The immature stages of *Phaulacridium marginale* (Walker) and *Sigaus campestris* (Hutton) (Orthoptera: Acrididae).

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by

NORTHCROFT, M.A.

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"No part of the insect fauna of New Zealand has been more neglected than the grasshoppers."

Hutton (1898).

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CHRISTCHURCH, N.

SECTION 1

Introduction.

New Zealand's economy is primarily based upon its extensive pastoral lands which are found in both Lowland and Alpine regions throughout the North and South Islands. Because of the economic value of these areas factors which affect their productivity are of great importance. Soil erosion, principally in Alpine country, is a source of particular concern. Research is therefore being concentrated on physical and biotic agents working in Alpine regions. The main aim of this research is to determine means by which factors responsible for initiation and acceleration of erosion may be controlled.

It has long been realised that damage is being caused by movement and grazing of sheep, deer and goats. Only recently, however, have suggestions been made that grasshoppers, also present in Alpine regions, may be a significant contributary factor in this process. In order to examine this suggestion it is necessary to know more about the biology and population dynamics of grasshoppers. Such research depends upon preliminary identification of species and of their nymphal instars. To date very little information is available on any aspect of morphology or biology of New Zealand grasshoppers.

This thesis is a study of the developmental stages of two species of grasshopper. The primary aims have been to establish the number of nymphal instars in each species, to describe and illustrate the anatomical differences between these instars (both within each species and between the two species), and to report any information obtained on the life histories, habitat preferences and the duration of the egg and nymphal stages of the two species selected.

Grasshoppers of the family Acrididae occur throughout New Zealand from sea-level to over 7,000 ft. The known fauna comprises twelve species belonging to six genera. Eleven of these species belong to the endemic genera Sigaus (5 species), Brachaspis (2 species), Paprides (2 species) and Alpinacris (2 species). The genus Phaulacridium is represented by one endemic species, P.marginale, which is closely related to the Australian species P.vittatum (Key, pers. comm.). The only species which is not endemic is the cosmopolitan Locusta migratoria. In this thesis the two species selected for study were Phaulacridium marginale (Walk.) and Sigaus campestris (Hutt.).

1.2. Instar number

Ramsey (1964) in his revision of the moult number in

Orthoptera concludes that the nymphal instars in the Acrididae range from four to nine, with five to six instars occuring most frequently. In recording the instar number, the figure given always excludes the moult of the vermiform larva or pronymph when the embryonic cuticle is cast off.

There are a number of methods used to determine the number of nymphal instars in grasshoppers: Uvarov (1966) notes that most of the available descriptions of instars are based on colour and pattern. However, in recent work other criteria have been used. Studies of certain species with eyestripes, for example Nomadacris septemfasiata and Schistocerca gregaria Albrecht (1955), have revealed that with each instar there is a regular increase in the number of eyestripes. This is the only known character that enables the number of nymphal instars in these species to be determined from examination of an adult. For those species lacking eyestripes other methods have been used, for example the number of antennal segments and changes occuring to the wings, elytra and genitalia; Burnett (1951), Carothers (1923), Richards and Waloff (1954) . In addition, measurements of dimensions of the head, pronotum and meso- and metathoracic legs have also been used by Richards and Waloff who also determined the number of instars by rearing nymphs. In this

study the methods used in determining the number of instars were: measurement of the specimens collected, examination of the rudimentary wings, elytra and genitalia, and rearing of P.marginale from egg to adult.

SECTION 2

2.1. Habitat

S.campestris and *P.marginale* are both found at sea level, *S.campestris* extending to altitudes of 4,000 ft., *P.marginale* to 3,000 ft. On Banks Peninsula where this study was carried out, *P.marginale* was widely distributed while *S.campestris* occurred in isolated populations of low density in association with *P.marginale*. Both species were found in sunny areas where the vegetation was not subject to intensive cultivation.

2.2. Study Area

The area selected for intensive study was at Sumner, a suburb of Christchurch, located at the foot of the Port Hills. The area was a level section approximately $\frac{1}{8}$ acre. This land was bounded on one side by a road and on all other sides by residential sections. Grasses covered most of the field with *Bromus carthariticus* as the dominant plant species, reaching a height of three feet in spring. Other species present included *Agrostis tenuis* (Brown top), *Holcus lanatus* (Yorkshire fog), *Trifolium repens* (White clover), *Dactylis glomerata* (Cocks-foot), *Lolium perenne* (Rye grass), *Taraxacum officinale* (Dandelion), *Hypochaeris*

radicata (Cat's ear), Crepis capillaris (Hawk's beard), Rumex acetosella (Sheep's sorrel).

A definite habitat preference was noticed while collecting. In January and February when numbers of both species were high the P.marginale population was distributed throughout the study area, except in tall grass. In contrast, the smaller S. campestris population was found only in the warmest corner of the field among the tall stands of Bromus carthar-ticus. A similar difference of site preference between the species was also observed in a nearby field. The study area was visited monthly throughout 1964 and samples were obtained for breeding and morphological studies.

2.3. Collecting.

Grasshoppers rely on cryptic colouration and motionless posture to avoid detection, betraying their presence by jumping. When the vegetation was disturbed the grasshoppers jumped, their position was noted and they were then tubed or netted.

2.4. Preservation.

Specimens collected were killed with ethyl acetate. All stages were preserved in 70% alcohol, because nymphal stages have a thinner cuticle than adults and collapse on

drying; only adults can be successfully pinned.

2.5. Laboratory culture of grasshoppers and nymphs.

a. Cages. Two types of container were used:

1. A plastic cannister 8" in diameter and 7" deep.
2. A glass jar 4" in diameter and 6½" deep.

The containers were fitted with a stocking sleeve held in position by an elastic band. The plastic container was adequate for keeping up to ten S.campestris or twenty P.marginale. Eventually not more than five nymphs were kept in a glass container, as overcrowding resulted in high mortality. A handful of dry straw and twigs was supplied for resting and moulting.

b. Feeding. Rat pellets (type b), fresh dandelion leaves standing in water, and a phial of water were found to be an adequate diet. The water phial and the dandelion container were plugged with cotton wool to prevent nymphs from drowning.

c. Cleaning. Uneaten dandelion leaves and dead grasshoppers were removed from the containers daily; faeces were removed weekly.

d. Temperature. Cages were kept on laboratory shelves at room temperature or in an incubator where the temperature was 78°F.

2.8. Field observations on Life Cycles.

General observations were made at Sumner on the life cycles of P.marginale and S.campestris during 1964-65. First instar nymphs of P.marginale were observed from October to the end of November. A similarly protracted hatching period is noted for British grasshoppers by Richards and Waloff (1954) who relate this to the position of the egg pod in the soil and also to the date on which the pod was laid. A comparative determination of the mean duration of each nymphal instar of P.marginale nymphs reared in the laboratory with those in the field was carried out during rearing experiments, when the nymphs were held at a constant temperature of 78°F. The average length of an instar under these conditions was ten days. This was shorter than would be expected in the field where mean temperatures are lower (McLintock, 1960 map 8). On the basis of laboratory results, the estimated time from hatching to the adult stage would be about forty days. A few adults were present in the field during late November. This represents the minimum expected time for nymphs hatching in the field in early October to reach the adult stage. Adults were abundant in the field during December, January, February and March. Following this period of general abundance a decrease in numbers took place and in May and early June only a few adults

remained. During late June, July, August and September no adult P.marginale were seen. In October, first nymphal instars were present. The apparently complete absence of adults and the presence of only first nymphal instars in October suggests strongly that P.marginale overwinters solely in the egg stage.

Mature adults of S.campestris were found from November to April. A collection in late January included only adults and early nymphs. During May, June and July no nymphs were observed. However, in mid-August on a day following an 18° frost twelve nymphs were collected (4th and 5th instars ♀, 3rd instars ♂). Nymphs were also present during September and October. The presence of nymphs in August, September, October and late January, and the presence of adults from November to April, suggests that this species overwinters in several stages, possibly also as eggs. Batcheler's observations on Brachaspis collinus at Cupola Basin (1966) suggest that very early instars may not be able to survive heavy frosts. Since eggs may not hatch during winter, these early instars may not normally be exposed to low temperatures.

Observations revealed that P.marginale and S.campestris show differences between their seasonal life histories.

P.marginale, which is closely related to an Australian species, has an apparently annual cycle; S.campestris seems to take more than a year from egg to adult form, which Bigelow (pers.comm.) suggests resembles the seasonal cycles of other New Zealand Alpine species. All these species have probably survived the Pleistocene glaciations in this country and are adapted to cold climate, becoming active during periods of warmth.

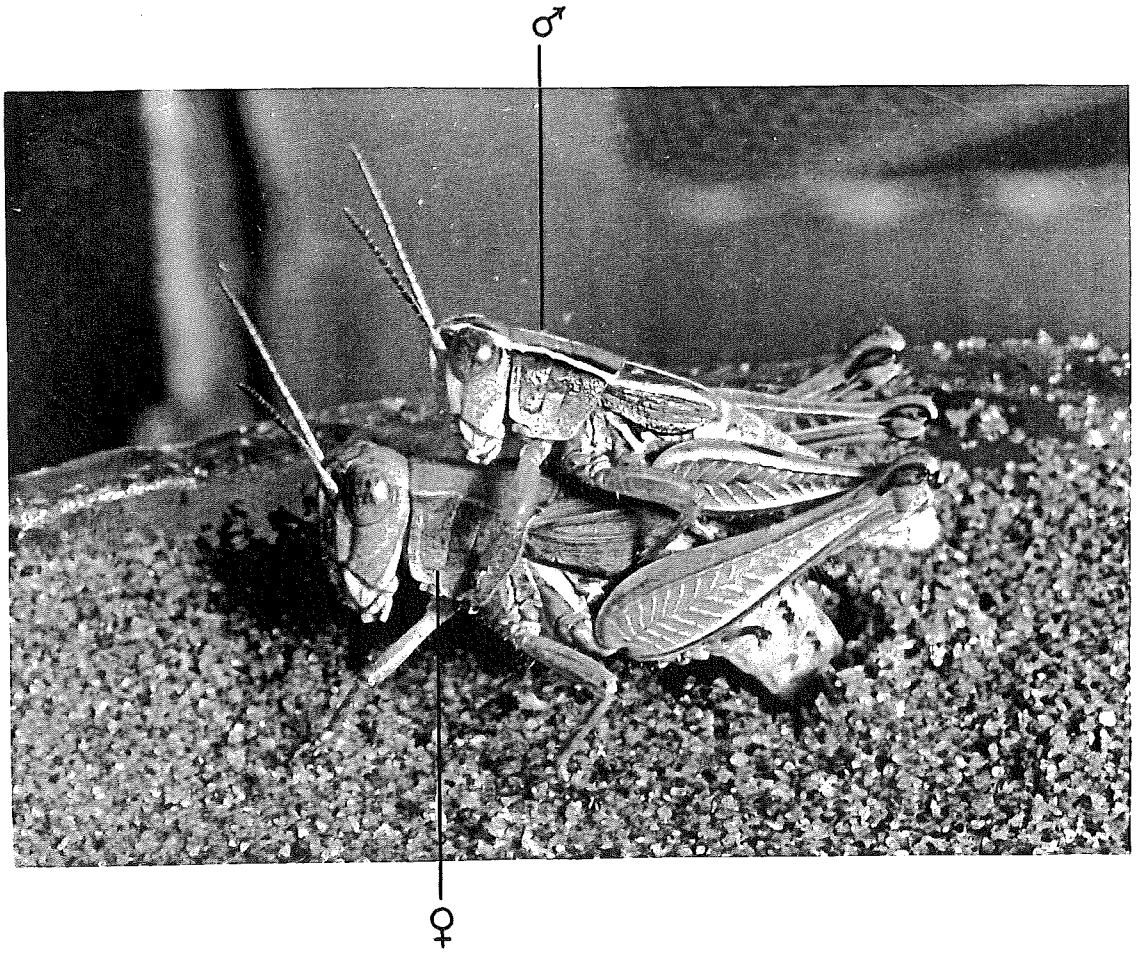


Fig. 3.1 Oviposition.
Phaulacridium marginale

SECTION 3

3.1. Pairing.

Pairing in P.marginale was observed both in the field and in the laboratory. It occurs without any preliminary courtship behaviour. The male jumps upon the female's back in an "ambushing" method of pairing which has also been observed with other non-stridulating species (Poulton, 1896; quoted by Uvarov, 1928). The male then rests upon the female with his prothoracic legs clasping the ventral edge of the pronotum, his mesothoracic legs gripped near the base of the female's mesothoracic legs with his metathoracic legs remaining free. Once pairing has occured separation does not take place readily. The female carrying the male is still able to walk and jump and even when collected in a vial or net they often remain together. The male may also accompany the female throughout oviposition (Fig.3.1).

3.2. Egg Laying.

The eggs are laid in egg-pods which are deposited in shafts excavated by the dorsal and ventral valves of the ovipositor. Soil is the usual oviposition site for grasshoppers, but a few lay in decayed wood, in the living stems of plants (Snodgrass, 1935) or the bases of plants (Richards

and Waloff, 1954).

In this study oviposition was only observed under artificial conditions in the laboratory. Here the eggs were laid in tightly packed moist sand inside four ounce plastic containers. Usually a single hole was bored and oviposition occured immediately. Some individuals bored several holes (range 1-7) before ovipositing. The reason for this was not ascertained but possibly the sand was not moist or compact enough for oviposition.

During oviposition the female balanced on her pro- and mesothoracic legs while her abdomen penetrated the soil (Fig.3.1). Sometimes in the course of oviposition the wall of the sand container was used as support for the prothoracic legs and the metathoracic legs were held above the ground at an acute angle so that the posterior ends of the femora touched one another above the abdomen in an inverted "V" shape.

The way in which the dorsal and ventral ovipositor valves were used for excavating was observed once, through the base of a container. The valves were being used to bore through a dry leaf. At first the paired valves were closed, and by extension of the abdomen pressed down onto the leaf. In this position the valves opened and shut a

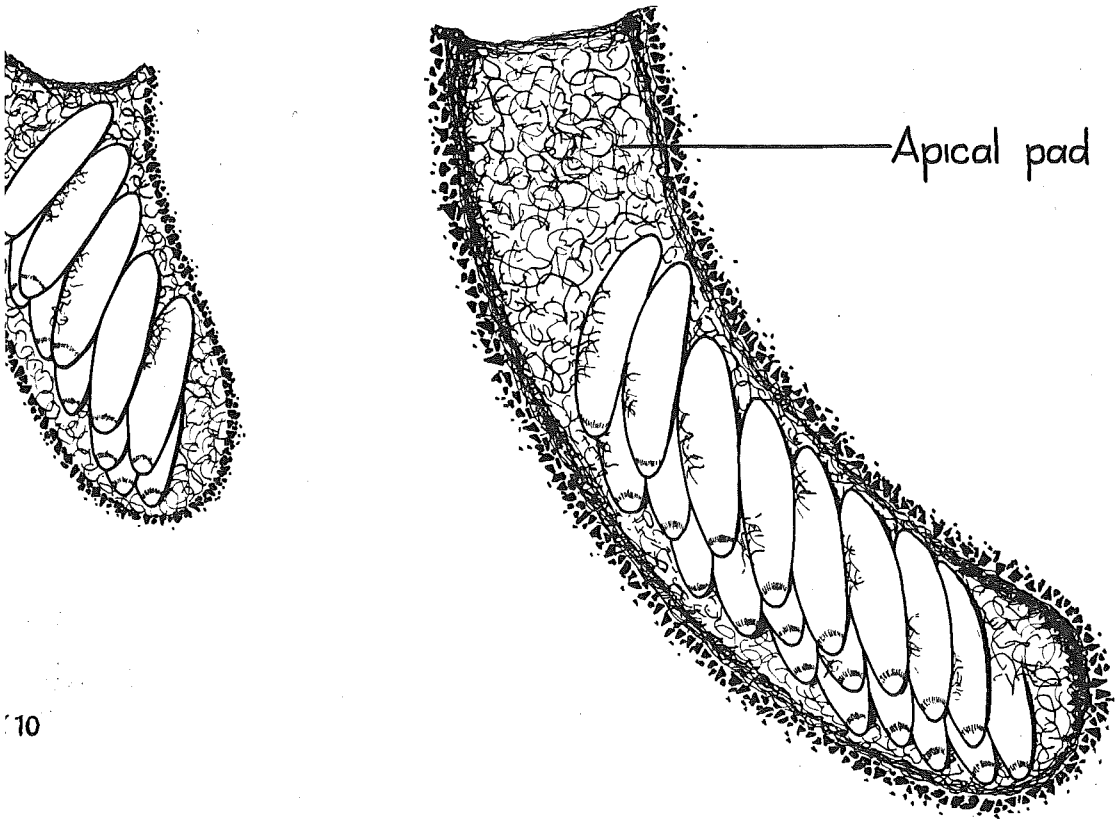
number of times tearing a hole in the leaf. The hole thus formed was enlarged by the curved tips of the dorsal valves pushing out the sides of the hole. These actions agree with Snodgrass's (1935) description of the operation of the ovipositor valves.

Following oviposition the apex of the egg pod was sometimes visible on the surface of the sand as a cream plug surrounded by a ring of loose sand. Frequently, however, the sand completely obscured the plug. To determine whether successful oviposition had taken place it was necessary, in this case, to scrape away the top few centimetres of sand in order to locate the egg pods.

3.3. Pods.

The shape of the egg pod conforms to the shape of the shaft made by the ovipositor. Pods of both P.marginale and S.campestris were straight or bow-shaped, as described and illustrated by Uvarov (1928) in his general description of grasshopper eggs. The concave side of the curved pod is uppermost, its distal end curving away from the female when laying; both types of pods were usually inclined from the vertical. Uvarov (1928) made the suggestion that the shape of the pod depends on the compactness of the soil in which

Fig. 3.2 Membranes shed by larvae of *Phaulacridium marginale* at hatching.



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Phaulacridium marginale *Sigaus campestris*

3.3 Egg-pods.

it is laid. Straight pods typically occur in very soft soil, while curved ones are present where the soil is compact. On a number of occasions in the laboratory egg pods were found deposited vertically against the side of the container.

The composition of the outer walls of the egg pods of both P.marginale and S.campestris is similar to that described by Richards and Waloff (1954) for the British grasshopper Omestris viridulus (L.). The outer wall of the egg pod is formed of a hardened cement secretion to which sand particles adhere. Internally a soft, spongy secretion lines the inner wall of the pod and a fine lamella of this secretion separates the individual eggs. The egg pod of S.campestris differs in construction from that of P.marginale in possessing a pad of frothy secretion at its mouth (fig.3.3). The presence or absence of an apical pad has been used by Richards and Waloff (1954) as a diagnostic feature in distinguishing the egg pods of British grasshoppers.

3.4. Eggs.

Within the egg pods of both P.marginale and S.campestris eggs are arranged in a linear fashion. The eggs

are cylindrical, elongate and slightly curved. At the time of deposition they are opaque and uniformly orange-brown in colour. Detailed descriptions of the structure of the shell of Acridid eggs have been given by Hartley (1961). Two membranes enclose the yolk and embryo, the chorion and the inner membrane. The latter in these two species is orange-brown and unsculptured. The chorion is a thin opaque covering faintly but distinctly hexagonally sculptured.

3.5. Hatching.

A detailed account of hatching in Acrididae has been given by Uvarov (1928). Observations made in the course of this study are in accord with his description. The hatching of a single specimen of P.marginale was observed. At the time of hatching the vermiform larva was enclosed in a transparent whitish membrane. While contained within this membrane the larva forced its way to the surface of the soil by a series of wriggling movements. On emergence the membrane was ruptured dorsally, and by movements of the body the nymph of the first instar released itself from the membrane. The membrane shed at this moult was visible as a small whitish object. Successive emergences of nymphs results in these membranes littering the surface of the

soil (fig.3.2). The nymph which emerged was creamy white with darkly pigmented eyes. Within fifteen minutes a gradual colour change took place until it became fully pigmented.

3.6. Diapause.

A natural state of arrested growth or diapause occurs in the eggs of many members of the Acrididae and serves to ensure that active stages are not present when environmental conditions are unfavourable. A winter diapause is characteristic of many grasshoppers living in temperate regions, for example it occurs in all five of the British species studied by Richards and Waloff (1954). Some species, e.g. Locustana pardalina (Walk), lay both diapause and non diapause eggs often mixed within the same egg pod, Dempster (1963).

The absence of P.marginale nymphs or adults in the field between late June and October and the presence of first instar nymphs in October suggests that the eggs of this species undergo diapause. While no experiments were specifically designed to test for the occurrence of diapause, two egg pods were considered to be in a state of diapause. It is characteristic of diapause that a period of cold is usually necessary for development to be resumed. Diapause

has been broken in a number of Acridids by cooling their eggs between 10°C and -7°C for 4 to 6 weeks, Demster (1963).

In this study two egg pods of P.marginale were subjected to temperatures of 5° - -8° C for 33 to 34 days and were then placed in an incubator at 66°-78°F. The eggs responded to this treatment by hatching in July and September, whereas in the field no eggs appeared to hatch before October. Egg pods laid during the months of April and March and held as controls in the laboratory at room temperature did not hatch until late November after a series of hot days.

SECTION 4

4.1. Development of wings, elytra and pronotum.

The general course of the development of the wings, elytra, pronotum and posterior abdominal structures in P.marginale and S.campestris was found to be similar to that given for other members of the Acrididae, for example Ander (1956) and Uvarov (1966). Substantial changes occur in the elytra and wings which develop from the lateral edges of the mesonotum and metanotum respectively. In the first instar the wing and elytral rudiments are only faintly visible as buds which may be indistinctly separated from the meso- and metanotum. These rudiments become more distinctly separated from the meso- and metanotum in subsequent instars. In the early instars the wing and elytral rudiments are small, short, and lie laterally, later becoming larger, elongate and reflexed dorsally. In the ante-penultimate and penultimate instars the wing rudiments increasingly overlap the elytral rudiments and the nymphs may often be mistaken for adults. However, as Uvarov (1921) has stressed, the adult may always be distinguished from these later stages, as in the adults the elytra cover the wings. Accompanying the development of the wings and elytra there is pronounced backward growth of the saddle-shaped pronotum, which in the adult covers both meso- and metanotum and may partly obscure

wing and elytral rudiments.

4.2. Development of the posterior abdominal structures.

The sexes have similar dorsal and lateral posterior abdominal structures. These structures increase in size in successive instars, approximately maintaining their initial proportions. Tergite IX is fused with tergite X which is posteriorly emarginate. A triangular median dorsal epiproct representing tergite IX is fused to this emarginate border of tergite X. The lateral paraprocts are formed from sternite XI. On each side of the epiproct there projects an unsegmented cercus, having a single papilla on its inside edge.

It is possible to distinguish the sexes of all instars by close examination of the ventral posterior abdominal structures. The first instar female has rudimentary dorsal and ventral ovipositor valves projecting from sternites VII and IX respectively. These valves elongate at each successive instar. Sternite IX and the inner valves are visible in early instars but are later obscured by the growth of the ventral valves. The first instar male has a single unpaired subgenital plate, formed from sternite IX. This plate is short, flat and mesally emarginate in the early instars, later increasing in breadth

and length, and in the adult it becomes a hooded structure enclosing the genitalia. Its posterior edge in the adult has a soft margin, the pallium. The subgenital plate has a proximal region and also a free distal region extending beyond the edge of tergite X; the demarcation between them is often visible as the hinge.

(For illustrations on the course of development of the pronotum, wings, elytra and genitalia see figs.4.1 - 4.17).

4.3. Diagnostic characters of S.campestris and P.marginale.

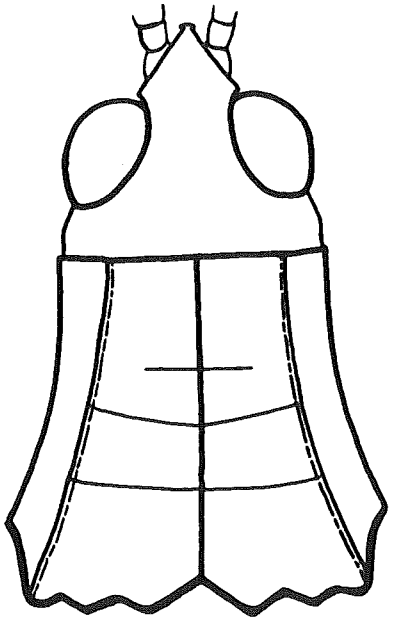
The following characters are used to distinguish between species:-

S.campestris	P.marginale
1. Antennal segments broad and flat (fig.4.2 a)	Antennal segments threadlike and cylindrical (fig.4.2 b)
2. Fastigium pointed (fig.4.2 c)	Fastigium rounded (fig.4.2 d)
3. Posterior edge of pronotum serrate (fig.4.1a,c)- not always obvious in early stages	Posterior edge of pronotum smooth (fig.4.1b,d).

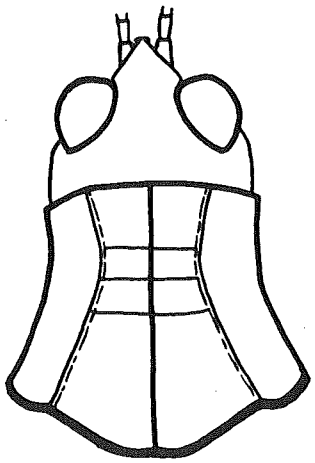
In addition the following can be used to distinguish adults:-

4. Elytra lie laterally (fig.4.1 c)	Elytra lie dorsally (fig.4.1 d)
5. Body length =	
Male 17.5 - 19.8mm	10.8 - 13.5mm
Female 27.8 - 34.4mm	14.4 - 18.2mm

For full descriptions see "Taxonomy and distribution of New Zealand grasshoppers (Acrididae)" Bigelow, in press 1966.

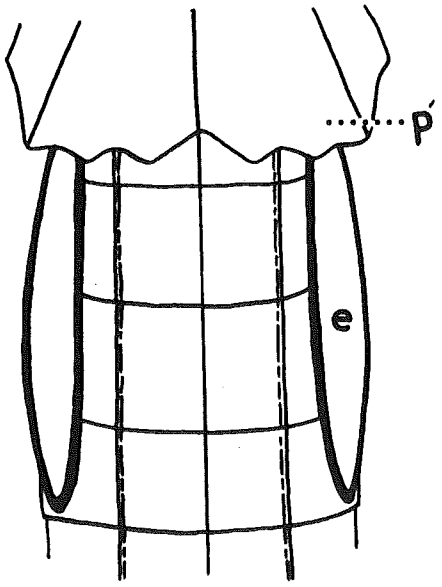


a *Sigaus campestris*

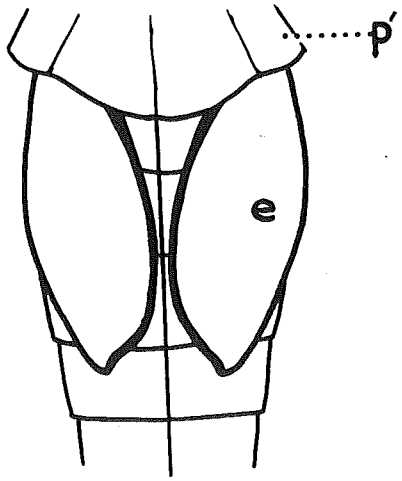


b *Phaulacridium marginale*

head and pronotum (dorsal view)



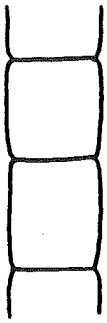
c *Sigaus campestris*



d *Phaulacridium marginale*

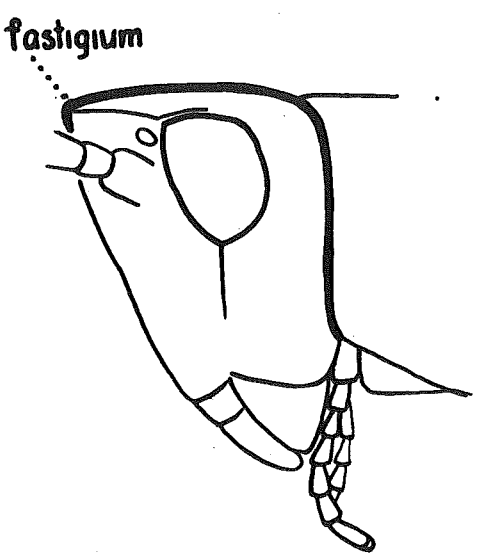
elytra (dorsal view)

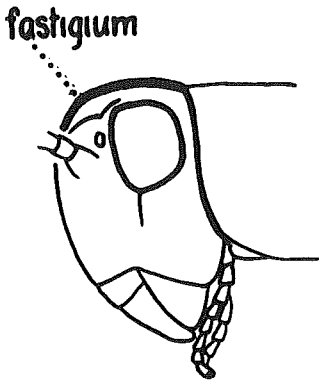
FIG 4.1 (a.b.c.d)



a *Sigaus campestris* b *Phaulacridium marginale*

antennal segments





c *Sigaus campestris* d *Phaulacridium marginale*

head (lateral view)

FIG 4.2 *(a.b.c.d.)*

4.4

Key to the nymphal instars and adults of P.marginale.

1 (2) Wing and elytral rudiments lying laterally. 3

2 (1) Wing and elytral rudiments reflexed dorsally 5

3 (4) Wing and elytral rudiments distinct. Postero-lateral margin of elytral rudiments pointed; those of wing rudiments rounded.....Instar II figs. 4.6 4.7 4.8

4 (3) Wing and elytral rudiments faint. Postero-lateral margins of elytral and wing rudiments both rounded.....Instar I figs. 4.3 4.4 4.5

5 (6) Wings completely covered by elytra..Adult figs. 4.15 4.16 4.17

6 (5) Wings not completely covered by elytra.

7 (8) Elytral rudiments not extending back as far as wing rudiments.....Instar III figs. 4.9 4.10 4.11

8 (7) Elytral rudiments extending back as far as wing rudiments.....Instar IV figs. 4.12 4.13

4.5

DIAGNOSES OF

INSTARS AND ADULTS OF

P. MARGINALE.

P.marginale

Instar 1.

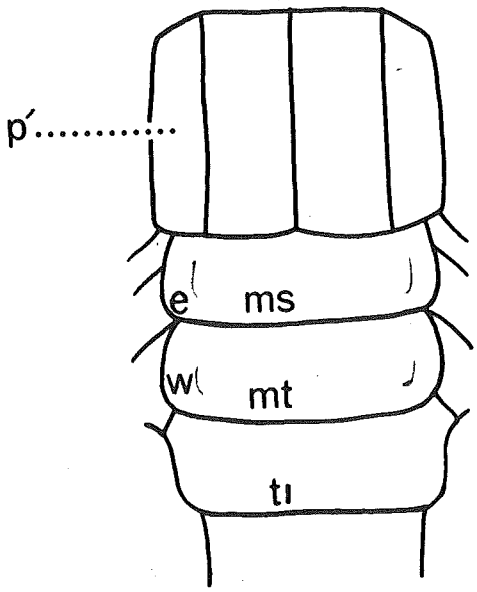
Body length between 3.8 - 6.3mm : male

3.6 - 6.1mm : female

Postero-lateral margins of mesonotum and metanotum rounded forming faintly visible wing and elytral rudiments (fig. 4.3 a). Wing and elytral rudiments lying laterally (fig. 4.3 b).

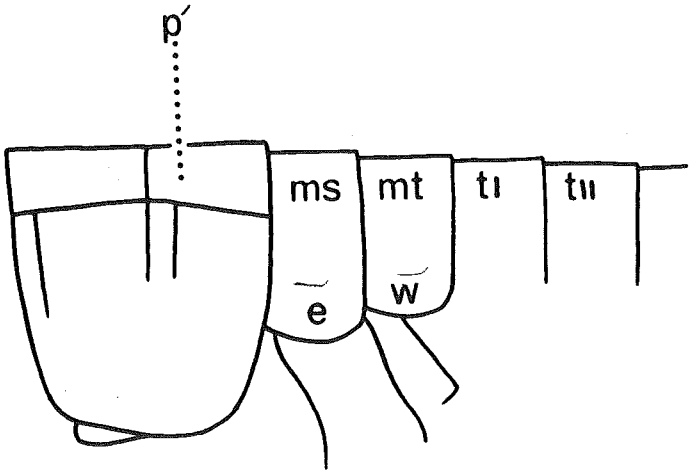
Female. Sternite VIII slightly concave bearing posteriorly a pair of rudimentary ventral valves. Sternite IX completely visible bearing posteriorly a pair of rudimentary dorsal valves (figs. 4.4 a, 4.5 a).

Male. Sternite IX flat; longer than sternite VIII (figs. 4.4 c, 4.5 b). Distal portion of sternite IX shorter and narrower than proximal portion (fig. 4.4 c, 4.5b). Posterior margin of distal portion of sternite IX concave (fig. 4.4 c).



X30

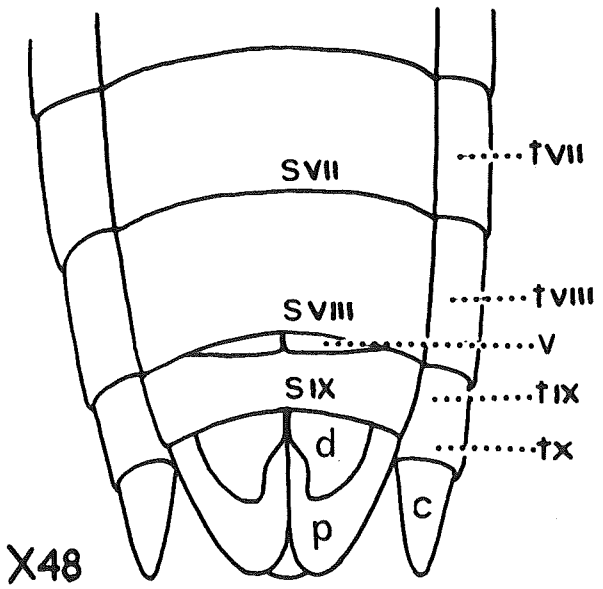
a *Phaulacridium marginale* (dorsal view)



X30

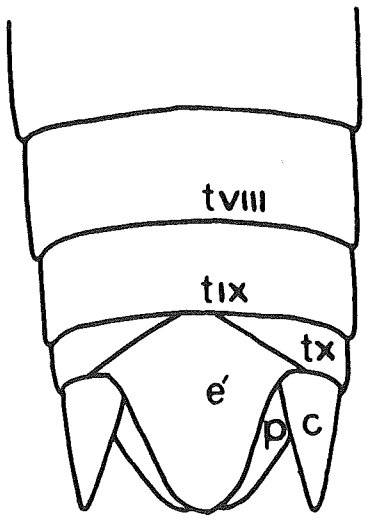
b *Phaulacridium marginale* (lateral view)

FIG 4.3 (a b) Thoracic and anterior abdominal segments First nymphal instar



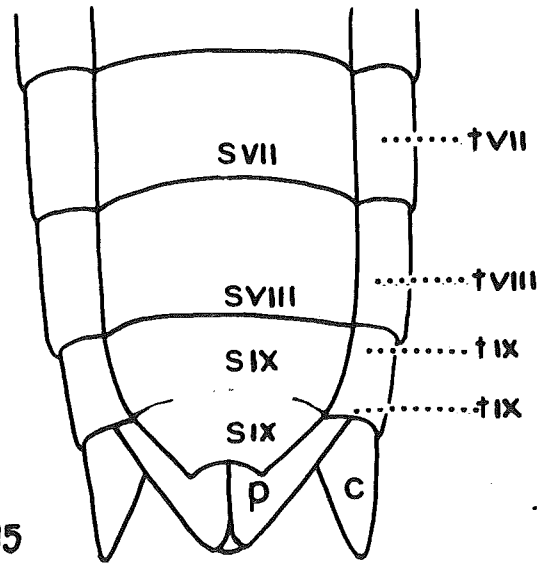
X48

a. Female (ventral view)



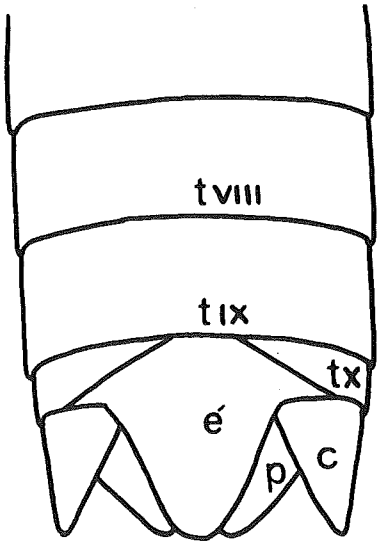
X36

b. Female (dorsal view)



X45

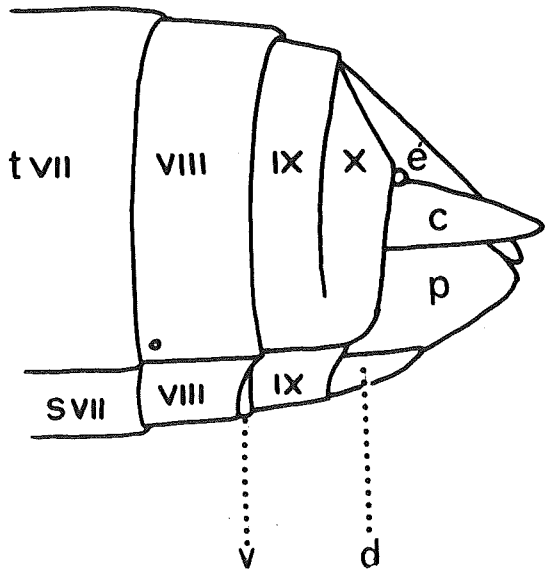
c. Male (ventral view)



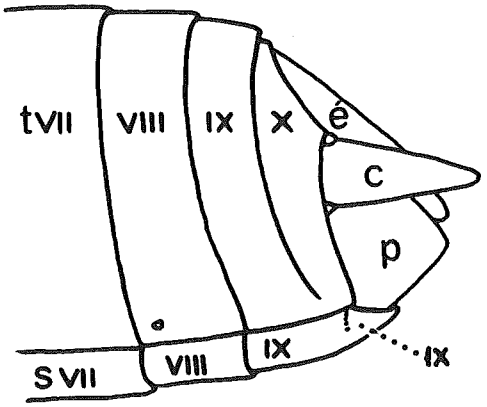
X45

d. Male (dorsal view)

FIG 4.4 (a b c d) *Phaulacridium marginale* First nymphal instar Posterior abdominal structures



a. *Phaulacridium marginale* : Female X 38



b. *Phaulacridium marginale* : Male X 42

FIG 4.5 *(a.b.)* Posterior abdominal structures (lateral view) First nymphal instar

P.marginale

Instar II

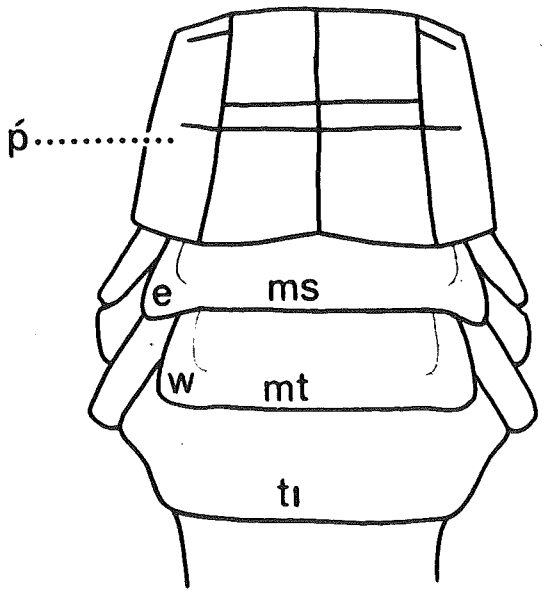
Body length between 5.2 - 7.7mm : male

4.9 - 8.1mm : female

Postero-lateral margins of mesonotum and metanotum forming distinct elytral and wing rudiments lying laterally. Elytral rudiments pointed, wing rudiments rounded (fig. 4.6 a b).

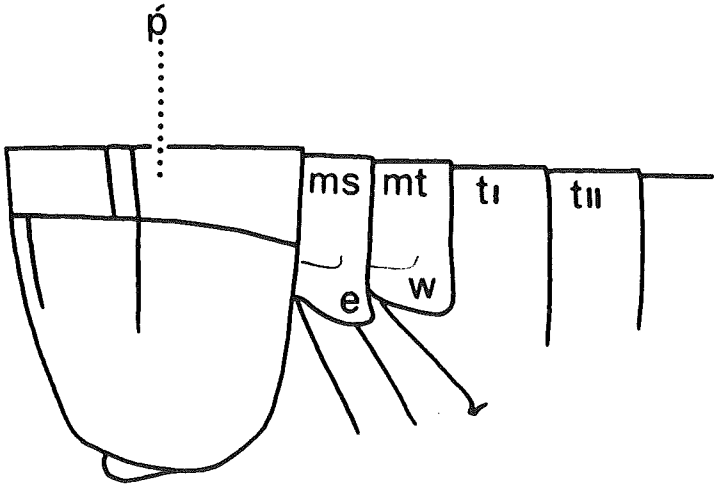
Female. Sternite VIII approximately equal in length to sternite VII. Posterior tips of the ventral valves overlapping bases of dorsal valves mesally obscuring sternite IX. Inner valves arise at the anteromedial margin of the dorsal valves just posterior to ventral valve tips (figs. 4.7 a, 4.8 a).

Male. Sternite IX longer than sternite VII. Distal portion of sternite IX shorter and narrower than proximal portion, lying horizontally (figs. 4.7 c, 4.8 b). Posterior margin of sternite IX slightly concave (fig.4.7 c).



X 20

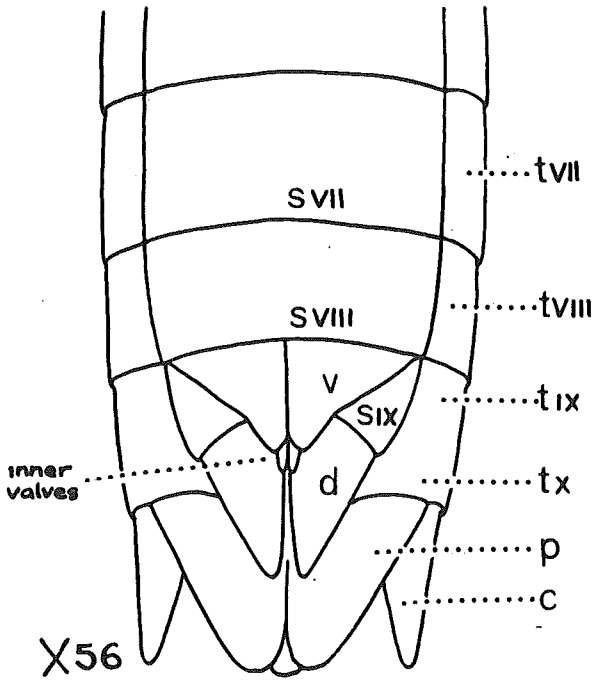
a *Phaulacridium marginale* (dorsal view)



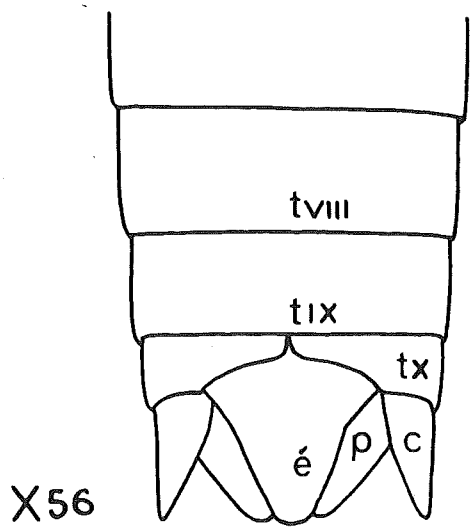
X 25

b *Phaulacridium marginale* (lateral view)

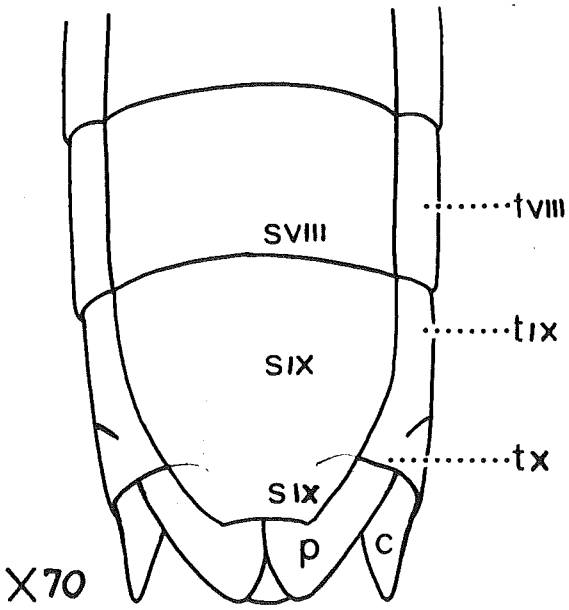
FIG 4.6 (a b) Thoracic and anterior abdominal segments Second nymphal instar



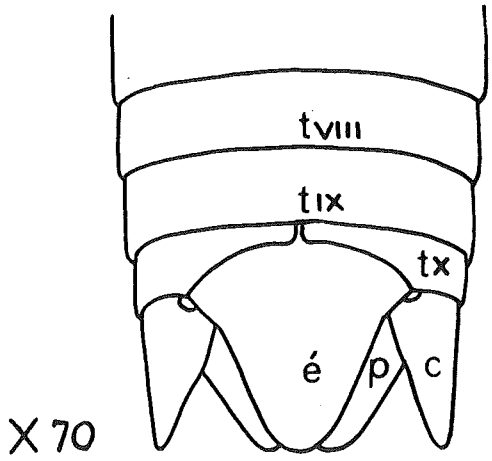
a. Female : (ventral view)



b. Female : (dorsal view)

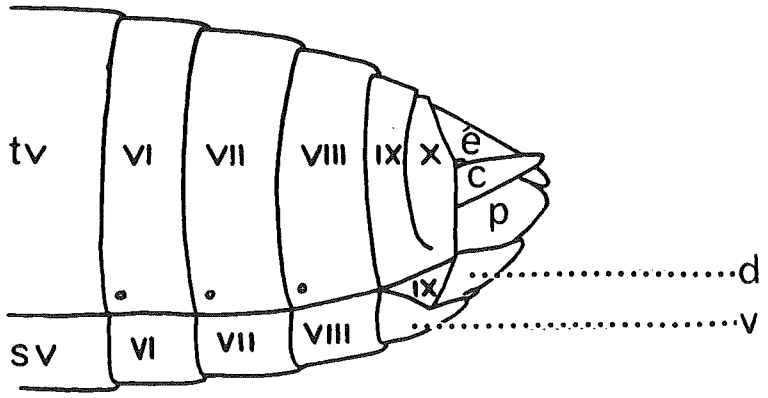


c. Male : (ventral view)

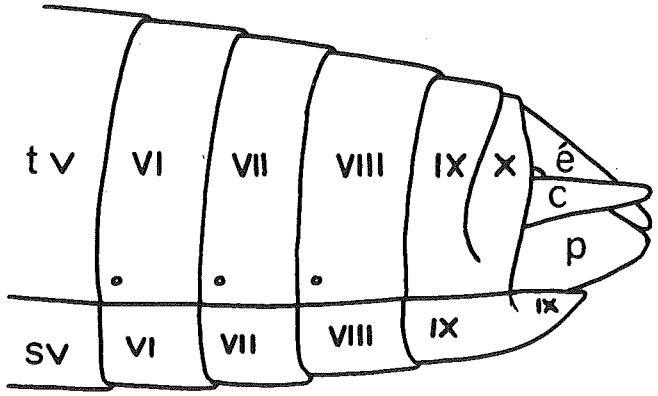


d. Male : (dorsal view)

FIG 4.7 (a.b.c.d.) *Phaulacridium marginale*: Second nymphal instar. Posterior abdominal structures



a. *Phaulacridium marginale* : Female X32



b. *Phaulacridium marginale* : Male X40

FIG 4.8 *(a. b.)* Posterior abdominal structures (lateral view) Second nymphal instar

P.marginale

Instar III.

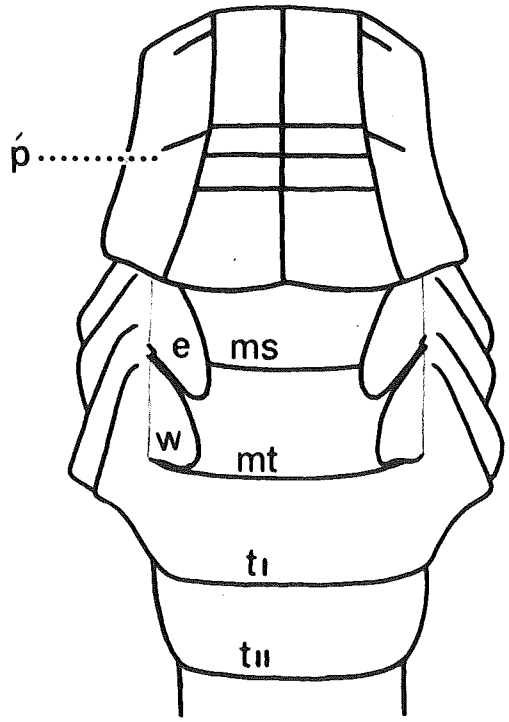
Body length between 6.4 - 11.0mm : male

7.4 - 11.4mm : female

Both elytral and wing rudiments pointed and reflexed dorsally. Elytral rudiments not extending back as far as wing rudiments (figs. 4.9 a b). Wing rudiments may partially overlap elytral rudiments.

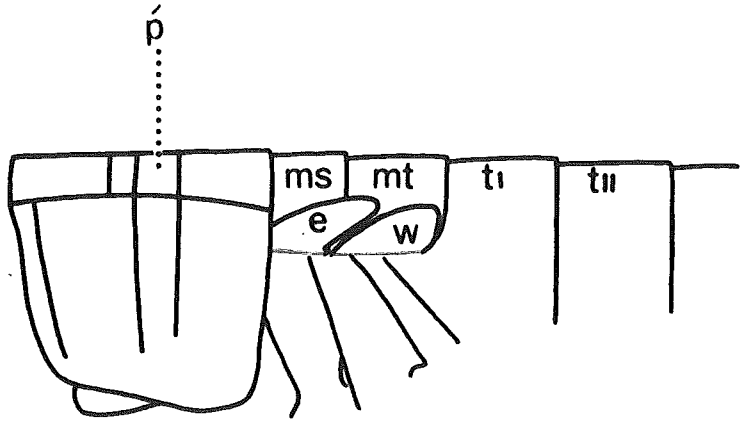
Female. Sternite VIII slightly longer than sternite VII. Posterior edge of sternite VIII with a single pointed median egg-guide. Sternite IX visible as small plates at the bases of tergites IX, X. Dorsal valves projecting slightly beyond the ventral valves. Neither pair of valves extending beyond the paraprocts (figs. 4.10 a, 4.11 a).

Male. Sternite IX longer than sternite VIII. Distal and proximal portions of sternite IX nearly equal in length (figs. 4.10 c, 4.11 b). Distal portion narrower than proximal portion., lying horizontally. The posterior margin of the distal portion of sternite IX convex (fig. 4.10 c).



X67

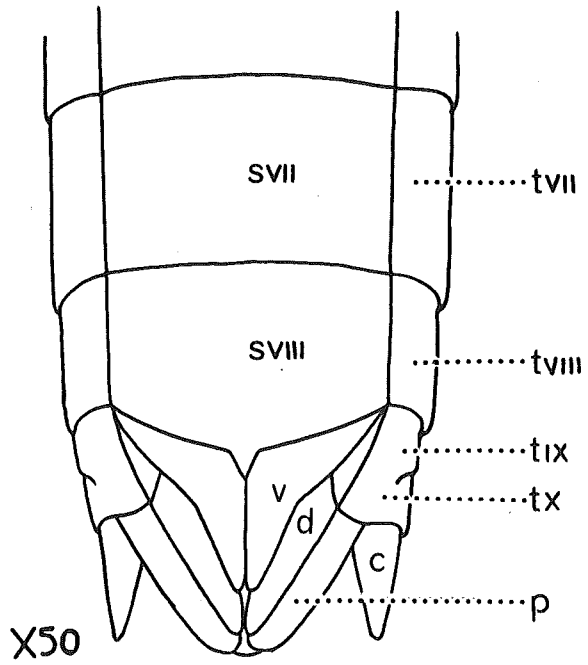
a *Phaulacridium marginale* (dorsal view)



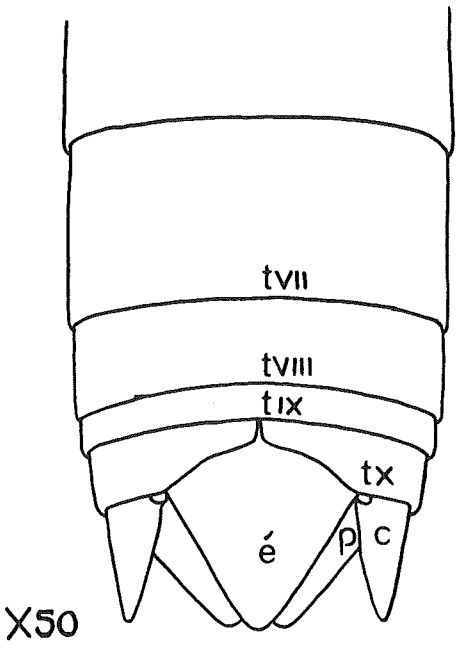
X60

b *Phaulacridium marginale* (lateral view)

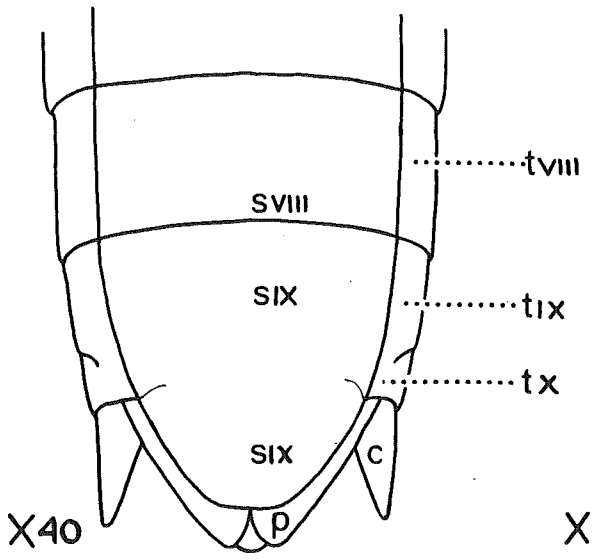
FIG 4.9 (a b) Thoracic and anterior abdominal segments
Third nymphal instar



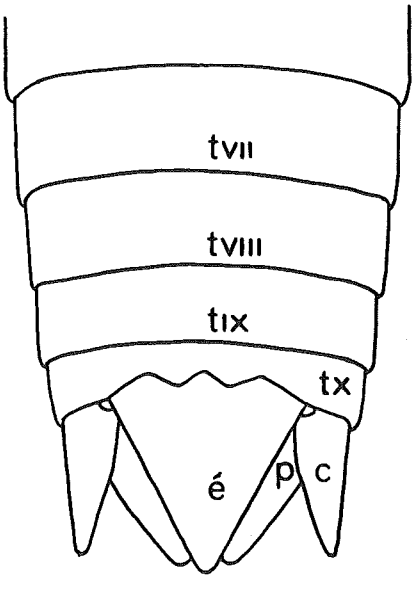
a. Female (ventral view)



b Female (dorsal view)

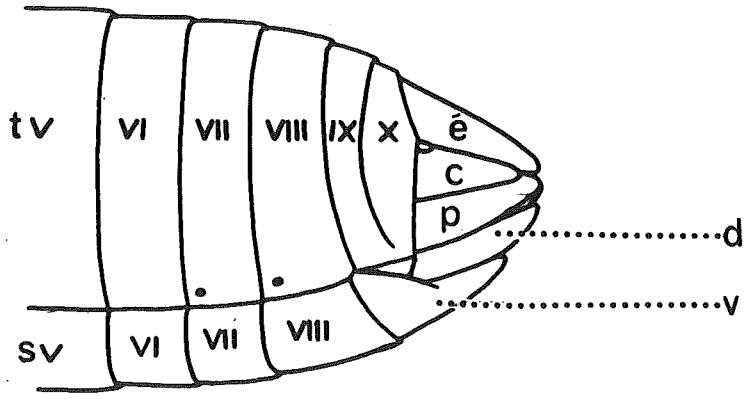


c. Male (ventral view)

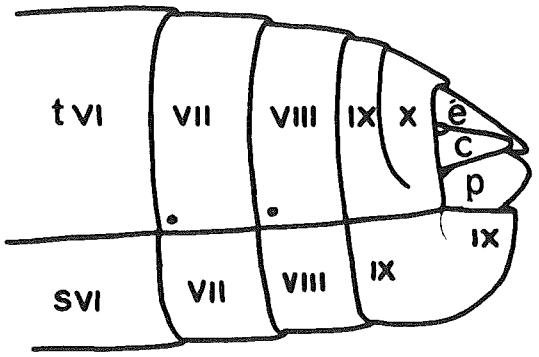


d Male (dorsal view)

FIG 4.10 (abcd) *Phaulacridium marginale* Third nymphal instar Posterior abdominal structures



a. *Phaulacridium marginale* : Female X19



b. *Phaulacridium marginale* : Male X30

FIG 4.11 *(a.b.)* Posterior abdominal structures (lateral view) Third nymphal instar

P.marginale

Instar IV

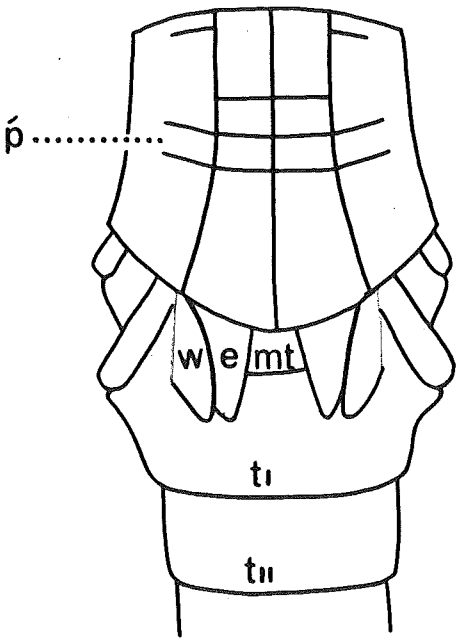
Body length between 9.2 - 15.7mm : male

10.3 - 16.6mm : female

Wing and elytral rudiments reflexed dorsally. Elytral rudiments extending back as far as wing rudiments. Wing rudiments partially overlapping elytral rudiments, (fig. 4.12 a b).

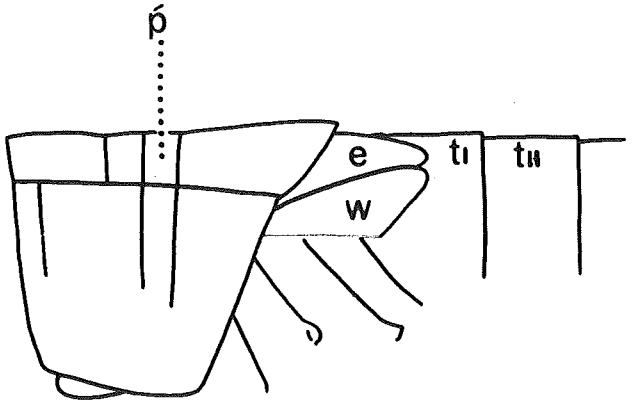
Female. Sternite VIII twice as long as sternite VII. Egg guide with paired lateral projections (fig.4.13 a). Sternite IX not visible. Both dorsal and ventral valves curved upwards; ventral valves pointing upwards (fig.4.14 a).

Male. Sternite IX more than twice the length of sternite VIII (fig.4.13 c). Distal portion of sternite IX longer than the proximal portion curving dorsally (fig.4.14 b). A pair of projections extending from the posterior margin of tergite X on either side of the dorsal midline (fig. 4.13 d).



X13

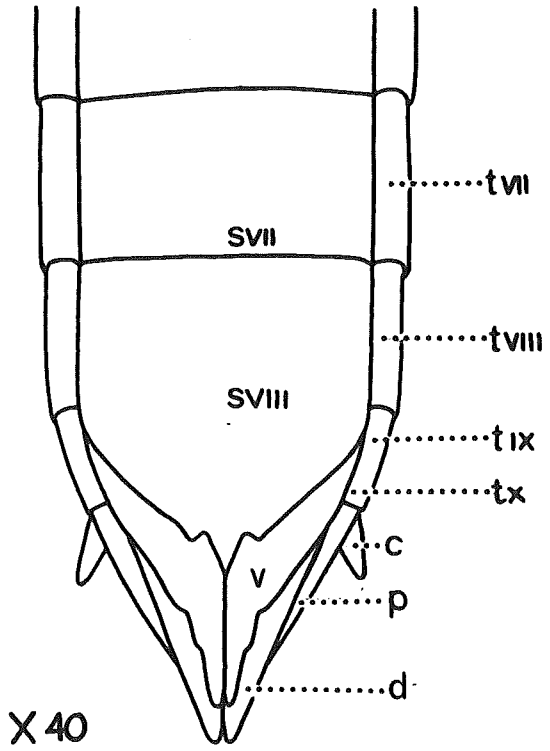
a *Phaulacridium marginale* (dorsal view)



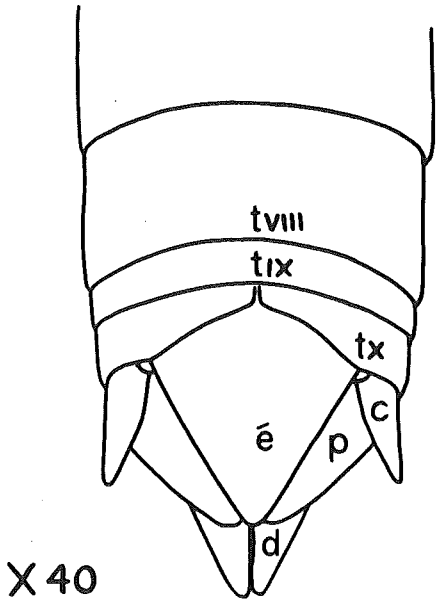
X13

b *Phaulacridium marginale* (lateral view)

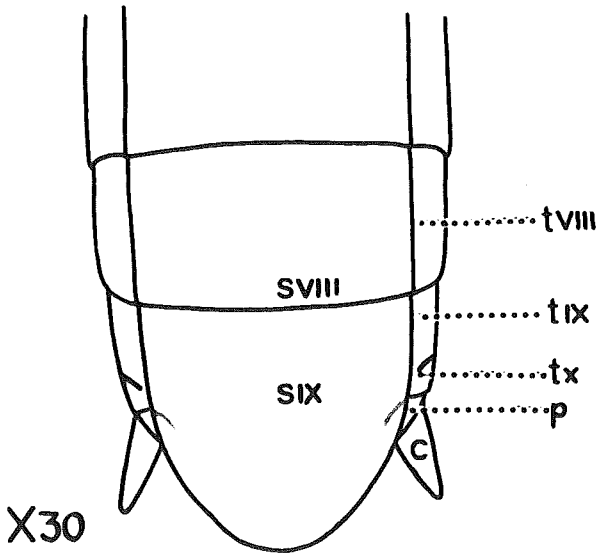
FIG 4.12 (a.b.) Thoracic and anterior abdominal segments Fourth nymphal instar



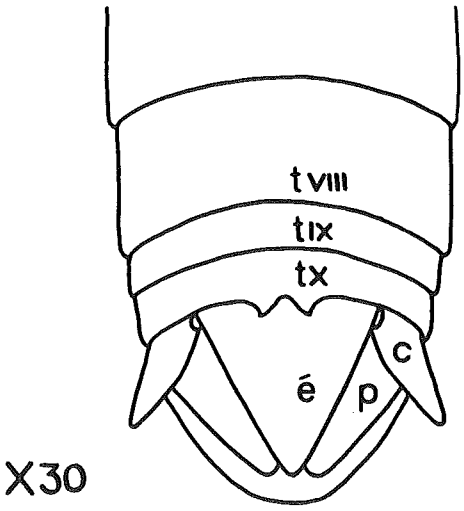
a. Female : (ventral view)



b. Female : (dorsal view)

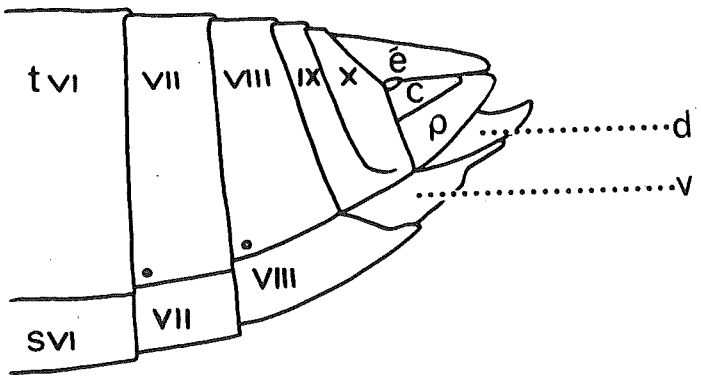


c. Male : (ventral view)

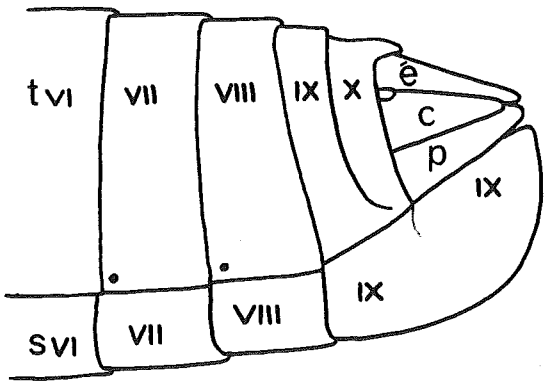


d. Male : (dorsal view)

FIG 4.13 (a.b.c.d.) *Phaulacridium marginale*: Fourth nymphal instar



a. *Phaulacridium marginale* : Female X20



b. *Phaulacridium marginale* : Male X30

FIG 4.14 (a. b.) Posterior abdominal structures (lateral view) Fourth nymphal instar

P.marginale

Adult

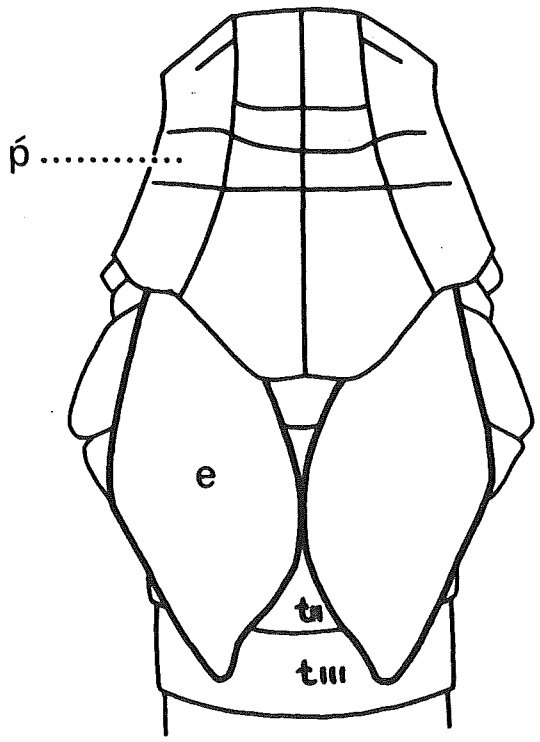
Body length between 10.8 - 13.5mm : male

14.4 - 18.2mm : female

Vestigial wings and elytra lying dorsally, elongated anteroposteriorly. Elytra extending to tergite III. Wings completely covered by elytra (fig. 4.15 a b).

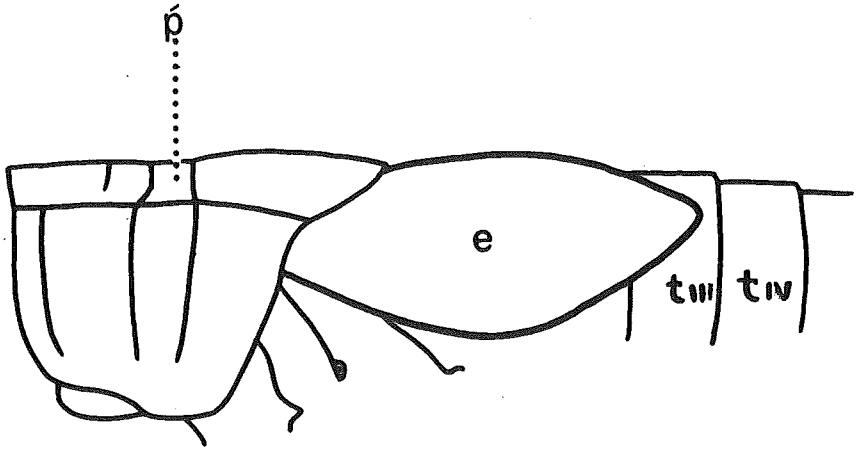
Female. Sternite VIII twice as long as sternite VII (fig. 14.6 a). Egg-guide three-pointed. A dark pigment spot behind the outer points of the egg-guide (fig. 4.16 a). Both dorsal and ventral valves projecting beyond the paraprocts (figs. 4.16 b, 4.17 a). Tips of the dorsal valves curving upwards and those of the ventral valves downwards (fig. 4.17 a).

Male. Sternite IX more than twice the length of sternite VIII (figs. 4.16 c, 4.17 b). Distal portion of sternite IX longer than the proximal portion with greatly increased dorsal curvature in comparison with previous instar (fig. 4.17 b). Projections from the posterior margin of tergiteX darkened (figs. 4.16 d, 4.17 b).



X15

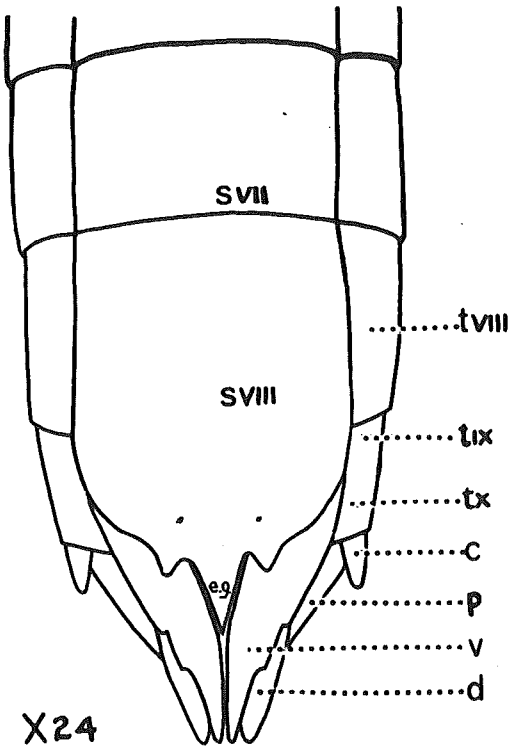
a *Phaulacridium marginale* (dorsal view)



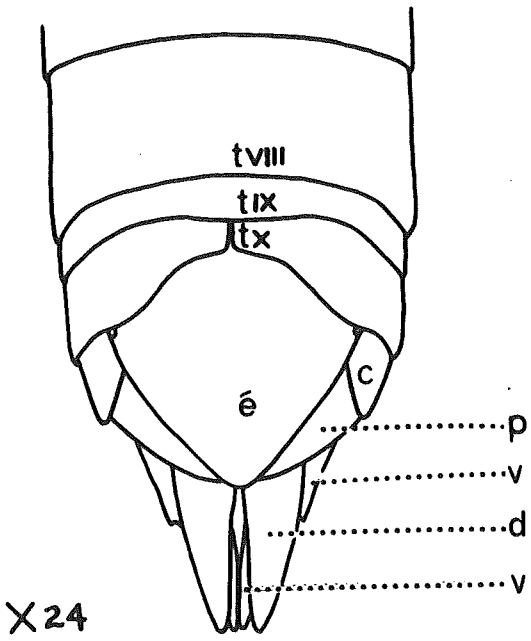
X15

b *Phaulacridium marginale* (lateral view)

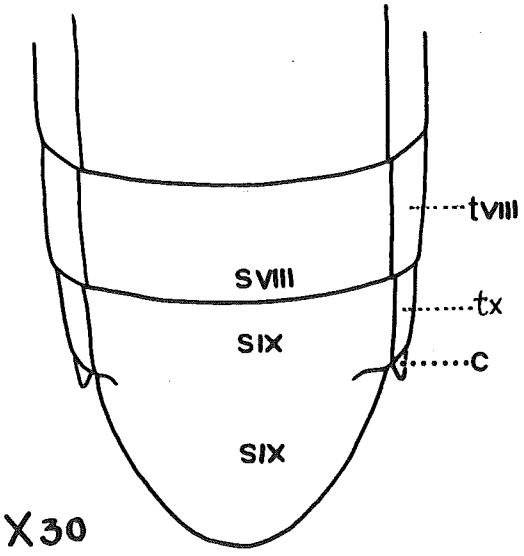
FIG 4.15 *(a b)* Thoracic and anterior abdominal segments Adult



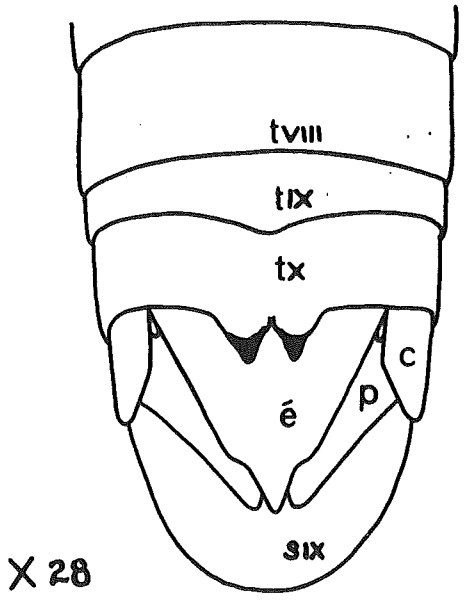
a. Female : (ventral view)



b. Female : (dorsal view)

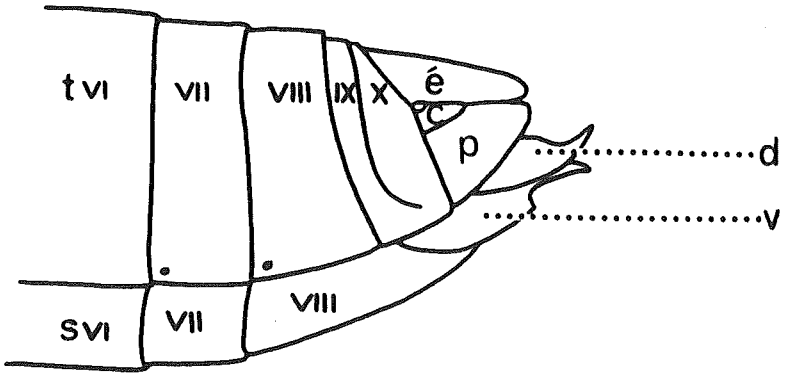


c. Male : (ventral view)

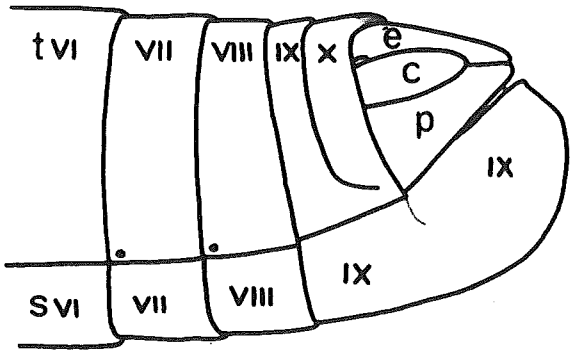


d. Male : (dorsal view)

FIG 4.16 (a.b.c.d) *Phaulacridium marginale* Adult
Posterior abdominal structures



a. *Phaulacridium marginale* : Female X 15



b. *Phaulacridium marginale* : Male X 24

FIG 4.17 *(a. b.)* Posterior abdominal structures (lateral view) Adult

4.6 ♀ S. campestris

Key to the nymphal instars and adult.

1 (2) Wing and elytral rudiments lying laterally 3.

2 (1) Wing and elytral rudiments reflexed dorsally 9

3 (4) Elytral rudiments pointed. Wing rudiments occasionally pointed, usually forming right angles at posterolateral corners..Instar IV
figs. 4.20, 4.30a, 4.31a

4 (3) Posterolateral margins of elytra and wing rudiments both rounded 5

5 (6) Sternite IX completely mesally obscured by the rudimentary ventral ovipositor valves..
....Instar III
figs. 4.19, 4.28a, 4.29a

6 (5) Sternite IX not completely mesally obscured by the rudimentary ventral ovipositor valves 7

7 (8) The anterior portion of sternite IX mesally obscured by the rudimentary ventral ovipositor valves.....Instar II
4.18, 4.26a, 4.27a

8 (7) The anterior portion of sternite IX scarcely obscured by the rudimentary ventral ovipositor valves.....Instar I

figs. 4.18
4.24 a b
4.25 a

9 (10) Wings completely covered by elytra....Adult

figs. 4.23
4.35 a b
4.36 a

10 (9) Wings not completely covered by elytra 11

11 (12) Elytral rudiments not extending back as far as wing rudiments.....Instar V

figs. 4.21
4.32 a b
4.33 a

12 (11) Elytral rudiments extending back as far as wing rudiments.....Instar VI

figs. 4.22
4.34 abc

4.7 ♂ S.campestris

Key to the nymphal instars and adult.

1 (2) Wing and elytral rudiments lying laterally 3

2 (1) Wing and elytral rudiments reflexed dorsally 7

3 (4) Elytral rudiments pointed. Wing rudiments occasionally pointed, usually forming right angles at posterolateral corners..Instar III
4.20
figs. 4.28 c
4.29 b

4 (3) Posterolateral margins of elytra and wing rudiments both rounded 5

5 (6) Distal portion of sternite IX shorter and narrower than proximal portion femur length 4.5mm.....Instar II
4.19
figs. 4.26 c
4.27 b

6 (5) (femur length female 3.5mm).....Instar I
(fig.4.18)

7 (8) Wings completely covered by elytra...Adult
(4.23
figs. 4.35 d
4.36 b)

8 (7) Wings not completely covered by elytra 9

9 (10) Elytral rudiments not extending back as far as wing rudiments.....Instar IV
4.21
figs. 4.30 c
4.31 b

10 (9) Elytral rudiments extending back as far as wing rudiments.....Instar V
4.22
figs. 4.32 d.4.33b

4.8

DIAGNOSES OF

INSTARS AND ADULTS OF

S.CAMPESTRIS

Sigaus campestris

WING BUDS AND ELYTRA.

Instar I male

Instar I and II female

Posterolateral margins of mesonotum and metanotum forming indistinct elytral and wing rudiments lying laterally. Both elytral and wing rudiments rounded (fig. 4.18 a b).

Instar II male

Instar III female

Posterolateral margins of the mesonotum and metanotum forming distinct elytral and wing rudiments, lying laterally. Elytral rudiments pointed, wing rudiments rounded (fig. 4.19 b).

Instar III male

Instar IV female

Wing and elytral rudiments distinct, lying laterally. Elytral rudiments pointed. Wing rudiments occasionally pointed, usually forming right angles at posterolateral corners (fig. 4.20 a b).

Instar IV male

Instar V female

Wing and elytral rudiments reflexed dorsally.

Elytral rudiments not extending back as far as the wing rudiments. Wing rudiments may partially overlap elytral rudiments (fig. 4.21 a b).

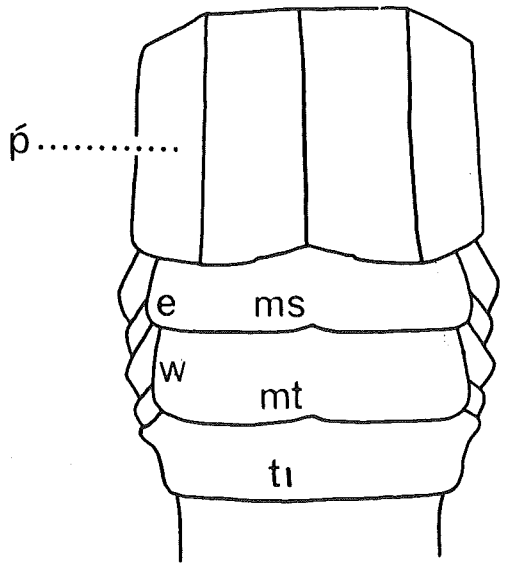
Instar V male

Instar VI female

Wing and elytral rudiments reflexed dorsally. Elytral rudiments extending slightly beyond wing rudiments. Wing rudiments slightly overlapping elytral rudiments (fig.4.22a b).

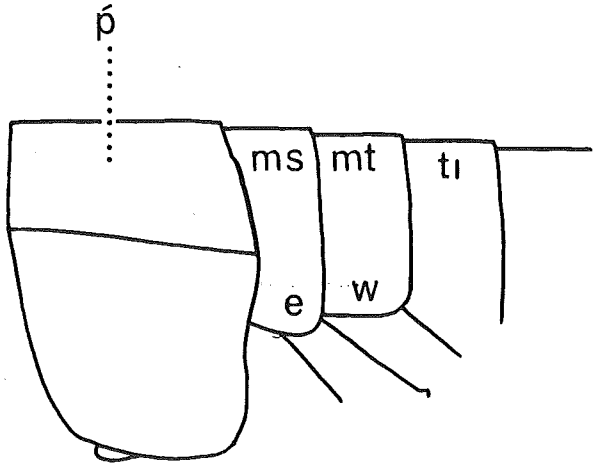
Adult male and female

Vestigial wings and elytra lying laterally, elongated anteroposteriorly. Elytra extending to tergite III. Wings completely covered by elytra (fig. 4.23 a b).



X 50

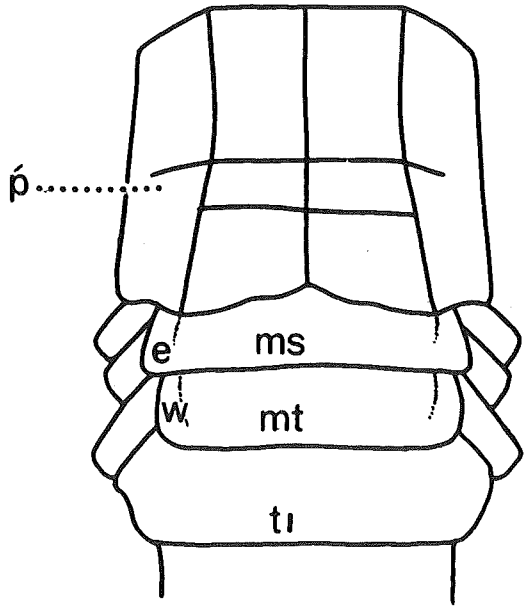
a. *Sigaus campestris* (dorsal view)



X 50

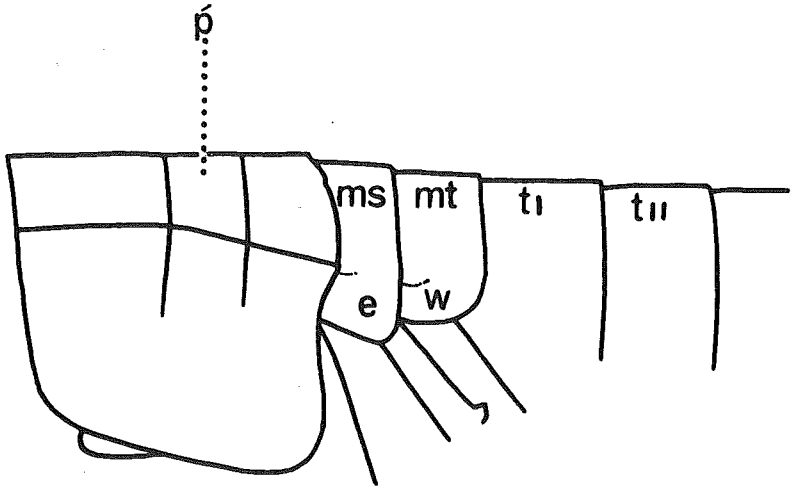
b. *Sigaus campestris* (lateral view)

FIG 4.18 *(a. b.)* Thoracic and anterior abdominal segment
First and second nymphal instars female
First nymphal instar male



X 27

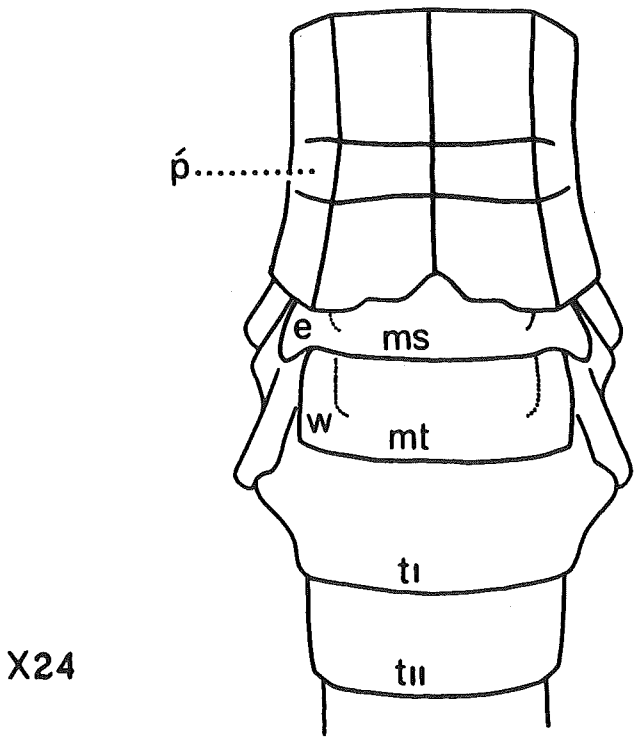
a *Sigaus campestris* (dorsal view)



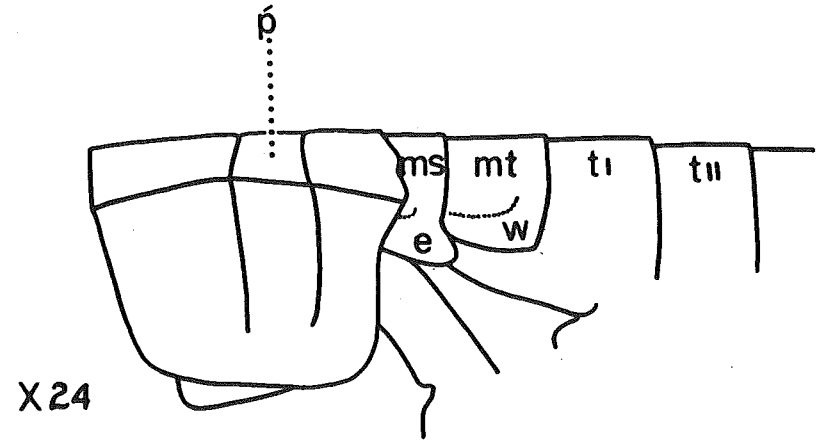
X27

b *Sigaus campestris* (lateral view)

FIG 4.19 *(a b)* Thoracic and anterior abdominal segments
third nymphal instar female
second nymphal instar male

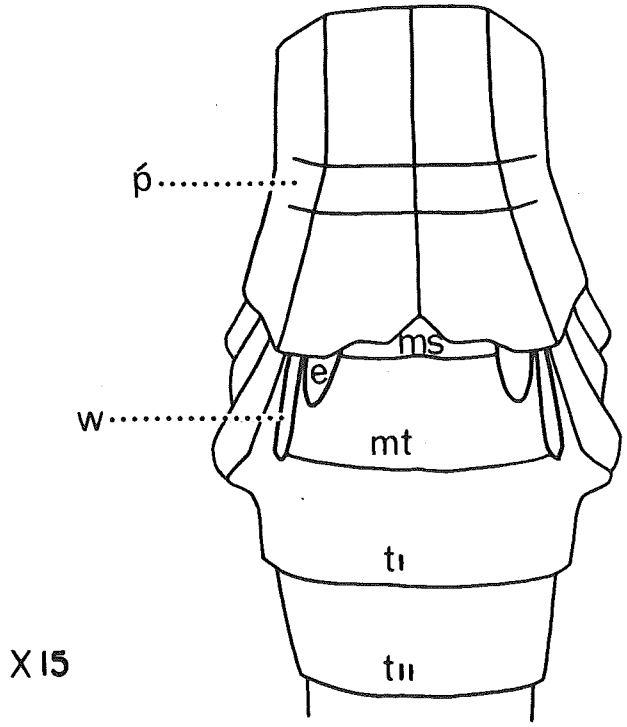


a *Sigaus campestris* (dorsal view)

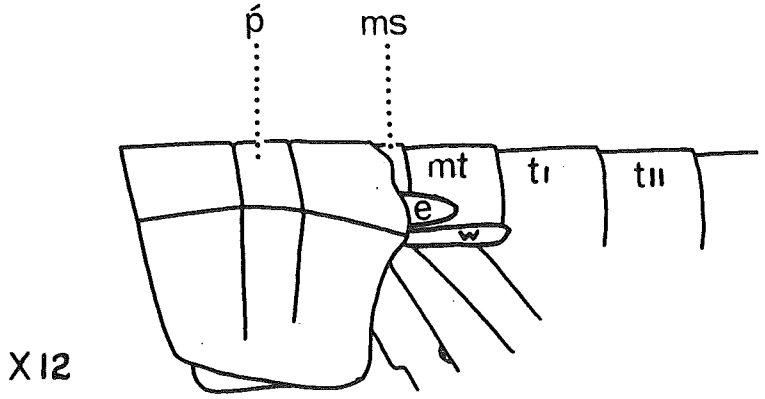


b *Sigaus campestris* (lateral view)

FIG 4.20 *(ab)* Thoracic and anterior abdominal segments
fourth nymphal instar female
third nymphal instar male

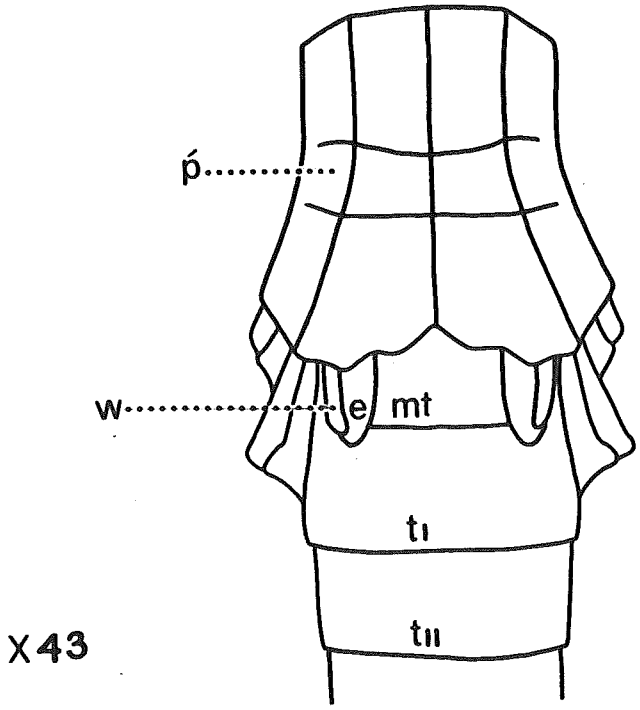


a. *Sigaus compestris* (dorsal view)

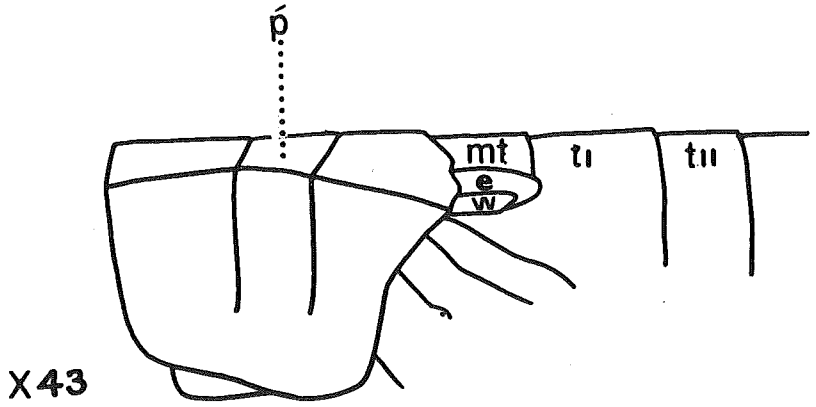


b. *Sigaus compestris* (lateral view)

FIG 4.21 *(a b)* Thoracic and anterior abdominal segments
Fifth nymphal instar female
Fourth nymphal instar male

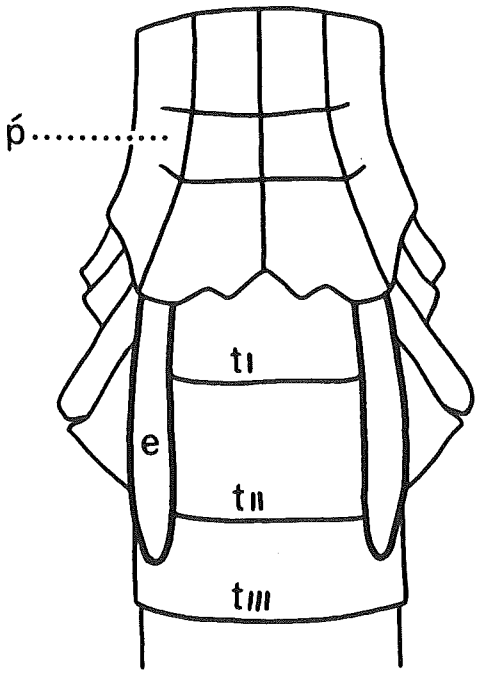


a *Sigaus campestris* (dorsal view)



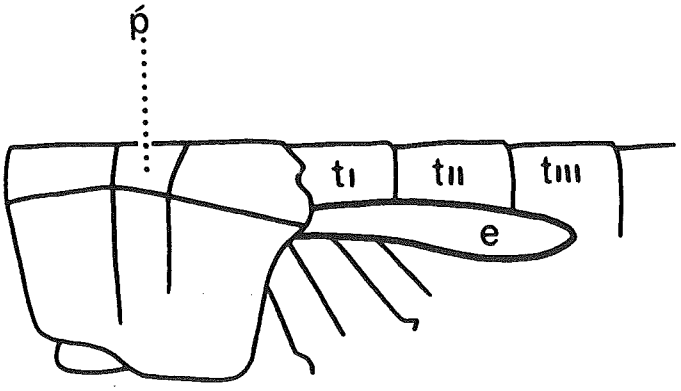
b. *Sigaus campestris* (lateral view)

FIG 4.22 (a b) Thoracic and anterior abdominal segments
sixth nymphal instar female
fifth nymphal instar male



X12

a *Sigaus campestris* (dorsal view)



X12

b. *Sigaus campestris* (lateral view)

FIG 4.23 (a. b.) Thoracic and anterior abdominal segments Adult male and female

Sigaus campestris

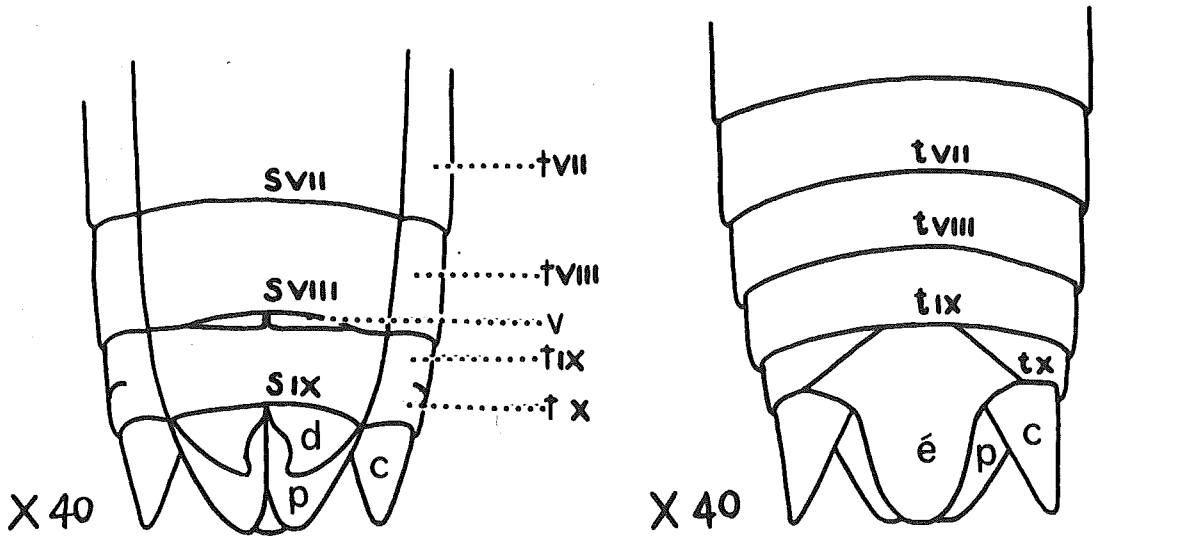
FIRST nymphal instar

Egg length 5.5mm

Body length 5.58mm : female

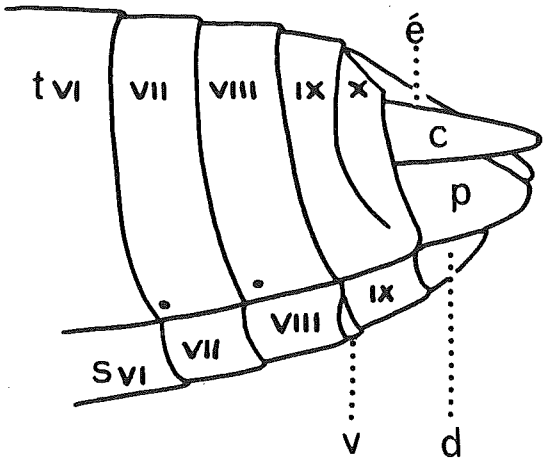
Female Sternite VIII slightly concave posteriorly and bearing a pair of rudimentary ventral valves scarcely obscuring the anterior portion of sternite IX. A pair of short dorsal valves projecting from the posterior edge of sternite IX (figs. 4.24 a b, 4.25 a).

Male Not seen. Assumed to be about the same size as first instar female with similar degree of development of wings and elytra, (fig. 4.18 a b).



a Female (ventral view) *b* Female (dorsal view)

FIG 4.24 (*a.b.*) *Sigaus campestris* First nymphal instar
Posterior abdominal structures



a. *Sigaus compestris* : Female X 40

FIG 4.25 (a.) Posterior abdominal structures (lateral view) First nymphal instar

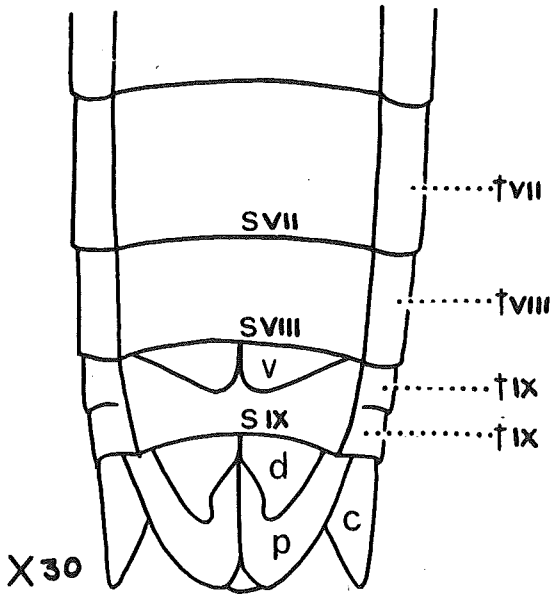
Sigaus campestris

SECOND nymphal instar

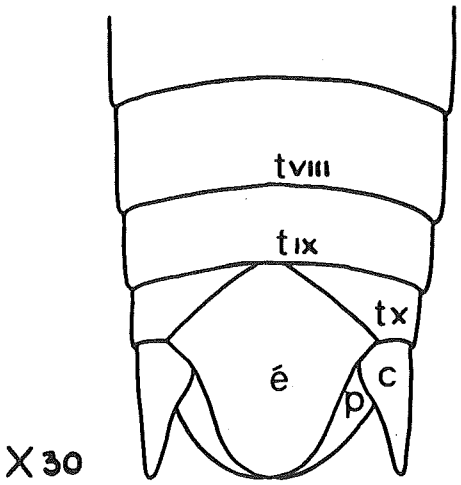
Body length between 6.3 - 10.4mm : male
7.7 - 10.0mm : female

Female. Sternite VIII slightly concave posteriorly bearing a pair of rudimentary ventral valves obscuring the anterior portion of sternite IX. A pair of short dorsal valves projecting from the posterior edge of sternite IX (figs. 4.26 a, 4.27 a).

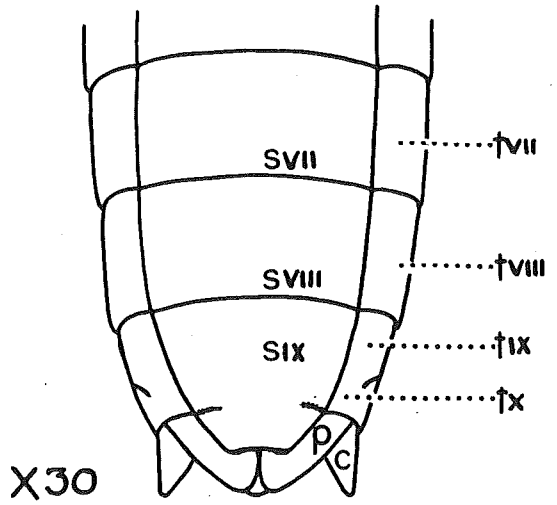
Male. Sternite IX longer than sternite VIII. Distal portion of sternite IX shorter and narrower than the proximal portion. Posterior margin of sternite IX slightly concave (figs. 4.26 c, 4.27 b).



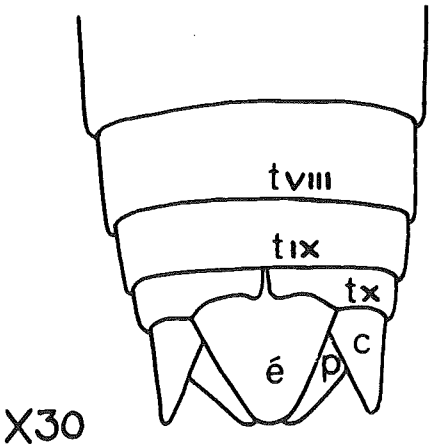
a Female (ventral view)



b Female (dorsal view)

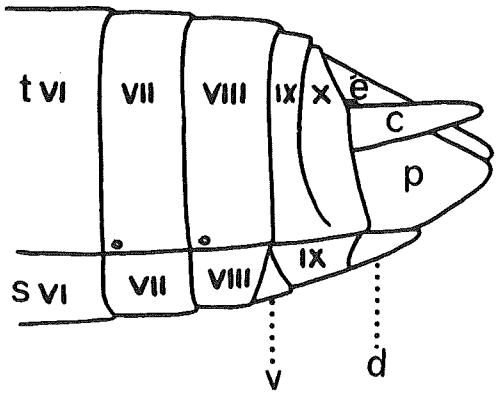


c Male (ventral view)

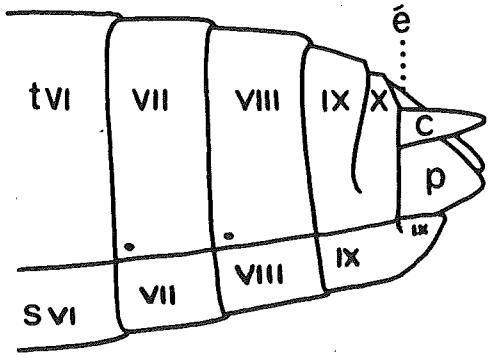


d Male (dorsal view)

FIG 4.26 (a.b.c.d) *Sigaus campestris* Second nymphal instar Posterior abdominal structures



a. *Sigaus campestris* : Female X34
(a.) Posterior abdominal structures (lateral view)
Second nymphal instar



b. *Sigaus campestris* : Male X30
FIG 4.27 (a. b.) Posterior abdominal structures (lateral view)
Second nymphal instar

Sigauscampestris

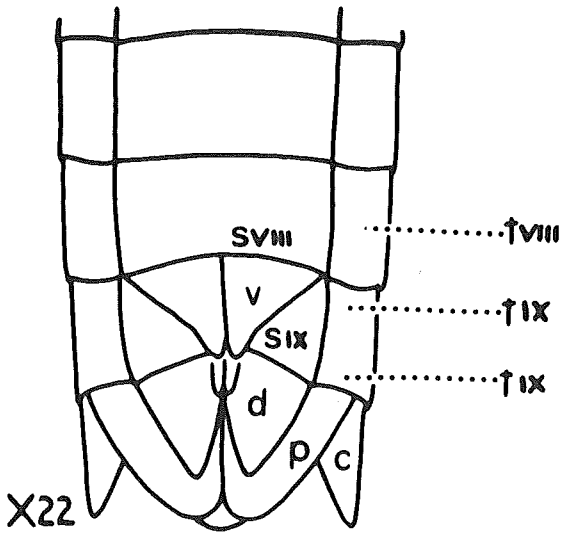
THIRD nymphal instar

Body length between 8.8 - 12.1mm : male

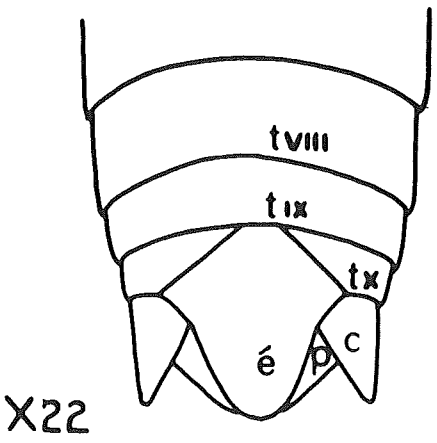
8.7 - 10.1mm : female

Female. Sternite VIII approximately equal in length to sternite VII. Sternite IX mesally obscured by the ventral rudimentary ovipositor valves. Posterior tips of ventral valves overlying bases of the dorsal valves mesally obscuring sternite IX. Inner valves arise at the anteromedial margin of the dorsal valves just posterior to the ventral valve tips (figs. 4.28 a, 4.29 a).

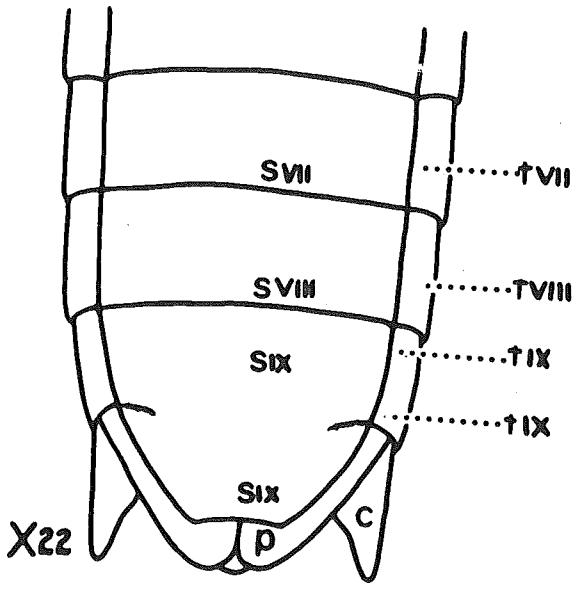
Male. Sternite IX longer than sternite VIII. The distal and proximal portions of sternite IX approximately equal in length. Distal portion narrower than the proximal portion (figs. 4.28 c, 4.29 b).



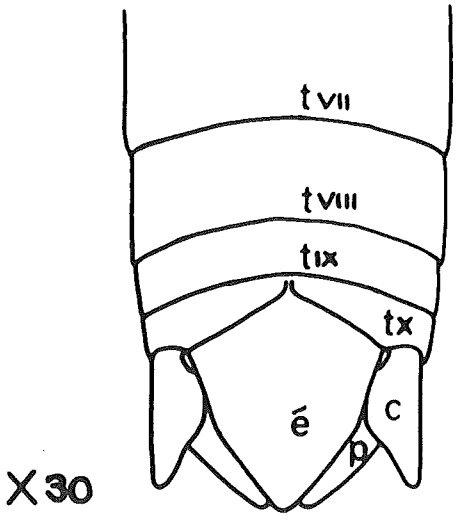
a Female (ventral view)



b Female (dorsal view)

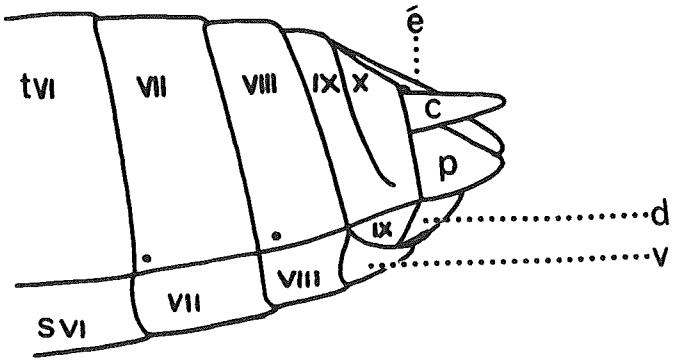


c Male (ventral view)

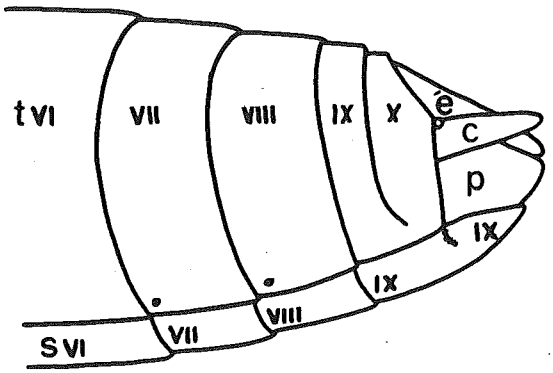


d Male (dorsal view)

FIG 4.28 (a.b.c.d) *Sigaus campestris* Third nymphal instar
Posterior abdominal structures



a. *Sigaus campestris* : Female X18



b. *Sigaus campestris* : Male X22

FIG 4.29 (a. b.) Posterior abdominal structures (lateral view) Third nymphal instar

Sigaus campestris

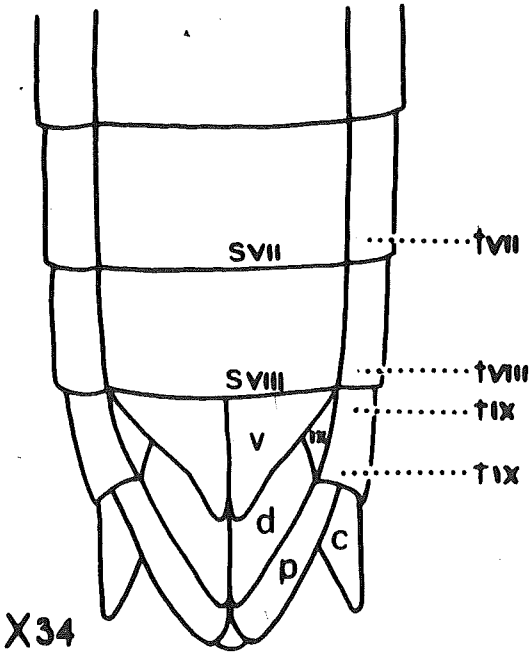
FOURTH nymphal instar

Body length between 10.5 - 15.5mm : male

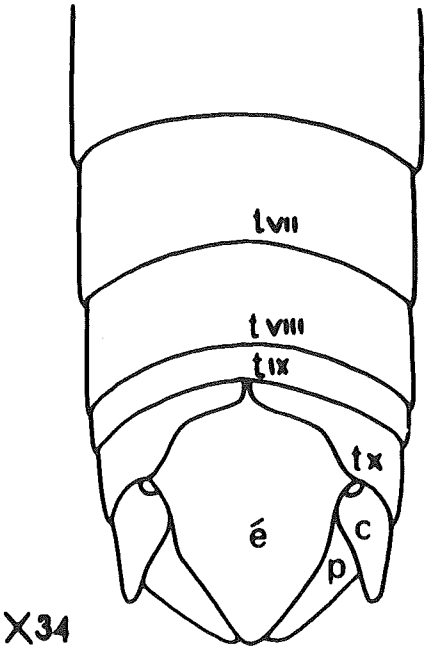
11.4 - 14.8mm : female

Female. Sternite VIII and sternite VII equal in length. The mesal part of the posterior edge of sternite VIII straight. Sternite IX present as triangular plates at bases of tergites X (fig. 4.30 a, 4.31 a). Dorsal valves projecting beyond ventral valves. Neither pair of valves extending beyond the paraprocts (figs. 4.30 a, 4.31 a).

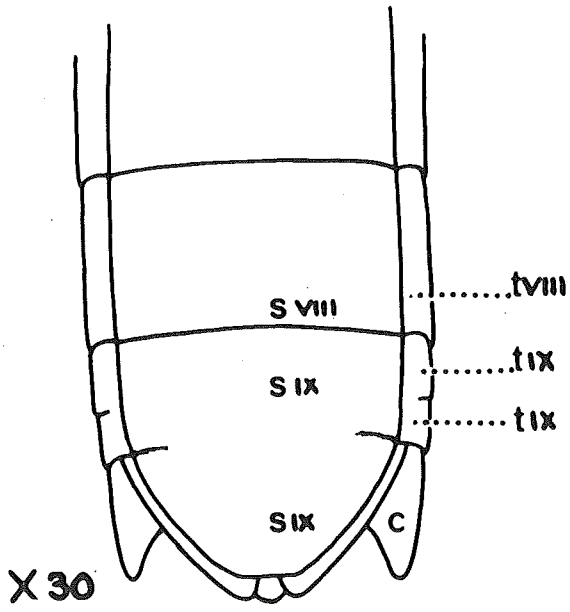
Male. Sternite IX twice the length of sternite VIII (fig. 4.30 a). Distal and proximal portions of sternite IX nearly equal in length. Distal portion narrower than proximal portion, lying horizontally (figs. 4.30 a, 4.31 a).



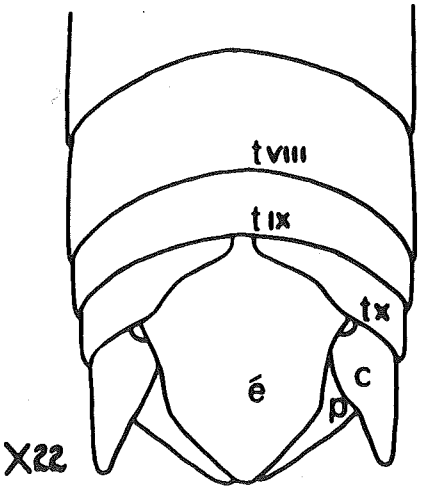
a Female (ventral view)



b Female (dorsal view)

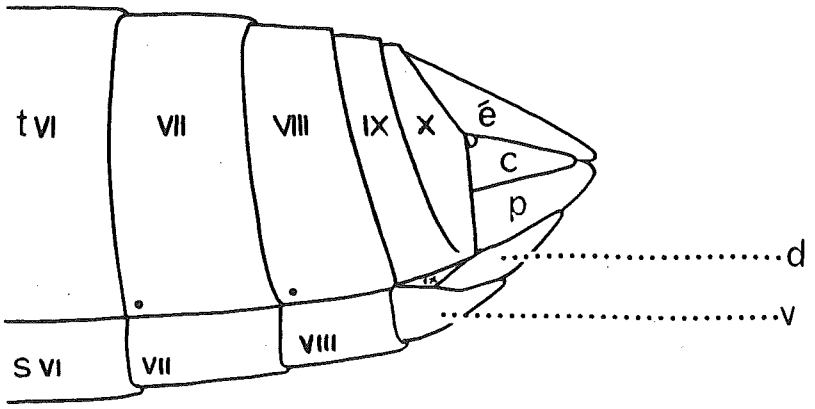


c Male (ventral view)

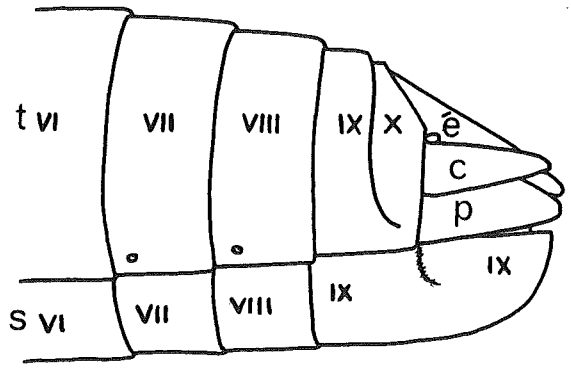


d Male (dorsal view)

FIG 4.30 (a.b.c.d) *Sigaus campestris* Fourth nymphal instar
Posterior abdominal structures



a. *Sigaus campestris* : Female X34



b. *Sigaus campestris* : Male X19

FIG 4.31 *(a. b.)* Posterior abdominal structures (lateral view) Fourth nymphal instar

Sigaus campestris

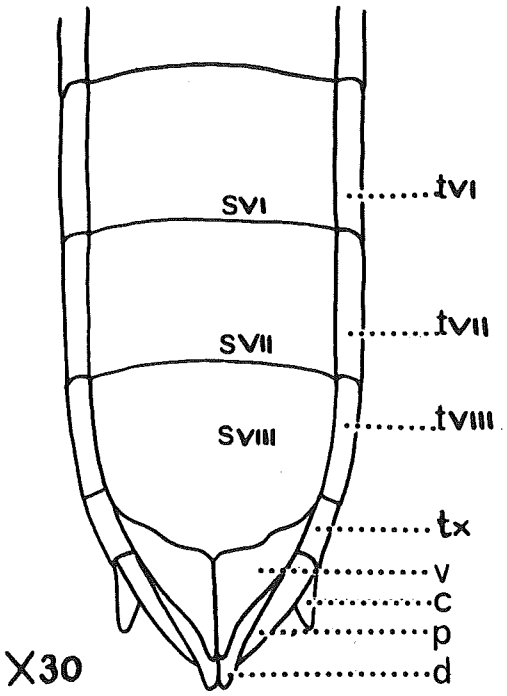
FIFTH nymphal instar

Body length between 15.6 - 17.3mm : male

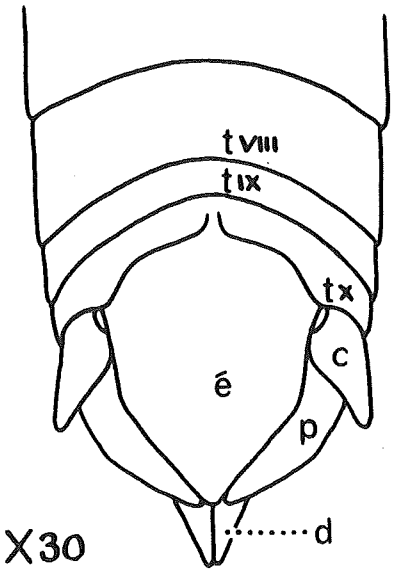
13.5 - 18.5mm : female

Female. Sternite VIII slightly longer than sternite VII. The mesal part of the posterior edge of sternite VIII with pointed projection, the egg-guide. Sternite IX not visible. Dorsal valves projecting beyond both ventral valves and paraprocts (figs. 4.32 a b, 4.33 a).

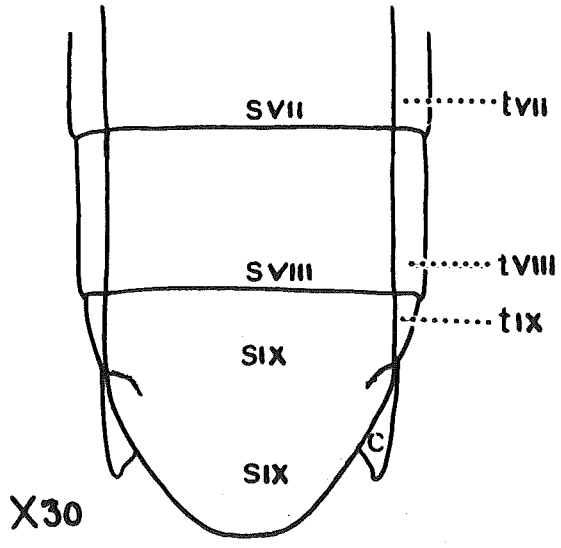
Male. Sternite IX longer than sternite VIII. Distal portions of sternite IX nearly equal in length to proximal portion, curving dorsally (figs. 4.32 d, 4.33 b). A pair of projections extending from the posterior margin of tergite X on either side of the dorsal midline (fig. 4.32 d).



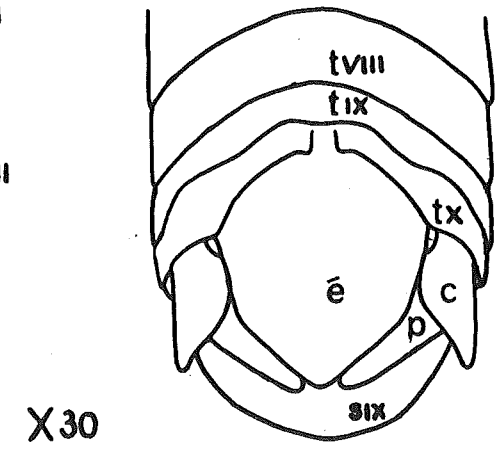
a Female (ventral view)



b Female (dorsal view)

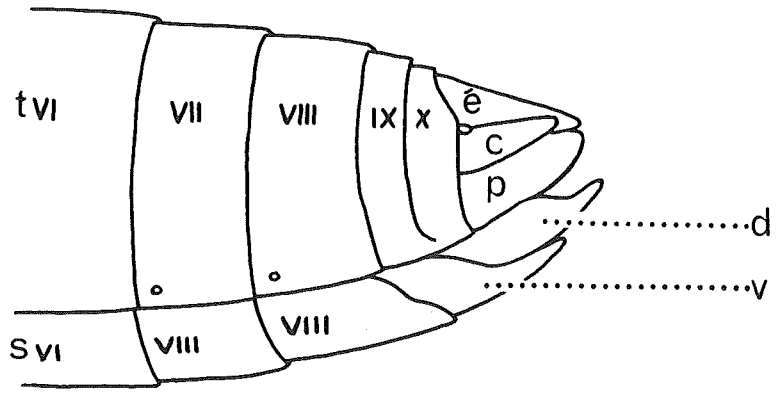


c Male (ventral view)

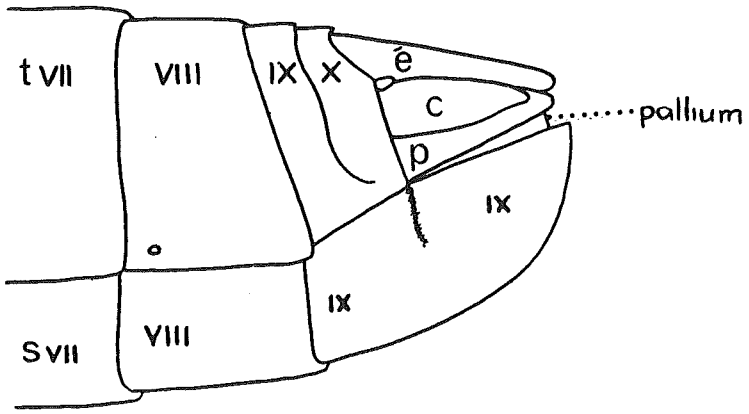


d Male (dorsal view)

FIG 4.32 (a. b. c. d) *Sigaus campestris* Fifth nymphal instar Posterior abdominal structures



a. *Sigaus campestris* : Female X25



b. *Sigaus campestris* : Male X30

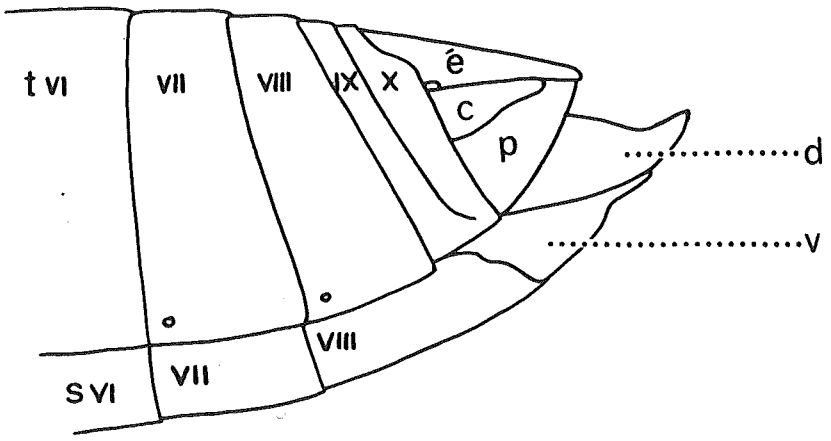
FIG 4.33 *(a. b.)* Posterior abdominal structures (lateral view) Fifth nymphal instar

Sigaus campestris

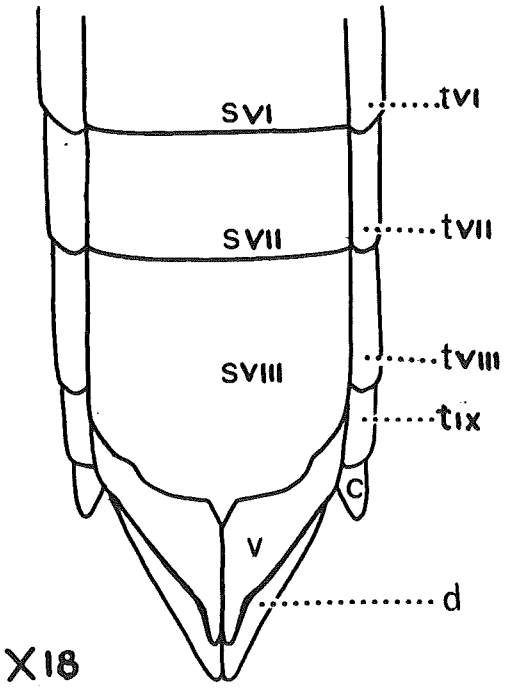
SIXTH nymphal instar

Body length between 19.25 - 25.2mm : female

Female. Sternite VIII twice as long as sternite VII. A small triangular egg-guide on posterior edge of sternite VIII between the ventral valves (fig. 4.34 a). Sternite IX not visible. Both dorsal and ventral valves extending slightly beyond paraprocts. Tips of dorsal valves curved upwards; tips of ventral valves pointing upwards (figs. 4.34 a b c).

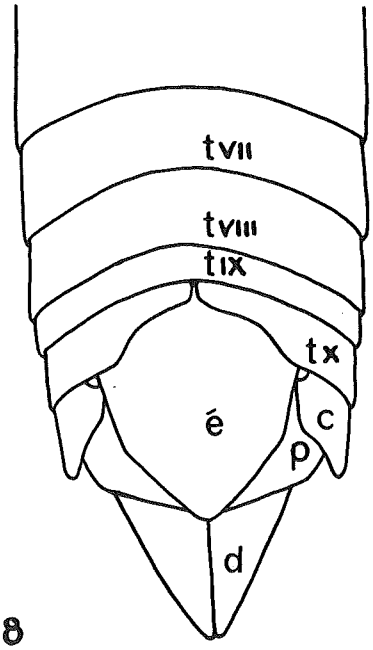


a. *Sigaus campestris* : Female X20



X18

b Female (ventral view)



X18

c Female (dorsal view)

FIG 4.34 *Sigaus campestris* Sixth nymphal instar

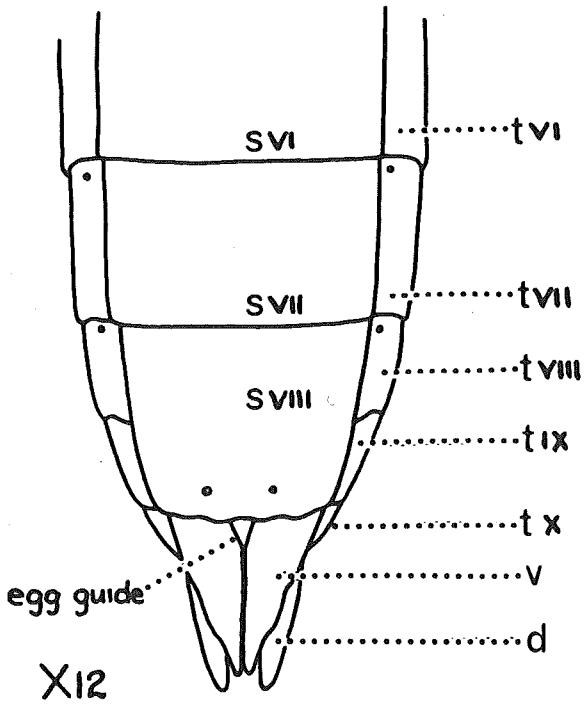
Sigaus campestris

ADULT

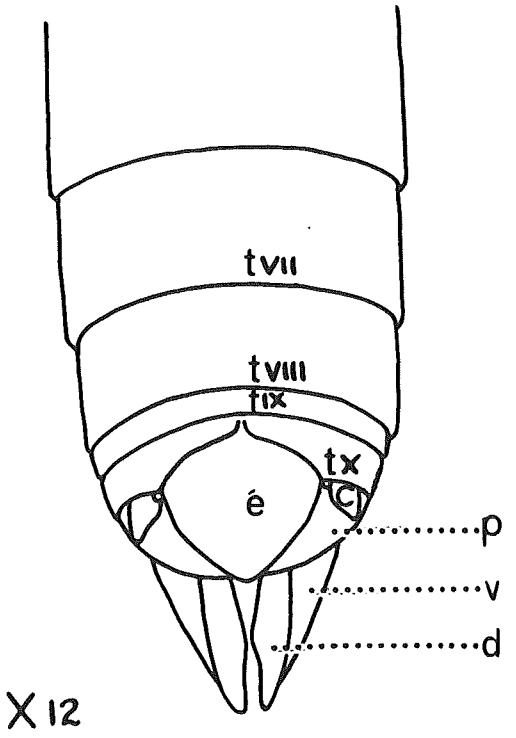
Body length between 17.5 - 19.8mm : male
27.8 - 34.4mm : female

Female. Sternite VIII longer than sternite VII (figs. 4.35 a, 4.36 a). A small triangular egg-guide on the posterior edge of sternite VIII between the ventral valves. Paired dark pigment spots on sternite VIII lateral to the base of egg-guide (fig. 4.35 a). Both dorsal and ventral valves projecting beyond paraprocts (figs. 4.35 a b, 4.36 a). Tips of dorsal valves curving upwards and those of the ventral valves downwards (fig. 4.36 a).

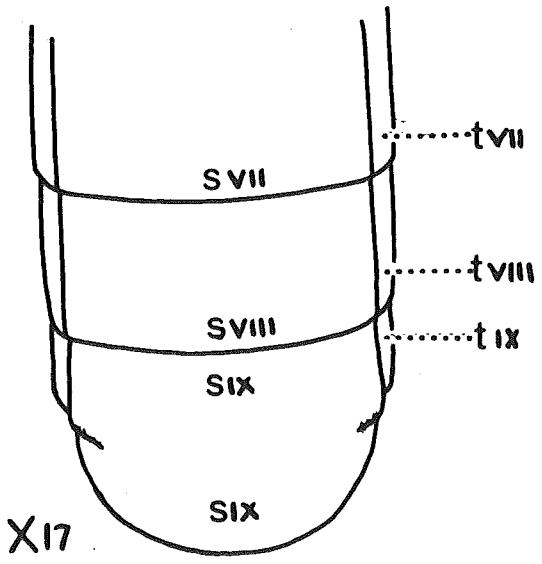
Male. Sternite IX more than twice the length of sternite VIII (fig. 4.36 b). Distal portion of sternite IX longer than proximal portion with greatly increased dorsal curvature in comparison with previous instar (figs. 4.35 d, 4.36 b). Tergite X with paired median projections (fig. 4.35 d).



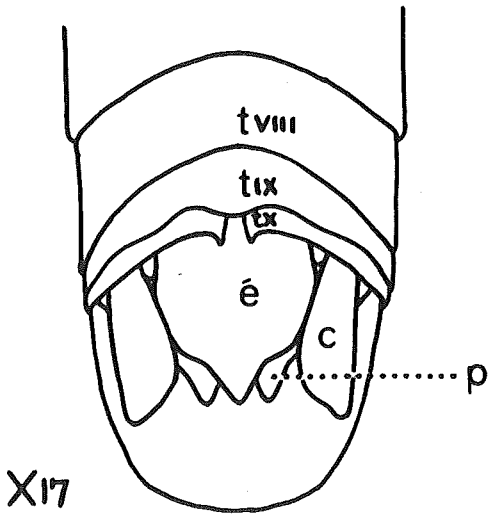
a Female (ventral view)



b Female (dorsal view)

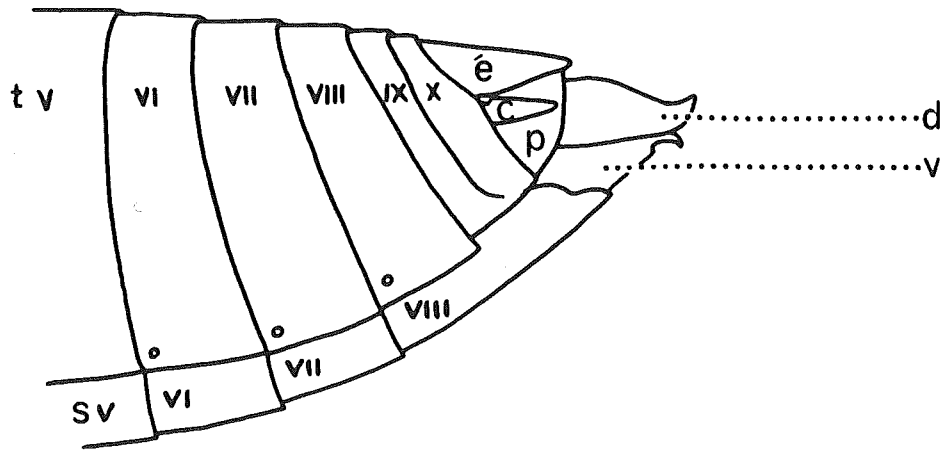


c Male (ventral view)

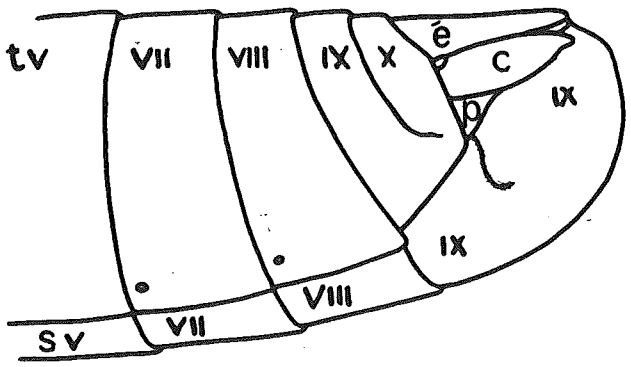


d Male (dorsal view)

FIG 4.35 (a.b.c.d.) *Sigaus campestris* Adult
Posterior abdominal structures



a. *Sigaus campestris* : Female X12



b. *Sigaus campestris* : Male X17

FIG 4.36 *(a.b.)* Posterior abdominal structures (lateral view) Adult

c = cerci

d = dorsal ovipositor valve

e = elytra

é = epiproct

e.g.= egg guide

ms = mesonotum

mt = metanotum

p = paraproct

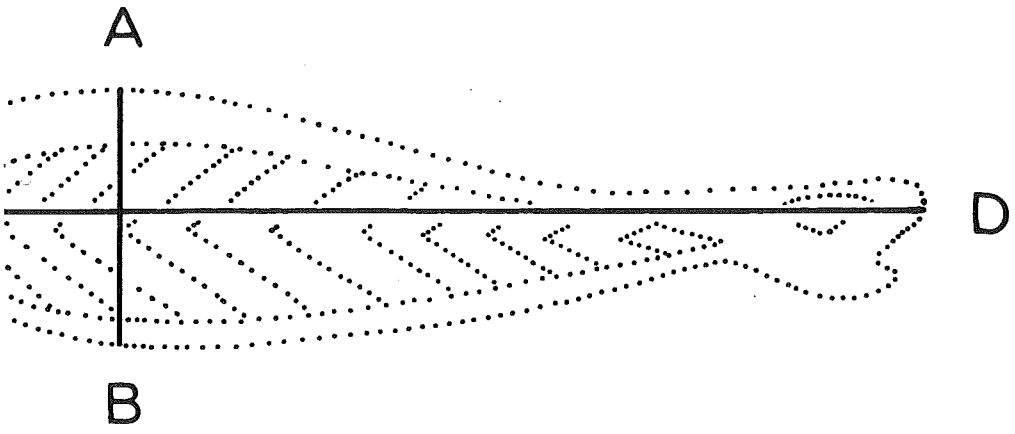
ṕ = pronotum

s = sclerite

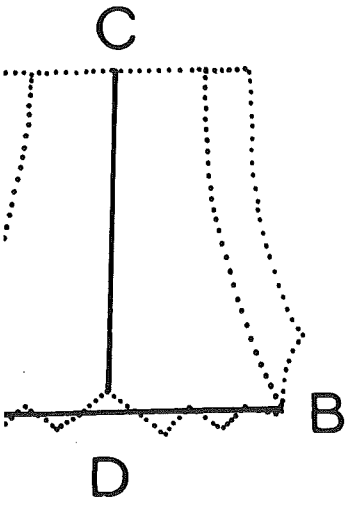
t = tergite

v = ventral ovipositor valv

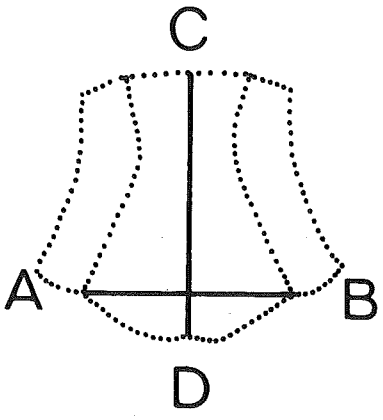
w = wing



't hind femur (outer aspect)



'us campestris
notum (dorsal view)
(a. b. c.)



c. Phaulacridium marginale
pronotum (dorsal view)

SECTION 5

Measurements.

Initially both species were grouped into instars by examination of the rudimentary wings, elytra and posterior abdominal structures. To ascertain the accuracy of these groupings, measurements of body, pronotum and femur were taken using an Olympus binocular microscope fitted with a graduated eyepiece. Body length was measured from the tip of the vertex to the end of the abdomen. As the abdominal segments were found to be subject to telescoping, the length of the body is not a precise measurement and therefore was used only as a guide to size in diagnosing instars. The measurements of the pronotum used were the mesal length and the greatest width between the carinae. To ensure accurate measurements, care was taken to distinguish the carinae when they were overlaid with colour markings. The greatest length and width of the outer aspect of the left hind femur were measured (fig. 4.37).

Samples of both species were taken from the single locality at Sumner over the period February 1964 to February 1966. Within a species, all specimens of each instar were lumped for measuring as the standard deviations

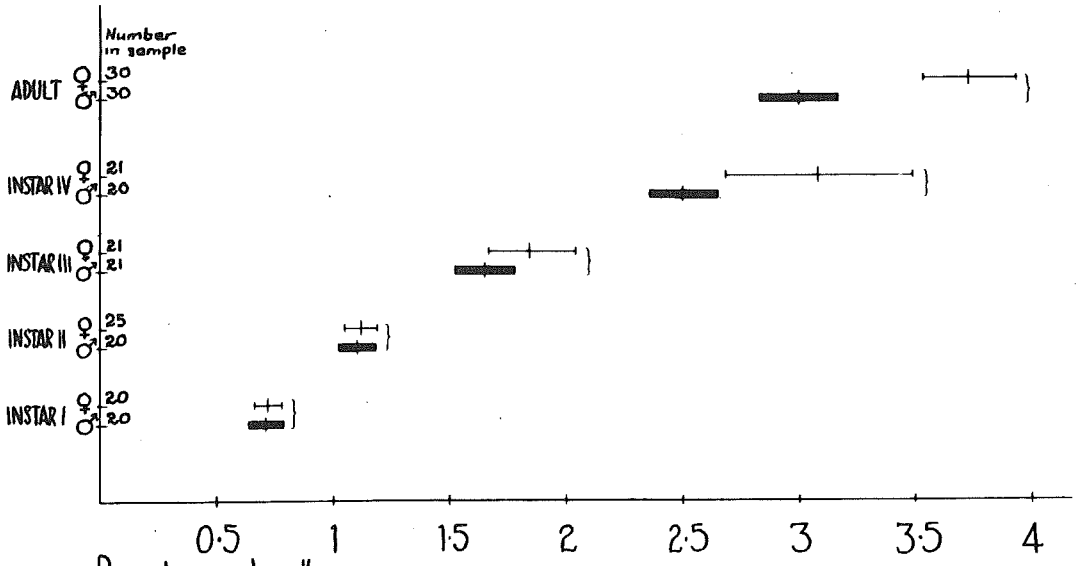


Fig 4.38 Pronotum length in mm

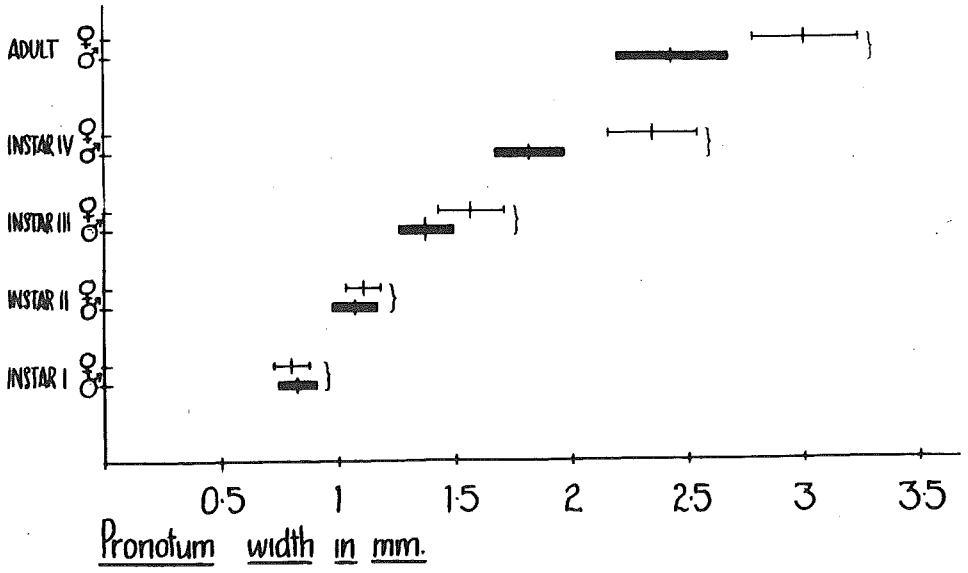
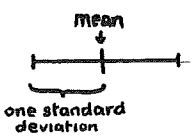


Fig 4.39 *Phaulacridium marginale*



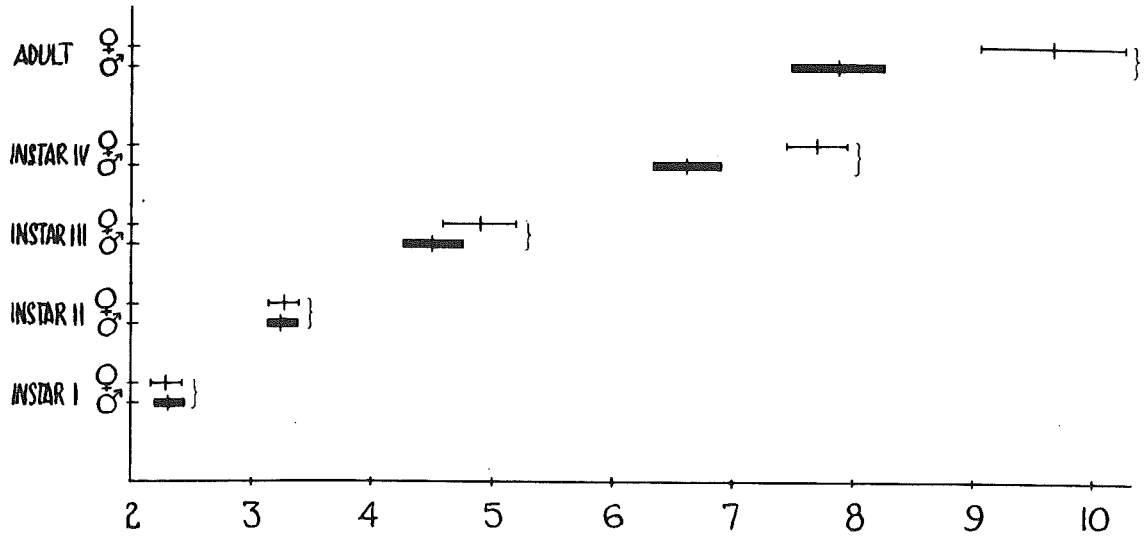


Fig 4.40 Femur length in mm.

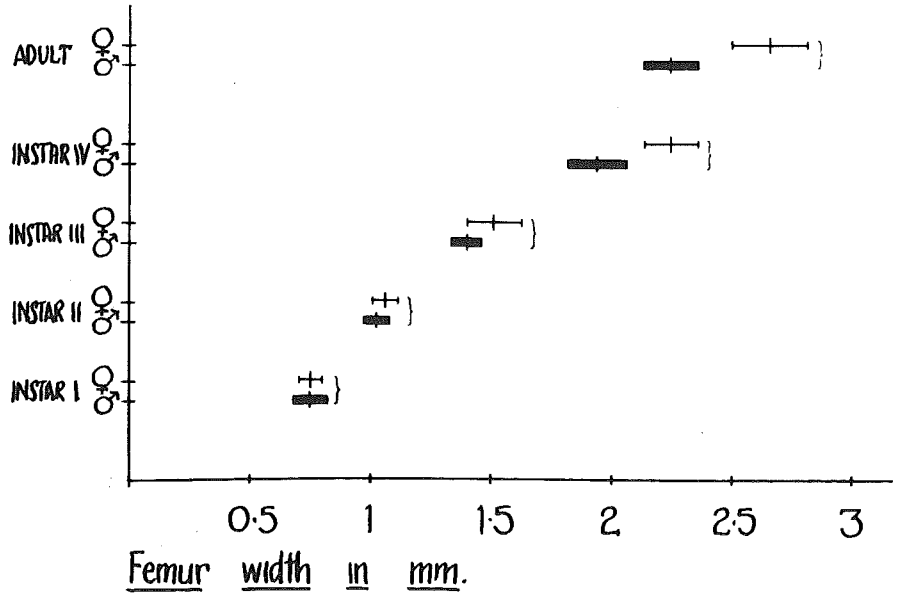


Fig 4.41 *Phaulacridium marginale*

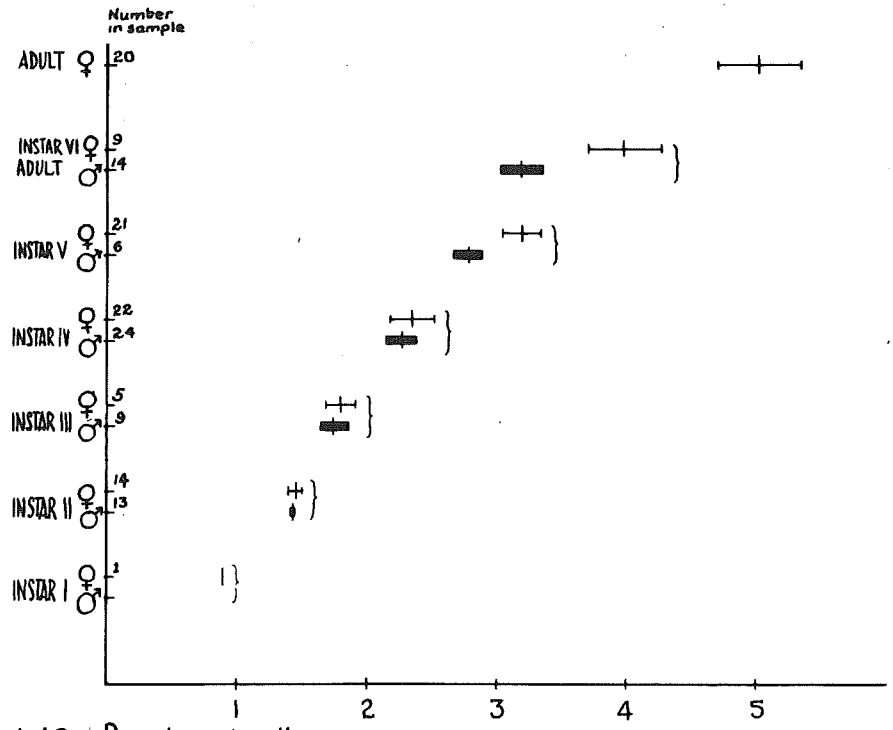


Fig 4.42 Pronotum length in mm.

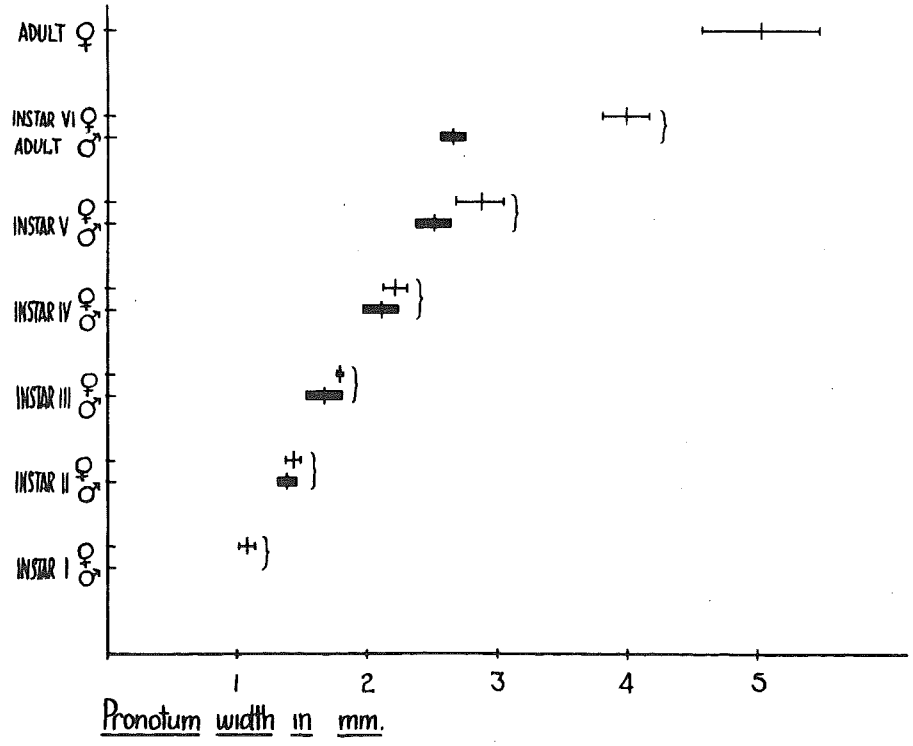


Fig 4.43 *Sigaus campestris*

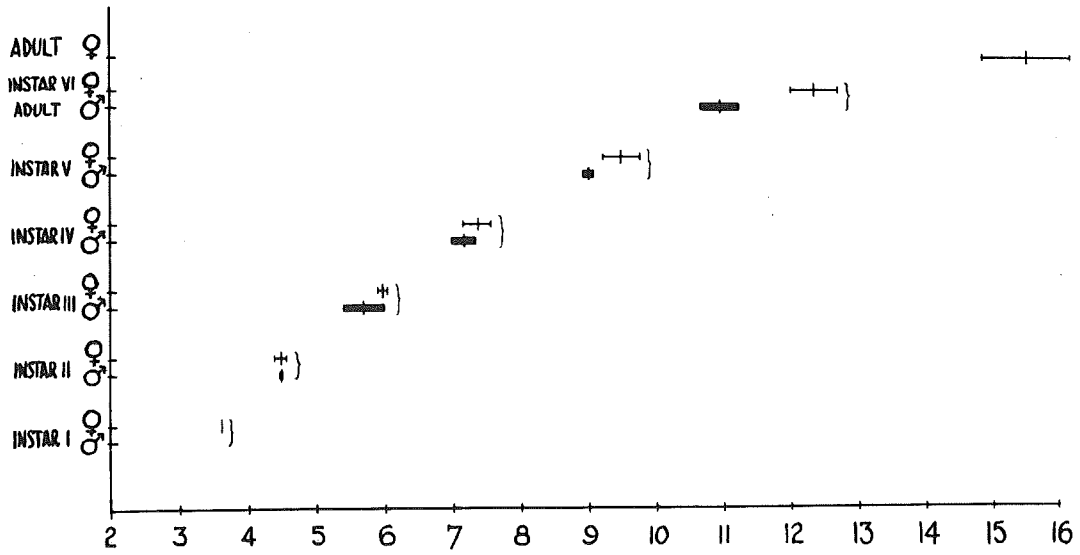


Fig 4.44 Femur length in mm.

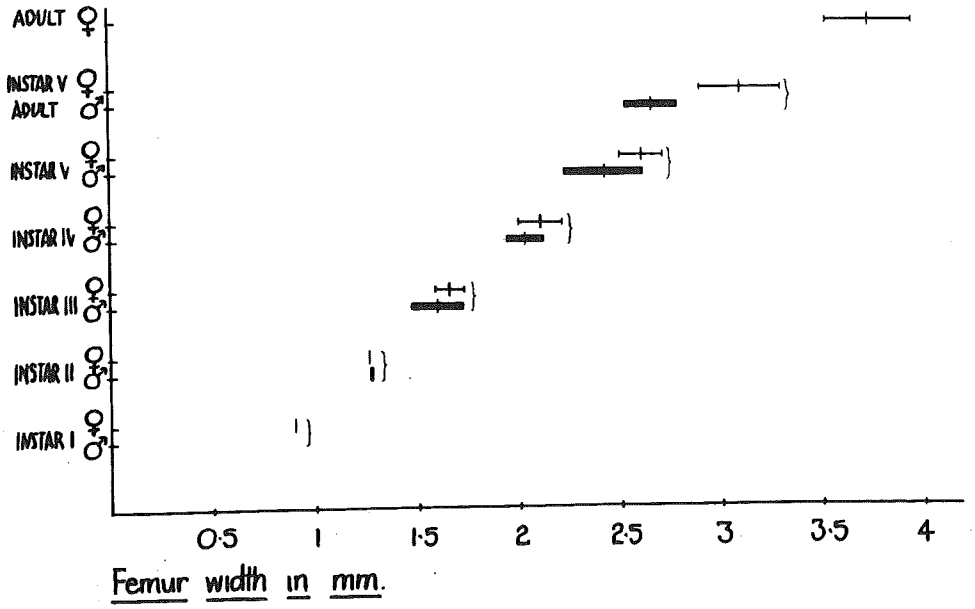


Fig 4.45 *Sigaus campestris*

of small samples of the same instar, collected at different times, did not reflect any large discrepancy within these composite samples.

Means and standard deviation of pronotum and femur length and width of both species are shown in figs.4.38 - 4.45. These measurements show not only growth but also progressive size differentiation between sexes within an instar. Measurements of P.marginale (figs.4.38- 4.41) affirm the morphological indication that both male and female have four nymphal instars. Accurate separation of the instars can be achieved by any one of the four measurements for the first three instars. These measurements cannot, however, be used for accurate separation of fourth instar nymphs and adults. However, if the sexes are taken separately all four measurements give good separation into instars.

No first instar males of S.campestris were found but measurements of first instar females probably indicate their size. Measurements of S.campestris (figs. 4.42 - 4.45) reveal that its life history differs from that of P.marginale, the males of S.campestris having five nymphal instars and the female six. As with P.marginale the four measurements give good separation of early instars, in this instance the first four instars. The remaining instars

are only separated accurately by the measurement of femur length. Taking the sexes separately, in the female all four measurements give good separation into instars, but in the male only pronotum length and femur length give good separation into instars.

In both species femur length gives good separation into instars at all stages, and is therefore a reliable characteristic for determination of instars.

SECTION 6

Discussion

The best means of instar determination was by measurement. Examination of wings, elytra and posterior abdominal structures were useful but less critical.

Rough groupings into instars were made on the basis of the development of rudimentary wings and elytra. Because of the very slight variation in form of the wing and elytral rudiments held laterally (before reversal), instars were not always easy to identify if this was the sole criterion used. Later instars could be identified without difficulty. The reversal of these rudiments divides the instars into two groups, those in which the rudiments lie laterally and those in which they are reversed. As Uvarov (1966) has noted, the instar in which reversal occurs varies according to the total number of instars, and may differ in the two sexes of the same species if they pass through different numbers of instars. This was shown to be true for P.marginale and S.campestris as tabulated below (fig.1).

Fig. 1

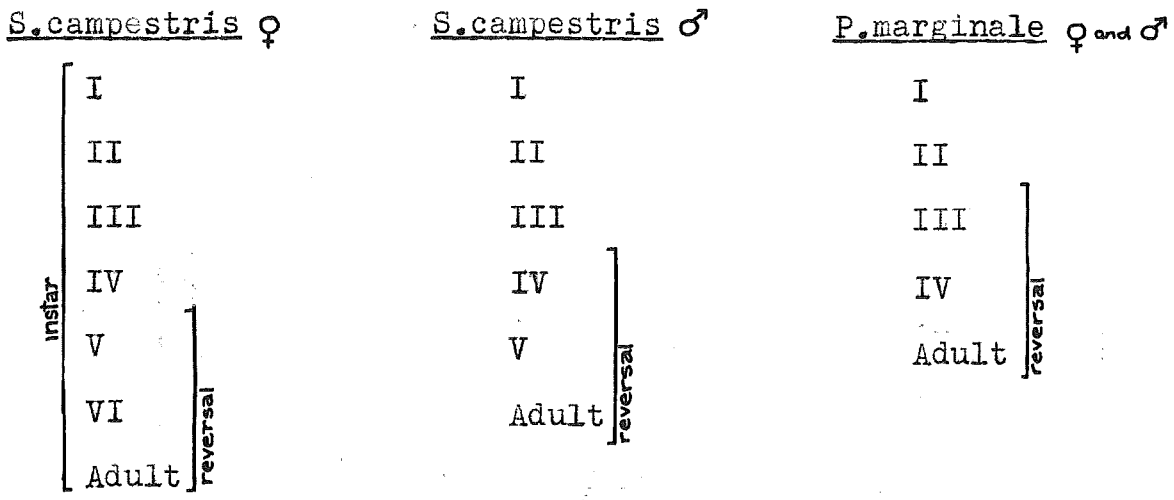
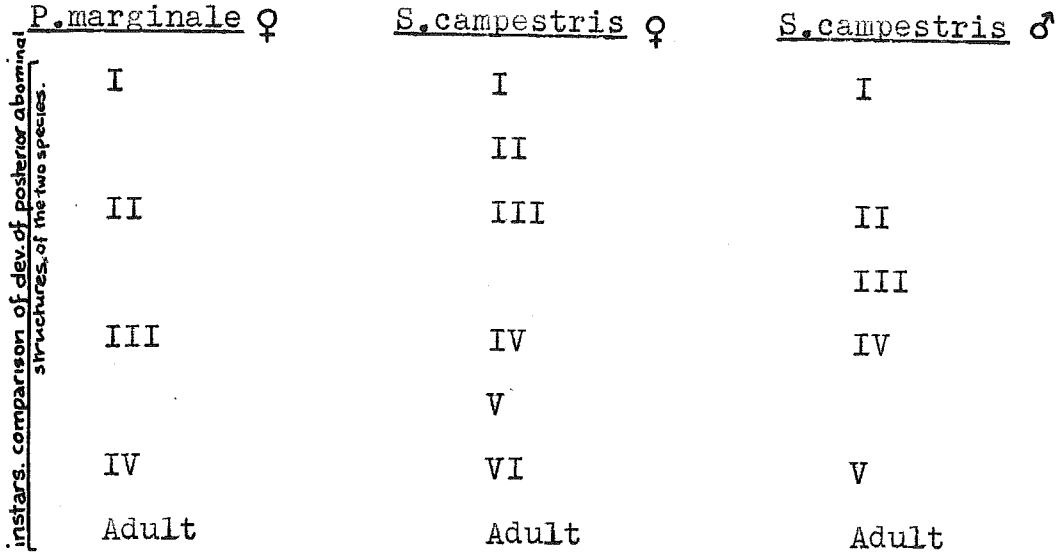


Fig. 2



A more exact grouping into instars was obtained by placing the sexes in order of development of the posterior abdominal structures. Development of the female posterior

abdominal structures takes place within four instars in P.marginale and in six in S.campestris. The extra instars in S.campestris appear to lie between the instars I and II, and III and IV of P.marginale. In males the extra instar in S.campestris appears to lie between instar II and III of P.marginale. There is no consistent trend shown by the posterior abdominal structures in relation to instar number, as there is with the reversal of wing and elytral rudiments (fig. 2).

The instar numbers of both species fell within the range of four to nine cited by Ramsey (1964). In accounting for species with higher instars Uvarov (1966) discusses evolutionary trends of primitive and advanced groups, sexual dimorphism, geographical variation and food. Uvarov suggests that where sexual dimorphism occurs the larger size of the female is always attained by the addition of one more instar than occurs in the male. Chopard 1938 (quoted by Ramsey) suggested that the larger the insect the greater the number of instars to be expected. This occurs in S.campestris where sexual dimorphism is more pronounced than in P.marginale.

Instar Identification.

Females of both species are readily identified in

all instars by examination of the genitalia, but identification of male instars solely on examination of the genitalia is difficult, as they do not show such distinct changes as the females. In both males and females it is not possible to identify the instar accurately from examination of wing and elytral rudiments prior to reversal. Care must be taken in distinguishing the antepenultimate and penultimate instars from the adult by noting that only in the adult do the elytra cover the wings.

Measurements of femur and pronotum confirmed the groupings made on the basis of descriptive evidence. Femur length was considered to be the most accurate means of identifying the instars of both species examined in this study.

SECTION 7

Final Comments

This study has been principally concerned with the developmental stages of two grasshoppers, Phaulacridium marginale and Sigaus campestris. Differences between their seasonal life histories were also noted, P.marginale apparently having a distinct annual cycle and S.campestris lacking a clear annual cycle. The difference in the life histories of P.marginale and S.campestris means that specimens of S.campestris occur in the field throughout the year, whereas no specimens of P.marginale are present during the winter months. It should be noted however that specimens of S.campestris, although present in the winter months, reveal themselves only on warm sunny days. Batcheler (pers.comm.) has found that the grasshopper Brachaspis collinus has a life history resembling that of S.campestris. It has been suggested by Bigelow (pers. comm.) that except for P.marginale all New Zealand's endemic grasshoppers may have this type of life history. It has been noted that P.marginale has close relations with an Australian species which may explain this exception.

As has been noted by Uvarov (1966) reliable

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descriptions and identification keys for nymphal instars are particularly needed for ecological studies in which it is essential to distinguish between species in mixed populations from their earliest instars. Most of the available descriptions are based on the colour and pattern of nymphs. However, recent workers are tending to rely on certain morphological characters and those of wing and elytral rudiments and posterior abdominal structures have been used with success. These characters were found satisfactory for both P.marginale and S.campestris and should also be useful for instar identification of the other New Zealand grasshoppers.

It needs to be emphasised that total body length is not an accurate means of nymphal identification as the abdominal segments are subject to telescoping. Femur length was found to be the best measurement for instar identification of P.marginale and S.campestris. Hudson (pers.comm.), measuring small samples of instars of ten species of New Zealand alpine grasshopper, has also found that femur length gives good separation into instars. Batcheler (pers.comm.) working with large samples of the alpine grasshopper Brachaspis collinus noted that femur length gave separation of all instars except first and

second. There is a possibility that this single character might be useful in large scale ecological work. There are a number of advantages that this measurement would have in estimating the relative numbers of instars in a sample. Once species identification of the nymphs was completed one hind leg could be removed from each nymph. These could then be sorted rapidly on squared graph paper. The relative numbers of each instar in the sample could thus be determined with comparative ease, using large samples, with scarcely any inaccuracy. Furthermore, a large sample of hind legs is far easier to handle than a sample of whole nymphs, since the legs, when detached, lie flat naturally in a position that makes their measurement easy.

The characters used for the identification of nymphal instars of P.marginale and S.campestris, especially femur length, should be useful for the instar identification of other New Zealand Acrididae. If this is so the present study may prove useful to workers engaged in studying alpine grasshoppers.

BIBLIOGRAPHY.

Albrecht, F.O., 1955. La densité des populations et la croissance chez Schistocerca gregaria (Forsk.) et Nomadacris septemfasciata (Serv.); la mue d'ajustement. J.Agric.trop.Bot.appl.2: 109-192.

Ander, K., 1956. Orthoptera Saltoria in S.L.P. Tuxen's Taxonomist's glossary of genitalia in insects.

Batcheler, C.L., 1967. Observations on Alpine Grasshopper in a Habitat modified by Deer and Chamois. Submitted for publication in Proc.N.Z.Ecol.Soc.

Burnett, G.F., 1951. Observations on the life-history of the Red Locust, Nomadacris septemfasciata (Serv.) in the solitary phase. Bull.Ent.Res. 42: 473-490pp.

Carothers, E.E., 1923. Notes on the taxonomy, development and life history of certain Acrididae (orthoptera). TRANS.AM.ENT.SOC., XLIX 7-23.

Chopard, L., 1938. La Biologie des Orthoptères. Encycl.ent., A, XX: 1-541pp.

Dempster, J.P., 1963. The Population Dynamics of Grasshoppers and Locusts. reprinted from Biological Reviews vol.38, 491-493pp.

Hartley, J.C., 1961. The shell of Acridid Eggs. Quarterly Journal of Microscopical Science, Vol.102 part 2, pp.249-255.

McLintock, A.H., 1960. A Descriptive Atlas of New Zealand. 110pp.

Poulton, E.B., 1896. On the courtship of certain European Acrididae. Trans.Ent.Soc.London: 233-252pp.

Ramsey, G.W., 1964. Moult number in Orthoptera (Insecta). N.Z. Journal of Science Vol.7, No.4.

Richards, O.W. and Waloff, N., 1954. Studies on the biology and population dynamics of British grasshoppers. Anti-Locust Bull. no.17: 182pp.

Snodgrass, R.E., 1935. The abdominal mechanisms of a grasshopper. Smithson. misc. Coll.94(6): 89pp.

Uvarov, B.P., 1928. Locusts and Grasshoppers. A handbook for their Study and Control. London, Imperial Bureau of Entomology. 352pp.

. . . . 1966. Grasshoppers and Locusts. A handbook of general Acridology. University Press, Cambridge. 481pp.

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