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SOME ASPECTS OF THE BIOLOGY
of the
TOBACCO BEETLE,
LASIODERMA SERRICORNE (F.)
(COLEOPTERA : ANOBIIDAE)

V.L. RAYNER
SOME ASPECTS OF THE BIOLOGY
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LASIODERMA SERRICORNE (F)
(COLEOPTERA : ANOBIIIDAE).

Thesis for the degree of B.Sc.,
University of Cape Town.

V.I. Rayner, B.Sc.,
University of Cape Town,
South Africa.

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I - INTRODUCTION.

Since about 1866 the "tobacco beetle," Lasioderma serricorne, has been recognized as a pest of considerable economic importance. In addition to cured tobacco, the larval stage attacks a great variety of other materials of both plant and animal origin.

Much of the work done on the biology of this beetle is fragmentary and not precisely recorded. The present author has aimed at correlating as much of the available valid information as possible and supplementing it with original records.

Further, most previous investigations have centred on control rather than bionomics. But a sound knowledge of bionomics is needed as a basis for an effective scheme of control. Therefore, as research had to be limited in some way, in this paper attention has been paid primarily to bionomics (with some relevant morphology). The section on control comprises only a few original observations, and this aspect offers a wide field for future research.
II - ORIGIN AND HISTORY.

The earliest record of the occurrence of *Lasioderma serricorne* comes from Egypt from the tomb of Tutankhamen. ALFIERI (1931) concludes that the beetles are probably indigenous to Egypt and states that they have scarcely altered morphologically in the 3,500 years that have elapsed.

However, there is no general agreement as to the original habitat of the beetle.

It was first reported in America in 1792, not on tobacco specifically, but as infesting "American dried plants" (RUNNER - 1919, p.10). Probably the first report of its occurrence on tobacco specifically was that in Europe in 1848. In 1861 it was recognised as being cosmopolitan, and in 1865 as being both cosmopolitan and chiefly, though not exclusively, a tobacco pest.

According to RUNNER (1919, p.11) the history of the species from an economic standpoint begins with a paper, published in America in 1885 - 86, in which its control is discussed.

In South Africa the earliest recorded specimens in the National Museum were collected in 1899, but the collection may not have been concomitant with the first appearance of the beetle in the Union.

In 1906 in the Transvaal, SIMPSON (1906) made the following report:

"Some months ago the importation of this beetle in consignments of cigarettes from Egypt drew our attention to the fact that this insect might gain a foothold in the tobacco stores, warehouses or drying sheds in the Transvaal and thus become troublesome to the tobacco industry of this colony."

These fears have now been realized and *Lasioderma serricorne* is regarded as an important pest of cured tobacco not only in the Union but also in many other countries, and especially in the warmer regions.
III - **ECONOMIC IMPORTANCE.**

Of a great variety of materials attacked by *Lasioderma serricorne*, cured tobacco sustains the greatest injury and is most important economically. (Unfermented tobacco is not attacked by this beetle).

In connection with attacks on cured tobacco the following points are noteworthy:-

1. **Both unmanufactured and manufactured tobacco is attacked.** However, it is probably in unmanufactured tobacco that most damage is done, as this is often stored for 2 years or longer to allow for a slow, natural fermentation; and this tends to provide the beetle with ideal breeding conditions over several undisturbed generations.

2. **A large number of different types or grades of cured tobacco are attacked, in contrast to the tobacco moth, *Ephestia elutella* Hb., which attacks only a limited number.**

3. **The larva actually consumes the tobacco, the adult apparently does not feed.** According to one report, (DELASSUS & LEFIGRE - 1931), the loss in weight of stored tobacco through larval consumption may amount to 5% after one year's storage and to more than 10% after 2 or 3 years. Nevertheless the insects need to be very numerous before the direct consumption of the tobacco becomes serious.

4. **All authorities are agreed that the actual amount of tobacco consumed is generally of far less importance than the contamination of the product through the presence of brown, dust-like frass, cast larval skins, pupal cells and dead beetles, which render the manufactured product unsaleable.**

The economic loss incurred by the tobacco beetle is probably created in 3 principal ways according to REED & VINZANT (1942, p.4). These are summarised below. Figures in brackets denote annual losses estimated in 1942 in the U.S.A.
U.S.A.

1. Loss in weight and quality of the leaf tobaccos infested. ($3,250,000 - 10,000,000).

2. The cost of replacing manufactured tobacco products that are found infested in wholesale and retail establishments. ($250,000 - $500,000). It is considered that there is a much greater potential loss in manufactured tobacco, since thousands of consumers never return infested goods, but instead change their brand of tobacco.

3. Loss on export shipments abroad, resulting from arbitration about infested lots of tobacco, and discrimination in foreign countries against the tobacco of the exporter because of insect infestation. ($250,000).

No figures appear to be available reflecting economic loss incurred by this beetle in South Africa.
Lasioderma serricorne is described as cosmopolitan in distribution having been freely transported by the commerce in tobacco and some of its other foods, to practically all parts of the world.

The little limitation there is on its distribution, is exerted mainly by temperature and to a lesser extent by humidity. It is most prevalent and important economically in tropical and sub-tropical regions. Here high temperatures and humidity accelerate development, which is continuous throughout the year. Its prevalence declines towards the poles.

In warm, temperate areas, as the Western Cape Province, infestation generally increases in the summer months and dies down in the winter when development in all stages is prolonged. In cool temperate areas, such as Great Britain, the insect is very inactive and little damage is done unless the foodstuff is stored at a minimum of 65°F (BOVINGDON - 1933). A long cold spell, such as 23 - 32°F for a period of over 5 days, will probably kill all the insects. (CRUMB & CHAMBERLIN - 1934). In very cold regions, the beetle may often have to be re-introduced and never become permanently established owing to low winter temperatures. This occurs in the northern parts of Russia. The beetle is normally confined to the southern districts as the northern cold, frost and sudden fluctuations of temperature are very detrimental to it. However, for a limited period it may do considerable damage, even in the north, if introduced in a favourable foodstuff during a favourable season. (SKALOV - 1931, and USTINOV - 1932).
V - MATERIALS ATTACKED.

As previously discussed, cured tobacco ranks as the most important material attacked by Lasioderma serricorne and, further, both leaf and manufactured tobaccos and a great variety of types and grades are susceptible.

In addition, however, the species has been recorded as occurring in at least 70 other materials. The occurrence of the beetle in some of these may have been more or less accidental, or the larva may not have been able to complete its developmental cycle in the material concerned. Breeding experiments will have to be carried out to determine the true range of materials liable to infestation.

Of these additional materials, most are vegetable substances and in particular those that are dried; but a few animal substances, also mainly dried, are included.

The following are a few of these additional materials:

- aniseed
- biscuits - various
- bamboo
- books - bindings & leaves
- cabbage - dried
- cane-work
- copra & copracake
- cotton bolls
- curry powder
- fish - dried
- flour - various
- fruit - dried & various
- gun-wads
- herbarium specimens
- insect specimens
- leather
- liquorice
- macaroni
- mealie meal
- pepper - various
- rattan work
- rice
- rugs
- seeds - of great variety
- spices
- starch
- tapestry
- turmeric
- upholstery - flax, tow, hemp, plush, silk, straw.
- wax
- woollens
- yeast.

7/... Text figs.
Text figs. 1 - 4 show infestation in leaf tobacco, cigarettes, an "army" biscuit, and mealie meal, respectively.

Fig. 1 - A tobacco leaf showing larval damage (x 0.4).

Fig. 2 - Infested cigarettes showing exit holes of adults (x 1.8).
Fig. 3 - An "army" biscuit showing larval tunnels and exit holes of adults. (x 1.6).

Fig. 4 - A mealie meal culture showing stages in pupal cells up against the glass. (x 0.7)
VI - SYSTEMATICS.

1. GENERAL CLASSIFICATION:

Lesioderma serricorne (F) has been placed in the family, Anobiidae, which is classified as follows, according to INWS (1948):

Order: Coleoptera
Sub-order: Polyphaga
Super-family: Diversicornia
Family: Anobiidae.

Further it is placed in the sub-family, Xyletininae, according to JUNK (1912), KEITTER (1911) includes 6 genera in this sub-family.

Originally the family, Ptinidae, was sub-divided into the Ptinini and Anobiini, but in 1830, Stephens raised the sub-family, Anobiini, to family status and later placed the genus, Lesioderma, which he erected in 1832, in this new family, Anobiidae.

The Ptinidae and Anobiidae were probably originally grouped together owing to their similarity in size and colouring and their similar habits.

Characters of the genus, Lesioderma Stephens.

The following is a condensation of the characters of the genus, Lesioderma:-

Body not exactly cylindrical, but oval or elongate-oval. Head strongly inflexed. Antennae serrate last three joints not bigger than the preceding ones. Sides of prothorax deflexed or slightly concave near the margin. Elytra punctate without order and not striate.

A sub-genus, Hypora, was described by Mulsant and Rey in 1864, and the species, Lesioderma serricorne, is included in this sub-genus.
2. SYNONYMY, CLASSIFICATION AND CHARACTERS OF
THE SPECIES, _SERRICORNE FABRICIUS._

a) SYNONYMY:

The most important points in the synonymy are as follows:

In 1792, the species was first described by Fabricius as _Ptilinus serricornis_. In 1806, Schönherr listed this as synonymous to _Ptilinus serricornis_. In 1825 Duftschmidt described it as _Ptilinus testaceus_. In 1832, Stephens transferred the species _testaceum_ to his newly-erected genus, _Lasioderma_. In 1837, Sturm listed it as _Xyletinus testaceus_. Thereafter, it was referred to, by various authors, as _X. flavescens_, _X. serricornis_, and _Pseudochiona (Hypora) serricornis_. It was not until 1865 that Le Conte described the beetle as _Lasioderma serricorne_.

As previously described, this species is popularly known as the "tobacco beetle." Synonymous common names have arisen from the variety of materials which _L. serricorne_ infests. Some of those recorded are the "cigarette beetle," "tobacco bug", "tobacco weevil", "cheroot beetle", and the "tow bug". This latter name originates from its habit of infesting types of upholstery fillings, such as tow, flax, hemp etc. (HARTNACK - 1939). The names, "tobacco flea" or "tobacco flea beetle" may have originated from confusion of the species with _Epitrix parvula_, which attacks growing tobacco (RUNNER - 1915).

The following references to the species and its synonyms are taken from JUNK (1912) and a few other sources:

_serricorne._


* The species discussed in this paper have been included in the accessions collection at the Division of Entomology, Rosebank, Cape Town, as No. 300.
35 species have been attributed by Junk (1912) to the genus, Lasioderma. The majority of these species occurs in the Palaeartic zone in places like Corsica, Algiers, France, Southern Russia, Greece and Spain. But several species have also been recorded in the U.S.A., Canary Islands and Japan. The species, serricorne, is listed as cosmopolitan.
cosmopolitan.

REITTER (1911, p.316) gives the following as the distinguishing characters of the species:

Whole body ferruginous or testaceous. Pubescence of prothorax entirely simple, directed backward and not parted in the middle. Length 2 - 2.5 mm.

An account of the general characters of the species in the various stages is given below.

c) CHARACTERS:

1) EGG

Size

The size of 340 eggs measured by the author was as follows:

- Length: 0.40 mm. (0.29 - 0.50 mm.)
- Diameter: 0.21 mm. (0.18 - 0.23 mm.)

These figures represent greatest length and greatest diameter. Eggs were held in position by placing on a slide made slightly sticky by a light smear of honey. This facilitated microscopical measuring.

RUNNER (1919) obtained the following measurements:

- Length: 0.45 mm. (0.44 - 0.46 mm.)
- Diameter: 0.20 mm. (0.19 - 0.21 mm.)

These figures show averages that agree closely with those obtained by the present author, but ranges that are smaller.

General description.

In shape, the egg is ovoid, elliptical, but the author has noted that most of the eggs are slightly asymmetrical, and that, while the cephalic pole is rounded, the opposite pole may be pointed (Pl. I, fig.A) or rounded (Pl.I, fig.B). Eggs may be somewhat distorted in shape when laid in very confined places, as narrow cracks or jammed in amongst other eggs, but this does not appear to affect hatching.

Translation by Dr. H. Andreae.
The surface of the egg, as described by RUNNER (1919), is smooth, without reticulation or sculpture except a portion at the cephalic pole which is covered with numerous papillae. (Pl. I, figs. A & B.).

In colour, the egg is pearly white at first, becoming more opaque and dull in colour as incubation proceeds.

ii) LARVA (Pl. I, fig. C).
Size.
The length of 2 groups of larvae was measured, one group having been killed by exposure in a cyanide killing bottle and the other by immersion for about 24 hours in kerosene.

Each group of larvae comprised 3 sets, namely, newly-hatched larvae, last-instar larvae reared on cigarette tobacco, and last-instar larvae reared on mealie meal. 100 larvae were measured in each set. Both sets of last-instar larvae were reared at 85°F and 75% relative humidity.

Newly-hatched larvae were collected and measured before any feeding took place, and last-instar larvae as soon as they started to construct their pupal cells.

Larvae were measured microscopically, and some difficulty was experienced owing to their curvature, especially the last-instar groups. In all cases, the larvae were arranged under the ocular micrometer scale with the dorsal side down, and gently straightened out by means of 2 dissecting needles. It was found easier to arrange the newly-hatched larvae on a slide made slightly sticky with a thin smear of honey.

Table I gives the average lengths obtained and the extremes (figures in brackets). In each set, the figures obtained through the two different methods of killing correspond closely and do not show that the cyanide had any contracting effect or that the kerosene had any swelling effect.
effect. It is presumed that either of these 2 methods is equally valid in larval measurements of this nature.
(Killing by immersion in boiling water, even for the shortest possible time, could not be used as it caused swelling and even bursting of the last-instar larvae reared on mealie meal.)

Table I: The lengths of different batches of larvae.

<table>
<thead>
<tr>
<th>DESCRIPTION OF LARVAL SET</th>
<th>KILLED BY MEANS OF CYANIDE</th>
<th>KILLED BY MEANS OF KEROSENE</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEWLY-HATCHED</td>
<td>0.49 (0.41 - 0.65)</td>
<td>0.50 (0.42 - 0.64)</td>
</tr>
<tr>
<td>LAST-INSTAR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOBACCO</td>
<td>3.01 (2.32 - 3.62)</td>
<td>2.90 (2.50 - 3.57)</td>
</tr>
<tr>
<td>MEALIE MEAL</td>
<td>3.45 (3.03 - 3.92)</td>
<td>3.41 (3.03 - 3.75)</td>
</tr>
</tbody>
</table>

A comparison between the 2 last-instar sets shows the greater size of larvae reared on mealie meal compared with tobacco. Amongst other developmental media, too, comparisons of this type can be made and it is apparent that, in general, quality of food affects larval size. This effect will be shown to persist through pupal and adult states.

General description.

The larva is scarabaeoid, and generally assumes a curved position, especially the older larvae.

The newly-hatched larva is semi-transparent. As it develops it gradually becomes more yellowish white in colour with chitinous parts brown. The presence of food in the alimentary canal or of faecal pellets or dust, from a dark foodstuff adhering to the larval hairs, may disguise the true yellowish white colour and give the larva a brownish appearance.
First-instar larvae are sparsely set with very long, pale hairs. Last-instar larvae are set entirely with long, silky yellowish brown hairs. The positions of some of these hairs have been described by Dr. Boving (RUNNER - 1919, p.14) as specific characters, as follows:

"Median region of epistoma with a row of 5 setae on each side, lateral regions naked; labrum with about 7 straight setae on the upper surface at each anterior corner, several long, medianly curved setae along the anterior margin and an oblique row of 3 shorter, stouter, hood-shaped setae on the under surface on either side of and posteriorly approaching the median line; clypeus naked; stipes labialis, mentum and submentum with long soft setae; maxillary articulating area not setiferous."

11) PUPA.

Size:
The length and width was measured of 4 groups of pupae, namely, female pupae reared on mealie meal, male pupae reared on mealie meal, female pupae reared on tobacco, and male pupae reared on tobacco. Each group comprised 100 pupae. All were reared at 85°F and 75% relative humidity. Measurements obtained, both averages and extremes (figures in brackets), are given in Table 2.

Table 2: The lengths and widths of 4 different groups of pupae.

<table>
<thead>
<tr>
<th>DESCRIPTION OF PUPAL GROUP</th>
<th>LENGTH (MM)</th>
<th>WIDTH (MM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FEMALE - MEALIE MEAL</td>
<td>3.25</td>
<td>1.56</td>
</tr>
<tr>
<td></td>
<td>(2.93 - 3.43)</td>
<td>(1.39 - 1.64)</td>
</tr>
<tr>
<td>MALE - MEALIE MEAL</td>
<td>2.99</td>
<td>1.44</td>
</tr>
<tr>
<td></td>
<td>(2.71 - 3.21)</td>
<td>(1.29 - 1.54)</td>
</tr>
<tr>
<td>FEMALE - TOBACCO</td>
<td>2.85</td>
<td>1.39</td>
</tr>
<tr>
<td></td>
<td>(2.46 - 3.14)</td>
<td>(1.21 - 1.57)</td>
</tr>
<tr>
<td>MALE - TOBACCO</td>
<td>2.62</td>
<td>1.27</td>
</tr>
<tr>
<td></td>
<td>(2.29 - 2.82)</td>
<td>(1.18 - 1.43)</td>
</tr>
<tr>
<td>AVERAGE</td>
<td>2.93</td>
<td>1.42</td>
</tr>
</tbody>
</table>

Table 2 shows the greater average size of pupae reared on mealie meal than of tobacco. It exemplifies the fact...
that the influence of quality of food on size, seen in the larval stage, persists in the pupal stage. Because it is possible to sex the pupae, a further size-factor can be diagnosed, namely, the difference in sizes of the two sexes - the average size of females is greater than that of males reared on the same foodstuff. The ranges, however, overlap to some extent, thus excluding measuring as a reliable means of sexing.

General description:-

The pupa (Pl. II, fig. A.) is naked and white with a very slight greenish tinge when first transformed. This colouration may be uniform, but, most frequently, some pigmentation of the eyes is evident as soon as the larval skin has been shed from them and before the skin has been shed from them and before the skin has reached the terminal segments of the emerging pupa.

The pupa has externally all the adult characters. The tips of the elytra attain the fourth visible ventral segment of the abdomen. The metathoracic legs lie beneath the elytra and do not attain the tips of the inner wings. The head is bent upon the thorax and beneath the pronotum.

RUNNER (1919) has ascribed to each of the ultimate and penultimate abdominal segments, a pair of fleshy, latero-ventral protuberances. He has, however, not discriminated between the terminal segments of male and female pupae, and has illustrated only a female pupa. The author has not been able to trace any literature referring to this sexual dimorphism among the pupae of this species, nor any illustration of the male pupa.

In the female pupa appendages are present of the ultimate pair of lateral lobes. These are very distinct and are absent in the male. (Compare text figs. 5 and 6; and on Pl. II, figs. A & B).
This clear structural difference provides a reliable way of sexing living pupae. This is of great practical importance in bionomical work, especially as there appears to be no way in which to sex living adults from external differences.
Two factors may, however, prevent sexing in this way. Firstly, the last larval integument may adhere to the terminal segments of the pupa in the position illustrated on Pl. I, fig. D.4. It may be impossible to remove the integument without injury to the pupa, but the number of times sexing is prevented in this way is insignificant. Secondly, in a very old pupa, when the lateral lobes are disappearing and the terminal segments have started to invaginate (described below), sexing in this way is impossible.

iv) ADULT.

Size.

The length was measured of 4 groups of adults, namely, females reared on mealie meal, males reared on mealie meal, females reared on tobacco, and males reared on tobacco. Each group comprised 300 individuals. All were reared at 85°F and 75% relative humidity. Measurements obtained, both averages and extremes (figures in brackets), are given in Table 3. Frequency distribution curves (Pl. IV, A & B) were constructed from the individual measurements.

### Table 3: The lengths of 4 different groups of adults.

<table>
<thead>
<tr>
<th>DESCRIPTION OF ADULT GROUP</th>
<th>LENGTH (MM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MALE - MEALIE MEAL</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>(2.08 - 2.84)</td>
</tr>
<tr>
<td>FEMALE - MEALIE MEAL</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>(1.71 - 2.59)</td>
</tr>
<tr>
<td>MALE - TOBACCO</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>(1.58 - 2.46)</td>
</tr>
<tr>
<td>FEMALE - TOBACCO</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td>(1.46 - 2.34)</td>
</tr>
<tr>
<td>AVERAGE</td>
<td>2.2</td>
</tr>
</tbody>
</table>

On Plate IV the average of all 4 groups, 2.2 mm., is denoted by mm. It is noted that the bulk of the mealie meal measurements is greater than the mean, while the bulk of the tobacco measurements is smaller. This illustrates the fact that influence of quality of food on larval size...
persists in the adult stage. It has already been seen in the pupal stage. The adults, themselves, very probably do not feed.

Dead adults were sexed after they had been measured. This method of sexing is described later. The difference in size of the 2 sexes seen in the pupae, is evident here too. The average size of the females is greater than that of the males within the same foodstuff.

The overlap of size-ranges of males and females is sufficient to preclude the use of size as a reliable criterion of sex. As far as is known, there are no external characters differentiating male and female adults.

General description.

The adults (Pl. II, Fig. C) is elongate-oval and moderately convex. It is a uniform brownish red or reddish yellow. The whole body is pubescent. The punctuation of the upper surface is fine, uniform, and not dense. That of the prothorax is directed backward and not parted in the middle.elytra are not striate.

The head is broad and strongly inflexed. The eyes are small. Antennae (Pl. II, Fig. D) are serrate and rather narrow. The second and third joints are smaller than the first, the third distinctly triangular; the fourth to tenth about as wide as long, the eleventh oval.

The thorax is strongly convex. Front angles are acute, but hind angles are wanting.
VII - BIONOMICS.

1. GENERAL TECHNIQUE.

a) Stock cultures:

A continuous supply of insects was obtained from about 20 dual-display jars filled with infested "army" biscuits and kept in a breeding room at 85°F and 60 - 70% relative humidity. These proved very satisfactory as stock cultures because about the only attention they required was the occasional addition of fresh biscuits. Mealie meal cultures were very suitable for experimental work but not as stock cultures as they declined too rapidly and had constantly to be renewed.

b) Experimental cultures:

(1) Mealie meal (Text fig. 4).

Mealie meal cultures for experimental work were set up as described by BARBET AL. (1947, p.2) but the mealie meal was used pure and not mixed with yeast.

Cultures were started and cleared as described in the same paper on pp. 3 - 4, and adults were handled as described on p.3. In bionomical work, wherever numbers of live adults had to be handled, this suction device was used, e.g. where adults were confined with sections of tobacco midrib to obtain egg cultures.

A culture in a pint fruit jar, started with 300 active, newly-matured adults, generally resulted in about 600 - 800 new adults. Where smaller cultures were required, as where jars had to fit into dessicators, a correspondingly small number of adults was introduced to prevent overcrowding.

In a mealie meal culture of this type, adults, on leaving the pupal cell, chew their way straight to the surface of the mealie meal where they are immediately visible. This fact enabled accurate estimates in large numbers to be made of the lengths of larval to adult stages, as 20/...follows....
follows:-

When a large batch of larvae hatched in a stock egg culture on the same day, this date was noted and the larvae collected by transferring singly on a pin-point to a small square of black paper. When all had been collected, the paper was placed face-down on the surface of a mealie meal culture, so that the larvae came in direct contact with the mealie meal.

As soon as larvae and pupae had developed and resulting adults became visible on the surface of the mealie meal, the date was noted, and the number of emergents. The culture was then completely cleared. This gave the time taken for the development of a known number of adults. This dating and counting was repeated for each daily batch. When all had emerged, the average length of the larval to adult stage \( x \) of the whole group of emergents, at the temperature and humidity to which the culture was exposed, could be calculated.

For all work in dessicators, about 100 - 200 larvae were placed in small jars about 10 cm. tall and 5 - 6 cm. in diameter.

Another advantage of a mealie meal culture is that, where pupation occurs up against the glass, (Text fig.4), daily developments in the pupal cells can be recorded. To make these records, an ink ring was drawn on the glass around a larva as soon as it started constructing a cell. The rings were numbered and a daily record of development in each cell was kept. When the adult finally left the cell, ring and number were erased. In this way, average prepupal, pupal and resting adult stages could be calculated; and also the total average prepupal to active adult stage \( y \). All the data could be obtained from one culture.
With reference to this technique, tall, narrow jars were preferable to short, wide ones. Further, where a larva was ringed and numbered, but disappeared from view through constructing one wall of the pupal cell up against the glass, or through crawling back into the mealie meal, ring and number were erased and the observations had to be discontinued. It was impractical to remove pupal cells from the culture under observation and break them open to record development as, among other difficulties, the pupal cells are hard and the occupants easily damaged.

In conclusion, a single mealie meal culture can give values for both x and y (described above); and a subtraction of y from x gives the average length of the larval stage for any particular set of conditions. This method was used in Table 8 in some instances.

ii) Tobacco:

Tobacco cultures, similar to the mealie meal type described above, were used when large numbers of adults were required, e.g. for determining sex ratios or obtaining copulating couples for oviposition and longevity experiments. Here, finely-divided tobacco, or shredded cigarette tobacco was used and tamped down well in the jar, as described by BARE etc (1947) for mealie meal.

On the whole, however, individual observations were made on larval development in tobacco by confining a single larva in a vial (about 1.5 cm. diam. and 5.2 cm. tall - hereafter referred to as a "small vial") with a small, flat square of leaf not bigger than 2" sq. This was renewed when necessary. An average-sized dessicator held about 50 of these vials comfortably.

In this way daily observations could be made, generally without opening up the vial and removing the contents. Pupal cells were often constructed up against the glass in which case observations could be made as with the mealie
meal cultures. Where, however, the contents of the pupal cell were not visible, the cell could easily be opened slightly, as it is much more delicate than that constructed in mealie meal.

When such observations began with newly-hatched larvae, the length of the larval, prepupal, pupal and resting adult stages could be accurately determined for a given set of conditions.

c) Observations on eggs:

(i) Large egg batches:

Where large numbers of eggs were required, as for determining viability and incubation period or obtaining newly-hatched larvae, the following procedure was adopted:

The lamina was stripped from the midrib of a tobacco leaf and the midrib cut into sections about 4 cm. long. Each section was smoothened off with a blade so that there were no depressions or irregularities except the one main central groove. This was also filed down so that it was even and very shallow.

Such a section of midrib was placed in a ½-pint fruit jar with about 200 active adults and left for 24 hours.

The adults generally laid the majority of their eggs in the central groove of the midrib. If this was suitably shallow and regular, the eggs could be clearly seen and, being laid one behind the other in the groove, could easily be counted. (Text fig.7). When counts were made, eggs that were not laid in the groove but irregularly over the midrib, or were so obscured as to make observations difficult, were destroyed by piercing with a very fine pin.

A section of midrib left for 24 hours with about 200 newly-emerged adults often had 50-200 eggs laid in the groove. For the bigger experiments such as exposure of eggs to cold or heat, about 6-12 jars were set up with midribs and adults, the adults being obtained from stock...
cultures or, sometimes, mealie meal cultures. If it was necessary, (as with these experiments on control) to determine viability alone, a couple of sections of midrib were placed in each jar and left for a couple of days before removing and counting the eggs. Where, however, the incubation period was required, a single midrib was placed in the jar for a maximum of 24 hours. All the eggs were presumed to have been laid on the day on which the midrib was removed from the jar. Subtracting this date from the date on which the first hatchings occurred, gave the period of minimum incubation.

Fig. 7 - A small section of tobacco leaf midrib showing eggs laid in the groove (x 26).

A jar of 200 active, newly-matured adults generally gave a supply of eggs over a period of about 4 days.

This technique was found to be more satisfactory than that described by BARE ETC. (1947, p.3). Further, it
involves no handling of the individual eggs. It was found impossible to make observations on the viability and incubation period of eggs by transferring them to slides made slightly sticky by a thin smear of honey, as is often suggested, as the eggs are generally glued down onto the surface on which they are laid and a large number are damaged on transference.

Midribs were handled by constructing trays (text fig. 8) as follows:–

A rectangle of corrugated cardboard about 4 cm x 10 cm. was fixed to a bigger piece of heavy cardboard by means of 2 paper clips. Midribs fitted neatly into the grooves of the corrugated cardboard, which were numbered for record purposes. The sides of the heavy card base were sloped so that two such trays fitted into the average dessicator.

Immediately on removal from the jars, the sections of midrib were placed in the trays. The whole tray was placed on the stage of the dissecting microscope for counting and general observations. Such trays of eggs kept in dessicators and at controlled temperatures and removed daily for observation, could give information on the viability and incubation period of large numbers of eggs and provide large numbers of newly-hatched larvae.

It is to be noted that larvae must be removed from the midribs as soon as they hatch. If not, they tend to start feeding on other unhatched eggs thus upsetting records; or they may burrow into the midribs spoiling them for future use.

11) Number of eggs per female

Where it was desired to record the number of eggs laid per female beetle, the following procedure was adopted:–

A mealie meal or tobacco culture was cleared and copulating couples removed from among the adults that emerged within the following 24 hours. Each couple was
Fig. 8 - A cardboard tray for holding tobacco leaf midribs on which eggs have been laid.

placed in a small vial. Each vial was numbered and a record kept of the date of emergence of the couple. After 24 hours the cultures were again completely cleared in readiness for the next batch of emergents. In this way the date of emergence of a couple was always accurately known.

A couple in copula could be gently transferred from the culture to the small vial without causing the beetles to separate. Therefore, it was considered that this transference did not disrupt the copulation in any way and had no detrimental effect on future egg-laying.

A small section of midrib was placed in each vial; each section was about 1.5 cm. long and cut with sloping ends to facilitate microscopic examination. Further, the section was smoothened off and the groove cut down so that it was shallow and even, as previously described. Vials were placed in dessicators at controlled conditions of temperature and humidity.

Whenever observations were made, generally every 2 or 3 days, the vials were removed, opened, and both vial and midrib examined microscopically for eggs. The majority of
the eggs were laid on the midrib and were easily located and counted. As some of the eggs were sometimes laid on the sides and base of the vial, these were also always examined microscopically and the eggs counted. As the surface was glass and the vial small, this examination was not difficult, especially if done against a black background. The muslin covers were never examined, as the proportion of eggs laid on these in a few test cases appeared to be negligible.

After an examination, the number of eggs was recorded, all the eggs were cleared from both midrib and vial, and the midrib and adult pair replaced in the vial. The vial, in turn, was replaced in the dessicator at the original temperature and humidity.

These small sections of midrib could be used repeatedly in this way, unless they became mildewy, in which case they were discarded and replaced by fresh ones.

From this type of experiment, the total number of eggs laid by a female could be calculated as well as her longevity and that of the male. As soon as one beetle died it was removed and sexed, as described below, and as the date of emergence was known, the longevity of males and females could be calculated separately.

d) Sexing of adults:

Pupae alone could be sexed from external differences, as previously described. With adults, couples in copula had to be collected for oviposition and longevity experiments to make sure that a true pair was obtained. When these died they were sexed. Samples of dead adults were also sexed to obtain sex ratios, (when not enough pupae were available), and to obtain figures on the correlation of size and sex.

Sexing was done as follows:-

Adults were placed separately in small vials with a little unheated 10% potassium hydroxide for about 24 hours
if specimens were old and dried, longer if fresh. It often facilitated sexing if the abdomen was dissected off and alone left to soak in the potassium hydroxide.

On removal, the beetle or abdomen was placed with ventral side up on a slide and examined microscopically. The shape of the genitalia "in situ" could be clearly seen through the sternites especially if the specimen was examined against a white illuminated background. Where the beetle had been left intact, it was necessary to arrange the abdomen so that light was not blocked from the dorsal side by the elytra.

The distinctive shapes showing through the sternites have been diagrammatically represented for the male (Plate III, fig. B) and the female (Text fig.9.). What these shapes represent is described below:

1) Male genitalia.

The male genitalia are shown on Plate III, dorsally (fig.A) and laterally (fig. C). Terminology is based on IMMS (1948, p.156) and SHARP & MUIR (1912). The author is well aware that this is a highly controversial field and that the terms used here are open to criticism. The nearest systematic relations described by SHARP & MUIR (1912) are various members of the Ptinidae, from which Lasioderma serricorne differs in certain respects. A description of the male genitalia of Lasioderma serricorne follows.

The aedeagus is strengthened with a thin, chitinous, rod-like supporting structure. (SS).

The aedeagus itself is composed of a proximal tegmen, a central median lobe (ML), and an internal sac (IS).

The median lobe is long, thin and curved with the point of articulation (PA) on the dorsal aspect. The median orifice (WO) is near the distal end on the ventral face. Through this orifice, the internal sac is evaginated. (Pl. III, fig.C). This sac bears an armature of stout

...29/...hooks....
hooks and hairs. It is the region of the aedeagus which completely enters the vagina of the female during coitus. At rest it is invaginated within the median lobe. The median foramen (MF) is near the proximal end of the median lobe on the dorsal face. Through this aperture, the ejaculatory duct (ED) passes.

The tegmen is the ring of sclerites around the proximal part of the median lobe and unites the aedeagus to the abdomen. It is composed of a basal piece (BP) and 2 lateral lobes (LL). The basal piece is a thin chitonous plate encircling the proximal end of the median lobe and joining at the point of articulation.

The lateral lobes lie laterally to the median lobe along its distal half. They are hairy distally.

ii) Female genitalia.

The female genitalia are shown "in situ" in text fig.9. The vagina is supported by a thin, chitonous supporting structure, and widens distally. At rest, the ovipositor lies telescoped within it. In this figure the ovipositor is shown partially evaginated.
Fig. 9 - Ventral view of abdomen of female showing genitalia in position - ovipositor partially evaginated.

e) Control of temperature and relative humidity.

To obtain the temperatures required for experimental work, the following devices were used.

- 105°F, 100°F, 95°F,
- 90°F and 75°F - two types of incubator.
- 85°F - a large breeding room.
- 70°F and 63°F - 2 brine-cooled rooms.
- 48°F - a large cool room for storing chemicals.
- 38°F - a household refrigerator.
- 10°F - a large fish-storage room.
- 5°F - a "deep-freeze" cabinet for making ice-cream.

lower temps - brine-cooled rooms.

Fluctuations in temperature were kept as low as possible with each device.
Relative humidity was controlled by doing all work in dessicators. These contained sulphuric acid solutions of various concentrations to control the vapour pressure of the air within the dessicator. Solutions were prepared according to tables compiled by Wilson (1921).

Within the small experimental cultures used, the temperature, to which the insects were exposed, was the same as the surrounding air temperature i.e. as the temperature recorded in the devices described above. It was decided to determine whether this applied to insect infestation in practice. For instance, was the temperature inside a bale of tobacco the same as the external air temperature? The determination was made as follows:

Temperature was recorded on a thermograph having two long heat-sensitive terminals. One terminal was placed at different depths and in different positions in the bale of tobacco and recorded internal temperature (A); the other was left outside the bale to record external room temperature (B). The test bale measured 34" x 28" x 24" and weighed about 220 lbs. It was covered with a single layer of waterproof paper, and a single layer of hessian external to this. Before recordings commenced the bale atmosphere was allowed to reach equilibrium with that of the store room. Average weekly temperatures are given in Table 4 for both A and B. Readings were spread over both winter and summer.

**Table 4:** Temperatures inside a bale of tobacco (A) correlated with external room temperature (B).

<table>
<thead>
<tr>
<th>DEPTH IN BALE (INCHES)</th>
<th>TEMP. (OF) A</th>
<th>TEMP. (OF) B</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>72</td>
<td>74</td>
</tr>
<tr>
<td></td>
<td>69</td>
<td>71</td>
</tr>
<tr>
<td></td>
<td>61</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>60.5</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>59</td>
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<tr>
<td>9</td>
<td>61</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>61</td>
<td>61</td>
</tr>
</tbody>
</table>

32/...Table 4 continued..
Table 4 shows that average external air temperatures only exceed average internal bale temperatures by about 1°F, over temperatures ranging from 57 - 72°F. The maximum difference recorded between A & B for any week was 3°F. These differences are not significant where general activity and development of the insect are concerned, unless critical temperatures are being considered.

Thus, for practical purposes temperature inside and outside a bale of tobacco can be considered the same; and if the atmosphere surrounding the bale has a temperature of x°F, then results obtained in experimental cultures at x°F can be applied to insects infesting the bale.

With reference to Table 4, it is to be noted that insect infestation seldom extends beyond 6 - 8".

<table>
<thead>
<tr>
<th>DEPTH IN BALE (INCHES)</th>
<th>TEMP. (°F)</th>
<th>TEMP. (°F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>60</td>
<td>62</td>
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<tr>
<td></td>
<td>59</td>
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<td>61</td>
<td>61.5</td>
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<tr>
<td></td>
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<td>60</td>
</tr>
<tr>
<td></td>
<td>59</td>
<td>60</td>
</tr>
<tr>
<td>AVERAGE</td>
<td>61.4</td>
<td>62.5</td>
</tr>
</tbody>
</table>
2. **THE EGG STAGE.**

a) **Viability and incubation period:**

Table 5 gives the viability and incubation period of eggs under 3 different sets of conditions, namely, 75% relative humidity and various temperatures, 44% relative humidity and various temperatures, and 85°F and various humidities. From the figures given, the graphs on Plates V (viability) and VI (incubation period) have been constructed.

In Table 5, each total number of eggs observed was composed of several different batches of eggs laid at different times, and the number of separate batches per condition was never less than 7, and sometimes as many as 27.

Hatching at the lower humidities was sometimes only partial, i.e. the larva chewed open the shell but died before leaving the egg completely. These were counted as hatched. Eggs were kept under observation for at least 30 days if there was no sign of hatching.

The average incubation periods given are the average minimum periods of the different batches (See TECHNIQUE - observations on eggs (i)).

Where mould developed at the highest humidities, it was scraped daily off both midribs and eggs as completely as possible. It obscured the eggs if left, but apparently had no detrimental effect on their actual development.

**Table 5:** The viability and incubation period of eggs at various conditions of temperature and relative humidity.

<table>
<thead>
<tr>
<th>TEMP. (°F)</th>
<th>R.H. (%)</th>
<th>TOTAL NO. OF EGGS</th>
<th>% HATCHED</th>
<th>AVERAGE INCUBATION (DAYS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>105</td>
<td>75</td>
<td>397</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>85</td>
<td>492</td>
<td>80.3</td>
<td>5.6</td>
</tr>
<tr>
<td>95</td>
<td>85</td>
<td>352</td>
<td>99.7</td>
<td>5.0</td>
</tr>
<tr>
<td>85</td>
<td>75</td>
<td>234</td>
<td>100</td>
<td>5.5</td>
</tr>
<tr>
<td>75</td>
<td>70</td>
<td>216</td>
<td>99.5</td>
<td>8.8</td>
</tr>
<tr>
<td>70</td>
<td>63</td>
<td>236</td>
<td>99.6</td>
<td>14.0</td>
</tr>
<tr>
<td>63</td>
<td>48</td>
<td>199</td>
<td>91.9</td>
<td>20.9</td>
</tr>
<tr>
<td>48</td>
<td>158</td>
<td></td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>

34/...Table 5 continued...
Table 5 continued...

<table>
<thead>
<tr>
<th>TEMP. (°F)</th>
<th>RH. (%)</th>
<th>TOTAL NO. OF EGGS.</th>
<th>% HATCHED</th>
<th>AVERAGE INCUBATION (DAYS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>105</td>
<td>44</td>
<td>150</td>
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</tr>
<tr>
<td>90</td>
<td>429</td>
<td>660</td>
<td>2.1</td>
<td>7.3</td>
</tr>
<tr>
<td>90</td>
<td>321</td>
<td>88.4</td>
<td>5.5</td>
<td></td>
</tr>
<tr>
<td>85</td>
<td>203</td>
<td>100.0</td>
<td>6.7</td>
<td></td>
</tr>
<tr>
<td>75</td>
<td>241</td>
<td>99.1</td>
<td>8.1</td>
<td></td>
</tr>
<tr>
<td>70</td>
<td>476</td>
<td>98.9</td>
<td>15.0</td>
<td></td>
</tr>
<tr>
<td>65</td>
<td>249</td>
<td>85.8</td>
<td>20.0</td>
<td></td>
</tr>
<tr>
<td>45</td>
<td>236</td>
<td>0.0</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>85</td>
<td>100</td>
<td>143</td>
<td>97.2</td>
<td>6.2</td>
</tr>
<tr>
<td>90</td>
<td>221</td>
<td>93.2</td>
<td>5.7</td>
<td></td>
</tr>
<tr>
<td>85</td>
<td>199</td>
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<td>100.0</td>
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<td>35</td>
<td>219</td>
<td>5.0</td>
<td>10.2</td>
<td></td>
</tr>
</tbody>
</table>

Tables and graphs give the following data with reference to viability and incubation period.

Viability:
1) Viability (Pl. V; fig.A) is practically 100% between 70 - 90°F for both 44% and 75% relative humidities.
2) At 75% R.H. it is also practically 100% at 95°F. There is a sudden drop to the upper critical temperature which lies between 100 - 105°F. At 44% R.H. this critical temperature is nearer 100°F.
3) The lower critical temperature for both humidities lies between 48 - 63°F. According to CRUMB & CHAMBERLIN (1934) this temperature is about 56°F.
4) At 85°F and various humidities (Pl. V, fig.B) viability does not decline significantly until the humidity has fallen below 32%. Thereafter it declines steadily.

Incubation period:
1) Incubation period (Pl.VI, fig.A) appears to be shortest at 90°F for 44% R.H. (5.5 days) and at 95°F for 75% R.H. (5.0 days).
2) Above and below optimum temperatures, the period lengthens to much the same degree for both 75 and 44% R.H.

35/.....3)At........
3) At 85°F, (Pl. VI, Fig. B) relative humidity has little effect on the incubation period, until the humidity falls below 23% when the period is prolonged.

b) Development.

The following are daily observations on the development and hatching of the eggs:

1st & 2nd day: Egg pearly white and transparent - slightly more opaque at cephalic pole.

3rd & 4th day: Rest of egg almost as opaque as cephalic pole which is no longer so clearly distinct.

5th day: Whole egg opaque. Larval mandibles pigmented and visible as two small triangles at cephalic end. Sometimes outline of larva faintly visible through shell.

6th day: Egg hatching. Larva generally chews through shell at approximately the posterior margin of the papillated region so that this lifts up like a cap and the larva emerges through this opening.

7th day: Larva often eats whole egg-shell, especially if no other food is available, when it may also attack other unhatched eggs.
3. **THE LARVAL STAGE.**

a) **Larval feeding:**

As previously discussed, it is the larval stage which actually consumes the infested commodity.

Of the great variety of materials attacked, two have been chosen for comparative developmental purposes. These are tobacco, chosen for its low carbohydrate content and great economic importance, and mealie meal, chosen for its contrastingly high carbohydrate content and because it is so satisfactory as an experimental medium.

The tobacco used throughout was 1st grade flue-cured Virginian leaf (class (b) FC/AS) defined in the GOV. GAZETTE EXTRAORD. (1939, p.824).

1) **Nutrition.**

Table 6 gives the constituents of generalised samples of the two experimental media. For the tobacco, nicotine content was obtained from BOVINGDON (1933) and the other percentages from WILEY (1914, p.730). For the mealie meal, all percentages were obtained from HENRY & MORRISON (1923, p.709).

Table 6: The constituents of tobacco and mealie meal.

<table>
<thead>
<tr>
<th>CONSTITUENT</th>
<th>TOBACCO</th>
<th>MEALIE MEAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture</td>
<td>E</td>
<td>10 - 25</td>
</tr>
<tr>
<td>Ash</td>
<td>15 - 25</td>
<td>10 - 20</td>
</tr>
<tr>
<td>Protein</td>
<td>7 - 13</td>
<td>9 - 10</td>
</tr>
<tr>
<td>N-free Carbohydrates,</td>
<td>8 - 10</td>
<td>1.5 - 2.0</td>
</tr>
<tr>
<td>extract</td>
<td>3</td>
<td>63 - 70</td>
</tr>
<tr>
<td>Fat</td>
<td>3</td>
<td>4.5 - 5.0</td>
</tr>
<tr>
<td>Nicotine</td>
<td>1 - 4</td>
<td>-</td>
</tr>
</tbody>
</table>

In Table 6, the figures given for the moisture content of tobacco apply to ordinary atmospheric humidities. Tobacco is very hygroscopic and the change of moisture content with air humidity is given in Table 7.
The figures in Table 7 have been obtained from BOVINGDON (1933, p.58), from the United Tobacco Co., and the moisture contents corresponding to 44% and 32% R.H. were determined by the author according to the method laid down by H.M. customs, which involved heating of samples in an electric oven for 15 hours at 100°C. These two humidities, 44% and 32%, were found to correspond to 9.5 and 7.8% moisture content respectively. Newly-hatched larvae at 85°F, developed on tobacco at 44% but not at 32% relative humidity. Thus the critical moisture content of tobacco for the development of newly-hatched larvae, lies between 7.8 and 9.5% at 85°F.

Table 7: The moisture content of conditioned tobacco leaf at various relative humidities.

<table>
<thead>
<tr>
<th>RELATIVE HUMIDITY (%)</th>
<th>MOISTURE CONTENT (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>3.7</td>
</tr>
<tr>
<td>32</td>
<td>7.8</td>
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<tr>
<td>44</td>
<td>9.5</td>
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<td>18.5</td>
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<td>75</td>
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<tr>
<td>80</td>
<td>26.5</td>
</tr>
<tr>
<td>100</td>
<td>67.2</td>
</tr>
</tbody>
</table>

Storage of tobacco at this low range of relative humidity would, therefore, control infestation, but is not practical as the tobacco becomes brittle and high losses in handling due to breaking and crumbling are caused. (NAUDE & SICHEL, p.1). High humidities during storage cause reduction in condition and the possible development of mould. Government regulations in various countries generally stipulate that tobacco must contain between about 11 - 14% of moisture by weight, and this is well within the limits of the moisture content required to make it susceptible to infestation by Lasioderma serricorne.
Even at a maximum of 4% (Table 6), the nicotine in cured tobacco has no apparent ill-effect on the development of the larvae. (BOVINGDON - 1933).

Table 6 shows that the chief difference between the constituents of mealie meal and tobacco is the amount of carbohydrate present, 64 – 72% total carbohydrate in the former, 11 – 13% in the latter. FRAENKEL & BLEZETT (1943) showed that the presence or absence of carbohydrates was a determining factor in the natural distribution of a variety of insects on different foods. The fact that Lasioderma serricorne can develop in the absence of carbohydrates means that it can infest a much wider variety of natural foods, than insects like Ephesia kühniella, Sitodrepa sp. and Silvanus sp. which must have carbohydrates.

Nevertheless it has been shown in this discussion that in mealie meal, with its high carbohydrate content, all stages of Lasioderma serricorne grew bigger than corresponding stages in tobacco, with its low carbohydrate content. Further, it will be shown that larval development is quicker in mealie meal and adult longevity greater. In this respect, although there are some conflicting reports, most authorities agree that the larvae attack the higher grade tobacco leaves more readily than the lower. The better grades are said to be sweeter, i.e. contain more sugars, than the lower.

The author has not traced any references to changes in the constituents of tobacco during curing, or to factors preventing attack on unfermented or growing tobacco. It is generally considered that the larvae "prefer" the older leaves in the most advanced stage of fermentation. According to RUNNER (1919) and others, the way in which leaf is cured sometimes affects its susceptibility to attack. Thus, flue-cured tobacco is often more readily attacked than fire-cured.
Further experiments by Fraenkel & Blewett (1944), point to the probable presence of intracellular symbionts in the larvae. These are considered to supply vitamins of the B group, enabling larvae to develop in foodstuffs lacking these vitamins. This may be a further factor enabling the larvae to attack such a variety of materials.

i) Feeding habits

According to Runner (1919) newly-hatched larvae can live for 5 - 10 days without food, but according to Van Der Veen (1940) they survive a maximum of 48 hours.

On emergence, they are much more active than at later stages and capable of crawling a considerable distance in search of suitable food. Also, in the earlier stages they tend to migrate from infested to uninfested materials. According to Van Der Veen (1940) they are able to chew through such wrappings as twill, packing paper, cellophane and sisal-kraft paper, and the perforations are so minute that they are practically invisible.

In leaf tobacco, larvae, as they feed, tunnel out long cylindrical galleries especially near the midribs. They tunnel in all directions making damage very diffuse. In samples of baled tobacco examined in Russia, 40 - 60% of the leaves bore traces of infestation, whereas, generally only about 2% of the leaf surface was actually destroyed (Ustinov 1932). Where several larval tunnels meet and cross, irregularly-shaped holes are formed (Text fig.1). Brown, dust-like frass is evident on an infested leaf.

Tobacco in the interior of bales is seldom attacked, damage generally being confined to the cut 6 - 8". According to Keuchenius (1917), this is probably because of the carbon dioxide, ammonia and other gases generated in the centre.

In mealie meal cultures, eggs are laid on the surface, and resulting larvae feed down into the mealie meal in all directions.
Larvae are negatively phototropic, at least in the immature stages, and when exposed, tend to hide in the folds of the leaf.

b) Larval development.

i) Rate of development:

With reference to rate of development, two tables (8 & 9) have been compiled not only for the larval stage, but also for the prepupal, pupal, resting adult, total larvae to active adult, and total egg to active adult stages in both mealie meal and tobacco at various temperatures and relative humidities.

Table 8:

Table 8 gives the average rate of development for each condition. Some of the averages are calculated, e.g. the egg to active adult stage, which is calculated using average incubation periods given in Table 5. Dashes denote no development of newly-hatched larvae was seen to occur, and blanks denote no observations made.

Table 9:

In Table 9, where possible, the range in days of rate of development for each set of conditions is given, and also the number of observations (figures in brackets) made to determine the averages in Table 8. Blanks denote no observations made, though they may have been calculated in Table 8. As all the egg to active adult stages have been calculated in Table 8, these columns have been omitted altogether in Table 9. Dashes denote that no development of newly-hatched larvae was seen to occur.

From the average "egg to active adult" stage as given in Table 8, the graphs on Pl. VII have been constructed. Tables and graphs show 3 of the factors that definitely influence rate of development, the fourth is controversial. The factors are as follows:—
Table 8: Rate of development of various stages at different temperatures and relative humidities in tobacco and mealie meal.

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<th>TEMP.</th>
<th>R.H.</th>
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<th>Pupa</th>
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- I4 -
Table 9: (1) The range, in days, of the developmental periods given in Table 8. (2) The number of observations made to determine the average lengths of stages in Table 8. (Figures in brackets).

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1) **Nature of larval foodstuff** - development in mealie meal is more rapid than in tobacco.

2) **Temperature** - In both media at 75% R.H., the optimum temperature-range, that causing most rapid development, is about 85 - 95°F. The upper critical temperature for newly-hatched larvae lies between 95 - 100°F, and the lower between 45 - 63°F, perhaps between 55 - 60°F. However, older larvae may be able to withstand this low temperature. Larvae, and in particular these older larvae, are the stage most resistant to low temperatures. In very severe winters, the larvae which remain dormant until temperatures rise, are most likely to survive. They are therefore considered to be the hibernating stage. If temperatures are low, but not quite low enough to cause actual hibernation, they make development continuous but extremely slow. Thus at 63°F it was observed that the larval stage was at least about 106 days in tobacco, and about 65 in mealie meal. Development was also protracted in subsequent stages, and to such an extent that lack of time prevented these observations being completed up to the time of writing.

At 44% R.H., the optimum temperature is slightly lower than at 75% R.H. Above and below this, development is prolonged and critical temperatures are much the same as at 75% R.H. Survival rate of newly-hatched larvae is very low at 95°F and 44% R.H. in tobacco.

3) **Relative humidity** - Larvae develop over a more limited range of humidity in tobacco than mealie meal. In the former the optimum is probably about 75%, while in the latter it is probably slightly higher. Above and below the optimum, in both cases, development is lengthened. Especially at higher humidities, where the foodstuff becomes mouldy, survival rate is very low, e.g. in tobacco at 85°F and 95% R.H.

The lower critical humidity lies between 32 and 44% for newly-hatched larvae in tobacco, but is even lower than
23% in mealie meal, and in this region development is very prolonged.

4). Some oviposition factor - The ranges given in Table 9. show that there is considerable variation in the rate of development of larvae even when kept under the same physical conditions and on the same foodstuff. Howe (1956) noted this in the case of "Pitius tectus" and suggests that the rate of development of a larva may be influenced by the age of the adult beetle at the time when the egg was laid. This applies even to a short period of egg-laying, namely 10 days.

A further factor influencing rate of development, and one not illustrated here, has been mentioned by Runner (1919), namely, the form of the larval foodstuff. Foods in a compact or concentrated form e.g. pressed yeast cakes and pressed plug chewing tobacco, caused a higher rate of development than more diffuse foods, e.g. loose, shredded tobacco.

ii) Ecdisis.

A variation in the number of moults per larval stage has been noted.

21 larvae were examined daily while feeding on leaf tobacco at 85°F and 75% relative humidity. Results were as follows:-

14 had 4 moults (6 stadia)
4 " 3 " (4 " )
3 " 5 " (6 " )

Thus the average larva probably moults 4 times.

The stadia ranged from 7 to 9.5 days. The three larvae with 6 stadia had perforce the longest period of larval development.

The larva is generally quiescent for about 24 hours before moulting and ceases to feed. Sometimes it constructs a rudimentary cell from which it emerges after moulting to continue feeding.
During ecdysis, firstly, a median dorsal split occurs in the head capsule of the old integument. This allows the capsule to slip forward over the larval head and to be worked down with the rest of the exuviae to the posterior region of the body where the whole of it is cast off. The process is the same as that illustrated for the emergence of the pupa (Pl. I, figs., D, 1 - 4). During the process, the larva contorts its body to work the integument down its length.
4. THE PREPUPAL, PUPAL AND RESTING ADULT STAGES.

a) Metamorphosis:

At the end of the final stadium, the mature larva constructs the pupal cell, generally near the surface of the foodstuff. In tobacco, this cell is fragile and composed of frass and small particles of tobacco cemented together by a secretion of the larva. The pupal cells are generally ovoid and large enough to permit free movement, but vary considerably in shape and completeness, this depending largely on the location of the cell and character of the food substance. In leaf tobacco, the larva frequently utilizes folds in the leaf for part of the cell. It may also use an angle between two surfaces of a container e.g. between base and sides of a vial. On a flat surface it simply forms a covering over itself. Within dense food substances, as mealie meal, the surrounding material forms the necessary protection, the walls of the cell being thinly lined, though the cells may be constructed up against the surface of the container (Text fig. 4). Sometimes no pupal cell is constructed. It is then difficult to determine the onset of the prepupal stage. In the pupal cell, the larva lies quiescent while it undergoes structural changes preparatory to pupation. This is termed the prepupal stage, and according to RUNNER (1919), the body contracts somewhat and becomes more deeply wrinkled. But the prepupa is apparently not distinguished by any other external modification.

Immediately before pupation the body straightens out. Then the last larval integument is shed (as illustrated on Pl. 1, figs, D, 1-4, and as previously described under larval ecdysis) and the pupal stage commences. The larval integument generally lies free in the pupal cell, but sometimes remains attached to the terminal segments of the pupa until pupation terminates.
Pupae turn around freely in their cells although they generally lie on their backs.

The following daily observations were made on the external changes occurring during the development of the pupa, and resting adult, at 85°F and 75% relative humidity:

1st day: Outer perimeter of eye, and then finally whole eye, lightly pigmented.

2nd day: Eyes uniformly light brown.

3rd day: Eyes very dark brown. Inner edges of mandibles light brown. Whole pupa tinged with a light brown especially the wings.

4th day: Inner edge of mandibles darker. Head more pigmented than the wings. Lateral lobes of terminal segments disappearing. A very thin, transparent membrane is visible covering the whole pupa.

5th day: Enveloping membrane shed. Wings moved to dorsal side. This marks the onset of the resting adult stage. Adult soft, light brown. Abdominal segments posterior to the 5th visible sternite invaginating but still protrude beyond the elytra.

6th and 7th day: Adult darker and hardening. Terminal abdominal segments invaginated further but still projecting beyond elytra.

8th day: Adult completely pigmented and hardened. Terminal segments have invaginated so that the posterior margin of the 5th visible sternite is applied to the posterior margin of the last tergite. Abdomen covered by elytra. Adult is now ready to leave pupal cell and this marks the onset of the active adult stage.

The active adult chews its way out of the cell to the surface of the commodity it is infesting. It is then that adult life, involving mating and oviposition, commences.
The "egg to active adult" developmental periods given in Table 8 therefore include the following stages: - egg, larva, prepupa, pupa, resting adult.

b) Rate of development.

The prepupal, pupal and resting adult stages are affected in much the same way by foodstuff, temperature and humidity as previously described for the larvae; but as these stages are shorter the effect is not always so conspicuous. This applies especially when comparing the effects of the two different foodstuffs, tobacco and mealie meal. The lengths of the stages under various conditions are given in Table 8.
5. **THE ADULT STAGE.**

a) **Feeding:**

There is no evidence that either sex feeds in the adult stage. The only damage done by the adult is the chewing of an exit hole to reach the surface of the commodity in which it has pupated. Typical exit holes in the wrappings of cigarettes are shown in text fig. 2. The adult apparently lives on the reserves of nourishment acquired in the pupal stage.

b) **Copulation:**

There is no definite pre-oviposition period, copulation and oviposition can commence as soon as the active adult stage is reached. The author noted that copulation sometimes occurred the instant that adults reached the surface of a mealie meal culture, after making their way from the pupal cell. All adults, used in oviposition and longevity tests, had copulated on the first day of active life.

Further, copulation was often noted to occur more than once in the life of a single beetle. Whether more than one copulation is necessary to the female for complete oviposition is not known. DICK (1937) has suggested, on the basis of experiments on *Tribolium confusum*, that besides supplying spermatozoa, additional copulations may have a stimulating effect on the rate of oviposition.

No eggs were obtained from virgin females by the author. This agrees with the observations of RUNNER (1919), DICK (1937) and POWELL (1931).

The position of the adults in copula is shown in text fig. 10. The male initially climbs on to the dorsal surface of the female and extrudes the copulatory organ into the vagina of the female, before climbing down to one side and moving round to face in the opposite direction.

This process may take a few seconds, but pairs can remain in copula for anything up to several hours. A few instances were recorded when the length of the copulation exceeded...
exceeded 24 hours. Pairs in copula were generally stationary, but could move about freely if disturbed.

Fig. 10 - An adult pair in copula - male on left. (x 23).

(c) **Oviposition.**

(i) **Deposition.**

Eggs are generally laid singly and glued down onto the surface on which they are deposited. They are most often deposited in cracks, crevices, grooves or folds. A surface with such inequalities e.g. the tobacco leaf and midrib, is preferable to a smooth surface, e.g. paper or glass.

Both physical form of the oviposition site and odour play a part in inciting egg-laying, but, according to POWELL (1931), DICK (1937) and others, odour is relatively unimportant in comparison with physical form. Thus sand, crushed glass, sawdust, iron filings, wool, glass-wool and powdered potassium dichromate incited oviposition, provided that the size of the particles supplied was small enough. (POWELL - 1931). Sometimes the female will not lay at all if no suitable site is present.

In all experiments, discussed here, on the number of eggs laid per female, the oviposition sites were constant,
namely, a section of tobacco midrib placed in a small glass vial.

According to VAN DER VEEN (1940), adults can gnaw their way out of the pupal cell to the surface of a foodstuff, but they never gnaw their way back into the substance to oviposit, even through such a delicate fabric as thin muslin covering a bale of tobacco. The female can, however, pierce a covering, like muslin, with her ovipositor, and lay an egg on its inner surface or directly on the substance beneath.

ii) Number of eggs per female:

The number of eggs laid per female was determined using adults reared on mealie meal. Preliminary experiments showed no apparent difference between the number of eggs laid per female reared on mealie meal and the number per female reared on tobacco. Therefore results of oviposition experiments given in Table 10 can apparently be applied to females reared on tobacco as well as on mealie meal.

Table 10 gives the average number of eggs laid per female at various temperatures and relative humidities. 30 females reared on mealie meal were used per condition. Couples in copula were collected and immediately transferred to the conditions to which they were to be exposed. In all cases this was the first copulation of each of the pair, and occurred within 24 hours after emergence from the pupal cell. Oviposition sites were constant throughout.

Observations are graphically represented on Pl. VIII.

Results show that the optimum temperature, (resulting in the largest number of eggs laid per female), is 70°F. Above and below this temperature there is a steady decline in number.

The upper critical temperature probably lies between 160 - 100°F. At 44% relative humidity it is probably slightly lower than at 75%.
Table 10: The average number (and range) of eggs laid at various temperatures and relative humidities by females reared on mealie meal.

<table>
<thead>
<tr>
<th>CONDITIONS</th>
<th>TEMP.</th>
<th>R.H. %</th>
<th>AVE. NO. EGGS/ FEMALE.</th>
<th>RANGE.</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td></td>
<td>75</td>
<td>4.5</td>
<td>0 - 24</td>
</tr>
<tr>
<td>95</td>
<td></td>
<td></td>
<td>9.0</td>
<td>0 - 46</td>
</tr>
<tr>
<td>85</td>
<td></td>
<td></td>
<td>24.4</td>
<td>0 - 75</td>
</tr>
<tr>
<td>70</td>
<td></td>
<td></td>
<td>36.8</td>
<td>0 - 77</td>
</tr>
<tr>
<td>63</td>
<td></td>
<td></td>
<td>30.0</td>
<td>0 - 77</td>
</tr>
<tr>
<td>48</td>
<td></td>
<td></td>
<td>0.2</td>
<td>0 - 3</td>
</tr>
<tr>
<td>38</td>
<td></td>
<td></td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>100</td>
<td></td>
<td>44</td>
<td>0.2</td>
<td>0 - 3</td>
</tr>
<tr>
<td>95</td>
<td></td>
<td></td>
<td>5.6</td>
<td>0 - 25</td>
</tr>
<tr>
<td>85</td>
<td></td>
<td></td>
<td>17.1</td>
<td>0 - 50</td>
</tr>
<tr>
<td>70</td>
<td></td>
<td></td>
<td>28.3</td>
<td>0 - 61</td>
</tr>
<tr>
<td>63</td>
<td></td>
<td></td>
<td>12.3</td>
<td>0 - 32</td>
</tr>
<tr>
<td>48</td>
<td></td>
<td></td>
<td>0.1</td>
<td>0 - 2</td>
</tr>
<tr>
<td>38</td>
<td></td>
<td></td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>100</td>
<td></td>
<td>95</td>
<td>37.2</td>
<td>10 - 79</td>
</tr>
<tr>
<td>95</td>
<td></td>
<td>87</td>
<td>33.4</td>
<td>0 - 105</td>
</tr>
<tr>
<td>85</td>
<td></td>
<td>75</td>
<td>24.4</td>
<td>0 - 75</td>
</tr>
<tr>
<td>70</td>
<td></td>
<td>44</td>
<td>17.1</td>
<td>0 - 50</td>
</tr>
<tr>
<td>63</td>
<td></td>
<td>9</td>
<td>14.8</td>
<td>0 - 46</td>
</tr>
</tbody>
</table>

The lower critical temperature lies between 38° - 48°F for both humidities. This result contradicts the statement made by RUNNER (1919, p.22) that "eggs usually are not deposited at temperatures below 70°F." At 85°F and various humidities, 95% R.H. gave the highest yield of eggs which declined as the humidity declined. The yield at 75% R.H. was higher for every temperature-group than at 44% R.H.

iii) Oviposition period:

DICK (1937) has grouped the Coleoptera into 4 types according to their oviposition cycles. He has classified Lasioderma serricorne as the first type, viz., species which live only a short time as adults and lay all their eggs within a few days.

As previously mentioned, there is no definite pre-oviposition period. Oviposition can occur within 12 hours after copulation, and copulation can occur immediately the beetle embarks on the active adult stage.
Further, there are no definite inter-oviposition periods. Eggs are laid irregularly throughout the oviposition period.

The oviposition period itself is by no means clearly defined, and was noted to be anything up to 30 days. However, in the case of 100 females kept under various conditions, an average of 57% of the total number of eggs was laid within the first 3 days after the initial copulation. After this period, the percentage gradually tailed off.

d) Sex Ratio

To obtain the sex ratio in mealie meal, a total of 1,200 pupae in 4 different batches was sexed. Pupal cells were dropped into boiling water to disintegrate them and random samples of the freed pupae were sexed. To obtain the sex ratio in tobacco, 420 adults were sexed in 6 different batches of 70 each. Results were as follows:-

<table>
<thead>
<tr>
<th></th>
<th>In tobacco</th>
<th>In mealie meal</th>
</tr>
</thead>
<tbody>
<tr>
<td>males</td>
<td>46.4%</td>
<td>47.9%</td>
</tr>
<tr>
<td>females</td>
<td>53.6%</td>
<td>52.1%</td>
</tr>
</tbody>
</table>

The results show a slight preponderance of females in both media. This agrees with reports of RUNNER (1919, p. 21) and REED etc. (1935).

e) Longevity

Table 11 gives longevity of males and females reared on mealie meal and tobacco at 4 different sets of conditions. Each average was obtained from observations on 30 individuals.

Table 11 shows that, on an average, adults reared on mealie meal live longer than adults reared on tobacco. This applies even when comparing the longevity of the male reared on mealie meal with that of the female on tobacco. Thus, in contrast to oviposition, it appears that longevity of the adult is influenced by the nature of the foodstuff on which it developed in the larval stage.
Table 11: The average longevity of males and females, reared on tobacco and mealie meal, at 4 different conditions of temperature and relative humidity. (Range in Brackets).

<table>
<thead>
<tr>
<th>CONDITIONS</th>
<th>LONGEVITY IN DAYS</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEMP. °F</td>
<td>R.H. %</td>
</tr>
<tr>
<td>95</td>
<td>75</td>
</tr>
<tr>
<td>95</td>
<td>44</td>
</tr>
<tr>
<td>85</td>
<td>75</td>
</tr>
<tr>
<td>85</td>
<td>44</td>
</tr>
</tbody>
</table>

Further, longevity is influenced by sex and physical conditions as shown in Table 12 and, graphically on Pl. IX.

30 adults were observed to obtain each average given in Table 12, and all adults were reared on mealie meal.
Therefore, the results are applicable only to adults reared on mealie meal. For those reared on tobacco, longevity can be expected to be somewhat shorter, to the degree shown in Table 11.

That there is a difference in the longevity of the two sexes is evident in Table 12 and Pl. IX. With the exception of longevity at 85°F and 87% relative humidity, the average longevity of the female is greater than that of the male exposed to the same set of conditions.

The effect of physical conditions on longevity is also evident in Table 12 and Pl. IX. Both sexes are influenced in the same general way by various temperatures and relative humidities. Longevity is greatest at 48°F, and above and below this temperature it decreases fairly rapidly. Average longevity of the 2 sexes at 38°F and 75% R.H. is 34.2 days, which is in close agreement with the figure obtained by SWINGLE (1938), namely, 33 days at 40°F.

At 85°F and various relative humidities, the greatest longevity for the male is attained at 87% R.H.; whereas for the female at 75% R.H. Above and below these humidities the longevity decreases. At 75% R.H., over the whole range of temperatures, the longevity is practically always greater than...
than at 44% R.H., when the same sexes are compared.

Table 12: The average longevity (and range) at various temperatures and relative humidities, of male and female adults reared on mealie meal.

<table>
<thead>
<tr>
<th>CONDITIONS</th>
<th>LONGEVITY IN DAYS</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>TEMP.</td>
<td>H.R.</td>
<td>MALE</td>
<td>FEMALE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(OF)</td>
<td>(%)</td>
<td>Average</td>
<td>Range</td>
<td>Average</td>
<td>Range</td>
</tr>
<tr>
<td>100</td>
<td>75</td>
<td>8.8</td>
<td>2 - 18</td>
<td>11.1</td>
<td>3 - 20</td>
</tr>
<tr>
<td>95</td>
<td>&quot;</td>
<td>16.8</td>
<td>5 - 23</td>
<td>20.3</td>
<td>11 - 29</td>
</tr>
<tr>
<td>85</td>
<td>&quot;</td>
<td>20.9</td>
<td>14 - 30</td>
<td>26.1</td>
<td>11 - 37</td>
</tr>
<tr>
<td>70</td>
<td>&quot;</td>
<td>34.5</td>
<td>22 - 46</td>
<td>45.1</td>
<td>16 - 57</td>
</tr>
<tr>
<td>63</td>
<td>&quot;</td>
<td>43.4</td>
<td>33 - 61</td>
<td>60.2</td>
<td>34 - 81</td>
</tr>
<tr>
<td>48</td>
<td>&quot;</td>
<td>88.0</td>
<td>34 - 124</td>
<td>112.1</td>
<td>54 - 142</td>
</tr>
<tr>
<td>38</td>
<td>&quot;</td>
<td>29.3</td>
<td>21 - 80</td>
<td>39.1</td>
<td>21 - 80</td>
</tr>
<tr>
<td>100</td>
<td>44</td>
<td>3.2</td>
<td>2 - 4</td>
<td>3.4</td>
<td>2 - 4</td>
</tr>
<tr>
<td>95</td>
<td>&quot;</td>
<td>13.0</td>
<td>9 - 17</td>
<td>17.8</td>
<td>9 - 21</td>
</tr>
<tr>
<td>85</td>
<td>&quot;</td>
<td>16.5</td>
<td>9 - 25</td>
<td>19.9</td>
<td>7 - 38</td>
</tr>
<tr>
<td>70</td>
<td>&quot;</td>
<td>34.2</td>
<td>23 - 53</td>
<td>40.8</td>
<td>8 - 65</td>
</tr>
<tr>
<td>63</td>
<td>&quot;</td>
<td>44.5</td>
<td>30 - 67</td>
<td>57.5</td>
<td>81 - 66</td>
</tr>
<tr>
<td>48</td>
<td>&quot;</td>
<td>83.2</td>
<td>27 - 122</td>
<td>111.0</td>
<td>60 - 135</td>
</tr>
<tr>
<td>38</td>
<td>&quot;</td>
<td>23.4</td>
<td>8 - 40</td>
<td>24.3</td>
<td>8 - 75</td>
</tr>
</tbody>
</table>

f) Tropisms and general activity.

Adults are positively phototropic up to a point. According to Reed et al. (1934), they are attracted to moderate light, but are repelled by sunlight or strong electric lights. This attraction towards moderate light is the principle used in various types of light traps.

Adults have a habit of feigning death when disturbed.

They are most active at high temperatures, and, though they may live for a considerable period at temperatures like 48°F, they are very inactive. They remain largely motionless; and with head flexed beneath the pronotum and legs drawn closely together, they appear lifeless.

They are fairly strong fliers. Of a number of individuals released out-of-doors on a calm day, several were noted to fly up over an 18 ft. roof. Runner (1919) observed beetles flying from one warehouse to another on the opposite side of a street.
6. **NUMBER OF GENERATIONS.**

In Cape Town about three overlapping generations a year are expected. There is no definite emergence period, but adults are more prevalent and active, and development quicker, in summer. Each stage of the insect may be found at almost any time during the year. There appears to be no definite hibernation, but a mere slowing up of development in each of the different stages during the comparatively mild winter.

The range of temperature and humidity producing this annual developmental cycle is given in Table 13.

**Table 13:** Temperature and relative humidity in a Cape Town tobacco leaf store.

<table>
<thead>
<tr>
<th>MONTH</th>
<th>GROUND FLOOR</th>
<th>BASEMENT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TEMP (OF)</td>
<td>H.H. (%)</td>
</tr>
<tr>
<td>March, 1950</td>
<td>73</td>
<td>72</td>
</tr>
<tr>
<td>April, &quot;</td>
<td>66</td>
<td>77</td>
</tr>
<tr>
<td>May, &quot;</td>
<td>63</td>
<td>79</td>
</tr>
<tr>
<td>June, &quot;</td>
<td>60</td>
<td>81</td>
</tr>
<tr>
<td>July, &quot;</td>
<td>56</td>
<td>79</td>
</tr>
<tr>
<td>August, &quot;</td>
<td>60</td>
<td>70</td>
</tr>
<tr>
<td>Sept., &quot;</td>
<td>61</td>
<td>71</td>
</tr>
<tr>
<td>Oct., &quot;</td>
<td>67</td>
<td>69</td>
</tr>
<tr>
<td>Nov., &quot;</td>
<td>68</td>
<td>66</td>
</tr>
<tr>
<td>Dec., &quot;</td>
<td>70</td>
<td>65</td>
</tr>
<tr>
<td>Jan., 1951</td>
<td>71</td>
<td>65</td>
</tr>
<tr>
<td>Feb., &quot;</td>
<td>75</td>
<td>65</td>
</tr>
<tr>
<td>Annual Average</td>
<td>66</td>
<td>71</td>
</tr>
</tbody>
</table>

To obtain monthly averages in Table 13, 2 thermohygrographs were run concurrently, one in the basement and one at ground floor level of a local tobacco store. Temperature and relative humidity at ground floor level showed greater daily fluctuations than in the basement, but it is noted that monthly and annual averages are very similar.

At ground floor level, the maximum temperature recorded during the 12 months was 88°F in March and January; the minimum was 46°F in July. The maximum relative humidity was 94% in April and July; and the minimum was 40% in December. These extremes never persisted for longer than
24 hours. The average conditions recorded during summer were 71°F and 68% relative humidity, while during winter they were 61°F and 75% Relative humidity.

Temperatures concurrently recorded in a ground floor laboratory in another suburb of Cape Town, were very similar to those recorded at ground floor level in the tobacco store. Thus, the series of temperatures given in Table 13 is probably typical for Cape Town.

According to JEPSON (1939), there may be 4 - 5 generations a year in a place like Mauritius, where annual average temperatures and relative humidities are higher than in Cape Town. In contrast, only one generation probably occurs in England where the mean outdoor temperature only exceeds 60°F during 1 - 2 months.
7. **CONCLUSIONS.**

Viability and incubation periods of eggs are influenced by physical conditions. Conditions causing the shortest incubation period (5 - 6 days) and the highest viability (99 - 100%) are probably about 85 - 95°F and 60 - 90% relative humidity.

Critical conditions for hatching are as follows:
- **Upper critical temperature** - 100 - 105°F
- **Lower** " " - 48 - 63°F (probably about 56°F)
- " " relative humidity - less than 9%

Rate of larval development is affected not only by physical conditions, but also by nature of foodstuff, form of foodstuff, and possibly by age of adult beetle at the time of oviposition.

Physical conditions causing the most rapid development appear to be the same as for the egg stage, namely, about 85 - 95°F and 60 - 90% relative humidity. Critical conditions for development of newly-hatched larvae are as follows:
- **Upper critical temperature** - 95 - 100°F
- **Lower** " " - 48 - 63°F, (probably between 55 - 60°F)
- " " relative humidity:
  - In tobacco - 32 - 44%
  - In mealie meal - less than 23%

The lower critical humidity-range corresponds to 7.8 - 9.5% moisture by weight in leaf tobacco at 85°F.

The effect of foodstuff has been shown through a comparison of developmental rates on mealie meal and tobacco. Development was more rapid on the former than on the latter. This may be due to higher total carbohydrate content of mealie meal (64 - 72%) compared with tobacco (11 - 13%).

At the optimum conditions previously mentioned, the average period of larval development on mealie meal was about 16 - 22 days, and on tobacco about 34 - 44 days.
According to RUNNER (1919), form of foodstuff is important in influencing rate of larval development. Thus foods in compact or concentrated form cause a higher rate than more diffuse foods. According to HONE (1950), referring to Ptiinus tectus, the rate of development of a larva may be influenced by the age of the adult beetle when the eggs were laid. Neither of these 2 factors has been investigated by the author.

Some variation in number of larval moults was recorded. The average larva appeared to moult 4 times (5 stadia).

The lengths of the prepupal, pupal and resting adult stages are influenced in the same way and by the same factors as affect the larval stage. The average lengths of these stages at the optimum conditions previously mentioned, are as follows:

In mealie meal,

- prepupa: $2.8 - 3.3$ days.,
- pupa: $3.2 - 3.9$ “
- resting adult: $4.0 - 4.2$ “

In tobacco,

- prepupa: $2.6 - 3.6$ “
- pupa: $3.8 - 4.5$ “
- resting adult: $3.6 - 4$ “

Reviewing the whole developmental cycle from egg to active adult, optimum conditions of $85 - 95^\circ F$ and $60 - 90\%$ relative humidity make the average cycle about $35 - 40$ days in mealie meal, and about $49 - 60$ days in tobacco.

Among factors influencing oviposition, are the nature of the oviposition site and physical conditions.

A rough surface is preferred to a smooth for oviposition, and odour plays a minor role compared to tactile stimulus. Sometimes a female will not lay any eggs if no suitable site is present.
The optimum conditions, for rate of development from egg to active adult, cause the shortest incubation periods of eggs, but not the greatest average number of eggs laid per female. This number is attained at the same humidity-range (60 - 90%), but the optimum temperature is lower (about 70°F). Under these conditions, the average number of eggs per female is about 20 - 37. At 85 - 95°F and 60 - 90% relative humidity it is about 9 - 35. The upper critical temperature for oviposition probably lies between 100 - 105°F, and the lower between 38 - 48°F.

Neither the number of eggs per female nor the sex ratio (females slightly outnumber males) is apparently influenced by larval foodstuff.

The effect of foodstuff is, however, seen in adult longevity, as well as the effect of physical conditions and sex.

On the whole, longevity is greater in mealie meal than tobacco, and greater in the female than the male. At 85 - 95°F and 60 - 90% relative humidity, longevity was as follows:

Mealie meal:
- female = 20 - 26 days.
- male = 16 - 23 ".

Tobacco:
- female = 14 - 17 "
- male = 13 - 15 "

Longevity is least at high temperatures (about 100°F), low temperatures (less than 38°F) and low relative humidities (less than 9%). It is greatest at about 48°F and 75 - 95% relative humidity.

To sum up, physical conditions most favourable for the development of the species appear to be 85 - 95°F and 60 - 90% relative humidity, when the "egg to active adult" stage takes about 35 - 60 days, depending on foodstuff and other factors.
The most favourable foodstuff appears to be one high in carbohydrate content and in compact or concentrated form.

In Cape Town, where average summer conditions are about 71°F and 68% relative humidity, and winter conditions about 61°F and 75% relative humidity, about 3 overlapping generations can be expected annually, with a period of very slow development during the winter.
As mentioned in the introduction, much of the work done on Lasioderma serricorne has been directed towards control. Despite all that has been written on the subject, no one completely satisfactory method of control has been revealed. The following methods have been used either singly or in various combinations:

- Heating; refrigeration; fumigation; spraying;
- dusting; exposure to low pressure, x-rays and electric currents; trapping by mechanical means; and attention to general cleanliness.

Whatever method is employed must not only be toxic to the insects, cheap, convenient and safe to use, but also, if tobacco is infested, must not leave any after-effects injurious to the smoker nor injure the aroma and smoking qualities of the tobacco.

Preventative measures include keeping tobacco factories and stores scrupulously clean and spraying bales, and the store generally, with some solution like 5% pyrethrins, every few days. If infestation is not held in check in this way, some supplementary measure must be used.

In previous investigations the accent has been on fumigation, especially with hydrocyanic acid gas and carbon bisulphide. There is some doubt as to the efficiency of the former in controlling the egg stage. Further, though apparently neither of these fumigants has any injurious after-effects on the smoker nor on the flavour of the tobacco, neither gas diffuses rapidly enough after fumigation. Traces of hydrocyanic acid gas have been apparent in bales of tobacco after 3 months of airing subsequent to fumigation. A further disadvantage of carbon bisulphide is that it is inflammable and explosive.
Among a great variety of other fumigants used, such as ethylene oxide, ammonia gas and methyl bromide, the latter seems to hold most promise of adequate future control. It has great penetrating powers, diffuses readily, is not inflammable or explosive, and apparently causes no alteration in taste or processing qualities of the commodity treated, and leaves no significant residue. It is highly toxic to man, however, and has to be handled with great care. An adequate dose for baled tobacco is considered to be 2 lbs/1,000 cubic ft.

Although control by refrigeration is at present more expensive than fumigation, there is a tendency to prefer it in tobacco factories as it does not endanger factory personnel in any way. This is a field for a great amount of experimental work, as much of the data available on temperatures and exposure periods is conflicting.

2. Original investigations

The present author, owing to limited time, was able to carry out only a few original investigations on two aspects of control, namely, refrigeration and heating.

1) Refrigeration

The egg stage alone was tested. Eggs had been laid on leaf midribs, as previously described, and were exposed naked and "in situ". About 200 eggs were exposed per condition.

Eggs were exposed to temperatures ranging from 2 - 10°F for varying periods. Results of observations are given in Table 14.

Results indicate that for an exposure of 12 hours, which is often termed the maximum exposure for practical purposes, a lower temperature than 50°F is required for complete control. Further, the larval stage is more resistant than the egg to low temperatures and should also be used in testing to determine the complete efficiency of temperature and exposure period.
Table 14: Percentage hatching of eggs exposed to Low temperatures for various periods.

<table>
<thead>
<tr>
<th>TEMP. OF</th>
<th>DURATION OF EXPOSURE (Hours)</th>
<th>PERCENTAGE HATCHING</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 2</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>15</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>9</td>
<td>8.0</td>
</tr>
<tr>
<td>7</td>
<td>10</td>
<td>7.8</td>
</tr>
<tr>
<td>8</td>
<td>11</td>
<td>6.8</td>
</tr>
<tr>
<td>9</td>
<td>12</td>
<td>5.0</td>
</tr>
<tr>
<td>10</td>
<td>6</td>
<td>30.0</td>
</tr>
</tbody>
</table>

It is noted that SWINGLE (1938) claimed complete mortality of eggs at 10°F after one hour. The reason for the discrepancy in the results is not apparent.

ii) Heating:

Before manufacture, tobacco is generally reconditioned, i.e. made more pliable with raising of the moisture content. This conditioning usually involves either a thermal vacuum process or steam-heating under pressure. The egg stage was exposed to both these processes which were as follows:

a) Thermal vacuum process.

A partial vacuum of 14 lb./sq. in. was created and broken by an injection of steam. The temperature rose to 180°F where it remained for about 3 min., falling to 150 - 155°F within the next 5 minutes.

Of 224 eggs exposed to this process, 0% hatched.

b) Steam-heating under pressure.

Steam was injected into a "steam-box" until the pressure reached 40 lb./sq.in. and the temperature reached about 160 - 170°F for 5 minutes.

Of 795 eggs exposed to this process, 0% hatched.

In each case, test-eggs were laid on midribs, as previously described, and each total number exposed was composed of several different batches tested at different times and in different positions in the "thermo-vector" and "steam-box." In the first process midribs were placed in
metal spikes (described by SMINGLE - 1938, p.7) and these were driven into the bales of tobacco. In the second process, where loose "hands" were exposed, midribs were placed in wire gauze capsules and these were bound into specially labelled "hands" generally near the butt-end.

Both these processes apparently control the egg stage completely. Whether this also applies to the larval stage is not known. If this is so, factories using these particular processes during reconditioning will ensure 100% freedom of their manufactured products from infestation, provided there is no subsequent recontamination during manufacture.

These processes are, however, not always applied to all types of tobacco, and some manufacturers do not use them at all, having preference for other methods of reconditioning, where pliability, flavour and other qualities of the tobacco are concerned.
IX - NATURAL ENEMIES.

The following natural enemies of Lasioderma serricorne have been mentioned in various works:-

**Coleoptera:**
- *Tenebrioides mauritanicus* L.
- *Thanerocerus girodi* Chevr. and *T. buqueti* Lef.

**Hymenoptera:**
- *Lariphagus distinguendus* Först.
- *Nortanua* sp.
- *Bruchophagus* sp.
- *Cephalonomia quadridentata* Duchaussay.

**Mites:**
- *Pediculoides ventricosus* Newp.
- *Moniezella* sp.
- *Seiulus* sp.
- *Chortoglyphus gracilipes*
- *Cheyletus* sp.
- *Rhegidia* sp.
- *Tyroglyphus* sp.

No one stage of the insect under discussion is immune to attack, but none of the natural enemies is considered to be of great importance from the point of view of biological control.

Of these, only 2 types were encountered by the author, namely, 2 species of mites, and the "cadelle," *Tenebrioides mauritanicus* L.

One species of mite was *Pediculoides ventricosus*, the other was doubtful, probably a *Gamasid* or *Parasitiform* mite. These mites were particularly troublesome among test eggs where they were well camouflaged, and where their attacks could seriously upset records on viability. They are considered to attack every stage of the insect.

*Tenebrioides mauritanicus* was found in cultures on "army" biscuits. It is predaceous to some extent on larvae and pupae.
From the preceding account of the biology of Lasioderma serricorne, it is apparent that this insect has characteristics which commend it to the attention of experimentalists. Like Tribolium confusum, described by Fark (1934), it is cosmopolitan and fairly easily obtainable; it has a moderately short life cycle; and it is easy to breed. With the idea in mind that it may be a useful test insect in both theoretical and practical problems, the present author has paid attention to techniques of rearing, sexing, handling and observation.

Theoretical problems in which Lasioderma serricorne has already been used as a test insect include the following:

a) Experiments by Fraenkel & Blewett (1934 & 1935) on the nutrition of the larval stage.

This stage can exist on a wide variety of materials; and it is of interest to determine what factors permit this wide choice of foods. In this connection, Fraenkel & Blewett have found that the larvae can develop in the absence of carbohydrates. They also suggest the probable presence of intracellular symbionts supplying vitamins of the B group and enabling larvae to develop in foodstuffs lacking these vitamins.

b) Experiments by Dick (1937) on oviposition.

The adult female will oviposit on a wide variety of substrata. Dick has studied the relative importance of tactile stimuli and odours in oviposition.

Further, Lasioderma serricorne, may well be used in the future as a test insect in theoretical problems so far applied only to other species by various workers. These include the following:

a) Experiments by Dick (1937) on copulation of Tribolium confusum.
Whether more than one copulation is necessary to the female for complete oviposition is not known. Dick has suggested that besides supplying spermatophores, additional copulations may have a stimulating effect on rate of oviposition. This may also apply to Lasioderma serricorne, where more than one copulation has frequently been noted in the life of a single adult pair.

b) Experiments by Howe (1950) on rate of development of larvae of _Ptilius tectus_.

Considerable variation was noted in rate of development of these larvae, even when kept under the same physical conditions and on the same foodstuffs. The present author noted similar variations amongst larvae of _Lasioderma serricorne_. Howe has suggested that the rate of development of a larva may be influenced by the age of the adult beetle at the time when the egg was laid. It is of interest to determine whether such a factor may operate in the case of _Lasioderma serricorne_, and if not, what factor does cause the variation.

c) Experiments by numerous authors on population densities among various test insects, e.g. _Tribolium confusum_ and _Sitophilus oryzae_.

It should not be difficult to rear experimental populations of _Lasioderma serricorne_ under controlled physical conditions and in suitable cultures, such as a known weight of mealie meal in a container of known volume.

d) Attempts to establish the phylogeny of the Coleoptera on the basis of the comparative anatomy of the male genitalia by Sharp and Muir (1912).

The present author has described the male genitalia of _Lasioderma serricorne_. The nearest relations described by Sharp and Muir are various Ptilidae. Structural differences between the genitalia of these forms and that of _Lasioderma serricorne_ exist, e.g. in the symmetry of the lateral lobes. Whether the difference is of such a degree as to give further
support to the separation of the Anobiidae from the Ptinidae, is yet another theoretical problem.

Economic entomologists have paid much more attention to Lasioderma serricorne than the theorists. As stated in the introduction to the paper, most experimental work on this insect has been directed towards practical control.

The present author, as previously mentioned in this discussion, has paid attention to techniques of rearing, sexing, handling and observation, with a view to the large-scale use of this insect in scientifically planned experiments on control. There has been a paucity of such experiments; for, despite the mass of work done on control, many experiments have been fragmentary and inadequately qualified by data relating to conditions prevailing during the experiments.

In addition to the techniques described, other biological data in this paper may be of use in planning control. Some of the applications of this biological, and in particular bionomical data to control are:

a) Descriptions of the various stages and type of damage done aid in determining the nature of infestation.

b) Data on the duration of the life cycle, activity and productivity under various physical conditions enables estimates to be made of the number of generations that can be expected in any location, where conditions of temperature and relative humidity are known. The nearer the known conditions approximate to the microclimate of the infesting insect, the more accurate will be the estimates.

Such knowledge further enables estimates to be made of the degree of infestation likely to occur at any place and at any time, and, consequently, of the stringency of the control measures to be applied.

c) Data on the habits of the insect can be applied in a variety of ways.
It has been shown that insects are not necessarily confined within the limits of the commodity they are infesting, e.g. a tobacco bale. Adults can chew their way out of a bale to mate, and females may lay their eggs not only on the surface of the bale and on tobacco debris in the vicinity, but also on rough surfaces and in cracks and crevices such as occur in wooden structures; walls and floors of a store-room. Here, too, adults may hibernate. Further, newly-hatched larvae are known to be very active and crawl far distances in search of food, and to be able to chew through such substances as packing paper and twill. Thus, infestation may easily spread from infested to uninfested materials.

These habits emphasise, firstly, the importance of cleanliness and removal of infested material. Secondly, they indicate that where a store has contained infested tobacco, though infested bales and debris have been cleared away, the store should also be completely sterilised before stocking it with clean bales. This is especially necessary if only a short time elapses between the clearance and the re-stocking. Sterilisation involves the destruction of eggs, larvae and any other stages found on the walls and floors, etc., of the store itself.

The habits and location of the various stages show that it is chiefly the adult and egg that may be found on the surface of a commodity, e.g. on the outside of a tobacco bale. It is these stages, therefore, which are most likely to be affected by a contact insecticide, applied, for instance, to the exterior of a bale, or to the walls and floors of a store-room. Such an insecticide must, therefore, be chosen for its effect on these particular stages.

In this connection, very tentative experiments by the author, indicated that DDT solutions (approximately 5%) caused less than 50% mortality among adults. At this

71/...concentration....
concentration, therefore, DDT does not appear to be a satisfactory insecticide for spraying store-rooms, and, further cannot be applied directly to the bales. Solutions like 5% pyrethrins appear to be much more satisfactory.

The positive phototropism of the adults is the principle used in various types of light traps, which have been found to aid in reducing infestation.

d) Data on the ranges of temperatures and humidities at which the various stages can develop, in particular, the upper and lower critical conditions, may be of importance.

When materials are put into storage at conditions outside the developmental range, e.g. 50 - 55°F, there will be no growth and reproduction amongst insects already present. However, this initial infestation, though checked, may not be completely destroyed unless a certain minimum period of storage is exceeded. Less than the minimum may merely cause quiescence with a return to original activity as soon as the material is removed from storage.

At the low temperature-range of 50 - 55°F, newly-hatched larvae do not apparently survive, and the percentage hatching of eggs, if any, is probably very low. (Table 5 shows that the author obtained 0% hatching at 48°F). But the period of storage will probably have to exceed 4 - 6 months before all original infestation will actually be killed. This minimum period needs to be more accurately determined.

It must also be determined what effect such long exposures to low temperatures will have on the condition of the material in storage.

e) Data on natural enemies may eventually lead to a method of natural control.

Finally, the author has attempted to contribute directly to economic entomology.

Lasioderma serricorne (in the egg stage) has been used as a test insect in a few original experiments on practical
control through heating and refrigeration. Refrigeration seems promising enough to be the subject of future research. Particular attention should be paid to the larva in future experiments, as this is the stage considered to be most resistant to low temperatures.

The most promising fumigant, at present, seems to be methyl bromide, and its use in control opens another avenue of research for economic entomologists.
SUMMARY.

From literature, the following information has been obtained:

1. Lasioderma serricorne (F) has been placed in the sub-family, Xyletininae, family, Anobiidae.
2. It is described as cosmopolitan but more prevalent and active in the warmer regions of the globe.
3. It attacks a great variety of materials but, at present, cured tobacco is most important economically. It has not been known to attack growing or unfermented tobacco.
4. The larval stage does the most damage, largely through contamination of the product, partly through direct consumption. The adult apparently does not feed.
5. None of the natural enemies is considered to be of great importance from the point of view of biological control. (A list of some of these has been compiled).

The following contributions have been made by the present author:

1. General descriptions have been given of egg, larval, pupal and adult stages and of their development, habits and metamorphosis. They have been illustrated and measured.
2. Measurement of both pupal and adult stages showed the difference in average size between the two sexes. However, owing to overlap of the size groups, measurements were not reliable criteria of sex. Thus other techniques of sexing had to be elaborated, as sexing was essential for some aspects of biotechnical work. The author's methods of sexing living pupae and dead adults have been described. In this respect, adult genitalia have been described and illustrated. No way is apparently known of sexing adults while still alive.
3. Measurements show the effect of larval foodstuff (exemplified by tobacco and mealie meal) on size of all stages. (Throughout the investigation, tobacco and mealie meal were used as experimental media for comparative developmental work. They differ largely in their carbohydrate content).

4. In addition to sexing, other techniques have been elaborated for bionomical work, and most of these have been described. Among these are techniques for observing eggs on tobacco leaf midribs and the stages in mealie meal cultures.

5. The following bionomical aspects have been studied:
   a) The effect of various physical conditions (in the normal range of tolerance) on:
      (i) viability,
      (ii) incubation period
      (iii) lengths of all stages
      (iv) oviposition rate.

      An estimate has been made of the number of generations that can be expected under the physical conditions experienced in Cape Town.

      The effect of extreme physical conditions on the egg stage have been studied from the point of view of control. A few experiments have been done, using low temperatures (0 - 10°F); and high temperatures (150 - 180°F), coupled with a partial vacuum or pressure.

   b) The effect of larval foodstuff (the two experimental media) on the lengths of the various stages, (including the adult). There is apparently no effect on oviposition rate.

   c) The difference in adult longevity of the two sexes, and the sex ratio in the two experimental media.
The present author has, with original observations, entirely covered the field suggested by the 5 sections given above. In addition, however, the work of other authors has sometimes been quoted for comparative purposes; or for supplementary purposes where no original observations have been made. Examples of the latter are:

a) The effect of form of foodstuff and age of adult as possible factors influencing rate of larval development.

b) The effect of site on oviposition.

c) The number of generations found under other conditions than those experienced in Cape Town.

d) A brief survey of methods of control.
XII - ACKNOWLEDGEMENTS.

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EXPLANATION OF PLATES.

PL. III.

BP - Basal piece
ED - Ejaculatory duct
IS - Internal sac
LL - Lateral lobes
MF - Median foramen
ML - Median lobe
MO - Median orifice
PA - Point of articulation
SS - Supporting structure

PL. IV. - refer to Table 3.

PLS. V to IX.

R.H. - Relative humidity.

PLS. V and VI. - refer to Table 5.

No hatching and, therefore, no incubation period observed under the following conditions:-

75% R.H. and 105°F

44% R.H and 105°F

48°F

PL. VII. - refer to Table 8.

No development of newly-hatched larvae observed under the following conditions:-

In mealie meal and tobacco at

75% R.H. and 100°F

44% R.H. and 100°F

48°F

55 - 60°F

In tobacco at

32% R.H. and 85°F

PL. VIII - refer to Table 10.

PL. IX. - refer to Table 12.
PLATE I

EGG.

A.  

B.  

C. LARVA.

D. STAGES IN EMERGENCE OF PUPA.

1.  

2.  

3.  

4.

0.2 MM.

1 MM.
PLATE III

MALE GENITALIA.

A. DORSAL VIEW

B. PLAN OF VENTRAL VIEW OF ABDOMEN SHOWING GENITALIA IN POSITION

C. LATERAL VIEW (SS. NOT SHOWN)

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PLATE IV

FREQUENCY DISTRIBUTION OF SIZE OF ADULTS

(MM represents mean of all four groups)

(A) Tobacco

(RIGHT)

(Male)

(Female)

(B) Mealie Meal

(RIGHT)

(Male)

(Female)
PLATE V

VIABILITY OF EGGS.

AT 75% RH AND 65% RH AND VARIOUS TEMPERATURES.

(A)

AT 85°F AND VARIOUS RELATIVE HUMIDITIES

(B)
PLATE VI

INCUBATION PERIOD OF EGGS.

(A) AT 75\% R.H. AND 44\% R.H. AND VARIOUS TEMPERATURES.

(B) AT 85\% R.H. AND VARIOUS RELATIVE HUMIDITIES.
PLATE VII
RATE OF DEVELOPMENT FROM EGG TO ACTIVE ADULT.

(A) AT 75% RH AND VARIOUS TEMPERATURES

(B) AT 75% RH AND VARIOUS TEMPERATURES

(C) AT 80°F AND VARIOUS RELATIVE HUMIDITIES
PLATE VIII

NUMBER OF EGGS PER FEMALE

AT 75% RH AND 44% RH AND VARIOUS TEMPERATURES

(A)

NO. OF EGGS/FEMALE

TEMPERATURE (°F)

AT 85°F AND VARIOUS RELATIVE HUMIDITIES

(B)

NO. OF EGGS/FEMALE

PERCENTAGE RELATIVE HUMIDITY
PLATE IX
ADULT LONGEVITY.

AT 75\% R.H. AND VARIOUS TEMPERATURES

(A)

TEMPERATURE (\(^{\circ}\)F)

MALES
FEMALES

LONGEVITY IN DAYS

120
110
100
90
80
70
60
50
40
30
20
10
0

B

AT 44\% R.H. AND VARIOUS TEMPERATURES

(B)

TEMPERATURE (\(^{\circ}\)F)

MALES
FEMALES

C

AT 86\% R.H. AND VARIOUS RELATIVE HUMIDITIES

(C)

PERCENTAGE RELATIVE HUMIDITY

LONGEVITY IN DAYS

30
25
20
15
10
5
0

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