Frontispiece

The Brown wattle mirid, Lygidolon laevigatum Reut. - male.

L. laevigatum - female.

T

ASPECTS OF THE MORPHOLOGY AND BIONOMICS OF Batrachomorphus cedaranus (Naudé) AND Lygidolon laevigatum Reut. ON BLACK WATTLE (Acacia mearnsii De Wild)

SR by

A

Allan Donovan Connell

NT Thesis (Ph.D.; Entomology) - University of Natal,
Pietermaritzburg, 1970

Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy in the
Department of Entomology, Faculty of Agriculture,
P PP
University of Natal, Pietermaritzburg.

CONTENTS

PAGE

INTRODUCTION

Certain species of Hemiptera, including both suborders Homoptera and Heteroptera, have for many years been known to cause damage to young wattle trees, *Acacia mearnsii* (de Wild) in Natal and the South-eastern Transvaal, as well as in the East African wattle growing areas. Species of Hemiptera most commonly encountered in Natal include the cicadellid *Batrachomorphus cedaranus* (Naudé) and the mirid *Lygidolon laevigatum* Reuter. Both species have a wide distribution in tropical and subtropical East Africa.

Ever since the insects were first recognised as pests in 1910 by Mr. C. Fuller, the term "froghopper" has been used in literature on the subject. However, as neither species is a true froghopper - a name given to members of the family Cercopidae - the writer will not use this term, and each insect will be referred to by its specific name. Common names suggested are : *B. cedaranus*; Green wattle leafhopper, and *L. laevigatum*; Brown wattle mirid.

In the past, all the work done on these Hemipterous pests of wattle, has been confined to investigations aimed at finding suitable control measures. Fairly detailed accounts of the damage caused can also be found in early papers, together with silvicultural methods which were recommended to prevent attacks. In the early nineteen-fourties Pyrethrum dusts were used in control (Ripley and Petty 1940). In 1950 fogging with toxaphene (1% oil solution) was instigated as a control measure.

Probably the main reason for the paucity of research on this problem in wattle is that it is difficult for the individual the almost complete lack of information on the biology and ecology of the two principal species prevented any attempt at forecasting outbreaks. Consequently this study, started in January 1967, has been very basic, with most emphasis on morphology, biology and ecology. Preliminary studies of control, both biological and chemical, have been conducted, but have of necessity had to take second place at this stage. Economic studies are more of a long-term project in a crop such as wattle, as data is required on the comparative values of the damaged and undamaged plantations, together with the cost of protective measures, before an assessment of the economic importance of the insects to the wattle industry, can be made.

PART I

TAXONOMY AND MORPHOLOGY

CHAPTER 1

THE TAXONOMY OF B. CEDARANUS AND L. LAEVIGATUM

1.1

INTRODUCTORY NOTES

The morphological studies conducted have been directed primarily at those features important in the taxonomy of the species involved. Basic external anatomical features are far better illustrated by drawings than by description, and the illustrations have been supplemented by tables of measurements. In both the Miridae and Cicadellidae but more particularly in the former family, features of the external and internal genitalia are widely used as taxonomic features, particularly between the genera within a tribe and between species within a genus.

Literature was frequently consulted during the morphological studies, particularly with regard to the reproductive systems of the families involved, in order that descriptions might be comparable with those of other authors. A study of the female reproductive system of L. laevigatum is of interest from a purely morphological point of view. In Miridae as well as in Reduviidae, Nabidae and Anthocoridae, the arrangement of the genital organs and genital ducts appears to be distinctly different from the arrangement in other Hemiptera as well as from insects in general. This will be further discussed in the relevant section on the female organs of L. laevigatum. Suffice to say that this is partly the reason for the detailed study submitted in the chapters on morphology.

1.1.1 Materials and methods

All specimens used in morphological studies were field collected throughout the wattle growing areas of Natal.

had been laid, and measurements taken immediately, but nymphs and adults were preserved in 70% alcohol. The majority of drawings of external features were made from untreated alcohol specimens.

The methods and techniques used during the course of the studies of genitalia were neither extensive nor complicated, and were more or less standard procedure. Whole abdomens were removed and placed in a hot 5 per cent. KOH solution until examination under a dissection microscope showed that all extraneous material had been cleared away. The specimen was then removed and placed in a watchglass containing water and dissected, using watchmakers forceps and fine "minuten nadeln" pins in cane holders.

The female genitalia of *B. cedaranus* are readily accessible but in the female of *L. laevigatum* certain sclerotised structures, notably the sclerotised rings and posterior wall of the genital chamber (bursa copulatrix), required careful removal for study and drawing. The following technique was found to be most successful and, with only very little practice, easily and swiftly performed. Using small scissors, the terga of the KOH-treated abdomen were cut along a mid-dorsal line. Then holding the tergum of the ninth segment (which remains uncut) all the terga and sterna were removed, including lastly those of the ninth segment itself. Thus only the valvulae and valvifers together with the rami of the valvulae, and the sclerotised portions of the genital chamber remain together. These latter structures are situated dorsally, at the base of the ovipositor. To expose them it was found best to separate the first (anterior) and second (posterior) valvulae which constitute the ovipositor blades. This was done by placing the specimen ventral surface up and then inserting a dissecting needle between the first and second tip separated the first valvulae from the second. This freed the first valvulae and their rami which remained joined by the dorsal wall (roof) of the genital chamber, containing the sclerotised rings. The second valvulae are inseparable and their rami and valvifers form the ovipositor sheath. Associated with the base of these structures is the posterior wall of the genital chamber, also of great taxonomic value, and this was separated from the second valvulae and the ovipositor sheath for the purpose of illustration.

Female cicadellids do not have the sclerotised genital chamber walls considered as important in the taxonomy of Miridae and are sufficiently large to make dissection of cleared specimens simple. The male of L. laevigatum similarly requires no specialist surgery to extract the aedeagus and claspers.

In the removal of the male genitalia of B. cedaranus the following quick method with KOH-cleared specimens was found satisfactory. The abdomen was anchored by means of fine forceps while the anal lobe was gripped by similar forceps. Gentle pulling almost invariably resulted in the anal lobe and pygofer hooks, together with aedeagus, connective and styles being neatly removed leaving the genital capsule (pygofer) intact.

Drawings were made from specimens either under water or glycerine (occasionally 70% alcohol) anchored by a tiny drop of petroleum jelly where necessary. Smaller organs were drawn from slides. Most illustrations were made with the aid of a Camera Lucida, while a squared ocular and co-ordinate paper were used in a few cases.

To confirm findings as well as to study other organs such as the salivary glands, serial sections were made of whole adults. Carnoy's and Zenker's fixatives were used, especially staining techniques were tested, namely Mallory's Triple Stain (Pathological technique 1918 pg. 112) and Jane E. Cason's modification of the Mallory Heidenhain stain (Gurr 1956). Both were chosen for speed of execution, but the latter proved quite suitable and was used almost exclusively.

1.1.2 Illustration technique

Illustrations were prepared in the following way. The original drawings were enlarged several times, and drawn in black india ink on a good quality white paper. These were then photographed and reproduced, from the negative, onto Kodagraph P84 photographic paper. The contrasty negatives required for such work were obtained by developing in Kodak D9 developer.

1.2

THE TAXONOMY OF LYGIDOLON LAEVIGATUM

1.2.1 Taxonomic summary

Order	Hemiptera
Suborder	Heteroptera
Superfamily	Cimicomorpha
Family	Miridae (Capsidae)
Subfamily	Mirinae
Tribe	Mirini Hahn 1831
Genus	Lygidolon Reuter 1907
Species	laevigatum Reuter 1907

Due to lack of sufficient data, Imms (1957) was not prepared to give formal subdivision of the Heteroptera into superfamilies. He did however adopt the time-honoured division into the two series Gymnocerata and Cryptocerata, based on obvious external characters and broadly speaking, subdivided into three series, the Geocorisae (land bugs), Hydrocorisae (water bugs) and Amphibicorisae (water surface bugs), a classification still in use (Leston et.al.1954). The latter workers proposed subdividing the Geocorisae into the two superfamilies Pentatomorpha and Cimicomorpha on the basis of two morphological types of accessory salivary glands and other features such as male genitalia, wing venation, the development of the female spermatheca and egg type. The Cimicomorpha have accessory salivary glands of the vesicular type with ducts not greatly convoluted (Southwood 1955). The Miridae are included in this group.

1.2.2 Family Miridae Hahn 1831

The family name Miridae has been the subject of considerable controversy as regards acceptability. However the name Miridae would seem to have precedence since the first genus described was Miris (Fabr. 1794), and Mirides (Hahn 1831) was the earliest name given to the family (Slater 1950). Despite this some authors, particularly Kullenberg (1947) still use the family name Capsidae.

The mirids are described as "medium to small ovate, oblong or slender, usually delicate insects. Colours dull or brilliant - never metallic. Head small, often sharply produced. Antennae four-segmented and slender the second segment usually very long, the third and fourth usually thinner. Eyes well developed, ocelli absent. Rostrum long, four-segmented, first segment as long or longer than the head. Hemelytra opaque or hyaline, with a cuneus usually present. Legs long and slender, tarsi three-segmented, rarely two-segmented." Imms (1957).

Members are largely herbivorous, but many species are distinctly predacious on small arthropods and a few are both

1.2.3 Subfamily Mirinae Hahn 1831

The primary character used in separating the Miridae into subfamilies has been the structure and arrangement of the arolia, while the presence of a pronotal collar is used to separate the Mirinae from the Orthotylinae (Carvalho 1955). This author described the following features of the Mirinae : "Tarsi with a pair of arolia present, closely approximate at their base, large and free, usually dilated. Arising between the claws they are divergent from base to tip". Tarsal claws more or less arcuate or bent at the middle, not sharply bent near the base (Brues et. al.1954). Pronotal collar always present and well separated from pronotum by a furrow (Carvalho 1955). Other authors have suggested the use of male genitalia for separation of subfamilies (Kelton 1959), but Kullenberg (1947) had earlier objected to this on the grounds that these structures, having the single function of inseminating the female, are likely to show some variation without impairment of function. On the other hand he considered that the female genitalia, with their three-fold function of coupling with the male genitalia, the receiving and retaining of the male products, and egg laying, were less liable to undergo any structural change, and therefore more reliable as taxonomic characters. Kullenberg also rejected the use of the arolia in subfamily taxonomy, as he considered them too liable to adaptation. However Carvalho (1955) continued to use the features of the arolia. Kullenberg also considered that the Mirinae did not constitute a distinct subfamily but only a tribe of the Capsinae. The Capsinae have been grouped into the tribe Mirini by Carvalho (1955), who considered them to be not distinct enough to be regarded as belonging to a separate subfamily.

More recent work by Leston (1961) and other workers has

1.2.4 Tribe Mirini Hahn 1831

Carvalho (1955) gives the characters of this tribe as follows:- first segment of hind tarsi not as long as second and third together (Fig. 6E). Pronotum without a lateral ridge. Pronotal collar distinct, separated from pronotum by a furrow (Fig. 4A). No species are myrmecomorphic as in the closely related tribe Herdoniini. Ostiolar peritreme prominent (Fig.4B), pronotal collar not as broad as width of calli. Species if dark usually shining. Hemelytra opaque, membraneous area two-celled (Fig. 4B small and large areole).

1.2.5 Genus Lygidolon Reuter 1907

The following is a summary of the characters of this genus given by Carvalho (1955) and Odhiambo (1960): Hemelytra with cuneus and membrane, the divisions into corium, clavus and embolium distinct; large areole rounded at apex; cuneus longer than wide. Dorsum although shiny, very densely covered with small shallow punctures; scutellum very finely transversely rugose. Odhiambo (1960) states that the dorsum is not glabrous as stated by Poppius (1912), but covered by minute pale hairs coming out of shallow punctures, although the hairs are easily rubbed off. Frons sparsely punctate and finely shagreened. Hind femora not extending beyond tip of abdomen, about one and a half times as long as fore femora; anterior tibiae cylindrical. Second antennal segment linear in thickness except at base where it is narrower, the segment as a whole as thick, or only slightly thinner than first segment; third and fourth antennal segments distinctly thinner. First tarsal segment slightly shorter than second. Rostrum long reaching at least to posterior margin of middle coxae. Eyes very large, compressed, smooth behind, touching the anterior angles of the pronotum and gula below, Odhiambo (1960) in his supplement to earlier generic diagnoses uses the criterion "metathoracic wings without a hamus". Davis (1961), however, considers the hamus to be absent in Miridae although Slater (1951) lists the condition of the hamus as a criterion used in separating the subfamilies of Miridae. Carvalho (1955) does not include the hamus in his key to the genera of Miridae of the world.

1.2.6 *Lygidolon laevigatum Reuter*

First described by Reuter in 1907 both sexes of this species have been thoroughly redescribed by Odhiambo (1960) who includes measurements, as follows:-

"*Male:*

Structure - Head appears twice as high as long when viewed from the side. Rostrum extends to apices of mid coxae; first rostral segment reaches base of fore coxae. Antennal segment II slightly thinner than segment I. Pronotum with posterior margin two and a half times as wide as anterior margin. Tibial spines about as long as tibial thickness; hind tarsus with segments II and III subequal.

Measurements (of nine males in mm., first figure representing the mean, figures in brackets the range):- Length of body 3.25 (2.9 - 3.55); width across hemelytra 1.49 (1.40 -1.54); length of head 0.64 (0.62 - 0.66); width across eyes 0.93 (0.90 - 0.96); width of eye 0.34 (0.32 - 0.35); width of interocular space of vertex 0.26 (0.24 - 0.28); ratio, vertex: eye 1 : 0.77 (1 : 0.69 - 1 : 0.85); length of antennal segments I 0.28 (0.26 - 0.30), II 1.14 (1.10 - 1.16), III 0.52 (0.46 - 0.58), IV 0.38 (0.32 - 0.44); median length of pronotum 0.74 (0.72 - 0.76), basal width 1.30 (1.24 - 1.38).

Colour. Shiny. Head fuscous to black; vertex extensively, or only at base, yellowish or yellowish-brown; bucculae pale towards apex. Pronotum, including propleura, black; posterior margin of disc narrowly and ventral margin of propleura broadly, yellowish-white; disc sometimes largely brownish-yellow. Scutellum black; apex broadly, or sometimes the disc largely, yellow. Clavus fuscous to black; basal margin near claval suture paler, brownish; sometimes this pale area more extensive, covering half or more of the clavus. Corium yellowish, sometimes with a brownish tinge; inner apical angle, sometimes enlarged with an irregular transverse band just before the cuneal fracture, and sometimes external margin of embolium except at base of apex, brownish to black. Cuneus yellowish; most of apical half fuscous to black. Membrane smoky-grey; veins towards apices, an area inside the large areole, a narrow area adjoining the inner lateral margin of cuneus towards apex, and a spot near the external margin of membrane, pale or whitish. Abdomen brown to fuscous; base and sometimes ventral aspect yellowish-brown; abdomen sometimes largely yellowish. Thoracic venter fuscous to black; probasisternum pale yellow; ostiolar peritreme partially, and sometimes also metepisternum and ventral aspect of mesobasisternum, yellowish-brown. Legs yellowish; coxae sometimes very narrowly yellowish-brown at base; distal halves of hind femora brownish or reddish-brown or with some reddish markings; tibiae narrowly at apex, the last tarsal segment, sometimes also bases of hind tibiae, infuscate; basal tarsal segment yellowish-brown; tibial spines black, those on fore tibiae yellowish-brown.

Female

Structure. Similar to that of the male.

Measurements (in mm. of seven females):- length of body 3.25 (3.1 - 3.5); width across hemelytra 1.65 (1.56 - 1.74);

interocular space of vertex 0.33 (0.30 - 0.36); ratio, vertex : eye 1 : 1.11 (1 : 1.03 - 1 : 1.20); length of antennal segments I 0.27 (0.26 - 0.28); II 1.06 (1.02 - 1.12); III 0.55 (0.48 - 0.60); IV 0.37 (0.30 - 0.44); median length of pronotum 0.79 (0.76 - 0.84), basal width 1.44 (1.32 - 1.56).

Colour. As in the male, except: the body tinged with red, especially on the paler areas; vertex and frons yellowish-red; pronotum and scutellum extensively or largely pale in colour; abdomen sometimes entirely yellowish-brown, or sometimes entirely black."

1.3

THE TAXONOMY OF BATRACHOMORPHUS CEDARANUS

1.3.1 Taxonomic summary

Order	Hemiptera
Suborder	Homoptera
Series	Auchenorrhyncha
Superfamily	Cicadoidea
Family	Cicadellidae (Jassidae)
Subfamily	Iassinae
Tribe	Iassini
Genus	*Batrachomorphus* Lewis
Species	*cedaranus* Naudé 1926

The suborder Homoptera is subdivided into three series, namely the Auchenorrhyncha Duméril 1806, the Sternorrhyncha Amyot and Serville 1843 and the Coleorrhyncha by Essig (1954). The Anchenorrhyncha are those species having the tarsi mostly three-segmented and the rostrum arising from the ventral base of the head. Imms (1957) uses a similar subdivision.

The Auchenorrhyncha are divided into two superfamilies, Cicadellidae.

1.3.2 Family Cicadellidae (Jassidae)

The members of this family have in the past been subdivided into a number of separate families but there has been lack of agreement between different authorities on their limits (Imms 1957). Brues et.al.(1954) retain this splitting of the group, but the majority of authorities now recognise the single family Cicadellidae (Imms 1957, Medler 1942, Beirne 1956).

1.3.3 Subfamily Iassinae

Although there has been much controversy and change in the subdivision of the Cicadellidae into subfamilies, recent workers have been consistent in their classification and have used the subfamily Iassinae (Linnavuori 1961, Beirne 1956). Earlier Naudé (1926) recognised the subfamily Bythoscopinae, as did Buys (1924) and even Medler (1942). The genera recognised by these three authors have been regrouped into a number of subfamilies (Beirne 1956), one of which is the Iassinae.

Members of the Iassinae are keyed by Beirne (1956) using the following features:- "Ocelli on margin or close to margin of vertex, or on the vertex itself. Frontal sutures ending at antennal pits (Fig.5A). Face flat or, usually, distinctly convex in profile". Kramer (1963) describes the Iassinae as "medium to large in size, always robust and stout, frequently somewhat depressed". To the above features he adds: "The crown is almost always of uniform width, never sharply produced. Surface of crown and pronotum transversely rugulose".

1.3.4 Tribe Iassini

There are two tribes in the subfamily Iassinae, the second being the tribe Gyponini (Beirne 1956). They are simply

Evans (1947) gives a complete description of the members of the tribe Iassini and states that the majority are arboreal insects, with several species occurring on Acacia spp. in Australia.

1.3.5 Genus Batrachomorphus Lewis

Considerable confusion has previously existed in the nomenclature of certain genera and species of the Iassinae. The two genera Iassus and Batrachomorphus are very closely related. Linnavuori (1957) describes the genus as follows: "Robust and somewhat flattened species. Head narrower than pronotum behind. Vertex short and broad, of uniform length, transversely furrowed. Face short and broad; anteclypeus parallel-sided (Fig. 5A); frontoclypeus heartshaped, slightly transversely rugulose. Pronotum transversely furrowed. Elytra with three closed subapical cells; appendix broad; first apical cell membraneous; submarginal vein evanescent apically, extending only to the base of the second apical cell (s. gen. Straganía) or extending to the apex of the second apical cell (Batrachomorphus s. str.). Flying wings with three apical cells. Dorsal surface of fore tibiae rather rounded, with a longitudinal furrow, reducing the angular appearance in cross-section characteristic of Iassus. Spinulation of hind knees 2 + 2 + 1 (Fig. 11D). Male genitalia: Plates often well-developed (except in some neotropical forms). Styles with a long apophysis. Pygofer strongly setose, side lobes with a ventral appendage. Anal tube normal without the appendages found in Iassinae. Penis simple; gonopore on the ventral surface."

1.3.6 Batrachomorphus cedaranus Naudé

Naudé (1923) described the species as follows:- "General colour dark green. Females 6 mm. long, 2 mm. wide; males 5 mm. long 1.75 mm. wide.

margin; the anterior half of the pronotum which is whitish and is regularly marked with dark green spots; the scutellum which is whitish with a large brownish green spot at each basal angle, and two smaller ones close together just in front of the middle, and has a black depressed crescentic line on the middle; the face which is white with many short yellow transverse arcs, the genae being pale green; the eyes are red, the ocelli greenish.

Vertex one-fifth as long as its breadth between the eyes. Pronotum two and a quarter times as wide as long, subangularly incurved behind. Scutellum about one and one-half times as wide as long. Elytra punctate and smooth, subhyaline towards the apex; venation indistinct. Face broad, one and a half times as broad as long, rounded at the base; clypeus one and a half times as long as wide.

Genitalia - Female: last ventral segment twice as long as the penultimate, sinuately truncate behind. Pygofers strong, two and a half times as long as the last ventral segment, spinose, equalling the ovipositor in length. Male: Last ventral segment one and a half times as long as the penultimate. Valve strong, pointed, convex, twice as long as the penultimate segment; plates absent; pygofers exceeding the valve and strongly overlapping."

CHAPTER 2

GENERAL APPEARANCE AND EXTERNAL MORPHOLOGY

In a study of this nature, it does not seem justified to embark on a lengthy description of the entire external morphology of each of the two species under consideration. The descriptions which follow will, therefore, be as brief as possible, with emphasis on those structures and features of importance in the taxonomic status of the group to which the species belongs, and in the taxonomy of the species itself. In doing this, illustrations will be used as much as possible.

2.1

LYGIDOLON LAEVIGATUM

2.1.1 Variations in colour

Odhiambo (1960) gives a fairly comprehensive colour description (§ 1.2.6) of both the male and female of this species. However, the colour variations described by him, vary according to the age of the specimen. During the present study these colour changes were carefully noted. Immediately after emergence as an adult, the female is green in colour, the clavus and corium of the wing usually more olive. Within forty-eight hours the pronotum is chestnut changing to yellowish anteriorly and with a black posterior border. The genal areas are ginger to blackish. The abdomen has two black areas ventrally. These latter consist of two feint bars one on each side of the abdomen, running parallel to the outer edge, along the mid-lateral region of the sternal plates. At this stage the scutellum is lightly coloured

Fig. 2A. L. laevigatum female, 48 hours after emerging as an adult.

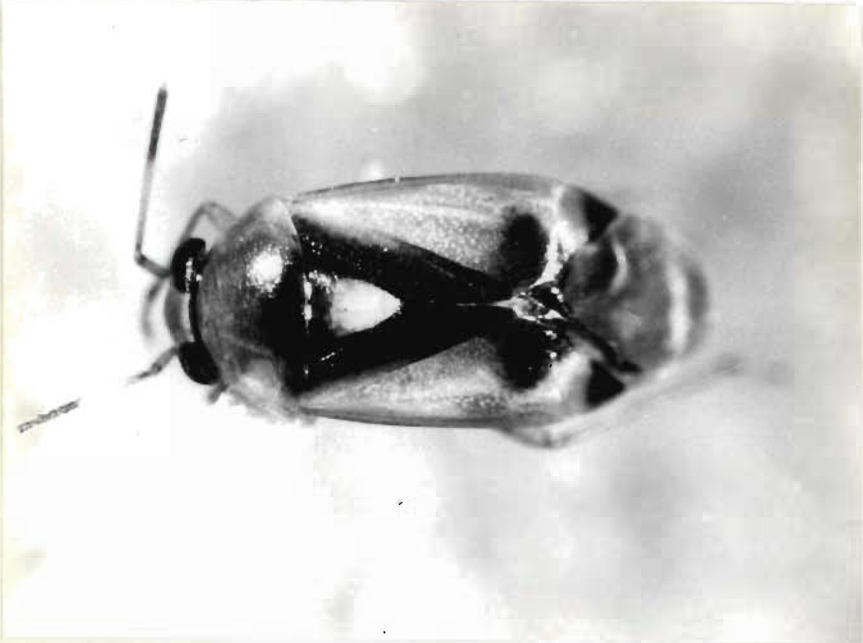


Fig. 2B. Darker colouring of the female at about 72 hours after emergence.

ovipositor region and genital segments become light chestnut and the pronotum is now completely chestnut, changing to black posteriorly in an area roughly equal in width and length to the mesoscutum (Fig. 2B). Legs cream to pale yellowish, showing no red. At this stage the colouring of the head, thorax and wings becomes more or less constant with little variation between specimens. The abdomen continues to change in colour.

At four days the only green to be seen on the body is on the anterior three visible sterna of the abdomen (sterna 2, 3 and 4). The black now extends to the lateral edges of the sterna and the whole area surrounding the ovipositor is chestnut. At five days the general appearance is darker, with the green of the abdomen receding and the ovipositor area darkening to black.

After a week the genital segments of the abdomen are often completely black, and the abdomen may be almost all black ventrally, with a silver pubescence. In other specimens this blackening is confined to the first genital segment and the two bands of black while the rest of the abdomen is yellowish tinged with red.

At ten to twelve days the abdomen is predominantly black in colour, with the posterior margins of the second sternum narrowly, and the third to sixth sterna broadly black. The formerly yellowish parts including the genital segments, become reddish-brown (Fig. 2C). In older females even the seventh sternum has its posterior half black. The black speckling and barring on the hind femur also changes gradually, to become reddish in the mature adult female.

The newly emerged adult male is all green, with the frons, the claval area of the wing, and the whole of the pronotum, olive-green. Within twenty-four hours, the frons and pronotum are completely black, except for a thin yellow posterior border on the latter (Fig. 3A). The vertex and each clavus are gingery black and the scutellum is black anteriorly, merging to yellowish posteriorly (Fig. 3A). The corium appears greenish, mainly due to the green of the body beneath, the embolium yellow. Powdery black markings are visible on the corium near the anal ridge, at the apex of the V formed by the clavus of each wing. The cuneus is yellow, but black apically, and the membrane of the wing is greyish. Ventrally the genital segment of the abdomen shows a slightly black shading.

Dorsally colour only changes slightly in intensity with age after this stage has been reached, although the scutellum becomes progressively more black until after about five days, when only a small area near the apex is yellowish. Ventrally, important colour changes occur on the abdomen, as in the female. The genital segment becomes light brown, and a bar of reddish to brown develops laterally on each side of the abdomen, and parallel to its outer margin when viewed ventrally. When five days old this bar is well developed and two blackish areas

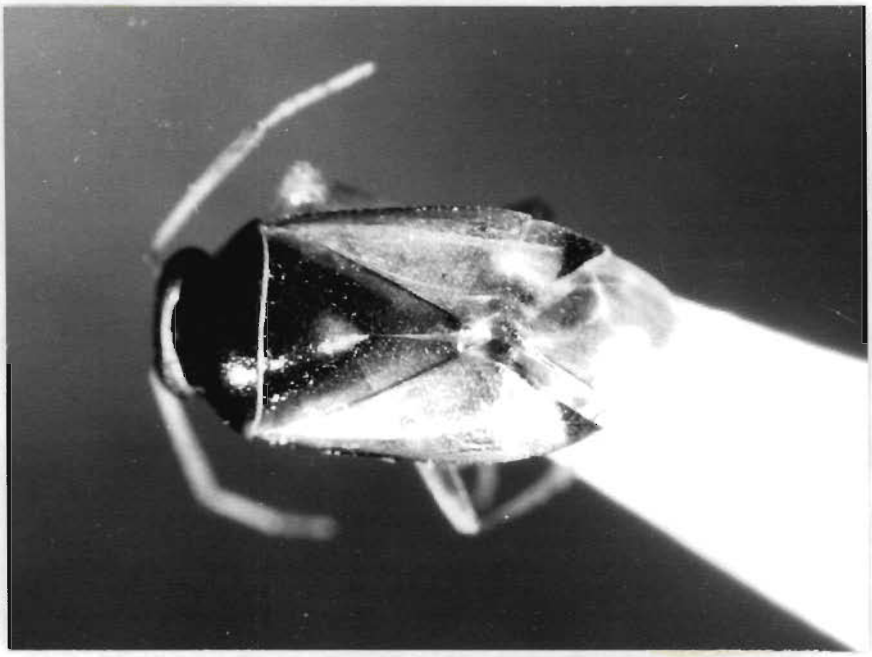


Fig. 3A. L. laevigatum. Adult male. Dorsal view.

Fig. 3B. L. laevigatum. Adult male. Ventral view.

in the fully coloured adult male the genital segment and bands are a deep rich red-brown to black, leaving only the central sternal areas and often the area outside each band, pale yellow.

2.1.2 General body shape and size

The measurements of body length and width presented in Appendix 1 compare favourably with those given by Odhiambo (1960). Measurements taken from twenty males and twenty females selected from insects collected over an extended period from various localities, show average male length as 3.19 mm.; average female length as 3.37 mm. This gives a difference of 0.18 mm., with a standard error 0.0583 for this difference. The value of t (38 DF) is 3.026, significant at the 1 per cent. level. Thus females are significantly larger than the males.

Body width measurements taken across the hemelytra behind the scutellum, are more variable, depending as they do on the positions of the hemelytra. The body of L. laevigatum is fairly wide, but this is the general body shape of many of the Mirini. L. laevigatum may be considered a fairly small species, since Miridae vary from 2 mm. to 8 mm. in length.

2.1.3 The head

The head of L. laevigatum is of the prognathous type and highly specialised to accommodate the sucking mouthparts and their associated structures.

On the head capsule the gular region is well-developed, as in most Heteroptera (Southwood 1953) (Fig. 4A). The clypeus is greatly enlarged and divided into the anteclypeus or tylus, (Figs. 4 and 5G) and the postclypeus. There is no suture between the two but the division is considered to occur where the clypeal folds end (Fig. 5G). Deep clefts separate the tylus from the lateral lobes of the head, called the juga (the mandibular plates

FIG. 4

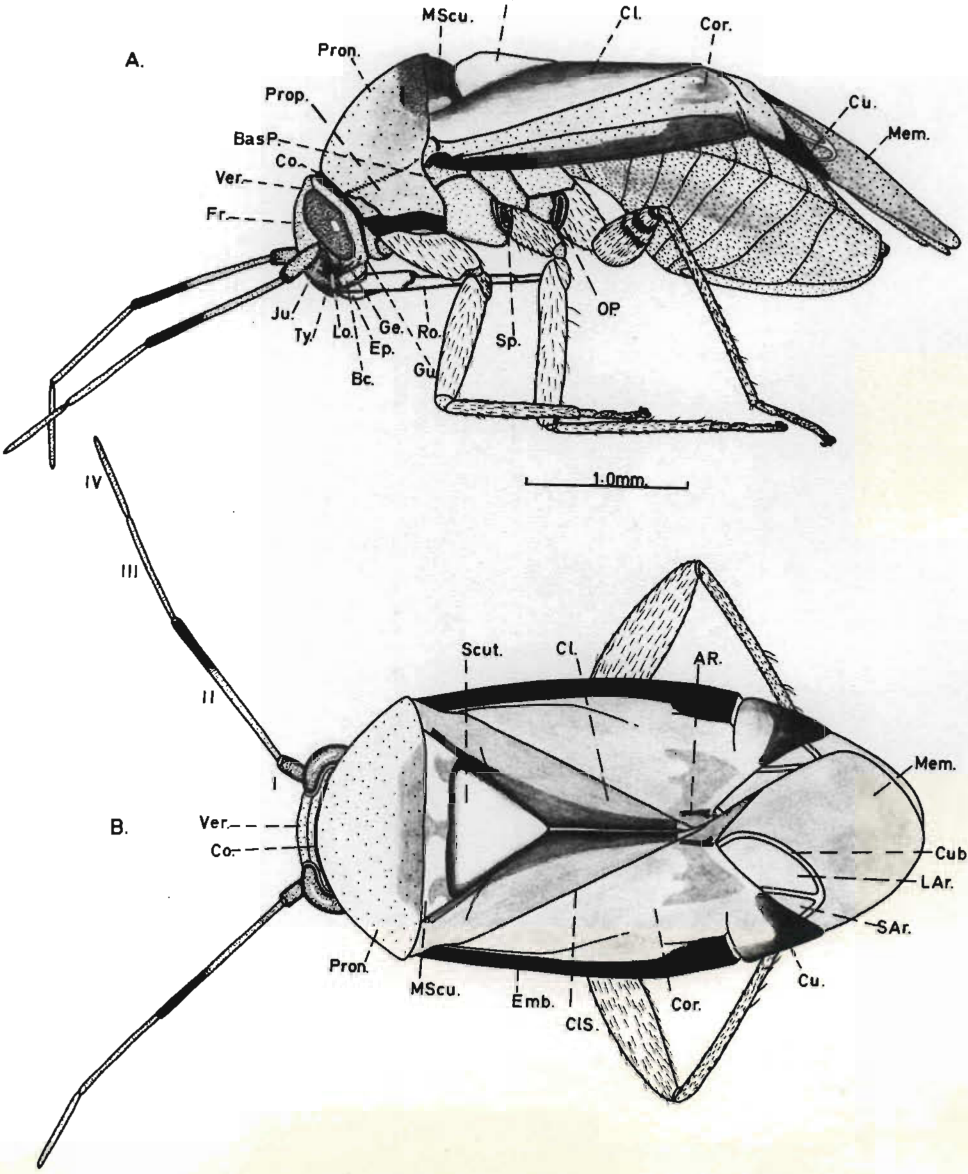


Fig. 4 Adult female *L. laevigatum*. A, lateral view. B, dorsal view. AR, anal ridge; Bas P., basalar plate; Bc., buccula; Cl., clavus; Cl S., claval suture; Co., collar; Cor., corium; Cu., cuneus; Cub., cubitus; Ep., epipharynx or labrum; Fr., frons; Ge., gena; Gu., gula; Ju., jugum; L Ar., large areole; Lo., lorum; Mem., membrane of hemelytron; M Scu., mesoscutum; OP., ostiolar peritreme; Pron., pronotum; Prop., propleuron; Ro., rostrum; S Ar., small areole; Scut., scutellum; Sp., mesothoracic spiracle; Ty., tylus; Ver., vertex.

FIG. 5

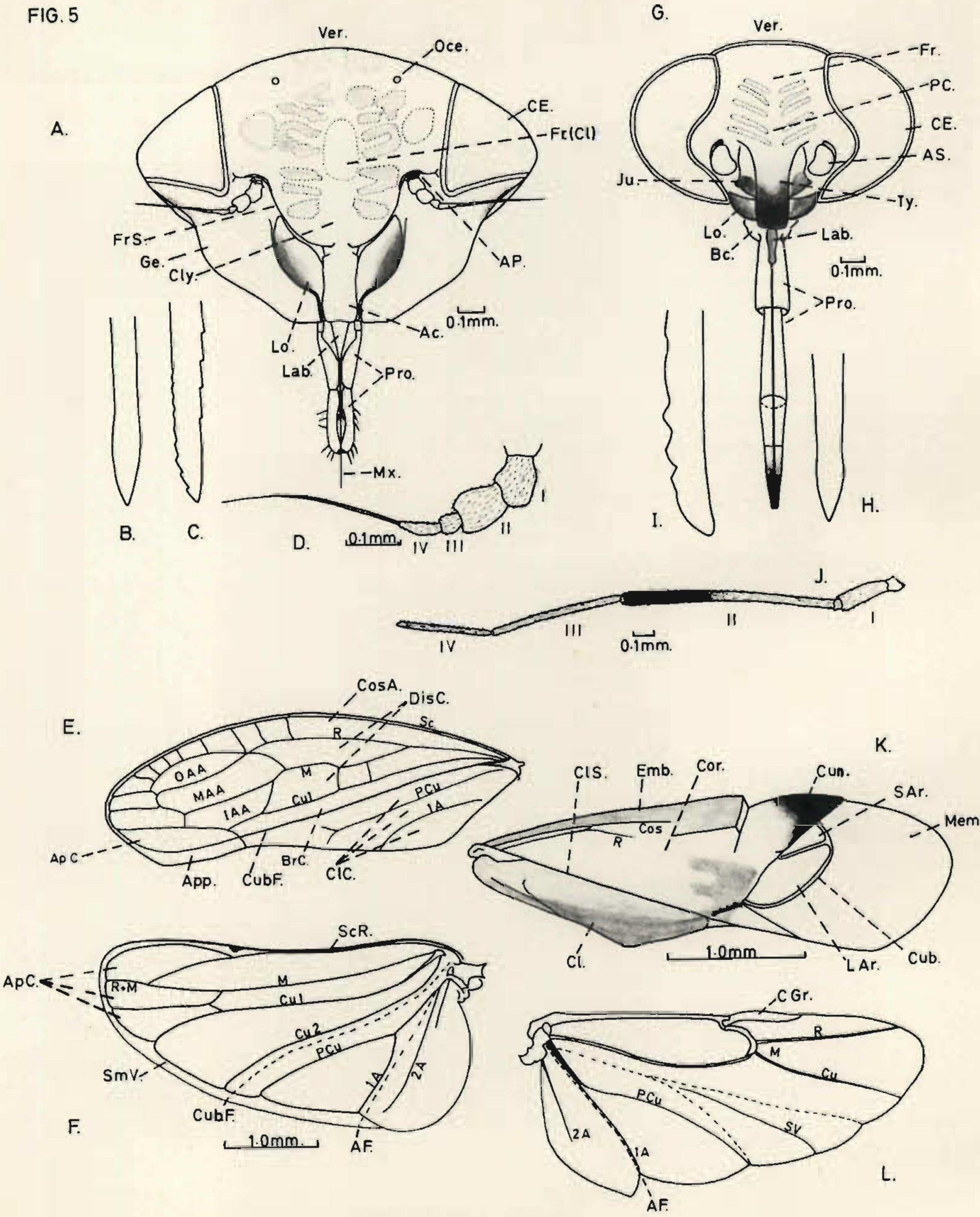


Fig. 5 Head, mouthparts, antennae and wings of: A - F, B. cedaranus. A, anterior view head. B, tip of maxilla. C, tip of mandible. D, antenna. E, Hemelytron. F, metathoracic wing. G - L, L. laevigatum. G, anterior view head. H, tip of maxilla. I, tip of mandible. J, antenna. K, Hemelytron. L, metathoracic wing. Ac., anteclypeus; AF., anal fold; AP., antennal pit; ApC., apical cell; App., appendix; AS., antennal socket; Bc., buccula; BrC., brachial cell; CE., compound eye; CGr., costal groove; Cl., clavus; ClC., claval cells; ClS., claval suture; Cly., clypellus; Cor., corium; CosA., costal area; Cub., cubitus; CubF., cubital fold; Cun., cuneus; DisC., discal cells; Emb., embolium; Fr., frons; FrS., frontal suture; Ge., gena; IAA., MAA., OAA., inner, median and outer anteapical cells; Ju., jugum; Lab., labrum; LAr., large areole; Lo., lorum; Mem., membrane; Mx., maxillae; Oce., ocellus; PC., postclypeus; Pro., proboscis; SAr., small areole; Ty., tylus; Ver., vertex.
Wing veins:- 1A., 2A., first and second anal veins; Cos., costa; Cu., cubital; M., media; PCu., postcubital; R., radius; Sc., subcosta; SmV., submarginal vein; SV.,

gena is a plate termed the buccula (Figs. 4 and 5G).

Sutures are absent in the posterior region of the head capsule of the adult, and there are no ocelli. The labrum is attached to the anterior margin of the anteclypeus, although directed ventrally due to the position of the head (Figs. 4 and 5G).

The mandibles and maxillae are each represented by a pair of stylets. The tip of each maxilla is simple (Fig. 5H) while the mandibular stylets are serrated on their outer edges (Fig. 5I). The labium is modified to form a four-segmented rostrum (Fig. 5G) and the maxillary and mandibular stylets are housed in a groove on its anterior surface.

The antennae (Fig. 5J) are long and four-segmented (as in all Miridae) and are attached to the head just below the centre of, and anterior to, the eyes (Fig. 5G). The segments are covered by fine hairs, with none of the long setae used in taxonomy of other groups of Miridae.

2.1.4 The Thorax

There is little information in the literature concerning the structure of the thorax in Heteroptera, the only major studies being those of Taylor (1918), Larsen (1945), Brindley (1934) and Southwood (1953). As observed by Southwood, there is a great deal of overlapping of tergal plates.

The pronotum (Fig. 4) is well developed and forms by far the greater portion of the dorsally visible thorax. Described by Southwood as saddle-shaped, it overlaps the mesothorax to the extent that only about the posterior third of the mesoscutum is visible externally. Laterally, the pronotum fuses with the epimeron which extends down immediately posterior to the first coxal cavity, where it ends. Anteriorly the point on the collar behind the eye (Fig. 4). Posterior to this suture on the propleuron, is the epimeron. Ventrally the collar gives way to the probasisternum which forms a wide precoxal bridge.

The mesothorax has a large mesoscutum (Fig. 4B) the greater part of which is hidden under the pronotum. Posterior to this is the scutellum (Fig. 4B), which extends backwards to cover most of the metanotum. Laterally the episternum and epimeron are separated by a well-defined pleural suture. The episternum is separated from the large bulky basisternum by a weak wavy suture.

The metathorax is entirely hidden by the wings, is greatly modified, and much reduced. The backward projection of the mesothoracic scutellum is reduced to a narrow band. Laterally the episternum (Fig. 4) is large, and according to Southwood(1953) overlaps the epimeron. Ventrally the basisternum is smaller than that of the mesothorax, but is nevertheless well developed.

2.1.5 Thoracic legs

In the Miridae the three pairs of legs are similarly developed and of similar function (Fig. 6). All three display a feature found in other Heteroptera, in which there appears to be two "segments" between coxa and femur. Southwood (1953) studied the muscles of this part of the leg and concluded that the second "segment" was in fact a basal part of the femur.

At the distal end of the tibia of the prothoracic leg is a fine comb-like structure termed the tibial comb by Knight (1921). It is comprised of fine, closely placed translucent spine-like teeth, numbering 14 - 16 in L. laevigatum. The comb is bordered on each side, by two large spines (Fig. 6D).

FIG.6

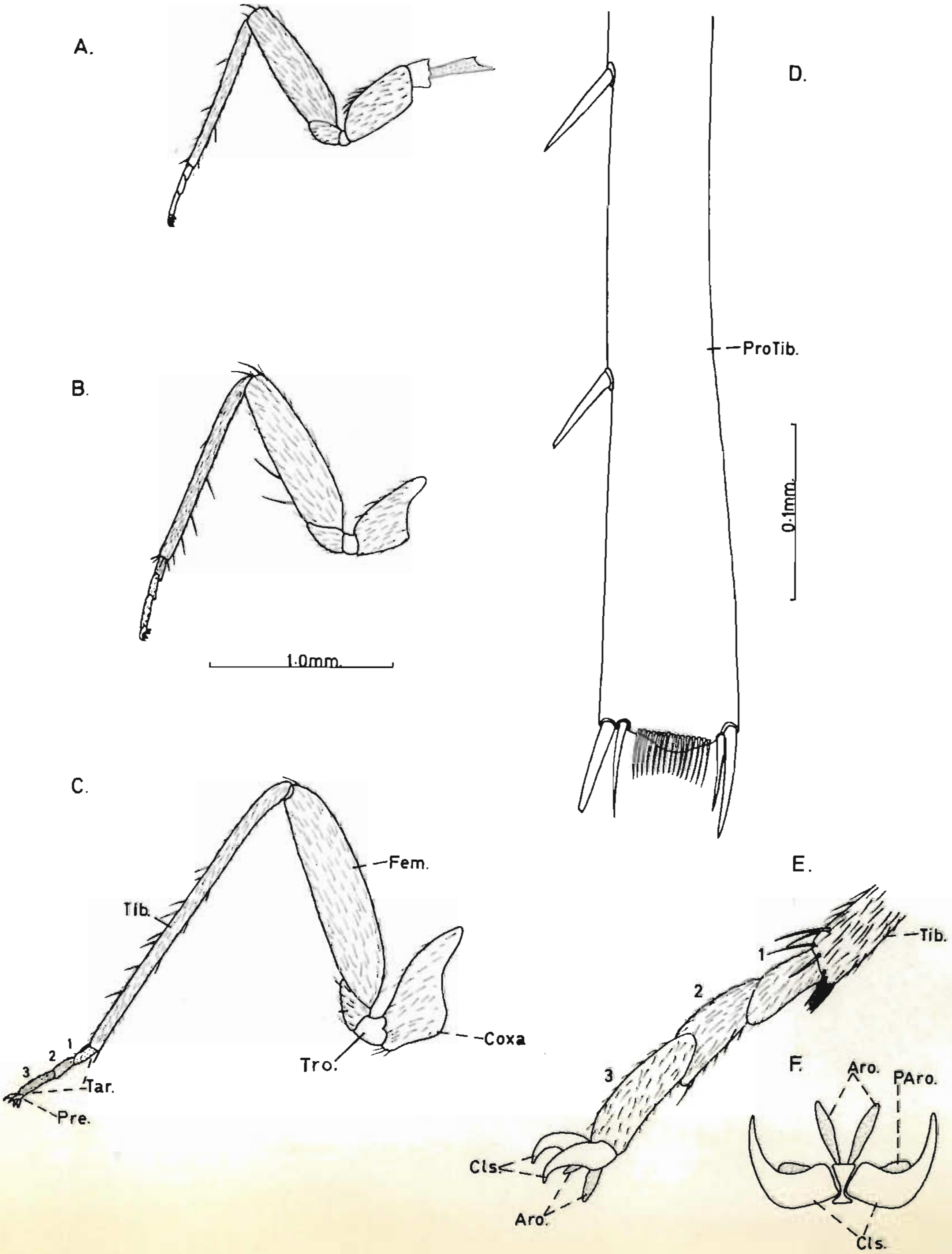


Fig. 6 Thoracic legs of L. laevigatum adults. A, prothoracic leg. B, mesothoracic leg. C, metathoracic leg. D, antennal comb at the apex of the prothoracic tibia. E, detail of metathoracic tarsus. F, detail of the pretarsus. Aro., arolia; Cls., claws; Fem., femur; P Aro., pseudarolia; Pre., pretarsus; Pro Tib., prothoracic tibia; Tib., tibia; Tro., trochanter.

pair of well developed, fleshy arolia and a pair of pseudoarolia (Fig. 6F).

Apart from a covering of fine hairs over all leg segments, the femora are densely covered by long hairs, the coxae more sparsely. A row of heavy setae occurs on the hind tibia, those on the other tibiae being less conspicuous. Medium length hairs are found on all tibiae as well.

2.1.6 Wings

The forewings of all Heteroptera are modified into hemelytra (Fig. 5E). Terminology given is that of Knight (1921). The hemelytra are covered by extremely fine hairs.

The membranous hind wings of Heteroptera have been studied by Davis (1961). He found the venation of Miridae to be very consistent, with no marked differences between subfamilies. The present investigation confirms this in that the venation of the hindwing of L. laevigatum is practically identical to that described and figured by Davis. The venation is characterised by Davis as follows: "Sc. indistinct and marginal, hamus lacking; M distinguishable only as a diagonal vein connecting R and Cu, only one secondary vein present; Pcu and 1st A joined proximally and strongly divergent distally, forming a Y-shaped pattern; 2nd A often obsolete." In L. laevigatum the 2nd A is fairly well-developed (Fig. 5F).

The hindwing has a groove along its costal edge which links with a spur near the apex of the clavus of the forewing (anal ridge) and serves to hold the two together in flight (Davis 1961).

2.1.7 The abdomen

The abdomen of the female is more or less boat-shaped and is relatively broader and deeper than that of the male (Figs.

FIG. 7

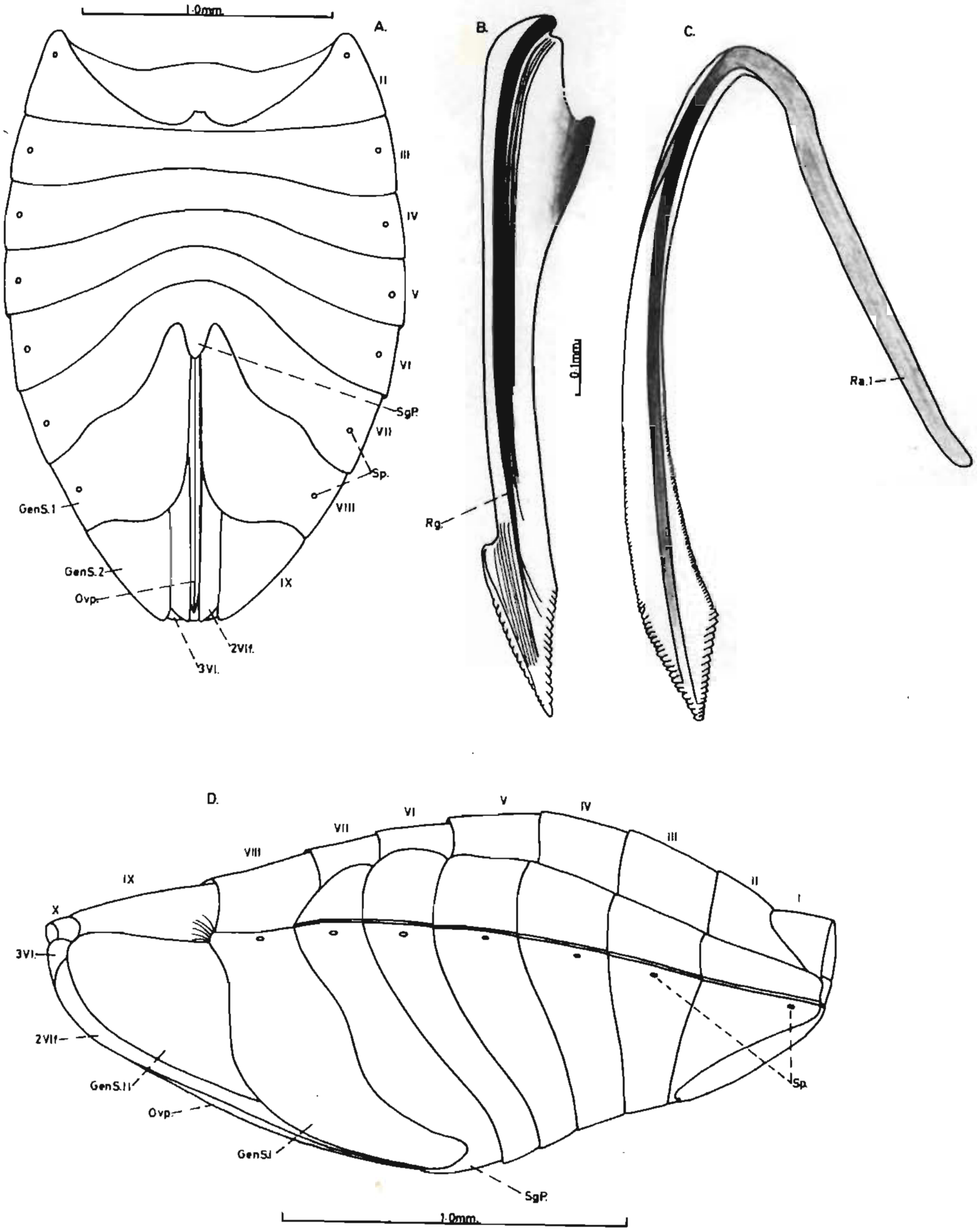


Fig. 7 Female abdomen and external genitalia L. laevigatum. A, ventral view abdomen. B, second or posterior valvulae. C, first or anterior valvulae. D, lateral view, abdomen. Gen S.1., Gen S.2., first and second genital segments; Ovp., ovipositor; Rg., ridge; Ra.1., ramus of first valvulae; Sg P., subgenital plate; Sp., spiracles; 3 Vl., third valvulae; 2 Vlf., second valvifers.

FIG. 8

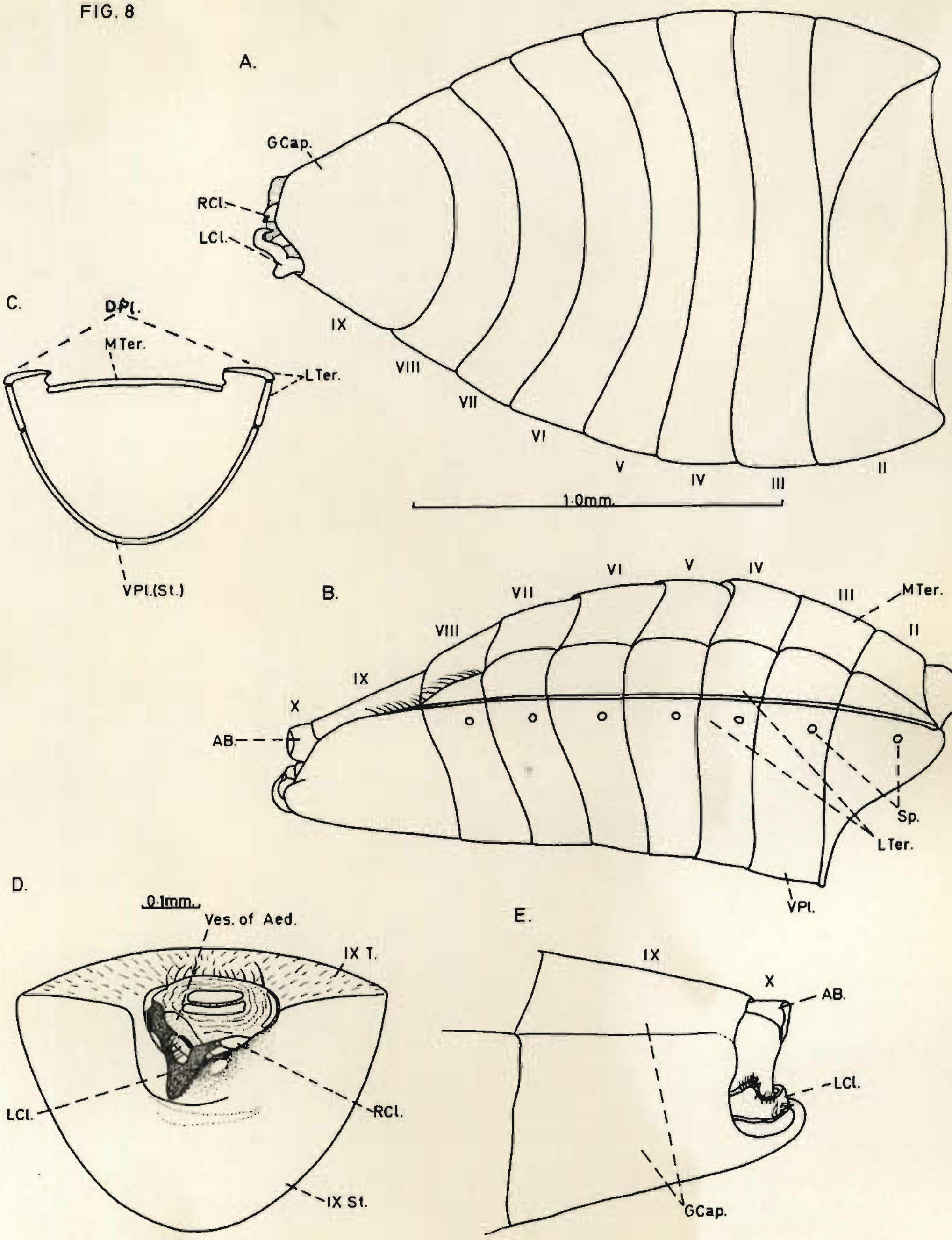


Fig. 8 Male abdomen and genitalia of *L. laevigatum*. A, abdomen ventral view. B, same, lateral view. C, transverse section through the abdomen (after Kullenberg, 1947). D, posterior view, terminalia. E, left lateral view, terminalia (genital capsule). AB., anal block; DPl., dorsal plate G Cap., genital capsule; L Cl., left clasper; L Ter., laterotergite; M Ter., median tergite; R Cl., right clasper; Sp., spiracles; St., sternum; T., tergum; Ves., vesica of aedeagus; V Pl., ventral plate.

although some are considerably modified. The eleventh is covered by the tenth. According to Davis (1955) the ventral portion of the first abdominal segment is reduced to an elastic membrane which joins the abdomen to the thorax. Dorsally the first segment is reduced to a small plate. The ventral portion of the second segment is reduced to a thin sclerotised strip, while dorsally and laterally the plate is fairly well developed. The following four abdominal segments are roughly similar in shape, consisting of broad plates which, in the female, arch increasingly in order of nearness to the genital segments. The seventh segment in the female has a pointed flap-like portion referred to as the subgenital plate. The terminal abdominal segments are discussed in Section 3.2.2.1.

In the male, segments three to eight are similar both dorsally and ventrally although they become increasingly arched towards the tip of the abdomen. The ninth abdominal segment is the genital capsule, discussed in Section 3.2.1.1.

As mentioned previously, a series of broad median tergites constitute what is known as the dorsal plate of the abdomen (Kullenberg 1947). Two membranous bands, extending from the anterior margin of the abdomen, continue through the seventh segment in the female, to some extent including the eighth in the male. These become greatly expanded in the young gravid female. Posteriorly the membranous bands on each side of the tergum approach and meet a thin membranous band termed the connexiva by Davis (1955) which extends to the posterior end of the ninth although its membranous appearance is lost in the eighth and ninth segments (Figs. 7D and 8B). This band is narrow and appears to act as a hinge, allowing that part of the tergal plate between it and the membranous area to be raised

This portion was termed the laterotergite by Kullenberg (1947) and extends down with the connexiva at its apex, to include a portion of the ventral plate (Fig. 8C). On the eighth and ninth segments of the male long fine hairs line the inner edge of the laterotergite (Fig. 8). Similar hairs are found on the posterior margin of this tergite on the female's eighth abdominal segment (Fig. 7).

Spiracles are found, just below the connexiva, on abdominal segments two to eight. From transverse sections made in this study it appears that these lie in tergal plates which have come to lie latero-ventrally on the abdomen. This was suggested by Kullenberg (1947) who considered that the ventral margins of the tergum could be represented by hypothetical lines running just below the abdominal spiracles. There is no obvious point of union between tergum and sternum.

2.2

BATRACHOMORPHUS CEDARANUS

2.2.1 Body colour and size

The general colour is light green, with two small conspicuous black spots near the posterior margin of the vertex, and the eyes reddish to bright red. The face is white with many transverse green lines on the clypeus. The anterior and posterior margins of the vertex, together with the area surrounding each of the black dots and a mid-dorsal line are pale white. The anterior third of the pronotum forms an arc of pale white, prominently marked in a pattern of green spots and markings. The scutellum is whitish with two brownish-green markings extending down from the pattern of the pronotum, two pairs of

FIG. 9

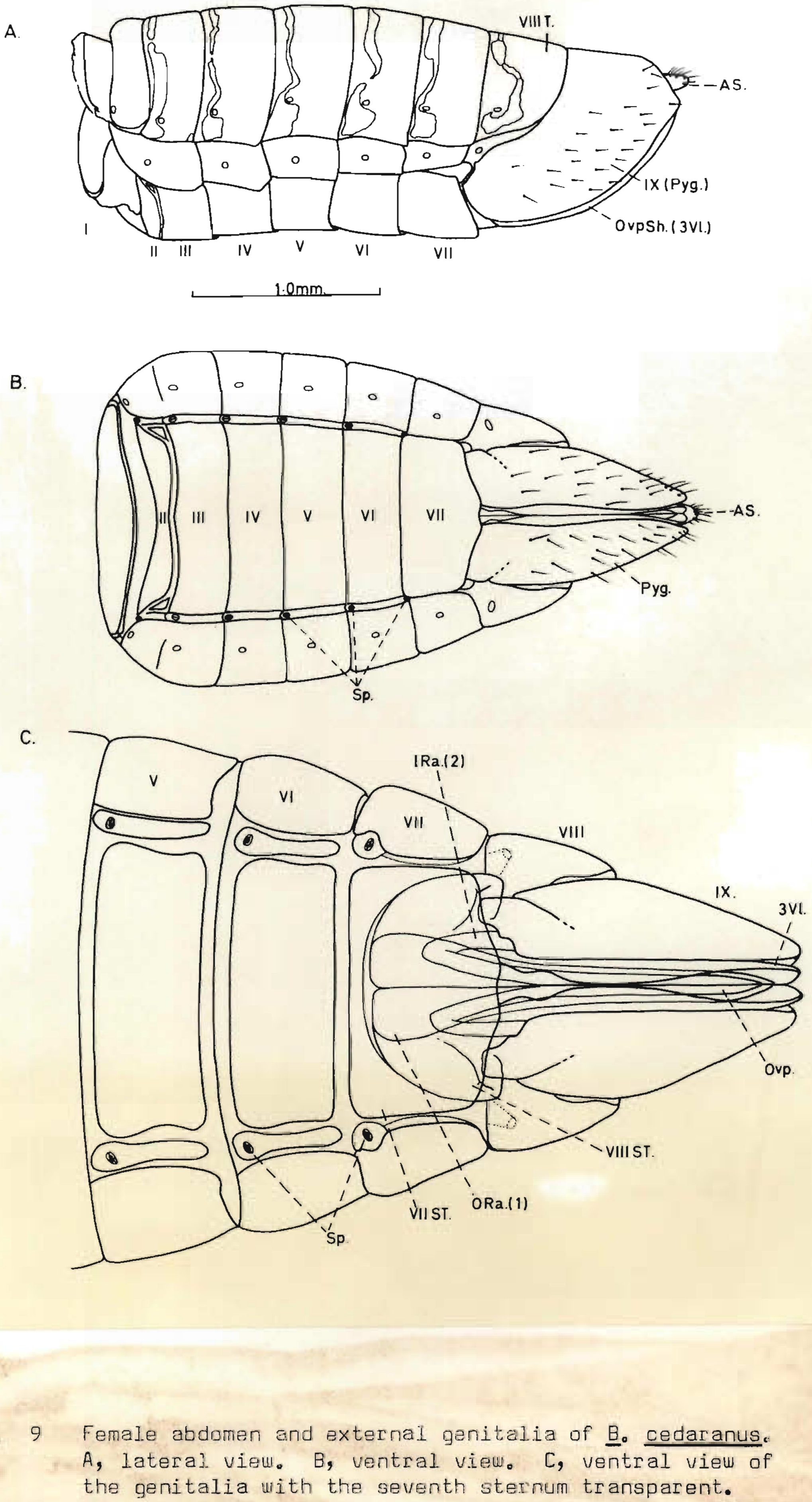


Fig. 9 Female abdomen and external genitalia of B. cedaranus. A, lateral view. B, ventral view. C, ventral view of the genitalia with the seventh sternum transparent. AS., anal style; I Ra., inner or second ramus; ORa., outer or first ramus; Ovp., ovipositor; OvpSh., ovipositor sheath; Sp., spiracles; ST., sternum;

On the abdomen the anterior margin of each tergal plate is white, more broadly laterally (Fig. 9A). The sterna are predominantly greenish and in the female the ovipositor is pinkish-brown.

Measurements taken from adults of B. cedaranus are presented in Appendix 1. These give average male length as 4.74 mm., average female length as 5.46 mm. The difference of 0.72 mm., has a standard error of 0.1422 mm. The value of t (38 DF) is 5.084, significant at the 0.1% level. Thus females are significantly longer than males.

2.2.2 The head

The anterior view of the head is illustrated in Fig. 5A. Even when feeding it is deflexed under the prothorax (Fig. 10A). As a result the only part of the head visible from above, is the narrow vertex, with a compound eye at each lateral extremity (Fig. 10B). This portion is in fact termed the crown by Evans (1946), defined as that part of the head which is visible from above and is on a plane with the pronotum. The term has no morphological significance and may comprise part of the frons as well as the vertex. Viewed anteriorly, the head is rather oval in shape, (Fig. 5A) and only slightly broader than long. The clypeal suture divides the clypeus into two regions. Dorsally the broad frons bears the compound eyes laterally and a pair of ocelli. Medially, between the downward curves of the clypeal suture on each side of the face, the clypeus extends down the length of the face to its anterior (ventral) margin. If we consider the head as prognathous for the purposes of description, then the posterior portion of the clypeus is the frons. Evans (1946) following Spooner (1938) named the part immediately anterior to the antennae, the anteclypeus. Other

FIG. 10

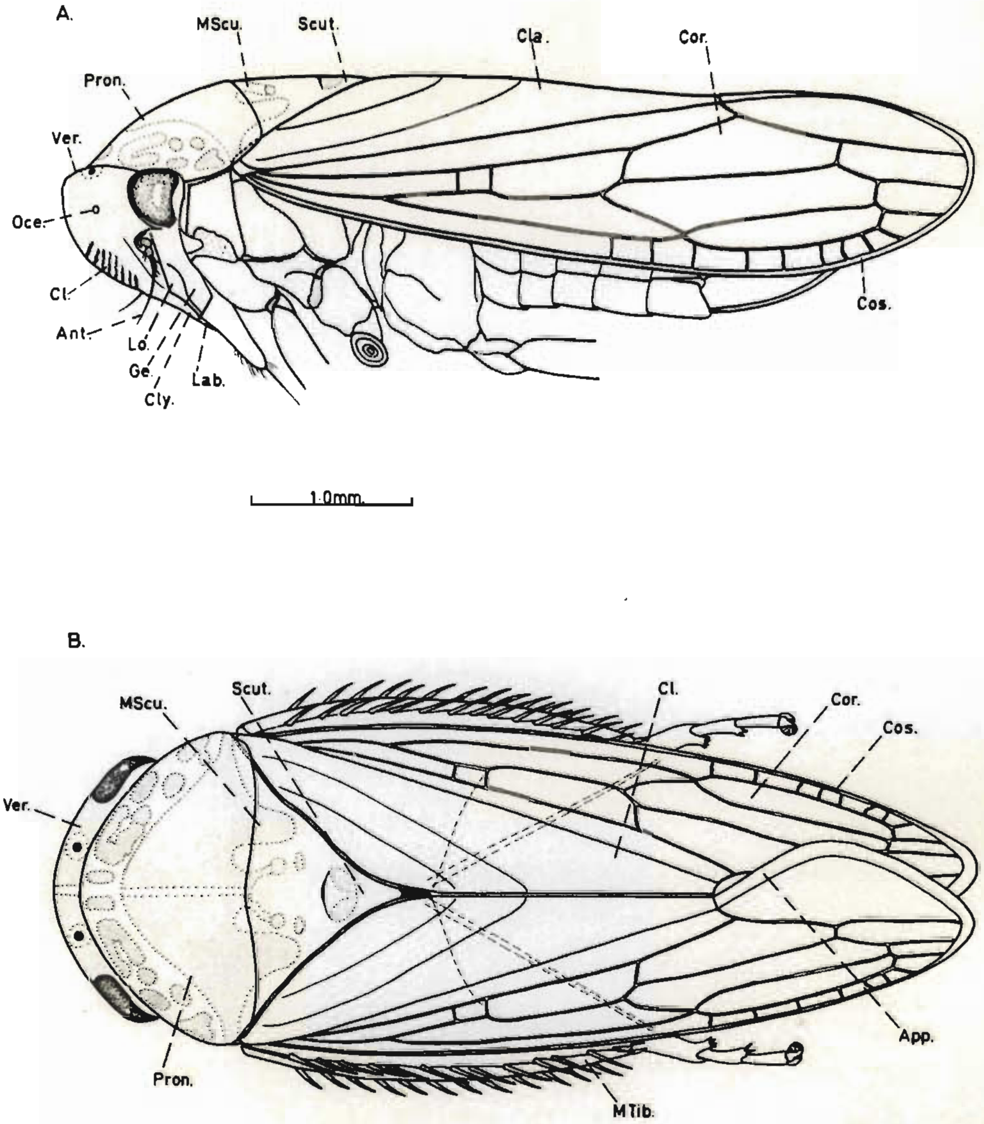


Fig. 10 Adult female *B. cedaranus.* A, lateral view. B, dorsal view. Ant., antenna; App., wing appendix; Cl., Clypeus; Cla., clavus; Cly., clypellus; Cor., corium; Cos., costa; Ge., gena; Lab., labrum; Lo., lorum; M Scu., mesoscutum; M Tib., metathoracic tibia; Oce., ocellus; Pron., pronotum; Scut., mesothoracic scutellum; Ver., vertex.

portion of the clypeus.

Immediately anterior to the anteclypeus is the small triangular labrum.

Lying along the margin of the anteclypeus and frons, on each side are two plates termed the lora(e) (Fig. 5A). Evans (1946) submits evidence for regarding the lora of Cicadellidae as derived from mandibles. Since the lora of Heteroptera (Section 2.1.3) are considered to be maxillary plates, and the juga as mandibular plates, there appears to be some confusion in terminology and origin of these structures. Laterally the lower portion of the face is made up of the maxillary plates, termed genae, lying below the compound eyes. These structures appear to correspond to the maxillary plates or lora of Heteroptera (Section 2.1.3).

The labium lies between and below the maxillary plates forming the three-segmented proboscis. It is grooved anteriorly to form a housing for the mandibular and maxillary stylets. The latter pair are tubular, while the former have serrated outer edges apically and even some serration on their inner edge (Fig. 5C). Apically the maxillary stylets are locked together, grooves on their inner surfaces being opposed to form two canals, one being a salivary and the other a food channel.

The antennae are fairly small, consisting of two basal segments and a filament. This latter part apparently consists of three thicker segments and a long thin portion which makes up about half the antennal length (Fig. 5D).

2.2.3 The thorax

The pronotum is large and lightly transversely furrowed. Superficially the dorsal part of the thorax appears similar to that of the mirid L. laevigatum. According to Evans (1946) the has resulted in a highly compressed metatergum, due to the backward projection of the mesotergum (Evans 1946). For further detail on the structure of the cicadellid thorax the reader is referred to Evans (loc. cit.). Although Evans considers the scutum to form the major portion of the mesonotum, taxonomists persist in referring to the visible area of the mesonotum as the scutellum. It is not within the scope of this investigation to confirm or reject the views of Evans.

Laterally and ventrally the episterna of the prothorax are reduced and the visible sternum is small. In the mesothorax, according to Evans (1946), each episternum is divided into an anepisternum and a pre-episternum, with an undivided epimeron. A small sternum is situated ventromedially between the pre-episterna, although these latter in fact meet ventrally and posterior to the sternal plate. In the metathorax the trochantins and coxae of the hind legs are so greatly enlarged that the episterna and epimera are concealed (Fig. 10A).

2.2.4 Legs

Legs of the pro- and mesothorax are similar, consisting of normally developed segments. The tarsus is three-segmented and the pretarsus has a pair of claws and a pair of fleshy arolia (Fig. 11).

The metathoracic legs are well-developed for the purpose of jumping, hence the appropriate name "leafhopper" often given to members of the family. The coxa is enormously enlarged (Fig. 11C) and has a greatly enlarged trochantin at its base. The femur is also much enlarged. The tibia is long and roughly quadrilateral in cross-section, with a row of spines on each edge. The two outward-facing rows of spines are slightly longer than tibial width, of strong construction with enlarged bases.

FIG. 11

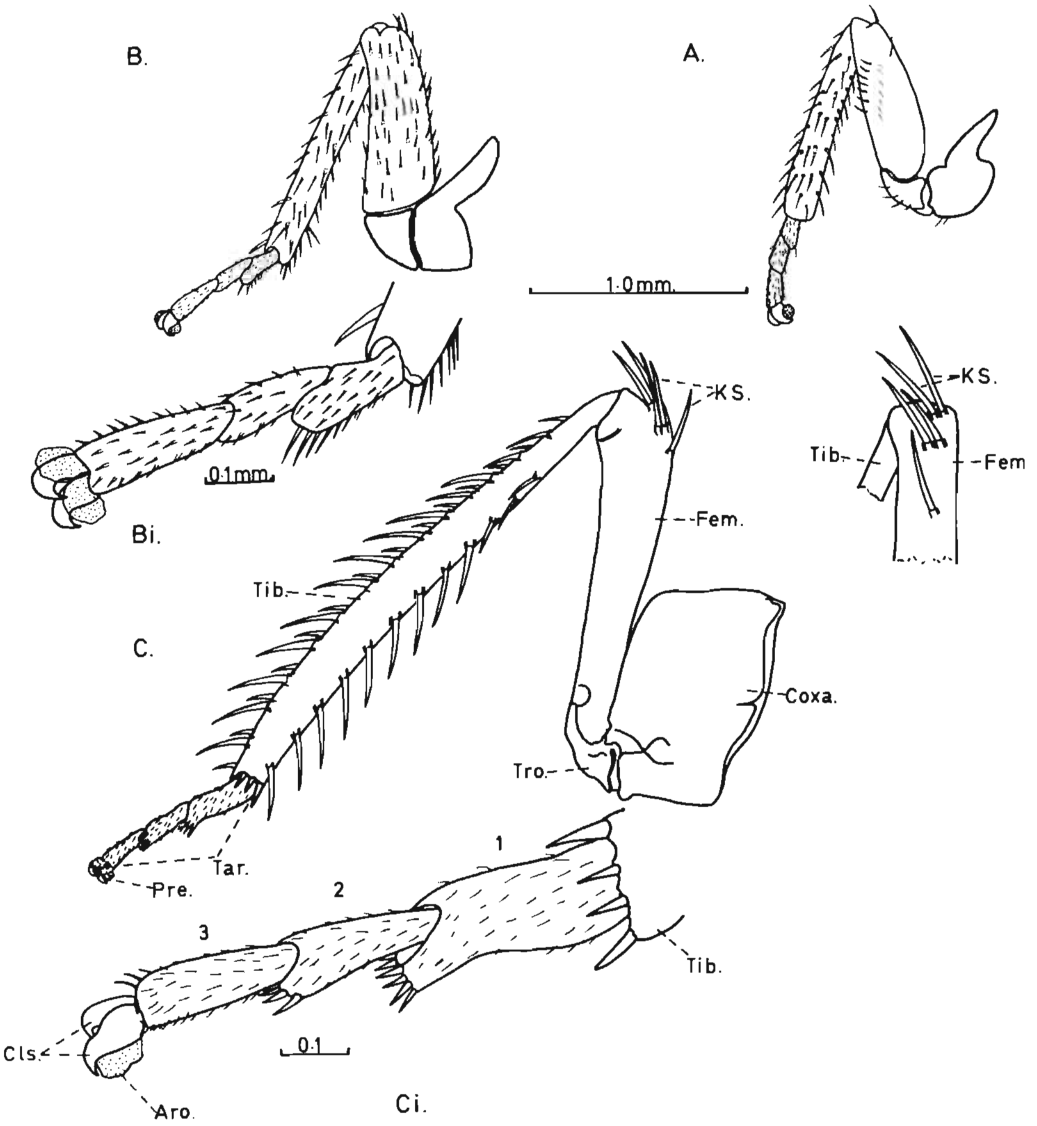


Fig. 11 Thoracic legs of B. cedaranus adults. A, prothoracic leg. B, mesothoracic leg. Bi, detail of the mesothoracic tarsus. C, metathoracic leg. Ci, detail of the metathoracic tarsus. D, dorsal view of "knee-spines". Aro., arolium; Cls., claws; Fem., femur; KS., knee spines; Pre., pretarsus; Tar., tarsus; Tib., tibia; Tro., trochanter.

either side of the femur when the leg is folded, the upper row consists mainly of fine spines interspersed with six or seven longer spines nearer the base of the tibia, in all numbering 42 to 45, while the lower row consists of nine to ten spines, slightly smaller than those of the two outward-facing rows, and without enlarged bases.

On the metafemur spines exist which are used as taxonomic features. These are at the distal end and lie in a 2 + 2 + 1 formation (Fig. 11D).

2.2.5 The wings

Some confusion has existed concerning the position and identity of the Cubital, Postcubital and Anal veins of the forewing. Davis (1961) states that the Cu_2 borders the cubital furrow posteriorly but, since it is weakly developed and inconspicuous, it is frequently indistinguishable. However the presence of this vein is indicated by the presence of a trachea clearly visible in newly moulted adults. The remaining veins of the clavus should thus be designated as the Pcu, 1st A and 2nd A respectively (Fig. 5E). Other veins and cells are consistently named as shown in the illustration. There are three closed subapical (anteapical) cells, and a broad appendix.

In the hindwing, Cu_2 lies anterior to the cubital furrows and posterior to the furrow is found the characteristic Y-shaped pattern of venation formed by veins which should be designated as Pcu and 1st A (Fig. 5F). The anal lobe contains a single vein, the 2nd A (Davis 1961).

A recurved toothlike lobe on the costal margin of the hind wing (Fig. 5F) acts as the mechanism for locking the fore and hind wings of the Auchenorrhyncha together. The lobe of the hind wing catches in the turned-under hind margin of the clavus

2.2.6 The abdomen

General shape of the male and female abdomen is shown in Figs. 9A and B and in Fig. 22. In both male and female all eleven basic abdominal segments may be readily recognised, segment ten being represented by the anal tube, (or anal block) usually hidden by the pygofer lobes, while the eleventh segment is the anal style (Ossiannilsson et. al. 1956).

The first abdominal segment is reduced to a small tergal plate which is visible immediately behind the scutellum of the metathorax. Ventrally it is membranous, serving to connect the thorax to the abdomen. The second abdominal segment is also reduced, both the tergum and sternum being much narrower than those of the third and following abdominal segments. Segments three to seven are basically similar, but in the female the eighth sternum (Fig. 26B) is modified to form the anterior or first valvifers to which the sabre-like sclerites, termed the first valvulae, are attached (Ossiannilsson et. al. 1956). The genital segments of the female will be discussed in Section 3.3.2.1.

In the male the eighth tergum is normal in shape while the eighth sternum is shovel-shaped and extended posteriorly to cover the much reduced ninth sternum, a small plate to which the subgenital plates are attached (Fig. 22C). Male genital segments are more fully discussed in Section 3.3.11.

CHAPTER 3

THE ORGANS OF REPRODUCTION

3.1

THE TERMINOLOGY APPLIED TO THE GENITALIC STRUCTURES OF TAXONOMIC IMPORTANCE IN MIRIDAE AND CICADELLIDAE

3.1.1 Miridae - male genitalia

The male genitalia of Miridae are very specialised, and show no affinities with those of any other Heteroptera (Pendergrast 1958). Several parts, particularly the claspers and certain details of the vesica, have been used extensively to define species and to a certain extent, to define their relationships. The first attempt at using the genitalia as a taxonomic tool was that of Reuter (1883) who illustrated the claspers to show differences between species (Kelton 1959). Knight (1923) was the first to consider the aedeagus in taxonomic studies. More recently the spiculum of the vesica has been used as a diagnostic character on its own (Kelton 1955) although this author did not use the spiculum separately in a later more extensive work (Kelton 1959).

In this study the structures beyond the phallobase are referred to as the vesica (Fig. 12A and B). This includes the distal portion of the ductus seminis, the gonopore, and the processes of the vesica, which in the Mirinae are usually in the form of spiculi or spines. The term phallus is used to designate the intromittent organ as a whole, while the phallobase is the sclerotised basal region of the phallus. The phallotheca is the structure enclosing the phallus when the phallus is in the normal position, while the

the clasping organ of male Heteroptera, the former being that in common use by North American specialists in Miridae, the latter was used by Kullenberg (1947). In this study they will be termed claspers. The harpagones of Snodgrass (1935) gonoforceps of Michener (1944) and gonostyli of Bonhag and Wick (1953) are synonymous with the two former terms. The terminology used for their various regions is that of Kullenberg (1947) modified by Kelton (1959) (Fig 12C, D and E).

3.1.2 Miridae - female genitalia

Although in the male genitalia, terminology of the structures used is neither extensive nor complicated, that of the female genitalia is fairly complex and often special techniques are required for dissecting out the required structures. An excellent paper by Kullenberg (1947) initiated the extensive search for taxonomic characters in the female Miridae. However, Kullenberg's terminology was essentially descriptive and too lengthy for general taxonomic use. Thus Slater (1951) used a series of letters to denote structures referred to in text, rather than attempting to name parts of unknown origin or function. Later Davis (1955) named several of the structures numbered by Slater.

The female mirid genital structures involved in taxonomic studies to date are all part of the genital chamber (bursa copulatrix of Slater 1951). This structure is situated dorsally above the base of the ovipositor (Figs. 16A and B). Kullenberg (1947) designated three anatomical regions of the genital chamber. These are the anterior wall, the posterior wall and the roof. Both the dorsal wall (roof) and posterior wall are important taxonomically. On the dorsal wall are found the sclerotised rings used by Slater (1951) and Kelton 1955 while the posterior subfamily relationships, and often of value in the identification of species. The different areas of the posterior wall were lettered by Slater (1951), while Davis (1955) named the wing-like portions the inter-ramal sclerite and the central portion was termed the sigmoid process by him (Fig. 19D).

3.1.3 Male genitalia - Cicadellidae

The principal genitalic features of taxonomic importance are the phallus or penis, the connective at the base of the penis and the movable styles or parameres, more or less elongate sclerotised processes which articulate with, and are situated one on each side of, the connective. The connective itself is a usually well sclerotised formation belonging to the phallobase and varying much in shape (Ossiannilsson et. al. 1956). Other characters such as the development, shape and arrangement of setae on the genital plates, and the presence or absence of setae on the pygofer lobes are used as taxonomic characters. The pygofer lobes, as well as the anal tube and the anal collar may be armed with sclerotised appendages varying in shape which are used in the taxonomy of the species involved.

3.1.4 Female genitalia - Cicadellidae

The various parts of the genitalia have been little used in the taxonomy of female cicadellids. The internal structures lack the sclerotisation of the female mirid genital chamber and have therefore been found of little taxonomic use so far. Apart from the hind margin of the seventh abdominal sternum which is often incised in a characteristic way, structures at the base of the ovipositor have recently been used in taxonomy by Cunningham and Ross (1965) in a study of *Empoasca* spp.

3.2

GENITALIA OF LYGIDOLON LAEVIGATUM

3.2.1.1 The genital capsule (Figs. 8D and E)

The genital capsule consists of the whole of the ninth abdominal segment, and is strongly sclerotised. Within the "genital chamber" is the anal tube, consisting of the tenth urite and a telescoped eleventh or true anal segment. Below this is the phallus and the movable copulatory hooks or claspers (parameres, Dupuis and Carvalho 1956) located at each side of the phallus.

3.2.1.2 The phallus (Figs. 12A and B)

The Mirinae represent a highly specialised group within the very specialised family Miridae. They appear to be a homogeneous group (Kelton 1959). The vesica is distinctive with the rim of the gonopore generally circular in outline, simulating a coiled spring. The vesica is a simple structure in *laevigatum*, showing none of the bulbous or tubular lobes found in other members of the subfamily. One simple spiculum is present. The seminal duct has a subapical expansion characteristic of the Tribe Mirini (Kelton 1959). The phallotheca is a simple partially sclerotised sheath.

3.2.1.3 The claspers (Figs. 12C, D and E)

Within the Mirinae the left clasper is gently or sharply curved, and the sensory lobe varies considerably in size and form. The right clasper is generally slender, with a prominent apical process (Kelton 1959). In *L. laevigatum* the left clasper has a sensory lobe of moderate size, and a sharply curved shaft with a small globular process at the tip. The right clasper has four large setae near the apical process, with a sharp constriction to form a narrow base.

3.2.1.4 The ductus ejaculatorius

FIG.12.

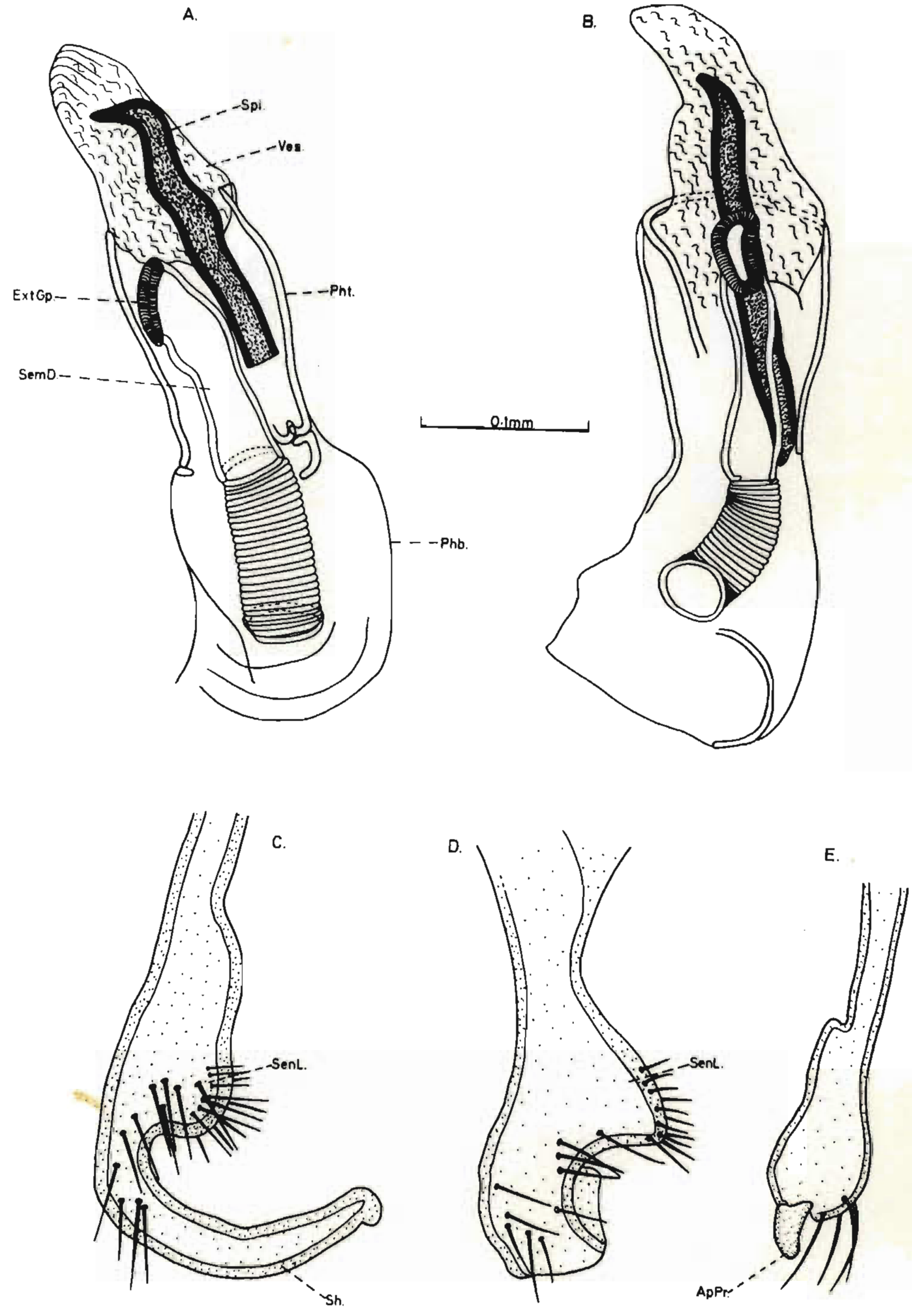


Fig. 12 Male genitalia of L. laevigatum. A, vesica (aedeagus) dorsal aspect. B, same, in lateral aspect. C, left clasper - dorsal view. D, same - left lateral view. E, right clasper. ApPr., apical process; Ext Gp., external gonopore; Phb., phallobase; Pht., phallotheca; Sem D., ductus seminis; Sen L., sensory lobe; Sh., shaft; Spi., spiculum.

ectoderm at the posterior end of the ninth abdominal segment, with which the vasa deferentia become connected (Snodgrass 1935). In the Miridae this is divided into three separate sections. Anteriorly, where the vasa deferentia join to become a common duct, Kullenberg (1947) retains the original term ductus ejaculatorius. He describes it as of variable length in Miridae, but usually short. The duct becomes greatly enlarged near its anterior end to become the ejaculatory bulb (bulbus ejaculatorius) (Fig. 13Ai). Posterior to the ejaculatory bulb the duct turns vertically downwards and immediately enters the phallobase to become the ductus seminus.

In L. laevigatum the two vasa deferentia appear to enter the ejaculatory bulb without uniting (Fig. 13A), so that no part of the duct can be termed the ductus ejaculatorius.

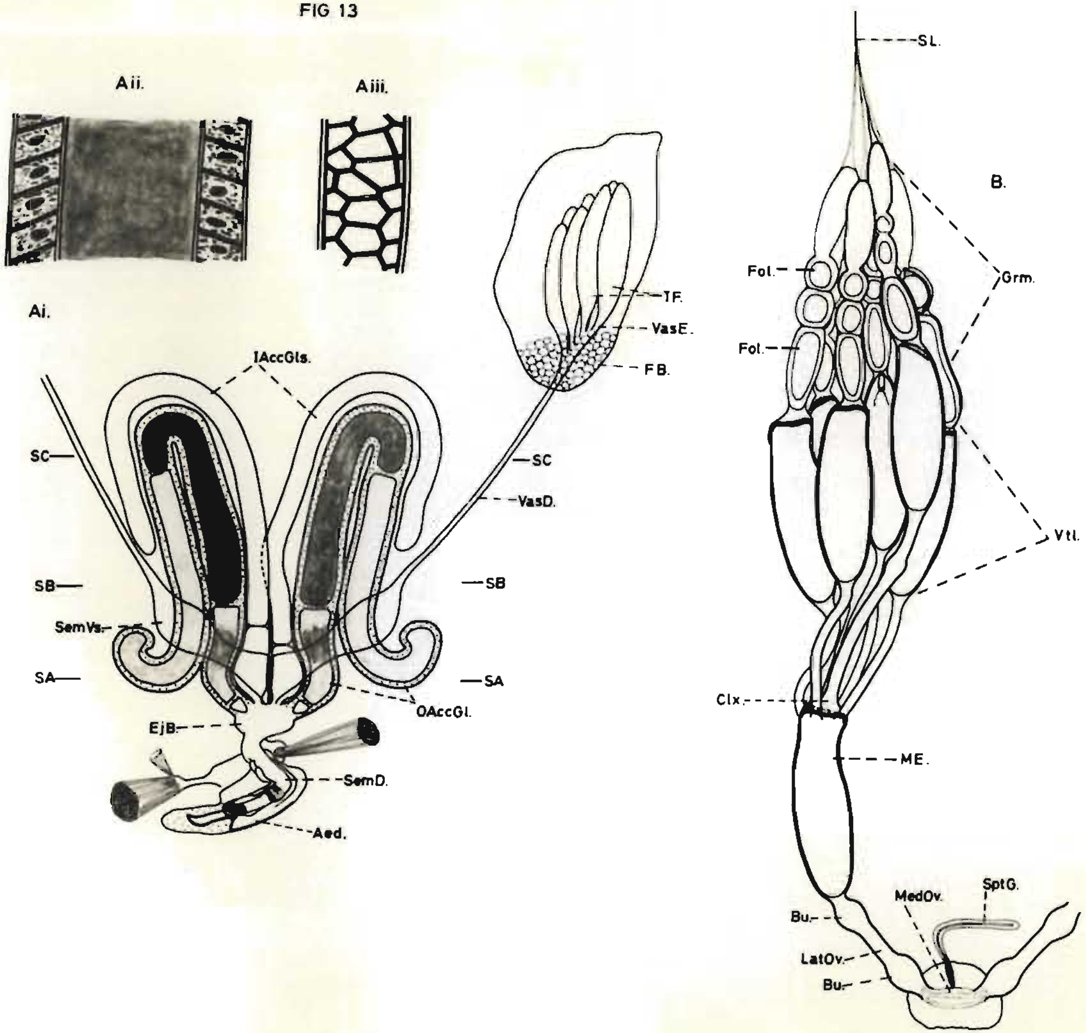
3.2.1.5 The accessory glands

Kullenberg (1947) described three pairs of accessory glands commonly associated with the male genitalia of Miridae as well as a glandular tissue associated with the seminal vesicle. He described the arrangement of the accessory glands of Lygus pratensis as being the most common type encountered. In this species the dorsal median gland of the median pair is much reduced while the ventral median gland is longer with a slightly swollen apex. The dorsal and ventral median glands are thus not a true pair being very seldom alike in size and shape. Inner and outer accessory glands of L. pratensis males are well developed.

In the male of L. laevigatum, the outer and inner lateral glands are similar to those found in other Miridae. The outer lateral glands are by far the larger, and are slightly thicker basally than towards their apical ends. The wall of the gland

Fig. 13 Internal reproductive organs of *L. laevigatum*. Ai, male organs. Aii, detail of outer accessory glands, in longitudinal section. Aiii, detail of cell shape of the inner accessory glands, as visible externally. B, female organs. Aed., aedeagus; Bu., bulbs of lateral oviducts; Clx., calyx; EjB., ejaculatory bulb; FB., fat body; Fol., follicle; Grm., germarium; IAccGls., inner accessory glands; LatOv., lateral oviduct; ME., mature egg; MedOv., median oviduct; OAccGl., outer accessory gland; SA., section A Fig. 14B; SB., section B Fig. 15A; SC., section C Fig. 15B; SemD., ductus seminis; SemVs., seminal vesicle; SL., suspensory ligament; SptG., gland of the spermatheca; TF., testis follicles; VasD., vas deferens; VasE., vas efferens; Vtl., vitellarium.

FIG 13


Aii.
Aiii.
Ai.
IAccGls.
SC
SB
SemVs.
SA
EjB.
SemD.
Aed.
OAccGl.
SA
SB
SC
VasD.
TF.
VasE.
FB.
B.
SL.
Grm.
Fol.
Fol.
Vtl.
Clx.
ME.
MedOv.
SptG.
Bu.
LatOv.
Bu.

nuclei (Fig. 13A). The lumen of the gland is divided into sections according to its contents. Apically is a portion of lightly coloured homogeneous secretion which stains pink with Cason's Stain. Centrally the content is granular and stains orange. Basally the content is similar to that found near the apex. The granular nature of the secretion in the major portion of the gland is conspicuous and Woodward (1952) suggests that the granules probably aid in nourishment of sperm in the anterior genital pouch of the female. It undoubtedly has a function of this sort but as mentioned later (§ 3.2.2.10) sperm is not permanently stored in the anterior genital pouch.

The inner lateral glands are of similar cellular structure to the outer lateral glands, but are narrower and have a very much thinner lumen. Basally the inner lateral glands are swollen (Fig. 13A) and at the point of enlargement is a thin barrier across the gland similar to those found in the outer lateral glands between the areas of different content. These barriers certainly appear to be of importance, as in the inner glands the lumen below the barrier contains a secretion which stains yellow with Cason's stain while above the thin barrier the lumen appears to contain only colourless non-staining secretion which is far less dense. In the outer lateral glands the barriers effectively separate the granules from the more homogeneous secretions.

In L. laevigatum, the dorsal median gland appears to be absent, while the ventral median gland is extremely reduced. For example in transverse sections of an adult male the ventral median gland was cut in eleven serial sections of six microns each, giving a total length of about 66 microns. Positionally the ventral median gland is no longer being cut.

Both pairs of lateral glands and the ventral median gland empty their contents directly into the ejaculatory bulb (Figs. 13A and 14A). The outer lateral glands enter the ejaculatory bulb laterally while the inner lateral glands enter it on its anterior wall but low down. The ventral median gland enters the ejaculatory bulb ventrally. Since the ejaculatory bulb is of ectodermal origin and all the glands enter it, these glands must be considered as ectadenia.

The positions of the glands in the body cavity and their positions relative to one another are clearly illustrated in Figs. 14A and B, and 15A and B.

3.2.1.6 The vasa deferentia and seminal vesicles

Pendergrast (1958) describes the vas deferens found in male Heteroptera as a simple tube with an epithelium usually invested by a sheath of circular fibres which may become greatly thickened posteriorly. In some Heteroptera the vasa deferentia are dilated apically to form a seminal vesicle. In others it is the middle or base which is enlarged.

In the Miridae this simple condition prevails, but the vasa deferentia are generally extremely thin, and usually with little or no muscular sheath. This type of vas deferens was found in several species by Kullenberg (1947) which led him to suggest that the mature sperms entered the seminal vesicle by their own motions, unaided by contraction of a muscular sheath. Kullenberg noted that some species, such as Megalocoleus molliculus (subfamily Phylinae), have a fairly well developed muscular sheath around the vasa deferentia, particularly near where they enter the ejaculatory duct.

The seminal vesicle consists, in the Miridae, of a basal

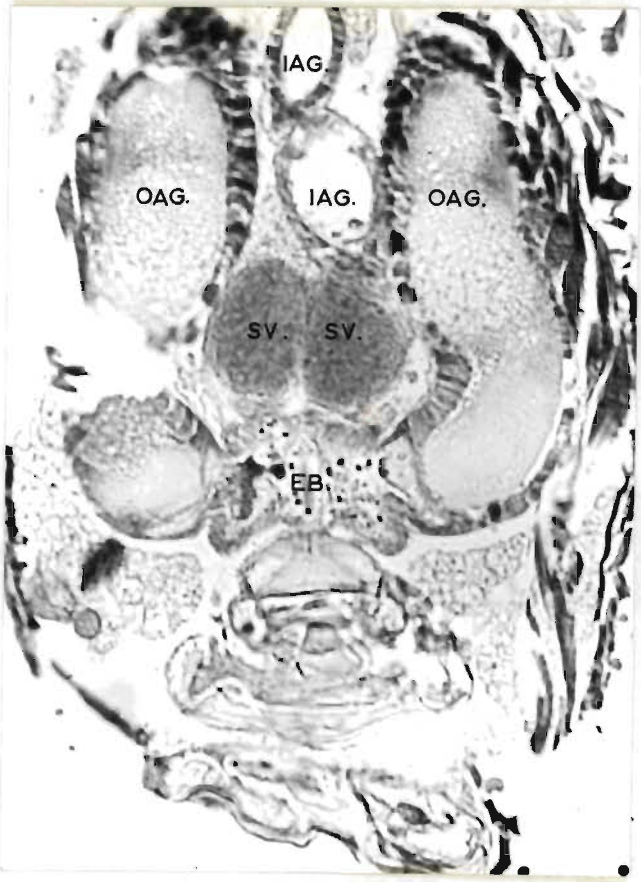


Fig. 14A. L. laevigatum male. Longitudinal section through the reproductive organs. EB., ejaculatory bulb; IAG., OAG., inner and outer accessory glands; SV., seminal vesicles.

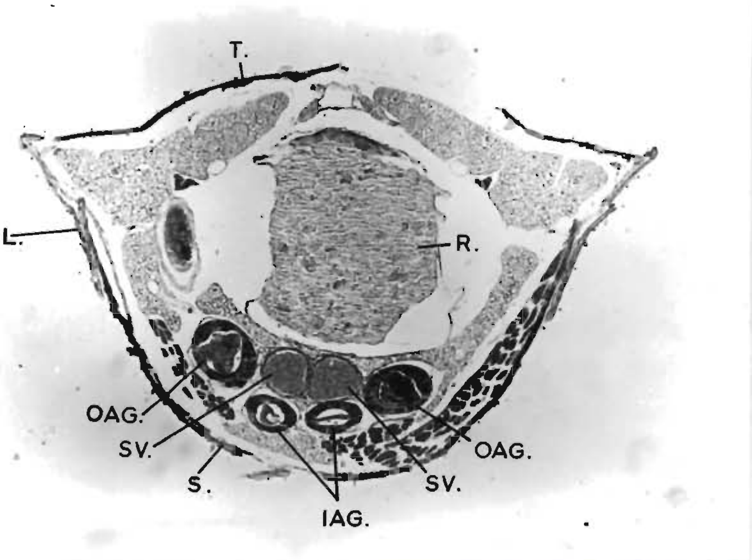


Fig. 14B L. laevigatum male. Transverse section through the abdomen and internal reproductive organs in the region of Section A of Fig. 13Ai. IAG., OAG., inner and outer accessory glands; L., laterotergite; R., rectum; S., sternum; SV., seminal vesicle; T., tergum.

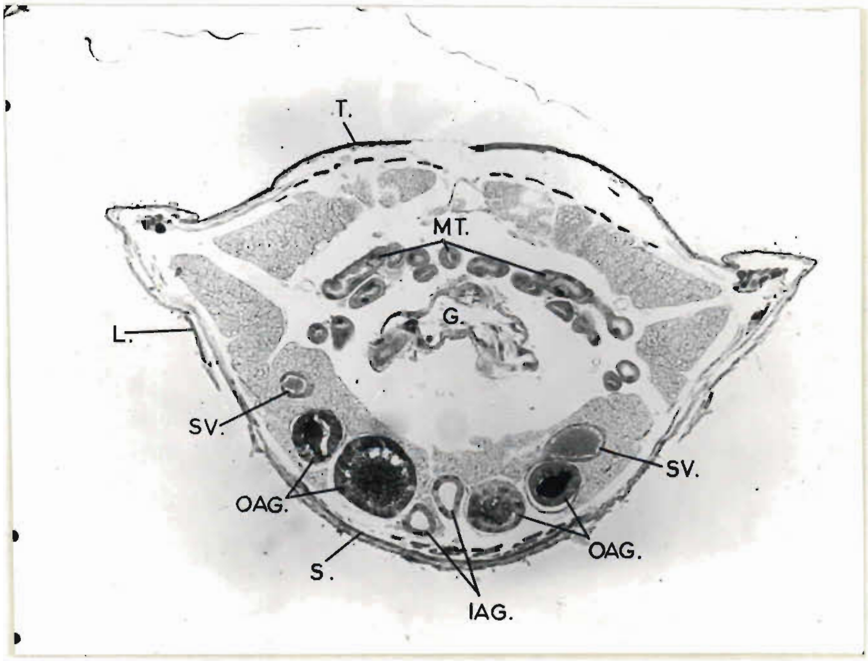


Fig. 15A L. laevigatum male. Transverse section through the abdomen and internal reproductive organs at the point shown as Section B in Fig. 13Ai. G., gut; IAG., OAG., inner and outer accessory glands; L., laterotergite; MT., malpighian tubules; S., sternum; SV., seminal vesicle; T., tergum.

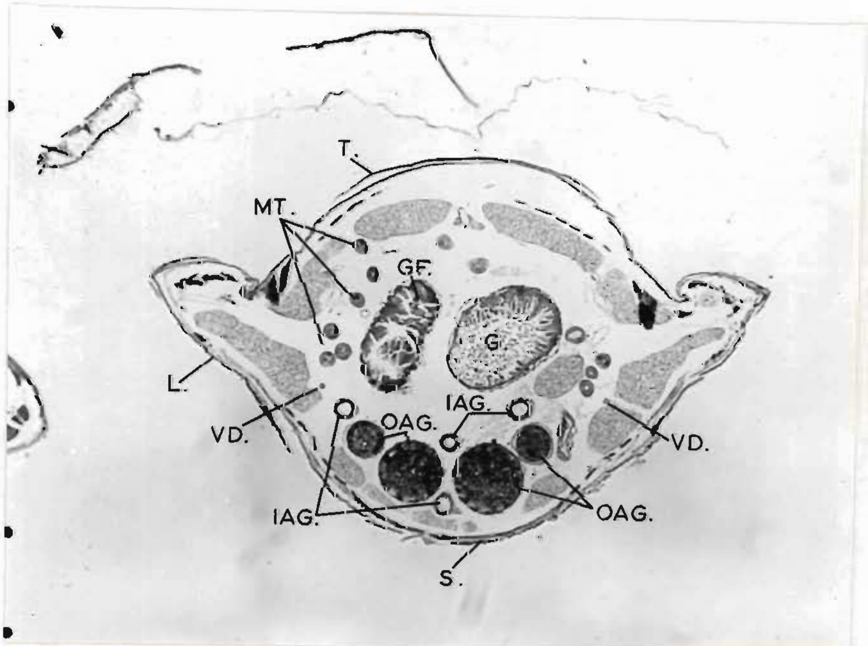


Fig. 15B As for Fig. 15A, at the point shown as Section C of Fig. 13Ai. GF., fold of the gut; VD., vas deferens. All other abbreviations as for Fig. 15A.

posterior to it, which unites with its compliment to enter the ejaculatory duct. The seminal vesicle itself, may be well defined and greatly distended (sausage shaped) as in Stenodema laevigatum (Woodward 1952) or inconspicuous and only slightly thicker than the vas deferens as in Phytocoris ulmi and Pantilius tunicatus (Kullenberg 1947). Kullenberg suggests that the former condition is probably found in the majority of species.

In Lygidolon laevigatum the vas deferens is extremely thin and relatively short (Fig. 13A and 15[illegible]). Posteriorly it is greatly distended to form a seminal vesicle. Each vesicle has a thin muscular sheath. The vesicle in this species has an unusual shape, being constricted centrally (Fig. 13A). A similarly shaped vesicle was illustrated by Boness (1963) for Exolygus rugulipennis. Structurally there appear to be two different parts of the seminal vesicle. The posterior bulb has a thin wall and in the adult male is tightly packed with mature sperms. The cellular lining of the anterior bulb (i.e. the bulb nearest the testis) is thicker and appears to have a secretory function. The content of this bulb is far less dense, with fewer sperms and more fluid. Kullenberg mentioned this secretion of the cells of the seminal vesicle, and named it "spermiensekret". This is possibly the source of the fluid in which the mature sperms travel from the testis to the seminal vesicle, although it may be for nourishment of sperm in the vesicles themselves.

As mentioned previously, in some species the seminal vesicles open directly into the ejaculatory bulb, a condition found in L. laevigatum. Thus there is no ejaculatory duct between the seminal vesicles and the ejaculatory bulb.

3.2.1.7 The testes and vasa efferentia (Fig. 13A)

numbers is as in the entire Heteroptera, namely one to eight. He also found marked modality in follicle number within subfamilies e.g. Phylinae, 3; Dicyphinae, 1; Orthotylinae, 2; Mirinae, 7. Of thirty-six Mirinae species examined, thirty-two had seven follicles per testis, three specimens had eight and one species, Notostira elongata, of which fourty-five individuals were examined, had three follicles per testis.

In L. laevigatum the typical Mirinae number of seven follicles per testis is found. These follicles are elongated with short vasa efferentia. The whole testis is enclosed in fat body.

3.2.2 Female

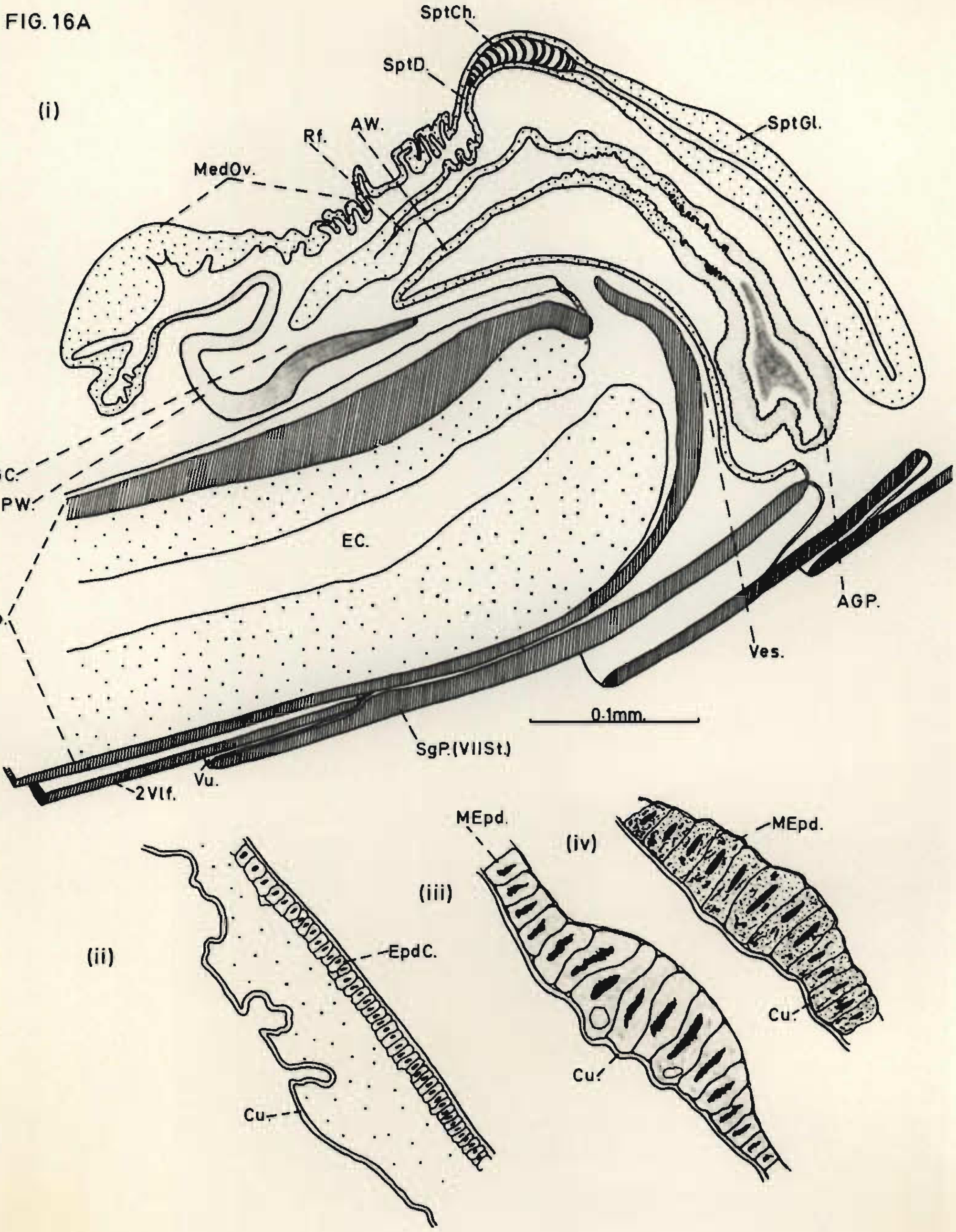
In female Miridae as well as in Reduviidae, Nabidae and Anthocoridae, the arrangement of the genital organs and genital ducts appears to be distinctly different from the arrangement in other Heteroptera as well as insects in general. Final determination of the homologies of certain structures of the female genitalia of mirids must await more extensive studies of the genitalia of other Hemiptera. However, Davis (1955) has made a study of several species and the terminology used by him has been adopted in this study, although some reference to that used by other authors is also made.

3.2.2.1 The genital segments

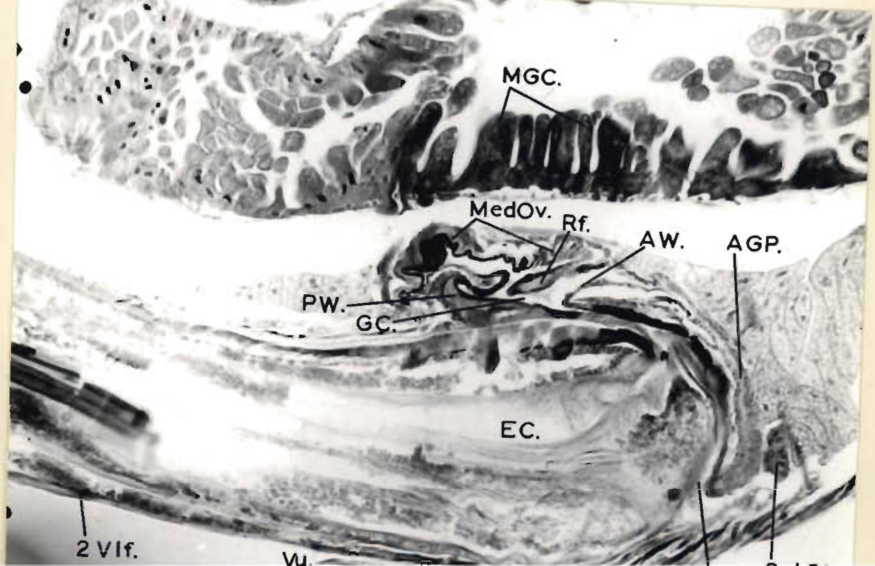
When viewed ventrally, the posterior third of the abdomen of the female is almost entirely covered by the first and second genital segments (Fig. 7A). These are the abdominal segments eight and nine. In this area the ventral plate of the abdomen is divided by the elongated second valvifers (Fig. 7A). The seventh segment has a pointed flap-like portion extending over the vulva (or secondary gonopore) and base of the

Fig. 16 Ai, Sagittal plane section through the female genitalia of L. laevigatum. Aii, detail of the wall of the anterior genital pouch. Aiii, detail of the ring gland cells. Aiv, detail of of the spermathecal gland. B, same, actual section of a virgin female L. laevigatum. AGP., anterior genital pouch; AW., anterior wall of the genital chamber; Cu., cuticular lining; EC., egg canal; EpdC., epidermal cells; GC., genital chamber; MedOv., median oviduct; MEpd., modified epidermal cells; MGC., mid-gut cells; Ovp., ovipositor; PW., posterior wall of genital chamber; Rf., roof (dorsal wall) of genital chamber; SgP., subgenital plate; SptCh., spermathecal chamber; SptD., spermathecal duct; SptGl., spermathecal gland; St., sternum; Ves., vestibulum; 2Vlf., second valvifer; Vu., vulva.

FIG. 16A


(i)
SptCh.
SptD.
SptGl.
Rf.
AW.
MedOv.
GC.
PW.
EC.
Ovp.
AGP.
Ves.
0·1mm.
SgP.(VIISt.)
Vu.
2VIf.
(ii)
EpdC.
Cu.
(iii)
MEpd.
Cu.
(iv)
MEpd.
Cu.

B.


MGC.
MedOv.
Rf.
AW.
AGP.
PW.
GC.
EC.
2 VIf.
Vu.

The sternal regions of the eighth and ninth segments are apparently inflexed to form the walls of the genital chamber and vestibulum (Snodgrass 1935). This latter is defined by Snodgrass as being "an external genital cavity formed above the seventh abdominal sternum when the latter extends beyond the eighth". It is therefore the opening anterior to the base of the ovipositor, which is covered by the subgenital plate (Figs. 16A and B).

3.2.2.2 The valvulae and valvifers

The ovipositor of L. laevigatum, as in other Miridae, consists of two pairs of valvulae or blades. The second valvulae are united for the greater part of their length (Fig. 17A) but remain separated at their distal ends (Fig. 17B). Proximally the median blades or second valvulae are swollen to form an enlarged base (Fig 18A). From the base sclerotised rods known as rami, extend in an arc, first dorsally (termed the fibula by Dupuis & Carvalho 1956), and then posteriorly, where they unite with the anterior dorsal margins of the second valvifers (Fig. 19A). The second valvifers (collectively termed the ovipositor sheath by Kullenberg 1947) are elongated plates which lie on each side of the ovipositor when it is in the rested position (Fig. 19A). They also appear to lock the ovipositor when in the erect position by becoming inflexed into the cavity in which the ovipositor usually lies, so that the anterior ventral margins of the valvifers close about the base of the ovipositor.

At the tip of the ovipositor, the apical blades of the second valvulae are covered by the more strongly serrated, knife-shaped cutting blades of the anterior or first valvulae. These are, unlike the second valvulae, entirely free of one

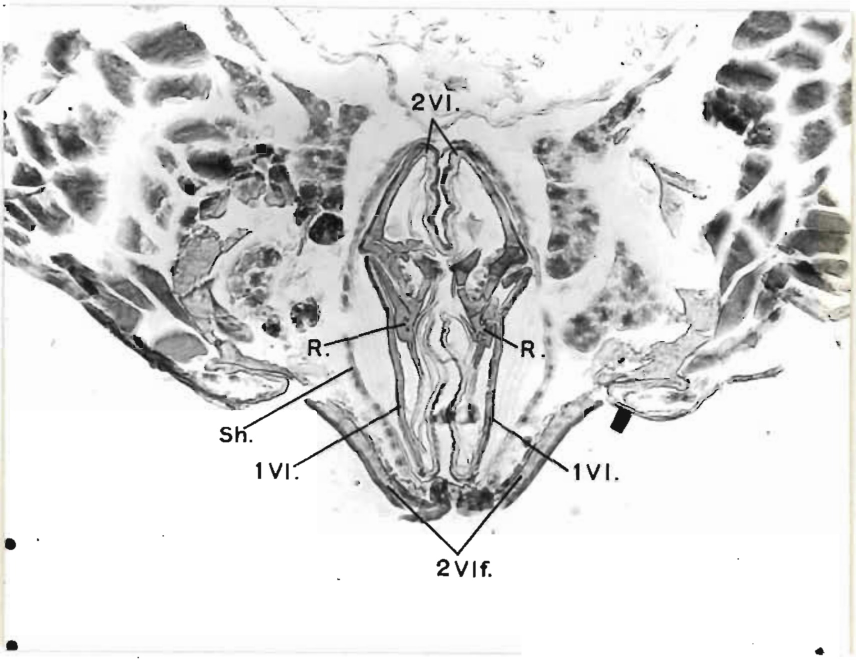


Fig. 17A L. laevigatum female. Transverse section through the ovipositor near the apex showing the united second valvulae (2Vl.) and the two separate first valvulae (1Vl.) attached to ridges on the second valvulae (R). Sh., sheath surrounding ovipositor; 2Vlf., second valvifers.

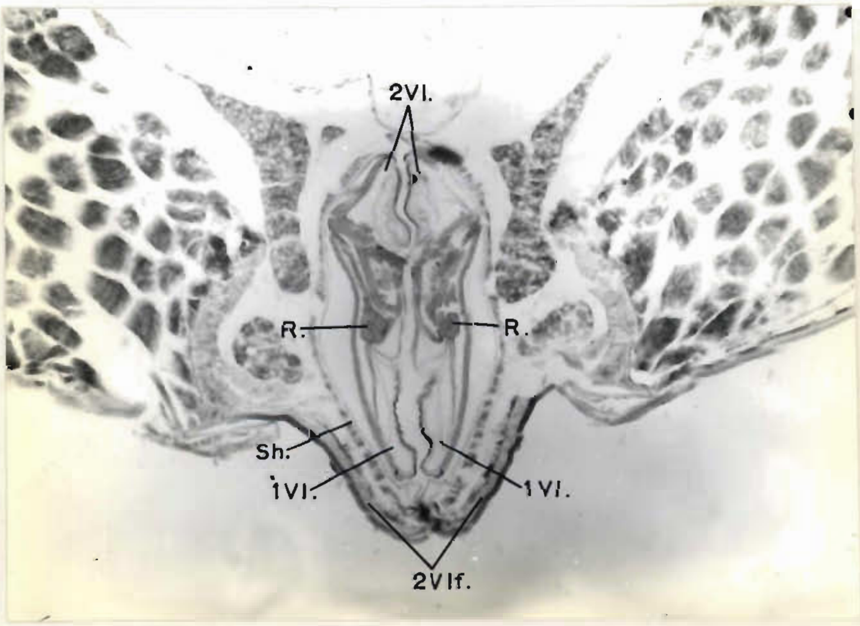


Fig. 17B L. laevigatum female. Transverse section through the ovipositor nearer the apex than Fig. 17B., showing the second valvulae ununited. Annotation as for Fig. 17A.

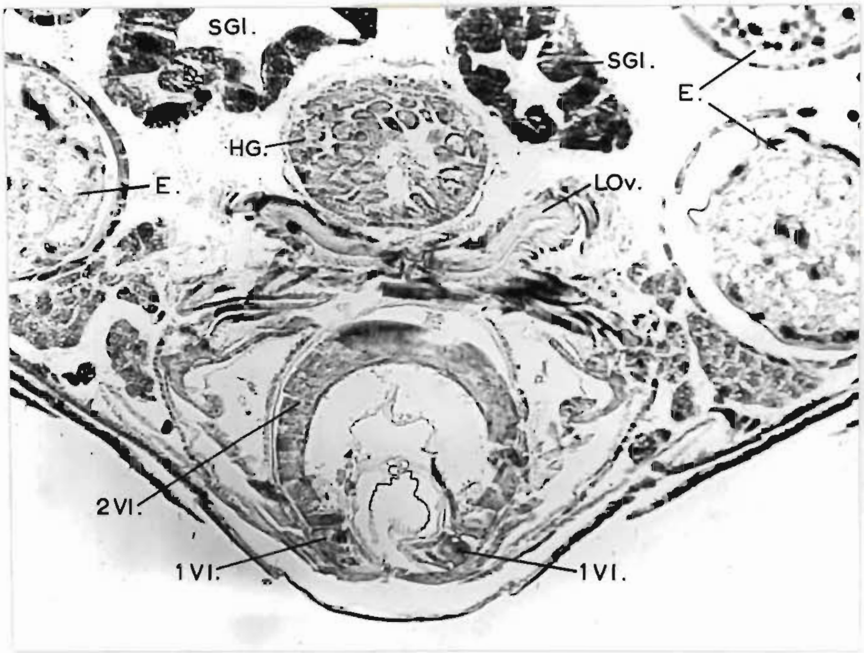


Fig. 18A L. laevigatum female. Transverse section through the base of the ovipositor. E., eggs; HG., hind gut; LOv., lateral oviduct; SGl., salivary gland; 1Vl., 2Vl., first and second valvulae.

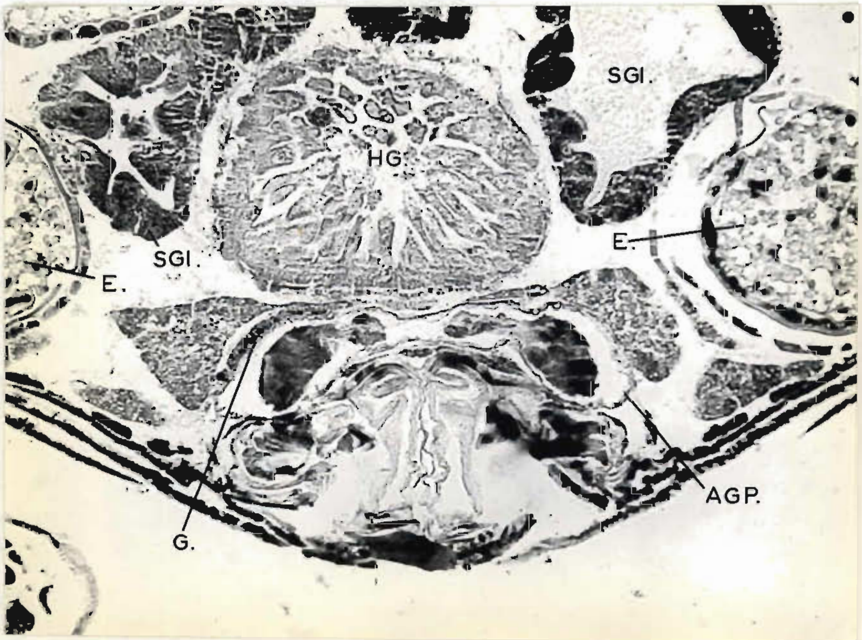


Fig. 18B L. laevigatum female. Transverse section through the anterior genital pouch (AGP.). E., eggs; G., glandular portion of the anterior genital pouch wall; HG., hind gut; SGl., salivary gland.

second valvulae (Fig. 18A). As they arch dorsally the two pairs of rami are closely linked and remain closely associated for a short distance before each first ramus extends postero-dorsally to become attached to a sclerotised plate. Davis (1955) considered this latter plate to be an inflection of the anterior margin of the ninth paratergite, and termed it the ramal plate (Fig. 19C). However Kullenberg (1947) considered there were two parts involved, namely part of the first valvifer itself as well as part of the eighth paratergite. This view has been supported by Scudder (1959), who states that "the structure called the eighth paratergum (by Southwood [1953] and Davis [1955]) is the fused first gonocoxa (valvifer) and paratergite VIII. This interpretation is supported by the musculature."

The first and second valvulae on each side, are connected laterally by means of a longitudinal ridge on the second valvulae, which fits in a corresponding groove of the first valvulae. The ridges on the second valvulae continue on the corresponding rami to the point where the latter become attached to the second valvifers (Fig. 19A). From being laterally placed apically on the second valvulae, the ridges gradually become ventrally situated towards the base of the ovipositor, and therefore are on the anterior surfaces of the rami as they arch dorsally, and on their dorsal surfaces as the rami extend posteriorly (Fig. 19A). The function of this type of attachment is to allow the first valvulae to slide back and forth in a parallel path while supported by the second valvulae. During oviposition first one of the first valvulae is thrust a short way into the tissue of the plant and then the other is protracted until a similar distance has been pierced. The

In L. laevigatum cutting teeth are well developed on the dorsal and ventral edges of the first valvulae between the apex and the broadest part of the blade. Anterior to this region the teeth are very much finer, and extend for about half the length of the valvulae (Fig. 7C). The second valvulae have fine teeth on the dorsal and ventral edges, at the apex only.

The entire ovipositor is separated from the body cavity by a thin membrane (Fig. 17A).

3.2.2.3 The genital chamber

The opening to the genital chamber is, during copulation, the vulva or secondary gonopore (Fig. 16A). This is covered by the subgenital plate, an extension of the seventh sternum. The passage leading from the vulva to the genital chamber is termed the vestibulum by Snodgrass (1935). The anterior wall of the vestibulum is the intersegmental membrane on the posterior margin of the seventh sternum. The posterior margin of the vestibulum is formed by the ovipositor. Kullenberg termed the passage from vulva to genital chamber the "vulva" and the external opening the "vulvamunding".

The genital chamber itself was divided into three regions by Kullenberg (1947) namely, the anterior wall (vordere Wand), the posterior wall (hinter Wand) and the roof (dach) or dorsal wall.

The anterior wall is the dorsal extension of the anterior wall of the vestibulum (Fig. 16A) and in actual fact very little of this forms the anterior wall, as it immediately gives way to the opening to the anterior genital pouch. That portion termed the anterior wall by Kullenberg (Fig. 16A) has been termed the ventral labiate plate by Davis (1955).

The roof of the genital chamber lies between the rami of

FIG. 19

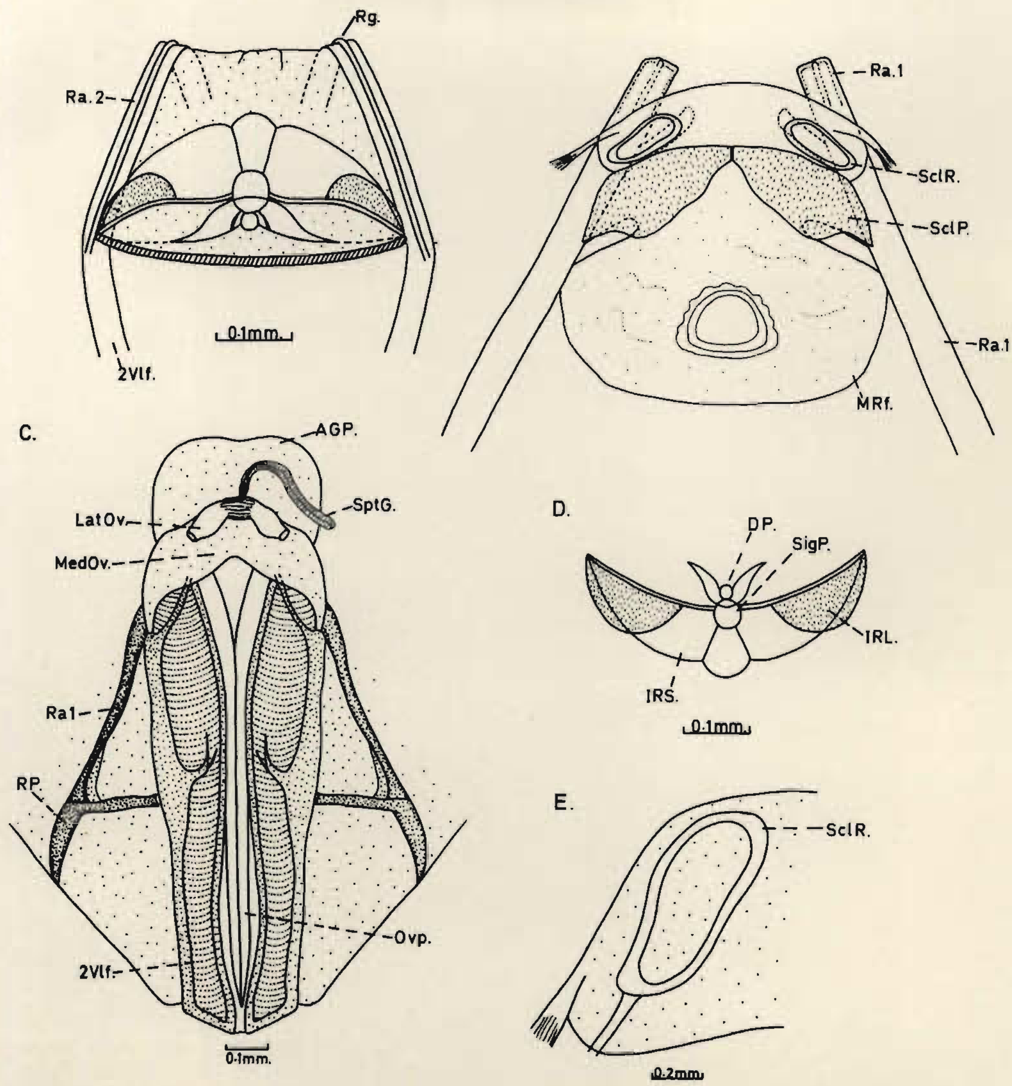


Fig. 19 Female genital structures. *L. laevigatum*. A, dorsal view of the structures of the posterior wall of the genital chamber, in position between the rami of the second valvulae. B, dorsal view of the sclerotised rings and plates of the dorsal wall (roof) of the genital chamber, in position between the rami of the first valvulae. C, dorsal view of the lateral and median oviducts and anterior genital pouch in position over the base of the ovipositor. D, detail of the posterior wall of the genital chamber. E, detail of a sclerotised ring. AGP., anterior genital pouch; DP., dorsal process; IRL., inter-ramal lobe; IRS., inter-ramal sclerite; Lat Ov., lateral oviduct; Med Ov., median oviduct; MRf., membranous portion of genital chamber roof; Ovp., ovipositor; Ra.1, Ra.2, first and second rami; Rg., ridge; RP., ramal plate; Scl P., sclerotised plate; Scl R., sclerotised ring; Sig P., sigmoid process; Spt G., Spermathecal gland; 2 Vlf., second valvifers.

first valvulae are appendages. As mentioned before (§ 3.1.2) parts of the roof are of importance as taxonomic characters. In sagittal plane sections it is that portion which forms the roof of the mouth of the anterior genital pouch (Fig. 16A). In dorsal aspect this is a plate of similar width to the mouth of the anterior genital pouch, and containing the sclerotised rings which are being used increasingly in female mirid taxonomy (Slater 1955). Those of L. laevigatum are very slender and elongated, the ring wider mesally than apically (Figs. 19B and E). Davis (1955) found that these rings encircle areas of glandular tissue in the roof of the genital chamber, and referred to them as "ringed glands". Immediately posterior to these rings in L. laevigatum are a pair of plates which are covered by minute aculeae. Also attached to the roof of the genital chamber is a structure termed the "dorsal sack" by Kullenberg. This is in fact the median oviduct or oviductus communis (Figs. 16A, 19C). It is fairly large in L. laevigatum, with a much convoluted wall anteriorly (Fig. 16A) and enters the genital chamber from above. In some species of Miridae the median oviduct is greatly enlarged and bulbous (Kullenberg 1947).

The posterior wall of the genital chamber is situated between the rami of the second valvulae (Fig. 19A) and being continuous with the second valvifers, may be considered to have been derived from the ninth sternum. In L. laevigatum it has a characteristic sclerotisation (Fig. 19D). The sigmoid process found centrally has a heavily sclerotised median process and a pair of wing-like structures constituting the dorsal structure described by Kelton (1955 A) in other Mirinae. This dorsal structure is covered by minute aculeae similar to those found

H. structure of Slater) and are also covered by minute aculeae. The lateral lobes of Kelton (1955 A) are not present in L. laevigatum. The dorsal portion of the posterior wall is membranous in Miridae (Davis 1955).

3.2.2.4 The anterior genital pouch (Figs. 16A and B)

Although this organ is termed the seminal depository by Davis (1955) the term is misleading since sperm is not retained there. The structure is of interest in that similar organs are reported to occur in only a few closely related families of Heteroptera, including the Nabidae and Anthocoridae (Davis 1955).

Due to its supposed function as an organ for the storage of sperm, it might be considered analogous to the spermatheca of other insects. Snodgrass (1935) however states that "the spermatheca is primarily an invagination of the integument at the posterior end of the venter of the eighth abdominal segment". As mentioned before (§ 3.2.2.3) the anterior wall of the vestibulum is the intersegmental membrane on the posterior margin of the seventh abdominal sternum. The anterior genital pouch is bordered dorsally by the so-called roof, and ventrally by the anterior wall, of the genital chamber (§ 3.2.2.3 and Fig. 16A), both of which are considered to be derived from the eighth abdominal sternum (Kullenberg 1947 and Davis 1955). Therefore the organ found in Miridae can not be considered analogous to the spermatheca of other insects.

The insect spermatheca arises as a median invagination of the eighth sternum just posterior to the gonopore. Johannsen and Butt (1941) state, however, that in later development the gonopore and opening of the spermatheca may be carried inward by the formation of a copulatory pouch (as in Miridae). Thus the gonopore may shift with changes in the genital chamber, but be considered anterior to the opening of the anterior genital pouch (§ 3.2.2.7). Normally too, the spermatheca has a slender duct (Snodgrass 1935) but the anterior genital pouch has a broad slit-like mouth lying laterally between roof and anterior wall of the genital chamber (Fig. 16A). There is also no sign of a muscular sheath as found surrounding the duct of a normal insect spermatheca.

In sagittal plane section the pouch is seen to be fairly narrow in L. laevigatum, (Fig. 16A) although this depends on the age and condition of the individual female. However, even at its most distended the organ is small in this species when compared with many other species examined personally and figured by Kullenberg (1947) and Davis (1955). In unmated females, it has a collapsed appearance, with a greatly folded inner lining (Fig. 16B). In newly-mated females it is often greatly distended (Fig. 19C) and consequently lies horizontally in the body cavity, while in mature laying females it has a more collapsed appearance although some content remains visible within its walls.

The inner lining of the pouch is cuticular, and is fairly variable in thickness, but unsclerotised and very pliable (Fig. 16Aii). The border with the haemocoel is lined with epidermis. Dorso-laterally the epidermal lining is differentiated into two large patches of glandular tissue consisting of cuboidal cells with lightly staining elongated or circular nuclei (Figs. 16Aiv and 18B). In the region of these glandular areas the cuticular lining is thin and normal. They are the ringed glands described by Davis (1955).

3.2.2.5 The spermatheca

In Miridae, a variably developed tubular organ which to the spermatheca of other insects. Being ectodermal in origin, it is lined internally with a thin unsclerotised cuticle. The spermatheca of *L. laevigatum* consists basally of a short thin-walled duct followed by a median portion with a wide internal diameter and a muscular sheath, termed the spermathecal chamber by Davis (1955). Internally the cuticle of this chamber is folded into rings, giving the appearance of a trachea when viewed in longitudinal section (Fig. 16A). Distally the spermatheca consists of large cuboidal glandular cells, of almost identical appearance to those of the glandular portion of the anterior genital pouch (Fig. 16A). In transverse section they are wedge-shaped surrounding a narrow duct. The lumen of this glandular portion is considerably more narrow than that of the median chamber.

Observations on the structure of the spermatheca of *L. laevigatum* are similar to those made by Davis (1955) on other Miridae. It is of interest to note that the spermatheca does not function as a storage organ for sperms. Its function appears to be purely glandular. This points to the possibility of it being an accessory gland. Galliard (1935) described a gland of similar structure to the spermatheca of Miridae, in the reduviid genera *Rhodnius* and *Triatoma*. Apart from being comparably situated, this gland had the three structurally different regions found in the mirid spermatheca , while the median chamber has similar cuticular ring-like folds and an outer layer of longitudinal muscles. Galliard considered it to be an accessory gland, with the function of secreting an adhesive substance for anchoring eggs to the substratum. However as Davis (1955) points out, apart from Galliard's description, there seems to be no mention of a muscular sheath may be considered to be a spermatheca. It may possibly have a spermatophilic function (§ 3.2.2.10).

Davis (1955) considered that the folds in the cuticular wall of the median chamber allow for shortening and lengthening of this portion of the spermatheca under the action of the longitudinal muscles, thereby forcing the contents of the gland into the median oviduct. In saline dissections I found it to be very active, most conspicuously so in young mated females, with continuous "wagging" movements.

3.2.2.6 Accessory glands

There do not appear to be any structures in Miridae analogous to the accessory glands found in most insects. As noted above (§ 3.2.2.5) the spermathecae of certain reduviids are considered to serve as sources of egg-cement, the function usually given to accessory glands.

Kullenberg (1947) noted the presence of glandular tissue at the base of the second valvulae. He found that in species producing greater quantities of egg-cement this tissue was better developed and suggested that it performed the function of accessory glands. Davis (1955) tends to refute this theory, since his studies revealed no cuticular lined ducts from this tissue, opening into the genital tract, and no homologies to the female accessory gland.

3.2.2.7 The median oviduct

The median oviduct is part of the secondary exit apparatus formed as a series of invaginations of the body wall, (Snodgrass 1935) and is generally tubular. In the Miridae the tubular median oviduct is replaced by a usually pouch-like structure situated above the genital chamber. It was termed the "dorsal sack" by Kullenberg (1947). While large a thick posterior wall.

3.2.2.8 The lateral oviducts

The lateral oviducts are short and each forms a narrow calyx (Fig. 13B). They are surrounded by a thin layer of circular and longitudinal muscles and have a greatly folded inner wall. Each has two distinct bulbs near the point of union with the median oviduct.

3.2.2.9 The ovaries

In Miridae the most common number of ovarioles per ovary is seven (Woodward 1950). This author noted that in most species for which numbers are known, the same number of testis follicles as ovarioles are found within a species. When they differ it is usually by one only.

In L. laevigatum there are seven ovarioles per ovary, although the author found one example of six in one ovary and seven in the other.

The ovarioles are of the acrotrophic type, with nurse cells in the upper part of each egg tube (Fig. 20A). Distally each ovariole is drawn out into a terminal filament. Follicle cells are binucleate (Fig. 20B). As the ovarioles mature there is an accumulation of eggs in successive stages of development and each ovariole increases considerably in length. A single fully mature ovary is large and in L. laevigatum may contain as many as eleven mature eggs per ovary, together with partly developed eggs.

3.2.2.10 The fate of sperm in the mated female

Kullenberg (1947) considered that the organ which received the sperm in the first instance at copulation, was the anterior genital pouch (vorderer sack). He noted, however, that in

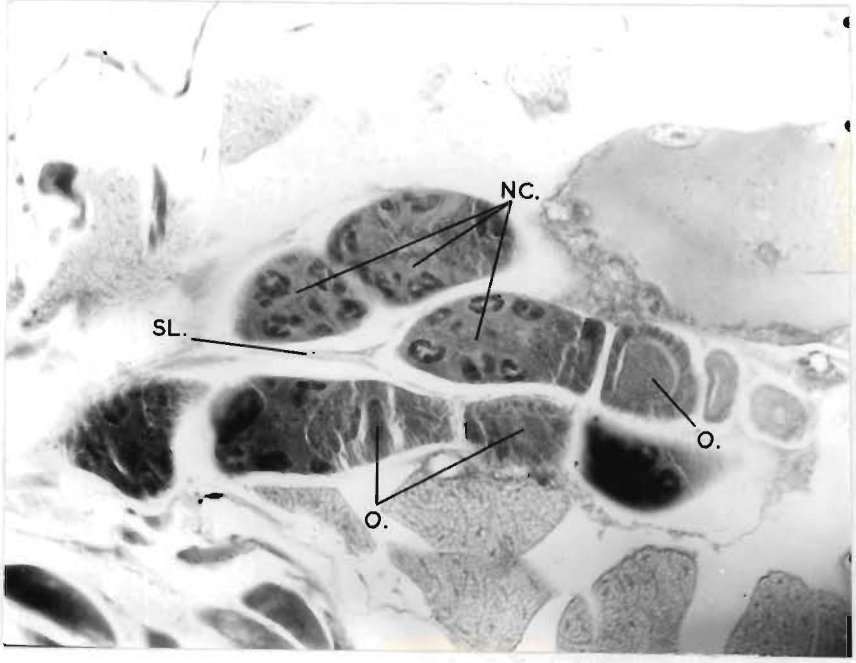


Fig. 20A Female L. *laevigatum*. Longitudinal section through the nurse cells at the apex of an ovariole. NC., nurse cells; O., oocyte; SL., suspensory ligament.

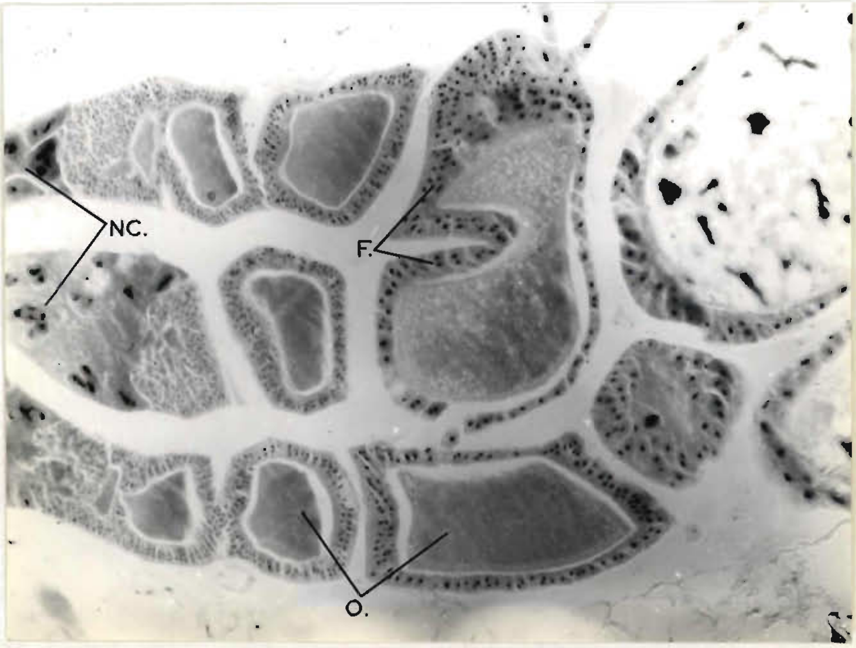


Fig. 20B Female L. *laevigatum*. Longitudinal section through ovarioles showing binucleate follicle cells. F., follicle cells; NC., nurse cells; O., oocyte.

oviducts and ovariole stems. He also noted that fertilisation of eggs occurred in the vitellarium. In an earlier paper (Kullenberg 1944) he mentioned that after copulation, the sperm in the anterior genital pouch (receptaculum seminis) migrated through the oviducts and ovariole stems into the proximal parts of each vitellarium. He also noted the presence of a spermatophore in the anterior genital pouch of the female. Davis (1955) merely records the structure, which he termed the seminal depository, as "apparently serving to receive and store sperm", while Woodward (1952) noted the dilated appearance of the bursa copulatrix (anterior genital pouch) in mated females of two mirid species studied, as well as noting that male accessory gland secretions "possibly help to nourish the sperm during retention in the bursa copulatrix of the female", thus suggesting at least a semi-permanent retention of sperm in the pouch.

By dissection in physiological saline (0.85% NaCl) an investigation was conducted to study female sperm storage in field-collected specimens. Of 36 females of L. laevigatum dissected and microscopically examined, none was found to have live sperm in the anterior genital pouch, although dead sperm was observed in one young female, newly mated, in which the pouch was greatly distended. In virgin females, the pouch is always empty, while in newly mated females the pouch is distended and contains a granular inclusion very similar to that produced by the male outer accessory glands. At this stage a loose heart-shaped structure can usually be seen in the pouch with an opening at the apex, facing the mouth of the pouch. It is a male ejaculation product which appears to form as a hard coat, only after entry into the anterior genital the secondary gonopore of the aedeagus. It would appear that this "spermatophore" is formed from the solution in which the sperms are conveyed during copulation, coming into contact with some secretion in the female anterior genital pouch, causing it to form a hard outer coat. However the sperm disperses within minutes, probably much of it before the outer coat forms. The sperm quickly migrates, probably under the influence of spermatophilic secretions from the spermatheca and some tissues of the lateral oviducts, or ovarioles, and enters the lateral oviducts. They become embedded in the thick wall of the lateral oviducts, at a point just before these latter enter the median oviduct (Fig. 21A and B). At this point, the lateral oviducts bulge noticeably. In actively laying females, most of the sperm can be found in these bulbs of the lateral oviducts, but small numbers of sperm can also be found in the vitellarium and the ovariole stem of each ovariole around fully developed eggs. As noted by Kullenberg, this is where fertilisation occurs.

The "spermatophore", containing a finely granular fluid, in the anterior genital pouch, together with, usually, a granular material similar to that of the outer accessory glands of the male, possibly acts as a source of nourishment for the sperm. The spermatheca, inactive in all virgin females dissected, but continually contracting and pumping in mated females, may have this function, but may also secrete a spermatophilic substance for guiding the sperm to the lateral oviducts. Kullenberg (1947) suggests that the ring glands may have a spermatophilic secretion as well, acting as first guide to the sperm in the anterior genital pouch. Even in young virgin females a finely granular secretion can be found in the lateral oviducts, probably having spermatophilic or nutritional functions.

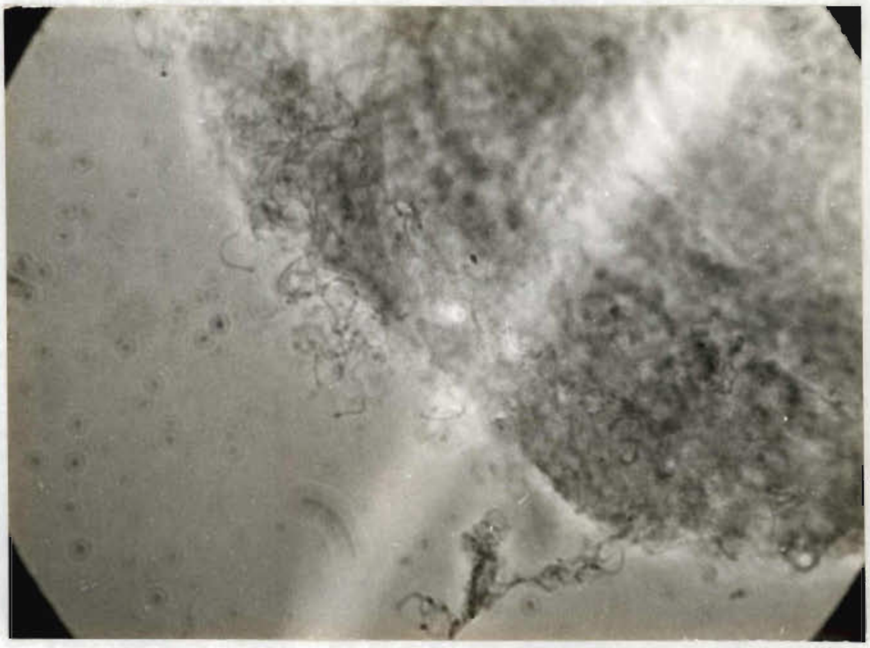


Fig. 21A Squash of the lower bulb of the lateral oviduct, of a mated female L. laevigatum, revealing a mass of sperm.

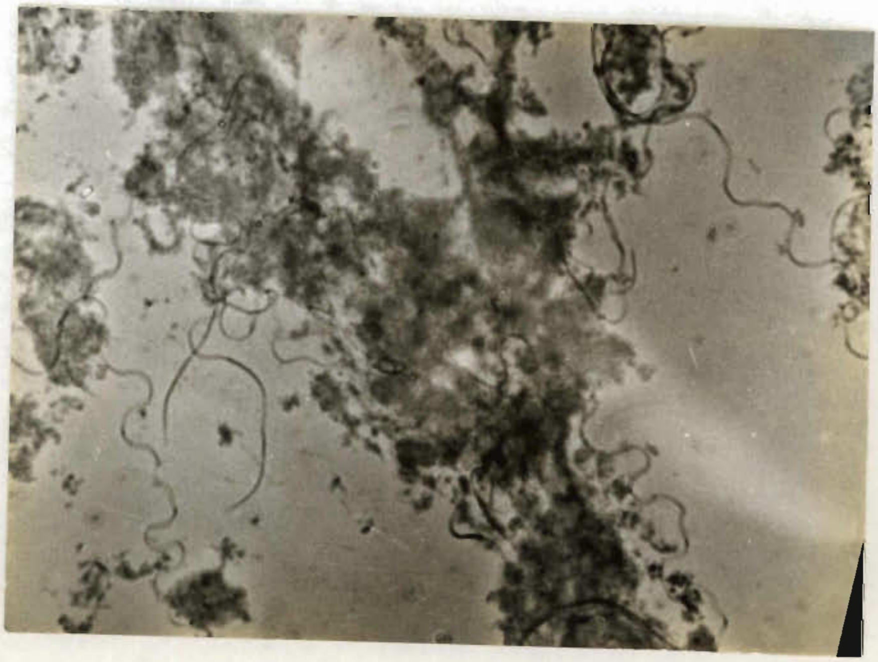


Fig. 21B Close-up of Fig. 21A.

Taylorilygus pallidulus (Blanch) (Mirinae : Mirini); *Sthenarus leucochilus* Reut., *Campylomma subflava* Odh. (Phylinae : Phylini) and *Orthotylus tabidus* (Stål) (Orthotylinae). Young newly mated female specimens of *T. simonyi*, *T. pallidulus* and *C. subflava* have been found with sperm in the mouth of the anterior genital pouch, the genital chamber and the median oviduct. A mature female of *C. subflava*, dissected under saline immediately after mating had occurred, was found to have a huge mass of sperm in the anterior genital pouch, all grouped together in the fluid in which they had been deposited. The sperm had obviously not had time to begin migrating, and no "spermatophore" had yet formed.

In all the species examined the sperms were found in the oviducts and ovarioles of ovipositing females. In *T. simonyi*, *T. pallidulus* and *O. tabidus*, the last to a lesser degree, sperm is stored and nourished in folds in the walls of the basal portion of each lateral oviduct, while in *C. subflava* and *S. leucochilus* the sperm migrates up into the ovarioles and is apparently nourished there. Obviously this situation also occurs in the former three species, but most sperm is always found in folds of the walls of the lateral oviducts, except in old mature females which are approaching the postreproductive stage.

In mated fully mature *L. laevigatum* females (and in all other species examined as well) the "spermatophore" becomes yellowish and the anterior genital pouch shrivels. Three specimens of *L. laevigatum* and one specimen each of *Orthotylus tabidus* and *Campylomma* sp. were found to have more than one "spermatophore" in the anterior genital pouch. One specimen of each of the former two species was found to have three observed mating, in which no sperm had yet migrated even from the anterior genital pouch (where is was deposited by the male) an empty shrivelled spermatophore was observed in the pouch as well as a bundle of fluid containing a mass of sperm, which was actively beginning to disperse. Evidence that the empty spermatophore came from an earlier mating was provided by the presence of sperm up in the vitellerium of each ovariole.

It therefore seems that the actual point of deposition of copulatory products by the male depends on the species involved but is usually at the mouth of, or within, the anterior genital pouch. In every case the sperm quickly migrates into the oviducts. Dead sperm was observed in the anterior genital pouches of several species besides *L. laevigatum*. The products of the male accessory glands are stored in the anterior genital pouch, and possibly the dead sperm is simply that which was due to some incumberance, unable to migrate into the oviducts, and therefore either remained in or was carried into the pouch, depending on where the ejaculatory products were deposited at mating. This dead sperm is probably later absorbed by the body fluids, as it was only found in the pouches of young mated females, never in older specimens.

As mentioned previously, the male ejaculatory products in the anterior genital pouch are initially a fluid mass, but later develop an outer coating to form a "spermatophore". Chemical action with a fluid secreted by the wall of the genital pouch is possibly responsible. Evidence that the moulding of the outer coat occurs in the anterior genital pouch is given by the shape of the spermatophore itself. In several species studied (*L. laevigatum*, *T. simonyi*, *T. pallidulus*) the anterior genital pouch is heart-shaped (Fig. 19C) and the "spermatophore" even when reduced in size and empty was distinctly heart-shaped in these

3.2.2.11 The genitalia during oviposition

During oviposition the ovipositor is erected, until it points almost vertically downwards. This brings the opening of the egg canal into a position directly below the genital chamber (Fig. 16A). At the same time part of the wall of the genital chamber is stretched posteriorly making a direct passage from lateral oviduct to egg canal.

3.3

GENITALIA OF B. CEDARANUS

3.3.1 Male

3.3.1.1 The genital segments

As in male Miridae, the ninth abdominal segment forms the genital capsule (Fig. 22). The ninth sternum is, however, separated in cicadellids, while the tergum and pleura are united to form a single plate, the pygofer (Young 1952). Typically the eighth sternum is normal and the ninth sternum forms a plate (valve), variously developed, to which a pair of subgenital plates are attached. These latter are generally not considered true appendages (Young 1952).

Atypically, the eighth sternum of *B. cedaranus* males is shovel-shaped (Fig. 22B), and extends posteriorly to cover the ninth sternum and its subgenital plates. The ninth sternum itself is much reduced, and the subgenital plates are small, bearing long thin setae.

Dorsally the genital cavity is covered by the tergal part of the pygofer and behind the latter, by the anal tube (Fig. 22C). This tube consists of the tenth abdominal segment and carries the terminal eleventh abdominal segment, the anal style. The pygofer lobes bear short strong setae. More slender setae

FIG. 22

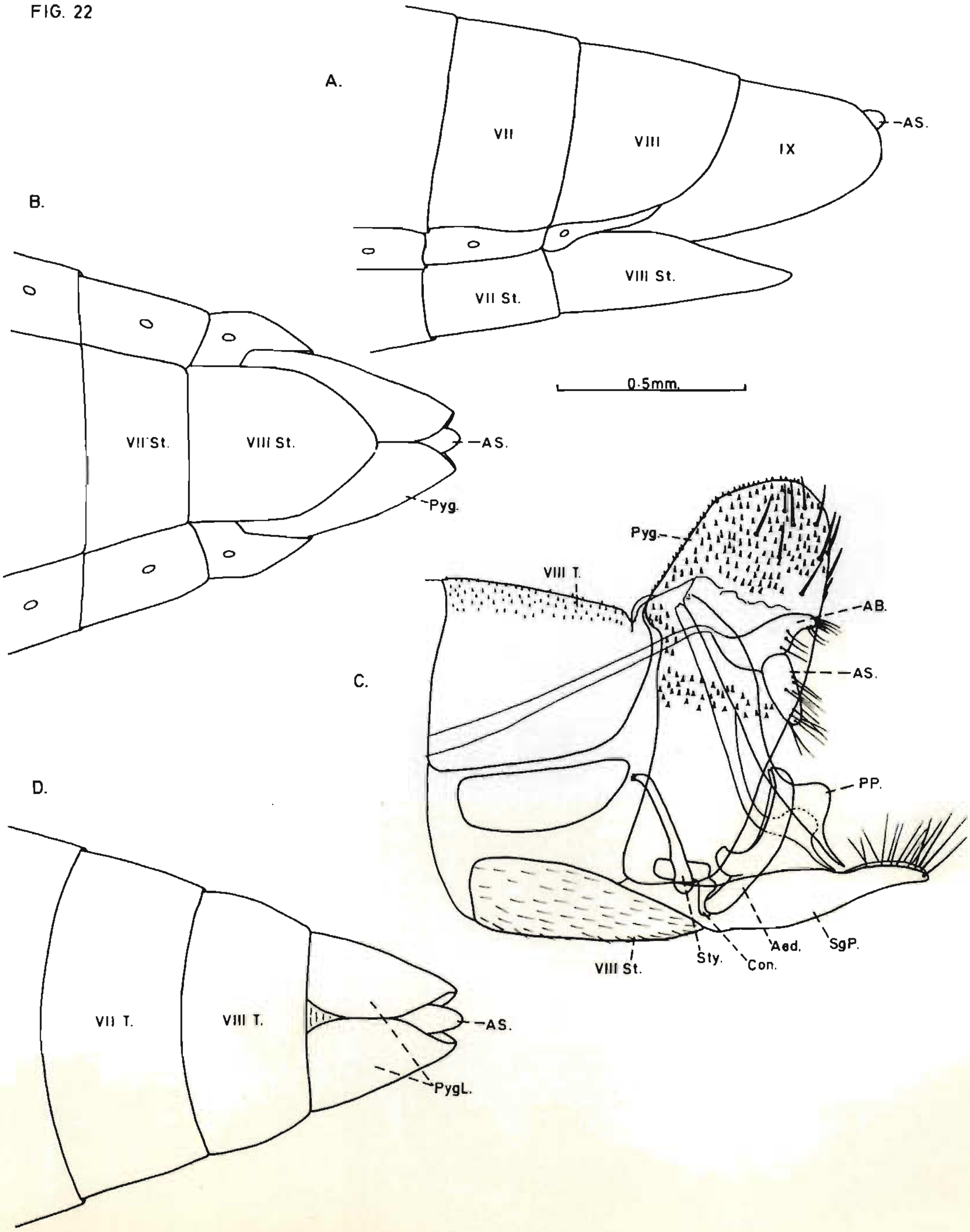


Fig. 22 External genitalia of the male B. cedaranus. A, lateral view. B, ventral view. C, a lateral semi-erect "see-through" view. D dorsal view. AB., anal block; Aed., aedeagus; AS., anal style; Con., connective; PP., pygofer process; Pyg., pygofer; Pyg L., pygofer lobes; Sg P., subgenital plate (paired); St., sternum; Sty., style; T., tergum.

The pygofer possesses a pair of processes or hooks, termed lateral parameres by Helms (1968), which articulate internally with the pygofer plates near the anal lobe (Fig. 22C). The shafts of these hooks are further attached for the major part of their length, to the thin membranous posterior wall of the genital chamber. Distally the hooks are free and lie externally, immediately above the subgenital plates (Fig. 22C). They function as claspers during copulation and are used in the taxonomy of the Iassini (Linnavuori 1957, Kramer 1963). Anal hooks are not present.

3.3.1.2 The aedeagus, connective and styles

The aedeagus is simple and slightly curved (Fig. 23D) lying just above the subgenital plates (Fig. 24A). In dorsal view a shallow apical notch is apparent, together with a series of angular serrations. The broader basal opening of the aedeagus is termed the genital atrium by Young (1952) and its border, the atrial rim (Fig. 23D). Paired dorsal apodemes are found on the posterior perifery of the genital atrium. The anterior or basal tip of the aedeagus articulates with the connective, which is essentially Y-shaped when viewed from above (Fig. 23C), strongly curved when seen in lateral view (Fig. 22C). Laterally the styles articulate on the lateral arms of the connective. These styles are simple, being slender and rodlike. They are moveably articulated internally to the walls of the ninth segment (Fig.22C).

3.3.1.3 The ejaculatory ducts

Both Evans (1931) and Gil-Fernandez and Black (1965) have described both paired and common ejaculatory ducts in the Cicadellidae, and in *B. cedaranus* by far the greater part of the ejaculatory duct is paired (Fig. 23B). Helms (1968) has provided ample evidence of the ectodermal origin of these paired ducts as found in *Empoasca fabae*. He found that the paired ducts, the ejaculatory bulb and the

FIG.23

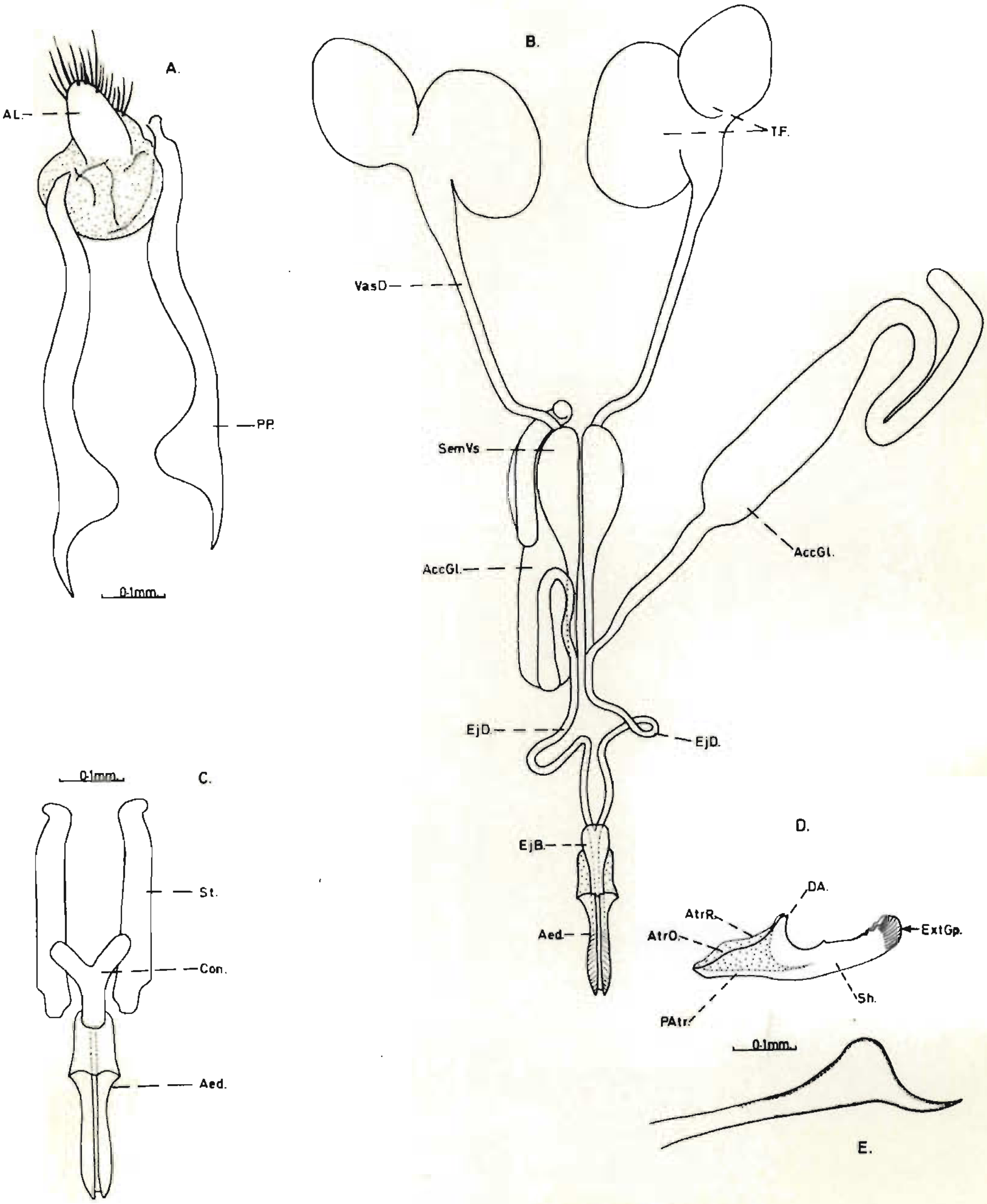


Fig. 23 Male reproductive organs and genitalia of B. cedaranus. A, pygofer processes or hooks. B, dorsal view of the reproductive organs as positioned in the abdomen. C, dorsal view of the aedeagus, connective and styles. D, aedeagus lateral view. E, lateral view apex of pygofer hook. Acc Gl., accessory gland; Aed., aedeagus; A L., anal style; Atr O., atrial opening; Atr R., atrial rim; Con., connective; DA., dorsal apodeme; EjB., ejaculatory bulb; EjD., ejaculatory duct; Ext Gp., external gonopore; P Atr. preatrium; PP., pygofer process; Sem Vs., seminal vesicle; Sh., shaft of aedeagus; St., style; T F., testis follicles; Vas D., vas deferens.

ducts finally unite after entering the ejaculatory bulb, close to the base of the aedeagus. The ejaculatory bulb has a large lumen and is enclosed in a thick muscular sheath (Fig. 24A) while the ducts have a thinner muscle sheath.

3.3.1.4 The accessory glands

A single pair of large accessory glands is associated with the male genitalia of Cicadellidae. In many species they are of more or less uniform width while in others they are greatly enlarged mesally. As mentioned before (§ 3.3.1.3) they are of ectodermal origin. In *B. cedaranus* they lie in very close association with the seminal vesicles, one having been teased out for the purposes of drawing (Fig. 23B). The gland ducts meet the ejaculatory ducts posterior to the seminal vesicles. In transverse section the cells of the enlarged portion of each gland are seen to be very elongated with a nucleus uniformly situated near the base of each cell (Fig. 24B). The content of the lumen remains unstained with Cason stain. Apically a narrower portion is found, the contents of which are granular and stain red with this stain (Fig. 25A). The cells are far less elongated.

Since spermatophores are not produced by Homoptera - Auchenorrhyncha (Helms 1968 from Maillet 1959), the male accessory glands secrete a seminal fluid that transports spermatozoa during copulation.

3.3.1.5 The vasa deferentia and seminal vesicles

The vasa deferentia of *B. cedaranus* are fairly large tubes (Fig. 23B). The posterior tip of each is dilated, forming a pair of seminal vesicles. These are pear-shaped in longitudinal section (Fig. 25B) while in transverse section they are more circular (Fig. 25A).

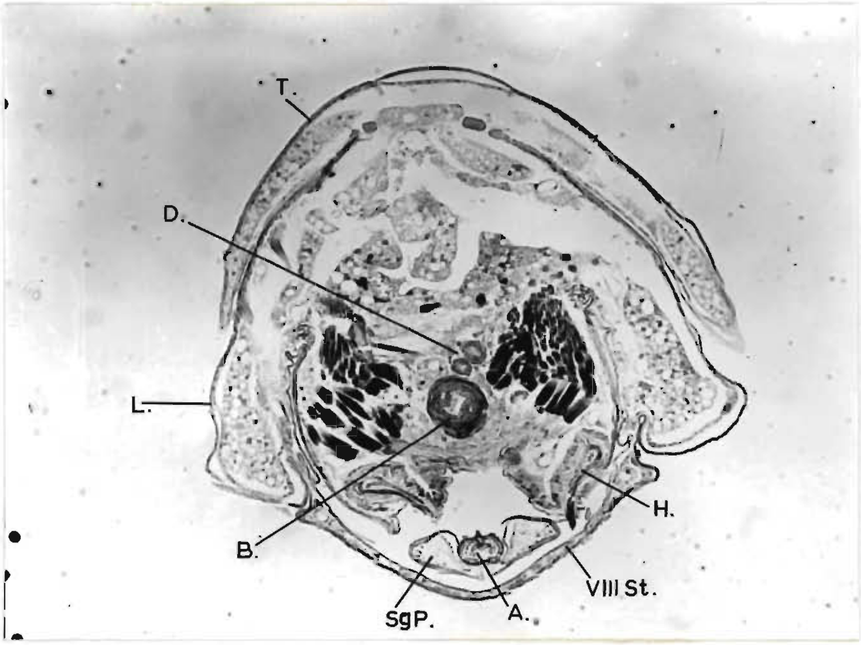


Fig. 24A Transverse section through the eighth abdominal segment of a male B. cedaranus. A., aedeagus; B., ejaculatory bulb; D., ejaculatory ducts; H., section through the pygofer hooks; L., latero-tergite; SgP., subgenital plate; VIIISt., eighth sternum; T., tergum.

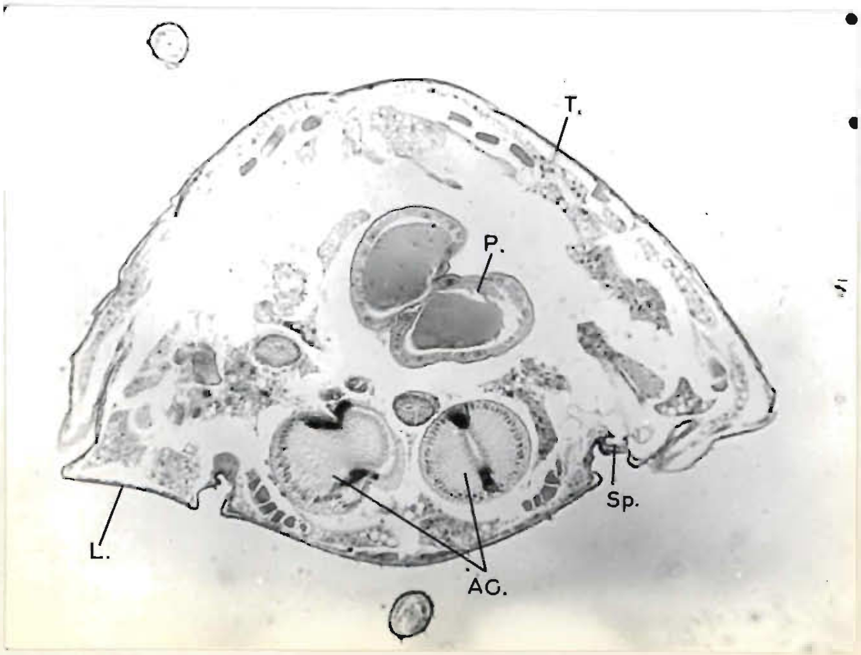


Fig. 24B Transverse section through the abdomen of a male B. cedaranus. AG., accessory gland; L., latero-tergite; P., anal vesicle of a pipunculid parasite larva; Sp., spiracle; T., tergum.

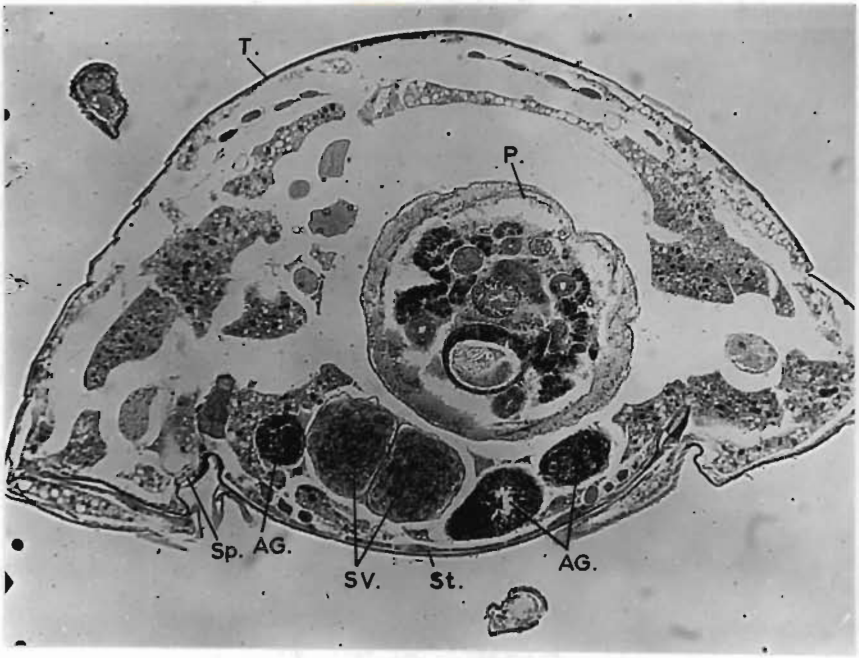


Fig. 25A Transverse section of a male B. cedaranus cutting the seminal vesicles (SV.) and accessory glands (AG.), slightly out of position due to the presence of a pipunculid parasite larva (P.). Sp., spiracle; St., sternum; T., tergum.

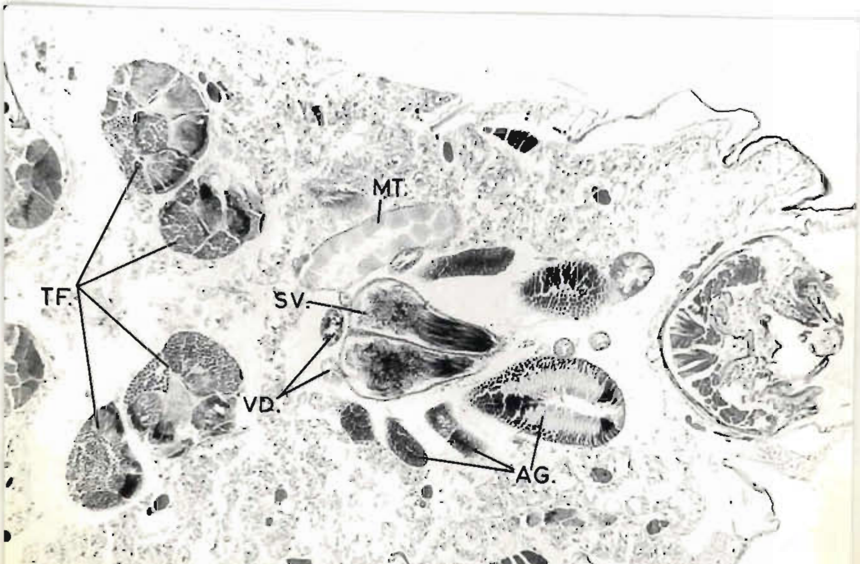


Fig. 25B Longitudinal section through the abdomen of an adult male B. cedaranus. Ag., accessory gland; MT., malpighian tubule; SV., seminal vesicle (paired); TF., testis follicles; VD., vasa deferentia.

each follicle contains spermatogonia, spermatocytes, spermatids and spermatozoa (Fig. 25B). No apical cells were seen in sections and Helms (1968) reports finding no evidence of apical cells in the testicular follicles of cicadellids.

3.3.2 Female. B. cedaranus

The external genitalia of the female B. cedaranus are of the type in which the ovipositor is formed of sabre-like valvulae on the venter of the abdomen. This type is most developed in Homoptera-Auchenorrhyncha but similar structures are found in the Miridae, as described previously (§ 3.2.2). Since the internal and external organs are fairly typical, little time will be spent on them.

3.3.2.1 The genital segments

The tergum of the ninth abdominal segment forms the pygofer (Fig. 26A). Dorsally, posterior to the pygofer is the anal tube, with its anal style. The last visible sternal plate is that of the seventh abdominal segment (Figs. 9A and B), with the shape of its posterior margin distinctive. It corresponds to the subgenital plate of female Miridae and is so named by some authors. Dorsally the eighth segment is fairly well developed, but ventrally the sternum is present only as part of the wall of the genital chamber (Fig. 27A) although the first valvifers and valvulae are derived from the eighth sternum.

3.3.2.2 The valvulae and valvifers

The ovipositor consists of the usual two pairs of blades or valvulae. The median or second pair are, as in the Miridae, united for most of their length, except at the tip, and are of a fairly uniform width throughout their length (Fig. 26B), being only slightly broader at the base. Basally they are united to

FIG. 26

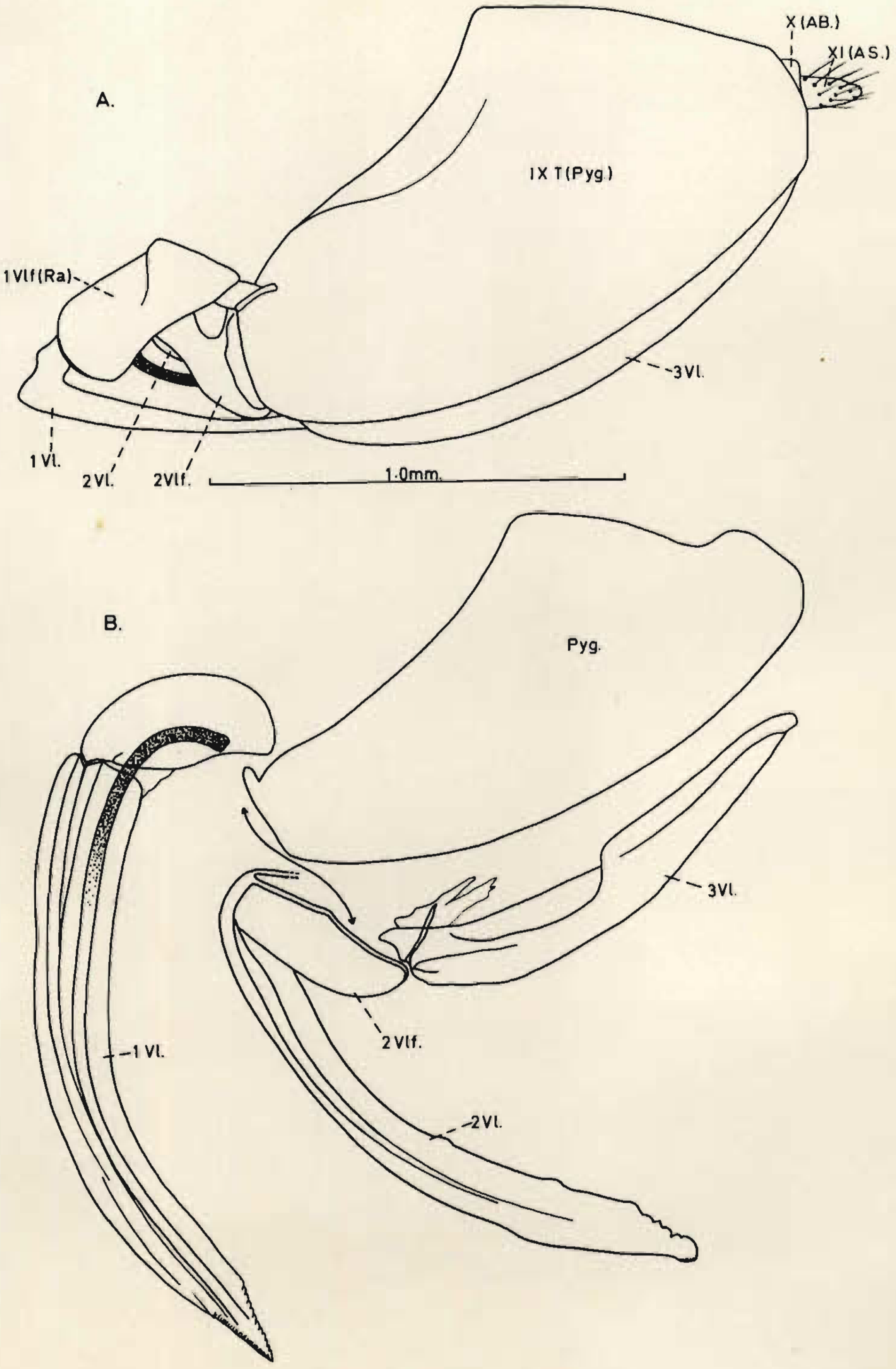
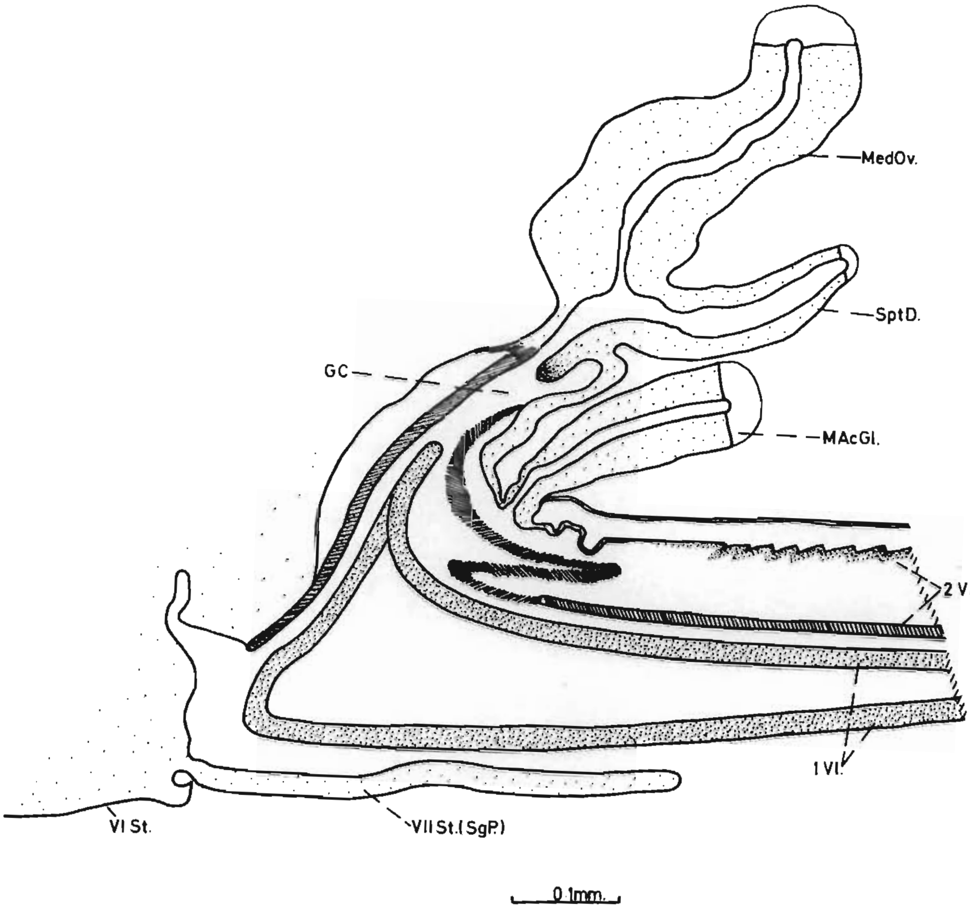
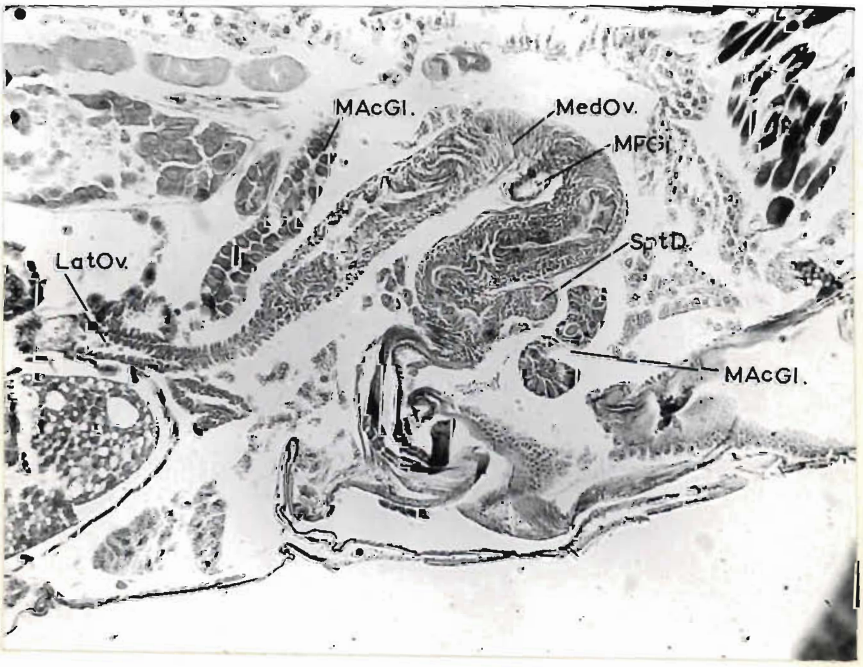


Fig. 26 External genitalia of the female *B. cedaranus*. A, lateral view. B, "exploded" view. AB., anal block or anal lobe (tenth abdominal segment); AS., anal style (eleventh abdominal segment); Pyg., pygofer lobe (ninth abdominal segment); 1 Vl., 2 Vl., 3 Vl., first, second and third valvulae; 1 Vlf., 2 Vlf., first and second valvifers (rami).

FIG. 27A


MedOv.
SptD.
GC
MAcGl.
2 Vl.
1 Vl.
Vl St.
Vll St.(SgP)
0.1mm.

B.


MAcGl.
MedOv.
MFGl.
SptD.
LatOv.
MAcGl.

C.

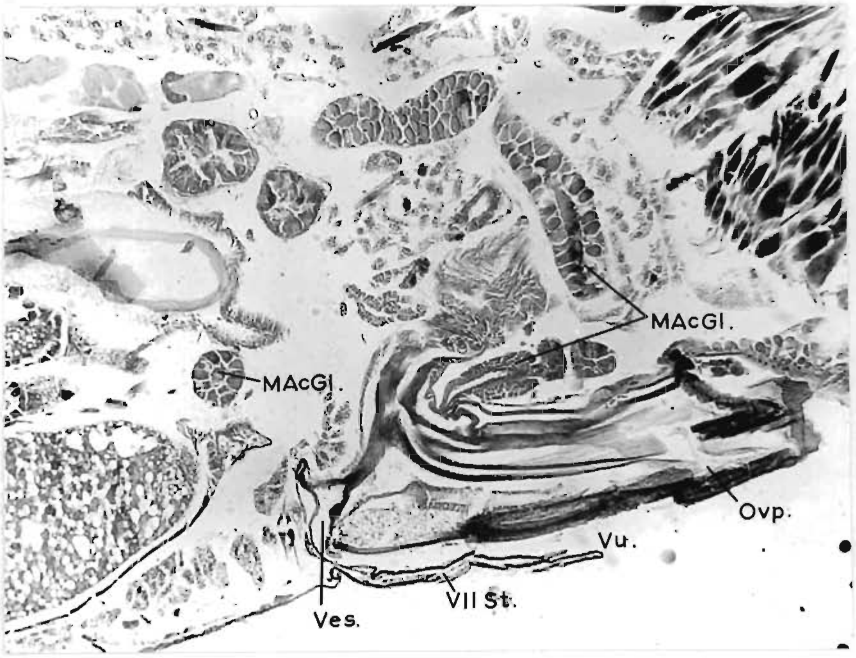


Fig. 27 Sagittal plane sections through the genitalia and reproductive organs of a female B. cedaranus. A, Semi-diagrammatic drawing from serial sections. B, photograph of one of the serial sections, cutting the median and lateral oviducts, the spermathecal duct and part of the genital chamber. C, Another section showing the opening of the major unpaired accessory gland into the genital chamber. GC., genital chamber; MAcGl., major unpaired accessory gland; MedOv., median oviduct; MPGl., major paired accessory gland; Ovp., ovipositor; SgP., subgenital plate; SptD., spermathecal duct; St., sternum; Ves., vestibulum; 1Vl., 2Vl., first and second valvulae; Vu., vulva.

ovipositor is housed when at rest (Fig. 28A). According to Helms (1968) both the second and third valvulae develop from the anterior margin of the ninth abdominal segment.

Apically the weakly sclerotised blades of the second valvulae are covered by the strong, serrated cutting blades of the first valvulae (Fig. 26B). The first valvulae are, as observed in L. laevigatum, hinged to the second valvulae (Fig. 28A), but unlike those of the L. laevigatum they too are linked to one another by similar longitudinal grooves and ridges basally. This allows the strongly serrated first valvulae to slide on one another as well as on the ridges of the second valvulae. The first valvulae are strongly developed along their entire length, and basally they unite with the first valvifers.

Recently use has been made of the structures at the base of the ovipositor in taxonomy of female Cicadellidae (Cunningham and Ross 1965). In research on the genus Empoasca these workers found that although there are obvious differences in the posterior margins of the seventh sternite in some species, these differences overlapped in at least a few species and in most cases many species. They found however that several excellent diagnostic characters exist in the region of the bases of the first valvulae and structures associated with them. These are best seen in abdomens cleared in KOH, and viewed laterally and ventrally (Fig. 9C). The structures include the base of the first valvulae, termed the outer ramus (Cunningham and Ross), and found to be both constant and distinctive. The inner rami (structure B Fig. 9C) were found to be similar in different species and therefore of little use in their taxonomy. Also the shape of the first valvifers was found to be useful.

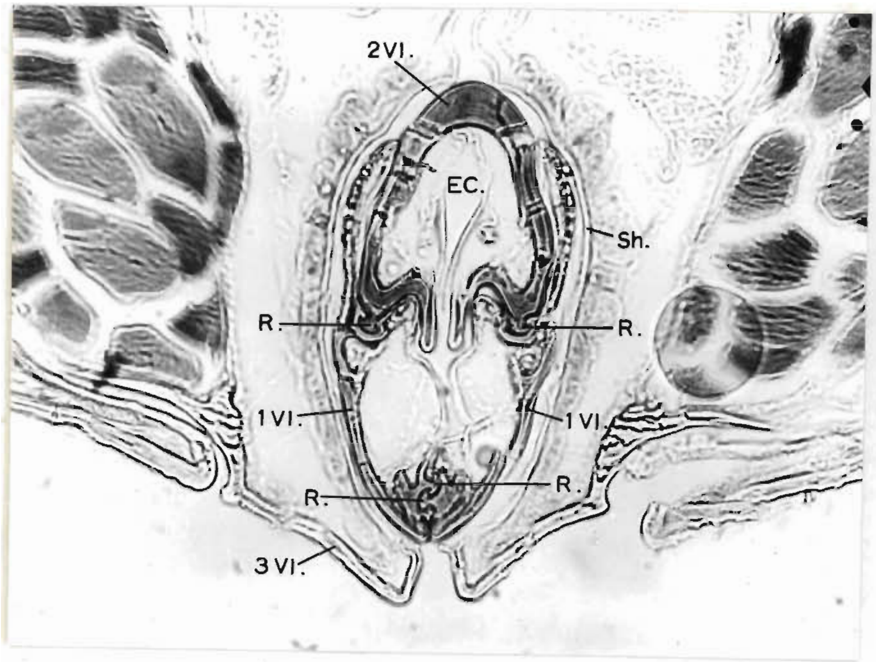


Fig. 28A Transverse section through the ovipositor of B. cedaranus showing the first valvulae (1Vl.) linked with the united second valvulae (2vl.), and to themselves by a series of parallel ridges (R.) and grooves. 3Vl., third valvulae forming the sheath (Sh.) in which the ovipositor is housed. EC., egg canal.

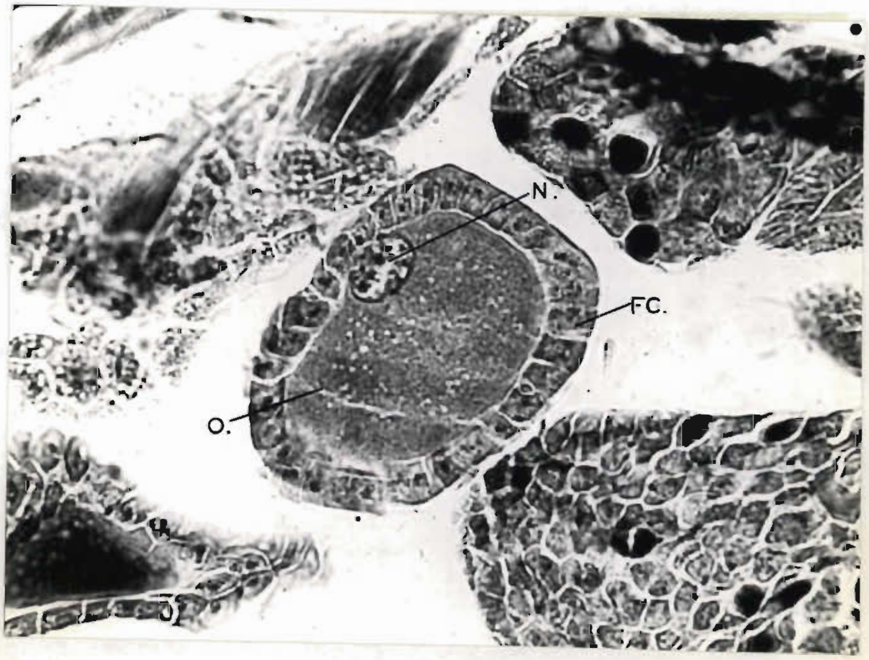


Fig. 28B Section through an oocyte in an ovariole of a B. cedaranus female. FC., mononucleate follicle cells; N., nucleus of oocyte; O., oocyte.

copulation, the vulva or secondary gonopore (Fig. 27), covered by the seventh sternum. The vestibulum lies between the bases of the first valvulae and the posterior intersegmental membrane of theseventh sternum. According to Snodgrass (1935) the genital chamber receives the median oviduct and the duct of the spermatheca into its anterior end. This therefore defines the extent of the genital chamber (Figs. 27A and C). Where the genital chamber takes the form of a tubular passage continuous with the median oviduct, it is distinguished from the latter as the vagina (Snodgrass 1935), a condition prevalent in the cicadellids (Kunze 1959).

3.3.2.4 The spermatheca

Opening into the anterior end of the genital chamber is the spermatheca, pear-shaped with a fairly thick duct (Fig. 30). It lies closely associated with the median oviduct and often against it, in the body cavity. It is inveloped in a strong muscular sheath and has a thin cuticular lining. In mated females the spermatheca becomes greatly distended. Helms (1968) reports finding no spermatozoa or secretory material in the spermathecae of mated female Empoasca fabae, but the author has observed them in the spermatheca of B. cedaranus (Fig. 29).

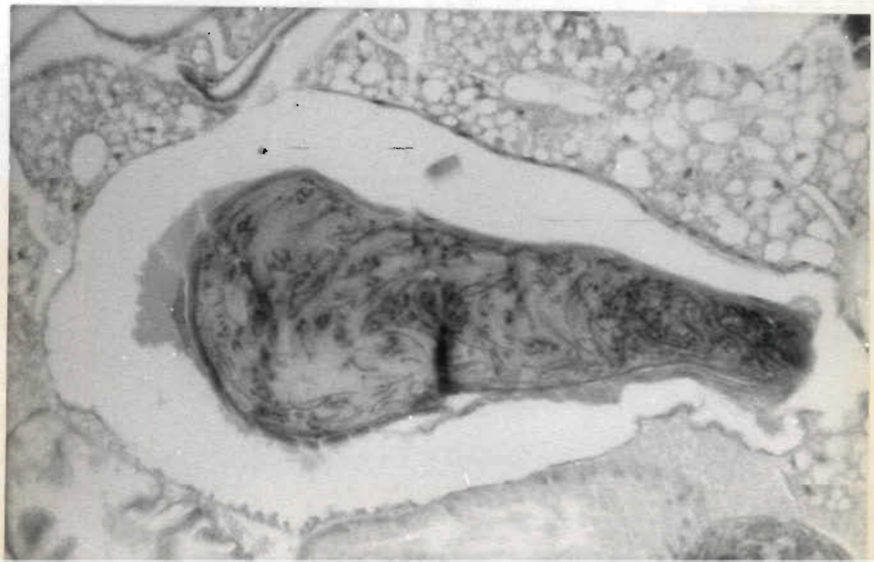


FIG. 30

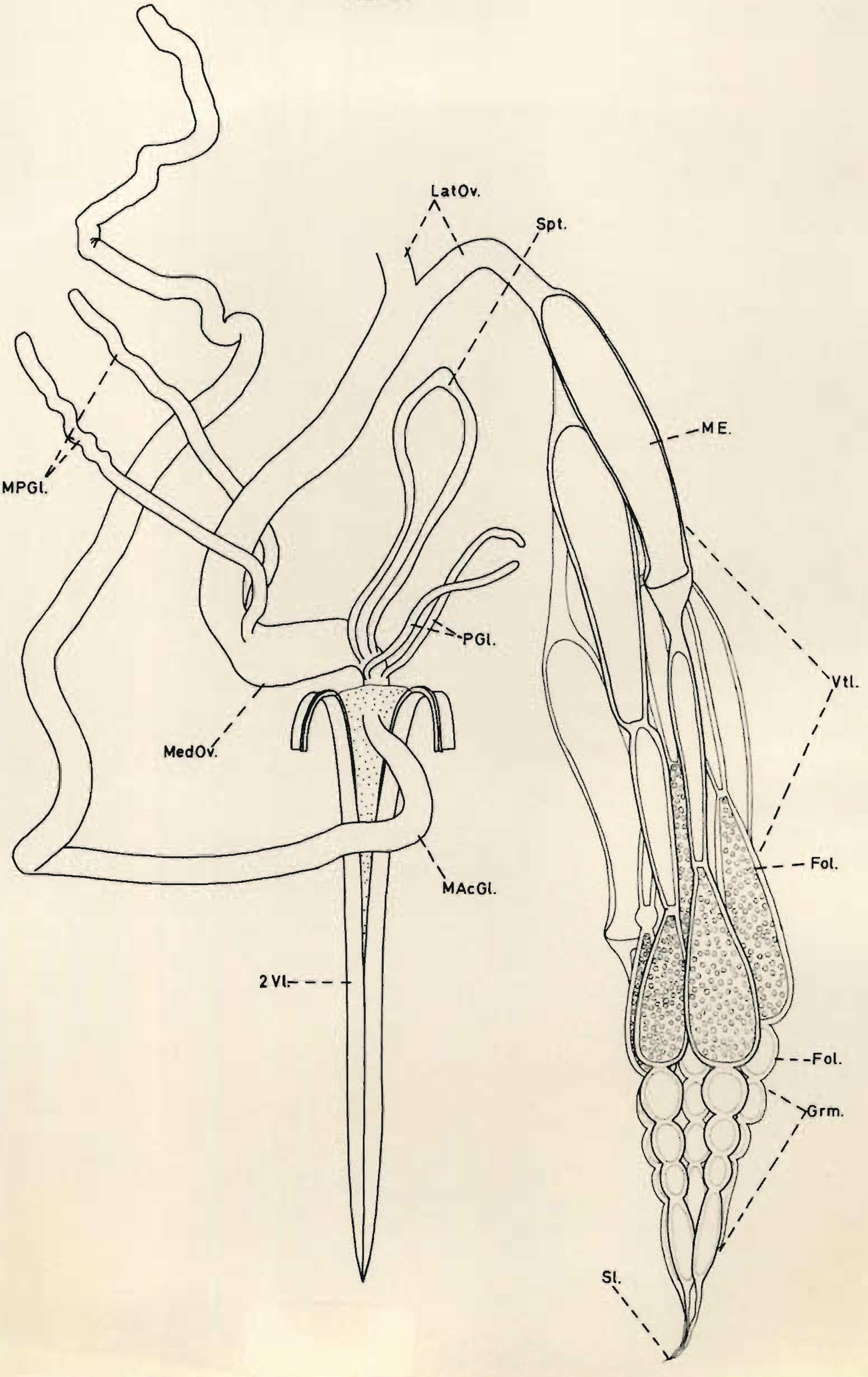


Fig. 30 The female reproductive organs of B. cedaranus. Dorsal view with the right ovary deflected posteriorly for inclusion in the drawing. Fol., follicular egg chamber each containing a developing oocyte; Grm., germarium; LatOv., lateral oviducts; M Ac Gl., unpaired major accessory gland; ME., mature egg passing through the calyx into the lateral oviduct. Med Ov., median oviduct; M P Gl., large paired glands of the median oviduct; PGl., small paired glands of the median oviduct; Sl., suspensory ligament; Spt., spermatheca; 2 Vl., second valvulae; Vtl., vitellarium

3.3.2.5 Accessory glands

A single large median unpaired accessory gland empties its contents into the genital chamber (Fig. 27A and C). The cells of this gland are large with large basal red-staining nuclei (Cason's stain) while the contents of the lumen stain orange. From its point of entry into the genital chamber between the rami of the second valvulae, the gland arches dorsally and then anteriorly (Fig. 27C). It then passes between the lateral oviducts (Fig. 27B) and comes to lie below the ovaries in the sternal region of the body cavity, extending forward to about the anterior margin of the fifth abdominal segment in a mature female. In young newly adult females, the gland is very much more slender and reduced.

Since the aperture of the gland is dorsal to the external genital opening, Helms (1968) suggests that it may secrete some protective solution around the egg at oviposition. He suggests that such secretions may polymerise or otherwise form a protective pocket in the host-plant tissues for the egg and developing embryo. A sheath of this sort was found surrounding eggs of B. cedaranus in wattle tissue (§ 5.2.1). Gil-Fernandez and Black (1965) refer to it as a colleterial gland, but offer no evidence.

Several authors have described small paired accessory glands opening into the genital tract near the median gland. A pair of glands comparable to these, are present in the female B. cedaranus (Fig. 30). These so-called glands are of uniform thickness, and have narrow ducts.

Of far greater functional importance are a pair of accessory glands which enter the median oviduct (Fig. 30). These glands consist of cuboidal cells. In the central and basal parts of the glands, the cells have diffuse, poorly staining nuclei but apically the nuclei are large, compact and stain deep red with

In the female B. cedaranus the median oviduct is fairly thick, with an intricately folded inner wall (Fig. 27B). It is surrounded by a thin muscular sheath. Lateral oviducts (Figs. 27B and 30) are relatively short and considerably thinner than the median oviduct.

3.3.2.7 The ovaries

The ovaries of B. cedaranus each have eight ovarioles. Each ovariole consists of a terminal filament, germarium, vitellarium and pedicel, and belongs to the acrotrophic type. The terminal filaments are united forming a suspensory filament attached to the fat body.

Within the germarium, a condition similar to that observed in the Empoasca fabae by Helms (1968) exists, namely that the cells of the apical half are macronucleate with coarse chromatin. These cells differentiate into large cells and oocytes. The latter lie in the basal portion of the germarium.

The follicular cells of a newly developing oocyte are columnar (Fig. 28B), but as the oocyte enlarges and moves down the ovariole, they become cuboidal and eventually squamous. Follicle cells are mononucleate, the nuclei ill-defined and granular (Fig. 28B).

PART II

BIOLOGY AND SOME ECOLOGICAL STUDIES

CHAPTER 4

BIOLOGICAL STUDIES ON LYGIDOLON LAEVIGATUM

4.1

INTRODUCTION

Due to a lack of suitable facilities for adequate control of temperature and humidity, the greater part of the study concerned with life-cycle duration was conducted in the field. During these studies fine gauze cages, about twelve inches long and with a six-inch diameter, were used for confining insects on young wattle trees. In order to give some idea of temperatures prevailing during periods of study, tables of mean weekly maximum and minimum temperatures are provided. (Appendices 3, 4 and 5). A table was also drawn up showing mean hourly values of temperature and relative humidity, for each month of 1967 (Appendix 6). All readings were taken in the field in the experimental area.

4.2

THE EGG STAGE

4.2.1 Oviposition sites

Eggs are laid in very young growth on young wattle trees. On the tips of shoots, eggs are often laid between the pinnae of tiny developing leaves, or within the apical bud. Another favoured site is in the tiny axil buds in the axils of the developing leaves. In young half-developed leaves, eggs may be laid in the rachilla, while in tiny folded leaves the fleshy also variation in the degree of penetration of the egg in the tissue. When laid between the folded pinnae of a tiny developing leaf, or in the apical bud of a shoot, the egg is almost entirely concealed, but no plant tissue is damaged (Fig. 31A). In the majority of cases, however, the egg is laid within living tissue, often with only its operculum showing. Occasionally half or less than half of the entire egg penetrates the tissue, the rest being easily visible (Fig. 31B). Data on 50 eggs examined from field-collected material is shown in Table 1.

Table 1. L. laevigatum. Egg position on field collected material consisting of 50 eggs.

Egg Penetrating Living tissue		Egg Between tissues or on surface	
Operculum only visible	Half or more of egg visible	Between pinnae or in buds	On the surface Entire egg visible
21	7	13	9

Eggs are usually laid singly although sometimes several in close proximity to each other may be found. Clusters of five have been noted, and even an extreme case of seven eggs clustered and stuck together, all penetrating the tissue of the plant and causing considerable bruising and even slight gumming, was recorded. Eggs were only considered as in a cluster if they touched one another along most of their length. The following is a table of egg cluster size and frequency on field collected material from young wattle plantations (N = 130)

No. of eggs per group	1	2	3	4	5	7
No. of such groups found	59	14	6	2	2	1

4.2.2 Size and shape of the egg

The measurements of newly-laid eggs together with those of eggs just prior to hatching, are given in table 2.

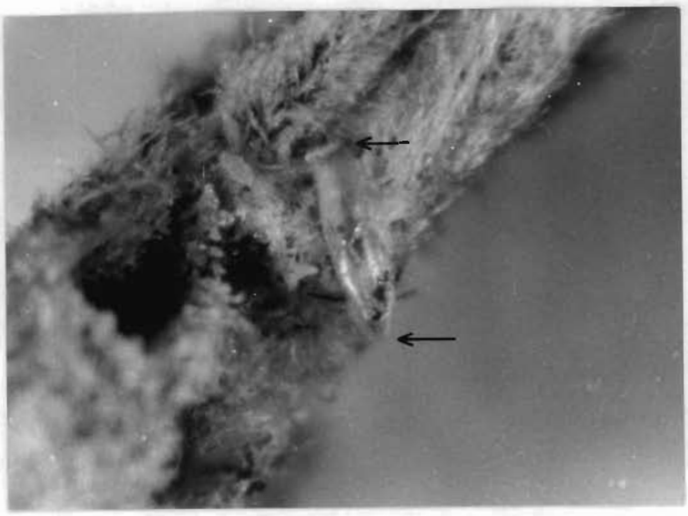


Fig. 31A An egg of *L. laevigatum*, entirely exposed.

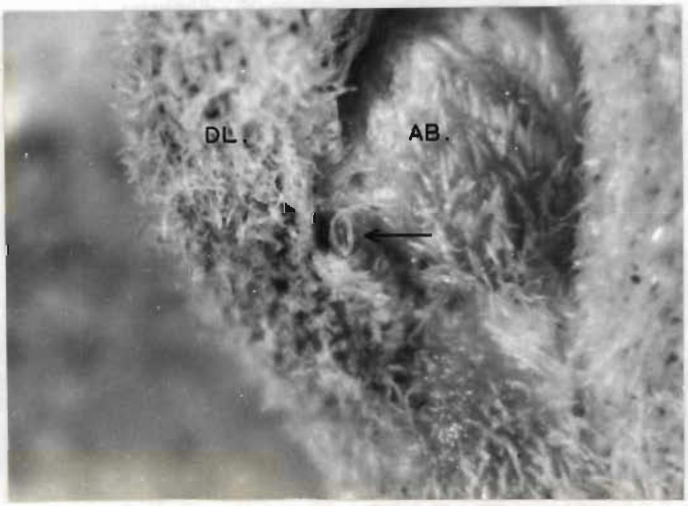


Fig. 31B Operculum of *L. laevigatum* egg buried between an apical bud (AB.) and a tiny developing leaf (DL.).

Fig. 31C Operculum of *B. cedaranus* egg after hatching. The operculum rim (OR.) and embryonic cuticle (EC.)

Table 2. L. laevigatum. Measurements of newly-laid eggs, (N = 10) together with those eggs just prior to hatching. All measurements in mm.

	Newly laid eggs			Eggs just prior to hatching	
	Length	Breadth	Operculum width	Length	Breadth
	0.75	0.20	0.20	0.86	0.21
	0.75	0.21	0.21	0.85	0.20
	0.76	0.20	0.21	0.88	0.22
	0.76	0.20	0.19	0.86	0.21
	0.79	0.23	0.20	0.85	0.20
	0.76	0.20	0.21	0.84	0.20
	0.81	0.23	0.20	0.88	0.23
	0.79	0.20	0.20	0.87	0.22
	0.79	0.21	0.18	0.87	0.21
	0.75	0.20	0.18	0.86	0.21
Mean	0.771	0.208	0.198	0.862	0.211

Newly-laid eggs average 0.77 mm. in length (N = 10) with a maximum of 0.81 mm. and a minimum of 0.75 mm. Mean maximum width is 0.208 mm. and mean width of the operculum, 0.198 mm. Eggs are narrowest just behind the operculum (Fig. 32A). They are cylindrical and slightly curved, and rounded at the posterior end, with an operculum which is laterally compressed and asymmetrical. The chorion is transparent, shiny and finely reticulated. Overall egg colour is cream.

4.2.3 Maturation changes in the egg.

For several days before the egg hatches the red eye patches of the developing nymph may be easily seen (Fig. 32A). At approximately this stage, the truncated anterior end of the chorion appears to rupture along its midline. The embryonic membrane becomes exposed and expands through this rupture, so that the finely sculptured chorion rim is no longer apical

4.2.4 Egg stage duration and fertility

Using a hand lens (10 x magnification) one is able to detect and examine eggs in the field and to note when they have hatched. Using this technique the fertility of eggs could be studied in the field. Of 96 eggs examined from the period 15th April 1967 to 1st May 1967, 75 hatched; 78 per cent. fertile. In order to check this, additional data was collected in January 1968. Of 25 eggs examined 21 hatched, giving an 84 per cent. fertility. No egg parasites were found. During August 1969, of 38 field collected eggs isolated individually in a search for egg parasites, 78 per cent. hatched, one of the eggs failing to hatch due to parasitism by a trichogrammatid parasite (§ 8.2.2.3).

Egg stage duration was studied by confining field collected females in the small gauze cages mentioned in § 4.1, on tender shoots for a period of 24 hours. The cages were then removed, together with the adults. The trees were examined every 24 hours and any newly hatched nymphs removed. Egg stage was calculated from day of cage removal to day of nymph emergence. Results are presented in Table 3, and represent data collected in the period March - June 1967 and January - February 1968.

Table 3. Incubation period in days, of eggs of L. laevigatum during the important outbreak months. Temperature data recorded in Appendices 3, 4, 5 and 6.

Month	1968 January	1968 February	1968 March	1967 April	1967 May	1967 June
Number of readings	17	23	18	21	12	16
Maximum (days)	8	9	9	11	12	14
Minimum (days)	6	7	7	8	9	10
Mean	7.3	7.7	8.1	9.4	10.8	12.3

4.3

THE NYMPHAL INSTARS

The nymphs of Miridae are generally active and mobile, while those of L. laevigatum are confined only by their feeding habits, since they feed on the tender growing tips of young wattle plants. As is the rule in this family there are five nymphal instars (Fig. 32). Metamorphosis is hemimetabolous.

4.3.1 The first-instar nymph

On eclosion, the first-instar nymph averages 0.59 mm. in length, but after feeding, increases considerably in size, to attain an average length of about 0.88 mm. (Appendix 2). The nymph is pale yellow with bright red eyes and translucent appendages. The body is sparsely covered by fine dark hairs, arranged in rows across the abdomen. The appendages and tergal plates are darker than the rest of the body. A dark spot occurs dorsally on the anterior margin of the fourth abdominal segment (Figs. 32B and C).

4.3.2 The later instar nymphs

Nymphs of the later instars differ from first-instar nymphs in colour, size, wing-pad development and arrangement of hairs (Fig. 32). They are predominantly light green, with red eyes which often become greyish in large nymphs. In the fifth-instar the tips of the wing-pads are black, the dark area increasing in size as the final moult to the adult approaches. The head, thorax and abdomen dorsally, and the legs and antennae, are sparsely coated with prominent black hairs. On the abdomen each segment has a row of hairs (Fig. 32G). The dorsal abdominal spot is well-defined in all instars but in these later instars is usually accompanied by a dull yellow area which appears to be

FIG. 32

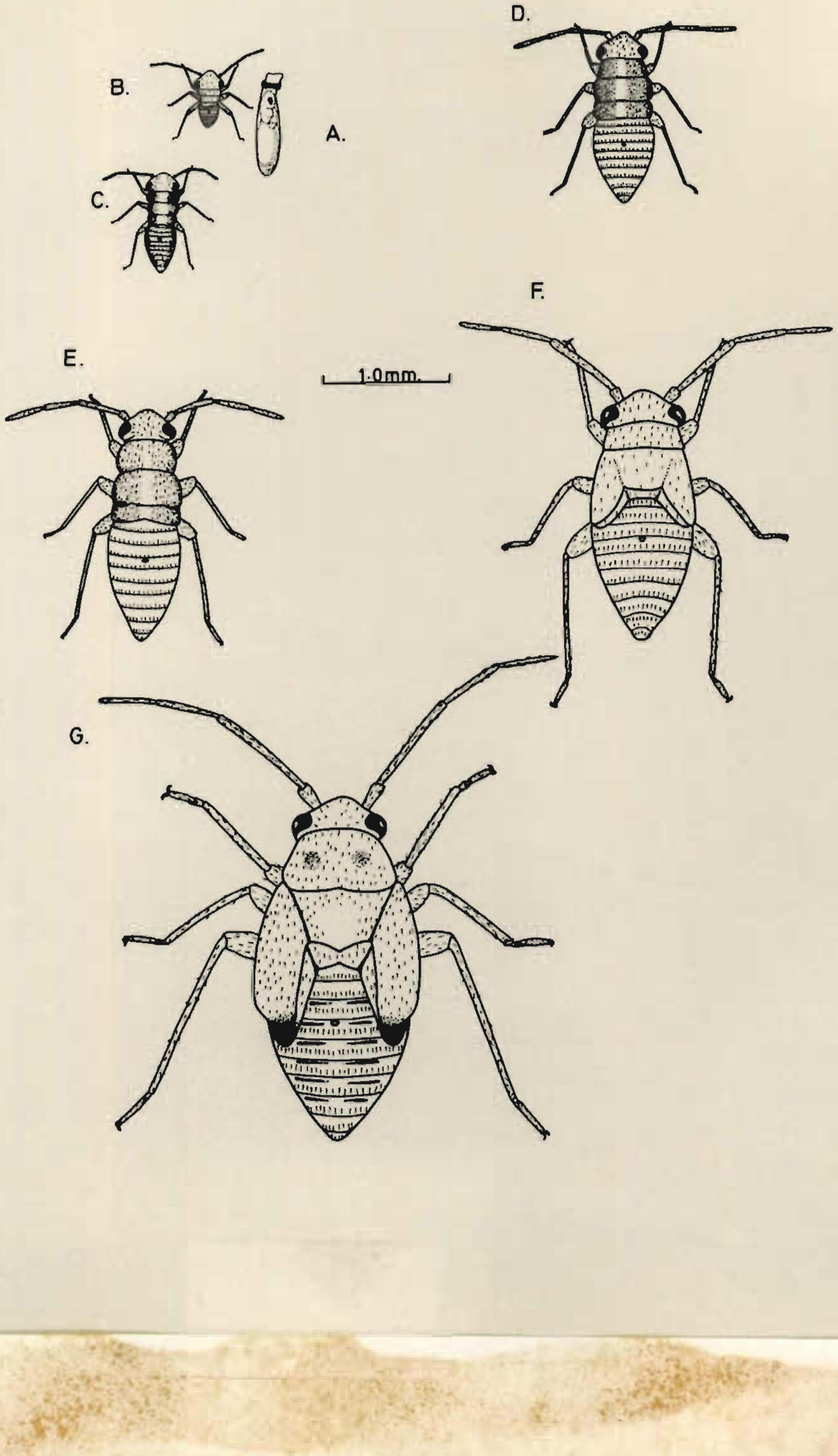


Fig. 32 Egg and nymphs of L. laevigatum. A, an egg shortly before hatching, with the developing nymph's eye visible through the chorion. B, first-instar nymph immediately after hatching. C, same, after feeding. D - G, second- to fifth-instar nymphs.

4.3.3 Duration of the nymphal instars

The durations of nymphal instars were investigated by confining newly emerged nymphs in cages in the field. Although this gave a good indication of nymph stage duration, individual instar times were often difficult to assess under such conditions, as shed ecdyses were lost and the nymphs themselves difficult to observe closely. Studies were therefore confirmed by data collected in the laboratory, from nymphs reared on potted wattle seedlings, and under lamp glasses. In the latter case foliage was changed every second day and kept moist using tubes of water. Nymphs were individually housed and carefully inspected daily for signs of having moulted. It was felt that the data on individual instar duration so obtained was applicable as overall nymph stage duration had been assessed in the field. Data from nymphs which developed from egg to adult in a similar number of days in the laboratory, confirmed individual instar times.

Table 4. Instar duration (in days) of <u>Lygidolon laevigatum</u> under field conditions. Prevailing temperatures during the study are recorded in Appendices 3, 4 and 6.

a) Period January to February, 1968:

INSTAR	1st	2nd	3rd	4th	5th	Total time as nymph
Number of Readings	20	20	20	20	20	25
Max. duration (days)	3	3	4	3	4	16
Min. duration (days)	2	2	2	2	1	12
Mean duration (days)	2.2	2.7	2.9	2.6	2.9	14.3

b) Period April to June, 1967:

INSTAR	1st	2nd	3rd	4th	5th	Total time as nymph
Number of Readings	22	19	19	18	17	25
Max. duration (days)	4	4	4	4	6	20
Min. duration (days)	2	3	3	2	3	15

4.3.4 Nymph survival rate in the field

Owing to the fact that the nymphs of *L. laevigatum* are highly mobile, an estimate of field survival rate is extremely difficult. By caging nymphs on trees, natural control agents, such as predators and parasites are interfered with, and although these may in some instances be negligible, parasites have been found to cause a high mortality. However, some indication of natural mortality can be obtained from the data collected during investigations into the overall nymph stage duration in the field. In order to obtain data on 50 individuals, it was found necessary to cage 67 nymphs. This allowed for a mortality of about 25%. Great care was necessary in transferring newly hatched nymphs to field cages, as they are extremely fragile and active.

4.3.5 Distribution of nymphs on the tree

As mentioned in Section 4.2.1, eggs are laid on the tender terminal shoots on actively flushing young wattle trees. Such areas are the natural feeding places of the adults, and both adults and nymphs appear unable to feed on the more mature foliage and terminals which are not in a condition of flush. The first-instar nymphs, in particular, are invariably found on the tiny terminal buds and between the pinnae of small developing leaves. Although highly active, first-instar nymphs do not move far from the empty egg-case. They commence feeding within minutes of hatching, and will recommence feeding very soon even after being thoroughly disturbed. This indicates that they require a great deal of moisture due to rapid desiccation. The second-instar nymphs also tend to feed on the very tender shoots, while the larger nymphs feed on the leaflets of new fully opened leaves, provided such leaves are still tender. Thus the instar, do appear to move about a little. More than two nymphs are very seldom found on the same terminal and later instar nymphs are usually found singly. This is despite the fact that as many as ten eggs may be encountered on a single terminal. Numbers of newly hatched nymphs can often be seen in close proximity to one another, but disperse more widely during their second- and third-instars.

4.4

THE ADULT STAGE

4.4.1 Preoviposition period

In these studies, adults were confined, in pairs, in eight to ten inch tall lamp-glass cages with fine gauze over the top, and standing in petri-dish lids. Within these cages small succulent terminals from young wattle trees were kept moist by standing them in tubes containing water. The foliage was renewed every second day, and the replaced foliage microscopically examined for eggs. In this way data on preoviposition period, fecundity and longevity were collected.

Data collected in May, 1968, from subsequent experiments revealed an average preoviposition period of eleven days (n = 9) indicating, possibly, the effect of temperature and other environmental conditions such as sunlight, humidity and host tree condition.

4.4.2 Fecundity of females

Oviposition studies on individual females revealed that eggs were not laid every day, and the maximum observed number of eggs laid in a 24 hour period, was 13. Mean number of eggs been considerably higher. Throughout the experiment care was exercised in presenting the insects with tender buds from young actively growing wattles, to ensure the presence of suitable oviposition sites.

Table 5. Data on preoviposition period, fecundity and longevity of Lygidolon laevigatum females during January and February 1968.

Female No.	Preoviposition Period	Total eggs Laid	Eggs per day during oviposition period		Longevity (Days)
			Maximum	Mean	
1	10	19	3	1.00	29
2	8	69	7	1.92	44
3	11	45	8	2.14	32
4	8	63	9	1.66	46
5	9	72	9	1.80	49
6	8	88	11	3.03	37
7	6	159	13	3.31	54
8	10	73	11	2.43	40
9	9	69	7	2.65	35
10	9	123	12	2.93	51
11	11	102	11	2.62	49
12	12	57	9	1.84	43
13	11	27	6	1.35	31
Mean	9.4	74		2.21	41.5

Dissection of field-collected females for various experiments has revealed a maximum of 24 mature eggs in a single mature female (assessed by colour of the abdomen § 2.1.1). A single specimen containing 39 mature eggs was encountered, but must be regarded as exceptional. Of 709 mature females dissected and found to contain eggs, the following were found to have 20 or more eggs per female.

No. of eggs per ♀	20	21	22	23	24

The full table of results from all 709 females is not presented, as they were collected at different times and localities with various factors affecting fecundity at these different times, and the data would therefore be misleading. However, the maximums given above serve to illustrate that the number of eggs per female is no indication of the egg-laying capacity of that female as egg development continues throughout the egg-laying life.

4.4.3 Factors affecting female egg-laying capacity

During the period February to August 1967, a marked change in the average number of mature eggs (eggs showing a fully developed operculum) per mature female, occurred in a plantation of young wattle trees at the Wattle Growers Union experimental station "Bloemendal" near Pietermaritzburg, as shown in the following table:

Table 6. Monthly averages of eggs per mature female for the period February to August 1967. All samples collected in Block 18, Bloemendal Field-Experimental Station, Pietermaritzburg.

Month	February	March	April	May	June	July	August
Average No. Eggs/♀	15.2	12.6	6.8	6.0	5.1	5.8	7.9
n	69	80	70	64	80	26	81

The samples for August were collected in extensive sweeps as the population was very much reduced in numbers at that stage (See data on population numbers § 6.2.2). To test whether the consecutive sample means were significantly different, the data was subjected to a F-test. The data was however not normal, and a transformation was required. Since the $(\text{range})^2$ was found to be proportional to the mean when plotted graphically for each treatment, a square-root transformation was made dissected during the course of the investigation.

The F-test showed the observed drop in fecundity to be statistically significant ($P = 0.01$). Individual t-tests conducted, showed that the reductions in the mean number of eggs per female recorded between February and March and between March and April were both significant ($P = 0.05$ and $P = 0.01$ respectively). The drops in fecundity recorded between the months of April and May, and between May and June, were not significant , but the overall drop between the mean values for April and June, was significant ($P = 0.01$). Similarly the rise in the mean value observed for July as compared with the June mean, was not significant, while the higher mean observed in August, as compared with the mean for July, was significant ($P = 0.05$). The overall rise in mean value observed between June and August was highly significant ($P = 0.01$).

It can be seen from an examination of these results, that a drop in mean number of eggs per female, occurred from February, to a minimum value in June, followed by a slight but significant rise, up to the end of August. In order to attempt an explanation of the cause of this drop in fecundity other experiments were conducted.

The minimum value observed in June 1967, together with the fact that a number of mature females in the sample showed failure of the reproductive organs to enlarge, and more fat body than usual in the abdomen, suggested that some sort of facultative diapause might occur, similar to that observed in L. hesperus by Beards & Strong (1966). From a sample of 15 mature females collected on June 19th 1967, five were found to be in the above condition while the mean number of eggs per female was 3.8. In most insect species having a facultative diapause, the principal precision, being unaffected by changes in weather and climate, but only by changes in latitude and season of the year (Beards and Strong 1966). Since the lowest mean and highest percentage of non-reproducing mature females was observed in mid-June, observations were resumed when a suitable population was found in the field in mid-June 1969 (Kirkfalls, Hillcrest, Natal). A sample from this population revealed no females in a non-reproductive state, and a mean of 8.0 eggs per female (n = 45). Diapause is defined as "a state of arrested development ...... - enforced by a physiological mechanism rather than by concurrently unfavourable environmental conditions" (Beck 1962). By this definition the observed drop in fecundity appeared to be in response to a concurrently unfavourable environment, and was therefore studied further.

4.4.3.1 The effects of soil moisture on egg production

Assuming that, in a normal young wattle tree, the soil moisture content would have an effect on the water relations in the plant, and hence, general tree condition, an experiment was conducted to assess the possible effect of water stress in the plant on female fecundity. In a 90 acre block of young 4 - 8 ft. wattle trees on the farm Kirkfalls, Hillcrest, samples of females were collected from three sites selected for their differing soil moisture contents. Samples of 1000 gms. of soil collected, weighed and oven-dried before reweighing, were used to estimate soil moisture content at each site. Soil was of the Msinga series, a moderately leached fairly deep red soil. The results of the experiment are recorded and analysed in Appendix 8. Since samples had a similar distribution to those of the previous experiment, the same transformation was used.

From the results of this test (Appendix 8) it can be seen sites. Females from the best-watered site (Site C) contained significantly more eggs than those from sites A and B. However, data from sites A and B were not significantly different, despite the different soil-moisture contents recorded.

4.4.3.2 The effect of food quality on egg production

In the previous experiment (§ 4.4.3.1) it was noticed that although the trees at Site A were obviously affected by a shortage of water, the trees at site B had been reduced to a similarly poor condition by the feeding of L. laevigatum adults and nymphs. It was therefore apparent that the trees at the two different sites had been adversely affected by two different factors. This resulted in a single factor being responsible for the reduced egg laying capacity of females, namely reduced food quality, although the result of two different causes.

To investigate the effect of food quality on the fecundity of females, a site was carefully selected in a 90 acre plantation of badly attacked trees at Kirkfalls, Hillcrest, 11th July, 1969. In this plantation the infestation had been initiated by adults migrating from slightly more mature trees (one year older) adjacent to the southern corner of the young plantation (Fig. 36A). Trees in the younger plantation but adjacent to the older trees were more heavily damaged, while those further away were only lightly damaged. Two samples of insects were collected, the first from actively flushing undamaged trees, and the second from the more heavily damaged young trees. These latter trees showed typical damage due to feeding and were therefore predominantly of poorer quality as food, although some had produced a new flush of foliage in response to good soil moisture conditions. The number of eggs per female was recorded by dissection. The data was subjected to a t-test, and the results presented in the

Table 7. Results of the statistical analysis of data based on the number of mature eggs per mature female (the latter assessed by body colour) from damaged and undamaged trees. Kirkfalls, Hillcrest. July 11th 1969.

	Undamaged trees	Damaged trees
n	34	71
Treatment totals	343	512
Treatment means	10.088	7.211

Pooled estimate of variance = 21.16 (103 D.F.)
Variance of the difference of the means = 0.9204
Standard Error of the difference = 0.9594
t. (103D.F.) = 2.999

The mean difference of 2.877± 0.959 eggs per female in favour of females collected on undamaged succulent trees is significant (P = 0.01).

This effect of food-quality is important in studies of the population dynamics of the species and will be referred to again in the section on ecology.

The rise in mean number of eggs per female observed at Bloemendal, Pietermaritzburg in July and August 1967 (§ 4.4.3) can now be explained from the data presented above. During that year, rains were consistent and copious until the end of April, the soil water content remaining high, and trees were growing rapidly. However, the heavy population of <u>L. laevigatum</u> damaged the trees to such an extent that by June the quality of the food available was having a marked effect on the egg production potential of the mature females. A late flush was noted during late June and July as trees recovered from the attacks, and this was confirmed by the observed rise in the mean number of eggs per female for July and August.

case of 13 females, showed a mean of 41.5 days and a maximum of 54 days. Although no detailed investigation on male longevity was conducted, cage experiments indicated that males survived for shorter periods than females under similar conditions. A study of the literature revealed that most workers found male Miridae to be shorter-living than the females, death intervening soon after mating had occurred.

4.4.5 Sex ratio in the field

During population studies throughout 1967 and 1968 at Bloemendal, Pietermaritzburg, sex ratio records were kept of all samples collected. Since each sample contained both males and females, "Student's" method of paired differences test was used to indicate any significant difference between the numbers of males and females encountered.

A total of 3330 males and 2895 females were used in the test, comprising 88 pairs. Males were significantly more numerous than females (P = 0.01), by a difference estimated at 4.94 ± 1.57 males per sample.

However, it has been found that when breeding is checked by unfavourable tree conditions, the shorter adult life of males results in a rapid change in the sex ratio, females becoming predominant. For example in early August 1967 two collections, on the 2nd and 10th August respectively, yielded a total of 114 females and only 50 males.

4.4.6 Adult mobility

Although flight studies were attempted, using a permanently tacky adhesive on boards at various heights in a plantation at Bloemendal, Pietermaritzburg during 1968, other activities prevented the experiment from being properly controlled, and it was abandoned. However, a number of careful

As mentioned earlier (§ 4.3.5) nymphs are fairly localised on trees, and provided trees are not touching, no movement, even from tree to tree, will occur. Adults are active and readily take to flight, and even slight jarring of a branch will cause adults to drop off and fly away. The presence of an observer is sufficient to cause them to dart around to the far side of the shoot on which they are perched, and may even set them to flight. The males are far more active than the females, and the activity of both sexes is increased during warm sunny days.

Flight studies of Heteroptera conducted by Southwood (1960) at Rothamsted Experimental Station from 1947 to 1956 indicated that 97 per cent. of all Heteroptera from light trap catches were Miridae. In the rather less biased suction traps they formed 56 per cent. of the total. Although Miridae dominated the light trap catches, less than 20 per cent. of the Miridae were taken at night. He also found that while equal numbers of males and females were taken during the day, the males greatly exceeded the females in the nocturnal captures. This excess of males was even more pronounced in ultra-violet trap catches.

4.4.7 Alternate host data

In and adjacent to wattle plantations a number of weed species are found on which adults of *L. laevigatum* has been collected. Amongst these are the following:-

Compositae	*Tagetes minuta*	Khaki weed
"	*Crassocephalum crepidioides*	
Phytolaccaceae	*Phytolacca octandra*	Inkberry.

The species has never been collected from any grass species, and on *P. octandra*, is usually found in association with *Taylorilygus simonyi*, a species of mirid often found on numbers in the young wattle plantations where these weeds were growing. Thus their occupation may have been due to some stress factor such as crowding or poor food quality.

The fact that wattle is so readily attacked resulted in a search for *L. laevigatum* on indigenous *Acacia* spp. Two of the most common species in the wattle growing areas are *Acacia nilotica* subsp. *kraussiana* and *A. karroo*. Both *L. laevigatum* and *Taylorilygus simonyi* were collected from young flushing trees of these two species as well as from the inflorescences of the latter. *Orthotylus tabidus* (Stål), a species of mirid commonly occurring on wattle, was also collected on *Acacia karroo* at the same locality in the Umlaas river valley, Camperdown.

Odhiambo (1960) records having collected a single *L. laevigatum* male on cotton at Serere Experimental Station in Uganda.

4.4.8 Overwintering

L. laevigatum has no true overwintering stage in the life-cycle, and breeding continues throughout the winter. Even under extreme conditions such as those experienced at Bloemendal, Pietermaritzburg during the mid-winter of 1967, when trees were in very poor condition, some breeding occurred (§ 6.2.2). Sampling in the second half of August yielded only a single male, but on 30th August nymphs were collected, obviously the progeny of females present in the field in early August (Fig. 34). Some of these reached the adult stage, and consequently five young females (determined by colour) were collected on 14th September 1967, during an extensive sweep of 100 trees. Many died of desiccation (§ 6.2.2). Under favourable tree conditions such as occurred during the winter of 1969 at Kirkfalls, During routine sampling in Block 18, Bloemendal (§ 6.2.2), specimens of L. laevigatum were occasionally collected throughout the winter and spring of 1967. On 4th October two mature females and a single male were collected, while on 12th October a single male was collected. Sampling was maintained for continuity and for determining the population of Batrachomorphus cedaranus which was present at the time.

In October 1967, adults and nymphs were collected from the flowers of mature wattle trees at block 21E, Bloemendal, some 150-200 metres from Block 18 (Fig. 36B). On 4th October 1967 adults and fourth- and fifth-instar nymphs were collected from these flowering trees. The adults were, judging by colour development, newly emerged, indicating that they had hatched from eggs laid about the first week of September. At this stage trees were covered with buds in the "yellow" stage, two to three weeks before flowering in the last week of September. Adjacent to these flowering trees, young wattle trees, 2 - 4 ft. high, planted as seedlings in paper sleeves in January 1967 were found to be harbouring some adults during October, possibly as a result of local movement from the flowering trees.

Too little is as yet known regarding the local movement and possible sustained flight of the species to offer valid comment on the possible origin of the adults found in the flowering trees in Block 21E. The presence of the species in small numbers within Block 18 was clearly established by sweeping, and it is probable that local movement was responsible, but the possibility of a longer range invasion by more sustained flight can not be ruled out, at least as a contributing factor, at this stage.

4.5

SUMMARY : BIOLOGY OF L. LAEVIGATUM

There is no definite overwintering stage, and the insects may continue to breed all year round provided conditions are favourable, although more slowly in the winter months. Eggs are laid in the tender terminals of young wattle trees, and the incubation period varies 6 to 8 days in summer, up to 14 days in winter. There are five nymphal instars, the overall nymph stage occupying from about 14 days in summer to a maximum of about 20 days in the field in early winter. Adult females have a preoviposition period of six to twelve days (mean 9.4 days) and females used in the investigation laid between 19 and 159 eggs with a mean of 74 eggs . Females live from 29 to 54 days (mean 41.5 days), while males are shorter lived. Sex ratio in the field favours males during active breeding, but as a population recedes, under unfavourable conditions, females become more abundant than males, presumably because of their longer life-span.

From the above it may be concluded that a single generation is completed in four to five weeks in summer and five to six weeks in winter. Several generations may therefore occur in a season.

CHAPTER 5

BIOLOGICAL STUDIES ON BATRACHOMORPHUS CEDARANUS

5.1

INTRODUCTION

Comments made in respect of the lack of suitable facilities for biological studies on *L. laevigatum* apply also in this instance. Studies on the two species were carried out simultaneously in the field, and the same temperature and humidity conditions existed (Appendices 3, 4, 5 and 6).

5.2

THE EGG STAGE

5.2.1 Oviposition sites

Under field conditions the site used most regularly for oviposition on wattle trees is the underside of the compound leaf rachis. The upper surface of the rachis is sometimes used, and on the underside of the leaf eggs may be found buried in the tissue of the petiole. Under crowded conditions on small potted trees some eggs may be embedded in the tissue of the branch at the base of the leaf, a condition which seldom occurs in the field.

Eggs are usually inserted in fully developed young leaves which are still lush and tender, although older, tougher leaves may also be used. Eggs are not laid in neat rows, but usually rather haphazardly as the female moves along the leaf rachis.

If undisturbed, a laying female may remain on a single even on the stem adjacent to the leaf. From a sparsely populated greenhouse (August 1967) a total of 633 eggs were collected, comprising 45 "batches", and giving an average of 14.1 eggs per batch. Of these 633 eggs, 59.2 per cent. were laid in the tissue of the underside of the leaf rachis, 16.1 per cent. on the upper surface, while 1.7 per cent. were laid in the rachillas of leaves and 4.9 per cent. in the tissue of the petiole. A further 18.0 per cent. were found embedded in the tissue of the stems adjacent to these leaves.

In the field eggs are found in smaller batches. For example, from 68 separate egg-batches observed in the field (December 1967), a total of 560 eggs were counted, giving an average of 8.2 eggs per leaf batch. Of these 72.9 per cent. were laid in the lower surfaces of the leaf rachides, 6.4 per cent. in their upper surfaces, while 18.4 per cent. of the eggs observed, were laid in the rachilla. Only 2.3 per cent. were laid in the leaf petiole, and no eggs were found laid in the plant stem adjacent to the leaves. The maximum number of eggs on a single leaf was 56.

In young tissues of newly opened leaves the ovipositor penetrates the xylem tissue of the rachis during oviposition, and the entire egg is buried within the tissue, almost at right angles to the surface of the rachis. Usually about half of the egg's length penetrates the xylem. In harder more mature tissues, especially when a stem is used for egg-laying, the ovipositor is unable to penetrate the xylem. The egg is then laid just beneath the surface between phloem and xylem in the region of the cambium.

Within the plant tissue the egg is completely surrounded by an outer coat of material probably secreted by the large female accessory gland during oviposition. This envelope is end of the egg is exposed to the air by splitting of the plant tissue, as usually occurs where a leaf rachilla is used for oviposition, the chorion, in the absence of the enveloping membrane, turns blackish. Each egg-slit has small threads of white substance over it, attached to the operculum, and these are possibly of the same substance which envelops the egg in the tissue (Fig. 31C).

5.2.2 Size and shape of the egg

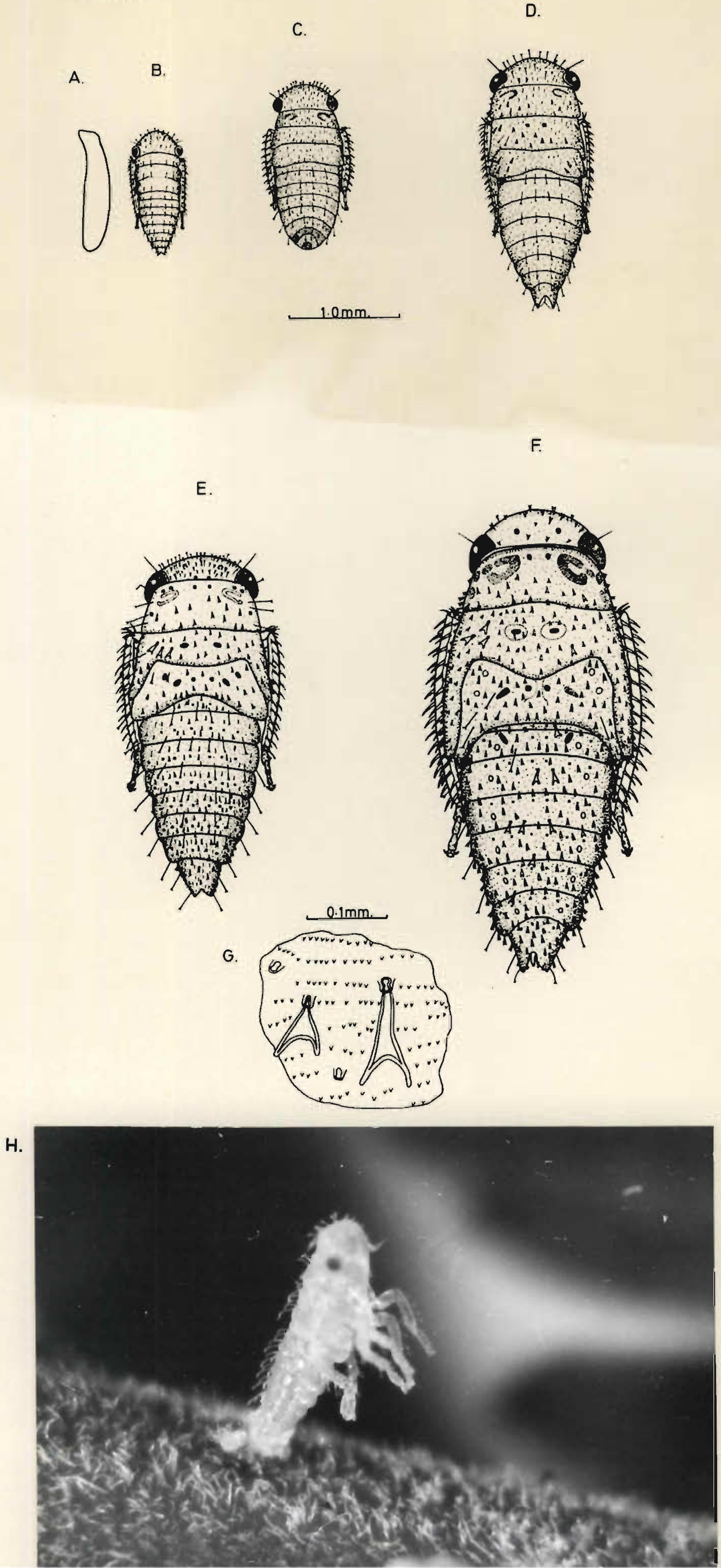
Table 8. *B. cedaranus*. Measurements of mature eggs from the ovaries. All measurements in mm.

	Length	Breadth	Anterior End Width
	1.08	0.27	0.21
	1.09	0.26	0.19
	1.11	0.30	0.19
	1.12	0.23	0.18
	1.07	0.27	0.18
	1.10	0.25	0.17
	1.08	0.25	0.20
	1.13	0.25	0.17
	1.17	0.28	0.19
	1.19	0.24	0.18
	1.09	0.25	0.19
	1.14	0.25	0.18
	1.12	0.27	0.19
	1.09	0.29	0.18
	1.10	0.25	0.21
	1.12	0.25	0.17
	1.09	0.26	0.21
	1.18	0.26	0.20
	1.12	0.25	0.21
	1.15	0.29	0.23
Means	1.117	0.261	0.1915

Table 8 gives measurements for 20 mature eggs dissected from females. These averaged 1.1 mm. in length with a mean

Fig. 33 Egg and nymphs of B. cedaranus. A, mature egg from the lateral oviduct of a laying female. B - F, first- to fifth-instar nymphs. G, detail cuticular hairs of a fifth-instar nymph. H, nymph hatching from an egg buried in the rachis of a wattle leaf.

FIG. 33



finely sculptured chorion rim found on the eggs of Miridae, and is smooth and white in colour. The chorion is translucent, so that the two red eye spots of the developing embryo within may be easily seen towards the anterior end of well-developed eggs dissected out of wattle leaves.

5.2.3 Egg stage duration and fertility

A considerable increase in numbers of B. cedaranus in the field at Bloemendal, Pietermaritzburg during the period September 1967 to January 1968 made it possible to conduct field studies. During November and December of that period the data shown in Table 9 on egg incubation period was collected. A mean incubation period of 18.4 days was obtained.

Table 9. Incubation period, in days, of eggs of B. cedaranus laid in wattle leaves during the period November December 1967.

Incubation period in days	15	16	17	18	19	20	21	22	23	24	25
Number of eggs in each class	5	14	46	22	44	13	5	3	4	4	1
Mean 18.4 days											

Data collected in the course of other experiments indicate that the incubation period is more than doubled during mid-winter. For example, 54 eggs laid by a female confined on a potted tree in an open nursery, from 1st to 15th June 1968 hatched between 22nd and 25th July, giving the minimum possible incubation period as 37 days.

Percentage egg hatch is fairly high and since the eggs are relatively easy to see and count (as compared with eggs of the mirid L. laevigatum), accurate figures are easily obtainable. During the incubation period studies of November and December 1967 an overall percentage hatch of 84 per cent. was achieved for 192 eggs.

5.3

THE NYMPHAL INSTARS

5.3.1 The first-instar nymph (Figs. 33B and H)

Immediately after hatching, mean body length is 0.94 mm. with a mean head width of 0.45 mm. (Appendix 2). After the first meal, mean body length increases to 1.16 mm. The nymph is pale yellowish or greenish and covered by rows of whitish hairs about 0.1 mm. long and with slightly split, y-shaped tips. There are eight rows of these erect hairs running down the length of the body from vertex to abdomen tip (Fig. 33B), one each on the lateral edge of the body (not visible in Fig. 33B) while the other six rows are dorsally situated, and arranged in pairs. There are four rows of hairs on each tibia. Each hair arises from a dark-brown pit, giving a spotted appearance. The underside of the abdomen is bare. Eyes are reddish internally, with a white cuticle. Some first-instar nymphs have a feint brownish band on each side of the thorax, running longitudinally.

5.3.2 The second-instar nymph

Second-instar nymphs average 1.56 mm. in length, and 0.61 mm. in head width (Appendix 2). Colour is predominantly greenish, with the prothoracic colour pattern of the adult already clearly visible. The eight rows of long, erect y-shaped hairs are interspaced by smaller more numerous y-shaped hairs of the type shown in Fig. 33G. These smaller hairs are randomly scattered over the entire dorsum and on the sterna of the abdomen. Well-developed strong spines replace the four rows of hairs on the hind tibiae, but interspersed with long hairs. Wing buds are discernible at this stage.

5.3.3 The third- and fourth-instar nymphs

In the third-instar nymph, mean length averages 2.05 mm., mean head width 0.81 mm. The underside of the body is still greenish, but dorsally colour may vary from light green or yellowish to light brown or light reddish-brown. The smaller y-shaped hairs are more numerous than in the second-instar. Eye colour is pale pinkish to red.

Mean length of the fourth-instar nymph is 2.89 mm., mean headwidth 1.06 mm. Overall colour is similar to that of the third-instar, with the tip of the abdomen brown. The mesothoracic wing-bud now extends posteriorly covering about half the length of the metathoracic wing-bud (Fig. 33E). Fourth-instar nymphs are even more profusely covered by the smaller variety of hairs than third-instar nymphs. Some of the long hairs of the fore and mid tibiae are replaced by thin hair-like spines.

5.3.4 The final (fifth) nymphal instar

This instar averaged 4.54 mm. in length and 1.36 mm. in head width for 20 specimens examined (Appendix 2). Colour is similar to that of the third-instar nymph, the usual colour above being greenish with brownish or reddish-brown tinges on eyes, posterior margins of thoracic terga, wing buds, the proximal third (or whole) of the meso- and metathoracic tibiae and ninth abdominal segment. There are also several brownish spots on the abdominal terga, and the last abdominal sternum is often very dark, especially in female nymphs. There are fewer of the smaller setae than in fourth-instar nymphs although the dorsum is often still well covered with them. Also many of the longer setae are absent giving the appearance of a more random distribution as opposed to the rows of these setae found in the thorax. Most of the shorter oblique-lying hairs are white as in other instars, but a few are dark-brown, especially on the meso- and metathorax. The prothoracic pattern of the adult is discernible as watery green patches of cuticle free of epidermal hairs.

The mesothoracic wing buds extend posteriorly to the tip of the metathoracic wing buds in this instar.

5.3.5 Duration of the nymphal instars

Data on the duration of the nymphal instars of individuals caged on trees at Bloemendal during the period November 1967 to January 1968 are given in Table 10. Cages were placed over terminals to include a single large young mature leaf on which nymphs were placed. Not more than five nymphs were isolated in each cage. The study was made easier by the fact that in the cages nymphs were relatively inactive, and were easily observed passing through their five developmental instars. Despite the fact that as many as five nymphs were reared to the adult instar on a single leaf, little observable damage was caused to the leaf. An extreme fifth-instar of 16 days duration, resulting in a total nymph period of 36 days for a single female, was omitted from the table. Temperatures and humidities in the field during the studies are recorded in Appendices 3, 4 and 6.

Table 10. Instar duration (in days) of B. cedaranus under field conditions Bloemendal, Pietermaritzburg November 1967 - January 1968.

	1st	2nd	3rd	4th	5th	Total
Number of readings	32	32	29	29	29	29
Maximum duration	8	8	7	9	11	34
Minimum duration	3	2	2	4	5	24
Mean duration	5.2	5.2	4.7	5.6	7.9	28.3

Data were also collected from nymphs on potted plants in obtained were comparable with those from field observations.

During December 1967 tests were conducted in a room maintained at a constant temperature of 26.7°C (80°F) and a relative humidity of 76 ± 2 per cent. Nymphs were reared in lamp glasses on foliage standing in water and changed every second day. Mortality of the 34 first-instar nymphs was as high as 59 per cent., while a further 12 per cent. died without becoming adults. A fault in the temperature regulation system caused the premature termination of the experiment. The four specimens successfully reared by then showed normal nymphal instar periods as compared with table 10. Three were males, with overall nymph stage durations of 27, 27 and 25 days, while the only female reared, took 30 days to pass through the nymphal instars. The high mortality recorded in first-instar nymphs seems to indicate that the temperature was too extreme in this test. The field-tests resulted in a first-instar mortality of only 8.6 per cent. (n = 35). However, overall nymph stage durations were comparable with those obtained in the field at Bloemendal during November and December 1967 (26.6 days for males, 29.5 days for females). It is therefore possible that optimum conditions for development lie somewhere between those in the field during the trial period (Appendices 3, 4 and 6) and those of the controlled room.

Data presented in Table 10 give a mean overall nymph-stage duration of 28.3 days. In other experiments further data was collected for a total of 96 individuals, which averaged 30.1 days. Separation of data on males and females reveals a slightly shorter male nymph-stage duration of 28.7 days (n = 27) compared with 30.0 days for females. However, statistical analysis of the data showed the difference of 1.3 days to be nonsignificant, Some nymph-stage duration data were collected from May to August 1967. During the period a total of 40 nymphs reared to adults in cages on young trees in the field at Bloemendal required an average of 54.9 days to complete their nymph instars.

5.3.6 Distribution of nymphs on the tree

After hatching, first-instar nymphs settle on the leaf rachis, usually up against the base of a rachilla, or on a rachilla itself. Except under crowded conditions very few leave the leaf on which they hatched, and nymphs will often develop right through to the adult stage on a single leaf. More mature nymphs are usually found on the leaf rachis, and also often on young tender shoots. The nymphs are inactive, usually moving only when disturbed, and they quickly re-settle. Often when disturbed nymphs will shake the abdomen rapidly from side to side, without moving position.

5.4

THE ADULT STAGE

5.4.1 Preoviposition period

The preoviposition period of females exposed to males for seven days from the time the females emerged as adults was usually seven days, and the mean for 15 individuals studied in lamp-glasses in the laboratory during October 1967 to January 1968 was 7.6 days (Table 11).

Table 11. Preoviposition period, fecundity and longevity in days of B. cedaranus females each caged with a male for seven days.

	Preoviposition Period	Eggs laid Per Female	Longevity
Number of readings	15	15	15
Maximum	9	152	80
Minimum	7	48	27
Mean	7.6	90.5	47.3

In order to eliminate the possible delaying effect of newly-emerged males, only males seven days old were used. A further 20 females in a second experiment, yielded a preoviposition period of 7.5 days (Table 12).

Table 12. Preoviposition period, fecundity and longevity in days, of B. cedaranus females each caged with a male throughout the experiment.

	Preoviposition Period	Eggs laid Per Female	Longevity
Number of readings	20	20	20
Maximum	9	161	68
Minimum	7	27	29
Mean	7.5	95.8	47.0

Most unmated females laid eggs, but the preoviposition period was greatly extended. Thus for 16 unmated females which laid eggs, the preoviposition period averaged 21.8 days with a minimum of ten days and a maximum of 52 days.

5.4.2 Female fecundity and adult longevity

Two studies were conducted in an investigation of female fecundity. In the first experiment, each female was paired with a single seven-day old male as soon as she reached the adult stage. Males were removed after seven days. New foliage was provided every second day and eggs were counted after each foliage change. In the second experiment a male was present conducted simultaneously in ten-inch high lamp-glass cages in the laboratory from November 1967 to January 1968. The results are recorded in Tables 11 and 12. No significant difference was recorded between numbers of eggs laid by the females in the two different experiments. The first experiment, however, did not exclude the possibility of multiple matings during the week in which males and females were confined together, and data were not obtained in respect of the number of matings.

Virgin females usually laid a few eggs, and the maximum life span was recorded for two specimens which each lived for 92 days, during which time they laid 17 and 27 eggs respectively. Of 18 caged unmated females, however, eleven died within three to five weeks.

Males have a much shorter life span, averaging 21.1 days for 21 males, with a maximum of 46 days.

5.4.3 Sex-ratio in the field

During population studies conducted at Bloemendal in 1967 and 1968, B. cedaranus was scarce. During routine sampling 557 males and 617 females were collected, of which 47.4 per cent. were males. However sub-totals of this data were so varied and often so low that a statistical analysis of the data was not possible. An interesting feature was the difference noted when comparing the sex ratio of high and low field population numbers. During regular sweeps on young trees at Bloemendal during 1967 and 1968 it was found that during most of the observation period, B. cedaranus was scarce, averaging only 4.5 insects per sample of 25 trees swept, and only 36.3 per cent. of the total of 366 specimens collected were males. During the period September 1967 to January 1968 when B. cedaranus was relatively abundant, with an average of 38.5

809 specimens collected were males. The scarcity of males in populations of low density is probably explained by their shorter adult life (§ 5.4.2).

5.4.4 Alternate host data

The low field populations of *B. cedaranus* which have prevailed during this study reduced the possibility of alternate hosts being found in the field, and laboratory studies on this aspect were not conducted. Although different species of weeds and other plants in and around wattle plantations were swept in search mainly for alternate hosts of the mirid *L. laevigatum*, *B. cedaranus* was never collected on any plant other than wattle. Several surveys of wild Acacias never revealed the presence of *B. cedaranus*, except for a single nymph collected amongst the inflorescences of an *Acacia caffra* in the Umlaas river valley, Camperdown, during December 1968.

5.4.5 Overwintering

The species continues breeding throughout the year and therefore has no true overwintering instar. They may be found throughout the winter in all instars of the life-cycle. Being hardier and less dependent on the succulence of the host tree for feeding and breeding, *B. cedaranus* is able to invade more mature trees. Examples were observed during July 1967 on the farm Groenekop in the Seven Oaks district where nymphs and adults were found on tiny shoots sprouting from the trunks of mature trees, as well as in the crowns of trees felled. Similar observations were made on 19th July 1967 on the farm Newlands near New Hanover, Natal, and while examining the crowns of trees during felling operations on Newlands in October 1967.

5.5

SUMMARY : BIOLOGY OF B. CEDARANUS

Eggs are usually laid in the tissue on the underside of the wattle leaf rachis. Often only a scar, made by the ovipositor, indicates the presence of an egg. Eggs hatch in about 18 days in summer under local field conditions (Pietermaritzburg) but this period is more than doubled in winter. The five nymphal instars are completed in an average of about 28 days in summer, extending to an average of almost 55 days in winter (May to August). The preoviposition period varies from seven to nine days, with an average of 7.5 days. In two separate experiments females laid an overall average of 93 eggs. Females lived for from 27 to 80 days, averaging about 47 days in both tests. Males were found to live for a shorter period, averaging 21 days. Sex ratio in the field was approximately 1 : 1 in an actively breeding population, although favouring females at times of very low field population numbers.

It may be concluded that the cicadellid _B. cedaranus_ has a life-cycle of about eight weeks in summer, and fourteen weeks in winter. This is much more extended than the four to five week life-cycle of the mirid _L. laevigatum_ during summer.

CHAPTER 6

POPULATION STUDIES

6.1

GEOGRAPHICAL DISTRIBUTION

The mirid *L. laevigatum* occurs in all the wattle-growing areas of Natal, the north-eastern Transkei and the Piet Retief area of the eastern Transvaal. Further afield the species is common on wattle throughout the Uasin Gishu and Central Province of Kenya where it causes damage to young trees (Sherry 1968; Elmar and Smith 1956). The species has been recorded in Tanzania (Odhiambo 1960), on wattles in Swaziland (Sherry 1968) and Odhiambo (1960) records two male specimens collected at Kawanda and Serere Experimental Station respectively, in Uganda.

The cicadellid *B. cedaranus* has a similar range in the wattle-growing areas of the northeast Transkei, Natal and eastern Transvaal, Swaziland, Kenya and Tanzania. The author has a sample collected on wattle on 31st March 1967 in the Eldoret area of Kenya, comprising 106 adult specimens of *B. cedaranus*, eight specimens of *B. segregatus* Naudé, ten specimens of *Coloborrhis corticina* Germ. and a few *Distantia* sp. Two isolated records of specimens collected in South Africa show that the range of *B. cedaranus* extends well out of the wattle areas. These records are of a specimen from Silverstrand, Cape eight miles west of Kleinmond collected on 19th December 1950, and another collected 10 - 15 miles south-east of Lydenburg, Transvaal on 7th May 1951 (Linnavuori 1961).

6.2

SEASONAL POPULATION FLUCTUATIONS

During the course of this study, several populations on farms within reasonable access to the Wattle Research Institute were kept under observation. By far the most detailed study was conducted in Block 18 of the Bloemendal Field Experimental Station, Pietermaritzburg during 1967 and early 1968, and in Block 20a from February to July 1968 (Fig. 36B). After this date neither species was present in the field in numbers sufficient for a population study.

6.2.1 Sampling Technique

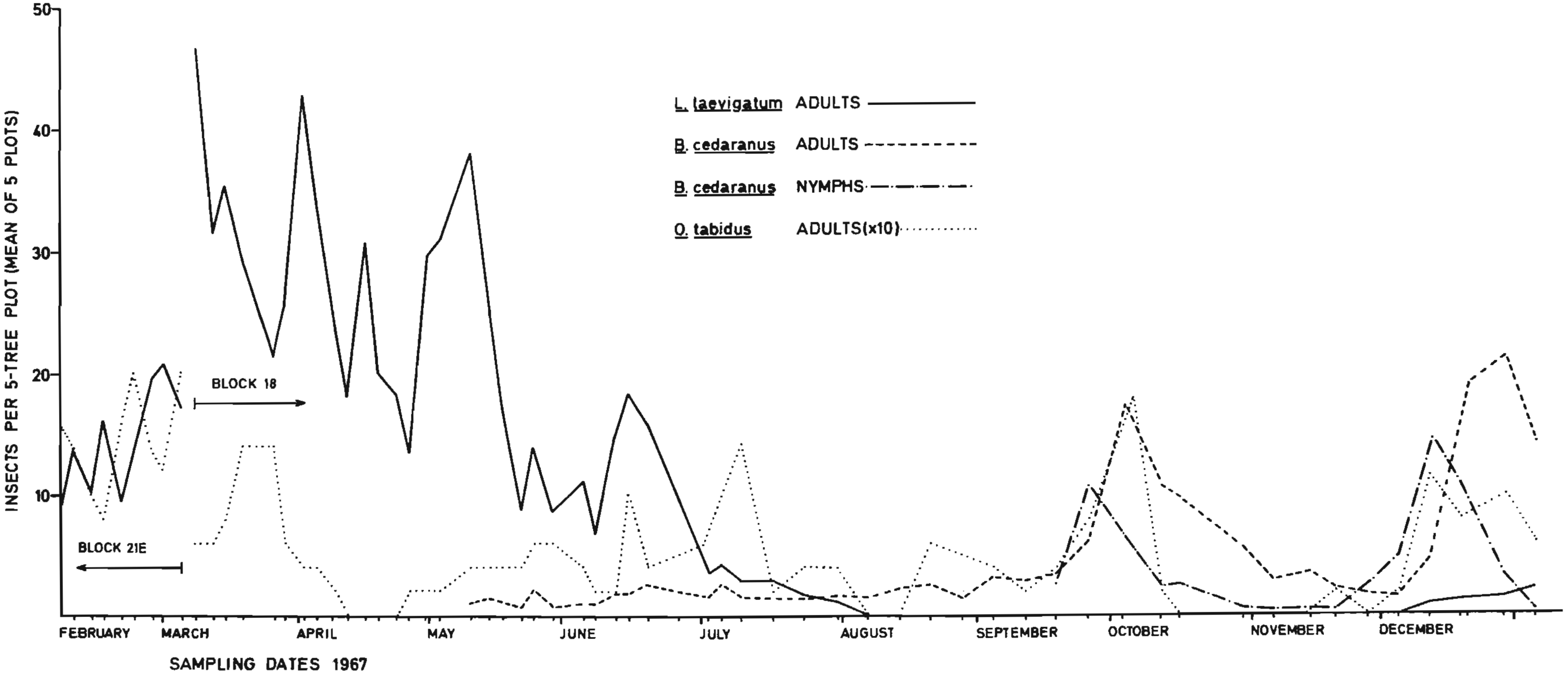
In an attempt to achieve some sort of standardisation in samples collected, sample plots, each consisting of five trees were selected at random. Each tree was swept on all sides with a hand-net of 18 inch diameter head. Five plots were sampled on each occasion, so that in all 25 trees were sampled. Insects from each plot were placed separately in containers for later identification and counting in the laboratory.

To obviate sampling of a single tree on two consecutive sampling days, groups of trees were used in rotation. Sampling technique had also to be modified to avoid the bias resulting from sampling trees of different heights. Only trees of from five to seven feet in height were sampled, and sampling areas were changed as soon as trees had outgrown this upper limit.

During 1967, *L. laevigatum* was abundant and two samples were collected, usually on Monday and Thursday, of each week, depending upon weather conditions.

Data on population numbers was confined to adults. This may not have been completely satisfactory, but in the early

FIG. 34



50
40
30
20
10
INSECTS PER 5-TREE PLOT (MEAN OF 5 PLOTS)
L. laevigatum ADULTS
B. cedaranus ADULTS
B. cedaranus NYMPHS
O. tabidus ADULTS(x10)
BLOCK 18
BLOCK 21E
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
SAMPLING DATES 1967

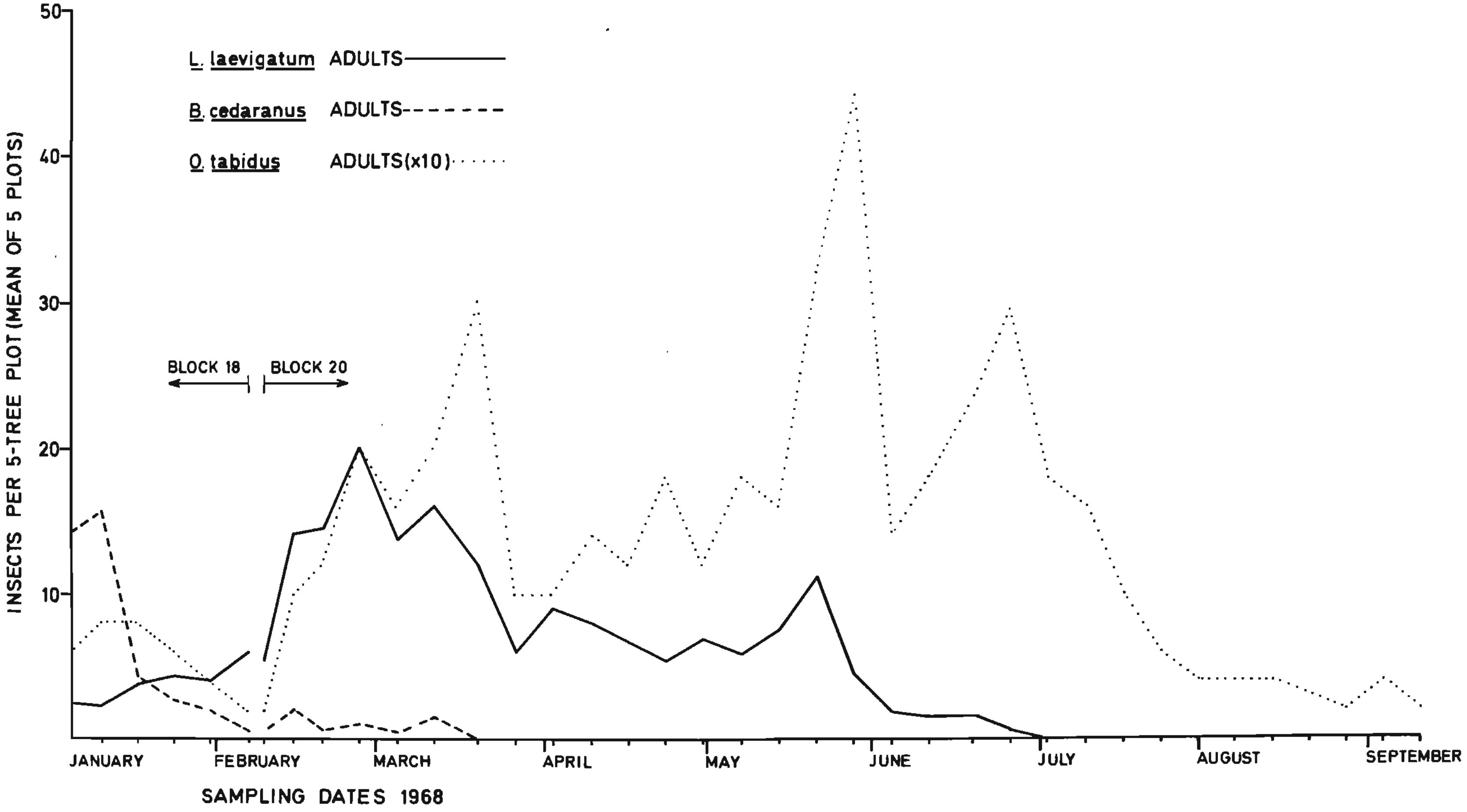
the nymphs of the different species of mirids, while the younger instars of both L. laevigatum and B. cedaranus are difficult to collect and count.

6.2.2 Seasonal fluctuations observed at Bloemendal, Pietermaritzburg, during 1967 and 1968.

The mirid L. laevigatum was abundant at Bloemendal during the summer of 1967. Abundant rains during early and mid-summer (Appendix 9) resulted in the young two to four-foot high trees of Block 18 being in lush condition suitable for rapid colonisation and population increase. Mirid numbers remained high throughout the summer (Fig. 34), becoming depressed as the trees lost condition due to mirid feeding damage and reduced soil moisture. By the first week of August 1967 standard sampling techniques were yielding no specimens of L. laevigatum. During the latter part of 1967, in the absence of L. laevigatum, the cicadellid B. cedaranus increased in numbers to a peak in the first week in October and another in early to mid-December. Each peak represents a generation emerging to the adult stage, evidenced by the large number of nymphs of B. cedaranus which were collected just prior to each of these peaks (Fig. 34). The reduced adult population after each peak is possibly due to migration out of the sample area.

In January 1968 the only area of Block 18C, suitable for population studies was used for an insecticide trial, and population studies were switched to Block 20a, approximately 200 metres SSW of Block 18, where an almost identical population was to be found. During February and March 1968 this plantation showed a moderate increase in numbers of L. laevigatum (Fig. 35) while numbers of B. cedaranus were low (less than two adults per sample of five trees).

FIG. 35



L. laevigatum ADULTS
B. cedaranus ADULTS
O. tabidus ADULTS(x10)
BLOCK 18
BLOCK 20
INSECTS PER 5-TREE PLOT (MEAN OF 5 PLOTS)
50
40
30
20
10
JANUARY
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
SAMPLING DATES 1968

such that, despite the presence of young trees in Block 19, which lies between the two previously infested areas of Blocks 18 and 20, no specimens of L. laevigatum were collected by periodic sampling. B. cedaranus was also so seldom collected that regular sampling was abandoned. The young trees were observed to be showing symptoms of lack of water throughout the mid-summer season and in view of the noted requirement of succulent tree condition for breeding of L. laevigatum (§ 4.4.3), it is apparent that this resulted in the absence of the species. Too little is known of the factors which affect populations of B. cedaranus to offer any explanation as to why this species did not increase in numbers during the same period. Since commencing this study in January 1967 the only increase in numbers of B. cedaranus encountered was that which occurred at Bloemendal in the early summer of 1967 (Fig. 34). However, population density was still relatively low.

6.2.3 Observations of various populations of L. laevigatum

In 1967 heavy infestations were reported from a number of farms throughout the wattle growing areas of Natal. At the farm Harden Heights in the Seven Oaks area a heavy outbreak was first inspected on 2nd March 1967. Trees were a year old and there was evidence that the insects had been present for several months. Sampling revealed an average of 48 adults per sample of five trees i.e. 9.6 adults per tree. Trees were very badly damaged, with very few pinnules and much branching (§ 7.4.2). A sample collected two weeks later on 15th March revealed far fewer L. laevigatum, except on the occasional tree still bearing green foliage. Most trees were so badly damaged that the mirids were apparently unable to feed and breed on them. A sample taken on 4th April contained an average of eight adults rainfall in this area fell in a pattern similar to that for Bloemendal. Precipitation was heavy in January and March, inducing the young trees to flush vigorously and thus producing conditions particularly suitable for the mirid to breed.

In 1968 the same plantation was sampled on 29th February. Although L. laevigatum was present, the infestation was lighter than the previous year, averaging 26 adults per five-tree sample. Trees were generally in poor condition, which together with a high degree of parasitism of nymphs by Euphorine wasps (§ 8.2.2.2), estimated at 68 per cent. by dissection, probably caused the drop in population numbers observed in a subsequent sample collected on 21st March. An average of only three adults per five-tree plot was collected.

In the summer of 1969 at Harden Heights a plantation of young two to five feet high wattles close to the previous plantation was observed. In mid-February sampling and close observation failed to reveal the presence of either L. laevigatum or B. cedaranus. On 15th April, close observation revealed characteristic pinnule damage, the early sign of the presence of L. laevigatum, in the south-west corner of the plantation. A few females were also observed, revealing a low population, which appeared to have moved from an adjacent plantation of ten to twelve feet wattles into the younger trees. On 23rd May more signs of damage were evident, the trees being four to eight feet high. Sampling yielded an average of only three adults per five-tree plot, but an average of nine fourth- and fifth-instar nymphs per plot, showed the insects to be actively breeding. However, on 17th July few L. laevigatum were found and most trees were free of them.

A similar 1969 population pattern was observed in a but numbers of L. laevigatum were slightly higher (11 adults per five-tree plot) and some light damage to trees was observed. By 17th July when this plantation was last visited, very few specimens were found, the population being too low to assess on adults or nymphs per five-tree sample plot.

A population of L. laevigatum was studied in a 90 acre plantation of young wattles on the farm Kirkfalls at Hillcrest, Natal, during 1969. Rainfall data are given in Appendix 11. The plantation (Fig. 36A) was joined on its southern border, by a six-acre stand of trees approximately a year older than those of the main plantation, and standing six to eight feet tall. An inspection in November 1968 failed to reveal the presence of the mirid, but on 6th February 1969, both adults and nymphs were found in the six-acre plot and adjoining younger two to three feet high trees. The population in the younger trees was obviously a result of local movement, some of the adjacent older trees showing slight signs of damage to terminals. A sweep of the young trees showed an average of five adults and five nymphs (fourth- and fifth-instar) per five-tree plot. On 6th March 1969 a sample in the same section of the plantation (Station C Fig. 36A) yielded an estimated population of 23 adults per five-tree plot. At this stage it was apparent that the mirids were confined to the southern corner of the plantation where the trees were actively growing, watered by a small stream. The extremely dry January experienced on the farm appeared to have affected most of the plantation to the extent that the young trees had a spindly upright growth form and no lush foliage. Good rains in the second half of February (77.7 mm.) and throughout March led to rapid appearance of succulent new growth on the young trees resulting in a rapid spread of mirids

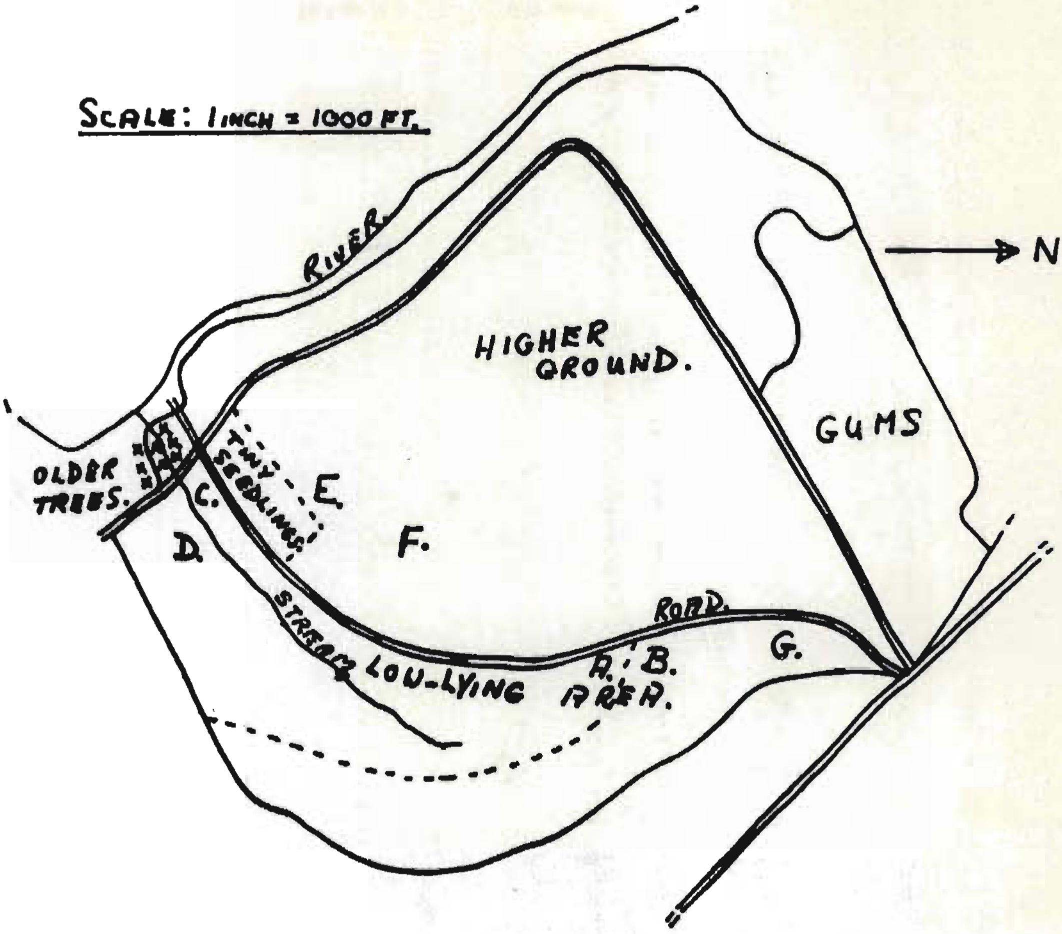


Fig. 36A Sampling stations in Block 3 Kirkfalls, Hillcrest, during population studies.

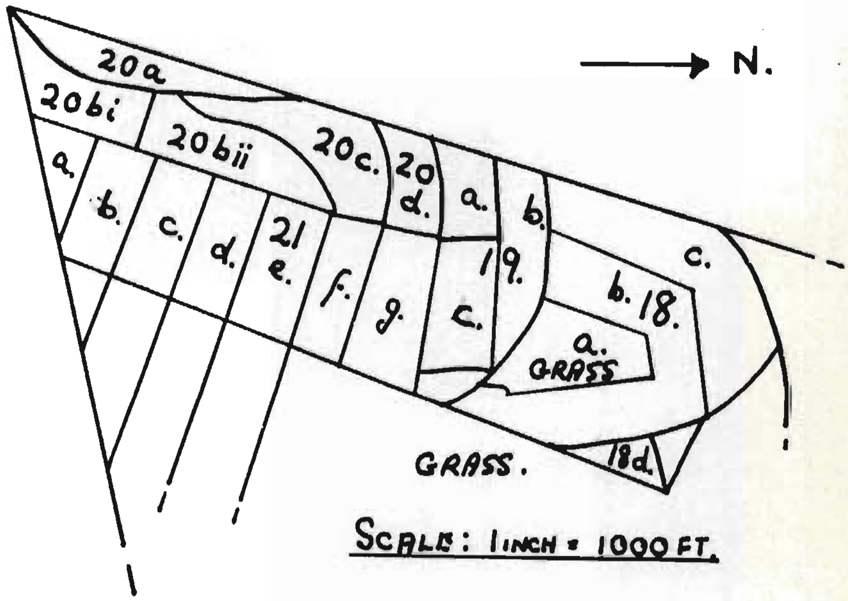


Fig. 36B Blocks used in population studies at Bloemendal experimental station Pietermaritzburg during 1967 and 1968.

conducted on 19th June at stations A, B, C, D, E and F (Fig. 36A).

Table 13. Sample counts of adults and nymphs of L. laevigatum collected at several sample stations. Kirkfalls, Hillcrest 19th June, 1969.

Sample station	No. of insects per five-tree plot Adults	Nymphs
A	34	26
B	28	22
C	70	30
D	37	43
E	50	85
F	54	86
Mean	45.5	48.7

On 14th August 1969 a similar sample survey was made, but samples were only collected from stations A, C and G (Fig. 36A).

Table 14. Sample counts of adults and nymphs of L. laevigatum collected at three sample stations. Kirkfalls, Hillcrest 14th August, 1969.

Sample station	No. of insects per five-tree plot Adults	Nymphs
C	4	2
C	3	0
A	16	5
A	21	8
G	24	11
G	15	5

On this occasion it was observed that the trees at station C were so badly damaged that despite favourable soil moisture most trees had no flush of green foliage. In view of the mirids need of tender succulent foliage for feeding and breeding (§ 4.4.3), the recorded drop in numbers at station C is not surprising, while the overall drop in numbers might also be

18th and 19th September revealed that trees in the low-lying more moist areas of the plantation were supporting a fairly high, actively breeding population of mirids, and at station A, three samples of five trees along timber piles (see § 6.3) yielded an average of 40 adults and ten nymphs per five-tree sample. In view of this extremely high local population within the plantation, together with a lower density at stations C and G (eight adults per five-tree sample) at the start of a new growing season, it was decided that this plantation should be sprayed. Aerial spraying with Dimethoate was carried out on 23rd September, and during sampling at stations A, B, C and D on 25th September no specimens of <u>L. laevigatum</u> were collected.

6.3

<u>RAINFALL AND POPULATIONS OF L. LAEVIGATUM</u>

Throughout this study it has been noted that populations of <u>L. laevigatum</u> increase after good rains. Studies of histograms, however, have not always revealed the pattern of rainfall required to make conditions favourable for an outbreak of mirids in a plantation. For example (Appendix 10) in the summer of 1968, despite a poor rainfall, mirids were present in a plantation of young trees on the farm Harden Heights (§ 6.2.3). However, it is reasonable to suppose that this was due to the presence of the mirids in the plantation the season before, the survivors creating a nucleus for re-infestation in 1968. On the farms Honey Grove (Harburg) and Harden Heights low numbers of the mirid (See § 6.2.3) were found in plantations in mid-April, 1969 following a dry January and a very much wetter late February and March (Appendix 11) Similar rainfall and a of four to six feet high trees on the farm Windy Hill in the Wartburg district. Populations were low due to the late appearance of favourable conditions.

The effective rainfall required to bring about a flush in young wattles will naturally vary according to a number of physical factors such as soil type and topography, while the period during which the trees are suitable as hosts to the mirid will depend on similar variable factors, together with the degree of habitat destruction caused by the mirids feeding on the trees. The common silvicultural practice of leaving brushpiles in plantations conserves moisture and trees planted in the rows next to these brushpiles are better watered and more succulent during dry periods than trees in adjacent rows. Such was the case in the plantation studied at Kirkfalls, Hillcrest, during 1969 (§ 6.2.3) where many tons of timber was left lying in rows in the plantation. Trees next to these rows of timber were noticeably more succulent, and contained a high mirid population, as shown by samples collected on 19th September (§ 6.2.3). Another factor would seem to have been the mild winter experienced on the farm, which resulted in continuous growth of the trees supporting a population of mirids until 23rd September when the insects were removed by chemical spraying.

6.4

OTHER SPECIES FOUND IN PLANTATIONS OF YOUNG WATTLES

6.4.1 Miridae

By far the most common mirid encountered in wattles, apart from L. laevigatum, was Orthotylus tabidus (Stål) with an average of slightly less than one adult per five-tree sample during the population studies at Bloemendal in 1967 and 1968 (§ 6.2.2). Three species of *Lygus* complex were also found in wattle plantations. *Taylorilygus simonyi* (Reut.), is almost identical in size to *L. laevigatum*. Although fairly frequently found on the wattles themselves, the species was more commonly collected on weeds, especially *Phytolacca octandra* (Inkberry). *T. simonyi* has a widespread distribution, the type specimens having been collected in Aden, while Taylor (1947) recorded the species from Uganda in East Africa, and Grahamstown and Durban, South Africa. The southern race, including the specimens collected on wattle during this study, differ from the type of *simonyi* and from Ugandan specimens, in having darker markings dorsally, but agree well in other respects, notably in the details of male genitalia (Taylor 1947). He records a number of plants known to be breeding hosts, particularly of the families Amarantaceae and Chenopodiaceae. *Taylorilygus pallidulus* Blanch, a cosmopolitan species (Kelton 1955), was recorded from Uganda by Taylor (1947) as *T. apicalis* Fieber, but later [Carvalho 1959 Arq. Mus. Nac. 48(4) : 265] *apicalis* was listed as a junior synonym of *pallidulus* (Fennah 1969). It is common on composites found in young wattle plantations, and is frequently encountered in samples from wattles although it is doubtful that the species breeds on wattle. Another species occasionally collected on wattle was simply identified as *Lygus* sp. by M.S.K. Ghauri of the British Museum (Natural History).

Three small species of mirid are commonly encountered, and the presence of nymphs indicate that they breed on wattle. All are approximately 2 mm. in length, and have been identified

Campylomma citrinella Odh. and *Campylomma subflava* Odh. The latter two have both been recorded from Uganda by Odhiambo (1959).

Other species of Miridae occasionally collected in sweeps include *Nesidiocoris tenuis* Reut., *Stenotus nigroquadstriatus* Kirk.(common on several grasses), *Lygus* sp. (also found on grasses); *Creontiades pallidus* (a third elongate grass species) *Deraeocoris ostentans* Stål, *Sthenarus leucochilus* Reut., and *Psallus* sp.

From the population studies made at Bloemendal there is some evidence of populations of *Orthotylus tabidus* (Stål) being influenced by the presence of *L. laevigatum*. However, this appears to occur only when numbers of *L. laevigatum* are so high, that severe damage to the trees results, and it is therefore probably caused by destruction of habitat, rather than competition for various habitat requirements. Thus, during February and March 1967 a steady population of one adult per five-tree plot of *O. tabidus* was present, but numbers were reduced to nil during mid-April (Fig. 34) when the *L. laevigatum* population was high, and trees were being severely damaged. *O. tabidus* appears to be slightly more tolerant of dry conditions, and remained in the field in low numbers through August and September when no *L. laevigatum* were being collected in samples (Fig. 34). During 1968 both species again occurred in the field together (Fig. 35) and in the absence of severe tree damage, *O. tabidus* attained a population higher than that of the previous summer. There appears to be no question of any mirid species competing in any way with *L. laevigatum* in the field, while populations of cicadellids have been too low to study in any detail. It is, however, of interest to note that

Bloemendal in the absence of *L. laevigatum* (Fig. 34).

6.4.2 Cicadellidae

Although no accurate data has been kept concerning their number, by far the most commonly encountered cicadellids in wattle are a small green *Empoasca* sp. and a similarly sized Gen. nr. *Hymetta* sp. (Cicadellinae : Erythroneurini). The former, although commonly present in fairly high populations in young wattles, appears to cause no damage to the tree, being confined to mature leaves of lower branches. The latter species, slightly smaller than *Empoasca* sp., is found feeding and breeding principally on dark mature leaves of lower branches. Their presence is indicated by whitish, almost thriplike, markings on the surface of pinnules, presumably caused during feeding. Their presence, however, does not appear to cause any leaflet shedding or poisoning of the tree.

Most common of the larger species is one identified as Gen. nr. *Allygus* sp. by M.S.K. Ghauri of the British Museum (Natural History). This species was encountered almost as commonly as *B. cedaranus*. Other species (identified by M.S.K. Ghauri) from wattle include *Penthimia vinula* Stål. and *Thaumatopoides* sp., *Jassus* sp., *Macropsis capensis* Cogan *Aletta fuscovaria* (Stål.) and *Erythroneura* sp. A sample of cicadellids collected on wattles at Eldoret, Kenya on 31st March 1967, consisted mainly of *B. cedaranus* but contained several specimens each of *Batrachomorphus segregatus* (Naudé) and *Coloborrhis corticina* Germ.

PART III

THE ECONOMIC IMPORTANCE AND CONTROL

CHAPTER 7

THE RELATIVE IMPORTANCE OF B. CEDARANUS AND L. LAEVIGATUM AS PESTS OF YOUNG WATTLE TREES

7.1

FEEDING LOCALITIES ON THE PLANT

Both species, being phytophagous Hemiptera, feed by piercing the tissue of the host plant. Adults and nymphs of *B. cedaranus* feed by piercing the tissue of a leaf rachis, rachilla, young shoot or the unspread pinnules of a young leaf. Nymphs and adults of *L. laevigatum* on the other hand feed on the pinnules of young mature or developing leaves, the tissues of tiny developing leaves and the meristematic tissue of terminal buds.

7.2

STYLET PENETRATION AND CELL DAMAGE

7.2.1 *B. cedaranus*

Due to the relatively settled feeding behaviour of this cicadellid, little trouble was experienced in obtaining specimens with their mouthparts in the tissue for detailed examination. However, any disturbance causes them to withdraw the mouthparts so attempts at dropping leaves containing feeding insects into hot and cold fixatives, and hot water (with wetting agent) met with little success. Dropping hot wax onto feeding insects was also not very successful and it was found that the best method was carefully to approach the feeding insect and

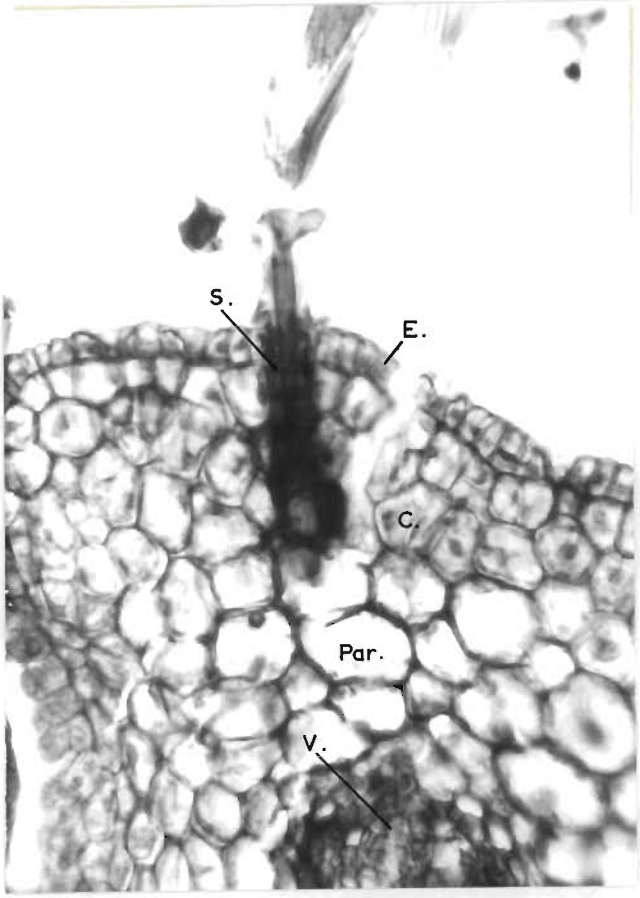


Fig. 37A Transverse section of a wattle leaf rachilla showing the mouthparts of a first-instar B. cedaranus nymph in chlorenchyma (C.) and parenchyma (Par.) cells. E., epidermis; S., salivary sheath; V., vascular tissue.

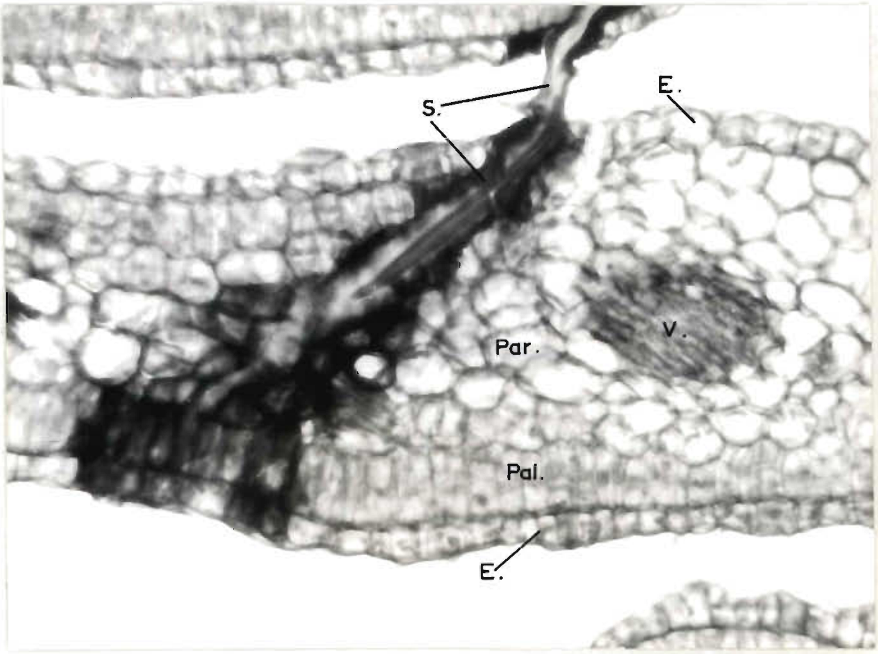
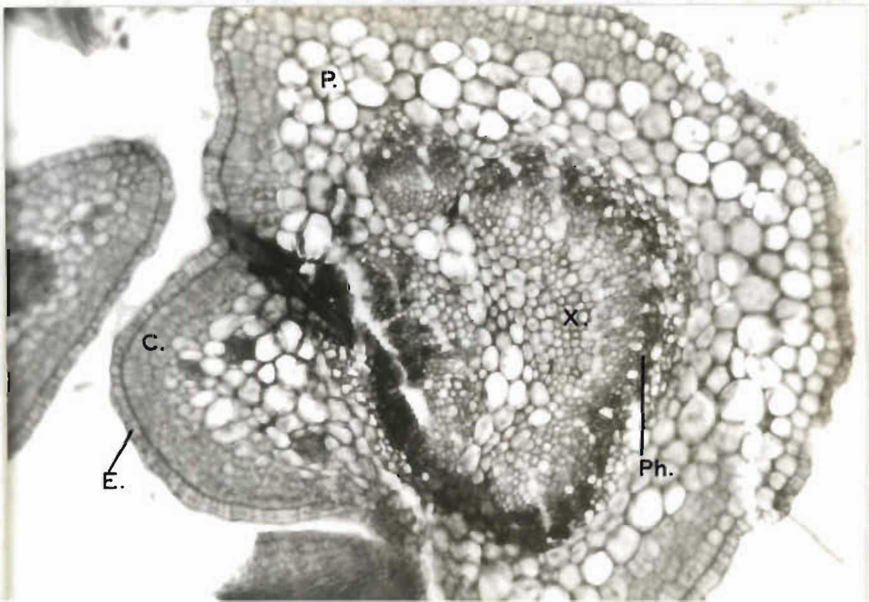


Fig. 37B Longitudinal section of a pinnule of a young developing wattle leaf, showing the stylet paths made by the mouthparts of a fourth-instar B. cedaranus being gently but firmly held, and then carefully placing it together with the leaf or shoot on which it was feeding, in Carnoy's fluid. After fixing, the plant tissue was trimmed and with the insect still in position embedded in paraffin wax. Sections were cut at 15 - 20 μ and stained in Jackson's Crystal Violet (Conn 1953).

Studying the cicadellid Eupteryx melissae Curtis, Pollard (1968) investigated stylet penetration. He found that the mandibular stylets were used for piercing the epidermis, and the maxillary stylets, being longer and more pliable, then easily penetrated palisade and parenchyma tissue without the support of the mandibular stylets. This was also found to be partly the case with B. cedaranus but the mandibular stylets usually penetrated half or more of the distance of the maxillaries. Feeding usually occurs in the parenchyma cells, (Fig. 37A) with a dark-staining sheath surrounding the stylets. Feeding on folded young pinnules often results in most of the leaf depth being penetrated (Fig. 37B). In such cases feeding stylets often penetrate the palisade tissue below the opposite leaf surface. Stylets occasionally reach the phloem of the vascular system, but this does not appear to occur commonly (Fig. 38).



The salivary sheath appears to be a gel-like substance, and remains even after the mouthparts have been withdrawn (Fig. 37B). It appears to be confined to the perifery of the mandibular stylets only, and therefore may be important as an anchor for these stylets while the maxillaries remain fairly mobile. Pollard stressed the importance of this function of anchorage of the mandibular stylets, both during feeding and moulting. Sometimes during feeding the maxillaries are partly withdrawn and re-inserted in a new path, resulting in branched feed paths, indicated by the deep-staining (crystal violet) reaction of the contents of damaged tissue (Fig. 37B).

7.2.2 L. laevigatum

Despite repeated attempts at obtaining specimens of L. laevigatum adults and/or nymphs with their stylets in the plant tissue, all the methods tried on B. cedaranus failed. Another technique using high voltage electric current was attempted (Emsley 1958). This method required a 12-volt battery and a 12-volt motor-car induction coil. The latter was earthed by high tension wire, to a spade electrode buried in the moist soil of the plant on which the insect was feeding, and from the outlet pole of the coil, a high tension wire carried the stepped-up voltage to a pointer electrode. This latter was then pointed at the insect and when the circuit was rapidly closed and then opened (by means of a switch near the battery) a spark passed from pointer to insect and via the plant to earth. Emsley obtained a half- to three-quarter inch spark but for various possible reasons the spark obtained in the present attempt was only about one-quarter of an inch. Also at the time of the experiment only adults were available, and they were strong

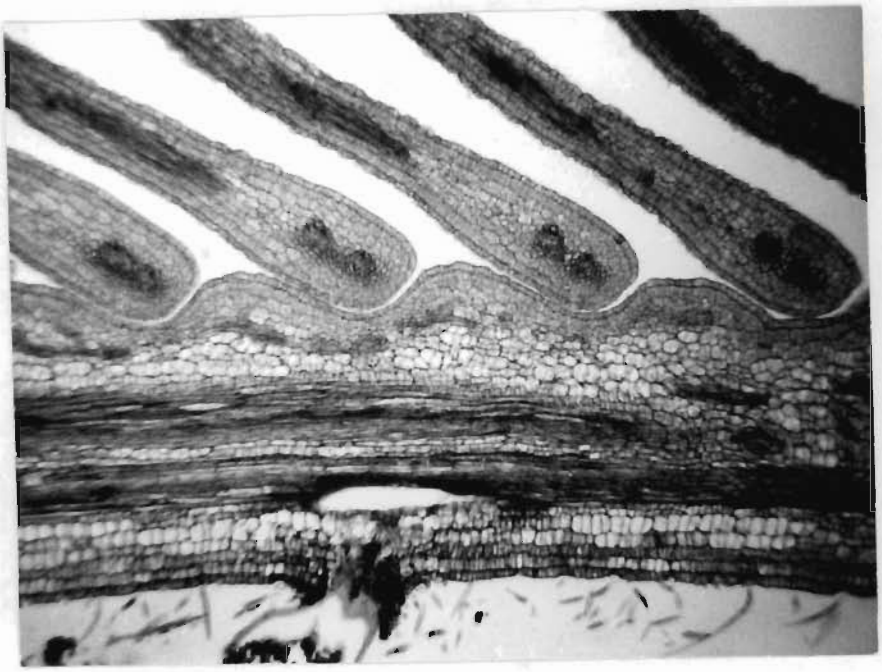


Fig. 39A Longitudinal section of a healthy young wattle leaf rachilla and pinnules, showing slight tissue damage during oviposition by L. laevigatum.

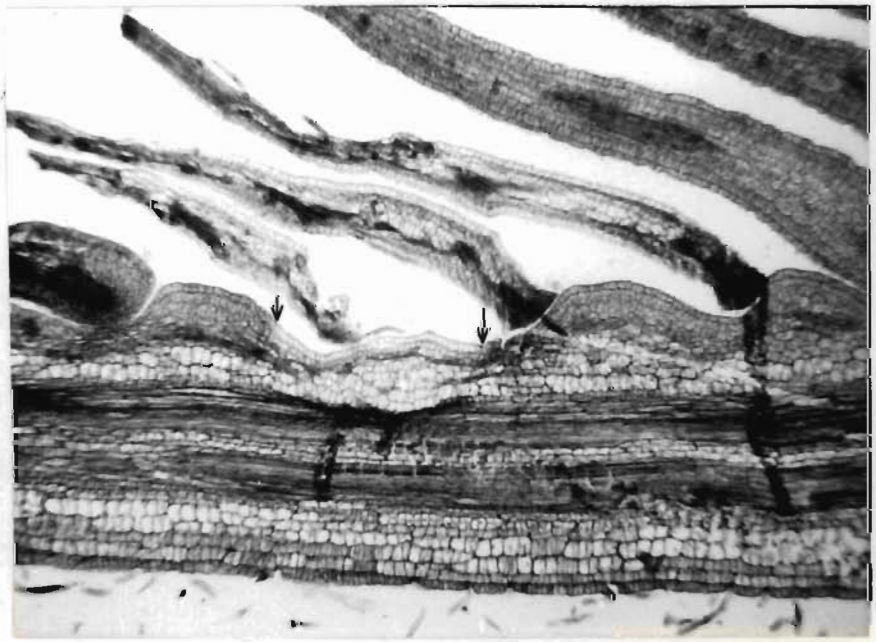


Fig. 39B As above, showing feeding damage with the contents of damaged cells removed, and the damaged area of the rachilla shrunken (arrowed). The crystal-violet staining contents of damaged cells in the pinnules are clearly visible, showing the extent of feeding damage.

The only indications of where *L. laevigatum* feeds, therefore, have been obtained from stylet paths in tissue sectioned after feeding, and from observations of field damage. From the former it would appear that stylet penetration is often fairly deep (up to about 0.6 mm.) and passes through various tissues including vascular bundles. Feeding occurs in most tissues. While studying Miridae, Smith (1926) similarly found that *Calocoris bipunctatus* Fab. and *Lygus pabulinus* Linn. fed on any part of the tissue pierced including vascular bundles while Awati (1914) figured the stylets of *L. pabulinus* in the xylem vessels of the host plant.

Some sections seem to indicate the complete destruction of cell contents of palisade, parenchyma and phloem cells leaving only cell walls (Figs. 39A and B, and 40), which later collapse to form the necrotic spots so characteristic of *L. laevigatum* feeding.

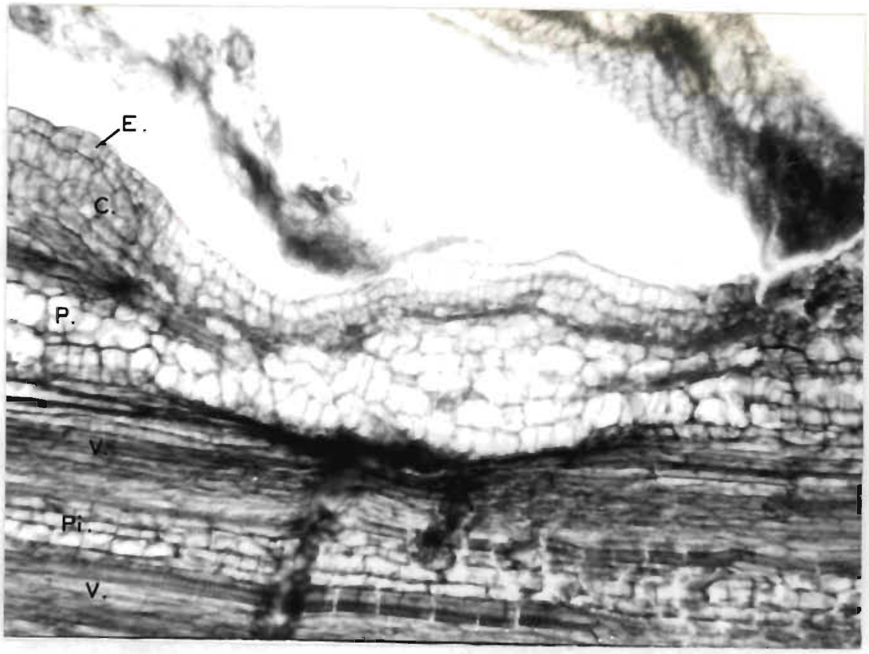


Fig. 40. Close-up view of Fig. 39B, showing cuticle, chlorenchyma and parenchyma cells with their contents removed. C., chlorenchyma; E., epidermis; P., parenchyma; V., vascular tissue; Pi., pith.

to be allied. Just as those bugs wash out the internal tissues of their prey with a stream of saliva, so the capsids kill the plant cells within a limited area and wash out their contents. In these processes the accessory salivary gland vesicles seem to be responsible for the maintenance of salivary circulation".

Continuous feeding by L. laevigatum in numbers sufficient to damage a young wattle tree badly, has a distinctly systemic toxic effect as well. Thus it is often observed in the field that trees subjected to continuous attack, shed practically all their pinnules, leaving only the rachis and rachillas of each leaf. The stem and branches of the tree take on a dull grey-green colouring, often far from the points of feeding. Even the pinnules of mature leaves not fed on by L. laevigatum are shed, indicating translocation of toxin within the plant, which in turn suggests that at least some saliva finds its way to the vascular system and in particular the xylem. Evidence of this was found by Smith (1926) while studying feeding habits of two species of Miridae.

7.3

THE SALIVARY GLANDS AND THEIR SECRETIONS

The salivary glands of B. cedaranus are typical of cicadellids, consisting of a pair of principal glands, each with a small accessory gland on a short duct. From the central portion of the principal gland (termed the hilus) a duct arises which joins the corresponding duct from the other principal gland to become the common salivary duct before entering the salivary pump. The glands are small and confined to the head

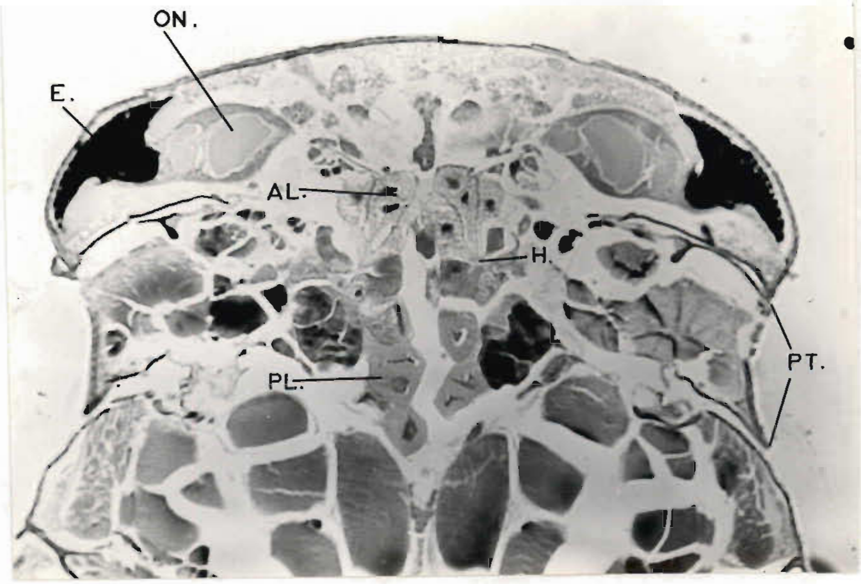


Fig. 41A Longitudinal section through the head and prothorax of an adult female *B. cedaranus* illustrating the size and position of the salivary glands. AL., anterior lobe of salivary gland; E., eye; H., hilus; ON., ocular nerve; PL., posterior lobe; PT., prothorax.

Fig. 41B Ventral view head and pronotum of an adult female *L. laevigatum* showing principal and accessory salivary glands. ASG., accessory salivary gland; ML., PL., median and posterior lobes of the principal salivary glands (PG.), T., tracheae.

In the terrestrial Heteroptera, there are two pairs of salivary glands, namely the principal salivary glands situated on either side at the front of the thorax and the accessory glands, one associated with each principal gland (Southwood 1955). Although usually bilobed (Southwood 1955) the principal glands of L. laevigatum have a third lobe protruding from the posterior lobe (Fig. 41B). The principal glands are also extremely large in comparison with those of many other mirids, extending from well into the thorax and head (Fig. 42A) to about the posterior margin of the fifth abdominal segment (Fig. 42B). The cells of the gland can be clearly seen in Fig. 42B, being large and bulbous. The accessory glands are fairly small and as in other mirids, thin-walled, and vesicular (Fig. 43A). Each is attached to its principal gland by a long thin duct which loops anteriorly into the head before entering the principal gland at the point where the salivary duct enters the principal gland (Fig. 43B). The salivary ducts join to form a common duct just before entering the salivary pump.

As observed by Goodchild (1952) an enormous destruction of plant tissue is characteristic of the feeding of mirids. This is produced by quite small numbers of bugs, by means of what is usually called the toxic saliva. Baptist (1941) found both an amylase and an invertase in the salivary glands of the mirid Lygus pratensis. Goodchild (1952) found amylases and esterases in the salivary gland secretions of cacao mirids, and considered that the strong acidity produced, possibly by the action of the esterases, was toxic to the plant cells. The amylase acts on insoluble carbohydrates. Goodchild also considered that the function of the accessory salivary glands was to absorb water

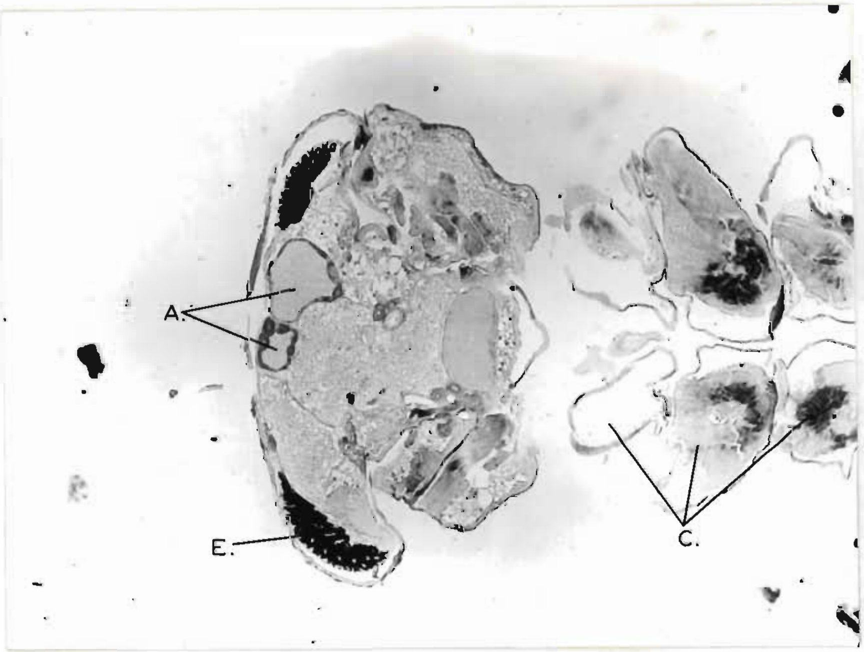


Fig. 42A Fifth-instar nymph of L. laevigatum. Longitudinal section of head showing the anterior lobes of the principal salivary glands. A., anterior lobes; C., coxae of thoracic legs; E., compound eye.

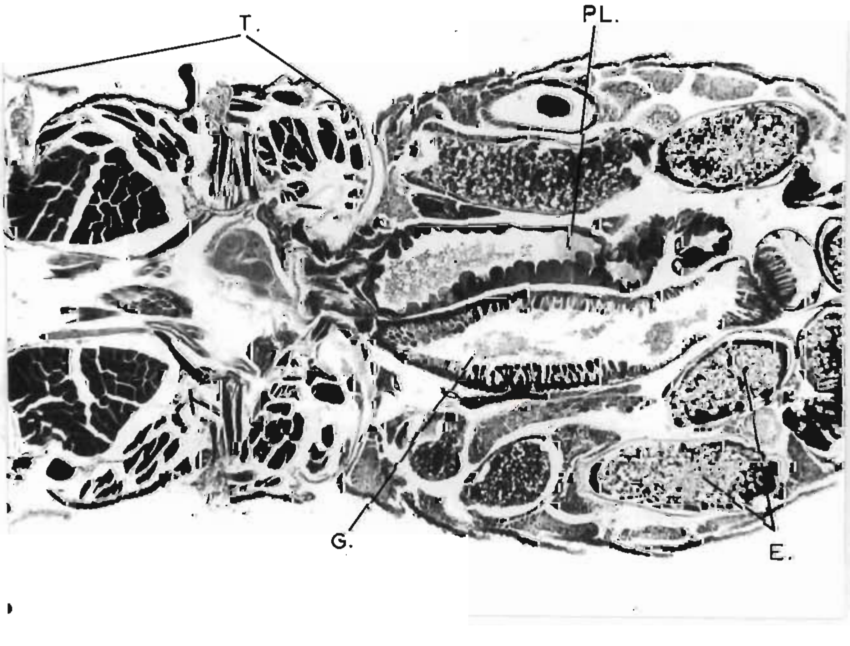


Fig. 42B Longitudinal section through an adult female L. laevigatum showing the posterior lobe of the principal salivary gland extending into the abdomen. The bulbous gland cells are easily visible. E., developing egg; G., gut; PL., posterior lobe; T., thorax.

Fig. 43A Fifth-instar L. laevigatum nymph. Ventral view head and salivary glands. ASG., accessory salivary gland; PG., principal salivary gland; D., duct of accessory gland.

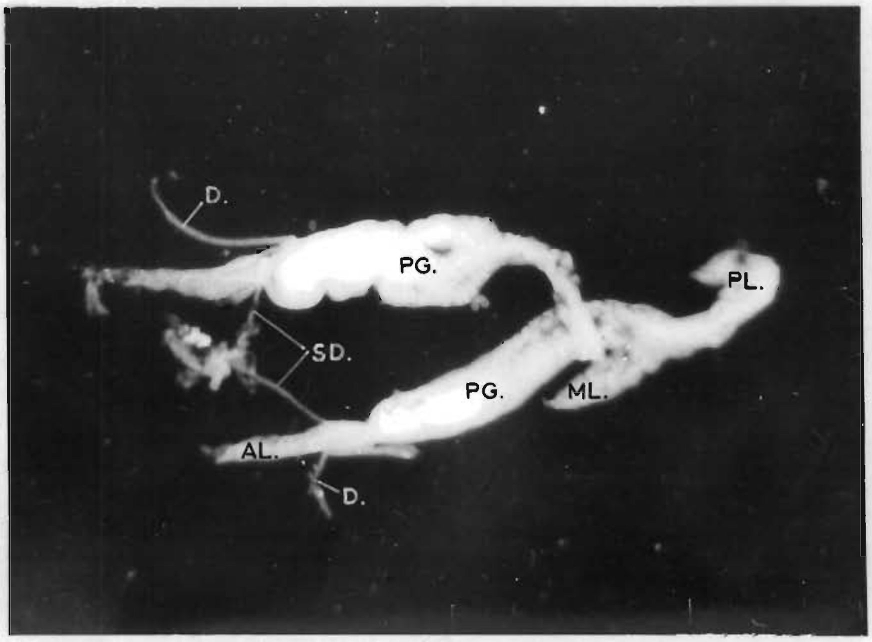


Fig. 43B As above, dissected out, showing the salivary ducts (SD.) from the principal glands to the salivary pump. AL., ML., PL., anterior, median and posterior lobes of the principal gland; D., accessory gland duct; SD., salivary duct leading to the salivary pump.

7.4

THE EXTERNALLY VISIBLE DAMAGE CAUSED BY FEEDING

During the initial stages of this investigation it became obvious from field observations, that *L. laevigatum* was capable of causing severe damage to young wattles, and all the types of damage previously described (Ripley 1926, etc.) were present in badly attacked plantations. However, these past reports referred only to "froghopper" damage, without identifying the species of insect present at the time. It was therefore felt necessary to conduct a simple test, in which adults of *B. cedaranus* and *L. laevigatum* were confined in cages on young potted trees during April 1967.

7.4.1 An assessment of damage caused by *B. cedaranus* and *L. laevigatum*.

Ten field collected adults of *B. cedaranus* (five male and five female) were confined on each of three young well-watered and succulent trees, with the same number of field-collected adults of *L. laevigatum* on three similar trees as a comparison. After three weeks the cages were removed and a visual inspection of the trees was made. Trees subjected to feeding by *L. laevigatum* showed typical damage (§ 7.4.2) but no feeding damage was visible on trees fed on by *B. cedaranus* adults. The only damage caused on these latter trees was a purely physical one, resulting from large numbers of eggs being laid in the rachides of several leaves and, probably due to crowding, also in some of the tender shoots. Damage of a similar nature was noticed when a high population of *B. cedaranus* built up on potted trees in a greenhouse at the Wattle Research Institute during July 1969, eggs laid by B. cedaranus females in the initial test, and although about 50 were allowed to reach the adult stage on each of the original trees, little damage was caused. Some pinnule shedding occurred, but since the nymphs and adults never feed from the pinnules, no necrotic spots appeared on these. Also a little stunting of internodes was noticed while the actively growing tree was being attacked, but the trees all recovered well after the insects were removed (each as it became adult).

In direct contrast the apical bud was destroyed on all three trees colonised by L. laevigatum and the typical side-branching which follows in the field, was observed.

7.4.2 External damage caused to young wattles by feeding of L. laevigatum.

The earliest damage first becomes visible on the pinnules of young mature leaves. Within four to five days of feeding, each feeding puncture becomes a small dark red-brown spot of 0.5 mm. to 0.8 mm. in diameter (Fig. 44B), equal in size on both the upper and lower surfaces of the pinnule and with all the tissue between dead and shrivelled. Where the spot occurs on the side of a pinnule, the latter becomes bent (Fig. 44C). Often, feeding near the apex of a pinnule results in the entire tip becoming shrivelled (Fig. 44D). Compared with a normal pinna (Fig. 44A), the pinnae of leaves subjected to feeding by L. laevigatum take on an extremely ragged appearance. This is particularly true in the case of nymphs which may spend several days feeding on a single leaf, with the result that a large percentage of the pinnules have at least one puncture mark.

When feeding occurs on young leaves of apical buds, stylets often penetrate the rachis of the leaf which becomes

Fig. 44A Undamaged pinnules of a wattle leaf pinna. (Magnified about 10x)

Fig. 44B Individual pinnules of a pinna damaged by feeding of L. laevigatum nymphs and adults.

Fig. 44C Pinnules bent as a result of feeding damage.

Fig. 44D Tips of pinnules shrivelled following feeding.

Fig. 45A A young wattle leaf with a severely bent rachis caused by the feeding of L. laevigatum damaging the growing tissue.

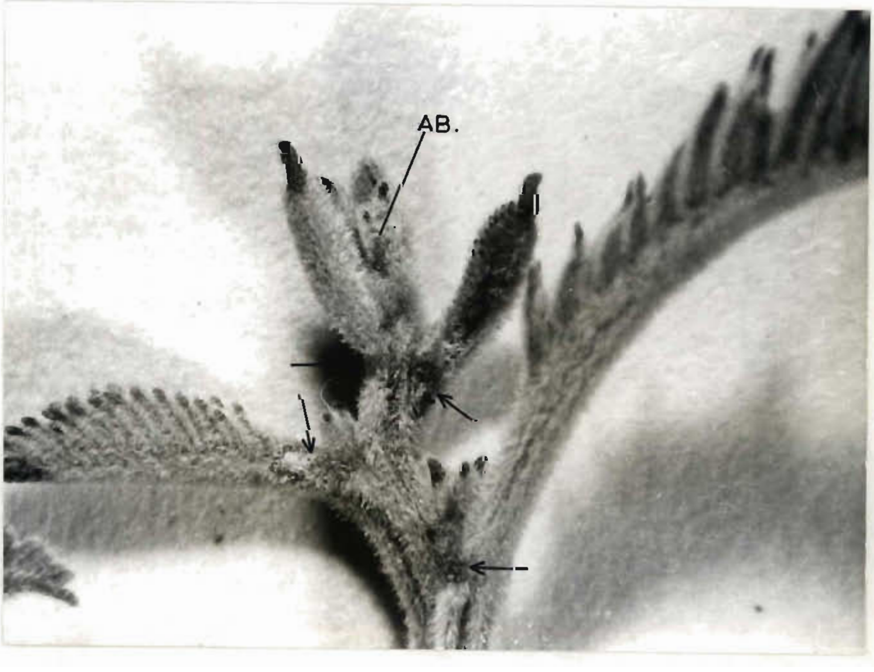


Fig. 45B Lesions containing patches of dead tissue after feeding by L. laevigatum, in the vicinity of an apical bud (AB.).

leaves. On the tender stems of terminal buds large yellowish to brown lesions result from feeding (Fig. 45B) and in this area, when stylets penetrate deeply and enter the terminal bud, the result is the death of the bud. Where this terminal bud is the apical bud of the young growing tree, its death means the removal of the source of growth-inhibiting hormone which the apical bud produces. As a result several side shoots in leaf axils immediately below the apical bud become dominant, resulting in forking.

Thus, after the destruction of the apical bud, subapical buds develop elongated shoots. With the continued presence of the mirid these new shoots are also pierced resulting in turn, in their death, and further shoots attempting to become dominant (Fig. 46A). Continued sprouting of shoots followed quickly by their destruction results in a "witches-broom" type of effect (Fig. 46B). In the nodes of leaves tiny bundles of shoots are often found, giving the appearance of abnormal hormonal control (Fig. 46A).

Ultimately continued uncontrolled feeding by increasing numbers of _L. laevigatum_ adults and nymphs destroys every terminal bud on the tree, and the writer has on several occasions seen young four- to eight-foot trees thus badly damaged. These trees also shed almost all their pinnules (Fig. 47A) and the bark becomes a dull greyish-green colour, blackish in places. Naturally such trees do not support the mirids, so that at this stage very few of the culprits are to be found in the plantation.

Young trees may be damaged two years in succession. Double leaders caused by the first season's attack are then subjected to further attack, severely damaging the young tree (Fig. 47B).

Fig. 46A Apex of a three-foot high wattle tree with multiple leaders and masses of tiny buds in leaf axils (arrowed) caused by the feeding of L. laevigatum. Hillcrest September 1969.

Fig. 46B "Witches-broom" caused by the continued feeding of L. laevigatum on apical buds and leaves. Hillcrest August 1969.

Fig. 47A A young tree badly attacked, showing some leaves which have dropped all their pinnules (arrowed). Bloemendal. March 1967.

Fig. 47B A young tree showing forking from a previous attack, and severe leader damage with multiple branching, caused by a further attack during January and February 1967. Bloemendal March 1967.

Fig. 48A A normal healthy young six-foot high wattle tree

Fig. 48B A young tree badly damaged by the feeding of *L. laevigatum*. Kirkfalls, Hillcrest, August 1969.

(See Sherry 1968 pp 369-375).

Fig. 49. A row of young trees showing multiple branching due to feeding by L. laevigatum the previous season. Photograph taken Bloemendal March 1968.

Damage is only very rarely caused to very young trees. The author has seen one to two foot high wattles badly damaged, but plants smaller than this were found difficult to colonise during biological studies in the field. It was thought possible that rain-splashed soil particles clinging to the plants, which were about nine inches high, may have been responsible for the high mirid mortality rate.

7.5

POPULATION DENSITIES CAUSING DAMAGE TO YOUNG WATTLES

The initial damage to pinnules described in § 7.4 is easily observed in the field by examination of leaves. It is a simple means of detecting L. laevigatum presence in a young plantation. The rapid appearance (four to five days) of these made regularly at least every two weeks, and if young trees are bordered by trees a year or two older, the young trees closest to these should be carefully inspected for evidence of mirids moving from the older trees.

One or two adults or nymphs on some trees, can easily be detected by this method, and as the population builds up, the number of damaged pinnules increases, as does ease of detection. Light damage with some side branching on most trees is caused by three to five adults per tree (trees three to five feet tall) assessed by sweeping. Nymphs are usually slightly more numerous than adults on trees where insects are actively breeding but this ratio depends on the breeding cycles and is quite variable. Moreover nymphs are not so easily swept from trees, so that counts have usually been confined to adults. Counts averaging six to ten adults per tree are high, and trees supporting such numbers soon show extensive branching with "witches-brooms" on the leader shoots of some trees. Some degree of pinnule shedding may also occur. An attack of this intensity over a period of about a month, will result in the final stage of a severe attack described in § 7.4, with pinnule shedding almost complete and all terminals damaged.

As indicated by nursery tests (§ 7.4.1) far higher numbers of B. cedaranus are required to cause any damage to trees, and damage is of a different nature to that caused by L.laevigatum. Such very high numbers of B. cedaranus have apparently occurred in the field in the past, with literally hundreds of adults and nymphs being collected by a sweep of the hat (G.A. Hepburn 1969 personal communication). Under such circumstances some damage may be caused to the trees, but such an outbreak has not been reported for many years, and was not observed during this investigation. It would appear that

CHAPTER 8

OUTBREAK OCCURRENCE AND CONTROL

8.1

OUTBREAK OCCURRENCE

8.1.1 Historical review

According to a paper in the author's possession, unsigned and undated but probably written by Dr. L.B. Ripley in about 1926, Mr. C. Fuller in 1910 noted a condition in young wattles, which resembled the fungus disease symptom known as "witches-broom". Fuller was of the opinion that L. laevigatum was mainly responsible for the damage. Ripley (1927) described the lesions figured in Figs. 44B, C and D (pinnule damage) but wrongly assumed that both L. laevigatum and B. cedaranus were capable of causing such damage. Thus in these early reports (Ripley 1926, 1927), B. cedaranus was considered the more important pest, a situation which remained until the findings of the present study revealed the importance of L. laevigatum. (§ 7.3).

Considerable damage was being caused during the 1920's (Ripley 1926, 1927, 1929) and some silvicultural control methods were instigated in an effort to reduce the damage. During many summers in the period 1930 to 1950 damage was apparently caused to young trees but reports are scarce. With the appointment of Dr. L.L.J. Ossowski as entomologist at the Wattle Research Institute in September 1949, more regular reports were forthcoming, published in the Annual Report of the Institute. However, those reports did not identify the species of insect or trees in most years. As many as 8,000 acres of young trees were reported to be damaged in the summer of 1952-3.

8.1.2 Present importance of L. laevigatum in young wattles

The overall importance of the species to the wattle industry is extremely difficult to assess. Although questionnaires on insect infestations are sent to farmers each year, these are in a great majority of cases, inadequately and inaccurately filled in, so that an assessment of overall acreage of young wattles damaged in any one year is virtually impossible. However, on the basis of a single farm unit, the importance of the pest can easily be assessed by damage caused to young plantations being re-established to wattle. Apart from the loss of growth resulting from a severe attack, the branching which results necessitates the added expense of corrective pruning (See Sherry 1968 pp 369-375). An assessment of the possible reduced value of timber and reduced bark yield obtained from a mature stand, on eight to ten year rotation, attacked years before as young trees, is a long-term project. An experiment has been designed in an attempt to estimate any such loss, and is to be attempted this summer if a suitable plantation of young trees is sufficiently heavily attacked.

8.2

THE CONTROL OF L. LAEVIGATUM AND B. CEDARANUS

8.2.1 Silvicultural methods

During the early development of the wattle industry, prior to the use of insecticides, a number of silvicultural practices were used in an attempt to reduce damage to young trees. As listed by Ripley (1927) these included avoiding thinning to be removed before attempting to prune the less severely damaged trees. Such advice is still applicable today.

In the late 1920's further attempts were made at controlling damage by intercropping young wattles with crops such as maize and millet. At the time it was believed that the insects clustered on the outer edge and apex of the tree due to being strongly photopositive, and that they would then leave the young wattles in favour of taller plants such as maize. While it is possible that such intercropping acted as a screen to some extent, neither species feeds readily on either maize or millet, and it is therefore doubtful that the insects would remain on either intercrop for any length of time. Protection might also have been afforded by competition rendering the young wattles less succulent and unsuitable for colonisation by *L. laevigatum*. Equally good protection was reported to have been afforded by certain weeds (notably *Erigeron canadensis* - Horseweed) overtopping the young wattles.

8.2.2 Biological control

8.2.2.1 Predators

Although no direct study was made of predators of *B. cedaranus* and *L. laevigatum*, a number of predatory insects and spiders which might be expected to prey on one or both species, commonly occur on young wattles. These include the larvae of a small green lacewing (Chrysopidae). Ripley (1926) mentioned a ladybird beetle (Coccinellidae) larva feeding on *B. cedaranus* nymphs but this has not been investigated.

A small green and white spider identified as *Oxyopes* sp. n.,(Oxyopidae),by B.H. Lamoral(1969), commonly encountered on

L. laevigatum adults, only to discard them quickly, possibly due to the release of an offensive odour from the metasternal stink glands.

8.2.2.2 Internal parasites of nymphs

Two such parasites have been found parasitising nymphs of *B. cedaranus*. The more important species, a pipunculid fly, was mentioned in literature by Ripley (1926). Specimens reared from nymphs were identified as *Pipunculus* (*Eudorylis*) *libratus* (Hardy) by Prof. D. Elmo Hardy of the University of Hawaii (Fig. 50A). A single specimen reared was identified as *P.* (*E.*) n. sp. nr. *mutillatus*. The fly appears to parasitise nymphs only, the mature fly larva emerging dorsally from the point of junction of thorax and abdomen of the fifth-instar *B. cedaranus* nymph (Fig. 50B). Occasionally the larvae emerge from young adults one to two weeks after the final moult. Pupation takes place within 24 hours in the soil, leaving the empty shell of the parasitised nymph clinging to a wattle leaf. The pupal period lasts 19 to 22 days (February to March 1968) in the laboratory.

Lack of suitably high populations of *B. cedaranus* in the field has prevented any assessment of the possible control potential of this pipunculid at high host density. The relatively high population of September 1967 to January 1968 was not subjected to high parasitism, being 18 per cent. of all fourth- and fifth-instar nymphs collected during that period. Although far less common in the field at that time, nymphs of the cicadellid Gen. nr. *Allygus* sp. (§ 6.4.2) were very highly parasitised by pipunculids (68 per cent.), but it was not established whether this was the same species of pipunculid, since none was reared to the adult. Several other species of

A

B

Fig. 50A *Pipunculus libratus* female.

50B *B. cedaranus* nymph shell. Note gap between thorax and abdomen through which parasite larva escaped.

Fig. 50C *Liodryinis* sp.

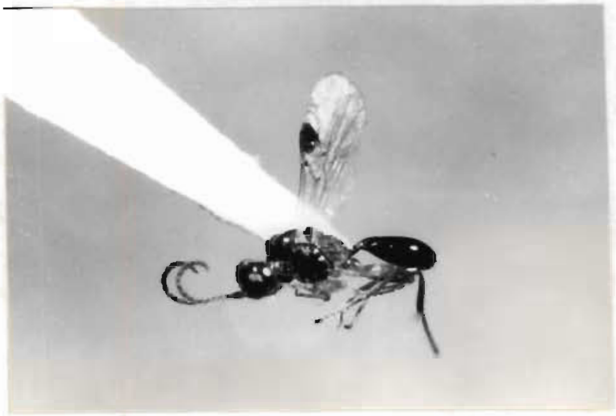
50D Ventral view of a parasitised B. cedaranus nymph

The other known parasite of B. cedaranus nymphs is the wasp Liodryinus sp. (Hymenoptera : Dryinidae. Fig. 50C). The species is however relatively rare, only an occasional parasitised nymph being encountered, showing the blackish external gall-like cyst or thylacium typical of parasitism by this family of wasp (Fig. 50D). An unusually high rate of parasitism was noticed in a plantation of young trees in the Piet Retief area of the Transvaal where 16 of the 23 fourth- and fifth-instar nymphs collected were parasitised. The wasp and parasitised nymphs have been collected in the Vryheid district and in the Natal midlands at Pietermaritzburg, Seven Oaks and Greytown.

The only two internal parasites so far found parasitising nymphs of L. laevigatum are Euphorus nigricarpus Szépligeti and E. praetor Nixon (Braconidae : Hymenoptera. Figs. 51A and B). Identification was confirmed by G.E.J. Nixon of the British Museum (Natural History). Both species have previously been found parasitising a number of mirid species in Uganda by Nixon (1947) who described E. nigricarpus and E. praetor as the two species of great importance in controlling L. vosseleri on cotton. On wattle they also parasitise Orthotylus tabidus Stål, and at times when L. laevigatum is scarce, this species probably acts as an important alternate host to maintain the parasite in the field. In view of the host range reported by Nixon, it is probable that other local species of mirid also act as hosts.

Parasitism is generally from 20 to 30 per cent. Few nymphs were collected at Bloemendal during 1967, as the parasites had not been detected, and adults only were being

A



B

C

Fig. 51A *Euphorus nigricarpus*.
51B *E. praetor*.

in the alcohol-preserved samples. Parasitism of the few nymphs in these samples was 21.4 per cent. In the summer of 1968 the mirid population at Bloemendal (§ 6.2.2) was more heavily parasitised, probably due to the build-up of parasites in the previous summer. In block 18c parasitism of all fifth-instar nymphs collected in January and February (assessment by dissection) was 69 per cent. (163 nymphs). An insecticide trial attempted during this period was a failure due to a similar reduction in numbers of insects collected from control plots after spraying, as that observed in the treated plots. Weekly samples in this experiment, from 30th January 1968 to 21st March 1968 showed 75 per cent. parasitism of fifth-instar nymphs collected. Since no other factors were observed which may have been responsible for the drop in population, it was considered likely that the euphorine parasites played an important part.

Regular sampling in Block 20 Bloemendal from February to early June 1968 revealed a 63.4 per cent. parasitism overall, comprising subtotals shown in Table 15.

Table 15. Parasitism of *L. laevigatum* by *Euphorus nigricarpus* and *E. praetor*. Block 20 Bloemendal during 1968 (Assessed by dissection of fifth-instar nymphs).

Month	Total	Parasitised	Percentage Parasitism
February	93	61	65.6
March	203	128	63.1
April	154	95	61.7
May	111	59	53.2
June	18	8	44.4

The monthly totals are not comparable since the number of samples taken each month was not constant. The drop in parasitism at low host density was observed by Nixon (1947) who noted "It is a general rule that parasites cannot attain a high percentage parasitism when the host is scarce, except in special circumstances". Nixon found a particularly high parasitism of Lygus vosseleri on cotton reaching 100 per cent. by the end of July at Kawanda, Uganda and remaining high until the mirid population dropped due both to the cotton plants drying out and parasitism. He noted that wet weather in September did not cause a second outbreak because adults were scarce and parasitism was still complete. Cotton appears able to support a higher population of mirids than can wattle, the latter being extensively damaged by relatively low populations of L. laevigatum. In contrast to Kawanda, Nixon found that at Serere, Uganda, where natural vegetation was rather different from that at Kawanda, parasitism of L. vosseleri on cotton was rare, despite parasitism of nymphs on grain crops in the area. Invasion of cotton after the grain harvest was rapid but the failure of the parasites to follow was thought to be due possibly to their being a different ecological race, and therefore searching different plant species for their hosts.

The parasites E. nigricarpus and E. praetor have been collected from various other localities besides Pietermaritzburg. In the Seven Oaks area on the farm Harden Heights an outbreak of L. laevigatum, sampled on 29th February 1968, showed 68 per cent. parasitism of fifth-instar nymphs. This plantation had been attacked the previous year (See § 6.2.3), and the high parasitism is therefore interesting as a similar increase in parasitism in the second year was noted at Bloemendal in 1968 (§ 6.2.2). In 1967 several samples established the parasitism at between 18

In 1969 parasitism was closely studied in the Kirkfalls, Hillcrest outbreak area (§ 6.2.3). Table 16 shows the sampling dates and parasitism recorded.

Table 16. Parasitism of L. laevigatum by E. nigricarpus and E. praetor. Kirkfalls, Hillcrest 1969

Date	Total	Parasitised	Percentage Parasitism
13/2/69	50	13	26
6/3	23	8	35
2/4	30	8	27
9/4	38	13	34
16/4	59	20	34
19/6	134	52	28

It was interesting to note that at Harden Heights (Seven Oaks district, Natal) a light outbreak of mirids (§ 6.2.3) was heavily parasitised (62 per cent.), showing that the parasites are at times capable of efficient searching and parasitism at low host density.

A serious outbreak of L. laevigatum on the farm Burn Tops east of Piet Retief, sampled on 4th June, 1969, was found to have 21 per cent. parasitism (115 fifth-instar nymphs dissected; 24 parasitised).

The overall impression gained is that these euphorine parasites are capable of considerably reducing populations of L. laevigatum, particularly in the second of two successive seasons of outbreak in a particular plantation. In isolated plantations parasitism is generally between 20 and 30 per cent., the parasites seemingly being able only to keep pace with mirid build up, without increasing sufficiently to increase substantially the percentage parasitism. Only after one season,

8.2.2.3 Egg parasites

Tiny wasps parasitising eggs of *B. cedaranus* and *L. laevigatum* have recently been investigated. Most specimens were collected by simply leaving foliage, known to contain eggs of the species of insect under study, in jars of water covered by gauze or plastic and collecting the wasps which subsequently emerged. However this did not exclude the possibility of eggs of other species being present. Individual field collected eggs of *L. laevigatum* were therefore dissected out of the tissue in which they had been laid and placed separately in tubes. Parasites of eggs of *B. cedaranus* were reared from eggs collected in the nursery at the Wattle Research Institute.

Identification of the species involved has not been attempted. Specimens of two egg-parasites of *L. laevigatum* have been sent away for identification, but the more recently obtained parasites of *B. cedaranus* eggs have yet to be dispatched.

Two parasites have so far been reared from eggs of *B. cedaranus*. Both were reared from eggs collected in Pietermaritzburg during August and September 1969. From 169 eggs isolated in the laboratory ten specimens of a small yellow as yet unidentified chalcidoid wasp (Fig. 52A) were reared, as well as two specimens of a species of Trichogrammatidae (Chalcidoidea). This constituted about 7 per cent. of the eggs collected.

Two hymenopterous parasites have been reared from the eggs of *L. laevigatum*. All eggs in this investigation were collected in the field at Kirkfalls, Hillcrest during August 1969. By far the most common species collected was a trichogrammatid (Fig. 52B).

Fig. 52A

Fig. 52B

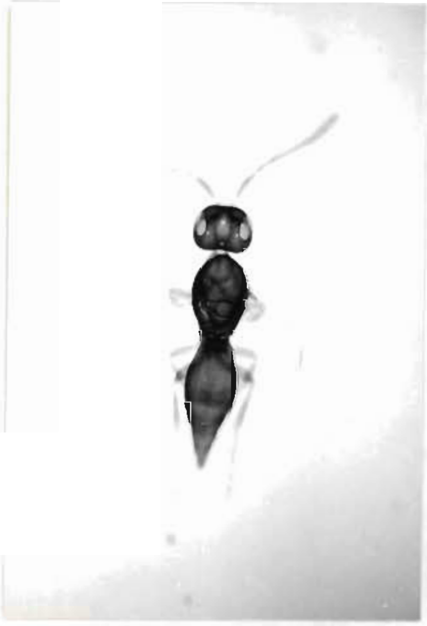


Fig. 52C

A Egg parasite of *B. cedaranus*.

B Trichogrammatid egg parasite of *L. laevigatum*.

C An egg parasite of L. laevigatum.

trichogrammatid, from eggs dissected from tissue and isolated, but not from foliage kept in plastic bags. It was found, however, that they took longer to emerge from the host egg than did specimens of the trichogrammatid, and it is likely that many individuals of the black species were killed within the egg as the surrounding plant tissue dried out, or became invaded by fungi.

From 160 eggs dissected out and isolated, ten trichogrammatids referred to in my collection as Species 1, emerged, the last three emerging on 13th October 1969, 21 days after the eggs were collected. Four days later three specimens of the small black parasite referred to above, emerged. In all ten specimens of the latter species were reared, giving a total egg parasitism of 12.5 per cent. made up equally of both species.

From foliage collected, a total of 149 specimens of Trichogrammatidae sp. 1 were reared. The number of eggs was estimated by rough counting, at 2,000, 7.5 per cent. parasitism. As mentioned previously, very few of the black species of egg parasite were reared from this foliage. Only 36 specimens were collected.

No data are available on the distribution of these egg parasites since the only mirid infestation available during the study was on the farm Kirkfalls, Hillcrest, Natal.

8.2.3 Chemical control

8.2.3.1 Historical review

Initially experiments were conducted in 1939 using a pyrethrum dust. Talc was found to be the best diluent (Ripley and Petty 1940). These authors noted that it was important to detect the presence of the insects before damage was noticed

During the late 1940's tests were conducted using pyrethrum and DDT, both in talc. In the laboratory 2 per cent. pyrethrum dust was found more effective than 5 per cent. DDT. against both nymphs and adults of B. cedaranus and L. laevigatum.

Tests with a 1 per cent. oil solution of Toxaphene were conducted by Ossowski (1950), at a rate of three gallons per acre, using a Tifa fogging machine. Control was not complete, and no indication of insect species involved was given. During 1951 further tests were conducted using 2½ per cent. and 1 per cent. solutions of Toxaphene in Diesoline applied with a hand-operated sprayer at a rate of two gallons per acre, and 4 per cent. gamma - BHC in Diesoline at a rate of 0.2 gallon per acre. A "Kyoritu" fogging machine was used. Good control was reported with both insecticides (Ossowski 1951).

8.2.3.2 Insecticide field tests conducted against L. laevigatum

In view of the reported success in the control of sucking bugs with toxaphene, about ten acres of young trees were fogged, using a Tifa fogging machine, on 15th and 16th March 1967. The success of this measure was however suspect even before confirmation by sweep samples, since the cover obtained with the method appeared (visually) to be rather inadequate. It was obvious that a more effective insecticide, applied by a method less susceptible to prevailing conditions than is fogging, was required.

Trial I

The presence of a fairly evenly spread population of L. laevigatum in Block 18 at Bloemendal, Pietermaritzburg, led to a field experiment conducted between 18th and 30th May 1967.

last being an experimental insecticide (at the time) presented as a sample by the manufacturer. Toxaphene was used as a standard, while dimethoate and sevin were both selected for their relatively low mammalian toxicity and for their different properties, the former having systemic action, the latter only contact action.

Each insecticide was to have been applied at a rate recommended for smallish shrubs or trees. These rates were as follows:-

T1 Control.
T2 Dimethoate e.c. (40% technical)12 fl.oz per morgen
T3 Sevin (85% wettable powder) 1 lb a.i. per morgen
T4 Menazon 10 fl.oz per morgen
T5 Toxaphene e.c. (62% a.i.by weight) 4 lb a.i. per morgen

However an error in making up the solutions resulted in $^{1}/_{5}$ this rate being applied.

The statistical design of the experiment was a 5 x 5 Randomised Block with $^{1}/_{20}$ acre plots, each plot consisting of six rows of trees nine feet apart (54 ft.) 40 ft. 4 inches long, being 2,178 sq. ft. or 0.05 acre. Each plot was separated from the next by 30 feet, while four rows of trees, nine feet apart, separated each line of plots. Each plot contained about 100 trees at three foot spacing. The field plan was as follows:

Block	Treatment				
1	T5	T4	T2	T3	T1
2	T3	T1	T5	T4	T2
3	T2	T4	T5	T3	T1
4	T3	T4	T5	T2	T1
5	T4	T5	T1	T3	T2

Insecticide application was by means of a "CP40" motorised knapsack sprayer. In order to ascertain the amount of liquid to spray all trees in the plot from both sides. Using this as a standard, the volume of each insecticide required to treat $^1/_4$ acre (five plots of $^1/_{20}$ acre each) was made up to 11.5 litres. In the field only 2,300 cc. was loaded into the sprayer at a time, thus ensuring proper dosage application for each plot. Controls were sprayed with water.

Plot sampling before and after spraying was randomised by simply selecting a random number from 1 to 20 as the first tree for sampling and then sampling every twentieth tree, since there were approximately 100 trees per plot, and five trees per plot were required for sampling at each occasion. On the first sampling furthermore, each sampled tree was marked, so that on the following occasion every eighteenth tree could be sampled, and then every sixteenth tree and so on, without the danger of any one tree being sampled twice during the course of the trial. Only the number of L. laevigatum adults in each sample was recorded. Samples were taken on the day before the trees were sprayed, and four, eight and twelve days after spraying.

Analysis and results

Due to the fact that only $^1/_5$ of the commercially recommended dosage was applied, kill within sprayed plots was less than 100 per cent. for all insecticides tested. This was fortunate for it simplified comparison of results. Appendix 12 shows the results of the plot sampling before and after treatment. Data were transformed [$y = \text{Log}\ (x + 1)$] for analysis. An analysis of variance and covariance applied to the before sampling and four days after spraying data established a highly significant response to insecticide (Appendix 13) but since the error regression was nonsignificant, the analysis was not continued.

Although toxaphene was found to be initially effective (Appendix 14) the residual effect was very short, and adults quickly reinfested toxaphene-sprayed trees. Thus in both dimethoate and sevin sprayed plots there were significantly fewer adults per sample eight days after spraying. No significant difference was detectable between the effects of dimethoate and sevin on both the fourth and eighth day after spraying. Menazon had no detectable insecticidal effect at the concentration used. Analysis of the sample data from twelve days after spraying (after transformation) gave a non-significant F-test. This was expected since the numbers of adults from all plots including controls, were reduced (Appendix 12) and fairly uniform.

Both sevin and dimethoate appeared promising and dimethoate was used for comparisons in further tests. In an attempt to assess the effectiveness of soil applied systemic insecticides (in granular form) an experiment was laid out in the field during January 1968 (Bloemendal Block 18). Unfortunately, however, the *L. laevigatum* population was suddenly reduced in all plots, including controls. An unusually high degree of parasitism was thought to have been responsible (§ 8.2.2.2). Throughout the rest of 1968 no suitable area for insecticidal tests was available.

Trial II

The object of this trial was to confirm the effectiveness of Dimethoate and to compare it with another systemic insecticide, Metasystox.

Procedure

The experiment was conducted from 1st to 16th April 1969

30 ft. 3 inches long, in a 5 x 5 Latin Square design.

Insecticides were applied at the following rates:-

T1	Control	
T2	Dimethoate 40% e.c.	12 fl.oz per morgen
T3	Dimethoate 40% e.c.	6 fl.oz per morgen
T4	Metasystox 25% e.c.	12 fl.oz per morgen
T5	Metasystox 25% e.c.	6 fl.oz per morgen.

Although the percentage active ingredient is lower in Metasystox, the cost is slightly higher so the same concentration as that for Dimethoate was used.

The method of application was the same as used in the previous experiments, but the error of the previous experiment was avoided and the correct dosages given above were applied. The volume of spray per plot was slightly increased. The required volume of insecticide to spray a $^{1}/_{30}$th acre plot was made up to 4.4 litres, giving a better cover. Sampling was as in Trial I, but ten trees per plot, instead of five as in the previous trial, were sampled on each sampling day. No pretreatment sample was made, samples being taken one, eight and fifteen days after spraying. Both adults and nymphs of <u>L. laevigatum</u> were counted (Appendices 15 and 16).

Results

Analyses of data from each of the sampling days revealed that on each occasion the F-test was highly significant ($P = 0.01$), revealing response to insecticide. Comparisons of insecticides alone revealed that Dimethoate was superior to Metasystox (Appendix 17). Although not statistically superior after one and eight days, Dimethoate gave better control and with additional replications, would probably have proved superior.

Since local flight activity probably has some effect on the numbers of adults collected on sprayed trees, it is of interest to study the numbers of nymphs collected (Appendix 16). This increased in control plots during the experiment, indicating considerable breeding activity. However, in the first and eighth day samples, very few were collected from any of the spray plots. After fifteen days, considerable numbers of nymphs were collected from treated plots, and analysis of these data (Appendix 18) revealed that Dimethoate was again superior to Metasystox, in killing newly hatched nymphs, indicating a superior residual systemic activity. An important fact revealed by these data, however, is that most eggs within the tissue at the time of spraying, were unaffected by the spray. Since these eggs would at most, take eleven days to hatch (those laid the day before spraying, Table 3 § 4.2.4) all the insecticides failed to have good activity for those eleven days. The fact that most of the nymphs collected from sprayed plots were in the second- to fourth-instar excludes the possibility that they hatched from eggs laid after spraying (Table 17).

Table 17. Numbers of nymphs of each instar (excluding first-instar) collected fifteen days after spraying Insecticide Trial II. Kirkfalls, Hillcrest, 16th April, 1969.

Treatment	Instar			
	2	3	4	5
Control	19	17	41	97
D6	17	16	14	3
D12	5	3	4	-
M6	37	43	29	5

hatched from the eggs less than a week after spraying, when only dimethoate at 12 fluid ounces per morgen was exerting a good level of control.

8.2.4 Discussion of chemical control measures

So far the best insecticide tested is Dimethoate 40% e.c., applied at a rate of 12 fluid ounces per morgen. This costs approximately R1.22 per morgen (R78.93 per 5 gal. drum) which is economically quite acceptable.

In view of the various parasites active in populations of L. laevigatum it has been felt that contact insecticides should be avoided. However, it would be an advantage if a systemic insecticide could be found having a slightly longer residual action in the plant. With this in mind further tests are planned using systemics. Other important properties are low contact action and quick absorption into the plant so that parasite mortality be reduced to a minimum. Unfortunately several systemics which suggest themselves, such as Azodrin and Phosphamidon (Dimecron) have a high mammalian toxicity.

SUMMARY

Two species of Hemiptera namely the cicadellid Batrachomorphus cedaranus (Naudé) and the mirid Lygidolon laevigatum Reut., have been considered responsible for the periodic serious damage to young wattles occurring in the wattle-growing areas of Natal and the south-eastern Transvaal.

The studies discussed in this thesis are divided into three parts, the first dealing with taxonomy and morphology. The taxonomy of the two species is only briefly discussed. Morphological studies are, for the most part, confined to adult features of importance in the taxonomy from family down to species level. This required fairly detailed studies of genitalia, particularly important in the males of both species and the female of L. laevigatum. Investigations into the taxonomically important structures of the posterior wall and roof of the female mirid genital chamber led to a study of the function of the anterior genital pouch. Previously described in the literature as an organ which "apparently serves to receive and store sperms" (Davis 1955) studies revealed that immediately after copulation sperm migrated into the lateral oviducts while only the contents of the male accessory glands remained in the anterior genital pouch. Findings were confirmed by studies on several other species of mirid commonly encountered in wattles. The eventual destination of sperm in the ovaries was found to vary in the different species examined. In L. laevigatum and two closely related Mirini, Lygus simonyi (Reut.) and L. pallidulus (Blanch.), the majority of the sperm was found in a bulbous portion of each lateral oviduct with only

sperm migrated up into the calyx and ovariole stalks.

The second part of the investigation deals with biology and ecology. The mirid has no definite overwintering stage, and can breed throughout the year provided the trees are succulent enough. Eggs are laid on the tender terminal shoots of the young wattles (in their first two seasons of growth). Older trees become too tough and can not be successfully colonised. Egg incubation period varies from six to eight days in summer, and increases to a maximum of 14 days in winter. There are five nymphal instars, the overall nymph stage occupying about 14 to 15 days in the field in summer, and up to 20 days in early winter (June). Adult females have a preoviposition period of six to twelve days (mean 9.4 days). Caged females laid 19 to 159 eggs (with a mean of 74 eggs per female) while living from 29 to 54 days (mean 41.5 days). Males have shorter lives than females. The sex ratio is 1.07 : 1, in favour of males. The whole life-cycle is completed in four to five weeks in summer, five to six weeks in winter. Several generations may therefore occur in a season and population buildup is rapid.

The entire life-cycle of the cicadellid is completed in eight weeks in the field in summer, and fourteen weeks in winter. Eggs are usually laid in the tissue on the abaxial surface of the leaf rachis. They hatch in about 18 days in November-December, but incubation period is more than doubled in winter. The five nymphal instars are completed in an average of 28 days in summer, extending to an average of 55 days in winter (May to August). The preoviposition period varies from seven to nine days. Caged females laid an average of 93 eggs with a maximum of 161 eggs laid by a single female. They lived an average of 47 days as

Field studies reveal that although several species of mirid are found on wattle, none in any way competes with L. laevigatum, or attains the densities of population recorded for this species. No high field populations of B. cedaranus were encountered during the study.

The breeding rate of L. laevigatum is considerably affected by the condition of the young wattle tree. The two most important factors in reducing the suitability of the tree as a host are soil moisture and the effect of mirids feeding on the tree. Succulent actively growing young trees are rapidly colonised, particularly if there are older plantations nearby, from which adults can move into the younger trees.

The effect of tree condition on the dynamics of L. laevigatum populations is reflected in populations studied in the field.

Part III deals with economic importance and control. Feeding studies revealed that while the cicadellid feeds mainly in the chlorenchyma and parenchyma cells the mirid penetrates all tissues and damages cells in a wide area around the feeding puncture. Toxins spread from feeding areas and exert a systemically toxic effect on the tree, causing it to shed pinnules, and discolouring the bark on shoots and stems. Local feeding on apical buds results in the death of the tissue and loss of apical dominance. Trees thus become extensively branched.

The biological control of both species in the field is assessed. Two species of hymenopterous parasites, Euphorus praetor and E. nigricarpus are fairly efficient in controlling populations of L. laevigatum, particularly in the second of two successive years of mirid presence in a single plantation.

namely Liodryinus sp. (Hymenoptera : Dryinidae) and Pipunculus libratus Hardy (Diptera : Pipunculidae).

A brief search for egg parasites revealed that the eggs of both species are parasitised. Seven per cent. of the eggs of B. cedaranus were parasitised by two unidentified species of chalcidoid wasp. Between 7.5 and 12.5 per cent. of eggs of L. laevigatum were found to be parasitised by two species of wasp, one a trichogrammatid (Chalcidoidea), the other, also a Chalcidoidea, unidentified.

The most successful insecticide tested against L. laevigatum is Dimethoate (40 per cent. e.c.) applied at a rate of 12 fluid ounces per morgen.

ACKNOWLEDGEMENTS

The author wishes to thank his supervisor, Prof. M.J. Oosthuizen, Head of the Department of Entomology in the Faculty of Agriculture, University of Natal, and co-supervisor, Mr. G.A. Hepburn, for their encouragement and guidance during this study, and invaluable criticism of the text.

Thanks are also due to Dr. R.M. Pringle of the Department of Biometry, for advice and assistance, and to Mr. J. Schoonraad for assistance with some of the microphotography. The author is also grateful to Mr. I.A. Hertogs for providing the extra hand often so essential during photographic processing and printing, and for assistance with other aspects of the photography. Thanks also to the many other helpers who contributed to this study.

Finally the author is indebted to the Committee of Control of the Wattle Research Institute for facilities provided and permission to submit the results as a thesis.

REFERENCES

AWATI, P.R., 1914. The mechanism of suction in the potato bug Lygus pabulinus Linn. Proc. zool. Soc. Lond. 28 : 685-733.

BAPTIST, B.A., 1941. The morphology and physiology of the salivary glands of Hemiptera - Heteroptera. Quart. J. micr. Sci. London. 83 : 91-139.

BEARDS, G.W. and STRONG, F.E., 1966. Photoperiod in relation to diapause in Lygus hesperus Knight. Hilgardia.37(10) : 345-362.

BECK, S.D., 1962. Photoperiod induction of diapause in an insect. Biol. Bull. Lancaster. 122 : 1-12.

BEIRNE, B.P., 1956. Leafhoppers (Cicadellidae) of Canada and Alaska. Can. Ent. Ottawa.88 Suppl. 2 : 1-180.

BONESS, M., 1963. Biologisch - ökologische Untersuchungen an Exolygus Wagner (Heteroptera, Miridae) Z. wiss. Zool. Leipzig.(A) 168 : 376-420.

BONHAG, P.F. and WICK, J.R., 1953. The functional anatomy of the male and female reproductive systems of the milkweed bug Oncopeltus fasciatus (Lygaeidae) J. Morph. Philadelphia. 93 : 177-284.

BRINDLEY, M.D.H., 1935. The metasternum and pleuron of Heteroptera. Trans. R. ent. Soc. Lond. 82 : 43-50.

BRUES, C.T., MELANDER, A.L. and CARPENTER, F.M., 1954. Classification of insects. Cambridge, Mass. Printed for the Museum of Comparative Zoology at Harvard College.

BUYS, J.L., 1924. The Cicadellidae of the vicinity of Ithaca, New York, with special reference to the structure of the gonapophyses. Cornell Univ. Agric. Expt. St. Mem. 80 : 1-115.

CARVALHO J.C.M., 1955. Keys to the genera of Miridae of the world. Bol. do Museu Praense Emilio Goeldi. 11(2) 1-151.

CONN, H.J., 1953. Biological stains. 6th Ed. The Williams and Wilkins Company Baltimore.

DAVIS, N.T., 1955. Morphology of the female organs of reproduction in the Miridae Ann. ent. Soc. Am. Columbus. 48 : 132-150.

---------- 1961. Morphology and phylogeny of the Reduvioidea. Part II Wing venation. Ann. ent. Soc. Am. Columbus. 54 : 340-354.

DE BACH, P. and SCHLINGER, E.I., 1964. Biological control of insect pests and weeds. London. Chapman and Hall Ltd.

DUPUIS, C. and CARVALHO, J.C.M., 1956. Taxonomists glossary of genitalia in insects. 28 Heteroptera : 158-169. Munksgaard, Copenhagen.

ELMAR, J.L. and SMITH, R.G., 1956. Some pests of black wattle in Kenya. East Afr. Agric. Jnl. XXI(4) 230-247.

EMSLEY, M.G., 1958. A technique for the examination of the feeding mechanism in phytophagous Heteroptera. Proc. R. ent. Soc. Lond. (A) 33(4-6) 93-94.

ESSIG, E.O., 1954. College entomology New York Macmillan.

EVANS, J.W. 1931. Notes on the biology and morphology of the Eurymelinae (Cicadelloidea). Proc. Linn. Soc. N.S.W. Sydney. 56 : 210-226.

---------- 1946. A natural classification of leaf-hoppers. Part I. External morphology and systematic position. Trans. R. ent. Soc. Lond. 96 : 47-60.

---------- 1947. A natural classification of leafhoppers Part 3. Jassidae. Trans. R. ent. Soc. Lond. 98 : 105-271.

FENNAH, R.G., 1969. British museum (Natural History) Personal communication.

GALLIARD, H., 1935. Recherches sur les rêduviidés hématophages <u>Rhodnius</u> et <u>Triatoma</u> Ann. de Parasitol. Humaine Compar 13 : 497-527.

GIL-FERNANDEZ, C. and BLACK, L.M., 1965. Some aspects of the internal anatomy of the leafhopper <u>Agallia</u> <u>constricta</u>. Ann. ent. Soc. Am. Columbus. 58(3) 275-284.

GOODCHILD, A.J.P., 1952. A study of the digestive system of the West African cacao capsid bugs (Miridae) Proc. zool.

HELMS, T.J., 1968. Postembryonic reproductive systems development in Empoasca fabae. Ann. ent. Soc. Am. Colombus. 61(2) 316-332.

IMMS, A.D., revised by RICHARDS, O.A. and DAVIES, R.G., 1957. A general textbook of entomology. London Methuen & Co.

JOHANNSEN, O.A. and BUTT, F.H., 1941. Embryology of insects and myriapods. Mc. Graw-Hill Book Co. Inc. New York and London. 462 pp.

KELTON, L.A., 1955A. Genera and subgenera of the Lygus complex (Miridae) Can. Ent. Ottawa. 87(7) 277-301.

---------- 1955B. Species of Lygus, Liocoris and their allies in the prairie provinces of Canada. (Miridae) Can. Ent. Ottawa. 87(12) 531-556.

---------- 1959. Male genitalia as taxonomic characters in the Miridae (Heteroptera) Can. Ent. Ottawa. 91 Suppl. 11 : 1-72.

KEMPTHORNE, O., 1952. The design and analysis of experiments. J. Wiley and Sons Inc. New York.

KNIGHT, H.H., 1921. Monograph of the North American species of Deraeocoris - Heteroptera, Miridae. Univ. Minnesota Agric. Expt. St. Tech. Bull. 1 : 76-210.

---------- 1923. The Miridae of Connecticut. In : The Hemiptera or sucking insects of Connecticut by W. Britton. Conn. Geol. & Nat. Hist. Surv. Bull. 34 : 422-658.

KRAMER, J.P., 1963. A key to the new world genera of Iassinae, with reviews of Scariodana and Pachyopsis Bull. Brooklyn ent. Soc. 63(2 & 3) 37-50.

KULLENBERG, B., 1944. Studien über die Biologie der Capsiden. Zool. Bid. Fran. Uppsala. 23 : 1-522.

---------- 1947. Über morphologie und funktion des kopulationsapparats per Capsiden und Nabiden. Zool. Bid. Fran. Uppsala. 24 : 217-418.

KUNZE, L., 1959. Die funktionsanatomischen grundlagen der kopulation der Zwergzikaden, untersucht an Euscelis plebejus (Fall.) und einigen Typhlocybinen. Dtsch.

LARSEN, O., 1945. Der thorax der Heteropteren; skelett und muskulatur. Acta Univ. Lund. (N.F.) Avd. 2, 41(3) 1-96.

LESTON, D., 1961. Testis follicle number and the higher systematics of Miridae. Proc. zool. Soc. London 137(1) 89-106.

LESTON, D., PENDERGRAST, J.G. and SOUTHWOOD, T.R.E., 1954. Classification of the terrestrial Heteroptera. Nature, London. 174 : 90-91.

LINNAVUORI, R., 1957. Remarks on the Iassinae. Ann. ent. fenn. Helsinki. 23(3) 144-149.

---------- 1961. South African Cicadellidae. South African Animal Life 8 : 452-486.

MAC CREADY, D., 1965. Flight range observations on *Lygus lineolarius* and certain other Hemiptera. J. econ. Ent. Baltimore. 58(5) 1004-5.

MEDLER, J.T., 1942. The leafhoppers of Minnesota. Univ. Minn. Ag. Exptal. Stn. Tech. Bull. 155 : 1-196.

MICHENER, C.D., 1944. A comparative study of the appendages of the eighth and ninth abdominal segments of insects. Ann. ent. Soc. Am. Colombus. 37 : 331-351.

NAUDÉ, T.J., 1923. Cicadellidae of South Africa. Thesis. Ohio State University.

NIXON, G.E.J., 1947. Euphorine parasites of capsid and lygaeid bugs in Uganda. (Braconidae) Bull. ent. Res. London. 37 : 113-129.

ODHIAMBO, T.R., 1959. Notes on the East African Miridae XII. Ann. Mag. nat. Hist. London. 13(2) 421-438.

---------- 1960. Taxonomic notes on three species of Mirinae including the descriptions of two new species. Proc. R. ent. Soc. London. (B) 29(9-10) 120-126.

OSSIANNILSSON, F., RUSSELL, L.M. and WEBER, H., 1956. Taxonomists glossary of genitalia in insects. 27. Homoptera. pp. 148-158. Munksgraad Copenhagen.

OSSOWSKI, L.L.J., 1950-1960. Annual reports of the Wattle Research Institute. University of Natal. Pietermaritzburg

PENDERGRAST, J.G., 1958. Studies on the reproductive organs of the Heteroptera with a consideration of their bearing on classification. Trans. R. ent. Soc. Lond. 109 : 1-63.

POLLARD, D.G., 1968. Stylet penetration and feeding damage of Eupteryx mellisae Curtis (Hemiptera : Cicadellidae) on sage. Bull. ent. Res. London. 58(1) 55-71.

POPPIUS, B., 1912. Die Miriden der Äthiopischen Region I Mirina Cylapina Bryocorina. Acta Soc. Sci. fenn. Helsinki 41(3) 76.

RIPLEY, L.B., 1926. Fmg. S. Afr. Pretoria. 1 : 17.

---------- 1927. "Froghopper" in wattles. Fmg. S.Afr. Pretoria. 2 : 423.

---------- 1929. Farm. in S. Afr. Pretoria. 4 : 239-40.

RIPLEY, L.B. and PETTY, B.K., 1940. Dusting for "froghopper" in wattles. Fmg. S. Afr. Pretoria. 15 : 218.

SCUDDER, G.G.E., 1959. The female genitalia of the Heteroptera : morphology and bearing on classification. Trans. R. ent. Soc. Lond. 111(4) 405-467.

SHERRY, S.P., 1968. The black wattle Acacia mearnsii (de Wild) PhD. Thesis Univ. Natal. Pietermaritzburg.

SINGH-PRUTHI, H., 1925. The morphology of the male genitalia in Rhynchyta Trans. R. ent. Soc. Lond. 1925 : 127-267.

SLATER, J.M., 1951. An investigation of the female genitalia as taxonomic characters in the Miridae (Hemiptera) Iowa St. Coll. J. Sci. 25 : 1-81.

SMITH, K.M., 1926. A comparative study of the feeding methods of certain Hemiptera and of the resulting effects upon the plant tissue, with special reference to the potato plant. Ann. appl. Biol. 13 :109-139.

SNODGRASS, R.E., 1935. Principles of insect morphology. Mc Graw Hill, New York.

---------- 1957. A revised interpretation of the external reproductive organs of male insects. Smitson. misc. Coll. Washington. 135(6) 1-60.

---------- 1955. The morphology of the salivary glands of the terrestrial Heteroptera and its bearing on classification. Tijdschr. Ent. Amsterdam. 98 : 77-84.

---------- 1960. The flight activity of Heteroptera. Trans. R. ent. Soc. Lond. 112(8) 173-220.

TAYLOR, L.H., 1918. The thoracic sclerites of Hemiptera and Heteroptera. Ann. ent. Soc. Am. Columbus. 11 : 225-254.

TAYLOR, T.H.C., 1945. Lygus simonyi as a cotton pest in Uganda. Bull. ent. Res. London. 36 : 121-148.

---------- 1947. Some East African species of Lygus with notes on their host plants. Bull. ent. Res. London. 38 : 233-258.

WOODWARD, T.E., 1950. Ovariole and testis follicle numbers in Heteroptera. Ent. mon. Mag. London 86 : 82-84.

---------- 1952. Studies in the reproductive cycle of three species of British Heteroptera with special reference to the overwintering stages. Trans. R. ent. Soc. Lond. 103(5) 171-218.

YOUNG, D.A., 1952. A reclassification of western hemisphere Typhlocybinae (Cicadellidae) Univ. Kansas Sci. Bull. 35(1) 3-217.

1. External body measurements from adults of *L. laevigatum* and *B. cedaranus*. All measurements in millimetres.

surement	*L. laevigatum*								*B. cedaranus*							
	Male				Female				Male				Female			
	n,	Max.,	Min.,	Mean	n,	Max.,	Min.,	Mean	n,	Max.,	Min.,	Mean	n,	Max.,	Min.,	Mear
gth excluding wings	20	3.77	2.94	3.20	20	3.72	3.09	3.37	20	5.76	4.02	4.74	20	6.18	4.70	5.46
ross head	10	1.03	0.92	0.99	10	1.01	0.97	0.99	10	1.47	1.38	1.42	10	1.60	1.49	1.56
gth - dorsal view	-	-	-	-	-	-	-	-	10	0.17	0.14	0.15	10	0.16	0.15	0.15
f face	10	0.71	0.59	0.65	10	0.71	0.67	0.69	10	1.08	0.98	1.04	10	1.13	0.98	1.08
tween eyes	10	0.29	0.25	0.26	10	0.39	0.33	0.35	10	0.88	0.83	0.87	10	1.01	0.90	0.96
eye	10	0.39	0.34	0.37	18	0.34	0.29	0.32	20	0.32	0.25	0.28	20	0.33	0.24	0.29
ross pronotum	10	1.44	1.28	1.38	10	1.54	1.40	1.48	10	1.73	1.59	1.67	10	1.91	1.75	1.84
ength pronotum	10	0.86	0.69	0.77	10	0.88	0.76	0.85	10	0.97	0.82	0.87	10	1.00	0.88	0.93
h across hemelytra	10	1.71	1.52	1.58	10	1.81	1.64	1.73	10	1.96	1.72	1.85	10	2.13	1.90	2.00
a length	25	3.45	3.06	3.28	38	3.57	3.19	3.44	40	4.31	3.91	4.06	37	4.75	4.17	4.52
segment I	18	0.29	0.25	0.28	20	0.29	0.25	0.26	-	-	-	-	-	-	-	-
segment II	16	1.30	0.98	1.25	19	1.12	0.99	1.08	-	-	-	-	-	-	-	-
segment III	15	0.67	0.54	0.61	18	0.69	0.60	0.65	-	-	-	-	-	-	-	-
segment IV	12	0.46	0.37	0.43	14	0.46	0.43	0.44	-	-	-	-	-	-	-	-
xcluding Segs. I and II	-	-	-	-	-	-	-	-	17	0.43	0.28	0.38	19	0.49	0.32	0.41
length	10	1.22	1.08	1.139	10	1.23	1.14	1.18	10	0.49	0.34	0.43	10	0.52	0.39	0.46

Appendix 2. Body length and head width, in millimetres, of nymphs.

L. laevigatum		Body length			Head width		
Nymph instar	n,	Max.,	Min.,	Mean	Max.,	Min.,	Mean
I newly hatched	10	0.69	0.49	0.59	0.30	0.27	0.29
I after feeding	10	0.94	0.83	0.88	0.31	0.29	0.30
II	20	1.35	1.05	1.19	0.43	0.39	0.41
III	20	1.80	1.37	1.65	0.55	0.51	0.53
IV	20	2.40	1.91	2.14	0.71	0.64	0.68
V	20	3.09	2.51	2.78	0.88	0.79	0.84
B. cedaranus		Body length			Head width		
Nymph instar	n,	Max.,	Min.,	Mean	Max.,	Min.,	Mean
I newly hatched	10	1.06	0.87	0.94	0.47	0.43	0.45
I after feeding	10	1.35	1.08	1.16	0.49	0.41	0.45
II	20	1.81	1.32	1.56	0.65	0.58	0.61
III	20	2.33	1.64	2.05	0.86	0.76	0.81
IV	20	3.39	2.43	2.89	1.13	0.94	1.06
V	20	5.44	3.53	4.54	1.52	1.26	1.36

Appendix 3. Mean weekly temperatures, in degrees Centigrade, for Bloemendal experimental station July 1966 - June 1967.

Week Ending	Max. Mean	Min. Mean	Means Av.	Week Ending	Max. Mean	Min. Mean	Means Av.
1966 July 3	24.6	8.6	16.6	1967 January 1	28.8	15.2	22.0
10	22.0	4.1	13.1	8	24.8	15.0	19.9
17	22.1	3.9	13.0	15	24.9	14.6	19.8
24	21.2	5.2	13.2	22	27.1	17.2	22.2
31	20.3	3.9	12.1	29	27.4	15.8	21.6
August 7	21.6	7.5	14.6	February 5	24.4	15.9	20.2
14	24.9	6.8	15.9	12	25.9	16.9	21.4
21	18.1	7.2	12.7	19	27.1	16.1	21.6
28	26.3	6.5	16.4	26	24.5	14.5	19.5
September 4	22.9	8.6	15.8	March 5	25.0	15.6	20.3
11	23.4	7.8	15.6	12	27.9	15.0	21.4
18	20.9	8.7	14.8	19	23.9	12.9	18.4
25	23.9	9.9	16.9	26	24.3	13.9	19.1
October 2	23.6	10.9	17.3	April 2	24.5	14.0	19.3
9	26.1	12.7	19.4	9	24.7	12.6	18.7
16	19.6	9.7	14.7	16	24.3	13.6	19.0
23	19.2	8.5	13.9	23	20.9	11.6	16.3
30	27.4	13.3	20.4	30	23.9	11.1	17.5
November 6	24.7	16.2	20.5	May 7	23.3	10.1	16.7
13	22.4	12.6	17.5	14	23.9	10.4	17.2
20	25.0	13.0	19.0	21	21.9	7.6	14.8
27	23.4	12.9	18.2	28	20.6	6.1	13.4
December 4	26.7	13.7	20.2	June 4	18.4	8.1	13.3
11	26.0	15.9	21.0	11	21.0	5.1	13.1
18	25.1	13.8	19.5	18	17.9	1.1	9.5
25	26.8	15.4	21.1	25	21.6	5.0	13.3

Appendix 4. Mean weekly temperatures in degrees Centigrade, for Bloemendal experimental station July 1967 - June 1968.

Week Ending	Max. Mean	Min. Mean	Means Av.	Week Ending	Max. Mean	Min. Mean	Means Av.
1967 July 2	21.2	5.9	13.6	31	27.1	14.9	21.0
9	18.1	2.8	10.5	1968 January 7	30.1	16.5	23.3
16	15.3	2.5	8.9	14	25.5	15.4	20.5
23	18.6	2.3	10.5	21	27.0	16.0	21.5
30	21.7	2.6	12.2	28	23.7	15.5	19.6
August 6	24.5	6.3	15.4	February 4	24.9	14.6	19.8
13	21.6	6.3	14.0	11	28.8	16.2	22.5
20	19.4	5.7	12.6	18	26.2	14.9	20.6
27	24.1	5.6	14.9	25	24.2	13.6	18.9
September 3	24.9	10.6	17.8	March 3	23.9	15.0	19.5
10	21.2	10.3	15.8	10	24.1	15.8	20.0
17	26.5	9.7	18.1	17	22.1	13.1	17.6
24	21.4	8.4	14.9	24	26.3	16.2	21.3
October 1	25.7	9.9	17.8	31	20.6	11.4	16.0
8	23.1	8.8	16.0	April 7	21.0	11.6	16.3
15	24.5	10.9	17.7	14	22.5	11.8	17.2
22	29.2	13.2	21.2	21	23.1	10.1	16.6
29	19.2	11.4	15.3	28	20.4	5.4	12.9
November 5	25.2	13.2	19.2	May 5	23.7	6.9	15.3
12	26.4	15.7	21.2	12	23.6	9.9	16.8
19	21.4	12.9	17.2	19	15.4	7.0	11.2
26	25.8	14.4	20.1	26	19.6	6.3	13.0
December 3	25.8	14.7	20.3	June 2	20.9	4.9	12.9
10	25.0	14.1	19.6	9	18.6	2.1	10.4
17	24.6	12.1	18.4	16	17.6	3.2	10.4
24	26.6	14.7	20.7	23	16.8	0.3	8.6

Appendix 5. Mean weekly temperatures, in degrees Centigrade, for Bloemendal experimental station July 1968 - June 1969.

Week Ending		Max. Mean	Min. Mean	Means Av.	Week Ending		Max. Mean	Min. Mean	Means Av.
1968					1969				
June	30	19.6	1.7	10.7	January	5	26.8	15.9	21.4
July	7	19.4	4.7	12.1		12	30.1	15.0	22.6
	14	19.4	3.4	11.4		19	27.9	15.6	21.8
	21	23.6	5.0	14.3		26	32.2	16.7	24.5
	28	23.0	5.7	14.4	February	2	30.6	18.4	24.5
August	4	21.3	6.6	14.0		9	29.4	17.7	23.6
	11	19.9	6.9	13.4		16	25.5	15.0	20.3
	18	19.0	7.1	13.1		23	26.5	16.9	21.7
	25	20.5	8.1	14.3	March	2	29.0	17.9	23.5
September	1	21.1	8.6	14.9		9	30.0	17.4	23.7
	8	21.4	7.4	14.4		16	23.2	14.1	18.7
	15	24.5	10.4	17.5		23	25.3	15.1	20.2
	22	25.9	9.9	17.9		30	22.9	13.1	18.0
	29	21.9	7.1	14.5	April	6	22.6	11.8	17.2
October	6	18.5	8.0	13.3		13	23.6	12.3	18.0
	13	24.4	11.0	17.7		20	23.4	12.9	18.2
	20	27.5	11.1	19.3		27	20.6	10.9	15.8
	27	19.1	11.5	15.3	May	4	21.9	10.7	16.3
November	3	23.7	12.6	18.2		11	18.8	7.9	13.4
	10	27.4	14.4	20.9		18	20.7	8.8	14.8
	17	16.3	7.3	11.8		25	17.6	8.7	13.2
	24	25.8	13.8	19.8	June	1	19.4	5.4	12.4
December	1	24.1	13.3	18.7		8	18.9	7.3	13.1
	8	26.4	15.6	21.0		15	16.9	5.9	11.4
	15	26.4	13.6	20.0		22	17.9	3.1	10.5
	22	30.5	16.4	23.5		29	20.6	4.4	12.5
	29	27.7	17.3	22.5					

Appendix 6.

Mean hourly values of relative humidity (%) and temperature(°C) at Bloemendal 1967.

Hours		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Yea
0100	%	87	93	93	91	87	78	76	76	83	89	85	89	86
	°C	17.1	16.6	15.8	14.2	12.0	9.2	8.0	10.6	11.0	11.1	13.4	13.7	12.
0200	%	90	92	93	91	87	78	77	75	83	89	85	89	86
	°C	16.9	16.4	15.7	13.9	11.7	8.8	7.5	10.3	10.5	10.9	13.3	13.6	12.
0300	%	91	92	93	92	87	78	76	73	82	90	86	90	86
	°C	16.6	16.3	15.6	13.5	11.3	8.5	7.2	10.0	10.4	10.6	13.2	13.5	12.
0400	%	92	91	94	90	87	77	76	75	81	90	86	90	86
	°C	16.4	16.1	15.3	13.4	11.0	8.5	6.8	9.8	10.1	10.5	12.9	13.3	12.
0500	%	91	92	93	91	88	78	76	75	81	88	89	89	86
	°C	16.4	16.0	15.0	13.1	10.4	8.1	6.4	9.3	9.9	10.5	12.9	13.4	11.
0600	%	90	92	93	91	88	77	75	76	81	87	88	88	85
	°C	16.8	16.2	15.0	13.0	10.1	8.0	6.0	9.0	9.9	11.4	13.5	14.5	12.
0700	%	85	88	92	89	86	79	75	75	79	83	83	85	83
	°C	18.0	17.3	15.7	13.9	10.8	7.9	6.1	9.5	11.2	13.0	15.1	16.1	12.
0800	%	79	82	87	84	83	76	71	69	71	71	76	73	77
	°C	19.5	18.7	17.1	15.4	12.3	9.2	7.1	11.9	13.2	14.8	16.5	18.0	14.
0900	%	72	76	78	76	76	67	69	57	60	60	72	65	69
	°C	21.0	20.1	19.0	16.8	14.4	11.7	8.8	15.1	16.1	17.0	18.1	19.4	16.
1000	%	67	69	72	71	67	56	59	46	51	54	67	59	61
	°C	22.2	21.2	20.6	18.2	16.6	14.2	11.1	17.5	17.9	18.5	19.2	21.0	18.
1100	%	64	67	68	64	55	48	49	37	42	50	64	54	55
	°C	23.1	22.0	21.5	19.6	18.5	16.2	13.4	19.2	19.3	19.7	20.2	21.9	19.
1200	%	62	66	62	59	49	42	43	35	40	48	61	52	52
	°C	23.7	22.7	22.6	20.7	19.6	17.5	15.1	20.7	20.0	20.2	20.5	22.6	20.
1300	%	61	65	62	58	47	39	39	32	39	49	61	52	50
	°C	24.3	23.4	23.1	21.2	20.2	18.3	16.2	21.4	20.4	19.8	20.3	22.6	20.
1400	%	63	67	63	59	49	37	36	32	40	53	64	55	51
	°C	24.0	22.9	23.0	21.5	20.2	18.6	17.1	21.3	20.4	19.2	20.0	22.2	20.
1500	%	66	74	66	65	54	37	36	35	43	57	69	61	55
	°C	23.4	22.4	22.3	20.4	19.6	18.4	17.2	20.2	18.8	18.1	18.9	21.0	20.
1600	%	70	80	76	69	62	41	38	40	50	62	73	67	61
	°C	22.6	21.1	21.0	19.5	18.1	17.1	16.5	19.1	17.9	16.8	18.1	19.9	19.
1700	%	77	87	82	78	73	50	45	49	58	69	76	73	68
	°C	21.3	19.9	19.6	18.2	16.2	15.0	15.1	17.0	16.1	15.4	17.2	18.5	17.
1800	%	83	91	88	83	79	56	51	58	69	77	80	76	74
	°C	19.7	18.6	18.3	16.8	15.0	13.8	13.6	15.0	14.2	14.0	16.3	17.2	16.
1900	%	87	93	91	86	83	61	57	68	77	84	84	80	79
	°C	18.8	17.9	17.4	16.1	14.3	12.7	12.5	13.9	13.2	13.0	15.3	15.9	15.
2000	%	89	93	93	87	85	64	63	71	81	88	83	86	82
	°C	18.1	17.5	17.0	15.6	13.8	12.1	11.0	13.2	12.4	12.4	15.0	15.2	14.
2100	%	90	93	93	89	86	69	69	72	81	89	83	87	84
	°C	17.8	17.3	16.6	15.2	13.6	11.2	10.3	12.6	12.1	12.0	14.6	14.9	14.
2200	%	91	91	94	90	87	73	72	73	81	89	83	88	84
	°C	17.5	17.2	16.4	15.0	13.0	10.5	9.7	12.3	11.8	11.7	14.3	14.6	13.
2300	%	90	91	94	90	88	75	73	73	83	89	83	89	85
	°C	17.3	17.0	16.2	14.6	12.6	10.1	9.2	11.7	11.4	11.4	14.1	14.1	13.
2400	%	88	90	94	91	89	76	75	75	83	90	84	89	85
	°C	17.2	17.0	16.1	14.4	12.2	9.6	8.8	11.2	11.2	11.1	13.9	13.8	13.
Mean	%	80	84	84	81	76	63	61	60	67	75	78	76	74
	°C	19.6	18.8	18.2	16.4	14.5	12.3	10.9	14.2	14.1	14.3	16.1	17.1	15.

Appendix 7.

To test whether the observed change in female fecundity in a population of <u>L. laevigatum</u>, during the period February to August 1967, was significant each month.
Data transformed: square-root transformation : $y = \sqrt{(x + \frac{1}{2})}$
Based on number of mature eggs per female, determined by dissection.

	T1 FEBRUARY	T2 MARCH	T3 APRIL	T4 MAY	T5 JUNE	T6 JULY	T7 AUGUST
n	69	80	70	64	80	26	81
Treatment Totals	270.94	282.39	175.18	143.54	165.91	58.62	222.98
Treatment Means	3.92666	3.52987	2.50257	2.23812	2.07387	2.25461	2.75283

<u>Analysis of variance</u>

<u>Source</u>	<u>DF</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>F required</u>
Months	6	206.67	34.45	35.8	2.80 (P=0.01)
<u>Error</u>	<u>463</u>	<u>445.13</u>	0.96		
Total	469	651.80			

Standard error of a single yield (transformed) = 0.9805
Coefficient of variation (transformed data) = 34.93%

t test results (t has 463 degrees of freedom) for transformed data.

	value of t	
T1 vs T2	2.46	*
T2 vs T3	6.40	***
T3 vs T4	1.56	NS
T4 vs T5	1.00	NS
T5 vs T6	0.82	NS
T6 vs T7	2.25	*
T3 vs T5	2.67	***
T5 vs T7	4.39	**

t values required	P = 0.05	1.960
	P = 0.01	2.576

Appendix 8.

The effect of soil moisture content (and therefore tree condition) on the fecundity of L. laevigatum females feeding on young wattles. (Transformed data based on number of mature eggs per mature female sampled at each site. Transformation $y = \sqrt{x + \frac{1}{2}}$). Data from Kirkfalls, Hillcrest, 1st July 1969.

Site		Water content of soil (by weight)
A	Hill top	11.1%
B	Hill slope below A	17.0%
C	Base of slope	25.8%

Site	A	B	C
n	27	19	36
Treatment totals	82.94	56.92	127.67
Treatment means	3.0719	2.9958	3.5460

Analysis of variance

Source	DF	SS	MS	F	F required
Treatments	2	5.234	2.617	4.73	3.15 and 4.98
Error	79	43.678	0.553		
Total	81	48.912			

Standard Error of a single yield (transformed data) = 0.744

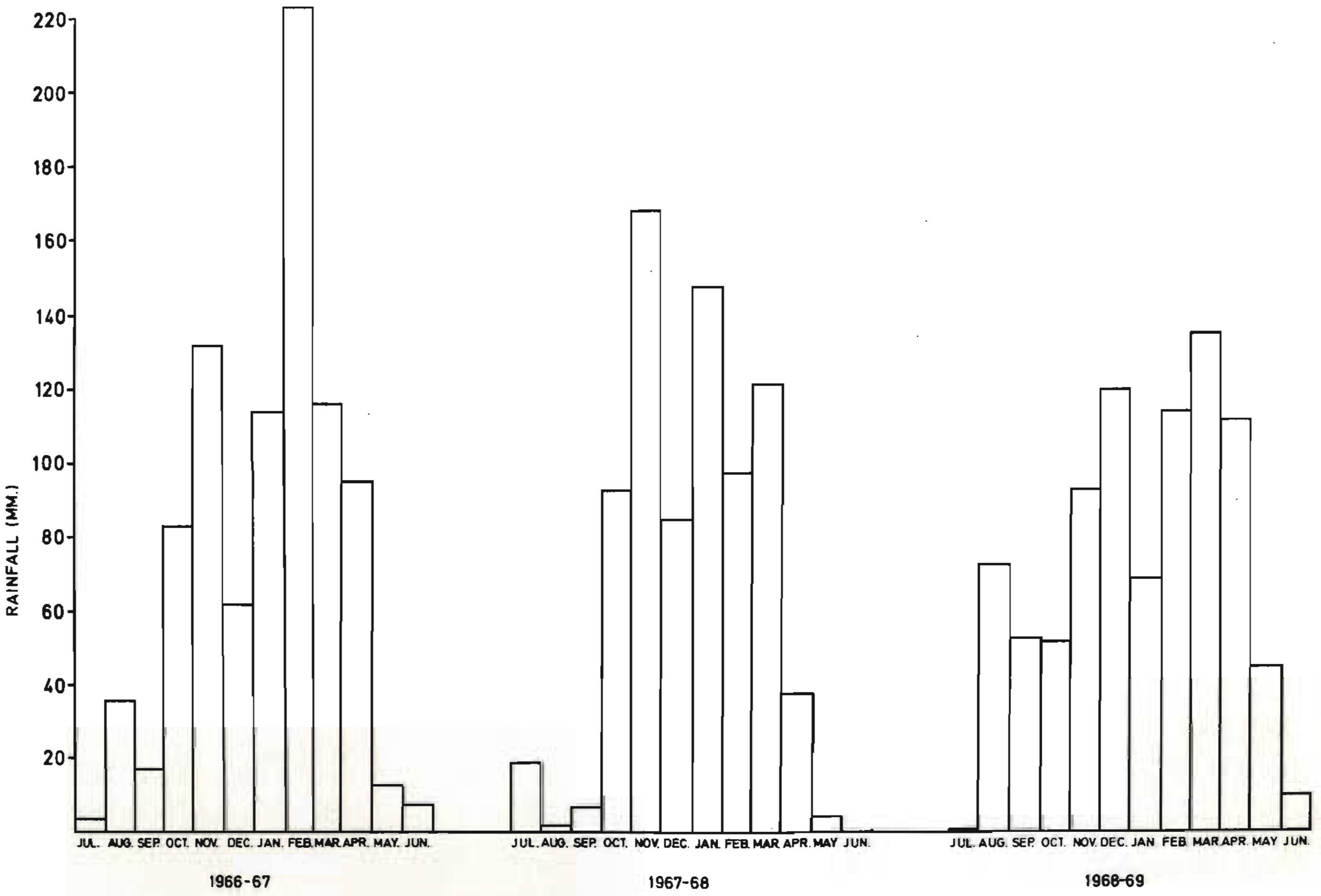
Coefficient of variation (transformed data) = 22.79%

t test results (transformed data) with 79 degrees of freedom.

Site	Value of t	
A vs B	0.342	NS
B vs C	2.611	*
A vs C	2.733	**

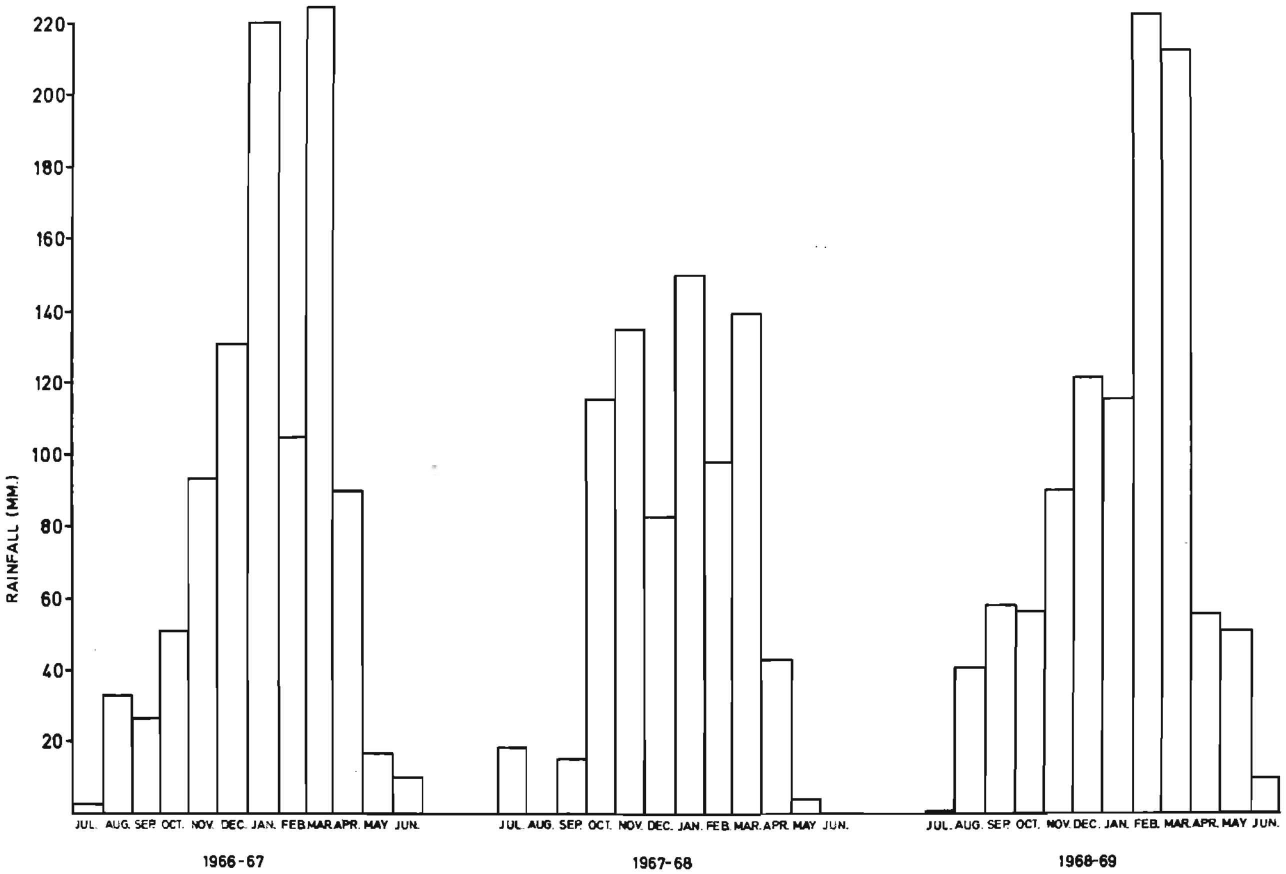
Required value of t(79DF)		
	P = 0.05	2.000
	P = 0.01	2.660

APPENDIX 9



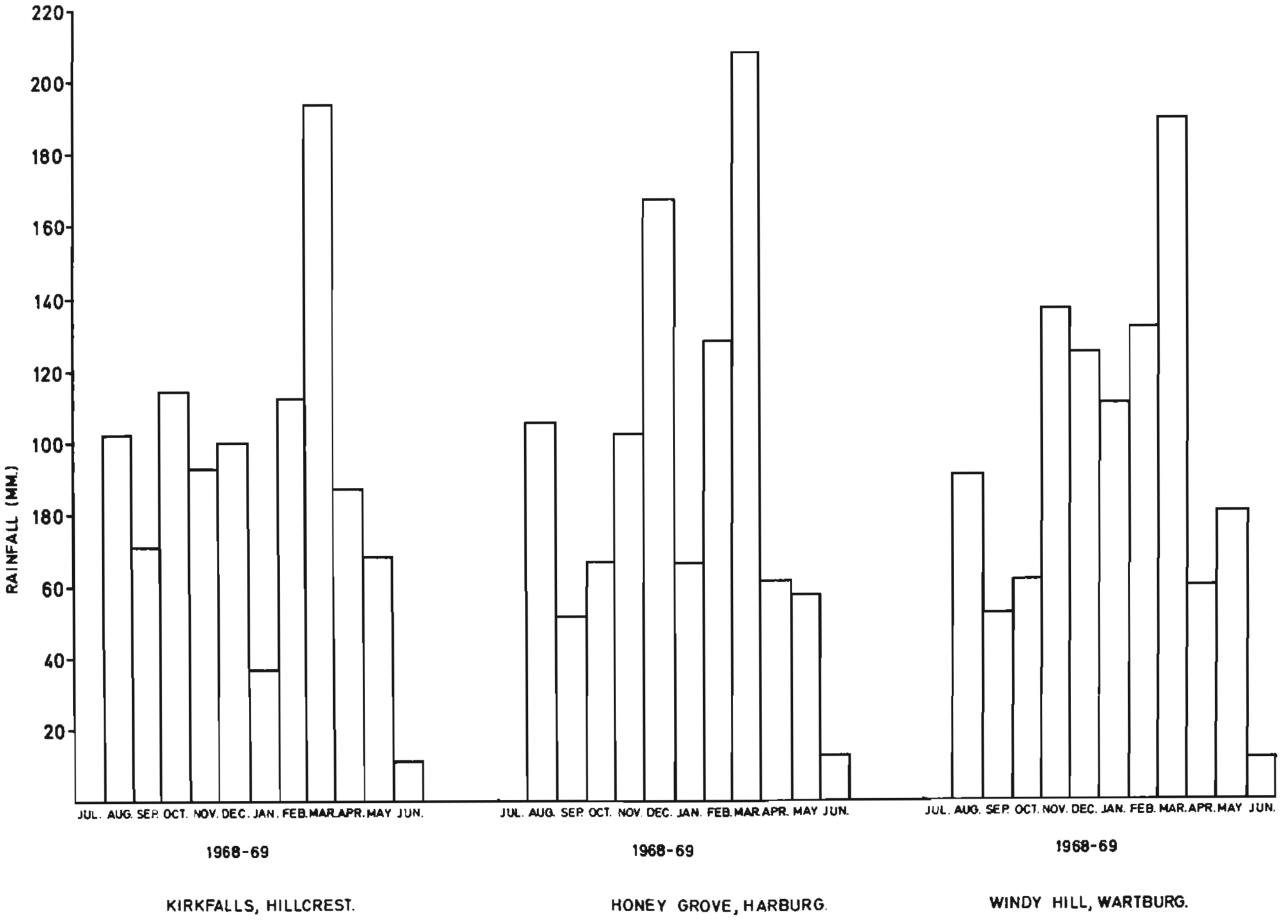
MONTHLY RAINFALL FIGURES. BLOEMENDAL EXPT. STN. PIETERMARITZBURG.

APPENDIX 10



MONTHLY RAINFALL FIGURES. HARDEN HEIGHTS, SEVEN OAKS.

APPENDIX 11



MONTHLY RAINFALL FIGURES.

Appendix 12.

Sampling results, based on adults of *L. laevigatum*, from each plot during insecticide trial I (§ 8.2.3.2).

	Replication				
	1	2	3	4	5
Treatment 1					
Before spraying	24	20	22	10	8
4 days after	25	33	26	12	11
8 days after	23	18	19	13	12
12 days after	7	4	13	6	3
Treatment 2					
Before spraying	21	28	14	12	10
4 days after	1	7	7	2	10
8 days after	3	12	11	3	6
12 days after	0	5	6	7	8
Treatment 3					
Before spraying	23	11	10	13	9
4 days after	8	3	9	4	5
8 days after	13	4	6	2	5
12 days after	2	1	3	4	11
Treatment 4					
Before spraying	22	17	5	18	24
4 days after	20	32	9	5	21
8 days after	11	13	27	13	14
12 days after	1	4	4	11	9
Treatment 5					
Before spraying	10	30	14	15	5
4 days after	11	13	4	2	10
8 days after	12	32	7	17	11
12 days after	4	6	4	3	5

Treatment 1 Control
" 2 Dimethoate (40% e.c.) 2.4 fl.oz per morgen
" 3 Sevin (85% w.p.) 0.2 lb a.i. per morgen

Appendix 13.

Analysis of data collected during insecticide Trial I (§ 8.**2.3.1**). Data based on numbers of L. laevigatum adults collected from five-tree samples within each plot.

/ Data transformed y = Log (x + 1) /

x = before spray sample totals.

y = 4 days after spraying sample totals.

		Treatments					
Blocks		T1	T2	T3	T4	T5	Block Totals
1	x	1.40	1.34	1.38	1.36	1.04	6.52
	y	1.41	0.30	0.95	1.32	1.08	5.06
2	x	1.32	1.46	1.08	1.26	1.49	6.61
	y	1.53	0.90	0.60	1.52	1.15	5.70
3	x	1.36	1.18	1.04	0.78	1.18	5.54
	y	1.43	0.90	1.00	1.00	0.70	5.03
4	x	1.04	1.11	1.15	1.28	1.20	5.78
	y	1.11	0.48	0.70	0.78	0.48	3.55
5	x	0.95	1.04	1.00	1.40	0.78	5.17
	y	1.08	1.04	0.78	1.34	1.04	5.28
Treatment Totals	x	6.07	6.13	5.65	6.08	5.69	29.62
	y	6.56	3.62	4.03	5.96	4.45	24.62

Analysis of variance and covariance

Fx 0.03 Fy 6.21 **

b = 0.1966

Test of significance of error regression

Appendix 14.

To compare the effectiveness of four insecticide treatments against L. laevigatum in young wattles (transformed data based on numbers of live adults sampled) four and eight days after spray application. Insecticide Trial I May 1967 (§ 8.2.3.2).

a) Four days after spray application.

Treatment	1	2	3	4	5
Treatment totals	6.56	3.62	4.03	5.96	4.45

F = 6.21 **

Standard Error of a single transformed treatment yield = 0.2283
Coefficient of variation (transformed data) = 23.2%
S. E. of a single transformed treatment total = 0.5104
LSD's (Two treatment totals) :

P = 0.05 - - - 1.53
P = 0.01 - - - 2.11

b) Eight days after spray application.

Treatment	1	2	3	4	5
Treatment totals	6.22	4.24	3.96	6.01	5.87

F = 5.5 **

Standard error of a single transformed treatment yield = 0.2042
Coefficient of variation (transformed data) = 19.41%
S.E. of a single transformed treatment total = 0.4566
LSD's (Two treatment totals) :

P = 0.05 - - - 1.37
P = 0.01 - - - 1.89

Appendix 15.

Sampling results based on adults and nymphs of L. laevigatum from each plot during insecticide trial II (§ 8.2.3.2).

Samples: A 1 day after spraying
B 8 days after spraying
C 15 days after spraying

Treatment		Replications				
		1	2	3	4	5
C	A	28	16	22	11	45
	B	48	40	25	4	43
	C	61	47	73	28	75
D6	A	0	3	3	3	3
	B	5	3	2	2	2
	C	18	27	20	9	24
D12	A	1	4	3	0	1
	B	7	4	5	3	10
	C	13	21	10	6	9
M6	A	2	5	6	5	4
	B	14	8	4	8	7
	C	38	53	19	13	35
M12	A	3	4	3	4	0
	B	17	4	5	4	8
	C	27	34	37	13	7

Treatment C Control
" D6 Dimethoate 6 fl.oz. per morgen
" D12 " 12 fl.oz. per morgen
" M6 Metasystox 6 fl.oz. per morgen
" M12 " 12 fl.oz. per morgen

Appendix 16.

Sample results based on nymphs only (of L. laevigatum) from each plot during insecticide trial II (§ 8.2.3.2).

Sample	A	1 day after sampling
"	B	8 days after sampling
"	C	15 days after sampling

Treatment		Replications				
		1	2	3	4	5
C	A	14	9	8	3	20
	B	32	19	13	1	22
	C	34	18	55	20	47
D6	A	0	0	0	1	2
	B	0	0	0	0	0
	C	10	16	14	2	11
D12	A	0	2	0	0	0
	B	0	0	0	0	3
	C	2	9	2	0	3
M6	A	0	0	1	1	0
	B	0	1	0	0	1
	C	25	46	13	7	29
M12	A	0	3	0	0	0
	B	0	0	0	0	0
	C	14	23	20	8	3

Treatments	C	Control	
"	D6	Dimethoate	6 fl.oz. per morgen
"	D12	"	12 fl.oz. per morgen
"	M6	Metasystox	6 fl.oz. per morgen
"	M12	"	12 fl.oz. per morgen

Appendix 17.

To compare the effectiveness of two insecticides each at two concentrations, against L. laevigatum in wattles. (Data based on numbers of adults and nymphs collected from each plot.) Trial II (§ 8.2.3.2).

a) One day after spray

Treatment	2	3	4	5
Treatment totals	12	9	22	14

S.E. of a single yield = 1.27
Coefficient of variation = 44.6%
LSD's (two treatment totals) = 8.7 ($P = 0.05$)
= 12.2 ($P = 0.01$)

b) Eight days after spray

Treatment	2	3	4	5
Treatment totals	14	29	41	38

S.E. of a single yield = 2.67
Coefficient of variation = 43.8%
LSD's (two treatment totals) = 18.4 ($P = 0.05$)
= 25.7 ($P = 0.01$)

c) Fifteen days after spray.

Treatment	2	3	4	5
Treatment totals	98	59	158	118

S.E. of a single yield = 8.5
Coefficient of variation = 39.3%
LSD's (two treatment totals) = 58.3 ($P = 0.05$)
= 81.7 ($P = 0.01$)

Appendix 18.

To compare the residual effectiveness within the plant of two systemic insecticides each at two concentrations, against L. laevigatum in young wattles fifteen days after spraying.
(Data based on numbers of nymphs only sampled)
Insecticide trial II (§ 8.2.3.2).

	Treatments				
Blocks	D6	D12	M6	M12	Block totals
1	10	2	25	14	51
2	16	9	46	23	94
3	14	2	13	20	49
4	2	0	7	8	17
5	11	3	29	3	46
Treatment Totals	53	16	120	68	257

Analysis of variance

Source	DF	SS	MS	F
Blocks	4	759		
Treatments	3	1116	372	7.5 **
Error	12	596	49.7	
Total	19	2471		

SE of a single yield = 7.1
Coeff. of variation = 55.3%
LSD's (2 treatment totals) = 48.6 (P = 0.05)
68.1 (P = 0.01)

D12 vs D6	37	NS
D12 vs M12	52	*
D12 vs M6	104	**
D6 vs M6	67	*
M12 vs M6	52	*
D6 & D12 vs M6 & M12	59.5*	