GROWTH AND DEVELOPMENT OF THE WINGS AND GENITALIA OF THE GRASSHOPPER *MELANOPLUS LAKINUS* SCUDDER (ORTHOPTERA, CYRTACANTHACRINAE)

by

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STATEMENT BY AUTHOR

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APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

William L. Nutting — 19 April 1963

WILLIAM L. NUTTING
Professor of Entomology

Date

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TABLE OF CONTENTS

Page

LIST OF FIGURES

ABSTRACT

A morphological study was made of the changes that take place in the thoracic nota, the wings, the terminal abdominal segments of the male, and the female genitalia of the grasshopper Melanoplus lakinus Scudder.

Wing-rudiments first appear in the fourth instar. Tracheae may be seen in the wing pads of the fifth instar. In the sixth instar epidermal cells cluster along the tracheae to form the thickened walls of the future veins. Growth of the wings is probably accomplished by cell division rather than by cell enlargement.

The nymphs of the male are characterized by the development of an enlarged ninth sternite. Those of the female on the other hand are distinguished by the elongation of the lobes of the ovipositor and degeneration of the ninth sternite. The first valvulae, originating from behind the eighth sternite, increase in size more rapidly than the third valvulae. The latter arise from the ninth sternite itself.

INTRODUCTION

Melanoplus lakinus Scudder is an important grasshopper pest in southern Arizona, doing considerable damage to sugar beets and garden flowers. This study was intended both as a basic contribution to the external morphology of the Cyrtacanthacrinae and as a practical aid to the identification of immature stages of both sexes of a single species in this subfamily.

Packard (1898) pointed out that by examination of the nymphs of any species of locust in its successive stages, one could see the wings arising as simple expansions of the postero-lateral edges of the meso- and metanotum. The grasshoppers and other orthopteroid insects are characterized by the gradual, external development of the wings. Comstock (1918) considered this feature of incomplete metamorphosis as being primitive. Holdsworth (1940) studied the wing pads of the early instars of the stonefly *Pteronarcys proteus* Newport and the relationship between the tracheae and the lacunae of the veins. He concluded that the lacunae were not induced by the developing tracheae. In 1942 he reported that the lacunae were not differentiated all at once, but progressively in successive instars. Smart (1956) studied the tracheae of the fore wing pad of the cockroach *Periplaneta americana* (Linn.) and found that development of the tracheae consisted of extra branching and a progressive increase in length and diameter.

Snodgrass (1935a) has provided some basis for an interpretation of the developing parts of the external genitalia in studies on a female cricket, Nemobius sp., and on male and female nymphs of a species of Melanoplus. Else (1934) has also provided material for comparison in a study of the developing male genitalia in Melanoplus differentialis (Thomas).

MATERIALS AND METHODS

Rearing the grasshoppers

The egg pods used were deposited by females of the short-winged form in a laboratory colony during the fall of 1963. Although it is not known whether the eggs of this species undergo a diapause, they were kept in a refrigerator from December 21, 1963, until February 7, 1964, at approximately 9^{o} C.

The grasshoppers were reared in an air-conditioned room at 75^{o} F. One-quart ice-cream cartons (8.5-10.5 x 14 cm.) provided suitable incubation containers when the central disc of the lid was replaced with 32-mesh Saran screening. Each incubator was two-thirds filled with moist sand and two egg pods were placed in each at a depth of one-half inch and approximately in the same position as they had been deposited by the female. The sand was moistened as necessary in order to promote the development of the eggs and to facilitate emergence of the nymphs. Ten such incubators were set up before a south window, where they received several hours of sunlight each day.

Grasshoppers used in the study hatched between May 17 and July 27, 1964. Window screen was sewed with fine wire into cylinders 24 cm. in diameter and 44 cm. high for rearing cages. Pie tins, 25 cm. in diameter, were used for the tops and bottoms of the cages. Wheat seedlings, grown in a layer of soil in the bottom pie tins, served as food for the grasshoppers. Ten to fifteen grasshoppers of approximately the same age were kept in each cage.

It became increasingly difficult to differentiate between the instars, since the grasshoppers molted at different times. This difficulty was overcome by the construction of smaller screen cages. These were cylinders 11 cm. in diameter and 24 cm. high. Wheat seedlings were grown in small plastic pots 13 cm. in diameter which were also used as bottoms for the cages. Petri dishes 14 cm. in diameter were used as covers. In each smaller cage only two grasshoppers were kept so that the ages of the different instars could then be exactly determined. A continuous supply of fresh food was assured by growing wheat seedlings in a number of pie tins and plastic pots. All cages were also kept on a bench in front of the windows. Gangwere (1960) and others have reported that most adult grasshoppers survive best when the temperature during the day is high and the relative humidity is low, and when they are exposed to sunlight for at least a part of each day.

Preparation of wings and genitalia for study

The grasshoppers were first anesthetized by exposure to CO_2. Both the fore and hind wing pads and wings were removed with a razor blade under a dissecting microscope. Some of these structures were stained to bring out certain features. They were washed in distilled water for about eight minutes, then dipped in a 5% aqueous solution of silver nitrate. The wing pads or wings were agitated in the solution in direct sunlight until they darkened to a suitable degree. They were again washed in distilled water and mounted in glycerine-jelly.

A Bausch and Lomb micro-projector was used for drawing the general features of the wing pads and wings. Further details were completed by using a compound microscope. Surface sculpturing on the wing pads and wings was drawn with the aid of a camera lucida.

Representatives of each instar were fixed in Bouin's fluid for twenty-four hours, then preserved in 95% alcohol. For the study of thoracic nota, terminal abdominal segments of the male, or female genitalia, the grasshoppers were pinned out in a wax-bottomed petri dish under 95% alcohol. A camera lucida was used for outlining these structures, while further details were added with the help of a dissecting microscope.

Since it was difficult to see clearly details of the female genitalia in the first instar, it was necessary to stain these specimens briefly in an aqueous solution of acid fuchsin.

RESULTS

Development of the thoracic nota and wings

First three instars (Figs. 1-3). The progressive growth and development of the thoracic nota and wings in each instar were studied and figured in a dorso-lateral view. In the first three instars the pronotum (Th_1) is much larger than the mesonotum (Th_2) or the metanotum (Th_3). The posterior part of the pronotum overlaps approximately one-half the mesonotum. The mesonotum similarly overlaps one-third or less of the metanotum. During this period the pronotum appears to increase somewhat more rapidly in size relative to the other two thoracic nota.

Fourth instar (Fig. 4). Rudiments of the wings appear for the first time as slight lobes on the postero-lateral corners of the meso- and metanotum.

Fifth instar (Figs. 5, 8-9). By this stage the pronotum has increased to such an extent that it completely covers the mesonotum and nearly one-half of the metanotum. The two pairs of wings now appear as distinct wing pads. The hind wings (h) are generally larger and darker and overlap the smaller, lighter fore wings (f). The latter extend back to about the middle of the metanotum while the former reach to about the middle of the first abdominal segment (IT).

Very small tracheal branches may be seen in both the fore (fig. 8a) and hind (fig. 9a) wings at this stage, although no definite veins are present. Snodgrass (1935b) has pointed out that in insects with incomplete metamorphosis the tracheae appear in the wings before the veins are formed. Unfortunately an analysis of the origins and progressive development of individual tracheal branches was beyond the scope of this study. Those which could be seen in the limited material available are indicated by dotted lines in the drawings. Details of the surface sculpturing, which appear to reflect the outlines of epidermal cells in many places, are shown in figs. 8b and 9b.

Large setae arise from thickened areas of the hind wing which foreshadow the veins of the adult wing.

<u>Sixth instar</u> (Figs. 6, 10-11). The pronotum still covers the mesonotum and much of the metanotum. Due to the increase in the size of the fore wing pads only a very small part of the metanotum can be seen. The hind wings still overlap the fore wings. The fore wing pads reach the anterior margin of the second abdominal segment (IIT), while the hind wing pads reach the posterior margin of the same segment.

A fore wing of this instar is shown in fig. 10a. As the wing increases in size, more and larger tracheal branches can be seen.

Figure 10b shows the surface sculpturing in the same part of the posterior margin of the wing. Figure 11a, b shows similar developments in the hind wing of this instar. The setae on the future wing veins have also increased in number.

In the fore (fig. 10a) and hind (fig. 11a) wings, the tracheal branches are now surrounded by clusters of epidermal cells indicated by the dotted lines. This was noted by Snodgrass (1935b) who pointed out that these epidermal cells form the thick cuticular layers that are to constitute the walls of the wing veins.

Adult (Figs. 7, 12-13). While the mesonotum is still concealed, the metanotum can be seen clearly in the short-winged adults. The fore wings completely overlap and cover the hind wings and extend as far as the anterior margin of the fourth abdominal segment.

The characteristic shape and venation of an adult fore wing are shown in fig. 12a. The tracheae were not visible within the veins in the preparations studied. The large setae may be seen proximally in the posterior part of the wing as well as on some of the cross-veins. Figure 12b shows the five- and six-sided figures making up the surface sculpturing on the adult fore wing.

Figure 13a, b shows corresponding features of the mature hind wing. The setae here are noticeably shorter. The surface sculpturing of the hind wing is strikingly different, for minute papillae (fig. 13b) are now found in place of the cell-like outlines of the same wing in the previous instar and of the fore wing in the adult.

Development of the terminal segments of the abdomen in the male

First instar (Fig. 14a, b). Dorsally (fig. 14a) the terminal abdominal segments through the ninth and the tenth are clearly visible (VIIIT, IXT and XT). The epiproct (Eppt) is the dorsal element of the eleventh segment. It is approximately conical in shape, with its broad base arising from the posterior margin of the tenth tergite. The cerci (Cer), apparently limb rudiments of the eleventh segment (Snodgrass, 1935a), arise laterally from the base of the tenth tergite. They are relatively large compared with the epiproct and extend considerably beyond it.

In the first instar the ninth sternite (fig. 14b, IXS) is much smaller than the preceding sternites and its posterior margin is concave. Most of the Paraprocts (Papt) are plainly visible, but they are not so long as the epiproct. The cerci are prominent and extend beyond the end of the epiproct.

Second instar (Fig. 15a, b). The only noteworthy changes in this instar are the considerable increase in size of the ninth sternite and the relatively smaller emargination at its tip. As seen ventrally most of the anterior parts of the paraprocts are covered by the ninth sternite. The cerci and the epiproct end at about the same level.

Third instar (Fig. 16a, b). Although the epiproct and paraprocts have maintained approximately the same proportions, the cerci are now definitely shorter than the epiproct. The ninth sternite shows further increase in size and is no longer emarginate apically. Part of the paraprocts protrudes above the ninth sternite. The cerci, although shorter than the epiproct, are still longer than the ninth sternite.

Fourth instar (Fig. 17a, b). At this stage a narrow, deep emargination appears medially on the posterior border of the tenth tergite, foreshadowing development of the furcula. The epiproct and paraprocts remain prominent. The cerci are relatively smaller and no longer have long, tapered tips. They are now considerably shorter than either epiproct or paraprocts.

The ninth sternite (fig. 17b) now shows a very slight upward curvature at the tip, as it begins to take on the shape of the future subgenital plate.

Fifth instar (Fig. 18a, b). As may be seen, rudiments of the furcula (F) show as two small medial lobes on the tenth tergite. The furcula normally develops from the anterior base of the tenth tergite and finally comes to rest upon it (Snodgrass, 1935a).

The cerci continue to decrease in relative size. As a result of its greater dorsal curvature, the tip of the ninth sternite, or distal sternal lobe (IXSL), is now visible from above. A thick membrane, the pallium (Pal), has also developed from the margins of this lobe, the entire structure now forming a genital chamber.

Sixth instar (Fig. 19a, b). The only changes at this stage involve the furcula, which now appears as a pair of well-separated lobes, and the cerci,which have become still shorter and more swollen basally.

Adult (Fig. 20a, b). The epiproct covers much of the paraprocts and the three structures are very nearly equal in size. The pallium has increased greatly so that it now covers the posterior third of the genital chamber. The lobes of the furcula are completely separated and extend posteriorly over the epiproct. The cerci have assumed their characteristic shape which serves as a feature very useful in the identification of this species.

Development of the genitalia in the female

First instar (Fig. 21). Rudiments of the first valvulae of the ovipositor are evident as a pair of flattened lobes (IVL) slightly protruding from behind the eighth sternite. The third valvulae (3VL) arise as conical lobes from the posterior part of the ninth sternite and actually overlap the bases of the paraprocts. The tip of the epiproct can be seen. The cerci extend considerably beyond the tip of the epiproct.

Second instar (Fig. 22). The first valvulae now appear as a pair of pointed processes which overlap more than two-thirds of the ninth sternite. The third valvulae have increased in size so that their medial margins are nearly contiguous. The cerci show a reduction in relative size and only extend for a short distance beyond the tip of the epiproct.

Third instar (Fig. 23). Here the first and third valvulae are approximately equal in size and shape. As the third valvulae have increased in size, the ninth sternite has correspondingly decreased. The cerci have decreased in relative size so as to be approximately equal in length to the epiproct.

Fourth instar (Fig. 24). In this stage the first valvulae cover nearly one-half of the third valvulae, while the latter cover most of the paraprocts. The cerci are smaller in size and no longer protrude beyond the posterior ends of the epiprocts and paraprocts. The posterior margin of the eighth sternite has developed a small median lobe between the bases of the first valvulae, which is the rudimentary egg guide (eg).

Fifth instar (Fig. 25). Nearly all of the ninth sternite and most of the third valvulae are now covered by the first valvulae. The paraprocts in their normal position are concealed ventrally by the third valvulae. The cerci show further degeneration.

Sixth instar (Fig. 26). The posterior ends of the first valvulae approach those of the third valvulae while the latter completely cover the paraprocts ventrally. The cerci can no longer be seen in ventral view although the size and shape of the left cercus is indicated by dotted lines.

The eighth sternite has increased considerably and the egg guide actually extends beyond the posterior margin of the now rudimentary ninth sternite.

Adult (Fig. 27). The first and third valvulae have both become approximately equal in length. The posterior ends of each are sclerotized and darkly pigmented. The cerci are extremely short and cannot be seen ventrally. The epiproct and paraprocts are also shorter and completely covered by the valvulae in ventral view. The egg guide is an elongate, triangular structure between the bases of the first valvulae.

DISCUSSION

The development of the thoracic nota in Melanoplus lakinus shows that the wing-rudiments on the meso- and metanotum first appear in the fourth instar and definitive wing pads in the fifth. Carpenter (1921), in a study of Melanoplus femur-rubrum (De Geer), found the wing-rudiments to be plainly visible in the third instar while the wing pads appeared in the fourth instar. However, he found that this species passed through only five instars before the adult stage was reached, while Melanoplus lakinus passes through six nymphal instars.

The size of the surface sculpturing pattern on the wings remains nearly the same throughout their development. If this pattern can be interpreted as a reflection of the epidermal cell boundaries, then the growth of the wings must be accomplished by continued cellular division rather than by cellular enlargement. The surface sculpturing on the thoracic nota, in the fourth and fifth instars at least, is the same as that on the wings.

The development of the major features of the male genitalia in Melanoplus lakinus was found to be essentially the same as that reported for Melanoplus differentialis by Else (1934). Through the first four instars in each species the ninth sternite or genital plate undergoes considerable broadening and elongation. The terminal emargination of this sternite disappears and the apex becomes turned up dorsally; this occurs in the third instar in M. lakinus and in the fourth in M. differentialis. The genital plate approaches the adult form much more closely during the fifth and sixth instars in M. differentialis than it does in M. lakinus, even though both insects pass through six numphal instars.

The ovipositor in M. lakinus follows the pattern of development worked out for an unknown species of Melanoplus by Snodgrass in 1935a. The first valvulae arise behind the eighth sternite as flattened lobes while the third valvulae develop as conical lobes directly from the ninth sternal plate. He pointed out that the second valvulae arise between the bases of the third valvulae, although he did not specify at what stage this occurred.

More extensive morphological work, particularly at the cellular level, is needed to clarify several interesting problems encountered during this study, for example, the cellular structure of the wings and its relation to the pattern of cuticular sculpturing, the formation of the wing veins, and the development of the concealed parts of the male and female genitalia. Probably the most profitable area would involve a comparative study of the growth and development of the wings in the two distinct forms of this species. Such information would provide a useful background for a physiological investigation of the factors controlling the production of long- and short-winged forms.

SUMMARY

A careful study was made of the morphological changes that take place in the thoracic nota, the wings, the terminal abdominal segments of the male, and the female genitalia of a common Arizona grasshopper, Melanoplus lakinus Scudder.

In the fourth instar the wing-rudiments first appear as lobes from the lateral edges of the meso- and metanotum. The wing pads of the fifth instar show significant development of the tracheae only. In the sixth instar the epidermal cells begin to cluster along the tracheae to form the thickened walls of the future wing veins. Growth of the wings appears to be accomplished mainly by cell division rather than by cell enlargement.

The enlargement of the ninth sternite forms a conspicuous character in the development of the nymphs of the male. The female nymphs on the other hand may be distinguished by the conspicuous lobes of the developing ovipositor and progressive degeneration of the ninth sternite. The first valvulae originate just behind the eighth sternite, while the third valvulae arise from the ninth sternite itself. The first valvulae increase in size more rapidly than the third although both of them reach approximately the same size in the adult.

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ABBREVIATIONS

Arabic numerals refer to thoracic segments; roman numerals refer to abdominal segments.

Cer, cercus

eg, egg guide

Eppt, epiproct

f, fore wing

F, furcula

h, hind wing

Pal, pallium

Papt, paraproct

SL, genital lobe

S, sternum

T, tergite

Th, thoracic segment

VL, valvula

Melanoplus lakinus Scudder

1. First instar. Dorso-lateral view of thoracic nota (X 50).

2. Second instar. Dorso-lateral view of thoracic nota (X 27).

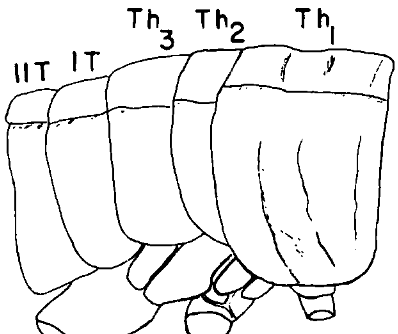
3. Third instar. Dorso-lateral view of thoracic nota (X 22).

4. Fourth instar. Dorso-lateral view of thoracic nota (X 14.5).

5. Fifth instar. Dorso-lateral view of thoracic nota (X 9).

6. Sixth instar. Dorso-lateral view of thoracic nota (X 9).

7. Adult. Dorso-lateral view of thoracic nota (X 4.7).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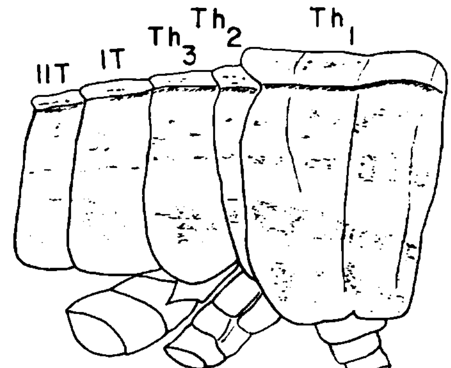
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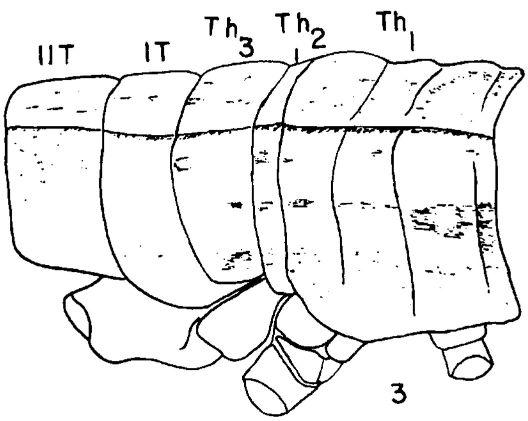
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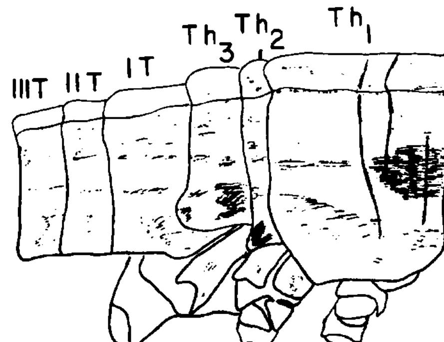
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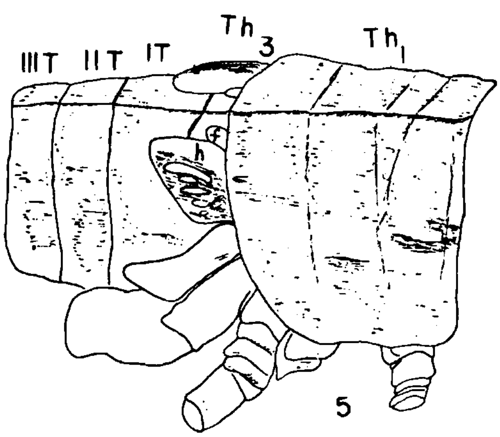
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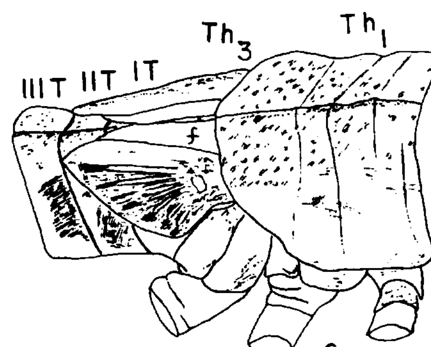
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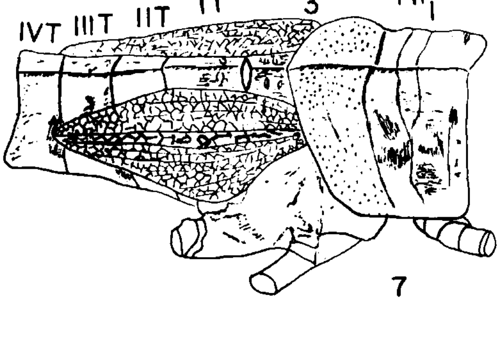
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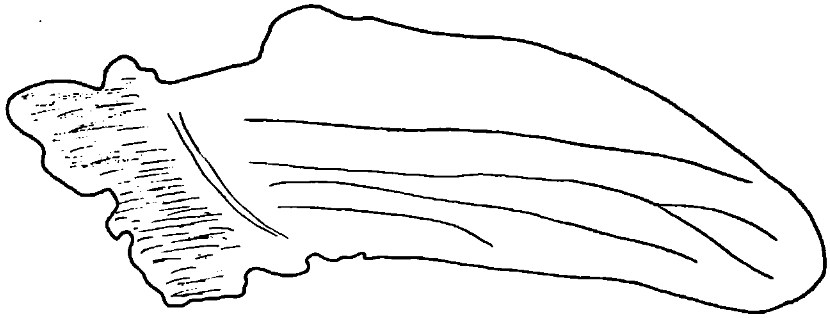
Melanoplus lakinus Scudder

8a. Fifth instar. Fore wing.(X 55).

8b. Fifth instar. Surface sculpturing of fore wing.

9a. Fifth instar. Hind wing (X 65.6).

9b. Fifth instar. Surface sculpturing of hind wing.



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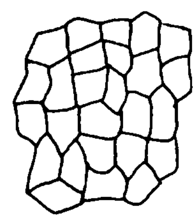

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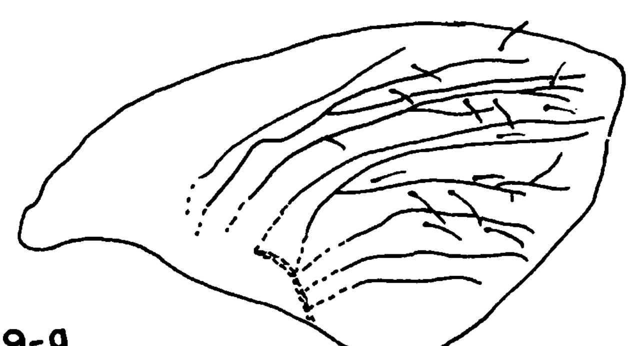

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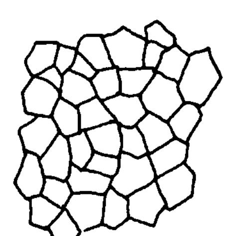


9-b I 0·01mm

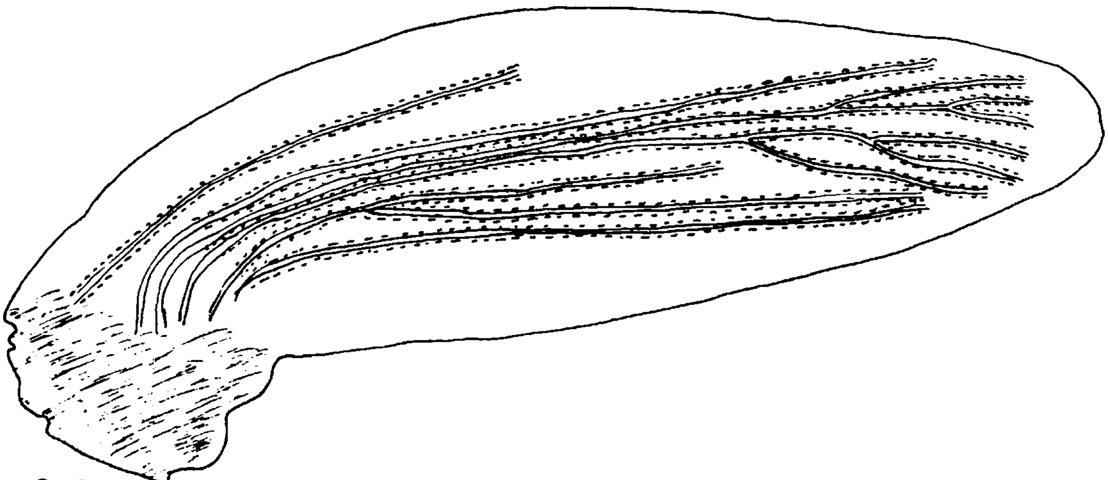
Melanoplus lakinus Scudder

10a. Sixth instar. Fore wing (X 42).

10b. Sixth instar. Surface sculpturing of fore wing.

11a. Sixth instar. Hind wing (X 43).

11b. Sixth instar. Surface sculpturing of hind wing.



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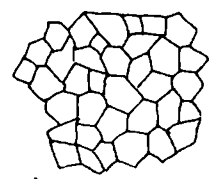

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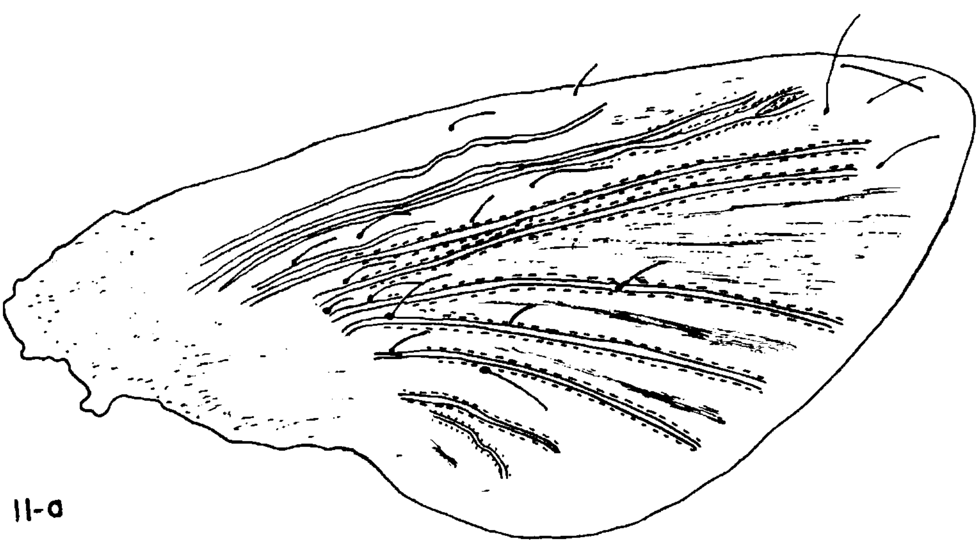

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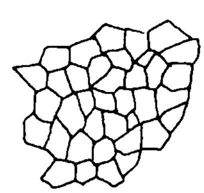


11-b I 0·01mm

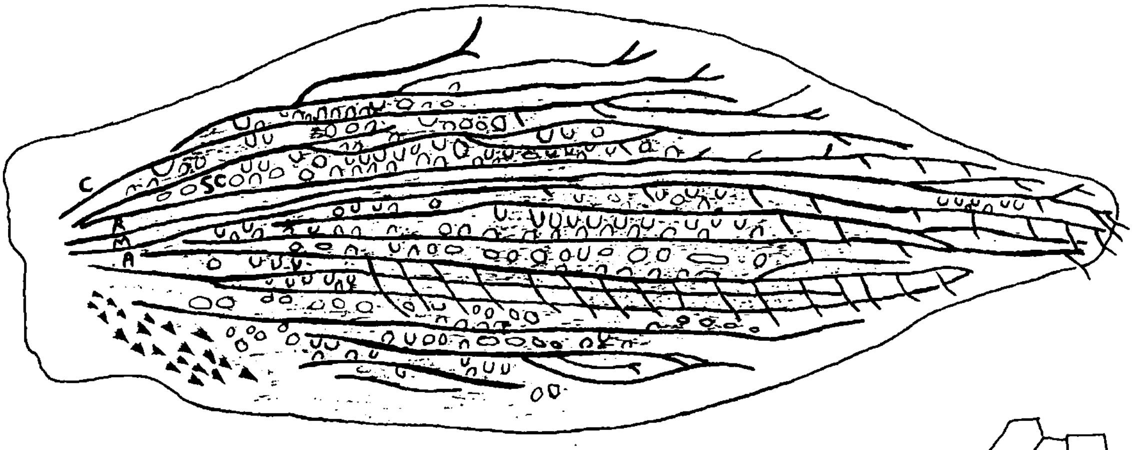
Melanoplus lakinus Scudder

12a. Adult. Fore wing (X 19.5).

12b. Adult. Surface sculpturing of fore wing.

13a. Adult. Hind wing (22).

13b. Adult. Surface sculpturing of hind wing.



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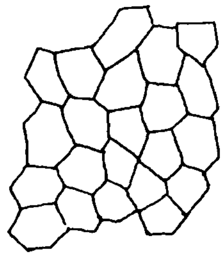
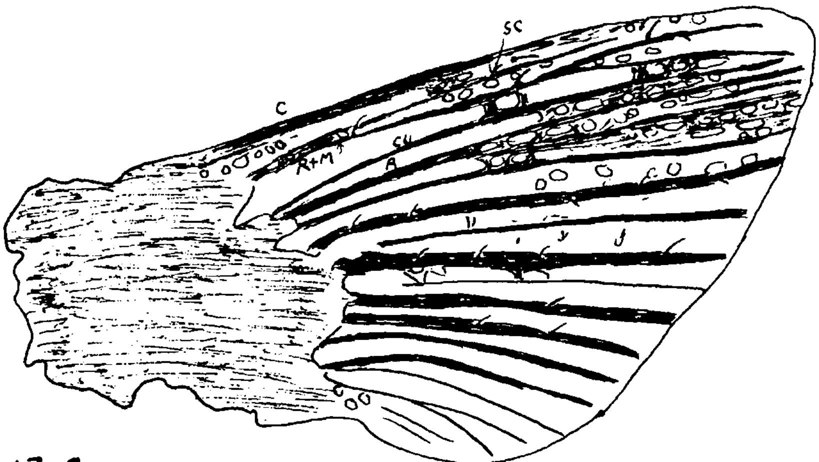
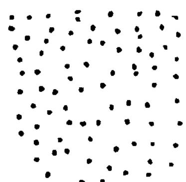


12-b I 0·01mm



13-a



13-b I 0·01mm

Melanoplus lakinus Scudder. Male.

14a. First instar. Dorsal view of terminal abdominal segments (X 54).

14b. First instar. Ventral view of terminal abdominal segments (X 42.7).

15a. Second instar. Dorsal view of terminal abdominal segments (X 58.7).

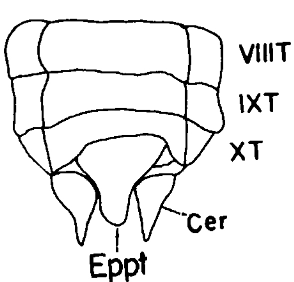
15b. Second instar. Ventral view of terminal abdominal segments (X 38).

16 a. Third instar. Dorsal view of terminal abdominal segments (X 54).

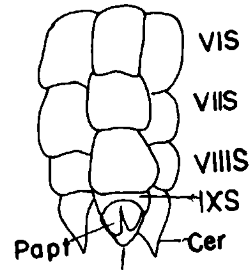
16b. Third instar. Ventral view of terminal abdominal segments (X 50).

17a. Fourth instar. Dorsal view of terminal abdominal segments (X 42.4).

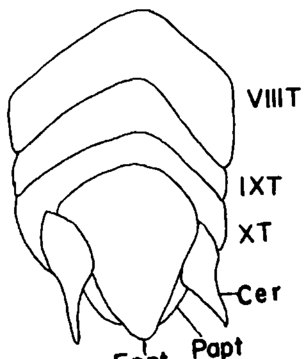
17b. Fourth instar. Ventral view of terminal abdominal segments (X 32).



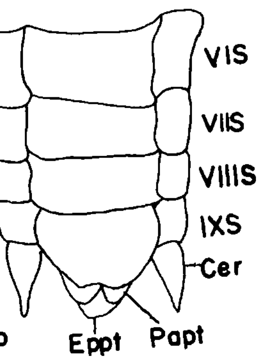
14-a



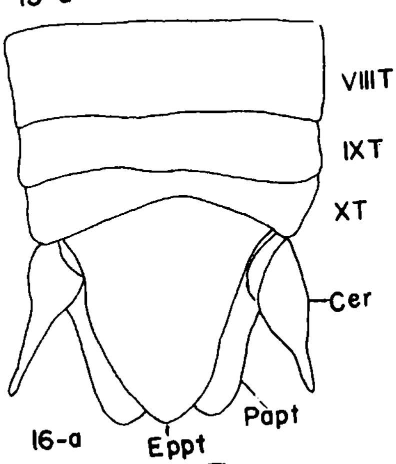
14-b



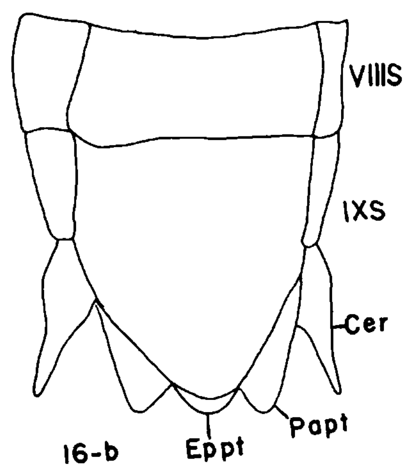
15-a



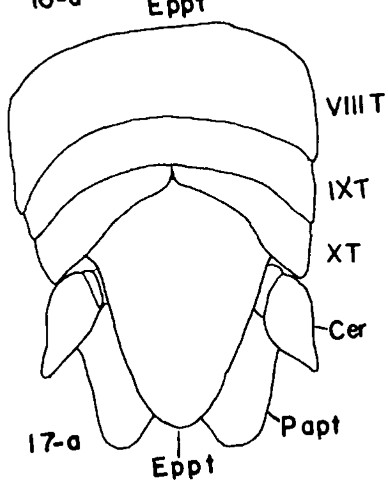
15-b



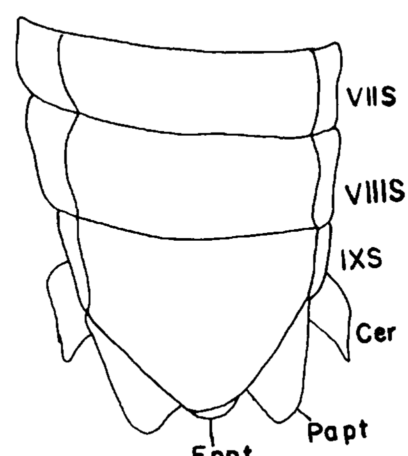
16-a



16-b



17-a



17-b

Melanoplus lakinus Scudder. Male.

18a. Fifth instar. Dorsal view of terminal abdominal segments (X 42).

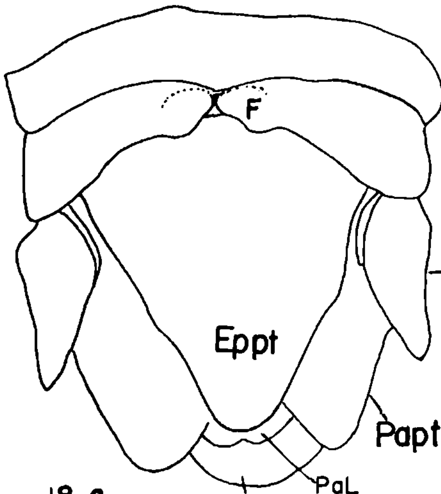
18b. Fifth instar. Ventral view of terminal abdominal segments (X 30).

19a. Sixth instar. Dorsal view of terminal abdominal segemtns (X 21.7).

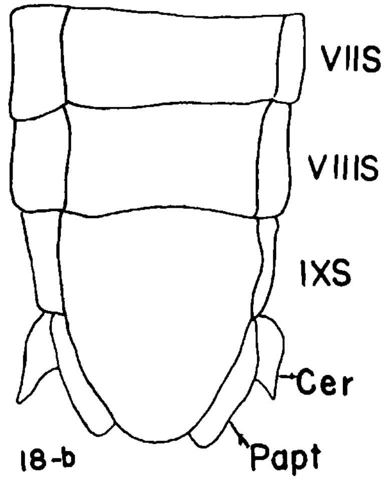
19b. Sixth instar. Ventral view of terminal abdominal segments (X 24).

20a. Adult. Dorsal view of terminal abdominal segments (X 13.7).

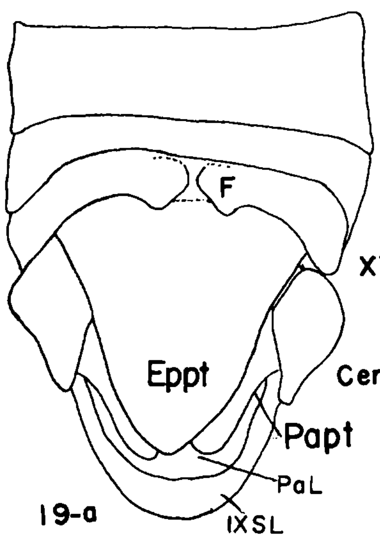
20b. Adult. Ventral view of terminal abdominal segments (X 14).



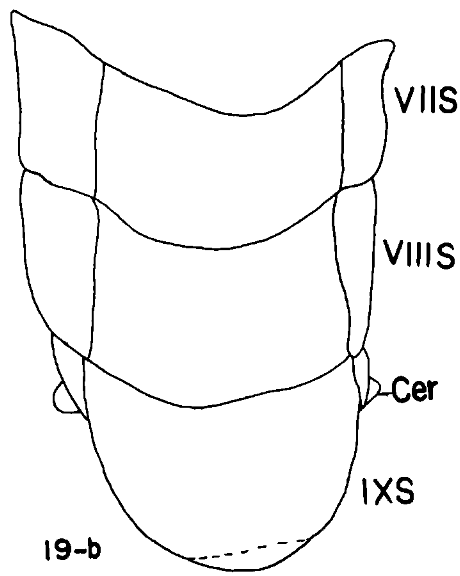
18-a



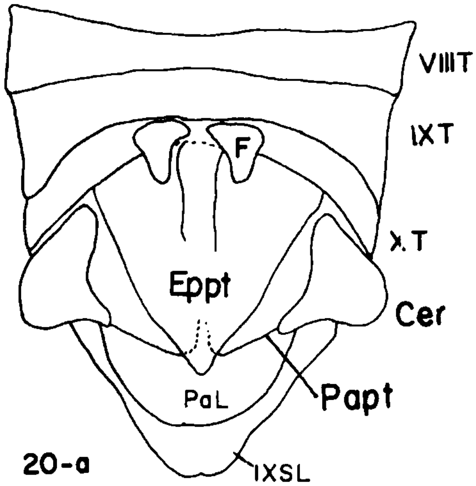
18-b



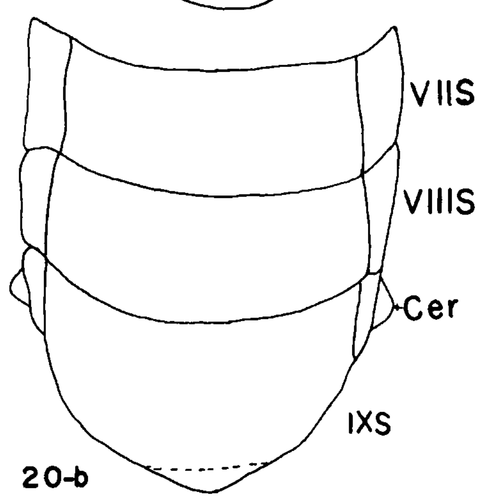
19-a



19-b



20-a



20-b

<u>Melanoplus lakinus</u> Scudder

Female. Ventral view of end of abdomen.

21. First instar (X 66).

22. Second instar (X 45.5).

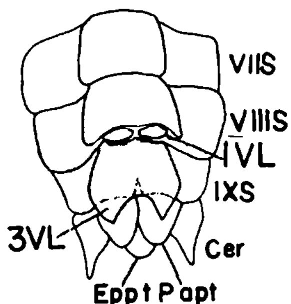
23. Third instar (X 40).

24. Fourth instar (X 55).

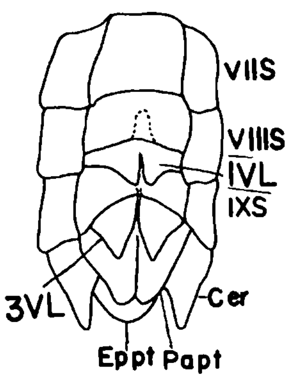
25. Fifth instar (X 40.7).

26. Sixth instar (X 38).

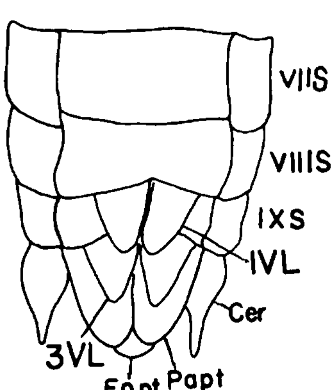
27. Adult (X 18).



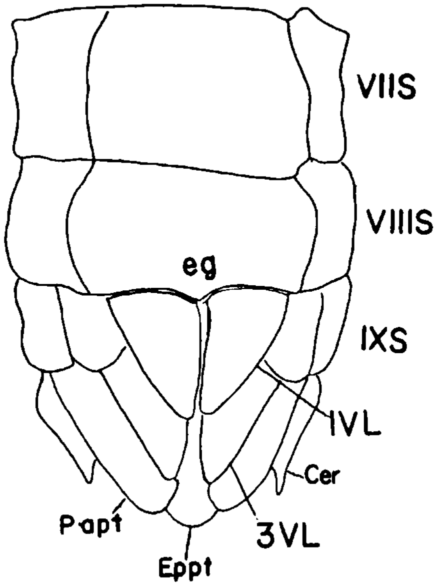
21



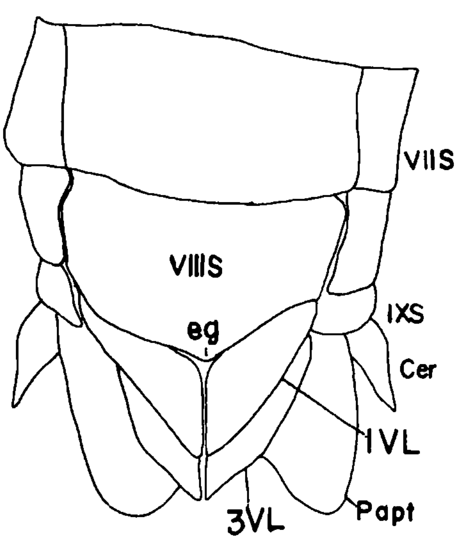
22



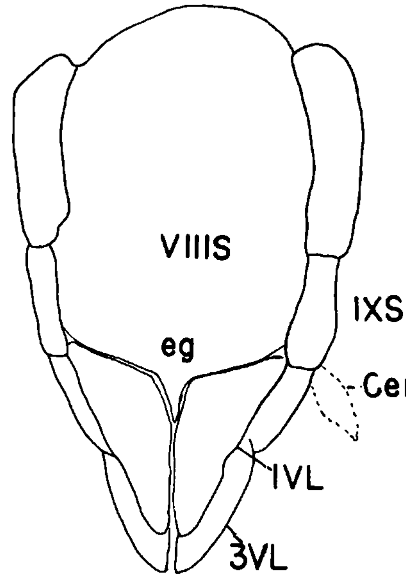
23



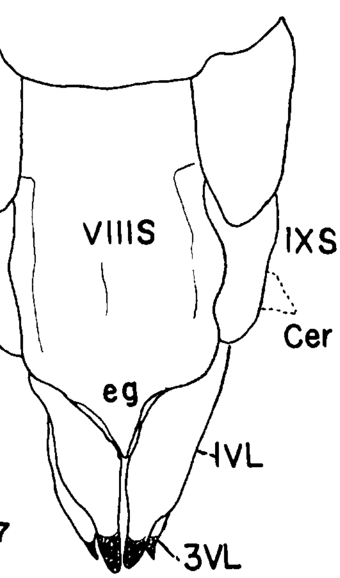
24



25



26



27