THE BIOLOGY AND MORPHOLOGY

OF

AGROTIS INFUSA (BOISD).

A thesis presented in fulfilment of the requirements for the degree of Doctor of Philosophy of the University of Adelaide.

by

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The following is a list of the abbreviations, together with their meanings, used in the text figures :

L A R V A

a.	antenna
a 1-2	adfrontal setae
ab.m	abductor muscle
adf	adfrontal sclerite
ad.m	adductor muscle
ads	adfrontal sensorium
adt	adfrontal suture
al	alacardo
an	antacoria
ar	antennaria
c 1-2	clypeal setae
cc	cervacoria
cca	attachment of cervacoria
ccc	chitinous cervacoria
cls	clypeo-labral suture
co	crochet
cs	clypeal suture; cutting surface (incisor region) (mandible)
ct	corpotentorium
cx	coxa
cw	claw
dg	distagalea
e 1-3	epipharyngeal setae (primary)
ea	epicranial arm
epm	epicranial parademe
es	epicranial suture
ex	epipharynx
f	frons
f_1	frontal setae
fcs	fronto-clypeal suture
fe	femur
fo	foramen
fs	frontal sensorium
hx	hypopharynx
hxs	hypopharyngeal setae
l	labrum
l 1-6	labral setae
las	setae on lacinia
lb.p.	labial palpus
ls	labral sensorium
m 1-2	mandibular setae
ma	muscle attachment
mc	median duct
md	mandible
mm	membrane
mnc	mandacoria
ms	molar surface (mandible)
mt	metatentorium
mxc	maxacoria
mx.p.	maxillary palpus
O 1-3	occipital setae
Oc 1-6	ocelli
p	planta
pa	post-gena
pap	post-genal parademe
pe	preclypeus
pf	palpifer
pg	proxagalea
pm	peritreme, parademe
po	post-clypeus
pox	post-pharynx
pp	palpiger
pr	precoila; Silk press, fringed processes
prts	pretarsus
pt	pretentorium
ptc	post-artis
ptl	post-coila
py	preartis
s	stipes
sa	subcardo
se	secondary suture
si	spinneret
sif	fringe of spinneret
sio	proximal fold of spinneret
sis	proximal sclerite of spinneret
sl	slit
sld	salivary ducts
sm	submentum
sms	submental setae
so	occipital sensorium
sp	stipula

spr	sensoria of palpiger
sps	stipular setae
sr	sensorium
sv 1-7	vertical sensoria
tb	tibia
td	tendon
tm	torma
tr	trochanter
ts	tarsus
v	vertex
v 1-14	vertical setae

I M A G O

a	antenna
a.c.	axillary cord
a.p.	anterior notal wing process
a.s.	antennal sclerite
a.so.	antennary socket
at	anterior arm of tentorium
B.a.	basalar sclerite
c	cardo
ct	corpotentorium
cv.sc.	cervical sclerite
cvx	cervix
cw	claw
cx	coxa
cx.m.	coxa meron
cx.v.	coxa vera
dt	dorsal arm of tentorium
e	compound eye
em	empodium
ep	epiphysis
epm 1	prothoracic epimeron
Epm 2	mesothoracic epimeron
Epm 3	metathoracic epimeron
eps 1	prothoracic episternum
Eps 2	mesothoracic episternum
Eps 3	metathoracic episternum
es	epicranial suture
ex	epipharynx
f.c.	fronto-clypeus
fe	femur
fl	flap (operculum)
fr	frenulum
ft	frontal lobe
ga	galea
ge	gena
h	hooks
h.l.	humeral lobe
jg	jugum
l	labrum
lb.p.	labial palpus
lc	lacinia
lrex	labrum-epipharynx
li	ligula
mn	membrane
mx.p.	maxillary palpus
O	occiput
oc	ocellus
P	patagia
	planta
	papilla-like setae
P.Eps 2	mesothoracic pre-episternum
P.Eps 3	metathoracic pre-episternum
pf	pilifer
ph_1	mesophragma
ph_2	metaphragma
pl	pulvillus
pmt	post-mentum
pn	pronotum
po	post-occiput
p.p.	posterior notal wing process
prmt	prementum
prs_2	metathoracic prescutum
prts	pretarsus
pt	posterior arms of tentorium
r	retinaculum, sclerotized rings
S	sternum ;
	stipes ;
	setae

S 1	mesoscutum
S 2	metascutum
	mesothoracic sternum
S 3	metathoracic sternum
S.A.	subalar sclerite
S.Eps 2	mesothoracic supra-episternum
sl_1	mesoscutellum
sl_2	metascutellum
sp	spiracle
T 3	metathorax
t	tegula, tentorium
t.a.	tegular arm
tb	tibia
tb.sp	tibial spur
$Th.sp._1$	Prothoracic spiracle
$Th.sp._2$	mesothoracic spiracle
t.p.	tegular plate
tr	trochanter
ts	tarsus
Tym	tympanum
U	unguitractor plate
V	vertex

ORGANS of REPRODUCTION

AcGls	Accessory glands
Aed	aedeagus
Af	anellifer
Am	ampulla
An	anus, anellus
Apo.ant.	apophyses anteriores
Apo.po.	apophyses posteriores
Brs.Dej.	anterior branches of ductus ejaculatoriùs
car.p.	carpus penis
co	costa
coe	coecum penis
cr	corona
crn	cornuti
crp.bu.	corpus bursae
cu	cucullus
db	ductus bursae
D.ej.	ductus ejaculatorius
ds	ductus seminalis
Enph	endophallus
Hp	harpes
Jx	juxta
lla	lamella antevaginalis
llp	lamella post-vaginalis
Ob	ostium bursae
Odc	median oviduct
Op	oviporus
Ov	Ovary
Pap.a	papillae anales
Pr.co.	process of costa
Res	reservoir of accessory gland
S	saccus
Sca	scaphium
Sg	signum
Sin.V	sinus vaginalis
Sl	sacculus
Spmt	spermatophore
Spt	spermatheca
Spt Gl	spermathecal gland
Ssca	subscaphium
Tes	testis
Tg	tegumen
Tu.a.	tuba analis
U	uncus
Va	valva
Vag	vagina
Vd	vas deferens
Vl	valvula
Vn	vinculum
Vsm	vesicula seminalis

SURFACE STRUCTURE and HISTOLOGY of the INTEGUMENT

b.m.	basement membrane
e.m.	ecdysial membrane
Endo	endocuticle
Epic	epicuticle
Epid	epidermis (hypodermis)
Exo	exocuticle
Meso	mesocuticle
pcp	pore canal plugs
Sc	scales

INTRODUCTION

Agrotis infusa (Boisd.) - (Lepidoptera: Agrotidae) is one of the many common species of endemic cutworms in Australia. Over a long period of years it has been recorded as causing considerable damage to a variety of crops and pastures, at irregular intervals. At times it has been credited with the total destruction of crops particularly wheat, at least in isolated patches (Froggatt 1899, 1911; Anon. 1919). It may be pointed out, however, that grave doubts exist as to the correctness of many of the identifications made by the earlier observers.

In spite of the many references about economic damage by the species over the last 60 years, its biology and behaviour have hitherto been little known. Recently Common (1954) made an important contribution leading to the better understanding of the adult behaviour of the species in the south-eastern part of Australia. From his field observations, supplemented by laboratory investigations, he drew the following conclusions:

1. The major part of the population of A. infusa in south-eastern Australia has but a single generation each year. In very favourable habitats, however, three or four generations annually are theoretically possible.

2. In the spring the moths migrate to the mountains (Australian Alps), where they aestivate gregariously, in a sexually immature condition, in crevices and small caves at altitudes above about 4000 feet. In the late summer and autumn, they migrate back to their breeding grounds.

3. From the preliminary data he suggests that a facultative diapause occurs during aestivation.

4. The migration, together with the facultative diapause, enables the moths to survive when adverse environmental conditions on the plains, mainly lack of suitable larval food, prevail.

It should, however, be noted that, because of the collection of a few impregnated females in spring in light traps at Canberra, and the presence of an occasional larva in gardens during summer in the same locality, he suggested that a small part of the population fails to aestivate.

Now, it is an accepted principle, that the biology of a species in one area cannot be interpreted in terms of its biology in a distant and climatically different one, and, the collection of a large number of moths of A. infusa in a light-trap at the Waite Agricultural Research Institute throughout the year, suggested that its biology in the neighbourhood of Adelaide, might differ considerably from that exhibited in south-eastern Australia. Partly because of these considerations, and partly because of the lack of information on the habits and the biology of the species, the present study was started late in 1955 and continued until 1957.

Besides the investigation of the general biology and the seasonal history of the species in South Australia, a second objective was to evaluate the influences of certain environmental factors, - mainly temperature, moisture and food, - on the rate and course of development, survival, fecundity etc., with a view to obtaining a better understanding of its innate capacity for increase, under different conditions. Morphological studies of the larva, pupa and adult were also undertaken

as they are of great taxonomic value, and are therefore useful for the correct identification of the species in its various stages. As with many other common agrotids, failure to appreciate its morphological characters has led to much confusion in the past through misidentification of the species recorded as doing economic damage.

REVIEW OF LITERATURE

With the exception of the recent work of Common (1954) and May and Passlow (1954), the records, concerning the species, consist of mere statements of assemblages or flights of moths, and larval infestations. No critical investigations about the biology or the ecology of the species, as a whole, have been published.

From the early days of European settlement in Australia, and long before any economic damage was assigned to the species, large aggregations of the moths in the Australian Alps, and their flights in large numbers in the coastal areas of New South Wales, attracted the attention of many naturalists.

Bennett (1834) seems to have been the first to report moth-assemblages at certain granite masses in the Bogong Mountains, (from which the popular name, "Bogong moth", was derived), during summer when the aborigines feasted on them. Bennett's account was confirmed by Scott (1873) who further reported on a large flight of moths which struck Sydney in 1867. Since then, similar observations have frequently been made (Helms 1890; Froggatt 1907; French Jr. 1915; McKeown 1935, 1942; McCarthy 1945; Common 1952, 1954).

The earliest mention of economic damage by the species is that of Olliff (1890), who reported that it sometimes attacked maize in New South Wales. Further, he claimed that the moths collected from the Australian Alps, were con-specific with those which appeared in vast numbers in Sydney

and elsewhere in 1867 and 1889.

Before the phenomenon of migrations of moths was investigated, and the main breeding grounds of the species were located, it was erroneously thought that breeding principally occurred at places of moth-assemblage in the mountainous country (Anon. 1893).

Frogatt (1899) made the first large scale observations on the localities of larval breeding during the widespread infestation of the Western Slopes and Tablelands of central New South Wales, extending for a distance of about 400 miles from Moree in the north, near Queensland, to Corowa and Albury in the south on the border of New South Wales and Victoria. Wherever infestation was observed, the caterpillars did considerably more damage on black soil flats than in the red soils of light texture, because of the favourable soil texture and type of vegetation of the former. A fungal disease, perhaps Entomophthora australiana McAlpine, was reported as destroying large numbers of larvae. Later, in October and November, two large swarms of moths were seen late in the evening feeding from flowers of small eucalypts and bushes of Leptospermum and Melaleuca spp.

Early in July 1900, larvae were again reported as causing great damage to crops and grass in the Whitton district of New South Wales (Anon. 1900). A heavy downpour of rain, about 2 inches within a few days, drowned many of the larvae, and their numbers were further diminished by subsequent infestation with fungus.

An extensive outbreak was reported from Broken Hill (New South Wales) in August 1901, where great damage was done to small herbage,

especially salt and blue bush (Froggatt 1901). Large numbers of larvae were destroyed by wild turkeys, cold weather, and fungal disease. Larvae were also collected from Condobolin and Trundle.

In August 1906, an infestation was reported from the flats at Tamworth (New South Wales) where grass and lucerne were damaged (Froggatt 1907). Froggatt (1910) also recorded a heavy infestation, in September 1909, over a large area, particularly in the Hay district of New South Wales, where saltbush was damaged to such an extent that the plains were almost denuded. About 72 per cent. of the pupae that were later collected from the infested area in December were found to be parasitised by a chalcid.

In September 1911, widespread attacks were recorded on wheat in isolated patches at Ganmain, Yanco, Narrandera and Grong Grong in New South Wales (Froggatt 1911). The caterpillars, which were nearly fullgrown, were found concealed under clods. In a paddock, in Ganmain District, 50 acres of wheat was completely eaten, and as in this area the straw from the previous harvest had been ploughed into the ground, it was thought that the eggs had been deposited upon the straw. The other part of the same paddock, where the previous crop had been cut for hay, and which, therefore, did not contain straw, was free from infestation. The correctness of this opinion is suggested by the study of the egg-laying habits of the moths during the course of the present work.

An outbreak which destroyed a young wheat crop at Bordertown (South Australia) was reported in September 1919 (Anon. 1919). Most of the larvae had pupated by the end of September and it was thought that a

second generation might develop in November.

This species, together with A. ypsilon Rott. and Euxoa radians Guen., was also considered to be responsible for serious damage to cotton seedlings in New South Wales (Gurney 1923), while in Queensland considerable injury by this species and Euxoa radians to cabbage and cauliflower was reported (Anon. 1925). Lyon (1925) made the rather unusual observation about injury by the larvae to young grape vines in the irrigated areas of the Murray Valley.

Newman (1927) reported this species to be numerous in some years in Western Australia but not as a frequently recurring serious pest there.

Tillyard (1926) stated that the moths sometimes flew on board ships far out on the Tasman Sea, and were also taken in New Zealand where, however, the species was not common. Hudson (1928) mentioned its occurrence at Invercargill and probably elsewhere in New Zealand.

In South Australia, maize was reported to be sometimes seriously infested by this species (Lea 1928). Evans (1943) recorded the species together with E. radians, to be injurious in Tasmania.

Common (1952, 1954), apparently was the first to make some critical studies on the insect (see INTRODUCTION). His field surveys in 1952 of the Western Slopes, plains and Tablelands of New South Wales showed the densest larval populations to occur on the heavy self-mulching soils of the North-West Slopes and plains. Linseed was severely damaged in Yetmen district (New South Wales) and at Milmerran on the Darling Downs. In pastures, on heavy soils, dense stands of Medicago spp. were heavily infested

but grasses such as barley grass (Hordeum leporinum Link.) on the lighter soils were completely free as were various Erodium and Geranium spp. In southern New South Wales the larvae were numerous especially in stands of Medicago spp. on self-mulching soils of the plains south of Hay. They were also numerous on heavy brown soils near Berrigan containing annual composites in a degenerate pasture, in sown pastures containing capeweed (Cryptostemma calendula Druce), on an alluvial river flat at Corowa, and on the Southern Tablelands and South Western Slopes. They were also observed, to a lesser extent, in subterranean clover pastures, lucerne fields, and in a mixed pasture of clover and oats.

The type of climate, soils and vegetation of the North West and South-West wheat belts of New South Wales, where the larvae were found to be numerous, were described.

The winter-surveys showed, by the presence of larvae, that in New South Wales and Southern Queensland the eggs had been laid by the moths in autumn. Moths reared from larvae, collected in the breeding grounds of New South Wales, or obtained from gregarious assemblages in mountains, showed a preoviposition period of from 24 to 66 days.

May and Passlow (1954) carried out systematic field trials to evaluate the effects on the larvae of modern organic synthetic insecticides during a widespread infestation of the pest in July-August of 1952, when the larvae damaged a wide range of crops, including seedling wheat, lucerne and barley, on the Darling Downs and in the South-Western agricultural districts of Queensland.

From the above review, it is obvious that the only exact studies of the species are those of Common (1954) and May and Passlow (1954). All previous accounts are almost entirely observational, and such a wide range of host-plants, from areas differing so greatly climatically, have been recorded, that some, at least, of the records are suspect. All too frequently these have been based on mere superficial inspection of the larvae, a practice that can easily result in misidentification of the species concerned.

MATERIALS AND METHODS

The cultures were started from moths caught in a light-trap at the Waite Agricultural Research Institute in the last week of August 1955. The moths were confined in a wire-gauze cage (about 14 inches long, 8 inches wide and 10 inches high), fitted with a removable top, and having a muslin sleeve at one end. The open bottom of the cage rested on sheets of brown paper on a table. A 20 per cent. sucrose solution, soaked in cotton wool in small glass vials, was provided as food. Some folded wax paper and pieces of blotting paper were put on the floor of the cage to afford shelter for the moths and to provide suitable sites for oviposition. When the latter began, the eggs, which were mostly laid on the blotting or wax paper, or the cloth cover of the removable top, were removed daily with a fine wet brush. As the eggs were firmly fastened to the objects with an adhesive material, they were first wetted to loosen them before attempting their removal. This technique enabled the eggs to be safely manipulated.

For noting speed of development, and survival of eggs at different temperatures and saturation deficits, 100 eggs were usually used for each treatment. They were arranged on a circular piece of blotting or filter paper which had previously been marked into 100 squares, and one egg was placed on each square. When the eggs were not to be kept at particular saturation deficits, the paper was kept constantly moist by adding a few drops of water at intervals. Eggs which were to be exposed to particular saturation deficits were kept in air-tight preserving jars on glass tripods

over the required mixtures of sulphuric acid and distilled water. Eggs exposed to 100 per cent. R.H. (0mm. saturation deficit) were kept over distilled water in similar jars.

Most of the larvae were reared collectively in small Petri dishes (3.5 inches in diameter) to about the third instar, when they were transferred to larger Petri dishes (7.5 inches in diameter x 1.5 inches deep). From the fifth instar onwards they were isolated and reared individually in small brown glass jars each of which contained a layer of plaster of Paris, about a quarter of an inch thick, at the bottom. The jars had metal screw tops. The food was changed daily and the dishes and the jars cleaned frequently. For determining the influence of different hosts on the survival and speed of larval development, the weights of the larvae and pupae, and the number of larval moults at different temperatures, the larvae were reared individually from the time of their emergence from the egg.

The weights of eggs, and early instar larvae were taken on a precision balance (capacity 50 mg) with which, by means of a Vernier scale, weights could be taken as low as 0.01 mg. The older larvae, prepupae, pupae and adults were weighed on a balance accurate to 0.1 mg.

For noting the influence of temperature, food etc. on the fecundity and fertility of moths, the latter were confined in pairs in large glass cylinders. Each female was enclosed with either one or two males according to the availability of the latter at the time. Both the females and males, which were confined together, usually emerged on the same day or at the most at an interval of one day. Small pieces of paper were provided as

previous experience showed that loose objects were preferred by the moths for oviposition. The tops of the cylinders were closed with muslin and kept in position by rubber bands. Most of the eggs were laid on the margins of the paper slips; fewer were laid on the cloth-cover. A few were, also, laid directly on the glass or the blotting paper at the bottom. The eggs laid by individual females were removed daily and subsequently counted.

For the morphological studies, either fresh specimens, or, specimens preserved in alcohol, were used. For the study of chitinous structures, both larvae and adults were boiled in 10 per cent. potassium hydroxide for 10 minutes, washed in distilled water and dissected. The dissected parts were either mounted direct in glycerol for temporary examination or made into permanent mounts in "Euparal". For the study of chaetotaxy, the external surface structure of the body wall etc. of the first instar larvae, the latter were mounted in "Euparal" after dehydration and clearing, or direct in Berlese's fluid. For the study of these structures in the final larval instar, the insect was cut longitudinally and ventrally along its entire length, boiled in 10 per cent. potassium hydroxide solution for 10 minutes and the body contents were removed in water. The clean exoskeleton was then flattened and kept so, by pressure from a glass slide, while being dehydrated in the various grades of alcohol. It was finally mounted in "Euparal".

For genitalia studies, the abdomens of male and female moths were boiled in 10 per cent. potassium hydroxide solution for about 15

minutes and then left in the solution for from 24-48 hours. The posterior abdominal extremity was gently pressed under water with a slight posterior movement so as to force out the genitalia,which are normally retracted within the body. The pre-genital abdominal segments were then removed taking special care to retain the bursa copulatrix attached to the female genitalia. After removing unwanted hairs and tissues in water, the genitalia were dehydrated in alcohol and mounted in "Euparal" or "Sira". The male genitalia were usually mounted with the two valvae flattened and the aedeagus either removed or left attached.

For the study of the structure of the cuticle of larvae, prepupae, pupae and adult, the insect was killed in chloroform. The head and the anal end of each were then cut out and the material fixed in freshly prepared Sanfelice's fluid for 24 hours. Of the adult, only the abdomen was fixed after removing it from the body; a posterior cut was made to facilitate entry of the fixative. The pupa, after being killed, was first fixed in Carnoy for 1 hour after which it was washed in 70 per cent. alcohol for 5 minutes. It was then opened ventrally and put in distilled water for 1 hour before fixing it further in Sanfelice's fluid for 24 hours. After fixation the material was washed in running water for 24 hours, dehydrated in the different grades of alcohol, and cleared in benzene. It was then embedded in paraffin wax (melting point 56°C). The sections were cut at a thickness of 5μ. The deparaffinized sections were stained by the technique of Lower (1955), dehydrated in alcohol, cleared in xylene and mounted in "Sira".

Most of the morphological sketches were drawn with the aid of a camera lucida; a few, however, such as the reproductive organs and genitalia, were drawn free hand.

DISTRIBUTION

Most of the recorded information regarding the distribution of A. infusa applies to New South Wales only, and is mainly due to Froggatt (1899, 1901, 1907, 1910 and 1911) and Common (1954). Both these workers observed the larval breeding grounds to be distributed over New South Wales from the Victorian to the Queensland borders, and comprising the Tablelands and Western Slopes. Both also observed the larvae to be numerous only on the heavy soils. The soil map shows that these areas have the grey and brown soils of heavy texture which form the bulk of the northern and southern wheat-belts of New South Wales, black earths and rendzinas which are deep uniform clays with a self-mulching granular surface and form wide, deep cracks on drying, and red brown earths and terra rossas with a heavy subsoil and lighter loamy surface. Common (1954) also observed some larval breeding in the podsolic soils of the coastal region of New South Wales. On determining the moisture-regimes of these areas it is found that all these lie in the semi-humid zone (mean rainfall season 9 months) to semi-arid zone (mean rainfall season 5 months). In addition to New South Wales, the only other definite available records of its distribution are from Queensland, where the species has been reported from Milmerran on the Darling Downs (Common 1954), and on the Darling Downs and south-western agricultural districts (May and Passlow 1954). The latter authors also mention a widespread outbreak in 1931 when larvae were observed as far west as Cunnamulla. The soil-types and the moisture-regimes of these localities are found to be similar to those of the outbreak-areas of New South Wales.

In parts further north to these outbreak areas of Queensland, though the soil types and moisture regimes are favourable, the distribution seems to be limited on account of higher prevailing temperatures during the main rainfall season.

In Victoria, though no definite records of its distribution are available, looking at the soil-types and moisture-regimes of that State, it is highly probable that the species is widely distributed there. French Jr. (1915) mentioned the presence of moths in all parts of Victoria and the destruction by the larvae of field and garden crops. Mr. J.Hogan, Senior Entomologist, in a personal communication, mentions the wide occurrence of the species especially at Dookie, Burnley, Mildura, Cohuna, Negambie, Maffra and Shepparton.

In Western Australia, Newman (1927) mentioned its occurrence as an infrequent pest. Mr. Jenkins, the Government Entomologist of the State, in a personal communication, states that the moths have been collected from Nungarin (Oct. 1946) and Carnarvon (Nov. 1950) and bred in the laboratory in January 1953 from larvae collected at Osborne Park (Perth). These records show that its distribution there also is limited principally to areas having between 5 and 9 months' rainfall season and relatively heavy soils in the agricultural districts of the south-west part of the State.

Nothing is known of its distribution in the Northern Territory, but considering the short rainfall season, high temperature and generally lighter or sandy soils it is inferred that the species does not occur there, at least in significant numbers.

The species has been recorded as doing economic damage in various parts of Tasmania (Evans 1943).

For South Australia, there are only two references to the species in literature. In September 1919, it was recorded as doing damage to young wheat at Bordertown (Anon. 1919). Lea (1928) made the general statement that it sometimes seriously infests maize. From information on the labels of specimens in the collections at the Waite Agricultural Research Institute and the South Australian Museum, however, important information concerning its distribution in this State was gathered. In October-November 1952, a number of adult specimens was collected from Mitchellville (Eyre Peninsula), sheltering under fallen wood. Others came from Wool Bay (Yorke Peninsula), and Strathalbyn, while an adult was reared from a pupa collected at Mangalo (Eyre Peninsula). A number of specimens, (emerged on 11.1.54), were reared from pupae collected at Mt. Schank, in the Lower South-East district. This is an important record showing breeding during summer and the absence of aestivation (at least in a part of population) as was also observed during the present study, in Adelaide (see "Seasonal History"). A number of specimens, in the South Australian Museum, was collected at Blackwood in a light-trap practically throughout the year. Specimens were also collected at lights in other suburbs of Adelaide in 1954-1957 during November, January and March, and at the Waite Agricultural Research Institute in the light-trap throughout the year in 1954-55 and 1955-56. Catches, however, were relatively larger during October-November and February-April than at other times of the year. Moths were also collected in a light-trap at Keith

during November-December 1956, and again in June 1957, when a few young larvae were also collected from lucerne. A few isolated full-grown larvae were collected in August-September 1955 from Waite Institute fields of young wheat and in home gardens at Fullarton. A field infestation was reported from Balaklava in the Lower North in November 1956. It was confined to a low-lying area which was previously subjected to flooding and had a young stand of lucerne. Damage was first noticed about 9.11.56. The area, when examined on 15.11.56, showed severe damage and large patches were almost bare. All stages of larvae were observed. A moth, found under a sod in the field, proved on dissection, to be fertilised with well developed ovaries and eggs descending through the common oviduct. This showed, beyond doubt, that moths of the spring generation were also reproducing, without entering aestivation. These observations suggested that the species is distributed throughout the agricultural areas of South Australia which have at least a 5 months' rainfall season. The most favourable soil types in this region seem to be red brown earths and terra rossas, spreading in a narrow strip from Adelaide in the south to Balaklava and Clare in the north; the less favourable soils are podsols and solonized brown soils.

Outside Australia, the species has only been reported from New Zealand (Tillyard 1926; Hudson 1928).

It is concluded, from these observations, that in Australia the important areas of distribution of this species occur between 35° and 25°

latitude and in this zone also only in the sub-humid and semi-arid agricultural regions with heavier soil types. The vast arid areas and also the warm sub-humid to semi-arid regions of northern and central parts of the continent are not favourable to its distribution.

GENERAL BIOLOGY

I. The Life-Cycle

A. The Egg

Pre-oviposition Period.- The female moths, on emergence from the pupae, contain large quantities of fat and the ovaries are immature. A few days after emergence, depending on temperature and the supply of food, the ovaries mature. The moths subsequently commence oviposition which is considerably accelerated if they have been previously fertilised, and obtained the right amount and quality of food. Mating takes place only after the moths have previously fed. Moths which have received water alone or neither food nor water, fail to copulate; the former lay few and infertile eggs only, whereas the latter invariably fail to oviposit. The pre-oviposition period varies from about 5 days to over 3 weeks depending on temperature, food and whether or not copulation has occurred. At about $20 \pm 2^{\circ}C$, when the moths were fed on 20 per cent. sucrose solution and allowed to mate, the period varied from 5 to 10 days.

Oviposition Period.- This varies from about 7 days to over 25 days depending on temperature and individual variation. Normally it ranges from 10 to 12 days at about $20 \pm 2^{\circ}C$.

Oviposition.- At the peak of oviposition eggs are deposited in quick succession at intervals of from less than a minute to 2 minutes. Without exception, they are laid at night only. In the course of a single night the highest number of eggs laid by a female was 907 (Table 1). Usually,

however, the number is less and varies from about 300 to 500. While ovipositing the female moth protrudes the ovipositor which is formed of the three terminal abdominal segments. She actively moves it from side to side and frequently touches the substratum with its tip, as if attempting to test its suitability for oviposition. The eggs may be laid singly, but usually several (from a few to over 400) are laid in an irregular mass and one above the other (Fig. 1). The usual sites of oviposition, as seen in laboratory cages provided with living plants (linseed and pea seedlings), small weeds, dried up leaves, stubbles, paper slips and loose clods of earth, were the loose objects lying on the soil surface. Loose clods of earth, dry leaves, stubbles, paper slips etc. were preferred to growing plants. This habit may account for the heavy infestation of a wheat field in which straw was ploughed into the ground after the previous harvest (Frogatt 1911). At times, a few eggs were laid on low growing weeds (in the cages) but very seldom on living crop plants. Exceptionally, however, the long, tortuous tendrils of pea plants, that were touching the ground and were, therefore, perhaps regarded as loose objects on the soil, were quite commonly selected. Sites at or near the margins of the paper slips, dried up leaves etc. had a high priority in selection (Fig. 1).

Fecundity.- The moths have a very high fecundity. The total number of eggs laid by a single impregnated female varies from about 1,000 to 3,000 (Table 1). The mean number of eggs laid at an optimum temperature per female is approximately 1,500 to 1,800. Table 1 shows the oviposition records of 17 females which were reared on Medicago spp. at 16°C, 22°C, and

Table 1

The oviposition record of 17 females at 20 ± 2°C

Days of oviposition	No. of females living	Daily oviposition by female																	Eggs
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1	17	150	86	156	90	351	230	15	4	318	1	1	1	281	301	118	336	15	2,454
2	17	175	799	172	91	495	429	332	377	412	540	462	663	883	332	333	145	20	6,660
3	16	4	535	402	414	298	479	393	322	264	30	263	412	-	345	421	232	21	4,835
4	16	17	356	262	907	262	141	407	301	168	131	207	151	-	209	186	190	6	3,901
5	16	8	228	258	115	132	114	344	142	184	570	57	160	-	246	132	172	34	2,896
6	14	-	159	249	316	-	55	342	187	68	375	41	62	-	187	137	154	468	2,800
7	12	-	47	99	243	-	56	151	53	70	207	-	-	-	158	143	54	187	1,468
8	11	-	-	113	342	-	56	204	25	6	199	-	-	-	142	71	103	209	1,470
9	11	-	-	115	3	-	89	116	23	4	150	-	-	-	91	35	86	272	984
10	10	-	-	120	1	-	50	66	15	3	11	-	-	-	92	-	50	312	720
11	6	-	-	-	-	-	49	135	76	-	-	-	-	-	57	-	40	336	693
12	6	-	-	-	-	-	43	67	50	-	-	-	-	-	78	-	14	329	581
13	4	-	-	-	-	-	-	70	13	-	-	-	-	-	17	-	-	282	382
14	4	-	-	-	-	-	-	90	1	-	-	-	-	-	56	-	-	103	250
15	3	-	-	-	-	-	-	60	-	-	-	-	-	-	2	-	-	90	152
16	2	-	-	-	-	-	-	17	-	-	-	-	-	-	-	-	-	49	66
17	2	-	-	-	-	-	-	55	-	-	-	-	-	-	-	-	-	81	136
18	2	-	-	-	-	-	-	27	-	-	-	-	-	-	-	-	-	58	85
19	2	-	-	-	-	-	-	22	-	-	-	-	-	-	-	-	-	68	90
20	1	-	-	-	-	-	-	14	-	-	-	-	-	-	-	-	-	-	14
21	1	-	-	-	-	-	-	21	-	-	-	-	-	-	-	-	-	-	21
Reproductive life of female (days)	Total eggs	354	2210	1946	2522	1538	1791	2948	1589	1497	2214	1031	1449	1164	2313	1576	1576	2940	
		5	7	10	10	5	12	21	14	10	10	6	6	2	15	9	12	19	30,658

Note 1. The highest number of eggs laid during period of oviposition is underlined.

2. The unusual trend of oviposition by female 17 was due to its laying infertile eggs for the first four days.

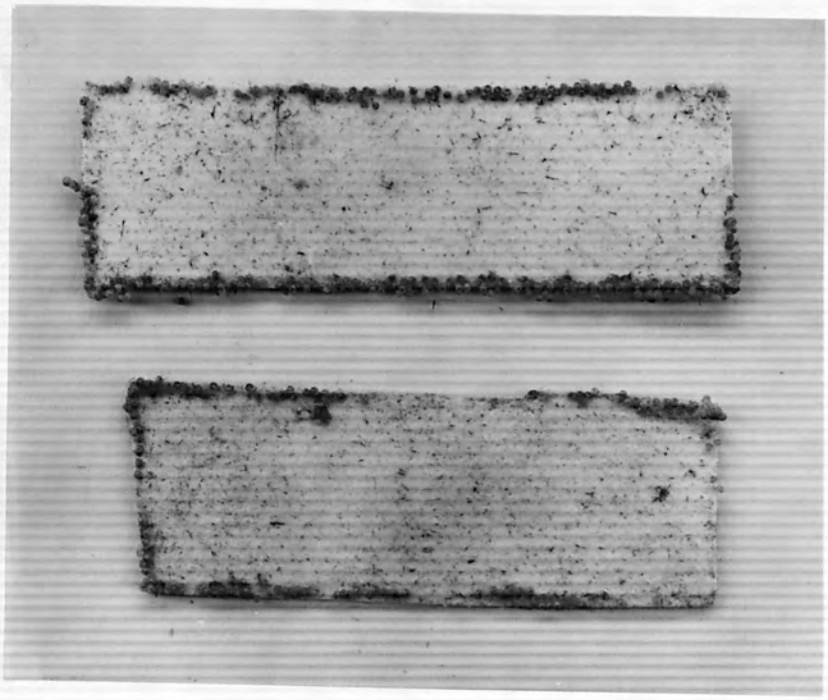


Figure 1. Egg masses at margins of paper-slips.

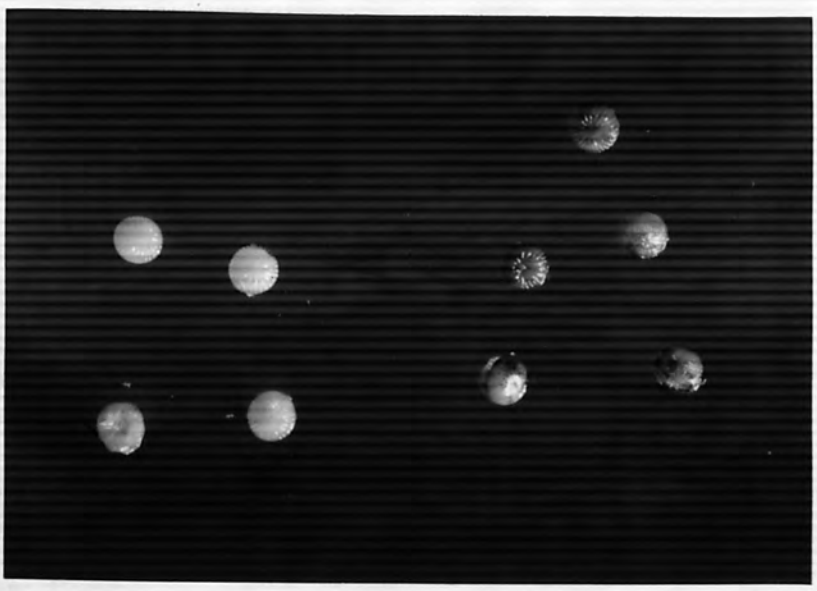


Figure 2. Changes in appearance of developing eggs.

26°C, respectively. They were separately mated at about 20 ± 2°C, and 20 per cent. sucrose solution was used as food.

Eggs Remaining in Ovaries of Dead Females

Dissections were made of several normally laying fertilized females after they had died to ascertain the state of the ovaries. None was found to have laid all the eggs of which she was potentially capable, and all contained both mature and developing eggs - from a few to over 800. The number of eggs remaining within the ovaries of dead females depends on the longevity of the moths in general and the length of the oviposition period in particular. As egg development continues, throughout the imaginal life, the eggs in the ovaries of dead females are always in various stages of development, and, for this reason, it is more or less impossible to determine the actual potential fecundity of the species.

Changes in External Appearance of Eggs with Development (Fig. 2)

Newly-laid eggs are uniformly cream-coloured. After about 1 to 7 days, depending on temperature, pale yellowish irregular markings appear which subsequently turn yellowish-brown and then deep reddish-brown. These markings take the form of an irregular circular spot at the anterior pole and an equatorial band near the middle of the egg. A little before hatching, the egg-colour changes to dark grey and the spot at the anterior pole turns dark brown. All these colour changes indicate the different stages of development of the embryo. When an egg, ready to hatch, is examined under low magnification, the fully-grown embryo can be seen within, its black prominent head and pro-thoracic shield in the anterior

part of the egg and the greyish body curled round in the middle of it. On the completion of embryogenesis, the larva is seen to make characteristic attempts to liberate itself.

Eclosion from the Egg.- The young larva begins to eat a hole through the chorion, and its minute reddish-brown mandibles can be seen at work under low magnification. It takes about 5 minutes to cut a hole large enough for it to crawl through. It then forces its head through the opening and slowly wriggles out by making characteristic peristaltic movements of the body. From 5 to 7 minutes are required for the larva to free itself from the egg, the chorion of which remains as a glistening, white, papery envelope.

Infertile Eggs.- Normally, the proportion of infertile eggs is small, rarely exceeding 3 per cent. In some cases, however, the percentage increased towards the end of the oviposition period, when it might be as high as 15 per cent. or even more. At unfavourable high or low temperatures, and especially at high temperatures, the percentage of infertile eggs increases rapidly; it may be, initially, as high as 30 to 50 per cent. and may reach 100 per cent. towards the end of the oviposition period. In a number of cases, when a female was confined with suitable food with a single male even at the optimum temperature of 20 $\pm$ 2°C and the moths were maintained at a favourable temperature, only infertile eggs were laid. This was possibly due to the sterility of the males, a phenomenon which was found to be fairly common and more widespread than sterility of the females. Infertile eggs can easily be distinguished by their failure to develop, and the consequent lack of the coloured spot and the band, the characteristic features of the fertile eggs. All such eggs shrink after a few days.

Abnormal Copulation and Reproduction - In experiments, to determine the fecundity and fertility of moths at different conditions of temperature (see "Experimental Biology"), many pairs were found to be unable to mate successfully and the females to lay fertile eggs. This was expecially so when moths were confined or reared at high constant temperatures. The temperature of confinement was more important than the rearing temperature. In nearly all such cases the males were sterile, being unable to complete spermatogenesis. Frequently, copulation began but the male was unable to transfer the spermatophore fully into the bursa copulatrix of the female to which, therefore, it remained attached by means of the partly everted spermatophore (Figs. 3, 4). In some cases, when the male did separate itself from the female, part of the tubular neck of the spermatophore remained permanently everted out of the female genitalia (Fig. 5, a and b). Such females laid only a few and infertile eggs because of the failure of the sperms to reach the spermatheca. Exceptionally, when more than one spermatophore were inserted in the female, and at least one was deposited in the bursa, fertile eggs were laid. The highest number of spermatophores found in a female was three; normally, however, a fertilized female contained only one.

Incubation Period.- The length of the egg stage varies considerably, depending on temperature. It is as short as 2.5 days at 34.°C, and extends to over a month at 9.3± 1°C.

Viability of Eggs.- Under suitable moisture conditions, the viability of eggs is unaffected by temperatures between 9°C and 34°C. Above or below this range, however,

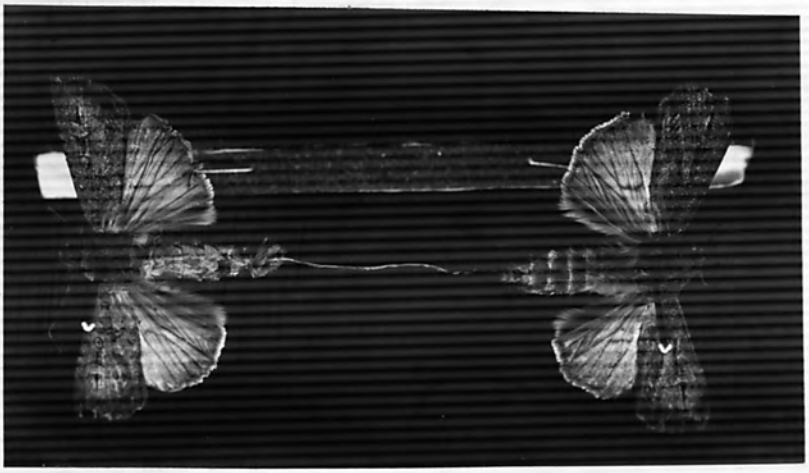


Figure 3. Abnormal copulation 1. (see Text)

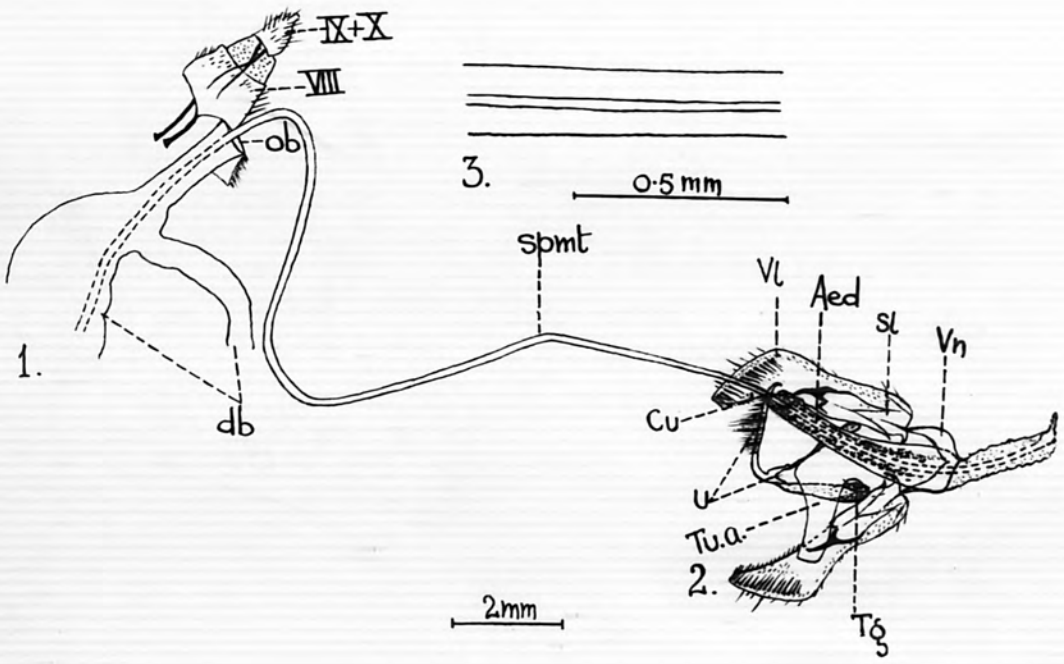


Figure 4. Abnormal copulation 2. (see Text).

(1) Female genitalia, and

(2) Male genitalia, attached with spermatophore (spmt).

(3) Longitudinal section of neck of spermatophore, to show the channel within.

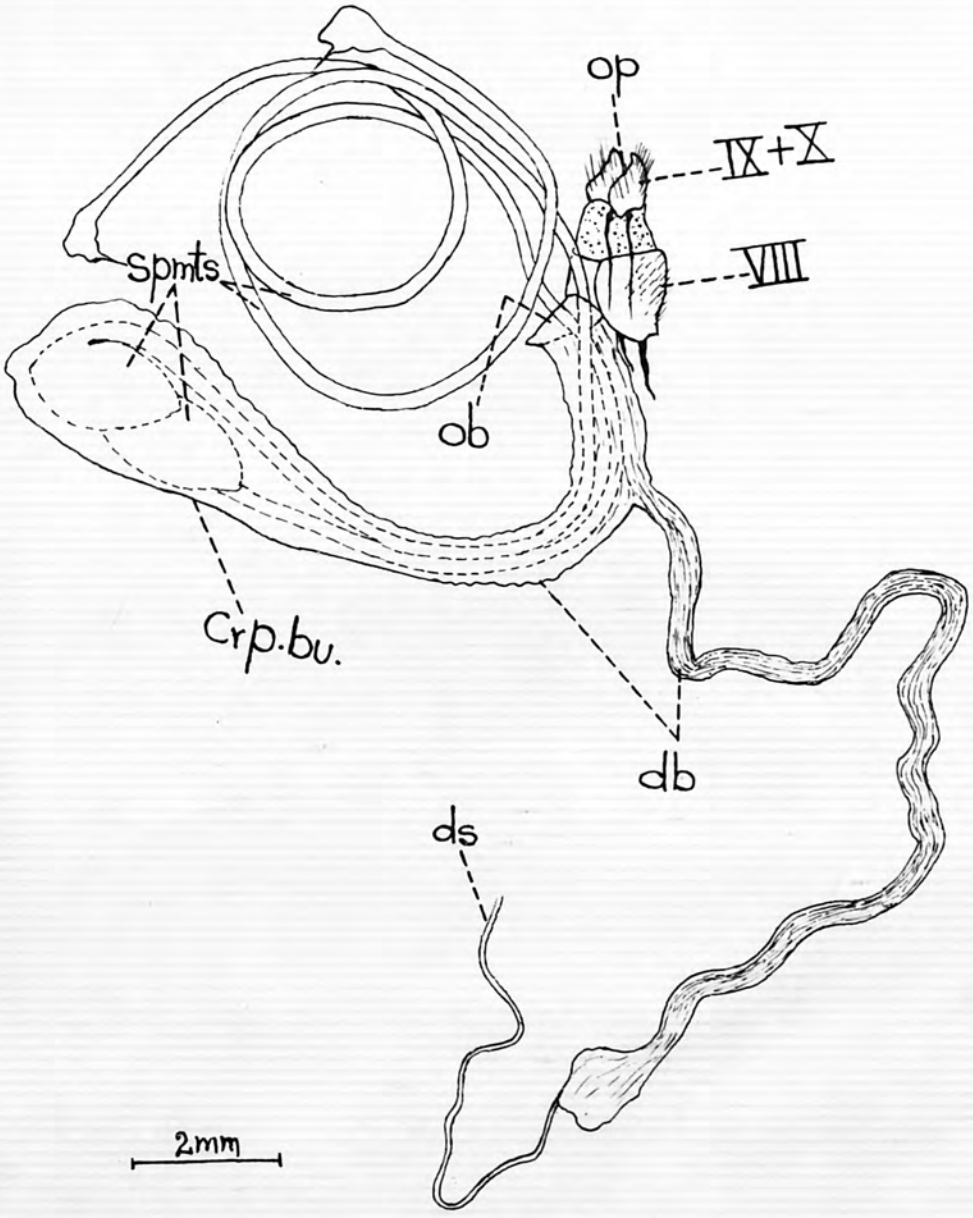


Figure 5. (a) Female genitalia with necks of spermatophores partly-everted after unsuccessful mating.

Figure 5. (b) Female with partly-everted spermatophores. Note attached egg mass.

it is progressively reduced. The eggs are highly resistant to desiccation, and even in a completely dry atmosphere up to 65 per cent. of eggs could hatch at the optimum temperature of 26°C. Near the extremes of the effective temperature range, the degree of desiccation that can be tolerated without injury, lessens. Under favourable conditions from 97 to 100 per cent. of fertile eggs complete their development and hatch.

B. The Larva and Pre-pupa

Soon after hatching, the larva eats a larger or smaller part of the chorion, a habit which is fairly general among lepidopterous larvae. Usually the feeding commences at the hole through which the larva has emerged. The entire eggshell is not consumed; the part attached to the substrate is usually left.

The number of larval ecdyses varied with the temperature. When this was favourable, the usual number of ecdyses was 6 or 7 but at higher temperatures (30°C, and above) the number increased to 8 or 9. In addition to temperature the quality of food may also exercise some influence on this, but this was not investigated.

Application of Dyar's Law.- Dyar's law applies to this species. To test its application, the width of the head capsules of a number of larvae, which passed through 7 and 8 instars respectively, was measured in different instars and the ratios of increase following each ecdysis was determined. From the different average ratios an overall average ratio was calculated (Table 2).

Table 2.

The application of Dyar's rule to the head widths of larvae undergoing 7 and 8 ecdyses, respectively

Larvae passing through	No. of larvae used	No. of instar	Mean width of head capsule	Mean ratios of increase	Overall average ratio
A. 7 stadia	5	1	0.280 mm	-	
		2	0.444 mm	1.59	
		3	0.643 mm	1.45	
		4	1.004 mm	1.56	1.52
		5	1.561 mm	1.56	
		6	2.304 mm	1.48	
		7	3.360 mm	1.46	
B. 8 stadia	6	1	0.284 mm	-	
		2	0.442 mm	1.55	
		3	0.638 mm	1.44	
		4	0.973 mm	1.53	
		5	1.411 mm	1.45	
		6	1.925 mm	1.36	1.44
		7	2.541 mm	1.33	
		8	3.623 mm	1.43	

There is a slight difference in the ratio of increase according to the number of ecdyses undergone. The larvae undergoing 8 ecdyses show relatively smaller increases in head widths and, therefore, a smaller overall average ratio of increase (1.44). Those undergoing 7 ecdyses show relatively larger increases in head widths and, therefore, a larger overall average ratio of increase, (1.52). In either case, the head width follows a more or less constant geometrical progression in successive instars from which it is possible to determine whether, or not, an ecdysis has been overlooked.

Process of Larval Moulting.- The details of moulting in all larval instars are essentially the same. Some time before actual ecdysis,

varying from a few hours to a few days according to the temperature, the larva discontinues feeding and becomes inactive. The body colour is slightly modified. Just before ecdysis occurs, the pro-thorax of the larva is conspicuously swollen posteriorly and the cervical region is considerably distended. These changes are brought about by the retraction of the relatively wider head of the next instar into the cervix of the moulting larva. The pale whitish-yellow head of the next larval instar, with its reddish-brown ocelli and mandibles, is clearly visible through the cervical membrane. Pressure applied by the new instar to the weaker membranous cervix causes it to rupture. The head capsule is thus shed separately and earlier than the remaining exuviae. More or less simultaneously with the shedding of the head capsule, the old partly digested cuticle splits along the mid-dorsal region as far as the second abdominal segment. The larva then begins to wriggle out gradually forcing the old cuticle behind by a series of convulsive contractions and expansions of the body. As the old cuticle is forced behind, the silvery-white cuticular linings of the tracheae are drawn through the spiracular openings of the emerging larva and stretched by being attached to the spiracles of the old cuticle. Within a few minutes moulting is complete and the exuviae is completely shed. Usually the anal claspers of the old cuticle remain attached to plant fragments or soil particles. Thus, the characteristic feature of the larval ecdysis is that the head capsule and the remainder of the exuviae are shed separately. Exceptionally, however, due to partial splitting round the cervix, the head capsule remains attached to the old cuticle

and is shed with it. The newly moulted larva is pale and dull in appearance; its body-surface is still wet with the moulting fluid, but dries after a few minutes. The head capsule, the pro-thoracic shield, the anal plate and the tubercles of the newly moulted larva are soft and white. The body colour begins to deepen about fifteen minutes after the larva has emerged but the head capsule, pro-thoracic shield, anal plate etc. take a much longer time to become sclerotized. The newly-moulted larva does not recommence feeding until some time after ecdysis, when the internal changes connected with moulting have been completed. Part of the exuviae is frequently eaten by the larva.

Larval Reactions to Light.- The first two larval instars are apparently not stimulated by light but are negatively geotropic. They, therefore, are found on the plants, feeding on the young foliage, irrespective of whether it is day or night. From the third instar onwards the larvae become increasingly negatively phototropic and positively geotropic. They begin to hide by day under the loose soil surface. The larvae in their two final instars are intensely negatively-phototropic. When exposed to light (in laboratory) in big rearing Petri dishes with food plants, they at once begin crawling away from a light-source and hide under the plant material provided as food.

Mode of Locomotion, and Reaction to Stimuli.- The first and the second larval instars adopt the semi-looper type of progression due to the fact that their first two pairs of prolegs are greatly reduced. Consequent upon the development of these, the later larval instars are able to move in the typical "caterpillar" manner. They seldom keep their bodies

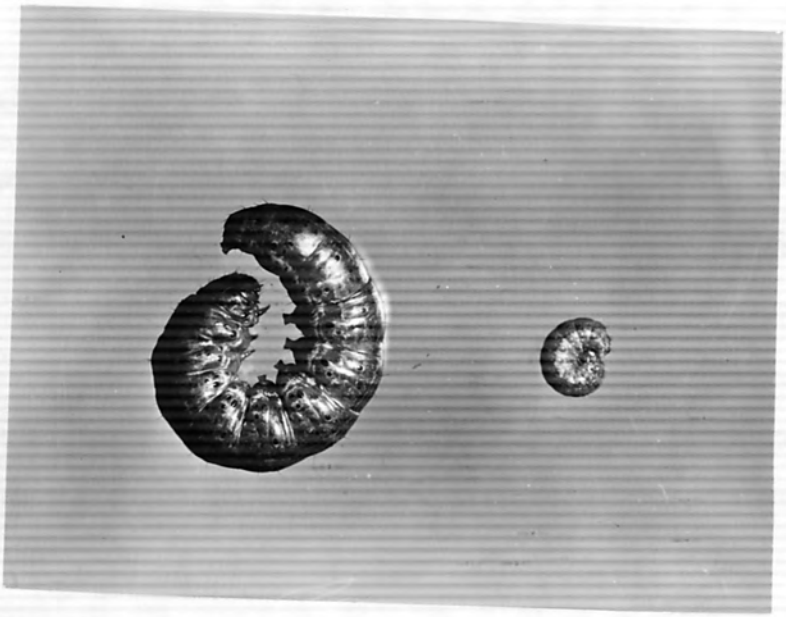


Figure 6. Larval reaction to tactile stimulation.

straight during locomotion but usually move with the posterior part of the body slightly curved to one side.

On disturbance, the larva, particularly from the fourth instar onwards, shows the characteristic habit of lying in the form of the letter 'C', or more often, of coiling itself in a spiral with the head concealed by the posterior end of the abdomen (see Fig. 6). This habit is also exhibited by the earlier instars though to a lesser extent, and also less frequently.

Mode of Larval Feeding (Figs. 7, 8).- The effect, on the plant, of larval feeding varies with the stage of development. Damage done by the first two instars is entirely restricted to the foliage. The first instars remove the leaf mesophyll irregularly from young leaves, forming small, white, papery patches. The second instar mostly skeletonizes the leaves by eating the soft leaf-tissue, and leaving behind a network of veins. The damage done by these two instars is comparatively small and not very obvious. From the third instar onwards the larvae display increasing appetites, causing relatively greater and more easily noticeable damage to plants. They begin attacking the tender stems, though the third and fourth instars still feed mostly on leaves. The third instar cuts holes between the prominent veins; the fourth instar, however, feeds on the entire leaf tissues by cutting irregular holes either at the leaf margin or in the lamina itself. The habit of cutting off the tender stems, usually near ground level, from the third instar onwards, coincides with the development of the positively geotropic and negatively-phototropic behaviour of the larvae. This habit is intensified in the two final instars which also show intense negatively

Figure 7. Larval damage to lucerne. Left - early instar damage; Right - older instar damage.

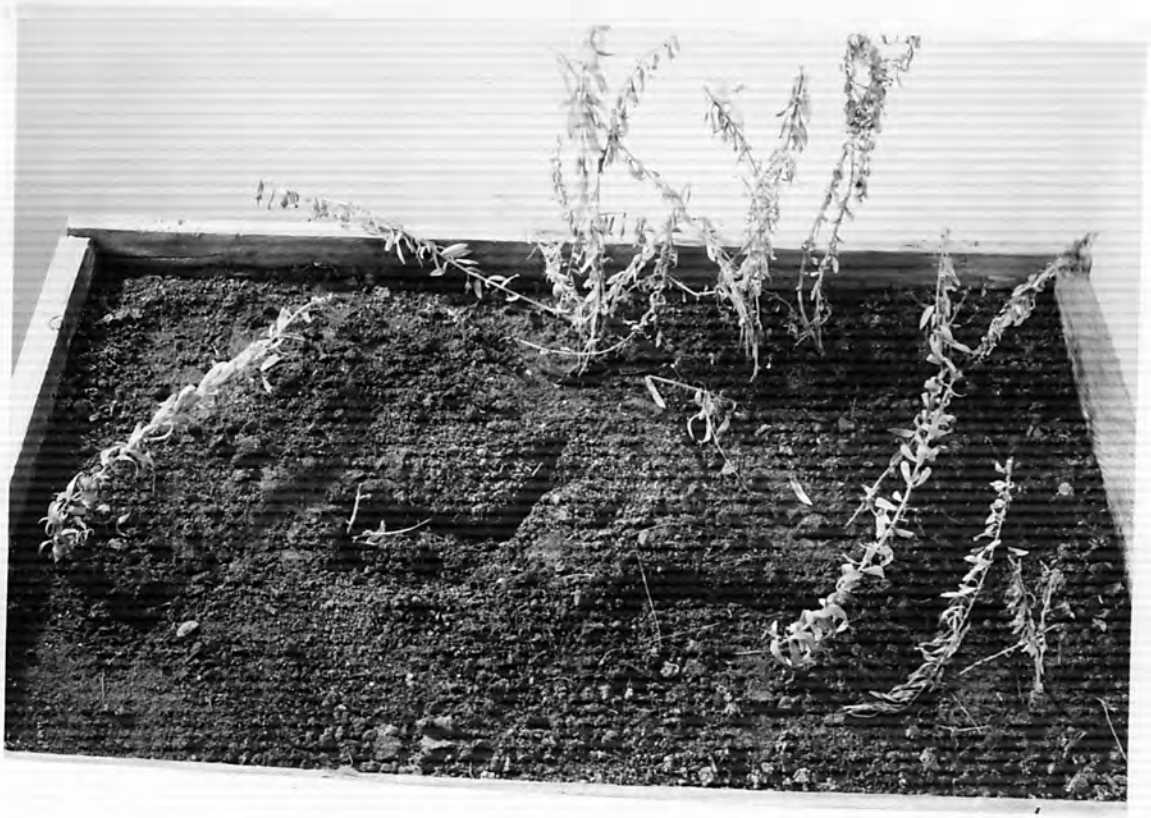


Figure 8. Larval galleries, exposed, in soil, and damage to linseed seedlings.

phototropic behaviour. In these stadia, the larvae come out of the soil only at night to cut off the stems of tender young plants, usually close to the soil surface. They drag the cut parts of plants, partly or wholly, into their burrows (Fig. 8), in which they lie concealed, feeding on them by day. Very young plants may be cut off even slightly below soil level, especially during the day. The older plants with relatively hard and woody stems, however, are cut off only at night, and at some distance above the soil surface where the stems are softer. At times, the final instar larvae may also damage plants by cutting through their roots. This type of injury was observed on lucerne in the Balaklava district of South Australia in November-December 1956. Many of the plants whose root systems were thus damaged still managed to survive and maintain growth. When, however, stock were subsequently allowed on the area, such plants were found to be easily removed due to mechanical disturbance, with only about two or three inches of roots remaining.

The characteristic feature of the damage is that it tends to be concentrated in patches which increase in area with the growth of the larvae. These patches probably correspond with areas in which large numbers of eggs are laid, possibly due to favourable factors in the micro-climate. As the plants are cut off near ground level these patches are denuded and become obvious. At times, when stems are incompletely cut through some distance above the ground, the parts beyond that point droop, and subsequently wither. This type of damage was seen both in cages in the laboratory and in the infested field mentioned above.

Economic damage by the species is irregular in its impact, and varies considerably in extent from year to year. It appears that when the environmental conditions for two or more consecutive years are favourable to the organism it builds up its population and causes appreciable damage.

Host Plants.- The species is polyphagous. It has been recorded as feeding on saltbush, bluebush, grasses, maize, wheat, barley, cabbage, cauliflower, vines, linseed, lucerne, Medicago spp., Trifolium spp., oats, annual composites like cape-weed (Cryptostemma calendula L.), peas, potatoes, cotton, and garden plants such as carnations, dahlias etc. (see Review of Literature). It is almost certain that in some of these records A. infusa has been confused with other species. Notwithstanding this, the range of plants on which it will feed is very wide. It is of interest to note that, whereas, in the earlier part of this century it has been mostly found to be destructive to saltbush, bluebush, wheat, barley, grasses and occasionally lucerne (Froggatt 1899, 1901, 1907, 1910, 1911; Anon. 1919), later records, chiefly by Common (1954), refer it to be most abundant in dense stands of Medicago spp., cape-weed, linseed and to a lesser extent in lucerne fields and mixed pastures of clover and oats. This suggests that with the large-scale spread of medics and cape-weed, subsequent to their introductions, and the diversification of agriculture in Australia, the pest has found these plants more attractive than others. On the other hand, it tends to cast doubts on the authenticity of some of the earlier records. During the course of the present study (1955-57) the larvae were found to be feeding on lucerne, Medicago spp., cape-weed and wheat.

Mode of Larval Movements in the Soil.- As mentioned above, older larval instars are positively geotropic and negatively phototropic. When such a larva is put on the soil surface and stimulated by light, it soon begins to burrow into the soil. If the surface is loose and relatively moist, larval penetration is greatly facilitated as are its movements within the soil. Such soils, therefore, are preferred by the species. When the larva begins to burrow, it forces its head into the soil, and then by a series of slight upward jerks and rhythmic body contractions and expansions loosens the soil particles. It then gradually pushes its body into the space made by the head and finally enters the soil. The larval movements within the soil are also effected in a similar manner. In the optimum environment, provided in laboratory cages, the old larvae were usually found at a depth of about three-quarters of an inch. They move in random fashion through the soil in search of food along horizontal galleries (Fig. 8). In the field, when the soil-surface was sufficiently moist and contained loose clods, the larvae were usually found concealed under these by day. As the heavier soils provide both the suitable moisture status and the clods on the surface, this particular habit, at least, partly accounts for its severe infestations on heavy soils (see Review of Literature).

Formation of Pupal Cell.- When fully fed, the final larval instar ceases feeding and evacuates the gut. Subsequently, it discharges a considerable quantity of water through the anus. No silk is produced during the formation of the pupal cell. The earthen cell is formed by means of the watery anal discharge combined with the body-movements of the active

phase of the prepupa. The prepupa in its initial stage, loses a great deal of weight, and discharges much pale yellowish fluid. During this discharge the prepupa makes typical rotary body movements, which compact the soil particles, provide a smooth inner surface to the cell, and make it sufficiently spacious for free movements of the pupal abdominal segments. The cell (Fig. 9) measures about 25 mm in length. Anteriorly, it has a width of about 15 mm, and posteriorly, about 10 mm. It is thus ovate in form. Its size is determined by the size of the individual prepupa. The active prepupa retains the capacity to crawl either forwards or backwards. On being disturbed it curls up slightly in the form of the letter 'C' (Fig. 9) but cannot completely coil itself. When it has discharged nearly all the excess water and has finished the formation of the cell, it becomes inactive. The only movements of which the inactive prepupa is capable when stimulated, are rotary movements of the abdomen. From the full grown larval to the inert prepupal stage the body contracts to about half the larval length, caused by the shrinkage of the intersegmental membranes. Simultaneously with the discharge of the excess water during the prepupal stage, numerous fat deposits are aggregated, most of which pass on from the pupa to the adult moth.

Occasionally, a fully-fed larva ceased feeding and entered the prepupal stage which lasted more than twice as long as normal. All such individuals failed to pupate but the derangement cannot be explained.

Duration of the Larval and Prepupal Periods.- The duration of the larval period is mainly determined by temperature though the quality of the food

Figure 9. Prepupa, pupal cell, and pupa.

also exercises some influence. The most rapid larval development takes place at 30°C, at which it occupies from 18 to 20 days. It is greatly prolonged at lower temperatures and is very variable near the threshold temperature of development; at 13°C it lasts from 81-102 days. At 8°C no larva completed its development, while a few only completed the third stadium in three months.

The prepupal period varied from two days at 30°C, to 15-16 days at 13°C, and as many as 23-24 days at 7°C, at which temperature mortality was very high.

The Final Larval Ecdysis.- Towards the end of the prepupal period when the formation of the pupa is complete, the remains of the larval cuticle form a thin covering around it. By a series of peristatic contractions and expansions of the last abdominal segments and aided by the cremaster of the pupa, which serves as an anchor, the posterior part of the old larval cuticle is pushed behind as a loose, contracted, empty sac. Pressure is thus brought to bear upon the anterior end of the larval cuticle. This pressure is further augmented by blood-pressure. Consequently, the larval skin splits medially along the dorsum of the larval pro-thorax and the dorsal thoracic region of the pupa soon protrudes through the split, which gradually extends for the whole length of the thoracic and head regions. In the latter, it extends along the stem and arms of the epicranial suture to the mandibular attachments. Subsequently, the head and the thorax of the pupa emerge through the opening. The larval skin continues to be pushed behind by rhythmic body movements and the cremaster of the pupa. From the first

appearance of the split, it requires some 10 minutes for the pupa to shed the larval exuviae completely. The ruptured head capsule lies just behind the cremaster and the remaining part of the exuviae forms a loose mass, lying at the posterior end of the pupal cell. The freshly cast exuviae is wet with moulting fluid and can be stretched to the full length of the larva. As it dries, it becomes much shrivelled and brittle. The final larval ecdysis differs from the previous ones in that the head capsule is not broken off along the cervix and shed separately from the remainder of the exuviae but remains attached to it. Pupation takes place at any time of the day and usually occurs two or three inches below the soil surface.

At times, as a result of abnormal moulting the larval cuticle splits only along the dorsal thoracic region and fails to extend to the head. Because of this the cephalic region of the pupa cannot free itself from the larval head capsule. The pupa thus remains attached to the larval skin at either end, and despite its efforts is unable to liberate itself. Such pupae are invariably injured by the rupturing of the soft cuticle of some part of the body and consequently die.

C. The Pupa and Moth

Duration of the Pupal Period. - Like the egg, larval, and prepupal periods, the pupal period is largely determined by temperature. The most rapid development, at 30°C, occupies 11-12 days. As the temperature falls, development is delayed until at 13°C it takes from 52 to 65 days. At 10°C the pupae failed to complete development though some were still alive at

the end of $3\frac{1}{2}$ months.

Eclosion of the Imago.- As the time for eclosion approaches, the moth starts to exert pressure on the pupal cuticle. As a result, part of the pupal case between the antennae and the ventral part of the head is ruptured. The split may also extend partly along the intersegmental region between the pro- and the meso-thorax, but these usually remain attached at the more highly sclerotized dark brown peritremal regions of the thoracic spiracles. Unlike larval ecdysis, the split does not extend medially along the dorsum of the thorax. With the rupturing of the pupal case, the antennae, the mouthparts and the legs of the moth are set free. With the help of movements of these appendages, the moth manages to struggle out of the pupal cuticle. Emergence of the moth may be completed within fifteen minutes. While it is emerging it simultaneously breaks open a circular hole at the anterior end of the cell. This hole is just large enough to allow the moth to squeeze through. It then makes its way to the soil surface by loosening the soil and pushing the loose particles aside. Emergence is greatly facilitated if the surface soil is friable and reasonably moist. In the laboratory the emergence of moths took place at any time of the day.

Abnormal Splitting of the Pupal Case.- Under unfavourably low relative humidities the pupae lose a high percentage of weight and show signs of desiccation by having the posterior abdominal segments distinctly contracted and constricted. Most of such pupae lose the mobility of their posterior abdominal segments and die. Some, which are more resistant and, therefore,

manage to survive, may undergo normal rupturing of their pupal cases; the moths, however, are unable to free their bodies from the pupal cases due to the abdomen of the pupae being constricted. At times, the pupal case breaks along the constricted part of the abdomen. When this happens the head and thoracic appendages are freed and the moths can fly and feed but as the posterior abdominal segments remain permanently encased within the broken part of the pupal case they can neither reproduce nor defecate and live for a short time only.

At times, the abdominal segments of the pupae become distended, possibly due to some abnormal physiological condition. Usually, when this happens, the pupal cell is broken near the middle of the abdomen, exposing the posterior part of the moth's abdomen. Such moths invariably fail to emerge.

On emergence, the whole body and the appendages of the moth are wet with moulting fluid, which soon dries. The wings of the freshly emerged moth are still of the same size as they were in the pupa. They are also similarly pressed and folded close to the body. This condition facilitates the movement of the moth through the soil. On reaching the surface, the moth usually rests head upwards on some herbage or other object and discharges the meconium through the anus, in the form of a number of thin pinkish-buff droplets. Simultaneously, the moth forces the blood into the wings which consequently are gradually expanded. During the expansion of the wings and for some time after, they are held vertically over the body as in the Rhopalocera. The wings are then gradually brought to the horizontal plane with the body and are then held in the characteristic manner. Intermittently,

however, the wings are raised vertically and lowered. When the wings have expanded and hardened, the moth is capable of flight.

Habits of the Moths.- The moths are usually active only at night when they leave their shelters and fly in search of food, mates or oviposition sites. By day they normally remain concealed, usually in numbers close together, with the anterior part of the body of one being covered up by the posterior part of the other, in such dark spots as under fallen tree trunks, clods of earth or stones, or within cavities in tree-trunks etc. This habit was also seen in the laboratory, when the moths were confined in cages for oviposition. When they were exposed to light, they quickly moved to dark places or under various objects.

Sex-ratio.- The numbers of male and female moths were usually found to be equal. Occasionally, however, one sex slightly outnumbered the other.

Longevity.- This varies considerably with temperature, and the presence or absence of food. When deprived of food or water they lived two days at 34°C to as long as 26 days at 6.8°C. The longevity of the moths, when provided with food and when they were reproducing, was about 3 to 7 times as long. Moths provided with water alone lived slightly longer than the ones which received neither food nor water (see "Experimental Biology"). The maximum longevity of moths kept with food, was 88 days at a constant temperature of 16°C, and 90 days at alternating temperatures of 20.0°C for 9 hours and 5.8°C for 15 hours daily.

D. Changes in Weight and Water-Content during the Life-Cycle

Determinations of the body-weight during the whole life-cycle

were made. The weights of the penultimate, and final larval, and the pupal exuviae were also determined, together with the body weights of larvae, prepupae and pupae.

The eggs were weighed, within 24 hours of oviposition (at 18°C) and were then kept at 18°C and about 50 per cent. R.H. They were re-weighed on the seventh day, just before hatching. The larvae in the first instar were weighed within 12 hours of hatching (at 18°C) and before the commencement of feeding. After feeding had begun they were re-weighed at intervals till the end of the instar. The penultimate instar was weighed on the fourth day of the stadium, while it was still feeding but was near the end of it, and re-weighed one day before ecdysis (on the fifth day). After ecdysis, the final larval instar was weighed daily until it was full-grown. The mean weight of the fully-fed larvae (reared at 26°C) was also determined and compared with that of the first instar (within 12 hours of hatching and before the commencement of feeding) and the increase in weight during the larval development was calculated. The prepupae, kept at 20 to 22°C, were weighed daily. The pupae, also kept at 20 to 22°C, were weighed in the beginning and at the end of their development, a little before the emergence of the moths. The moths were weighed soon after emergence and re-weighed after 24 and 48 hours, when kept without food or water at 22°C and about 60 per cent. R.H. One moth, which was weighed 24 hours after emergence (without food or water), was then provided with 20 per cent. sucrose solution and re-weighed after another 24 hours to determine the effect of food on its weight.

The changes of weight during the whole life-cycle of the species are shown in Table 3, and represented graphically in Figs. 10 and 11. Weights of the penultimate and final larval and pupal exuviae are given in Table 4 and the water-content of the larvae, prepupae and pupae in Table 5.

Table 3

Changes in weight of developing egg and weight of first larval instar on emergence

A.

Stage of Development	No. of Eggs	Mean Weight (mg)	Decrease in Weight (%)
Within 24 hours of oviposition (at 18°C)	50	0.0634	-
Just before hatching (on 7th day at 18°C)	46	0.0604	4.73
1st instar, within 12 hours of hatching at 18°C (without food)	70	0.048	24.3

Table 3 (Cont'd)

Increase in weight of 1st instar compared with weight of final larval instar

B.

Stage of Development	No. of Larvae	Mean Weight (mg)	Increase in Weight (%) (Approximate)
1st instar, newly emerged (within 12 hours of hatching at 18°C, without food)	70	0.048	-
1st instar, (after 24 hours of feeding at 18°C)	27	0.095	98
1st instar, (6 days after emergence at 18°C)	10	0.355	600
1st instar, (7 days after emergence at 18°C prior to ecdysis)	10	0.270	500
Full-grown larva (Reared at 26°C)	18	889.0	2,000,000

Table 3 (Cont'd)

Decrease in weight following ecdysis of penultimate larval instar and subsequent increase during development of final larval instar

C.

Stage of Development (20 to 22°C)	Number	Mean Weight (mg)	Decrease or Increase (%)
Penultimate Instar (feeding, 4th day of stadium)	2	478.0	-
Penultimate Instar, 1 day before ecdysis (5th day of stadium)	2	456.4	- 4.52
Final Instar, just after ecdysis	2	443.8	- 7.16
" " , 1 day " "	2	574.8	+ 29.52
" " , 2 days " "	2	687.2	+ 54.84
" " , 3 days " "	2	710.1	+ 60.00
" " , 4 days " "	2	752.5	+ 69.56
" " , 5 days " "	2	750.5	+ 69.10
" " , 6 days " "	2	790.4	+ 78.10
" " , 7 days " "	2	845.3	+ 90.47
" " , 8 days " "	2	970.0	+118.57
" " , 9 days " "	2	1019.1	+129.60

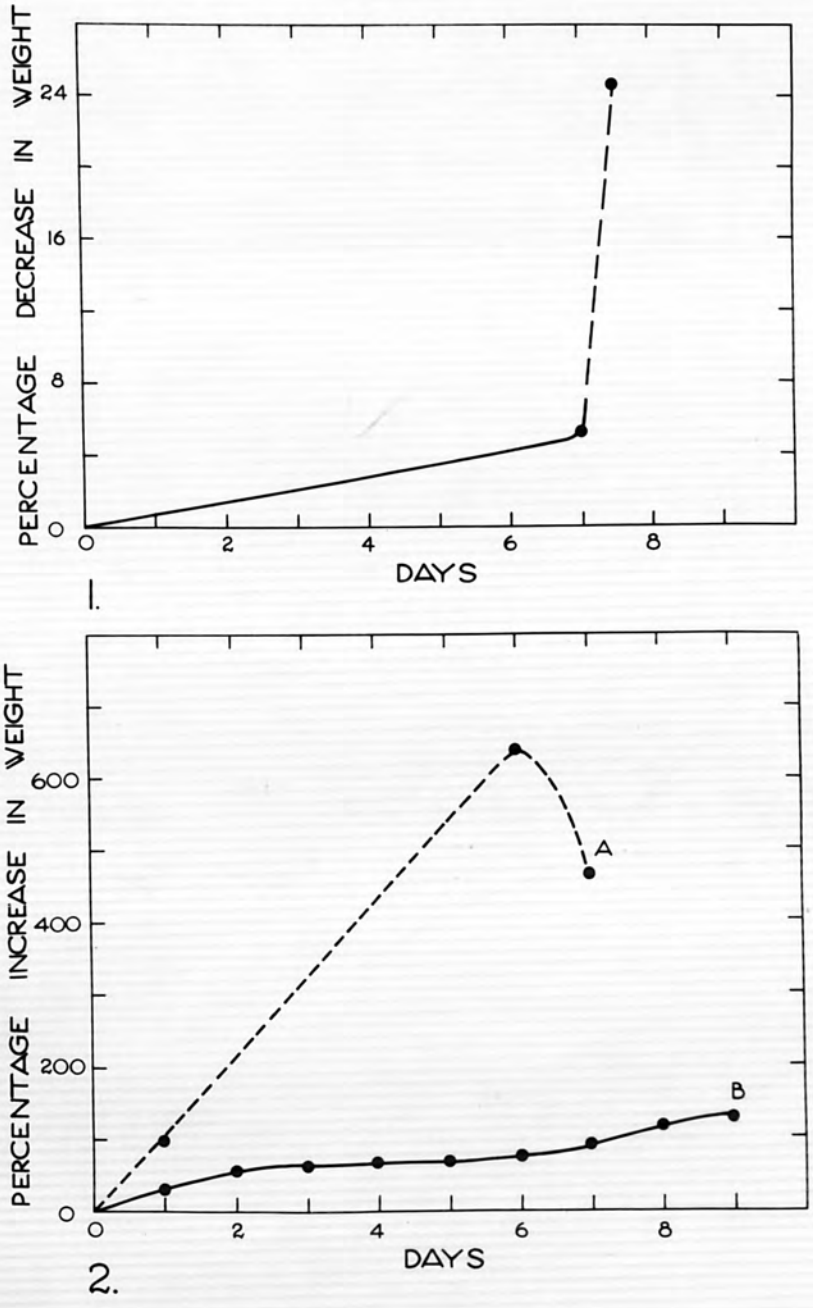


Figure 10. (1) Percentage decrease in weight during egg development (solid line), and within 12 hours of hatching (broken line); 18°C.

(2) A. Percentage change in weight; first larval stadium; 18°C.

B. Percentage increase in weight; final larval stadium; 20-22°C.

Table 3 (Cont'd)

Loss of weight from beginning of pre-pupal period to emergence of imago

D.

Stage of Development (20 to 22°C)	Number	Mean Weight (mg)	Loss of Weight (%)	Loss over Previous Weight (%)
Prepupa, (1st day)	19	817.0	8.10	-
" , (2nd day)	19	605.8	31.85	-
" , (3rd day)	19	440.5	50.40	-
" , (4th day)	19	397.3	55.30	-
" , (5th day)	19	384.1	56.80	-
Pupa (6th day after beginning of prepupation)	19	360.3	59.50 [1.]	-
Pupa (17th day after pupation)	17	329.0	63.00	8.7
Moth (unfed, within 12 hours of emergence)	14	200.4	77.5 [2.]	39.0

1. Includes 1.5% loss due to weight of newly-cast exuviae.
2. Includes about 1.0% loss due to weight of newly-cast exuviae.

Table 3 (Cont'd)

Loss of weight of moths under different conditions

E.

Conditions under which moths were kept (at 22°C)	Stage of imaginal Life	No. Moths	Mean Weight (mg)	Loss (%)
A. Without Food	a) Soon after emergence	3	250.0	-
	24 hrs. after "	3	183.5	26.6
	b) Soon after emergence	1	112.9	-
	24 hrs. after "	1	86.7	23.2
	48 hrs. after "	1	79.0	30.0
B. Without Food for 1 day, Then with Food (20% sucrose solution)	Soon after emergence	1	287.0	-
	24 hrs. after "	1	219.1	23.7
	48 hrs. after "	1	266.2	7.3

Loss of weight during the early part of imaginal life is mainly due to expulsion of meconium.

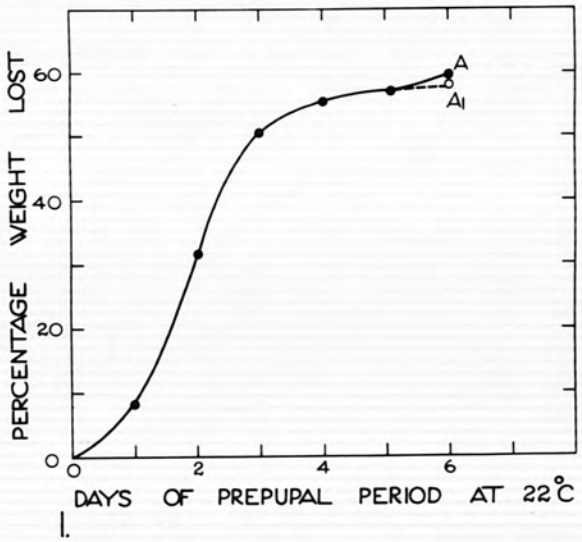
Figure 11

Figure 11.

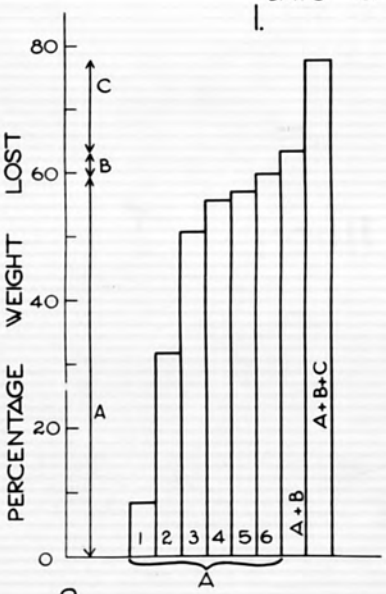
1. Percentage loss in weight during pre-pupal period; 20 - 22°C.
   $A - A_1$ = loss due to exuviae (1.5%).

2. Percentage loss in weight during
   A - pre-pupal stage; 20 - 22°C
   A + B - prepupal and pupal stages - including weight of larval exuviae (1.5%); 20 - 22°C
   A + B + C - pre-pupal, pupal, and imaginal stages, moths 12 hours old; no food. Including weight of pupal exuviae 1% ; 20 - 22°C

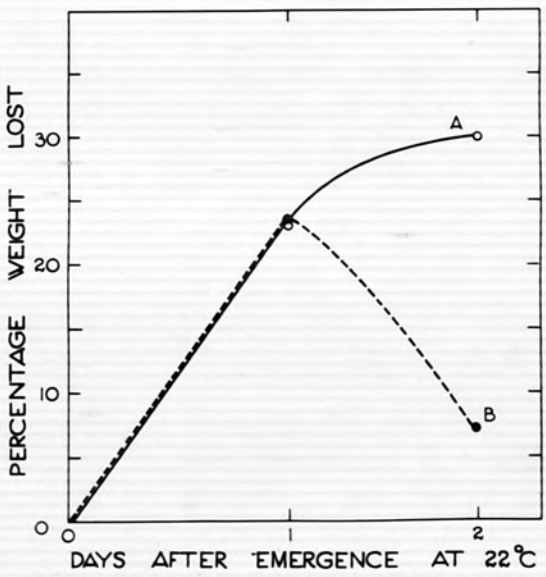
3. Percentage loss in weight during first two days of imaginal life :
   A No food
   B No food on first day; fed on second day.


PERCENTAGE WEIGHT LOST
0
20
40
60
A
A1
0
2
4
6
DAYS OF PREPUPAL PERIOD AT 22°C

1.


PERCENTAGE WEIGHT LOST
0
20
40
60
80
C
B
A
1
2
3
4
5
6
A+B
A+B+C
A

2.


PERCENTAGE WEIGHT LOST
0
10
20
30
A
B
0
1
2
DAYS AFTER EMERGENCE AT 22°C

3.

Fig. 11

Table 4

Weights of the Penultimate larval, Final larval, and Pupal Exuviae

Description of Exuviae	No. of exuviae Weighed	Mean Weight of newly-cast Exuviae (mg)	Mean Oven-Dry Weight of Exuviae (mg)
Penultimate larval	8	-	2.025 (Head capsule 0.583) (Rest of exuviae 1.442)
Final larval	17	12.7	8.3
Pupal	15	8.6	5.4

Table 5

Water-content of Larvae, Prepupae and Pupae

Stage	No. of insects used	Mean Water-Content (%)	Variation in Water-content (%)
1st Instar larva (within 12 hours of hatching; unfed)	67	75.00	73.0 to 77.0
Fully-fed larva	13	90.20	89.0 to 92.0
Pre-pupa (advanced stage)	5	76.20	75.9 to 77.0
Pupa (12 hours after pupation)	4	73.55	73.0 to 74.1

II. Description of Stages

A. The Egg (Figs. 1, 2)

The egg is dome-shaped, flat and smooth at the posterior end for attachment to the substratum but rough and sculptured on the remaining exposed region. It is slightly narrower posteriorly, widest near the middle and provided with an obtusely rounded anterior end. It measures about 0.5 mm in width and about 0.35 mm in height. The micropylar region, at the anterior end, is somewhat raised, and more or less circular. The sculpturing consists of a series of longitudinal ribs and transverse carinae. There are 14 primary polar ribs which converge towards the anterior, where they become obsolete. Between these primary ribs run secondary ribs which are, in all, about 20 in number. A series of fine transverse undulating carinae, not as high and prominent as the ribs, pass round the egg. Between the ribs and the carinae are slightly depressed oval areas. Newly-laid eggs are glistening and cream-coloured, but change colour as they develop (see "Life Cycle").

B. The Larva (Fig. 12)

Although the number of larval instars may vary from 6 to 9, their general colour pattern and external characters are not affected thereby. For the description of the different larval instars, those undergoing six ecdyses were selected.

First larval instar.- The newly-emerged first larval instar measures about 1.7 mm in length and about 0.25 mm in thickness, but it increases

Figure 12. The seven larval instars.

to 3.5 mm in length and 0.5 mm in thickness by the end of the stadium. The general body colour of the newly-emerged larva is pale yellowish-white, tinged with pale red dorsally. Once the larva starts feeding, the anterior part of its body assumes a greenish appearance due to the food's being visible through the semi-transparent cuticle. Subsequently, the colour becomes yellowish-orange with a pale pink dorsal suffusion. The ventral surface remains pale yellowish-white. The head capsule, the pro-thoracic shield and the anal plate are dark brown and highly sclerotized. On the head capsule, the black ocelli, the reddish-brown mandibles and the whitish, slender antennae are easily visible. The width of the head, about 0.28 mm, is distinctly greater than that of the body at the beginning of the stadium, thereby making it very prominent. Subsequently, the body-width increases while that of the head remains unchanged, so that by the middle of the stadium, body and head-widths are equal. By the end of the stadium, the body-width exceeds that of the head. The tubercles are yellowish-brown and very prominent. Each is surrounded by a very narrow whitish annulus and bears a minute seta which is clubbed at its tip. The thoracic- and pro-legs are white, and of the latter only the last three pairs are functional. The second pair are much reduced, and the first are vestigial. There are five narrow, white longitudinal lines along the body - a mid-dorsal, two right and left dorso-laterals and a right and left lateral. The mid-dorsal line ends at the posterior margin of the pro-thoracic shield. The spiracles are small, circular and yellow, and are smaller than the tubercles, except on the pro-thorax

and the eighth abdominal segment. The body segments are distinct.

Second larval instar.- The second larval instar measures 3.5 mm in length and 0.5 mm in thickness immediately after the first ecdysis; it later increases to about 6 mm in length and 1.0 mm in thickness. The head and the pro-thoracic shield become pale yellowish-brown with dark brown tubercles and irregular brown markings. The ocelli, mandibles and antennae retain the first instar coloration. The anal plate becomes pale yellow. The general body colour is pale pinkish-yellow with a green tinge, particularly towards its anterior part. The dorsal surface is suffused with pink except around the tubercles which have narrow white annuli. The mid-dorsal longitudinal white line, unlike that of the first instar, continues on to the pro-thoracic shield. The two dorso-lateral white lines, and the somewhat broader white lateral line resemble those of the first instar. Tubercles and clubbed setae are also similar to those of the first instar. Spiracles are small, circular and light brown in colour. The ventral surface is pale yellow, as are the thoracic and pro-legs. The two anterior pairs of the latter are still reduced, the first more pronouncedly so. The body segments are distinct.

Third larval instar.- Initially, the third larval instar measures about 6 mm in length and from 1.0 to 1.25 mm in thickness, but later increases to about 10 mm and 1.5 to 1.75 mm respectively. The body colour remains practically unchanged. The body segments are distinct caused by light green inter-segmental depressions. Each body segment is bi-annulate. A slightly yellow dorsal longitudinal band, including the mid-dorsal longitudinal white line extends from behind the head to the last abdominal segment. The dorso-lateral

and lateral white longitudinal lines are present. The head is light yellow, with minute brown markings on the epicranium, and bears black tubercles with their setae. The pro-thoracic shield is light brown, with pale yellow spots, and it has the medial dorsal longitudinal line. The last abdominal segment is slightly darker dorsally and the mid-dorsal line is somewhat broader here than elsewhere. The thoracic- and pro-legs are white; the claws and crochets are brown. The four posterior pairs of pro-legs are well developed. The most anterior pair are still reduced, and bear fewer and smaller crochets than do the others. The tubercles are dark with white annuli, and the setae are minute and clavate. The brown spiracles are more or less circular in shape.

Fourth larval instar.- The fourth larval instar measures about 10 mm in length and 1.5 mm in thickness initially, but later increases to 17-18 mm and 2.5 mm respectively. Soon after ecdysis all the parts which are later sclerotized, are pale yellowish-white. The body is dark with pale yellow tubercles dorsally, but ventrally, it is white, tinged with green and semi-transparent. Some time after ecdysis, the colour of the dorsal surface becomes dull pinkish-grey with a slight green tinge. The dorsal longitudinal yellow band, bearing the mid-dorsal longitudinal white line, passes along the full length of the body. The dorsum of the last abdominal segment has two short longitudinal pink stripes, one on either side of the mid-dorsal longitudinal white line. The two dorso-lateral and a broader lateral yellowish-white, lines are present as before. The head is pale yellow with pale brown markings. The antennae are prominent and

yellow. The ocelli, six on either side of the head, are dark brown. The postero-dorsal four form an arc, and are closer together than the antero-ventral pair which are a little separated. The pro-thoracic shield is yellow with dark brown markings, and bears the mid-dorsal longitudinal line. The ventral surface of the body, and the thoracic-, and pro-legs are pale greenish-white. Although all the pro-legs are now well developed, the first are still somewhat smaller and weaker than the others. The intermediate spiracles are circular and black; the pro-thoracic and the eighth abdominal ones are, however, oval and comparatively large. The tubercles are fully pigmented, being blackish-brown with narrow white annuli. The setae are simple and non-capitate.

Fifth larval instar.- The fifth larval instar measures about 17 mm in length and 2.5 mm in thickness initially but 28-30 mm, and 4 mm, finally. The newly-moulted larva is grey with a yellowish-grey dorsal longitudinal band. The mid-dorsal and the two dorso-lateral longitudinal lines are very faint. The lateral white line is more prominent. The head is creamy-white with pale reddish-brown mandibles, brown ocelli, and light yellow prominent antennae. The pro-thoracic shield is white with grey spots. The dorsum of the last abdominal segment is also white with two grey short, parallel longitudinal stripes. The tubercles are unpigmented. Later, the general body colour changes to grey, tinged with pink. The head capsule becomes sclerotized and light yellowish-brown in colour, with many minute brown spots. The pro-thoracic shield is also sclerotized and dark brown, with yellow spots, and is marked by the mid-dorsal longitudinal line. The two short parallel longitudinal stripes on the

dorsum of the last abdominal segment became dark. The dorsal longitudinal band remains yellowish-grey. The mid-dorsal, dorso-lateral and the lateral longitudinal lines are white. A minute dorso-lateral white spot on each body segment is situated behind the spiracle, just above, and touching, a tubercle. The ventral side of the body, and thoracic- and pro-legs are pale greenish-white and semi-transparent. The outer surfaces of the thoracic-legs are yellowish-brown pigmented. All the pro-legs are now well-developed. The crochets are arranged in uni-ordinal, semi-circular, meso-series on the inner sides of the plantae. The plantae are white, each with a central brown-pigmented spot which marks the region of muscle attachment. The spiracles are black and oval. The tubercles are dark-brown with pale whitish annuli. The setae are minute, simple and non-capitate.

Sixth larval instar.- The sixth larval instar initially measures about 28-30 mm in length and 4 mm in thickness; when fully-fed it increases to between 42-50 mm in length and 5.5 to 6.5 mm in thickness. The general body colour of the newly-moulted larva is grey; the head, the pro-thoracic shield, the tubercles, and the dorsum of the last abdominal segment are pale yellowish-white. Some time after ecdysis, when the sclerotization has been completed and feeding resumed, the general colour of the dorsum is dark olive green. The pale yellow dorsal band, bearing the mid-dorsal longitudinal white line, passes from behind the head to the last abdominal segment. The two dorso-lateral, pale, white longitudinal lines are discontinuous; the upper is indistinct, the lower more obvious. The

lateral longitudinal white line is very distinct. The head capsule becomes light yellowish-brown with dark spots and sculpturing. The pro-thoracic shield is sclerotized, dark, and bears the mid-dorsal longitudinal line. The dorsum of the last abdominal segment has two short parallel longitudinally-running dark stripes, one on either side of the white mid-dorsal line. The latter is somewhat broader in this region. The tubercles are dark and polished and their setae are short and simple. The spiracles are black and elliptical. The ventral surface of the body, the pro-legs and the inner sides of the thoracic-legs are green and semi-transparent. Through the thin ventral cuticle certain of the internal structures, such as tracheae, Malpighian tubules, fat-bodies etc., are clearly visible. Externally, the thoracic-legs are sclerotized and are yellowish-brown in colour.

C. The Pre-pupa (Fig. 9)

There is a progressive contraction of the body during the pre-pupal stage, which is initiated soon after the fully-grown larva has stopped feeding. Within from 1 to 6 days, depending on temperature, the length approximates to that of the pupa. The inert prepupa measures from 18 to 25 mm, in length and 5.5 to 7.05 mm, in thickness.

Dorsally, the prepupa is dark grey with a green tinge. The yellow dorsal longitudinal band is about 3 mm broad; the body is dark greyish-green medially. The white mid-dorsal, and the two dorso-lateral longitudinal, lines are very indistinct. The lateral white line is indistinguishable from the general yellowish-white colour of the ventral surface. The numerous fat bodies, within the body, are visible through the semi-transparent ventral

body wall. The dorso-lateral region, on either side, is dark olive-green and 3 mm broad. Laterally, below the lower dorso-lateral pale white longitudinal line, and just above the spiracle, there is a small pale yellowish-white conspicuous spot on each segment. The head is yellowish-brown. The pro-thoracic shield is blackish-brown with small yellow patches. The dorsum of the last abdominal segment resembles that of the final larval instar. The tubercles, situated on the dorso-lateral surface, are pale grey; those of the dorsal surface are dark brown. The spiracles are black and elliptical. The segmentation is very distinct due to deep inter-segmental infoldings which develop as a result of the contraction. The prepupa is more or less fusiform, tapering more towards the posterior end. The thoracic-legs and the pro-legs are more or less empty and flaccid due to histolysis of their tissues.

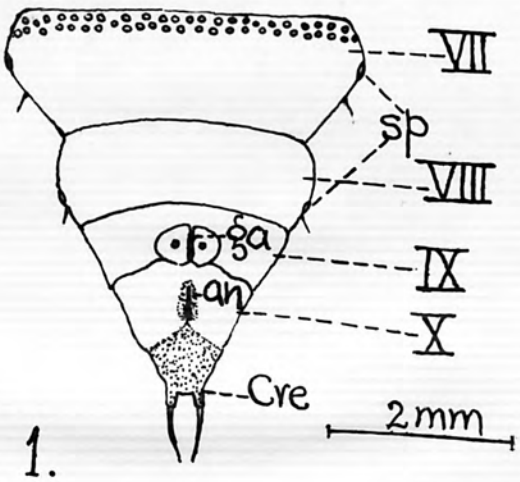
D. The Pupa (Fig. 9)

The pupa is typically obtect and measures from 16 mm, to 22 mm, in length and from 5 to 7 mm, in width. On the head, the vertex, the fronto-clypeus, the labrum-epipharynx, the pilifers and the compound eyes are visible, whereas the antennae, the labial palpi, and the proboscis extend over the ventral region of the thorax and the anterior part of the abdomen. The three thoracic segments are distinct, dorsally. The meso-thorax is larger than the meta-thorax as much of the latter is concealed under the hinder part of the meso-thorax. A single pair of prominent dark brown elliptical spiracles, situated dorso-laterally, are present between the pro- and the

meso-thorax. The second pair of thoracic spiracles are concealed under the folded wings. The wings and the legs are folded over the body. The hindwings are, for the most part, concealed beneath the forewings. The abdomen consists of ten distinct segments, all exposed dorsally. Ventrally, the folded wings cover the abdomen up to about the fourth abdominal sternum; the remainder is exposed. The movable segments are the fourth, fifth and sixth. The inter-segmental regions between these and between the sixth and seventh segments are markedly constricted. The anterior regions of the fourth to the seventh abdominal segments are highly sclerotized and are provided with numerous pits of different sizes (Fig. 13). The smaller pits are usually situated anteriorly and the larger, posteriorly. They are more numerous on the dorsal than on the ventral surface. Dorsally, these sclerotized regions are distinctly elevated above the general body surface. The first thoracic spiracles are concealed by the hindwings. The spiracles on the second to the seventh abdominal segments are well developed, elliptical and dark-brown in colour, whereas those on the eighth abdominal segment are somewhat reduced. A few minute setae are present on the abdomen, usually a pair on each segment posterior to the spiracles. The terminal segments of the pupa show important sexual differences.

The Sexual Differences

The Male Pupa (Fig. 13,1). The ninth abdominal sternum, near its caudal margin, bears the genital aperture between two semi-circular slightly-raised plates each of which has a deep brown circular spot in the middle. The tenth abdominal sternum bears the anal aperture in contact with the cremaster. The region on either side of the anal aperture is



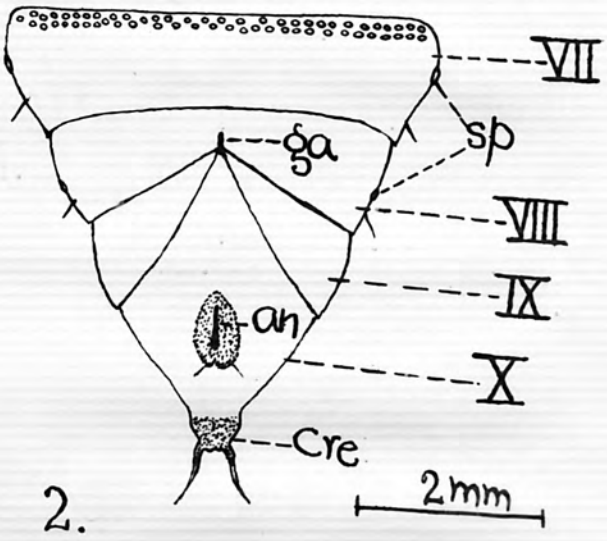


Figure 13. Terminal segments of male (1) and female (2) pupae
an = anus; cre = cremaster; ga = genital aperture; sp = spiracle

slightly elevated. The dark brown cremaster is highly sclerotized, and has a pair of short distal processes, each bearing a short, thin spine.

The Female Pupa (Fig. 13, 2). The posterior margin of the eighth abdominal sternum shows an emargination into which fits the anterior margin of the ninth sternum. The posterior margin of the ninth sternum, in turn, is even more deeply emarginate and into this fits the anteriorly-produced tenth sternum. The genital aperture is situated on the posterior part of the eighth sternum. The anal aperture, which is conspicuously larger than the genital aperture, is borne near the posterior margin of the tenth sternum, but is not in contact with the cremaster. The latter, as in the male pupa, consists of the highly-sclerotized, blackish-brown termination of the tenth abdominal segment which is produced into two short processes, each bearing a pair of fine spines.

Three stages of pupal development were selected for description.

The white pupa is the stage immediately after emergence. It lasts for from 2 to 6 hours, depending on temperature and other factors. It is yellowish-white in colour. The fat-bodies are visible through the semi-transparent abdominal body wall as also are the lateral tracheal trunks and their branches. A mid-dorsal longitudinal pale green line on the dorsal surface of the abdomen indicates the location of the heart. The characteristic pits are present on the abdomen as are a few pale brown tubercles with minute setae. The veins of the wings are very distinct. The spiracles are pale yellowish-brown. The last abdominal segment is pale

brown ending in the brown cremaster. In about half an hour, slight reddening of the dorsal surface of the abdomen begins, and the body wall gradually becomes opaque.

Within a few hours, sclerotization is more or less complete, and the colour of the pupa changes to pale reddish-brown. The spiracles also darken. The brown pupal stage may itself be sub-divided into four stages:

The first is of short duration during which the larvel ocelli are still present on the head.

The second begins with the disappearance of the larval ocelli, which are replaced by the reddish compound eyes of the adult.

The third is marked by the change in colour of the compound eyes to dark brown and of the pupa, as a whole, to deep reddish-brown. Areas adjacent to the inter-segmental regions between the fourth and fifth, the fifth and sixth, and the sixth and seventh abdominal segments turn dark reddish-brown.

In the fourth, the orbicular and reniform can be distinguished with the black fascia between them. The latter is continued beyond the reniform and is pointed distally.

The dark pupa is the final phase of pupal development, when the future imago is more or less complete, the general colour changes to dark brown, more particularly on the wings. Due to the darkening of the pupa, the black fascia, the orbicular and the reniform become less conspicuous.

E. The Imago (Fig. 14)

The male varies considerably in colour pattern, from a form with

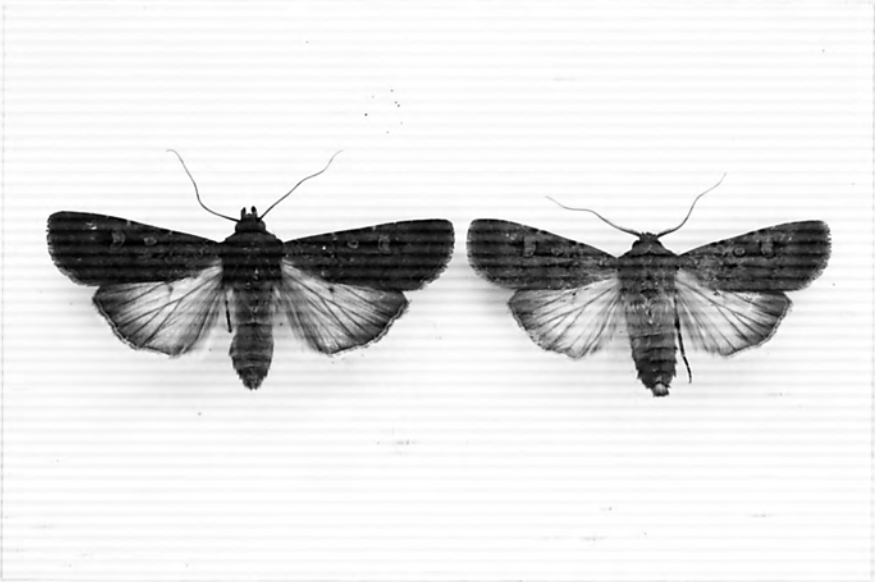


Figure 14. Imagines : female (left); male (right).

greyish-white wings to that with greyish-brown, or even fuscous wings. These variations were observed in the progeny of a single female. Temperature was found to have no recognizable effect on colour variation.

The females are more constant in colour pattern, the head, the thorax and the forewings being usually dark, and the abdomen and hindwings lighter and greyish. A few females may, however, show a brownish tinge on the forewings.

Considerable variations in size of imagines occurs according to the conditions to which larvae have been subjected. Temperature has an important influence on this as also has the food (see "Experimental Biology").

The body length of males varies from 16.0 to 20.5 mm, and the wing expanse from 32.0 to 43.0 mm. The corresponding measurements for the females are from 16.0 to 21.0 mm, and 32.0 to 45.0 mm, respectively. A general description of the imago was published by Hampson (1903) who, under the names, Euxoa infusa (p.164) and Agrotis spina (p.367), confused two colour-variants of this species.

III. Seasonal History

The seasonal history of the species has not hitherto been well known. Common (1954) concluded that the major part of the population in south-eastern Australia has but a single generation annually. He, however, considered that in favourable habitats three or even four annual generations were possible.

The present study showed that in the neighbourhood of Adelaide (South Australia) the species breeds throughout the year. Though economic

damage was reported and observed only from June to December, information derived from the catches in a light-trap at the Waite Institute showed that the species is active throughout the year, though most moths were caught during spring and autumn.

Throughout the summer, particularly in 1957, females collected in the light-trap, were dissected regularly to determine the extent of ovarial development and whether or not they had been impregnated. Over this period, both fertilized females, with well-developed ovaries, and unfertilized females, with immature ones, were collected (Table 6). From the presence or absence of the spermatophore in the bursa it was easily determined whether or not the moths had been fertilized. Of the moths with immature ovaries, many were newly-emerged as was shown by their complete and undamaged investment. This indicated that emergence was continuing throughout the summer. Nearly all females, which had been fertilized had mature ovaries, exhausted fat-bodies and eggs descending from the ovarioles into the oviducts. Some females had laid most of their eggs as the posterior parts of the ovarioles were empty and the fat-bodies nearly exhausted. From the evidence of laboratory experiments (see "Experimental Biology"), the presence of fertilized moths, capable of laying fertile eggs throughout the summer was to be expected. From similar evidence it could also be predicted that larvae were capable of developing continuously over the same period, especially in more suitable localized areas such as relatively moist or shady places where the soil was not too dry and food was still available.

Table 6

Showing results of dissections of Female Moths, collected at light-trap, in the Waite Agricultural Research Institute, during summers of 1956 and 1957 regarding the state of ovaries, fat-bodies and bursa copulatrix

Serial No. of Females Dissected	Date of Catch	State of Ovaries	State of Fat-bodies	State of Bursa Copulatrix
1	20.2.56	Immature	Well-developed	Without spermatophore
2	"	"	"	"
3	26.2.56	"	"	"
4	28.2.56	Mature	Emaciated	With spermatophore
5	"	Mature; eggs passing through oviducts	"	"
6	29.256	Mature; eggs passing through oviducts	"	"
7	29.2.56	Mature; eggs passing through oviducts	"	"
8	1.3.56	Immature	Well-developed	Without spermatophore
9	18.12.56	Mature; eggs passing through oviducts	Emaciated	With spermatophore
10	9.1.57	Mature	"	Without spermatophore
11	10.1.57	"	"	With "
12	13.1.57	Immature	Well-developed	Without "
13	"	"	"	" "
14	"	Mature	Emaciated	With "
15	17.1.57	Immature	Well-developed	Without "
16	"	"	"	" "
17	"	"	"	" "
18	21.1.57	"	"	" "
19	22.1.57	Mature; eggs passing through oviducts	Emaciated	With "
20	24.1.57	Mature	Well-developed	Without "
21	5.2.57	Mature; more or less empty	Emaciated	With "
22	"	Mature; posterior parts of ovarioles empty	Well-developed	Without "
23	6.2.57	Immature	"	" "
24	6.2.57	Mature; eggs passing through oviducts	Emaciated	With "
25	10.2.57	Mature; eggs passing through oviducts	"	" "
26	12.2.57	Mature; eggs passing through oviducts	"	" "
27	"	Mature; eggs passing through oviducts	"	" "
28	13.2.57	Maturing	Well-developed	Without "
29	17.2.57	"	Emaciated	" "
30	19.2.57	Mature; eggs passing through oviducts	Well-developed	" "
31	"	Immature	"	" "
32	19.2.57	"	"	" "
33	23.2.57	Mature; eggs passing through oviducts	Emaciated	With "
34	27.2.57	Mature; eggs passing through oviducts	"	" "
35	4.3.57	Immature	Well-developed	Without "
36	6.3.57	"	"	" "
37	7.3.57	"	"	" "
38	"	"	"	" "
39	9.3.57	Mature; eggs passing through oviducts	Emaciated	With "
40	19.3.57	Mature; eggs passing through oviducts	"	" "
41	"	Immature	Well-developed	Without "

These observations, together with those made in the field, and the natural occurrence of fully-grown larvae during most of the year, indicate that the species has more than one generation annually and is active throughout the year, particularly in favourable areas. Laboratory investigations concerning the speed of development at different temperatures suggest that the species is capable, in nature, of having six annual broods in the neighbourhood of Adelaide. Taking 8°C as the approximate threshold of development, the total day-degrees required for one life cycle from egg to egg, according to Blunck's formula, are about 835 to 850. In the vicinity of Adelaide the total day-degrees in a year, at which the development of the species can go on, amount to 5175. Theoretically therefore, six generations a year are possible. Such, however, could occur only under the most favourable environmental conditions encountered in small localized areas.

No evidence of aestivation was obtained in laboratory experiments nor was such found from observations made in the field. Though some females showed pronouncedly-delayed pre-oviposition periods this was associated with with male-sterility or with abnormal or unsuccessful mating.

IV. Natural Factors of Control

Before considering the natural agencies which exercise control over this species in South Australia, it may not be out of place here to review briefly the observations of other workers. Frogatt[§] (1899, 1901, 1910) recorded high mortalities of larvae due to heavy rains and subsequent flooding, cold weather, fungus disease, cannibalism, and birds. He also

Figure 15. Diaea variabilis Koch feeding on Heliothis larva.

Figure 16. Chrysopa larva feeding on second larval instar of A. infusa.

noted heavy parasitism of pupae by a chalcid. Common (1954) observed birds and other agents to exert some control.

In the course of this study the following natural factors had a direct or indirect influence in controlling population numbers:

Predators: A spider, Diaea variabilis Koch (Thomisidae; Fig. 15) was found feeding on young caterpillars of A. infusa and also of Heliothis punctigera (Wallengren), in the laboratory, when it was accidentally put in a rearing dish with the lucerne, used as food. Similarly, a Chrysopa larva (Fig. 16) was found feeding on eggs and first and second larval instars. It consumed several larvae and eggs in succession.

Insect Parasites: Two tachinids were reared from the larvae. About 60 per cent. of the fourth and fifth larval instars collected from Balaklava (South Australia) on 12th November 1956, were parasitized by Chaetophthalmus bicolor Macq. (Fig. 17) and died in their final instar. Another somewhat larger tachinid, Tritaxys heterocera Macq. (Fig. 18) parasitized a number of prepupae and pupae, and occasionally fully-grown larvae, which were reared from eggs in the laboratory, and fed on lucerne collected from the field. The lucerne apparently bore the parasite's eggs which, when consumed by the larvae, began their development. The adult parasites emerged during November-December (1955). The full-grown parasitic larva emerged by cutting a hole at the anterior part of the host body, after which it soon pupated. The pupal period, at 16°C, varied from 32 to 44 days (average 38.25 days); the imaginal life at the same temperature and without food varied from 9 to 13 days (average 10.5 days).

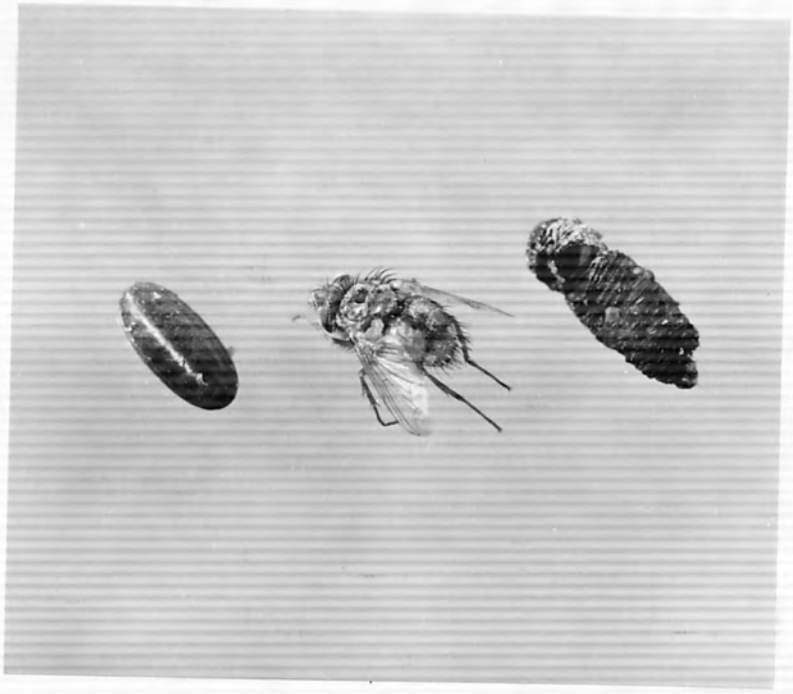


Figure 17. Chaetophthalmus bicolor Macq.
Puparium, adult, and dead host larva showing emergence hole of parasitic larva.

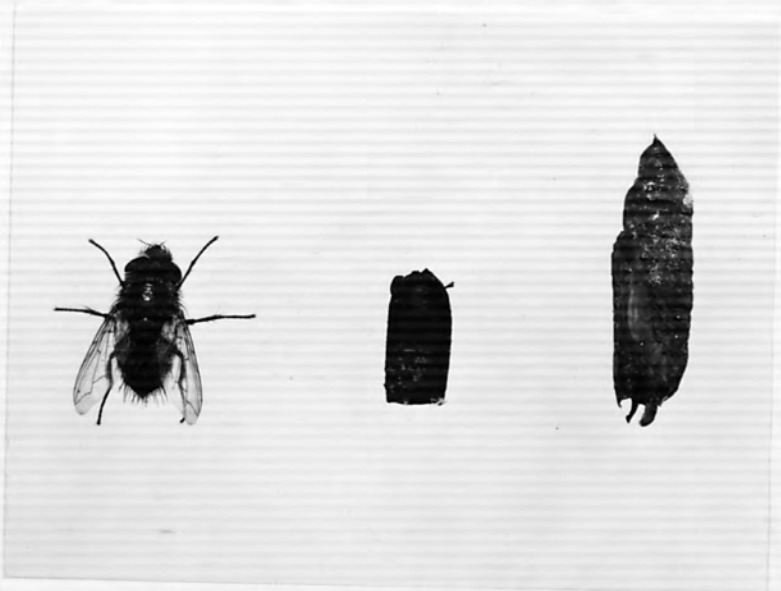


Figure 18. Tritaxys heterocera Macq.
Adult, broken puparium, and parasitized pupa.

Bacterial Disease.- Several large colonies of larvae reared in the laboratory, were destroyed by a bacterial disease, which was identified as Bacillus thuringiensis by Mr. J.R.Harris of the Soil-Microbiology Section of the Division of Soils (C.S.I.R.O.). The disease, though more virulent at higher temperatures, was also active at lower temperatures. It was found to be commonly associated with overcrowding of larvae especially when the rearing of successive generations had lowered their vitality. Infected larvae showed a decreased rate of development. The latter was also irregular and this resulted in great variations in size of larvae of the same age. Diseased larvae fed very slowly and displayed little activity. At a later stage they ceased feeding, and discharged through the anus a whitish fluid which contaminated both food and rearing dishes. In the final stage the larvae became incapable of moving and their bodies were much contracted and completely covered by the discharge. The disease seemed to spread rapidly due to the combined effects of contamination of food by the discharge, and cannibalism.

Cannibalism.- The tendency towards cannibalism among larvae of this species was less than in some others, e.g. Heliothis spp. in which it has been thoroughly studied. It was exhibited only by final larval instars when reared collectively. Usually the weaker, inactive or diseased larvae were eaten. As sick or dead larvae were invariably consumed, this habit probably assisted in the rapid spread of disease-carrying organisms. The whole body is not eaten; usually the head and the final abdominal segment are left.

Overcrowding.- Overcrowding alone was found to reduce larval survival considerably (see "Experimental Biology"). Overcrowding, however, at one time or another, produces a deficiency of food which, by lowering the general vitality, aids the spread of disease, cannibalism etc.

Type of Food.- The lack of suitable food exercises some control over the numbers of this species. As will be shown later, survival and rate of larval development, as well as the weights of larvae and pupae, are greatly affected by the suitability or otherwise of the food eaten. Thus, of cape-weed, lucerne and wheat, the first was found to be the most suitable and the last the least suitable.

EXPERIMENTAL BIOLOGY

I. The Egg

For the experimental work described in this section, all eggs used had been laid within the 24 hours preceding the commencement of the experiment, unless otherwise specified.

In each experiment, all eggs were kept until no further hatching occurred.

Dashes in tables usually indicate "No observations made".

1. Effect of Different Constant Temperatures on the Rate of Development and Survival of Eggs

At each of the selected temperatures, 100 eggs were placed on blotting paper and kept continuously moist for the duration of the experiment, in a closed container. Counts of eggs hatched were made at twelve-hourly intervals.

Results are shown in Table 7 and Figures 19 and 20.

Table 7

Effect of Temperature on Rate of Development and Survival of Eggs

Temperature °C	Mean Incubation Period (Days)	Index of Development	Eggs Hatched (%)	Details about the Distribution of Hatching	
				Time (Days)	Eggs Hatched (%)
9.3 ± 1.0	32.47	3.08	97	30.5	1
				31.0	0
				31.5	0
				32.0	41
				32.5	22
				33.0	31
				33.5	0
				34.0	1
				34.5	0
				35.0	1
13.1 ± 0.3	17.65	5.60	96	16.0	5
				16.5	10
				17.0	3
				17.5	0
				18.0	30
				18.5	48
16.0	10.10	9.90	99	9.5	15
				10.0	74
				10.5	10
18.4 ± 0.2	6.86	14.60	98	6.5	27
				7.0	71
20.0	6.00	16.66	99	6.0	99
22.2 ± 0.3	4.90	20.40	94	4.5	6
				5.0	88
26.0	3.60	27.77	97	3.0	37
				3.5	60
30.2 ± 0.2	2.60	38.50	100	2.5	100
33.8 ± 0.2	2.40	41.70	100	2.0	4
				2.5	85
				3.0	11

Note: The eggs, which failed to hatch, were usually infertile.

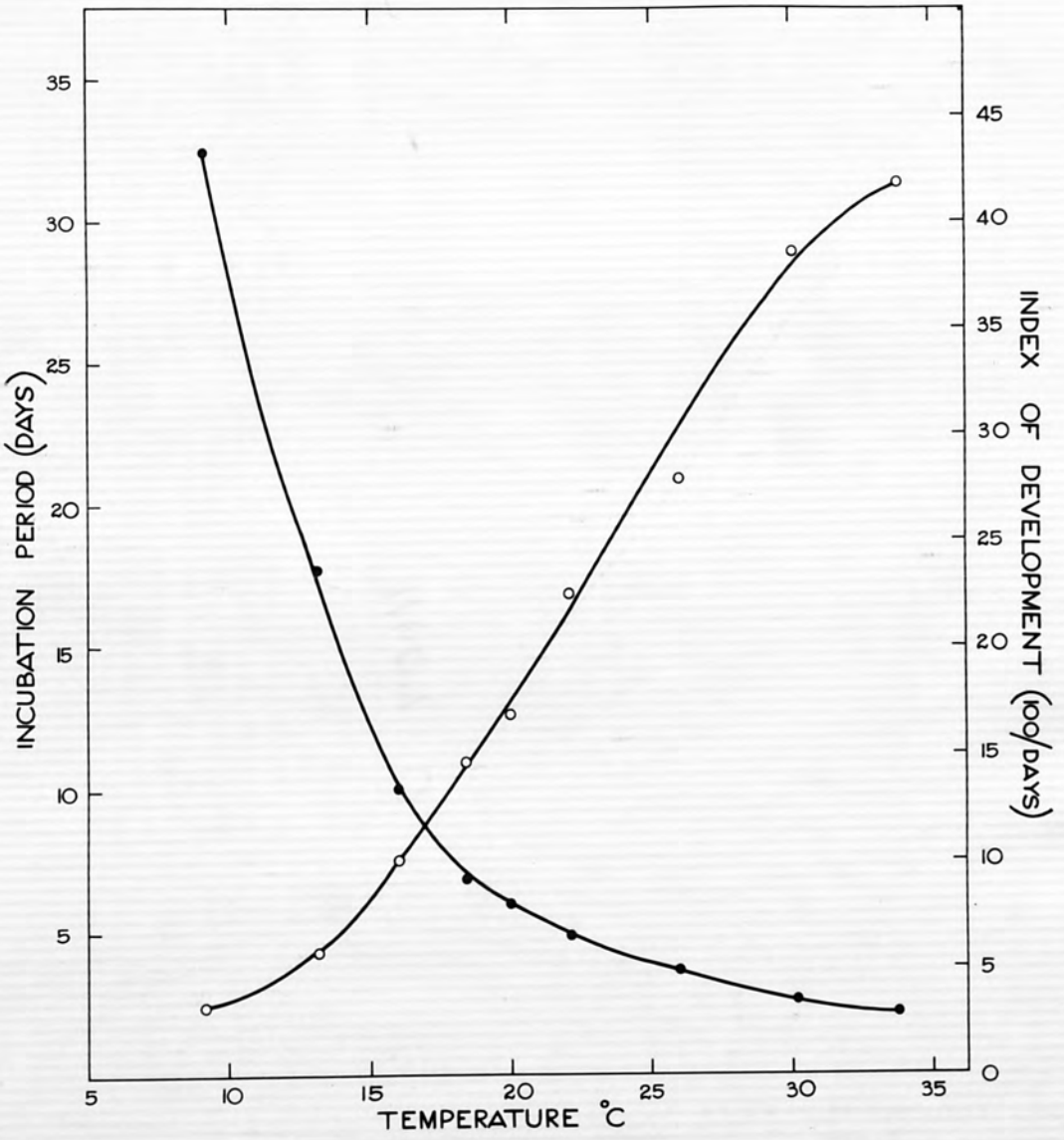


Figure 19. Mean incubation period and indices of development of eggs at different temperatures.

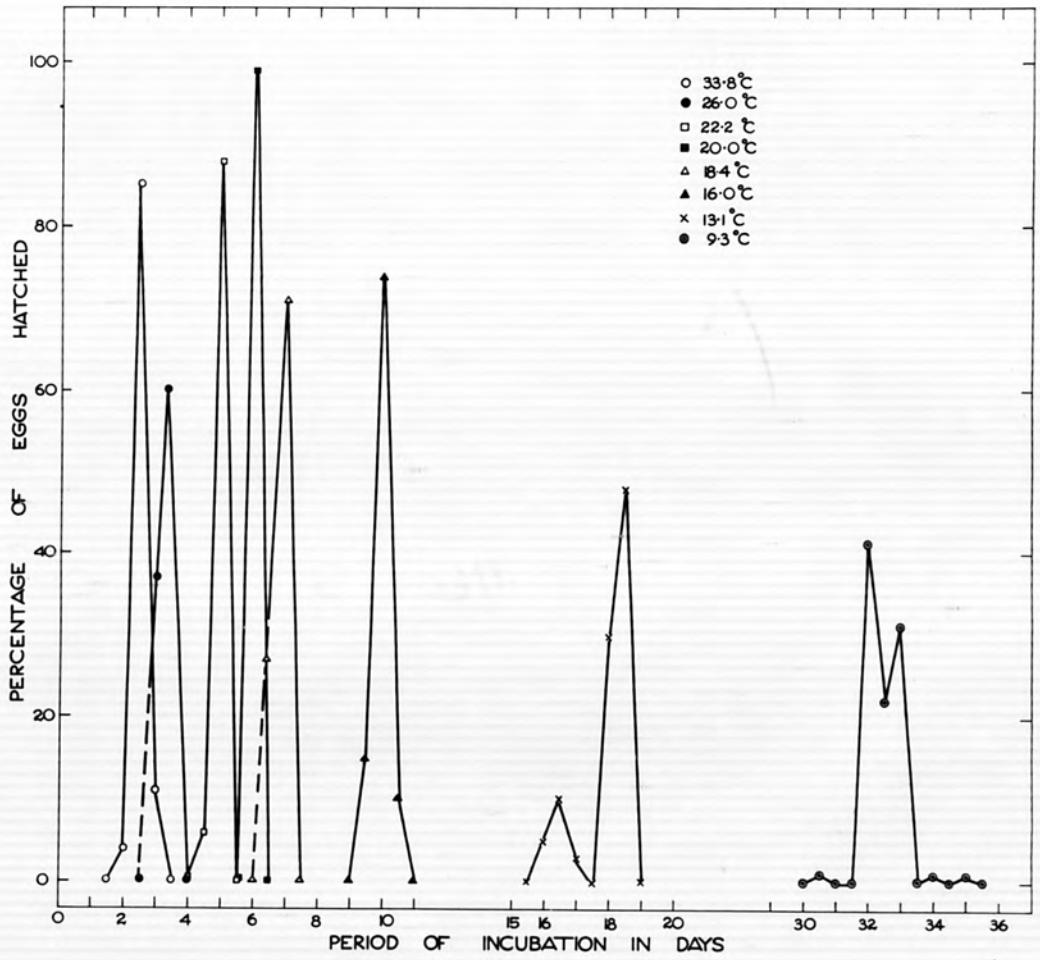


Figure 20. Distribution of hatching at different constant temperatures

Conclusions:

1. There was no significant difference in percentage of eggs hatched over a temperature range of 9.3°C to 33.8°C.
2. Between 13.1°C and 30.2°C, rate of development was directly proportional to increase in temperature. Outside this range rate of development was not proportional to temperature, though rate of development at 33.8°C was higher than at 30.2°C.
3. Between 18.4°C and 30.2°C hatching was completed within 24 hours. Outside this range, hatching occupied a longer period. At 13.1°C and below, hatching was very irregular and occupied a much longer period. Low temperatures are, therefore, unfavourable to development, an effect which is masked if total hatching alone is considered.

2. Effect of Different Combinations of Temperature and Saturation Deficit on Rate of Development and Survival of Eggs

At each combination, 100 eggs were used. The eggs were kept in air-tight jars containing the required mixtures of sulphuric acid and distilled water. Hatchings were recorded at 12-hourly intervals, except the first reading at 20.1°C, which was taken ten hours before the second.

The following combinations were used

Temperature	Saturation deficits
12.9 ± 0.2°C	0, 3, 6, and 9 mm
20.1 ± 0.1°C	0, 3, 6, 9, and 14 mm
30.0 ± 0.1°C	0, 3, 6, 9, 14, and 20 mm
34.5 ± 0.1°C	0, 3, 6, 9, 14, 20/25 and 30 mm

The eggs used at 34.5°C were laid by moths caught in a light-trap. Those used at other temperatures were laid by moths reared in the laboratory. Results are shown in Table 8 and Figures 21, 22.

Table 8

Effect of Different Combinations of Temperature and Saturation Deficit on Rate of Development and Survival of Eggs

Temperature °C	Saturation Deficit (mm)	Mean Incubation Period (Days)	Index of Development	Total Eggs Hatched (%)	Distribution of Hatching	
					Time (Days)	Eggs Hatched (%)
12.9 ± 0.2	0	15.85	6.31	81	15.0	5
					15.5	40
					16.0	18
					16.5	12
					17.0	5
					17.5	1
	3	15.67	6.38	83	15.0	6
					15.5	49
					16.0	23
					16.5	4
					17.0	0
					17.5	1
	6	16.14	6.20	71	15.5	20
					16.0	20
					16.5	24
					17.0	5
					17.5	2
	9	16.71	6.00	7	16.0	1
					16.5	3
					17.0	2
					17.5	1

(Cont'd)

Table 8 (Cont'd)

Temperature °C	Saturation Deficit (mm)	Mean Incubation Period (Days)	Index of Development	Total Eggs Hatched (%)	Distribution of Hatching	
					Time (Days)	Eggs Hatched (%)
20.1 ± 0.1	0	6.03	16.60	73	5.7	24
					6.0	30
					6.5	19
	3	5.95	16.81	74	5.7	30
					6.0	35
					6.5	8
					7.0	1
	6	6.07	16.47	72	5.7	15
					6.0	40
					6.5	15
					7.0	2
					7.5	0
	9	6.26	16.00	68	5.7	6
					6.0	26
					6.5	34
					7.0	1
					7.5	1
	14	6.50	15.38	65	6.0	9
					6.5	49
					7.0	6
					7.5	1
30.0 ± 0.1	0	2.60	38.46	74	2.5	59
					3.0	15
	3	2.54	39.37	75	2.5	70
					3.0	4
					3.5	1
	6	2.57	38.91	67	2.5	58
					3.0	8
					3.5	1
	9	2.63	38.03	67	2.5	55
					3.0	9
					3.5	3
	14	2.66	37.60	71	2.5	50
					3.0	19
					3.5	2
	20	2.77	36.10	61	2.5	28
					3.0	33

(Cont'd)

Table 8 (Cont'd)

Temperature °C	Saturation Deficit (mm)	Mean Incubation Period (Days)	Index of Development	Total Eggs Hatched (%)	Distribution of Hatching	
					Time (Days)	Eggs Hatched (%)
34.5 ± 0.1	0	2.09	47.85	100	2.0	83
					2.5	16
					3.0	1
	3	2.16	46.30	100	2.0	67
					2.5	33
	6	2.40	41.67	97	2.0	21
					2.5	75
					3.0	1
	9	2.43	41.15	98	2.0	14
					2.5	83
					3.0	1
	14	2.53	39.56	88	2.5	82
					3.0	6
	20	2.50	40.0	82	2.5	82
	25	2.53	39.56	49	2.5	46
					3.0	3
	30	2.62	38.17	62	2.5	47
					3.0	15

Note: The higher percentage of survival at 34.5°C was due to the difference in the source of eggs. (See Page 81).

Conclusions:

1. A saturation deficit of 3 mm was the optimum for development and survival. A saturation deficit of 0 mm retarded development slightly but higher saturation deficits had a greater depressing effect. Saturation deficits above 3 mm had a linear relation with rate of development.
2. At 34.5°C most rapid development was 0 mm. With higher saturation deficits rate of development decreased linearly.

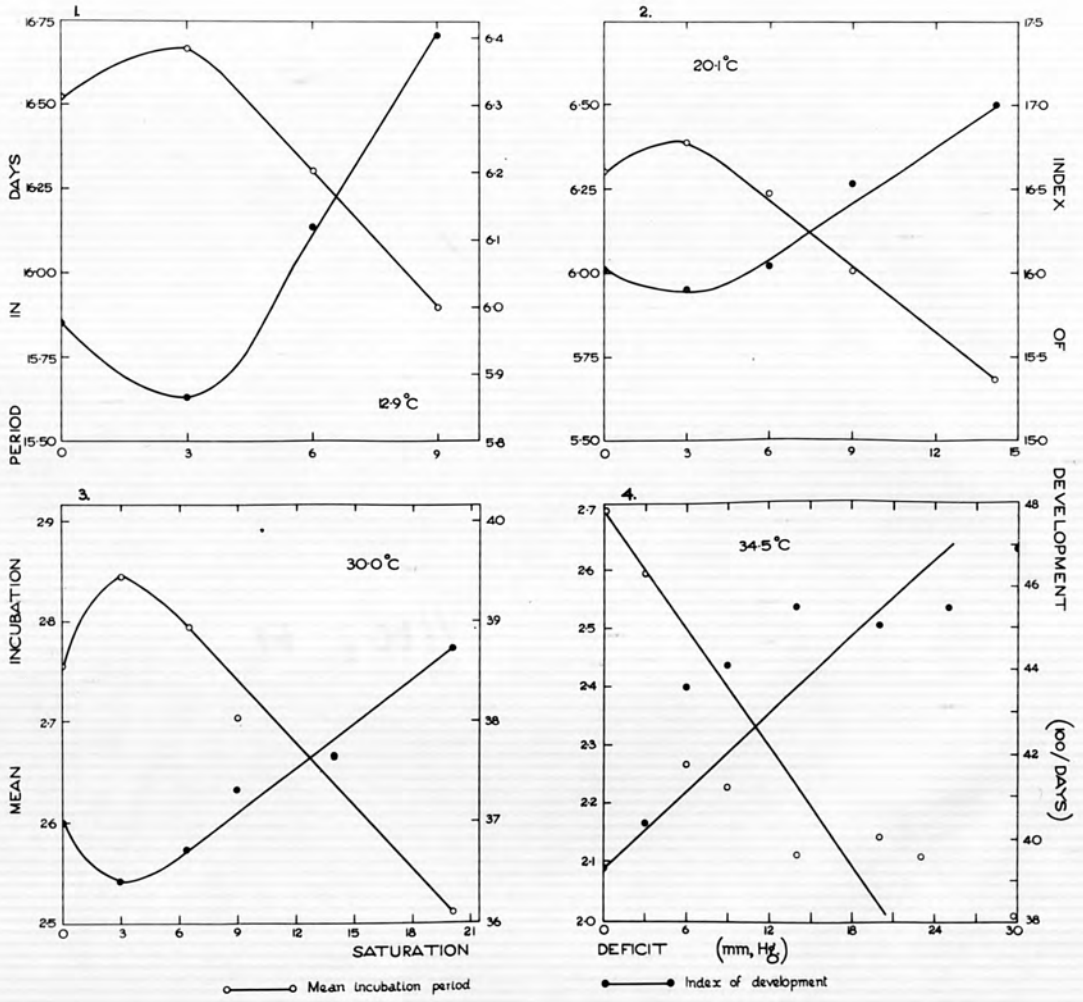


Figure. 21 (1-4) Mean incubation period and indices of development of eggs at different combinations of temperature and saturation deficit.

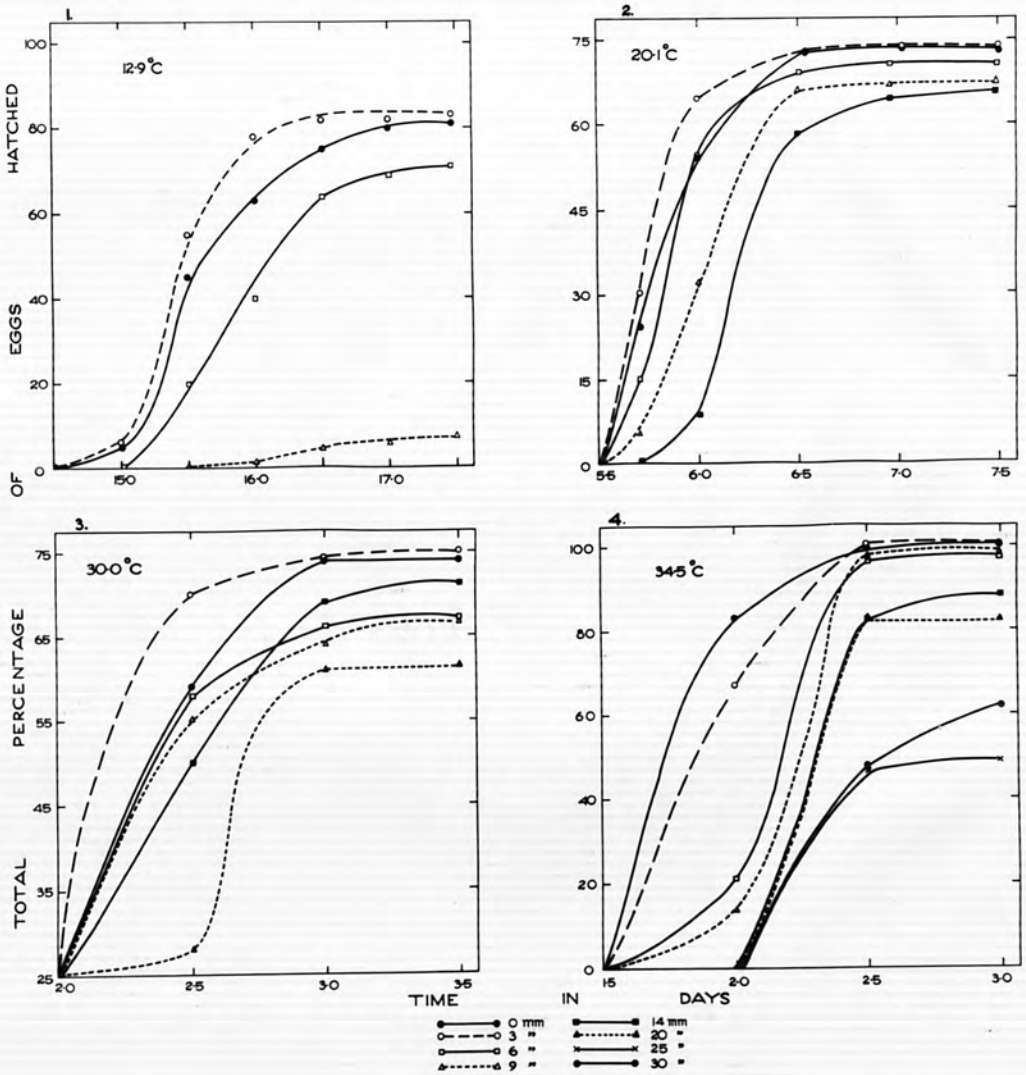


Figure 22. (1-4) Hatching and survival of eggs at different combinations of temperature and saturation deficit.

3. Higher saturation deficits usually reduced survival, at all temperatures. This effect was more pronounced at the extremes of the range.

4. Eggs are highly resistant to desiccation, especially at 20.1°C and 30.0°C.

3. Effect of Low Temperature on Survival and Development of Eggs

Experiment I. Effect of different periods of exposure at 7.0 ± 0.2°C on survival of eggs

Ten batches, each of 100 eggs, were used. Each batch was kept at 100 per cent. R.H. in an air-tight jar. Nine batches were exposed to 7.0°C for 10, 15, 20, 25, 30, 35, 40, 60 and 75 days respectively. As time of exposure was completed each batch was transferred to, and thereafter retained at, a temperature of 26°C until no further hatching occurred. The tenth batch was maintained throughout at 26°C as a control. The total number of eggs that hatched in each batch was recorded.

Results are shown in Table 9 and Figure 23(1).

Table 9

Effect of Different Exposure Periods at 7.0 ± 0.2°C on Survival of Eggs

Treatments	Total Eggs Hatched (%)	Mean Incubation Period at 26°C (Days)
10 days at 7.0°C, thereafter at 26°C	81	2.95
15 " " " "	71	2.80
20 " " " "	58	-
25 " " " "	43	-
30 " " " "	18	-
35 " " " "	8	-
40 " " " "	0	-
60 " " " "	0	-
75 " " " "	0	-
At 26°C throughout	95	3.60

Experiment II. Effect of exposure to a temperature of 7.0 ± 0.2°C on Survival of Eggs which had completed about 80% of their development before being coded

Two batches, each of 100 eggs, were kept at a constant relative humidity of 100 per cent. One batch was kept throughout at 20°C, the other was transferred to 7°C after having developed for five days at 20°C.

Results are shown in Table 10.

Table 10

Effect of exposure to a temperature of 7.0 ± 0.2°C on eggs which have already completed 80% of their development at 20°C

Treatments	Eggs Hatched (%)	Remarks
20°C throughout	99	Hatching complete in 1 day
20°C for first 5 days, thereafter at 7°C	98	Hatching distributed over 8 days

Experiment III. Effect of <u>different exposure periods</u> at <u>0.8°C</u> on <u>survival</u> and <u>rate of development</u> of Eggs

Fifteen batches, each of 100 eggs, were exposed for periods varying in length from one day to 15 days at 0.8°C. At the end of each period, each batch was transferred to, and kept at 26°C until hatching was complete. An additional batch of 100 eggs was kept throughout at 26°C. The eggs were kept continuously moist. Total hatching was recorded for each batch.

Results are shown in Table 11 and Figure 23(2).

Table 11

Effect of different exposure periods at 0.8°C on survival and rate of development of eggs

Treatments	Eggs hatched (%)	Mean incubation Period at 26°C (Days)
1 Day at 0.8°C thereafter at 26°C	99	-
2 Days " "	100	-
3 Days " "	97	-
4 Days " "	94	3.50
5 Days " "	92	3.56
6 Days " "	94	3.60
7 Days " "	85	3.73
8 Days " "	83	3.82
9 Days " "	84	3.93
10 Days " "	73	4.00
11 Days " "	76	4.09
12 Days " "	59	4.20
13 Days " "	32	4.25
14 Days " "	5	4.35
15 Days " "	0	-
At 26°C throughout	99	3.45

Experiment IV. Effect of different exposure periods at 0.8°C on survival of eggs which had already completed 50% of their development

Six batches, each of 100 eggs, were kept constantly moist, and maintained at 26°C until about half the development was completed. Five batches were then transferred to a temperature of 0.8°C for 6, 7, 8, 9 and 10 days respectively, at the end of which they were returned to 26°C and maintained at this temperature until hatching was complete. The sixth batch was kept throughout at 26°C. Total hatching was recorded for each batch.

Results are shown in Table 12.

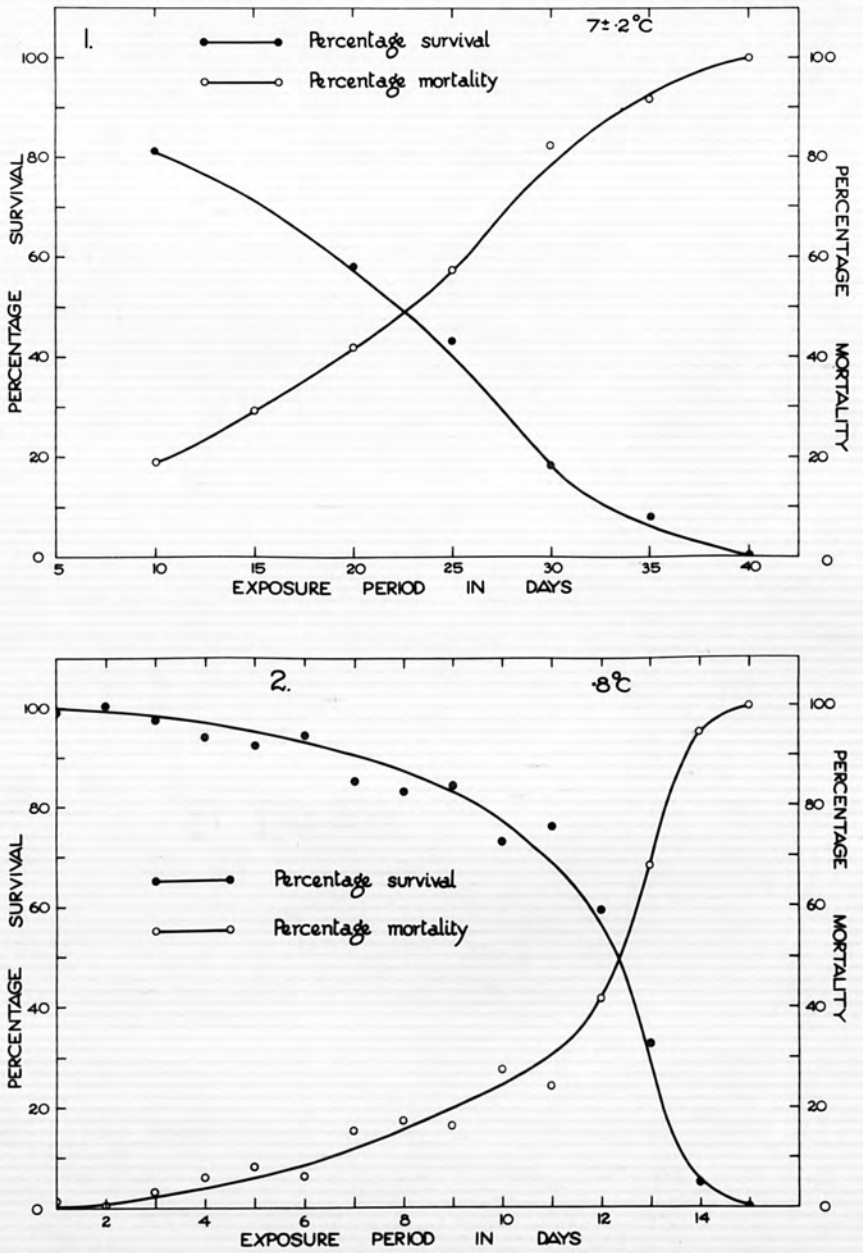


Figure 23. 1. Percentage survival of eggs exposed for varying periods to 7°C.

2. Percentage survival of eggs exposed for varying periods to 0.8°C.

Table 12

Survival of eggs, which had already completed 50% of development, when exposed for different periods at 0.8°C

Treatments	Eggs hatched
6 Days at 0.8°C; thereafter at 26°C	100
7 Days " "	96
8 Days " "	100
9 Days " "	97
10 Days " "	99
At 26°C throughout	99

Note: Lack of sufficient eggs prevented longer exposure periods being tested.

Conclusions:

1. At 7.0°C, though some development is possible, long exposures are injurious. Eggs which had already completed about 80 per cent. of their development could complete it at 7.0°C. There was no difference in survival of eggs, though hatching was irregular and distributed over a much longer time. The development of newly-laid eggs could not proceed beyond a certain initial stage. As the time of exposure increased so also did injury. Exposure for 40 or more days to this temperature killed all the eggs.

2. At 0.8°C, exposures for short periods (1 to 3 days) did not affect survival, but longer exposures were injurious. Exposures longer than four days diminished survival, and prolonged development. Exposure for fifteen or more days killed all the eggs. Eggs, which had already undergone about half their development were more resistant than were those whose development was only beginning.

4. Effect of High Temperatures on Survival of Eggs

Four experiments were done with newly-laid eggs to determine the influence of high temperatures on survival. The eggs were kept constantly moist. A batch of 100 was used for each treatment.

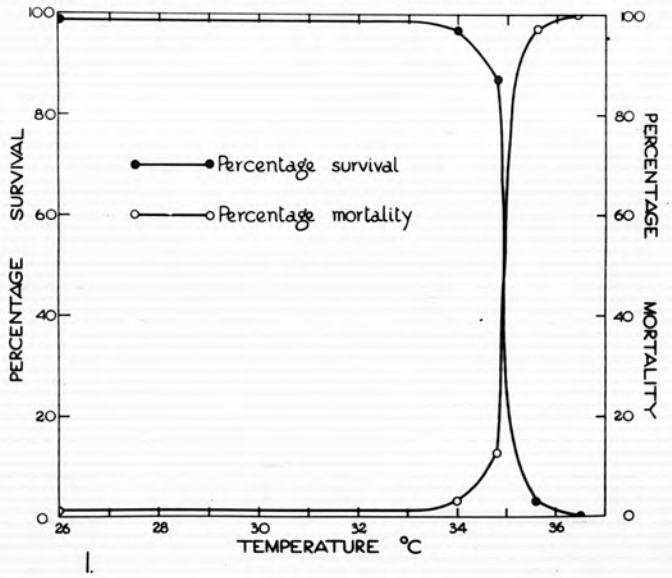
Results are shown in Table 13 and Figures (24(1-2).

Table 13

Effect of high temperatures on survival of eggs

Experiment No.	Treatments	Eggs Hatched (%)
1	34.0 ±·2°C throughout	97.0
	34.8 ±·2°C "	87.0
	35.6 ±·2°C "	3.0
	36.5 ±·2°C "	0
	26°C "	99.0
2	38.5 ±1°C throughout	0
	38.5 ± 1°C for 12 hours and at 26°C for 12 hours daily	38.0
	26°C throughout	71.0
3	40 ± 1°C for 12 hours; thereafter at 26°C	91.0
	" 18 hours "	74.0
	" 24 hours "	64.0
	" 28 hours "	46.0
	" 32 hours "	9.0
	" 36 hours "	1.0
	" 40 hours "	0
	26°C throughout	99.0
4	50 ± 0.7°C for 60 minutes; thereafter at 26°C	84.0
	" 90 minutes "	8.0
	" 100 minutes "	0.0
	26°C throughout	95.0

Notes: Eggs of each batch were retained until hatching was complete. Eggs used for the second experiment came from moths reared in the laboratory. All others were laid by those caught in a light-trap.



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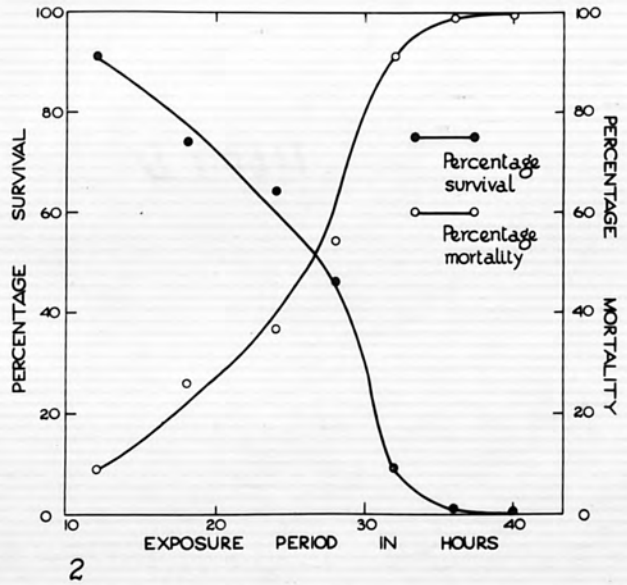


2

Figure 24. 1. Percentage survival of eggs at upper range of effective temperatures.

2. Percentage survival of eggs exposed for varying periods to 40°C.

Conclusions:

1. The injurious effects of high constant temperatures began to show at 34.8°C and even an increase of as little as 0.8°C greatly decreased survival. A constant temperature of 36.5°C was fatal to all eggs.
2. Although a constant temperature of 38.5°C killed all eggs, the same temperature when alternated with 26°C for equal periods each day enabled a high proportion to survive.
3. Exposure for 12 hours at 40°C had little effect on survival. Exposure for 18 hours or more to this temperature increasingly reduced the proportion which hatched. No eggs could survive 40 hours' exposure.

From the above, it is clear that the summer temperatures of Adelaide (mean about 21°C) would have no harmful effect on the eggs.

5. Effect of Different Saturation Deficits for Short Exposures to 50.5°C on the Rate of Development and Survival of Eggs.

Nine batches, each of 60 newly-laid eggs, were used. Two exposure periods, namely, 80 and 90 minutes and four saturation deficits of 0, 3, 9 and 20 mm were used. At the end of each period of exposure, the eggs were transferred to 29.7°C and kept at a relative humidity of 100%. An additional batch of 60 eggs was kept at 29.7°C and 100% relative humidity throughout as control.

The number of eggs hatched was recorded at 12-hourly intervals. Results are shown in Table 14 and Figures 25 (1-2).

Table 14.

Effect of Saturation Saturation Deficit for Short Exposures to 50.5°C on Development and Survival of Eggs.

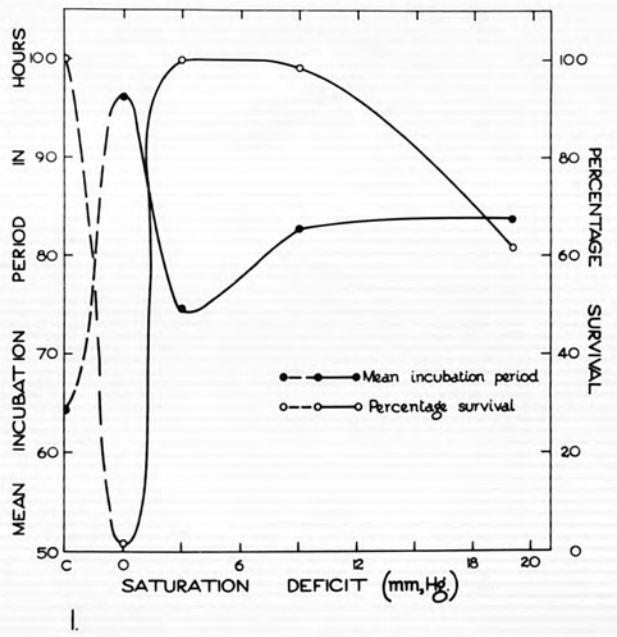
Exposure Period (Minutes)	Saturation Deficit (mm)	Mean Incubation Period (Hours)	Eggs Hatched %	Eggs hatched after - 60hrs. (%)	72hrs. (%)	84hrs. (%)	96hrs. (%)	108hrs. (%)
80	0	96.00	1.66	0	0	0	1.66	0
	3	74.60	100.00	0	80.00	18.34	1.66	-
	9	82.60	98.33	0	18.33	75.00	3.34	1.66
	20	83.70	61.66	0	1.66	60.00	0	0
90	0	0	0	0	0	0	0	0
	3							
	9							
	20							
Control	(at 29.7°C and 100% R.H. throughout)	64.40	100.00	63.33	36.67	-	-	-

Figure 25 (1-2)

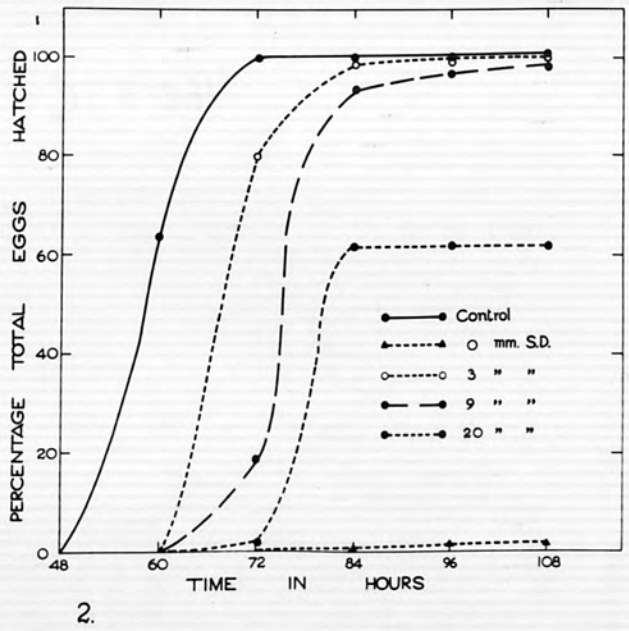
Figure 25.(1-2)

1. Incubation period and percentage survival of eggs exposed for 80 minutes at 50.5°C to different saturation deficits (control - broken lines - at 29.7°C throughout).

2. Hatching and survival of eggs exposed for 80 minutes to 50.5°C at different saturation deficits before transference to 29.7°C and 0 mm saturation deficit. (Control - solid line - at 29.7°C throughout).


MEAN INCUBATION PERIOD IN HOURS
PERCENTAGE SURVIVAL
Mean incubation period
Percentage survival
SATURATION DEFICIT (mm.Hg.)
C
0
6
12
18
20

1.


PERCENTAGE TOTAL EGGS HATCHED
Control
0 mm. S.D.
3 " "
9 " "
20 " "
TIME IN HOURS
48
60
72
84
96
108

2.

Fig. 25 (1-2)

Conclusions :

1. Irrespective of the saturation deficit, all exposures at 50.5°C for 80 minutes, had an injurious effect on the eggs. This was greatest at 0 mm and least at 3 mm. At the latter saturation deficit, survival was not affected but hatching was delayed.
2. At all saturation deficits, exposures to 50.5°C for periods of 90 minutes were lethal.

6. Effect of Age on Survival of Eggs, subjected to a High Lethal Temperature for Short Periods.

The eggs, used, came from one female and were 24 and 48 hours old (at 20°C) respectively. Three exposure periods, 80, 90 and 100 minutes, were tested at 50± .7°C. After the completion of each exposure, the eggs were transferred to and maintained at 26°C. A control batch was kept throughout at 26°C. The eggs were kept constantly moist in closed dishes.

Results are shown in Table 15.

Table 15.

Showing the Effect of Age on Survival of Eggs at a High Temperature.

Treatments	Eggs Used		Eggs Hatched		Survival %		Mean Incubation Period (Days) at 26°C	
			Age of Eggs.					
	1 Day	2 Days	1 Day	2 Days	1 Day	2 Days	1 Day	2 Days
50± 0.7°C for 80 minutes.	40	60	17	16	42.5	26.7	4.8	5.1
50± 0.7°C for 90 minutes.	40	60	5	0	12.5	0	4.9	-
50± 0.7°C for 100 minutes	40	60	0	0	0	0	-	-
Control: 26°C throughout	40	60	40	60	100.00	100.0	3.5	3.3

Conclusions :

The eggs which have developed for 1 day at 20°C are more resistant to high temperature than are those which have developed for two days.

7. Effect of a Dry Atmosphere on Survival and Development of Eggs at Different Temperatures.

Six batches, each of 75 eggs, were placed in airtight containers over silica gel granules and subjected to constant temperatures of 34.5°C, 29.8°C, 26°C, 20.0°C, 13.6°C and 9.3°C, respectively. A seventh batch was kept at 100% relative humidity, and 26°C to serve as a control.

Results are shown in Table 16 and Figure 26.

Table 16.

To Show Effect of a Dry Atmosphere on Survival and Development of Eggs at Different Constant Temperatures.

Temperature	Eggs Used	Eggs Hatched	Survival (%)	Mean Incubation Period (Days).
34.5°C	75	0	0	-
29.8°C	75	32	42.6	3.3
26.0°C	75	49	65.3	4.0
20.0°C	75	38	50.6	6.6
13.6°C	75	31	41.3	17.5
9.3°C	75	0	0	-
Control: 26°C 100% R.H.	75	74	98.7	3.7

Remarks: Many eggs that failed to hatch contained well developed embryos.

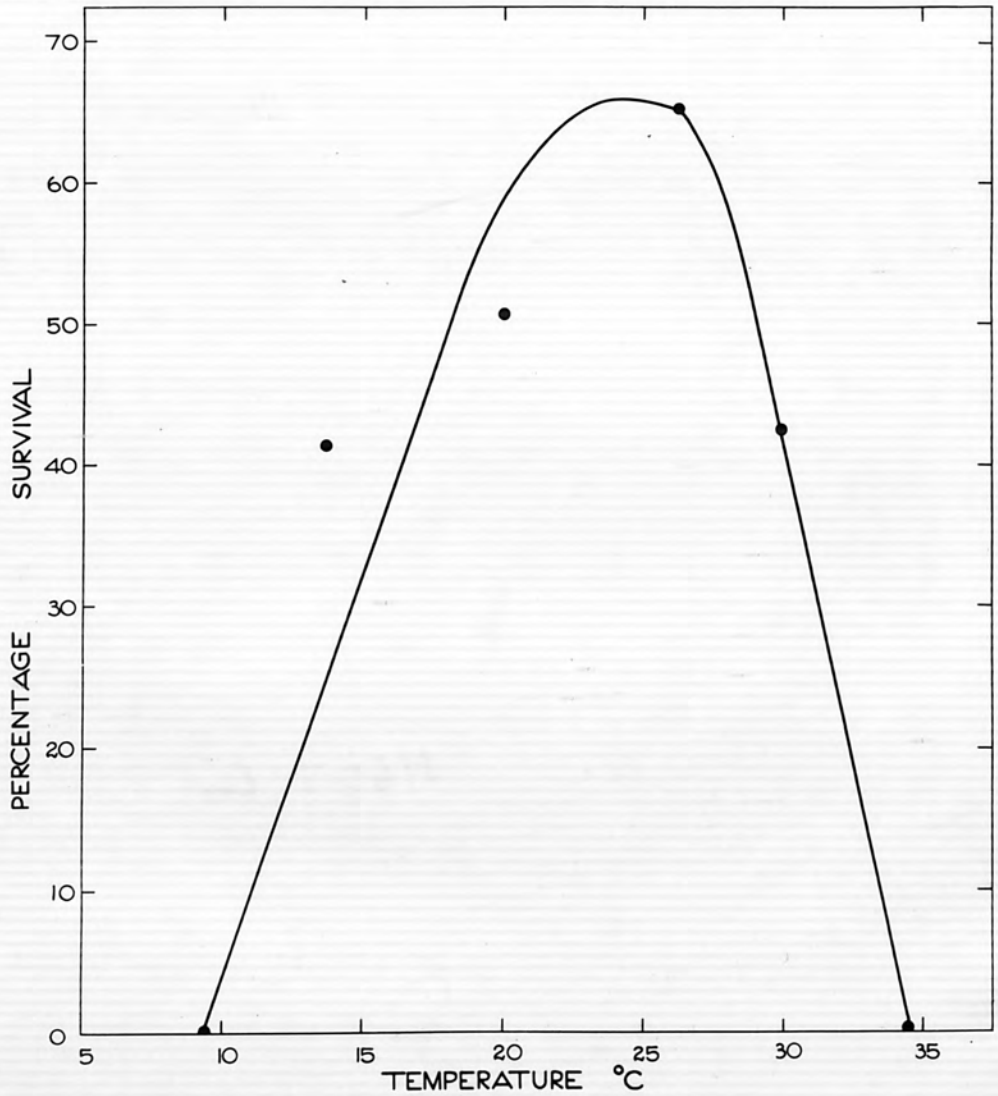


Figure 26. Percentage survival of eggs in a dry atmosphere at different constant temperatures.

Conclusions:

1. Eggs are highly resistant to desiccation.
2. In dry air, a temperature-range of from 20.0°C to 26.0°C is most favourable to development.
3. At 34.5°C and 9.3°C, eggs cannot survive in dry air.

8. Effect of Varying Moisture Status of the Environment on Survival and Time of Development of Eggs.

Four batches, each of 75 eggs, all from the one female and within 24 hours of laying, were used. The batches were treated as follows:

1. In air of 100% relative humidity.
2. In continuous contact with a free water surface.
3. Continously submerged in water.
4. In a dry atmosphere.

All the batches were kept at a uniform temperature of 26°C throughout. The results are shown in Table 17.

Table 17.

Effect of varying moisture status on survival and time of development of eggs.

Treatments	Eggs Used	Eggs Hatched	Survival %	Time of Development (Days)
100% R.H.	75	74	98.66	3 to 4
In contact with free water	75	71	94.66	3 to 4
Submerged in water	75	26	34.66	5 to 8
In dry atmosphere	75	49	65.33	4 to 5

Conclusions:

1. There was little difference in survival or time of development between eggs in a saturated atmosphere and those in contact with free water.
2. Survival was the least in eggs submerged in water; time of development was much prolonged and hatching was very irregular.
3. Although time of development was prolonged in a dry atmosphere, a large proportion of eggs still hatches.

From the above, it can be deduced that egg-development is virtually independent of external moisture and oxygen.

9. Effect, on General Vitality, of Rearing Successive Generations in the Laboratory, as shown by Viability of Eggs.

This experiment compares the viability of eggs of laboratory-reared females with those caught in a light-trap. 100 eggs of each were kept moist at a uniform temperature of 22°C until hatching was complete.

Results are shown in Table 18.

Table 18.

Comparison of viability of eggs of female caught in light trap with those of laboratory-reared female.

Kind of Female	Total Eggs	Eggs Hatched (%)
Collected at light trap	100	97
Reared in laboratory	100	77

Conclusion:

The eggs of laboratory-reared females appear to be less viable than are those of females in nature, indicating a general lowering of vitality.

II. LARVAL and PUPAL STAGES.

1. Rate of Development and Survival of Larvae in relation to Temperature.

Batches of 100 larvae were reared at nine different temperatures (see Table 19). They were fed on barrel medic (Medicago tribuloides), and a high relative humidity was maintained throughout. Duration of the larval and prepupal periods of each was recorded.

Results are shown in Table 19 and Figure 27 (1-4).

Table 19.

Rate of Development and Survival of Larvae

in relation to Temperature.

Temperature °C.	No. First Laval Instar.	No. Became Prepupal.	No. Pupated	Survival (%)	Mean Laval Period (Days)			Development per Day (%)		
					Larval	Prepupal	Total	Larval	Prepupal	Total
6.8	100	Nil	Nil	0.0	-	-	-	-	-	-
8.0	100	Nil	Nil	0.0	-	-	-	-	-	-
13.4	60	3	3	5.0	101.30	12.50	113.80	0.99	8.0	0.88
16.0	60	46	41	68.3	48.90	7.10	56.00	2.05	14.2	1.80
20.1	40	32	31	77.5	31.20	4.00	35.20	3.20	25.0	2.86
22.0	20	16	16	80.0	26.30	2.95	29.25	3.80	34.0	3.45
26.0	90	72	70	77.7	20.30	2.04	22.40	4.90	49.0	4.40
30.2	70	47	45	64.3	17.20	2.00	19.10	5.80	50.0	5.26
34.5	100[1]	10	4	4.0	28.80	3.10	31.60	3.50	32.26	3.16
					(Average of 10)	(Average of 4)	(Average of 4)			

1. Kept in saturated atmosphere.

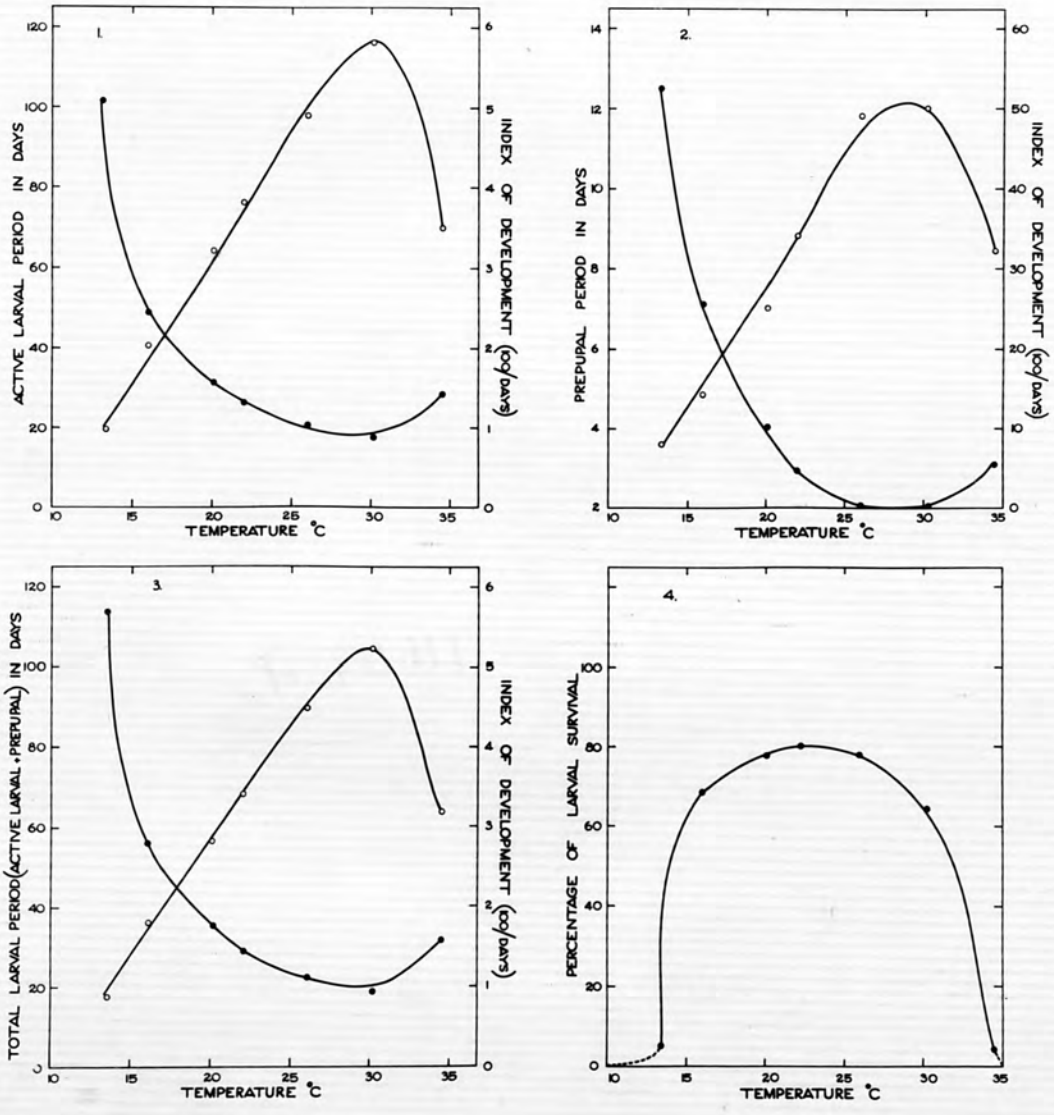


Figure 27. (1-4) Lengths of larval, pre-pupal, and total larval periods with indices of development, and percentage of larval survival at different constant temperatures.

Remarks:

At 6.8°C no larva survived for more than 54 days; All died in one or other of their first two stadia. Development was very slow.

At 8.0°C, 62, 28 and 2 larvae respectively entered their 2nd, 3rd and 4th stadia. None completed development.

At 34.5°C, of a first batch 130 larvae, all died in different stages of development, mostly during moulting.

Of a second batch of 100 maintained at 100% relative humidity only 10 became prepupae of which 4 pupated but then died.

Conclusions:

1. At 6.8°C and 8.0°C, though some development occurs, it cannot be completed.

   At 13.4°C, survival is low. The optimum range is from 20°C to 26°C. Development cannot be completed at 34.5°C unless in a saturated atmosphere when a small proportion survives.

2. From 13°C to 30°C, rate of development increased with rise in temperature. Above 30°C, the rate of development diminished.

2. Relation between Rate of Development of Larvae, Survival of Larvae and Pupae, and the nature of the Food.

Preliminary experiments suggested that development and survival of larvae were influenced by the food eaten.

For this experiment, the three most widely distributed food plants, and those most subject to damage by the species, - wheat, lucerne and capeweed (Cryptostemma calendula Druce), - were fed to batches of

30 newly-emerged first larval instars. Only young leaves and shoots were used.

A uniform temperature of 22.5°C was maintained throughout. The larvae were reared individually and weighed on the 16th and 22nd days after the commencement of the experiment, and the pupae on the second day of pupation.

Results are shown in Table 20 and Figure 28 (1-6).

Table 20.

Effect of Food on Survival and Rate of Development of Larvae and Pupae.

Food Plant	Larvae Used	Survival				Time of Larval Development (Days)	Mean Larval Weights (mg)		Pupal Weights (mg)		
		Pupated	Larval Survival (%)	Moths Emerged	Pupal Survival (%)		16th Day	22nd Day	Mean	Maximum	Minimum
Cape Weed	30	24	80.0	23	95.8	36.75	117.0	421.4	424.8	547.4	341.6
Lucerne	30	10	33.3	9	90.0	45.75	47.4	162.1	365.7	477.0	267.8
Wheat	30	6	20.0	5	83.3	45.42	31.97	127.2	237.3	326.1	96.6

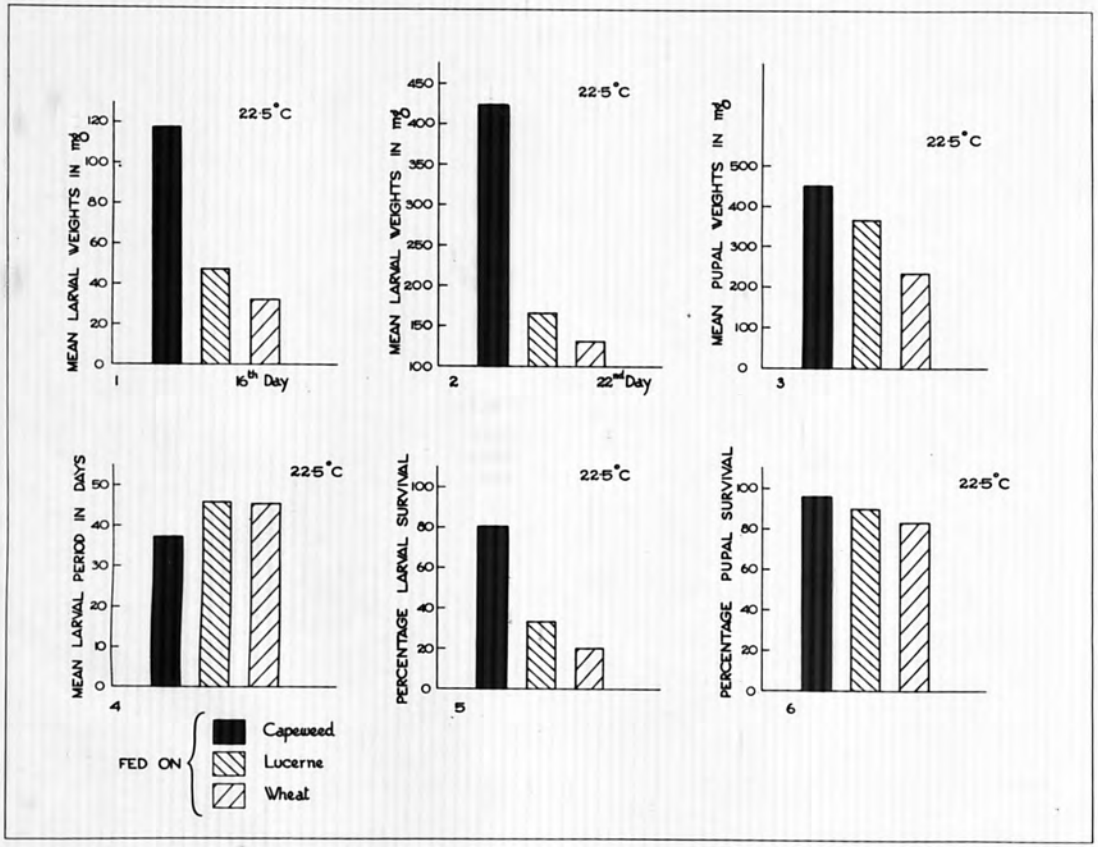


Figure 28. (1-6) Effect of the food plant on weights of larvae (16th and 22nd days) and pupae, on the mean larval period and on percentage larval and pupal survival, 22.5°C.

Remarks:

Young larvae feeding capeweed showed, at times, the unusual habit of feeding entirely within the leaf-tissue like a leaf-miner.

Conclusions:

1. Larval survival on capeweed was significantly higher than that on either lucerne or wheat; that on lucerne was, significantly higher than on wheat. No significant differences in pupal survival were observed irrespective of the food.
2. Larvae fed on capeweed developed most rapidly, their period of development being significantly shorter (1% level) than that of the other two batches between which there was no significant difference.
3. Weights of larvae and pupae, fed on capeweed, were significantly higher (0.1% level) than those of the other two groups. The weights of those, fed on lucerne, were, significantly higher than those, fed on wheat.
4. Of the three food plants, capeweed was therefore the most suitable.

3. Effect of Partial Submergence in Water on Survival of First Larval Instars.

As eggs are usually laid on debris on the soil, or even on the soil itself, both they and first larval instars are liable to partial submergence, for varying periods, during heavy rain. This experiment determined the resistance of the larvae to such conditions.

First larval instars, soon after emergence, were dropped into water on the surface of which most of them floated. When each period of treatment was completed, they were transferred to food. Living,

dead and missing larvae were counted 24 hours later. For the duration of the test, a batch of similar larvae was normally fed as a control. All larvae were maintained at a uniform temperature of 20°C.

Results are shown in Table 21.

Table 21.

Effect of Partial Submergence in Water on Survival of First Larval Instars.

Period in Water (Hours)	Larvae Used	Larvae at Conclusion of Treatment		
		Living	Dead	Missing
4.00	20	19	1	-
6.00	20	19	1	-
8.00	20	15	1	4
10.00	20	17	-	3
12.00	20	11	1	8
20.00	50	50	-	-
25.30	50	49	-	1
29.30	50	49	-	1
36.00	50	44	6	-
48.00	50	37	12	1
Control	70	70	-	-

Note: Most larvae floated on the surface and their alimentary tracts contained bubbles of gas.

Conclusion:

Periods of partial submergence of up to 30 hours have little effect on survival. As the period is extended beyond this time, a decreasing proportion of the larvae survives.

4. Different Combinations of Temperature and saturation Deficit in relation to Survival of Starved First Larval Instars.

As the eggs are, usually, not laid directly on the host plants, the first larval instars have to undego a short period of starvation while they wander in search of food. During this period they are liable to to desiccation. This experiment was devised to determine resistance of the larvae to the different combinations of temperature and saturation deficit, shown in Table 22.

At each combination 75 larvae were used, divided into three equal batches. These were placed over the required sulphuric acid - water mixture in an air-tight jar. Mortality counts were made at 10 hourly intervals. The criterion for death was failure of the larva to respond when pressed with a fine brush.

Mean survival times for each combination are shown in Table 22.

Table 22.

Mean Survival time of Starved First Larval Instars at Various Combinations of Temperature and Saturation Deficit.

Temperature.	Saturation Deficit (mm)							
	0	3	6	9	14	20	25	30
	Mean Times of Survival (Hours)							
20°C	58.85	53.74	51.73	47.65	42.3	-	-	-
26°C	50.40	44.84	41.00	37.00	29.00	25.10	-	-
30°C	33.34	26.45	25.51	23.23	22.22	21.84	-	-
34°C	28.24	-	21.11	22.88	20.83	18.21	12.50	10.66

Conclusions :

1. At any particular temperature the survival period decreased with increasing saturation deficit.
2. At any particular saturation deficit the survival period is reduced with the increase in temperature. Thus, at 0 mm a rise in temperature from 20°C to 34°C more than halves the survival period at 20°C.
3. High saturation deficits combined with high temperature are particularly injurious.

5. Effect of Different Combinations of Temperature and Saturation Deficit on Survival of Starved Fifth Larval Instars.

The combinations of temperature and saturation deficit tested are shown in Table 23. All the larvae used had been reared at 26°C and were of approximately the same age. 25 individual larvae, were tested at each combination.

Mortality counts were made at 12-hourly intervals.

Results are shown in Table 23.

Table 23.

Mean Survival times of Starved, 5th Larval Instars at various combinations of temperature and Saturation Deficit.

Temperature	Saturation Deficit (mm)					
	0	3	6	9	14	20
	Mean Survival Times (Hours)					
20°C	89.00	89.90	88.83	86.80	80.32	-
34°C	54.10	54.78	48.44	51.80	46.44	41.04

Conclusions :

1. Fifth-larval instars are more resistant than are first larval instars to similar combinations of temperature and saturation deficit.

2. Temperature has a greater influence on survival at any saturation deficit than has the latter at the same temperature.

6. Relation between Temperature, and Evaporation from Dead Fully-fed Larvae, in Dry Air.

Fully-fed larvae of the same age were stupefied in a cyanide bottle. Subsequently their mouths and spiracular and anal orifices were plugged with wax. They were then returned to the cyanide bottle until dead.

When dead, each was weighed and quickly transferred into an air-tight vessel containing silica gel granules. Four larvae were used at each temperature. At the end of one hour each larva was reweighed and the loss of weight determined.

Results are shown in Table 24 and Figure 29.

Table 24.

Loss of Weight of Dead Fully-fed Larvae when exposed to dry air at different temperatures.

Temperature	Mean Loss of Weight per Larva per Hour (mg).
20°C	6.45
26°C	7.42
29.8°C	12.18
34.5°C	26.20
42°C	39.20

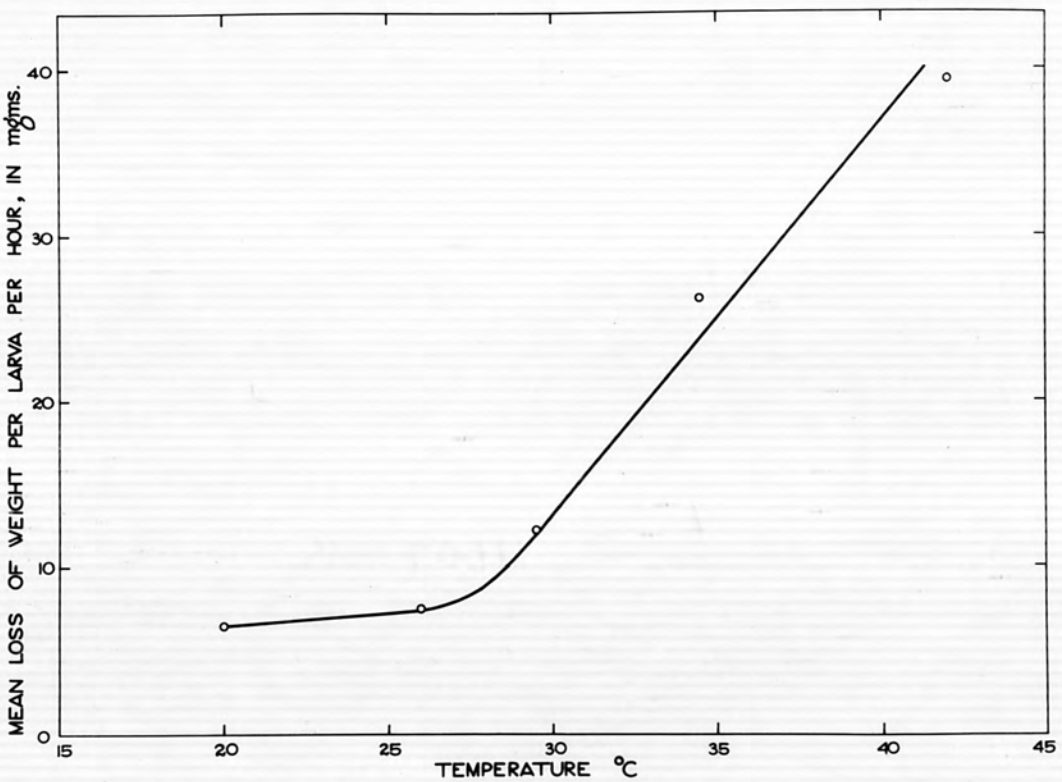


Figure 29. Loss of weight from dead larvae exposed for one hour to a dry atmosphere at different constant temperatures.

Conclusions :

Between the various temperatures used, starting with 20°C, the losses in weight amounted to 15%, 64%, 115% and 50% respectively.

This would seem to indicate that between 29.8°C and 34.5°C some change occurs in the larvae which make them more susceptible to water loss than at any other of the temperatures used.

While these results were obtained with dead larvae, it is possible that living ones may react similarly, and hence be particularly liable to desiccation within the temperature range from 29.8°C to 34.5°C.

7a. Relation between Temperature and Number of Larval Ecdyses.

The la rvae were reared, individually, at different temperatures on young shoots of Medicago spp. and at optimum humidity. Exuviae were removed regularly and the number of ecdyses for each larva recorded.

Results are shown in Table 25a.

Table 25a.

Temperature in Relation to Number of Larval Ecdyses.

Temperature °C.	Total No. of Larvae	No. of Larvae Passing Through Ecdyses			
		6	7	8	9
34.3 ± 0.2	16	-	-	-	16[1]
Room temperature during summer [max. 35.0 min. 22.0]	12	-	4	6	2
29.8 ± 0.2	11	-[2]	3	8	-
26.0	30	9	19	2	-
20.0	17	2	15	-	-
16.0	1	1	-	-	-
13.0	2	1	1	-	-

1. Most of the larvae died after passing through 9 ecdyses.
2. Larvae fed daily on lucern-shoots whose cut ends were kept in water at 4.0°C for 1 day to deliberately increase water content.

Comments :

Below 26°C, larvae tended to have 6 or 7 ecdyses. Above 26°C, the number tended to increase. The minimum number was 6, the maximum 9. Increasing the water content of the food tended to increase rate of larval development and to decrease the number of ecdyses.

7b. To determine whether Number of Larval Ecdyses is related to Sex of the individual.

12 larvae were simultaneously reared under identical conditions at room temperature during summer (see Table 25a). The number of individual ecdyses was noted, and after pupation, the sex of each was determined.

Results are given in Table 25b.

Table 25b.

Showing numbers of ecdyses, and the sexes of the individuals.

Total No. of Larvae Observed	Larvae undergoing Ecdyses					
	7		8		9	
	Male	Female	Male	Female	Male	Female
12	0	4	2	4	0	2

Conclusion :

There is no relation between sex and number of ecdyses.

8. Effect of Temperature on Rate of Development and Survival of Pupae.

Pupae, obtained from larvae reared at different constant temperatures, were retained at these temperatures for this experiment. They were kept in isolation at a relative humidity of 75%. Dates of pupation and also of emergence of moths were recorded at 12-hourly intervals during the time of pupation and the emergence of adults.

Results are shown in Table 26 and Figure 30.

Table 26.

Relation between Temperature, and Rate of Development and Survival of Pupae.

Temperature °C.	No. of Pupae Used	No. of Moths Emerged	Pupal Survival (%)	Mean Pupal Period (Days)	Index of Development
6.8	10	0	0	-	-
9.0	10	0	0	-	-
13.4	3	3	100.0	61.0	1.6
16.0	41	40	97.6	35.6	2.8
20.1	29	27	93.1	23.0	4.4
22.0	16	16	100.0	18.75	5.3
26.0	70	68	97.1	14.37	7.0
30.2	45	40	88.8	11.15	9.0
34.5	8	0	0	-	-
	20[1]	6	30.0	11.38	8.8

1. Pupae kept at 100% relative humidity.

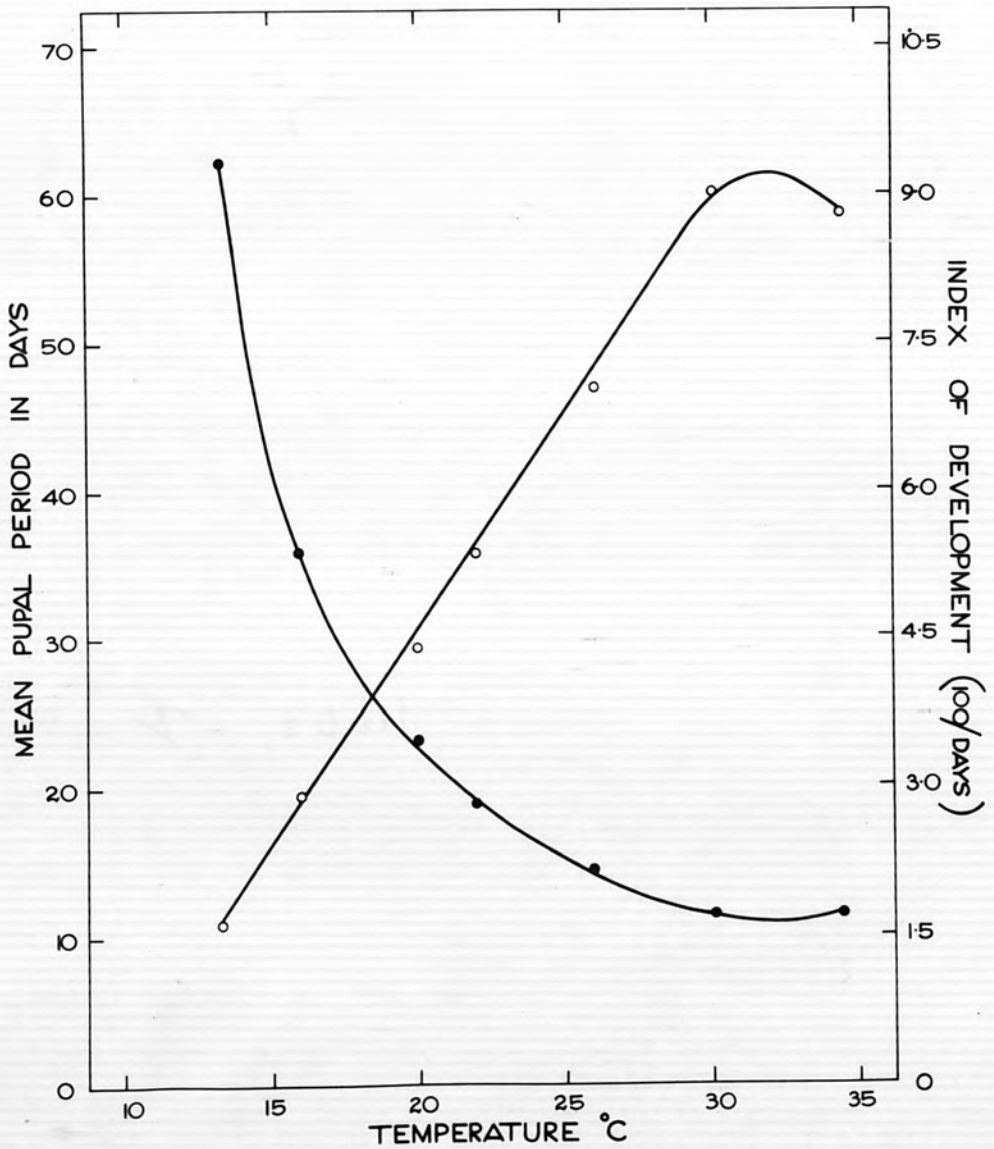


Figure 30. Mean pupal period and indices of pupal development at different constant temperatures.

Remarks :

At 34.5°C, the greater part of pupal development took place but, could be completed only when the relative humidity was 100%. Even under these conditions only 30% the pupae produced moths.

At 6.8°C pupae showed no signs of development.

At 9.0°C, the development was only partial.

Conclusions :

1. Complete development was possible between 13.4°C and 34.5°C.
2. Rate of pupal development increased with rise in temperature from 13.4°C to 30.2°C but slightly decreased at 34.5°C.
3. There was no significant difference in the pupal survival between 13.4°C and 30.2°C. At 34.5°C, however, survival was very significantly less (0.1% level).

9. Effect of Different Constant Temperatures on Pupae Which had Undergone 70% of their Development at 26°C.

This experiment supplements the previous one. Of 40 pupae which had undergone 70% of their development at 26°C, 14 were retained throughout at this temperature. The remainder were divided into four batches and treated as indicated in Table 27, where also the results are shown (compare with experiment 8).

Table 27.

Showing effect of exposure to different constant temperatures of pupae which had undergone 70% of their development at 26°C.

Treatments	Pupae	Moths	Pupal Survival (%)	Mean Pupal Period (Days)	Index of Development	Mean Period of 30% Development (Days)	Index of Development for final 30%
26°C, throughout	14	14	100	14.4	7.0	-	-
26°C for 10 days, thereafter at 34.5°C	8	8	100	13.0	7.7	3.0	10.0
26°C for 10 days, thereafter at 18°C	6	5	83.3	20.0	5.0	10.0	3.0
26°C for 10 days, thereafter at 13.4°C	6	6	100	31.2	3.2	21.2	1.4
26°C for 10 days, thereafter at 6.8°C	6	1	16.3	60.0	1.7	50.0	0.6

Conclusions :

1. At 34.5°C, the rate of the remaining 30% development was more rapid than was that of the whole development at that temperature, the indices of development being 10.0 and 8.8, respectively. The survivals for 30% and 100% development at the temperature were 100% and 30%, respectively. This shows that full exposure for the whole period of development is more injurious than a partial one.
2. At 13.4°C, the remaining 30% development was completed at a rate slower than that of the whole development at that temperature, the indices of development being 1.4 and 1.6, respectively.
3. At 6.8°C, though no external indication of development was obtained when pupae were kept at that temperature from the beginning of pupation and all died, the remaining 30% development could still be completed at 26°C, with a survival of 16.3%.

10. Effect of Different Combinations of Temperature and Saturation Deficit on Rate of Development and Survival of Pupae.

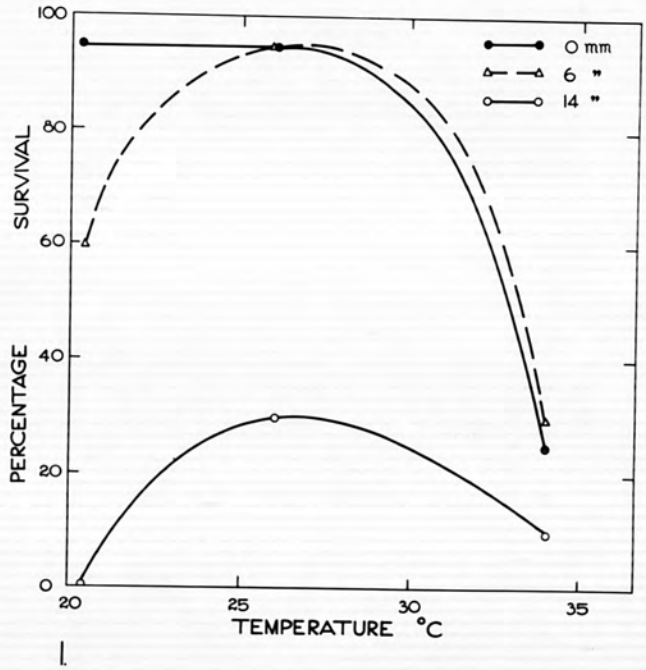
The pupae, used in this experiment, were obtained from larvae reared in isolation at a mean temperature of 20°C. Within 12 hours after pupation, when the pupal skin had hardened sufficiently to enable safe handling, the pupae were kept under the conditions shown in Table 28. At each saturation deficit - temperature conbination, 20 pupae were kept, individually, in numbered containers. Dates of commencement of the experiment and of emergence of individual moths were recorded.

Results are shown in Table 28 and Figure 31 (1-2).

Table 28.

Effect of temperature and saturation deficit on rate of development and survival of pupae.

Temperature	Saturation Deficit (mm)											
	0				6				14			
	No. of Pupae Used	No. of Moths Emerged	Survival (%)	Mean Pupal Period (Days)	No. of Pupae Used	No. of Moths Emerged	Survival (%)	Mean Pupal Period (Days)	No. of Pupae Used	No. of Moths Emerged	Survi-val(%)	Mean Pupal Period (Days)
34°C	20	5	25	10.15	20	6	30	11.38	20	2	10	11.00
26°C	20	19	95	14.37	20	19	95	14.60	20	6	30	14.03
20.3°C	20	19	95	22.53	20	12	60	22.04	20	0	0	-



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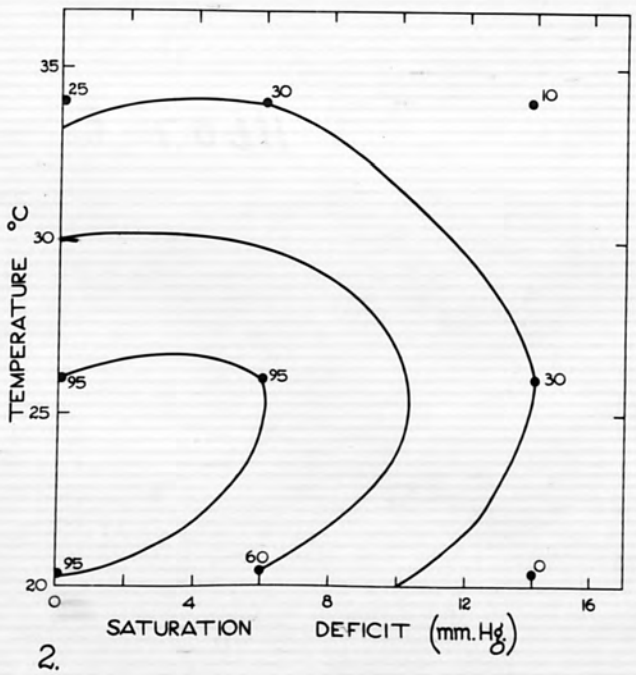

2.

Figure 31. (1-2) Percentage survival of pupae at different combinations of temperature and saturation deficit.

Remarks :

The moths that emerged at 0 mm saturation deficit and 34°C were morphologically abnormal with crumpled wings which could not be expanded. Such moths lived for from 1 - 2 days only, even when provided with food and kept at a favourable temperature.

Many of the moths which emerged at 14 mm saturation deficit also had crumpled wings. When provided with food, they lived longer than those which had emerged at 0 mm saturation deficit and 34°C. Most of the pupae kept at 14 mm saturation deficit, were visibly partially desiccated, their posterior abdominal segments being retracted and constricted.

Conclusions :

1. There was no significant difference between mean pupal periods due to variation in saturation deficit at a particular temperature.
2. The highest survival was at 0 mm saturation deficit, at all temperatures (except 34°C), and at 26°C, at all levels of saturation deficits.
3. The injurious effects of high saturation deficit were most pronounced near the lower and upper ends of the effective temperature-range.

11. Water Losses from Pupae at two different Saturation Deficits.

Soon after pupation, four pupae were kept at 0 mm saturation deficit, and five at 12 mm saturation deficit at a temperature of 29.8°C. Of the second batch, one pupa was killed in a cyanide bottle at the end of seven days, and thereafter, maintained at the same saturation deficit and temperature. Pupae were, individually, weighed daily.

Results are shown in Table 29 and Figure 32.

Table 29.

Water losses from pupae at two different saturation deficits.

Saturation Deficit (mm)	No. of Pupae	Period After Pupation (Days)	Mean Weight (mg)	Progressive Mean Loss of Weight	
				(mg)	(%)
0	4	0	302.6	-	-
		1	301.2	1.4	0.46
		2	300.7	1.9	0.63
		3	300.4	2.2	0.73
		4	299.7	2.9	0.96
		5	299.1	3.5	1.16
		6	297.8	4.8	1.60
		7	296.2	6.4	2.10
		8	294.4	8.2	2.70
		9	292.9	9.7	3.20
		10	290.9	11.7	3.90

(Continued)

Table 29 (Continued)

Water losses from pupae at two different saturation deficits.

Saturation Deficit (mm)	No. of Pupae	Period After Pupation (Days)	Mean Weight (mg)	Progressive Loss of Weight	
				(mg)	(%)
12	4	0	300.7	-	-
		1	292.9	7.8	2.6
		2	289.7	11.0	3.6
		3	287.0	13.7	4.6
		4	284.5	16.2	5.4
		5	281.5	19.2	6.4
		6	277.7	23.0	7.6
		7	273.6	27.1	9.0
		8	268.4	32.3	10.7
		9	262.9	37.8	12.6
		10	257.4	43.3	14.4
		11	245.4	55.3	18.4
	1	0	296.3	-	-
		1	292.4	3.9	1.3
		2	290.1	6.2	2.1
		3	288.5	7.8	2.6
		4	286.5	9.8	3.4
		5	283.9	12.4	4.2
		6	280.6	15.7	5.3
		7	276.5[1]	19.8	6.7
	Killed ----	8	234.8[2]	61.5	20.8
		9	206.4	89.9	30.3
		10	186.1	110.2	37.2
		11	166.0	130.3	44.0
		12	143.0	153.3	51.7
		13	120.0	176.3	59.5

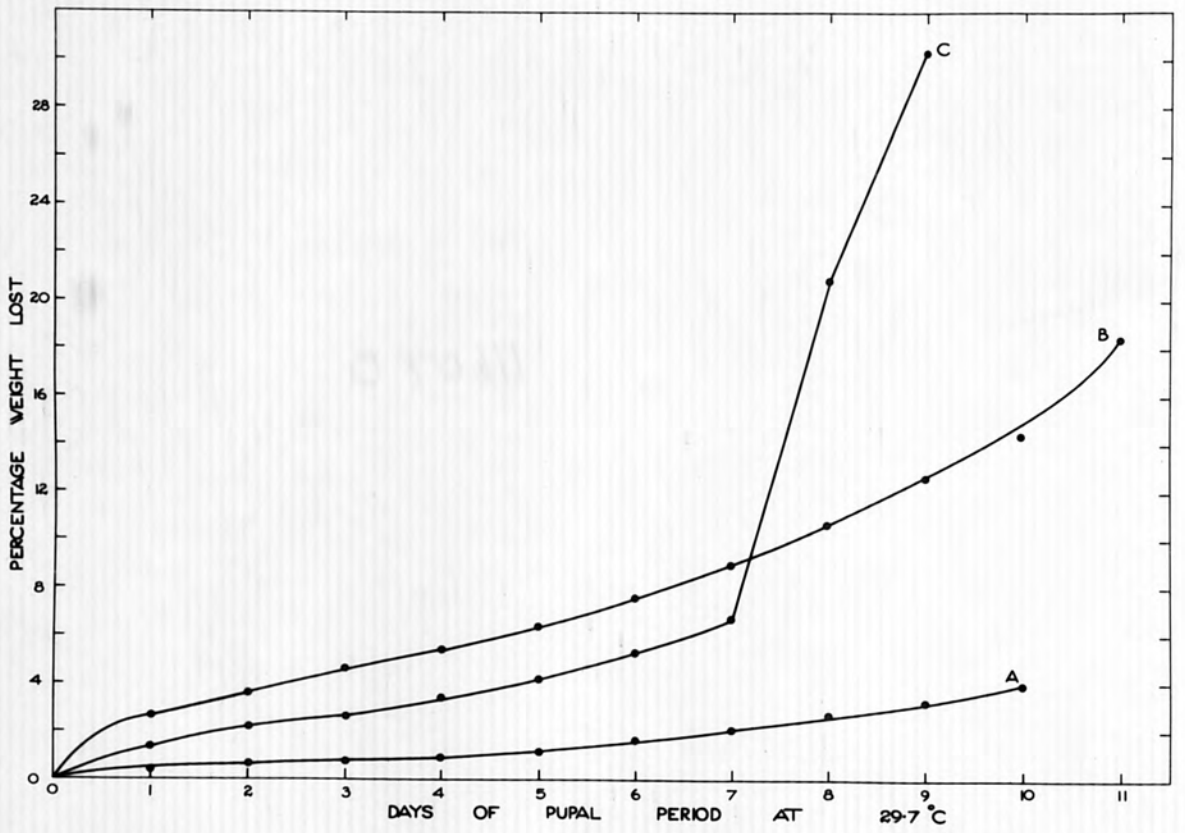

Figure 32. Percentage loss of weight from pupae at 29.7°C at different saturation deficits :
A. 0 mm; B. 12 mm; C. 12 mm (pupa killed at end of 7th day).

1. Final weight of pupa while alive.

2. Weight of pupa 1 day after killing.

Conclusions :

1. Loss of weight increased with saturation deficit. Thus, at 12 mm saturation deficit the loss was five times as great as at 0 mm.

2. The loss by evaporation increased suddenly with the death of pupa. Since the killing agent used would have the minimum effect on the cuticle, this suggests that water retention is principally dependent on some internal living, water-retaining mechanism, and is not merely the passive retention of water by the cuticle.

12. Effect of Temperature, during larval development, on Weight and Linear Dimensions of Pupae.

Pupae, from larvae, reared at different constant temperatures (See Experiment 1.), were individually weighed and measured. In measuring length, the spines of the cremaster were disregarded and widths were taken diametrically across anterior of abdomen.

Results are shown in Table 30 and Figure 33.

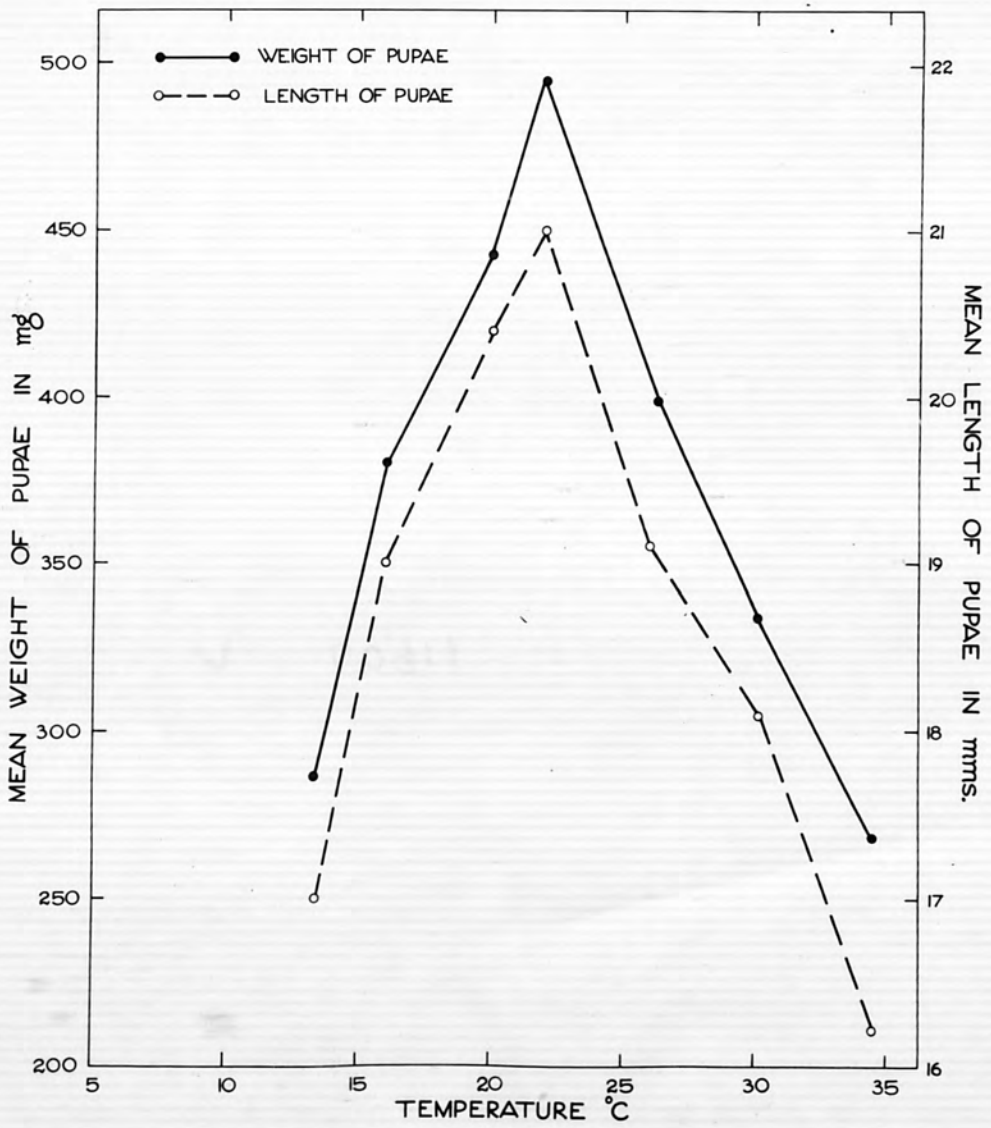

Figure 33. Relation of rearing-temperature to mean weight and length of pupa.

Table 30.

Effect of temperature on weight and dimensions of pupae.

Temp. of Rearing °C.	Pupae Weighed	Extreme Weights (mg)		Mean Weight (mg)	Pupae Measured	Mean dimensions of Pupae (mm)	
		Lower	Upper			length	breadth
13.4	4	201.5	342.6	286.2	4	17.0	5.08
16.0	43	304.0	486.8	380.9	41	19.0	5.82
20.0	30	363.0	501.4	443.9	30	20.4	6.10
22.0	16	432.0	637.6	495.1	16	21.0	6.40
26.0	61	290.2	496.0	398.5	30	19.1	5.85
30.2	43	227.5	448.0	334.5	30	18.1	5.70
34.5	4	211.4	350.6	268.0	4	16.3	4.94

Comments:

Maximum weights and dimensions were those of pupae reared at 22°C. Above and below this temperature, both weights and dimensions decreased progressively, the differences in weights being highly significant (almost all at 0.1% level)

13. Effect of Crowding on Colour-Variation, Speed of Development, and Survival of Larvae, and Weights of Pupae.

The larvae, used in this experiment, came from eggs laid by a single female, caught in a light trap. They were reared collectively until the end of second instar after which they were divided into 3 batches (A, B, and C) and reared under the following conditions for the remainder of the developmental period.

Batch A, of 30 larvae, was reared individually in circular

containers, 1.5 inches in diameter. This allowed an area of 1.8 square inches to each larva.

Batch B, of 15 larvae, was reared collectively throughout in a circular dish, 7.5 inches in diameter, the density of larval population being 1 larva per 2.9 square inches.

Batch C, consisting of 25 larvae, was reared collectively throughout in a dish, 7.5 inches in diameter, an area of 1.8 square inches per larva.

The entire rearing was done at 26°C and the larvae were fed on lucerne. The colouration in Table 31 is that of the final larval instar.

Results are shown in Table 31.

Table 31.

Effect of crowding on larval-colouration, survival, speed of development and weights of pupae.

Details of Observations.	Larvae reared singly Batch A 1.8 sq.inch/larva	Larvae reared 15 together Batch B 2.9 sq.inch/larva	Larvae reared 25 together Batch C 1.8 sq.inch/larva
A. Larval colour			
(i) General body colour (dorsal surface)	Pale olive green	Blackish-dark	Similar to Batch B but more pronounced.
(ii) Mid dorsal longitudinal band.	Yellowish-grey, distinct.	Greyish indistinct	
(iii) Head	Pale reddish-brown	Brown or dark brown	
(iv) Ventral surface	White greenish tinge	Dark.	
B. Larvae reached final instar (%)	63.3	53.3	48.0
C. Larvae survived to pupate (%)	50.0	13.3	0
D. Mean Larval Period (Days)	29.8	31.0	-
E. Mean Weights of Pupae (mg)	386.3	211.5	-

Conclusions :

1. Larvae which were reared collectively were darker than those reared individually, but there was no correlation between colour and space per larva.

2. Development was slightly more rapid and survival significantly higher in larvae reared individually.

3. The pupae that developed from larvae, reared singly, were significantly heavier than the others.

III THE IMAGO.

1. Effect of Feeding on Longevity of Moths at Different Temperatures.

The moths, which were kept without food or water, at different temperatures, had been reared throughout at these temperatures except those, kept at 34°C, 13°C and 6.8°C, which had been reared at 26°C. Each was kept in isolation from the time of its emergence from the pupa. The period of survival of each moth was recorded.

The moths, provided with food or water had been reared at 26°C ; Males were usually included with them. The food was 20% sucrose solution.

Results are shown in Table 32.

TABLE 32.

Effect of feeding or starvation on longevity of moths at different temperatures.

Temperature ^{0}C.	Longevity without food or water (Days).				Longevity with food (Days)				Longevity with water only (Days)	
	Mean	Mini-mum	Maxi-mum	No. of Moths	Mean	Mini-mum	Maxi-mum	No. of Moths	Mean	No. of Moths.
34.0	2.04	1.50	2.75	6	7.15	3.50	11.50	10	3.75	12
29.8	2.69	2.00	3.00	4	15.18	6.00	34.00	19	-	-
26.0	4.00	3.50	5.00	4	29.90	18.00	43.00	9	6.5	13
22.0	8.00	7.50	10.00	12	-	-	-	-	-	-
20.0	9.70	7.00	12.00	24	34.44	18.00	65.00	9	-	-
16.0	10.21	7.00	12.00	7	46.77	18.00	88.00	9	-	-
13.0	12.50	9.00	18.00	6	30.00	18.00	39.00	7	-	-
10.0	-	-	-	-	39.00	19.00	69.00	11	-	-
6.8	26.50	22.00	31.00	2	-	-	-	-	-	-
34.0 for 9 hrs; then 26.0 for 15 hrs.	-	-	-	-	12.17	2.00	44.00	12	-	-
34.0 for 9 hrs; then 20.0 for 15 hrs.	-	-	-	-	20.30	10.00	48.00	10	-	-
29.8 for 9 hrs; then 26.0 for 15 hrs.	-	-	-	-	15.30	5.00	27.00	11	-	-
29.8 for 9 hrs; then 20.0 for 15 hrs.	-	-	-	-	21.80	10.00	32.00	12	-	-
20.0 for 9 hrs; then 5.8 for 15 hrs.	-	-	-	-	58.40	28.00	90.00	9	-	-

Comments :

1. Decrease in temperature favoured longevity. Thus, at 6.8°C, moths kept without food or water lived 13 times as long as at 34°C. Maximum longevity of feeding moths at constant temperatures occurred at 16°C. Longest survival of feeding moths, however, was recorded for those kept at alternating temperatures of 20° and 5.8°C. (see Table 32).
2. When temperatures of 34° and 26°C or 34°C and 20°C were alternated, longevity of feeding moths was greater than at a constant temperature of 34°, but was less than at constant temperatures of either 26° or 20°C.
3. Moths which fed lived longer than others.

Conclusions :

1. Moths live longer at low temperatures.
2. Feeding greatly increases longevity.

2. Effect of Saturation Deficit During the Pupal Period on Longevity, Fecundity and Oviposition of Moths.

The larvae were reared under uniform conditions at 25°C and were fed on lucerne. The resulting pupae were kept at 0 and 9 mm saturation deficits, respectively, at 26°C, until the moths emerged. When this occurred, they were maintained at 26°C and fed on 20% sucrose solution. Two males which emerged from pupae reared at the same saturation deficits were enclosed with each female.

Two females from each treatment were used for the experiment.

Results are shown in Table 33 and Figure 34.

Table 33.

Effect of saturation deficit during the pupal period on longevity, fecundity and Oviposition of moths.

Saturation Deficit (mm)	Mean Longevity (Days)			Mean Pre-Oviposition Period (Days)	Mean Rate of Oviposition per Day									Mean Fecundity	Mean Oviposition Period (Days)	Mean No. Eggs in Dead Females
	Females (2)	Males (4)	♂ + ♀ (6)		1	2	3	4	5	6	7	8	9			
0	14.5	19.0	17.3	7	148	216	382.5	239.5	275	152	129	56	8.5	1606.5	9	27.5
9[1]	9.25	15.5	13.4	4.5	120.5	179	203.5	72	51.5	-	-	-	-	626.5	5	100

1. One female laid infertile eggs only.

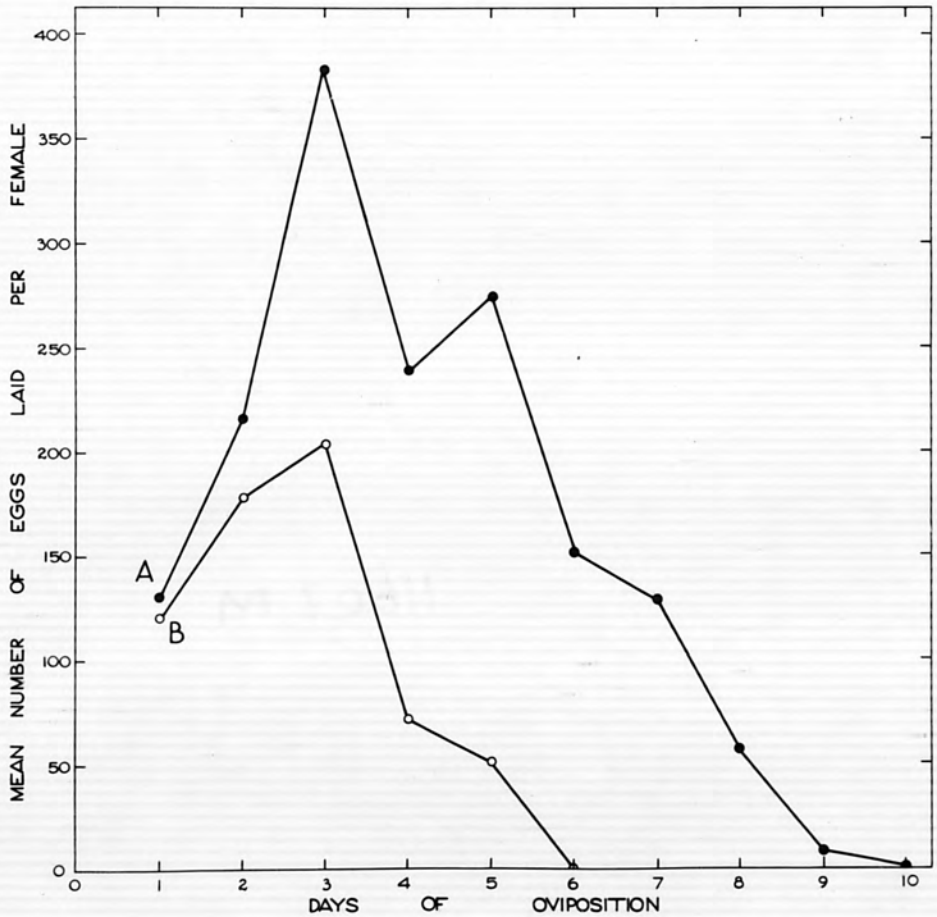

Figure 34. Effect on fecundity and rate of oviposition of different saturation deficits during pupal period.

A. pupae at 0 mm; B. pupae at 9 mm

Comments :

The ~~two~~ moths which emerged from pupae kept at 0 mm saturation deficit had significantly greater longevities than those from pupae kept at 9 mm saturation deficit. Their preoviposition and oviposition periods were longer. They had significantly higher rates of oviposition and laid more eggs. Of the eggs which they were potentially capable of laying, they laid a higher proportion than did the two females of the other group. It should be noted, however, that the second set of figures is unreliable. One of the two females did not copulate. Copulation stimulates the female to lay more eggs than she otherwise would.

Conclusion :

The data were obtained from two sets, each of two females only, and no valid conclusions can therefore be drawn from them. They suggest, however, that reproduction etc., may be affected by variations in saturation deficit experienced by the female while in the pupal stage.

3. Effect, on Oviposition, of Transference of Moths, Ovipositing at an Optimum Temperature, to a Temperature of 10°C.

Moths which emerged from pupae kept at 0 mm saturation deficit and 26°C were used. Two females, each with two males, were confined at 26°C throughout. Two other females, each again with two males, were kept at 26°C till the end of the fourth day of oviposition, after which they were transferred to 10°C. The moths were fed, daily, on 20% sucrose solution.

Results are shown in Table 34 and Figure 35.

The Table 34.

Effect, on Oviposition, of Transference of Moths, Ovipositing at an Optimum Temperature, to a Temperature of 10°C.

Temp. Conditions.	Mean Longevity (Days)			Mean Pre-Oviposition Period (Days)	Mean Rate of Oviposition on Day ----									Mean Fecundity	Mean Oviposition Period (Days)	Mean No. of Eggs left in Dead Female
	Females (2)	Males (4)	♂ + ♀ (6)		1	2	3	4	5	6	7	8	9			
At 26°C throughout	14.5	19.0	17.3	7	148	216	382.5	239.5	275	152	129	56	8.5	1606.5	9	27.5
					1	2	3	4	5	6	7	8	9			
At 26°C for first 4 days of Oviposition then at 10°C.	28.0	20.5	23.0	6	90.5	208.5	295.5	383.5	22	57.5	30	72	7.5	1446.5	22	307.5
					10	11	12	13	14	15	16	17	18			
					32.5	55	45	38.5	22.5	12.5	15	18	10			
					19	20	21	22								
					15.5	6	7.5	1.5								

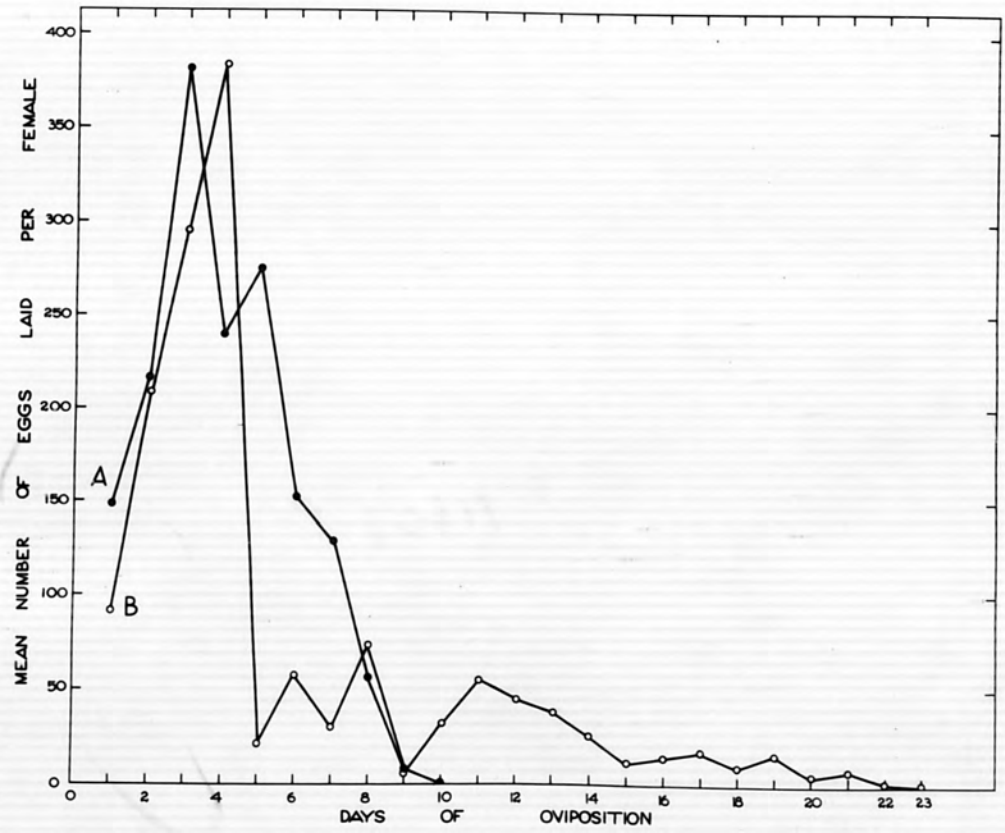

Figure 35. Eggs laid at different temperature conditions - A. 26°C throughout; B at 26°C for 4 days, thereafter at 10°C.

Conclusions :

1. Transfer to 10°C of moths ovipositing at 26°C caused the oviposition rate to decrease suddenly and the oviposition period to be much prolonged. 67.7% of the eggs were laid during the first four days ; laying of the remainder was distributed over the next 18 days.
2. The females which remained at 26°C throughout laid comparatively more eggs than those which were transferred to 10°C.
3. Many more eggs remained in the ovaries of females transferred to 10°C as compared with the females which remained at 26°C throughout.

4. Effect of Different Temperatures of Rearing on Weights of Female Pupae and Fecundity of Moths.

Larvae were reared collectively during earlier instars and singly during the final two, at temperatures of 29.8°, 26.0°, 22.0° and 16°C, on Medicago spp. The pupae of the females moths, used in the experiment, were weighed one day after pupation. The females on emergence were confined at 20°C, each with a single male. They were fed daily on 20% Sucrose solution.

Oviposition for each female was recorded; a separate record was kept of the females laying fertile and infertile eggs.

Results are shown in Table 35 and Figure 36.

Table 35.

Effect of Temperature of Rearing on Weights of Female Pupae and Fecundity of Moths.

Temp. of Rearing (°C)	No. of Females			Mean Weights of Female Pupae (mg)	Preoviposition Period (Days)			Oviposition Period (Days)			Fecundity			Mean No. of Fertile Eggs	Mean No. of Infertile Eggs.
	Total No.	No. Laying Fertile Eggs	No. Laying In-fertile Eggs.		Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum		
29.8	6	2	4	297.4	9.3	12.0	6.0	12.0	22.0	6.0	988	1742	229	553	435
26.0	10	7	3	306.5	8.2	10.5	6.0	10.4	16.0	2.0	1098	2313	38	940	158
22.0	11	11	0	436.0	11.6	25.0	4.0	15.1	26.0	3.0	1927	2948	994	1927	0
16.0	9	9	0	398.0	4.2	8.0	2.0	8.3	14.0	5.0	1516	2214	354	1516	0

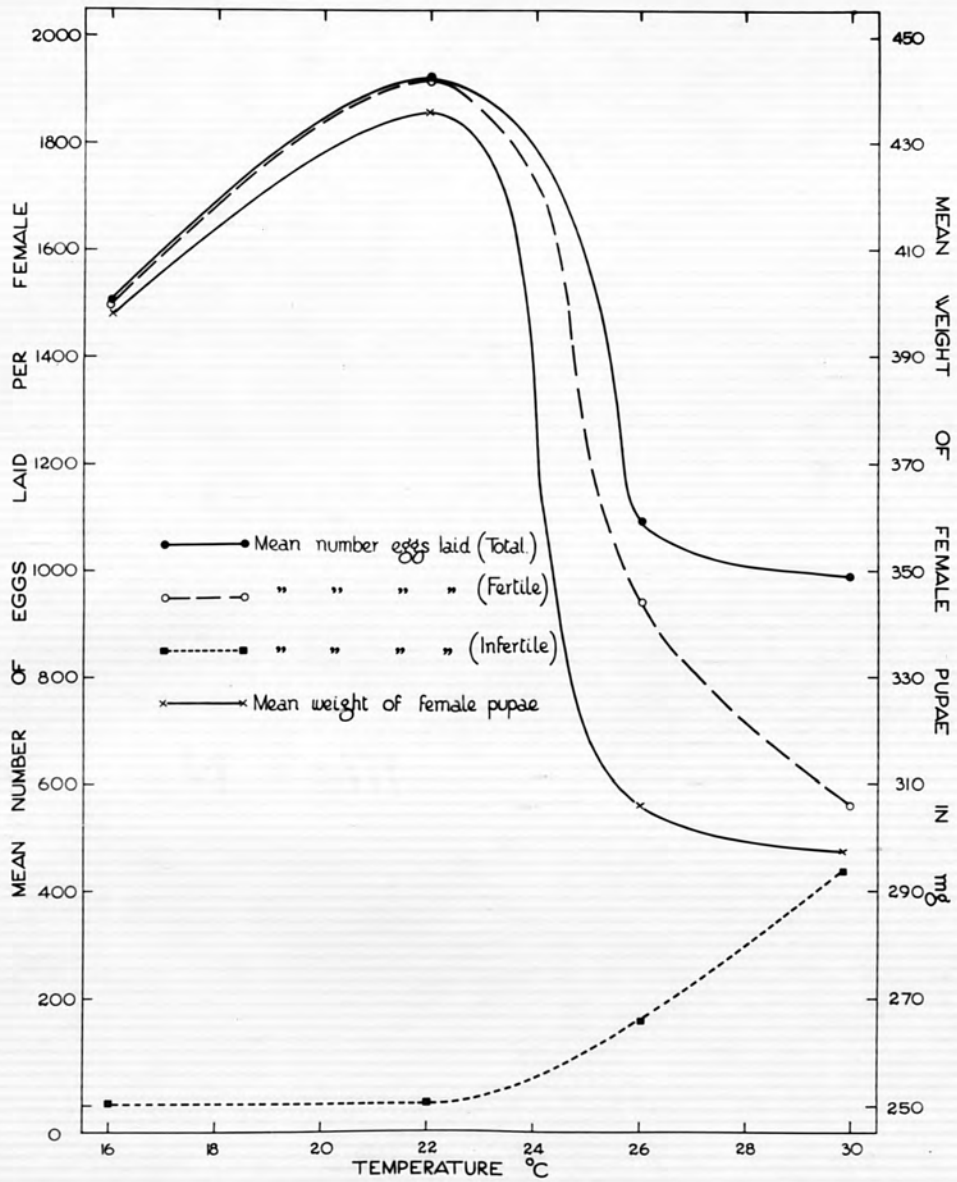

Figure 36. Relation between rearing temperature, weights of female pupae and fecundity of resulting moths at 20°C.

Comments :

Most of the pairs, reared at 29.8°C, and some of those, reared at 26°C, failed to accomplish successful copulation. Some were unable to disengage themselves and died in this condition. When this occurred, the females were unable to oviposit. If separation was accomplished, the partly-everted spermatophore frequently remained permanently attached to the female genitalia (Figs. 3 to 5), and such females laid few and infertile eggs only.

Conclusions :

1. Temperature of rearing exercised a definite influence on fecundity. Pupae reared at 22°C were the heaviest and the moths from these had the greatest fecundity and longevity.
2. The females that developed at 22°C and 16°C all laid fertile eggs; at higher temperatures the proportion of infertile eggs increased. Of the females developing at 26°C and 29.8°C respectively, 30% and 66% laid infertile eggs only.
3. Moths reared at 16°C had the shortest pre-oviposition and oviposition periods, and the highest oviposition rate.
4. 22°C is the optimum temperature of rearing for procreation.

5. Effects of Different Temperature Conditions, during Imaginal Life, on Fecundity.

Moths, from Larvae, reared at 25°C, were used at the various temperature conditions set out in Table 36. They were fed on 20% sucrose solution.

For each set of temperature conditions (see Table 36), four pairs were confined, except at 29.8°C, when 9 pairs were tested, and

at alternating temperatures of 34°C and 26°C, and 29.8°C and 20°C, when 5 pairs were used.

When possible, each female was confined with two males, but at 26.0°, 20.0°, 16.0° and 13.0°C, only one male was present because of an insufficiency of males at the time.

Results are shown in Table 36 and Figure 37.

Table 36.

Effects of Different Temperature Conditions, during Imaginal Life, on Fecundity.

Temp. Conditions (°C)	No. of Females				Preoviposition Period (Days)			Oviposition Period (Days)			Fecundity				
	Total No.	No. Laying			Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean (Fertile & Infertile Eggs)	Maximum	Minimum	Mean Fertile Eggs	Mean Infertile Eggs
		Fertile Eggs	Infertile Eggs	No Eggs											
34.0	4	0	0	4	-	-	-	-	-	-	-	-	-	-	-
29.8	9	0	7	2	6.5	16	1	6.1	13	2	484.3	2375	10	0	484.3
26.0	4	2	2	0	20.0	26	10	10.8	17	7	945.5	1695	370	653.3	292.2
20.0	4	2	2	0	23.3	33	17	10.5	15	6	1219.2	2015	792	752.7	466.5
16.0	4	3	0	1	20.7	25	16	15.3	17	12	697.0	1876	44	697.0	0
13.0	4	2	2	0	13.0	17	11	14.5	26	1	934.0	1511	2	696.5	237.5
10.0	4	1	3	0	21.5	32	12	9.8	12	8	206.2	348	9	87.0	119.2
34.0(9hrs) +26.0(15hrs)	5	4	1	0	4.5	8	3	6.2	13	3	1049.2	2019	445	885.8	163.4
34.0(9hrs) +20.0(15hrs)	4	4	0	0	5.8	7	5	6.5	10	4	1784.0	2529	985	1784.0	0
29.8(9hrs) +20.0(15hrs)	5	5	0	0	6.8	10	3	5.4	14	1	1246.6	2360	438	1246.0	0
20.0(9hrs) +5.8(15hrs)	4	2	2	0	26.5	41	19	21.3	30	14	776.0	1383	354	555.5	220.5

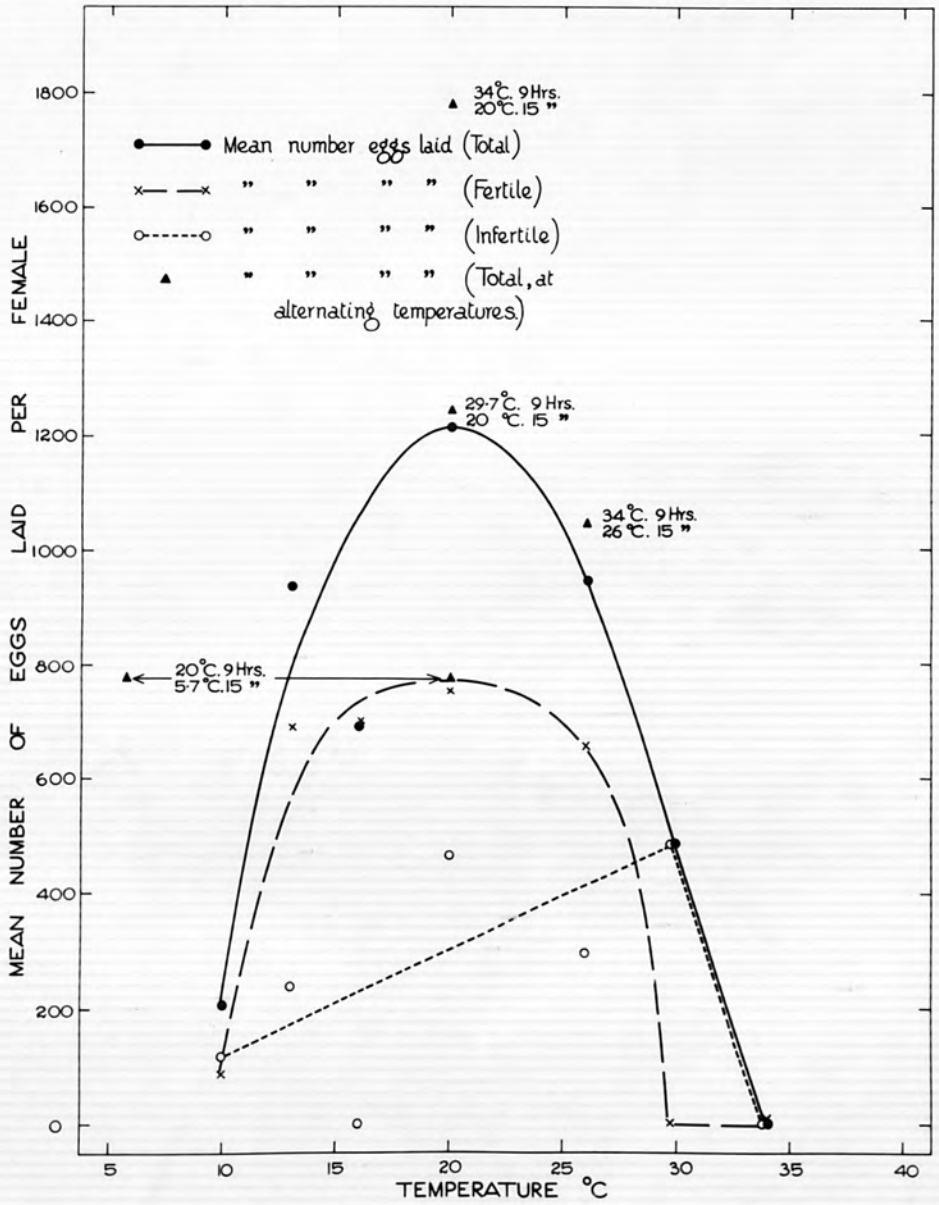

Figure 37. Relation between temperature at time of oviposition and fecundity.

Comments :

1. At a constant temperature of 34°C, no female laid any eggs. Dissection of females after death showed the ovaries to contain few and degenerate eggs.
2. Of the nine females kept at 29.8°C, two failed to oviposit. The remaining seven laid relatively few eggs all of which were infertile. In some cases mating was unsuccessful, as was shown by the partly everted spermatophore remaining attached to the female genitalia (see preceding experiment). In all others, the bursae of dead females contained no spermatophores.
3. At 26°, 20°, and 16°C, pre-oviposition periods were unusually prolonged; at the first two temperatures this was particularly so with the females which laid only infertile eggs.
4. Between 29.8°C and 10°C, maximum oviposition occurred at 20°C; fecundity decreased both above and below this temperature.
5. Though at constant temperatures of 34° and 29.8°C no fertile eggs were laid, the same temperatures when alternated daily with temperatures of 26° and 20°C had a beneficial effect on oviposition. Under the latter conditions, not only did nearly all females lay fertile eggs, but they laid more than did moths kept constantly at 26° or 20°C.
6. Oviposition was much reduced when females were kept constantly at 10°C; at alternating temperatures of 20°C and 5.8°C, the beneficial effect of the higher temperature more than compensated for the depressing effect of a temperature of 5.8°C.

7. At all temperatures, females laying fertile eggs, laid a greater number than those laying infertile eggs.

6. Effect of Fertilization on Oviposition.

The moths used in this experiment were all reared at 16°C under similar conditions. Five females were kept without males in groups of three and two. Five other females were individually confined, each with two males. Moths were kept at a uniform temperature of 20°C, and were fed on 20% sucrose solution daily. A record of oviposition by each set of moths was kept.

Results are shown in Table 37.

Table 37.

Effect of Fertilization on Oviposition.

Treatments	Total No. of Eggs Laid.	Mean No. of Eggs Laid per Female	Remarks.
5 females, no males	2,540	508	Eggs infertile
5 females, each with 2 males	8,629	1,726	Eggs fertile

Comments :

Fertilized females laid three and a half times as many eggs as unfertilized ones.

Conclusion :

Fertilization stimulates oviposition.

7. Influence of Food on Reproduction.

Moths were confined at 20°C under the five sets of conditions, as set out in Table 38.

Where "food" is mentioned, this means 20% sucrose solution.

Results are shown in Table 38.

Table 38.

Effect of Food on Reproduction.

Treatments	Moths Confined	Eggs Laid		Remarks on Dead Females.
		Number	Condition	
1. Neither Food nor water.	1 pair	0	-	Ovaries immature, bursa without spermatophore
	1 pair	0	-	" " "
2. Water for first 2 days; then neither food nor water.	1 pair	235	Infertile	Ovaries partly developed bursa without spermatophore.
3. Water only	1 pair	0	-	-
	1 pair	0	-	-
	1 pair	5	Infertile	-
	1 pair	70	"	Ovaries developed; bursa without spermatophore
	2 females + 1 male	1675	"	" " "
	3 females no males	236	"	-
	1 female + 3 males	0	-	Ovaries immature, bursa without spermatophore
	1 female + 2 males	0	-	" " "
4. Females fed for 1 day; then confined with unfed males without food or water.	1 female + 2 males	0	-	Ovaries developed; bursa without spermatophore.
	1 female + 2 males	72	Infertile	Ovaries degenerated, bursa without spermatophore.

Table 38 (Continued)

Treatments	Moths Confined	Eggs Laid		Remarks on Dead Females.
		Number	Condition	
5. Females and males fed for first 2 days; then water only.	1 pair	1480	Fertile	Ovaries developed, bursa contained spermatophore.
	1 pair	273	Infertile	Ovaries developed, bursa without spermatophore.

Note : The presence or absence of a spermatophore in the bursa indicated whether or not copulation had occurred.

Comments :

1. Copulation failed to occur unless both males and females had fed.
2. With neither food nor water the ovaries failed to develop. With water only, some ovarial development occurred but only few and infertile eggs were laid.
3. If both males and females were allowed to feed for two days, and then kept with water only, copulation could occur and fertile eggs could be laid, but not necessarily so (see 5 in Table 38).

Conclusion :

Feeding of both males and females is essential for mating to take place and fertile eggs to be laid.

M O R P H O L O G Y

The morphology is discussed under four headings :

1. The Larva.
   (a) Chitinous structures of the head
   (b) Chitinous and sclerotized structures of the appendages
   (c) The spiracles
   (d) The chaetotaxy

2. The Imago.
   Chitinous structures of the body; the wings and their venation; the body investment

3. The Organs of Reproduction
   (a) The organs of copulation and oviposition
   (b) The internal organs of reproduction

4. The Surface Structure and Histology of the Integument.
   (a) The surface structure of the larval cuticle
   (b) The histology of the integuments of larva, pre-pupa, pupa and imago

1. 1. The LARVA.

The Head (Figures 38 and 39).

The head of the first larval instar (Fig. 38 (2)) is uniformly blackish brown, and bears setae most of which are clavate.

The inverted Y-Shaped epicranial suture is well developed. The adfrontal sutures being obsolete, the adfrontal sclerites are wanting. The vertical triangle is poorly developed, and the frons is relatively longer than in the final larval instar. The mean lengths of the frons and epicranial stems of the four specimens measured were 0.102 mm and 0.0516 mm respectively, giving an epicranial index of 1.98. The width at the base of the frons (100 μ) is approximately equal to its length. The clypeus and labrum, respectively, measure 120 μ and 95 μ transversely, and 45 μ and 42 μ longitudinally. The tormae are 10 μ long. The clypeal suture is irregular and wavy. The antennae, including the antacoriae, are 55 μ long. The longest antennal seta, on the distal end of the 2nd segment, measures 80 μ. The largest setae on the head (v_2) are 105 μ long, and the smallest (0_1, 0_2 and 0_3) 3 μ. The mandibular teeth (Fig. 38 (4)) are fine and sharp.

The Head of the Final Larval Instar (Fig. 39 (1))

The epicranial suture (es) takes the form of an inverted 'Y'. Its stem, 0.56 mm long, lies along the mid-dorsal region, and the two arms, each 1.56 mm long, diverge antero-laterally. The stem of the epicranial suture is somewhat reduced due to its dividing posteriorly. There is a deep emargination of the posterior wall of the cranium ; the triangular area so formed , the vertical triangle, is occupied by the membranous cervacoria (cc). Its apex is highly sclerotized. The epicranium, which

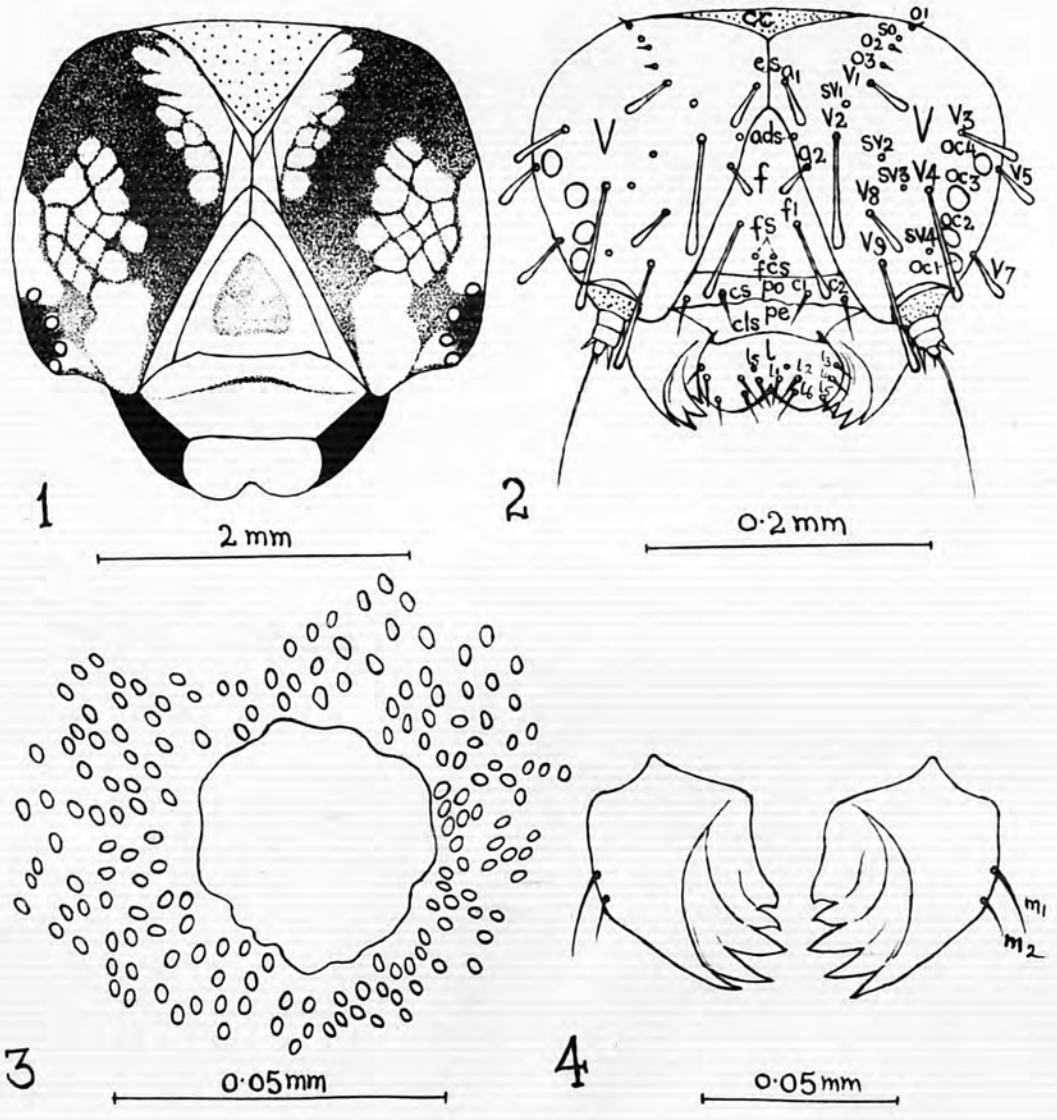

Figure 38. 1. Head of final larval instar to show colour pattern and sculpturing (Dorsal).

First larval instar :

2. Head showing setae and sensoria (Dorsal).

3. Isolated granules and a tubercle.

4. Mandibles.

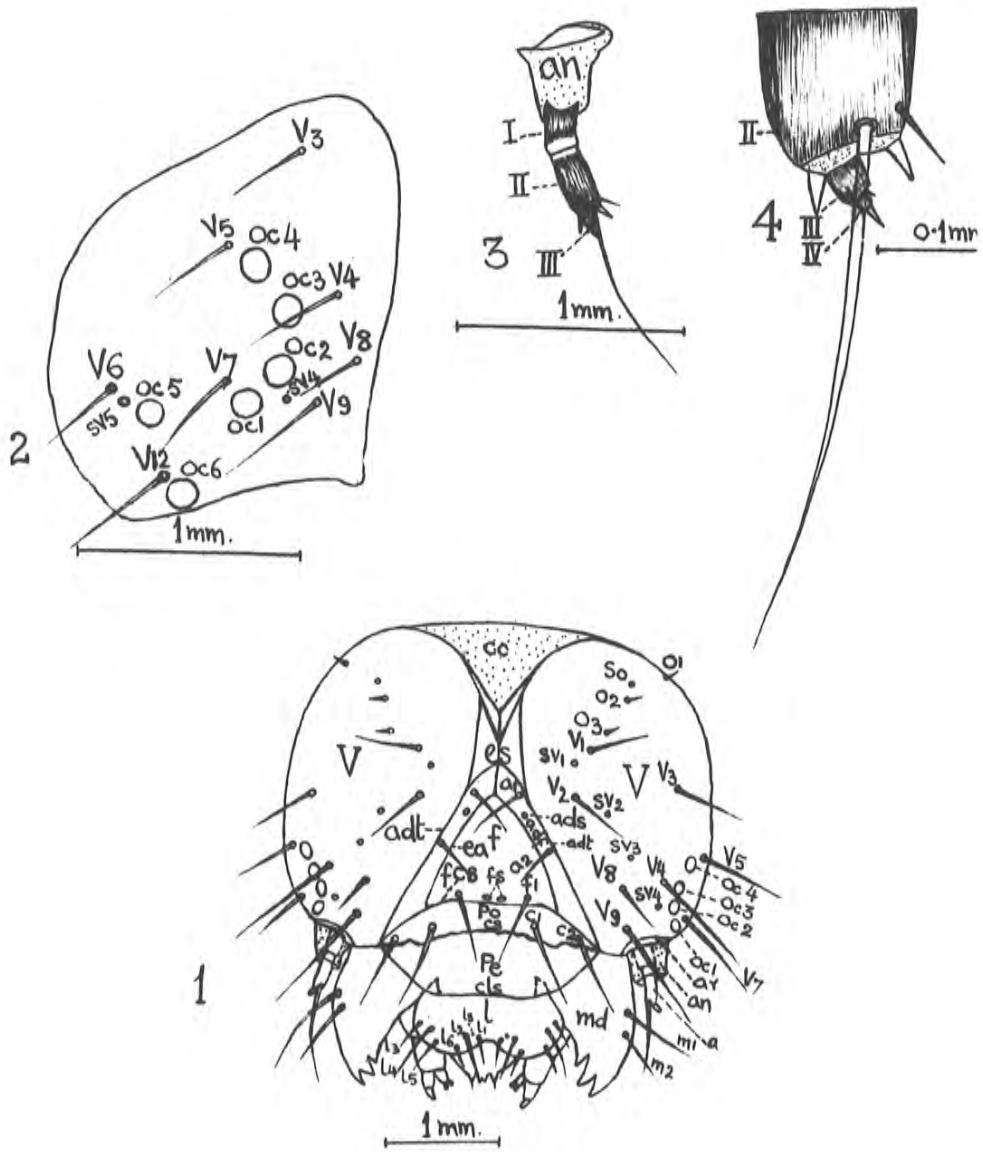

Figure 39. Final larval instar

1. Head showing setae and sensoria (Dorsal).
2. Part of epicranium showing ocelli.
3. Antenna.
4. Distal part of antenna.

lies on either side of the epicranial suture and comprises the greater part of the head, comprises the fused vertex, occiput and postgenae.

A pair of secondary sutures, the adfrontal sutures (adt), which are sub-parallel to the epicranial suture on the outer sides, enclose between them and the primary epicranial suture, very narrow elongate plates, the adfrontals (adf). Ripley (1923) suggested that the outer sutures are the secondary ones, and the inner, the primary or epicranial suture.

The frons (f) is triangular in form, with slightly convex sides which are bounded by the arms of the epicranial suture. It measures 0.9 mm longitudinally from the apex to the base and 0.94 mm across the base. The lengths of the frons and the stem of the epicranial suture being 0.9 and 0.56 mm respectively, the epicranial index is 1.62. The fronto-clypeal suture (fcs) is distinct. It turns slightly upwards at the sides, for a short distance, and is slightly concave medially and anteriorly.

The clypeus is large and more or less hexagonal inform, the two outer angles being acute. The two lateral surfaces are more or less convex, and the two median ones slightly concave. It is 0.70 mm long and 1.75 mm between the two outer angles. The clypeal suture subdivides it into a broader ante- or pre-clypeus (Pe) and a narrower post-clypeus (PO); it is more or less zig-zag, and slightly convex medially towards the post-clypeus. The pre-clypeus and the post-clypeus, respectively, are 0.45 mm and 0.25 mm long.

the Labrum (l) is separated from the clypeus by a distinct clypeo-labral suture. It is a large unpaired sclerite. A prominent anterior cleft, 0.15 mm deep, makes it bilobed. It measures 1.26 mm transversely

and 0.53 mm longitudinally. The anterior and outer margins of its lobes are strongly convex; posteriorly it is slightly convex.

The postgenae (Fig. 46, pa). Ventrally and medially, the vertex extends for some distance on either side beyond a secondary lateral suture. As occipital sutures are wanting, the limits of the vertex and the postgenae are not clearly defined. Though the lateral sutures are not homologous with the occipital sutures, Ripley (1923), for convenience, referred to the plates mesad of these sutures as the post-genae, a practice which is here adopted. The postgenal plates do not fuse medially but remain some distance apart, being connected by a narrow band of the cervacoria (cc). Anteriorly, the two postgenal plates together with their cervacorial attachment form a deep concavity into which fits the base of the composite structure, formed by the two maxillae and the labium. At the posterior margin of each postgenal plate is a narrow strip of sclerotized cervacoria (ccc) which is folded. Around the postero-lateral margin of the foramen (fo), a secondary infolding (se) separates a thin crescentic secondary sclerite (se) from the remainder of the vertex on either side.

The colour of the head of the final larval instar (Fig. 38 (1)) is light yellow to yellowish-brown withdark brown patches and sculpturings. The part of the vertex situated below, and more or less bounded by ocelli 1 to 4 is dark brown. In the middle of the epicranium is a dark brown well developed sculpturing in front of which and just above the ocelli is a faint brownish patch. A prominent dark brown longitudinal more or less irregular band traverses the whole length of the upper part of the epicranium. There is a narrow elongate pale yellow area between it and the median stem of the epicranial suture, and

the margin of the vertical triangle. Mesad of this band, and extending towards the pale yellow area is a small sculptured area. The region laterad of the well developed sculpturing and posterior to the ocelli, and that lying anterior to the sculpturing are also pale yellow. The adfrontals, the frons, the clypeus and the labrum are pale yellow except for the central region of the frons, which may be light brown. Along the clypeal suture, is a very narrow transverse dark brown stripe. The pre-clypeus is white.

The coloration of these patches and the degree of sculpturing varies greatly among individuals.

The Organs of Ingestion.

In addition to the labrum, the mouthparts comprise the epipharynx, the mandibles and the maxillolabial-hypopharyngeal complex.

The epipharynx (Fig. 42 (2), ex) is membranous. It is continous latero-ventrally with the hypopharynx and posteriorly with the post-pharynx (pox). Near its distal margin, on either side, it bears three short, stout setae (e_1 - e_3). The middle seta is longer (0.14 mm) than the other two, which are more or less sub-equal (0.06 - 0.07 mm). Several minute setae, similar to those on the hypopharynx, but smaller, are present on the epipharynx and extend to the post-pharynx. Laterally, the posterior margin bears a pair of highly-sclerotized, short stout sclerites, the tormae (tm), which are slightly curved mesad and extend entad of the clypeo-labral suture, projecting posteriorly.

The mandibles (Figs. 40, 41, 42 (3), md) are hard, compact structures of the chewing type. Each is 1.23 mm in length from the median posterior projection to the apex, and 0.77 mm in width across the middle. The first or outermost tooth is somewhat smaller than the 2nd and the 3rd teeth, and is situated close to the second. The 2nd and the 3rd teeth are sub-equal and are the longest as well as the sharpest. They form the incisor region (cs) of the mandible. The two inner teeth (nos. 4 and 5) are smaller, blunt and rounded, and form the molar area (ms). Each mandible is attached to the head just mesad of the antacoria (Figs. 40,41, an) by a narrow membrane, the mandacoria (Fig. 40, mnc), and to the lateral margin of the maxilla by a relatively wider membrane, the maxacoria (Fig. 40, mxc). Each articulates dorsally by means of a ginglymus or preartis (Fig 40, py), which is 0.25 mm wide, and the precoila (Fig 40, pr), which is 0.15 mm wide. Ventrally it has a large globular condyle, the post-artis (Fig 41, ptc) which articulates with the post-coila (ptl). The latter is 0.175 mm in diameter and 0.105 mm in depth. The abductor muscles (Fig 42 (3) ab.m.) are smaller and weaker than the adductor muscles (ad.m.). Mandibular glands are wanting. Extending from the teeth inwards are highly sclerotized blackish brown regions which reinforce the mandibles. Each mandible bears two setae dorsolaterally of which proximal (m_1) is larger than the distal one (m_2).

The Maxillo-labial-hypopharyngeal complex (Figs. 42 (4)). This acts as a lower lip and comprises the united maxillae, labium and hypopharynx. Its base is attached by a membrane (cc) to the post-genal plates (Fig. 46, pa) for the most part, and to the cervacoria in the middle (Fig. 46, cc).

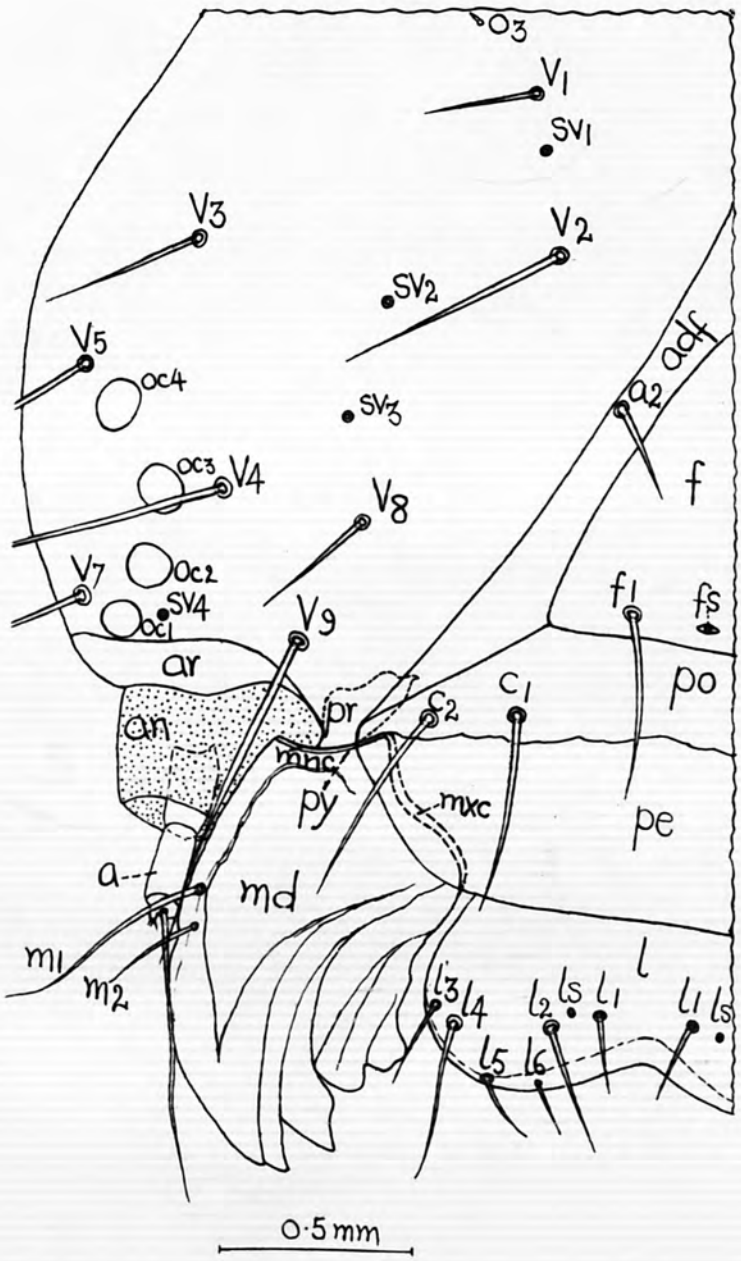

Figure 40. Final larval instar
Part of head (Dorsal).

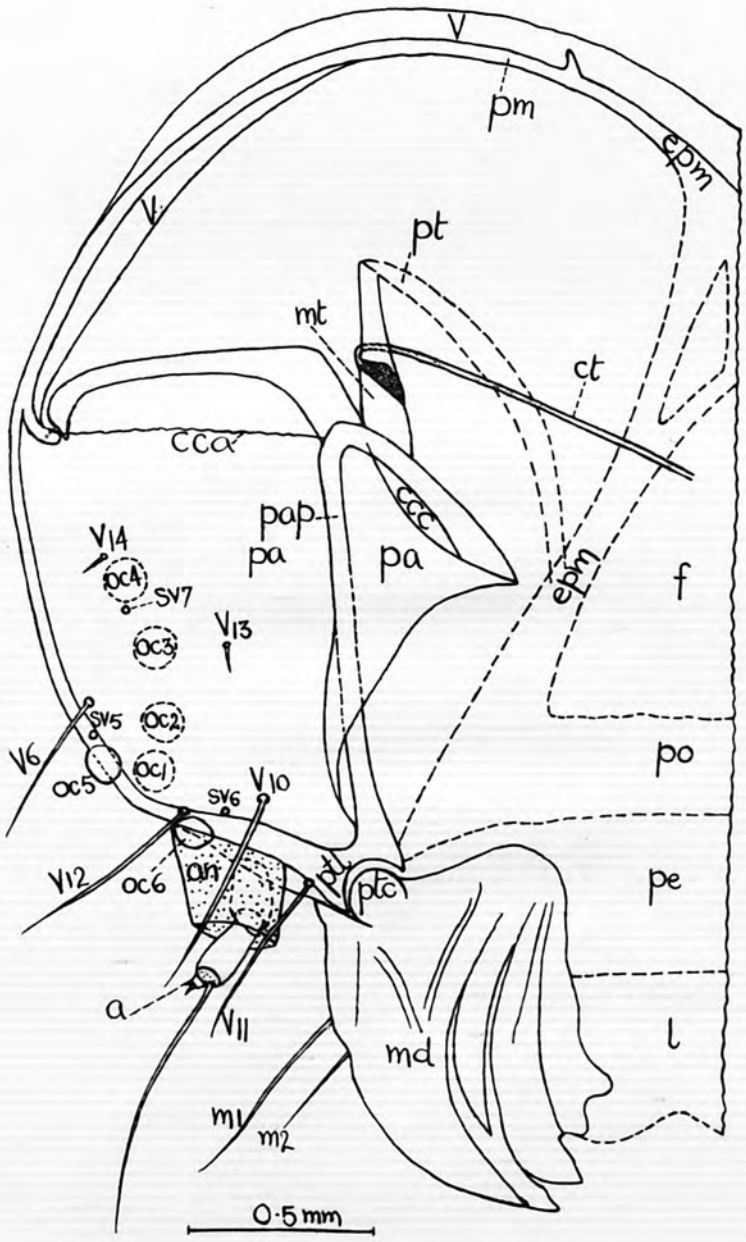

Figure 41. Final larval instar
Part of head (Ventral)

The Maxillae (Fig. 42 (4,5)) are highly specialized. The cardo, articulates with the anterior margin of the post-genal plate. Its proximal part, the sub-cardo (sa), articulates with the post-gena; its distal part, the alacardo (al), is attached to the stipes. Medially, the sub-cardo is produced to form a finger-like free projection which extends above the sclerotized lateral plate of the submentum and provides a point for muscle attachment. The outer and more distal part of the cardo is membranous; the remainder is sclerotized. Its length and [the maximum] width are 0.8 mm and 0.7 mm, respectively. The stipes (s) is attached to the alacardo basally and to the submentum medially. The medio-proximal, and the medio-distal parts, of the stipes are membranous. The former bears a large seta. A median transverse secondary suture (se) divides the stipes into two parts. The lateral region of the sclerotized portion of the stipes bears a large seta, close to and laterad of the seta of the membranous part. The maximum dimensions of the stipes are 0.8 mm in length and 0.665 mm in width. At the distal end of the stipes is located a sclerotized plate, the palpifer (pf). Distally, this bears the three-segmented maxillary palpus (mx.p.). Between the sclerotized palpifer and the segments of the maxillary palpus, are membranous regions. The maxillary palpus measures 0.455 mm in length. The first and second segments are 0.245 mm and 0.140 mm long, respectively. The third segment is 0.07 mm long and tapers from the base. [Apically, it] bears four minute setae, one ventrally and three dorsally. The membranous region between the palpifer and the first segment of the maxillary palpus bears a seta about 0.4 mm long. The galea is differentiated into the basal narrow and membranous proxagalea (pg) and the distal sclerotized distagalea (dg); the latter is 0.105 mm in length. The distal end of the distagalea

bears two processes each of which terminates in a small knob (glc). The lacinia is reduced, membranous and more or less indistinguishable from the proxagalea. It bears two setae (las) which are characterized by being blunt and rough at their tips. The distal end of the first maxillary segment bears two setae. The entire maxilla measures 1.8 mm in length from the base of the cardo to the tip of the palpus.

The labium (Fig. 42 (4)) lies between the two maxillae to which it is proximally attached for about two-thirds of its length, the distal third being free. The submentum (sm) is well developed. It is largely membranous except for two latero-proximal sclerotized yellowish brown triangular plates whose bases lie at the proximal margin of the submentum. Their outer and inner sides are somewhat convex and concave, respectively. As the inner finger-like projection of the cardo moves above this part of the submentum, the sclerotization provides added strength. The submentum has two partially developed sutures between the submental plates, more or less close to and parallel with, the inner margins of the latter, and extending for about three-fourths of their length. A pair of large setae (sm.s.), about 0.315 mm long, are present in the middle of the submentum, which is 1.12 mm long and 0.925 mm across the base. Laterally, the submentum is attached throughout its entire length to the cardo and stipes on either side. Basally, it is attached to the concave anterior margins of the postgenal plates and to the cervacorial connection of the latter, in the middle, by narrow membranous part (cc) of the cervacoria. The mentum is undifferentiated. The distal part of the labium, the pre-mentum or stipula (Figs. 42 (4), 43 (1), sp), is highly specialized and quite distinct from

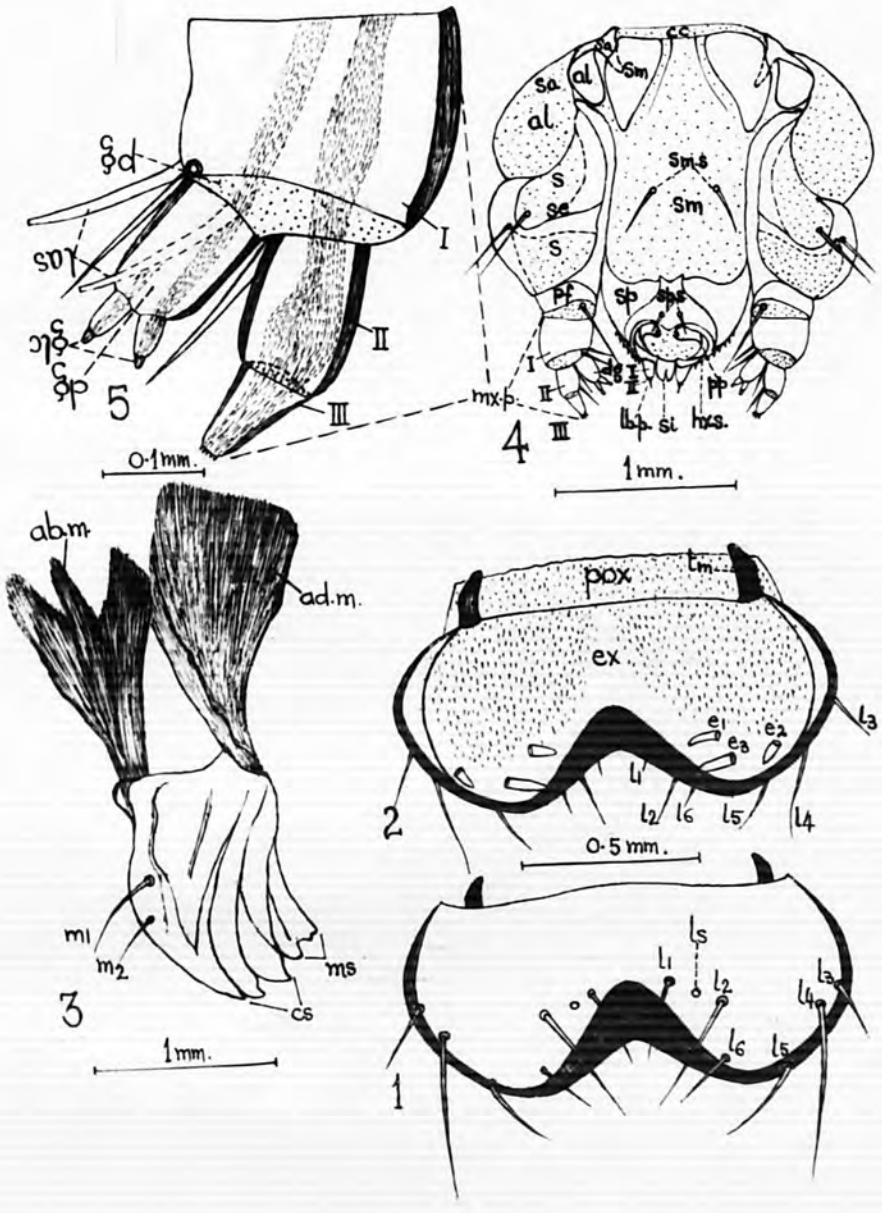

Figure 42. Final Larval Instar - Mouthparts

1. Labrum.
2. Epipharynx and post-epipharynx.
3. Mandible.
4. Maxillo - labial - hypopharyngeal complex (Ventral).
5. Distal part of maxilla (Ventral).

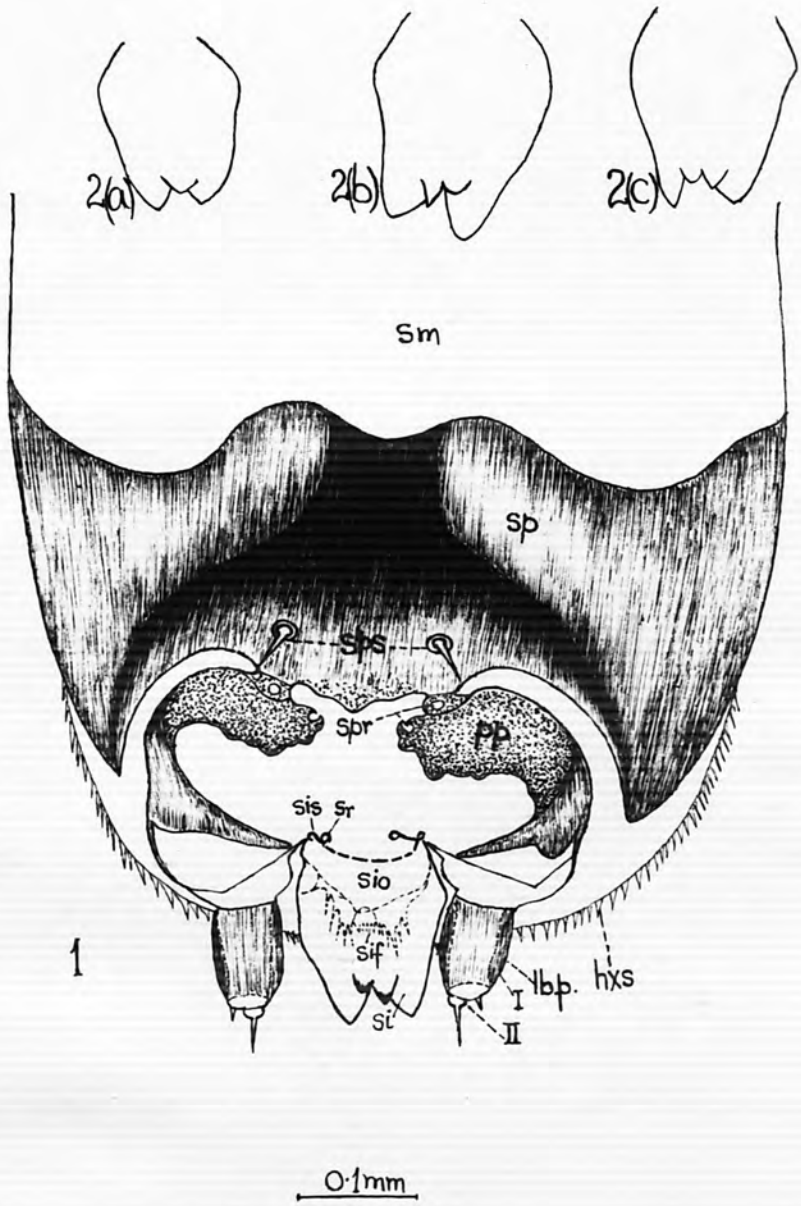

Figure. 43 Final larval instar

1. Distal part of labium (Ventral). 2. Spinnerets showing variations in inner lobes.

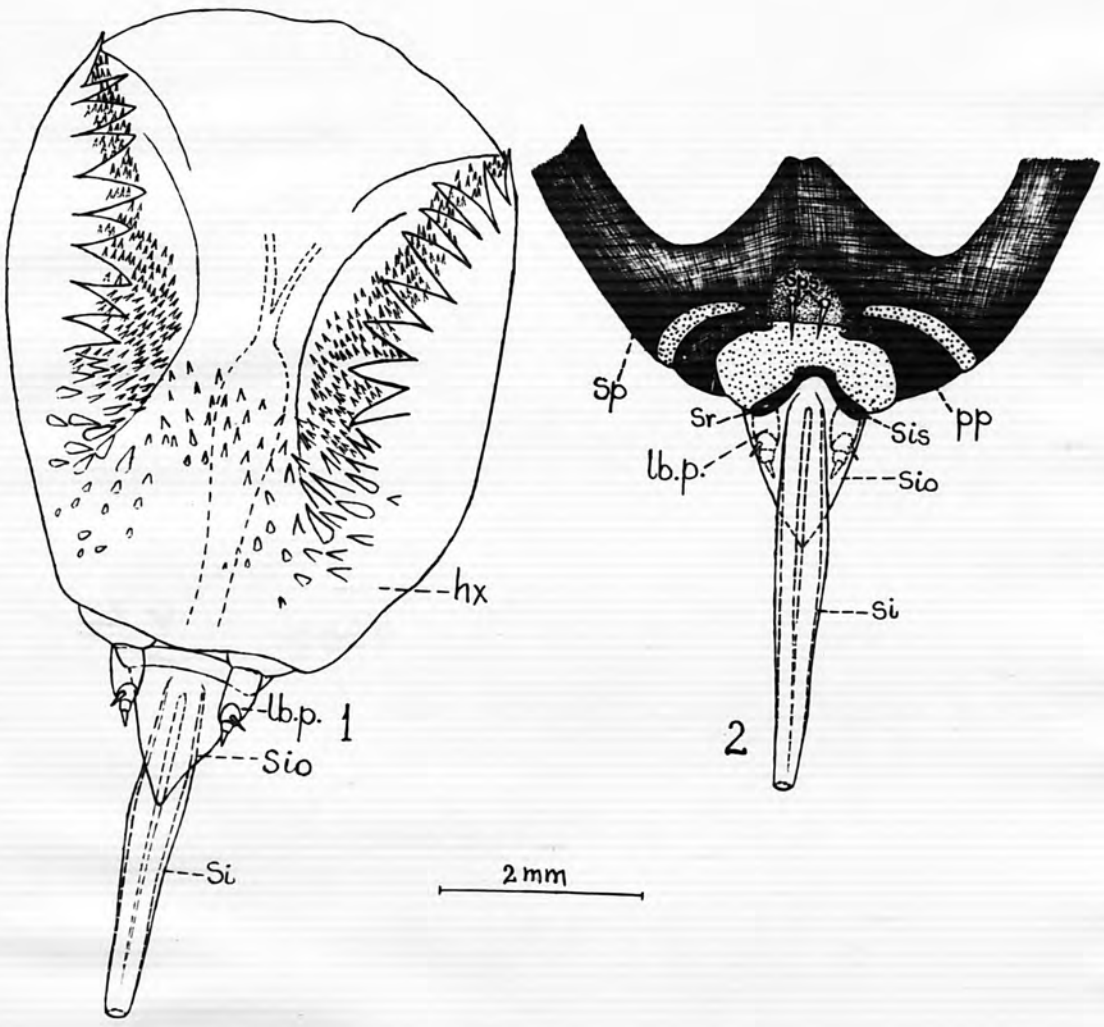

Figure 44. Heliothis punctigera Wall.

1. Hypopharynx and distal part of labium (Dorsal).
2. Distal part of labium showing spinneret (Ventral).

the submentum. It is sclerotised proximally and membranous distally. Latero-proximally, to the sclerotised part are attached the maxillae. The remainder of the stipula is a free, semicircular lobe lying between the maxillary palpi. The sclerotized region of the stipula is further differentiated into a medio-distal dark brown area and latero-proximal brown one. The former bears a pair of stipular setae (sps). Distally it is concave at the sides with a slight protrusion in the middle. On either side of the protrusion, and anterior to the concave margin of the stipule, is a palpiger (pp). This is a narrow crescentic sclerite connected to a membrane distally. There is a narrow membranous area between the sclerotized stipula and the palpiger. Anterior to the stipular setae, the two are fused. In the middle of this fused area is a sensorium (spr). A second sensorium is situated mesad of the first at the tip of the palpiger. These sensoria are about 10 μ in diameter. The proximal and the lateral margins of the palpiger are smooth and convex; the distal margin is uneven. The labial palpus (lb.p.) is very small and two-segmented. The proximal segment is relatively very large (0.09 mm in length and 0.06 mm in width). The distal end of the first segment bears a minute seta. The second segment is minute and dome-shaped. It bears a fine teminal seta. The labial palpus, including the terminal seta, is about 0.105 mm long.

The Spinneret (Fig 43 (1-2 a,b,c), si) and the spinning apparatus (Fig. 45, pr) - The spinneret is short and flat. It tapers slightly towards the base but more so distally, where it is only half the width of its broadest part. Distally, it is deeply emarginate medially. Two pairs of lobes are usually present. The dorsolateral pair are much larger than the medioventral pair which are adjacent to the base of the

emargination. At times, these smaller inner lobes are fused (Fig. 43, 2 (a)). On the dorsal side, the spinneret is supported by a thin transverse basal sclerite (sis) which extends ventrally only at the sides, each of which bears a sensorium. On the dorsal surface of this sclerite is a prominent rounded membranous fold (sio) at the base of the spinneret. Anterior to the fold, and dorsally, is a fringe (sif) which exudes silk, not as a definite thread but as a gummy secretion. As this is secreted, it is formed, by the fringe, into a flat ribbon.

The spinning apparatus, consisting of the large silk press (Fig. 45, pr) and the associated ducts, lies between the labium and the hypopharynx. The two ducts (sld) from the silk glands unite to form a short median duct (mc) which opens into the base of the silk press which is wider anteriorly and tapers posteriorly. Between the posterior end of the press and the median duct is a prominent constriction. The press is sclerotized and provided with powerful muscles. It discharges through a narrow duct connected to the spinneret.

The structure of the spinneret of this species strongly suggests that this organ is a modified ligula formed from the paraglossae and the glossae. The outer pair of lobes most probably represent the paraglossae and the shorter inner pair the glossae. Though the inner lobes are distinct (Fig. 43 (1-2 b, c)) in most larvae, they tend to fuse. In a few specimens, actual fusion to form a small median lobe (Fig. 43, 2 (a)) was observed. Though early workers, Packard (1898) and others, regarded the spinneret as a modified hypopharynx, later workers have described a separate hypopharynx in addition to the spinneret. Berlese (1909), Dampf (1910), Imms (1948) etc., considered the spinneret to be formed

from the fused glossae and paraglossae. Ripley (1923), while accepting this view advanced certain arguments in support of his hypothesis that the spinneret, in caterpillars, evolved secondarily, and had, therefore, no homologue in the insect-labium. This, however, seems to be too extreme a view, based on too many suppositions. Its position on the labium and its generalized, ligula-like structure in Agrotis strongly suggests that it represents the ligula of the labium. The presence of two pairs of lobes on the spinneret also shows that the proximal sclerite (sis) and the fold (sio) cannot be regarded, as was suggested by Dampf (1910), as homologous with the paraglossae. They are apparently secondary adaptations for the support of the spinneret. The generalised structure of the spinneret in this species is to be correlated with the fact that silk production is very limited. Though the spinneret is generalized, it has developed, in common with many other agrotids, the secondarily specialised condition of having the characteristic fringe (sif). This fringe is supposed to distribute the gummy secretion of the silk glands over the inside of the earthen cocoon prior to pupation. By contrast, in other species of the Agrotidae which secrete silk as a definite thread, e.g. Heliothis punctigera Wallengren (Fig 44 (1-2)), the spinneret is a long tube formed of the fused glossae and paraglossae, and the fringe is wanting. The large proximal fold (sio) on the dorsal side, and the well developed, sclerotized, proximal sclerite (sis) are secondary adaptations for the support of the long spinneret.

The hypopharynx (Fig. 45, hx) is connected with the dorsal surface of the labium. It is a membranous lobe forming a low mound on the floor of the prepharynx. It covers the entire surface of the stipula and extends slightly beyond it on either side. Posteriorly it extends as far as the submental setae. It is provided with numerous yellowish brown specialised setae or papillae arranged in a definite order. The number and arrangement of these differ in closely related species. Thus, in Heliothis punctigera Wallengren (Fig. 44 (1) hx) they are fewer and smaller and the distal lobe is only weakly developed.

The hypopharynx consists of three regions :

1. The anterior lobe rests on the distal part of the stipula. Its anterior and outer margins are semicircular; the posterior margin is straight in the middle but has a slight concavity at either side. It bears numerous setae. Those situated on its anterior and outer margins are directed anteriorly and project beyond the distal border of the labium. The lateral setae are directed inwards and those on the median part, posteriorly. The distal setae are smaller than the others.

2. The posterolateral lobes are higher than the ventral lobe and are oblong in form. The outer margin of each has a thin sclerotized longitudinal bar which articulates with the distal part of the stipes. The disto-lateral setae are directed medially and anteriorly; the others are directed medially and posteriorly. The lateral setae, situated in an arc, are the largest; between these and the lateral sclerotized bar is a non-setiferous area.

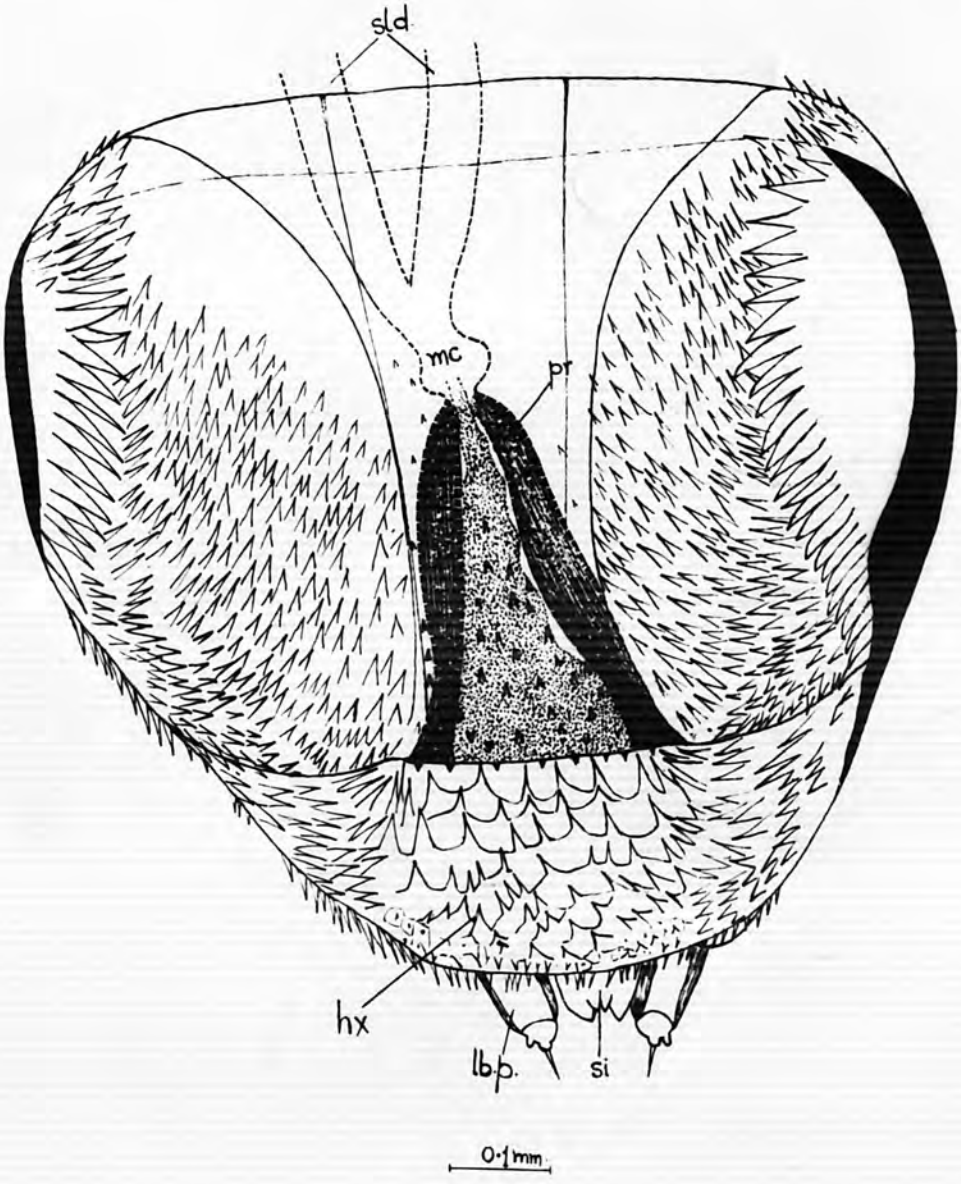

Figure 45. Final larval instar

Distal part of labium showing hypopharynx, silk-press with ducts and spinneret.

3. The postero-medial region is situated between the two lateral lobes and is somewhat depressed. Only few and very small setae are present. Three sutures are present, two lateral and longitudinal and a third basal and transverse. The latter extends over the postero-lateral lobes.

The entire hypopharynx measures about 0.84 mm longitudinally and about 0.91 mm laterally across the base.

The Ocelli (Figs. 39 (2), 41, $oc_1 - oc_6$). Six ocelli are present on either side of the vertex behind the insertions of the antennae. Ocelli 1 to 4 are dorsal and arranged in an arc having a ventral curvature. Ocelli 1 and 2 are situated closer together than any other two adjacent ones. Ocelli 5 and 6 are situated ventrally and are separated from the rest. Ocellus 5 is behind, and ocellus 6 in front, but ventrad, of the first ocellus. Each ocellus is located on a narrow, circular sclerite, and measures about 140 μ in diameter. The distances between the ocelli, 1 - 4, beginning with the first, 1 to 5, and 5 to 6 are 60, 105, 105, 210 and 280 μ respectively.

The antennae (Figs 39 (3-4), 40, 41, a) are short structures located just behind the bases of the mandibles. Each is attached to a sclerotized antennaria (ar) with a large membranous antacoria (an) by which it may either be retracted into or protruded from the head. The antenna is four-segmented. The two basal segments are large and sub-equal, the third is very small, and the fourth is so minute as to be visible only under high magnification. The first three segments are separated by membranous areas (the coriae), which allow free movement. The distal end of the second segment bears five setae. Two are long and attenuate, one of them being much longer than the whole antenna. The other three are

conical. Two of them are large and sub-equal but the third is minute. The distal end of the third segment bears three small conical setae. The fourth minute segment bears a single thin seta. The four segments, beginning with the basal one, measure 210 μ, 225 μ, 35 μ and 10 μ in length. The largest seta, on the second segment, is about 770 μ long.

The endo skeleton of the head (Fig. 46) is formed by a number of prominent heavily sclerotized sutural infoldings, the parademes. The tentorium is much reduced and of unusual form. The corpotentorium (ct) is represented by a fine transversely placed membranous thread attached on either side to a sclerotized narrow part to which are also joined the pretentorium (pt) and the metatentorium (mt). The pretentoria (homologous with the anterior arms of the tentorium) are formed by invaginations at the bases of the epicranial parademes (epm). Externally, therefore, their positions can not be ascertained. Moreover, the pretentorinae are not located at the ends of the fronto-clypeal suture but have migrated posteriorly on the epicranial parademes. Each pretentorium first extends posteriorly, then ventrally and finally anteriorly to meet the metatentorium of its side. The pretentoria are semi-hardened. The metatentoria (homologous with the posterior tentorial arms) are very short, and some what broader than the pretentoria. They are membranous and originate at the bases of the posterior ends of the postgenal parademes (pap). Hence, the positions of the metatentorinae are not externally visible. To give support and strength to the postgenae, a large tendon (td) originates just outside the base of the metatentorium from the posterior end of the post genal suture and extends laterad to be inserted in the end of the parademe (pm).

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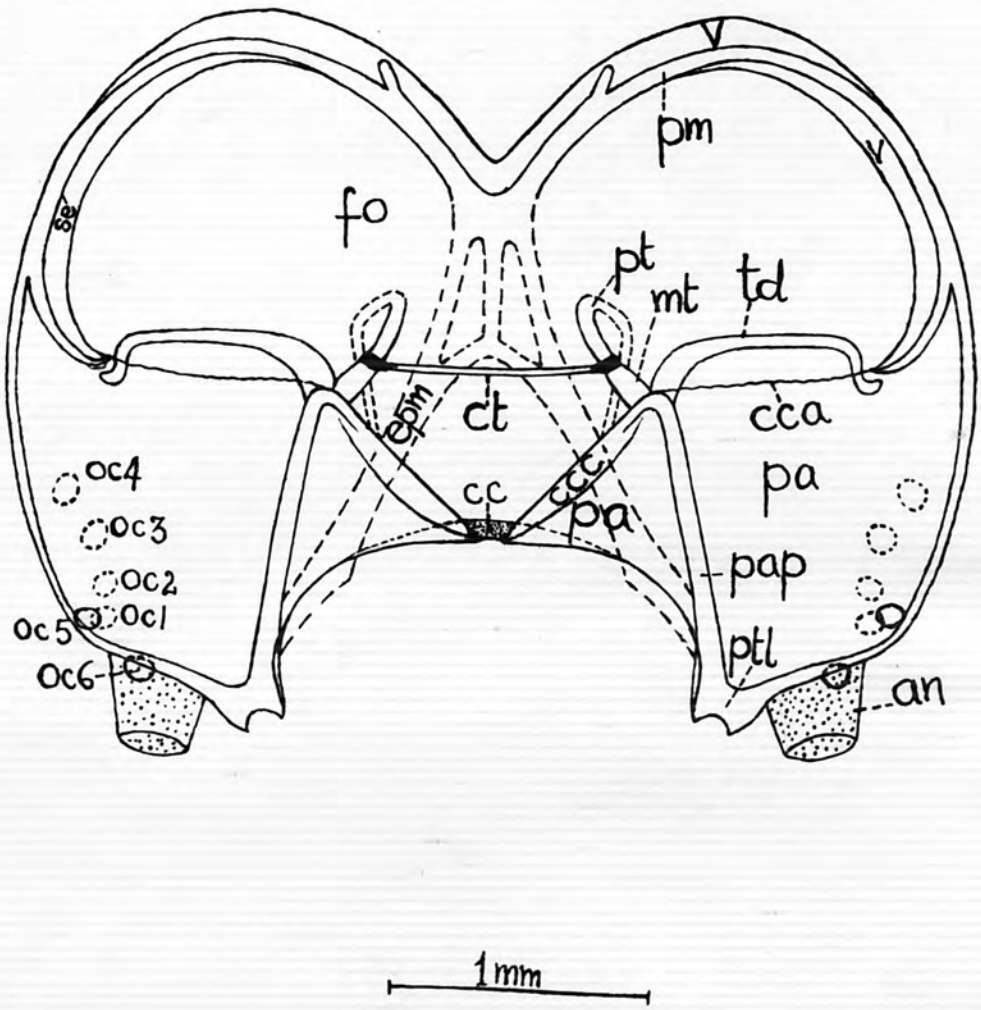

Figure. 46. Final larval instar

Head (ventral), showing endoskeleton as seen through foraminal opening.

Since the poorly developed tentorium is incapable of performing its normal functions, these are assumed by a number of deeply inflexed hardened structures, the parademes, along the epicranial and some secondary sutures. These comprise the epicranial (epm), posterolateral (pm), postgenal (pap) and the weakly developed fronto-clypeal, parademes.

Structurally, the thoracic legs (Fig. 48 (1)) of all instars resemble each other. Each is jointed. The coxa is large and broad, the femur, tibia, and tarsus are well developed and of nearly equal length. The pretarsus is small and bears a small claw. The length of the leg of the final instar is 1.62 mm, whereas that of the first instar is 0.15 mm.

The prolegs (Figs. 47 (1-4), 48 (2-4)) of the first and final instars differ considerably, and are therefore separately discussed.

a) The prolegs of the first larval instar (Fig. 47 (1-4)). Only 3 pairs of well developed prolegs are present, namely those on the 5th, 6th and the 10th abdominal segments. Those of the 4th abdominal segment are much reduced and each has a single small crochet. The prolegs of the third segment are vestigial,, being represented by a pair of small swellings. Those of the 4th segment are 40 μ in length, whereas the last three pairs are from 96 - 100 μ in length. The width of the plantae of the prolegs of the 4th segment is 20 μ, while those of the 5th and the 6th abdominal segments are 40 μ, and of the anal claspers 65 μ. The number of crochets varies on different pairs of prolegs and even on the prolegs of the same pair. Usually, the anal claspers have the largest number. The crochet - formulae of two larvae

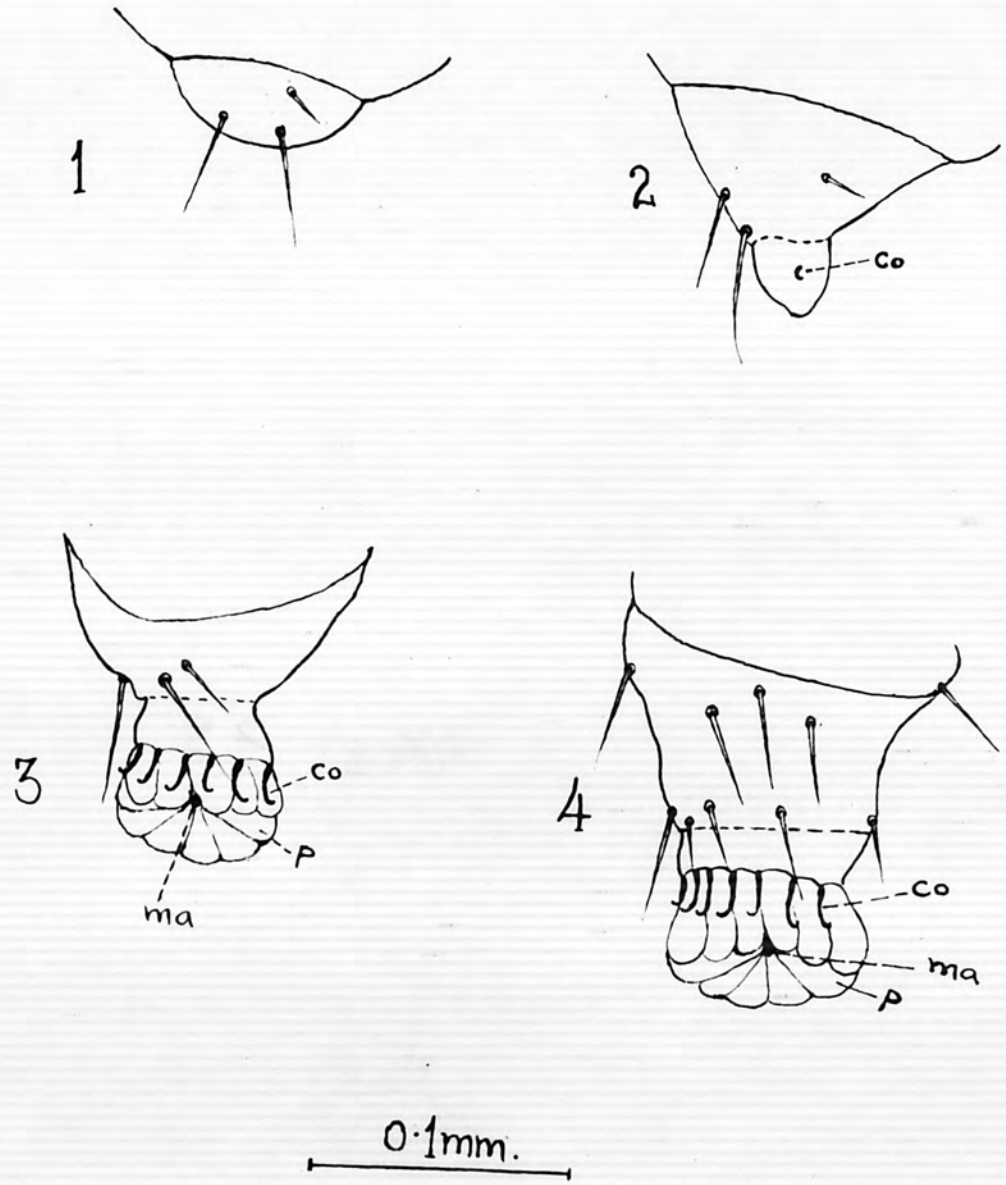

Figure 47. First larval instar

1. First proleg; 2. second proleg; 3. third proleg; 4. anal clasper.

examined were :

1. $\frac{0}{0}$, $\frac{1}{1}$, $\frac{6}{5}$, $\frac{6}{6}$ and $\frac{7}{7}$;

2. $\frac{0}{0}$, $\frac{1}{1}$, $\frac{5}{6}$, $\frac{5}{5}$ and $\frac{8}{8}$.

b) The Prolegs of the Final Larval Instar (Fig. 48 (2-4))

All five pairs are well-developed, fleshy structures. The median prolegs measure 420 μ in length; in width they are 1050 μ at the base and 525 μ at the planta. The anal claspers are larger. Each median proleg bears 4 setae and the anal clasper 8 setae and 2 sensoria. The crochets (co) are arranged in uniordinal mesoseries on the inner side of the planta. The middle crochets are the longest (360 μ) and the outer ones the shortest (240 μ). In the centre of each planta is a minute sclerotized dark brown spot (ma) indicating the place of muscle attachment. Several folds connect the planta with the muscle attachment; these allow for retraction of the planta.

The crochet formulae for four larvae examined were :

1. $\frac{15}{18}$, $\frac{23}{22}$, $\frac{20}{\text{nil}}$, $\frac{21}{23}$ and $\frac{19}{22}$

2. $\frac{14}{15}$, $\frac{16}{17}$, $\frac{18}{17}$, $\frac{17}{17}$ and $\frac{20}{19}$

3. $\frac{16}{19}$, $\frac{20}{19}$, $\frac{22}{20}$, $\frac{20}{23}$ and $\frac{21}{21}$

4. $\frac{15}{17}$, $\frac{18}{19}$, $\frac{20}{19}$, $\frac{20}{20}$ and $\frac{20}{20}$

The Spiracles

The spiracles of the first larval instar are circular in form. They are pale in colour, with light yellowish-brown peritremes and white lips. The spiracles of the prothorax and the 8th abdominal segment

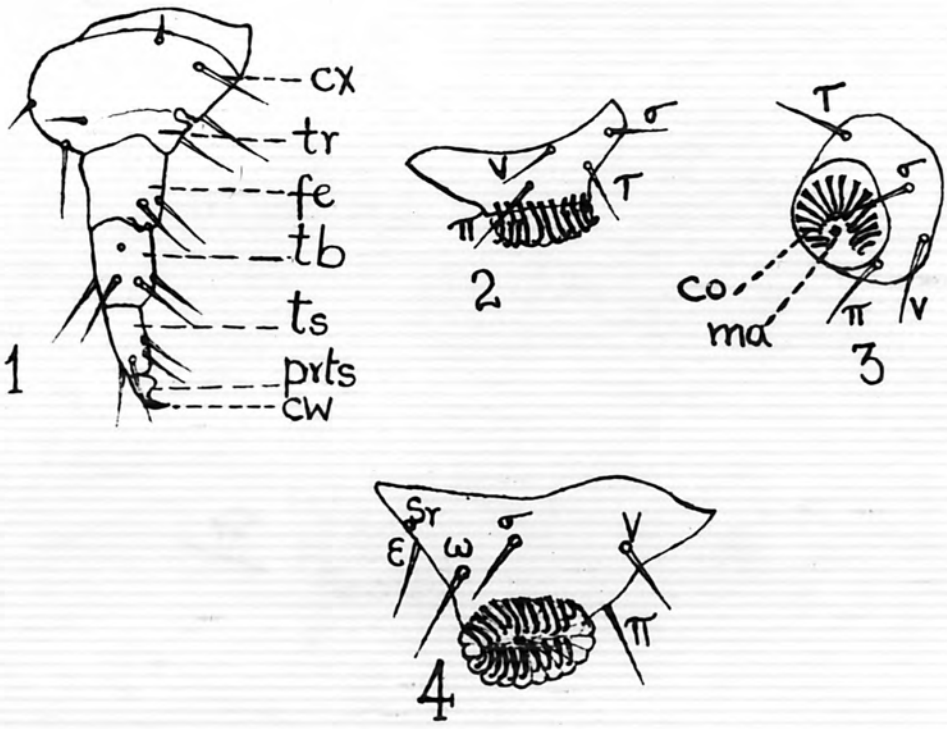

Figure 48. Final larval instar

1. Prothoracic leg (posterior); 2. Median proleg (lateral);
3. Median proleg (Apical); 4. Anal clasper (median)

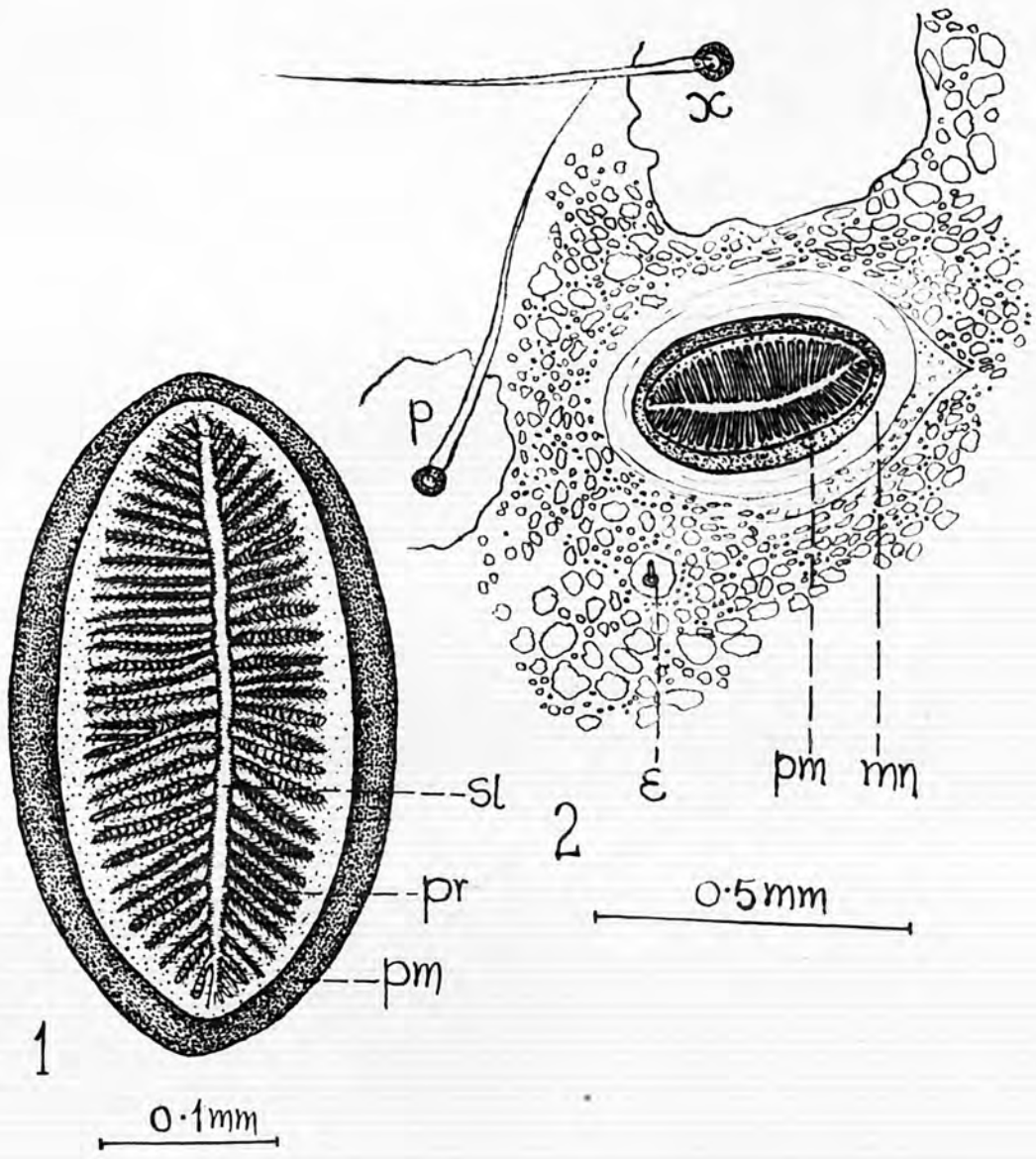

Figure 49. Final larval instar

1. spiracle; 2. part of cuticle with spiracle.

are the largest, measuring about 20 μ and 15 μ in diameter respectively. Other spiracles present on the 1st to the 7th abdominal segments, are about 10 μ in diameter.

The spiracles of the final larval instar (Fig. 49) are elliptical in shape. Those of the prothorax and the 8th abdominal segment are the largest, measuring about 490 μ in length and about 245 μ in width. The intermediate spiracles are smaller. Each is provided with a sclerotized dark-brown peritreme (pm) and inner fringed brown lips (pr). Though most of the fringed processes reach the inner margin of the lip, a few fail to do so. They are united by brown sclerotized rod-like connections. They bear minute hairs and their apical margins are finely serrated.

The Chaetotaxy

According to Fracker (1915), Ripley (1923) and Currie (1931), and others, whose system of nomenclature is here followed, three types of setae have been recognised :-

1. The primary setae borne on setiferous tubercles which are definite in number and position in all instars.
2. The secondary setae which have no fixed positions.
3. The subprimary setae which, though borne on setiferous tubercles having constant positions, are distinguished from primary setae by not being present in the first larval instar.

The chaetotaxy of the head and body segments of first and final instars was studied from a comparative point of view.

The chaetotaxy of the head.

The chaetotaxy of the head of the first and the final larval instars is fundamentally alike. Whereas all the setae on the head of the final instar are simple, most of those of the first instar are clavate.

(a) the dorsal surface (Figs. 38 (2), 39 (1)). The occiput has three minute setae, O_1, O_2 and O_3, - with a sensorium, so, between O_1 and O_2. On the vertex are 8 setae, V_1 to V_5 and V_7 to V_9, and 4 sensoria, - SV_1 between V_1 and V_2, SV_2 between V_2 and V_3, SV_3 between V_2 and V_4 and, SV_4 between V_4 and V_9. In the adfrontal region there are 2 setae, - A_1 and A_2, - with a sensorium (ads) between them. In the first instar, however, as the adfrontal is not differentiated, they are situated on the vertex. The frons bears distally a seta, f_1 and a sensorium, fs, on either side. The clypeus has 2 setae on either side, C_1 and C_2, on the region of the post clypeus. The labrum bears 6 setae, l_1 to l_6, with a sensorium, ls, between l_1 and l_2, on either side.

(b) The ventral surface (Fig. 41). This was studied only in the final larval instar. There are 4 large setae, V_6, V_{10}, V_{11} and V_{12}, two minute setae, V_{13} and V_{14}, and 3 sensoria, SV_5, SV_6 and SV_7.

The chaetotaxy of the body segments.

The setal maps of the body segments of the first and the final larval instars are shown in Figures 50 and 51 respectively. In the final instar, all setae are simple; in the first instar, all setae, except those mentioned in Table 39 are clavate.

Table 39.

Simple setae of body segments of first larval instar.

Segment	Setae
Prothorax	Xa, ε, η, ν, π, σ, τ, and ω.
Mesothorax	Xb, Xc, Xd, τ, ω, and σ.
Metathorax	Xa, Xb, Xc, Xd, τ, ω, and σ.
1st abdominal segment	X, ε, ω, σ, and π.
2nd & 3rd abdominal segment	X, ε, ω, σ, ν, and π.
4th to 8th " "	X, ε, ω, σ, and π.
9th abdominal segment	X, ω, σ, and π.
10th " "	All except P.

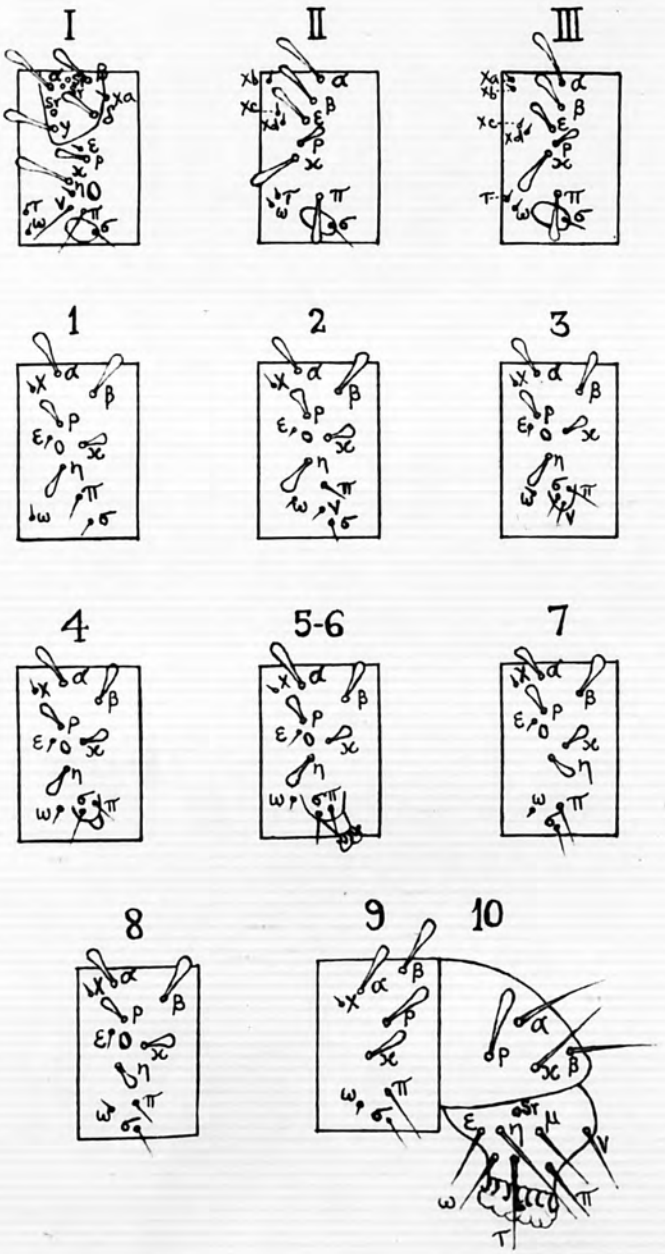

Figure 50. First larval instar
setal maps of thoracic (I to III) and abdominal (1 to 10) segments.

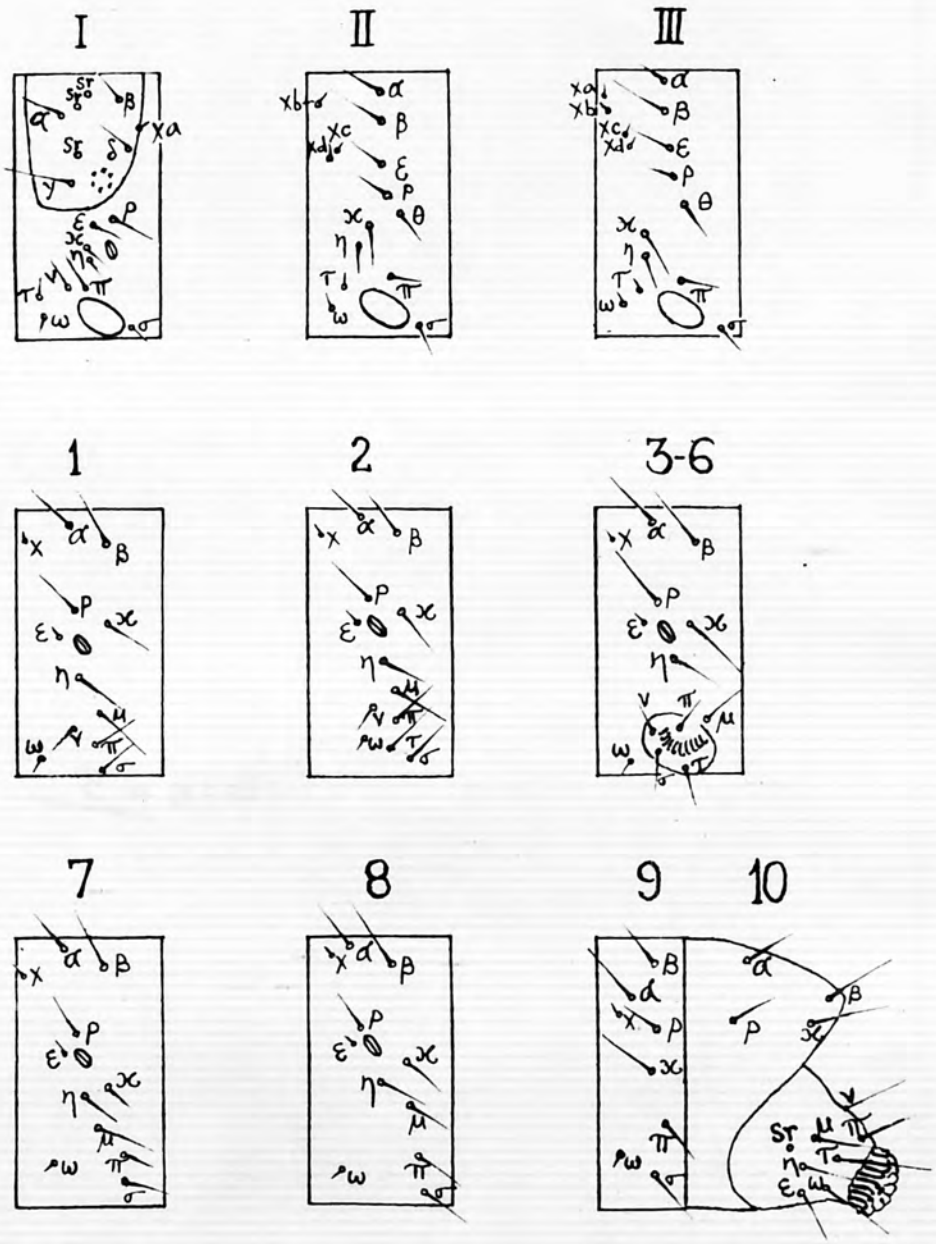

Figure 51. Final larval instar

Setal maps of thoracic (I to III) and abdominal (1 to 10) segments.

The setae present on different body segments of the first and final larval instars, together with their names are shown in Table 40. Subprimary setae are separately indicated.

Table 40

Setae of the Body Segments of the First and Final Larval Instars

Segment	Setae of 1st Larval Instar		Setae of Final Larval Instar	
	No. of Setae	Setae Present	No. of Setae	Setae Present
Prothorax	14	α, β, γ, δ, ε, ρ, ϰ, η, ν, π, σ, τ, ω, and χa (migrated from mesothorax)	14	Same as in 1st instar
Mesothorax	12	α, β, ε, ρ, ϰ, π, σ, τ, ω, χb, χc and χd.	14	All of 1st instar + θ and η (subprimary setae)
Metathorax	13	All of mesothorax + χa	15	All of 1st instar + θ and η (subprimary setae)
1st Abdominal	10	α, β, ρ, ε, ϰ, η, π, σ, ω, and χ.	12	All of 1st instar + μ and ν (subprimaries)
2nd Abdominal	11	All of the 1st abdominal segment + ν	13	All of 1st instar + μ and τ (subprimaries)
3rd Abdominal	11	-do-	13	-do-
4th-6th Abdominal	10	All of the 1st abdominal segment	13	All of 1st instar + μ, τ and ν (subprimaries)
7th-8th "	10	-do-	11	All of 1st instar + μ (subprimary)
9th Abdominal	8	α, β, ρ, ϰ, π, σ, ω and χ.	8	All of 1st instar
10th Abdominal	12	α, β, ρ, ϰ, ε, η, μ, ν, π, τ, ω and σ[1].	12	All of the 1st instar

1. σ , located medially on the anal clasper, is not shown in the setal maps. It is shown in Fig 48 (4).

Note : In addition to the setae, there are in both instars, three sensoria on either side of the prothoracic shield, and two on the anal claspers (an outer and a middle one).

2. THE IMAGO

I. The Head (Fig. 52.)

The head is more or less globular. The epicranial suture (es) runs transversely just in front of the antennal bases; posterior to it are the well defined vertex (v) and occiput (O). The post occiput (po) is a small triangular sclerite. Anterior to the epicranial suture is the fronto-clypeus (f.c.) which is formed by the fusion of the frons and the clypeus. It occupies practically the entire region of the "face". The genae (ge) are small and narrow, situated on either side of the fronto-clypeus below the compound eyes. The post genae are situated behind the genae.

A pair of prominent ocelli (oc) are present on the vertex behind the antennal sclerite (a.s.) and close to the compound eyes. Each ocellus is dome-shaped, 0.175 mm in diameter and dark brown in colour except centrally where it is colourless.

The compound eyes are globular structures, situated one on either side of the fronto-clypeus. Each eye is formed of several hexagonal facets (Fig. 54 (2)) all of uniform size. Each eye has a dark-brown circular inner disc. Externally, it is greyish-white with several small black spots.

The antennae are composed of eighty or more segments. The scape is the thickest. The pedicel, is about half as thick as the scape. The remaining segments comprise the flagellum which gradually tapers to a fine point. The entire antenna is 12 mm in length. In

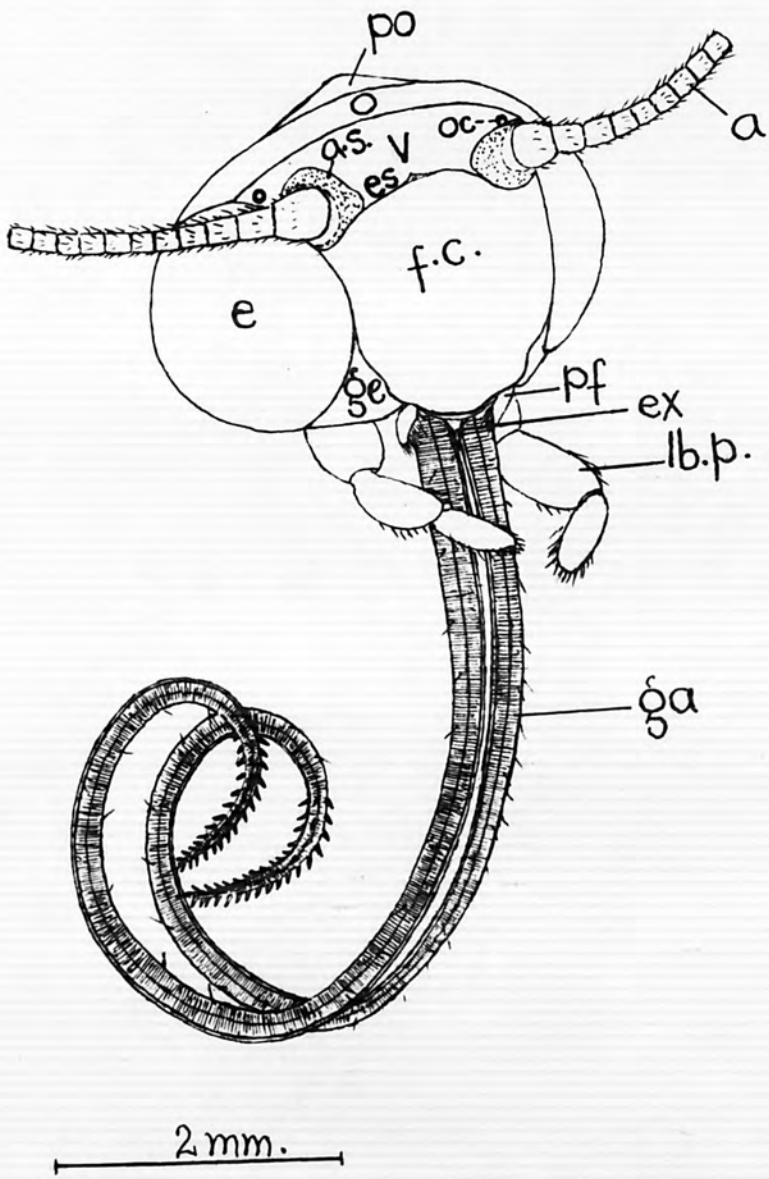

Figure 52. Imago - Head

the female the antennae are ciliate (Fig. 52). In the male they are bipectinate (Fig. 55 (2)) with processes only on the basal two-thirds; the apical third is ciliate. The processes of the basal segments are small, and gradually increase in length over the basal sixth of the antenna. The largest are situated between 3 and 4 mm from the base. Between 5 and 8 mm from the base they again gradually diminish in length and are wanting on the distal third. The processes bear dense prominent hairs on their surfaces. The longest are situated at the tips of the processes. Each antenna is situated just behind the transverse epicranial suture near the compound eye and in front of the ocellus in a socket (Fig. 54 (3), a.so.), surrounded by the antennal sclerite (a.s.)

The Mouthparts (Figs. 53 ; 54 (1)).

The labrum (Fig. 53 (3), 1) is a slender transverse piece entirely concealed by the hoodlike fronto-clypeus. The lateral, rounded pilifers (pf) and the median, pointed epipharynx (ex) project beyond the anterior margin of the fronto-clypeus. Mandibles are wanting.

Each Maxilla (Fig. 53 (2)) consists of a small, basal, triangular cardo (c) and a distal large elongate stipes (s). The latter bears on its outer side a reduced maxillary palpus (mx.p) and distally a reduced lacinia (lc) which is more or less fused with the base of the long galea (ga). The maxillary palpus is very short and is two-jointed. The first segment is minute. The terminal segment is comparatively large and rounded, and nearly as thick as the whole length of the palpus. It is haired distally. The two long tubular galeae form the proboscis. Each galea is a hollow tube channelled along its inner face and interlocked with the other galea by special hooks (Fig. 54 (1), h) on its

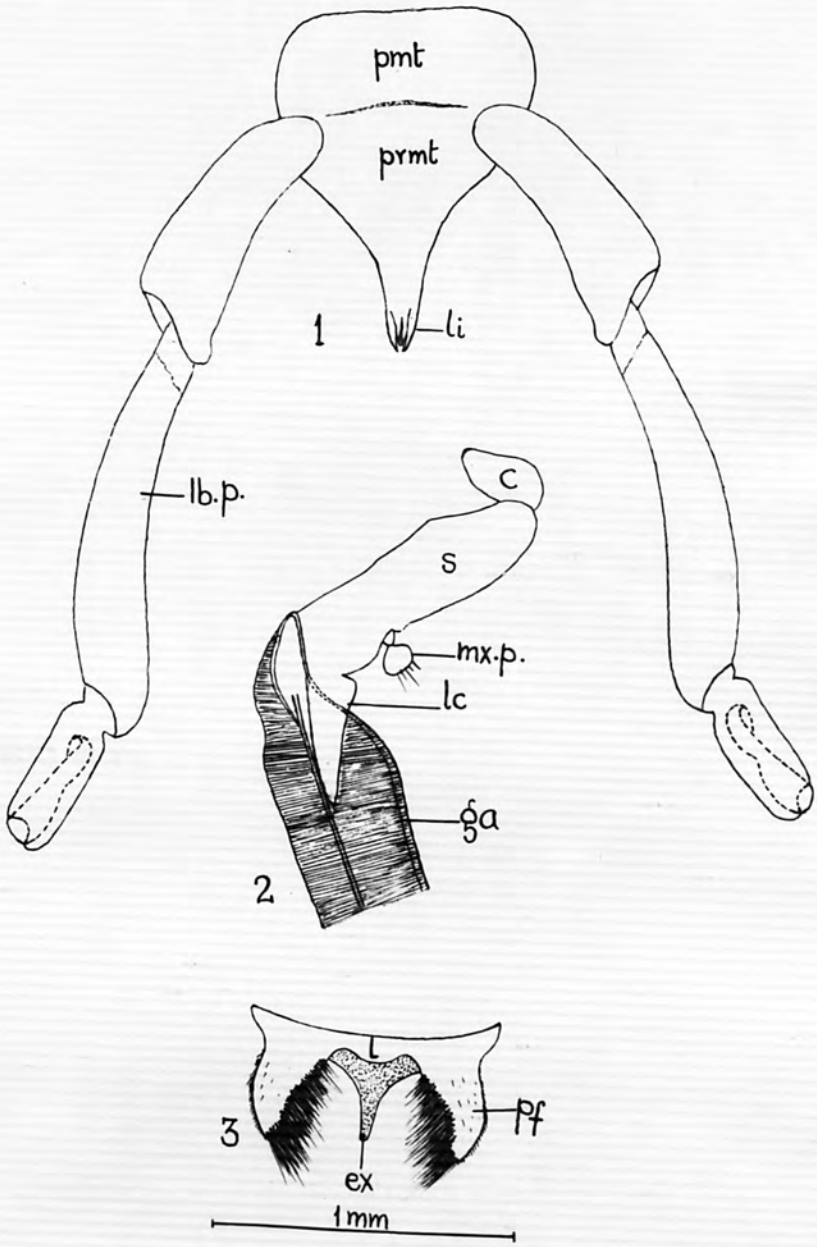

Figure 53. Imago - Mouthparts :
1. labium (ventral); 2. base of maxilla (median);
3. labrum - epipharynx (dorsal).

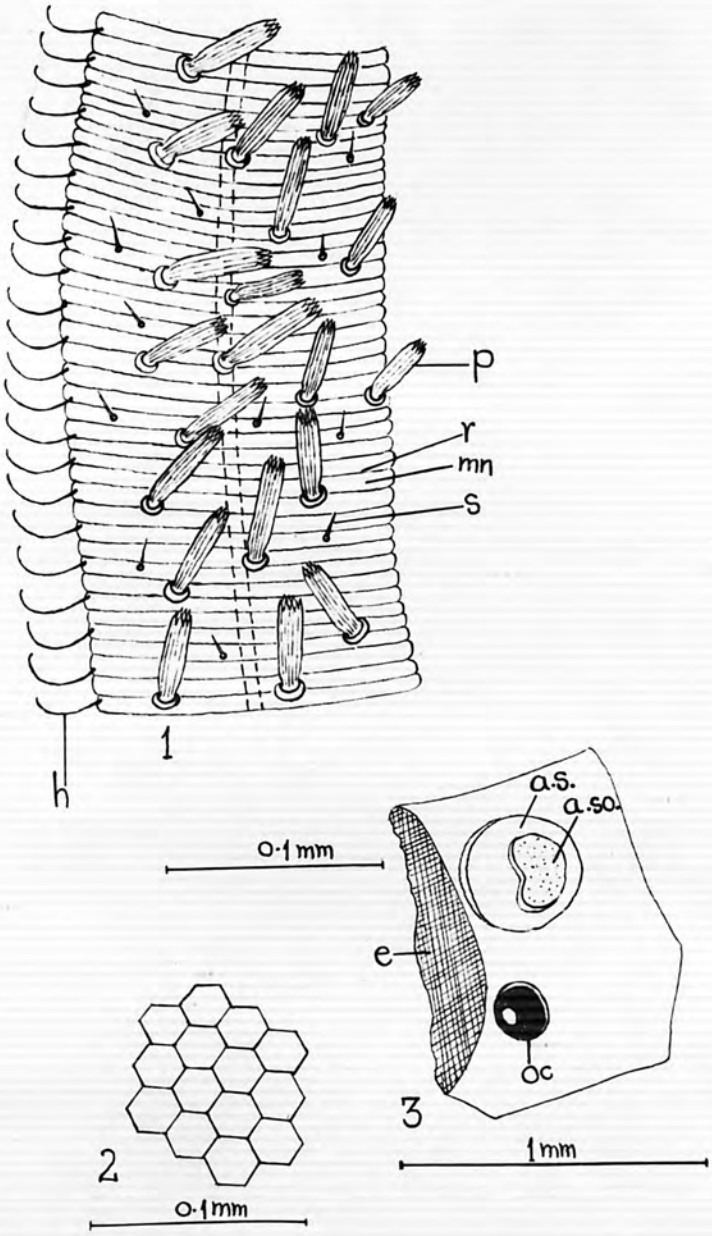

Figure 54. Imago
1. distal part of galea; 2. part of compound eye; 3. part of head.

inner face. Dorsally the galea is raised mid-longitudinally and slopes on either side. Throughout its length, it is formed of numerous deep brown sclerotized rings (r) connected by thin membrane (mm).

Two types of setae are present on the galea: simple unmodified setae which are sparsely distributed all over it, but especially on the outer surface, and highly modified papilla-like setae (p) which are situated only on the terminal two millimetres of it. These specialised setae are scale-like; they are longitudinally ridged, and their distal ends are notched. The base of each maxilla is situated on either side of the labium; these together occupy the whole ventral surface of the head.

The labium (Fig. 53 (1)) consists of a broad, basal post-mentum (pmt), and a distal tapering pre-mentum (prmt). The ligula (li) is imperfectly differentiated into paraglossae and glossae. The labial suture is distinct. The labial palpus is three-segmented, its 1st, 2nd and 3rd segments being, respectively, 0.7, 1.05 and 0.6 mm in length. The two palpi are upturned in front of the head, one on either side of the proboscis, and are held close to each other. The third segments of the palpi are directed forwards, and each contains an eversible sac.

The Endoskeleton of Head (Figs. 55 (1-2)).

The endoskeleton or the tentorium is ⋎-shaped and formed of two sclerotized yellowish brown apodemes. Each of its anterior arms (at) is invaginated from the slight concavity behind the pilifer, on either side of the fronto-clypeus. They are the longest arms of the tentorium. Each widens considerably at the middle. Just behind the median

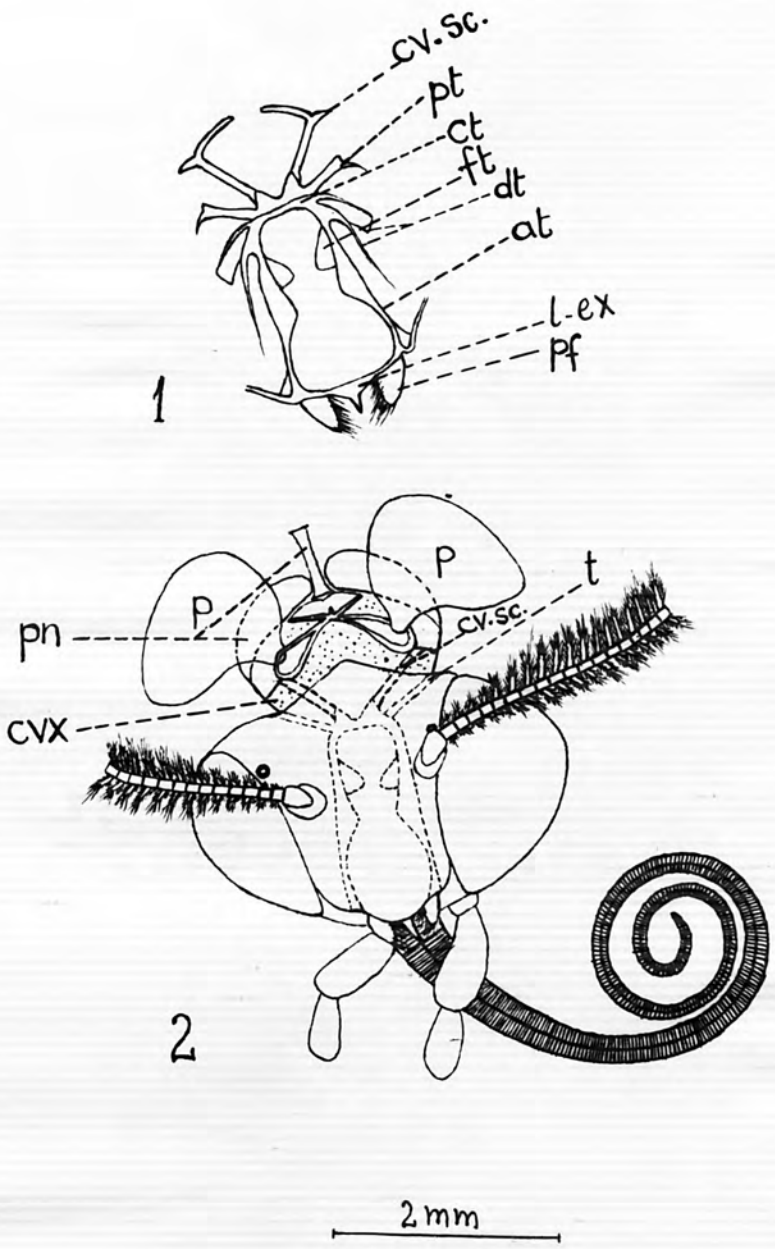

Figure 55. Imago

1. Tentorium - labrum epipharynx - cervical sclerites.

2. Head, cervix and prothorax (dorsal).

expansion of each anterior arm is a triangular plate like projection (ft). These plates seem to be remnants of the frontal plate of the tentorium in generalized insects. The dorsal arms (dt) arise from the sides of the corpotentorium and extend dorsally to the antennal bases and the compound eyes. The posterior arms (pt) are shorter than the anterior and are formed by the invaginations from the lower ends of the post-occipital suture. The corpotentorium (ct) is formed by coalescence of parts of the anterior, posterior and the dorsal tentorial arms. It is slender, and its posterior margin bears two prominences to which are secondarily attached the cervical sclerites (cv.sc.). The corpotentorium and the posterior arms run transversely dividing the occipital foramen into two parts.

The Cervix (Figs. 55 (2), 56 (5), cvx).

The cervix is the slender membranous intersegmental membrane uniting the head with the prothorax. It is well developed. On either side of it is a deep brown, sickle-shaped sclerite (Fig. 56 (5), cv.sc.) formed by fusion of the two lateral cervical sclerites. The cervical sclerite shows further specialization by the fusion of its anterior end with the posterior prominence of the corpotentorium. Each consists of a straight, anterior horizontal bar, and a transversely placed slightly-curved posterior bar, which articulates above with the episternum and below with the sternum of the prothorax. This cervical sclerite serves as a fulcrum between the head and the thorax. To it are attached the muscles which control movements of the head.

II. The Thorax (Figs. 55 (2), 56, 57).

The prothorax (Figs. 55 (2), 56 (1,5)) is the smallest segment of the thorax being narrow and collar-like. Anterior to the slender pronotum, in the membranous region, are situated a pair of cup like depressions bounded by narrow sclerotized margins. In these fit the short, rounded elongations of the patagia (p). The latter are well developed, flat, lobed, erectile structures. They are inclined posteriorly and laterally. The pronotum is extended posteriorly in the form of a narrow stalk concealed by the anterior margin of the mesonotum. A narrow dorsolateral sclerite, on either side, is the epimeron (Fig. 56 (5), epm1), which is located behind the patagia and articulates with the posterior margin of the upper part of the episternum (epsl). The episternum is situated below the patagia. It articulates with the prothoracic leg ventrally, and the sternum and the cervical sclerite anteriorly. The first thoracic spiracle is well developed and is situated behind the epimeron in the intersegmental membrane.

The mesothorax (Figs. 56 (2), 57) is the largest of the thoracic segments. Its tergum (Fig. 56 (2)) is very large and convex, and is differentiated into a narrow bandlike prescutum, a large scutum and a rhomboidal scutellum. The prescutum is concealed under the anterior part of the scutum. The scutum (S_1) is the largest tergite of the mesothorax. Its anterior margin is smooth and rounded and the posterior is concave. It has two longitudinal subdorsal sutures demarcating the lateral parts of the scutum which bear the tegular plates (t.p.) for the

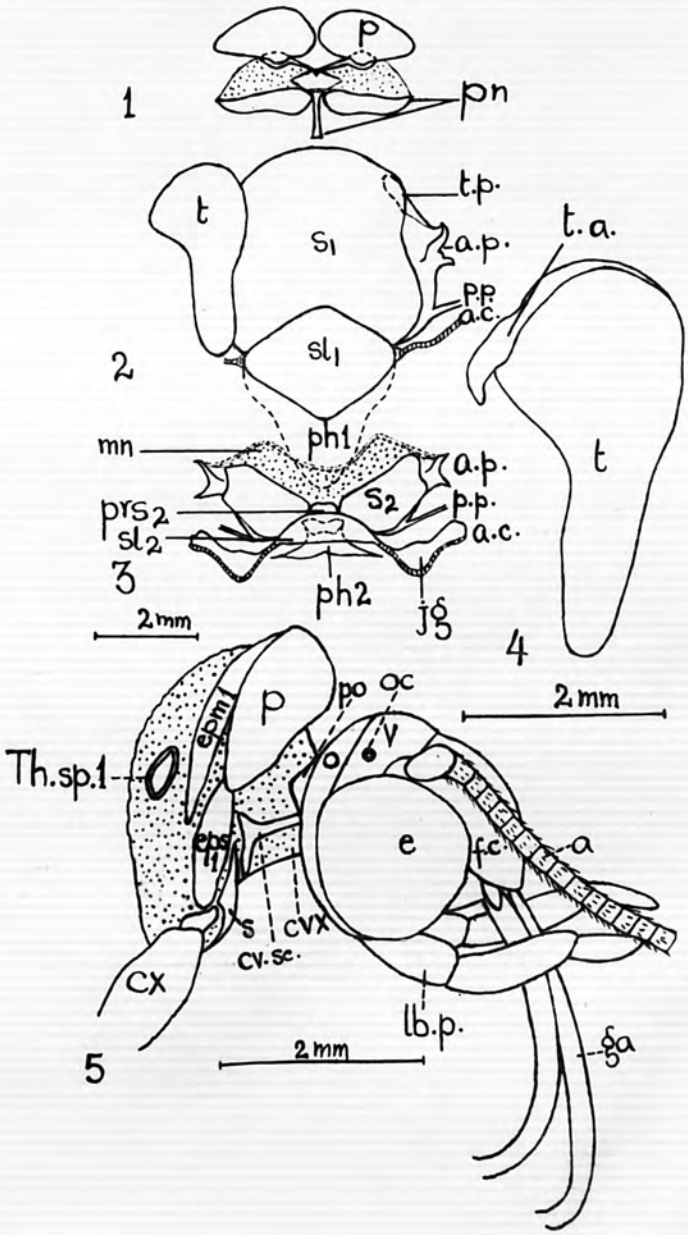

Figure 56. Imago

1 - 3. The three thoracic segments (dorsal); 4. tegula (median); 5. head cervix and prothorax (lateral).

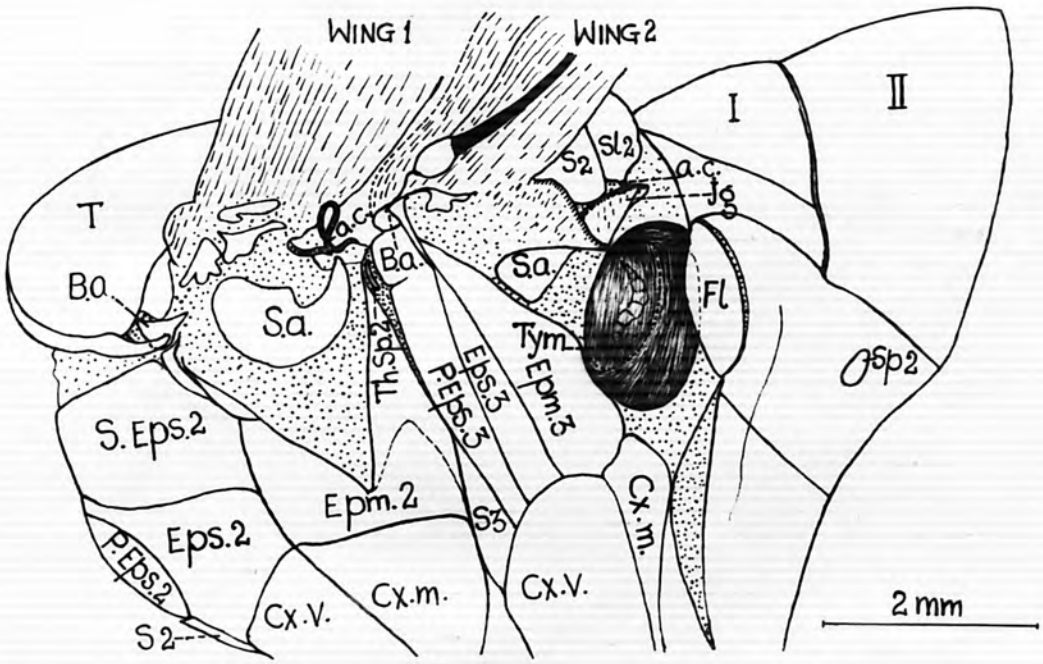

Figure 57. Imago
Pterothorax and "base" of abdomen (lateral).

attachment and support of the tegula (t), and the anterior and posterior notal wing processes (a.p. ; p.p.). The scutellum (sl_1) is a convex lobe jutting anteriorly into the concavity of the scutum and extending posteriorly to the emargination of the meta-tergum. On either side, it bears the axillary cord (a.c.) which bounds the posterior margin of the membranous wing base. Behind the scutellum is a large triangular sclerotized mesophragma (ph_1), that descends far down into the interior of the body for muscle attachment.

The tegulae (t) are very large, elongate structures, each supported by, and attached to, the tegular plate (t.p.) of the mesonotum. Each is further supported from below by the tegular arm (t.a.), which is attached to the antero-ventral margin of the tegula. The tegular arm extends postero-ventrally in the form of an inwardly-curved process that rests on the base of the pleural wing process. The tegula is placed longitudinally on the lateral region of the mesoscutum overlying and protecting the basal articular area of the forewing. It is broader at the anterior end, and elongate posteriorly. Both its ends are rounded. Posterior to its widest region the inner margin is slightly concave at the middle and the outer margin more so.

The <u>mesopleuron</u> (Fig. 57) consists of a well developed episternum (Eps.2) and epimeron (Epm.2.). A broad upper, and a narrow, anterior part of the episternum are differentiated by secondary sutures into the supra-episternum (S.Eps.2.) and the pre-episternum (P.Eps.2.). The epimeron is deeply notched. Above it is the well-developed membrane containing the large, more-or-less crescentic subalare (s.a.). The upper end of the pleural suture is produced to form the pleural wing----

process posterior to the supra-episternum. Above and slightly anterior to the pleural wing process is the small basalare (B.a.). The Mesosternum (S_2) is the largest of the thoracic sterna. It is narrow between the coxae but anterior to these it widens and extends in front of the lower part of the episternum. In the narrow membranous region between the upper parts of the epimeron of the mesothorax and the episternum of the metathorax lies, somewhat concealed, the second thoracic spiracle (Th.sp.2).

The metathorax (Figs 56 (3), 57) is much smaller than the mesothorax. Its tergum (Fig. 56 (3)) is anteriorly emarginate and fits snugly against the rhomboidal mesothoracic scutellum. A delicate membrane (mm), which lies concealed under the posteriorly extended mesoscutellum, connects the two together. The prescutum (prs 2) is very small and slender, lying between the bases of the scutum, and concealed under the median posterior part of the meso-scutellum. The scutum (S_2) is divided into two broad oblique plates fitting closely to the meso-scutellum. Apically, it bears the anterior notal wing process (a.p.) and posterolaterally, the posterior notal wing process (p.p.). The metascutellum (sl_2) is a median sclerite with a rounded anterior margin which supports the scutum on either side of the prescutum. Its posterior margin is straight. Laterally, it bears the axillary cord (a.c.), which, posteriorly, bounds the jugal lobe (jg) of the hind wing. A short but broad metaphragma (ph_2) is invaginated into the body from the middle of the metascutellum. The metapleuron (Fig. 57) consists of a narrow elongate episternum (Eps.3) and epimeron (Epm.3). The anterior part of the episternum, differentiated by a secondary suture, is known as the pre-episternum (P.Eps.3.). Above the epimeron and

lying behind the pleural wing process in the membrane is the large triangular subalare (s.a.). Above the episternum and just in front of the pleural wing process, is the small rectangular basalare (B.a.). The metasternum (S_3) is similar to the mesosternum but is comparatively smaller. It is represented by a narrow posterior strip between the coxae and the wider anterior part lying in front of them and the episternum. The tympanal organ (Fig. 57, Tym) is a well developed cavity, situated in the large membranous region of the metapleuron behind the epimeron (Epm.3.) and below the subalare. It is oval in form and measures 1.7 mm long and 1.4 mm wide. Posteriorly, it is partly covered with a flap (Fl), the tympanal operculum, which is attached to the anterior margin of the pleuron of the first abdominal segment. It is differentiated into a shallow sclerotized posterior part and a membranous deeper anterior part. In the deeper membranous part is a spindle-shaped structure, which lies just under the integument. Because of a series of swellings, it appears segmented. It possibly represents Müller's organ (Imms, 1948) which forms the termination of the auditory nerve.

Thoracic appendages

Each thoracic segment bears a pair of legs (Fig. 58)

The coxa (cx) is attached by a fine membrane, the coxal corium, to the pleuron and the sternum of the segment. The coxa of the foreleg is freely-movable (Fig. 56 (5), cx), but those of the mid and hind legs are so embedded in the pleural and sternal regions (Fig. 57) as to have little mobility. Greatest freedom of movement is at the coxo-trochanteral joint where there are two articulations. The anterior one consists of a small coxal condyle and a socket in the trochanter. The posterior

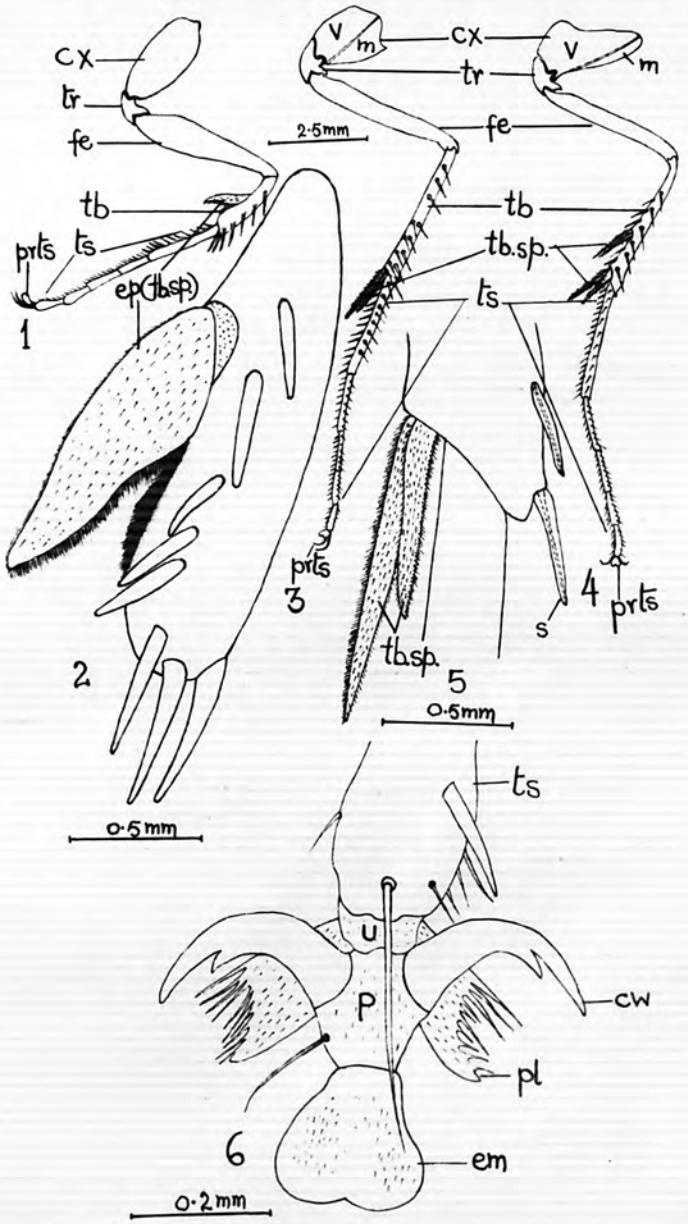

Figure 58. Imago

1. 3. and 4. Fore, mid, and hind legs; 2. fore tibia; 5. enlargement of distal part of hind tibia showing tibial spurs; 6. pre-tarsus (dorsal).

one consists of a prominent condyle on the trochanter and an equally prominent coxal socket. The coxa of the foreleg is elongate, simple and undifferentiated in structure. Those of the mid and hind legs are conical and thickset; each is differentiated, by a longitudinal suture, into an anterior, coxa vera (cxv), and posterior, coxa meron (cxm).

The trochanter (tr) is the smallest leg segment. It is somewhat wider at the distal end. The trochanter of the foreleg is smaller than those of the others which are about equal in size. Proximally, the trochanter articulates with the coxa. Distally, it has an emargination into which fits the slender proximal extremity of the femur.

The femur (fe). The femora of the fore, mid and the hind legs measure about 3 mm, 5 mm and 4 mm in length, respectively. They are devoid of characteristic setae which are present on the lower parts of the legs.

The tibia (tb). The fore-tibia is the smallest of the three, being about 1.75 mm long. It is slightly broader at the distal end, and bears two rows of stout spines, about 7 or 8 in each row. Those near the distal end are stouter and longer than those towards the femur. A prominent leaf-like structure, the epiphysis (ep) is attached by a membranous base to the inner side of the tibia about midway along it. It seems to be a modified tibial spur. It takes the form of a double walled pocket, which is closed and somewhat convex above, but open and concave below. Distally, it tapers to a point. Its lower margins, bounding the open pocket, are provided with a conspicuous fringe of setae. The outer wall of this structure is deep brown but the inner is much paler being yellowish-white. The part of the tibia immediately beneath this structure is provided with a thick pad of black scales. The tibia of the middle leg

measures about 4 mm in length. Its spines, which are arranged in two rows of eight, are somewhat smaller and finer than are those of the fore-tibia. A pair of stout spurs of unequal length are borne distally on its anterior surface. The spurs, themselves, bear several minute hairs. The tibia of the hind leg is the longest of the three, measuring about 5 mm in length. It bears two rows of spines and two pairs of spurs on its anterior surface. The upper apir of spurs are borne at about 3 mm from the proximal end, and the second near the distal end. The lower pair are somewhat smaller than the upper.

The tarsus (ts) is the longest part of the leg and is divided into 5 tarsomeres. The metatarsus of each leg is the longest of all the tarsal joints, being only slightly less than half the length of the entire tarsus. The tarsi of the fore, mid and the hind legs measure 4, 7 and 7.25 mm in length, respectively. Each bears several small spines arranged in four longitudinal rows.

The pretarsus (Fig. 58 (6)). Just below the last tarsal segment is a small proximal plate, the unguitractor plate (u) to which is attached a larger sclerite, the planta (P), which bears a pair of lateral claws (cw) and median pad-like empodium (em). A pair of leaf-like pulvilli (pl) arise from the unguitractor plate below the claws, which are curved and sickle-shaped. Each claw is bifid, having a minute tooth at about two-thirds of its length from the base. The distal margin of the empodium is weakly emarginate. The distal margin of each pulvillus is produced into a fringe of about 10 slender processes. Both empodium and the pulvilli are provided with many minute tenant hairs.

The wings (Figs. 59, 60). The forewings are narrow and elongate about 17-20 mm in length and 8-10 mm in width at the distal end. The hind wings are relatively shorter and broader, being about 13-16 mm in length and about 11-14 mm in width across the outer margin. The wings are very narrow at their attachments. Each is connected to the notum of the segment by the anterior and posterior notal wing processes between which and the wing are three sclerotized articulatory sclerites. These articulate between themselves, the notal wing processes and the hardened bases of the wing veins. The membranous wing-base is strengthened by its thickened hind margin, the axillary cord (Fig. 56 (2-3), a.c.), which is attached to the scutellum of the segment. The base of the hind wing is posteriorly produced as a lobe, the jugum (Fig. 56 (3), jg). Ventrally, each wing is supported on the pleural wing process and articulates with the larger subalare and the smaller basalare.

Wing-venation. The venation of both wings is more or less similar. In discussing the venation, the Comstock - Needham system as used by Tillyard (1926) is adopted here.

In the forewing (Fig. 59), the following veins are present : Sc; R_1; R_2; R_3, R_4; R_5; M_1; M_2; M_3; Cu_{1a}; Cu_{1b}; 1A+2A and 3A.

Sc is a simple unbranched vein. R is a strong vein dividing midway into R_1 and Rs, the latter further subdividing into 4 branches - R_2, R_3, R_4 and R_5. The basal parts of R_2 and R_3, together, form the anterior boundary of the prominent areole or radial cell, and the stem of $R_4 + R_5$ formsits posterior boundary. The areole is quadrangular. R_5 is differentiated from the stem of $R_4 + R_5$ at the distal end of the areole. M and its branches are obsolete within the basal cell; they

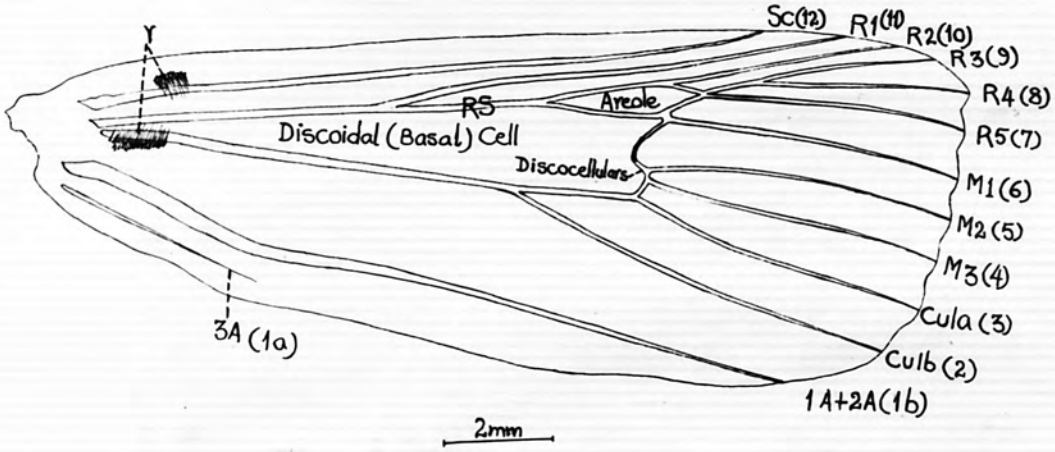

Figure 59 Forewing of female, showing retinaculum (r) and veins (named and numbered).

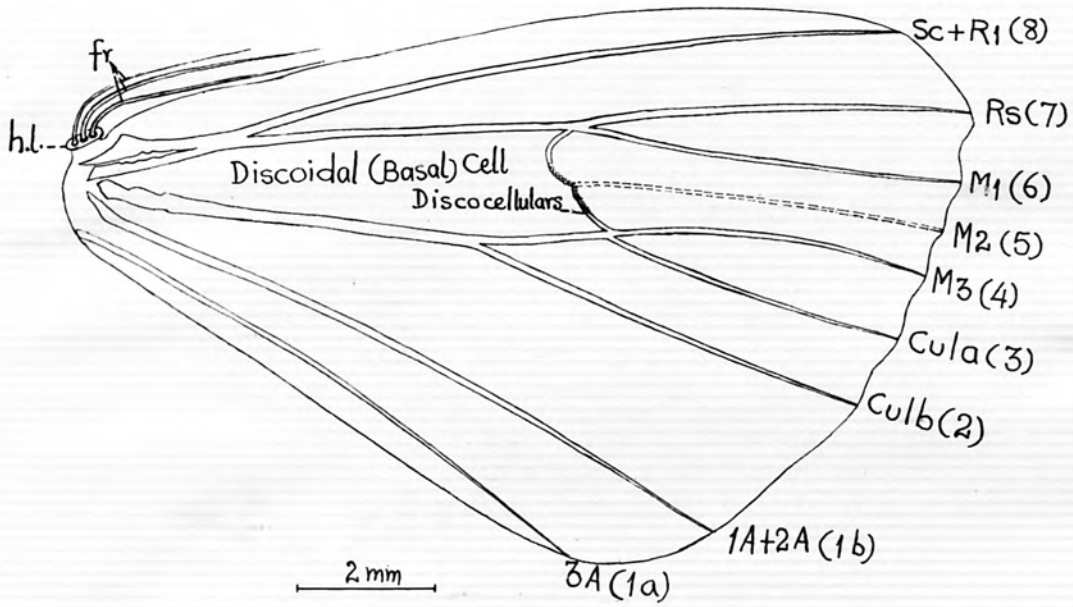

Figure 60. Hindwing of female, showing frenulum (fr) and veins (named and numbered).

are represented by three branches only - M_1, M_2, and M_3. M_4 is fused with Cu_{1a} and is represented only by a short cross vein connecting M_3 with Cu_{1a}. Cu_1 is a strong vein dividing distally into Cu_{1a} and Cu_{1b} in about the middle of the wing. The basal cell is bounded anteriorly by R, Rs and the stem of $R_4 + R_5$, distally, by short cross veins, the discocellulars, and posteriorly by Cu_1 and the basal part of Cu_{1a}. It is not completely closed basally but remains open by a very small gap where R and Cu_1 do not unite. At the middle of the discocellulars, a vein is vestigial, only the spiral taenidia being present. Cu_2 is wanting. 1A and 2A are completely fused forming a stout vein (1A + 2A). 3A is only partly developed.

In the hindwing (Fig. 60) Sc + R_1; Rs; M_1; M_2; M_3; Cu_{1a}; Cu_{1b}; 1A + 2A; and 3A are present. Sc and R_1 are fused for most of their lengths, but free basally. Rs is reduced to a simple vein without branches. M_1 unites with Rs at the upper angle of the basal cell. There is no areole. M_2 is obsolescent. Cu_1 is a stout vein, dividing into Cu_{1a} and Cu_{1b} distally at about two-thirds the distance of the basal cell from its base. M_3 unites with Cu_{1a} at the lower angle of the basal cell which is bounded anteriorly by R for a short distance at the base and then by Rs, distally by the discocellulars, and posteriorly by Cu_1 and the basal part of Cu_{1a}. As in the forewing, it is open basally. The middle of the discocellulars shows only spirally coiled taenidia. 1A and 2A are completely fused. Unlike that of the forewing, 3A is complete.

The wing-coupling device (Figs. 59, 60, 61 (1-2) consists of the retinaculum (r) in the forewing and the frenulum (fr) in the hindwing. The structure of both the retinaculum and the frenulum differs according

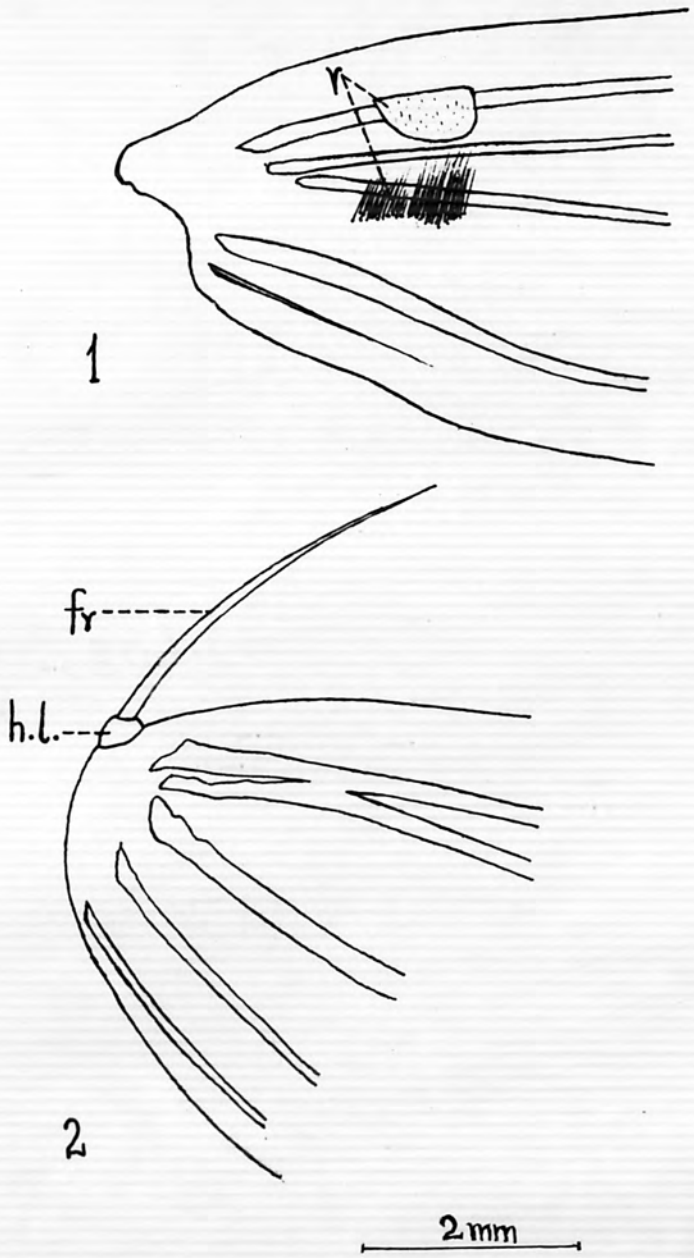

Figure 61. (1-2) Wing bases of fore and hind wings of male, showing retinaculum (r.) and frenulum (fr.)

to the sex. The retinaculum of the female (Fig 59, r) consists of two tufts of hairs on the underside of the wing. The smaller anterior tuft arises from the membrane just anterior to vein Sc and the bigger and denser tuft from the wing membrane just behind Cu_1. The retinaculum of the male (Fig. 61 (1), r) differs from that of the female in that the anterior tuft of hairs is replaced by a membranous fold or hook attached to the membrane anterior to vein Sc. Its free margin is rounded. The frenulum of the female (Fig. 60, fr) consists of 3 spines which are borne on the elliptical and narrow humeral lobe (h.l.). The two inner spines are sub-equal and relatively stouter than the outer which is smaller and finer. The frenulum in the male (Fig. 61 (2), fr) consists of a single stout spine, situated on the dome shaped humeral lobe.

III. The Abdomen.

The abdomen measures about 12-15 mm in length. Its first segment is represented by a well-developed, sclerotized narrow, tergum and a membranous, somewhat vestigial sternum which is entirely concealed by the coxae of the hindlegs. The first visible sclerotized sternum, therefore, is that of the 2nd segment. Laterally, the first segment bears the tympanal opercula (Fig. 62 (1), fl), which conceal the first abdominal spiracles. Each is more or less triangular in shape. The visible number of abdominal segments differ according to the sex. In the female (Fig. 62 (2)), seven segments are visible dorsally and six ventrally. The 8th, 9th and 10th segments, which are modified to form the female genitalia, are normally telescoped into the 7th which forms the apparent termination of the abdomen. At its posterior end, the 7th

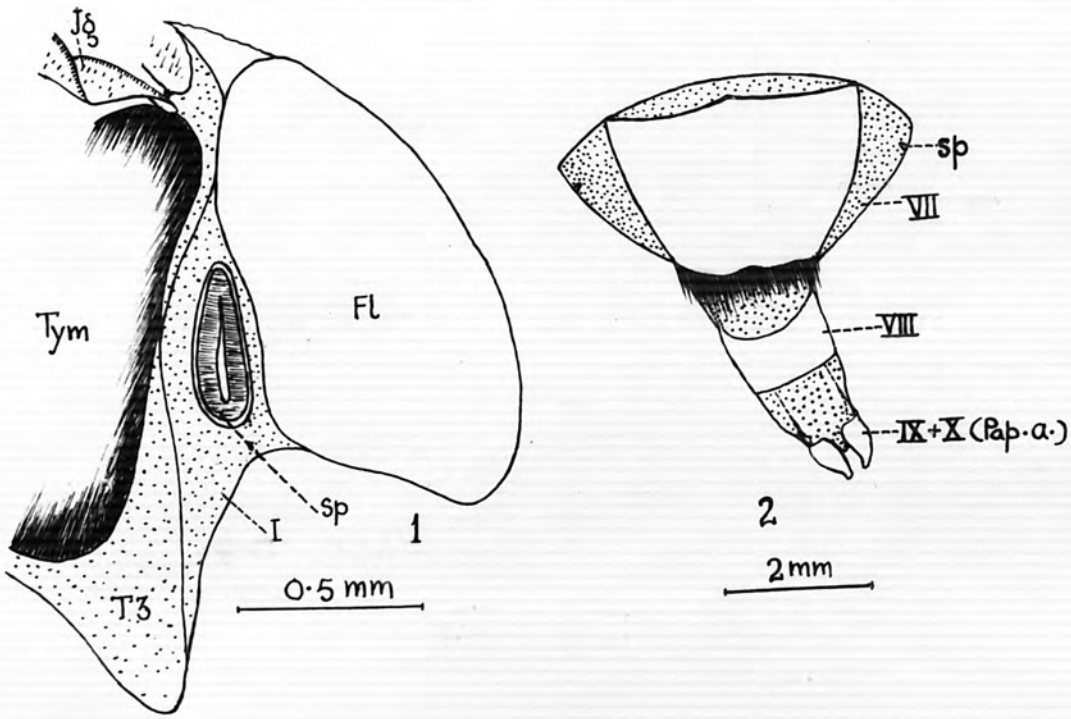

Figure 62. Imago

1. A part of tympanum on metathorax, and the operculum and spiracle on first abdominal segment. (Operculum turned back)
2. Termination of female abdomen with ovipositor extended (dorsal).

abdominal segment bears a conspicuous tuft of dense dark hairs. In the male (Fig. 67 (4), the visible number of abdominal segments is eight dorsally and seven ventrally. The last two segments, the 9th and 10th, are modified to form the male genitalia and are normally completely retracted inside the body. The caudal end of the 8th abdominal segment and the modified 9th and 10th segments bear long dense dark hairs which form tufts at the posterior extremity.

Seven pairs of spiracles are present on the first seven abdominal segments; the 8th have atrophied.

The Body Investment

More than twelve different kinds of scales are present. Those of the forewings, hindwings and the body vary greatly in shape and size (Figs. 69, 70). The greatest variety is found on the wings. On the forewings, (Fig. 69) types a - d are very common, whereas, type g is confined to the outer margins. On the hindwings, (Fig. 70 (1)) numerous unmodified hairs, (type a) are present. The commonest scales on them are types c and d which are much shorter and broader than are the scales of the forewings and their apical margins are weakly dentate. The scales on the outer margin (type b) are similar to those of the forewings. On the body (Fig. 70 (2)), a variety of scales is present. The less-highly developed scales and hairs (types c,d,e) are very common. Some very highly modified scales (types a,b,f,g) are also present. Most of the body scales are characterised by conspicuous apical fringes.

All the scales have characteristic longitudinal ridges which increase their stiffness. They are normally present only on the outer surfaces of the scales; at times, some may be present on the ventral

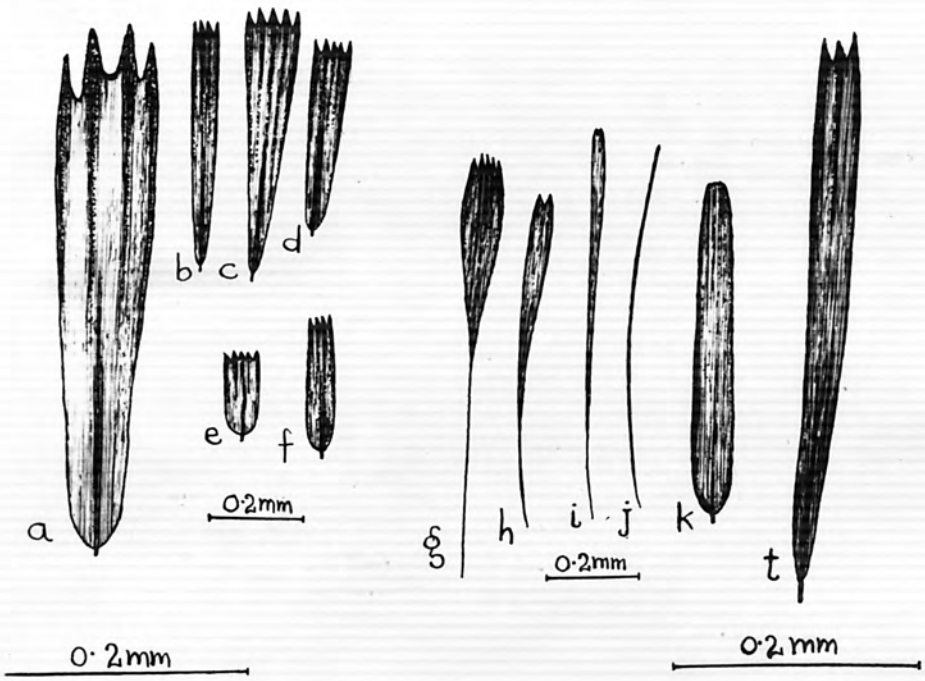

Figure 69. Investment of fore-wing.

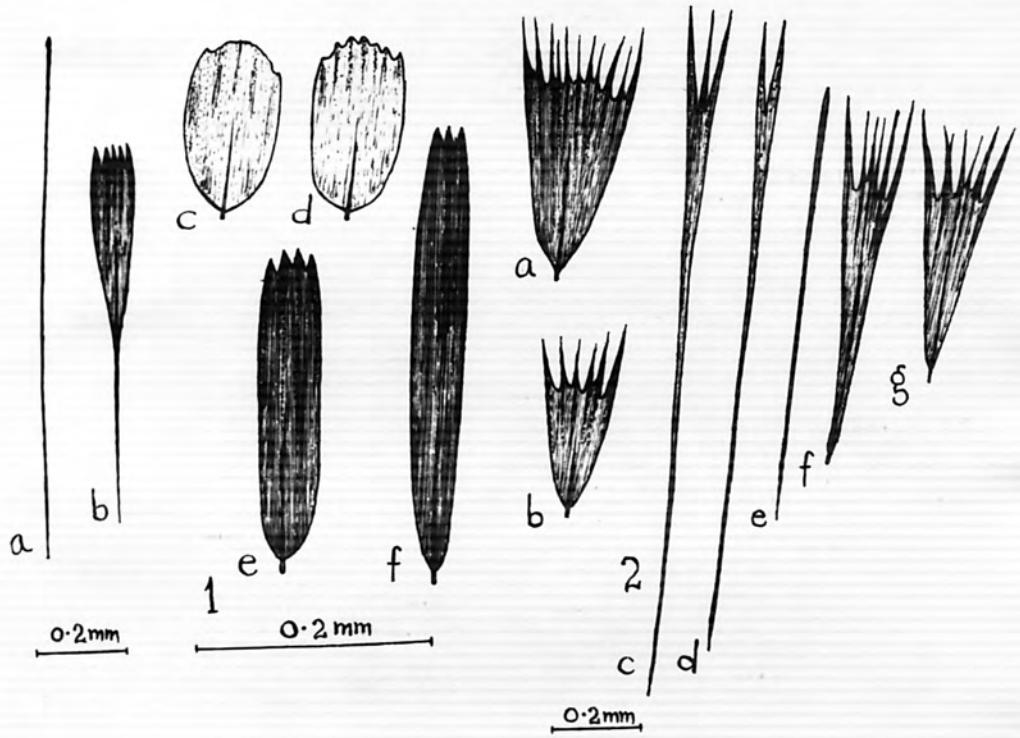

Figure 70. 1. a - f investment of hind-wing.
2. a - g investment of body.

surface (Fig. 80 (1)). All scales are provided with short fine bases for articulation with cuticular sockets.

3. THE ORGANS OF REPRODUCTION

(a) The Organs of Copulation and Oviposition.

In describing the genitalia, the nomenclature of Klots (1956), Sibatani et al (1954) and Okagaki et al (1955) is here adopted.

The Female Genitalia (Figs. 5 (a), 63 (1-2)) are of the ditrysian type which is characterized by the presence of two widely-separated reproductive openings - the ostium bursae (ob), and the oviporus or ostium oviductus (Fig. 5 (a), 71 (3), op). They are formed from the greatly modified eighth, ninth and the tenth abdominal segments. The eighth segment is distinct but the ninth and tenth are fused. The intersegmental membranes between the seventh and eighth segments, and between the eighth and the fused ninth and tenth, are very large allowing for telescoping of the segments. The eighth abdominal segment is sclerotized dorsally, laterally and lateroventrally. The midventral region is membranous. Situated midventrally on the anterior end of the eighth abdominal segment is the genital chamber or sinus vaginalis (sin.v.), which consists of a deep ingrowth of the body wall. Its receptive opening, the ostium bursae (ob), is the anterior gonopore which permits of impregnation of the female. It is situated in the intersegmental region between the seventh and the eighth abdominal sterna. The ostium bursae is bounded anteriorly by a sclerite, the lamella antevaginalis (lla), and posteriorly by a membranous plate, the lamella post-vaginalis (llp) which together comprise the genital plate. Into the ostium bursae opens the ductus bursae (db) which extends anteriorly

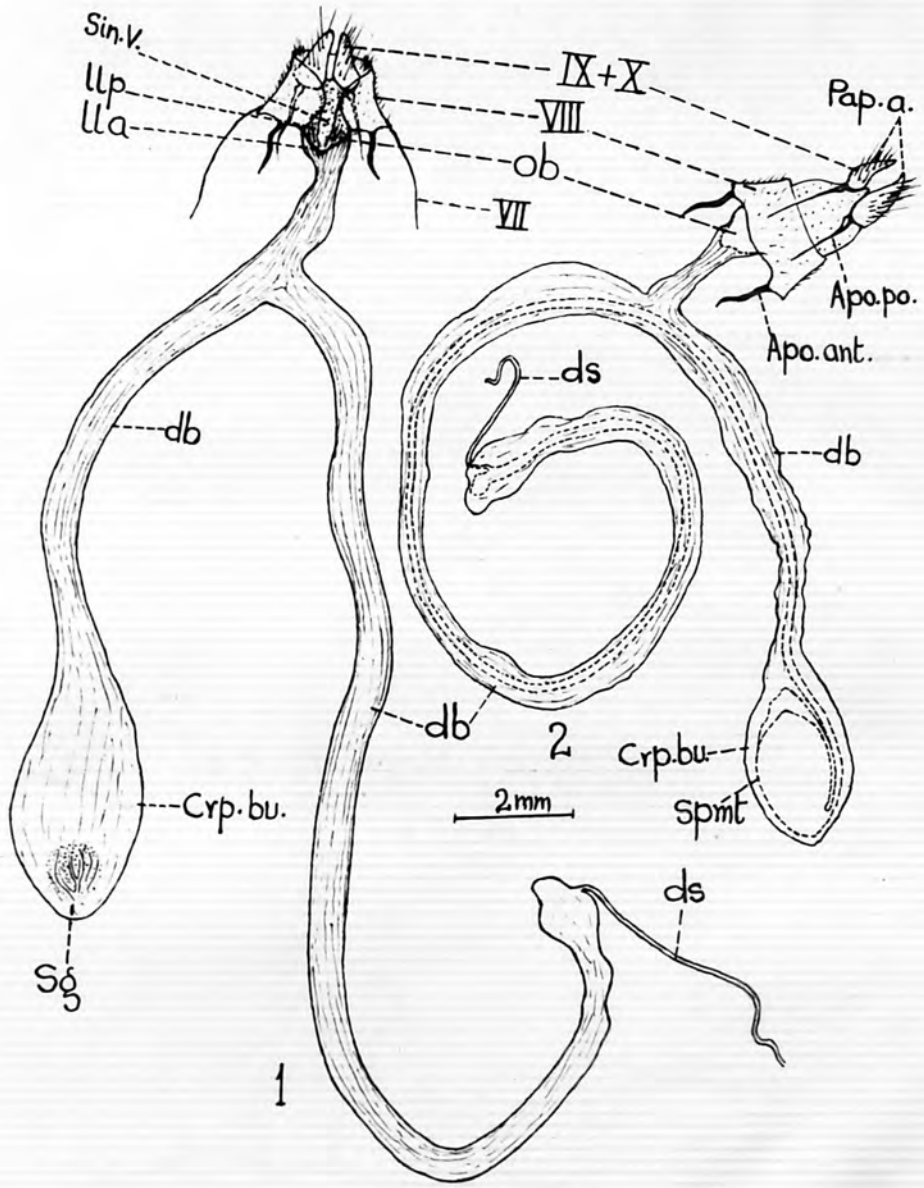

Figure. 63. Female genitalia

1. without spermatophore (ventral).
2. with spermatophore (dorsal).

within the abdominal cavity below the common oviduct. From the ostium bursae for a distance of 800 μ the ductus bursae bears numerous small conical projections (Fig. 64). A short distance from the ostium bursae, the ductus bursae bifurcates, the shorter duct leading to the corpus bursae (crp.bu.) and the longer to the ductus seminalis (ds). The ostium bursae, the ductus bursae and the corpus bursae together comprise the bursa copulatrix (Klots, 1956). The ducts leading to the corpus bursae and to the ductus seminalis are 6 mm and 20 mm in length, respectively. The ductus seminalis is thus much longer than the whole abdomen and is spirally coiled. The corpus bursae is much wider than the ductus bursae. It is sac-like and has two scobinate brown signa (Figs. 63 (1) Sg and 65 (1,3)), one much larger than the other. The larger signum (Fig. 65 (3)) is yellowish-brown with brown scobinations. It is sub-oval and has one or more irregular folds or furrows which are part of the numerous folds of the ductus bursae and corpus bursae. These folds seem to allow for expansion of the ductus and corpus bursae, to accomodate the spermatophore. The pattern of the folds on the signum varies greatly in different individuals (Fig. 66 (1-4)). The smaller signum (Fig. 65 (1)) is oval and pale yellowish-brown in colour. The brown sclerotized scobinations are not confined to the signa, but cover the entire surface of the corpus bursae. Those situated on and around the signa are more sclerotized, larger, and closer together than elsewhere. As their distance from the signa increases, they become less sclerotized, more-widely separated, and reduced in size (Fig. 65 (2)). Their apparent function is to strengthen the walls of the corpus bursae. The end of the ductus bursae, which is connected to the ductus seminalis,

Figure 64. Basal part of ductus bursae.

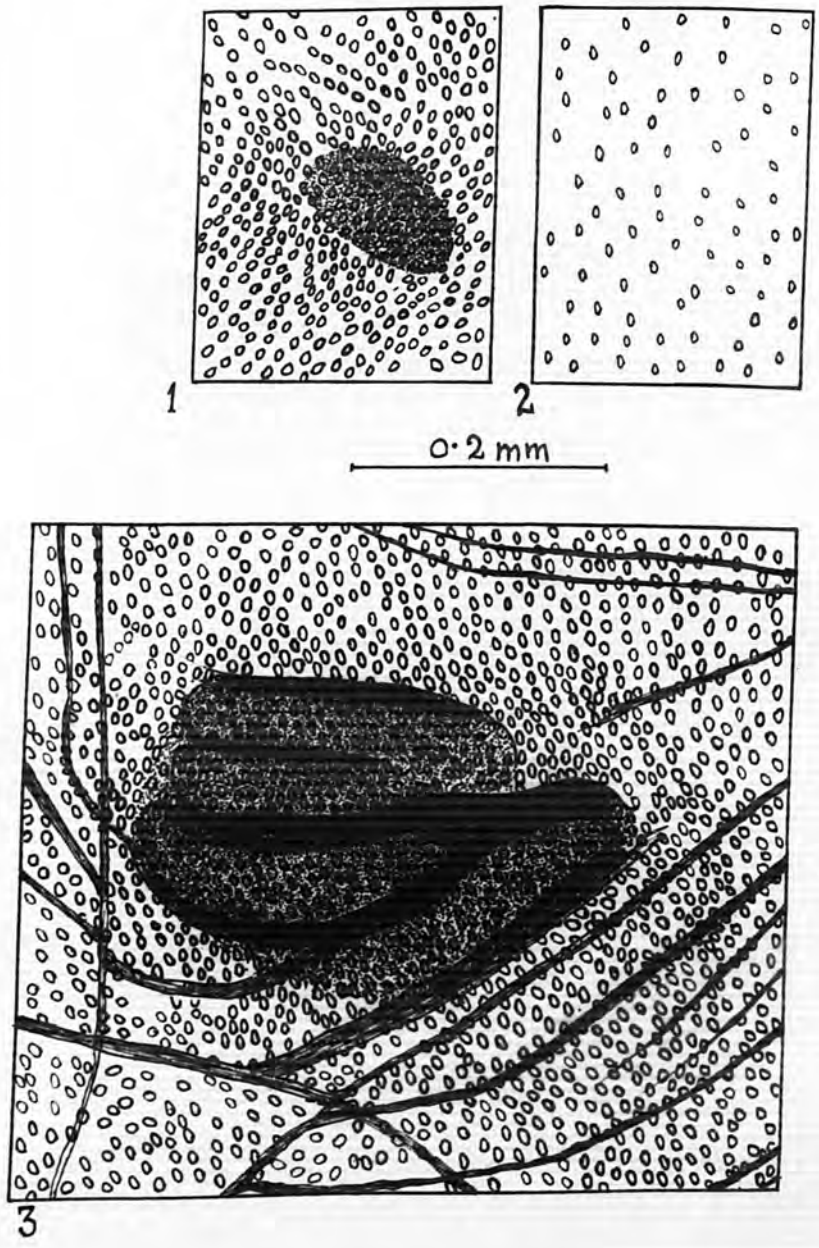

Figure 65. 1. scobinate area on and around small signum;
2. scobinations at 1200 μ from small signum;
3. scobinations and folds on and around large signum.

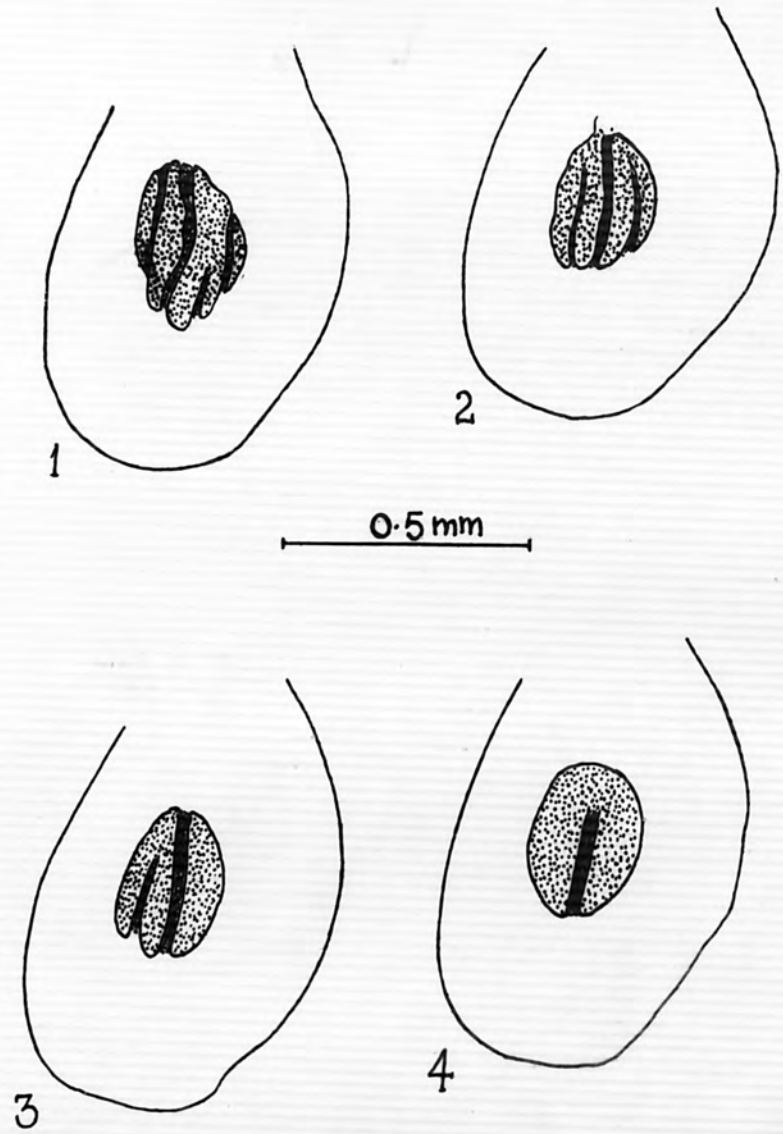

Figure 66. (1-4) Fold variations of large signum.

is slightly swollen. The ductus seminalis is very narrow and opens from the swollen end of the ductus bursae at a point near its tip.

The ninth and tenth abdominal segments are much reduced, and have fused. The most important structures of this region are a pair of soft, elongate, pointed, hairy lobes, the papillae anales (Pap.a.). Their inner margins are convex basally and concave apically while their outer margins are uniformly convex. Between these papillae is situated the anus and the oviporus (Fig. 71 (3)). From the anterior margins of the papillae, a pair of long, slender, sclerotized apophyses posteriores (Fig. 63, Apo.po.), extend into the body. Their bases are flattened to form small sclerotized plates which taper posteriorly where they are loosely attached to the anterior ends of the papillae anales. A pair of apophyses anteriores (Apo.ant.), proceed within the body from the antero-subdorsal edges of the eighth segment. These are smaller and stouter than the apophyses posteriores. They are firmly fused with the eighth segment and are undulate. Both pairs of apophyses provide points of attachments for muscles which control the movements of the genitalia during oviposition.

The Male Genitalia (Figs. 67, 68) are formed from the greatly modified ninth and tenth abdominal segments. The intersegmental membrane uniting the eighth and ninth segments is extensive, enabling retraction of the genitalia within the body.

The ninth abdominal segment is represented by the tegumen (Tg) which forms its tergum, the vinculum (Vn), which forms its sternum, and a pair of valvae (Va), which are thought to be modified remnants of its appendages.

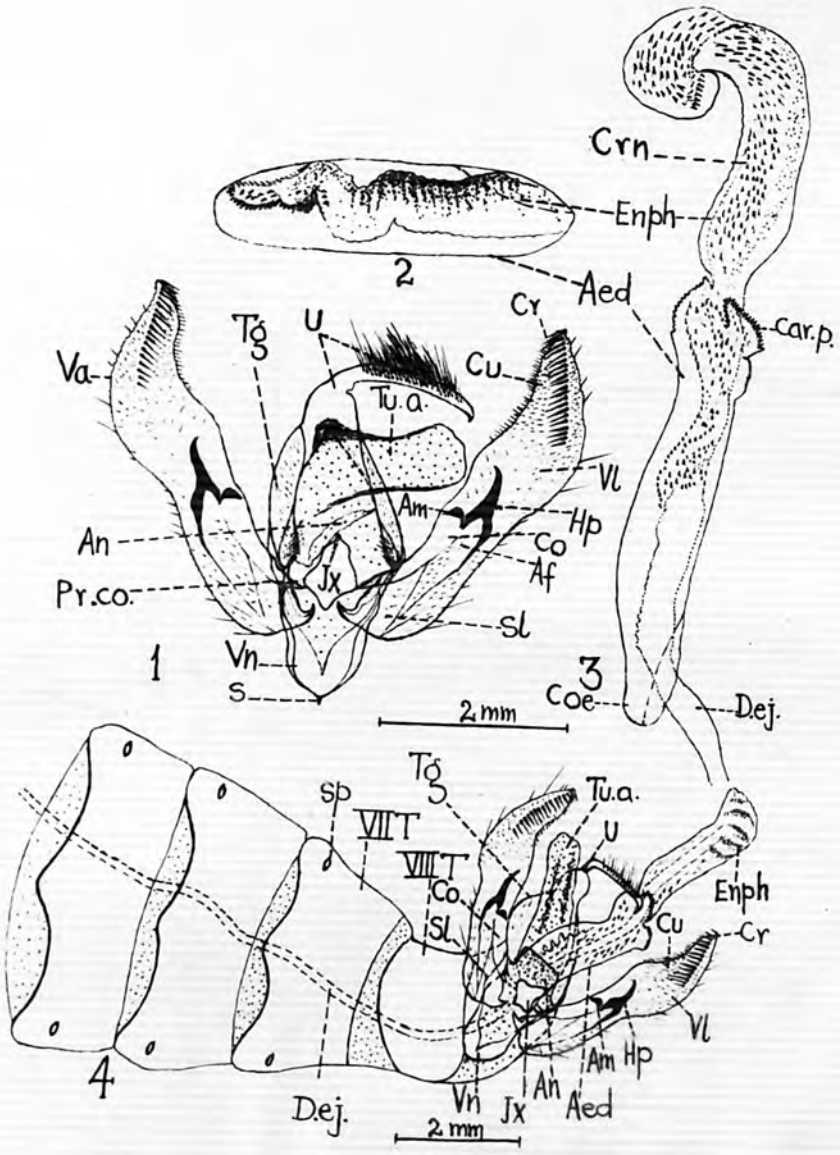

Figure 67. Male genitalia

1. Complete genitalia (ventral); 2. Phallus with endophallus retracted; 3. Phallus with endophallus everted; 4. Termination of male abdomen, genitalia extended.

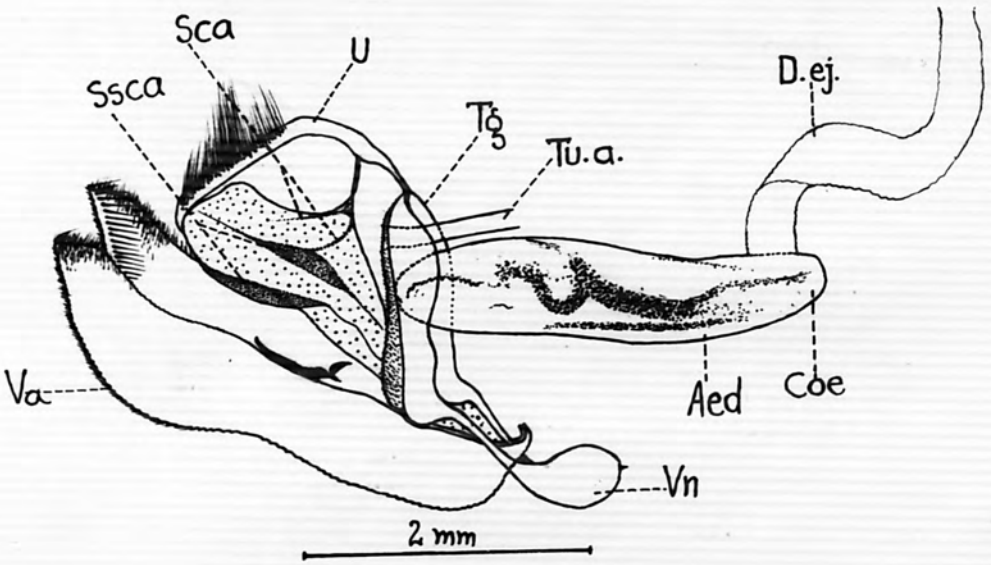

Figure 68. Male genitalia (lateral).

The tegumen is a sclerotized, well developed, roof-like structure, united posteriorly and dorsally with the uncus (u) and anteriorly and ventrally with the dorsal arms of the vinculum. Its antero-ventral rounded extremities articulate with the costa of the valvae.

The vinculum is U-shaped externally and V-shaped internally. It is dorsally produced in the form of a pair of long slender arms which unite with small posterior extensions of the tegumen (Fig. 66). The fusion between them is complete resulting in the obliteration of any sign of union. Between the arms of the vinculum lie the bases of the valvae attached to lateral extensions of the anellus. From the middle of the anterior margin of the vinculum a short, slender process, the saccus (s), proceeds anteriorly into the eighth segment.

The valvae or paired claspers are elongate and flattened, and are shaped as in Fig. 67 (1). Most of the surface of each is rough due to the presence of modified setae. The dorsal surfaces of the costa and sacculus, however are smooth.

Each valva is differentiated into the following parts :

The costa (Co), a narrow dorsal sclerite in its basal part, is wide distally and tapers basally where it is produced as a short conical extension (Pr.Co) that reaches the juxta at its base. Near the base of the costa, on its dorsal margin, is a shallow socket-like area for articulation with the antero-ventral extremity of the tegumen.

A sacculus (Sl) forms the ventro-proximal region of the valva. It is well developed, sclerotized and yellow in colour. The base of each is extended to form a dorsally and posteriorly inclined hamate structure between the vinculum and the juxta (Jx).

The cucullus (cu) is the well developed dorso-apical region of the valva. It bears a row of about 20 stout spines, the corona (cr). The cucullus is sclerotized and yellow in colour.

The valvula (vl) is the middle region of the valva. It is lightly sclerotized and is yellowish white in colour. The part of the valvula ventrad of the corona is thinner than the cucullus and extends to the tip of the valva.

The ampulla (am) is sclerotized and brown. It is small and rounded apically, and has a flat base. It is situated in the central part of the valva near its dorsal margin. Ventrally it is closely associated with the base of the harpe.

The harpe (Hp) is a sclerotized, deep-brown, stout pointed process, situated ventrad of the ampulla, near the centre of each valva. Its free distal part is directed posteriorly with a slight dorsal curvature. Its base is concave, the extension of its sides anteriorly forming dorsal and ventral arms. The dorsal arm is small and terminates near the ventral end of the ampulla. The ventral arm is much longer and thinner and extends for almost the whole length of the sacculus.

The tenth abdominal segment is represented solely by its specialized tergum or uncus (u). This consists of a long slender process, which is directed ventro-anteriorly by curvature near its base. Its remaining part is straight, except for its curved tip. Except at its basal curvature and near the tip, it bears stiff hairs on its posterior surface. Basally, the uncus is fused with the posterior part of the tegumen.

The tuba analis (Tu.a.) is a membranous tube situated ventrad

of the tegumen and uncus and between the valvae.

The scaphium (Fig.68, sca) is poorly developed,fine and U-shaped.

The subscaphium (Fig. 68, ssca) is well developed in the form of two ventrally situated, parallel, yellowish, longitudinal strips. The tuba analis is the posterior part of the digestive tract, and so far as the author is aware, no other function has been assigned to it. Dissections of this structure showed that it does not consist of the posterior part of the digestive tube only, but that there is an additional external membranous covering, with sclerotizations,the scaphium and subscaphium, formed from the dorsal part of the diaphragma. In the course of the present work, it was observed that, during copulation, it is capable of making active movements, during which it presses against the aedeagus. From this it is suggested that it may play some part in guiding the aedeagus during copulation.

The diaphragma is a transverse membrane at the posterior end of the abdomen, extending from the tegumen dorsally to the vinculum and ventrally to the bases of the valvae. It is supposed to be derived mainly from the intersegmental membrane between the 9th and 10th abdominal segments but may contain elements of the 11th segment (Klots, 1956). The anellus (An) is the part of the diaphragma through which the aedeagus emerges and which forms a membranous pocket by being doubly folded. It permits of retraction and protrusion of the aedeagus during copulation. The lateral extension of the anellus attached to each valva below the base of the harpe has been termed the anellifer (Af) by Sibatani et al (1954). Just below the anellus, and above the bases of the valvae, is a shield-shaped sclerotized plate, the juxta (Jx). Its posterior end

is produced as a fine tapering process, which, is folded back dorsally on itself.

The phallus (Fig. 67 (2-3)) comprises the basal aedeagus (Aed) and the distal eversible endophallus (Enph). The aedeagus is highly sclerotized, and brown in colour except for a small part at one side of its base which is pale yellow. Through this part enters the ductus ejaculatorius. The part of the aedeagus anterior to the point of entry of the ductus ejaculatorius is the caecum penis (Coe). The endophallus is much longer than the aedeagus within which it is capable of being retracted. The wall of the endophallus is whitish and membranous. It bears several minute conical brown spines, the cornuti (crn). At its base, there is a group of highly sclerotized, deep-brown serrate structures arranged close together in two or three irregular rows, forming an arc. These are the carpus penis (Carp.p.)

The ductus ejaculatorius (D.ej.) is attached to the terminal end of the endophallus. When the latter is everted during copulation, the ductus is drawn through the entire length of the phallus and opens at its distal end.

(b) The Internal Organs of Reproduction.

The female reproductive system (Fig. 71 (2-3)) consists of a pair of gonads or ovaries, two lateral oviducts, the median oviduct leading to the vagina, the copulatory pouch or bursa copulatrix, the spermatheca and a pair of accessory glands.

Each Ovary (ov) consists of four ovarioles, which are long slender tubes tapering distally. The slender thread-like terminal

filaments of the ovarioles unite with one another and terminate in a slightly thickened mass. In newly-emerged females, the ovaries are immature, very small and slender. A few days after emergence and feeding of the females, the ovaries enlarge and mature. A mature ovary may be as much as 60-75 mm in length or about 5 times the entire length of the abdomen. Each is folded upon itself about four times so that it can be accomodated within the abdominal cavity. The folded ovarioles are held in position by tracheal connections and fat bodies. Each mature ovariole contains numerous ova arranged linearly, in successive stages of development.

The Lateral Oviducts - Each group of ovarioles converges posteriorly to open into the anterior end of the lateral oviduct. The eggs, on being discharged from the ovarioles, pass through the lateral oviducts before entering the median oviduct.

The Median Oviduct (Odc) - The two lateral oviducts unite posteriorly to form the median oviduct, which leads to the tubular vagina. Into the anterior part of the vagina also open the ductus seminalis (ds) and the spermathecal duct (spt). The duct of the accessory glands opens dorsally into its posterior part. After the commencement of oviposition the median oviduct and the vagina contain eggs throughout the reproductive life. As these pass from the median oviduct into the vagina they are fertilised by the sperm, discharged from the spermatheca.

The Bursa Copulatrix is specialised since the ductus bursae has a long branch spirally coiled, whose distal end is connected to the vagina by a very long ductus seminalis (ds) just below the orifice of the spermathecal duct (see "The Female Genitalia"). The bursa copulatrix of a fertilised female usually contains one, but sometimes two or even

three spermatophores (Fig. 5 (a), 63 (2), spmt). Each spermatophore consists of a bulbous oval "body", about 2.5 mm in length and 1.5 mm in width across the middle, contained in the corpus bursae, and a long slender neck. The latter proceeds from one end of the "body" and turns back, lying close to one side of it. It then extends beyond the body in the form of a slender hard tube, about 29 - 30 mm in length. The neck traverses the whole length of the ductus bursae from the corpus bursae to the attachment of the ductus seminalis. It is hollow (Fig. 4 (3)). Sperms pass through it and the ductus seminalis into the vagina before being stored in the spermatheca. As the bursa copulatrix is devoid of muscular walls the sperms move from the bursa to the vagina by their own motility. The wall of the spermatophore is very hard, glossy and transparent. It is formed by the cement-like secretion of the male accessory glands, discharged together with the sperms. A spermatophore which is full of the sperms, is deep brown due to the colour of the sperms being visible through its transparent wall. When the sperm supply is depleted, it loses its colour.

The spermatheca or receptaculum seminis (spt) provides storage for sperms. A long slender blind tube, the spermathecal gland (Spt.Gl) leads to the storage pouch or the spermatheca proper, which is elongate in form. The spermathecal pouch has a brown, sclerotized dorsal wall and a white, membranous, ventral one. The dorsal wall is more or less flat but the ventral is strongly convex. The distal end of the spermatheca, connected to the spermathecal gland, is curved downward, whereas its proximal end is inclined upwards and is connected to the spermathecal duct. The latter is slender, and opens at the anterior part of the vagina just dorsad of the opening of the ductus seminalis. The spermatheca

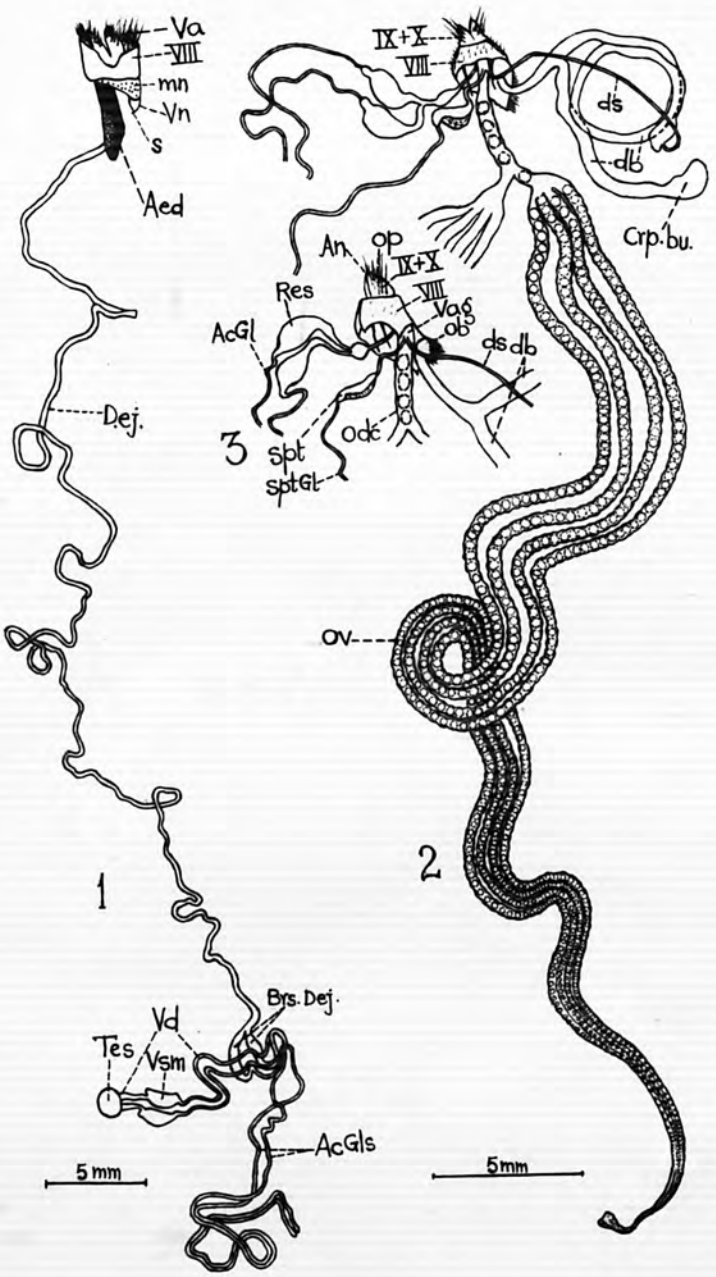

Figure 71 Internal organs of reproduction.
1. Male (lateral); 2. Female (dorsal); 3. Basal parts of female reproductive organs (lateral).

has a powerful muscular coat which regulates the flow of sperms into the vagina as required.

The Accessory Glands (Ac Gl) are very slender, long and tortuous. Each leads to an elongate, large bladder-like reservoir one end of which is produced to form a short neck, constricted distally. The two ducts unite posteriorly to form a small bulbous part which leads to a median duct. The latter opens on the posterior dorsal wall of the vagina. The fluid secreted by these glands forms a cement-like adhesive coating round each egg before it is laid which fastens it to the substratum.

The Male Reproductive Organs (Fig. 71 (1)).

The Testis (tes). Although in primitive Lepidoptera the two testes are separate, in higher forms they are fused to form a single median gonad. To this group belongs A. infusa in which the testis is globular, has a smooth surface and is pale yellow in colour.

The Vasa Deferentia (Vd) are the paired ducts leading from the testis. Some distance from it each duct widens to form a saclike vesicula seminalis (vsm). Posterior to the vesiculae seminales, the vasa deferentia continue as slender convoluted ducts which open into the anterior branches of the common ejaculatory duct. The entire length of the vasa deferentia including the vesiculae seminales is about 12.5 mm.

The Ductus Ejaculatorius (D.ej) is formed by an invagination of the bodywall and is, therefore, wholly ectodermal in origin. It is a slender, extremely long highly-convoluted tube, measuring about 90 mm in length from the aedeagus to the commencement of its anterior branches (Brs.Dej), which are about 4 mm long and twice as wide as the common ejaculatory duct. The whole duct and the vasa deferentia have strong

muscular coats which control expulsion of the sperms.

The Accessory Glands (Ac Gls) are paired, slender, much convoluted blind tubes, 37.5 mm long. They are connected posteriorly with the anterior branches of the ejaculatory duct. Their function is to secrete the viscid substance which forms the hard, glossy capsule of the spermatophore. The accessory glands together with the ductus ejaculatorius are about nine times as long as the entire abdomen and are able to be accomodated in it because of their convolutions.

4. The SURFACE STRUCTURE and HISTOLOGY of the INTEGUMENT.

The surface structure of the larval cuticle.

The cuticle of the first instar is thin and white. On its surface are prominent yellowish brown tubercles, and numerous isolated, minute, pale yellowish brown granules (Fig. 38 (3)). The tubercles are larger, more convex and more pigmented than the granules. Most of them measure 35 μ in diameter but the largest are 60 μ. The granules are convex, smooth, and oval, and measure 3.5 μ across their longer diameter. They are irregularly distributed, and are separated by intervening areas of thinner cuticle.

The cuticle of the final larval instar is almost entirely covered with convex circular pigmented granules of different sizes each bounded by a narrow depressed irregular margin. Under low magnification, many of the smaller granules are invisible, so that the larger ones appear isolated (Fig. 72 (2)). Under higher magnification, many smaller granules are seen between the larger ones (Fig. 72 (1)). The largest measure from 60 to 72 μ in diameter, the smallest from 8-12 μ. Granules are wanting on sclerotized areas such as the prothoracic shield, the anal plate and the spiracles. They also do not occur on certain localised, membranous, oval or elliptical areas (Figs. 73, 74, 75), on the membranous part around each spiracle (Fig. 49 (2)), or on the plantae of the prolegs. The oval membranous areas measure 60 to 72 μ in length and 48 μ in width, the elliptical ones 84 - 96 μ in length and 24 μ in width. The number and arrangement of the membranous areas differ from

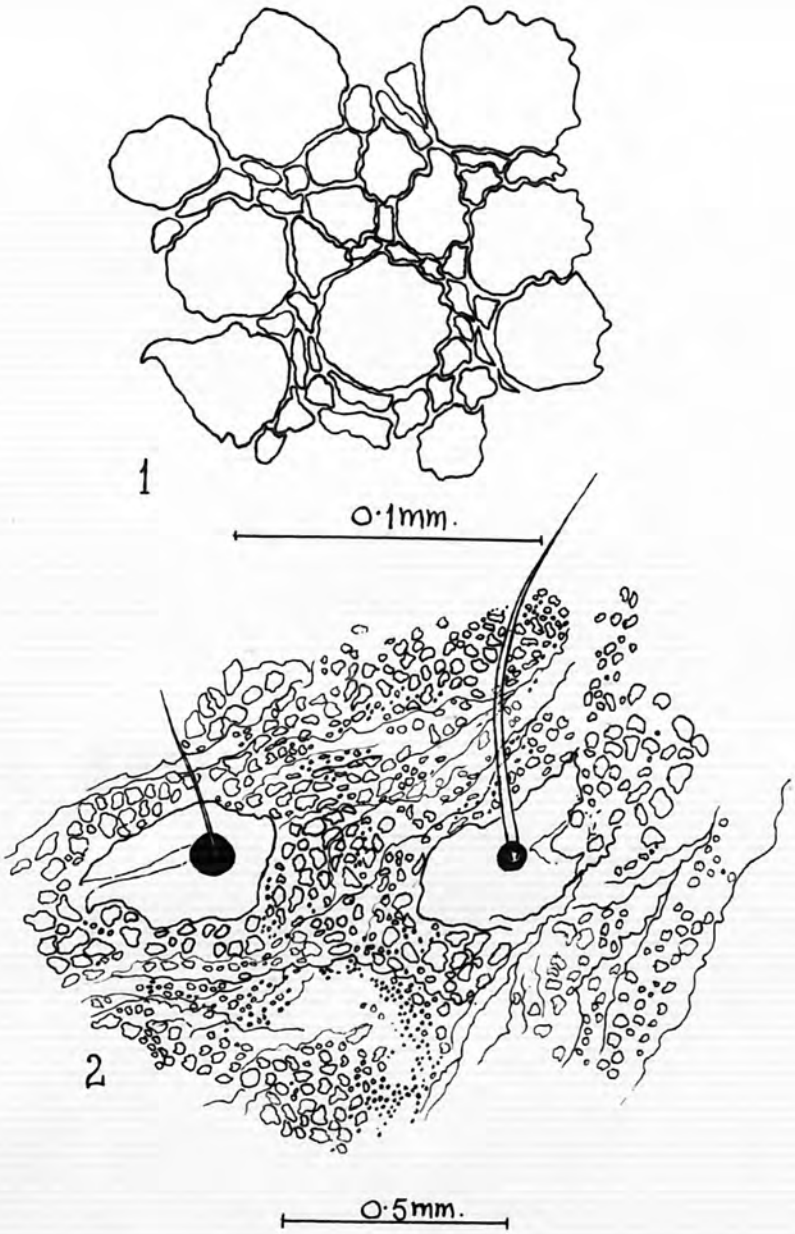

Figure 72. 1. Cuticular pigmented granules of final larval instar (much enlarged).
2. Cuticular surface of final larval instar (under low magnification).

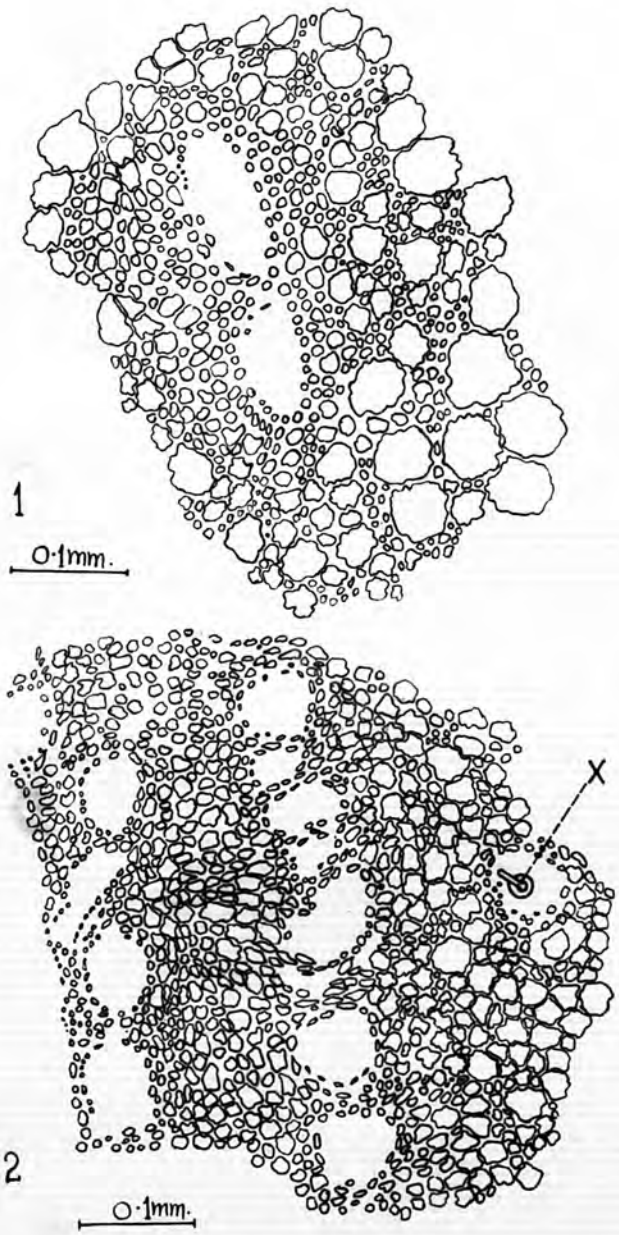

Figure 73. Nongranular, nonpigmented elliptical or oval membranous areas surrounded by granules of cuticle of final larval instar.

Figure 74

Figure 74.

Final larval instar - cuticle (surface view)

1. Prothoracic shield showing bases of setae, sensoria, depressed oval areas and lateral patches of black spots

2 and 3. Nongranulated oval areas on dorsa of thorax (2) and abdomen (3) in relation to setae, whose positions are shown by Greek letters.

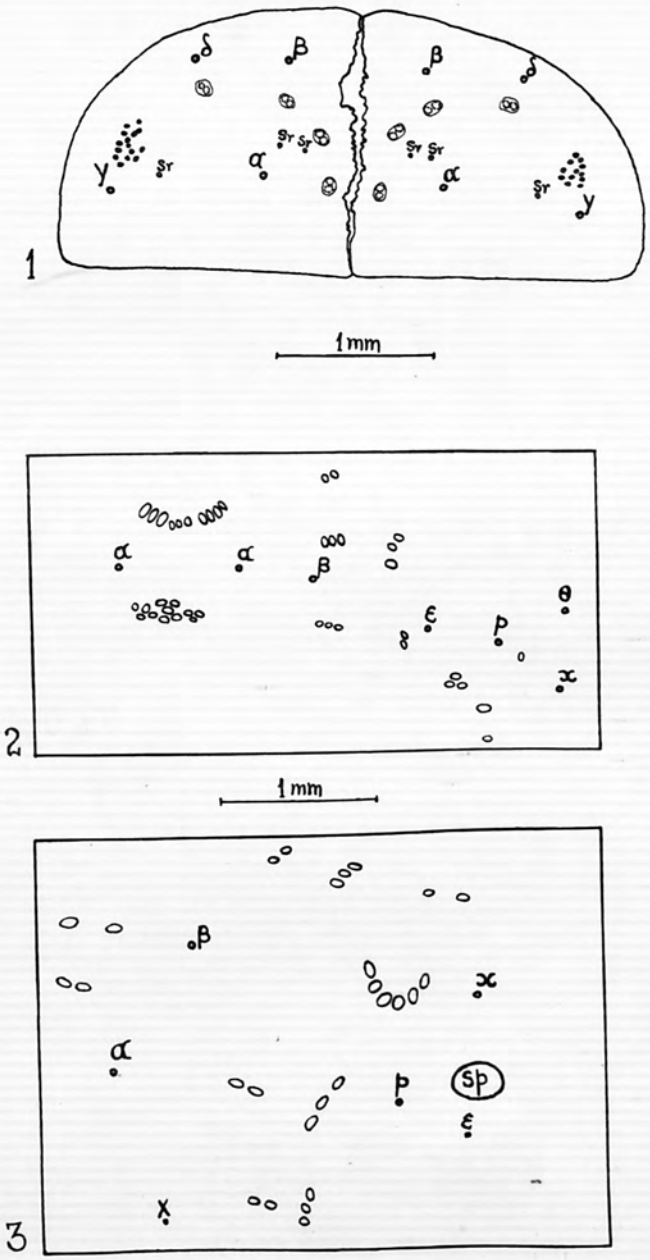

Fig. 74

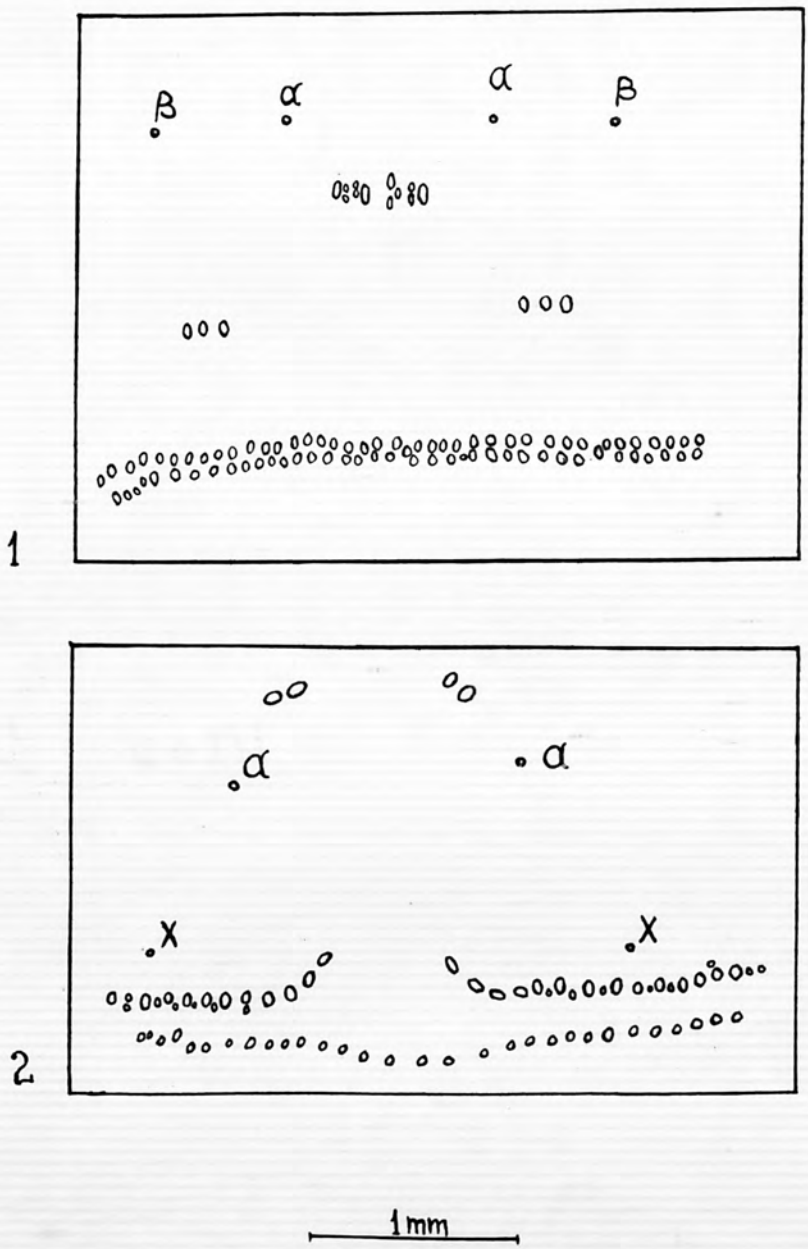

Figure 75. 1 and 2. Nongranulated oval areas on dorsum and intersegmental region of thoracic and abdominal segments in relation to setae, whose positions are shown by Greek letters.

place to place (Figs. 74,75). There are few on the cuticle of the segments, but they are numerous in the intersegmental membranes where they are arranged in two rows. In the intersegmental membranes of the thoracic segments (Fig. 75 (1)) both rows are close together, more or less straight and uninterrupted. In the membranes, uniting abdominal segments, (Fig. 75 (2)) the rows are separated, and, in addition, although the anterior one is continuous, the posterior one is broken at the mid-dorsal region, the two parts extending slightly posteriad. Usually, only small granules surround the membranous areas (Fig. 73 (1-2)).

The prothoracic shield (Fig. 74 (1)) is sclerotized. On either side of it are four oval depressions, each of which has two round membranous areas. Laterally, and posterior to seta 'Y', is a group of minute dark spots.

The granules vary greatly in their degree of pigmentation. Those of the dorsal surface are deeply pigmented and give the larva its olive-green appearance. Those situated on white or light coloured areas are unpigmented, though their sizes and arrangement are similar to those of the dorsal granules.

The dark brown tubercles are higher, larger and more convex, than the granules.

The Histology of the Integuments of Larva, Prepupa, Pupa and Imago.

1. The Integument of the Final Larval Instar (Fig. 77 (1))

The Epicuticle

The epicuticle is a little less than 2 μ in thickness. It appears to consist of two layers, the outer pale grey and the inner dark. These probably represent the lipoid and cuticulin layers, respectively. Based

on microscopical examination and chemical evidence, Lower (1957) suggested that the epicuticle of Persectania is formed of two layers, the outer containing lipoid, and the inner proteinaceous, which perhaps correspond to the lipoid and cuticulin layers of Sarcophaga (Dennell, 1946).

The epicuticle is thrown into many convex or dome shaped granules of various sizes (see "Surface structure of the larval cuticle"). Between adjacent granules, the epicuticle is infolded. During the growth of the instar, the granules separate and become flatter than those of the larva immediately before or after ecdysis (Fig. 76 (1-2)). They vary from 6 to 70 μ in diameter, and from 4 to 12 μ (occasionally as much as 16 μ) in height. Because of the presence of raised granules, the epicuticle resembles that of Persectania (Lower, 1957), in which species, however, the granules ("plates" of Lower) are smaller, and of more uniform dimensions. It differs from that of Diataraxia (Way, 1950), whose epicuticle is tuberculate.

The Procuticle.

Richards (1951) advocated the use of the name "procuticle" for that part of the cuticle which contains chitin. He (1952) further distinguished in the procuticle from one to three zones - the exocuticle, the mesocuticle and the endocuticle. This terminology was adopted and recommended by Lower (1956, 1957) and is herefollowed.

In Agrotis infusa, the procuticle consists of a very thin impregnated mesocuticle, the solidified terminal ends of pore canals (the "pore canal plugs") and a very thick endocuticle. The characteristic dark brown turbinate bodies forming the exocuticle in Persectania (Lower, 1957) are absent in this species.

(a) The mesocuticle forms a very thin layer lying just inside the epicuticle of the granules. It is stained reddish-brown by the routine stain. It varies from 1 to 4 μ in thickness in different granules, and is absent inside the infolded epicuticle between adjacent granules.

The pore canal plugs, which taper inwards, are also confined to the granules. They stain similarly to the mesocuticle with which their outer broader ends are connected. Much the greater part of each, however, is embedded in the endocuticle.

The endocuticle constitutes the whole of the remaining procuticle, and over 90% of the entire cuticle. It is strongly basiphil to dyes and is stained green by the routine stain. It varies from 32 to 80 μ in thickness, and consists of several layers which can easily be distinguished under a light microscope. The endocuticle is differentiated into a thin outer endocuticle and a very thick inner endocuticle. The outer endocuticle stains more deeply than does the inner and is composed of thinner, more-closely placed laminae. In Diataraxia, a similar arrangement was considered by Way (1950) to be, in part, an effect of growth. He believed that the outer endocuticle was subjected to more stretching than the inner; its laminae were, in consequence, thinner than those of the inner part. This also may apply to A. infusa, in which the outer endocuticle is secreted during moulting, when, and for some time after ecdysis, it is much convoluted due to the form of the epidermis which secretes it (Fig. 76 (1,2)). After ecdysis and subsequent growth, the cuticle is stretched, resulting in the granules losing some of their convexity and the outer endocuticle becoming regular. Some time after ecdysis, when the growth rate declines, the epidermal cells become

regular, and secrete an even inner endocuticle which is less subject to stretching during the remaining part of the stadium.

The Epidermis principally consists of cuboidal cells, about 6 μ thick, contiguous with the endocuticle. The nuclei are large and oval and display prominent nucleoli.

The Basement Membrane is an extremely thin, delicate and structureless membrane which forms the inner boundary of the epidermis. Lower (1957) observed the basement membrane to be secreted concurrently with the cuticle, to grow with the latter, and similarly to be digested during ecdysis. Like the procuticle, chitin has been demonstrated as one of its constituents.

2. The Integument of the fifth Larval instar before Ecdysis (Fig.76(1))

The larva used was one which had completed about three-quarters of the quiescent phase which follows cessation of feeding.

The Old Cuticle

The old partly-digested cuticle consists of the typical larval epicuticle, and a very thin, outer endocuticle about 4 μ thick. The greater part of the endocuticle has been digested and absorbed, giving rise to a digestive space between the old and new cuticles. The mesocuticle and the pore canal plugs are wanting, having been digested. In Persectania also, the pore canal plugs are completely digested during moulting (Lower, 1957); in Diataraxia, however, they remain undigested and are shed with the exuviae (Way, op. cit.)

The ecdysial membrane lies convoluted in the digestive space. Though, like endocuticle, it is strongly basiphil, and is stained green

with the routine stain, its separate identity is undoubted. It is an independent structure having no connection, with the endocuticle. It is the first secretory structure of the epidermis during moulting (Richards, 1955; Lower, 1957). As the moulting fluid has to diffuse through this membrane, Lower has suggested that it may contain, besides chitin, other unknown substances which make it resistant to the moulting fluid.

The Cuticle of the New Instar.

The cuticle of the new instar consists of a thin epicuticle, and an endocuticle, about 4μ thick, formed of closely packed laminae which are indistinct. The mesocuticle and pore canals are indistinguishable under the light microscope. Whereas the old cuticle is relatively even, with somewhat flattened granules, those of the new cuticle are more convex and have deeper inter-granular folds to permit of future growth during the next stadium.

The epidermis consists of cells of various shapes and sizes, and varies from 4 to 10 μ in thickness. Most of the cells show prominent convex outer surfaces. These enable them to secrete new cuticle of the characteristic granular form. The varying sizes and convexities of the outer cellular walls determine the sizes and heights of the granules. The inner walls of the cells are even. The cell-walls are well defined and distinct and the nuclei are particularly large.

The basement membrane bounds the inner surface of the epidermis. In many parts it is free and, therefore, is most distinctly seen internal to the walls separating adjacent cells due to slight concavities at these regions.

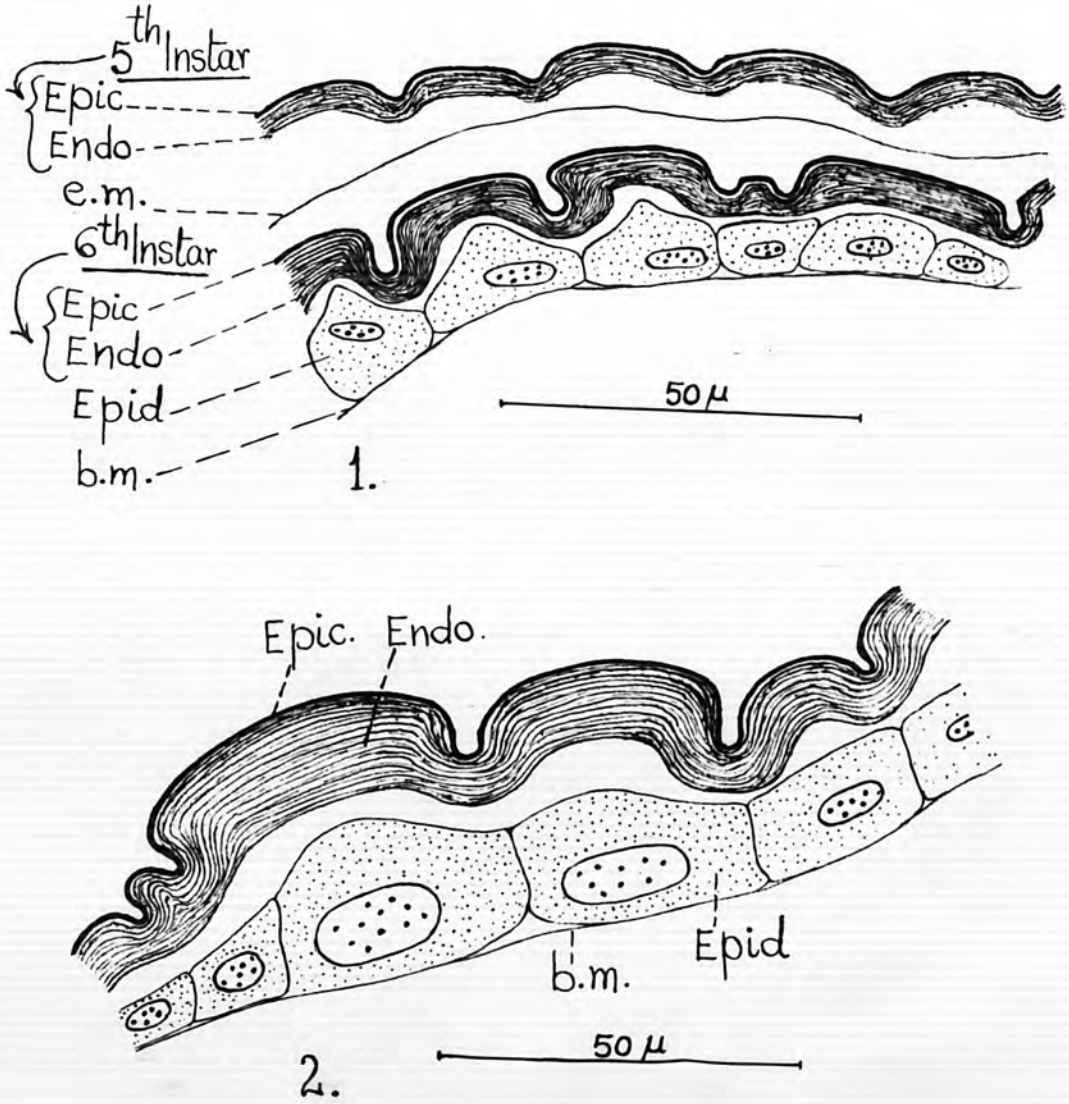

Figure 76. 1. Cuticle of fifth larval instar immediately prior to ecdysis.

2. Cuticle of newly-moulted sixth larval instar.

3. The Integument of the Newly-Moulted Sixth Larval Instar (Fig. 76 (2)).

This resembles the new cuticle of the larva immediately prior to ecdysis. The granules are prominently convex with deep inter-granular folds. Usually, between the larger granules, smaller ones are situated. They vary, in diameter, from 6 to as much as 50 μ ; their height ranges from 4 to 20 μ. Just below the very thin epicuticle in some granules, a very thin indistinct zone of mesocuticle is present but for the most part, the procuticle alone consists of the entire endocuticle ~~only~~. The laminations are more distinct than before ecdysis. The endocuticle varies from about 6 to 10 μ in thickness. The epidermis varies in thickness from 6 μ, where it is cuboidal, to 20 μ across the largest and most irregular cells. The outer surfaces of most of the cells are convex, projecting into the granules, though not to the same extent as before ecdysis. The cell walls are distinct, and the basement membrane well developed.

4. The Integument of the Inert Prepupa (Fig. 77 (2)).

The integument of the inert prepupa is that of the final larval instar, slightly modified. The granules, are larger and less convex than earlier, due to stretching of the cuticle during growth of the final larval instar. The subsequent substantial decrease in body-length as the insect becomes prepupal does not affect their shape or size since shortening is almost entirely caused by infoldings of the intersegmental membranes. The epicuticle, mesocuticle and the pore canal plugs are essentially similar to those of the final larval instar. The endocuticle is much thicker, varying from 70 to 220 μ in thickness. Its numerous laminations are distinct. The epidermis comprises more or less columnar cells, about

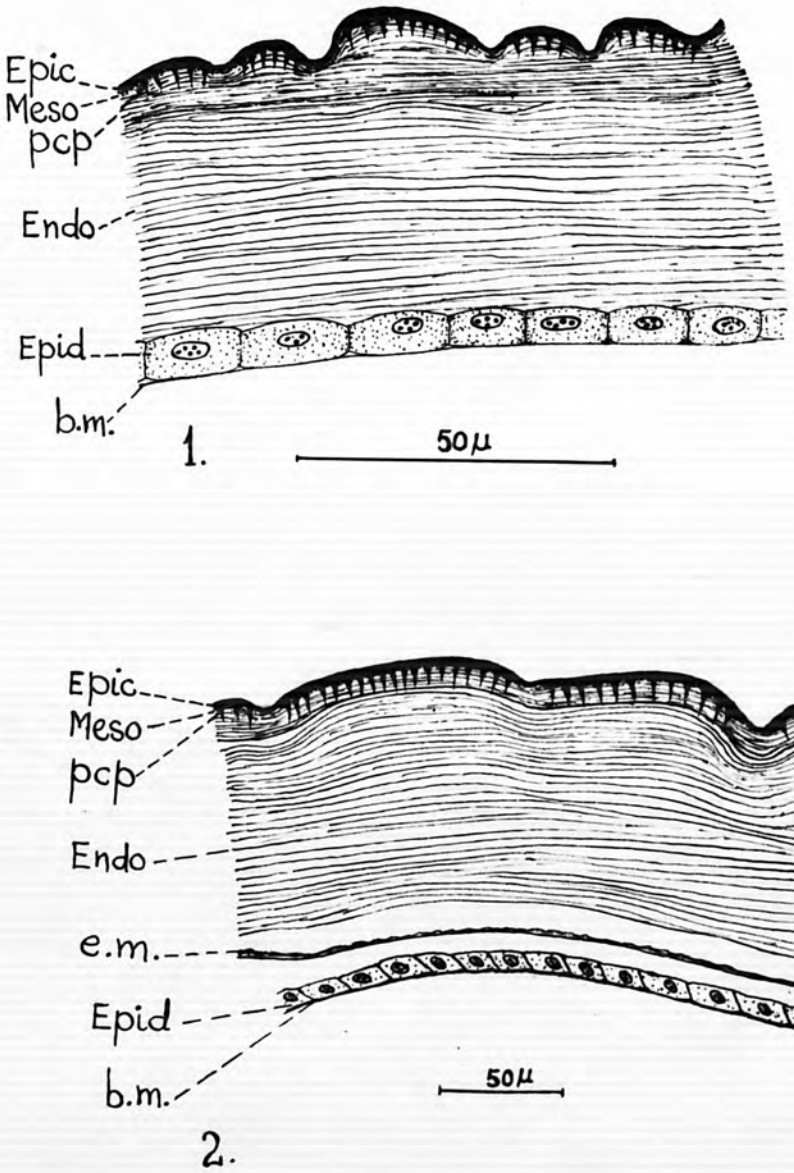

Figure 77. 1. Cuticle of final larval instar.
2. cuticle of pre-pupa.

15 μ thick. It has retracted from the cuticle, and has secreted the ecdysial membrane which appears to be two-layered. The ecdysial membrane has separated from the epidermis, but secretion of the pupal cuticle has not yet begun. The basement membrane is indistinct.

5. The Integument of the White Pupa (Fig. 78 (1)).

Only the integument of the pupal abdomen was studied. The epicuticle is very thin, being less than 1 μ in thickness. The entire procuticle is only about 6-7 μ thick. The amber-coloured, sclerotized exocuticle, and the endocuticle are very narrow zones. The mesocuticle constitutes the greater part of the cuticle. The latter is very soft and the pupa, in this stage, is very susceptible to damage. A peculiar feature of the pupal cuticle is that it is divided into blocks due to its being septate. While cutting sections, the cuticle often breaks into its constituent blocks at the septal lines of weakness. This type of structure of the pupal cuticle was first noted by Kühn and Piepho (1938) in Ephestia. Lower (1957) suggested that the septa may permit of the diffusion of fluids during the formation of the pupal cuticle. Should this be demonstrated in the future, it would explain the absence of, and the lack of necessity for, pore canals when the pupal cuticle is being secreted. Apparently, its mode of secretion in A. infusa is not unlike that in Persectania. The epidermis principally consists of fusiform cells, about 30-40 μ in thickness. These are separated medially by gaps, the cells being connected with one another externally just inside the cuticle and internally against the basement membrane. The latter is very irregular which is perhaps brought about by the great elongation of the cells, and

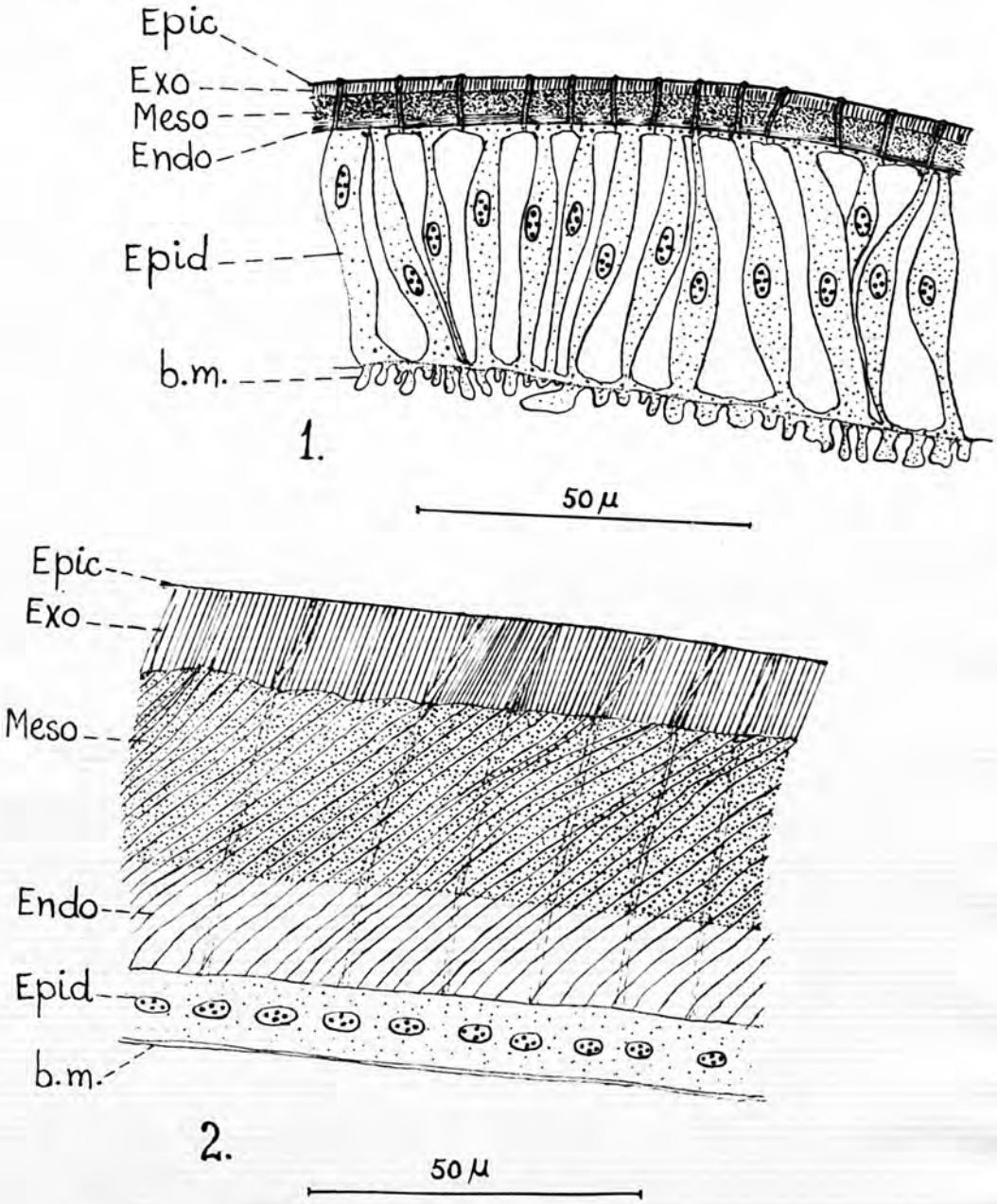

Figure 78. 1. Cuticle of white pupa.
2. Cuticle of brown pupa.

may perhaps allow for their flattening after secretion of the cuticle has been completed.

6. The Integument of the Brown Pupa (Fig. 78 (2)).

About 4 hours after emergence, the white pupa becomes reddish-brown in colour. Sclerotization of its cuticle is important as the hardened pupa is more resistant to mechanical damage and perhaps also to desiccation.

The epicuticle is very thin (less than 1 μ in thickness) and apparently remains unchanged. The thickness of the whole cuticle has increased to between 24 and 40 μ. The sclerotized amber zone (exocuticle) is now 6-10 μ thick; the mesocuticle is the widest zone (8-20μ thick), while the endocuticle is thin (4-10 μ thick). The septa are clearly visible. The epidermal cells, unlike those of the white pupa, are cuboidal and about 6-7 μ in thickness. They are in close contact with the cuticle and are bounded internally by a thin basement membrane.

7. The Integument of the Dark Pupa (Fig. 79).

In this stage , development of the imago is almost complete and digestion of the pupal cuticle has practically ceased. The epicuticle, the exocuticle and the mesocuticle have undergone no change. Most of the endocuticle has been digested, its outer remnant being only 2-4 μ in thickness. Just inside the endocuticle is the ecdysial membrane. The epidermis has already secreted 6 μ thick imaginal cuticle, most of which is mesocuticle. It has cup-like depressions in which the bases of scales are seated. As they lie flat against the surface of the

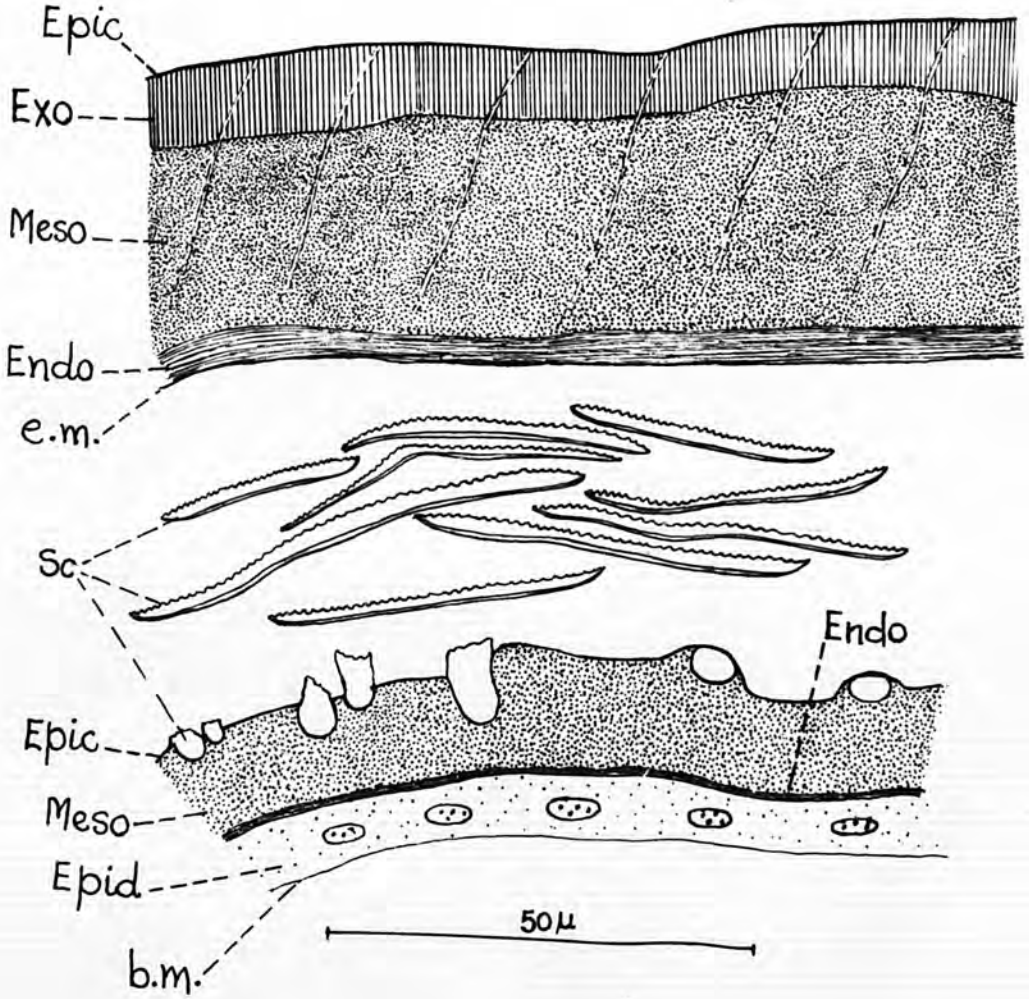

Figure 79. Cuticle of dark pupa.

imaginal cuticle, most of the scales are cut transversely in sections. They are firmly pressed between the imaginal and pupal cuticles. Due to the scale-sockets, the epicuticle is interrupted. The endocuticle is very thin - about 1 μ in thickness. The epidermis consists of cuboidal cells whose lateral walls are indistinct. The basement membrane is very thin and almost indistinguishable.

8. The Integument of the Imago (Fig. 80 (1-2)).

The epicuticle is extremely thin measuring 0.5 μ in thickness, and is discontinuous due to its being perforated by the scale-sockets. The amber coloured exocuticle varies in thickness from place to place and is confined to the dorsal and ventral surfaces where it is from 3-4 μ in thickness. It is formed by sclerotization of the outer part of the mesocuticle, and contains the sockets of scales and setae. Most of these are cut transversely in sections, though a few are cut longitudinally. When this happens, the scales remain attached to the cuticle in their sockets. (Fig. 80 (2)). The mesocuticle and endocuticle measure 4 μ and 2-4 μ in thickness, respectively. The epidermis is about 6 μ in thickness; its cell walls are indistinct. In most places it seems to have undergone degeneration and consists of fragmented and separated parts. The very thin basement membrane is visible, though indistinctly, where the epidermis is intact.

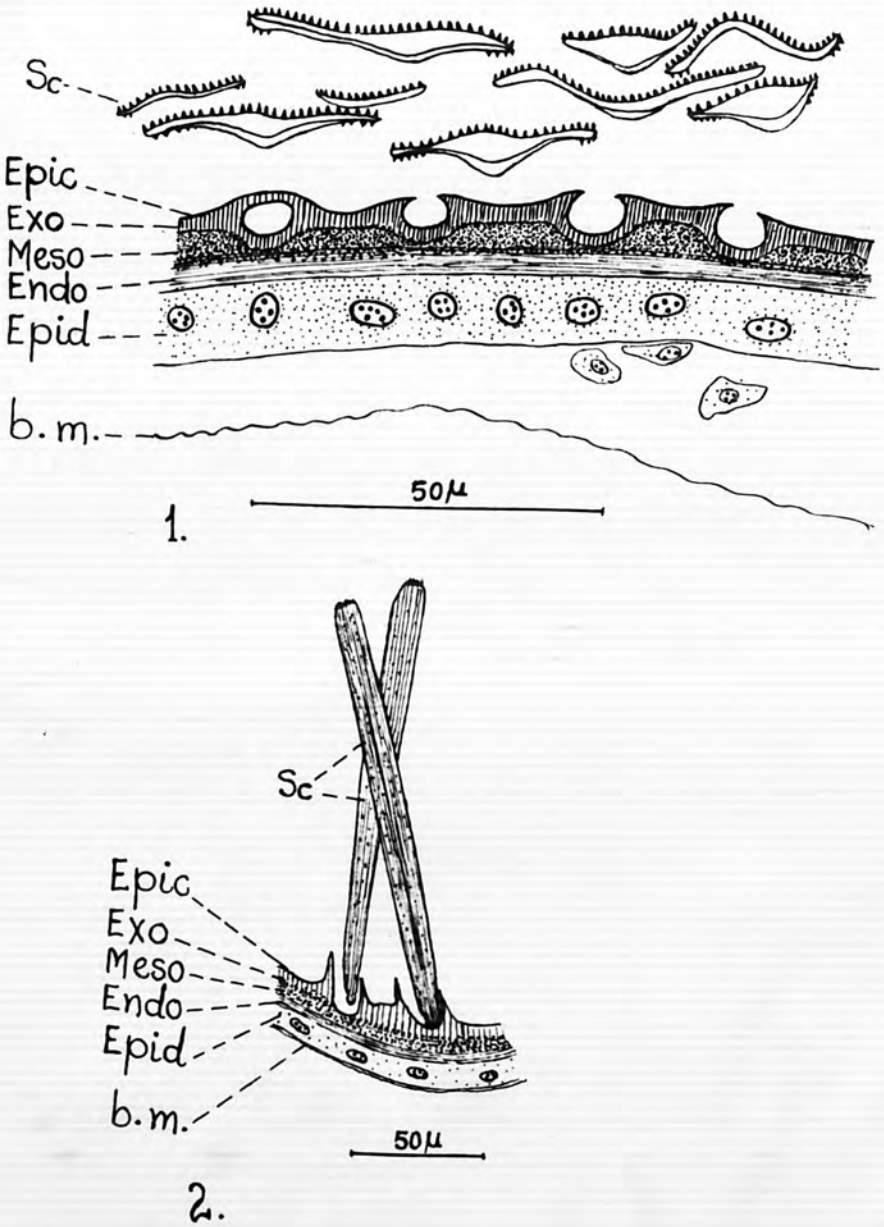

Figure 80. Abdominal cuticle of imago

1. Scales cut transversely; 2. scales in sockets.

DISCUSSION

I. INTRODUCTION

At the time the present study was begun practically nothing was known about the biology, seasonal occurrence and distribution of A. infusa in South Australia. Only two references to it, in that region, are in literature (Anon, 1919; Lea, 1928), which briefly refer to it as attacking crops of wheat and maize respectively. Whether or not the identification was correct cannot be said, for in many of the older records, in eastern Australia, the species was confused with others whose larvae superficially resemble those of A. infusa.

The task undertaken was, therefore, a twofold one: A study of the external morphology of the post-embryonic stages was undertaken, chiefly because of its intrinsic interest, but also to facilitate identification of the species. Another part of the work consisted of a study of the biology of the species with particular reference to the effects of different environmental factors. As a result of the experiments performed an attempt has been made to determine the optimum conditions for its development, survival and reproduction, to show how the environmental facotrs exercise a control on the abundance of the species and to use all the data so obtained, supplemented with data from light-trap captures at the Waite Research Institute and field-records, to show its seasonal occurrence and distribution in South Australia.

The morphological studies being self-explanatory, this discussion is, therefore, concerned with co-ordinating and interpreting the

the experimental data on various stages.

2. E G G

Effects of Temperature and Moisture on Development and Survival of Eggs.

(a) Effects of Temperature on eggs kept at 100% R.H. or in contact with moist substratum

The survival of eggs was not affected and normal hatching (94 to 100%) occurred within the temperature range from 9.3°C to 34.5°C (Tables 7 and 8). The only injurious effect observed in eggs kept at the high and low temperatures was that the hatching was irregular and distributed over a comparatively longer period (Fig. 20). Between 13.1°C and 30°C, the rate of development increased proportionately with rise in temperature, though the development at 33.8°C was still faster than that at 30.2°C. The development at 30.2°C (2.6 days) was 6.8 times as rapid as that at 13.1°C; the most rapid development at 33.8°C (2.4 days) was 13.5 times as rapid as at 9.3°C (32.47 days) (Table 7, Fig. 19).

At constant temperatures of 7°C and 36.5°C no eggs survived (Tables 9 and 13). Much lower or higher temperatures, however, could be tolerated with little injurious effect upon survival, provided exposure-periods were not too prolonged. Thus, exposure up to 6 days at 0.8°C had practically no effect on survival (Table 11); 12 hours' exposure at 40°C had little adverse effect and 40 hours' continuous exposure to this temperature was required for complete mortality (Table 13). Of the eggs, which were kept for 12 hours at 38.5°C and the remaining 12 hours

at 26°C daily, the survival was more than 50% of that of the control batch at a constant temperature of 26°C (Table 13).

Sixty minutes' exposure at 50±.7°C had little effect on survival whereas 100 minutes' exposure gave 100 per cent mortality.

(b) Effects of Moisture on Development and Survival of Eggs.

Moisture, in comparison to temperature, had little, though still noticeable, effect on development and survival of eggs. At 12.9°C, 20°C and 30°C, development was most rapid at 3 mm saturation deficit and was slightly retarded at 0 mm and increasingly so at higher saturation deficits. There was a positive linear relation between saturation deficits above 3 mm and the period of development (Table 8, Fig. 21). At 34.5°C, the development was most rapid at 0 mm saturation deficit and the development was gradually retarded with increasing saturation deficits.

At 20°C, survival was least affected by saturation deficit but at 12.9°C a saturation deficit of 9 mm (=11% R.H.) reduced the survival considerably, which was partly due to the lower vitality of the eggs, obtained from laboratory bred moths. Though most of the embryos had developed they failed to emerge. 20 mm saturation deficit (=37.1% R.H.) at 30°C, and 20, 25 and 30 mm saturation deficits, equivalent to 49%, 37% and 24.8% relative humidities, respectively, at 34.5°C, also noticeably reduced the survival of eggs (Table 8). Even in a completely dry atmosphere, however, 41% to 65% of the eggs hatched at intermediate temperatures of 13.6°C to 29.8°C, the highest survival of 65% being at 26°C; at 9.3°C and 34.5°C, at which normal hatching occurred at optimum

moisture condition, no eggs survived (Table 16). Even when completely submerged in water as many as 34.66% eggs hatched at 26°C. Taking all these data into consideration, 26°C is apparently the most suitable temperature for egg development at extremes of moisture conditions. At the upper and lower ends of the effective temperature-range the eggs are less resistant to desiccation. At 50.5°C, an exposure of 80 minutes at 3 mm (=96.8% R.H.) and 9 mm (=90.3% R.H.) saturation deficits had no effect on survival which was due to the ability of the eggs to cool by gradual evaporation; at 20 mm saturation deficit (=78.4% R.H.) survival was reduced to only 61.6%, which was due to excessive evaporation, and at 0 mm saturation deficit the survival was practically nil (1.66%) due to the inability of the eggs to cool by evaporation.

These data suggest that, in shade, the mean air-temperatures of Adelaide during summer and winter, which seldom go above 21.6°C and below 10°C respectively, would have no injurious effect on survival of eggs. As the mean relative humidity during summer is not below 43%, moisture would also not affect the egg-survival. The same would apply to most of the agricultural parts of South Australia which lie in relatively cooler and moister regions. Long periods of submergence, due to heavy rains, also would have little effect on egg-survival.

Even the extremes of air-temperature in Adelaide, (not more than 40°C in summer nor below 3.6°C in winter), would not be injurious as they seldom last long enough to be so. The temperature at the soil-surface in exposed bare situations may, however, rise to about 43 C in summer. If this high temperature acts continuously long enough which,

however, ordinarily is not the case, it may, with the associated low relative humidities, reduce the survival of eggs in such exposed places.

3. L A R V A

Temperature in Relation to Development and Survival of Larvae at a high Optimum Relative Humidity.

(a) Rate of Development and Survival

Larval development could be completed at temperatures from 13.4°C to 34.5°C, though at both these extremes of temperature survival was only 4 - 5 percent. At 34.5°C, there was no survival under the usual conditions of rearing and all the larvae died at different stages, while moulting, due to desiccation, except at 100% R.H., when only 4% survived. The rate of development increases proportionately with rise in temperature form 13.4°C to 30.2°C, at which the development was most rapid, (Table 19, Fig. 27). At 34.5°C, the rate of development was considerably retarded. The period of development at 30.2°C (19.0 days) was 6.0 times as rapid as that at 13.4°C (113.8 days). At 8°C and 6.8°C, though some development took place, the feeding and growth were very slow and all larvae gradually died during 1st to 4th stadia.

At temperatures between 20°C and 26°C, there was practically no real difference in survival, which was 77.5 to 80 per cent, when the same food (Medicago tribuloides) was used. This temperature zone is, there-

fore, the optimum one. The highest survival of 80% was at 22°C. At 16°C and 30.2°C the survival was reduced to 68% and 64% respectively. Above 30.2°C and below 16°C the survival was considerably reduced.

(b) Course of Development

Besides the rate of development, temperature also exercised a definite influence on its course. The number of larval ecdyses increased from 6 to 9 with rise in temperature. At temperatures below 26°C the usual number was 6 to 7; above it the number increased with rising temperature, being usually 8 at 29.8°C and 9 at 34.5°C (Table 25a). Other conditions being identical, temperature, during the larval stage, affected the extent of growth as well. The maximum growth, as seen by the weight and linear dimensions of pupae soon after their being sclerotized, was at 22°C, when the average weight and length of the pupae were 495.1 mg and 21.0 mm respectively. At temperatures above as well as below 22°C both the weight and linear dimesnions of pupae were increasingly reduced (Table 30, Fig. 33). This difference in growth is apparently due to the difference in the rate of feeding, assimilation and energy spent at different temperatures.

Though the most rapid larval development occurred at 30°C, taking into consideration the survival and the extent of growth, temperature of 20 - 22°C was the most suitable one; at these temperatures the development was also fairly rapid. As these temperatures prevail in Adelaide at 2" to 6" soil-depth, where the larvae usually live, from September to November (Spring) and March to April (Autumn), these two periods are most suitable for larval growth and survival.

These results also show that in Adelaide and most agricultural tracts of South Australia, where the mean air-temperature and soil-temperature, at 1" depth in exposed, bare ground, during summer, rarely go above 21.7°C and 30°C respectively, normal larval breeding and survival are possible. Scarcity of food, however, would be a limiting factor. In sheltered situations, areas under irrigation and low-lying places, which are relatively moist, cool, and where food is available, larval breeding can continue throughout summer. In winter, survival would be reduced due to low mean temperatures (10°C - 11°C), and especially so in unusually cold and wet years, though food is abundant. Autumn and Spring, with mean air-temperatures of 14°C to 20°C and soil-temperatures (at 1" depth) of 20°C to 24°C, together with adequate moisture and food, are the two ideal seasons for survival.

Different Combinations of Temperature and Moisture in relation to Survival and Water-loss from Larvae.

The effect of combinations of temperature and saturation deficit was measured on the length of survival of starved first and fifth larval instars. Judging from the period of survival, the first instar, because of its greater area exposed in comparison to the volume of the body, was found to be twice as susceptibel as the fifth instar (Tables 22 and 23). The survival period of both larval instars decreased, at any one saturation deficit, with rise in temperature, so also, at any one temperature, with increase in saturation deficit. This reduction in survival was much more pronounced in the first than in fifth instar. Thus, the survival

period of the first instar was reduced from 58.85 hours at 20°C and 0 mm S.D. to 18.21 hours at 34°C and 20 mm S.D. and to 10.66 hours at 34°C and 30 mm S.D.; that of the fifth instar was reduced from 89.00 hours at 20°C and 0 mm S.D. to 41.04 hours at 34°C and 20 mm S.D.

Water-loss by evaporation through the cuticle of dead full grown larvae in a dry atmosphere was found to increase more rapidly as temperature rose above 29.8°C to 34.5°C. This shows that at 34.5°C the total larval mortalities under usual conditions of rearing, as referred to previously, were at least partly due to excessive evaporation, though this can not be asserted definitely since the water retaining mechanism in living larvae is more efficient than in dead ones.

Type of Food in relation to Development and Survival of Larvae.

Both the development and survival of larvae were greatly influenced by the type of larval food. When the larvae were fed on cape-weed, lucerne, and wheat, at 22.5°C, those fed on cape-weed developed in a much shorter time (36.75 days) than the others, which required slightly more than 45 days.

Larval survival was even more affected. Of those fed on cape-weed, lucerne and wheat, survivals were 80%, 33% and 20%, respectively. Besides the highest rate of development and survival, the larvae, fed on cape-weed, also were heaviest as were the pupae, which developed from them. The larvae, fed on wheat, and the pupae, which developed from them, weighed the least, (Table 20, Fig. 28). Thus, of the three food plants used, cape-weed was the most suitable, and wheat the least.

Medicago tribuloides appears to be as good a food as cape-weed

or even better, as the larval survival on it, at 22°C, was also 80% (Table 19), and the pupae, which developed from these larvae, weighed even more than those from larvae fed on capeweed (Table 30).

These results show that the availability of a particular type of food-plant in a locality may be an important factor in determining survival and development of the species. Spring, and, to a lesser extent, Autumn, are the two periods in the year when not only more suitable temperature and moisture conditions prevail but also right type and quantity of food is available.

Partial Submergence in Relation to Survival of 1st Larval Instar.

Submergence up to 29½ hours had practically no effect on survival. 36 and 48 hours of submergence, however, killed 12% and 24% of the larvae respectively (Table 21). This resistance to submergence of first larval instars seems to be due to their ability to float for most of the period. The larvae could float because of the lightness of their bodies and due to the air-bubbles in their guts that, probably, further reduced their specific-gravity. This is important for survival in nature. Flooded conditions, due to heavy rains, are extremely unusual in South Australia and even under these conditions a large proportion of the first instars would escape drowning by floating on the surface, which the older larvae are unable to do.

Larval-crowding in Relation to Development, Survival and Colour-Variation.

(Table 31)

It was found that the area per larva, by itself, was without

influence. On the other hand, the close association of larvae with one another was found to have a decisive influence. Such close associations in nature, would, however, only result from high larval densities in cases of mass outbreaks. The larvae which were reared in isolation, with a surface-area of 1.8 sq. inch for each larva, were pale olive-green with pale reddish-brown head capsules; their survival was significantly higher but the period of development, though slightly less, was not significantly different. Their pupae weighed significantly more. The larvae which were reared collectively, with an area of 1.8 sq. inch or 2.9 sq. inch per larva, developed a darker colour; their survival was much reduced and their pupae weighed appreciably less. This shows that high larval densities in nature would cause appreciable reduction in survival, and lighter pupae.

4. P U P A.

Temperature in Relation to Development and Survival of Pupae (R.H. 75%)

The rate of pupal development increased proportionally with rise in temperature from 13.4°C to 30.2°C. At 34.5°C, the rate was somewhat slower than that at 30.2°C, (Table 26). The most rapid pupal development at 30.2°C (11.15 days) was 5.5 times as rapid as the period of development at 13.4°C (61.0 days).

There was no real difference in pupal survival at temperatures between 13.4 and 30.2°C; at 30.2°C, however, it was somewhat lower (88.8%) than at other temperatures (93 to 100%). At 6.8°C, 9.0°C and 34.5°C,

there was no survival. At the last temperature, however, 30% of the pupae survived when kept at 100% R.H. (Table 26). Even at 6.8°C some development occurred, as 16.3% of the pupae, which had already completed 70% of their development, at an optimum temperature, completed the remaining 30% development at this temperature (Table 27).

Moisture in Relation to Development, Survival and Loss of Weight of Pupae.

The rate of pupal development was not affected by the difference in saturation deficit at the same temperature (Table 28).

The pupal survival, however, was considerably influenced due to saturation deficit. The maximum survival of 95% was obtained at 26°C with saturation deficits of 0 mm and 6 mm (=76% R.H.) and at 20°C with a saturation deficit of 0 mm. At the latter temperature 6 mm S.D. (=65.8% R.H.) reduced the survival to 60%. The saturation deficit of 14 mm (= 44.5% R.H. at 26°C, and 20.0% at 20°C) significantly reduced the survival at 26°C as well as 20°C to 30% and 0%, respectively. It is thus seen that, whereas at 0 mm S.D. survival was the same both at 26°C and 20°C, higher saturation deficits reduced it at 20°C significantly more than at 26°C. At 34°C, the survivals at saturation deficits of 0, 6 and 14 mm were significantly lower than those at 26°C (Table 28, Fig. 31). The pupae, like eggs, were thus most resistant to effects of desiccation at 26°C. Their survival, however, was much reduced at higher saturation deficit at all temperatures.

Water-loss from pupae was directly influenced by saturation

deficit. Thus, at 29.8°C, the pupae kept at 0 mm and 12 mm saturation deficits lost 3.9% and 18.4% of weights, respectively, during pupal development (Table 29). At 12 mm S.D., whereas water-loss from living pupae was slow and gradual, that from dead pupa was very rapid and sudden. Thus, the living pupae have some active internal water-retaining mechanism, besides the passive cuticle, which is responsible for retaining water and limiting its loss.

These data show that, in comparison with eggs, pupae are less resistant to extremes of temperature and saturation deficits. During summer, when the average mean monthly soil-temperature, at one inch depth, of Adelaide ranges at about 30°C, the amount and the distribution of rain seems, therefore, to influence pupal survival and the autumn brood considerably. Long dry spells of hot summer weather seem to reduce pupal survival greatly and, therefore, the autumn brood. Mild summers with well distributed rains would enable a high pupal survival and big autumn broods.

5. I M A G O

Moisture during Pupal Development in Realtion to Longevity and Fecundity of Moths.

Moths that emerged from pupae kept at 9 mm saturation deficit (64.3% R.H.) at 26°C had shorter pre-oviposition and oviposition periods than those which emerged from pupae at 0 mm S.D.; they also laid only 39% of the eggs laid by the latter (Table 33).

Thus, besides reducing the pupal survival, the long spells of dry weather in summer may also reduce the longevity and fecundity of the moths appreciably by acting on pupae.

Imaginal Food in Relation to Longevity and Reproduction.

The longevity of moths, which received 20% sucrose solution, as food, and which reproduced, was 3 to 7 times as high as that of the moths which neither received food nor water but were kept at the same temperatures. The longevity of moths which were provided with water alone was more than that of moths which received neither food nor water but was still much less than of those, with food (Table 32).

Without food and water or with water alone, mating failed to occur and, in the latter case, only a few infertile eggs were laid. Feeding of both sexes was necessary for mating and normal reproduction. Even when the moths were provided with food for asshort a period as the first two days of imaginal life it was enough for normal reproduction

to occur, (Table 38). The availability of nectar-bearing flowers in nature is, therefore, an essential requirement for reproduction and the lack of them in summer or winter may be a factor in limiting the population.

Temperature, during Imaginal Stage, in Relation to Longevity of Moths and Reproduction.

Whether with food, with water alone or under starvation, longevity was much influenced by temperature. Under starvation, the longevity of 26.5 days at 6.8°C was 13 times as great as that at 34°C. With food, the highest longevity of 58.4 days, at alternating temperatures of 20°C for 9 hours and 5.8°C for 15 hours daily, was 8.17 times the longevity at 34°C (Table 32). The longevity of moths, kept with food, at alternating high and low temperatures was usually significantly higher than that of moths which remained constantly at a high temperature.

Temperature also had a great influence on reporduction (Table 36, Fig. 37). At 34°C, mating failed to occur, no eggs were laid and eggs in ovaries were usually degenerate. At 29.8°C, only unsuccessful attempts of mating were observed and only a very few infertile eggs were laid. Normal reporduction took place between 26°C and 10°C, the lowest temperature tested. Of the temperatures tested, highest fecundity was at 20°C; at lower temperatures fecundity gradually decreased. Fecundity at 10°C and 26°C, respectively, was only 16.9% and 77.5% of that at 20°C.

When the moths were kept at alternating temperatures of 34°C or 29.8°C for 9 hours and 26°C or 20°C for 15 hours daily, not only was

normal reproduction possible but the fecundity was even higher than that at constant temperatures of 26°C or 20°C. This stimulating effect of alternating temperatures on fecundity was particularly well marked at 34°C for 9 hours and 20°C for 15 hours.

Even when the moths were kept at as low a temperature as 5.8°C for 15 hours daily, and then transferred to 20°C for the remaining 9 hours, normal reproduction occurred and the mean number of eggs laid (776) was significantly higher than that (206.2) at a constant temperature of 10°C, though still considerably less than that at a constant temperature of 20°C.

This shows that in Adelaide, and the South and South-East parts of South Australia, with average summer and winter air-temperatures of about 21.6°C and 10°C, respectively, normal reproduction is possible throughout the year and that fecundity in summer could be much higher than in winter. In spring and autumn, with mean air-temperatures of 16°C to 20°C, the fecundity should be intermediate between that in summer and winter. Though temperature in summer is thus favourable for fecundity, shortage of nectar may be a limiting factor to a certain extent.

Temperature, during Immature Stages, in Relation to Weights of Pupae, and Fecundity at 20°C.

Temperature during rearing not only influenced the weights of pupae but also the fecundity (Table 35, Fig. 36). The pupae which developed from larvae reared at 22°C weighed the highest and the moths emerging from them also had the maximum fecundity. The fecundity of

of moths which emerged at 29.8°C, 26°C and 16°C was significantly less and their pupae also weighed less. The moths which emerged by rearing at higher temperatures, i.e. 26°C and 29.8°C, laid the least number of eggs; many made only unsuccessful attempts of mating and laid only infertile eggs. All the moths which emerged by rearing at 22°C and 16°C laid fertile eggs.

This suggests that in Adelaide, and similar other relatively cooler and moist places in South Australia, where summer breeding is possible, the moths, emerging during summer, because of mean soil-temperature of about 30°C at 1 inch depth and 26°C at 6 inch depth, where the immature stages are found, should potentially have lesser fecundity and more chances of unsuccessful mating. Similarly, those emerging from the immature stages which develop in winter, due to low soil-temperatures of about 11 to 12°C at 1 to 6 inches depth, should have lesser fecundity. On the contrary, due to favourable soil-temperatures of about 16°C to 24°C, the moths, emerging from immature stages which develop during spring and autumn, should have higher fecundity.

To summarise, the egg stage is the most resistant one to effects of temperature and desiccation, the larvae and pupae being less so. The first larval instars are particularly susceptible to high temperature and saturation deficit. Survival of larvae and pupae during winter and summer conditions of Adelaide seems to be reduced - during winter due to low temperature and wet conditions and during summer chiefly due to lack of food. If long dry spells of summer prevail, the pupal survival may be considerably affected, so also the larval, particularly of the first larval

instar. The optimum temperature, for the development and survival of eggs and pupae, at which they are most resistant to desiccation, is 26°C; that for the maximum growth and survival of larvae is 22°C, which was also the optimum temperature for reproduction while acting on the immature stages as well as the imaginal stage.

6. Seasonal Abundance and Occurrence of A. infusa in South Australia.

There is strong evidence, afforded by light-trap and field data, experimental results, discussed above, and continuous rearing throughout the year in the laboratory, that the habits and behaviour of the species in Adelaide and south and south-east of South Australia differ greatly from those in eastern Australia, where the major part of the population is recorded to have but one annual generation (Common, 1954). Light-trap data for a part of 1954, 1955 and 1956, at the Waite Institute, show that moths are active at all times of the year but that peak populations are present in the spring and the autumn (Fig 81). The data suggest that successive generations develop throughout the year but that the more favourable environmental conditions enable larger survivals of the spring and autumn broods.

Experimental rearing at different temperatures suggests that the average temperatures prevailing in winter in the south and south-eastern parts of South Australia considerably decrease both rate of

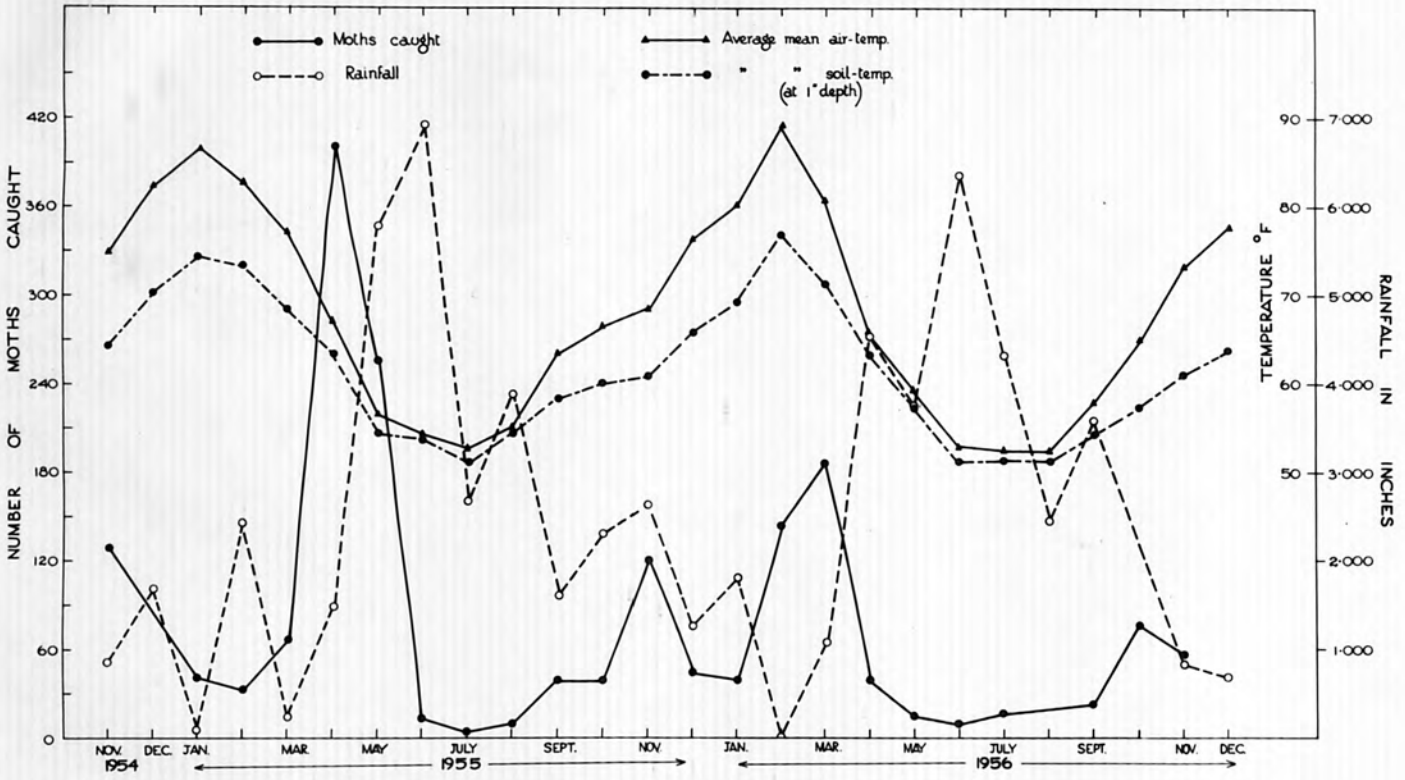

Fig. 81 : Light-trap catches of A. infusa (Boisd.) showing seasonal abundance.

development and survival, facts which are reflected in the poor light-trap catches during that time. As the temperature rises in spring, development is accelerated and survival increases, resulting in larger catches during November. During the summer (December to February), high maximum soil-temperatures (up to 43°C at 1 inch depth, and 31°C at 6 inch depth), deficiency of larval food, and high saturation deficits seem to cause a reduction in the population, which, however, is still larger than the population in winter. Examinations of the state of bursae and ovaries (Table 6) of females caught over the summer showed that the species was reproducing during all that period; while the experiments at alternating temperatures of 34°C and 26°C or 20°C (Table 36) confirm that normal reproduction is possible at the summer air-temperatures (mean 21 to 22°C) experienced in Adelaide and most of the south and south-east parts of South Australia. Food for the adults is also available during summer as most of the eucalypts, lucerne etc. flower at that period. A succession of generations, therefore, ensues during the summer, at least in areas where suitable environmental conditions prevail. In autumn, when temperatures, relative humidity, and moisture-status of the soil are again favourable, the numbers increase to the maximum for the year. The amount and distribution of rainfall in January and February, the two hottest summer months, seem to greatly influence the survival and the time of emergence of the autumn generation. From the rainfall and light-trap data during 1955 and 1956 (Fig. 81) it seems that should the rainfall during this period exceed 2.5 inches and be fairly distributed, the autumn generation is large, as happened in 1955. The size of the autumn brood

is also dependent on the weather conditions of the previous winter and spring. As rainfall during January-February falls short of 2 inches and is uneven in distribution, the numbers of the autumn generation are proportionately reduced. Time of large autumn emergences of moths seem to be correlated with time and amount of precipitation during January-February. In 1955, light-trap catches increased in March and reached a maximum in April after a rainfall of 2.440 inches in February followed by 0.155 inch in March. In 1956, on the other hand, when the total precipitation of 1.800 inches, during this period, occurred relatively earlier, i.e. in January, the autumn emergences were also correspondingly earlier, the catches increasing in February and attaining a maximum in March.

The maximum autumn catches in March 1956 were, however, much smaller than those in April 1955, which seems to be due to reduction in survival brought about by extra wet winter of 1955, and the unusually hot and dry February of 1956, when no rainfall was recorded and the maximum soil-temperatures at 1 inch and 6 inches depths soared up to 43.3°C and 31°C, respectively.

Besides the light-trap data and dissections of female moths caught during summer, some field collections provide further confirmatory evidence for the continual breeding of the species during summer. In the Waite Institute collection, there are a number of adult specimens which emerged on 11.1.'54 from pupae, collected at Mt. Schank, in the South-East. During field-infestation in Balaklava in November-December 1956 a female moth, found under sod in the infested field, showed, on dissection, the presence of a spermatophore in the bursa and the eggs passing through the common oviduct. This showed that the spring generation moths had been

normally reproducing.

7. Distribution of A. infusa in South Australia.

Experimental data on larvae, pupae and imagines suggest that the species is unable to breed in dry arid regions which are associated with high temperatures. Survival of both larvae and pupae is considerably reduced at high temperatures (above 30°C) and saturation deficits. At a constant temperature of 29.8°C reproduction fails, though at alternating temperatures of 34°C for 9 hours and 26°C for 15 hours daily (mean temp. 30°C) normal reproduction is possible. Normal reproduction is also possible at 10°C and at alternating temperatures of 20°C for 9 hours and 5.8°C for 15 hours daily, though fecundity is reduced (Table 36). Survival of larvae is also greatly influenced by the type of food plants. Distribution of the species, therefore, seem to be mainly limited by the total amount of precipitation and its distribution, temperature and, soil type, which, in turn, sustains particular type of vegetation.

Experimental results show that, provided proper moisture conditions and food are available, the species can breed at temperatures of mean values from 10°C to 30°C. With temperatures below 13°C and especially above 30°C larval survival is considerably reduced. At 34.5°C, there is no larval survival unless a R.H. of 100% is maintained when also survival is negligible (Table 19).

From these experimental data so also the data of recorded captures of different stages of the species (Fig. 82) it is seen that the major part of the State in the North and North-West, comprising desert loams, sandhills and stony deserts, is non-habitable by the species. Besides the unsuitable soil types, the lack of proper moisture (annual rainfall being below 10 inches) and proper food plants make this vast stretch of land entirely unsuitable for the breeding of the species, even if favourable temperatures prevail during part of the year, as in winter. During most of the year, however, temperature is also unfavourably high. The normal maximum and mean air-temperatures, during summer, rise above 90°F (32.2°C) and 75°F (24°C) respectively, and the normal maximum and mean soil-temperatures, at 1 inch depth, above 115°F (46°C) and 90°F (32.2°C) respectively. These soil temperatures at the prevailing high saturation deficits would be completely lethal to larvae and pupae.

Most of the South and South-East of the State, comprising Eyre Peninsula, Yorkes' Peninsula, the wheat belt and South-East, which receive an annual precipitation of more than 10 inches (Fig. 82) and have a rainfall season of 5 months and above, are habitable. This conclusion is based both on the suitability of the environmental conditions and the recorded data of captures at different localities, as presented in Fig. 82. These areas have relatively heavy soils, which seem to be more suitable for the species, and proper food, as well as favourable temperatures, at least during a part of the year. According to the extent of suitability, these can be differentiated into (a) permanently habitable, and (b) potentially habitable areas.

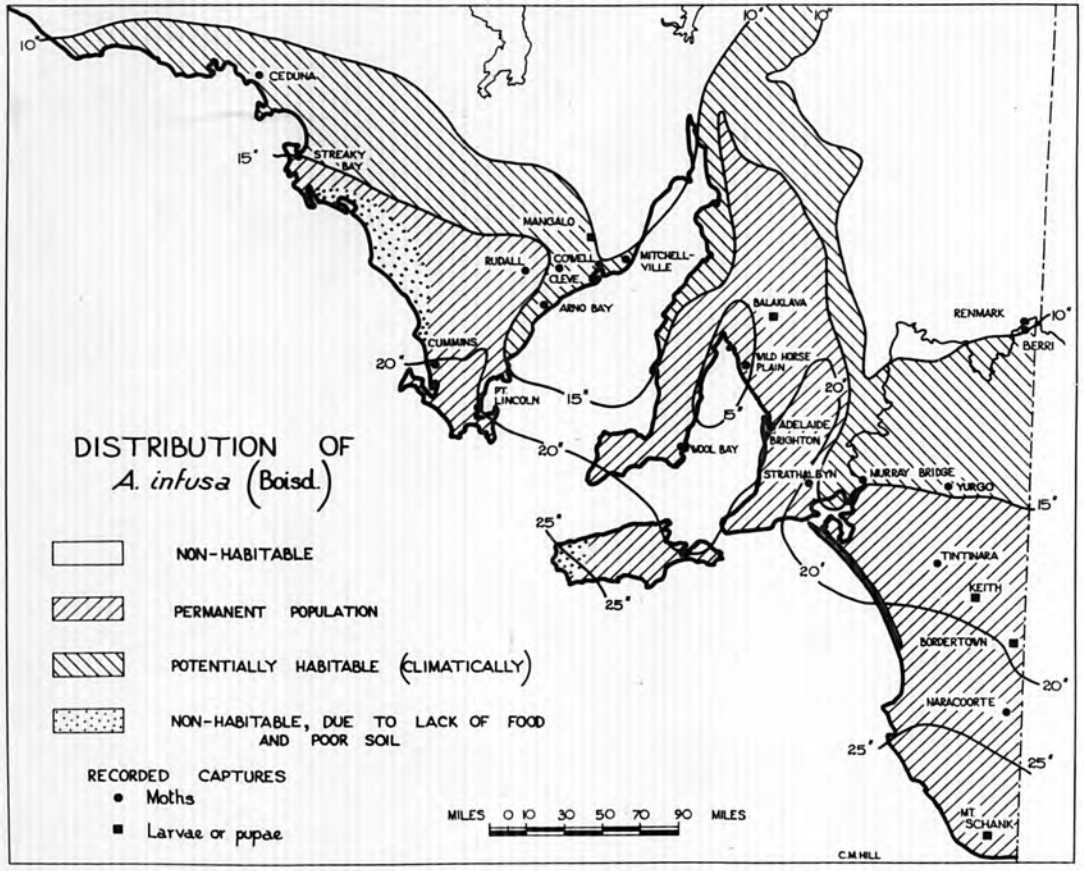
DISTRIBUTION OF
A. infusa (Boisd.)
NON-HABITABLE
PERMANENT POPULATION
POTENTIALLY HABITABLE (CLIMATICALLY)
NON-HABITABLE, DUE TO LACK OF FOOD AND POOR SOIL
RECORDED CAPTURES
Moths
Larvae or pupae
MILES 0 10 30 50 70 90 MILES
C.M. HILL
CEDUNA
STREAKY BAY
MANGALO
RUDALL
COWELL
CLEVE
MITCHELL-VILLE
ARNO BAY
CUMMINS
PT. LINCOLN
WOOL BAY
BALAKLAVA
WILD HORSE PLAIN
ADELAIDE
BRIGHTON
STRATHALBYN
RENMARK
BERRI
MURRAY BRIDGE
YURGO
TINTINARA
KEITH
BORDERTOWN
NARACOORTE
MT. SCHANK
10°
15°
20°
25°

Fig. 82

(a) Permanently habitable areas present more suitable environment for the permanent existence of the species and its breeding throughout the year. In particularly favourable years the species can build up populations large enough to cause appreciable economic damage. These areas lie mostly in semi-humid zone with 7 - 9 months' mean rainfall season and an annual rainfall of 15 inches and over. The normal maximum and mean air-temperatures, during summer, are ordinarily below or about 81°F (26.6°C) and 65 - 70°F (18.3 - 21.1°C), respectively, which give the normal maximum and mean soil-temperatures, at 1 inch depth, of below or about 108°F (42.2°C) and 81 - 86°F (27.2 - 30°C) respectively, in exposed and bare situations. As these temperatures would be relatively less under vegetation and in moist places, the species can breed throughout the summer in such places, the evidence of which has been provided under the discussion of Seasonal Occurrence.

(b) Potentially (climatically) habitable areas lie just north of the permanently habitable areas and have an annual rainfall of about 10 inches or a mean rainfall season of about 5 months. These areas are favourable for breeding of the species only during a limited part of the year, i.e. winter and spring, and especially so in certain favourable years when rainfall is more than average and temperatures milder.

Some parts, e.g. Renmark and Berri (Fig. 82), which lie in the arid zone with less than 10 inches annual rainfall and should normally be non-habitable, have been artificially rendered suitable for breeding of the species due to irrigation, at least during a part of the year when temperature conditions are favourable. On the other hand, some places,

e.g. a part of western Eyre's Peninsula and Kangaroo Island, which, though climatically suitable and lie within permanently habitable areas, are non-habitable due to poor soil and lack of vegetation.

SUMMARY.

The biology and certain aspects of the morphology of Agrotis infusa (Boisd) have been studied.

The species has a very high fecundity; the moths on emergence, have invariably immature ovaries and die before laying all the eggs which they are potentially able to produce. Habits and behaviour of the species have been noted.

Various stages in the life-cycle and sexual differences in pupae are described.

Changes in weight during the course of the life-cycle and water contents of first larval instars, before commencement of feeding, fully-fed larvae, inactive prepupae and pupae have been determined. During egg-development there is a very slight decrease in weight; weight of first larval instars, before commencement of feeding, is however, much less than the original weight of eggs due to the weight of the chorion. The weight of fully-fed larvae, when reared at 26°C, increases about 2,000,000% over the original larval weight at hatching. Increase in weight during the first larval instar is much higher than that during final larval instar.

A considerable weight is lost (about 60%) during the prepupal stage, almost entirely due to water-loss. During the pupal stage, however, comparatively little weight is lost. Within a period of about 12 hours after emergence, the moth loses a substantial amount of weight due almost entirely to expulsion of the meconium. Whereas the moths,

kept under starvation, continue to lose weight, those, provided with food, regain most of the weight lost.

The water-content of first larval instars, before commencement of feeding, is very nearly the same (75 to 76%) as that of the inactive prepupa after the larva has lost all the extra water; that of the fully fed larva is much higher (90%) and the pupa a little less (73.5%).

Different biological agencies and phenomena, found to exercise control of numbers have been recorded.

The comparative morphology of the chitinous structures of the first and final larval instars, with particular reference to the final instar, is described.

The chitinous structures of the imago, including the organs of reporduction, have also been described.

Surface structure of the larval cuticle of the first and final instars has been studied.

The histology of the cuticle of the fifth larval instar before ecdysis, the newly moulted 6th larval instar, the inactive prepupa, the pupa in three stages of development, and the imago has been studied and relevant comparisons made with the structure of the cuticle of Persectania ewingii (Wwd) and Diataraxia oleracea L, the two other agrotids, studied by Lower (1957) and Way (1950) respectively.

At suitable moisture conditions normal egg-development occurs at temperatures from 9.3°C to 34.5°C. At intermediate temperatures development is more uniform and hatching is complete within a shorter time than at extremes of the temperature-range.

At a constant temperature of 7°C, though some development occurs,

complete egg-development fails to be accomplished. Continuous exposures of up to 6 days at 0.8°C had little injurious effect on survival of eggs; longer exposures, however, increasingly reduced the survival and delayed the period of development. Eggs which have already completed 50% of development are more resistant to low temperature than are newly laid eggs.

At at constant temperature of 36.5°C, there is no survival of eggs. Short exposure periods to much higher temperatures can, however, be tolerated without effect on survival, though development is delayed. Continuous exposures for 40 hours to 40°C and 100 minutes to 50±0.7°C are necessary for 100% mortality.

Eggs are highly resistant to desiccation. This resistance is highest at 26°C and decreases with higher or lower temperatures. Thus even in completely dry atmosphere as many as 65% eggs hatch at 26°C but no eggs survive at 9.3°C and 34.5°C, which allow normal survival under suitable moisture conditions. Saturation deficit of 3 mm has been found to be the most suitable for egg development.

Exposure for 80 minutes to 50.5°C is most injurious at 0 mm S.D. and least so at 3 mm S.D., at which survival is unaffected and development is only slightly delayed. Higher saturation deficits, e.g. 9 and 20 mm, increasingly reduce survival and delay development.

2-day-old eggs are comparatively less resistant to high temperature than 1-day-old eggs.

Even in complete submergence full egg-development occurs at an optimum temperature though survival is appreciably reduced.

Viability of eggs, laid by laboratory-reared moths, was found to

be significantly less than that of eggs, laid by moths, captured in nature.

Complete larval development takes place at temperatures from 13.4°C to 34.5°C. At 34.5°C, this is possible only at 100% R.H. and there is only very little survival. Though the most rapid development occurs at 30.2°C, the highest survival is at 20°C to 26°C, particularly at 22°C. At 8°C and 6.8°C feeding is very slow and, though some development takes place, all the larvae gradually succumb in early instars.

The pupae which develop from larvae reared at 22°C are the heaviest and largest of all those reared at the whole temperature-range. With the fall or rise in temperature beyond 22°C both the weights and linear dimensions of pupae are increasingly reduced.

The type of food greatly influences the larval development and survival as well as the extent of growth, as measured by weights of larvae and pupae. Of the different foods, tested, barrel medic and capeweed are the most suitable and wheat the least.

Survival period of both the first and fifth larval instars is reduced with higher temperatures and saturation deficits. First instars are, however, much more susceptible than are older larvae.

Partial submergence of first larval instars up to 29½ hours has no adverse effect on survival.

Loss of weight, due to evaporation, through the body cuticle of dead fully-fed larvae, in dry atmosphere, rises gradually as the temperature increases from 20°C to 26°C. It is comparatively more from 26°C ~~and~~ to 29.8°C and the highest with the temperature increase from 29.8 to 34.5°C.

Temperature also influences the number of larval ecdyses. At temperatures below 26°C, the usual number of ecdyses is 6 to 7; with higher temperatures the number increases to a maximum of 9 at 34.3°C. Some evidence has also been obtained as to the effect of quality of food on the number of larval ecdyses. No correlation has been found between the sex and number of larval ecdyses.

Collective-rearing throughout the period of larval development greatly reduces the larval survival and pupal weights, slightly delays larval development, and causes the larvae to be much darker than those reared in isolation.

Complete pupal development with normal survival occurs at temperatures from 13.4°C to 30.2°C. At 6.8°C and 9°C though some development takes place, full development fails to be accomplished. At 34.5°C, though full development can occur, survival is greatly reduced.

Pupae, which have developed to 70% at 26°C, on transfer to a higher temperature (34.5°C), complete the remaining development at the rate somewhat greater than that of the full development at the latter temperature; on transfer to a lower temperature (13.4°C), however, the remaining development occurs at the rate lower than that of the full development at low temperature.

The pupae are much less resistant to desiccation than are the eggs. Their resistance to desiccation is highest at 26°C. Loss of weight, due to evaporation, from living pupae, is gradual and increases with saturation deficit; it, however, is very rapid and sudden with the death of the pupa.

Imaginal longevity, whether with or without food or with water

alone, increases greatly as the temperature decreases from 34°C. The moths, provided with water alone, live longer than those which are provided with neither water nor food; those which are fed, live significantly longer than their counterparts which are starved or provided with water alone.

Longevity, pre-oviposition and oviposition periods as well as fecundity of the moths, which emerge from pupae, kept at 9 mm saturation dificit, at 26°C, are significantly less than are those of moths that emerge from pupae kept at 0 mm saturation deficit.

Temperature of rearing has been found to exert a profound, though indirect, effect on fecundity of moths - through its direct effect on the weight. Pupae reared at 22°C weigh the highest and the moths which emerge from them have the greatest longevity and fecundity. Many of the moths, reared at 26°C and more so at 29.8°C, fail to mate successfully, have a much lesser fecundity and lay a higher percentage of infertile eggs.

Temperature, during the imaginal stage, also influences the fecundity and reproduction. Of the moths confined at constant temperatures, those kept at 20°C laid the highest number of eggs. At 29.8°C and above successful mating failed to occur. Moths kept at 34°C for 9 hours daily and then at 26°C or 20°C, not only reproduced normally but laid more eggs than those kept at 26°C or 20°C constantly.

Fertilized females lay considerably more eggs than unfertilized. Feeding of moths is essential for mating and normal reproduction. Moths kept without food or water fail to oviposit; those kept with water alone lay only a few infertile eggs.

Both on the basis of experimental results, light-trap catches

and dissections of female moths caught during summer, it has been concluded that the species can breed throughout the year in Adelaide and similar other mild parts of South Australia with annual rainfall of at least 15 inches. Spring and autumn, however, are the most favourable periods for survival.

Distribution of the species in South Asutralia has been recorded.

A C K N O W L E D G M E N T S

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