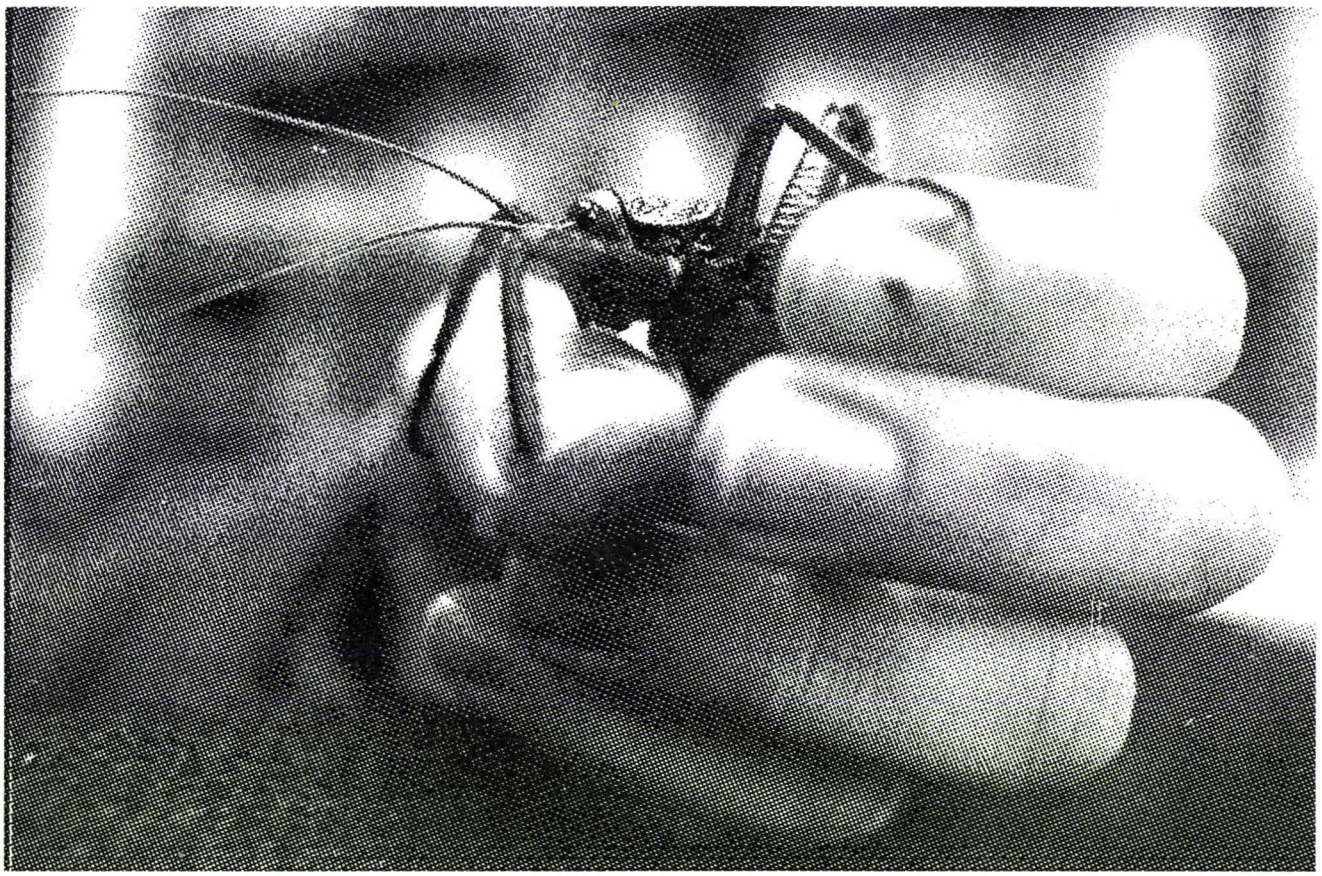
Reproduction and behaviour of the Mahoenui Weta, *Deinacrida* n.sp.

A thesis presented in partial fulfilment of the requirements for the degree of Masterate of Science in Ecology at Massey University.



Sub adult female Mahoenui weta *Deinacrida* n.sp. in hand (Photograph by Penny Aspin).

Elizabeth Domett

1996

Massey University Library
Thesis Copyright form

Title of thesis: Reproduction and behaviour of the Mahoenui weta *Deinacrida* n.sp.

1) I give permission for my thesis to be made available to readers in Massey University Library under conditions determined by the librarian.

2) I agree that my thesis, or a copy, may be sent to another institution under conditions determined by the librarian.

3) I agree that my thesis may be copied for Library use.

Signed E Jomitt

Date 29/2/96

The copyright of this thesis belongs to the author. Readers must sign their name in the space below to show that they recognise this. They are asked to add their permanent address.

NAME AND ADDRESS DATE

ACKNOWLEDGEMENTS

I wish to thank the following people for their input and advice. Firstly to my supervisors, Drs Ian Stringer and Murray Potter and to my husband Sam who aided me with editing, advice, field work, travel and assistance where necessary. To the people of the Department of Ecology, the Department of Plant Biology and the Department of Production Technology, Massey University, who contributed advice and many hours of their own time. To both of my families for continued support and advice. For my friends for always being willing to help. To the Thrower family for computer assistance. To Greg Sherley for providing some of the weta in my study, and the Department of Conservation for allowing me access to their land. Thanks also to Ngati Rauputu for allowing me access to his land. My thanks also to those people who provided assistance and have been accidentally left out of these acknowledgements.

Abstract

The morphology and histology are described for the entire male internal reproductive organs of the Mahoenui weta. These show many similarities to other Stenopelmatidae. Testes follicles of Mahoenui weta have the usual structure for Stenopelmatidae with basal sections surrounding the ends of the vasa efferentia. Epithelial cells of the vasa efferentia, vasa deferentia and seminal vesicle have similar basophilic cytoplasm. Muscle layers are best developed around the seminal vesicle and the accessory glands. The ejaculatory duct has a cuticular intima and is enclosed by a muscular sheath. The development of the external genitalia from the 8th to the 10th instar is followed and discussed. The morphology of the external reproductive genitalia is close in form to that of the Rhaphidophoridae.

The morphology and histology of the entire female reproductive organs of the Mahoenui weta are described. The morphology and histology of female Mahoenui weta are very similar to those of other Orthoptera. The histology is particularly close to that of the Acrididae. Ovaries and ovarioles have the usual structure for Stenopelmatidae. The follicles are enclosed within a follicular epithelium and the ovarioles are enclosed within an outer ovariole sheath layer of connective tissue. The epithelial cells of the ovarioles and lateral oviducts have basophilic cytoplasm. The vagina is lined with a cuticular intima and is surrounded by a muscular sheath. The external genitalia are described from 8th to 10th instar Mahoenui weta and their probable functions are discussed.

The behaviour of captive Mahoenui weta was observed, using infra-red time lapse video. Data were recorded from the months of December, January, February, March and July. Weta ate most often in January, March and July, and most mating activity occurred during January. Mahoenui weta were consistently most active at 60-80% of total night-time and showed less activity closer to sunrise or sunset. Mating and moulting are discussed.

Incubation time of Mahoenui weta eggs was recorded using eggs laid in a previous study (Richards 1994). The time of hatching and the behaviour of newly hatched nymphs was recorded over several days using video equipment. All eclosion occurred at night, with time of eclosion ranging from 8 pm to 3.30 am over the three

nights. Weta were free of the egg and walked within 17 minutes of the egg appearing on the soil surface. All hatched weta died within three days of eclosion. The external appearance and histology of eggs is described. Mahoenui weta eggs have many features in common with other Orthoptera.

Mahoenui weta were exposed to 12 different plant species commonly fed to them in captivity, and present in the Mahoenui weta reserve. The weight of plant material eaten was recorded to determine which species of plant the weta preferred. Mahoenui weta showed the greatest preference for kowhai followed by gorse, broom, buttercup, tawa, karaka, coprosma, camellia, lemonwood, mahoe, houhere and hoheria. There was a marked preference for legume plant species over non-legumes.

Table of contents

List of figures and tables

Chapter One

General Introduction

1.1 Ecology and History

Mahoenui Weta, *Deinacrida* n.sp., are among the smallest of the Giant weta belonging to the family Stenopelmatidae (Orthoptera). Their distribution is now confined to several small localities in the North Island of New Zealand. They are commonly found on farms in the Te Kuiti area surrounding the Mahoenui weta reserve (Figures 1.1 and 1.2). The weta was first discovered at Mahoenui in 1962 and was originally classified as *D. heteracantha* White by Watt 1963. It is now thought that the Mahoenui weta is a separate subspecies or a new species. It differs from *D. heteracantha* in having different shaped notches on the subgenital plates (Meads 1990) and adult Mahoenui weta only reach a third of the size of *D. heteracantha*.

Mahoenui weta have not been formally described, and therefore is not eligible to be listed as a protected species. In 1990 the Department of Conservation purchased 250 ha of gorse shrubland at Mahoenui to provide a reserve for this weta. The reserve is grazed by cattle in winter, and by feral goats all year round.

Mahoenui weta are nocturnal, arboreal and largely solitary and their current habitat is comprised almost entirely of introduced gorse, *Ulex europaeus* L. (Figures 1.3 and 1.4).The gorse offers both a plentiful food supply and protection from predators. The weta will readily eat several native plant species, but none offer the protection that introduced gorse does. Some giant weta species have managed to survive only on several offshore islands, for example *D. fallai* Salmon on the Poor knights Islands (Richards 1973), and *D. rugosa* Buller on Stephens Island (Meads 1990). Other giant weta, such as *D. connectens* (Ander) Ramsay and *D. tibiospina* Salmon still survive on the mainland of New Zealand but they are confined to remote alpine areas of the South Island. (Meads 1990).

Sherley and Hayes (1993) studied the habitat use, life cycle and aspects of the behavioural ecology of the Mahoenui weta. They concluded that the weta occur mostly

on steep (>21°) slopes with north to east facing aspects, areas regularly used by cattle and goats, open areas, and middle-aged gorse bushes (7-13 years) or old and senescent trees (>15 years old). Dark brown and yellow morph weta were found, respectively, in the following ratios: 77% and 23% of males and 61% and 39% of females. They stated that the species is apparently monogamous. An egg stage of about 10 months is followed by nine nymphal instars which continue for about a year until the weta reach sexual maturity. Sherley and Hayes (1993) concluded that egg laying probably occurs in late autumn and that hatching followed a year later. Adulthood is reached in late summer, when copulation occurs. A wide range of instars is present at any given time of the year and growth rate may be seasonably variable.

Little information exists on the specific reproductive structures and behaviour of the Mahoenui weta. Chapters two and three of this thesis describe the internal and external reproductive structures, and histology, of female and male reproductive organs of Mahoenui weta. In chapter four behaviour patterns are investigated, with particular reference to light/dark cycles. In Chapter five egg hatching and egg histology are described. The soil conditions and time of hatching are recorded. Captive Mahoenui weta readily eat several species of plant, both native and exotic, but no research has been done to quantify the extent of any preferences for certain species. Chapter six describes investigates food preference and makes predictions on the pre-European diet of this weta. An overall synthesis of the thesis is presented in chapter seven.

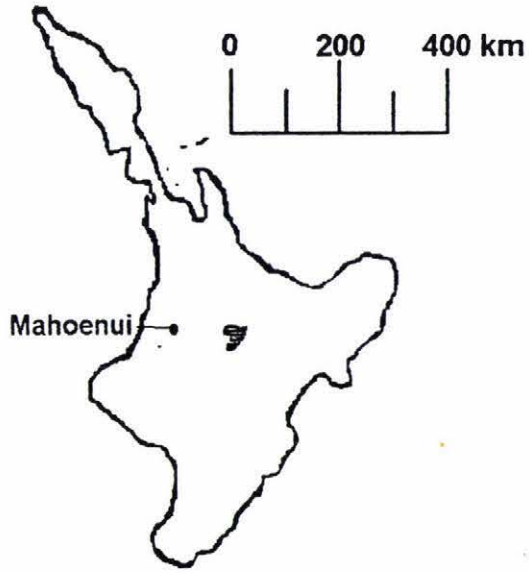


Figure 1.1: North Island of New Zealand, showing location of Mahoenui.

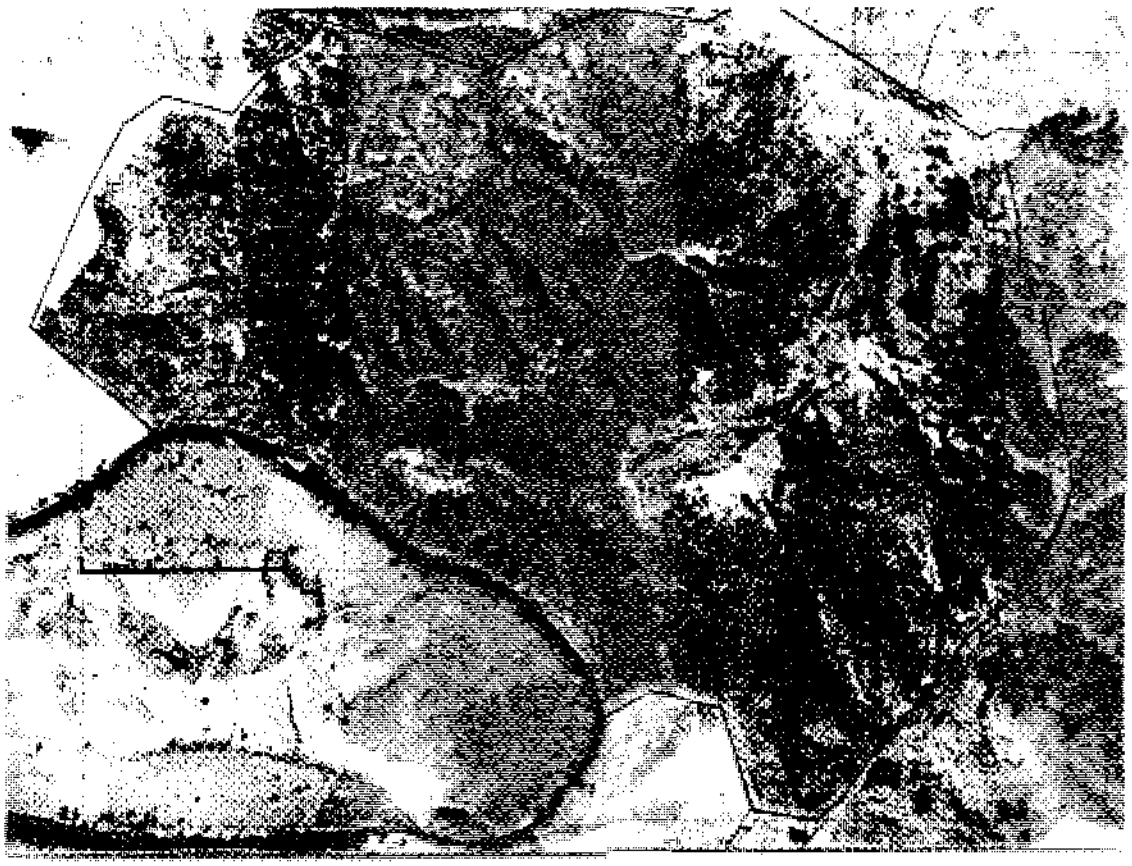


Figure 1.2: Aerial view of the Mahoenui weta reserve. Black outline shows borders of reserve.

Figure 1.3: Gorse in Mahoenui weta reserve.

Figure 1.4: Looking out over Mahoenui weta reserve.

Chapter Two

The Male Reproductive System of *Deinacrida* n.sp. Mahoenui (Orthoptera: Stenopelmatidae)

Abstract

The morphology and histology are described for the entire male internal reproductive organs of the Mahoenui weta. These show many similarities to other Stenopelmatidae, and their histology is particularly close to that of the Acrididae. Testes follicles of Mahoenui weta have the usual structure for Stenopelmatidae with basal sections surrounding the ends of the vasa efferentia. Epithelial cells of the vasa efferentia, vasa deferentia and seminal vesicle have similar basophilic cytoplasm. Muscle layers are best developed around the seminal vesicle and the accessory glands. The ejaculatory duct has a cuticular intima and is enclosed by a muscular sheath. The parameres and the penis hook into the female's genital chamber during copulation. The development of the external genitalia from the 8th to the 10th instar is followed and discussed. The morphology of the external reproductive genitalia is similar to that of other Stenopelmatidae and is close in form to that of the Rhaphidophoridae.

2.1 Introduction

The male reproductive system of the Mahoenui giant weta, *Deinacrida* n.sp., has not been described before although a comparison of the external reproductive structures of *Deinacrida fallai* Salmon and *D. heteracantha* White was published by Richards (1973). Amongst other Stenopelmatidae, Cary (1981) described the external reproductive morphology of *Zealandosandrus gracilis* n.g. and Sandlant (1981) described the external reproductive morphology of *Hemideina femorata* Hutton. Maskell (1927) described the reproductive structures and the histology of *Hemideina thoracica* (White) and Ander (1939) discussed the reproductive morphology of a variety of other Stenopelmatidae.

Detailed morphological and histological analyses are available for some other Orthoptera. Early works are those of Snodgrass (1933,1937) who published extensive

works on the genitalia of Orthopteroid insects, and Matsuda (1976) who reviewed Orthoptera genitalia.

Here I present the first detailed description of the reproductive system of the male Mahoenui giant weta.

2.2 Methods

Two adult males were taken immediately after natural death, and dissected under Clark's insect saline (Hale 1965). The abdomens were cut open dorsally and the entire specimens were then fixed with Formol-Alcohol fixative for 48 hours. Transverse and longitudinal serial sections of excised reproductive organs were made using normal histological techniques as described in Humason (1967). Sections were fixed, dehydrated in a graded alcohol series, then cleared first in chloroform and then in Xylene. The tissue was embedded in paraffin, sectioned at 2-8μm (usually 5-6μm), and stained with Mayer's haematoxylin and eosin. Photomicrographs were taken using Kodak Ektrachrome Elite 200 and Kodak Ektrachrome 64T Tungsten professional colour reversal films. Either Nomarski or Interference Contrast Microscopy was used to view the slides of prepared reproductive organs.

All drawings were made from specimens using graph paper and a microscope equipped with a squared eyepiece graticule. Measurements smaller than about 2mm were made with a microscope fitted with a calibrated eyepiece micrometer.

2.3 Results

The internal reproductive organs

The internal reproductive organs comprise paired testes and vasa deferentia, a fused seminal vesicle, and an ejaculatory duct. The paired testes lie dorsally in the abdomen and medially to a fused seminal vesicle. The vas deferens travel posteriorly from the testes and join the ejaculatory duct at the distal end (Figure 2.1).

The fused seminal vesicle lies anteriorly and dorsally to the ejaculatory duct. The junction with the ejaculatory duct is difficult to observe. The ejaculatory duct is continuous from the fused seminal vesicles and is single, extending posteriorly into the external penis, which consists of three lobes. A pair of tubular accessory glands branch

separately from the ejaculatory duct. Posteriorly the paired vas deferens branch separately from either side of the ejaculatory duct (Figure 2.1).

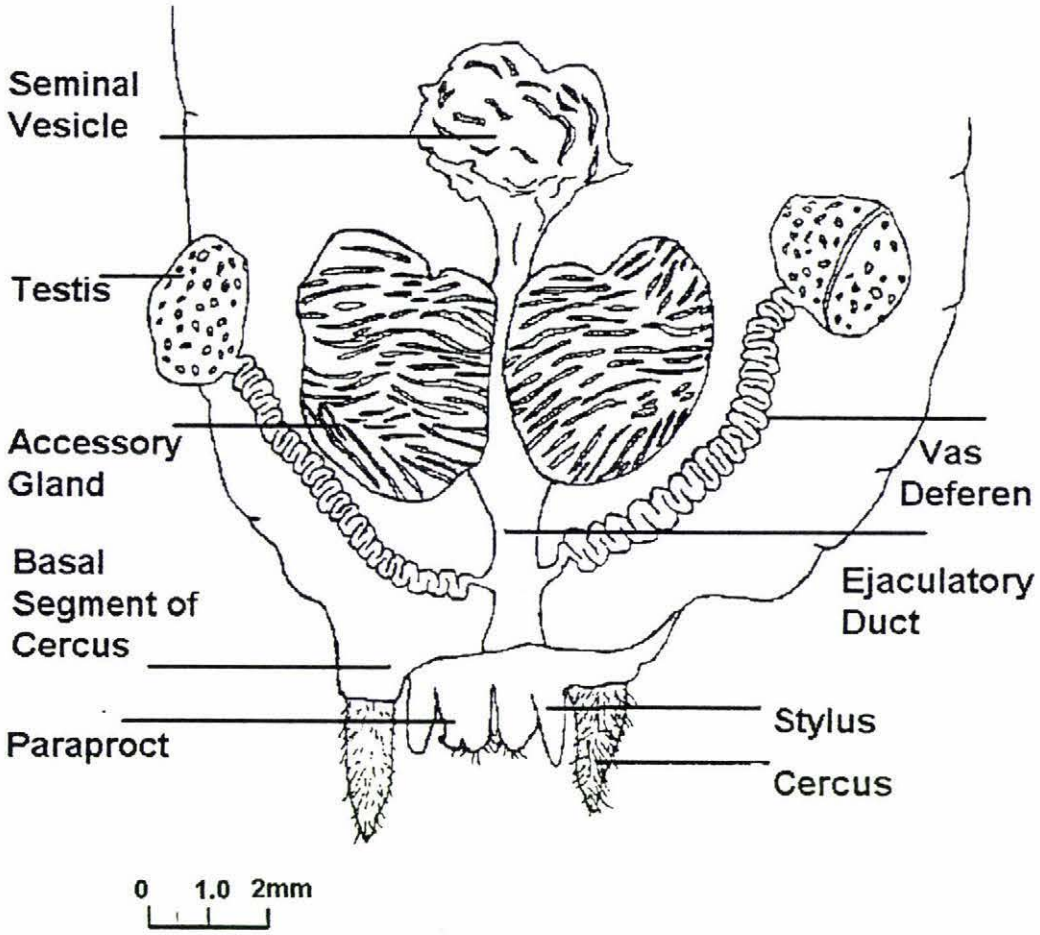


Figure 2.1: The morphology of the male Mahoenui weta internal reproductive structures.

Figure 2.2: Mahoenui weta. Dissection of abdomen, showing reproductive organs.

Figure 2.3: Mahoenui weta. Dissection of abdomen, showing accessory glands and seminal vesicle.

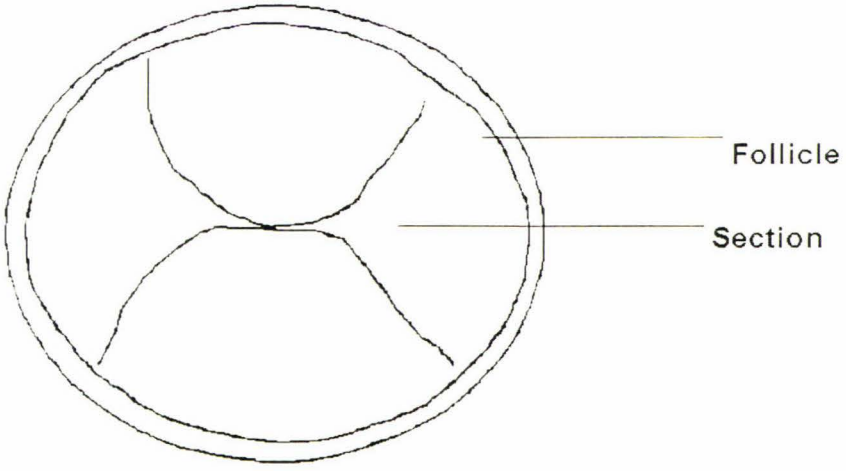


Figure 2.4: Mahoenui weta follicle, showing sections within.

The testes

The testes are yellow brown and each is enclosed within an exterior sheath forming a rounded structure. Each testis consists of 67 follicles which are bound together within an outer connective tissue sheath. Each follicle is itself bounded by an inner connective tissue sheath. They are held in place by tracheae which penetrate between follicles and hold them in place. There is connective tissue present between the walls of the follicles. Each follicle is spherical in cross section and has a mean diameter of 0.38mm ± 0.02 SD. Each follicle connects to the vas deferens by a vas efferens, which lies wholly within the outer connective sheath. Where the vas deferens joins the testis it is 1.2mm in diameter narrowing to 0.2mm at it's furthest extent. Internally, each follicle is divided into 4-8 sections (Figure 2.4). No attempt was made to follow spermatogenesis in this study but sections of the testes show that the earlier stages consisting of spermatogonia and cysts of synchronously dividing cells are concentrated in a thick disc-like region at the apical end. Here the follicle is not subdivided into sections. Latter immature cysts tend to be concentrated near the outer surface of the sections and the remainder of the interior is packed with cysts of mature spermatozoa. Spermatozoa finally become free from their cysts when they reach the vas efferens (Figures 2.5 and 2.7).

The vasa efferentia

The vasa efferentia connect the testis follicles with the ends of the vasa deferentia (Figure 2.6). They are thin transparent tubes with diameters of 0.2mm or less and lengths of approximately 4.8mm. Each vas efferens is lined with an epithelial layer of cuboidal to columnar cells which vary from about 0.01 to 0.04mm in height (Figure 2.6). These rest on an outer basement membrane and have a smooth well defined border with the lumen. Their cytoplasm is basophilic. The lumen of the vas efferens is approximately 0.05mm in diameter. Free spermatozoa were visible within an eosinophilic matrix. No bundles of spermatozoa were visible here, unlike in *H.*

thoracica as reported by Maskell in 1927. A thin layer of muscle fibres forms a reticulum.

The vasa deferentia

Each vas deferens is opaque white in colour. The distal ends are located medially to it with respect to the testis follicles to which it is connected by the vasa efferentia. Each vas deferens forms a regular convoluted tube, which moves towards the ejaculatory duct ventrally and medially until it joins it posteriorly (Figure 2.1) . At this point both straighten out and dilate slightly into the ejaculatory duct. Each vas deferens varies between 6mm to 7mm in length, although this is hard to measure accurately because of their coiled and elastic nature. They have maximum diameters of 0.2mm.

Histologically the vasa deferentia are lined with an epithelium of columnar cells which vary in height from 0.01 to 0.06mm (Figure 2.8). Their cytoplasm is as basophilic as that of the epithelium lining the vasa efferentia. The vasa deferentia are surrounded by a sparse layer of predominately circular muscle fibres.

The ductus ejaculatorius

The ejaculatory duct has the same histology of that of the vas deferens except that it has a cuticular lining continuous with that of the body wall. The columnar cells vary in height from 0.05 mm to 0.06mm (Figure 2.11). The predominately circular muscular sheath gradually increases in thickness from one to about five cell layers thick.

The accessory gland and seminal vesicle

The accessory gland and seminal vesicle both have an outer sheath that is continuous with the circular muscle layer of both the ejaculatory duct and vas deferens (Figure 2.9).

The accessory glands form a pair of large tubes bound within an outer sheath. They occupy most of the volume of the body cavity (Figures 2.2 and 2.3) and appear fused due to their compact nature. They are salmon pink in colour grading towards white at the midline of the body.

The accessory glands lie free within the hemocoel except for their tracheal supply. When dissected out they have a diameter of 3.5mm and a length of 4.5mm. They are attached to the fused seminal vesicle via the muscular sheath.

In cross section the tubules within the accessory glands are round to oval in shape. They are lined with a layer of columnar cells which are about 1.2μm high and 1μm wide. The diameter of the tubules varies from 0.10 mm to 0.13 mm (Figure 2.9). These cells rest on an outer basement membrane, and an outer muscle layer is sometimes present. They are arranged approximately radially about the lumen of the follicle within the gland. The secretion within the glandular tubule is eosinophilic and homogenous. The nuclei of the columnar cells are basophilic. The nuclei are central and have diameters of about 8μm.

The seminal vesicle is very similar histologically to that of the accessory glands. However, the colour of the gland is opaque to translucent white, and the clear fluid contents are visible within. The muscular sheath encloses the columnar epithelium which is invaginated to form pockets (Figure 2.10). The tubules in the seminal vesicle follow the same pattern as that of the accessory gland, except the average height of the columnar cells is 3μm and the nuclei within are <2μm high. The eosinophilic secretion within the tubule has spermatozoa within it.

The Exterior genitalia

Development of the male external genitalia from instar 8 to instar 10

Eighth instar male weta paraprocts form simple lobes, which are symmetrical when viewed from above (Figure 2.13). Cerci are short, pointed, and quite wide at the anterior end (Figure 2.14). The epiproct is wide at the anterior edge and gently curves in a double reverse ogive from the centreline at the posterior end, to the corners of the anterior (Figure 2.13). The subgenital plate is small and slightly notched. The styli are short and wide at the anterior end (Figure 2.15).

Paraprocts of ninth instar weta are larger than those of eighth instars and possess a well defined lobe on their posterior end. The cerci are longer than those of instar eight, but their bases share the same diameter, so giving ninth instar cerci a narrower cone shape (Figure 2.16). The epiproct is soft edged and is triangular when viewed from above (Figure 2.17). The subgenital plate is wider at the anterior edge than that of

eighth instar weta, but it is not much longer. As a result it is now a broad triangle shaped plate (Figure 2.18). Styli are longer and narrower than those of eighth instar weta.

Paraprocts of tenth instar adults are as large as those of ninth instar weta but are more defined, with a blunt, hook-like shape forming on the outer edge of each paraproct. Cerci are not much longer than those of ninth instar weta and have the same overall shape. The epiproct is the same general shape as instar nine weta but has a slightly broader anterior edge (Figure 2.19). The subgenital plate is as wide overall as in ninth instar wetas but is longer (Figure 2.20). Styli are very long, and narrower than those of ninth instar weta (Figure 2.21).

Table 1: Dimensions of male reproductive organs of The Mahoenui Weta *Deinacrida* n.sp. (from two field collected specimens).

		Mean	SD	Range
Testis follicle	max diameter	0.38	0.02	0.07
Testis	max diameter	2.25	0.06	0.1
vas deferens	length	5	0.99	1.4
	width	0.2	0.07	0.1
Accessory gland	length	4.8	0.28	0.4
	width	4	0.14	0.2
Seminal vesicle	max	3.25	0.35	0.5
Ejaculator duct	width	0.5	0.57	0.1
	length	10.5	0.71	1

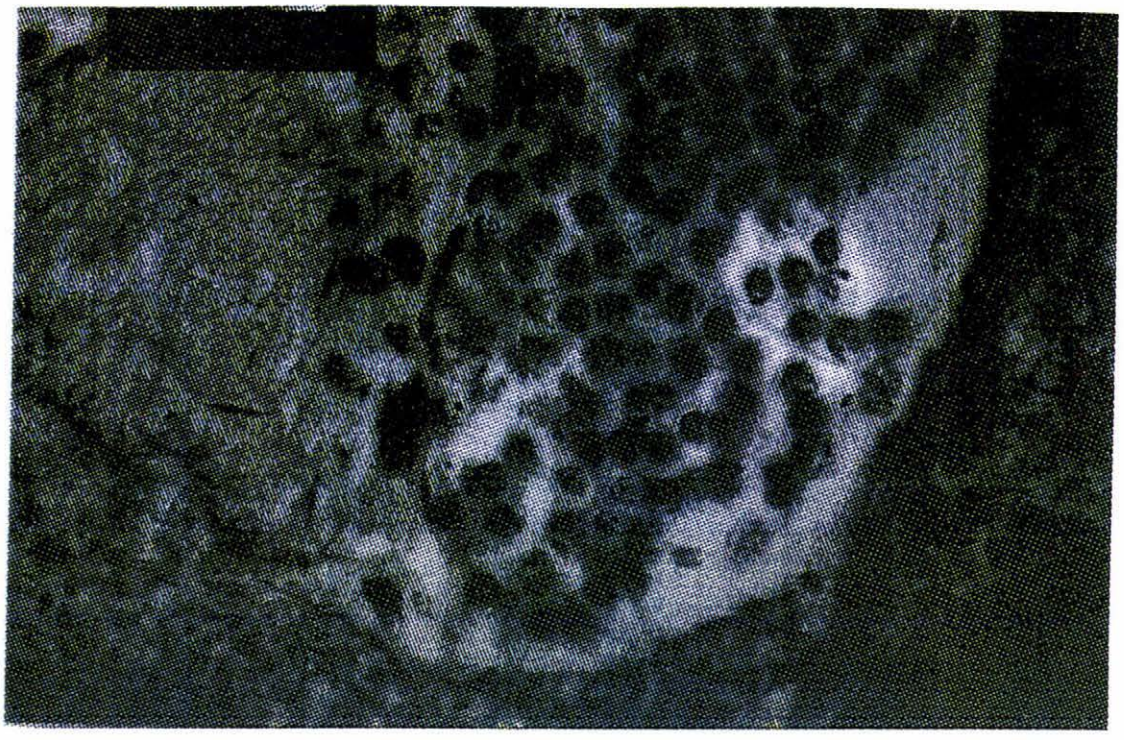


Figure 2.5: Mahoenui weta testis, transverse section in situ.

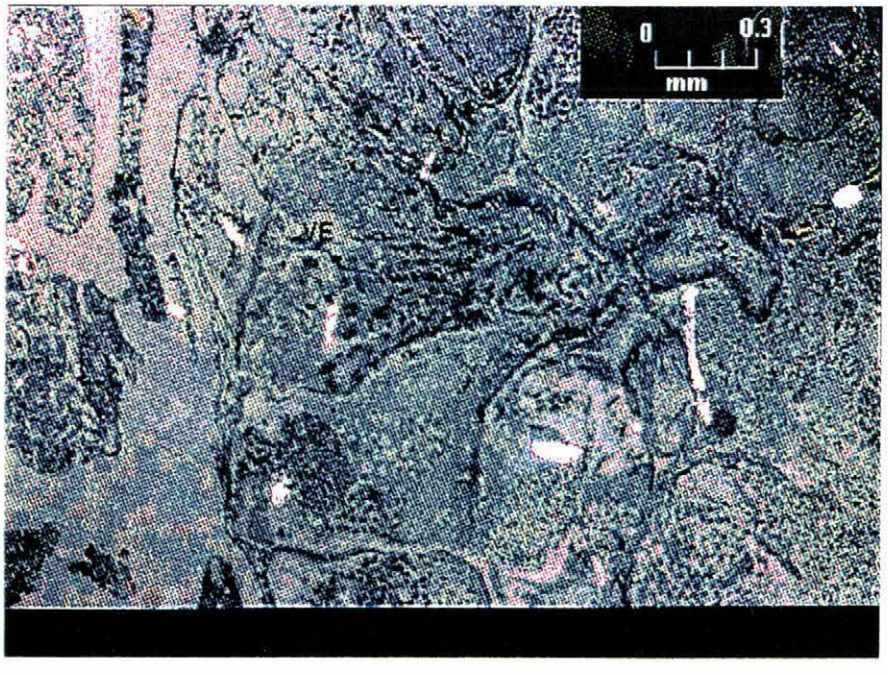


Figure 2.6: Vas efferens (VE) of Mahoenui weta in testis, oblique Section.

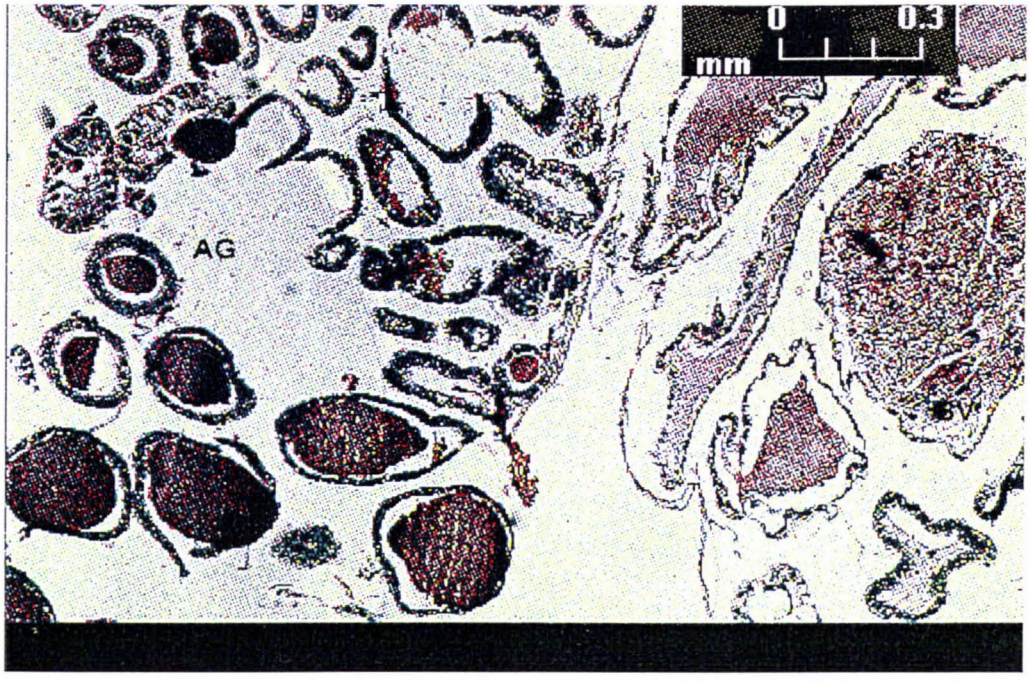


Figure 2.9: Accessory gland (AG) and seminal vesicle (SV) of Mahoenui weta, transverse section.

Figure 2.10: Mahoenui weta seminal vesicle, oblique section.

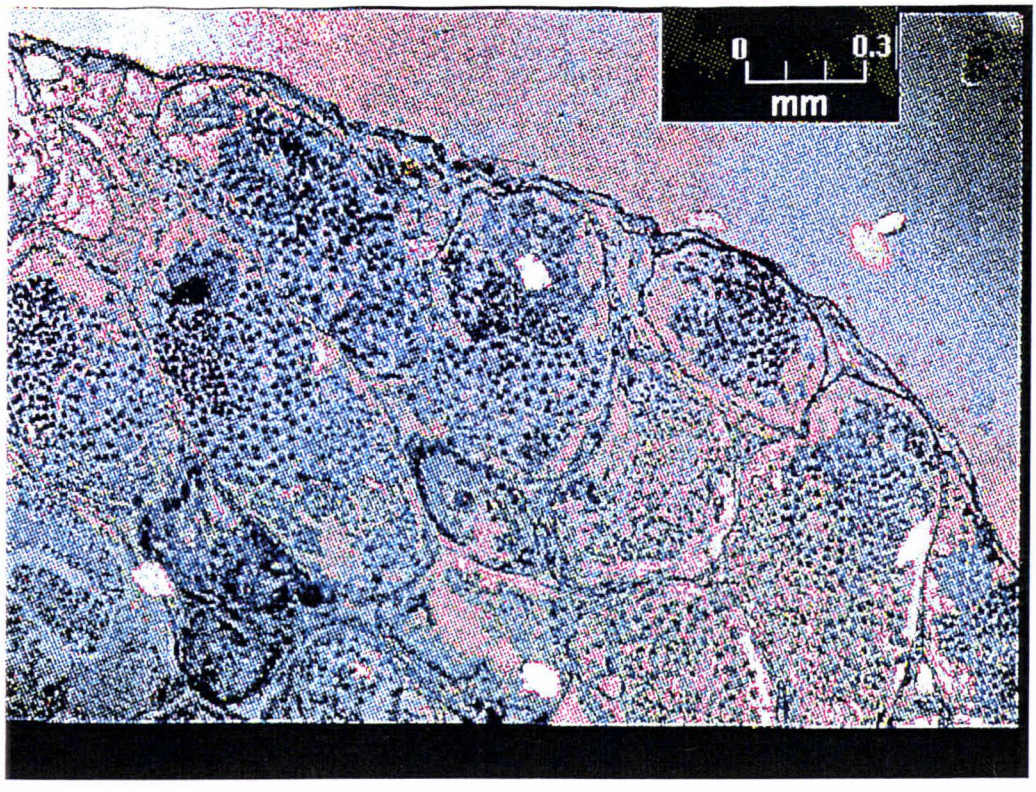


Figure 2.7: Mahoenui weta testis, transverse section.

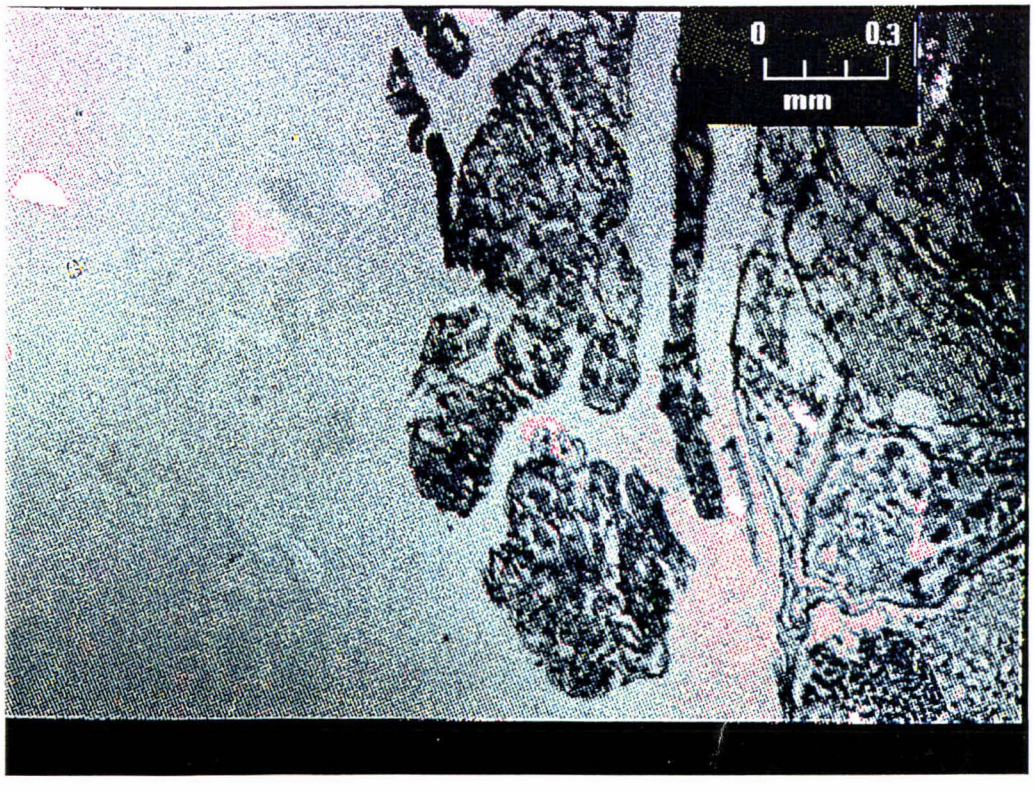


Figure 2.8: Mahoenui weta vas deferens, oblique section.

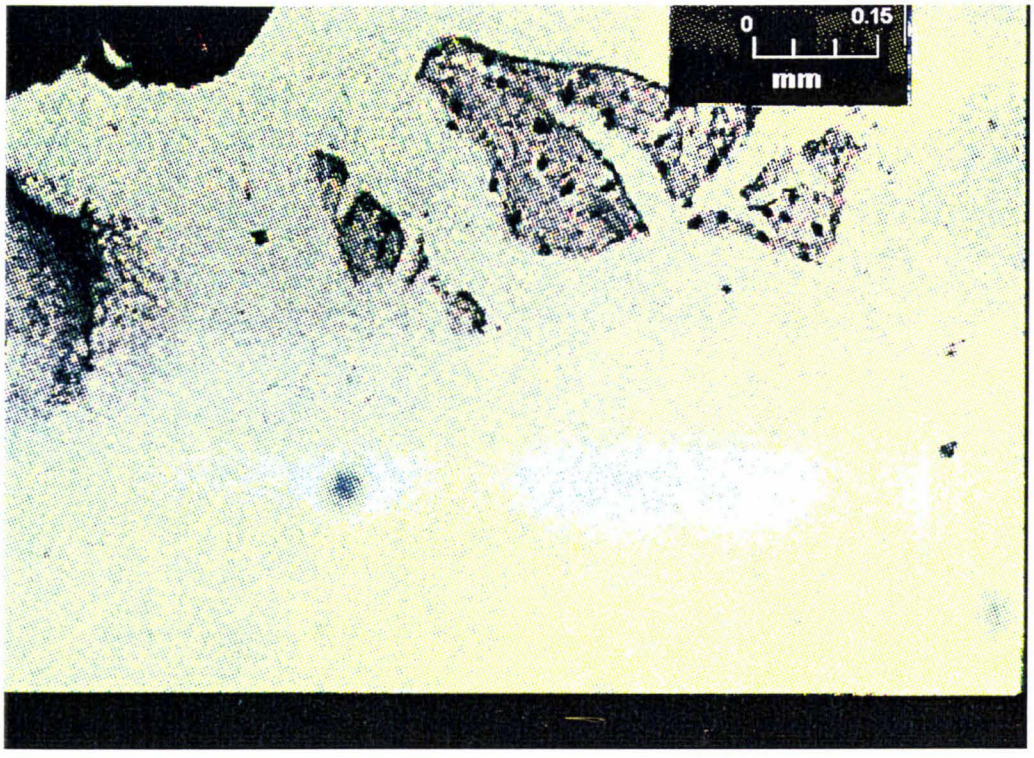


Figure 2.11: Mahoenui weta ejaculatory duct, longitudinal section.

(For photographs of the external genitalia of the male Mahoenui weta: Instars 8-10 refer figures A.1 - A.9 in appendix)

Figure 2.12: Key for external genitalia of the male Mahoenui weta.

C - Cerci

PP- Paraprocts

SGP- Sub genital plate

P- Penis (Phallus)

SVIII- Sternum Plate 8

SVII- Sternum Plate 7

SVI- Sternum Plate 6

TX- Tergum Plate 10

TIX- Tergum Plate 9

TVIII- Tergum Plate 8

EP- Epiproct

S- Stylus

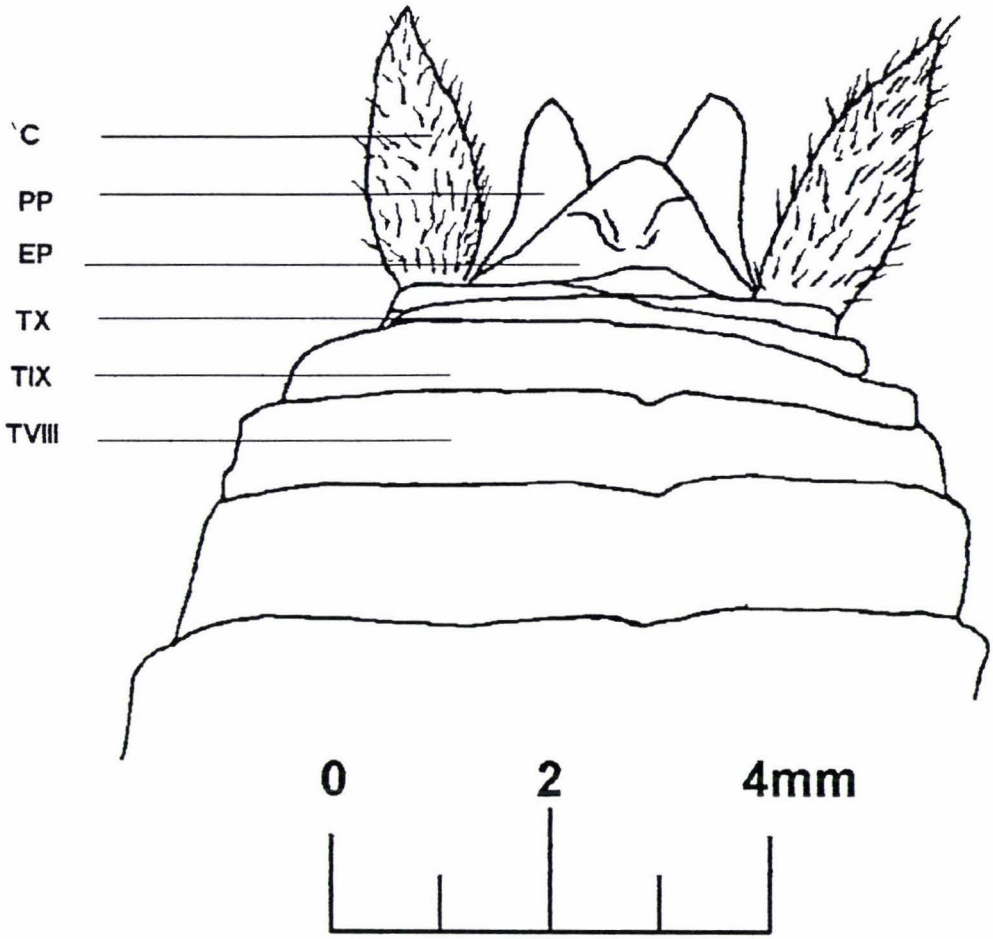


Figure 2.13: External genitalia of eighth instar male Mahoenui weta, dorsal view

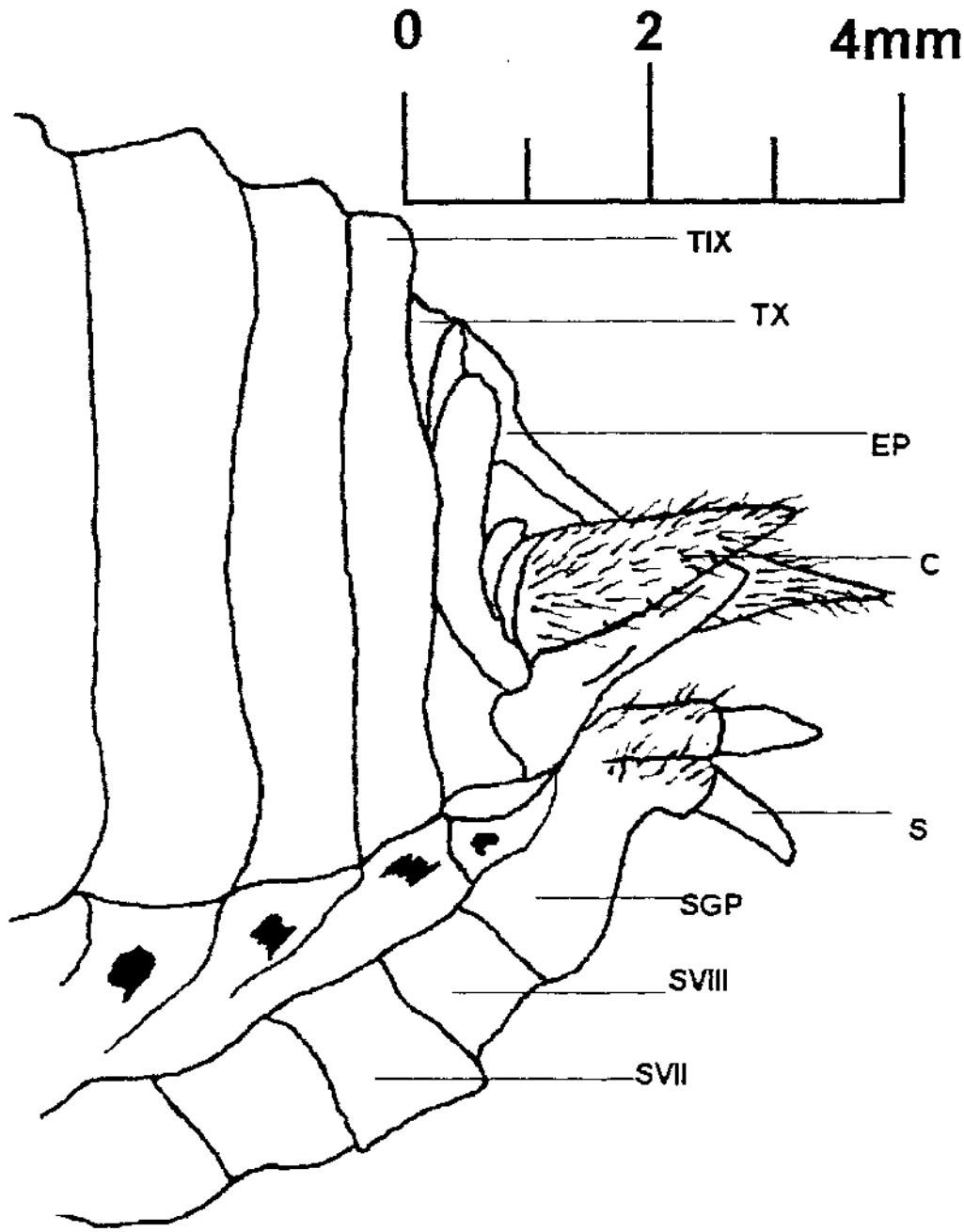


Figure 2.14. External genitalia of eighth instar male Mahoenui weta, lateral view.

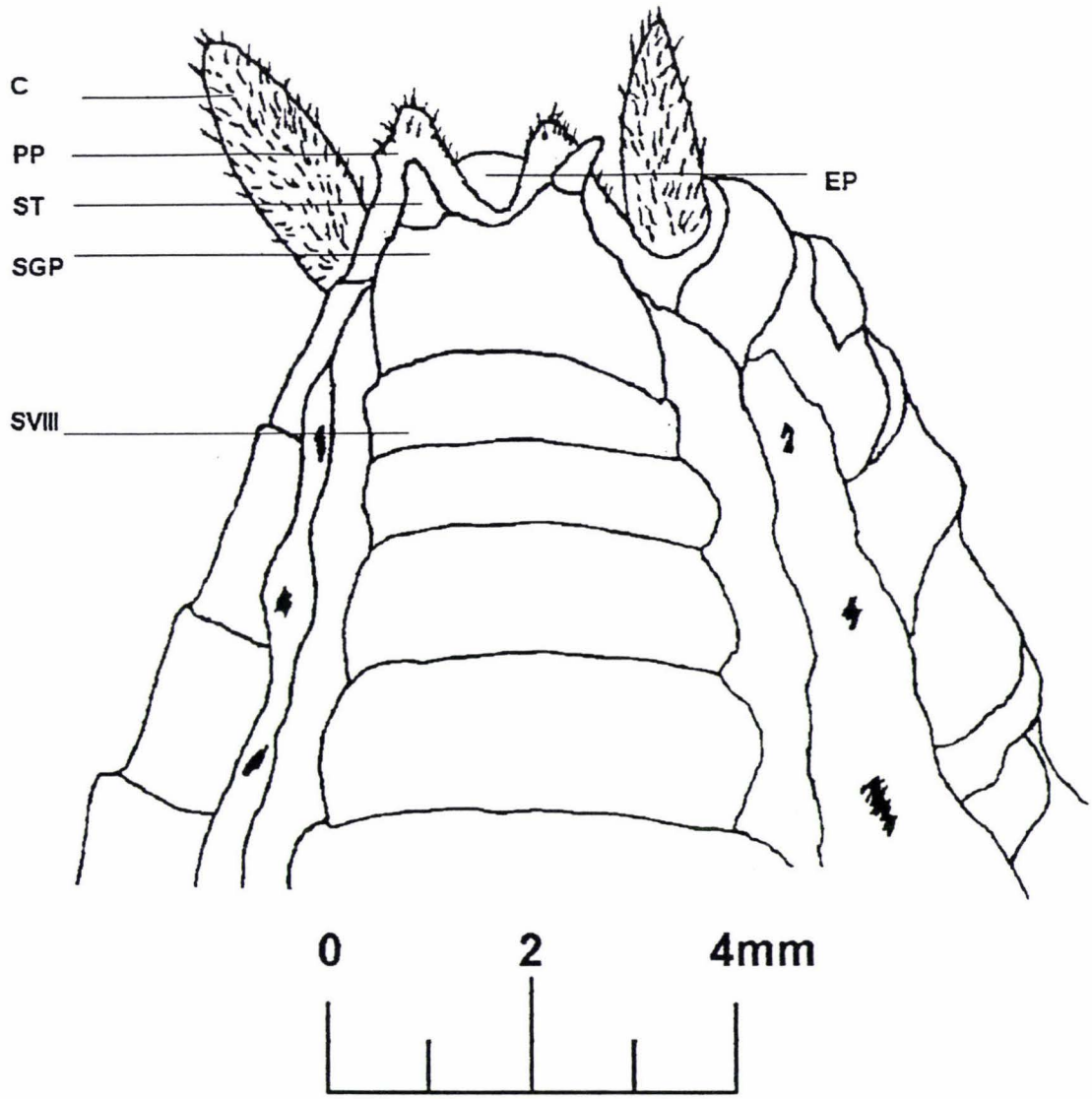


Figure 2.15: External genitalia of an eighth instar male Mahoenui weta, ventral view.

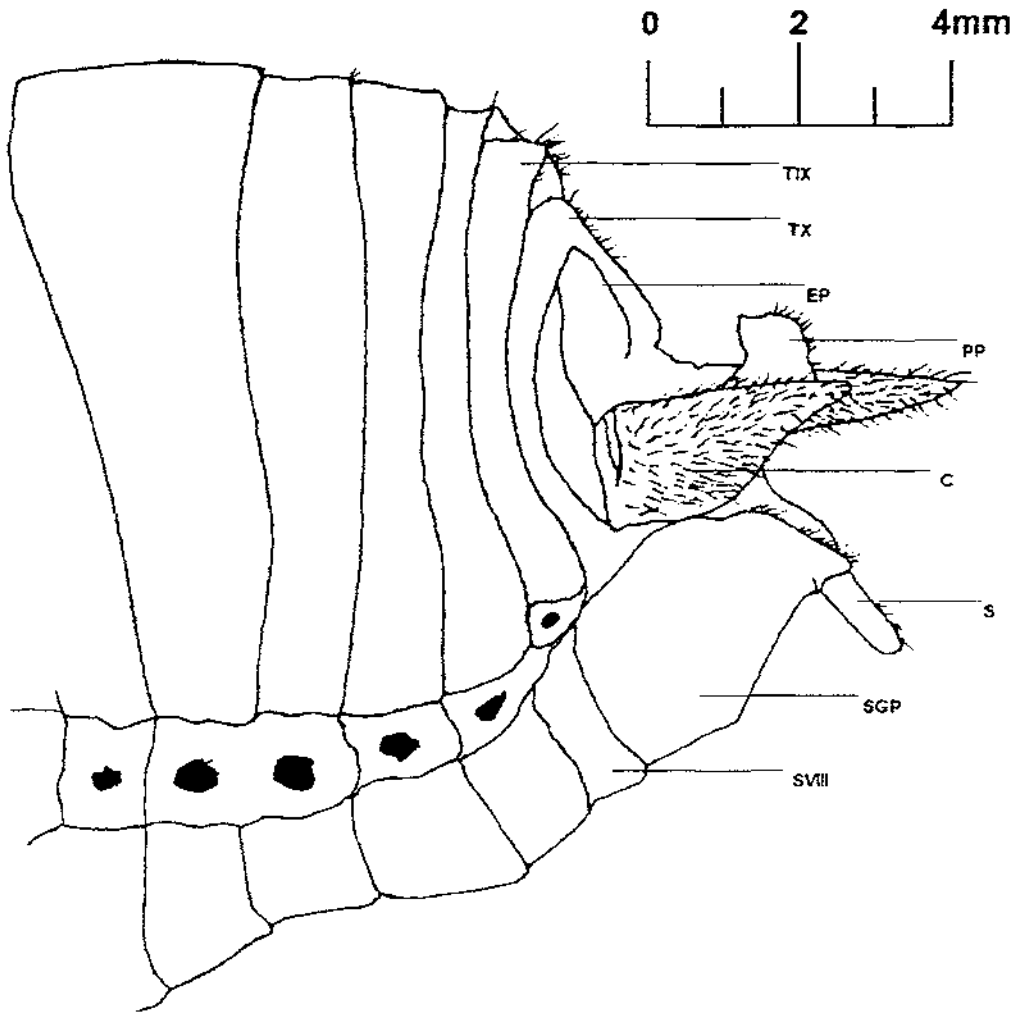


Figure 2.16: External genitalia of ninth instar male Mahoenui weta, lateral view.

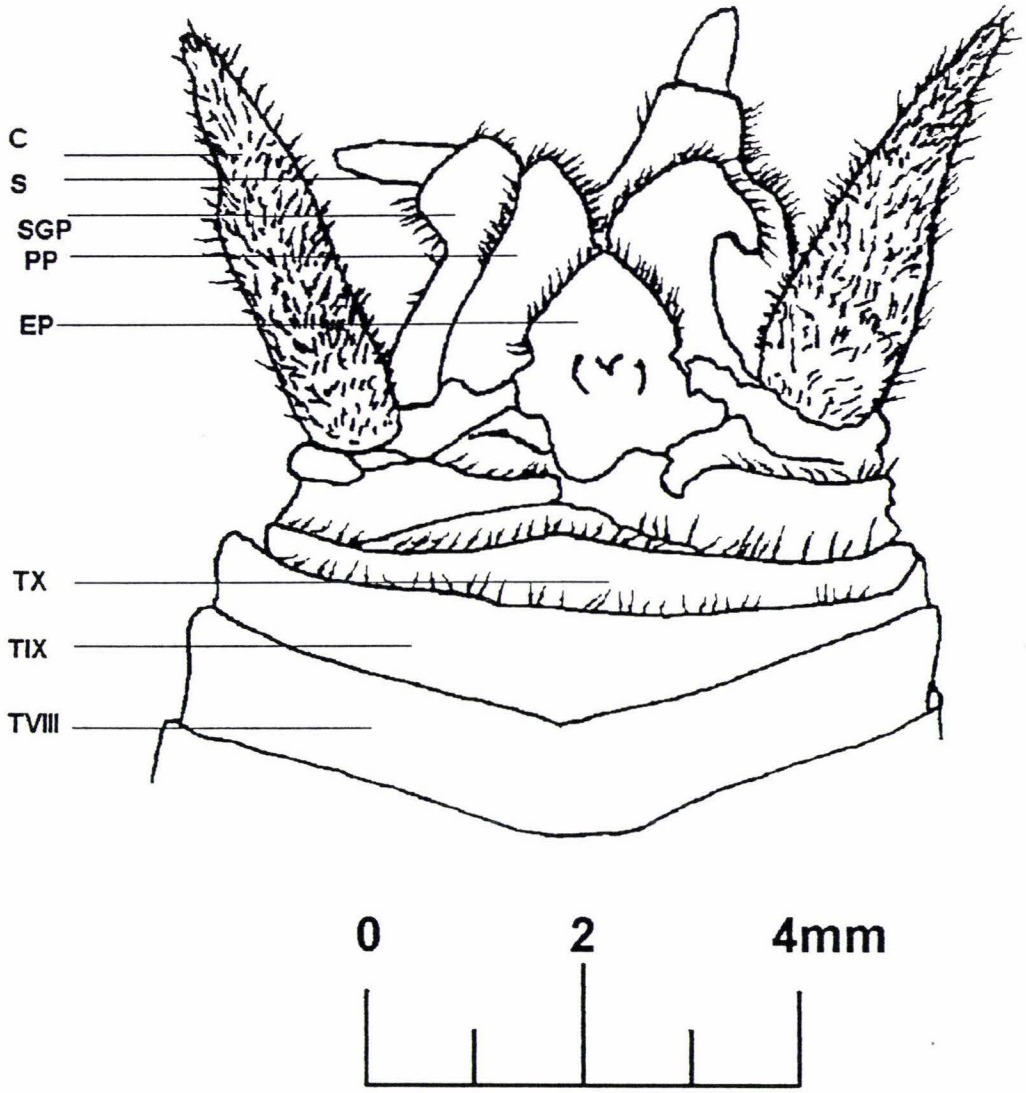


Figure 2.17: External genitalia of ninth instar male Mahoenui weta, dorsal view

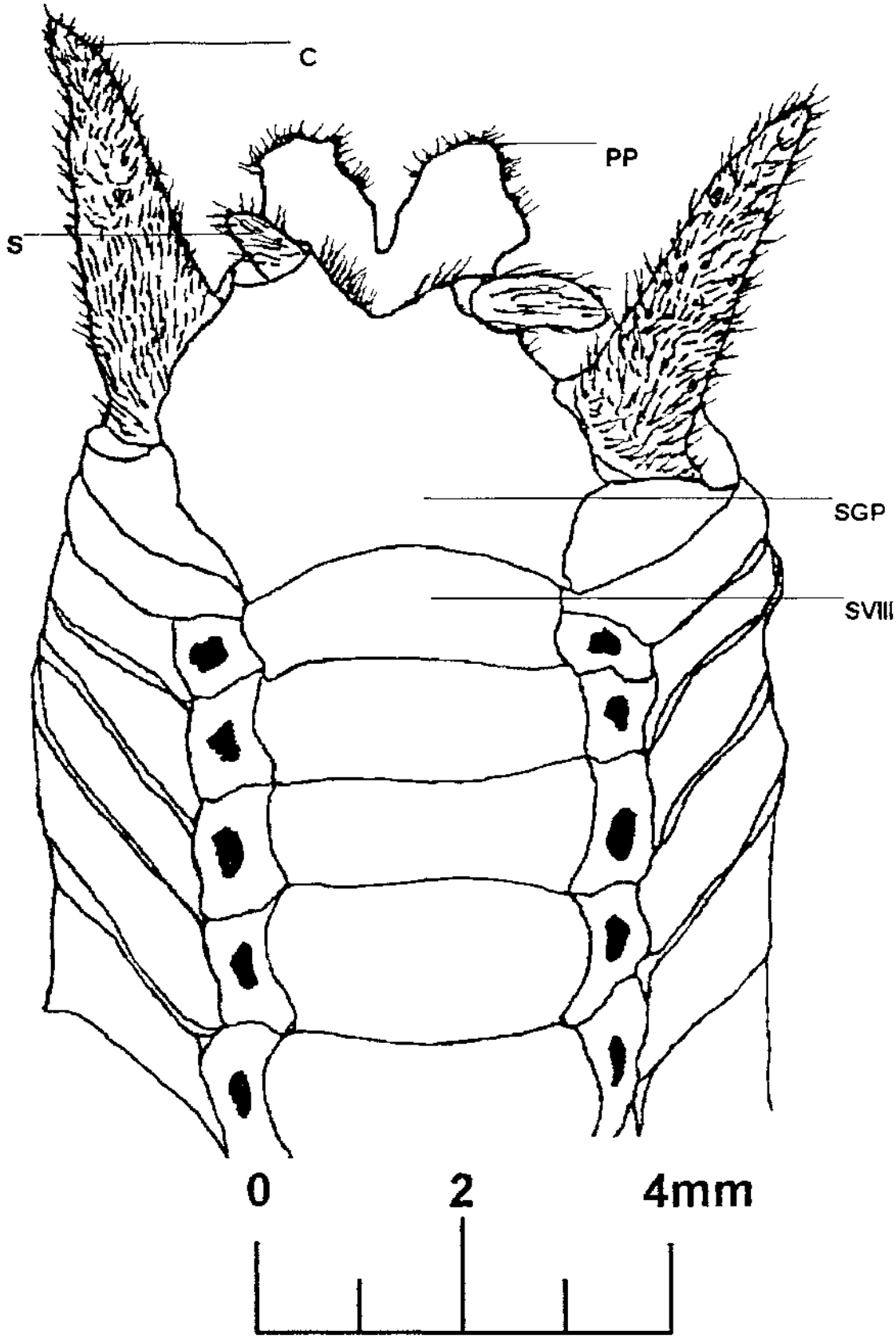


Figure 2.18: External genitalia of ninth instar male Mahoenui weta, ventral view.

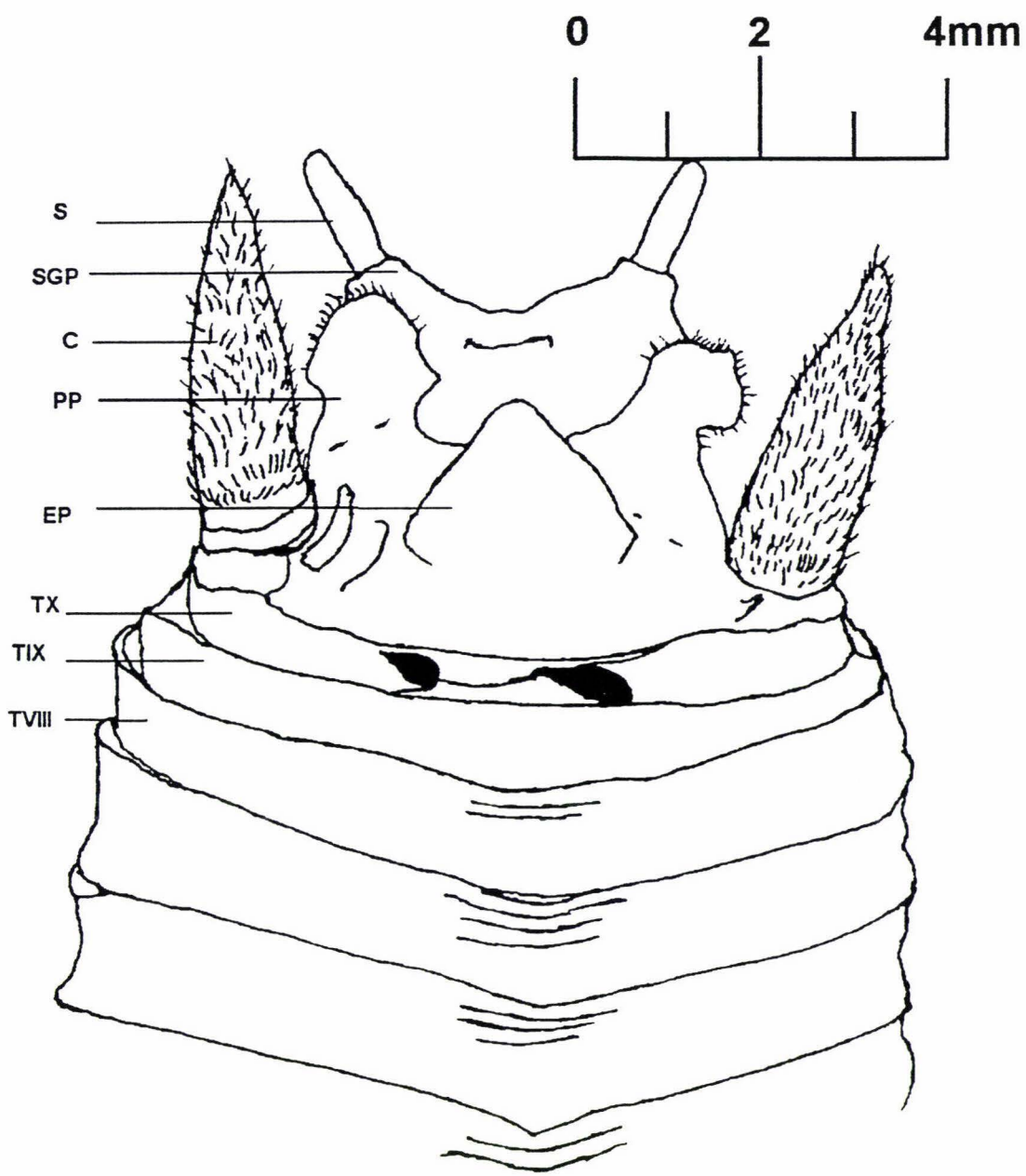


Figure 2.19: External genitalia of tenth instar male Mahoenui weta, dorsal view.

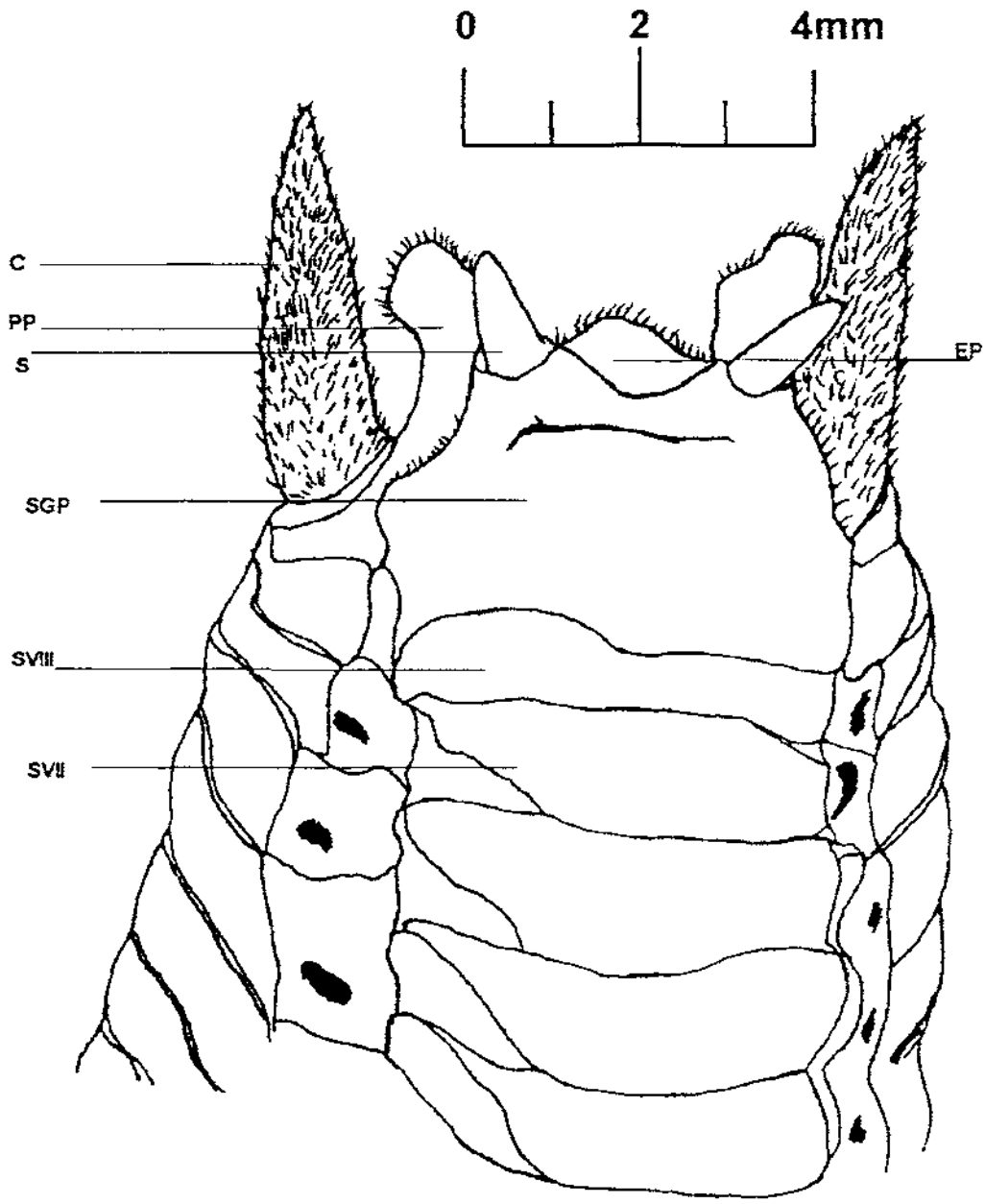


Figure 2.20: External genitalia of tenth instar male Mahoenui weta, ventral view.

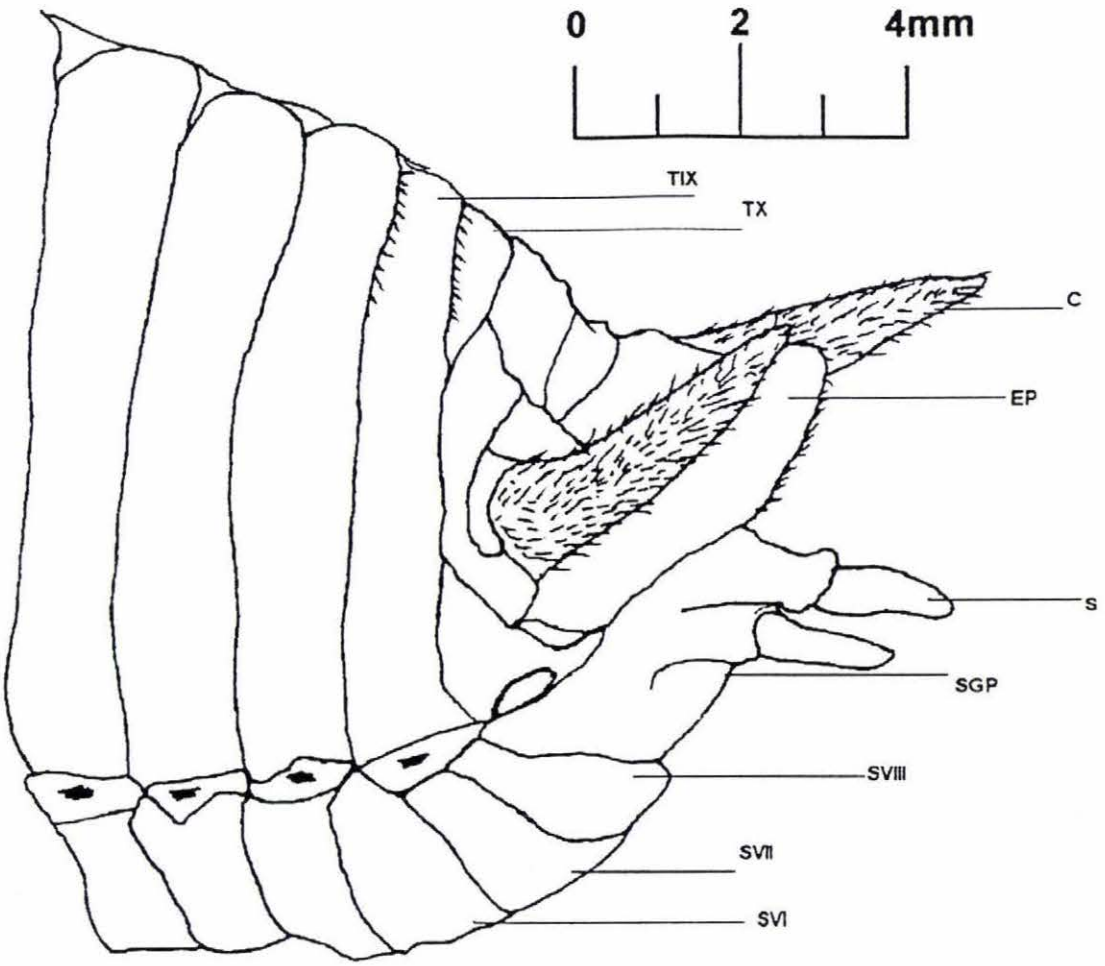


Figure 2.21: External genitalia of tenth instar male Mahoenui weta, lateral view.

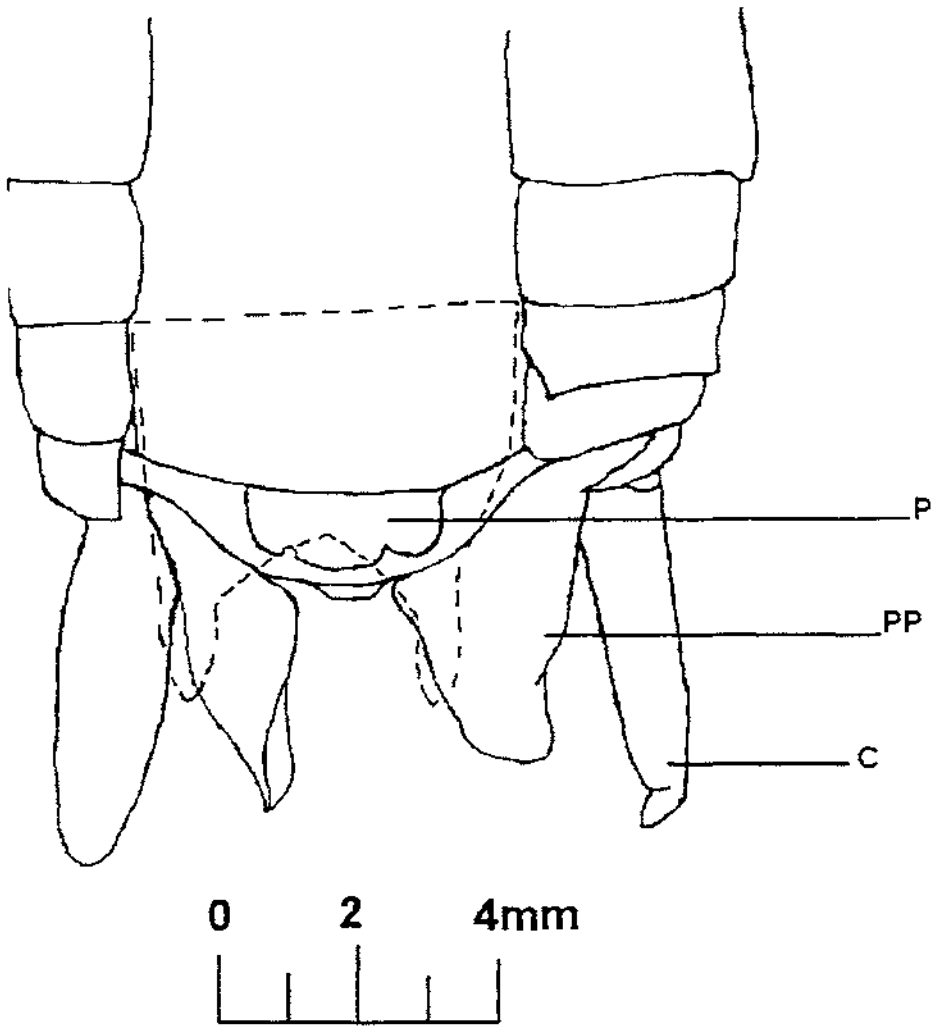


Figure 2.22: External genitalia of tenth instar male Mahoenui weta, with subgenital plate removed (dotted line denotes position of removed plate), to show penis.

2.4 Discussion

The reproductive structures of the adult male Mahoenui weta are similar to other Orthoptera (Snodgrass 1937, Matsuda 1976, Schwalm 1988). The Mahoenui weta

differs only in the relatively large size of the accessory glands. In these glands some fusion has taken place to accommodate the glands within the body. While the seminal vesicle is completely fused, the accessory glands are only partially fused.

In other respects the testes of the Mahoenui weta correspond in form with the genus Tachycines of the Orthoptera (Matsuda 1976). Development of the testis from this 'simple' form involves the formation of a common base for numerous follicles that enter the anterior end of the vasa deferentia (Matsuda 1976). The testis of the Mahoenui weta are not compressed as reported in Acrididae (Uvarov 1966). The accessory glands are best correlated with Onesto's 1st major kind of accessory gland in that they lie ventrally and are very large (Matsuda 1976).

The general morphology and histology are very close to that of Acrididae (Akhatar and Ashrafi 1965). Although the individual shapes of organs differed, the histology was almost identical, except the size of all cells differed between families. Also, the Mahoenui weta's ejaculatory duct contained no longitudinal muscle, while that of Acrididae did.

In Acrididae the secretion of the accessory glands is thought to have a stimulatory effect on the motility and activity of the oviduct in vitro (Paemen et al 1990). These glands are responsible for the production and secretion of a proteinaceous fluid which enables the transport of spermatozoa to the female during copulation. The accessory glands may have a similar function and be responsible for the production of the secretion surrounding the sperm in the spermatophore (Maskell 1927).

The histology of *H. thoracica* shows the closest similarity to that of Mahoenui weta, and this is to be expected as they are both in the Stenopelmatidae (Maskell 1927). A possible difference arises in the muscle layers of the ejaculatory duct. In the Mahoenui weta I found only circular muscle in the ejaculatory duct while Maskell did not specify the direction of the muscle in *H. thoracica.* The ejaculatory duct is lined by a cuticular intima in both species. The penis appears to be tri-lobed from above in both *H. thoracica* (Maskell 1927) and the Mahoenui weta (Figure 2.22). In other respects the external genitalia differs little from that of other weta (Richards 1953, Sandlant 1981, Cary 1981, Wahid 1978).

A comparison of development between external reproductive structures in the Stenopelmatidae was conducted by Cary (1981). He found that the subgenital plate

elongated and broadened anteriorly as *Z. gracilis* developed from 1st instar to adult. He also noted that the posterior lobes of paraprocts became larger and curved more in the dorsal direction and that the tenth abdominal tergite was greatly modified to form two anteriorly pointing hooks. The phallus appeared as fleshy lobes that protruded and the cerci were more rounded at their tips. In the Mahoenui weta the penis does not protrude from the body cavity and instead lies under the subgenital plate as in *H. thoracica* (Maskell 1927). The Mahoenui weta has no heavily sclerotized hooks that are modified from the tenth abdominal tergite and cerci become more pointed and elongate in the Mahoenui weta during development, while those of *Z. gracilis* become more rounded at their tips as the weta develops into the final instar.

Chapter Three

The Female Reproductive System of the Mahoenui weta *Deinacrida* n.sp. (Orthoptera: Stenopelmatidae).

Abstract

The morphology and histology of the entire female reproductive organs of *Deinacrida* n.sp, excluding the spermatophore, are described. Follicular degeneration after ovulation and sperm transfer were not investigated. The morphology and histology of female Mahoenui weta are very similar to those of other Orthoptera and their histology has many similarities to that of the tree weta. The histology is particularly close to that of the Acrididae. Ovaries and ovarioles have the usual structure for Stenopelmatidae. The follicles are enclosed within a follicular epithelium and the ovarioles are enclosed within an outer ovariole sheath layer of connective tissue. The epithelial cells of the ovarioles and lateral oviducts have basophilic cytoplasm. The vagina is lined with a cuticular intima and is surrounded by a muscular sheath. The external genitalia are described from 8th to 10th instar Mahoenui weta and their probable functions are discussed.

3.1 Introduction

No thorough study of the female reproductive organs of *Deinacrida* n.sp. has been published. The only information concerning this is by Richards (1973), who compared the external reproductive structures of *D. fallai* (White) Salmon and *D. heteracantha* White and Ramsay (1965) who investigated the external genitalia of the female instars of *D. rugosa* Buller. Ander (1939) published a comprehensive review of the reproductive system of Ensifera, mentioning several of the Stenopelmatidae including external morphology of *Hemiandrus* n.sp.

Information concerning the reproductive organs of other Stenopelmatidae is provided by Sandlant (1981) who described the external reproductive morphology of *Hemideina femorata* Hutton, and Cary (1981) described the external reproductive morphology of *Zealandosandrus gracilis* n.g. Maskell (1927) provided diagrams of the

internal reproductive organs and some of the histology for *Hemideina thoracica* (White).

Detailed morphological studies have been published for other species of Orthoptera. Snodgrass (1933,1935) published extensive works on the genitalia of Orthopteroid insects, and Matsuda (1976) presented a review on Orthopteran genitalia. Here I present the first detailed description of the reproductive system of the female Mahoenui giant weta.

3.2 Methods

Two adult females were taken immediately after natural death, and dissected under Clark's insect saline (Hale 1965). Two adults and two sub-adults were used for taking external measurements. Abdomens of entire specimens were opened and fixed with Formol-Alcohol fixative for 48 hours. Transverse and longitudinal serial sections of entire abdomens of female Mahoenui weta were made using normal histological techniques as described in Humason (1967). Sections were fixed, dehydrated in a graded alcohol series, then cleared first in chloroform and then in Xylene. The tissue was embedded in paraffin, sectioned to 2-8μm (usually 5-6μm), and stained with Mayer's haematoxylin and eosin. Tissues containing eggs were coated with celloidin to prevent the yolk fracturing when cut. Photomicrographs were taken with using Kodak Ektrachrome Elite 200 and Kodak Ektrachrome 64T Tungsten professional colour reversal films. Either Nomarski or Interference Contrast Microscopy was used to view the slides of prepared reproductive organs.

All drawings were made on graph paper from specimens under a microscope equipped with a squared eyepiece graticule. Measurements smaller than about 2mm were made with a microscope fitted with a calibrated eyepiece micrometer.

3.3 Results

The internal reproductive organs of the female

The internal reproductive organs consist of paired ovaries attached to lateral oviducts that converge to form a ventral vagina. A spermatheca branches off the vagina dorsally (Figures 3.1 and 3.2).

The ovaries

Each ovary in ninth instar weta consists of 36 panoistic ovarioles that are translucent white in colour for most of their length (Figure 3.2). These appear to degenerate to approximately 19 in the mature adult. Each ovariole is enclosed within an ovarial sheath and the ovarioles of each ovary are enclosed within an outer ovary sheath. The ovarioles have layers of fat between them. Numerous tracheae also run from the thin connective tissue sheath to the body. Within each ovariole a series of oocytes are visible that increase from translucent white apically through yellow to a dark brown colour basally in the mature egg.

Each ovariole comprises a terminal filament, germanium, vitellarium, and pedicel. The terminal filaments of each ovary fuse together to form a common terminal filament. This runs dorsally and medially within the abdomen and eventually joins to the end of the terminal filament from the opposite ovary and then attaches to the pericardial diaphragm. Posteriorly, the terminal filament of each ovariole increases gradually in width and joins the germanium at a slight swelling. Following this the vitellarium forms the largest part of the ovariole and finally the pedicel connects the ovariole to the calyx of a lateral oviduct and it either forms a short constricted tube behind the last oocyte or is distended with mature ova if the lateral oviducts are also filled. The calyx usually occupies the last third of the ovary.

Ovaries vary considerably in size depending on the degree of development of the oocytes within them. When these are all immature, the ovaries occupy ventral positions within the fifth to sixth abdominal segments and each ovariole can be as small as 6.25mm long. A single ovary can, however, contain 55 or more mature ova and then it occupies most of the ventral and lateral space within the abdomen between segments three to eight. Each ovariole and its terminal filament can then reach up to 21.5 mm long.

The terminal filament appears to be composed entirely of muscle anteriorly. The combined muscle fibres range in size from 0.07mm to 0.30mm thick. These terminal filaments each continue with a layer of circular muscle around the sheath of each ovary. The muscle cells have a width of 2μm and a length of 0.06mm. An outer

layer of longitudinal muscle lies on top of the circular muscle and its cells have dimensions of 0.03mm to 0.02mm. The epithelial cell layer enclosing an ovariole range in size from 0.06mm long and 0.02mm wide to 0.02mm long and 0.01mm wide depending on their position along the ovariole and the extent of its distension (Figure 3.3). The epithelial cells are cuboidal to columnar and lie on an outer basement cell membrane and their inner surface have microvilli. Their cytoplasm is basophilic and their nuclei are centrally located within the cells and have diameters of about 1μm. Internally the ovariole has a maximum diameter of just over 1mm then tapers to its junction with the terminal filament.

Germanial cells start off with a basophilic cytoplasm. As they progress down the ovariole their cellular contents change and become eosinophilic in the mature egg. The nucleus of the cell remains basophilic and central in the early stages and has a diameter of about 0.01mm. The cell gradually increases in size until it reaches the dimensions of the mature egg (refer chapter 5).

The calyx is formed at the lower end of the ovary between the pedicels and oviduct proper, and forms a storage place for the eggs before ovipostion.

Oviduct and vagina.

From the calyx the oviduct of each side continues as a short narrow tube that is translucent white. This unites with the other oviduct to form the vagina. The vagina opens by a slit-like aperture upon the upper surface of the subgenital plate.

The lateral oviducts are identical to the pedicel and the rest of the ovariole in histology, but the pedicel and the oviduct differ in that their columnar cells do not have villi. Their columnar cells vary in height from 0.02mm to 2.5μm (Figure 3.4) .These cells rest on a outer basement membrane. The oviducts have the same muscle layer as the ovariole. The inner muscle layer is often up to three to five muscle fibres in thickness and these are for the most part circular.

The vagina has dimensions of 1.2mm by 0.8mm. The vagina has the same histology as the rest of the oviduct, differing in that it has a cuticle layer continuous with that of the outer exoskeleton.

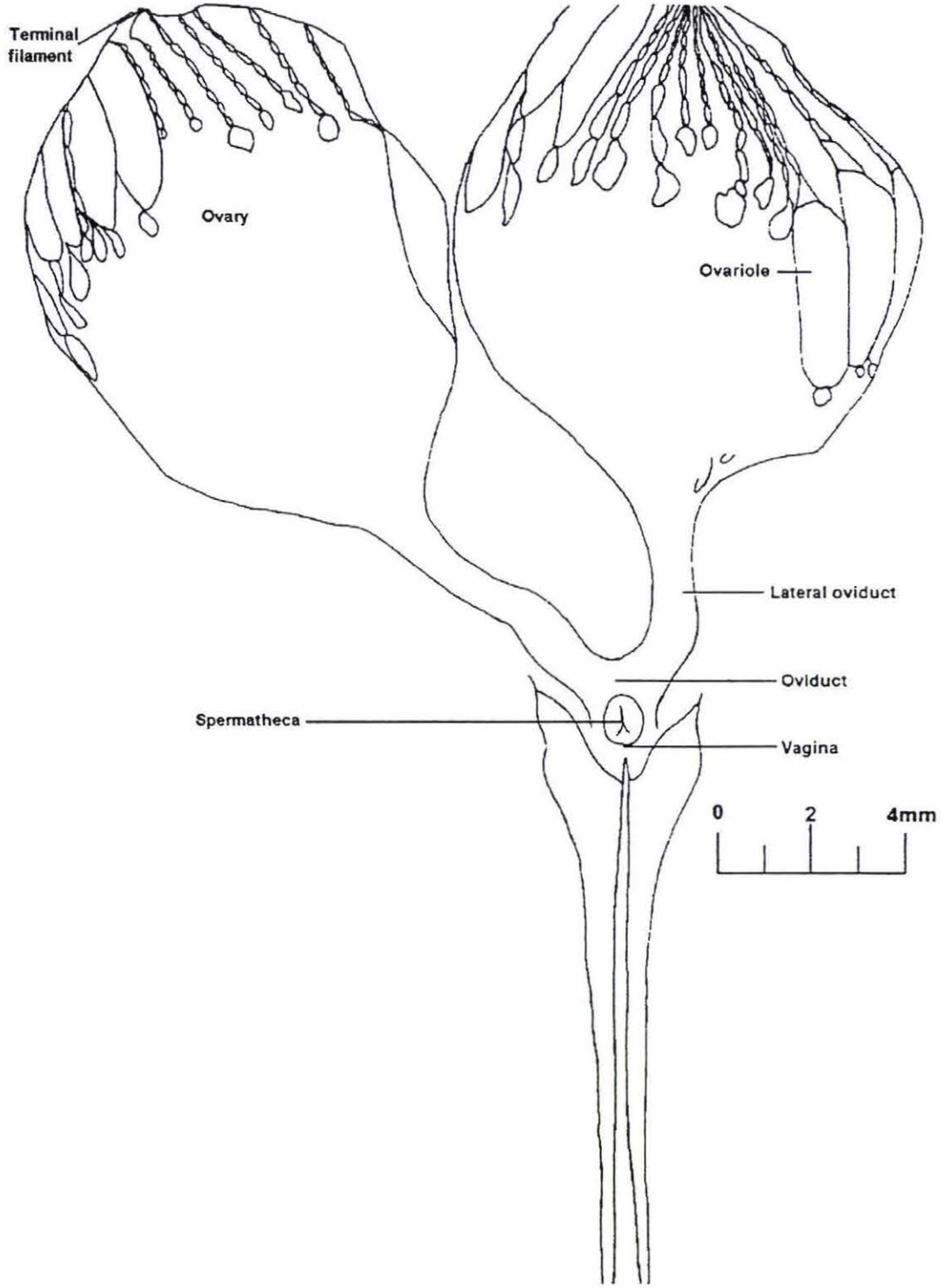


Figure 3.1: Internal reproductive structures of adult female Mahoenui weta.

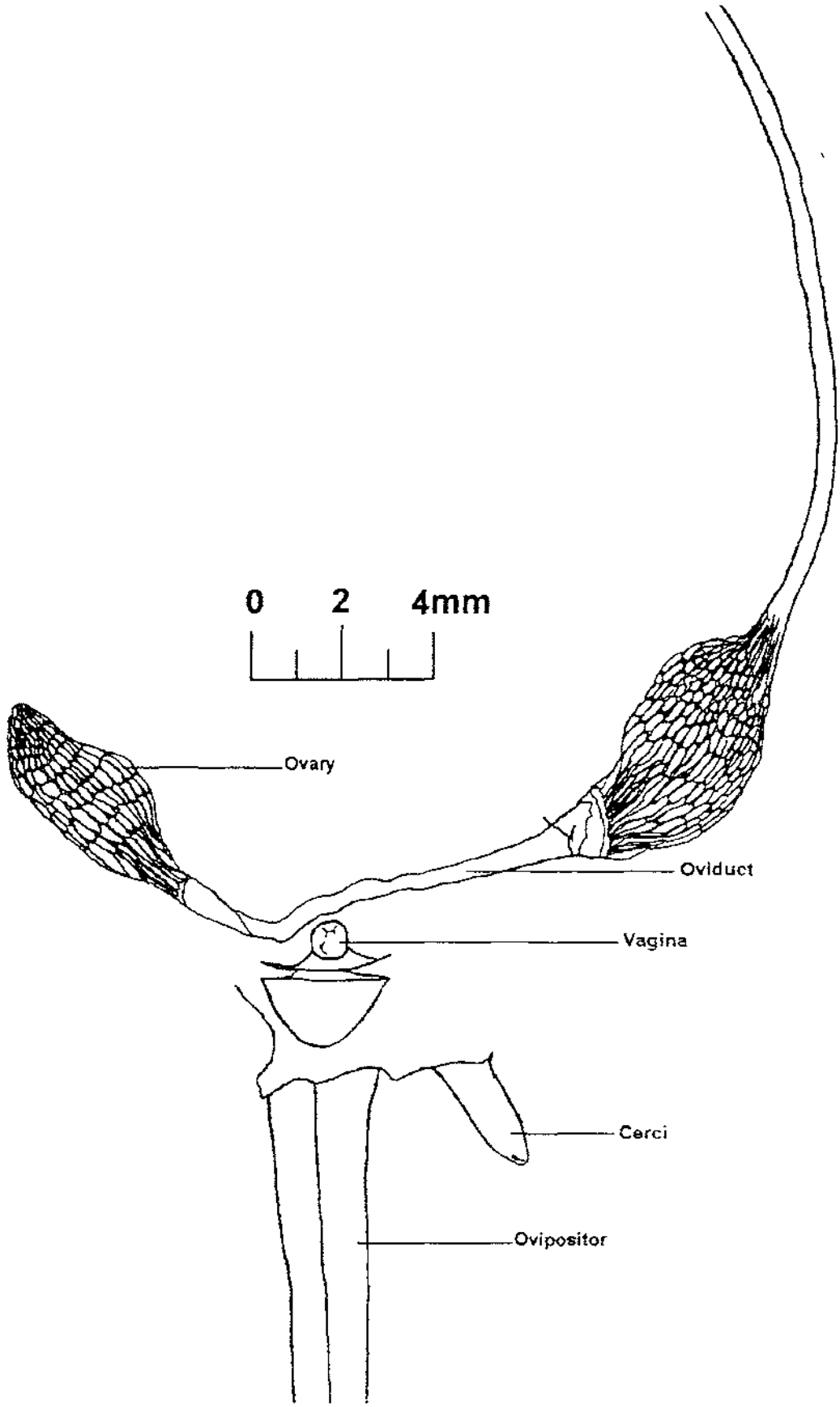


Figure 3.2: Ninth instar Mahoenui weta female reproductive organs.

Spermatheca

The spermatheca is a median blind tube that arises dorsally to the vagina and its distal end is bent back upon itself, before dilating into a sac. It is translucent white in colour. The spermatheca is dorsal to the vagina and ellipsoidal in cross section, with dimensions of 0.24mm by 0.50mm and the closed, flattened tube it forms bends back upon itself. The histology of the spermatheca is the same as that of the oviduct except that the order of the muscle layers is reversed, so the circular muscle layer is encountered first with the longitudinal layer second. The inner layer of the spermatheca is lined with an intima (Figure 3.5).

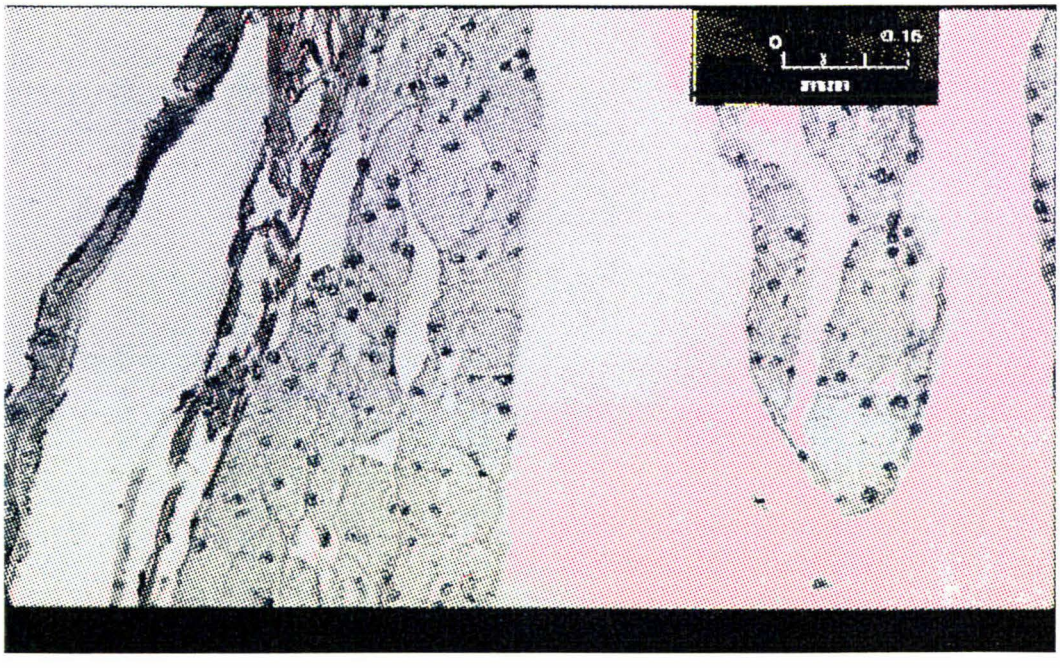


Figure 3.3: Mahoenui weta ovariole sheath, longitudinal section.

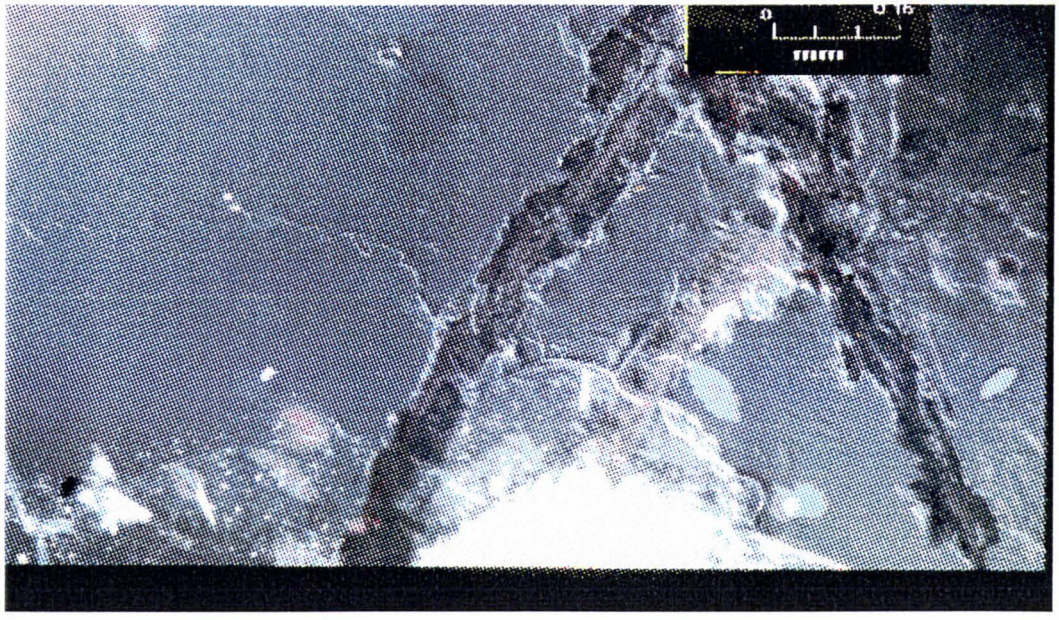


Figure 3.4: Mahoenui weta lateral oviduct, transverse section.

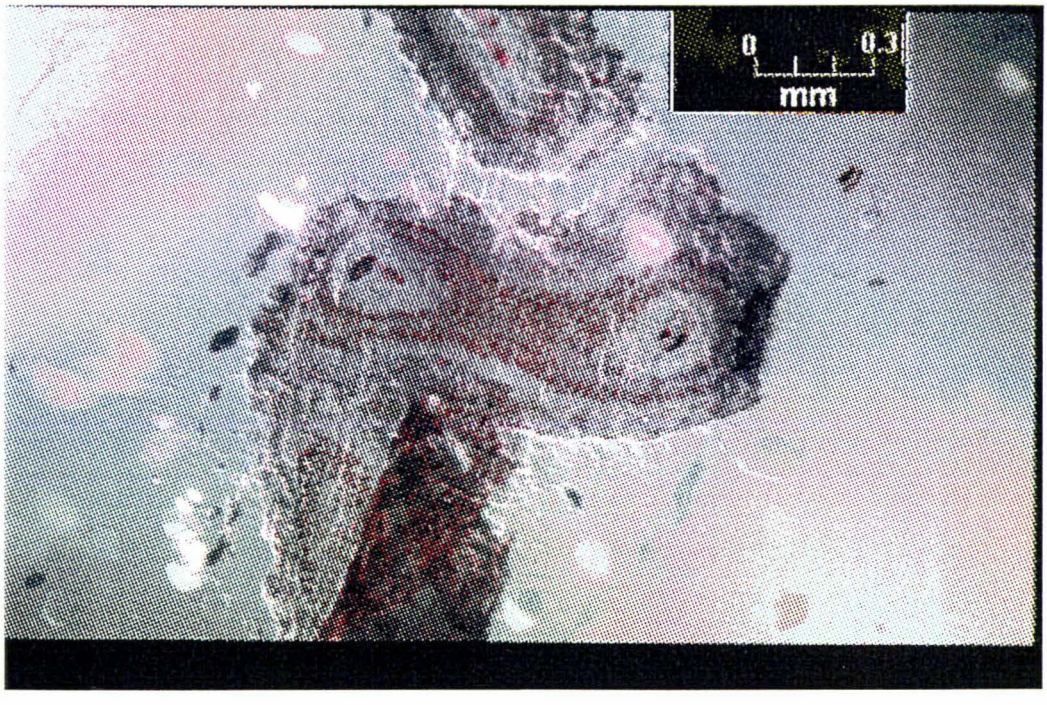


Figure 3.5: Mahoenui weta spermatheca (Cut through twice due to bent nature), transverse section.

Table 3.1 Dimensions of female reproductive organs of the Mahoenui weta *Deinacrida* n.sp. from four field collected specimens.

		Mean	SD	Range	Mean	SD	Range	(mm)
ovariole+ terminal filament	length	21.5	0.71	1	12.5	0.71	1	
	max width	0.35	0.07	0.1	1	0	0	
Spermatheca	length	1.25	0.07		1.45	0.07	0.1	
	max width	0.4	0	0	0.5	0	0	
vagina	length	0.8	0	0	1.2	0	0	
	width	0.75	0.07	0.1	0.8	0	0	
		9th	Instar		10th	Instar		

total sample size four

Development of the external genitalia of female Mahoenui weta from instar 8 to instar 10.

The paraprocts of eighth instar weta are long and narrow, with pointed posterior ends. The cerci are short and very broad at the base while the epiproct is wide at the anterior edge and is gently curved in the same shape as an eighth instar male weta (Figure 3.7). The subgenital plate is small and slightly notched (Figure 3.8). The ovipositor is short and broad when viewed from above and does not narrow noticeably towards the posterior end. When viewed from the side the ovipositor narrows slightly from anterior to posterior, and it curves slightly upwards at the blunt tip (Figure 3.9).

Ninth instar weta paraprocts are both narrower and longer than those of eighth instar weta. The cerci are slightly longer than in the eighth instar, but is the same width at the anterior end. The epiproct is as wide at both the posterior and anterior ends as that of the eighth instar, but it is slightly longer, imparting a more gently curved posterior profile (Figure 3.10). The subgenital plate is broad at the anterior edge and narrows sharply towards the posterior end. There is a well developed notch and the corners of the posterior edge of the sub genital plate are sharp (Figure 3.11). The

ovipositor is much longer than that of an eighth instar weta and it narrows sharply from anterior to posterior when viewed from above. When viewed laterally, the ovipositor has a very broad anterior end and it narrows gently to a sharp point at the posterior end (Figure 3.12).

Tenth instar paraprocts are long and narrow with slightly hooked ends. The cerci and epiproct appear no different to those in ninth instar weta (Figure 3.13). The subgenital plate is the same general shape of that in ninth instar weta, although it is slightly longer (Figure 3.14). The ovipositor is the same shape as that of ninth instar weta, but it is larger in all dimensions and it is slightly more curved when viewed laterally (Figure 3.15).

First instar weta could not be sexed as both male and female had styli present on the subgenital plate (Figure 3.16).

(For photographs of the external genitalia of the female Mahoenui weta: Instars 8-10 refer figures B.1 - B.8 in appendix.)

Figure 3.6: Key for external genitalia diagrams of the female Mahoenui weta.

C - Cerci

PP- Paraprocts

SGP- Sub genital plate

SVIII- Sternum Plate 8

SVII- Sternum Plate 7

SVI- Sternum Plate 6

SV- Sternum Plate 5

TX- Tergum Plate 10

TIX- Tergum Plate 9

TVIII- Tergum Plate 8

TVII- Tergum Plate 7

EP- Epiproct

S- Stylus

ADP- Invagination of ninth sternum associated with formation of apodeme

INBV- Inter-basivalvular sclerite

VII- Second valvifer

VI- First valvifer

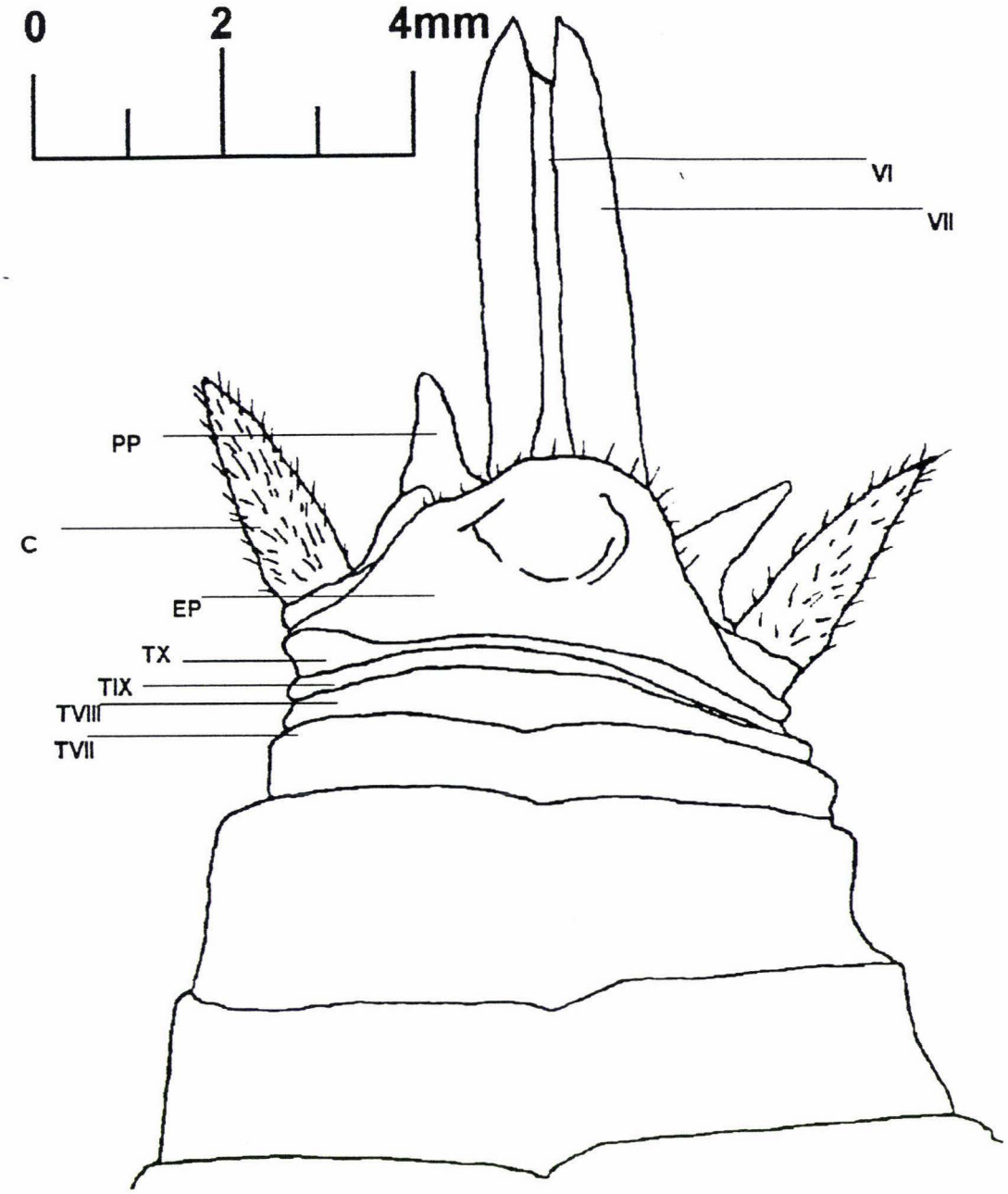


Figure 3.7: External genitalia of eighth instar female Mahoenui weta, dorsal view.

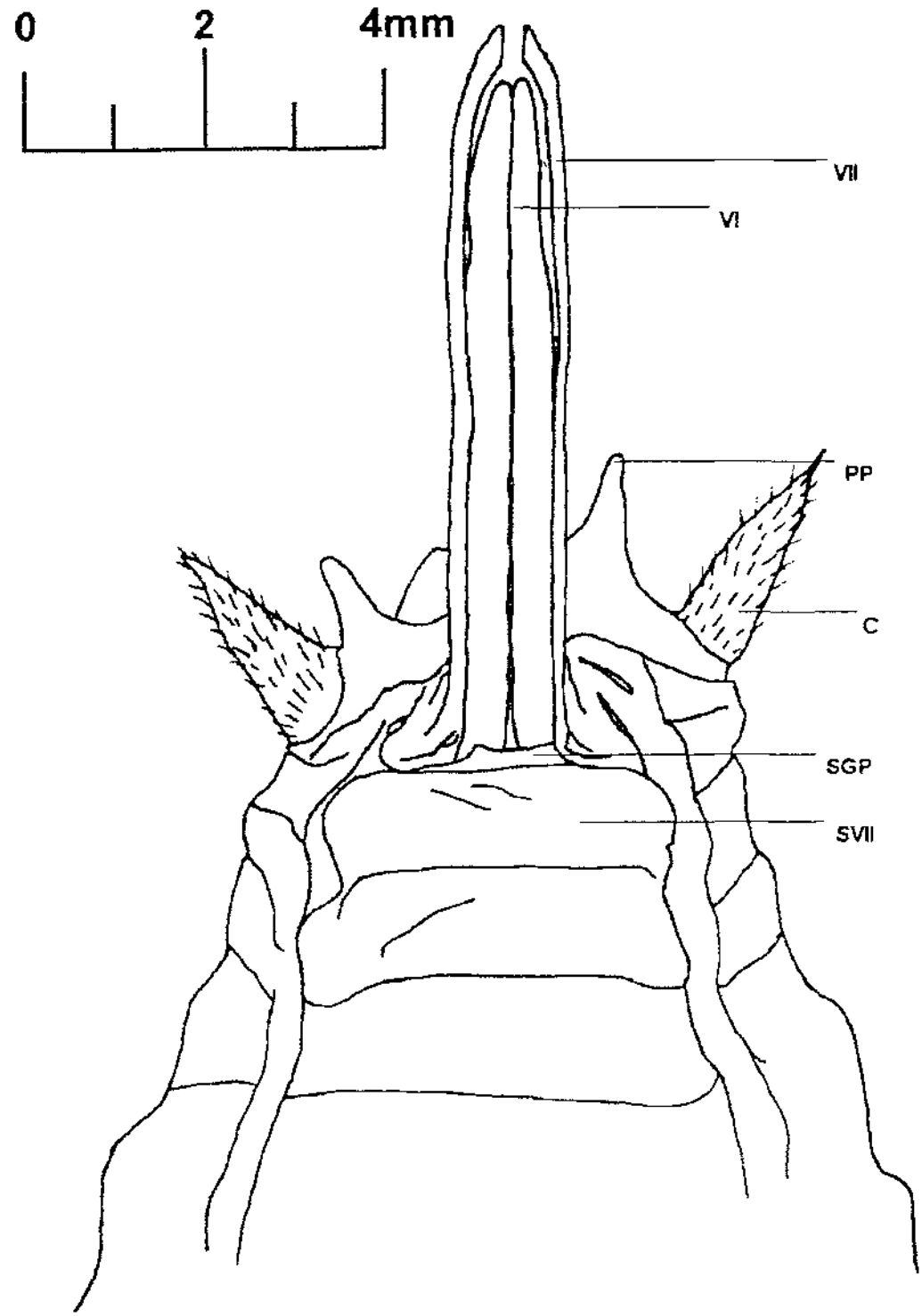


Figure 3.8: External genitalia of eighth instar female Mahoenui weta, ventral view.

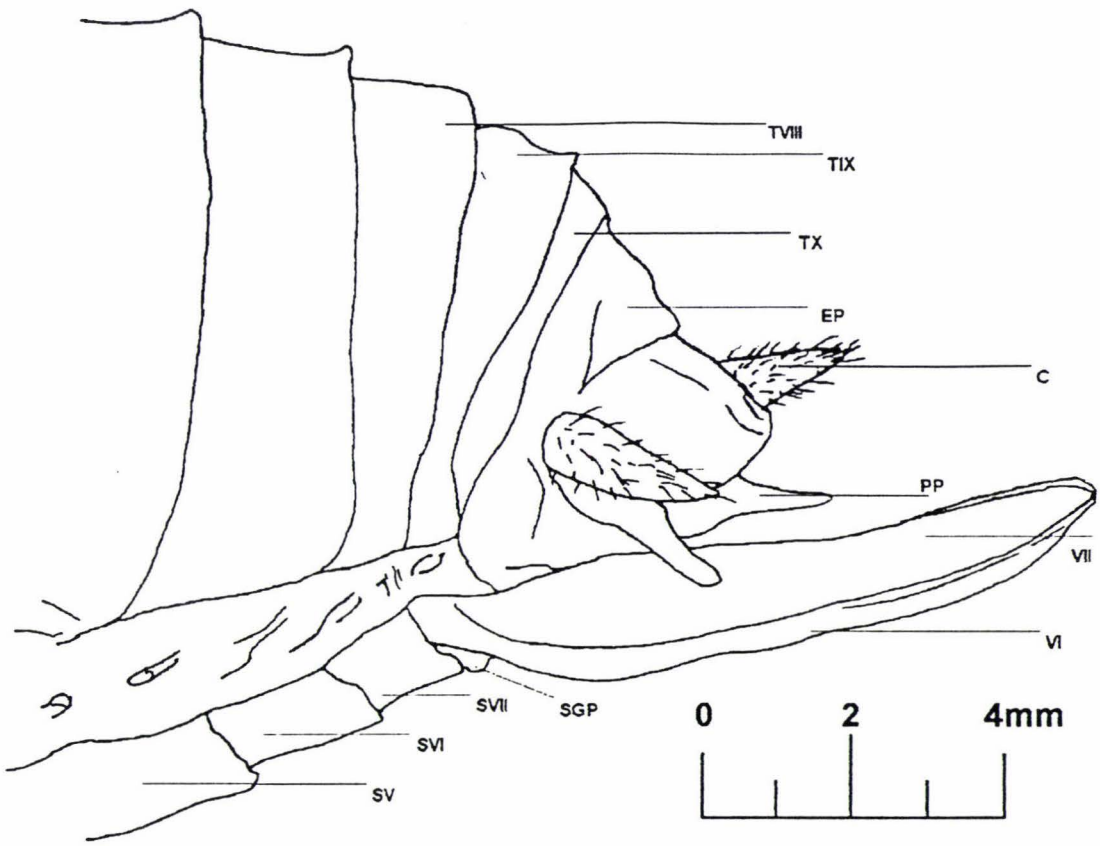


Figure 3.9: External genitalia of eighth instar female Mahoenui weta, lateral view.

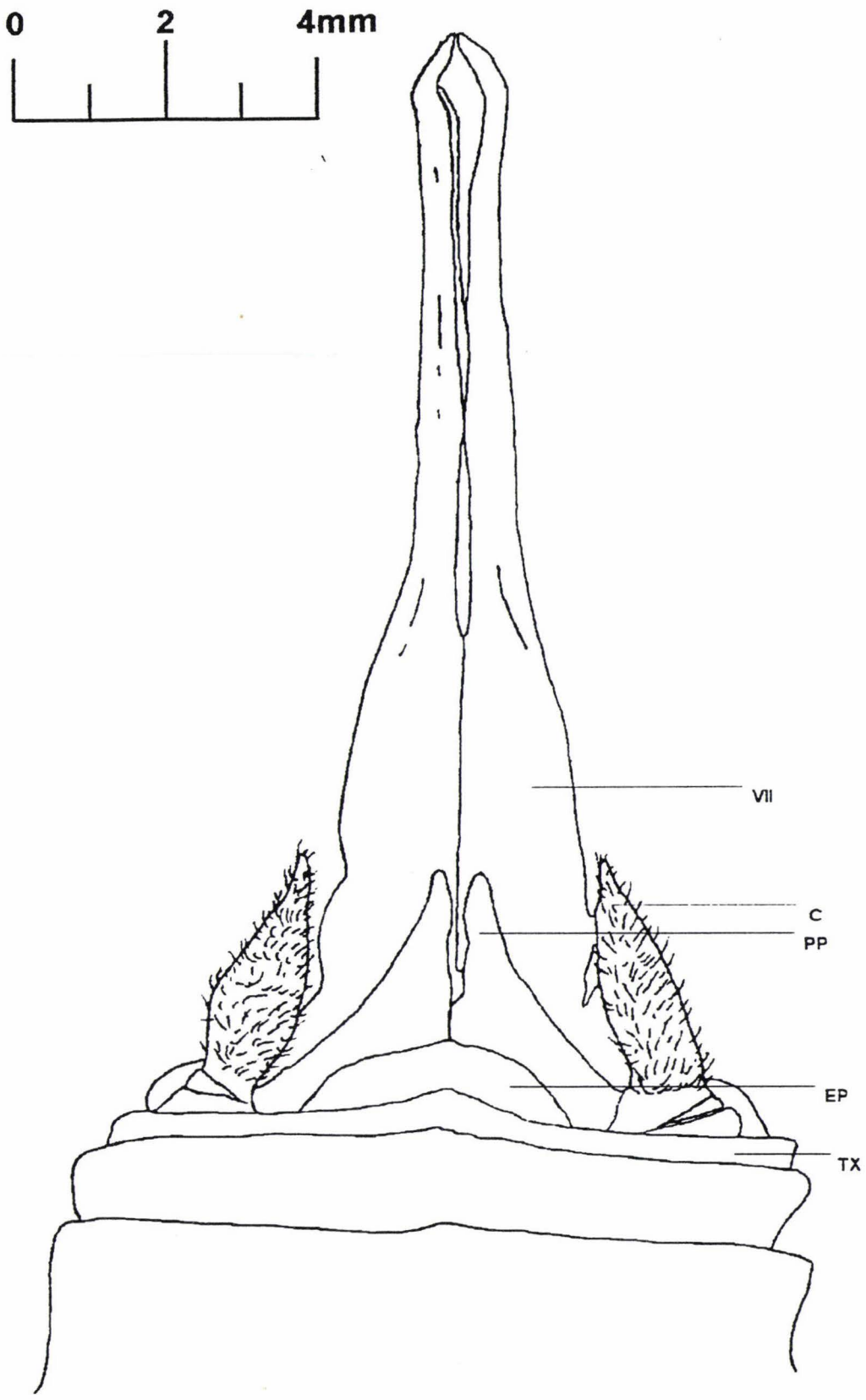


Figure 3.10: External genitalia of ninth instar female Mahoenui weta, dorsal view.

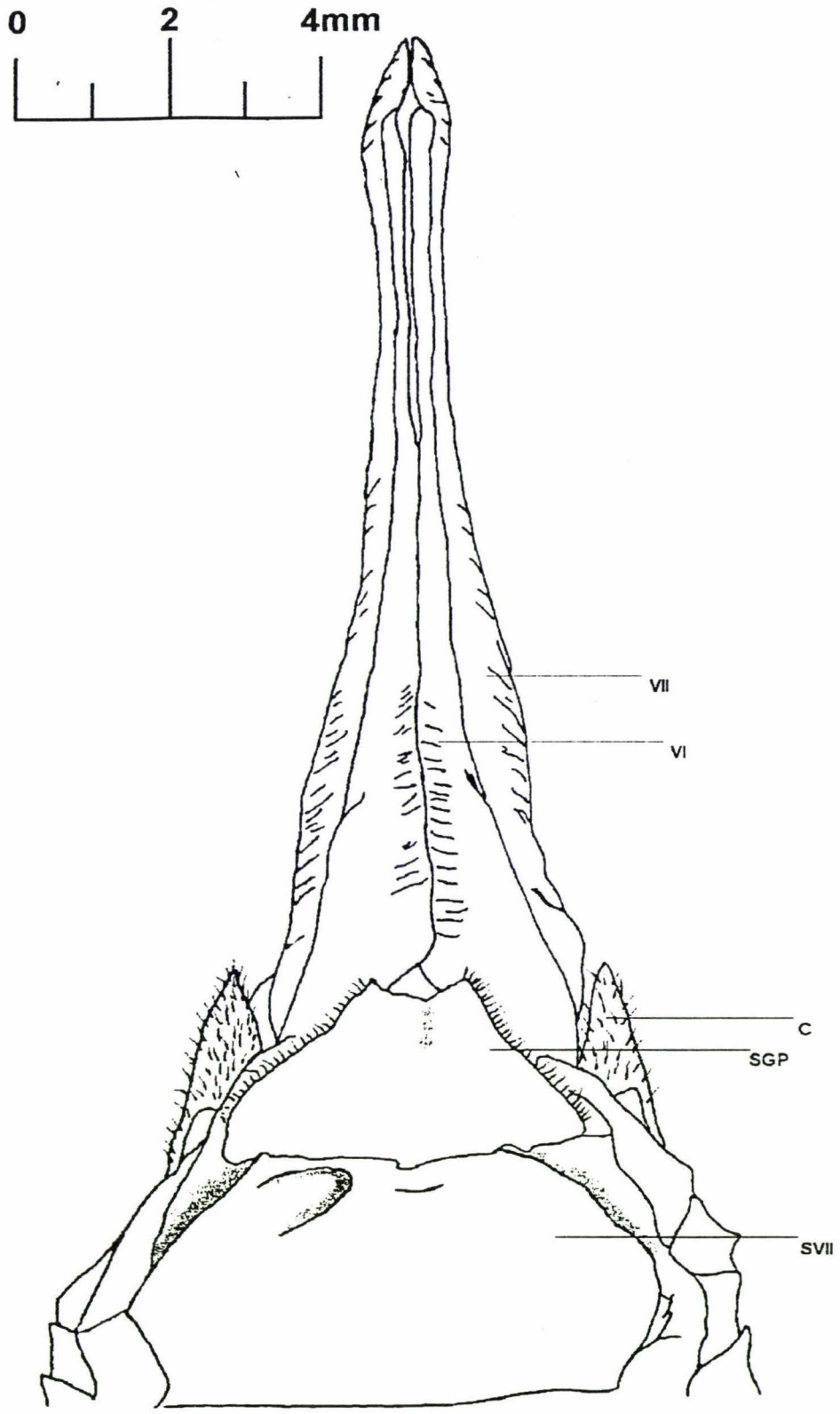


Figure 3.11: External genitalia of ninth instar female Mahoenui weta, ventral view

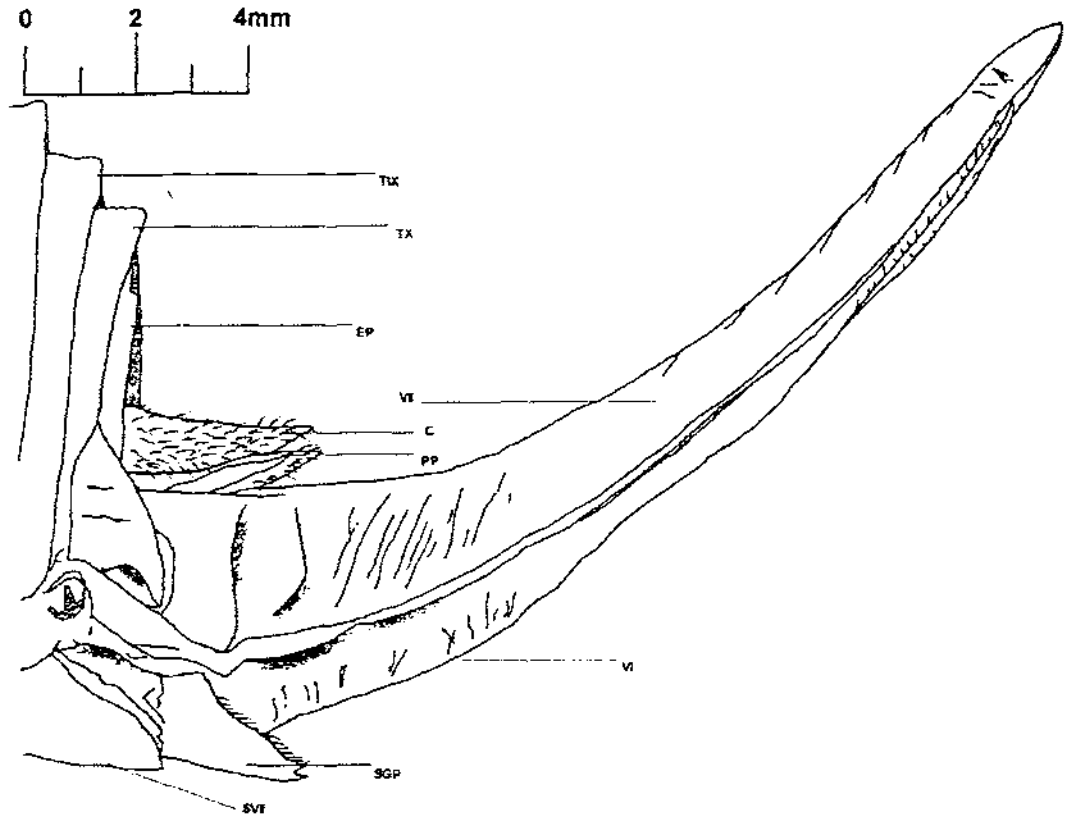


Figure 3.12: External genitalia of ninth instar female Mahoenui weta, lateral view.

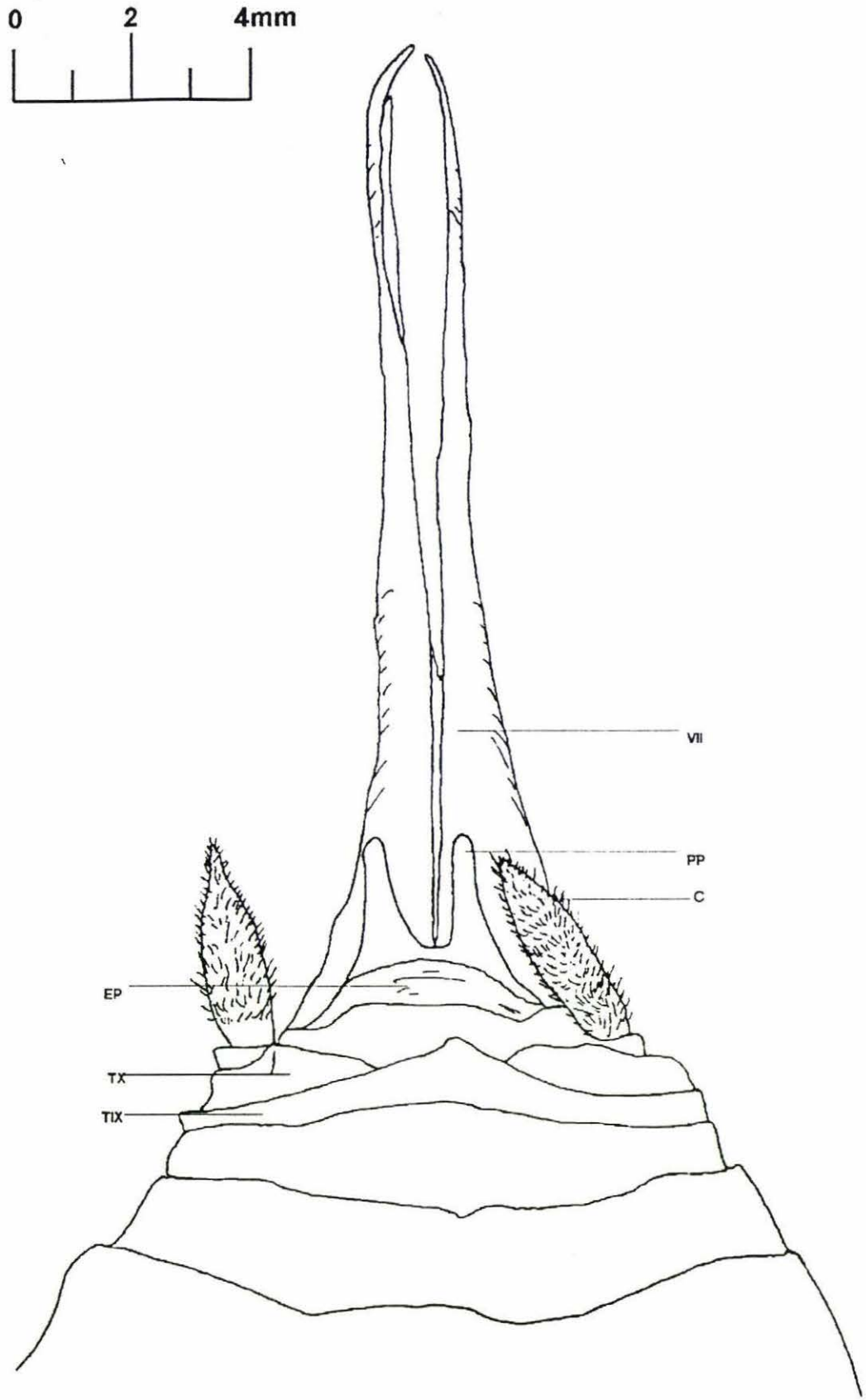


Figure 3.13: External genitalia of tenth instar female Mahoenui weta, dorsal view.

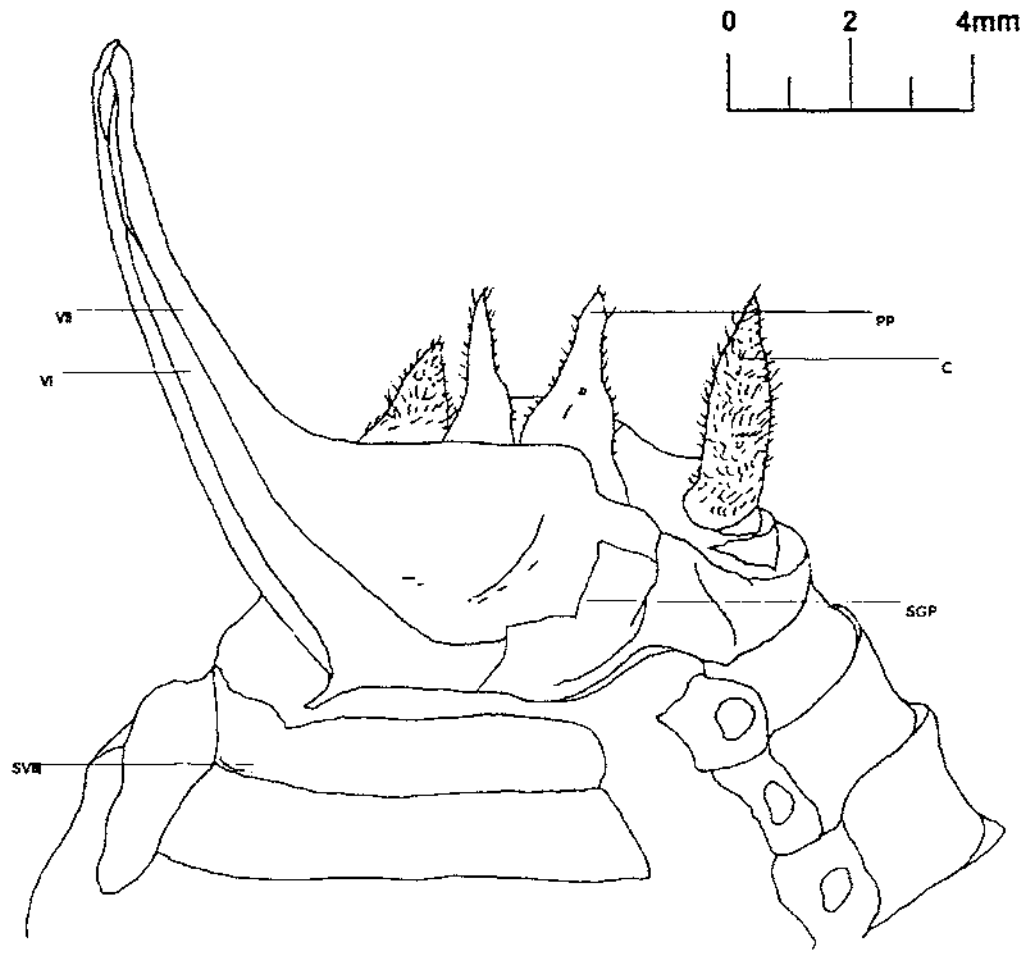


Figure 3.14: External genitalia of tenth instar female Mahoenui weta, ventral view.

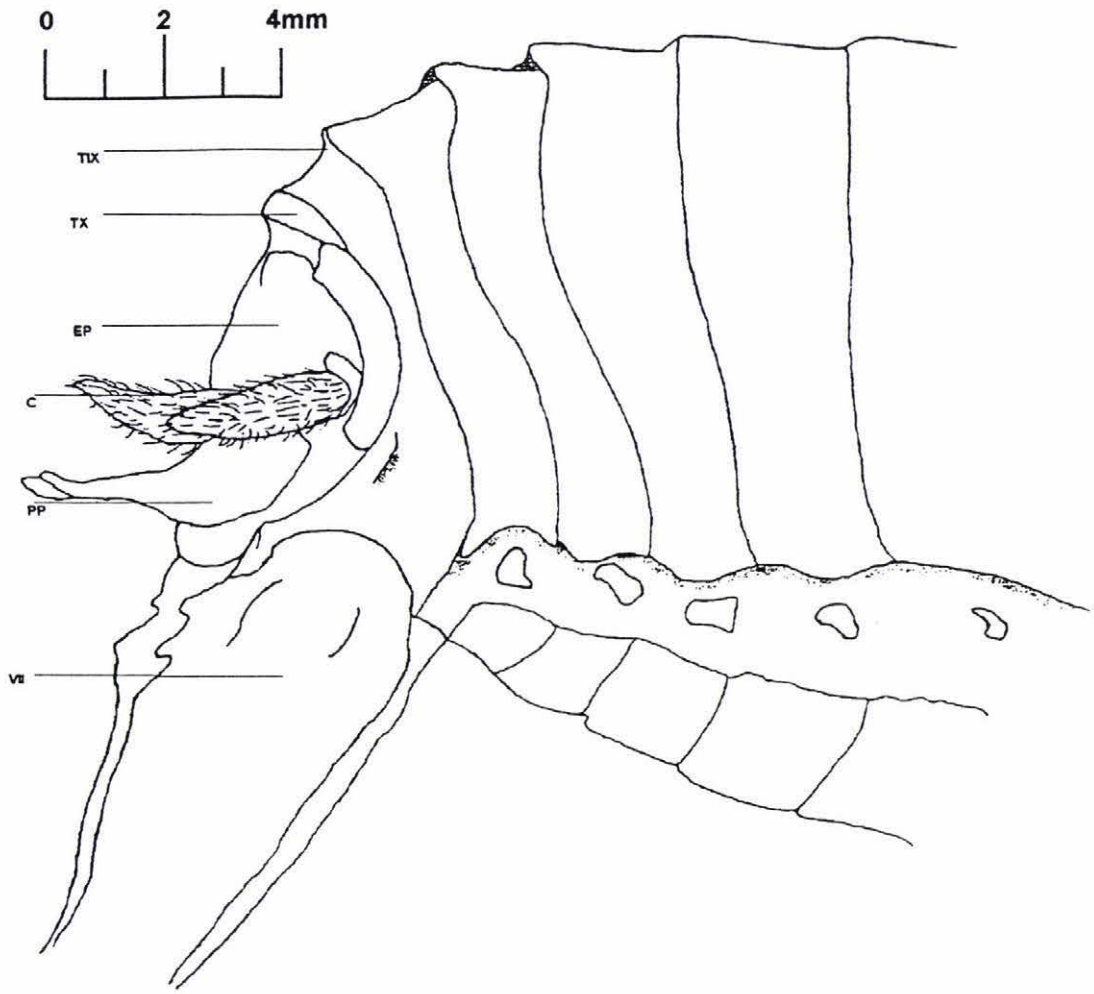


Figure 3.15: External genitalia of tenth instar female Mahoenui weta, lateral view.

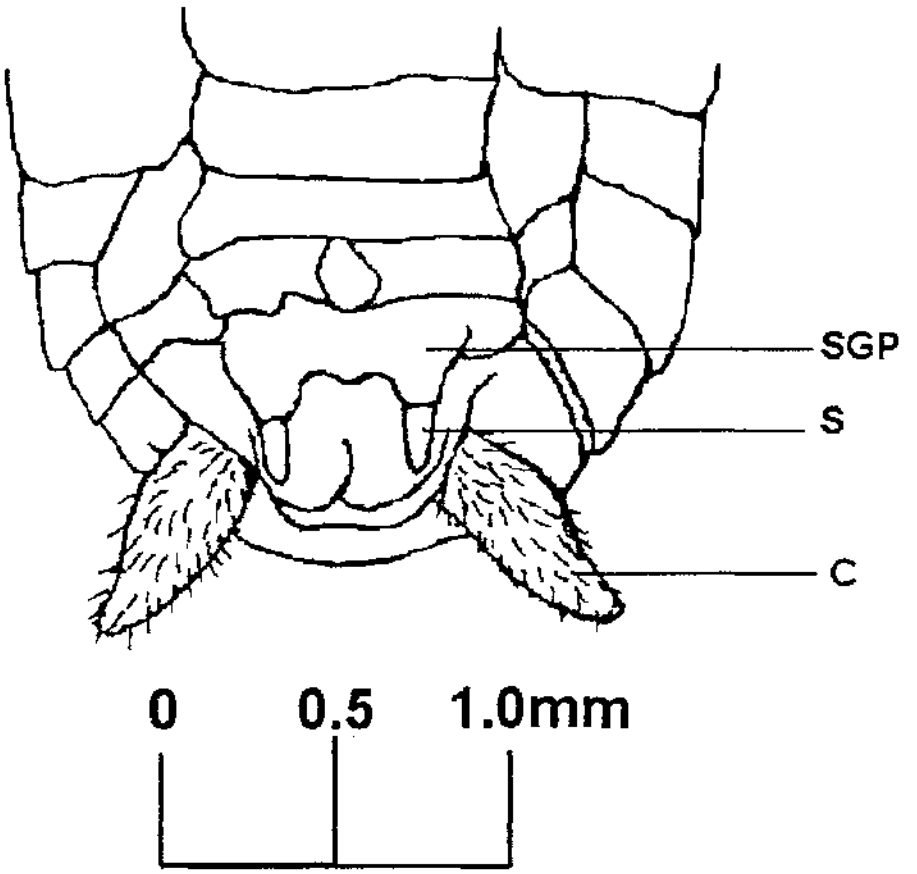


Figure 3.16: External genitalia of first instar Mahoenui weta, ventral view.

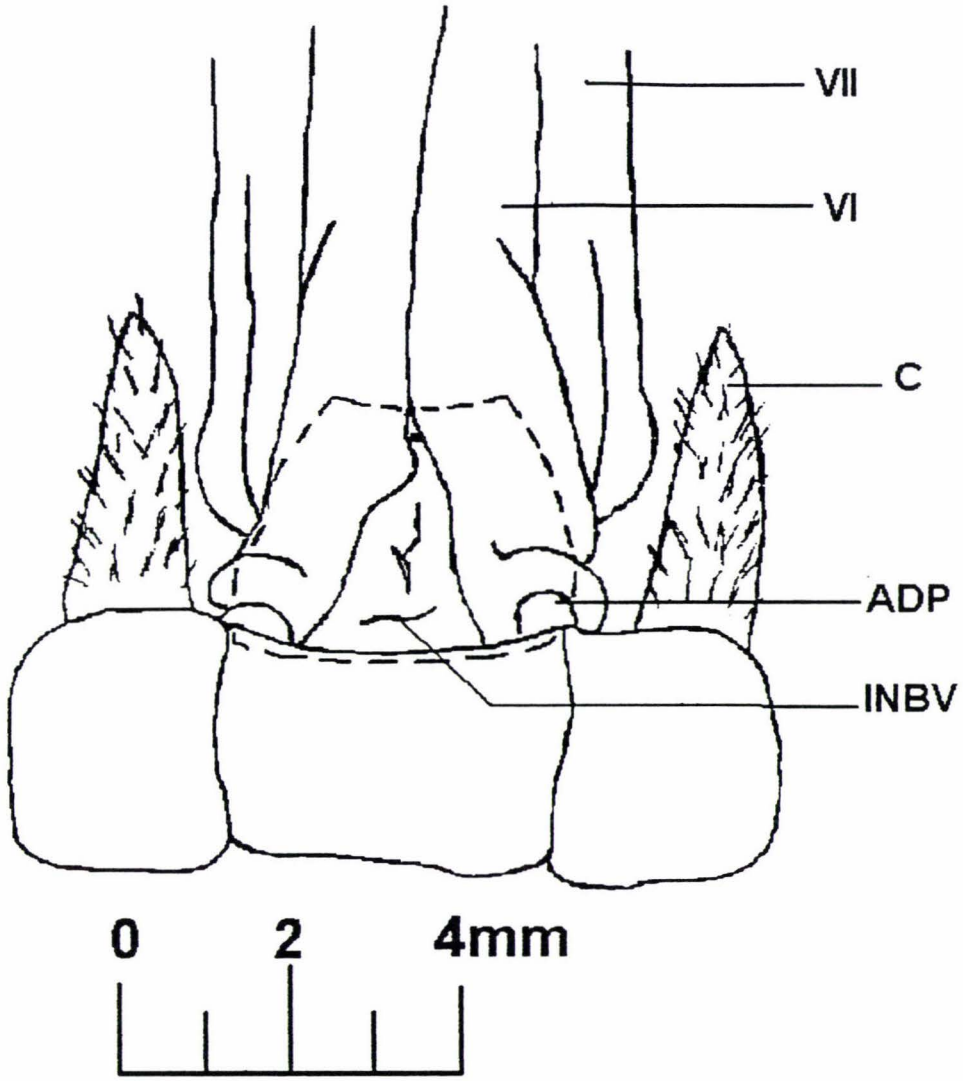


Figure 3.17: External genitalia of an adult female Mahoenui weta, ventral view, with subgenital plate removed to show structures beneath. (Dotted line indicates position of removed plate).

3.4 Discussion

The morphology and histology of the female Mahoenui weta conforms to the normal pattern exhibited by female Orthoptera (Snodgrass 1935, Matsuda 1976, Schwalm 1988). In the Mahoenui weta each ovary consists of approximately 36 ovarioles in the 9th instar weta but these appear to degenerate to approximately 19 in the mature adult. Although follicular degeneration was not investigated in this study, it is not known to occur in some Orthoptera (Phipps 1966, Singh 1958). It was difficult to

estimate ovariole numbers with confidence, as only two subadults and adults were measured. The ovarioles are "cluster shaped' and conform to Ander's (1939) second type of ovariole. Ander regarded the second type as more advanced and the first combed shape to be more primitive (Ander 1939).

The general morphology and histology of Mahoenui weta correspond closely with that of Acrididae (Akhatar and Ashrafi 1965). The major difference is that the ovarioles of Acrididae were not reported to be covered in an outer ovary sheath whereas such a sheath was reported in other Stenopelmatidae by Maskell (1927). Cell size and ovariole number also differ between Acrididae and Stenopelmatidae. Within the Stenopelmatidae ovariole number is dependent upon the size of the animal.

Morphology and histology of Mahoenui weta was almost identical to that of *H. thoracica* (Maskell 1927). The only difference noted was that the Mahoenui weta has both circular and longitudinal muscle around the spermatheca while in *H. thoracica* the muscle fibres run in all directions around the spermatheca (Maskell 1927).

The external genitalia, as in the male Mahoenui weta, differed little between species of weta (Richards 1961, Sandlant 1981, Cary 1981, Wahid 1978, Ramsay 1965). The only major difference is in the length of the ovipositor and this is related to the size of the species.

When the genitalia was examined at the first instar level there was no noticeable difference between the sexes due to the fact that both male and female first instar weta have styli that fall off the female later. This is consistent with Ramsay's (1965) findings that sexing of first instar *D. rugosa*, was not possible.

Chapter Four

Behaviour of the Mahoenui weta *Deinacrida* n.sp. (Orthoptera: Stenopelmatidae) in captivity.

Abstract

The behaviour of captive Mahoenui weta was observed, using infra-red time lapse video. Data were recorded from the months of December, January, February, March and July. Weta ate most often in January, March and July, and most mating activity occurred during January. Mahoenui weta were consistently most active at 60-80% of total night-time and showed less activity closer to sunrise or sunset. Mating and moulting are described in detail.

4.1 Introduction

Barrett (1991) published a book on the captive rearing of weta and also mentioned some aspects of Mahoenui weta behaviour. Field (1980) reported that the most common nightly activity of *Deinacrida connectens* (Ander) Ramsay was perching and wandering around the cage. The behaviour of endangered animals is important to researchers, as it enables informed decisions to be made on the best methods to ensure the survival of that species. Data on diet, habitat choice, activity, and mating system are invaluable to conservation plans for any species.

Richards (1994) found that the level of activity in Mahoenui weta increased in captivity as they were not exposed to some environmental conditions, such as frost and rain. The objectives of this chapter were to study the Mahoenui weta in an artificial environment and quantify levels of individual behaviours as well as behaviour activity periods, both seasonally and nightly. The data obtained were then linked with the results of Richards' (1994) study to enable comparisons between behaviour in the field and laboratory to be made.

4.2 Methods

Weta were captured when required from land surrounding the Mahoenui Reserve, near Te Kuiti, New Zealand. Mature weta were used for observing

reproductive behaviour and ovipositon. Weta were assigned to a perspex cage either as individual males, individual females, in male/female pairs, or in mixed sex groups of any number. The perspex cage measured 50cm high by 80cm square, and had a wood framed lid covered in wire mesh. Water was provided ad libitum, as was vegetation for the weta to eat and to shelter in. Soil was provided for oviposition. The cage was kept at ambient room temperature with natural day/night cycles. Weta were filmed using a Panasonic WV-BP 310 closed circuit TV camera with an infra-red sensitive low light lens. A microscope light covered with a Lee 57 infra-red filter was used for illumination. Behaviour was recorded on a Panasonic AG-6124 time lapse video recorder on lapse modes of 24hrs/1hr of tape, 72hrs/1hr of tape and 120hrs/1hr of tape. Observations were made from the video tapes at 5 minute intervals. Each night from average sunset to sunrise per month was divided into subsets of 100% to allow comparison of different night durations due to time of year. Behaviour was scored as either hiding, sitting, ovipositing, eating, moving, mating, interacting with other weta, or drinking.

4.3 Results

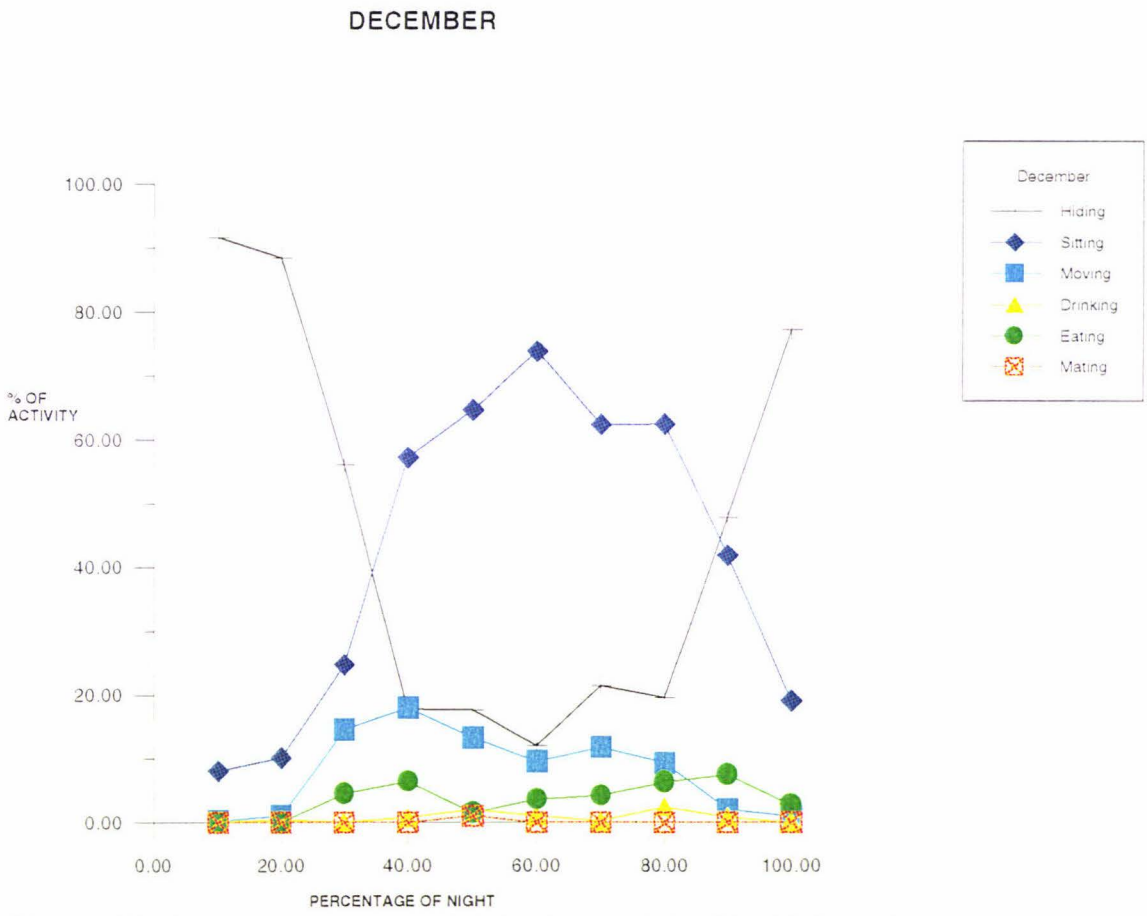


Figure 4.1: Average percentages of behaviour exhibited by Mahoenui weta over eighteen nights of observation during December. (Three adult females and two adult males).

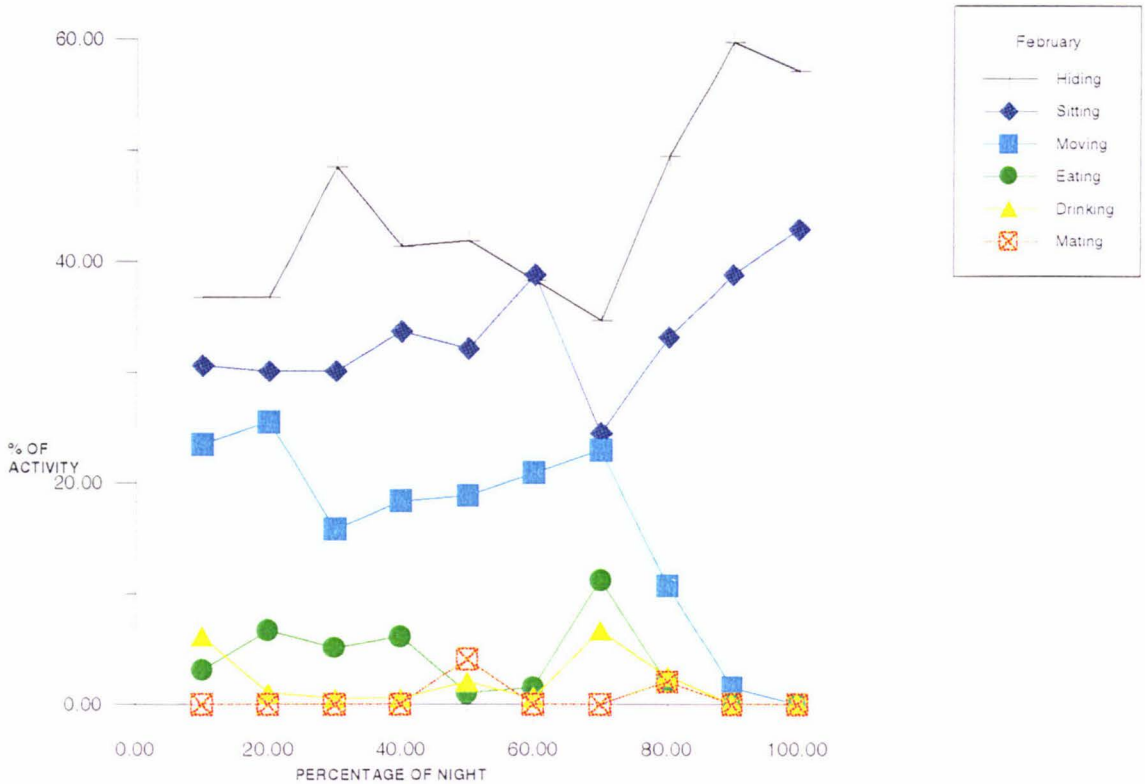


Figure 4.3: Average percentages of behaviour by Mahoenui weta over nine nights of observation during February. (One adult female and one adult male).

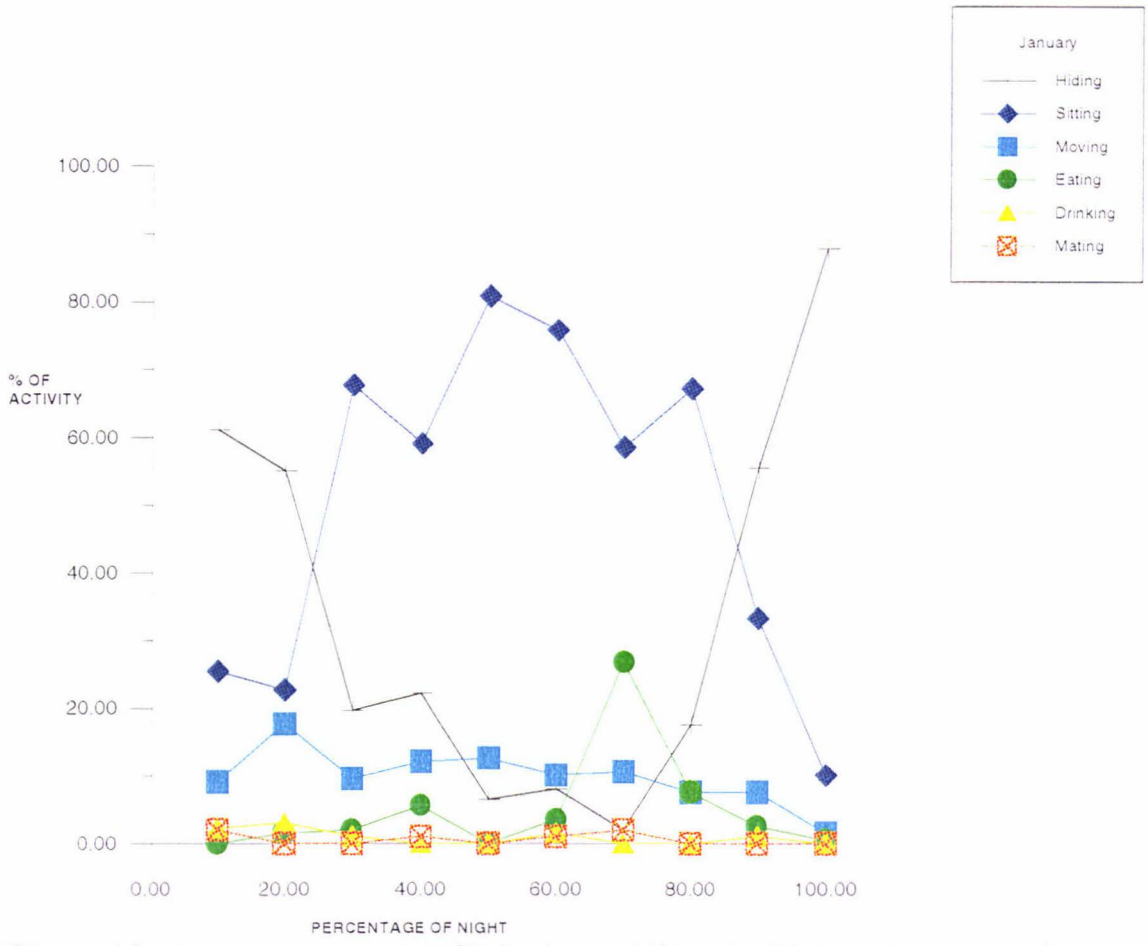


Figure 4.2: Average percentages of behaviour exhibited by Mahoenui weta over four nights of observation during January. (Three adult females and two adult males).

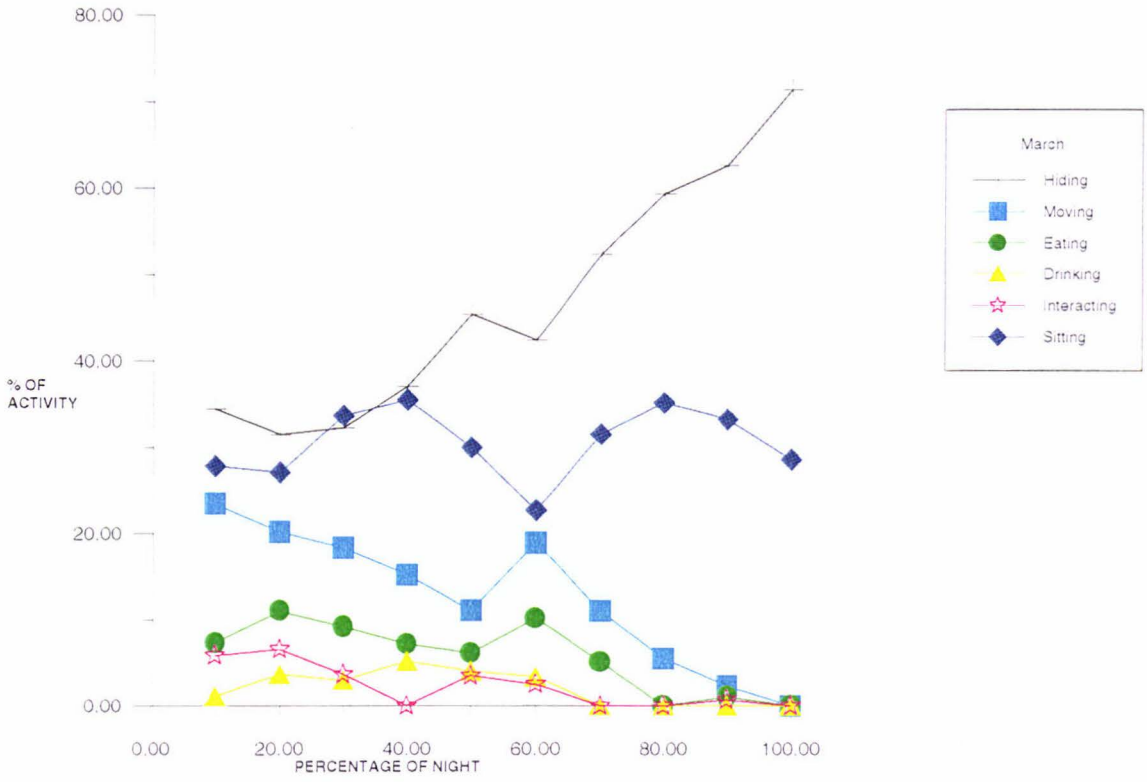


Figure 4.4: Average percentages of behaviour exhibited by Mahoenui weta over sixteen nights of observation during March. (One subadult female and two subadult males).

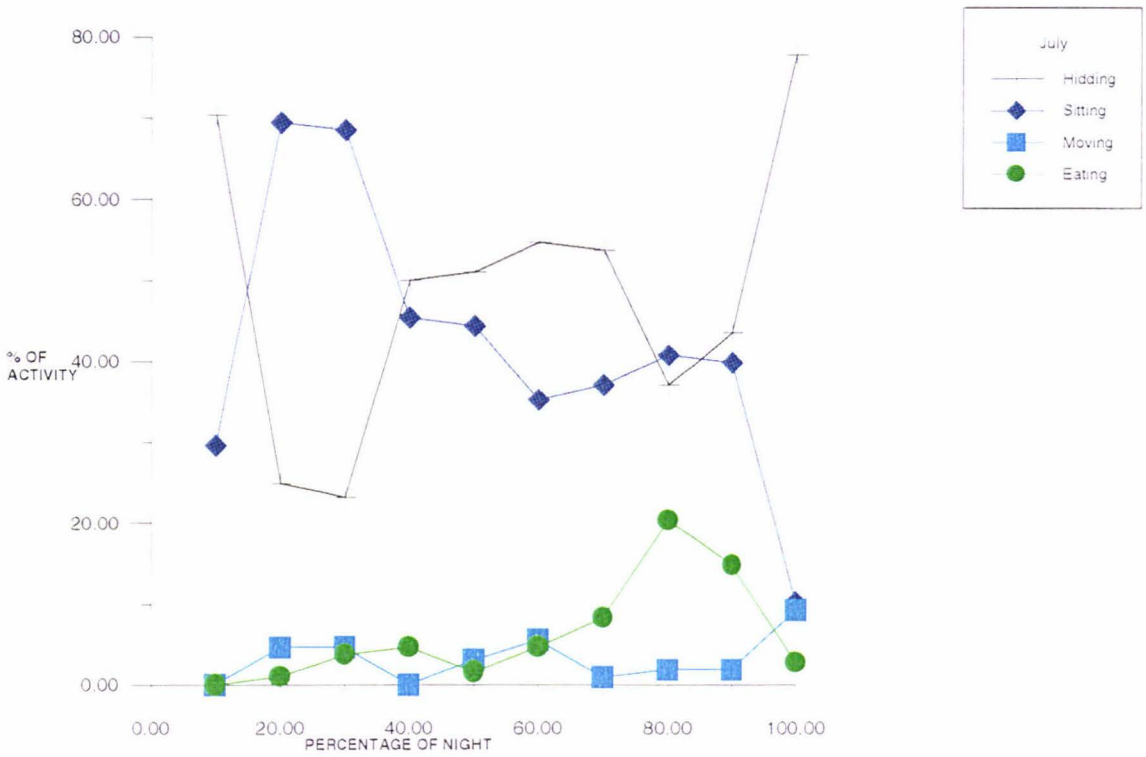


Figure 4.5: Average percentages of behaviour exhibited by Mahoenui weta over thirteen nights of observation during July. (One subadult female and one subadult male).

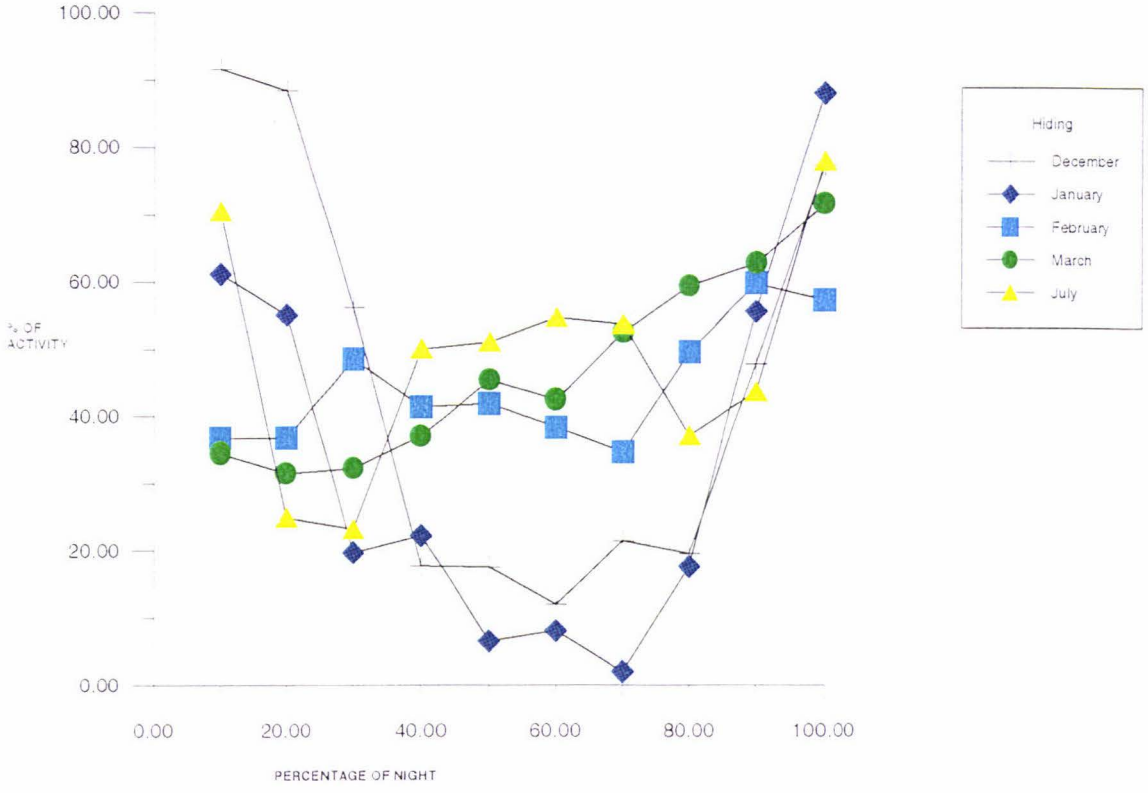


Figure 4.6: Percentage of hiding activity throughout night per month.

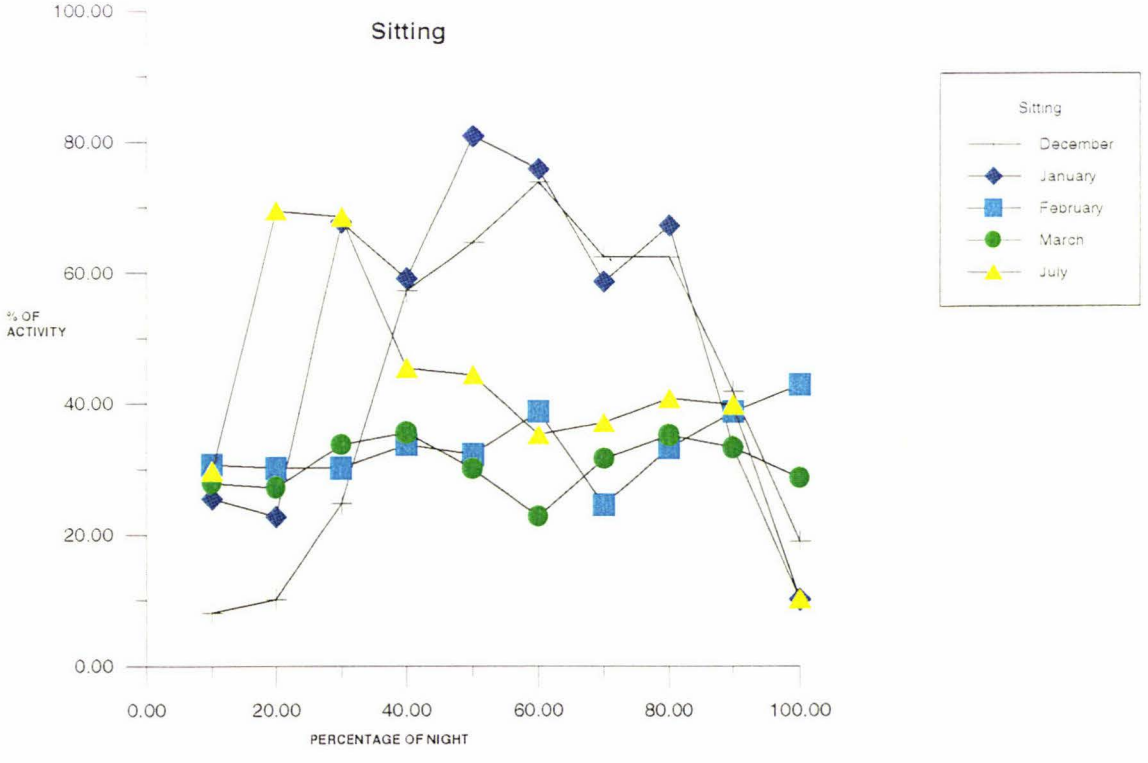


Figure 4.7: Percentage of sitting activity throughout night per month.

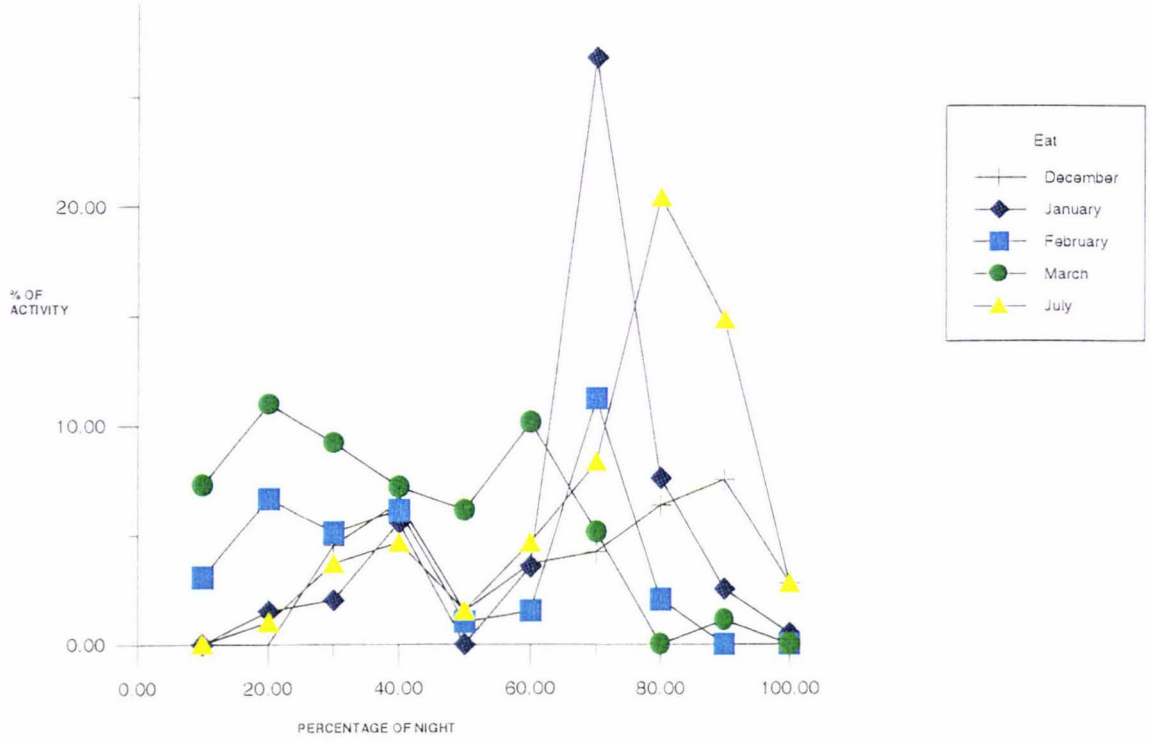


Figure 4.8: Percentage of eating activity throughout night per month.

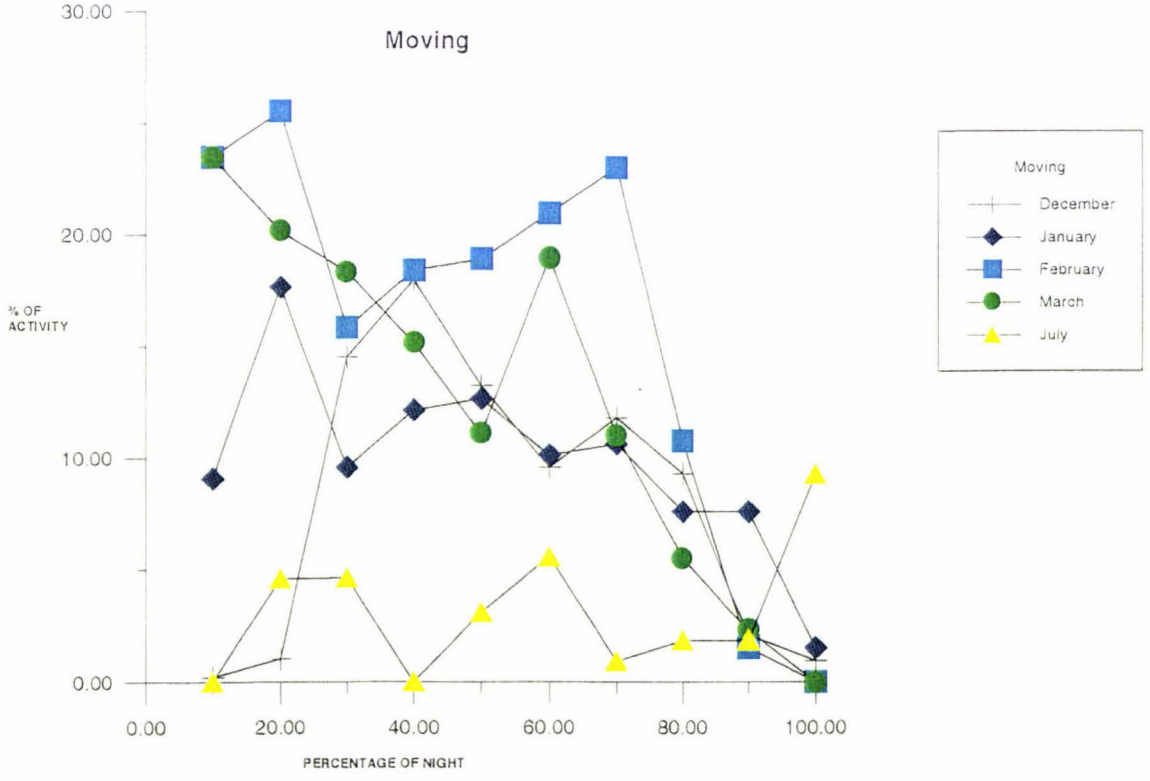


Figure 4.9: Percentage of moving activity throughout night per month.

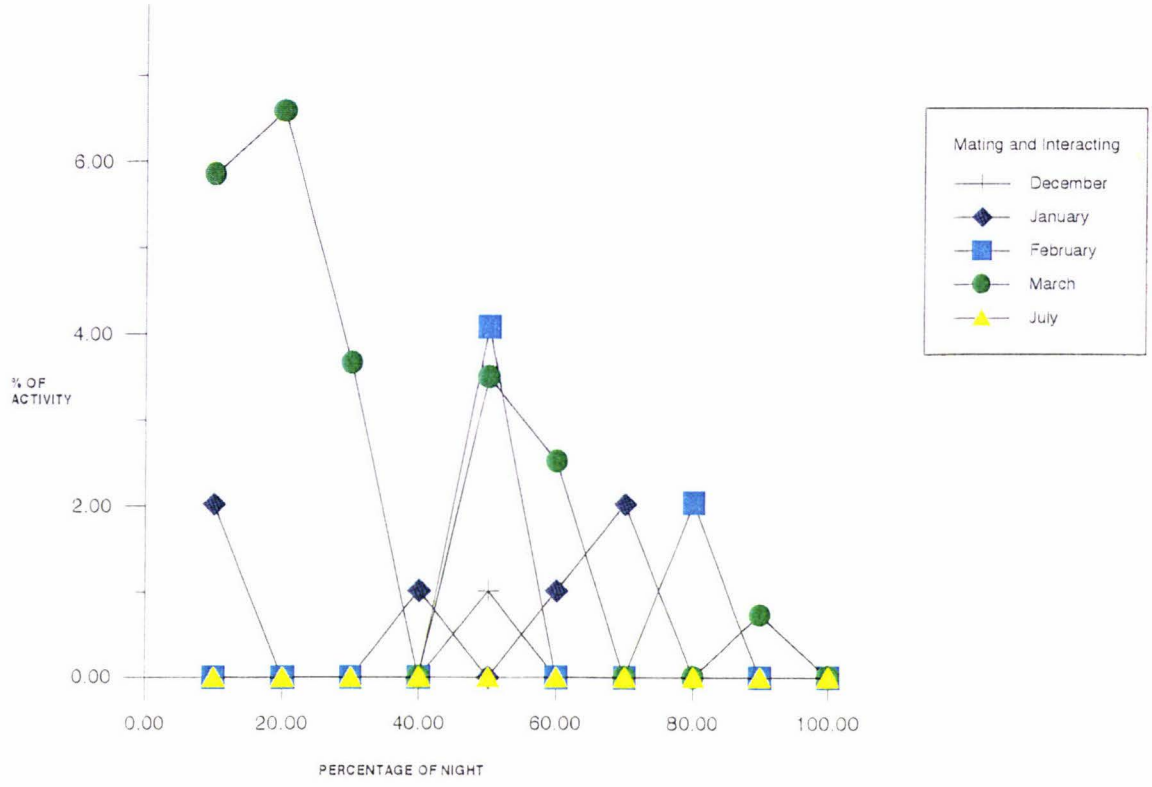


Figure 4.10: Percentage of attempted mating and interaction activity throughout night per month.

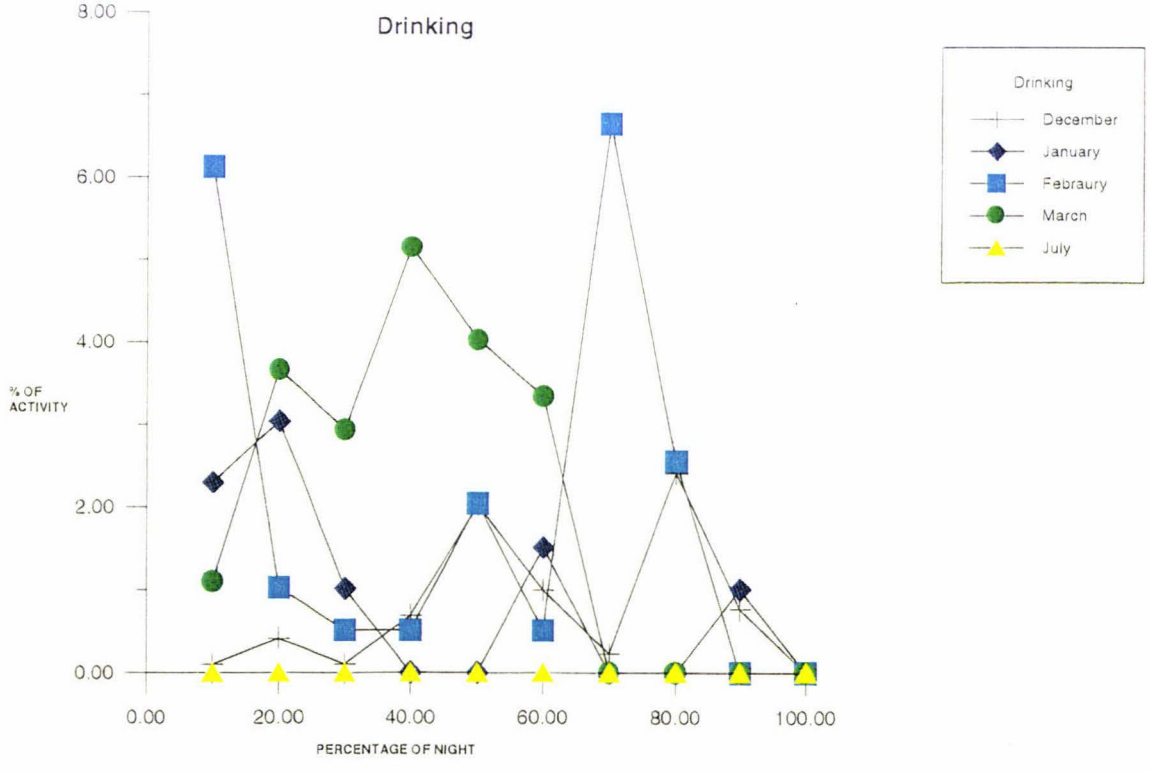


Figure 4.11: Percentage of drinking activity throughout night per month.

Seasonal activity of the Mahoenui weta varied over the five months that samples were taken (Figures 4.1, 4.2, 4.3, 4.4, 4.5). Behaviour appeared to be affected by seasonal temperature fluctuations, with greater total activity in the summer months (Figures 4.2, 4.3). Weta predominately hid under vegetation during the month of July when they were generally less active than in December, January and February. Each category of behaviour is examined below.

Hiding

Hiding behaviour was classified as when the weta was not visible (Figure 4.6). Hiding gradually increased during the night, reaching a peak during the last 10% of the night in February, March and July. Hiding behaviour in both December and January started off high at the start of the night and dropped to a low after 60% of night had elapsed. It then increased again at the end of the night. Hiding in December and January was inversely correlated with sitting behaviour in the same months (Figures C.12 and C.13 in appendix). Hiding behaviour occurred most frequently on a per night basis in

per night were; March (46.8%), December (44.9%), February (44.3%), and January (33.5%) (see table C.6 in appendix).

Sitting

In general sitting behaviour increased very slightly throughout the night except in the months of December and January where it reached a maximum in the middle of the night (Figure 4.7). This behaviour followed an inverse correlation with hiding in December and January. In December and January, sitting behaviour reached a maximum at around the 60% of the night. The time spent sitting per night was highest in January at 50%, followed by December (42.4%), July (42%), February (33.4%), and March (30.5%) (see table C.7 in appendix).

Eating

Eating was least frequently observed in December and February (Figure 4.8). Weta began feeding soon after nightfall, rising and falling throughout most of the night. However it decreased to zero shortly before dawn. Eating was lowest in December and February. In January and July eating reached the highest peaks at 75% and 80% of night respectively. The most time spent eating per night was in July, with 6.1%, followed by March (5.7%), January (4.9%), December (33.7%), and February (3.6%) (see table C.9 in appendix).

Moving

Movement was classified as when the weta was walking, rather than moving antennae or legs without ambulation. Movement was high after the first 25% of night had elapsed in all five months when it was monitored (Figure 4.9). In general it gradually decreased towards dawn. The exception occurred in July when movement increased in the last half of the night. February, March and July showed maximum activity at 65%, 60% and 60% periods of night respectively. Time spent moving per night was highest in February, at 15.8%, followed by March (12.5%), January (9.8%), December (8.0%), and July (3.1%) (see table C.8 in appendix).

Mating and Interactions

The category mating and interactions measured both the attempted copulations and physical contacts between individuals (Figure 4.10). No actual copulations were achieved during the night and attempts lasted for less than five minutes. A single mating attempt was recorded in both December and February, occurring halfway through the night. In January there were regular attempts at mating observed at time intervals of about 10% time of the night. In March and July only subadults were used and so all behaviour percentages for these months were interactions, rather than mating attempts. Time spent interacting and mating was highest in January and February (both 0.6%), and lowest in December (0.1%). The interaction only scores for March and July are 2.2% and 0.0% respectively (see table C.11 in appendix).

Drinking

No drinking was observed in July, but drinking occurred frequently in February and March (Figure 4.11). In February drinking reached a maximum at the beginning and at the end of night, while drinking in March peaked in the middle of the night. Drinking in January declined gradually throughout the night, while drinking in December occurred consistently throughout the night. The most drinking per night occurred in March, at 2.1%, followed by February (1.9%), January (0.88%), December (0.77%), and July (0.0%) (see table C.10 in appendix).

Video recording and observations on mating.

Several observations were made of weta mating, although film of mating is limited to one three hour video tape. Near the start of tape (2.19 p.m) the male approached a female from behind and lightly touched the back of the female with his palps. The female weta was still for approximately 15 seconds, then moved quickly away. The male followed the female until the female wedged herself into a crack between two feeding jars. The male then walked randomly around the bottom of the cage, waving his antennae for 20 seconds, then returned to the spot where he had first found the female.

The male then searched the bottom of the cage until he located another male sitting up against the corner of the cage. The searching male then approached the other male, lightly touching the second male's back with his palps. When the other male began to crawl up the wall of the cage, the searching male seized the other male's left hind leg in his mouthparts and held the other male weta. When the other weta kicked violently at the searching male he let go of the leg and the other male escaped up the wall of the cage.

The searching male then followed a fairly direct path into another corner of the cage, where a second female was sitting. Once again, the searching male lightly touched the female's back with his palps. The second female also moved away, and wedged herself in the same gap as the first female. The male immediately headed directly towards the two females. The searching male then reversed, and moved backwards into the gap containing the two female weta. The first female remained in the gap, but the second female moved a short distance away out of the gap, to sit in the open part of the cage.

The male was now orientated at 90 degrees to the female (Figure 4.12), with both genitalia in close proximity. At approximately five minute intervals over the next hour, the male would push his genitalia up against the female's. While both the female's and male's abdomens would 'pump' (the abdomen would expand and contract) over this period, no close connection of the genitals was seen. Eventually the female moved, or was pushed, so that her body was lying almost horizontal to the ground. Connection between the two genitalia was then established. Both the female and male's abdomens pumped during this stage.

The two weta disengaged 34 minutes later but otherwise remained in the same position. No spermatophore was observed to pass between the two weta. The male then repeatedly pushed his genitalia up against the female's, and connection was re-established five minutes later. Once again, both weta's abdomens pumped during this period. Both weta disengaged 11 minutes later. This pattern continued until the end of filming at 5:00 p.m, with disengagement and reattachment occurring every 20 minutes or so.

Figure 4.12: Mahoenui weta mating.

Video recording of moulting

An opportunistic recording of a moulting female weta was made when one of the captive weta had progressed to the stage where the last two or three segments were still covered by the exuviae. A home video camera was quickly obtained and filming commenced at 8:34 p.m. Eclosion had commenced an unknown time before filming.

At 8:34 p.m the weta was hanging upside down from a twig by the hind legs, with the exuviae covering two to three of the last abdominal segments. The hind legs were still covered, as were the antennae, and obviously the ovipositor. The rest of the body including the head was free of the exuviae. At 8:39 p.m the hind legs were pulled from the exuviae and were held close to the body with the other legs, away from any vegetation (Figure 4.13). By 9:07 p.m, abdominal pumping became pronounced, occurring slowly at about eight to 10 seconds per cycle.

9:10 p.m; the weta's head had begun to touch the floor of the cage as the weta dropped from the exuviae. The forelegs now rested on the floor. Every three to four minutes the weta would twist and turn violently as if to pull from the exuviae. The last quarter of the antennae were still within the exuviae, and the weta's head moved back and forth, alternately tightening and slackening the antennae. The resolution of the video image was not good enough to show clearly, but it may be that the weta seized hold of the antennae with her mouthparts while moving the head back and forth.

9:16 p.m; the weta freed the antennae and began to push against the exuviae with her hind legs. It may be at this point that the weta received the laterally bent hind

legs present when examined the next day, the camera angle being such that it is hard to judge lateral bends in the leg. At 9:32 p.m the weta began using her middle legs as well as the hind legs to push against the exuviae.

10:15 p.m; the weta pulled free of the exuviae and hung below it using all it's legs. Abdominal pumping continued and the weta remained still in this position until video tape ends at 11:59 p.m. The exuviae was only partially eaten.

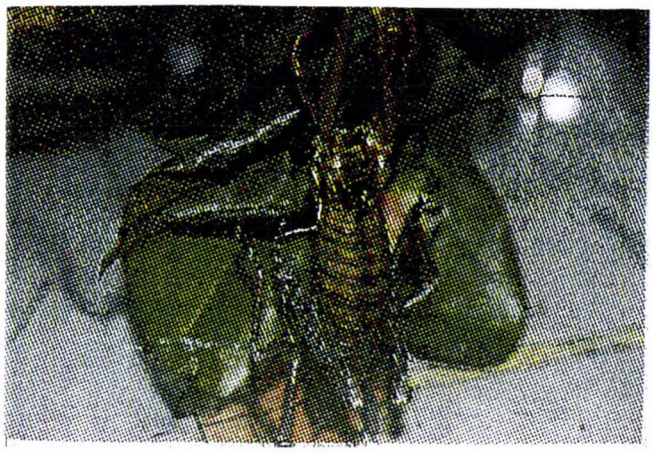


Figure 4.13 Mahoenui weta moulting.

Observations on defence behaviour

Weta defended themselves in a number of ways. Passive defence was possible through a number of spines on the tibia which protected the weta from predation and made extraction from gorse difficult. Active defence involved a threat posture with hind legs held forward above the abdomen (Figure 4.14), while the weta stridulated and made a ticking sound. Weta also bit when extremely provoked, but rarely broke human skin. Smaller instars also regurgitated when provoked.

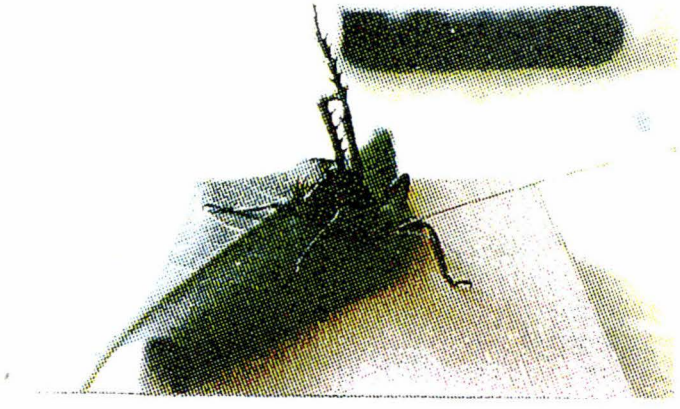


Figure 4.14 Mahoenui male weta showing defence posture.

4.4 Discussion

Seasonal differences in behaviour pattern of captive Mahoenui weta are obvious in the behaviours of hiding, drinking, eating, and sitting. For the behaviour category 'hiding', two months, (December and January) show a different pattern to the three other months. Hiding activity reached a maximum at the beginning and end of each night, while for the other three months, hiding increased gradually throughout the night, with no obvious maximum. Obviously hiding will be inversely correlated with the total of the other behaviours, and this difference between months in hiding behaviour appears to relate to changing patterns of all the other behaviours. Hiding was classified as when a weta was not visible in the video recording, so the results from the hiding behaviour are likely to be inaccurate, as the weta could be moving down the back of the cage behind the vegetation. Indeed, there was a strong correlation between hiding and sitting scores for December and January, suggesting that the peaks in activity for these months were due to weta sitting behind vegetation while in the other months, they tended to sit where the camera could record them. The average time spent per night hiding was between 44.9% - 48.6%, with the only exception being January (33.5%).

Drinking behaviour appears to relate quite well to seasonal variation in climate. There is a pattern present, with the weta drinking infrequently in December (0.77%), increasing through January and February, peaking in March (2.1%), and dropping away to nothing in July. February to March were very dry months that year, and the weta drank nothing in July, when the vegetation provided appeared to have a much higher moisture content.

Weta fed later in the night during January and July, with feeding occurring at a low, variable level throughout the entire night for the other months. Weta were making the most mating attempts during January, and the large peak in feeding present may be a result of higher energy requirements for the processes of mating and copulation. Weta tended to spend more time eating in March and July, as ambient temperature dropped. My data (Figure 4.8) indicate a feeding maximum just before dawn. This is consistent with Richards' (1994) finding that her captive weta returned to feed 1-1.5 hours before

dawn. Richards' weta showed two activity peaks during the night that were not present in my data.

Weta sat for consistent times throughout the night for February and March, with the data for July reaching a maximum early in the night and falling into line with that for February and March at 60% of night time. The major differences between sitting behaviours occur between December and January, and the other months. Sitting for December and January peaked at 60% of night and fell away the closer to nightfall or dawn. As explained earlier when considering hiding, this could be an artefact of weta sitting in different areas of the cage that could not be recorded by the video camera. It would appear that weta in captivity spend approximately the same amount of time sitting per night throughout all the months studied. Average time spent sitting per night varied between 42% and 50% for December, January and July, with February and March at 33.4% and 30.5% respectively. The weta were more active in February and March than in the other months, and this accounts for the low sitting scores for these months.

Mating attempts were low during December and February, reaching a very high level during January, and the only successful copulations were observed during the day. The most interaction per night occurred in March, when all weta present were sub-adult instars (see table C.11 in appendix).

Movement followed the same pattern for every month, except July. These findings contrasts with those of Richards (1994), who found that the Mahoenui weta showed levels of movement that remained constant between summer and winter. For the other four months, movement peaked early in the night and fell towards dawn. Movement in July remained at low, varying levels throughout the entire night. The average time spent moving per night was certainly lowest for July, and no real conclusions can be made as to why movement is following a different nightly pattern, as well as a much lower nightly average. It could be that the weta were spending more time in one spot feeding, as the average time spent feeding for July was higher than all other months. In July, a cold month, the weta were moving less and eating more.

General activity levels rose for the summer months. This is consistent with Richards' (1994) findings on the Mahoenui weta and Moller's (1985) findings on *Hemideina crassidens* (Walker). Moller found that activity increased with both

humidity and temperature. Townsend's (1995) findings on *H. ricta* (Walker) also support this as her weta were found less often during the month of August and were more active during December and January. *H.ricta* could be observed at any time throughout the hours of darkness and were found to emerge on average 2h 24min after official sunset (Townsend 1995).

Both Townsend (1995) and Richards (1994) found captive weta were more active than those in the field. In both cases weta were more easily observed in captivity and hence more events were probably recorded in the laboratory. Moulting descriptions in Richards' (1994) study of the Mahoenui weta were consistent with observations in my study. However the moulting observed in the present study took longer than Richards' described. This may have been due to the constant activity around the weta, and white light needed for filming with a home video camera.

The mating behaviour of the Mahoenui weta in captivity shows that there is a certain element of chance in the opportunity of any individual weta to reproduce. The male searches for the female almost randomly, even when the female is near. In the reserve this may be an even greater chance of not mating, due to the larger distances to be travelled to find mates. The fact that the female always moved away from a courting male implies some form of mate choice on the part of the female. In all observed matings though, the male never ceased to chase the female. I have no evidence that the female moving away from the male may sometimes result in the male giving up pursuit. Therefore, it cannot be concluded whether there is any mate choice depending on the abilities or tenacity of the male. In Richards' (1973) study of *D. heteracantha* White the female will wander off if the pair are disturbed but the male quickly searches for her and they will remate. The male is the dominant partner in this relationship. The major difference with Richards' (1973) *D. heteracantha* and *D. fallai* (White) Salmon was that the female mounted the male on most occasions, which was not observed in the Mahoenui weta.

There was little aggression observed between the weta, except in situations where a male approached another male and lightly touched it's back with his palps. Usually this resulted in the male that was being approached kicking the approaching male. Usually this was thought to be a result of the approaching male mistaking the other for a female, but there is some evidence from the recordings that may favour

another explanation. In the video of mating, when one male approaches another and uses his palps on the other male's back, he also grabs hold of the target male's rear leg with his mouthparts. This hold was quite tenacious, as the weta kicked several times with his free leg before the other male would let go. Aggression in this manner may be directed towards a potential competitor, with one male attempting to drive off the other while there are females present. Alexander (1967) found that male field crickets, while attempting to mate with other males, would sometimes bite the recipient's cerci, hind legs, or tegmina.

The palpitation of the other male's back may be more a way of simply identifying the sex rather than the opening round of courtship. This is unlikely, however, as non mating weta have never been seen to use these actions when in close proximity to other weta. There is unfortunately not enough data here to support either a mistaken identity explanation, nor a potential competitor explanation.

Palpation is common in potentially mating weta. Richards (1994) found that Mahoenui weta males palpated the female prior to mating. Field (1993) found that *H. ricta* Hutton palpated the potential partner before copulation was initiated, while Moller (1985) also observed male *H. crassidens* palpating female's abdomens and following them around. Richards (1973) found that no other premating behaviour other than palpitation was observed and no stridulatory signals were heard in either *D. heteracantha* or *D. fallai*. Alexander (1967) found that Field Crickets initiated copulation by palpitation and antennal contact and suggested it was because of chemo-receptors present on palpi and other portions of the mouthparts. Unlike Mahoenui weta however, the female Field Cricket responds to the male calling, rather than the male actively searching out females. Richards (1973) noted that sex recognition was entirely by contact. Townsend (1995) thought that there may be a sexual attractant pheromone used by female *H. ricta*.

It took at least an hour for the weta to connect their genitalia once they were in position, and they only connected when the female's abdomen was lying almost horizontally on the ground. This could be a result of that particular position, as Mahoenui weta have also been seen to mate 'end to end' (Richards 1994), and one of the participants in the video may have been unprepared for which position was being used. No spermatophore was observed to be passed between the two weta. This could

be because of the camera resolution or angle, and there was a lot of abdomen pumping by both participants. It could have been an unsuccessful mating attempt, but as filming was finished before final disengagement spermatophores may have been passed later. The mating of the Mahoenui weta appears to be identical to the matings observed in *D. fallai* (White) Salmon and *D. heteracantha* (Richards 1973). However in contrast to Fields' (1980) observation that the *D. connectens* male appears to play a passive role in courtship, the male Mahoenui weta actively chases the female, especially in the presence of another males and has been observed to attempt to copulate with more than one female. These mating attempts on multiple females indicate that the Mahoenui weta may be polygynous, at least in the restricted conditions of captivity. Females in captivity tend to cluster together in groups of up to five, and this is a possible explanation for the male attempting to mate with multiple females. Barrett (1991) also thought that the weta was polygynous, in comparison to Richards' (1994) theory that they are monogamous. Mate guarding was not apparent in captivity, except to the extent that the male would remain with the female in copulatory position attempting copulation for up to 14 hours. This amount of time is consistent with Richards' (1973) findings on *D. fallai* and *D. heteracantha* whose matings periods lasted from 9-16 hours.

The moulting behaviour of the Mahoenui weta follows very closely that of other *Deinacrida* and the Orthoptera in general. It closely follows Moller's (1985) description of *H. crassicruris* (Walker). It has been suggested that bent legs, fairly common in Mahoenui weta, are obtained when the freshly moulted weta has little room when resting soon after moulting. In the moulting video it can be seen that the weta pushes against the exuviae with it's hind legs as it attempts to pull the final two segments of abdomen from the exuviae, and this may well be the reason why that weta had laterally bent hind legs when examined later.

Mahoenui weta defence behaviour is typical of that of other *Deinacrida*, as described by Field (1980) for *D.connectens*. Defence behaviour seems to be almost identical in the majority of Stenopelmatidae but varies within the Orthoptera in general (Robinson 1970).

Most weta have the primary defence of being nocturnal (Ordish 1992). The only exception to this was Messenger's (1991) observation that *H. monstrosus* (Walker)

appeared to be active during the daylight. *H. monstrosus* also showed another unusual defence response of raising its tusks and rasping them together (Bellingham 1991). The defence display described for *D. fallai* and *D. heteracantha* by Richards (1973) also showed no difference from that of the Mahoenui weta. The majority of weta show the defence display as exhibited by *Hemideina* (Field 1993) and *Deinacrida* species differ only in that they are also capable of making an abdominal 'tick' sound as well as stridulating (Richards 1994).

Chapter Five

Egg Histology and Hatching Time.

Abstract

Incubation time of weta eggs was recorded using eggs laid in a previous study (Richards 1994). The time of hatching and the behaviour of newly hatched nymphs was recorded on several days using video equipment. All eclosion occurred at night, with the time of eclosion ranging from 8 pm to 3.30 am over a period of three nights. Weta were free of the egg and walked within 17 minutes of the egg appearing on the soil surface. All hatched weta died within three days of eclosion. The external appearance and histology of eggs is described. Mahoenui weta eggs have many features in common with other Orthoptera.

5.1 Introduction

Richards (1994) reported that incubation time of Mahoenui weta eggs was inversely related to mean temperature. She also found evidence that they underwent diapause over winter. Richards (1973) suggested that winter diapause also occurred in *Deinacrida heteracantha* White eggs. There has been no histological study of Mahoenui weta eggs, although the histology of other Orthopteran eggs is well known (Uvarov 1966). Here I describe the structure and histology of Mahoenui weta eggs. In addition, low light video recordings were taken of the eggs during eclosion. This provided an estimate of timing of Mahoenui weta eclosion and of their behaviour after eclosion.

5.2 Methods

Weta eggs of known oviposition dates were obtained in soil from Grace Richards. These eggs had been oviposited during December 1992, and had not hatched during the course of her study. They were retained to see whether they remained viable for periods in excess of two years incubation. The eggs were left undisturbed in the original soil where they had been oviposited. The soil was kept outside in a plastic tub 8 cm in diameter and 10 cm deep, exposed to the weather, until eclosion began. When eclosion commenced, the soil was taken into the laboratory and watered once every two

days. A low light television camera was used to document the time of night when weta began eclosion, and the behaviour of the nymphs directly after hatching. New born weta were supplied with cabbage leaf and gorse for food. Eggs were also sectioned for histology (See methods Chapter 2).

5.3 Results

Eggs for sectioning were taken from deceased females, rather than from eggs that had been laid. The eggs of the Mahoenui weta average 6.45 mm long (Table D.3 appendix) and are deep brown to black in colour. Fox (1991) reported that the average length of eggs removed from adult females Mahoenui weta was 5 mm. This suggests that the egg increases 1 mm in length before the nymph hatches. The unlaid Mahoenui weta egg has all the layers present in other Orthopteran eggs (Uvarov 1966). These comprise the yolk, which is acidophilic, the vitelline membrane which is also acidophilic, and the chorion, hypoderm and extrachorion which are all basophilic (figure 5.1).

Eggs hatched during the months of December 1994, and January and February 1995 after spending between 24 and 26 months in the soil (Richards pers. comm. 1994). The eggs used in this study showed a 100% hatch rate, with 104 eggs hatched and no unhatched eggs were left in the soil. The egg rose to the surface by being flexed by the nymph inside, before eclosion occurred.

Eclosion was observed on six individuals. This occurred between 8 pm and 3.30 am over a three night period (Table D.1 in appendix). As a typical example, an egg surfaced at 3.21 am, and after 13 minutes the weta was out of the egg. Nine minutes later the cuticle had hardened enough for the weta to walk away and hide. Time from egg surfacing to finish of eclosion ranged from 13 to 17 minutes. All new born weta died within three days of hatching, with several of the nymphs appearing to have drowned in small droplets of condensation. Identifying the sex of the new born weta was attempted by examining their genitalia (figure 5.2), but no difference in genitalia shape or form between sexes were observed.

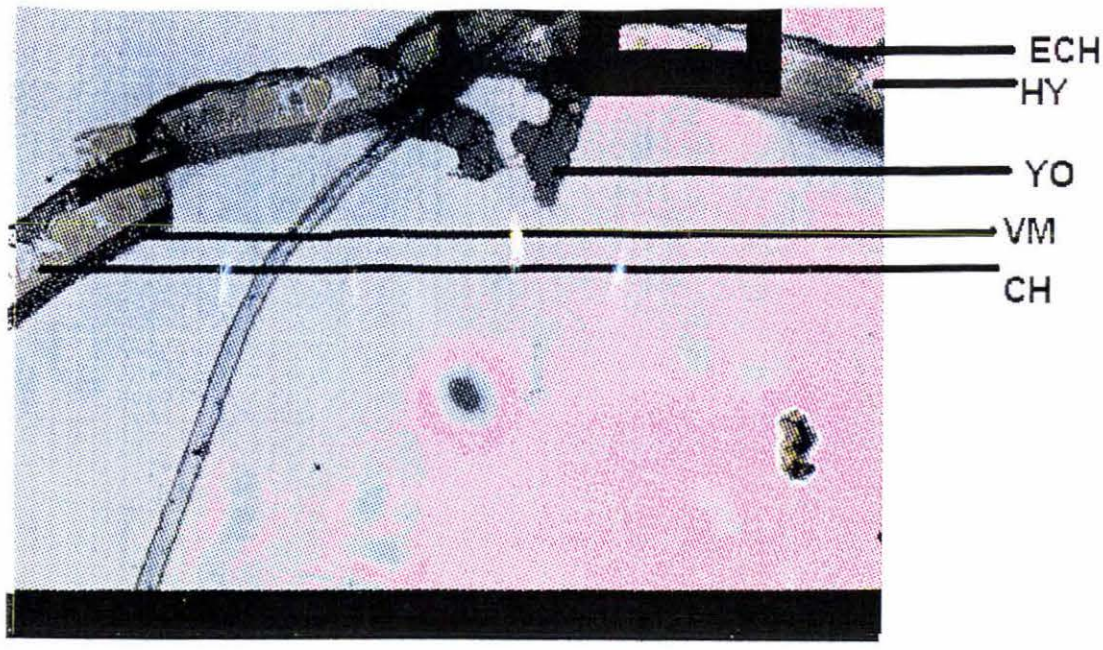


Figure 5.1 :Section through an unlaid egg of the Mahoenui weta.

ECH- Extrachorion

HY- Hypoderm

YO- Yolk

VM- Vitelline membrane

CH- Chorion

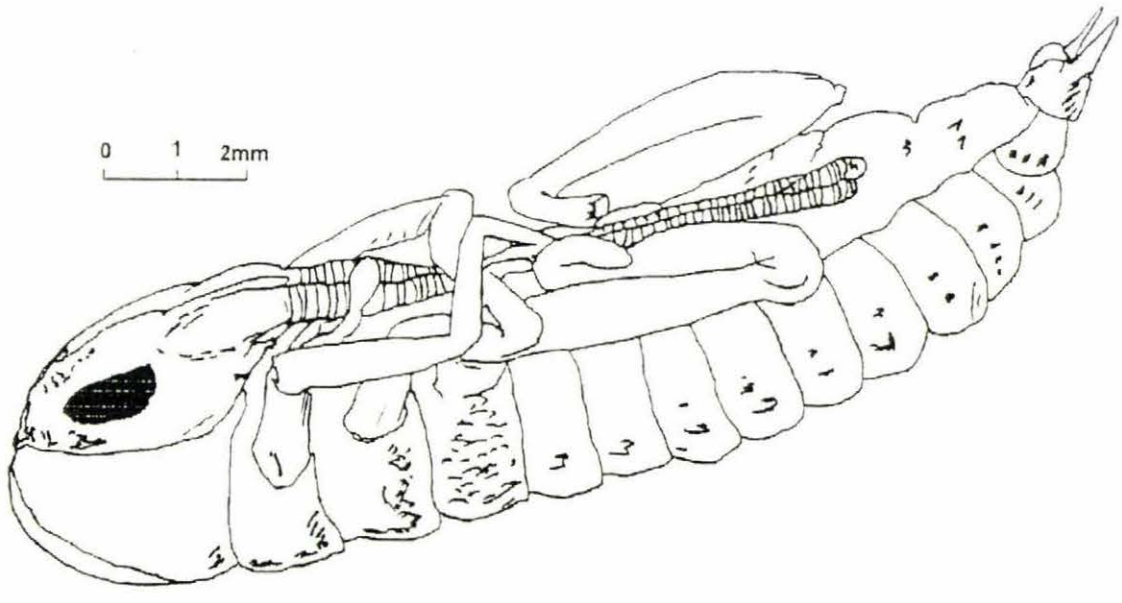


Figure 5.2: Newly hatched Mahoenui weta.

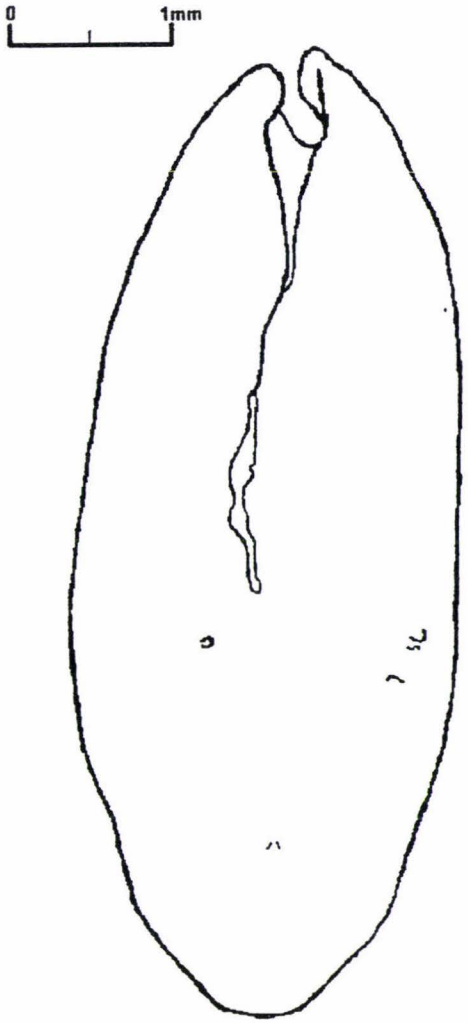


Figure 5.3: Egg shell of newly hatched Mahoenui weta.

5.4 DISCUSSION

Externally the egg of the Mahoenui weta (figure 5.3) is similar to that of *D. heteracantha* (Richards 1973), and the interior layers are similar to those of most Orthoptera (Uvarov 1966). Hatching occurred most commonly around 2:00 a.m, and no weta hatched during daylight hours. Emergence time may be related to temperature, and the associated risk of dehydration to incompletely hardened nymphal cuticle.

The newly hatched weta had spent 24 to 26 months in the soil, longer than any other Mahoenui weta eggs that have been known to survive. This incubation time is also far longer than the 141 days of incubation for *D. heteracantha* eggs observed by Richards (1973). In her study, Richards (1994) observed eggs that hatched out after ten months in the soil. These had a hatching rate of 58 out of the 300 eggs laid, a 19% hatch rate. The eggs used in the present study showed a 100% hatch rate. In the present study the eggs may have been subject to a winter quiescence and this has been observed in other Orthopteroid insects. Bennett (1981) noticed unseasonal hatching of both New Zealand stick insects and mantids. Wahid (1978) found that eggs in *Hemiandrus* sp. have a winter quiescence and the presence of contact water was essential for the egg development.

Once an egg reached the surface of the soil, 13 to 17 minutes elapsed before the weta hatched. Richards' (1994) eggs differed in that the eggs usually remained on the soil surface from a few days to a few weeks before hatching occurred. This could make eggs susceptible to predation and fungal attack (Wahid 1978).

All weta eclosed in this study moved very lethargically, and died two to three days after hatching. Reasons for their death could be related to lack of correct food for small weta (cabbage and gorse was supplied), or high levels of humidity in the weta containers (several weta appeared to have drowned in droplets of condensation). The most likely explanation is that the weta had spent such a long time in the eggs that their nutrient reserves had run out and so at eclosion they had little ability to survive.

Chapter Six

Comparative Feeding Preferences Of The Mahoenui Weta *Deinacrida* n.sp.

Abstract

Mahoenui weta were exposed to 12 different plant species commonly fed to them in captivity, and present in the Mahoenui weta reserve. The weight of plant material eaten was recorded to determine which species of plant the weta preferred. Mahoenui weta showed the greatest preference for kowhai followed by gorse, broom, buttercup, tawa, karaka, coprosma, camellia, lemonwood, mahoe, houhere and hoheria. There was a marked preference for legume plant species over non-legumes.

6.1 Introduction

Mahoenui weta are polyphagus and omnivorous; they eat a wide variety of different plants as well as small dead insects, and even raw sheep liver (Barrett, 1991; Richards, 1994). Barrett (1991) advised that gorse, taupata, karamu, *Hebe*, mahoe, *Buddleia*, ngaio, willow, plantain, *Euonymus*, dandelion, karaka, gum, ngaio and *Coprosma* along with fresh liver or mince should be regularly supplied to captive Mahoenui weta to maintain them. He also suggested that 1st instar weta should be kept separately in captivity as they are cannibalistic. In the Mahoenui reserve the usual diet of these weta is apparently gorse *Ulex europaeus* L., although other species are eaten, such as dandelion, plantain and various grasses (Sherley and Hayes, 1993; Richards, 1994). It is not known, however, whether gorse is their preferred diet or whether native species such as kowhai, which might once have been located in the reserve, are preferred.

Here I test whether Mahoenui weta show any preference for the plants commonly fed to them in captivity (Barrett 1991), and compare these preferences with that for gorse.

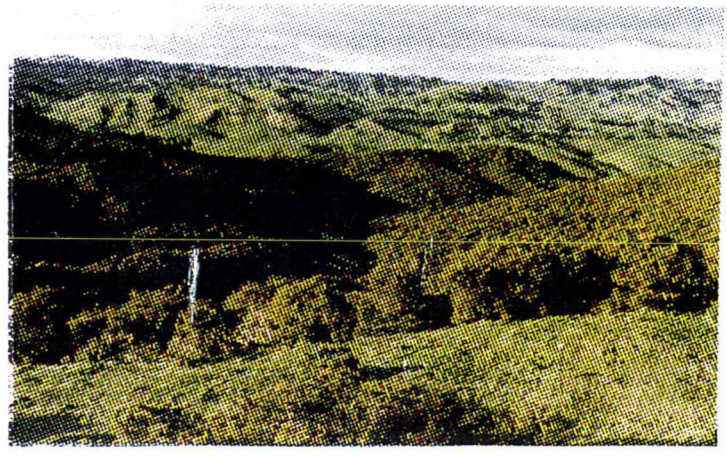


Figure 6.1: Mahoenui Study site, showing extensive Gorse *U. europaeus* cover, including pasture and some native species in the gullies (Mahoe, Cabbage Tree and Tawa.)

6.2 Method

Six weta were housed separately in Perspex tanks, 35cm by 30cm by 35cm high, covered with metal mesh screens. Instars 6-10 were used. Instar was determined by measuring pronotum length or body weight as described by Sherley and Hayes (1993). The weta were kept in a constant temperature room at 18±1°C, with a photoperiod of 16:8 (L:D) h. Water was provided ad libitum through absorbent cord protruding out of the lids of small water filled vials. All weta were provided with the same single plant species for a period of 12h, then the weight of plant consumed was estimated as follows. A record of leaf area was taken before each sample was exposed to weta, by photocopying the plants intended for each tank. These leaves were then inserted through the lids of vials containing water, and each vial was then placed in a tank with a different weta. After removal, each set of leaves was superimposed on the matching photocopy made before the trial, for that leaf set. The difference in leaf shape between the leaf set and photocopy was traced out and removed from the photocopy. The sections of paper were then weighed and multiplied by a ratio to convert paper area to leaf weight. The ratio of plant weight to paper area was calculated for each plant species by comparing the weight of 10 (1cm by 1cm) squares of each leaf type and 10 (1cm by 1cm) squares of photocopy paper.

Gorse, kowhai, buttercup and tawa were treated differently as the leaves did not lie flat for photocopying. Instead leafy twigs of these plants were placed in six separate vials with water. Each vial with its set of leafy twigs was weighed individually and put in the constant temperature room with an individually housed weta. Each vial was individually re-weighed at the end of the 24h period, to give weight loss due to consumption and transpiration. Due to the high transpiration rates of these plants, six separate vialed plant samples similar to those exposed to weta were weighed and put in the constant temperature room without weta. Average weight loss due to evaporation and transpiration over the six control vials was subtracted from each weta-exposed vial weight.

Weta were deprived of food for 12h between successive trials. Plant species used in these trials were kowhai *Sophora tetraptera* J.Mill, gorse *Ulex europaeus*, broom *Cytisus scoparius* (L.) Link, buttercup *Ranunculus aborrtivus* L., tawa *Beilschmiedia tawa* (A. Cunn) Benth. et Hook., karaka *Corynocarpus laevigatus* J.R. et G. Forst, coprosma *Coprosma robusta* Raoul, camellia *Camellia japonica* L., lemonwood *Pittosporum eugenioide*, A.Cunn, mahoe *Melicytus ramiflorus* J.R et G. Forst, houhere *Hoheria sextylosa* Col. and hoheria *Hoheria angustifolia* Raoul.

Feeding trial design was conducted using four female and two male weta, a sample size that sits on the minimum requirement for a Kruskall-Wallis test. One male (No. 7) ate very little vegetation during the tests, and died shortly after. A second set of experiments using the same method was made using six weta, some of whom had come from the first experiments, and some new weta, again four females and two males. Resulting data showing weight of plant type eaten for each weta were analysed statistically using Kruskall Wallis in the Minitab statistical program.

6.3 Results

Legumes, especially gorse and kowhai were readily consumed by the captive weta (figs 6.2 & 6.3). These weta showed the following preference, highest to lowest, for the 12 plant types used in the study; *S. microphylla> U. europaeus> C. scoparius> R. abortivus> B. tawa> C. laevigatus> C. robusta> C. japonica> P. eugenioides> M. ramiflorus> H. sextylosa > H. angustifolia* (Table 6.1).

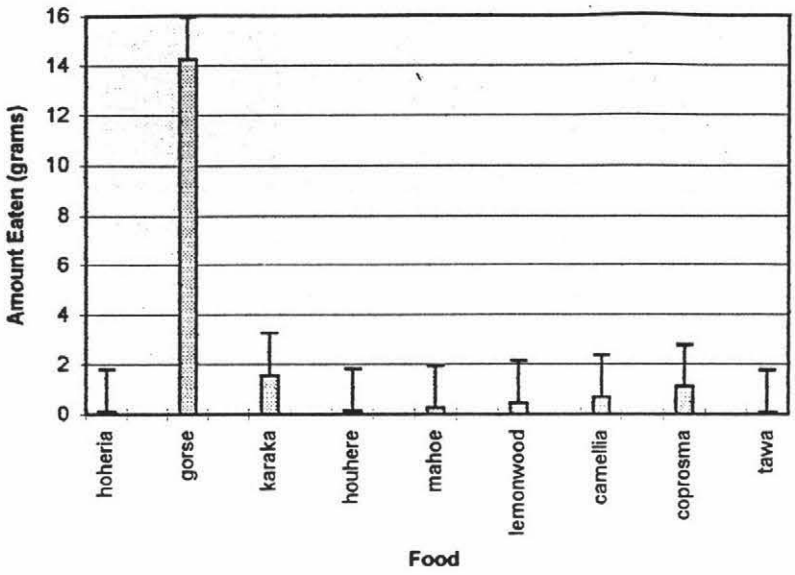


Figure 6.2: Mean ± SE of weight of each plant species eaten by Mahoenui weta in trial one.

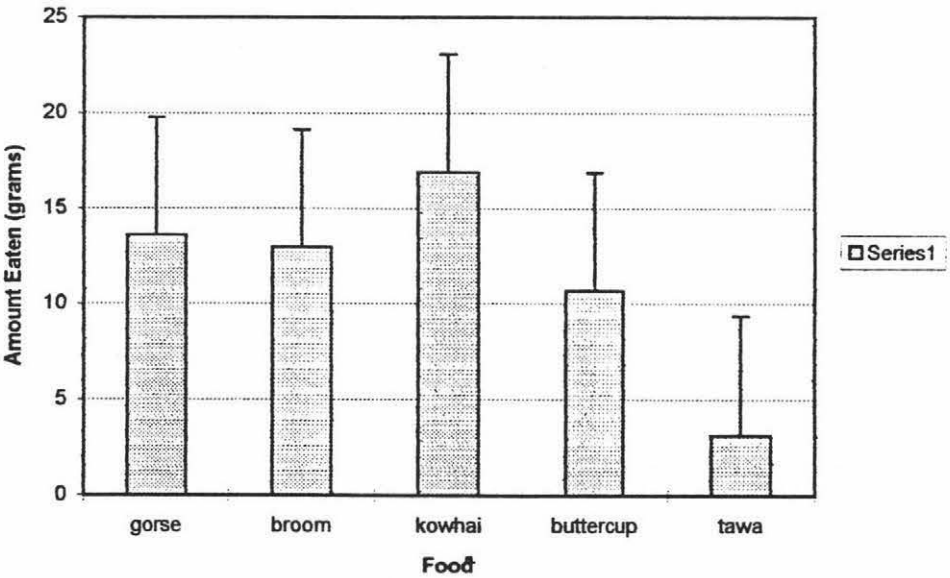


Figure 6.3: Mean ± SE of weight of each plant species eaten by Mahoenui weta in trial two.

Table 6.1: Weight of each plant species eaten by Mahoenui weta averaged over both trial one and two.

Amount of Plant Food Eaten. (averaged over both trials) (g)	Plant	Trial 1 or 2
16.90	Kowhai	2
13.92	Gorse	1,2
12.97	Broom	2
10.68	Buttercup	2
1.63	Tawa	1,2
1.55	Karaka	1
1.11	Coprosma	1
0.69	Camellia	1
0.45	Lemonwood	1
0.26	Mahoe	1
0.14	Houhere	1
0.11	Hoheria	1

Trial One H=27.9 d.f.=8 p=0.001

Trial Two H=18.05 d.f.=4 p=.001

The null hypothesis that there was no difference between the amount of food types consumed was rejected and the alternative hypothesis that there was a difference in the food types eaten was accepted at the 99% confidence level.

The weta clearly preferred kowhai and gorse over any other plant species tested, and they also showed a preference for legume species over non-legumes. Plant species that were significantly high in preference were gorse in the first trial and kowhai in the second. Species that were significantly low in preference were hoheria and houhere in the first trial and tawa in the second.

6.4 Discussion

The preference shown by the weta for legumes may be related to the nitrogen content of the leaves, and the protein provided by the flowers of these legumes (Sherley and Hayes 1993). Richards (1994) found that weta preferred pods and flowers of gorse over the leaves when these were provided in captivity. My results indicate that the possible pre-European diet of the Mahoenui weta could have included kowhai as a common food. Research conducted by Richards (1994) failed to find any conclusive data from food preference trials and concluded that the weta showed no plant species preference.

Legumes grown for foraging and grazing domesticated animals are recognised for their value as both shelter and a ready protein and nitrogen source (Speedy and Pugliese 1992) and many major insect pests feed on legume crops for their high food value (Singh et al 1978). Although plant nutrient data were unavailable in this study, statistical tests conducted in the food preference trials show an overwhelming preference for plant species within the legume family, both native and exotic. This suggests that Mahoenui weta consume gorse due to the protein and nitrogen availability contained within. Kowhai contains cytosine, (Crowe 1990), which does not appear to deter weta from eating the plant which contains high levels of this substance. Buttercup contains ranunculin throughout the plant (Crowe 1991), and weta did not appear to be

deterred by this. Secondary plant compounds did deter *Locusta migratoria* Reiche and *Schistocera gregaria* (Forskall) from eating plants (Cottee et al 1988), suggesting that *Deinacrida* n.sp Mahoenui weta may have a wider alkaloid tolerance than other Orthoptera.

Further research through more extensive plant choice and higher number of weta is needed to accurately assess what the weta's original diet was before European colonisation and the introduction of gorse.

Several factors may have affected the reliability of my data, notably the small sample size (six weta). This was unavoidable due to the low number of weta taken due to the endangered nature of Mahoenui weta and the low density of the study site population (Sherley and Hayes 1993). Another factor affecting reliability of data is that weta stop eating several days before and after moulting. No weta moulted during the trials but it is hard to predict when a weta will moult, and some may have moulted between trials. This may have affected the appetite of some weta.

During the food preference study, when flowers of gorse or kowhai were provided, the amount of pollen visible in the faecal pellets appeared to increase. This suggests that the weta were concentrating their feeding on parts of the flower that contain pollen. This warrants further investigation.

The question has to be asked whether weta living in the Mahoenui reserve gain some advantage from eating gorse over other plant species, or whether they have been living in the reserve for so long that they have adapted to a new diet. As there were no tests made on the nutritional content of the plants involved it cannot be concluded that eating gorse provides a nutritional advantage for weta over other plant species. My results show however, that weta ate far more gorse and kowhai than any other plant species. When available, weta concentrated on the gorse flower, consistent with Richards (1994). There may be some advantage from eating gorse beyond it's advantage as a shelter plant. As both gorse and kowhai are legumes I believe that Mahoenui weta prefer these species because of the high levels of nitrogen commonly found in legumes. This could have a large bearing on management strategies for the weta as knowledge of legume preference and stability of diet over time may allow conservation managers to introduce preferred species into the weta reserves. For the Mahoenui reserve this could involve planting kowhai amongst the gorse, allowing the

weta to continue to use the gorse for protection from predators, but supplementing their current diet.

Chapter Seven

Summary

Chapter 2;

The male reproductive structures of Mahoenui weta are similar to those of other Orthoptera, but differ in that the accessory glands are relatively larger than in other species. The accessory glands are partially fused to compensate for a relative lack of available space in the abdomen. The accessory glands best fit with Onesto's first major category of accessory gland in that they lie ventrally and are very large [(in Matsuda 1976)]. The seminal vesicle is completely fused. The general morphology and histology of Mahoenui weta reproductive structures are very close to that of Acrididae, although individual organ shapes differ and all cells were larger in Mahoenui weta. The penis of Mahoenui weta does not protrude from the body cavity as is usual for *Hemiandrus* n.sp., but instead lies under the sub genital plate, as in *Hemideina thoracica.*

Chapter 3;

The morphology and histology of the reproductive system of female Mahoenui weta conforms to the general pattern exhibited by female Orthoptera. Ninth instar ovaries consisted of approximately 36 ovarioles, but these degenerate to approximately 19 in the mature adult. General morphology and histology also corresponded closely with that of Acrididae. The major difference between Mahoenui weta and Acrididae was that Mahoenui weta ovarioles are covered in an outer sheath, while those of Acrididae are not. Cell size and ovariole number also differed between Acrididae and Mahoenui weta.

External genitalia was very similar to all other species of weta, although ovipositor size differs in relation to size of species. There was no discernible difference in sex within first instar weta, both sexes having styli, which are later lost in the female.

Chapter 4;

Seasonal differences in behaviour of Mahoenui weta are evident in hiding, drinking, eating and sitting. Weta were generally more active in summer, when hiding and sitting were less frequent. Drinking occurred most often in the dry months of

February and March. Weta spent more time feeding in the colder months of March and July than in the other months examined. Mating attempts occurred most often in January. Previous researchers found that captive weta are more active in captivity than in the field, although this could be a result of weta being seen more often in the confined conditions of captivity.

Mating in Mahoenui weta appears to have an element of chance. The male spends large amounts of time searching for females, even in very confined conditions. Palpitation of the female's back always preceded attempted copulations, but palpitation did not always result in a copulation. The female was often observed to move away from the male when the male palpated her abdomen. Moving away from the male as a form of mate choice is discussed. Once attachment between the female's and male's genitalia was successful, the pair would often spend up to 14 hours subsequently disengaging and reattaching approximately every five minutes. No spermatophore was observed to be passed from the male to the female.

Antagonistic behaviour and stridulation is rare in captive Mahoenui weta. Antagonistic behaviour was observed only once, when a male attempted to copulate with another male and this resulted in the second male kicking the first with his hind legs and then moving away. Moulting behaviour matches very closely that of other *Deinacrida* species.

Chapter 5;

Externally, the egg of the Mahoenui weta is similar to that of *D. heteracantha*, and the interior layers of the egg are similar as those in other Orthoptera. Mahoenui weta eggs were obtained form a previous study and eclosed after incubating for an average of 24 months. This exceeds the 10 months incubation time previously reported. Eclosion occurred most often around 2:00 am. All weta that hatched died after several days, suggesting that the long incubation time subsequently reduced nymphal survival. Egg hatching success was 100% for 185 nymphs, contrasting with a previous study where the success rate was 19%.

Chapter 6;

Mahoenui weta showed a strong preference for legume plant species and readily ate Kowhai and Gorse. This could be related to the high nitrogen content of these plants. Mahoenui weta also appeared to be attracted to the flowers of gorse, possibly because of the high protein levels in the pollen. Mahoenui weta are resistant to plant secondary compounds, such as cytosine in Kowhai and ranunculin in Buttercup, that deter other Orthoptera from feeding on them. It is suggested that conservation plans for Mahoenui weta should include ensuring the availability of legumous plants for feeding.

APPENDIX

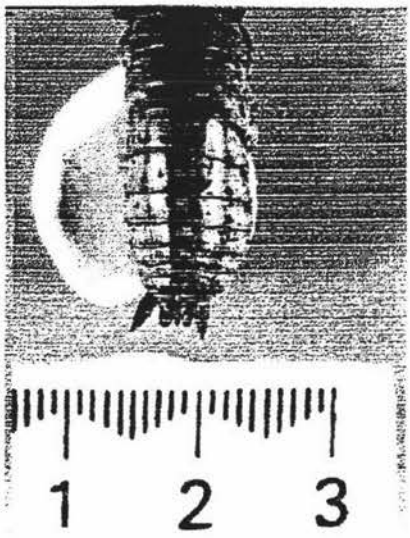


Figure A.1: Eighth instar male Mahoenui weta, dorsal view.

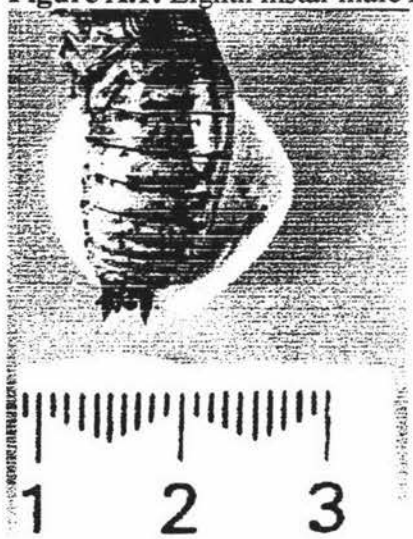


Figure A.2: Eighth instar male Mahoenui weta, lateral view.

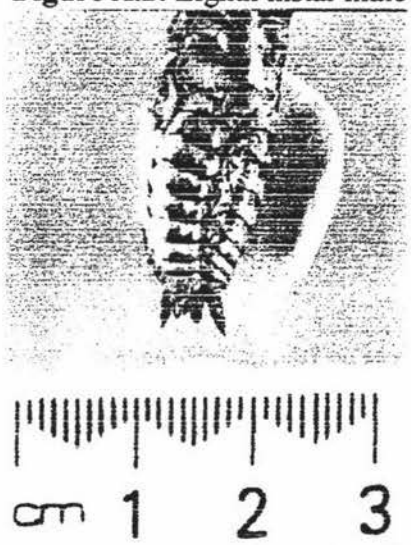


Figure A.3: Eighth instar male Mahoenui weta, ventral view.

Figure A.4: Ninth instar male Mahoenui weta, dorsal view.

Figure A.5: Ninth instar male Mahoenui weta, lateral view.

Figure A.6: Ninth instar male Mahoenui weta, ventral view.

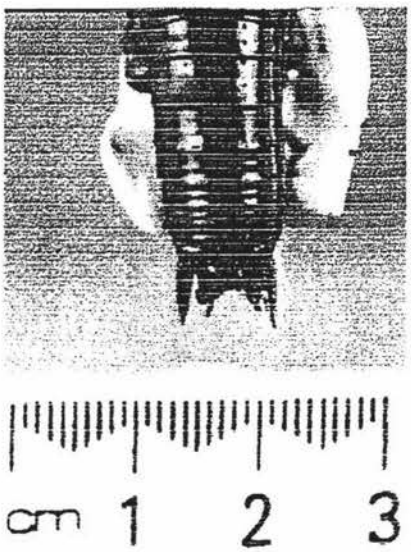


Figure A.7: Tenth instar male Mahoenui weta, dorsal view.

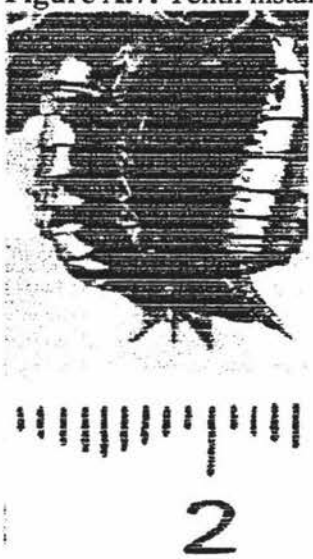


Figure A.8: Tenth instar male Mahoenui weta, lateral view.

Figure A.9: Tenth instar male Mahoenui weta, ventral view.

Figure B.1: Eight instar female Mahoenui weta, Dorsal View.

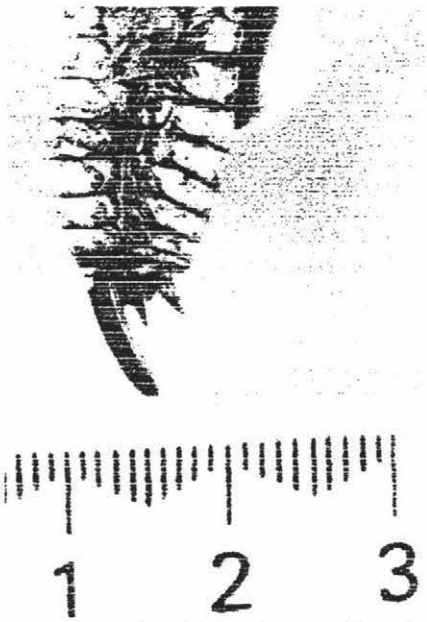


Figure B.2: Eighth instar female Mahoenui weta, lateral view.

Figure B.3: Eighth instar female Mahoenui weta, ventral view.

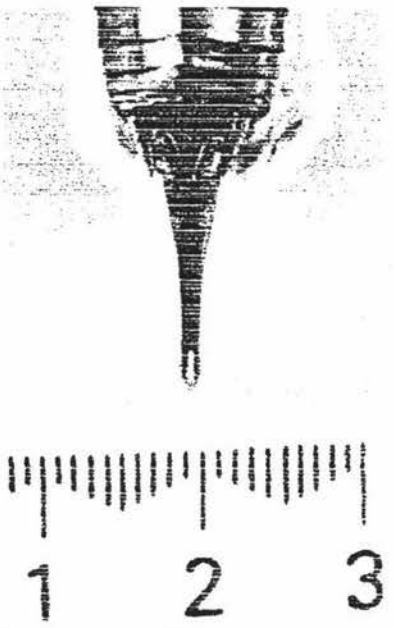


Figure B.4: Ninth instar female Mahoenui weta, dorsal view.

Figure B.5: Ninth instar female mahoenui weta, lateral view.

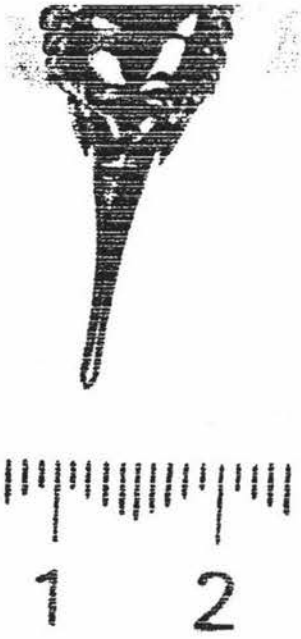


Figure B.6: Ninth instar female Mahoenui weta, ventral view.

Figure B.7: Tenth instar female Mahoenui weta, dorsal view.

Figure B.8: Tenth instar female Mahoenui weta, lateral view.

Table C.1: Percentage of behaviour throughout percentage of night for December.

% of night	hide	sit	move	drink	eat	mate	Total
10	91.59	8.1	0.21	0.1	0	0	100
20	88.41	10.15	1.03	0.41	0	0	100
30	56.13	24.72	14.52	0.1	4.53	0	100
40	17.73	57.16	17.95	0.69	6.47	0	100
50	17.6	64.6	13.24	2.02	1.53	1.01	100
60	12	73.78	9.56	1	3.66	0	100
70	21.44	62.33	11.78	0.23	4.22	0	100
80	19.56	62.4	9.29	2.41	6.34	0	100
90	47.76	41.85	2.08	0.77	7.54	0	100
100	77.22	19.04	0.96	0	2.78	0	100

Table C.2: Percentage of behaviour throughout percentage of night for January.

% of night	hide	sit	move	eat	drink	mate	Total
10	61.11	25.48	9.09	0	2.3	2.02	100
20	55.05	22.73	17.66	1.52	3.04	0	100
30	19.7	67.7	9.57	2.02	1.01	0	100
40	22.22	59.09	12.12	5.56	0	1.01	100
50	6.57	80.8	12.63	0	0	0	100
60	8.08	75.76	10.1	3.54	1.51	1.01	100
70	2.02	58.6	10.61	26.75	0	2.02	100
80	17.64	67.2	7.58	7.58	0	0	100
90	55.56	33.33	7.58	2.52	1.01	0	100
100	87.88	10.1	1.52	0.5	0	0	100

Table C.3: Percentage of behaviour throughout percentage of night for February.

% of night	hide	sit	move	eat	drink	mate	Total
10	36.73	30.61	23.47	3.07	6.12	0	100
20	36.73	30.1	25.51	6.64	1.02	0	100
30	48.47	30.1	15.82	5.1	0.51	0	100
40	41.33	33.67	18.37	6.12	0.51	0	100
50	41.84	32.14	18.88	1.02	2.04	4.08	100
60	38.27	38.78	20.92	1.52	0.51	0	100
70	34.69	24.49	22.96	11.22	6.64	0	100
80	49.49	33.16	10.72	2.04	2.55	2.04	100
90	59.7	38.78	1.52	0	0	0	100
100	57.14	42.86	0	0	0	0	100

Table C.4: Percentage of behaviour throughout percentage of night for March.

% of night	hide	sit	move	eat	drink	interacting	Total
10	34.43	27.84	23.47	7.3	1.1	5.86	100
20	31.5	27.1	20.17	10.98	3.66	6.59	100
30	32.23	33.66	18.32	9.2	2.93	3.66	100
40	37.06	35.47	15.15	7.18	5.14	0	100
50	45.36	29.94	11.06	6.13	4.02	3.49	100
60	42.42	22.7	18.9	10.13	3.33	2.52	100
70	52.38	31.5	10.99	5.13	0	0	100
80	59.34	35.16	5.5	0	0	0	100
90	62.64	33.23	2.3	1.1	0	0.73	100
100	71.43	28.57	0	0	0	0	100

Table C.5: Percentage of behaviour throughout percentage of night for July.

% of night	hide	sit	move	eat	Total
10	70.4	29.6	0	0	100
20	24.93	69.44	4.62	1.01	100
30	23.15	68.52	4.63	3.7	100
40	50	45.37	0	4.63	100
50	51.01	44.34	3.1	1.55	100
60	54.63	35.19	5.55	4.63	100
70	53.7	37.04	0.93	8.33	100
80	37.04	40.74	1.85	20.37	100
90	43.52	39.81	1.85	14.82	100
100	77.78	10.18	9.26	2.78	100

Table C.6: Percentage of hiding throughout night per month.

Dec	January	February	March	July	% of night
91.59	61.11	36.73	34.43	70.4	10
88.41	55.05	36.73	31.5	24.93	20
56.13	19.7	48.47	32.23	23.15	30
17.73	22.22	41.33	37.06	50	40
17.6	6.57	41.84	45.36	51.01	50
12	8.08	38.27	42.42	54.63	60
21.44	2.02	34.69	52.38	53.7	70
19.56	17.64	49.49	59.34	37.04	80
47.76	55.56	59.7	62.64	43.52	90
77.22	87.88	57.14	71.43	77.78	100
449.44	335.83	444.39	468.79	486.16	Total
44.9	33.5	44.3	46.8	48.6	Average

Table C.7: Percentage of sitting throughout night per month.

Dec	January	February	March	July	% of night	
8.1	25.48	30.61	27.84	29.6		10
10.15	22.73	30.1	27.1	69.44		20
24.72	67.7	30.1	33.66	68.52		30
57.16	59.09	33.67	35.47	45.37		40
64.6	80.8	32.14	29.94	44.34		50
73.78	75.76	38.78	22.7	35.19		60
62.33	58.6	24.49	31.5	37.04		70
62.4	67.2	33.16	35.16	40.74		80
41.85	33.33	38.78	33.23	39.81		90
19.04	10.1	42.86	28.57	10.18		100
424.13	500.79	334.69	305.17	420.23	Total	
42.4	50	33.4	30.5	42	Average	

Table C.8: Percentage of moving throughout night per month.

Dec	January	February	March	July	% of night	
0.21	9.09	23.47	23.47	0		10
1.03	17.66	25.51	20.17	4.62		20
14.52	9.57	15.82	18.32	4.63		30
17.95	12.12	18.37	15.15	0		40
13.24	12.63	18.88	11.06	3.1		50
9.56	10.1	20.92	18.9	5.55		60
11.78	10.61	22.96	10.99	0.93		70
9.29	7.58	10.72	5.5	1.85		80
2.08	7.58	1.52	2.3	1.85		90
0.96	1.52	0	0	9.26		100
80.62	98.46	158.17	125.86	31.79	Total	
8	9.8	15.8	12.5	3.1	Average	

Table C.9: Percentage of eating throughout night per month.

Dec	January	February	March	July	% of night	
0	0	3.07	7.3	0		10
0	1.52	6.64	10.98	1.01		20
4.53	2.02	5.1	9.2	3.7		30
6.47	5.56	6.12	7.18	4.63		40
1.53	0	1.02	6.13	1.55		50
3.66	3.54	1.52	10.13	4.63		60
4.22	26.75	11.22	5.13	8.33		70
6.34	7.58	2.04	0	20.37		80
7.54	2.52	0	1.1	14.82		90
2.78	0.5	0	0	2.78		100
37.07	49.99	36.73	57.15	61.82	Total	
3.7	4.9	3.6	5.7	6.1	Average	

Table C.10: Percentage of drinking throughout night per month.

Dec	January	February	March	July	% of night
0.1	2.3	6.12	1.1	0	10
0.41	3.04	1.02	3.66	0	12
0.1	1.01	0.51	2.93	0	30
0.69	0	0.51	5.14	0	40
2.02	0	2.04	4.02	0	50
1	1.51	0.51	3.33	0	60
0.23	0	6.64	0	0	70
2.41	0	2.55	0	0	80
0.77	1.01	0	0	0	80
0	0	0	0	0	100
7.73	8.87	19.9	20.18	0	Total
0.77	0.88	1.9	2.1	0	Average

Table C.11: Percentage of attempted matings and interactions throughout night per month. (Note, in March and July only subadults were observed, so activity covers only interactions for those months.)

Dec	January	February	March	July	% of night
0	2.02	0	5.86	0	10
0	0	0	6.59	0	20
0	0	0	3.66	0	30
0	1.01	0	0	0	40
1.01	0	4.08	3.49	0	50
0	1.01	0	2.52	0	60
0	2.02	0	0	0	70
0	0	2.04	0	0	80
0	0	0	0.73	0	90
0	0	0	0	0	100
1.01	6.06	6.12	22.85	0	Total
0.1	0.6	0.6	2.2	0	Average

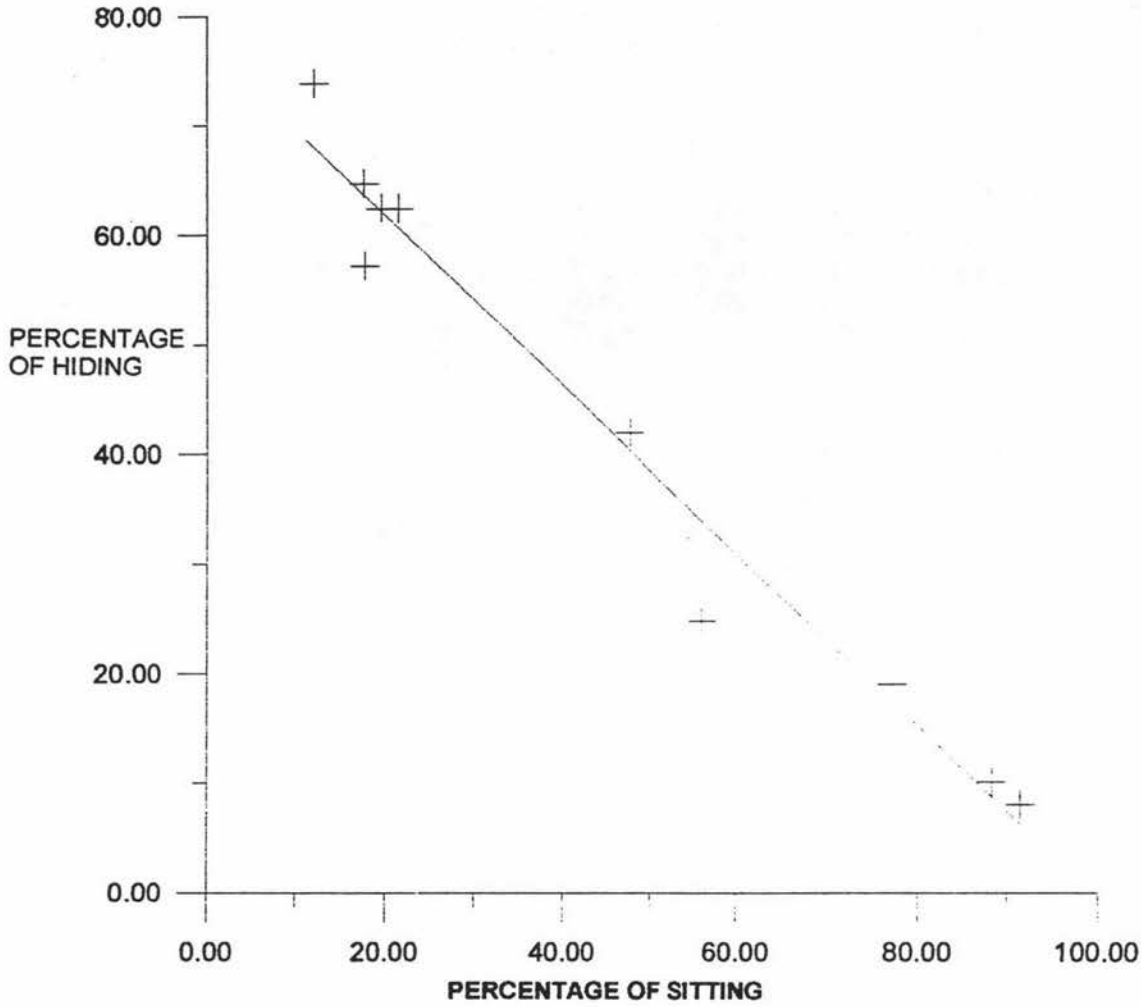


Figure C.12: Scatterplot of percentage of hiding versus percentage of sitting for December.

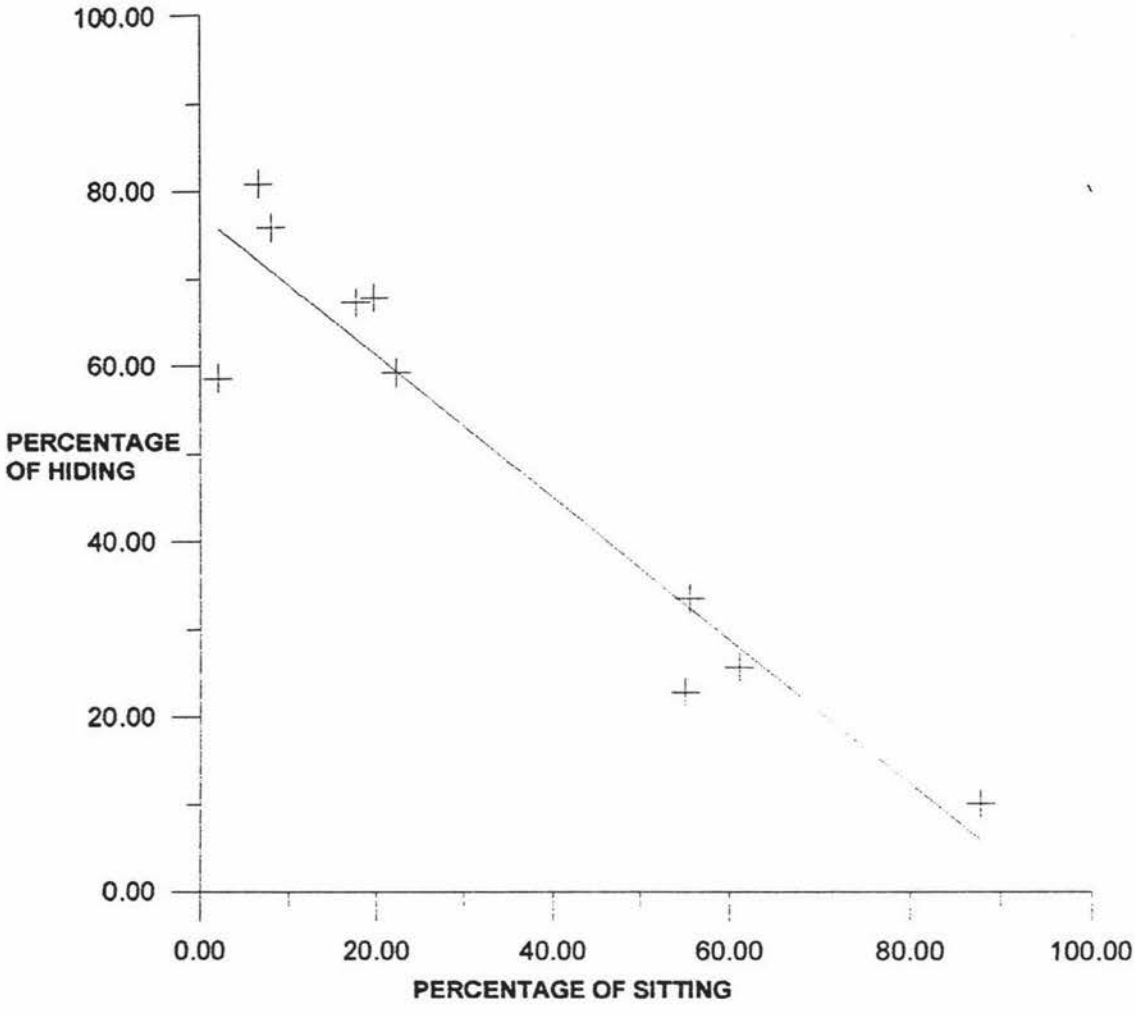


Figure C.13: Scatterplot of percentage of hiding versus percentage of sitting for January.

Table D.1: Time of Hatching for three nights observed on video.

Date	Time
28/12/94	20:10
29/12/94	00:22
29/12/94	01:27
29/12/94	03:21
30/12/94	01:04
30/12/94	04:51

Table D.2: Date of birth and number hatched for first instar weta.

D.O.B	NUMBER
2/12/94	2
19/12/94	1
20/12/94	1
24/12/94	1
25/12/94	1
27/12/94	3
28/12/94	1
29/12/94	3
30/12/94	2
2/01/95	8
3/01/95	12
4/01/95	1
6/01/95	2
8/01/95	6
9/01/95	2
10/01/95	4
14/01/95	7
20/01/95	41
4/02/95	3
5/02/95	1
6/02/95	5
TOTAL	104

Table D.3: Hatched egg length and mean egg length.

EGG LENGTH mm		TOTAL	MEAN LENGTH
10.3	6.3	671.8	6.45
10.2	5.35		
10.25	6.05		
10.45	6.2		
7.4	5.45		
7.4	6.25		
6.15	6.25		
6.2	6.3		
6.3	6.05		
6.3	6.35		
6.4	6.15		
6.25	6.35		
7.05	6.25		
7.35	6.15		
7.3	6.1		
7.3	6.35		
7.3	6.4		
6	6.25		
6.3	6.25		
7.4	7		
6.2	6.2		
7.1	6.45		
6.3	6.35		
7	6.1		
6.25	6.3		
6.35	6.25		
6.2	6.25		
6.3	6.15		
6.35	6.1		
6.3	6.05		
6.3	6.1		
6.3	6.1		
6.3	6		
6.3	6.15		
6.3	6.25		
6.4	6.25		
6.2	6.3		
6	6.4		
6.05	6.2		
6	6.25		
6.25	6		
6.3	6.2		
6.15	6.15		
6.25	6.1		
6.4	6.2		
6.1	6		
5.45	6		
6.15	6.25		
6	6.2		
6.2	6.3		
6.2	6.2		
6.45	6.2		

Table E.1: Weta used in Trial 1 and 2.

weta no.	Trial 1 instar	weight	prontum	sex
7	8	5.1	0.82	M
1	9	6.87	0.96	F
3	9	7.23	0.97	F
g	8	4.5	0.9	F
a	9	4.93	0.96	F
b	6	2.82		M
	Trial 2 instar			TOTAL
16	8	7.77		F
9	9	5		M
11	10	12.63		F
7a	8	7.82		F
8	7	6.68		F
1	9	5.98		M
				TOTAL

Table E.2: Amount eaten in grams of plants for Trial 1.

Trial 1 weta no.	8/06/94	10/06/94	12/06/94	14/06/94	16/06/94	18/06/94	20/06/94	22/06/95	24
	Hoheria	gorse	karaka	Houhere	mahoe	lemon	camellia	coprosma	taw
7	0	0.324026	0	0	0	0	0	0.004835	
1	0	1.81296	0.30036	0	0.00828	0.041474	0.012424	0.087417	
3	0	0.868563	0.767049	0	0.09072	0.007137	0.260896	0.34812	0.0
g	0.05974	5.941481	0.015179	0.072794	0.0487	0.036458	0.11477	0.198042	0.0
a	0	2.030106	0.293578	0	0.06672	0.130768	0.202323	0.267859	0.0
b	0.05379	0.05379	3.908393	0.17375	0.065549	0.05033	0.237074	0.097022	0.1
Total	0.11353	14.25837	1.549916	0.138343	0.26475	0.452929	0.687435	1.106249	0.0

Table E.3: Amount eaten in grams of plants for Trial 2.

	23/11/94	25/11/94	27/11/94	28/11/94	30/11/94
Trial 2					
weta no.	gorse	broom	kowhai	buttercup	tawa
16	1.324605	3.102430	3.129607	1.713495	0.371389
9	1.726670	2.250546	3.001427	2.138720	0.448688
11	4.915517	2.201591	3.890126	1.212135	0.368823
7a	2.434862	2.369694	1.840249	1.503890	0.758673
8	1.582612	2.091464	2.767509	1.549383	0.407324
1	1.603523	0.957781	2.265932	2.567235	0.813661
Total	13.58779	12.97350	16.89485	10.68486	3.168561

REFERENCES

Akhtar, S. and Ashrafi, S.H. (1966). "Morphometrical and histological study of the reproductive system of Desert Locust, *Schistocerca gregaria* (Forskal) Orthoptera Acrididae." Pakistan Journal of Scientific and Industrial Research **9(2)**: 140-145.

Alexander, R. D. (1961). "Aggressiveness, territoriality and sexual behaviour in Field Crickets (Orthoptera: Gryllidae)." Behaviour **17**: 130-223.

Ander, K. (1939). "Vergleichend-anatomische und phylogenetische Studien uber die Ensifera (Saltatoria)." Opuscula Entomologica, supplement. **2**: 306pp.

Barrett, P. (1991). Keeping Wetas in Captivity. Wellington., Wellington Zoological Gardens.

Bellingham, M. (1991). "Field observations on two species of tusked weta." The Weta. **14**: 30-32.

Bennet, B. G. (1981.). "Unseasonal hatching of Orthopteroid insects." The Weta. **4**: 20-21.

Cary, P. R. L. (1981). The biology of the weta *Zealandosandrus gracilis* (Orthoptera: Stenopelmatidae). Christchurch, University of Canterbury.

Cottee, P. K, Bernays, E.A, Mordue, A.J. (1988). "Comparisons of deterency and toxicity of selected secondary plant compounds to an oligophagous and a polyphagous acridid." Entomol. exp. appl. **46**: 241-247.

Crowe, A. (1990). Native edible plants of New Zealand. Auckland, Hodder and Stoughton.

Field, L. H. (1980). "Observations on the Biology of *Deinacrida connectens* (Orthoptera: Stenopelmatidae), an alpine weta.." New Zealand Journal of Zoology **17**: 211-220.

Field, L. H. (1993). "Observations on stridulatory, agonistic, and mating behaviour of *Hemideina ricta* (Stenopelmatidae: Orthoptera), the rare Banks Peninsula weta." New Zealand Entomologist. **16**: 68-74.

Fox., F. K. (1991). "Mahoenui giant wetas at the Otorohanga Kiwi House." The Weta. **14**: 28-30.

Gregory, G. E. (1965). "The formation and fate of the spermatophore in the African Migratory Locust, *Locusta migratoria migratorioides* Riche and Fairmaire." Transactions of the Royal Entomological Society London **117**(2): 33-66.

Hale, L. J. (1965). Biological Laboratory Data. London, Methuen and Co. Ltd.

Humason, G. L. (1967). Animal Tissue Techniques. San Francisco and London, W.H. Freeman and Company.

Maskell, F. G. (1927). "The anatomy of *Hemideina thoracica*." Transactions of the New Zealand Institute **57**: 637-670.

Matsuda, R. (1976). Morphology and Evolution of the Insect Abdomen. Hungary, Permagon Press Ltd.

Meads, M. J. (1990). The Weta Book: A Guide to the Identification of Wetas. Lower Hutt, DSIR Land Resources.

Messenger, G. (1991). "Entomological notes from the Far North." The Weta. **14**: 22-23.

Moller, H. (1985). "Tree wetas (*Hemideina crassicruris*) (Orthoptera: Stenopelmatidae) of Stephen's Island, Cook Strait." New Zealand Journal of Zoology **12**: 55-69.

Ordish, R. G. (1992). "Aggregation and communication of the Wellington weta *Hemideina crassidens* (Blanchard) (Orthoptera: Stenopelmatidae)." New Zealand Entomologist. **15**: 1-8.

Paemen, L, Schoofs, L, De Loof, A. (1990). "Presence of myotropic peptides in the male accessory reproductive glands of *Locusta migratoria*." Journal of Insect Physiology **36**(11): 861-867.

Phipps, J. (1966). "Ovulation and oocyte resorption in Acridoidea (Orthoptera)." Proceedings of the Royal Entomological Society London **41**(4-6): 78-86.

Ramsay, G. W. (1965). "Development of the ovipositor of *Deinacrida rugosa* Buller." Proceedings of Royal Entomological Society of London.(A) **40**(4-6): 41-50.

Richards, A. M. (1953). The anatomy, morphology and habits of *Pachyrhamma fascifer* (Walker, 1869) (Orthoptera, Raphidophoridae). M.Sc Thesis. Wellington., Victoria University College.

Richards, A. M. (1961). "Revision of the Raphidophoridae (Orthoptera) of New Zealand. Part viii. The species *Turbottoplectron cavernae* (Hutton) 1900." Transactions of the Royal Society of New Zealand Zoology. **1**(9): 121-37.

Richards, A. M. (1973). "A Comparative Study of the biology of the giant wetas *Deinacrida heteracantha* and *D. fallai* (Orthoptera: Henicidae) from New Zealand.". Journal of Zoology. **169:** 195-236.

Richards, G. E. (1994). Ecology and behaviour of the Mahoenui Giant Weta (*Deinacrida* n.sp.). M.Sc Thesis. Massey University, Palmerston North.

Robinson, M. H. (1970). "The defense behaviour of some Orthopteroid insects from Panama." Transactions of the Royal Entomological Society. **69**: 281-291.

Sandlant, G. R. (1981). Aggressive behaviour of the Canterbury weta *Hemideina femorata* (Orthoptera: Stenopelmatidae). M.Sc thesis. Christchurch, University of Canterbury.

Schwalm, F, Ed. (1988). Insect Morphogenesis. Monographs in Developmental Biology. Pratteln. Thur AG Offsetdruck.

Sherley, G. and L. M. Hayes (1993). "The conservation of a giant weta (*Deinacrida* n.sp. Orthoptera: Stenopelmatidae) at Mahoenui, King Country: habitat use, and other aspects of its ecology." New Zealand Entomologist **16**: 55-68.

Singh, T. (1958). "Ovulation and corpus lutem formation in *Locusta migratoria migratorioides* Reiche and Fairmaire and *Schistocerca gregaria* (Forskal)." Transactions of the Royal Entomological Society of London **110**: 1-20.

Singh, S. R., Van Emden, H. F, Ajibola Taylor. T. (1978). Pests of grain legumes: Ecology and control. London, Academic press.

Snodgrass, R. E. (1933). "Morphology of the insect abdomen: II, The genital ducts and the ovipositor." Smithsonian Miscellanous Collections **89(8)**: 1-148.

Snodgrass, R. E. (1935). Principles of insect morphology. New York and London, McGraw-Hill Book Company, Inc.

Snodgrass, R. E. (1937). "The male genitalia of Orthopteroid insects." Smithsonian Miscellanous Collections **96(5)**: 1-107.

Speedy, A. and P. Pugliese (1992). Legume trees and other fodder trees as protein sources for livestock. Rome, Food and agriculture organisation of the United Nations.

Townsend, J. A. (1995). Distribution and Ecology of the Banks Peninsula Tree Weta, *Hemideina ricta.*

Uvarov, B. (1966). Grasshoppers and Locusts. Cambridge, Cambridge University Press.

Wahid, M. B. (1978). The biology and economic impact of the weta, *Hemiandrus* sp. (Orthoptera: Stenopelmatidae) in an apricot orchard, Horotane Valley. Christchurch, Lincoln College, University of Canterbury.: 231.

Watt, J. C. (1963). "The rediscovery of a giant weta, *Deinacrida heteracantha*, on the North Island mainland." New Zealand Entomologist. **3**(2): 9-13.