spread considerably through the plantation, and was then heavily infesting between 300 to 400 acres of almost exclusively P. patula and P. leiophylla,

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and this despite the fact that a large number of caterpillars had during the previous summer succumbed to a caterpillar wilt disease." A striking characteristic of this infestation was the fact that all the compartments heavily defoliated the previous season were now singularly free from larvae, while fresh compartments were being heavily defoliated. In 1931 it was also reported from the Belfast and Harrismith plantations that the insect was defoliating large areas there.

From then onwards reports were received showing that the insect occurred in numerous other plantations in the Eastern Transvaal and Natal, although no further serious damage was reported until 1934, when a large area in the Driekop plantation in the Pilgrimsrest district was damaged by the insect, and again during 1938 in the Spitzkop plantation in the Sabie district.

In 1935, i.e. six years after the first outbreak in the Jessievale plantation, it was reported that 800 acres of P. patula were being defoliated there and in the next year 1,870 acres were defoliated in the same plantation. The latter defoliation was partially arrested by insecticidal application.

In 1935, 1937 and 1940 reports were received that large areas of the Harrismith plantations had been defoliated, and damage recurred at Belfast during 1938. No further damage in any plantation other than those at Jessievale has been reported in the Union since 1940.

The history of the outbreaks in the various localities mentioned above is summarised in Table 15. From this we may deduce that (a) the insect was noticed only in certain plantations (b) in others one to four outbreaks occurred with no subsequent recurrence, and (c) there is one plantation only where there have been periodic and regular outbreaks ever since the insect was first recorded in it.

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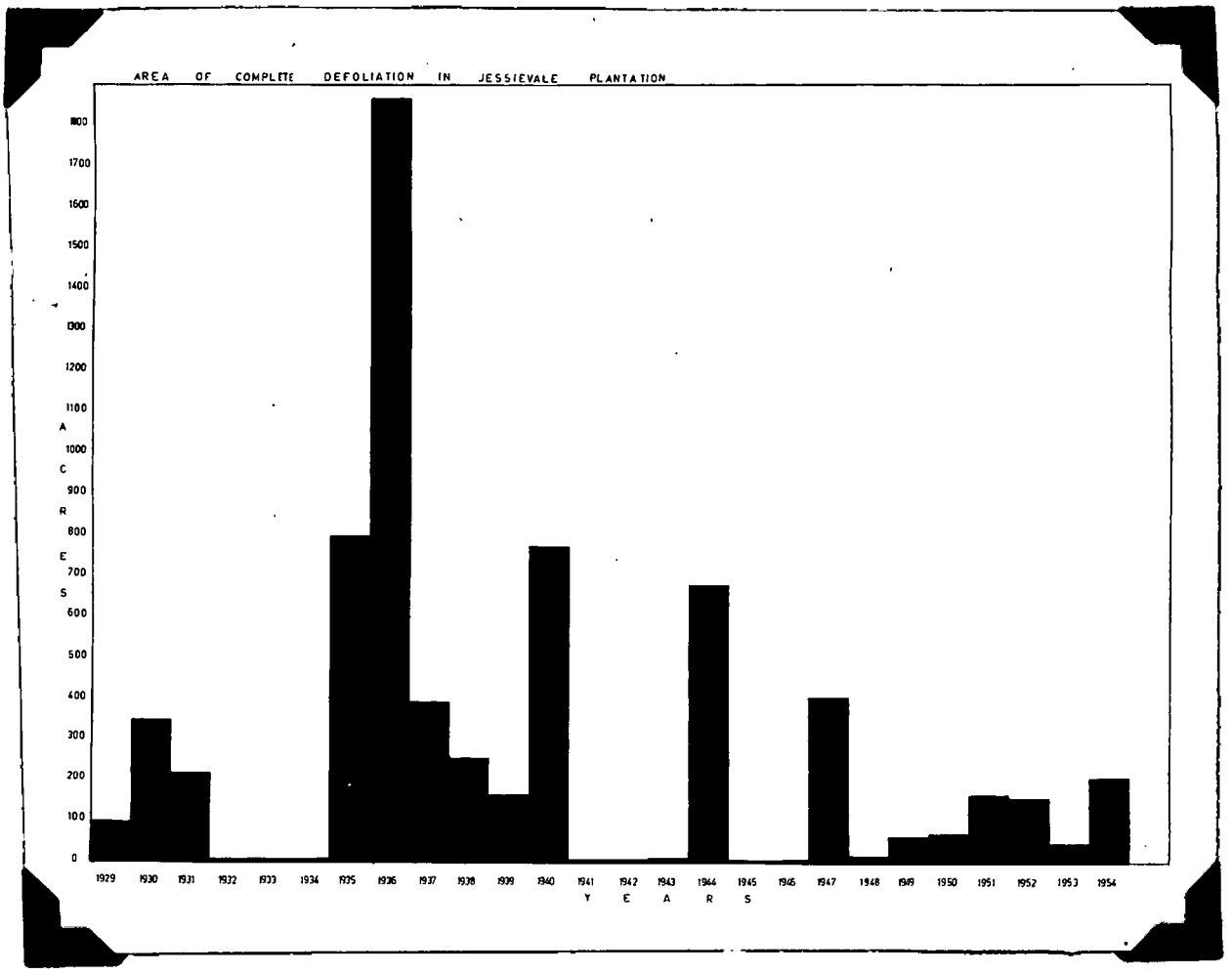

Fig. 70.

Complete defoliation in acres at Jessievale since 1929.

From a study of table 15 it would appear that the outbreaks occur in cycles of 5 - 8 years, e.g. at Belfast in 1930 and then again in 1938; at Harrismith in 1930, 1935, 1937 and 1940, which probably represents two cycles in different areas lasting from 1930 - 1937 and again from 1935 - 1940.

Recorded outbreaks of E. terminalis in Pinus plantations.

Plantation	First Outbreak	Second	Third	Fourth	Fifth
Jessievale	1929	1930	1935	1936	1937
Belfast	1930	1938	-	-	-
Harrismith	1930	1935	1937	1940	-
Driekop	1934	-	-	-	-
Spitzkop	1938	-	-	-	-

Table 15.

According/.....

According to Fig. 70 it would appear that the maximum area of complete defoliation in the Jessievale plantations was reached during 1936, the seventh year after the first outbreak was recorded. Since then there have been noticeable but progressively less extensive peaks of defoliation during the years 1940, 1944, 1947 and 1954. Since fig. 70 reflects complete defoliation only, it does not give a true reflection of the actual insect population density during the period under review. From the period of peak populations at Jessievale during the year 1936, damage to a greater or lesser extent has been brought about each successive year up to the present.

2. AREAS OF ABUNDANCE.

(a) General classification.

The insect occurs commonly in three types of areas, a) in its natural habitat; b) in the pine plantations where it is always present in noticeable numbers but where no outbreaks occur; c) in the pine plantations where periodic outbreaks are regularly recorded.

In the first area the population density is very low, so low in fact that the writer had to search over long periods in order to be able to establish the host plants on which larvae occur in their natural habitat, and after eleven such plant species had been found, the total number of larvae collected on them did not even exceed a hundred.

In the second area of abundance the insect does not occur in large numbers, although the population is heavier than that encountered in the natural habitat; in the third area of abundance the insect may always be found without trouble, even though there may be no outbreak in the season during which the search is conducted.

According to Cook (1929) and Uvarov (1931) the density of the population of every insect species varies, and

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its distribution may be subdivided into special areas or degrees of abundance. Uvarov (1931) states that "the area of specific distribution" is the area where the insect always appears, but is constantly kept in check by its controlling factors, with the result that it never becomes a pest.

In the case of E. terminalis, Uvarov's "area of specific distribution" would include the natural habitat of the species, where it is always present but kept down at a low level by controlling factors, as well as those plantations of exotic pines where the controlling factors regularly operate to such an extent that the insect, though more abundantly present than in its natural habitat, never becomes a pest.

The third area of abundance mentioned above corresponds with that presented by Cook (1929) as an "area of occasional abundance". In such areas, e.g. the Jessievale plantations, the insect may always be found, but it emerges as a pest only during those periods when the limiting factors temporarily cease to exert their influence.

In these three areas the density of the population naturally varies from year to year, but the variation will be smallest in the area where the population is normally at its lowest level and, conversely, it will be highest in the area where the population reaches its highest level. However, as Solomon (1949) puts it: "In a precise sense, populations often vary greatly in numbers, in a very broad sense they may be regarded as fairly constant."

The difference in density of the populations in the various areas is also due to the varying composition of the environmental resistance factors, while the oscillation

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is caused year after year by the variation in the efficiency of the sum of the different factors, as a result of the influence exerted on them by external factors. Smith (1935) states that the oscillation of a population is merely due to the fact that the effective rate of increase fluctuates with time; in other words, that the fraction of the progeny per parent which survives is not constant.

In order to understand better the causes of varying areas of abundance it is advisable to discuss each area separately, as the operation of the various factors differs according to the area.

(b) Natural Habitat.

The natural habitat of E. terminalis is the area where the insect occurs, and where no artificial influences have yet influenced the controlling factors. In this area there is still a perfect equilibrium. According to Clausen (1936) "the fundamental basis of biological control lies in the natural equilibrium which exists between all elements of the plant and animal world. Originally before movements of the plants and animals from country to country took place through human agency, there existed a condition of relative stability among all these elements." This condition still prevails in the natural habitat of E. terminalis.

In examining controlling factors which constitute the environmental resistance in the natural habitat the parasites will firstly be discussed.

(i) Influence of parasites on populations.

In the pine plantations no less than eleven indigenous insect parasites that thrive on E. terminalis have been discovered up to the present and this number may be taken as the possible minimum that attacks the pest. Ripley et al. (1934) pointed

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out that in the case of the wattle bag worm, Acanthopsyche junodi Heyl., certain indigenous parasites did not follow the insect from its normal habitat to the planted wattle plantations. Since these parasites prefer sunshine, the conditions prevailing in the plantations were apparently unfavourable to them. There is thus the possibility that this might also apply in the case of E. terminalis and that more parasites may be present in the natural habitat than are found in the plantations.

In this connection it may be mentioned that when E. terminalis occurs in exotic wattle trees, unknown parasites are always observed associated together with the known ones in the vicinity of the larvae in the trees. Although E. terminalis may very easily be reared on the leaves of wattle trees no outbreaks of this insect ever occur in wattles, even when these trees adjoin sections of P. patula where heavy defoliation occurs. This has been noted on many occasions in the Jessievale plantation.

The question therefore arises whether there are certain parasites which follow the insect into the wattle trees, Acacia mollissima - which is closely related to Acacia caffra, one of the indigenous hosts of E. terminalis -, and not into the Pinus plantations. It may be noted that the unknown parasites observed in the infested wattle trees are not in search of other host insects, since E. terminalis is the only insect occurring on these trees in the area concerned.

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In view of the fact that it has been proved by the writer that certain of the parasites of E. terminalis are not specific, (see chapter VIII) it may be assumed that the parasites in the natural habitat do not depend solely on E. terminalis for maintaining their numbers, and would hence form a stable and controlling factor in that habitat.

In the natural habitat with its mixed flora, there may also be other predators such as birds, small beasts of prey and insects which do not occur in the sterile Pinus plantations, and their possible controlling influence should thus be regarded as additional.

(ii) Influence of host plants on population.

The influence which the host plants may have on the decreased indensity of the population in the natural habitat is an indirect influence of the climate. It was shown experimentally that there is only one generation per year, and as the larvae of E. terminalis take 8 - 10 months to complete their cycle, they require food during this period for sustenance. Three of the eleven host plants in the natural habitat are deciduous, viz. Acacia caffra, Ziziphus mucronata, Rhus pyroides, and a further three viz. Dombeya pulchra, Rhus rehmanniana, Rhus dura, defoliate in areas where frost occurs. As a result of this, there is a period of 2 - 4 months during which food is very scarce. During this period larvae which are not ready yet to pupate will show a high mortality, and this will mean a considerable decrease in the density of the population in

winter./...

winter.

Due to the fact that the insect occurs in such small numbers in the natural habitat, it was not possible to investigate the influence of the different controlling factors more accurately.

(c) Plantation habitat in which E. terminalis occurs but not as a pest.

With the exception of the Jessievale plantation, and a few other minor ones in the immediate vicinity of it, outbreaks of E. terminalis do not occur today in any of the Union's plantations of exotic pines.

The population density of E. terminalis in the plantations under consideration is higher than in the natural habitat, as the insect's presence can easily be detected and on any hot day throughout the year moths flying around may be encountered under the trees.

The host plants play no direct part in the control of the insect as is the case in the natural habitat, being available in abundance throughout the year.

In view of the fact that no other Lepidopterous insect occurs in the plantations, the parasites are dependant on one host insect only namely E. terminalis. Their density is therefore unstable and as a controlling factor they cannot be as efficient in the plantations as they are in the natural habitat. As a result the density of the E. terminalis populations is usually higher in plantations.

In an attempt to ascertain the percentage of the population that is destroyed by parasites, a number of trees in the Spitzkop plantation were thoroughly searched from top to bottom for eggs and larvae. The search yielded 20 eggs masses containing a total of 3,645 eggs, of which 3,125 had been parasitised by one species of egg parasite, which

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amounts to 85.73% of the total. According to Tooke (1938) 88% of the E. terminalis eggs collected by him in the Sabie areas were parasitised. Only ten larvae were found, of which two were parasitised. By searching over a large area of the forest floor at different sites of the same plantation 58 cocoons were found, of which 54 pupae or 93.1% were parasitised. There is reason to believe that the % of parasitism in this case is relatively high. In Belfast plantation, of 75 larvae collected, no less than 49 larvae or 65.5% were parasitised.

In this unnatural habitat the effect of all the factors of the environmental resistance together is definitely not as severe as in the natural habitat, with the result that the population density is higher.

They prevent however an increase indensity to a level where the insect would cause damage of economic importance.

(d) Plantation habitat in which E. terminalis occurs as a pest.

In the aforementioned areas it was difficult to determine accurately the influence of the different controlling factors on the density of the E. terminalis populations, but judging from available data it would appear that the parasite complex is the most important controlling factor.

The influence of the factors constituting the environmental resistance in the Jessievale plantation could be deduced with a greater degree of accuracy since all the material necessary for such a study is availabe during an outbreak. The various factors are of course intermingled, but to be able to understand the complex as a whole, they were studied separately.

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In view of the fact that outbreaks occur only in the Jessievale plantation and a few smaller ones in the immediate vicinity of it, it seems obvious that in this area there are certain environmental resistance factors that do not exert the same influence on the population as in the areas where no outbreaks occur. It was found that the most important difference between this area and the others was found in the parasite complex. In the Jessievale plantations the number of parasitised E. terminalis is relatively small. As soon as the population density reaches a peak level, however, certain fungal parasites spread and decrease the population to a level from which it once more has to build up gradually.

The reason for this low percentage of parasitism was only discovered after intensive study and collecting. It was then found that the main difference between the area of specific abundance and the area of occasional abundance lies in the fact that in the former area the generations of E. terminalis, which has only one generation per year, are mixed, i.e. all the stages may be found throughout the year. While in the latter area, i.e. Jessievale, the stages of the single generation occur successively, i.e. the moths are found mainly in November, December and the beginning of January, the eggs mainly in December and January, the larvae only from January to October, and pupae only from October to December. (Fig. 71).

The parasite complex at Jessievale, consisting of egg parasites, two groups of larval parasites, the first of which attacks only the small, and the second only the larger larvae, and pupal parasites, can operate only during restricted periods each year when the instar required as host is present in the plantation. As a result the parasites in this area have not sufficient time to increase to

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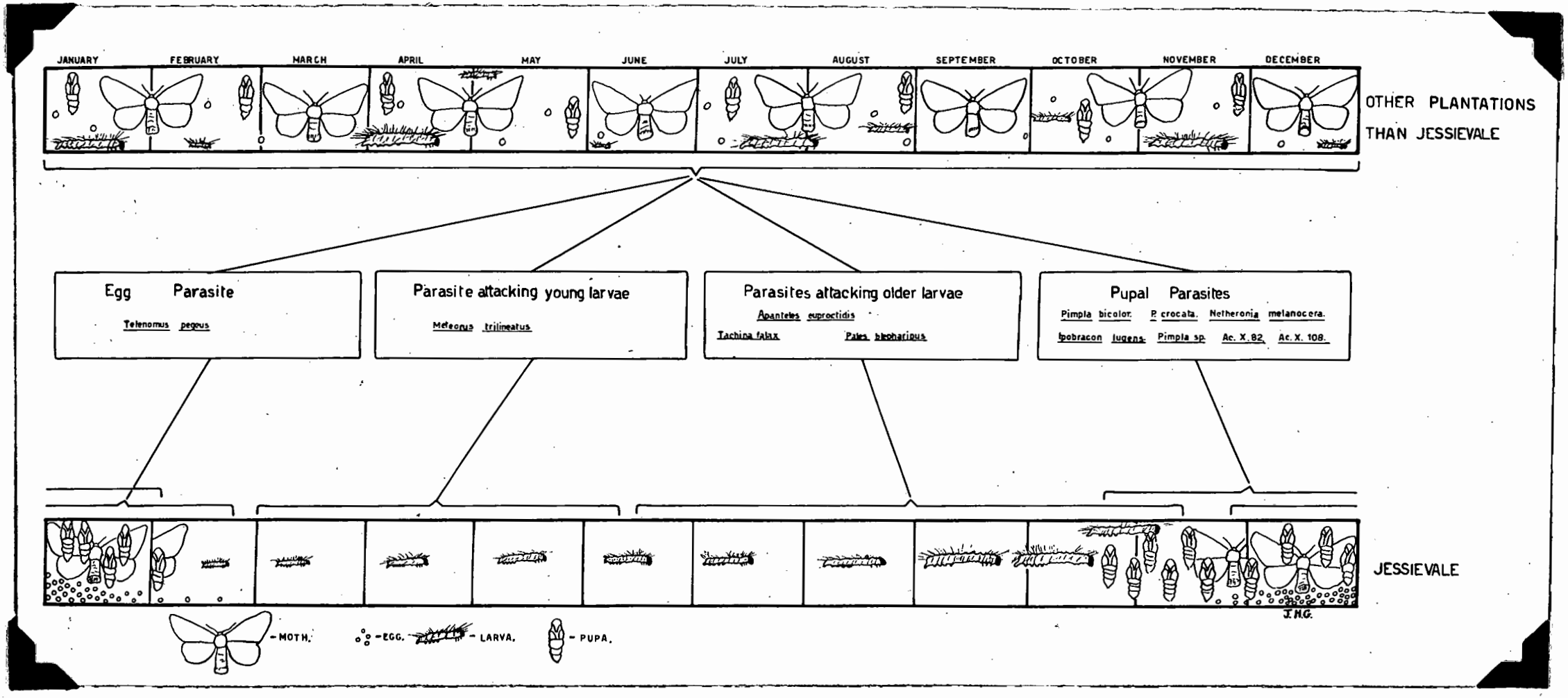

Fig. 71.

The area of specific abundance and that of occasional abundance (Jessievale) and the influence on the parasite complex.

numbers which would have a decisive controlling influence.

The main factors that control the pest periodically are fungal parasites of the larva and pupa. But unfortunately in the case of the larva it only operates efficiently when the larval numbers attain peak density, and in the pupa it only operates if the climate conditions are favourable.

The result is that the population of the insect at Jessievale occurs in rough cycles in the various compartments. At peak population density the fungus parasite operates efficiently and the population of the pest rapidly drops to a basic minimum. Thereafter it gradually increases, with the parasites as a factor exerting an influence on the rise of the logistic curve, eventually returning to a density where the fungus parasite may operate efficiently once more.

In compartments of young Pinus patula stands, outbreaks never occur before the trees are 7 to 10 years old. This lapse of time is necessary to enable the E. terminalis population to build up from the lowest to the peak level at which it is able to defoliate the trees completely. The outbreaks always occur a year or so after the lower branches in stands of young Pinus patula have been pruned to a height of eight feet. Before that time the trees are so dense that it is practically impossible even to walk among them. For some time the idea was prevalent that, owing to the density of these stands of trees, conditions in such compartments prevent outbreaks. That this is wrong, was proved at Jessievale in compartment C26, where one section was purposely left unpruned and yet, all the trees in the entire area, including those that had been left unpruned were defoliated the following year when they reached the age of eight years.

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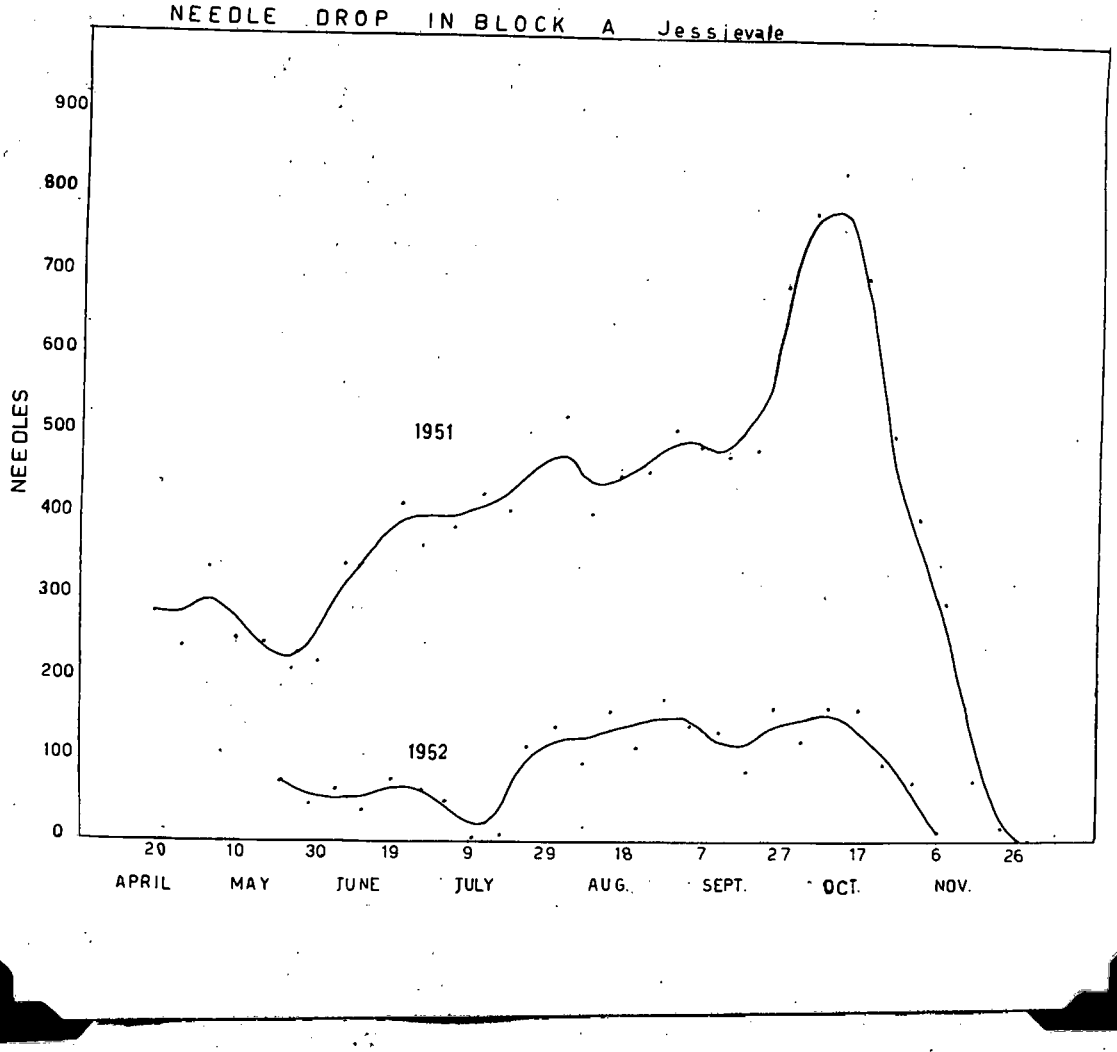

Fig. 72.

Severed needle drop in Block A.

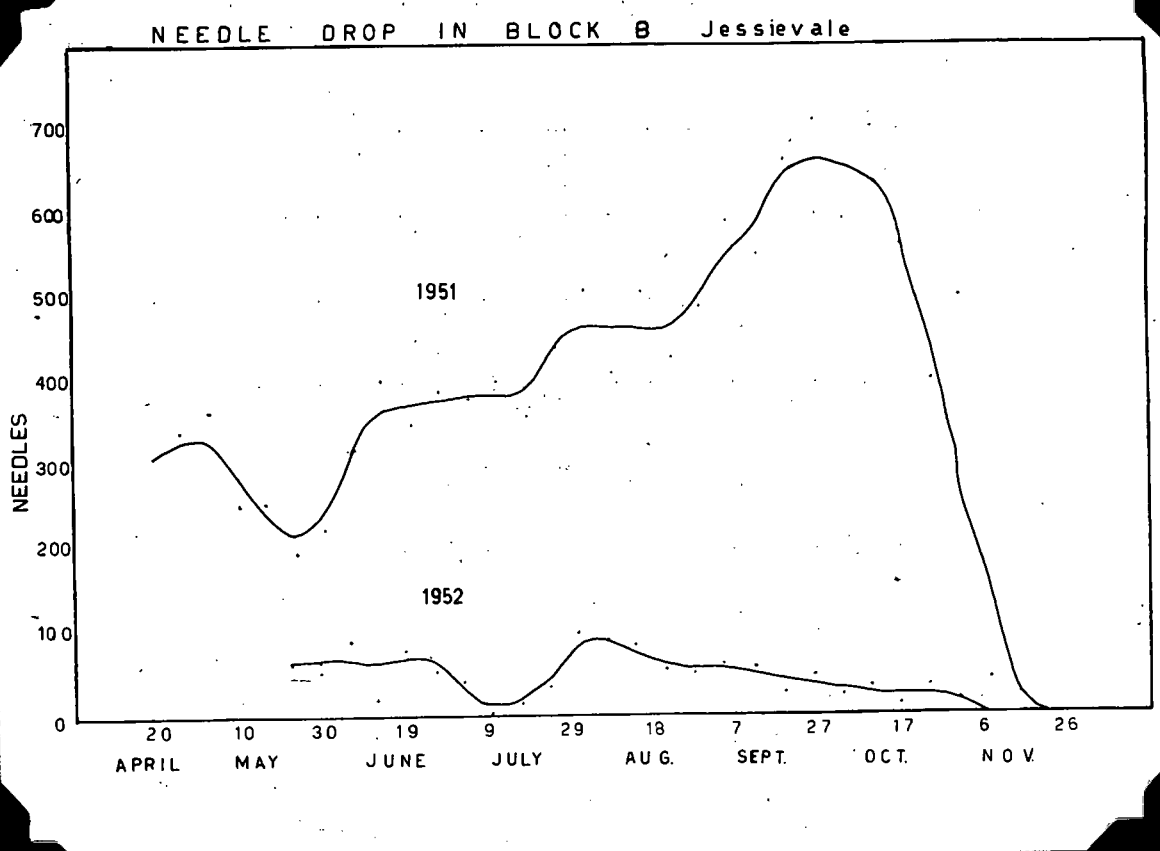

Fig. 73.

Severed needle drop in Block B.

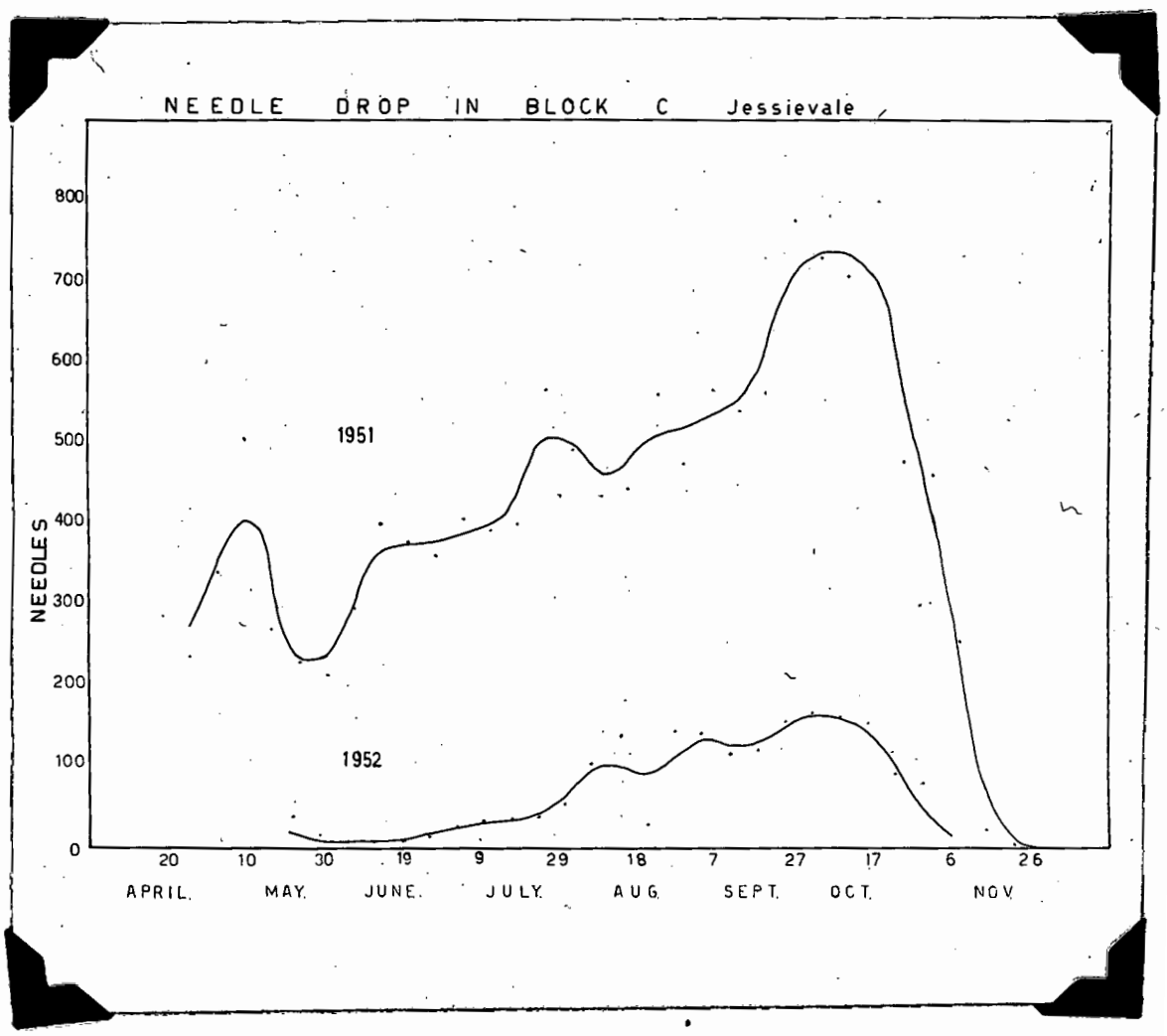

Fig. 74.

Severed needle drop in Block C.

In the older trees a shorter time than 8 - 10 years is required for the building up of the next cycle. After the disease has decreased population density, a relatively high population remains to serve as a nucleus from which the next cycle will develop. When the age of the trees exceeds 14 years, very little visible damage is done, despite the fact that the population of the insect will again increase to the same density as that which causes complete defoliation of younger trees. This fact was confirmed by severed needle counts in different age groups of Pinus patula trees.

In order to carry out such an experiment, it had first of all to be established in which areas outbreaks could be expected. This was done by ascertaining in which compartment a high moth population was present during December and January in the various areas. The areas selected for observation were those where moth density was highest.

Of three observation sites selected, the first consisted of 9 year old trees standing 300 stems per acre, the second 14 year old trees with 200 stems per acre, while the third consisted of a stand of trees 25 years old, standing 130 stems per acre.

In each of the areas daily counts were taken for 25 weeks of the number of needles severed by the larvae on 12 sq.ft. of ground surface. This was done by placing on the ground in each area at three fixed separate sites; three boxes each 2 feet square and 9 inches deep, and collecting from them and counting each morning all the needles that had been severed and fallen. By comparing the number of needles eaten in the various areas, an estimation could be made of the relative population densities infesting the three areas.

From/.....

Date. Week ending.	Severed Needles Dropped.		
	Block A.	Block B.	Block C.
18. 4.51	282	312	288
25. 4.51	253	343	239
2. 5.51	342	368	342
9. 5.51	257	256	507
16. 5.51	249	258	271
23. 5.51	213	198	230
30. 5.51	221	226	215
6. 6.51	349	330	298
13. 6.51	341	404	401
20. 6.51	423	350	378
27. 6.51	406	390	361
4. 7.51	393	383	408
11. 7.51	433	402	395
18. 7.51	414	360	401
25. 7.51	461	448	568
1. 8.51	530	511	492
8. 8.51	409	411	437
15. 8.51	457	510	445
22. 8.51	462	431	563
29. 8.51	519	492	473
5. 9.51	497	591	559
12. 9.51	483	553	543
19. 9.51	490	661	564
26. 9.51	697	711	779
3.10.51	789	591	730
10.10.51	840	704	707
17.10.51	703	561	800
24.10.51	468	404	480
31.10.51	403	502	463
7.11.51	298	4	254
14.11.51	78	27	21
21.11.51	24	0	6
28.11.51	0	0	0
Total	13,184	12,731	13,618

Table 16.

Total number of severed needles dropped per square foot weekly in infested areas in Block A, B and C in the Jessievale Plantation during 1951.

Date. Week ending	Severed Needles dropped.		
	Block A.	Block B.	Block C.
23. 5.52	71	65	38
30. 5.52	46	53	6
6. 6.52	63	91	8
13. 6.52	38	20	9
20. 6.52	77	77	6
27.6. 52	68	55	13
4. 7.52	49	41	27
11. 7.52	2	1	31
18. 7.52	8	13	30
25. 7.52	117	36	39
1. 8.52	143	100	54
8. 8.52	98	90	102
15. 8.52	167	84	138
22. 8.52	119	54	28
29. 8.52	175	51	144
5. 9.52	144	61	141
12. 9.52	135	58	118
19. 9.52	87	28	121
26.9. 52	157	49	156
2.10.52	123	24	168
9.10.52	156	34	162
16.10.52	154	12	156
23.10.52	97	36	91
30.10.52	75	17	80
6.11.52	12	0	13
	2,381	1,150	1,879

Table 17.

Total number of needles severed per square foot weekly in the same area as in Table I during 1952.

Year.	Block A.	Block B.	Block C.
1951	13,184	12,731	13,618
1952	2,381	1,150	1,879

Table 18.

Total number of needles severed per sq.ft. in the infested areas during 1951, and in 1952 when the population was ba to a basal minimum level.

From the graphs in fig. 71, 73 and 74 which were prepared using the data compiled in tables 16 and 17, it can be observed that the population in the three areas must have been of practically equal density despite the fact that there was not the same degree of visible damage. In the young trees the insect population had brought about total defoliation; in the 14 year old trees there were visible signs that the foliage of the trees was less dense than normal; in the 25 year old trees there was no visible sign of damage. According to Graham (1952) the loss of leaves in a large tree must exceed 50% before the tree appears to be abnormal.

It is thus clear that the cycles of E. terminalis infestation continue in the older trees, even if there are no visible signs of defoliation. It is certain that this defoliation, although not apparent, will exert an influence on the growth of the tree, although perhaps not to the same extent as in younger trees that have been totally defoliated.

An important question that still goes unanswered in the Jessievale area, is why the generations of E. terminalis are not mixed as in the other areas. It is most unlikely that there have been no migrations from outside into this plantation which could have given rise to generations differing from those already existing in it. It would therefore appear that there are certain climatic factors which prevent the development of mixed generations in this area, that are not to be found in the other areas.

The various climatic conditions prevailing at Jessievale and other areas affected by E. terminalis was investigated, but no light was thrown on the problem.

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For example, the climate of Harrismith differs from that prevailing at Jessievale in that the winters and summers are colder, and in addition it is slightly drier. Conversely we have the Sabie area which differs from Jessievale in that it has a warmer winter and summer and a higher rainfall.

Judging from tests performed on pupae, larvae and eggs to determine which instars and stages are most sensitive and subject to climatic variations, it would appear that there is not a single month at Jessievale which is climatically unsuited to the survival of any stage of this insect.

The only other possibility is that here may be micro-climatic conditions peculiar to the Jessievale area which are not clearly registered by our standard meteorological instruments. Extensive investigations which will take years to complete, using much more sensitive instruments are at present being undertaken by the writer in order to collect data about the micro-climate. It will not be possible to throw light on this aspect of the problem until such time as this investigation has been completed.

It is of interest to note that the plantations at Spitzkop and Driekop were the first in which a state of equilibrium has been restored after the occurrence of the initial outbreaks. These two plantations adjoin dense indigenous forests, while the other plantations are fairly distant from them.

The equilibrium prevailing in the indigenous forests could therefore extend much more readily into the Spitzkop and Driekop plantations, while it would have taken a much longer period in the case of other plantations. The policy of the Dept. of Forestry is to preserve any indigenous forests, no matter how small in extent, present

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in plantation areas, is thus one which is most commendable (Fig. 75). It is unfortunate that most of the commercial tree-planting organisations have not adopted this extremely sound policy.

Fig. 75.

Plantations and indigenous bush intermingled.

3. THE PARASITES AND THEIR CONTROL OF E. TERMINALIS.

(a) Insects parasitising E. terminalis.

When the study of E. terminalis was embarked upon by the writer in 1949, it was a known fact that there were four indigenous insect parasites, an egg parasite, one on the larvae and two pupal parasites, (Tooke 1938) but what role they fulfilled in the control of the pest was not known. In order to ascertain which parasites occur in the plantations and also the part played by them in the control of E. terminalis, large numbers of the different stages of the insect were collected every year in the Jessievale plantation in those areas where outbreaks occurred.

The parasites are classified according to the stages of E. terminalis attacked by them.

(i) Egg Parasites.

The most important egg parasite, Telenomus

phegeus/.....

phegeus, Nixon, (Fig 93) was discovered by Tooke (1938) in the Sabie area, where it was found to have parasitised 88% of the eggs of E. terminalis. The only other egg parasite was collected by the writer from the Jessievale plantation. This parasite, the identity of which has not been established, occurred in only one egg mass of E. terminalis in 1950, and has not subsequently been taken again. It is possible that this is a parasite which normally occurs only in the natural habitat and was unable to adapt itself to conditions prevailing in the plantations.

The technique for determining the percentage of egg parasitism was as follows:

During the period in which eggs could be obtained at Jessievale, regular weekly samples were collected. Each mass was then kept separate in a sealed test tube. All parasites that emerged, as well as the number of eggs in each test tube were counted. The percentage of parasitism was then calculated.

The highest percentage egg parasitism by Telenomus phegeus in the Jessievale plantation occurred during 1950 when 22% of the eggs were destroyed. In other years the percentage was much lower: in 1951 : 0.576%; in 1952 : 11.99%; in 1953 : 2.06% and in 1954 : 4.00%.

The main reason for the low percentage of egg parasitism lies in the fact that during the severe winters at Jessievale there are no eggs in which the parasites can breed. In spite of this there are sufficient of them left to parasitise the eggs once more in the next season. How they manage to survive during the period when no eggs of E. terminalis are available, is not at all

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clear, since no hibernation of the parasite in eggs has as yet been observed. Furthermore, no eggs of other species of Lepidoptera in which they could possibly breed are to be found in the plantation.

In tables 19 and 20 the data obtained during the years 1950 - 1954 concerning the percentage of egg parasitism are given, and in fig. 76 these are indicated graphically.

According to χ^2 there are no significant differences between maximum % parasitism of eggs during 1950 and 1952 (χ^2 = 3.226 D.F. 1) nor during the years 1953 and 1954 (χ^2 = 0.611 D.F. 1) but significant differences exist between the figures recorded for the years 1950 and 1954 (χ^2 = 12.461 D.F. 1) and also during 1952 and 1954 (χ^2 = 6.654 D.F. 1). The factors responsible for these significant differences in parasitism are not clear, but presumably they may be ascribed to variations in micro-climatic conditions prevailing in the areas where the parasites overwinter, as the percentage of parasites which survive the winter would have a profound influence on the number of eggs parasitised during the next season.

Year.	Maximum % eggs parasitised.
1950	22.0
1951	0.576
1952	11.99
1953	2.06
1954	4.00

Table 20.

Maximum percentage eggs parasitised at the Jessievale plantation during the years 1950-54.

(ii)/.....

Year.		Year.		Year.	
1950.		1951.		1952.	
Date Collected.	% Parasitism.	Date Collected.	% Parasitism.	Date Collected.	% Parasitism.
23. 1.50	0	29.1. 51	0	23. 1.52	0
5. 2.50	0	5. 2.51	0	30. 1.52	0
12. 2.50	7.84	12. 2.51	0	1. 2.52	1.45
19. 2.50	9.33	19. 2.51	0	8. 2.52	1.50
26. 2.50	13.33	5. 3.51	0	18. 2.52	3.21
6. 3.50	16.95	12. 3.51	0.27	27. 2.52	5.78
12. 3.50	15.60	19. 3.51	0.50	3. 3.52	9.91
19. 3.50	17.69	26.3.51	0.58	18. 3.52	10.12
27. 3.50	21.40			28. 3.52	11.59
2. 4.50	22.00				
No. of eggs used	20,372		16,449		20,098

1953.		1954.	
20. 1.53	0	15. 1.54	0
31. 1.53	0	21. 1.54	0
5. 2.53	0	30. 1.54	0
10. 2.53	1.36	8. 2.54	0
20. 2.53	1.31	17. 2.54	2.30
27. 2.53	2.00	25. 2.54	1.99
10. 3.53	2.06	27. 2.54	3.05
		11. 3.54	4.00
No. of eggs used	15,980		16,752

Table 19.

Egg parasitism at Jessievale.

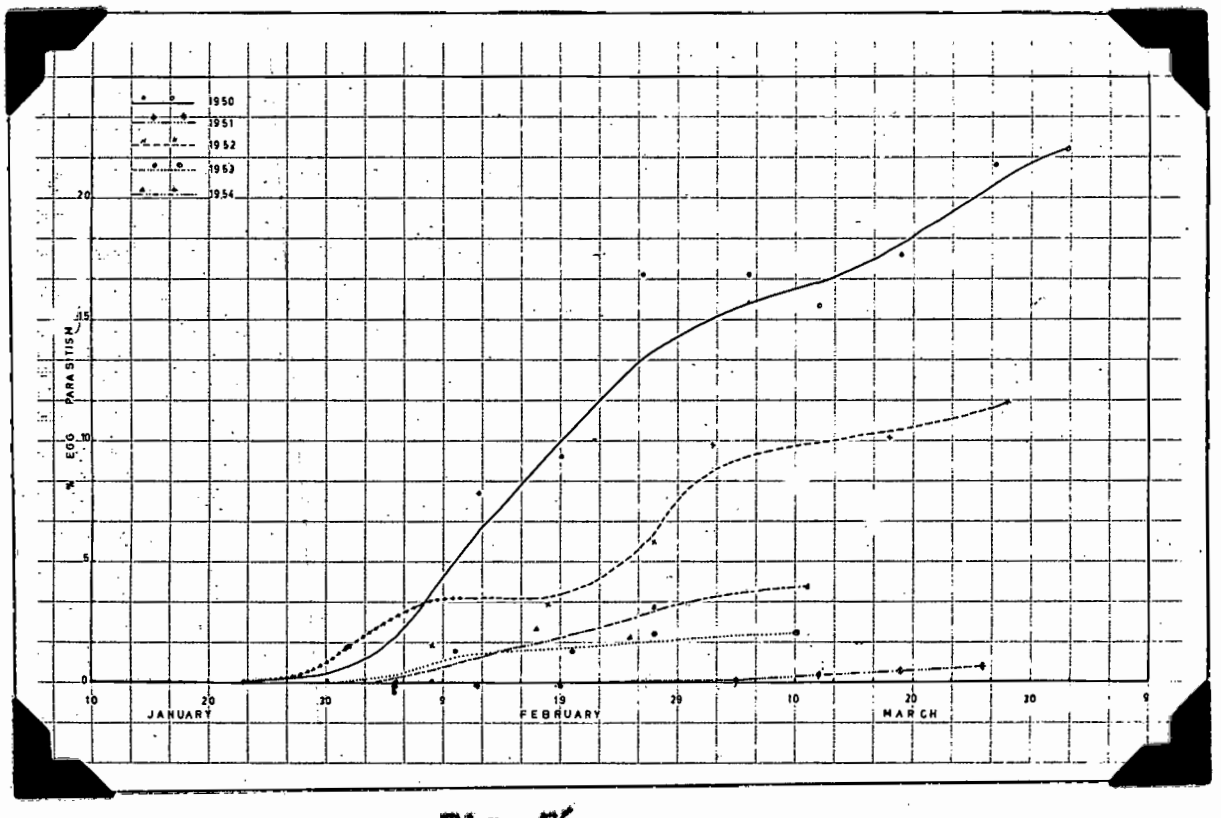

Fig. 76.

Egg parasitism at Jessievale during the years 1950 - 1954.

(ii) Larval Parasites.

The following four indigenous parasites of larvae of E. terminalis were found in the Jessievale plantation:

(i) Meteorus trilineatus, Metiorinae, Braconidae Hyman. (Fig. 100).

(ii) Apanteles euproctidis Ull. Braconidae. Hym. (Fig 77 & 78).

(iii) Tachina fallax Meig. Tachinidae Diptera (Fig. 112).

(iv) Pales blepharipus B.B. Tachinidae Diptera (Fig. 79).

Various techniques, of which dissection of larvae is the most common, are employed to determine the degree of larval parasitism. Although this technique does indicate the percentage of larvae which have been parasitised, it is not possible to establish the degree to which the individual parasitic species are exercising control unless the taxonomy of the various immature stages of all the parasites concerned is known. In order to solve this problem, the writer made use of the celluloid and organdie cages that have been described in Chapter V, in order to keep the host larvae alive until such time as the parasites emerged. This technique involves much work, especially when large numbers of larvae are used, but it seemed to be the only accurate method of determining which parasite species were present.

The four larval parasites recovered could be divided into two classes according to the instars of the host larvae that were attacked.

Meteorus trilineatus constitutes the first class and only attacks larvae from the second to the 5th instar. As will be shown later in the

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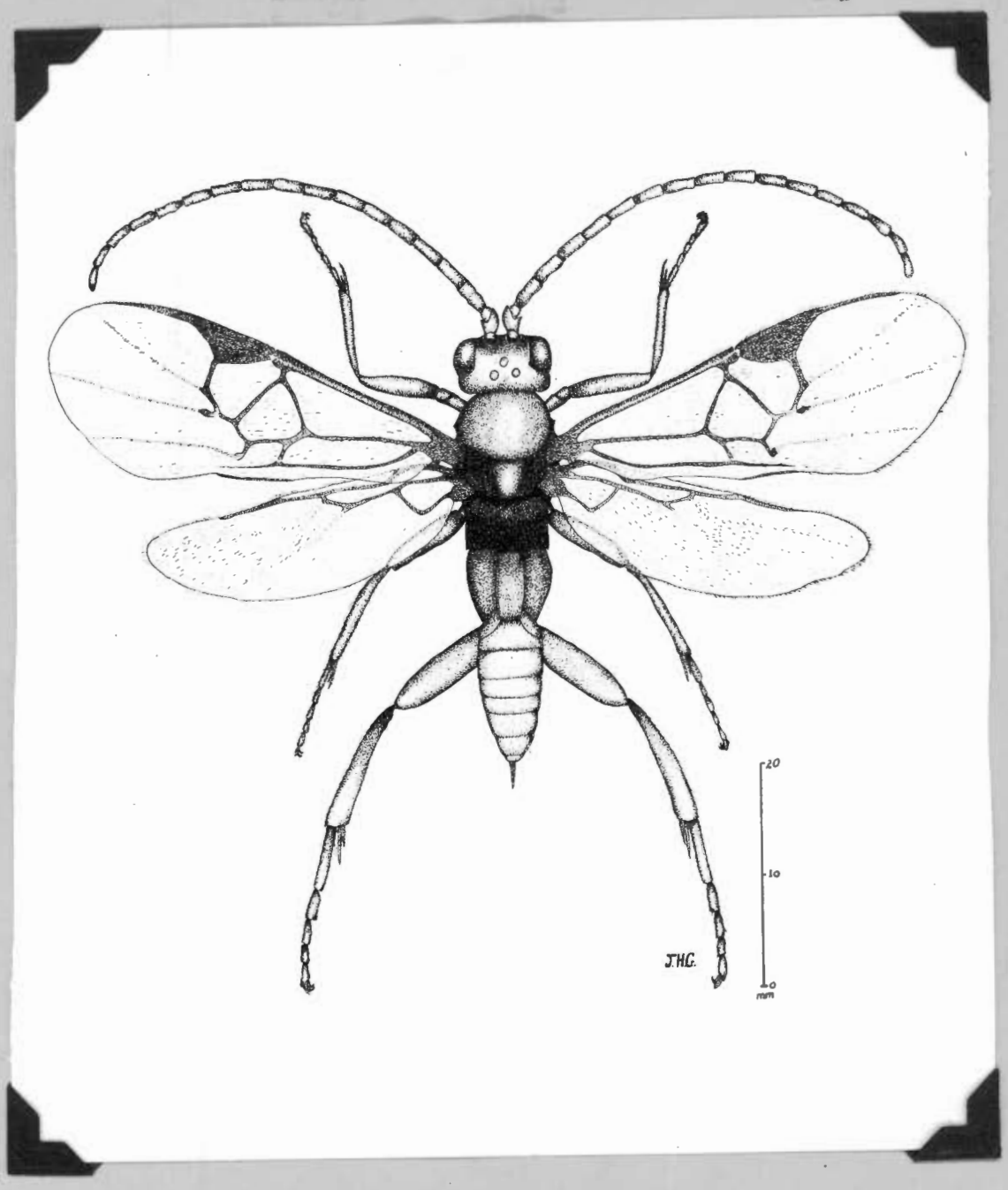

Fig. 77.

Apanteles euproctidis.

Fig. 78.

E. terminalis larvae covered with A. euproctidis cocoons.

biology of Meteorus trilineatus, they are unable to attack older larvae.

The second class is composed of three larval parasites, which parasitise chiefly the sixth instar and upwards.

Tachina fallax always prefers the older larvae if there is a choice between the last three stages, but does not attack those below the sixth instar. Pales blepharipus, which is also a Tachinid, will presumably do the same, but unfortunately this could not be determined in the laboratory as all the attempts to breed the parasite failed. The larvae of both parasites frequently pupate only after the infested E. terminalis larva has pupated.

Of the three parasites, Tachina fallax and Pales blepharipus are the most important and they occur in even numbers in parasitised larvae, whilst Apanteles euproctidis occurs very rarely. In the six years during which the writer has regularly kept larvae of E. terminalis under observation, a total of only 44 were found that had been parasitised by Apanteles euproctidis.

Out of every E. terminalis larva parasitised by Apanteles euproctidis from 17 - 34 parasite larvae emerged which as a rule spin their cocoons in two rows, one on each side of the host larva (Fig. 78). Only in one case was a larva of E. terminalis parasitised by A. euproctidis in the laboratory. Forty days after the eggs had been deposited in the E. terminalis larva, 23 larvae of the parasite emerged and spun their cocoons. Four days later all the adult parasites emerged from the cocoons within a period of 5 minutes.

In/.....

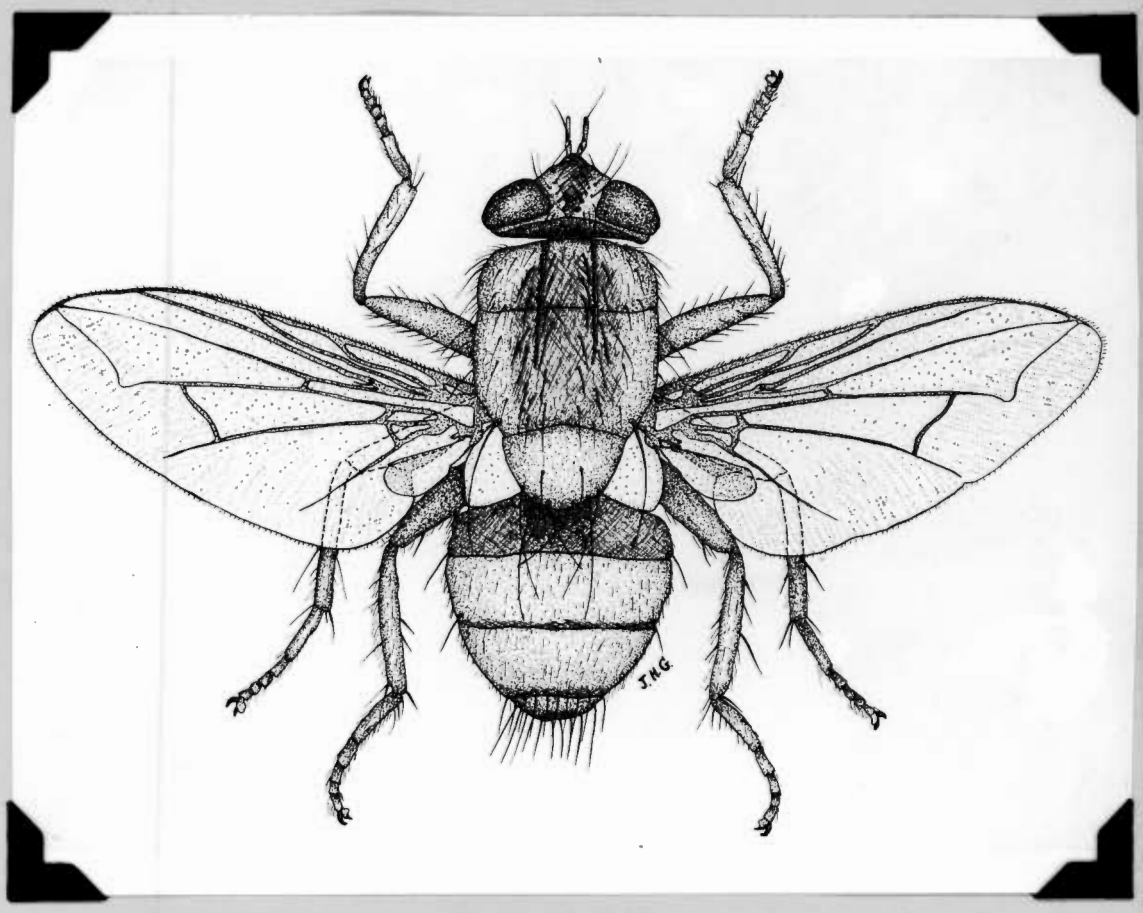

Fig. 79.

Pales blepharinus.

In compartment B.42 of the Jessievale plantation, which adjoins a ravine in which indigenous shrubs grow, literally thousands of dried, dead E. terminalis larvae covered with old cocoons resembling those of Apanteles suprocristalis, were found in 1949 on the stems of the Pinus patula trees. What was characteristic of the larvae was that all were orientated on the trunks with their heads pointed downwards, as if they had been descending the trees but had been too weak to do so. However, since then this parasite has never again been found in anything like large numbers, and there is no reason to believe that it is of any appreciable economic importance in controlling this pest at Jessievale.

It would appear that this parasite migrated into the plantation from the indigenous vegetation adjoining it but did not penetrate into it to any extent. It is possible that this is a case similar to that described by Morgan (1910) (Clausen 1940), namely that Apanteles congregatus is a general parasite on its host when the host attacks wild Solanaceae, but when the host attacks tobacco, the parasite seldom occurs.

According to Ullyett (1946), Apanteles flaviventris sp. nov. and Apanteles acraeae are parasites of E. terminalis. The cocoons of the former species are very frequently found on P. patula, in localities where E. terminalis does not occur. The writer has collected no evidence to support Ullyet's statement that those two species are parasitic on E. terminalis. Although both parasites do occur in areas where E. terminalis is found, neither species was taken from approximately

10,000/.....

YEAR					
1950		1951		1952	
Date Collected	% Parasitism	Date Collected	% Parasitism	Date Collected	% Parasitism
30. 5.50	0	25. 5.51	0	20. 5.52	0
8. 6.50	1.3	7. 6.51	0.7	30. 5.52	0
14. 6.50	0.9	12. 6.51	2.4	5. 6.52	0.91
22. 6.50	3.5	1. 7.51	4.0	11. 6.52	1.51
30. 6.50	1.8	26. 7.51	3.2	18. 6.52	3.70
8. 7.50	6.7	1. 8.51	0.5	25. 6.52	1.20
2. 8.50	3.2	16. 8.51	0.66	2. 7.52	0.71
19. 8.50	1.8	29. 8.51	1.25	7. 7.52	0.93
19. 9.50	0.72	4. 9.51	2.2	25. 7.52	0.99
14. 9.50	0.80	12. 9.51	3.7	3. 8.52	1.35
2.10.50	2.1	20. 9.51	4.7	7. 8.52	2.00
2.11.50	4.0	10.10.51	5.3	1. 9.52	2.78
8.11.50	5.3	17.10.51	5.90	25. 9.52	3.1
				1.10.52	3.98
				11.10.52	4.70
Total No. of Larvae used	1,648		1,931		1,145

1953		1954	
28. 5.53	0.15	24. 5.54	0.2
8. 6.53	0.72	9. 6.54	1.7
15. 6.53	1.91	25. 6.54	2.6
28. 6.53	2.50	9. 7.54	2.0
7. 7.53	0.83	17. 7.54	0.6
15. 7.53	0.81	29. 7.54	0.7
25. 7.53	1.30	11. 8.54	0.5
3. 8.53	1.28	23. 8.54	1.2
15. 8.53	1.80	8. 9.54	2.0
1. 9.53	2.22	24. 9.54	2.6
19. 9.53	3.15	4.10.54	3.6
1.10.53	4.05	22.10.54	4.0
10.10.53	4.60	29.10.54	5.0
Total No. of Larvae used	1,373		1,780

Table 21.

Larval parasitism at Jessievale Plantation.

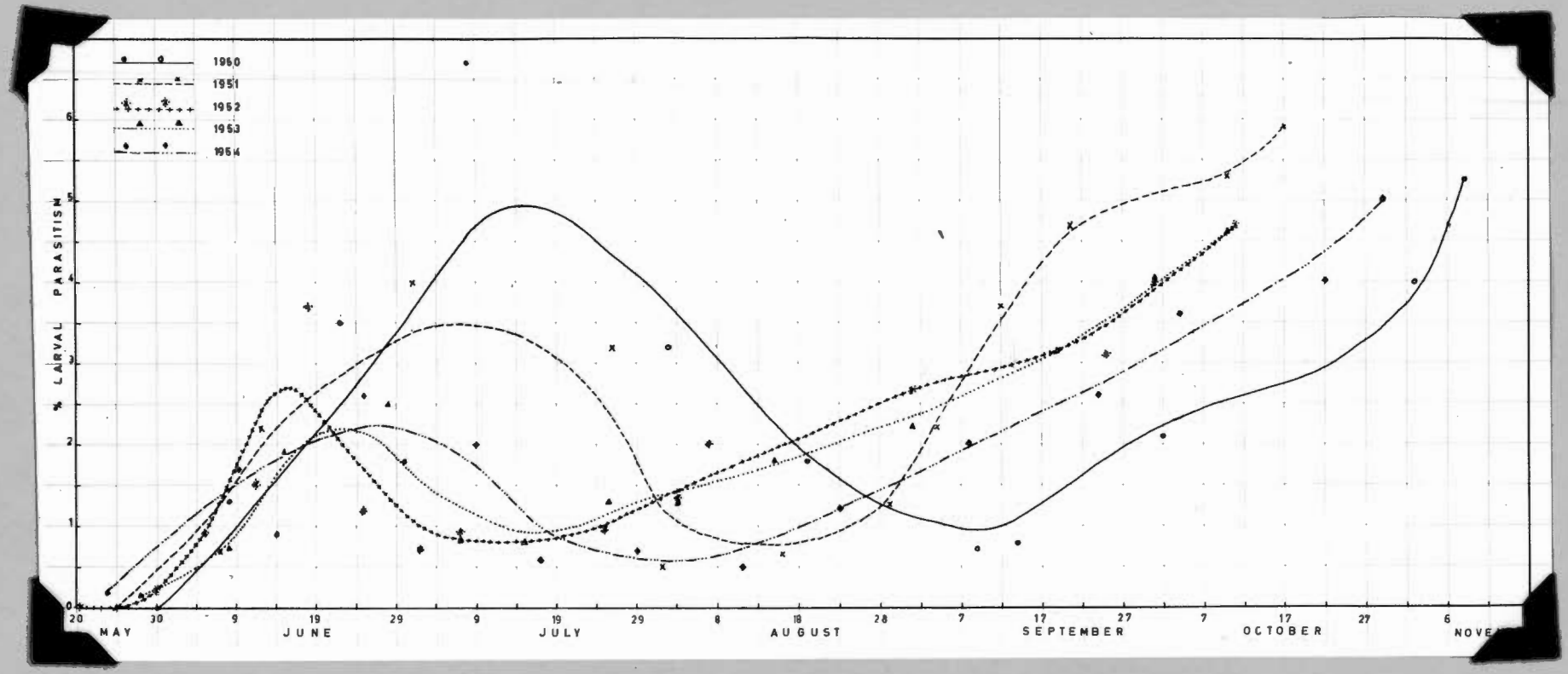

Fig. 80.

Larval parasitism during 1950-1954 at the Jessievale Plantation.

10,000 E. terminalia larvae examined by the writer during the course of 5 years.

Another parasite at present found in the Jessievale and Spitzkop plantations is Compsilura concinnata Meig. This parasite was imported from the U.S.A. in 1942 and released in these areas with the object of controlling E. terminalia . This step had been taken before it was realised how many indigenous parasites of E. terminalia already occurred in the plantations, and although the Compsilura concinnata was recovered from both areas by the writer during 1950, it has been established that the number of larvae attacked by the parasite in the Jessievale plantations is extremely small, and the liberation of this parasite has thus clearly not contributed much to the control of E. terminalia.

That Compsilura concinnata has succeeded in adapting itself very well to conditions in S.A. is proved by the fact that the writer has already found the parasite 20 miles west and 10 miles south of Jessievale in other plantations. In the Spitzkop area it has been found 10 miles north of the plantation in larvae of Nudaurelia cytherea, collected by the writer in an indigenous forest.

In view of the fact that the biology of the parasite has been worked out by several writers in Europe and the U.S.A., it was not considered necessary to undertake further biological studies on this insect.

In the graph in fig. 80 plotted from the data in table 21, two peaks may clearly be observed in the percentage of larvae attacked by parasites. The'

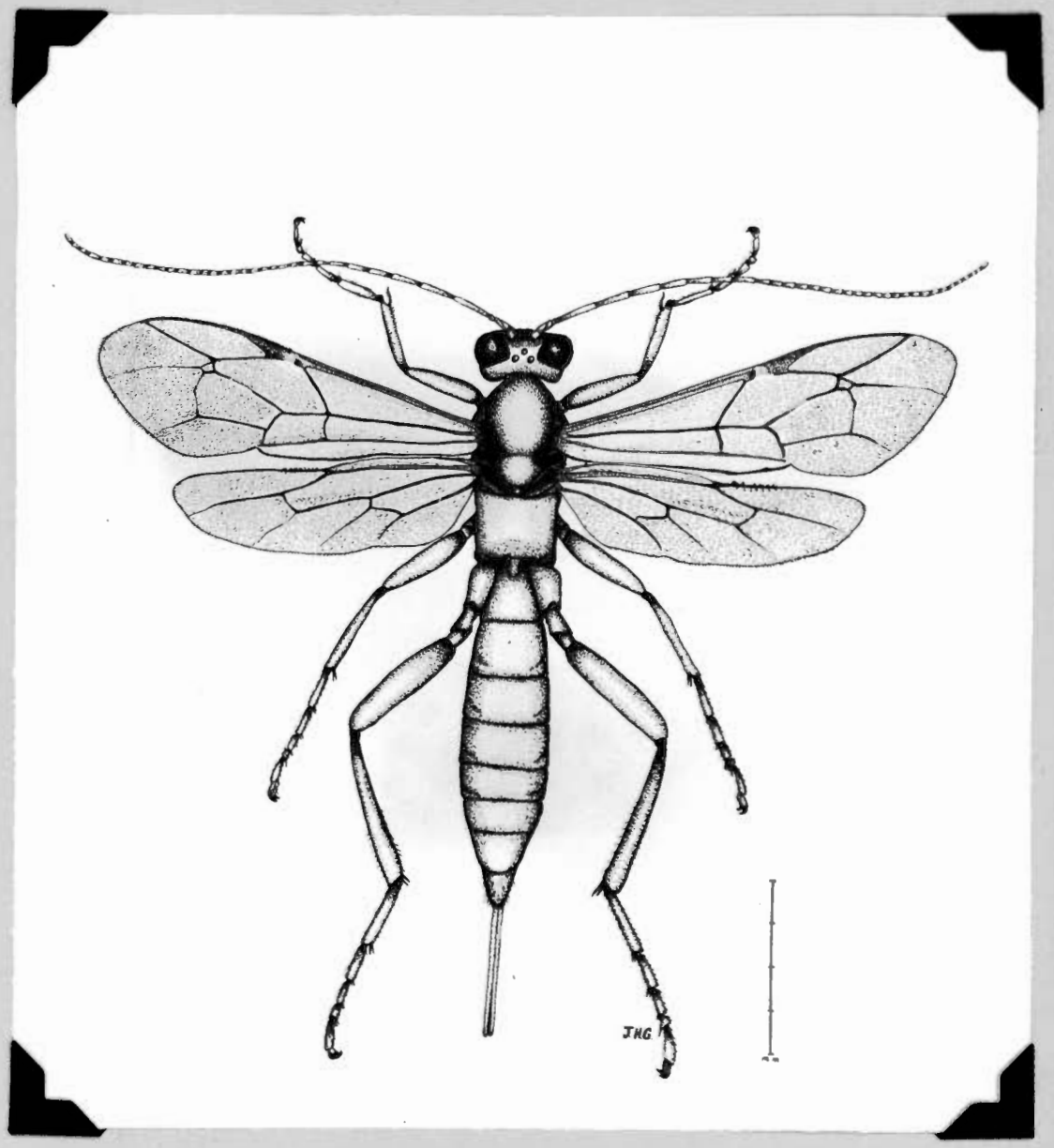

Fig. 81.

Pimpla crocata.

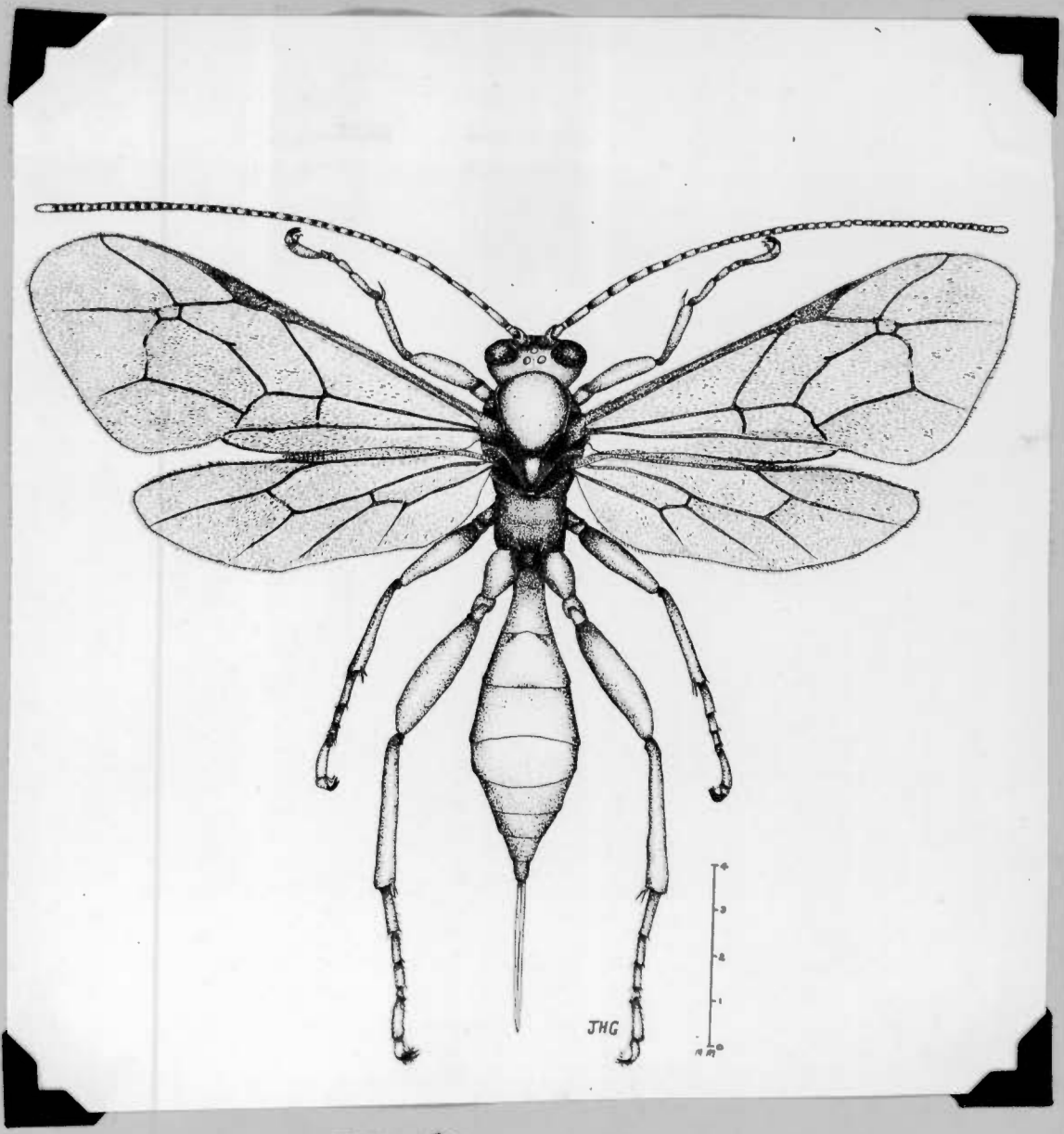

Fig. 82.

Netheronia melanocera.

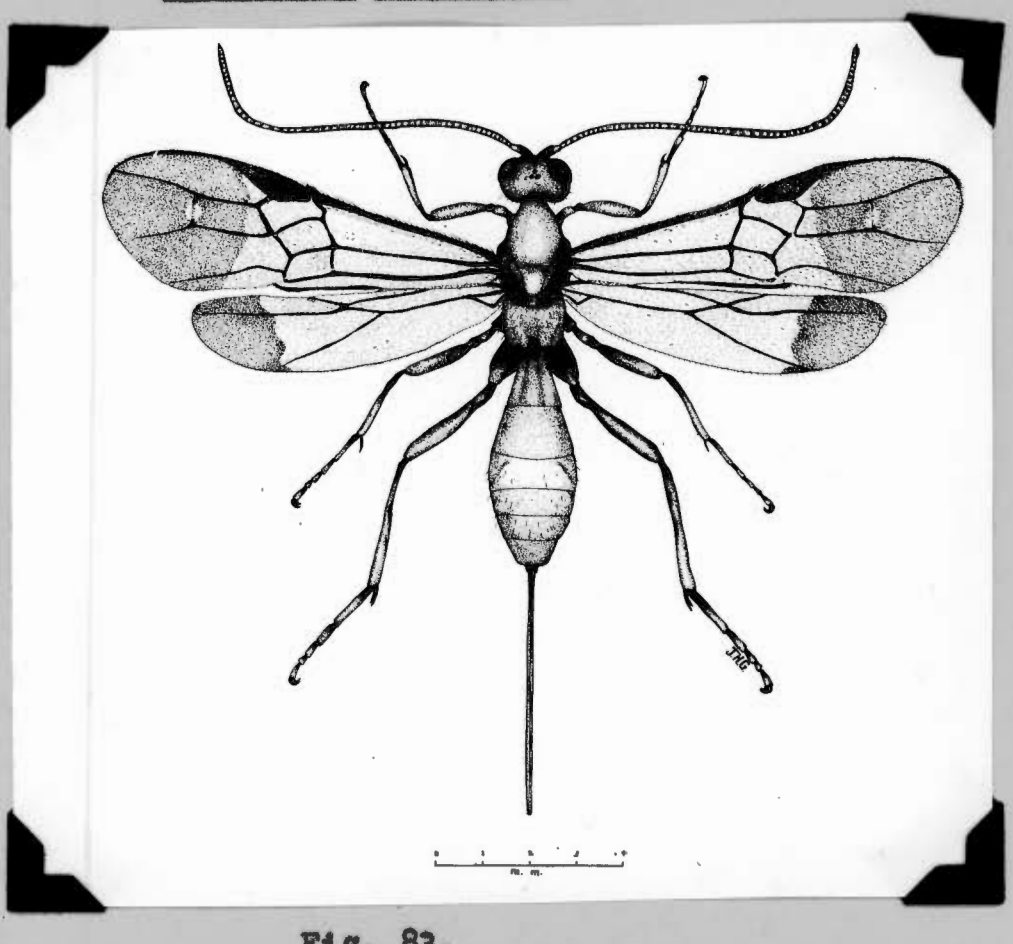

Fig. 83.

Inobracon lugens.

two peaks may be ascribed to the two groups in which the larval parasites occur. Meteorus trilineatus alone is responsible for the first peak, while the second peak is caused mainly by Tachina fallax and Pales blepharipus. The trough in the centre of the graph is due to the fact that the larvae become too big for Meteorus trilineatus to parasitise, and secondly, the winter months initially curb the activity of the second group of larval parasites. The climax of the second peak appears only after the larvae have pupated, and can only be determined by making pupal collections.

(iii) Pupal parasites.

In order to determine which parasites attack the pupae and the part played by them, pupae were collected when available every week for 5 years and kept under observation in the laboratory.

The pupae were maintained under conditions resembling as closely as possible those prevailingin the plantation, in cages covered with glass on one side to allow light to penetrate from one side only. As soon as the parasites and moths appear, they are attracted to the light and settle on the glass lid where they are caught.

The following parasites were obtained in this manner.

(i) Pimpla bicolor Bouche Ichneumonidae Hymenop. (Fig. 123)

(ii) P. crocata Tosq. Ichneumonidae Hymenop. (Fig. 81)

(iii) Nathoronia melanocara Higr. Ichneumonidae Hymenop. (Fig. 82)

(iv) Iphbracon Lugens Br. Baconidae Hymenop. (Fig. 83)

Three parasites were also obtained, Ac. X.82, Ac.X.84 and Ac.X.108 (Fig 84). Of these three, only Ac. X.84 was identified as a Pimpla sp., while the identity of the other two has not been determined.

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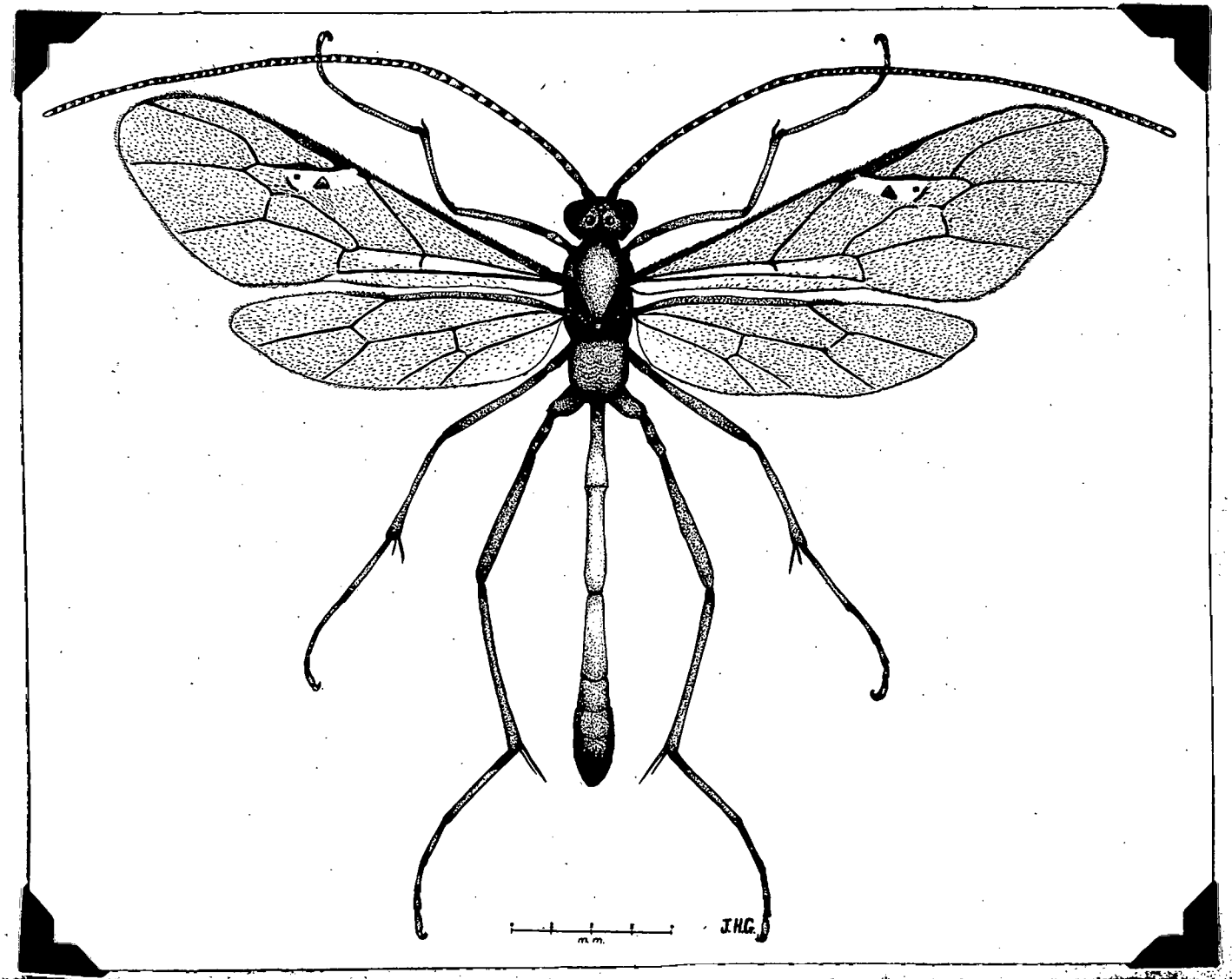

Fig. 84.

Ac. X. 108.

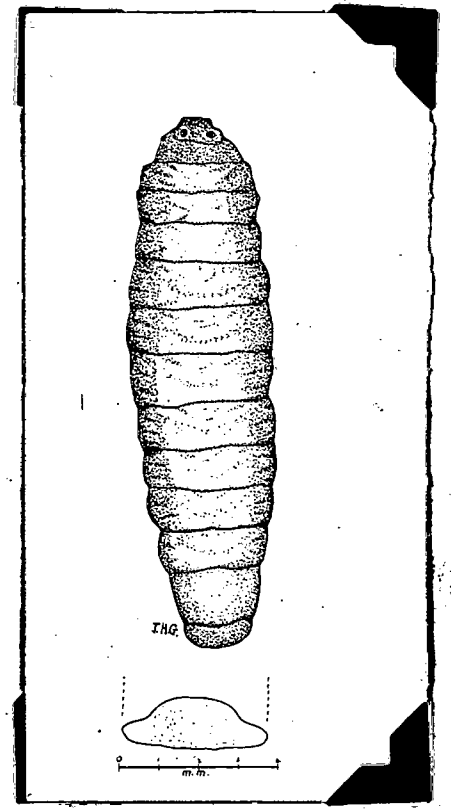

Fig. 85.

Full-grown larva of Ac. X. 108.

YEAR					
1950-1		1951-2		1952-3	
Date Collected	% Parasitism	Date Collected	% Parasitism	Date Collected	% Parasitism
23.11.50	1.5	30.10.51	2.1	20.11.52	4.75
8.12.50	0.5	6.11.51	7.7	24.11.52	4.5
15.12.50	1.7	13.11.51	10.0	29.11.52	7.3
22.12.50	2.8	22.11.51	12.7	1.12.52	8.0
3. 1.51	3.5	29.11.51	11.8	5.12.52	7.9
11. 1.51	6.0	12.12.51	13.5	10.12.52	8.5
19. 1.51	7.2	21.12.51	14.1	13.12.52	8.5
26. 1.51	6.4	3. 1.52	14.3	21.12.52	9.0
4. 2.51	9.6			26.12.52	11.3
8. 2.51	8.3			29.12.52	16.1
15. 2.51	14.8			5. 1.53	17.9
				10. 1.53	18.0
No. of pupae used	8,144		6,728		11,021

1953-4		1954-5	
17.11.53	0.3	15.10.54	2.7
24.11.53	1.6	18.10.54	2.3
1.12.53	0.8	20.10.54	5.3
9.12.53	2.2	6.11.54	6.8
19.12.53	2.2	10.11.54	6.7
30.12.53	3.2	23.11.54	6.6
7. 1.54	3.6	29.11.54	8.65
14. 1.54	6.1	9.12.54	8.7
21. 1.54	10.5	15.12.54	8.4
2. 2.54	11.7	21.12.54	9.8
10. 2.54	15.3	23.12.54	10.2
		9. 1.55	12.7
		13. 1.55	12.7
		2. 2.55	14.7
No. of pupae used	6,759		12,223

Table 22.

Pupal parasitism at Jessievale.

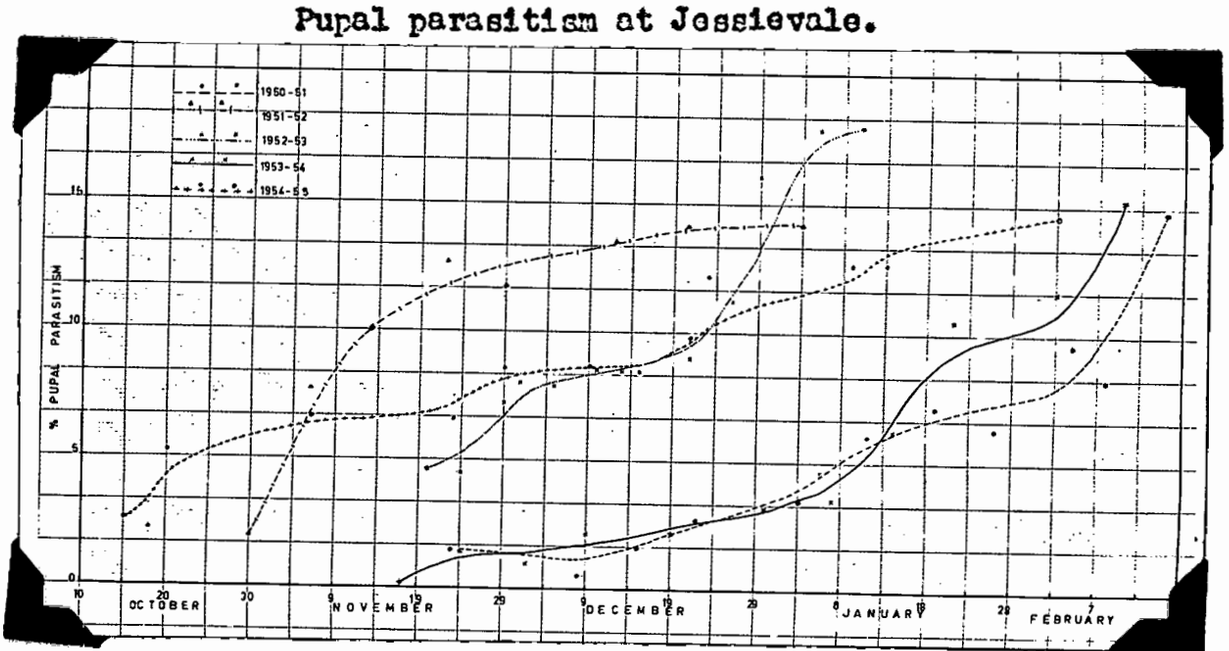

Fig. 86.

Pupal parasitism during the years 1950-55 at Jessievale.

Of all the pupal parasites it was only possible to infest pupae and rear to maturity the three Pimpla spp., Nethoronia melanocera Higr. and Ac.X.82 in the laboratory. Ipobracon lugens Br. and Ac.X.108 were obtained from pupae collected in the plantation but all attempts to infest pupae with these parasites have been unsuccessful. It may even be that these two species, like the Tachinids mentioned above, are larval and not pupal parasites. However, in the laboratory they did not oviposit in larvae exposed to them.

The only parasite of the above mentioned seven that has any value in the control of E. terminalis pupae in Jessievale is Pimpla bicolor Bouche. The others occur in such small numbers that in most years they cannot even be traced in pupal collections. For this reason the graphs in Fig. 86 that were plotted from the data compiled in table 22 reflect only the percentage parasitism by Pimpla bicolor. The biology of P. bicolor has been worked out and appears later in this thesis.

There is no significant difference between the lowest % of pupal parasitism, which was recorded during 1951, and the highest percentage which occurred during 1952 (X^2 = 0.4238 D.F.1), which once more indicates the stability of effect of this group of parasites in controlling E. terminalis.

The highest percentage of parasitism that occurred in the pupa was 18.0% in 1952/53, while the lowest was 14.3% in 1951/52. The pupal parasites, particularly P. bicolor, are therefore much more stable than the egg or larval parasites, where the variation in the different years was considerably higher.

(iv) Combined influence of all the parasites on the E. terminalis population.

The maximum number of E. terminalis of all stages destroyed by parasites between 1950 and 1954 occurred in

1950 when it reached only 41.29%.

In table 23 the percentage parasitism that occurred in the Jessievale plantation from 1950-54 is reflected.

% destroyed by Parasites.					
Year	Eggs	Young larvae	Older larvae	Pupae	Total population parasitised
1950	22.00	6.7	5.3	14.8	41.29
1951	0.58	4.0	5.9	14.3	23.03
1952	11.99	3.7	4.7	18.0	33.77
1953	2.06	2.5	4.6	15.3	22.84
1954	4.00	2.6	5.0	14.7	24.23

5/145.16 (29.03)

Table 23.

Average of population destroyed in 5 years : 29.03%

According to de Bach and Smith[1947] a "parasite, to regulate the population density of its host, that is, if it is to hold the population density within limits, avoiding either excessive increase or extermination, it must have the ability to destroy a greater fraction of the host population when the density of the latter is higher than when it is low".

The average number of the population of E. terminalia destroyed by parasitism over a period of 5 years in the Jessievale plantation, in those areas only where the population was at its peak level amounted to a mere 41.29%. For parasites to play an appreciable roll in controlling build-up of the host insect, it is generally accepted that parasitism should at least exceed 90%. It is thus clear that the parasites of E. terminalia do not play a major part in suppressing E. terminalia populations in the Jessievale plantation.

(b) Parasitic fungi in the control of E. terminalia.

The factors playing the most important part in the

control/...

control of E. terminalis in the Jessievale plantation, are fungal parasites amongst the larvae and pupae. The most important fungal parasite amongst the larvae, is the grey or locust fungus, Empusa grylli Fress., and amongst the pupae, the fungus Isaria farinosa (Dicks.) Fr. Polihydra and bacterial diseases also occur amongst the larvae, but they are of minor importance when compared with Empusa grylli.

(1) Fungal parasites of the larvae.

The grey or locust fungus (Fig 87 and 88) which is the most important factor in the control of E. terminalis larvae was found on locusts in South Africa as early as 1896. Various workers, such as Skaife (1925), McMartin (1935) and Schaefer (1936) investigated the occurrence of the disease on the red locust, Nomadacris septemfasciata.

Their general conclusions were that the fungus could not be bred and that it was not at all clear how the disease was transferred from one insect to another.

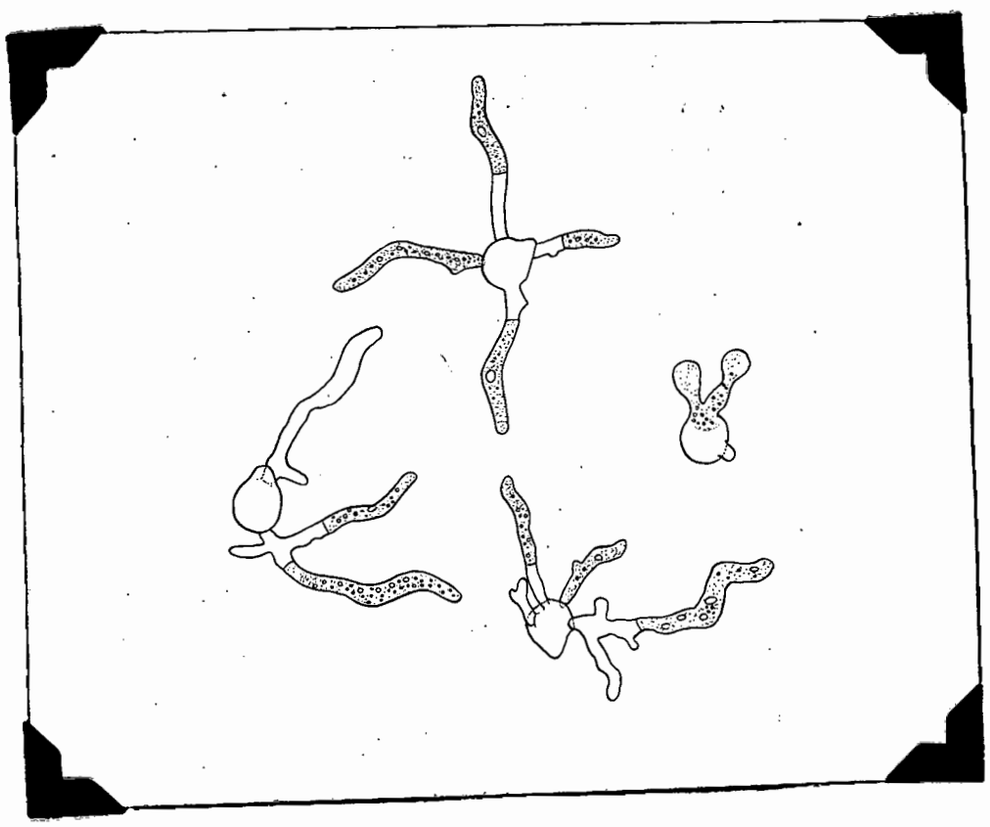

Fig. 88.

Germinating conidia of E. grylli.
(After E. Schaefer).

A general/.....

Fig. 87.

Larvae attacked by E. grylli.

Fig. 89.

Plots where larval counts were carried out.

Fig. 90.

Plot organised for larvae to pupate.

A general opinion was that an outbreak of Empusa grylli had to be preceded by copious rains, as in most cases the disease was noticed on locusts only after such rains had fallen. McMartin (1935), however, found that an outbreak of the disease amongst insects occurred before heavy rains, which can be confirmed by the observations in the Jessievale plantation.

After a study of the occurrence of this parasite on E. terminalis, it was concluded that it was chiefly a density mortality factor, as the larvae become infected by the fungus at the stage when they had reached peak density of population.

The fact that the fungus occurs amongst locusts after heavy rains, is probably related to the fact that large numbers of locusts hatch after such rains, with the result that their population density is high enough to cause such an epidemic.

In the Jessievale area it was frequently seen that where the population of E. terminalis in a compartment was high enough to cause defoliation, they perished in large numbers from Empusa grylli infection, while in adjoining compartments where the population was at a lower level, it was a rarity to discover a larva that had succumbed to the fungus.

The critical density to be reached by the E. terminalis population before this fungal parasite operates at peak efficacy in the Jessievale plantation is equal to the population density required to bring about complete defoliation of compartments of 8 - 10 year old P. patula trees. As shown in Fig. 72, 73 and 74, the population that defoliate young trees is unable to cause visible damage to larger and older trees, and the reason why the larger trees are not defoliated is because the fungus wipes out the population of E. terminalis before the pest is able to reach the

required density to do so. This density varies between 30 and 40 larvae in the crown per sq. foot of soil surface below a tree, since this is the number of larvae per square foot needed to defoliate an 8 - 10 year old tree.

In order to ascertain the exact number of larvae that succumb to this parasite, the following experiment was carried out in the Jessievale plantation during 1951.

In an area where an outbreak of E. terminalis threatened, four plots of 40 x 40 feet on the forest floor were completely cleared of leaves and other debris. The ground was levelled and firmed down where loose. (Fig. 89).

The plot was then completely fenced in by stocking round it logs of 9 inches diameter in three tiers. The outside of this fence was banked up to the top with soil. There was no point in the fence through which larvae could escape. Larvae that had fallen from a tree by accident into the enclosure climbed up the 27 inch fence for only a small distance, then returned to the soil surface.

The four plots contained an average of ten trees each, and their crowns, and the crowns of the trees outside the plot touched to form a closed canopy. Each morning all the larvae that had died and dropped to the ground during the past 24 hours were collected and counted.

When the time arrived for the larvae to pupate, the plots were organised in such a way that they were able to pupate within the area and could easily be retrieved (Fig. 90). The rough bark around the basis of the tree trunks in the enclosure was removed to prevent the larvae from pupating unseen in the crevices in the bark. Round the trunks and along the inside of the fence a strip of needles 6 inches wide and 3 inches deep was stacked on the ground. Distributed over the plot small round billets of wood, 4 inches thick and 12 inches long were stacked in

groups/...

groups of three, the bottom two being placed parallel to and in contact with each other, the third one being placed on top of the basal billets. The shelter served as an excellent place for pupation.

The needles and billets were examined once each week, the pupae present were collected and counted.

In the four plots covering 64,000 square feet, 17,495 larvae pupated and 187,000 (91.48%) larvae had died of diseases consisting mainly of Empusa grylli. The average density in this area was therefore 32.08 larvae per sq. ft. of ground surface.

The pupae collected in these plots were not used to determine the percentage of parasitism or to determine the percentage of pupae killed by Isaria farinosa, in view of the fact that they had not pupated in their normal sites.

(ii) Fungal parasites of the pupa.

The only fungal parasite occurring amongst the pupae of E. terminalis in the Jessievale plantation is an entomophagous fungus, Isaria farinosa (Fig. 91 and 92). In America (Hewitt 1912) and the British Isles (Petch 1948) this fungus is well known as a parasite of the pupae of insects. The infected pupae of E. terminalis collected by the writer in 1950 in the Jessievale plantation provides the first known record of this fungus from South Africa according to the division of Botany of the Dept. of Agriculture.

Fig 91.

Euproctis terminalis attacked by Isaria farinosa.

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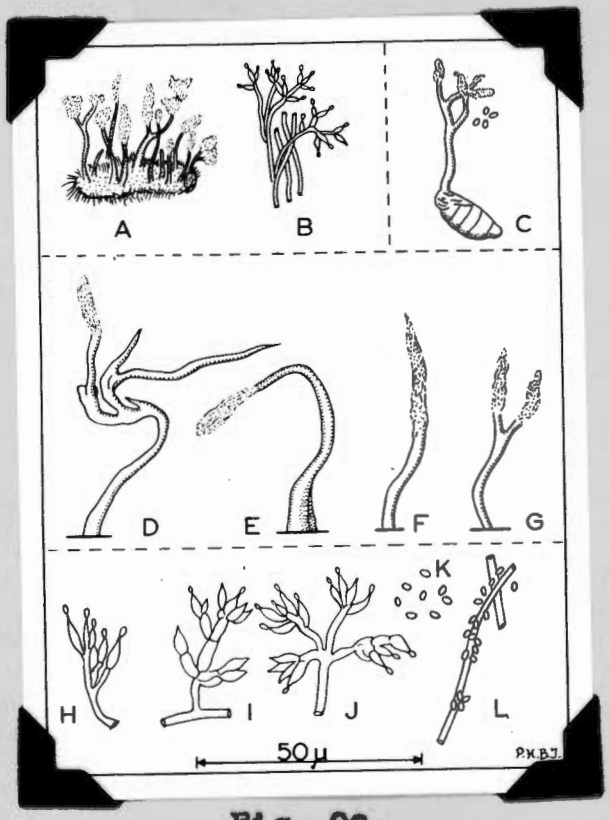

Fig. 92.

Isaria Farinosa Fr.

A. Habit of the fungus on dead caterpillar of Bombyx rubi, after Tulasne.

B. Fertile hyphae ending in conidiophores and conidia, after Tulasne.

C. Habit, after Ferraris.

D, E, F, G.
Habit of the fungus on Euproctis terminalis at Jessievale, magnified.

H, I, J.
Fertile hyphae with conidiophores and conidia from Jessievale specimens.

K. Conidia from Jessievale specimens.

L. Hyphae with detached conidia adhering to them, from Jessievale specimens.

This fungus developes in the pupae lying under the needle mat and pushes its fertile hyphae from the pupa to the surface of the ground where they become white due to the large number of conidia on them. The conidia scatter on the forest floor as a result of the action of wind and rain, and the E. terminalis larvae moving about in search of a suitable place to pupate, become infected with the conidia, and the fungus then developes in them.

In fig. 92, which Dr. P.H.B. Talbot was kind enough to prepare, the different stages in the development of the

fungus/.....

fungus are pictured.

Adult E. terminalis larvae on the point of pupating were allowed to crawl over infected pupae covered with white conidia, in the laboratory, and in six of the ten larvae, Isaria farinosa developed in the pupae, while the other four appeared normal and emerged as moths. It appears, therefore, that the fungus, unlike Empusa grylli, is not difficult to transmit to healthy insects.

Judging by the periods of outbreak of this fungus in pupae, it appears that conditions of high moisture are required for the disease to develop. Table 24 shows that during the years 1951/53 a considerable number of pupae were killed by Isaria farinosa, while in the years 1949-50 and 1954 there were so few that the figures were in every case only a fraction of one percent. In the years when the outbreaks occurred, the rainfall was above normal in the three months during which the pupae were present in the Jessievale plantation. In the other three years the rainfall was below normal. The highest percentage of pupae was destroyed by this disease during 1951.

		Rainfall in m.m.			
Year	% pupae dead	October	November	December	Total.
1949	-	91.4	92.2	174.8	358.4
1950	-	66.3	82	215.7	364.2
1951	74	125.4	41.7	229.0	396.1
1952	66	46.6	225.5	175.1	447.2
1953	62	64.8	305.0	75.1	445.1
1954	-	100.9	178.4	53.7	330.0

Table 24.

Isaria farinosa outbreaks and rainfall during pupal period at Jessievale.

Combined/...

Combined influence of the environmental resistance factors on the E. terminalis population.

Up to the present the attention has been drawn, and as far as possible in percentage form, to the proportion of E. terminalis populations annually destroyed individually by the various factors comparing the environmental resistance of the insect.

The only year during which full information was obtained concerning the controlling influence of each factor was 1951, and in table 25 is reflected the combined influence of all the environmental factors in an area where a complete defoliation has occurred.

It can be clearly seen from the table that during 1951, as experimentally determined, 99.71% of the E. terminalis population was destroyed by the various controlling factors, Empusa grylli clearly being the factor responsible for most of the mortality.

Eggs	Parasites in young larvae	Insect Parasites in older larvae	Empusa grylli	Insect Parasites in pupae	Isaria farinosa	Total % of population destroyed.
0.58%	4.0%	5.9%	91.48%	14.3%	74.0%	99.71%
		97.38%		88.3%		

Table 25.

The sum of the environmental resistance factors at Jessievale during 1951.

The various factors which collectively serve to control E. terminalis vary considerably in their individual effectiveness. By referring to Table 25 it will be seen that there is no significant difference between the controlling influence exerted by the egg parasites, and these affecting the young as well as the old larvae (X^2 = 3.070.D.F.2), but there is a significant difference betwee parasitism by

all/.....

all the above mentioned parasites and the pupal parasites ($X = 3.0705$ D.F.2). It would thus appear that of the insects parasitising E. terminalis the pupal parasites have the highest value.

Although there is no significant difference between the effectiveness of the fungus parasites, Empusa grylli and Isaria farinosa ($X^2 = 0.444$ D.F.1) it must not be lost out of sight that I. farinosa destroys relatively only a small proportion of the total population.

During the years 1949/50 and 1952/54 it was possible to determine only the controlling influence of the insect parasites and the fungus Isaria farinosa. An experiment such as described to determine the exact larval mortality due to E. grylli, is an enormous task that could unfortunately not be carried out each year.

In view of the fact that, in any compartment in which an outbreak occurs, thousands of dead larvae infested by E. grylli may always be found, it can be accepted that this disease, in any such year, plays as vital a part in reducing the population density in the affected areas as it did during 1951 when the detailed survey and analyses could be made.

During the year immediately following one when peak populations of E. terminalis have been nearly completely wiped out by E. grylli, no fresh outbreaks will occur in that particular section of a plantation. In the graphs plotted in Fig. 72, 73 and 74 the drop of severed needles, during the year after such a peak population has been nearly wiped out by the fungal parasite, is compared with that recorded during the preceding year. It is abundantly clear that the population level the year after the parasites had played their part was extremely low. From this point the cycle begins anew, the population density increasing progressively from year to year until once more the critical level is reached and E. grylli once again exerts its vital controlling influence.

CHAPTER VIII.

THE BIOLOGY OF THE MORE IMPORTANT INSECT PARASITES OF E. TERMINALIS.

1. TELENOMUS PHEGEUS. NIXON.

Adult. Telenomus phegeus (Fig. 93) belongs to the family Scelionidae, all the known members of which are parasitic upon the eggs of insects. The genus Telenomus is known to be parasitic only upon the eggs of Lepidoptera and Hemiptera.

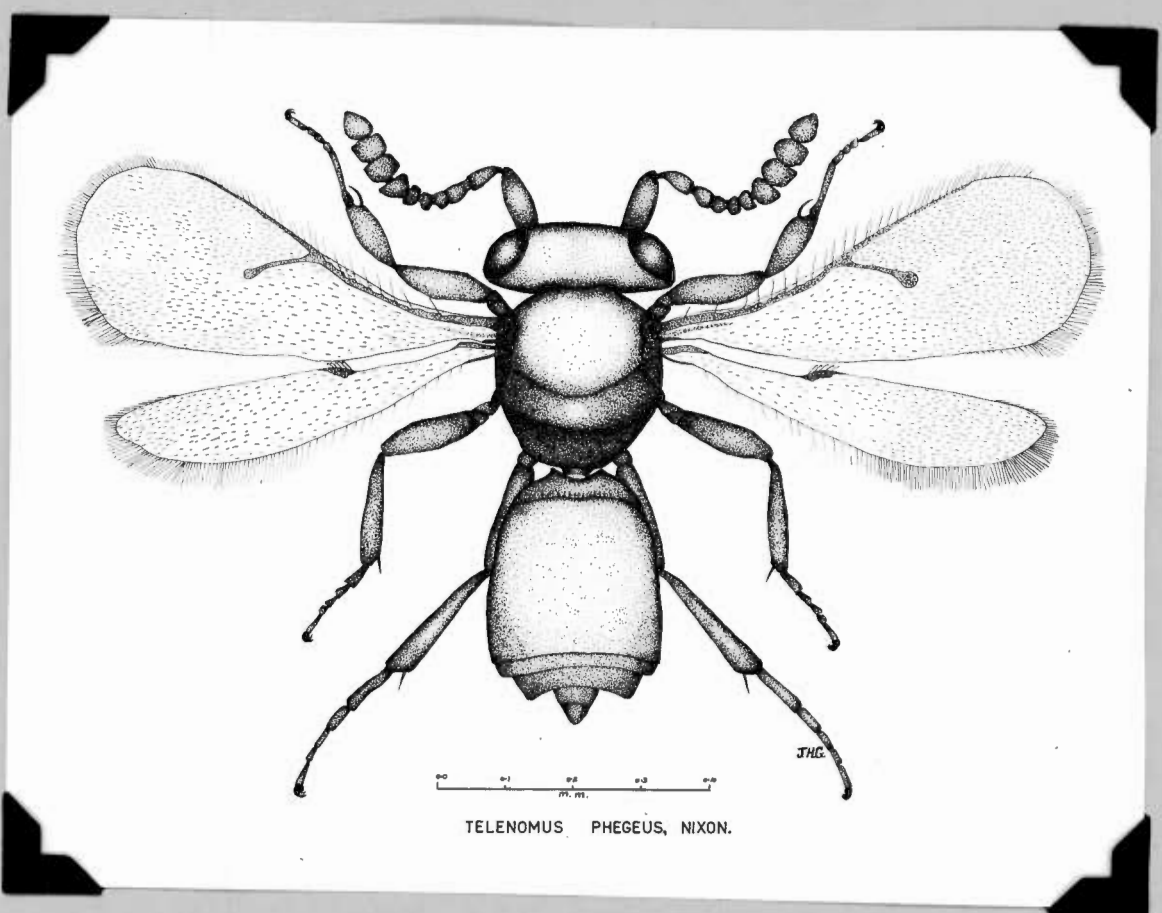

Fig. 93.

The adult Telenomus phegeus Nixon.

(a) Breeding Technique.

This minute parasite, which attacks the eggs of Euproctis terminalis breeds very readily under laboratory conditions,/....

conditions, and to study its biology, the freshly laid eggs of E. terminalis were used. The eggs were removed from the hair mass, with which the moth covers them, and were evenly spread on wetted gummed paper to which they adhere as the gum dries. Sections of this paper with the desired number of eggs on them were cut for experimental use.

(b) Feeding and longevity of adults.

All experimental work was done under laboratory conditions at 20°C.

The parasites were reared in Petri-dishes or glass vials containing a small pad of moist cotton wool and were found to thrive on a honey diet provided that it was made available to them in such a way that they did not get stuck in it. In order to prevent this, a drop of honey was placed on the side of the Petri-dish or glass vial and a piece of perforated paper was then firmly pressed over the honey, covering it and thus adhering to the side of the glass container. The parasites were then able to feed safely through the holes in the paper.

The influence of food and water on the longevity of 55 parasites are given in table 23, where it is clearly shown that starvation and lack of moisture tend to shorten the life of the insect.

	With food and water.	Without food and water.
Average period in days.	16	7
Standard deviation	± 5.467	± 0.1054
Significant difference	1.4212	

Table 23.

Longevity of adults.

(c) Oviposition/...

(c) Oviposition.

The males are normally the first to hatch and immediately the females emerge from the eggs they mate with them. The females start ovipositing the same day on which they emerge.

The Euproctis eggs on the gummed paper were kept in Petri-dishes for easy observations under the microscope. It was found that when a female is released into a dish containing eggs, she immediately approaches them, climbs on to an egg, rapidly tapping it with her antennae, and then alights from it to go to another egg to repeat the performance or to start preparing to oviposit. In order to do this, she sits right on top of the egg, bends her body downwards, extending the ovipositor, and with the help of backward and forward movements of the abdomen, pushes the ovipositor obliquely through the side of the egg. She normally remains in this position for an average period of 3 - 3½ minutes, although some females have been observed to remain for as long as 15 minutes.

Salt (1936) states that one of the factors by means of which the parasite Trichogramma can distinguish between parasitised and unparasitised eggs is a chemical trace left on the surface of the egg. He maintains that this chemical trace is not a body odor of the parasite, but a more specific smell probably produced by glands on the tarsi, and that it is left not only on hosts, but also on the substratum on which the parasite walks. Owing to this method of discrimination, the parasite sometimes mistakes healthy for parasitised hosts, and these, therefore escape parasitism and are important in the population problem.

In T. phegeus, however, this method of distinguishing between parasitised and unparasitised eggs is further developed. After the parasite has oviposited in the egg, she withdraws the ovipositor, and with the extruded ovipositor, she brushes the eggs with a circular movement.

This action renders the egg immune to any further

parasitization/....

parasitization. In this instance a smell is probably produced by the glands of the genitalia which acts as a discriminatory odor, and the parasites thus never mistakes an egg that has been treated in this manner for an unparasitised one.

The only instances where two females were observed to oviposit in the same egg, was where they started to oviposit in the same egg at the same time.

When the parasite attacks an egg cluster which is still covered by the long hairs from the anal tuft of the female moth, it will either insert its ovipositor right through the hairs or make its way through the hairs and oviposit when in contact with the actual eggs.

Under normal conditions, eggs up to the age of four days are readily parasitised, but thereafter females will only occasionally attack the eggs. This phenomenon is also mentioned by Moutia et. al. (1952) in their work on the egg parasite Platytelenomus hylas. Nixon. It was found however, that if eggs were kept in cold storage at a temperature at which the E. terminalis embryo could not start developing, they were readily parasitised even if the eggs were kept for as long as 30 days, but if kept for longer than this, the parasites were more reluctant to oviposit.

Balduf (1926) has, however, observed that Telenomus cosmopenlae Gahan, will oviposit readily and with success in the egg of its host, even if the embryonic nymph of the host has so far developed that its pink eyes are visible through the chorion.

In order to study the parasite in the egg of its host, the strongly chitinised chorion had to be broken and in so doing the contents of the egg was so disturbed that it was impossible to determine exactly where the parasite egg was situated. Clausen (1940), however, found that the egg of Telenomus ulyatti floats free in the yolk between the amnion and serosa, and that the young larva lies in

the/.....

the outer yolk layer and is attached by its mouth-parts to the serrosa.

By opening the egg of E. terminalia it is easy to determine whether it has been successfully parasitised or not. The contents of the parasitised eggs are much less viscous than those of healthy eggs. Through this fact no time was wasted in searching through an unsuccessfully parasitised egg for the parasite.

The colour of a newly laid egg of E. terminalia is a light pastel green which gradually changes to a buff-yellow in two days. The colour change occurs even when the egg has been successfully parasitised.

The egg retains the buff-yellow colour until the parasite larva within it starts to pupate when it changes into a dirtywhite colour. As the pupa becomes darker, the eggs show up first and later the whole pupa becomes faintly visible through the chorion. (Fig. 98).

The eggs of the silkworm were tried as an alternative host, but T. phaeeus would under no circumstances accept them.

(d) Biotic Potential.

In most of the Scelionidae the reproductive capacity is relatively low. The average number of E. terminalia eggs a T. phaeeus female was able to parasitise successfully was 48, the maximum being 76.

This parasite is exclusively a solitary one, and even in the rare instances where two females oviposited in one egg at the same time, only one parasite emerged.

(e) Life cycle and morphology of the immature stages.

To establish the life cycle of this parasite, parasitised E. terminalia eggs were opened at regular intervals and observations made.

The complete life cycle of T. phaeeus takes from 17 - 23 days, whereas T. cosmoeplas (Balduf 1926) completes

it's/.....

it's life cycle in 9 - 10 days.

The egg hatches within 24 hours after oviposition.

The development of the first instar takes from 70 - 84 hours to be completed, after which the larva moults to enter the second instar, which lasts 16 - 20 hours. Thereafter, by a further moult the larva passes into the 3rd or final instar which has a duration of 20 -24 hours, followed by pupation. The pupal period is extended over a period of 15 - 16 days.

Instar	Average Duration.	Standard deviation.
Egg	24 hours	± 1.304
First larval instar	75 hours	± 1.582
Second " "	18 hours)	± 2.889
Third " "	22 hours)	
Pupa	16 hours	± 1.479

Table 24.

The duration of the immature stages of T. phegeus in hours. The information was obtained by opening 150 parasitised E. terminalis eggs.

Egg. (Fig. 94)

The egg is ovate with a slender stalk, there being no visible demarcation between the stalk and the egg. The chorion is smooth and devoid of sculptures. The total length of the egg is 0.2 mm. while the stalk is 0.075 mm. long. The contents of the egg has a granular appearance in contrast to that of the stalk which is clear.

First Instar. (Fig. 95)

The first instar is transparent on eclosion and a typical teleaform larva, which is described by Clausen (1940) as follows:-

"Body segmentation not visible, but the cephalothorax and abdomen seperated by a constriction; the mandibles very

large/...

large, usually fleshy and directed ventral; the abdomen almost spherical, with one or more rings of long delicate spines, and a long heavily sclerotised bladelike process directed ventral on the last segment."

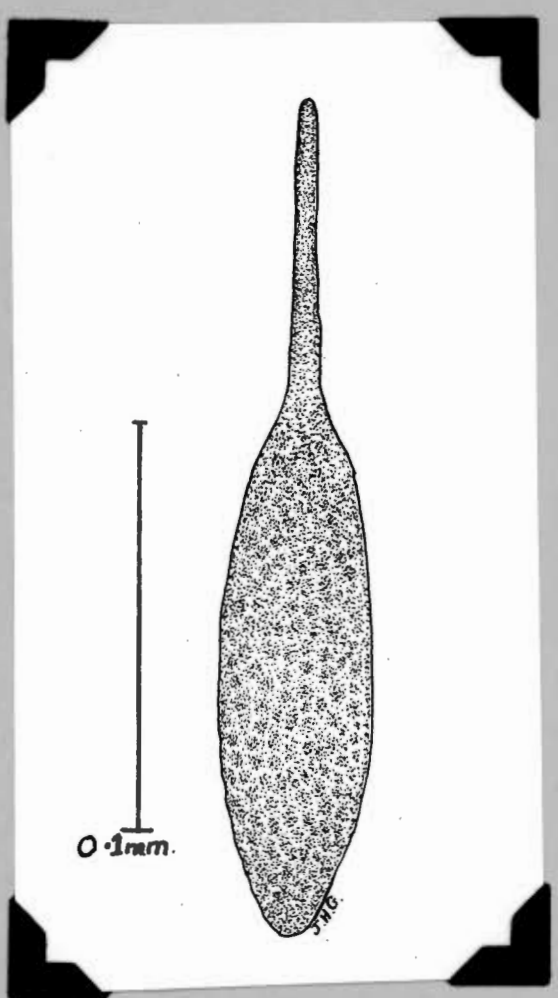

Fig. 94.

The egg of Telenomus phegeus.

The only respect in which T. phegeus differs from the above description is that the blade-like process or tail, is fleshy and not heavily sclerotised. Anteriorly the tail has a short spine on its dorsal line.

The two fleshy, sickleshaped mandibles are continuously moving up and down, and they probably break down the contents of the egg with these movements. Below the mandibles, on the median ventral line, is a fleshly process, which may probably represent the rudiments of the labium.

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The abdomen increases greatly in size as the larva grows older. The growth, relative the time in hours, is shown in figure 97.

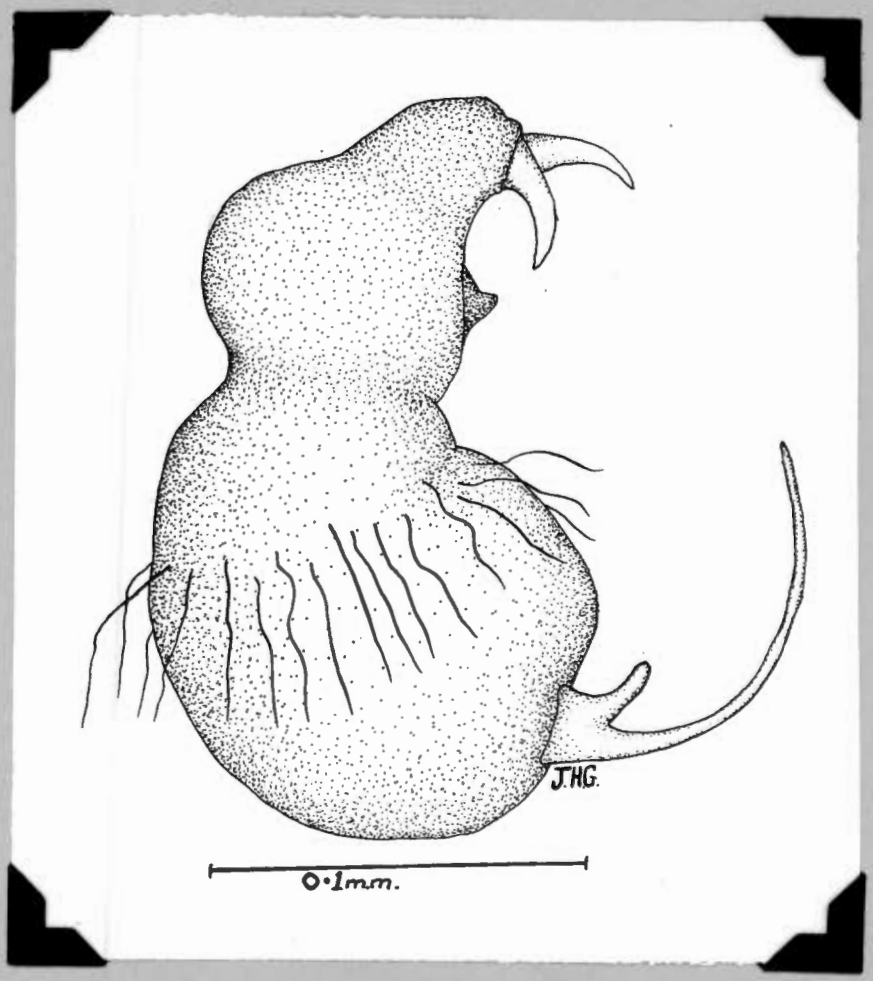

Fig. 95.

First instar of T. phegeus.

Second and third Instars. (Fig. 96).

The second and third instars have lost the sickle-shape mandibles, the tail, and the setae. Only a faint segmentation is visible on the sac-like body.

These two instars look so much alike, that if it was not for the fact that a second instar larva was by chance found to be moulting, the writer would have presumed that there were only two instars. If any spiracles are present, they must be very rudimentary, as I could be observed. I none

Fig. 96/....

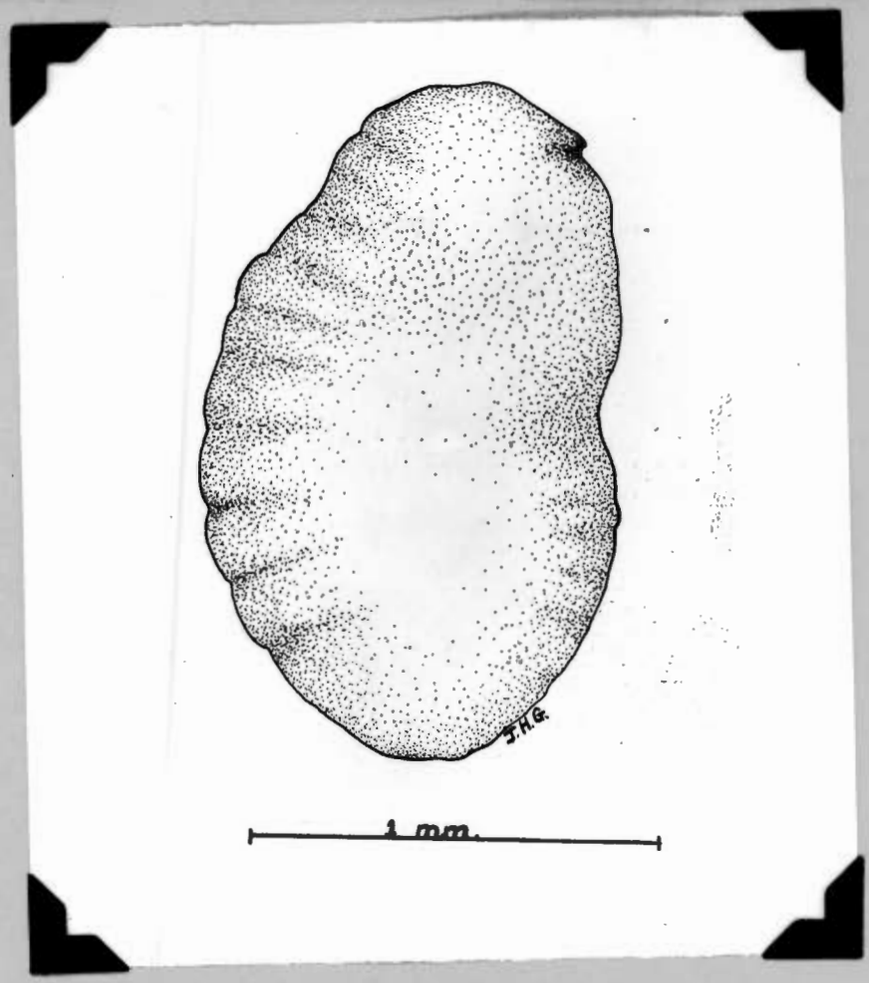

Fig. 96.

Last instar larva of T. phegeus.

By the time the larva pupates, it has consumed the entire contents of the egg, except for a solid greenish substance which is found flattened inside the egg against one side of it. This subsistance is probably the undigestable food and the larval skins and excretae. Balduf (1926) observed the same substance in T. cosmopenlae, but in this case it was yellowish in colour.

Pupa. (Fig. 98).

The pupa, which is slightly curved in the egg, is at first white, but it gradually becomes darker in colour until it is a dark brownish-red. The compound and eyes exhibit this colour change before the rest of the pupa and for this reason they are the first organs to be observed through the chorion. Within 36 hours the whole pupa becomes darkly pigmented and is then quite visible through the charion.

Fig. 97/.....

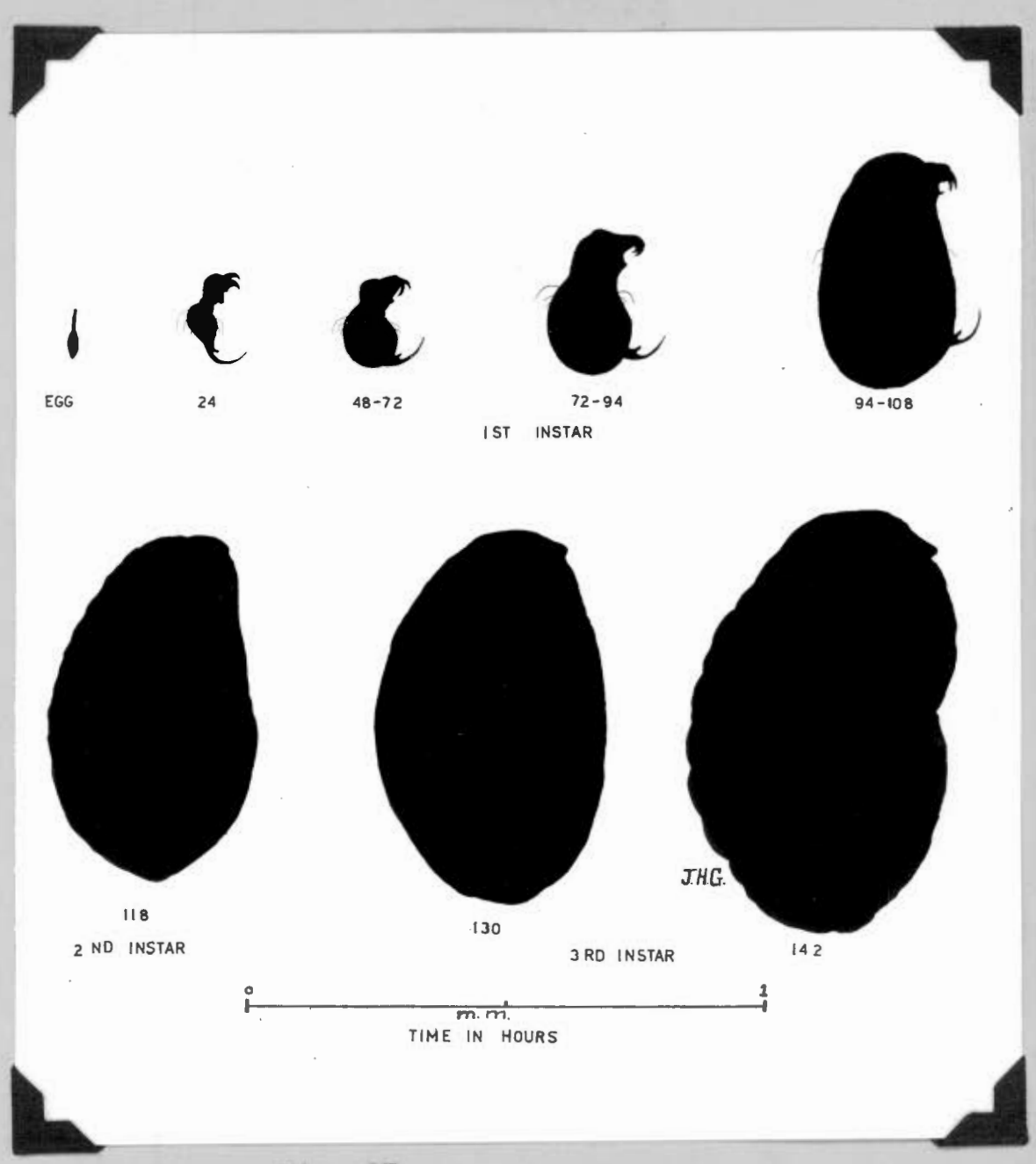

Fig. 97.

The growth, relative the time of the larval instars of Telenomus phoreus

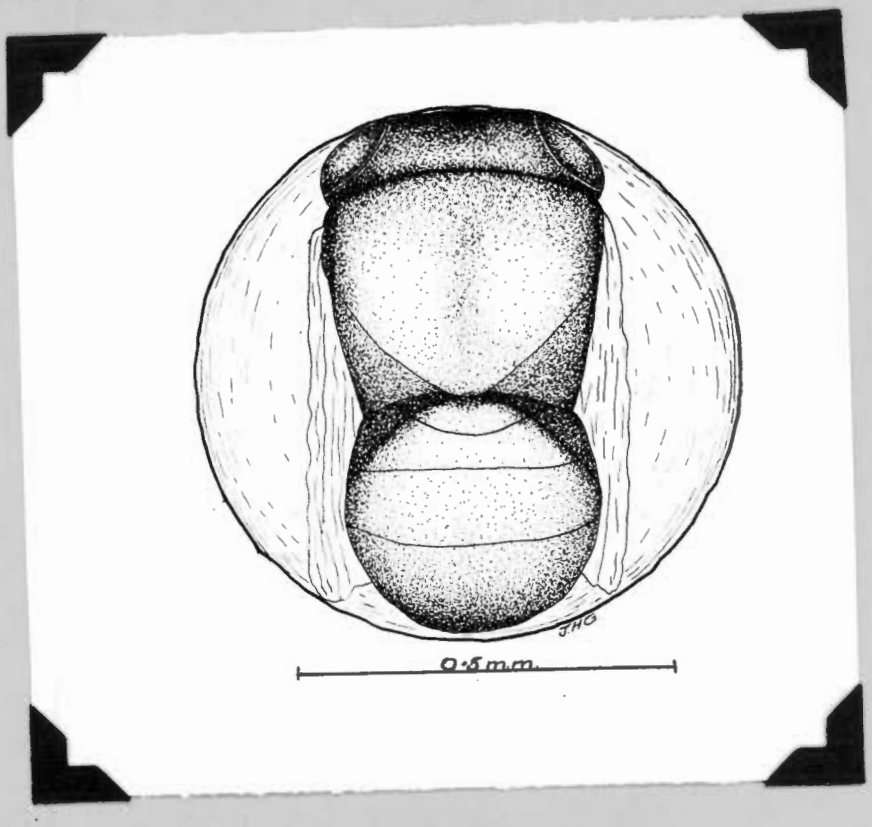

Fig. 98.

The pupa of T. phoreus.

Fig./99/.....

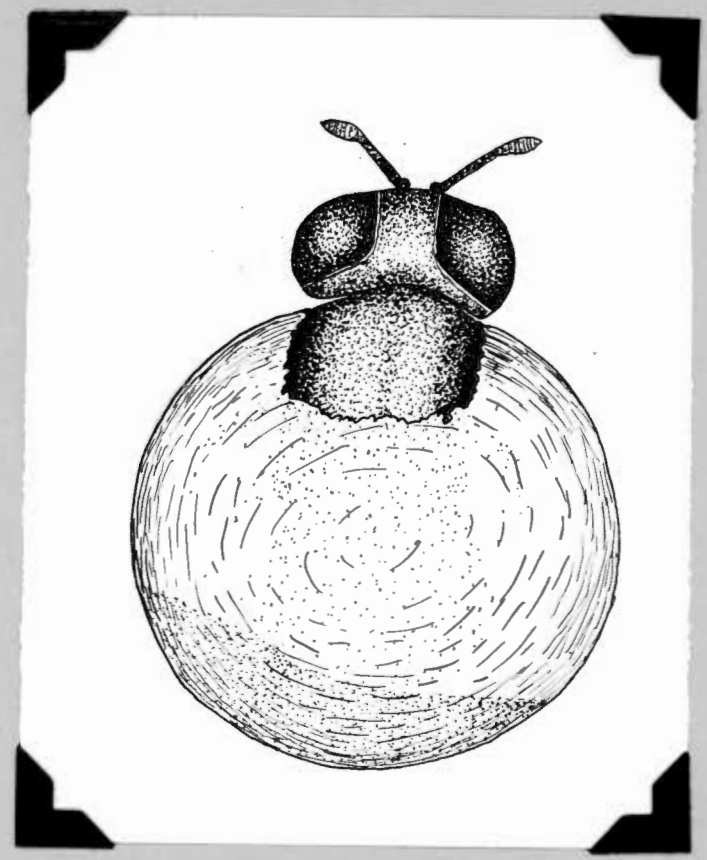

Fig. 99.

The emerging adult T.phaeeus.

The adult emerges by cutting an irregular hole (Fig. 99) with its mandibles through the chorion of the egg of the host.

2. METEORUS TRILINEATUS.

(a) Feeding and longevity of the adult.

Meteorus trilineatus (Fig. 100) were kept in wooden boxes with glass tops, and fed on honey and sugar spread over moist cotton wool. It is possible that they do not feed in the pine plantations owing to the lack of flowers from which to obtain nectar, but amongst the indigenous forests and shrubs they probably live much longer, as there is an abundance of flowers from which they can obtain nectar. It may be noted here that food is not necessary for normal parasitism to occur. If the adults do feed, however, they live longer, up to 40 days, and are therefore able to parasitise more larvae; adults which were kept without food only lived for an average of 28 days.

Fig. 100/.....

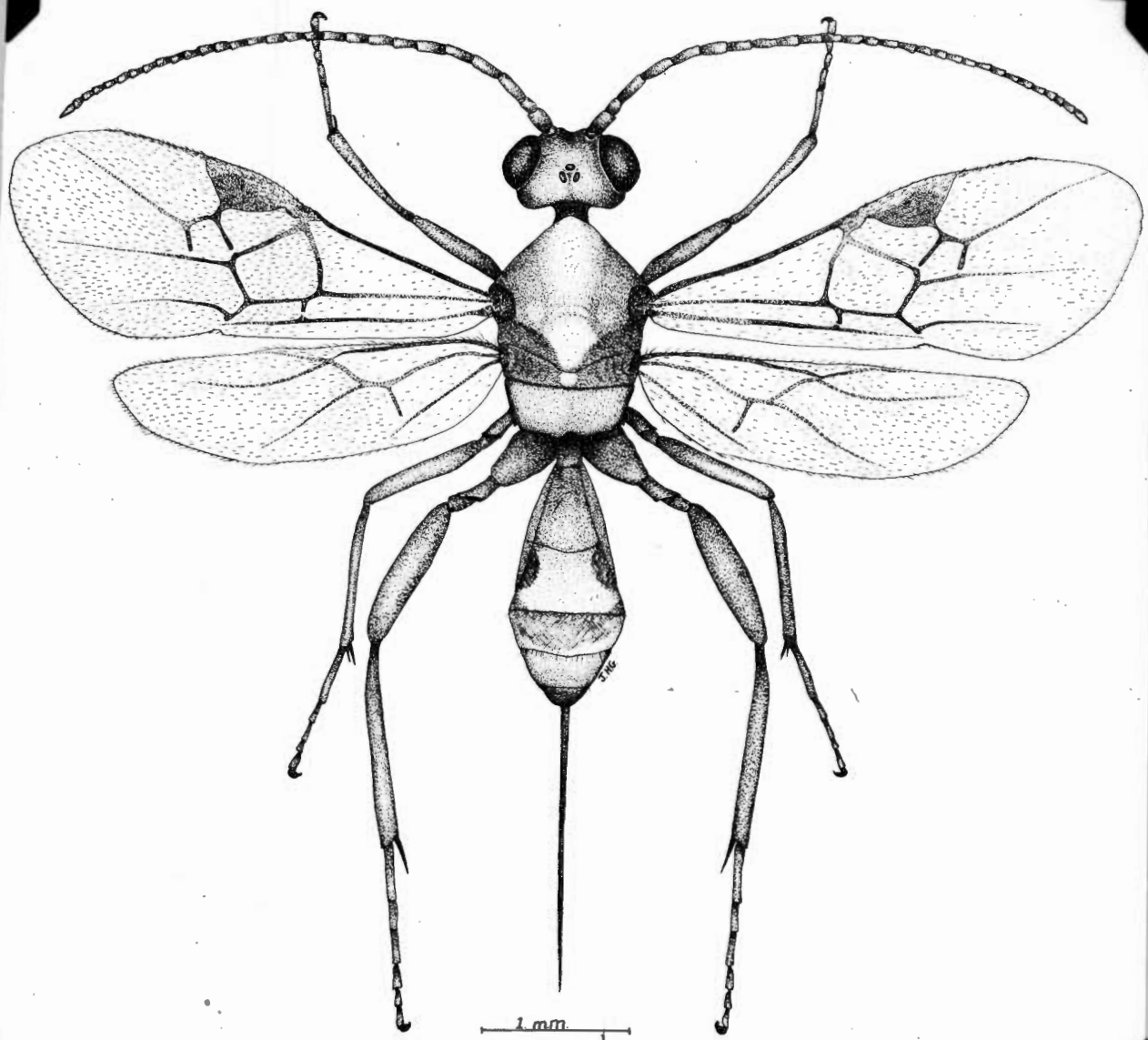

Fig. 100.

Meteorus trilineatus.

It has been observed in some cases that adult parasites feed on the blood which oozes out of the wound made by the ovipositor while laying the egg. The phenomenom was never observed in M. trilineatus, although blood droplets were often formed on the wounds, especially in young larvae.

(b) Mating and oviposition.

Mating takes place soon after emergence and in some cases the male will follow the female for quite a while before copulation occurs.

Oviposition may commence as soon as 10 hours after emergence.

The female M. trilineatus apparently recognizes the host by rapid, continuous tapping on the larva with

the/.....

the antennae. Following such recognition she becomes very excited and will return to repeat the performance. She then raises herself on her legs, bending the abdomen downwards and forwards, so that the ovipositor is parallel with the venter and projects between the anterior legs. At this stage she slowly advances towards her victim.

If the larva does not move she will remain momentarily motionless before thrusting the ovipositor into it. If, however, the larva should show signs of movement she will, without hesitation, quickly thrust the ovipositor into it, withdrawing it almost at once, and leaving only one egg in the body of the host. The whole process of oviposition is completed within a few seconds.

Epiparasitism* was frequently observed in the laboratory if parasites were confined in a cage with one or more Euproctis larvae.

Larvae which were dissected were often found to contain a number of eggs or young parasitic larvae lying in the haemocoel. As many as seven eggs were observed in some larvae, but, except in one instance wherever epiparasitism occurred it was found that only one parasite emerged. In this one case, two adult parasite larvae emerged from one Euproctis larva. Quite often more than one dead first instar larvae were found together with a live one. In such cases, the surviving larva appeared to have fed on the dead ones. (Fig. 101). This phenomenon was never observed in material collected in the field.

* This term was suggested by Haviland (1922) for cases where a single host has been successfully parasitised by several individuals of the same species of parasite.

Fig. 101./.....

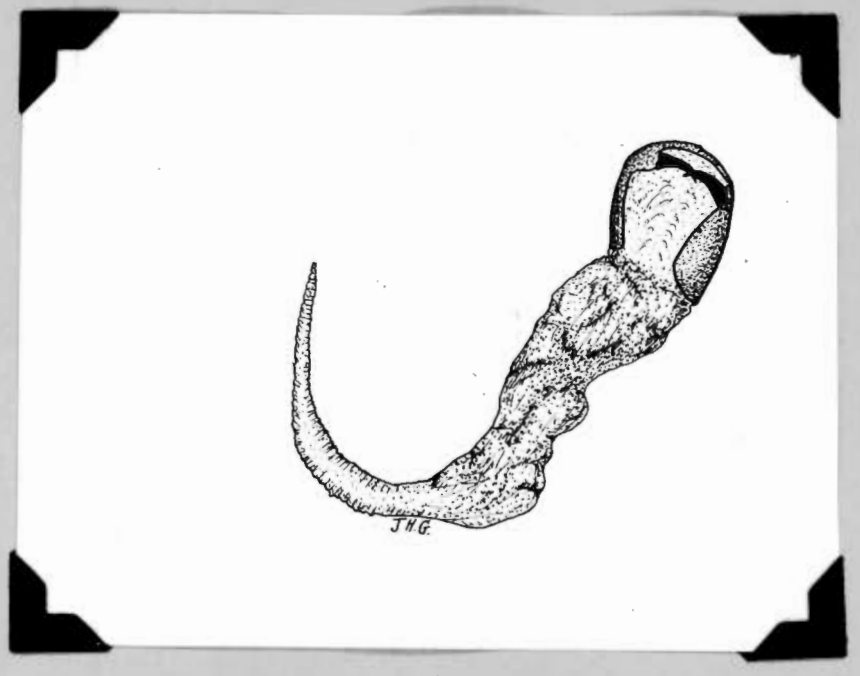

Fig. 101.

Dead First instar larva.

When the ovipositor is thrust into the Euproctis larva, it is accompanied by pronounced writhing movements on the part of the larva. This continues for a couple of seconds after which the larva will crawl quickly away. If the same larva is shortly afterwards again approached by a parasite, it will lift its head and thorax and swing them violently to and fro the moment the parasites antennae touches it. In many cases this movement is successful in chasing the parasite away.

Oviposition takes place readily and rapidly. In one instance a female M. trilineatus parasitised seventeen larvae in half an hour. In many cases, however, a successful thrust of the ovipositor through the larval skin does not necessarily ensure successful parasitation, since it has been observed that out of 105 larvae attacked, only 80 parasites eventually emerged.

The parasite does not appear to choose any particular spot on the larva in which to oviposit, although the thoracic region was found to be the area most commonly attacked. In certain cases the parasite tried unsuccessfully to parasitise the larvae in the head capsule.

A series of laboratory experiments were conducted to determine whether M. trilineatus could reproduce parthenogenetically.

In order to ascertain this; cocoons were isolated,

on/.....

on to a petri-dish, and all unfertilized females which emerged were placed together in specially constructed cages. (Fig. 102) with unparasitised Euproctis larvae.

The cage consisted of a celluloid cylinder, two inches high, and just wide enough to fit closely into the bottom half of a 10 c.m. Petri-dish. The bottom half of another Petridish of similar size was placed on top of the cage to serve as a lid. The behaviour of the parasites placed in this type of cage could be studied with ease under a binocular miscroscope.

Fig. 102.

Parasite cage.

In all cases they readily parasitised the larvae and a number of adults emerged from them. From this evidence it can be concluded that M. trilineatus is not only parthenogenetic, but also arrhenotokous, as the ovipositing virgins constantly produced nothing but males. Fertilized females, on the other hand, produced males and females in approximately equal numbers.

(c) Instars of E. terminalis parasitised.

Only larvae from the second to fourth instars can be successfully parasitised. The parasites often attempt

to/.....

to oviposit in caterpillars of a later instar, however, but are never successful, as they are unable to penetrate the thick integument. In such cases the parasite may apply so much pressure in trying to pierce the integument that it has often been observed to dislodge the larva. It has been noted, however, that newly moulted larvae of the fifth instar are quite often successfully parasitised, but this is not possible once the chitin has hardened.

When the first instar, or very young second instar larvae are parasitised they usually die, probably as a result of the wound caused by the ovipositor, and also through shock. This is not the case with the older instars.

In the younger larvae a drop of fluid always oozes out of the wound, but this very seldom happens in older larvae.

For the first five to six days after parasitism the larva feeds normally, but there after it remains stationary in one spot, spins a few silk threads onto the surface on which it is resting and remains there until it dies.

When the parasite is fullgrown, it gnaws a hole through the larval integument, through which irregular rupture it wriggles, and commences spinning its cocoon. The Eumroctis larva continues to live for another ten days, but never pupates.

(d) Life cycle and morphology of the immature stages.

Egg: The egg (Fig. 103) which is oviposited in the host larva is attached by a pedicel to the internal organs of the larva. Many authors seem to doubt that the pedicel is ever used as an organ of attachment, but Faure (1926) also observed the same phenomenom in Apanteles glomeratus.

The pale brownish-yellow egg is cylindrical in shape, being rounded at the end bearing the micropyle, while at the opposite end is situated the slender tapering pedicel.

The total length of the egg is 0.2mm., while the pedicel is 0.06 mm. long. The thin transparent chorion

bears/.....

bears minute hexagonal markings.

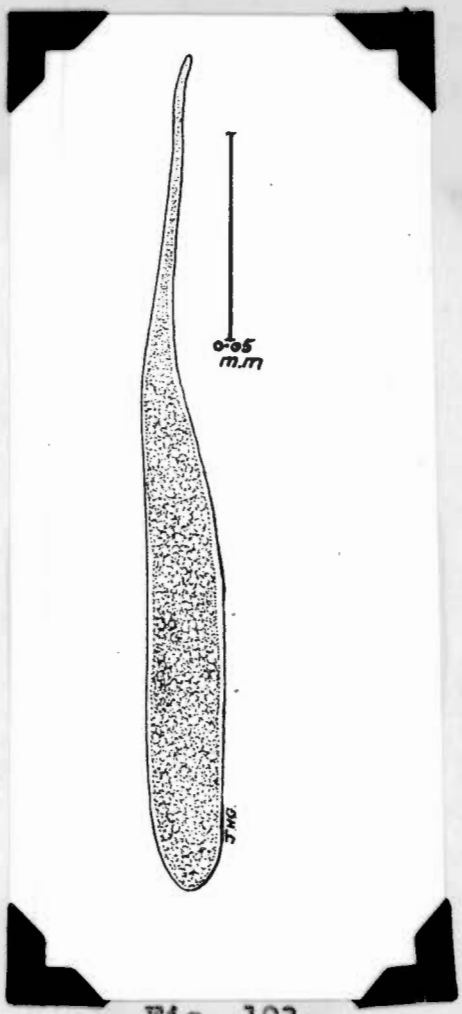

Fig. 103.

The egg of M. trilineatus.

After the egg has been laid, the embryo starts to develop, and the egg increases in size. The stalk, however, remains the same size throughout. The embryo increases so much in size that just before the larva hatches - after 120 hours - the egg, excluding the stalk, attains a length of 0.8 - 0.9 mm. with a width of 0.3 mm. at its widest point. (Fig. 104). This increase in size during incubation is mainly found in the Euphorinae and Metiorinae of the family Braconidae, and it is probably due to absorption of fluids from the host by the developing embryo.

When the larva hatches from the egg it is completely enclosed in a membrane, called the trophic or throphamnion membrane. (Fig. 105). The membrane occurs in the Braconidae, and specially in the subfamilies, Migrogastrinae, Meteorinae, Eupharinae and Opinae. In Meteorus nigricollis, however, the membrane does not cover the larva after it has hatched, but remains in the egg shell.

Meteorus/.....

Meteorus trilineatus, on the other hand, is enclosed by this membrane for about 48 hours after it has hatched.

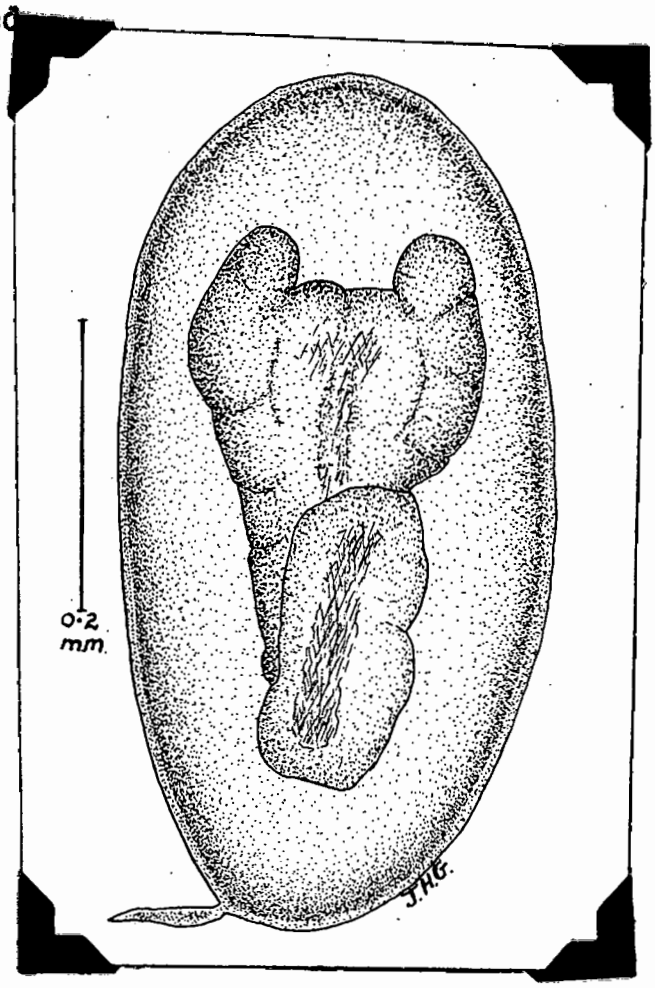

Fig. 104.

Ventral aspect of embryo.

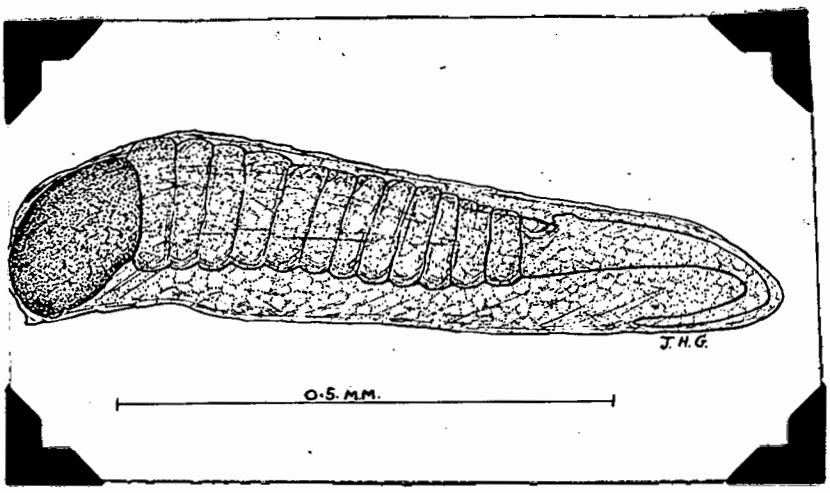

Fig. 105.

The trophic membrane consists of one layer of transparent hexagonal cells and as the larva grows in this "envelope" the cells of the membrane also increase in size.

The/.....

The cells continue growing after the larva has broken out of the "envelope". At first this torn membrane retains its shape and form, but after 24 hours the membrane cells, which have now become spherical in shape, break apart and resemble a bunch of grapes. The individual cells begin to float free in the body of the host and maintain an independant existance. Since the cells are able to increase in size they must be able to absorb nutritive matter from the blood of the host. Jackson (1935) put forward the theory that the cells store up fat absorbed from the body fluids of the host.

At the time when the larva ruptures the membrane, the cells are 0.025 mm. in diameter, but after 164 hours they have become spherically shaped, loose cells with a diameter varying from 0.05 to 0.12 mm. This represents a volume increase of about 100 times. The cells are light yellowish in colour and consists of a granular structure. No nucleus is visible.

In the third larval instar period of the parasite we find that all the trophic cells have disappeared, and it is very likely that they are eaten by the second and third instars.

First Instar. (Figs. 106 and 107).

As soon as the larva is ready to emerge from the membrane, it becomes very active. It is of the caudate larval type, which Clausen (1940) defines as distinctly segmented, the body usually somewhat elongated, and the last segment modified into a fleshy tail-like organ.

The caudate larvae are usually found in the Meteorinae and Aphiidinae. There are thirteen well defined body segments, the last one being drawn out to form the "tail".

The tails or anal vesicles of Apanteles, Microgaster and Microplitis differ morphologically from that of Meteorus and Dinocampus. According to Ullyett (1944) it

is/.....

is here formed by the evagination of the proctodaeum which becomes prolapsed through the anus.

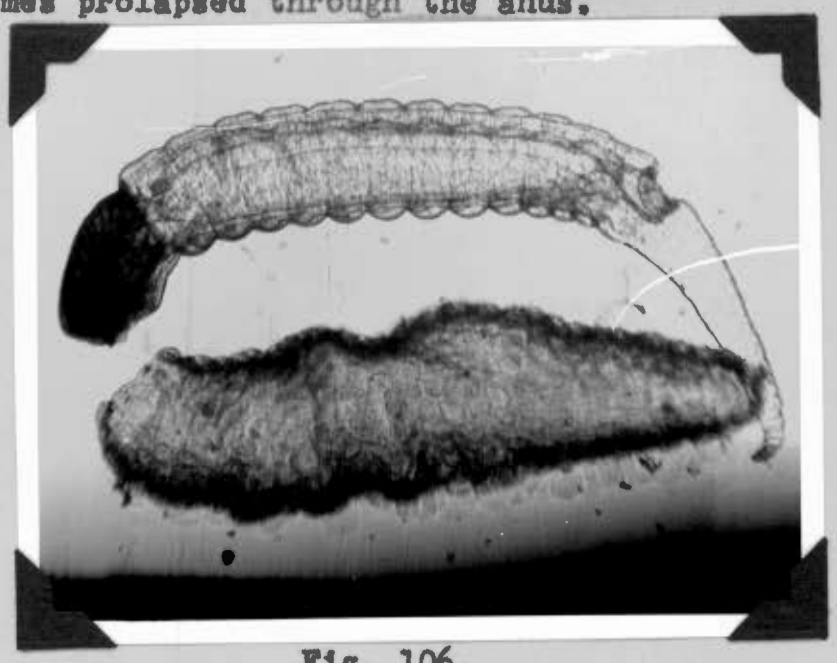

Fig. 106.

Newly hatched larva next to trophic sac.

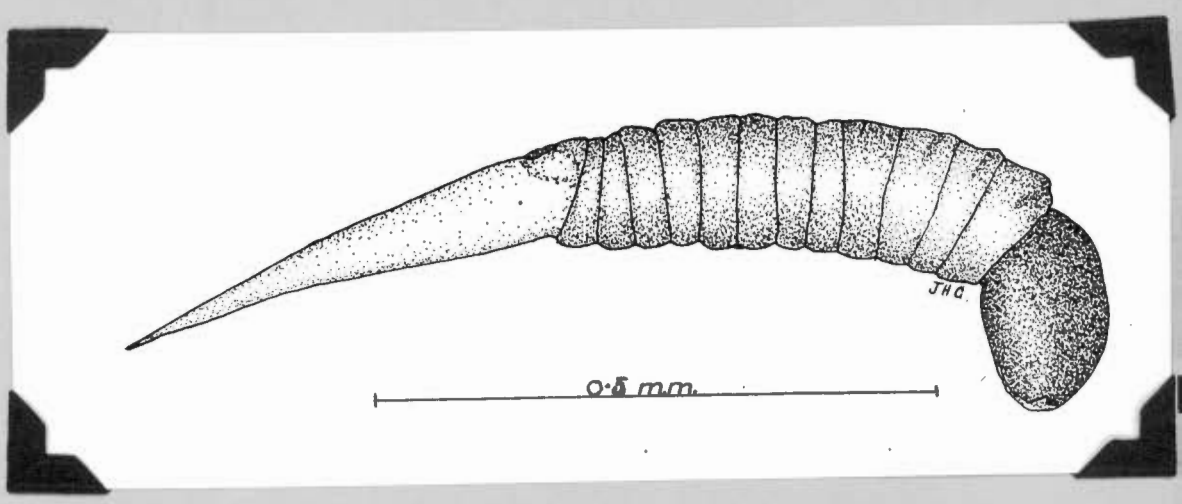

Fig. 107.

First instar larva showing the last segment which is drawn out into a tail.

The tail or last segment is at its widest at its point of origin, that is, next to the twelfth segment, and tapers off to a point. It is a transparent organ lined with a hypodermal layer and filled with blood, which circulates freely within it.

The total length of the newly hatched larva is

1 mm./.....

1 mm., the tail being 0.4 mm. in length. Seen from the lateral view, the larva is slightly convex. In most of the Meteorus species setae or tubercles or both are found on the skin, but in the case of M. trilineatus the skin is smooth and shiny.

Head and Mandibles. (Fig. 108).

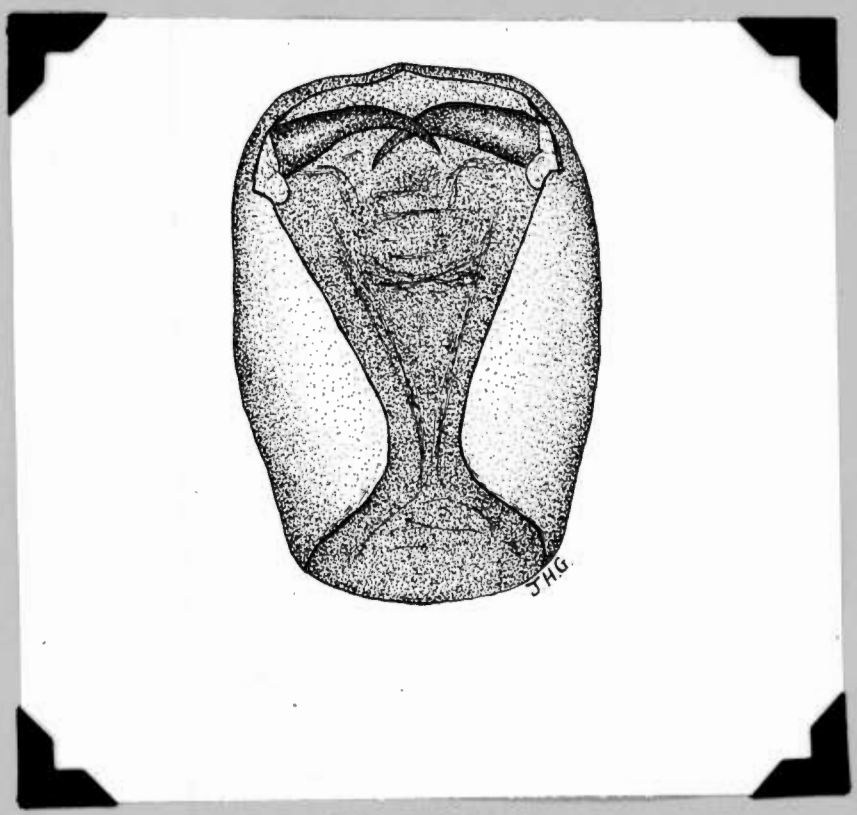

Fig. 108.

Head of first instar larva.

The head consists of a golden brown, heavily chitinized, ventrally flattened head capsule. It bears two very sharply pointed, sickle shaped mandibles. In M. trilineatus, the mandibles are smooth with no lateral teeth. The mandibles are continually in motion, and probably serve to break up the fat bodies of the host.

Tracheal system.

A primary tracheal system is found in this instar, and since respiration is apneustic, spiracles are absent.

The tracheal system consists of two main longitudinal trachea which lie on either side of the body, being joined in the first segment by a dorsal and ventral commisure. The larva lives submerged in the liquid medium of the host's

body/.....

body, and as it has no connection with its tracheal system or with the outside atmosphere, and has no gills, it must breathe through the skin, thus being dermatopneustic.

After 120 hours the first instar moults to become the second instar.

Function of the tail.

Many functions such as locomotion, (Seurat 1899)* excretion (Weissenberg 1909)* and respiration (Tothill 1922)* have been ascribed to this appendage. For a long time, the function of respiration was assumed to be the most likely but Thorpe (1932) proved without doubt, with the aid of luminiscent bacterium, Bs. phosphorescens that the tail is not associated with any oxygen uptake at all.

Ullyett (1944) ascribed a new function to the tail. In a study of Anopheles spp. he observed how the tail was used to rupture the chorion of the egg. Just before the larva hatches, it starts rhythmical backwards and forwards movements with the tail, actuated by the muscles of the posterior abdominal segments. The dorsal surface of the tail is closely adpressed to the chorion, thus enabling a sawing motion along the midventral line, while the head remains completely motionless. After some time, the chorion rips suddenly along that line, and sets the larva free.

In M. trilineatus the emergence from the egg may possibly be caused by the internal pressure set up by the growing embryo, as now movements can be seen at this stage. The emergence of the larva from the trophic membrane is, however, helped by the movement of the tail in a modified manner to that described above.

The tail is folded under the ventral surface of the larva in the trophic membrane. (Fig. 105). By contracting the abdominal muscles the larva forces blood into the

tail/.....

*Publications not seen by writer. (Ullyett 1944)

tail, causing it to straighten and press against the posterior end thus forcing the larva forward. This process continues for some time until the anterior portion of the membrane is ruptured, and the larva pushed out. The sawlike motion of the tail on the posterior end does not cause the sac to rapture as in Angitia. The mandibles are not used in this process, and only start functioning after the larva has emerged.

These observations suggest that at least one of the functions of the tail is the same as that described for Angitia, although the actual method of emergence differs from that described by Ullyett.

Second Instar.

There is a marked difference in the first and second instar larvae. (Fig. 109)

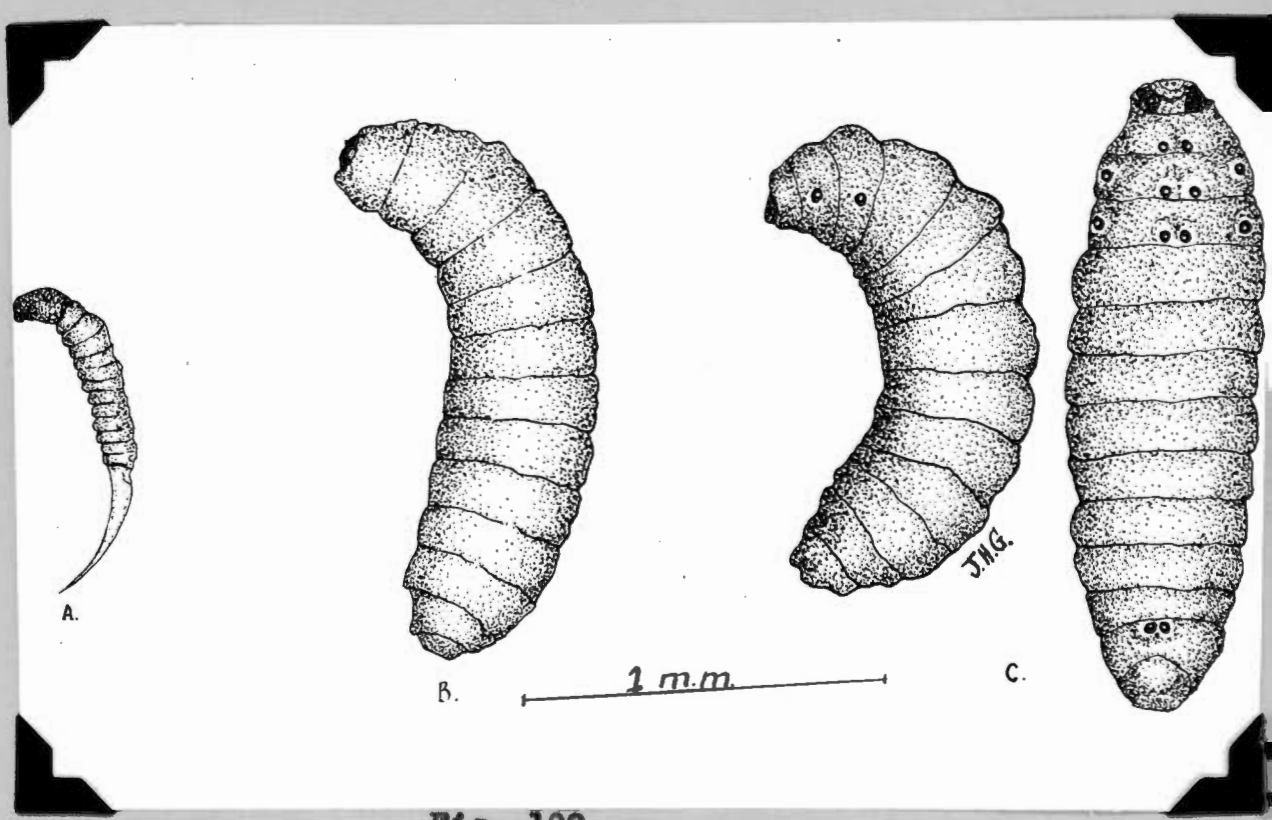

Fig. 109.

The three larval instars of Meteorus trilineatus.
A. First instar, B. second instar, C. Lateral and ventral view of the 3rd instar.

In moulting, the larva loses its tail as well as the large heavily sclerotized head with the falcate mandibles. It is now a typical hymenopterous form type. The mandibles are simple and barely visible. The tracheal system is still apneustic.

After/

After 56 hours the larva moults to become the 3rd instar.

Third and last Instar. (Fig. 119c)

The last instar is still a typical hymenopteriform larva. It differs from the second instar only in that it now possesses two pairs of spiracles and four pairs of tubercles. The spiracles are situated laterally and slightly to the ventral side of the second and third segments. The tubercles are situated in pairs on the ventral surface of the 1st, 2nd, 3rd and 12th segments.

When the larva is 88 hours old it is ready to pupate, and it then gnaws a hole through the body wall of the host, through which it emerges and starts to spin its cocoon. The larva pupates 48 hours after the cocoon has been completed. These figures were arrived at from observations on 20 parasites.

Mouth parts of last instar larva. (Fig. 110)

In 1930 Thorpe described the morphological characters of the mouth parts of a number of Hymenopterous parasites, and he was probably the first author to use these characters as a basis to classify them into genera and species. The terminology he used was later followed by Salt (1931) and Rosenburg (1934). Vance and Smith (1933), however proposed a new terminology to describe the different structures.

In this thesis the author has followed the terminology proposed by Thorpe.

In the fullgrown yellowish-white larva the brown mandibles and facial rods are clearly visible. Their relative position to one another is given in figure 106.

Labial ring.

The U shaped labial ring is very prominent and well defined in this species. At the posterior it is broad and well defined, whereas in Meteorus chrysophthalmus Nus, it is very indistinct. Fig. 110/....

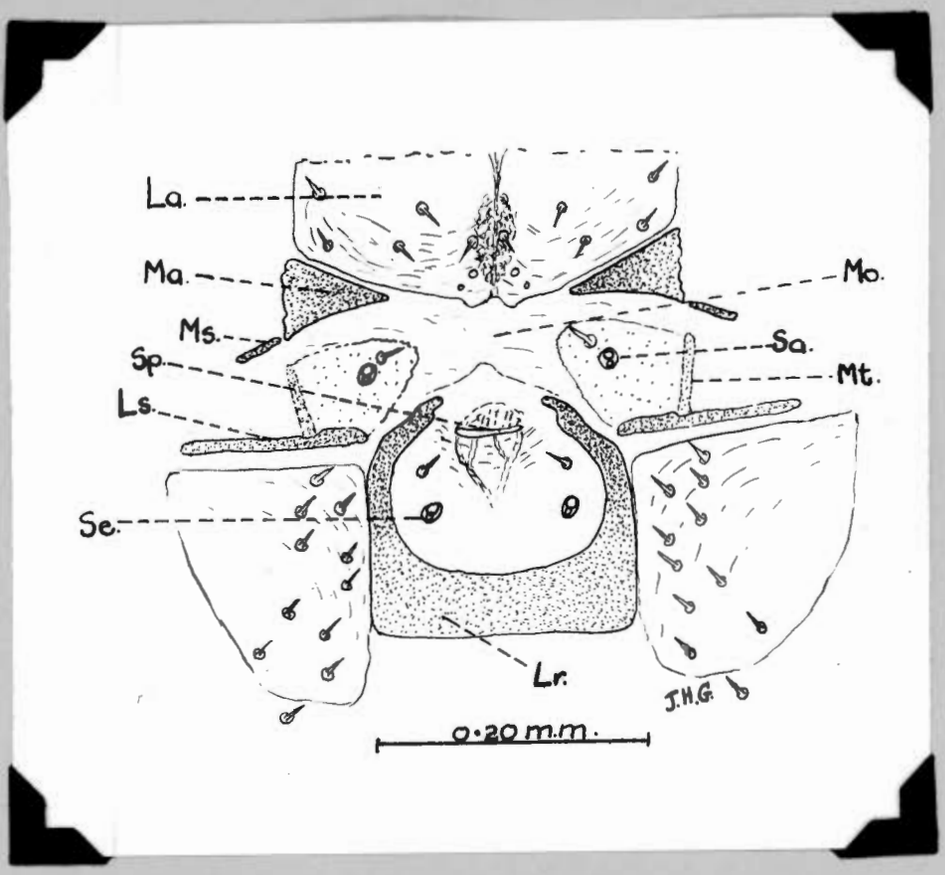

Fig. 110.

Mouth parts of the last instar larva.

La. - Labrum. Lr. - Labial ring. Ls. - Labial struts.
Ma. - Mandibles. Mo. - Mouth opening. Ms. - Mandibular struts.
Mt. - Maxillary struts. Sa. - Maxillary sensillae Se. - Labial sensillae.
Sp. - Spinneret.

Labial struts:

The labial ring is supported by two well sclerotised labial struts, situated one on each side of the ring.

Maxillary struts:

About $^1/_3$ from its anterior end the labial strut has a branch, the maxillary strut which runs to the posterior angle of the base of the mandible, and which, in contrast to the labial strut, is very poorly sclerotised.

Mandibular struts:

The mandibular struts have degenerated to such an extent that only a small poorly sclerotised vestigial structure remains.

Mandibles/.....

Mandibles:

The mandibles are small and not very heavily sclerotised. Their blunt smooth points are directed forwards.

Spinneret:

The spinneret is slightly sclerotised and is situated just below the mouth opening at the dorsal end of the labium.

Sense Organs:

There are two pairs of sense organs -

(1) The Labial Sensillae which are situated within the labial ring, and,

(2) the maxillary sensillae which are situated just below the mandibular bases.

These sensillae are all alike and consist of a circular sclerotised area with one large and one small papilla situated next to each other. Thorpe considers that these sensillae probably represent labial and maxillary palpi.

Setae:

The positions of the setae are shown in figure 43. It is possible that a number of these, especially those on the labium, are sensillary.

Antennae:

The antennae consist of smooth circular areas on which two small sensillary papillae are found.

Pupa.

The pupa is a typical exarate or free pupa. The appendages are free of any secondary attachments to the body, and the abdominal segments are capable of free movement.

At first the pupa is whitish-yellow in colour, but it gradually darkens until it becomes dark brown, with the thorax, which is almost black, being the darkest

region/....

region.

The size of the pupa, which is similar in male and female, varies according to the size of the host, the average length being 2.4 mm. The female pupa is however easily distinguishable from that of the male on account of the presence of the ovipositor which is clearly visible.

Cocoon. (Fig. 111).

As soon as the larva emerges from the host, it starts spinning its cocoon.

Fig. 111.

Cocoon of Meteorus trilineatus and the ~~dormant~~ moribund Euproctis larva from which the larva came.

At first it spins some loose silk threads on and around the now ~~dormant~~ moribund larva, on which to anchor its cocoon. It then proceeds to spin the elongated cocoon which is of a uniform brown colour, with some slightly lighter, loosely woven silk threads over the compact cocoon. The cocoon varies in length from 4.0 - 5.0 mm., the broadest part being from 1.5 - 2 mm. in width. The average pupal period lasts for 9 days, with a maximum of 19 days, and a minimum of 3 days and 3 hours, at a temperature of 18°C.

When the full-grown parasite emerges it cuts a

circular/.....

circular lid, which remains attached to the cocoon by means of the loose coarse silk covering the cocoon, off the one end of the cocoon and emerges through the opening thus formed.

3. TACHINA FALLAX. MEIG. (= xanthaspis Wied).

Tachina fallax is a Dipterous parasite of Euproctis terminalis larvae, belonging to the family Tachinidae. Baer (1921) mentions Dendrolimus pini L. as also being a host of T. fallax.

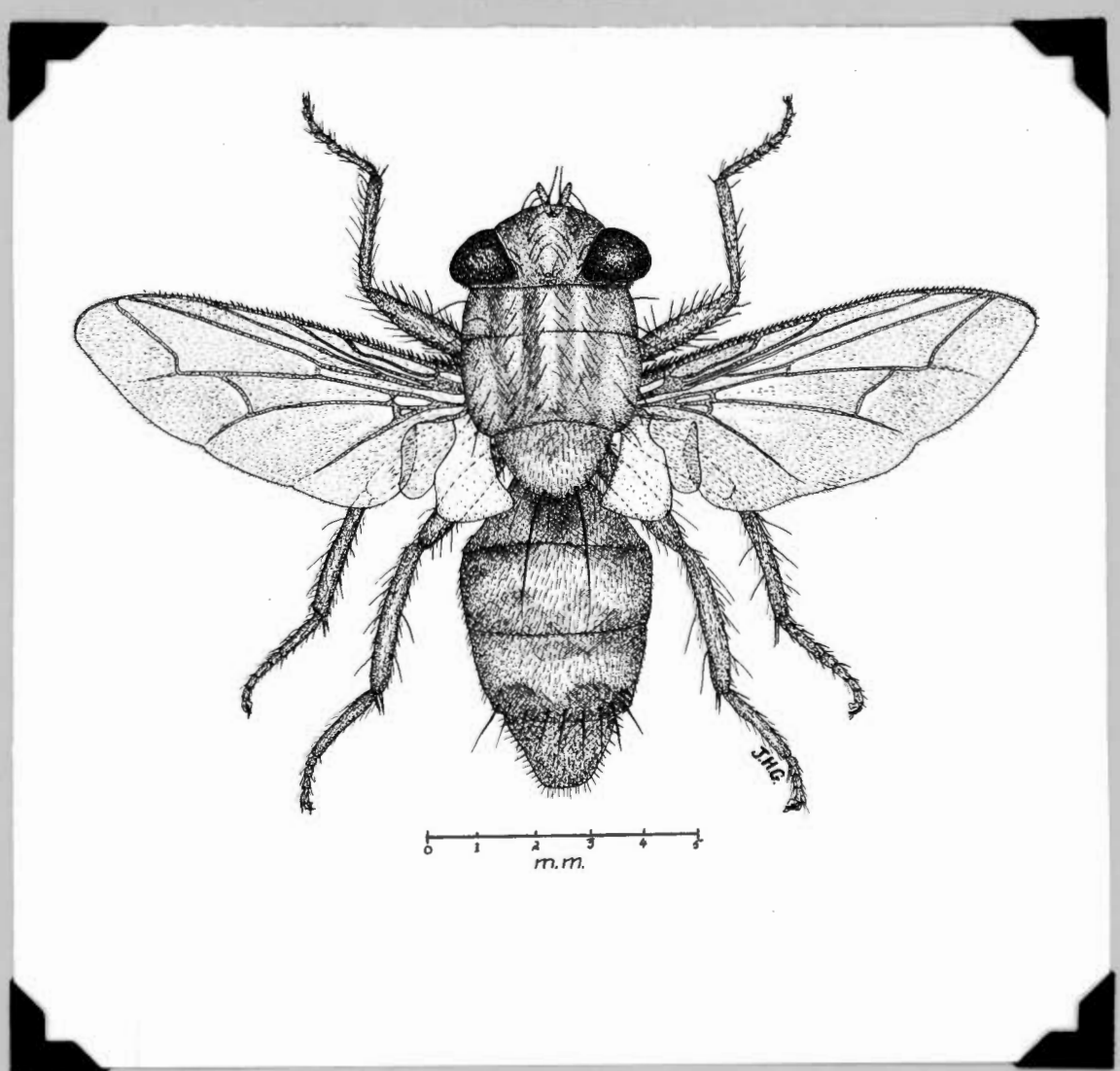

Fig. 112.

Tachina fallax Meig.

(a) Feeding and longevity of the adult.

In studying the biology of this larval parasite, the adults were kept in wooden cages, 12 inches square, 3 inches high, and fitted with a sliding glass top.

Holes/.....

Holes, one inch in diameter were drilled into two sides of the cage, and covered with fine copper gauze to ensure ventilation.

On one of the two remaining sides two more holes were drilled. These holes through which adult parasites were introduced into the cage, were closed with rubber or cork stoppers.

The food of the parasite under natural conditions was never determined, but in captivity, however, they were found to feed readily on crushed raisins, together with honey sweetened water, absorbed in cotton wool.

In captivity it was found that flies which were fed lived longer than those that were not. (Table 25) The results in the following table which were obtained from 20 individuals illustrates this point.

	With food	Without food
Average days alive	16	3
Standard deviation	± 1.362	± 1.1995
Significant difference	0.3977	

Table 25.

Longevity of adult.

(b) Mating and oviposition.

Many species of the Tachinidae family only mate, provided the optimum range of temperature, light and humidity, which is normally quite narrow, is just right, but T. fallax was found to mate very readily under laboratory and artificial light conditions.

Mating takes place within the first 24 hours after emergence, and may take from 30 seconds to 30 minutes.

Oviposition./...

Oviposition.

The females commence ovipositing three days after emergence. In many species of this family, the embryonic development of the egg has already started, but this is not the case in T. fallax, where there is, at the time of oviposition, no sign of development.

The female fly prefers to oviposit on the last two larval instars of E. terminalis, but when these are not available, she will also oviposit on larvae of the sixth instar.

In addition to the larvae of E. terminalis, the parasite was found to oviposit just as readily on silkworm larvae, and the latter were used in most of the biological studies.

The eggs are normally deposited directly on the head of the larvae, but in some exceptional instances they may be deposited on the prolegs or on the protharax. Before ovipositing, the female fly examins the host carefully by tapping the larva with her front legs. Sometimes she even climbs onto the larva and walks up and down on it, after which she alights, and only then will she oviposit by pushing her abdomen downwards and forwards through her legs, depositing an egg on the head. Should the larva move just before the egg is deposited she follows it and waits in this position for the right opportunity, but should the larva move the moment the egg is deposited, the fly will return and press on the egg with the ovipositor, thus securing it firmly to the larva.

The parasite is solitary in habit and never more than one parasite was ever found to emerge from a single host.

Each ovary consists of 25 tightly packed ovarioles. The relative position of the male and female genitalia is shown in figures 113 and 114.

Figure 113./....

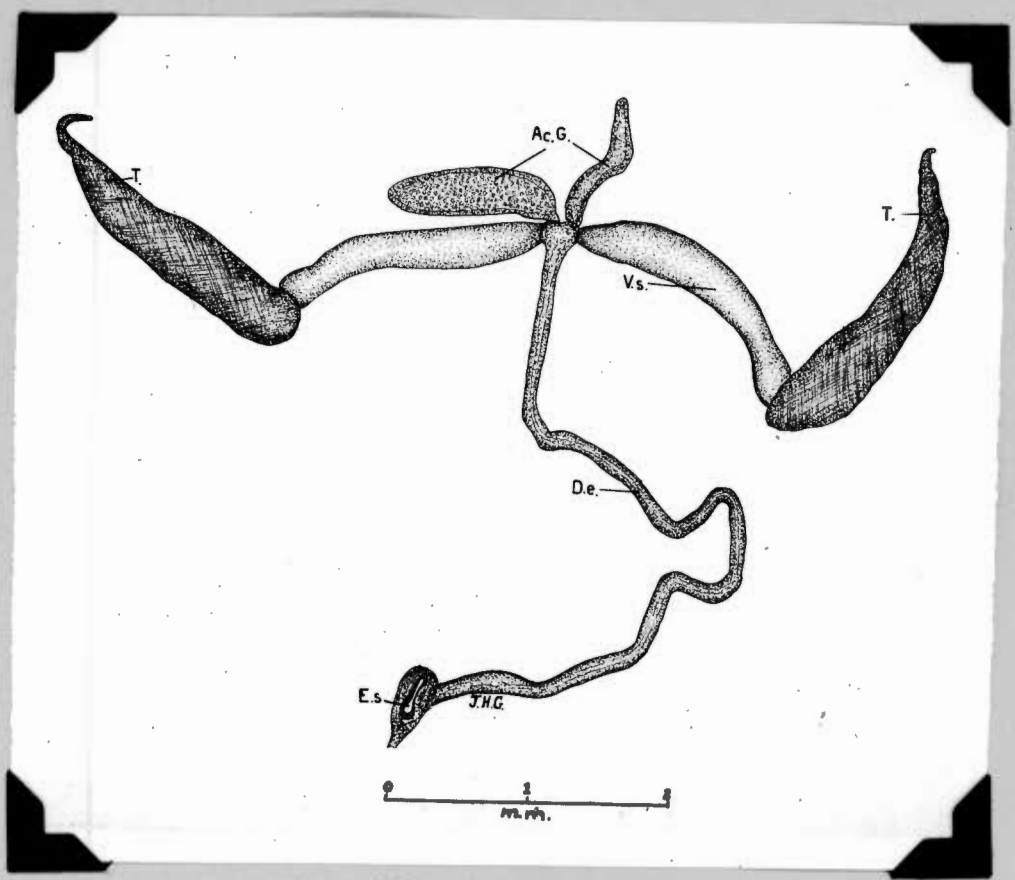

Fig. 113.

Male genitalia.

Ac.G. - Accessory glands. T. - Testes.
D.e. - Ductus ejaculatoris
E.s. - Ejaculatory sac.
V.s. - Vesicula seminalis.

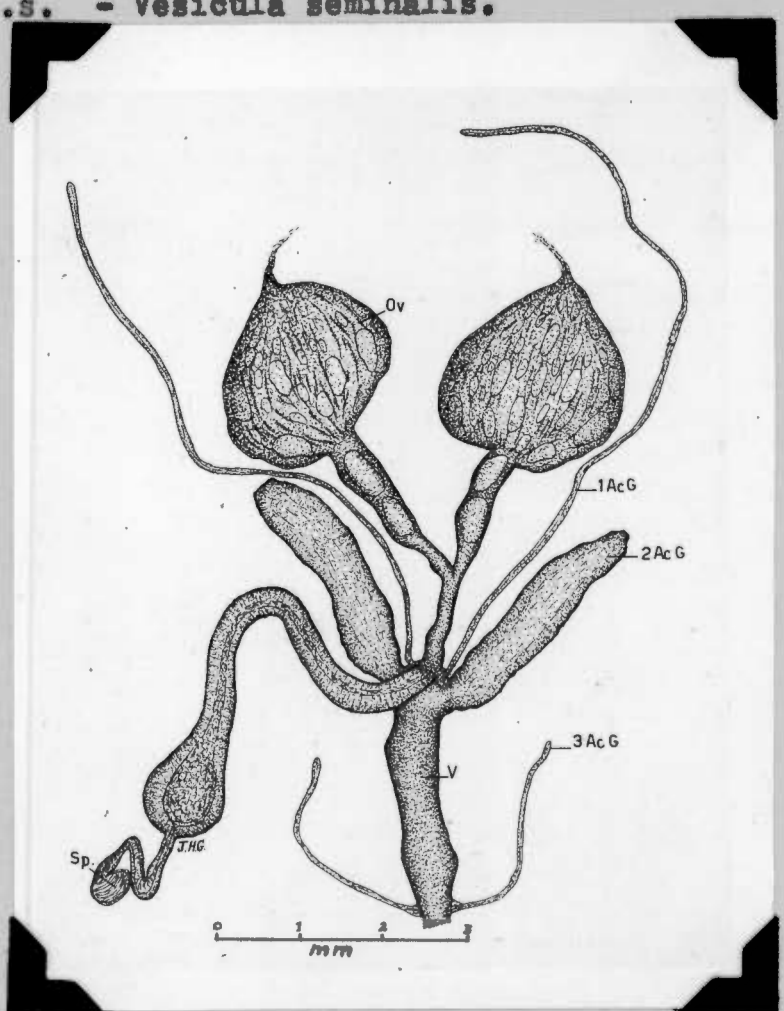

Fig. 114.

Female Genitalia.

Ov.- Ovaries. Ac.G. - Accessory glands.
V.- Vagina. Sp. - Spermatheca.

Under/...

Under natural conditions rarely more than one egg is oviposited on a single larva. But if a female fly is confined with one larva only, she might oviposit as many as 27 eggs on the same larva.

If females are kept without ~~feed~~ a host for a long period they start ovipositing their eggs on leaves, the side of the cage, or even on the heads of the other females present.

(c) Life cycle and morphology of the immature stages.

The time taken for the entire embryonic development of 35 eggs, which commences after it has been deposited, was found to vary from 48 to 55 hours and, although the eggs were all kept under the same temperature and humidity conditions, those which were removed from the host hatched 4 - 6 hours sooner than those which remained on it.

Tothill et al (1930) states that in the case of the Tachinid Ptychomyia the duration of the egg stage varied from 30 minutes to 100 hours, with an average hatching period of 40 hours.

When ready to emerge, the young larva bores through the ventral side of the egg directly into the body of the host. The first sign of hatching is the appearance of the bucco-pharyngeal apparatus through the thin ventral side of the egg, in the act of cutting a small opening through which the larva emerges. Should the egg be removed from the host, prior to hatching, the larva emerges normally until a few anterior segments are visible, but it then remains in that position until it eventually dies. (Fig. 115b)

Metcalfe (1922) reports that in the case of Sturmia nidiola, the host will make vigorous attempts to destroy the hatching larva before the latter has made its way inside, and occasionally these efforts are successful, particularly if the egg of the parasite was

deposited/.....

deposited near the posterior end of the host, where it may be crushed by the mandibles.

In E. terminalis, however, the larva does not show any discomfort when the egg hatches and the parasite bores unhindered into its head. The only way - and that is purely fortuitous -, by means of which the E. terminalis larva gets rid of the parasite egg, is by moulting. If the larva moults within 55 hours after the egg is deposited, the unhatched egg is shed together with the old skin.

Respiration.

While in the host, the larva meets its oxygen requirements by means of a special respiratory funnel, which is connected to the atmosphere, through the integument of the host. (Fig. 115c) This funnel is not attached to a trachea or spiracle as in Blepharipa scutellata. (Howard et al 1912)

The funnel which is of integumentary origin, originates at the point of entry into the host, that is, in all cases, directly underneath the egg.

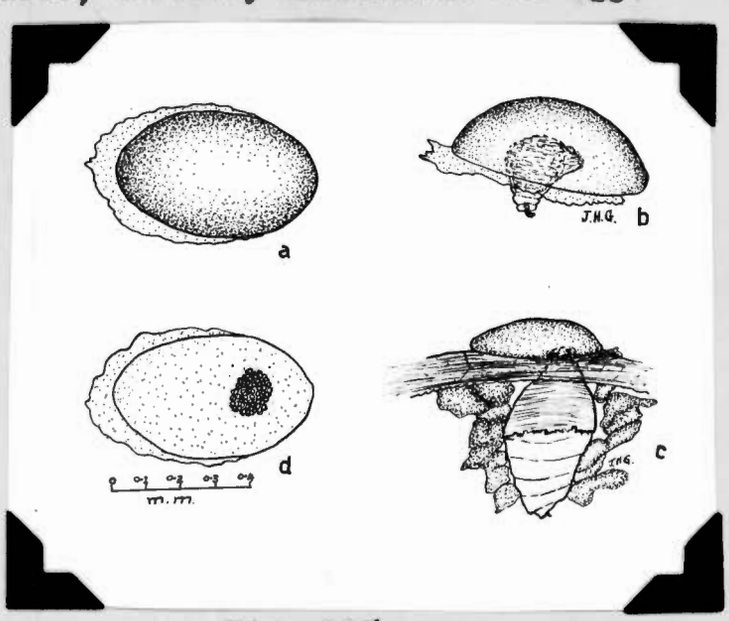

Fig. 115.

a. Dorsal view of egg. b. Lateral view of egg with larva emerging. c. Young larva and respiratory funnel. d. Ventral view of egg with the microphyle.

The moment the parasite larva enters the body of the host, the dark coloured funnel commences to develop, enveloping tightly several of the posterior segments of

the/.....

the parasite's body, on the last of which is situated a pair of spiracles. The funnel increases in size as the larva grows.

It is only in the third instar that the larva, after breaking the connection with the respiratory funnel moves freely in the body of the host.

Activities of the parasite larva.

Although, as previously ~~been~~ stated, as many as 27 eggs may be deposited on one host larva, only one adult parasite will emerge, the others being killed mainly during the 1st instar. If a larva, on which several parasite eggs were deposited, is dissected shortly after the eggs have hatched, a number of very young first instar larvae will be found dead in the near vicinity of a live one, some have been dislodged from their breathing funnels. If the dissection is done a little later, it will be found that there are still fewer live parasite larvae, and that the dead ones now include larger first instars. Should a larva be dissected at an even later stage two or three second instars might be found, but mortality will continue until only one is left.

The probable explanation of this is that the strongest parasite larva in a group, from its position in its breathing funnel, kills all the others within reach. As the remaining larvae grow, they are soon able to reach each other, and thus the process of selectivity continues until only one larva survives.

The young first instar larva, which is always attached to its breathing funnel, is situated in the head of the host, but as it grows, it extends into the thorax, where it moults and feeds until the third instar is reached. At this stage of development it leaves the breathing funnel and moves about freely in the abdominal region of the larva. It is during this instar that the host is killed.

By/.....

By the time the parasite leaves the host, practically all the tissues, with the exception of the skin, have been devoured.

Pupation:

When ready to pupate, the full grown larva gnaws a hole through the integument of its host. It was found that in the majority of cases, the host, although able to spin a cocoon prior to death was only rarely able to pupate. When this silken cocoon is present, the parasite gnaws a very regular, circular hole, 2.45 to 2.5 mm. in diameter through the silk at one end of it through which it emerges.

The parasite never pupates inside the cocoon of the host. Baldwin et al (1947) have shown that the Tachinid, Phorocera hamata always pupates within the cocoon of the host, but before pupating, the parasite larva will prepare an emerging hole.

The complete chitinisation of the puparium is completed in 10 to 12 hours, and during this process the colour changes from a buff-white to dark reddish-brown.

The puparium is always found next to the cocoon of the host, and very often among the loose silken threads.

The adult fly emerges by forcing off the two parts of the perculum (fig. 121c) by the expansion of the ptilinum. In most cases, the emergence of the fly from the puparium takes place in the early hours of the morning.

The data, in table 26, which were obtained from rearing 80 parasites, gives the duration of the egg, larval and pupal instars at 20°C.

	Egg	Larval instars	Pupa
Average	50 hours	19 days	12 days
Standard deviation	±1.095	±1.534	±1.107

Table 26.

Duration of the immature stages.

The egg/...

The egg. (Fig. 115)

The broadly oval, ventrally flattened egg is a typically macrotype pattern. The chorion on the dorsal surface is smooth, whitish in colour, opaque and thick, whereas the chorion on the ventral side is thin and more or less transparent. The micropyle is situated in this surface. (Fig. 115d)

At the junction of the flat, ventral surface and the lateral area, is a marginal flange which varies in size from egg to egg. This flange is possibly a portion of the hardened secretion with which the egg is attached to the larval head.

The eggs of T. fallax have no special way of hatching, as is the case with some of the other macrotype eggs. The larva simply bores through the ventral surface of the egg into the host.

The average dimensions of 25 eggs are 0.54 mm. to 0.56 mm. in length, 0.30 to 0.31 mm. in width and 0.22 to 0.23 mm. in hight.

First Instar. (Fig. 116)

The first instar is a tachiniform larval type. There are twelve well defined segments on which are situated bands of spinelike cuticular armature, (Fig. 117 c.) the longest spine being 0.001 mm. in length. The colour of the larva is buff-white. The posterior segments carries two inconspicuous spiracles, which open near the dorsal surface of the segment. (Fig. 116 c.) A few setae whose relative position on the figure are present in the near vicinity of the spiracle.

By measuring 10 newly hatched larvae, it was found that they were an average of 0.6 mm. long, and grow to approximately 1.5 mm. before moulting.

The bucco-pharyngeal armature, (Fig 116 a.) is well developed and strongly chitinised. It has no

articulations,/....

articulations, because the median tooth, as well as the intermediate and basal regions are fused. The median tooth, which is directed forwards and downwards, bears a row of teeth on its dorsal margin.

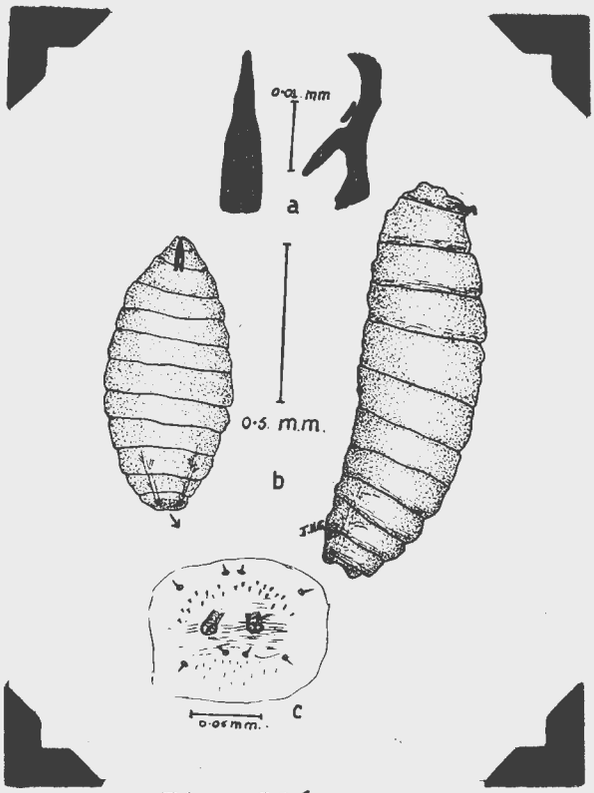

Fig. 116.

a. Dorsal and Ventral view of the buccopharyngeal apparatus.

b. Newly hatched and slightly older first instar larva.

c. Spiracles on last segment.

The dorsal and ventral wings of the basal region are not as strongly sclerotised as the median region. The ventral and dorsal wings are deflected ventrally. The salivary sclerite, which is well chitinised and prominent, is situated just ventral to the intermediate region.

Baer (1920) in his description of T. larvarum uses the term hypopharyngeal sclerite ("hypopharyngealsklerit") for this plate or salivary sclerite.

The anterior region is about 2½ times as long as the dorsal length of the median tooth taken from the dorsal notch.

Second instar:

The main differences between the first and second instars, apart from their size, is the armature on the

integument/...

integument, the spiracle, and the bucco-pharyngeal armature. The armature on the segments is relatively longer and there is a difference between those occuring on the anterior, middle and posterior region of the larva. (Fig. 117, a.b.c.)

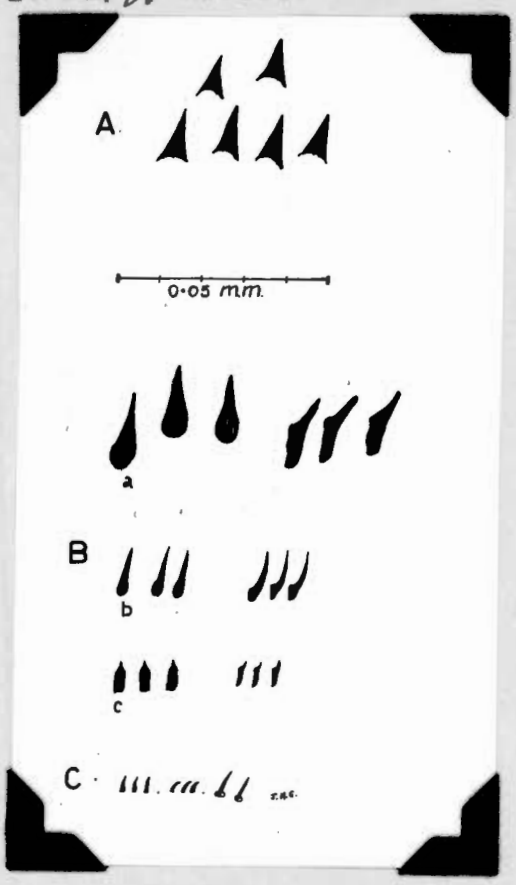

Fig. 117.

A. Armature on last instar larva.

B. Armature on second instar larva.

a. Anterior region.
b. Middle region.
c. Posterior region.

C. Armature on setae of the first instar.

The posterior spiracles (Fig. 115b) are more prominent than in the first instar, although they are not much more heavily chitinised and in addition to the posterior spiracles, an anterior pair is also present on the posterior margin of the second segment. (Fig. 118). The bucco-pharyngeal armature hereto is well developed and strongly chitinised, (Fig. 119) and the anterior, intermediate and basal regions are again fused, the main difference between the two instars, being that the anterior, ventrally curved, region row consists of a narrow, long distinctly paired mandibular hook.

Fig. 118/.....

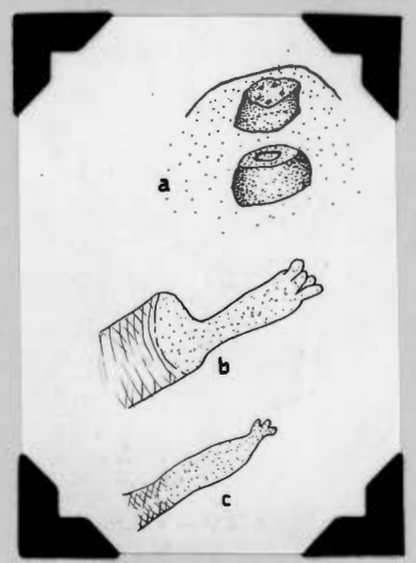

Fig. 118.

a. Maxillary organ and antenna - last instar.
b. Anterior spiracle - last instar.
c. Anterior spiracle - Second instar.

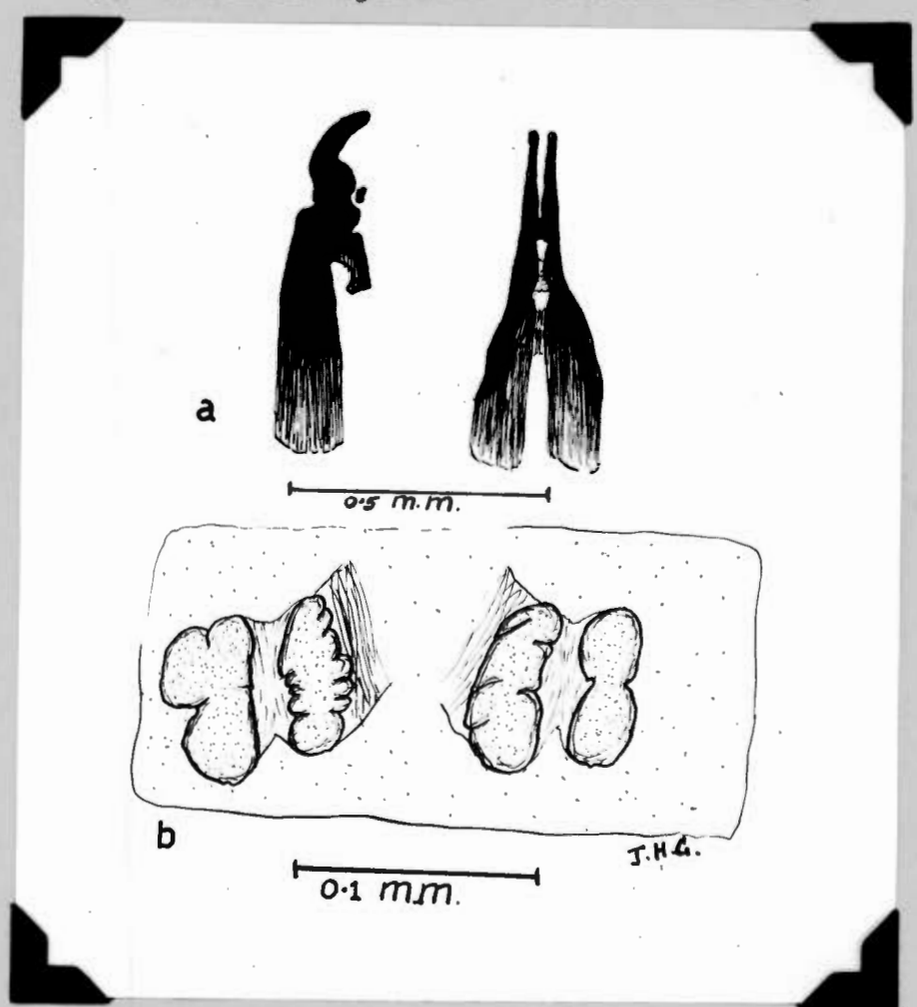

Fig. 119.

a. Bucco-pharyngeal armature of the second instar larva.
b. Posterior spiracles - second instar larva.

The salivary sclerite is not fused to the intermediate region and the anterior and intermediate regions are of the same length. As in the first instar the basal region consists of two wings, the dorsal one, being about

3 times/.....

3 times longer than the ventral one, and also much wider. The dorsal and ventral margins of the dorsal wing are straight, without any notches or depressions. The caudal region of the dorsal wing, and the dorsal region of the ventral wing exhibit a lower degree of chitinisation than the other parts of the wings. The average length of this instar before moulting is 7 mm.

Third instar:

The antennae and maxillary organs (Fig. 118a) of this instar, are poorly chitinized, but clearly visible.

The shape of the armature on the segments is triangular as shown in figure 117A.

The bucco-pharyngeal armature, as in the previous two instars is heavily chitinised, but the three regions are fused and are capable of articulation. (Fig. 120)

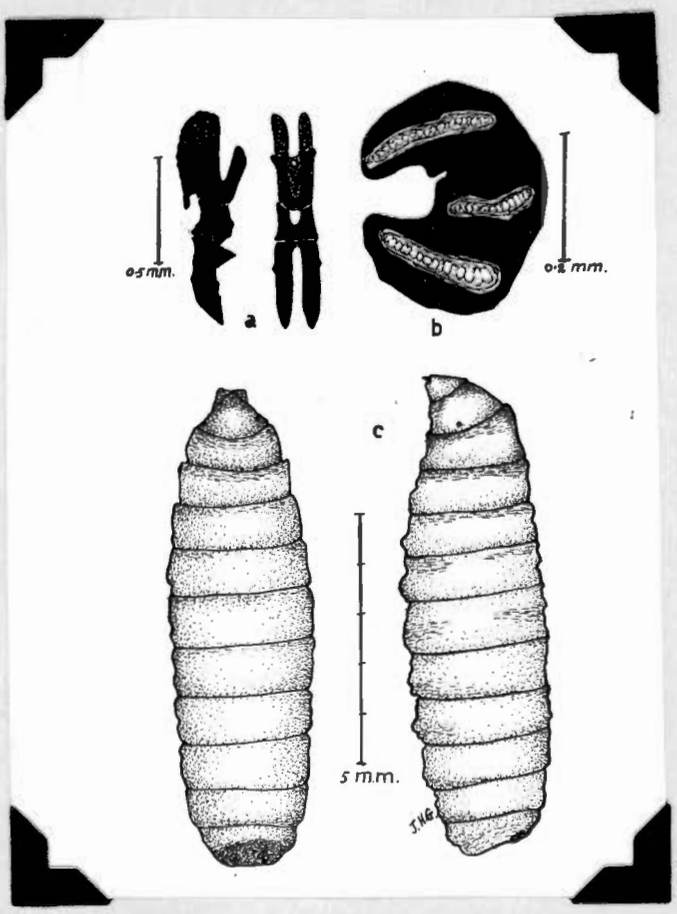

Fig. 120.

a. Bucco-pharyngeal armature.
b. Spiracle (Dorsal.)
c. Dorsal and ventral view of larva.

The median tooth is again paired and has a

rough/.....

rough dorsal margin. In this instar, a downwardly projecting process, the ventral ~~apophipis~~ apophysis occurs on the ventral surface of the anterior region at its point of articulation with the median region. (Fig. 120a.)

Here again the anterior sclerite is heavily chitinised. The salivary sclerite is not visible in this instar, but the projection on the ventral surface of this region could possibly be regarded as the fused sclerite. In Sturmia Jones (1938) found a hypopharyngeal sclerite between the ventral apophysis of the mandibular sclerite and the fused salivary sclerite. In T. fallax, however, this sclerite seems to be absent or fused in such a manner that it is not visible.

The basal region has an anteriorly directed process on the broad dorsal wing.

Only a third of the anterior region of the dorsal wing is heavily chitinised.

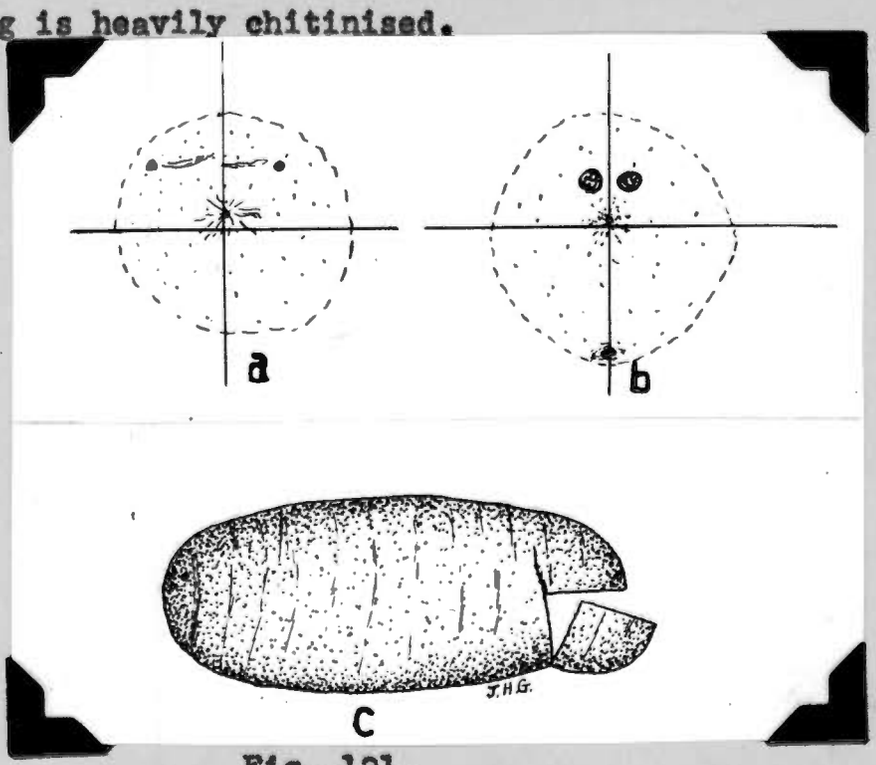

Fig. 121.

Puparium.

a. Anterior spiracles.
b. Dorsal spiracle and anus.
c. Puparium showing the puparial cap.

The lower wing is directed slightly downwards and is heavily chitinised throughout. It is about half the length of the dorsal wing and very much narrower. The length of this instar varies from 8 - 10 mm. before

pupation/....

pupation.

Pupa: (Fig. 122).

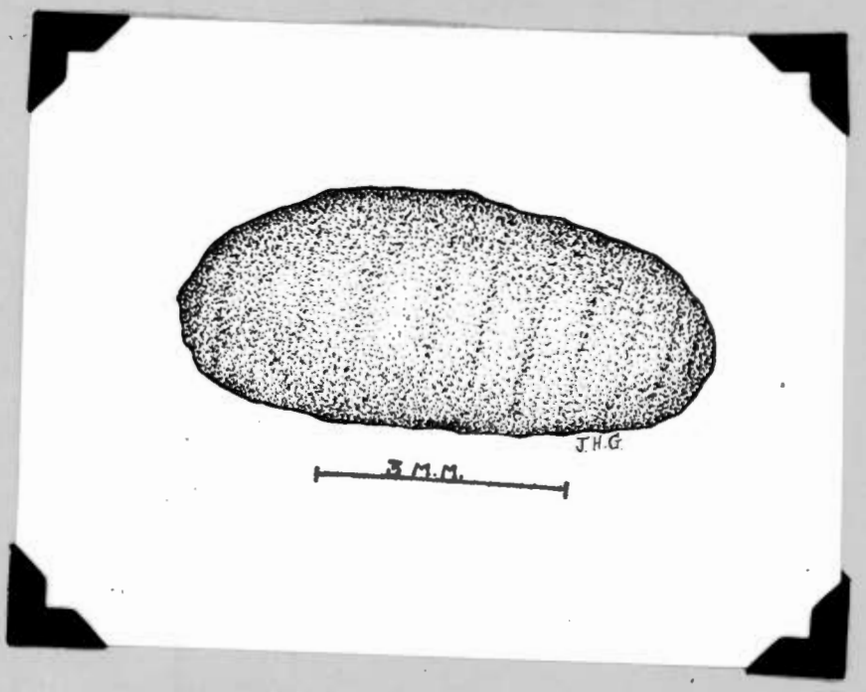

Fig. 122.

Pupa of T. fallax.

The barrelshaped puparium varies from 7 - 9mm. in length, the middle segments being the broadest. The segmentation is poorly defined, and only indicated by slightly darker areas and very slight ridges. The posterior spiracles, the anus and the anterior spiracles, are those of the third instar, and their relative position on the pupa are shown in figure 121 a & b.

4. PIMPLA /.....

4. PIMPLA BICOLOR. BOUCHè. ICHNEUMONIDAE.

Pimpla bicolor, (fig. 123) the most important parasite of the Euproctis terminalis insect parasite complex, is a true internal pupal parasite, and has never been observed to attack the larvae. This, however, is not always the case with Ichneumid parasites, since Clausen (1940) has recorded that the Ichneumid Aylophrurideа agrili Vees, will attack the larvae of its host in the autumn and in Spring, attack the pupae.

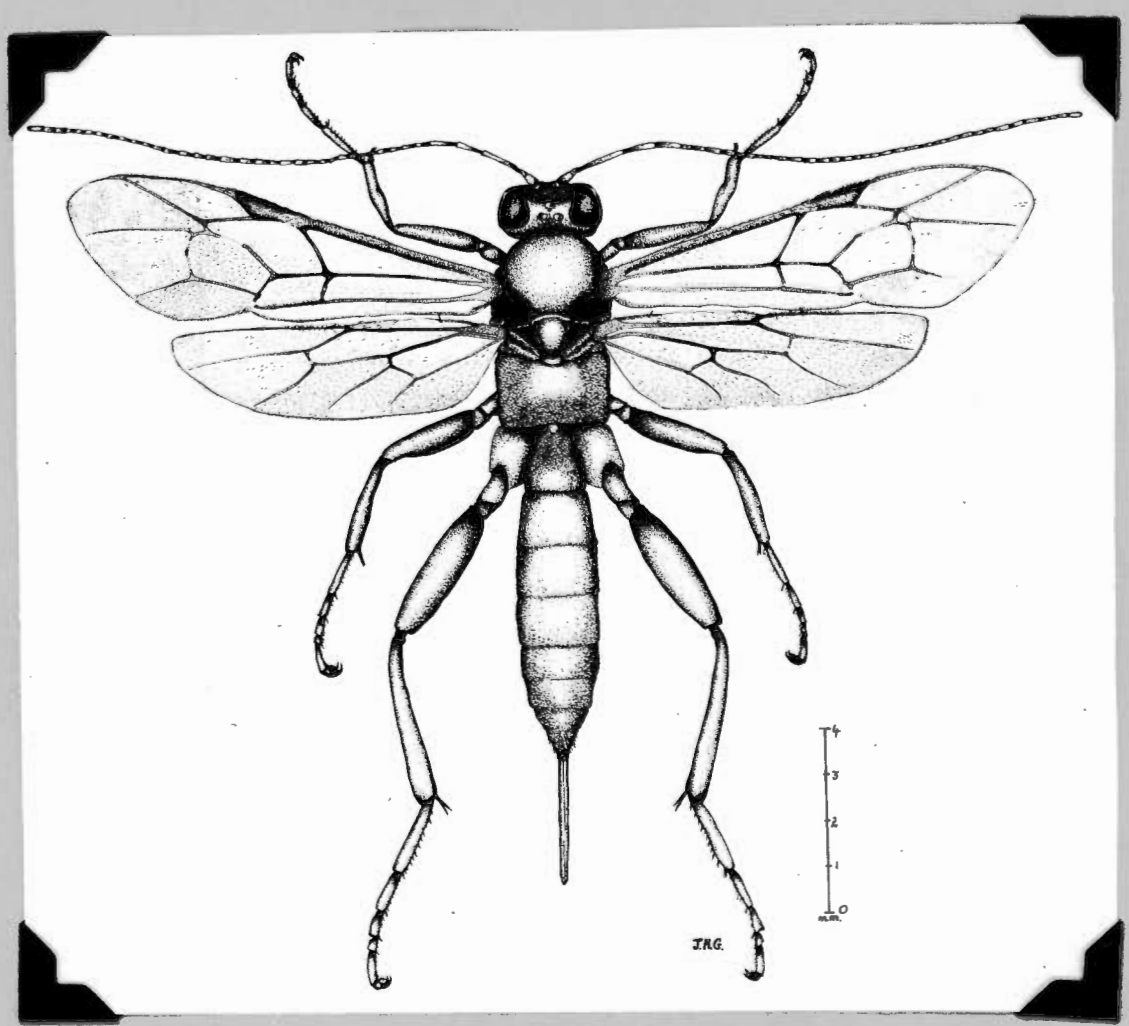

Fig. 123.

Adult Pimpla bicolor female.

The adult Pimpla bicolor has well developed wings and is a very active flyer. In plantations where there is an abundance of E. terminalis pupae, this parasite may be observed in and about the heaps of debris under which most Euproctis pupae are found.

Although the Pimpla adults are very photopositive, they will readily seek out the pupae in the dark areas under the debris.

(a) Feeding/.....

(a) Feeding and longevity of the adults.

The adults of P. bicolor were kept in wooden boxes with a sliding glass top, and were fed on honey, sugar and water. If the adults were deprived of food and water it was found that there was a marked difference in their life span, (Table 27) although they oviposit normally without food.

	With food.	Without food.
Mean	16	8
Standard deviation	± 2.270	± 1.374
Significant difference	1.4795	

Table 27.

Longevity in days.

Experiment carried out with 25 parasites.

In only two instances has P. bicolor been observed to feed in the cultivated plantations. The first occasion was on honeydew from aphids, and the second, on the nectar of the flowers of a bulbous plant, Eucomis humilis, which occurs along the sides of roads in the plantation, and flowers in December.

(b) Oviposition.

The female parasite pierces the cocoon with her ovipositor and lays her eggs inside the pupa where the complete development of the larval instars and the pupa takes place.

Genitalia.

The reproductive organs of the male and female are of the typical Ichneumonid type. (Figs. 124 & 125).

Fig. 124/....

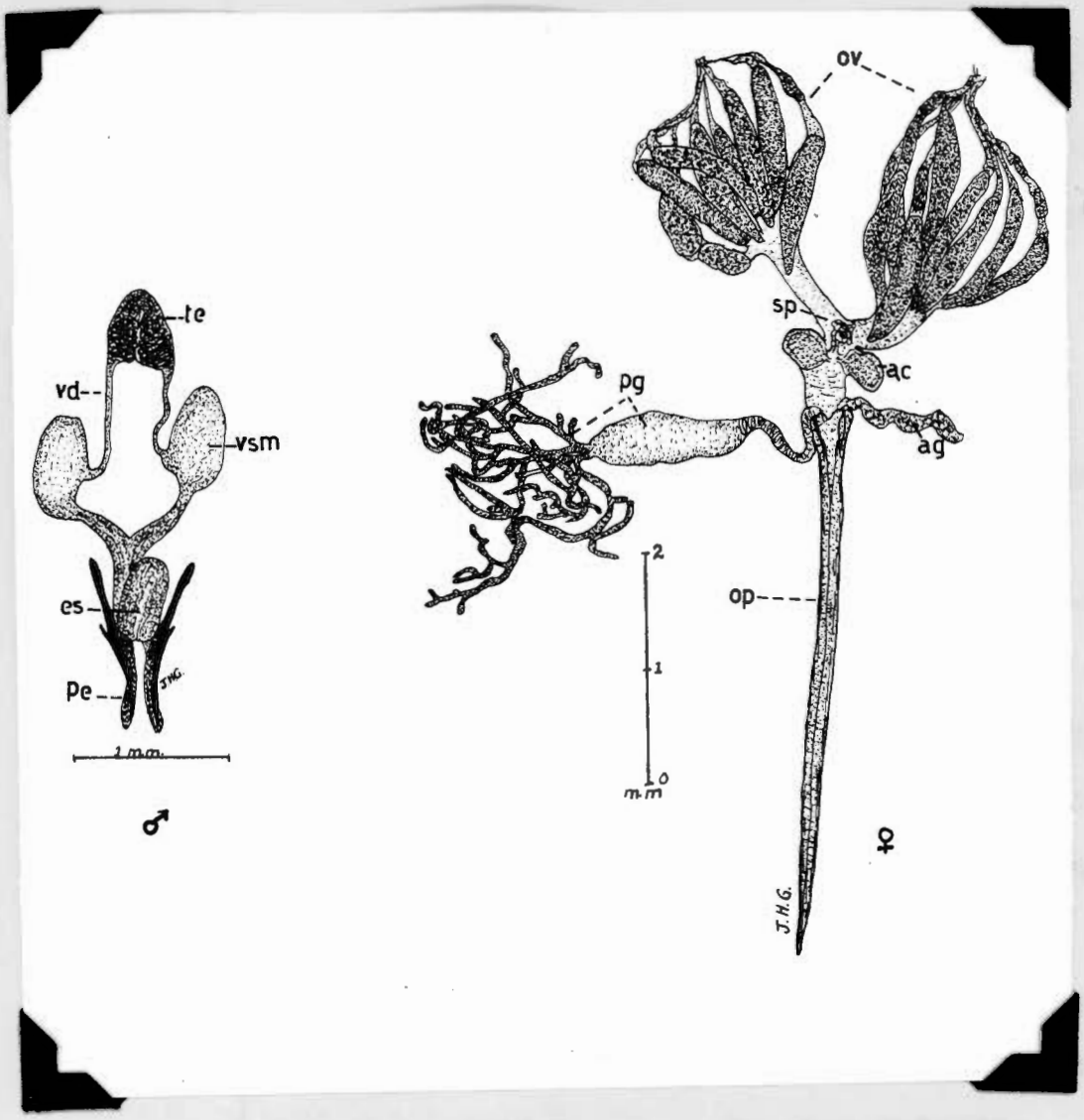

Fig. 124.

Male and female genitalia of
P. bicolor.

ac. - accessory gland
es. - ejaculatory sac.
ov. - ovaries.
pg. - poison gland and sac.
te. - testes
vsm.- vesicula seminalis.
ag. - alkine gland
op. - ovipositor
pe. - penis.
sp. - spermatheca
vd. - Vas deferens

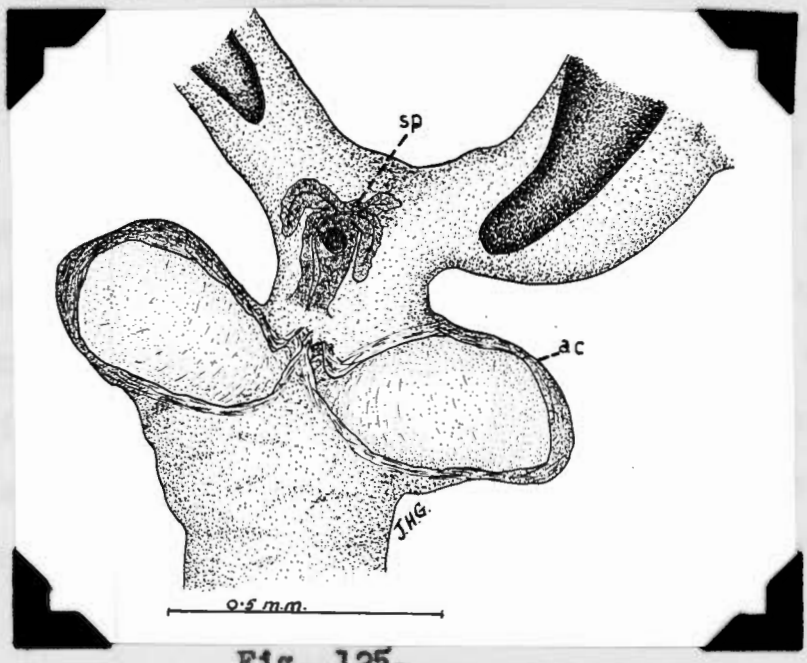

Fig. 125.

Enlargement of the spermatheca
of the genitalia.

sp. - spermatheca. ac. - accessory gland.

The ovaries consits of eight ovarioles, with only one

matured/....

mature egg in each. The relative position and shape of these organs are shown in fig.124 with an enlargement of the spermathecal area in fig. 125.

The young females mate the same day on which they emerge and start ovipositing the following day.

The female parasites are attracted to the pupae by their odour. This has been clearly demonstrated by crushing a pupa in the hand. The parasites were immediately attracted by the odour and settled on the hand as close to the crushed pupa as possible. In tests made by the writer it was found that if a choice was offered to the parasite between naked pupae and those contained in the cocoons, the parasite invariable oviposited in the latter. It would appear, therefor, that for puposes of oviposition, the cocoon fulfills an important role although not necessarily an essential one. It also fulfills a mechanical function, since the parasites make use of it to obtain a more secure foothold when thrusting the ovipositor into the pupa. They very often become dislodged if they try to oviposit on a naked pupa.

Marsh (1937) observed that the parasite Spilocryptus is only attracted to the larvae when they begin spinning. This he ascribes to an odour response. In P. bicolor, however, the naked pupae covered in a piece of cotton wool, is just as readily parasitised as those in the cocoons. In this case the attraction appears to be caused by the sense of touch. It has been observed that if a piece of cotton wool is placed in a cage with female parasites, they will even lay their eggs in this cotton wool with no pupae present to impart any odour.

Oviposition takes place anywhere in the pupa and no area appears to have any special preference. The female will, however, only lay her egg if she can thrust her ovipositor deeply into the pupa, and she will thus continue searching for such a suitable spot until she

eventually/....

eventually finds one for e.g. from the tip of the pupa it will be thrust obliquely into the pupa.

The female often feeds on the body fluids which adhere to the ovipositor after oviposition has taken place, but she never enlarges the wound with her mandibles to feed on the tissues of the pupa, as some members of this family will do.

On an average the egg hatches after 44 hours and in no instance has an increase in size been noted during the incubation period. The embryonic development commences as soon as the egg is laid, and this may easily be observed through the transparent chorion. (Fig. 126)

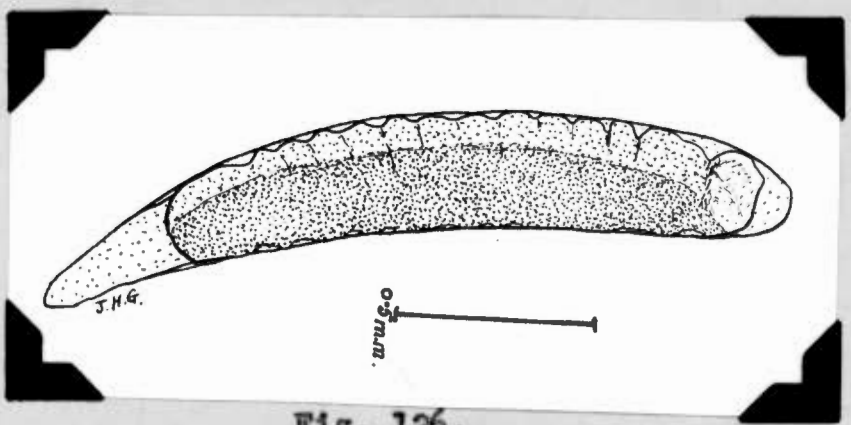

Fig. 126.

Egg just before hatching.

When the larva is fully developed, the egg is ruptured at the posterior end and through this opening the larva emerges. Whether the young larva causes this rupture in the chorion with its mandibles, or whether it is due to internal pressure is not clear. (Fig. 127). When epiparasitism occurs with P. bicolor, only one parasite survives, the other larvae in the pupa being killed in the first and second instars.

Since the first instar is more mobile and its mandibles are better adapted for fighting, the older instars are usually the ones to suffer. Dead first and second instar larvae which were examined were always found to be covered with scars that could easily have been caused by the mandibles of another larva.

It/.....

Fig. 127.

The larva of P. bicolor hatching from the egg.

It has been observed that if a single E. terminalis cocoon with a pupa is placed among female parasites, they will immediately start to oviposit in it, and up to 121 eggs have been found in a single pupa.

When the parasite larva is ready to pupate, it has usually consumed all the food available in the pupa, and only the chitinised exterior shell, completely filled with the parasite larva is left. The larva pupates in this chitinised shell without spinning a cocoon.

A very small percentage of the parasites go into diapause, to emerge several months later in mid-summer. Diapause was never observed in material reared in the laboratory, but in material from field collections, a small number of overwintering adult larval parasites are always to be found in some of the old pupal cases.

During the three months in which E. terminalis pupae are found at the Jessievale plantation there are two generations, with a possible third, but in the other plantations there are more generations, as in these localities

the/.....

the pupae are found throughout the year.

In collections made from the field it was found that males predominate, the ratio of males to females being two to one. This figure was obtained from an examination of 1722 adult parasites reared from a field collection. In P. pondorum, however, Clausen (1940) found that the set ratio is four females to one male.

(c) Life cycle and morphology of the immature stages.

Under laboratory conditions, it was ascertained that at a temperature of 22°C and relative humidity of 60%, P. bicolor took in 10 cases from 24 to 63 days to develop from egg to adult. (Table 28).

Development in days	
Average	30
Standard deviation	± 6.218

Table 28.

Time taken for the imature stage of P. bicolor to develop.

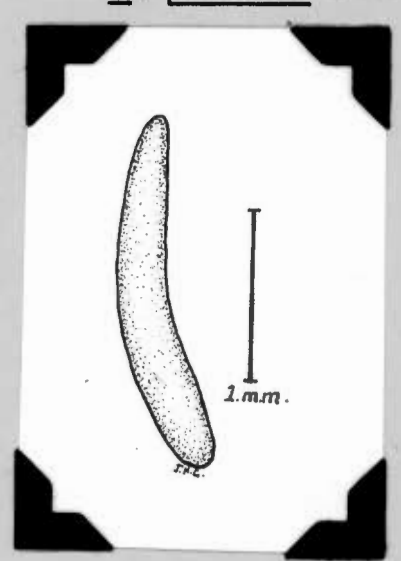

Fig. 128.

The egg of P. bicolor.

The transparent white egg has an elongated sub-reniform shape, with the one end slightly broader than the other. The length varies from 2 - 2.2 mm. and the maximum breadth varies from 0.3 - 0.4 mm. There is no pedicel or stalk

ner/....

nor are there any markings present on the chorion.

First Instar.

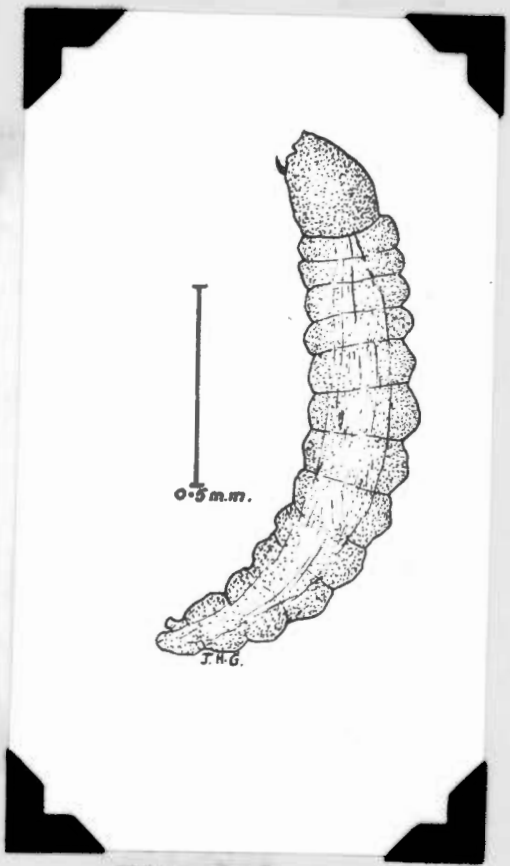

Fig. 129.

First instar of P. bicolor.

The first instar larva (Fig. 129) is of the hymenopteriform type. The yellowish white cylindrical body consists of 13 segments, with no setae or chitinised spines on them. The head is slightly darker than the body and poorly chitinised. The average length of the newly hatched larva is 1.5 mm. The mandibles, which are inconspicuous on account of their relatively light colour, are slightly curved, sharp and approximately 0.7 mm. long.

Although the larva has a well developed trachael system there are no spiracles present. In the first and also in the second instars the trachael system has special branches which show extensive ramifications just under the skin, and these probably function as a modified gill-like organ.

Imms (1918) found that the first instar of P. [illegible] possessed nine pairs of spiracles

Second Instar.

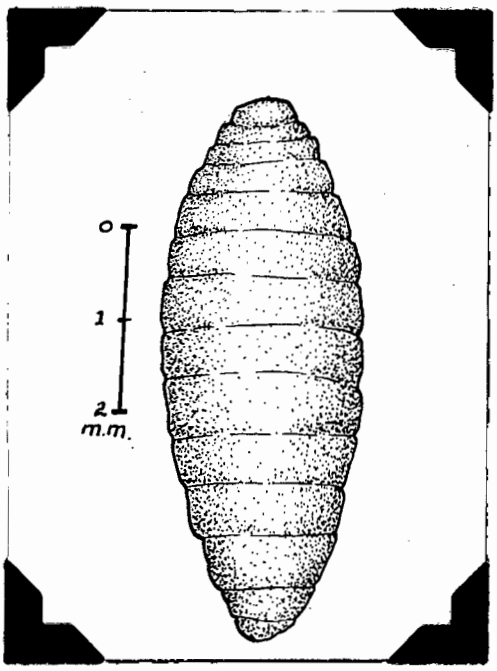

Fig. 130.

Second instar of P. bicolor.

The second instar larva (fig. 130) differs only slightly from that of the first instar. The head is now the same colour as the body and is relatively much smaller. The body is much wider in relation to its length, a newly moulted 2nd instar being 6 mm. long and 2.2 mm. wide at the 7th segment. No further development has taken place in the tracheal system.

Third and last instar: (Fig. 131)

It is quite common to find three larval instars in the Ichneumonidae, although some species have been found to have 4 and 5 larval instars. After careful observations only 3 instars could be found in P. bicolor.

Fig. 131./.....

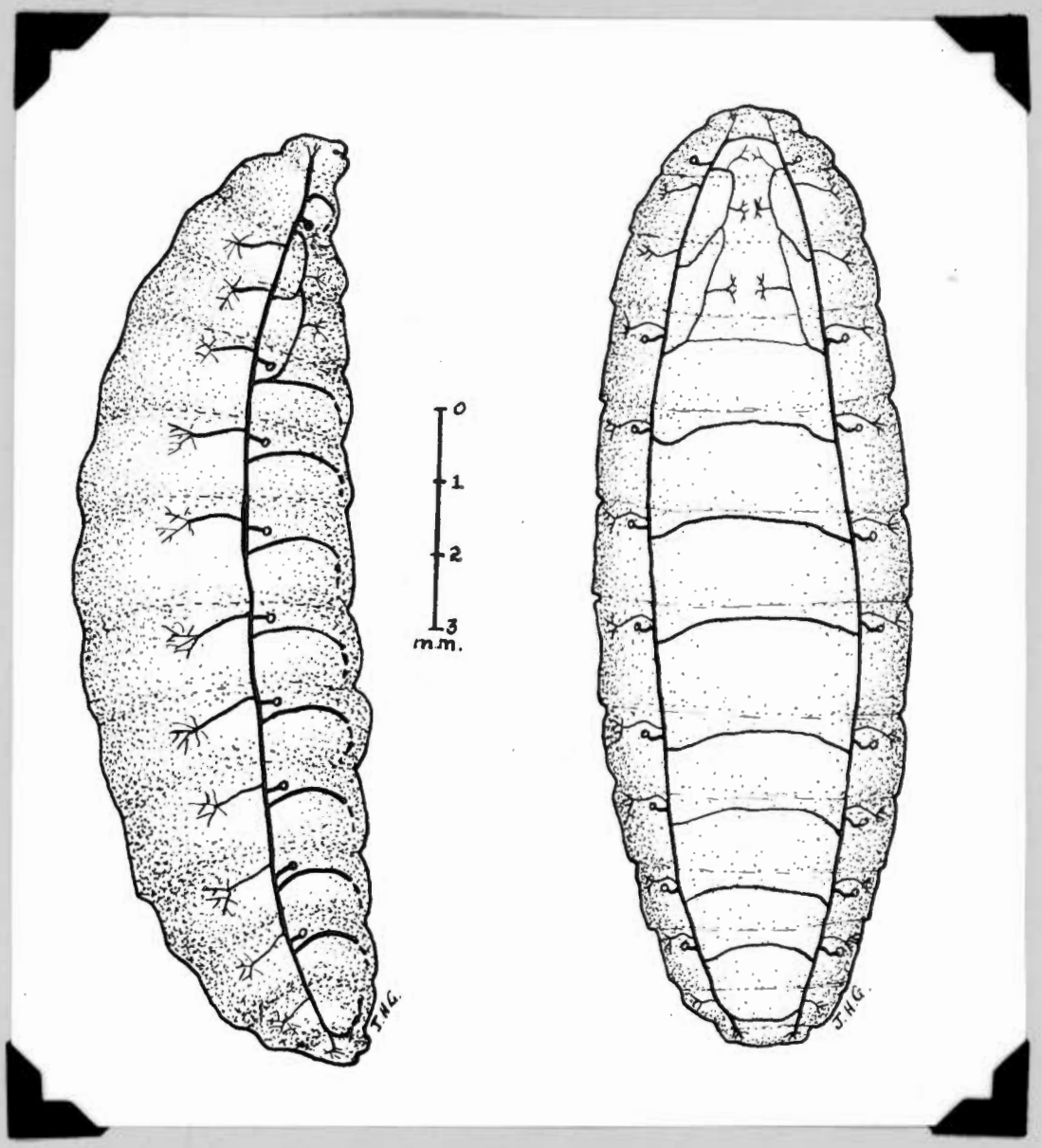

Fig. 131.

Lateral and dorsal aspect of the third and last instar of P. bicolor.

The average length of the newly moulted larva is 11 mm., with an average width of 4.5 mm. and the integument of the well defined body segments is smooth and shiny.

In this instar the tracheal system has become further developed, nine spiracles now being found. The first pair is situated at the posterior margin of the first body segment, and the second to the ninth pairs are situated near the anterior margin of segments four to eleven.

The tracheal system consists of two main longitudinal trunks which are connected by an anterior commissure in the 12th segment. In the fourth to the twelth segments the main longitudinal trunks are further connected by eight ventral commissures, which leave the lateral trunks slightly posterior to the spiracles.

The dorsal tracheal, which leave the two main trunks/...

trunks slightly anterior to the spiracles, proceed dorsally where they divide to supply the dorsal section of the segments with tracheoles.

In addition to the main trunks there are two lateral trunks, extending from the posterior margin of the first segment to the anterior margin of the fourth segment. They are connected to the main trunks by three branches, one in the first, one in the third and one in the fourth segments.

Mouthparts: (The terminology used is that proposed by Thorpe (1930) and Salt (1931)).

The facial rods, mouth parts and facial setae of the last instar P. bicolor larva and their relative position to one another, are shown in figure 132.

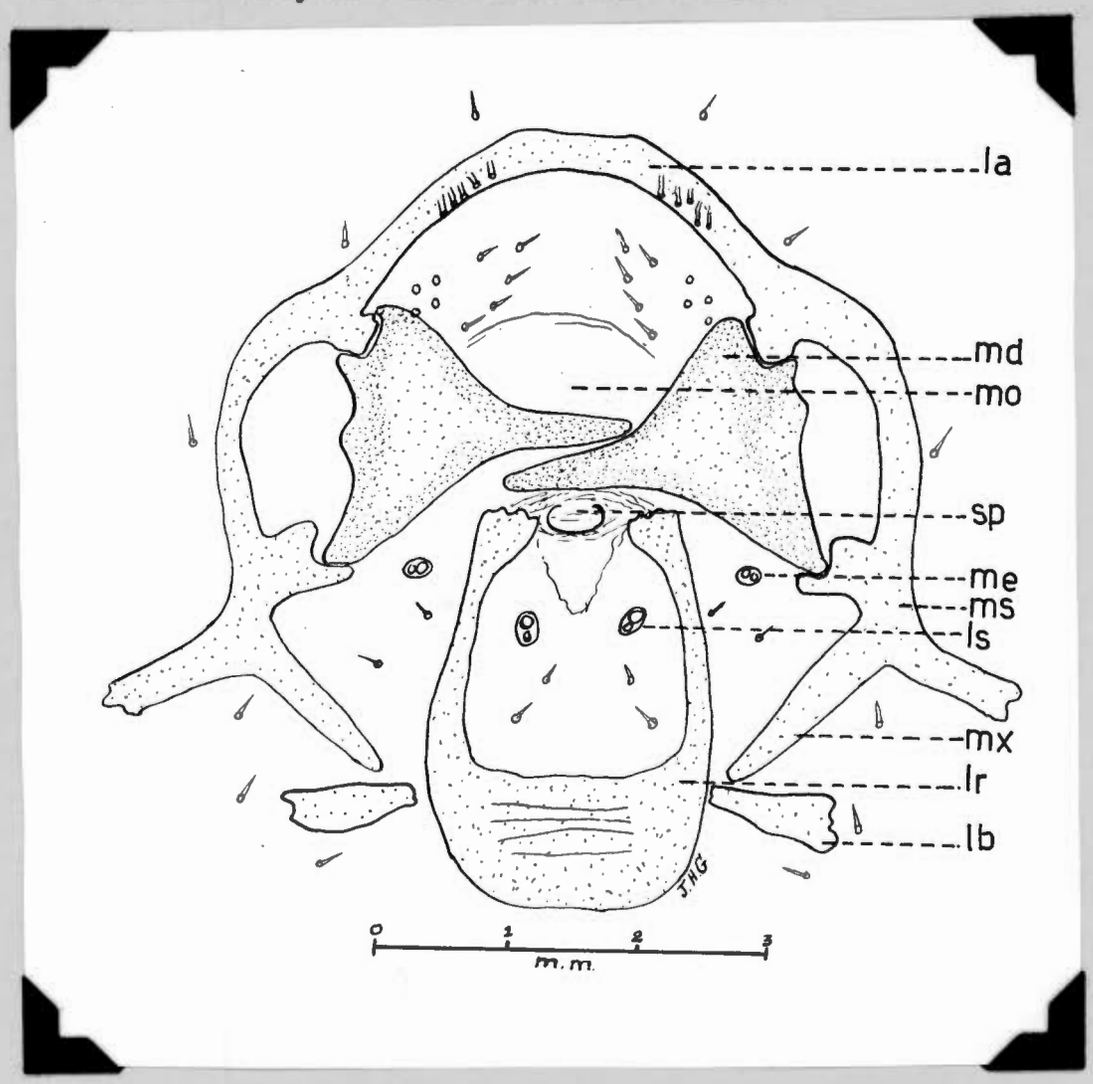

Fig. 132.

Mouthparts of the adult larva of P. bicolor
la. - labral arch. lb. - labial strut. lr. - labial ring.
ls. - labial sensillae md. - Mandible me.- maxillary sen-(silla
mv. - mouth opening. ms. - mandibular strut.
mx. - maxillary strut.

Labial ring./...

Labial ring.

The U shaped, pigmented, labial ring (lr) which surrounds the labial area below the mouth, is well defined, is very broad at its lower margin, and is nearly closed at the end nearest the spinneret.

In P. detrita Hlgr., P. ruficollis Grav. and P. brevicornis Grav. the lower margin of the labia ring has lobes, but in P. bicolor, however, the margin is smooth and the lobes are absent.

Labial struts. (lb)

On each side of the labial ring, at the base, there is a simple rudimentary labial strut, the inner ends of which almost reach the labial ring.

In P. ruficollis Grav. the inner end of the labial struts are fused with the maxillary struts, whereas in P. examinator Gray. and P. bicolor, they are free and confused.

Maxillary struts. (Mx)

The maxillary struts extend downward to the lower margin of the labial ring, and are fused at the other end with the mandibular strut. The mandibular struts are fused with the labral struts, which in their turn are fused with each other to form a labral arch, as is the case with P. detrata and P. brevicornis. (Salt 1931)

Mandibles. (md)

The triangular shaped mandibles are well sclerotised and are sharply pointed, with the sharp ends as straight as in P. detrata, but unlike P. detrata, there are no bristle-like setae on them. They articulate with the labral and mandibular struts.

Sense organs. (ls, me)

The labial sensillae (ls) are situated just below the spinneret in the area surrounded by the labial ring. The maxillary sensillae, (me) on the other hand are situated

below/.....

below and towards the base of the mandibles.

The relative position of the setae are shown in the figure.

The antennae which consist of one segment are cone shaped appendages situated on a circular raised area.

Pupa. Fig. 133.

The prepupa is of the same yellowish white colour as the mature larva. The segments of the larval body here commences to divide into the head, thorax and abdominal regions, and the eyes, which at this stage also start developing are clearly visible in the head region.

The pupa is of the common exate Ichneumonid type. The colour is mainly white, but it gradually darkens, and eventually the head and thorax turns black, while the abdomen and legs turn into a madder brown.

Alternative host.

The silk worm, Bomby mori. was used as an alternative host in studying the biology of P. bicolor.

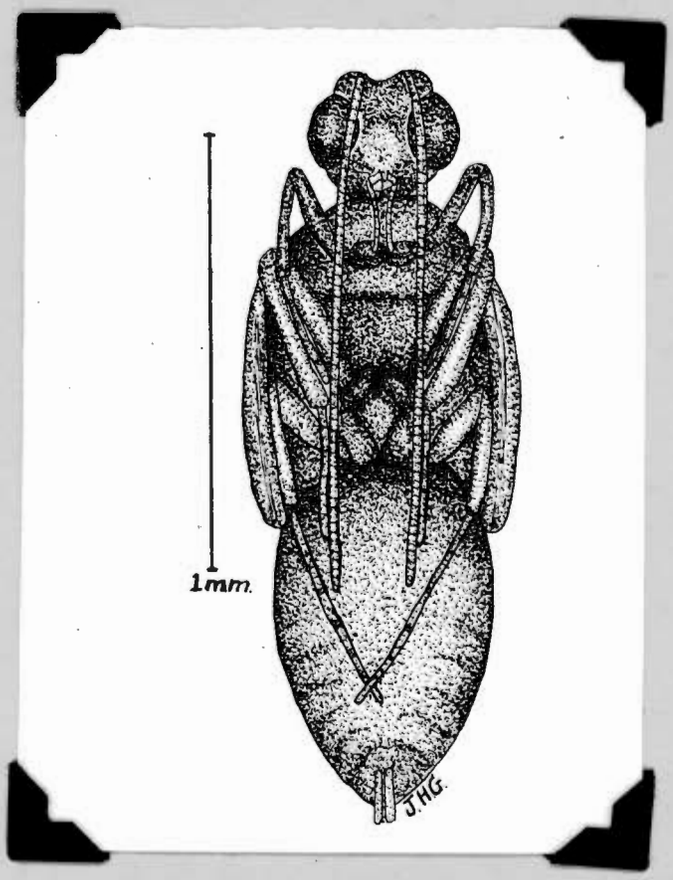

Fig. 133.

Pupae of P. bicolor.

This parasite finds it very difficult to penetrate/..

trate the thick silk of the cocoon with its ovipositor, but it will readily oviposit if some of the silk is removed, thus enabling the ovipositor to penetrate the cocoon more easily. The removal of the silk is, however, a laborious task, hence all the pupae were removed from their cocoons and were thinly covered with cotton wool. The parasites were then found to oviposit readily and without any difficulty.

The ideal pupae are the smaller ones, since a very peculiar phenomenon was observed when large silk worm pupae were used. In these cases the last instar of the parasite grew about 4 mm. longer than the normal ones found in Euproctis pupae, and instead of pupating and emerging as outsize adults, they died in every instance.

CHAPTER IX.

INFLUENCE OF DEFOLIATION ON P. PATULA.

When a leaf-eating insect destroys a high percentage of the foliage of the tree, transpiration and photosinthesis are decreased in proportion to the degree of defoliation. During such periods the wood increment and height of the tree will be correspondingly below normal. When a tree of known history is felled and the annual rings are examined, periods of severe defoliation are thus characterised by the narrow annual rings which reflect decreased growth. False or additional annual rings are in cases put on by trees, which may confuse interpretation, but in trees of known history these may readily be differentiated from those caused by insect-defoliation. (Figs. 134 and 135.)

The narrow annual rings resulting from defoliation of a tree by insects closely resemble those caused by forest fires, according to Craighead (1927), but if the history of a tree or plantation compartment is known, it can be determined which of these two agencies is responsible for the low increment. The climatic conditions prevailing during successive years from the time of planting should also be borne in mind when wood increments are assessed, since it is a known fact that during years of drought trees grow very little and the annual rings would be proportionately narrow.

Complete defoliation of a P. patula tree by E. terminalis is preceded by a period of a few years during which the insect population progressively increases to the peak level which results in 100% defoliation. During this period of waxing populations there is a corresponding increase in foliage destruction and decrease in the annual wood increment, the increment reaching its lowest level during the year of complete defoliation. In the year after complete defoliation, the increment still remains below the normal

level,/.....

level, although the insect population then drops to a very low level.

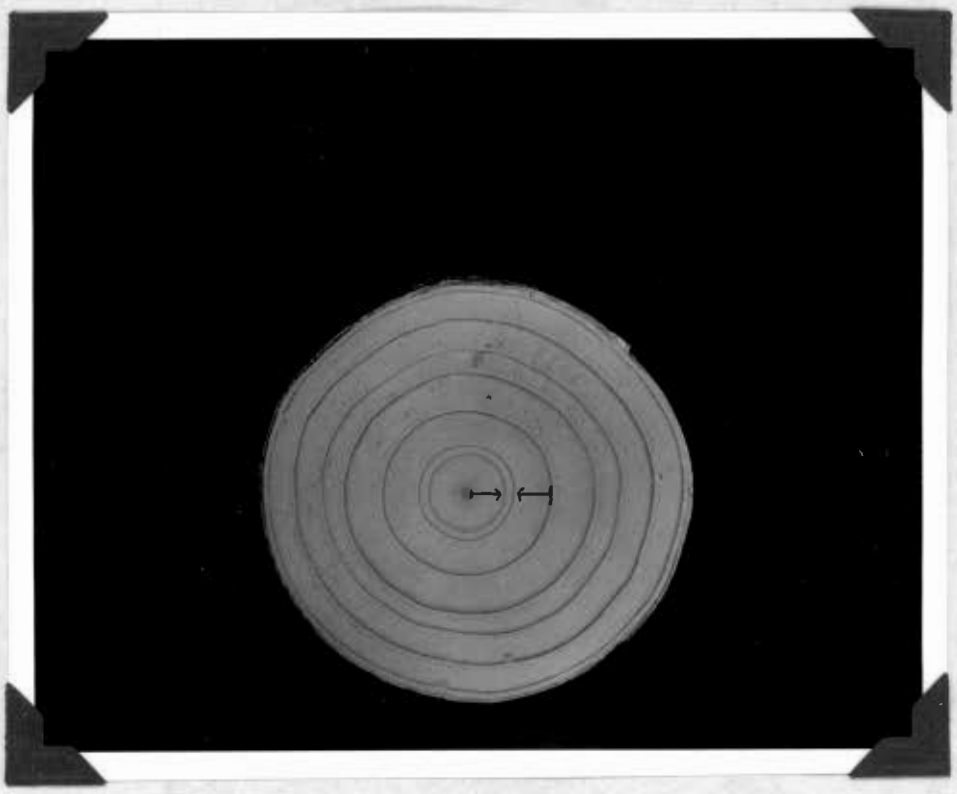

Fig. 134.

Section of a P. patula tree from Block C17, 35 feet from the ground, showing clearly the effect of a complete defoliation during the 1948-49 season, reflecting on the annual rings the loss of growth.

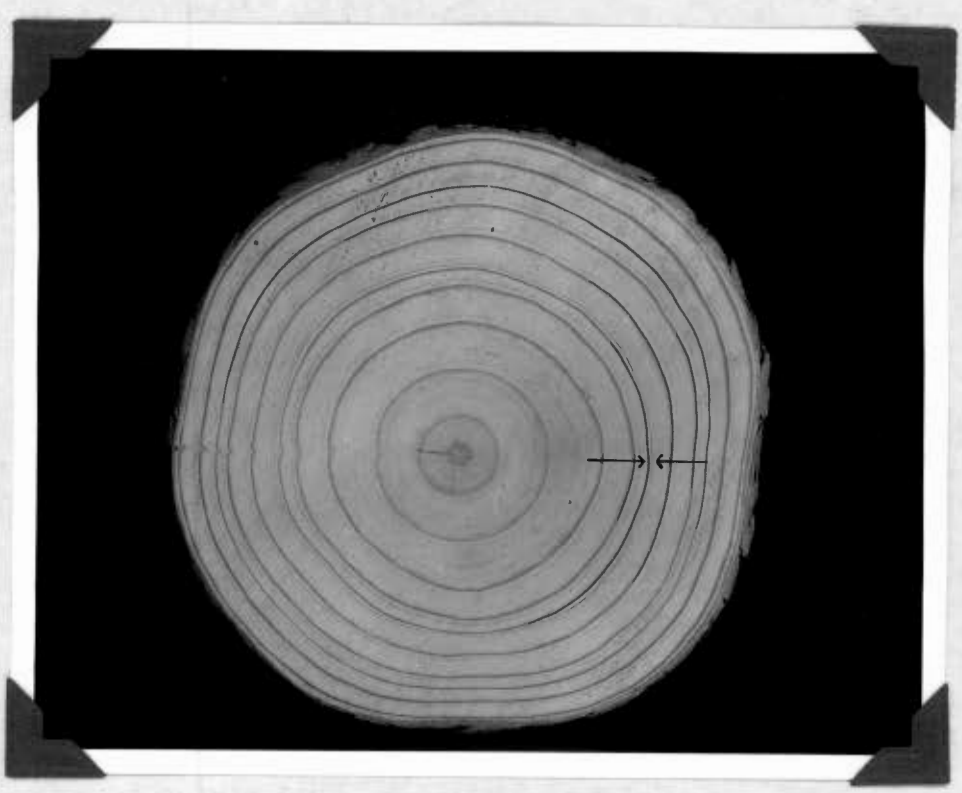

Fig. 135.

Section from the same tree as potrayed in figure 134 - 15 feet from the ground.

Fig. 136/.....

Fig. 136.

Complete defoliation of *P. patula* at the Jessievale plantation.

Fig. 137.

Complete defoliation of *P. patula*, 5 miles south of Jessievale.

Fig. 138.

Normal stand of *P. patula* at Jessievale plantation.

Graham (1952) shows that the annual rings of trees in the U.S.A. indicate a very low rate of growth for several years after complete defoliation. In this country, however, it is clear that P. patula trees recover after a year, and in the second year after complete defoliation, register the normal increment.

In most publications dealing with defoliation of trees, the indirect results of such setbacks are discussed, the direct results being very rarely studied. According to Chapman (1924) "the cubic volume of trees and logs affords the only basis of accurate and permanent scientific records and a universal standard of measurement. For this purpose the cubic foot should be used as the standard unit." The writer accordingly made volumetric analysis of the growth of a number of trees of known history, including complete defoliation by E. terminalis during the summer of 1948-1949, to assess the direct results of the insect attack in terms of loss of timber.

To calculate the volume of a tree for any particular year within its period of growth from the annual rings, Smalian's formula (Chapman 1924) is utilised.

In figures 139 and 140 two graphs provided by the Department of Forestry are given. The graph in Fig. 140 reflects the normal annual increase in the total volume of wood of a P. patula tree, while the graph in Fig. 139 shows the proportionate increase in the volume of wood from year to year. From these graphs it can be deduced that the rate, at which the volume of a tree is increased, waxes progressively from year to year until at least the 18th year, whereafter a stable increment is recorded.

For the volumetric analysis made by the writer, 6 P. patula trees were selected at random in compartment C.17 of the Jessievale plantation, were felled, and using Smalian's formula, the volume of each tree for each year from the third year after planting onwards, was calculated.

The/.....

The results are compiled in Table 29 and graphically portrayed in Fig. 141. The annual increase in height of these trees during the period under consideration was also computed.

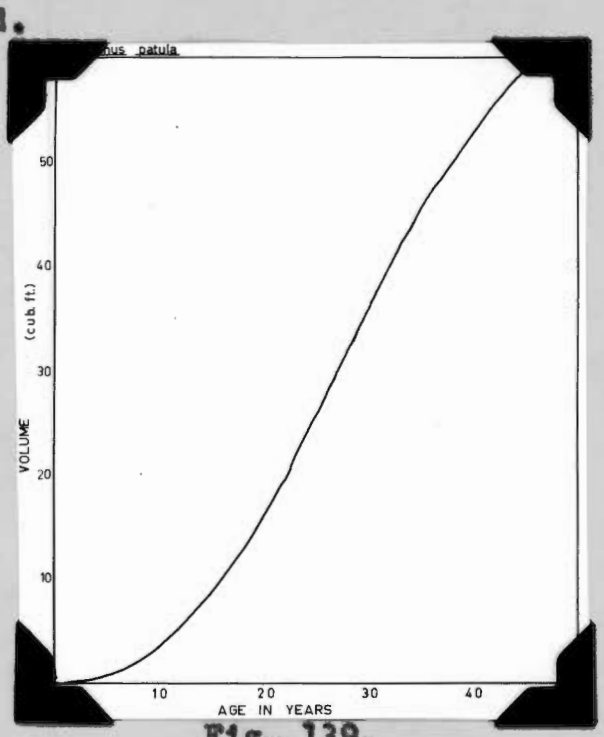

Fig. 139.

The normal proportionate annual increase in cubic feet of a P. patula tree.

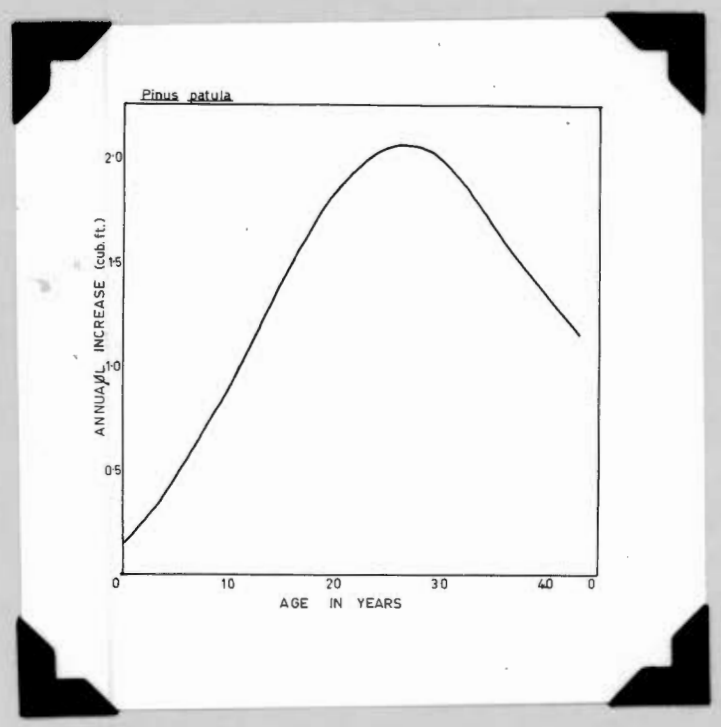

Fig. 140.

The normal annual increase in the total volume of wood of a P. patula tree.

Table 29./.....

Year.	Height in ft.	Wood. (Cub. ft.)	Difference in wood increase from year to year.
1942	8.79	0.0426	0.0426
1943	16.62	0.2076	0.1650
1944	21.12	0.6443	0.4367
1945	26.71	1.3270	0.6827
1946	33.66	2.3256	0.9986
1947	37.71	3.2673	0.9417
1948	41.41	4.1214	0.8541
1949	42.62	4.5293	0.4079
1950	47.08	5.4328	0.9035
1951	51.58	7.2911	1.8583
1952	55.17	8.4463	1.1552
1953	58.88	10.3319	1.8856
1954	63.17	12.5951	2.2632

Table 29.

The height and volumetric analysis of six P. patula trees from compartment C.17 Jessievale.

From the graph in Fig. 141 it will be seen that during each year up to and including 1945 - 1946, the average increase in the volume of a tree each year exceeded that of the preceding year. During the years 1946 - 1947 to 1949 - 1950 incremental losses due to the defoliation by E. terminalis are clearly apparent. If the increment recorded for the year 1945-1946 is taken as the standard normal annual increment against which losses during the period of defoliation are assessed, the figures reflecting annual losses would be very conservatively estimated. This is very clearly demonstrated when the average increment of 0.9986 cubic feet per tree recorded during 1945 - 1946, the year before losses due to defoliation became apparent, is compared with the average increment of 1.8870 cubic feet recorded during 1950 - 1951, the first year after

losses/.....

losses due to defoliation are no longer visible.

However, taking the potential annual increment for the four year period 1946-1947 to 1949-1950 at the standard, conservative figure of 0.9986 cubic feet per tree, the total loss per tree as a result of insect attack is assessed at 0.8870 cubic feet of timber.

The trees in the compartment from which samples were taken, were planted during 1940 at a rate of 500 trees per acre. It is the policy of the Department of Forestry to decrease this rate by thinning to one of 300 per acre when the trees attain an age of 6 - 8 years; this was done during 1950 in this specific compartment. Working again on a conservative basis of only 300 trees per acre, the loss of timber increment attributable to E. terminalis defoliation would amount to 266.1 cubic feet per acre.

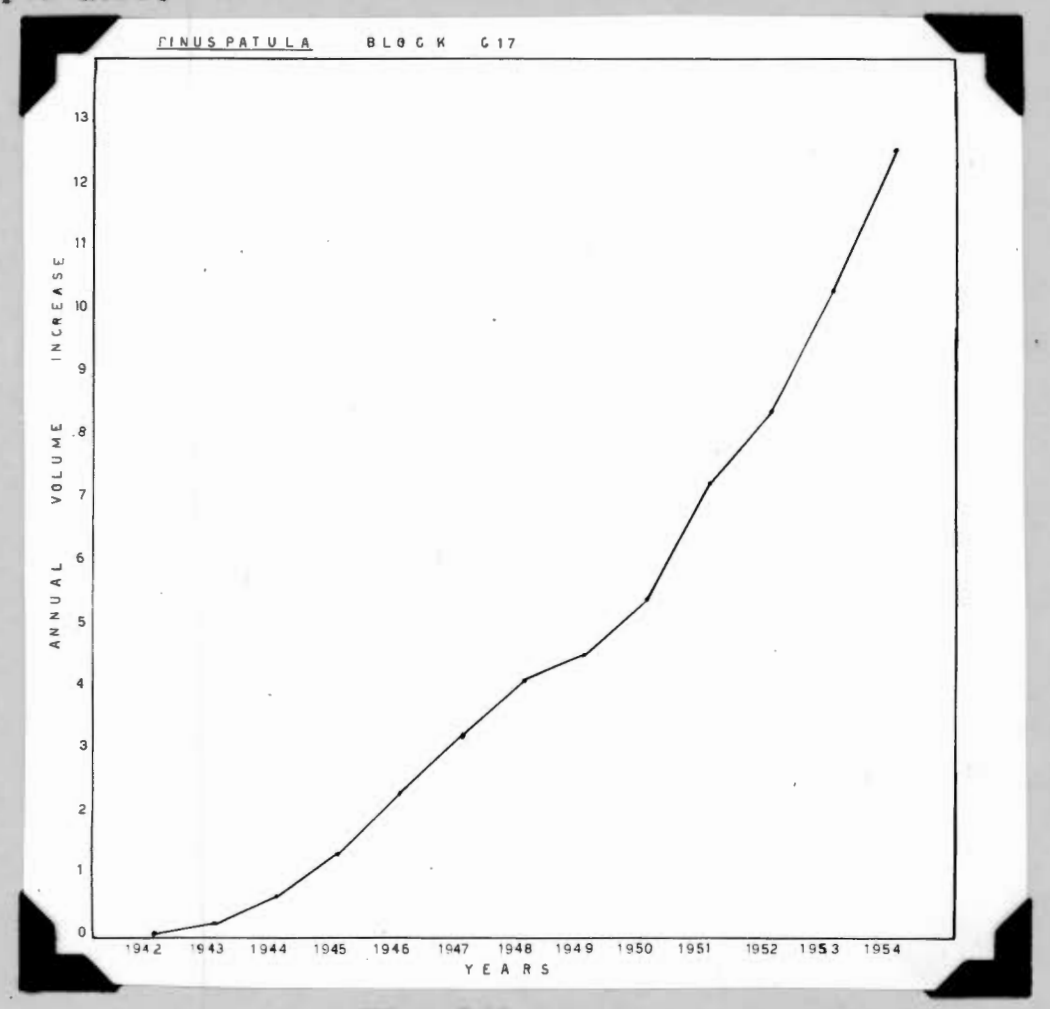

Fig. 141.

Annual average increase in volume of wood in Block C17 at the Jessievale plantation.

Since/.....

Since 1929 smaller or larger areas of P. patula at Jessievale have each year been completely defoliated and from then up to and including 1954 a total of 6,360 acres have been affected in this way. The total loss of timber in this area to be laid at the door of E. terminalis during the past 26 years at Jessievale can thus be estimated conservately at 1,692,396 cubic feet, or a yearly average of 65,092 cubic feet.

This estimate includes only those sections which at some time or another were completely defoliated. To this should still be added the damage done to trees which were defoliated to a lesser degree by lighter infestations not recorded.

The annual rate of increase in height of the trees is also adversely affected by infestations of E. terminalis, as a glance at Fig. 142 will reveal. Normally the annual height increment decreases progressively with age. To err on the conservative once more, in this calculation the figure for 1950-1951, namely, 3.59 feet is accepted as the standard potential increase for the preceding years against which losses can be calculated. Considering only the year 1948 - 1949 we find that the actual average height increment was 1.21 feet in the defoliated compartment. Subtracted from the conservatively estimated potential increment, the loss in height due to defoliation may be assessed at 2.38 feet per tree, or an aggregate loss during that particular year of 714 feet per acre.

Apart from losses in volume of timber and height of trees, the shock of complete defoliation is great, and trees so affected die very easily if subjected to drought in their weakened state. Under such conditions considerable mortality has been recorded. In addition it should be borne in mind that trees weakened by defoliation are extremely vulnerable to attack by bark-beetles, as shown by Graham (1952) in the U.S.A. There is a

constant/.....

constant danger that exotic insect species may be imported into South Africa from abroad. Plantations weakened by defoliation would serve as ideal localities wherein such exotics could establish themselves, and so become focal centres from which the pests could spread to other parts of the country.

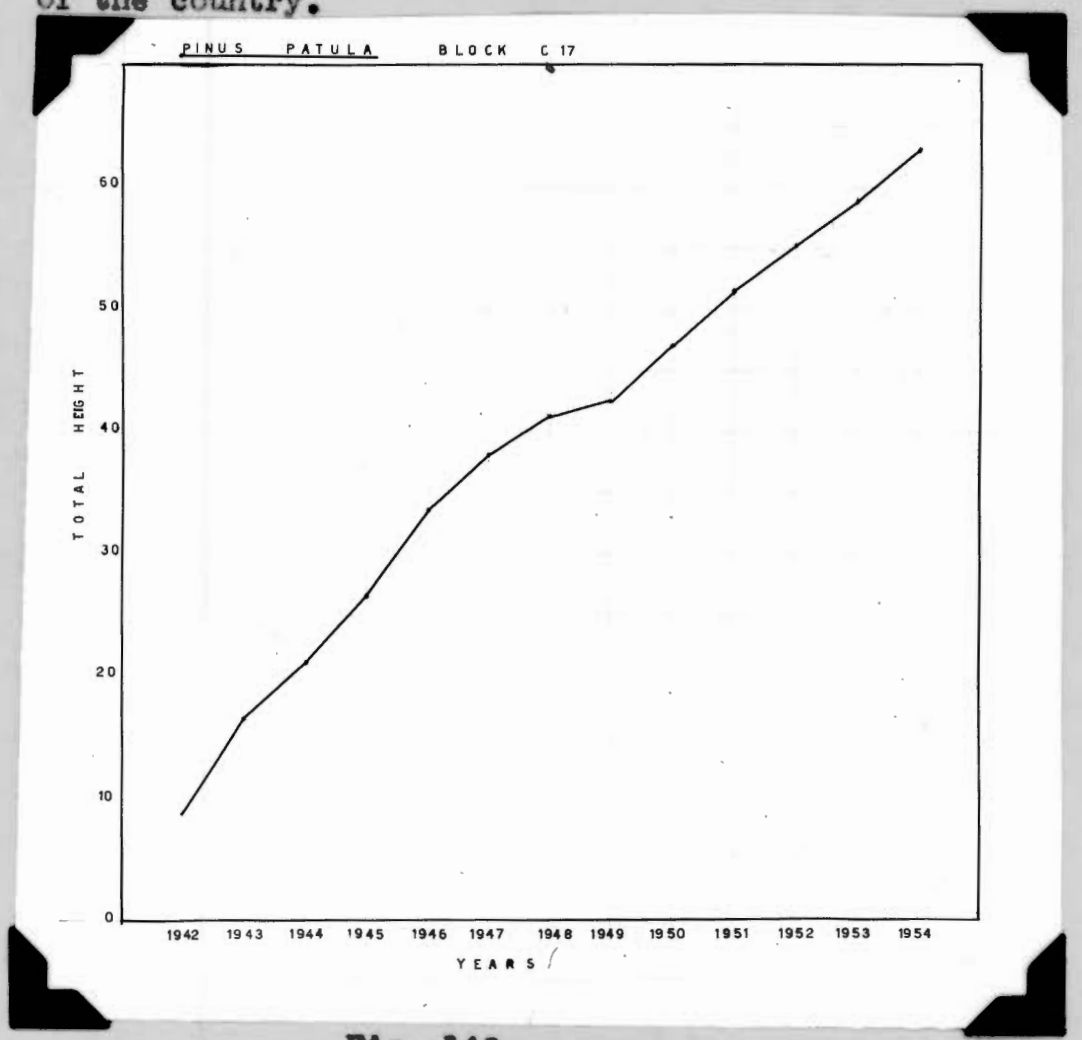

Fig. 142.

The average annual rate of increase in height of P. patula Block C.17, at the Jessievale plantation.

CHAPTER XI.

CHEMICAL CONTROL.

1. HISTORICAL.

Extensive experiments on the control of E. terminalis by chemical means, were started as early as 1931, and an account of this work was given by Tooke (1938). At that time it was found that calcium and lead arsenates were the most promising insecticides for the control of this pest. In recent years, however, the search for new insecticides has resulted in the release of several new compounds into the field of chemical control of insects, and as it was felt that these might prove more effective than the insecticides previously used. Petty (1948) carried out tests with some of these formulations which were available at the time.

2. THE EFFICACY OF SOME OF THE LATEST INSECTICIDES.

a. Technique.

The results of tests carried out by the author using some of the very latest insecticides available is included in this thesis. These tests may be regarded as a continuation of the work done by Tooke, and carried on by Petty.

The insecticides tested were applied as dusts, using the apparatus described by Petty (1948). The rate of application in the laboratory experiments was 0.7 m.g. per sq.c.m. which is the equivalent of 7 lb. per acre in field application.

To determine the relative susceptibility of the different instars of E. terminalis to the insecticides used, fourth and sixth instars were used as test insects. In the tests both the larvae and the pine foliage on which they were fed were dusted. The larvae were then exposed to the treated foliage - ten larvae to a petri-dish - for 24 hours in every case, after which the first

mortality counts were taken. The larvae were then transfered to clean petri-dishes containing fresh untreated foliage and further mortality counts made at 24 hour intervals.

Twelve groups of ten larvae each were used for each insecticide and for the controls in respect of both the 4th and 6th instar larvae. The total number of test insects used for each insecticide was therefore 240.

In order to have the insect material as uniform as possible, only larvae feeding normally for 24 hours prior to the commencement of the experiments were included in the tests, and subsequent to the application of insecticides they were kept under constant temperature and humidity conditions (70-75% R.H. and 75°F.)

b. Results of toxicity tests.

The average percentage mortality obtained with the various poisons obtained from twelve replications are presented in tables 30 and 32, and the analysis of variance in tables 31 and 33.

c. Conclusions.

1. Up to, and including the 4th instar larvae

a. When rapidity of action and final mortality produced are considered, the three organic phosphates, Parathion, E.P.N.300, and Malathion are more efficacious than the chlorinated hydrocarbon insecticides D.D.T., Toxaphene, Strobane, Dieldrin and Aldrin, under the conditions of these experiments.

b. D.D.T. and Toxaphene come next in order of merit by Strobane, Dieldrin and Aldrin.

No.	Insecticide used.	Dosage lbs. per Acre.	Experiment.	Mortalities (%)				Totals.	General treatment mean (%
				24	48	72	144		
1	2½% Parathion.	7	1	100	100	100	100	400	99.75
			2	98	100	100	100	398	
			Total	198	200	200	200	798	
			Mean	99.0	100.0	100.0	100.0		
2	5% ~~Strobane~~ E.P.N. 300	7	1	100	100	100	100	400	100.0
			2	100	100	100	100	400	
			Total	200	200	200	200	800	
			Mean	100.0	100.0	100.0	100.0		
3	5% Malathion	7	1	98	98	98	98	392	98.5
			2	95	98	100	100	393	
			Total	193	196	198	198	785	
			Mean	96.5	98.0	99.0	99.0		
4	5% D.D.T.	7	1	77	95	100	100	372	89.13
			2	50	93	98	100	341	
			Total	127	188	198	200	713	
			Mean	63.5	94.0	99.0	100.0		
5	2% Toxophene	7	1	50	85	92	100	327	76.38
			2	33	59	92	100	284	
			Total	83	144	184	200	611	
			Mean	41.5	72.0	92.0	100.0		
6	10% Strobane	7	1	48	73	88	100	309	67.75
			2	17	47	72	97	233	
			Total	65	120	160	197	542	
			Mean	32.5	60.0	80.0	98.5		
7	2% Dieldrin	7	1	49	87	98	100	334	73.25
			2	34	55	72	91	252	
			Total	83	142	170	191	586	
			Mean	41.5	71.0	65.0	95.5		
8	2½% Aldrin	7	1	23	65	77	98	263	62.88
			2	34	45	68	93	240	
			Total	57	110	145	191	503	
			Mean	28.5	55.0	72.5	85.5		
9	Control		1	0	0	0	0	0	0
			2	0	0	0	0	0	
			Total	0	0	0	0	0	
			Mean	0	0	0	0		
Total				1006	1300	1455	1577	5338	-
General Experimental mean				62.88	81.25	90.94	98.56	-	-

TABLE 30.

Insecticidal tests carried out on fourth instar larvae of *E. terminalis.*

2. Sixth instars larvae.

a. Against the older larvae both Parathion and E.P.N. 300 are significantly superior to the other insecticides when judged by general efficacy which includes final mortality and rate of mortality.

b. D.D.T. comes next in order of merit followed by Toxaphene, Malathion, Dieldrin, Strobane and Aldrin.

Variance due to	D.F.	S.S.	M.S.	F.	
				Calc.	At P=0.05
Treatment (T)..	7	11,103.07	1,586.12	16.1617	2.30
Observation Periods (O)...	3	11,403.82	3,801.27	38.7329	2.90
T & O Interaction.....	21	9,148.05	435.62	4.4387	1.91
Error	32	3,140.50	98.1406	1.000	-
Total	63	34,795.44	-	-	-

Significant differences.

a. Between treatments. - 9.2478
b. Between S.S. observation periods - 8.4108
c. Between T & O interaction - 28.6054

Table 31.

Analysis of variance of data in table 30.

No.	Insecticide used.	Dosage lbs. per Acre.	Experiment.	Mortalities (%)				Totals.	General treatment mean (%)
				24	48	72	144		
1	2½% Parathion	7	1	100	100	100	100	400	100.0
			2	100	100	100	100	400	
			Total	200	200	200	200	800	
			Mean	100.0	100.0	100.0	100.0		
2	5% E.P.N.300	7	1	97	100	100	100	397	98.50
			2	95	98	98	100	391	
			Total	192	198	198	200	788	
			Mean	96.0	99.0	99.0	100.0		
3	5% D.D.T.	7	1	28	58	92	100	278	73.13
			2	37	78	92	100	307	
			Total	65	136	184	200	585	
			Mean	32.5	68.0	92.0	100.0		
4	2% Toxaphene	7	1	20	48	78	98	244	64.75
			2	32	68	77	97	274	
			Total	52	116	155	195	518	
			Mean	26.0	58.0	77.5	97.5		
5	5% Malathion	7	1	65	78	80	85	308	83.25
			2	87	88	90	93	358	
			Total	152	166	170	178	666	
			Mean	76.0	83.0	85.0	89.0		
6	2% Dieldrin	7	1	5	15	32	75	127	49.75
			2	55	58	68	90	271	
			Total	60	73	100	165	398	
			Mean	30.0	36.5	50.0	82.5		
7	10% Strobane	7	1	10	32	50	83	175	41.25
			2	8	22	43	82	155	
			Total	18	54	93	165	330	
			Mean	9.0	27.0	46.5	82.5		
8	2½% Aldrin	7	1	0	10	17	55	82	27.75
			2	8	23	37	72	140	
			Total	8	33	54	127	222	
			Mean	4	16.5	27.0	63.5		
9	Control	7	1	0	0	0	0	0	0
			2	0	0	0	0	0	
			Total	0	0	0	0	0	
			Mean	0	0	0	0		
Total				747	976	1154	1430	4307	
General Experimental Mean				46.69	61.00	72.13	89.38	-	-

TABLE 32.

Insecticidal tests carried out on seventh instar larvae of E. terminalis.

Variance due to.	D.F.	S.S.	M.S.	F	
				Calc.	At P=0.05
Treatment (T).	7	39,219.49	5602.784	53.2331	2.30
Observation Periods (O).	3	15,602.42	5200.806	49.41383	2.90
T & O Interaction	21	8,710.45	414.788	3.94093	1.91
Error	32	3,368.00	105.250	1.000	-
Total	63	-	-	-	-

Significant differences.

a. Between treatments - 10.475
b. Between S.S. observation periods - 7.406
6. Between T. & O interaction - 29.589.

Table 33.

Analysis of variance of data in table 32.

General recommendations.

A. Should it become necessary to undertake chemical control of E. terminalis, the most effective insecticides for instars above the fourth are Parathion and E.P.N. 300, at the conclusions indicated in table 2. Against the younger instars than this, equally good results should be obtained with Parathion, E.P.N. 300, and Malathion.

b. Indications are that D.D.T. Toxaphene, Strobane and Dieldrin, although inferior to the organic phosphate materials, appear to be sufficiently toxic to afford a fair degree of control when used against larvae up to the fourth instar, while the same applies to D.D.T. and Toxaphene in respect of larvae older than the 4th instar.

S U M M A R Y.

1. After obtaining locality records of E. terminalis from all museums in Southern Africa as well as the British Museum, a map has been prepared showing the distribution of this insect in South Africa. Available data indicate that E. terminalis is limited in its distribution to areas with an annual rainfall of 725 m.m. or higher.

2. By combining the results of climatic studies with data obtained from laboratory experiments designed to determine the influence of temperature and relative humidity on this insect, it has been possible to delimit the probable distribution area of the species in the Union of South Africa, as well as to explain why it does not occur in other areas.

3. The morphology of the moth, including a study of the genitalia of both sexes, is described in detail. Mating and oviposition are dealt with, and details are given of the combined effect of relative humidity and temperature on the longevity of the moth. It is shown that, contrary to common belief, there is no mass migration of moths from defoliated to undefoliated compartments.

4. The structure and appearance of the egg is described. Using special technique to obtain and maintain constant relative humidities, the influence of various combinations of temperature and relative humidity on the incubation of the egg has been determined.

5. A description is given of the external morphology of the larval stages, which includes the various types of setae, and setal maps of the first and last instars. The technique used to obtain accurate setal maps is described in detail. The attachment of the poison

set a/

setae, as well as the origin of the poison and its effect on man, are dealt with.

6. A study has been made of the effect of climate, particularly temperature, on the colour of the integument of the larvae. Climatic influence on such colouration is illustrated by sketches of typical examples.

7. A key, based chiefly on colour differences, is given by means of which the various larval instars may be distinguished from each other.

8. The types of cage developed for rearing and keeping the larvae under observation and described. The movements and habits of the larvae from the time of hatching to pupation are dealt with.

9. As the result of intensive surveys over vast areas of indigenous flora, a list of the natural host plants of the larva has been compiled. A list of the exotic plants in South Africa attacked by this insect is also given. It is shown that the feeding habits on exotics differ considerably from those observed when indigenous broad-leafed plant species are attacked.

10. The combined influence of various combinations of temperature and relative humidity on the third and seventh instar larvae is determined by laboratory experiments.

11. A method is described by which density of larval populations in pine plantations can be assessed without resorting to the unpleasant task of actually counting the larvae on sample trees. This is done by counting needles and faecal pellets dropped from infested

trees/.....

trees on sample areas of known dimension on the forest floor over a fixed period of time, the results being correlated with the average temperatures which prevailed during the sampling period. Population density may be determined at a glance, using the graph prepared for this purpose.

12. The external morphology of the pupa is described and the influence of temperature and relative humidity on the duration of the pupal stage in its natural habitat is determined.

13. The history of outbreaks of E. terminalis in plantations of exotic trees in South Africa is reviewed and from this it is deduced that in any particular section of a plantation outbreaks occur in rough cycles of from 6 to 8 years.

14. The habitat of the insect is subdivided into three types according to the density of the insect. The various factors which together constitute the environmental resistance of E. terminalis and serve to control this pest are analysed in the three areas of abundance, with special emphasis on the area in which it occurs in pest proportions. In the areas where regular outbreaks occur,

it/.....

it is shown that various insect and fungal parasites influence the population density of E. terminalis. It is shown that the insect parasites play a minor role in the control of the host insect, whereas the main controlling factor is Empusa grylli; unfortunately this fungal parasite is effective only when the population density of the host insect reaches very high levels, i.e. at the stage when heavy defoliation of trees is apparent. The main controlling influence on E. terminalis is thus a density dependant factor.

15. The biology and morphology of the main insect parasites, ~~in both their larval and adult stages are~~ is described. This study includes

(a) the egg parasite, Telenomus phoreus,

(b) two larval parasites, Meteorus trilineatus and Tachina fallax, and

(c) the pupal parasite, Pimpla bicolor.

16. The direct loss in timber increment as a result of total defoliation by E. terminalis has been determined for Pinus patula trees in the Jessievale plantation. This was done by volumetric analysis of trees which were totally denuded a few years ago. Based on this analysis, and knowing how many acres of trees in this area had been completely defoliated during the 25 years since this pest first commenced damaging this plantation, an estimate is given of the total loss of timber to data in this area due to E. terminalis attack.

17. From the studies made, it is clear that the natural enemies of E. terminalis in certain plantations such as Jessievale, are unable to prevent

periodic/.....

periodic complete defoliation. Secondly, that the loss of timber increment due to such epidemics in these areas is so severe that chemical control of the pest would be an economically sound investment. For this reason experiments were carried out with the most promising of modern insecticides against third and seventh instar larvae to determine which of these can be used most efficiently and cheaply to control the pest. The results of these tests are given.

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