Frontspiece: Adult *Scolypopa australis* Walker feeding from a leaf.

ASPECTS OF THE BIOLOGY OF
Scolypopa australis WALKER (HOMOPTERA: RICANIIDAE)

A thesis
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ABSTRACT

Aspects of the biology of *Scolypopa australis* Walker (Homoptera: Ricaniidae) were studied in the Waikato region. Attempts were made to fill some gaps in the knowledge of what is in New Zealand an important species. A general outline of the life history of *S. australis* is given, followed by studies of three particular facets of the species' biology. A large experiment was set up to study the egg diapause but was not a success, and consequently little information of the embryonic diapause was obtained. The morphology of the chorion of the egg was studied with both the light and electron microscopes, and a quantity of information about the external and internal architecture of the shell was obtained. The egg bears an anterior micropylar process which contains both the single micropyle and the air-containing meshwork layer of the chorion where it meets the atmosphere. The egg has no hydropyle. An inner meshwork layer of the chorion is visible with the light microscope. Measurements were made of six different body parts on each of 220 *S. australis* nymphs, and it was found that the width of the post-clypeus and the length of the proboscis can be used to define the five nymphal instars. No comprehensive bibliography of the species has ever been published, thus reasonably exhaustive lists of references are given. More accurate information on the habits and distribution of the species outside New Zealand is given.

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1. INTRODUCTION

A general account of most aspects of the biology of *Scolypopa australis* Walker was given by Cumber (1966). In this present work more detailed studies of a limited number of aspects of the insect's biology were carried out. An account of the life history is given, and this is followed by studies on embryonic diapause, egg morphology and chorion structure, and morphometrical analysis of nymphal instars.

The experiments on diapause were carried out under natural and artificial conditions. As it was originally intended to make these a major part of the thesis, a considerable amount of time and effort was invested in this work. Unfortunately, for reasons which are described elsewhere, almost no results were obtained and no positive conclusions can be drawn from this work.

In the study of egg chorion morphology the scanning electron microscope was used. This work produced some new information on egg structure and also enabled the writer to gain experience in scanning electron microscopy.

Although *S. australis* is both plentiful and of economic importance in New Zealand, no comprehensive bibliography has been published. In Section 2.4 a brief review of the literature on the species is given. The synonmy of the species is also listed completely for the first time, and information on the distribution of *S. australis* in Australia, which is generally lacking, is also presented here (see Section 4.1).

2. *SCOLYPOPA AUSTRALIS*

2.1 GENERAL REMARKS ON *SCOLYPOPA AUSTRALIS*

The vine-hopper, *Scolypopa australis* Walker 1851 (Homoptera: Ricaniidae) is generally assumed to be a native of Australia. It is first recorded in the New Zealand literature by Distant (1878), and less than twenty years later it was described by Broun (1896) as being "... almost ubiquitous, so far as the North is concerned."

S. australis was probably brought into the country accidentally as eggs overwintering in plant stems; this hypothesis being strengthened by the presence in New Zealand of the egg parasite *Centrodora scolypopae* Valentine 1966 (Hymenoptera: Aphelinidae), which is thought to be of Australian origin (Cumber, 1966). However *S. australis* may have arrived in New Zealand on several occasions, and the possibility of adults being transported across the Tasman Sea by the prevailing winds should not be overlooked. A number of insect species are thought to have arrived in New Zealand by this means, e.g. *Vanessa kershawi* McCoy (Lepidoptera: Nymphalidae) (Gibbs, 1969); *Eriococcus orariensis* Hoy (Homoptera: Coccidae) (Hoy, 1959, 1961); *Hypolimnas bolina nerina* (F) (Lepidoptera) (Ramsay and Ordish, 1966). The subject is reviewed by Tomlinson (1974).

S. australis is now common throughout the warmer parts of the North Island and in the Nelson and Marlborough districts, and lives in great numbers on a wide variety of native and exotic plants in household gardens, scrublands, and bush areas. The nymphs and adults feed on the plant sap for long periods causing general loss of vigour and wilting, and in the passionfruit (*Passiflora edulis* Sims) at least, may prevent maturation of the fruit (Cottier, 1956). The insect produces honeydew on which grows the sooty mould fungus that disfigures the passion-fruit (May, 1965). *S. australis* is a vector of the bacterium *Erwinia amylovora* Burrell, causative organism of fireblight, a disease affecting some orchard trees (Tillyard, 1926b).

S. australis is also responsible for the production of toxic honey in New Zealand (Palmer-Jones, 1965; Paterson, 1947). The insect feeds on the native shrub tutu (*Coriaria arborea* Lindsay), which contains a highly poisonous picrotoxin known as tutin (Sutherland and Palmer-Jones, 1947a). This is changed in the insect's body to a hydroxytutin called hyenanchin (mellitoxin) which is passed out in the honeydew (Palmer-Jones and White, 1949). The production of honeydew from a dense population of late-instar nymphs and adults can be quite considerable, and in dry weather accumulates on the plant. In the absence of a good supply of floral nectar, honey bees (*Apis mellifera* L.) will collect the honeydew and incorporate it into the honey (Sutherland and Palmer-Jones, 1947b). When taken by man, even in small quantities, this honey produces very violent reactions, and may result in death. As a result of the discovery of the relationship between the poisonous plant and the two insects (Paterson, 1947), about 2,600 km^2 of the Bay of Plenty was declared a restricted area in terms of the Apiaries Act. The Coromandel Peninsula was similarly restricted in 1974.

2.2 DISTRIBUTION

S. australis is distributed in New Zealand throughout Northland, Auckland, Waikato and the coastal regions of the Bay of Plenty, Hawke's Bay, Taranaki and Manawatu. It is also present in the northernmost parts of Nelson and Marlborough (Cumber, 1966). *S. australis* does not appear to have expanded its New Zealand range in recent times. The transport of plant material within the country would permit the distribution of eggs, but the limits to distribution seem to be largely climatic (see below). *S. australis* has not, for instance, established itself in Canterbury (W. P. Thomas, pers. comm.).

Davilevskii (1965: 19) remarks that "it has long been known that the northern limits of insect distribution (in the northern hemisphere) coincide with the isotherms of winter minima." The relationships between insects and climate in temperate regions are a little more complex than those discussed by Danilevskii, but it is interesting to note the close correlation between the distribution of *S. australis* and the average July 8°C isotherm (Kisdon, 1950), the 12°C isotherm of July daily maximum temperature (Coulter, 1973), or the 12°C isotherm of mean annual temperature (Wards, 1976). This suggests that the distribution of *S. australis* is determined largely by climatic factors.

In Australia the species occurs east of the Great Dividing Range in Victoria, New South Wales, and southern Queensland. It appears to be confined mainly to the coastal regions of these areas. In 1975 it was reported for the first time from Launceston, Tasmania (R. J. Hardy, pers. comm.). (See also discussion in Section 3.1 (Diapause), and Australian locality list in Appendix 1).

S. australis is also found on Lord Howe and Norfolk Islands (D. F. Waterhouse, pers. comm.). Reports of the species from Fiji (e.g. Melichar, 1923; Kirkaldy, 1906) all derive from one mention by Froggatt (1900), which must be held in doubt as "no species even like it are found there" (R. G. Fennah, pers. comm.). Fennah has also remarked (Fennah, 1950: 3) that "The record of occurence (in Fiji) of... *Scolypopa australis* (Walker) (Kirkaldy, 1906) (is) considered erroneous."

2.3 SYNONYMY

Scolypopa australis was first described as a species of *Pochazia* from "New Holland" (i.e. Australia) by Walker (1851). Walker in 1858 transferred it to the genus *Flatoides*. Stål (1859) erected the genus *Scolypopa* and *S. australis* was placed in it as a new species, *S. urbana*. Stål in 1862 synonymised this with Walker's *Pochazia australis* and placed it in the genus *Ricania*. In 1898 Melichar replaced it in the genus *Scolypopa* Stål. Its synonymy, therefore, is as follows:

Walker, F. B. 1851. *List of the Homopterous insects in the British Museum.* *2*: 430. (*Pochazia australis*)

Walker, F. B. 1858. *List of the Homopterous insects in the British Museum.* Supplement p. 102. (*Flatoides australis*)

Stål. 1859. *Berliner Ent. Zeit.* *3*: 325. (*Scolypopa urbana*)

Stål. 1862. *Öfv. Svenska Vet. Akad. Föhr.* *19*: 491. (*Ricania australis*)

Melichar, L. 1898. *Ann. Nat. Hofmus. Wien* *13*: 255, 278, Pl. xi, fig. 24 (*Scolypopa australis*).

Although *Scolypopa australis* is by no means confined to the passion vine (*Passiflora edulis*), it is now almost universally referred to as the "passion vine-hopper". This somewhat misleading name is relatively recent, having been first used by Tillyard (1926a). Previously it had been referred to as "Tree hopper" (Broun, 1896) and "Vine-Hopper" (Kirk, 1903). Froggatt (1900) refers to the insect as the "Passion-vine Frog Hopper" because "... when you touch one he jumps like a frog, from which habit this group of insects have gained their popular name of frog-hoppers." Helson (1974) calls this species the "passion vine leaf-hopper".

However, these names mostly refer to families of insects belonging to the super-family Cicadoidea which are not related to *S. australis*, e.g. Membracidae (tree hoppers), Cercopidae (frog hoppers), and Jassidae or Cicadellidae (leaf hoppers). Insects of the superfamily Fulgoroidea are often called "plant name"-hopper, where "plant name" represents the name of the host plant. Because of the wide range of host plants of *S. australis*, passion vine-hopper is a rather deceptive name for this species.

Although the insect lives on many sorts of shrubs, it also inhabits all types of vine, including those of horticultural importance, and so the name "vine hopper" is suggested as a suitable compromise between habit and scientific accuracy.

2.4 BILBIOGRAPHY OF *SCOLYPOPA AUSTRALIS*

2.41 Brief mention in scientific journals.

New Zealand: Broun 1896, 1898; Cumber 1954, 1959; Distant, 1878; Hutton, 1897; Kirk, 1903; Kirkaldy, 1908; Myers 1922, 1923; Thomson, 1922; Tillyard, 1926b; Valentine, 1967; White, 1879; Worley, 1928.

Overseas: Anon, 1973b; Froggatt, 1900; Kirkaldy, 1906; McKeown, 1944; Tillyard, 1923.

2.42 Listed

New Zealand: Hutton, 1904; Valentine, 1967.

2.43 Description in popular and technical entomology texts

New Zealand: Child, 1974; Cottier, 1956; Ferro, 1976; Helson, 1974; May, 1965; Miller 1955, 1971; Sharrell, 1971; Tillyard, 1926a.

Overseas: Evans, 1952; Woodward *et. al.*, 1970.

2.44 Bibliographies

Melichar, 1923. Lists some of the taxonomic works given in Section 1.4.

Metcalf, . Contains a bibliography of *S. australis* for the years 1851-1952. It is farily comprehensive for the earlier years, and contains a few references in the overseas literature not given here.

Miller, 1956. All the references listed by Miller are also given in this chapter.

Musgrave, 1932. Has no references to *S. australis*.

2.45 References to the species' involvement in honey poisoning in New Zealand.

Clinch and Turner, 1968, 1975; Hodges and White, 1966; Palmer-Jones, 1965; Palmer-Jones and White, 1949; Paterson, 1947; Sutherland and Palmer-Jones, 1947b, Anon, 1949.

2.46 Mentioned as a pest of passion fruit in New Zealand.

Davidson, 1918; Greig, 1943, Helson, 1974.

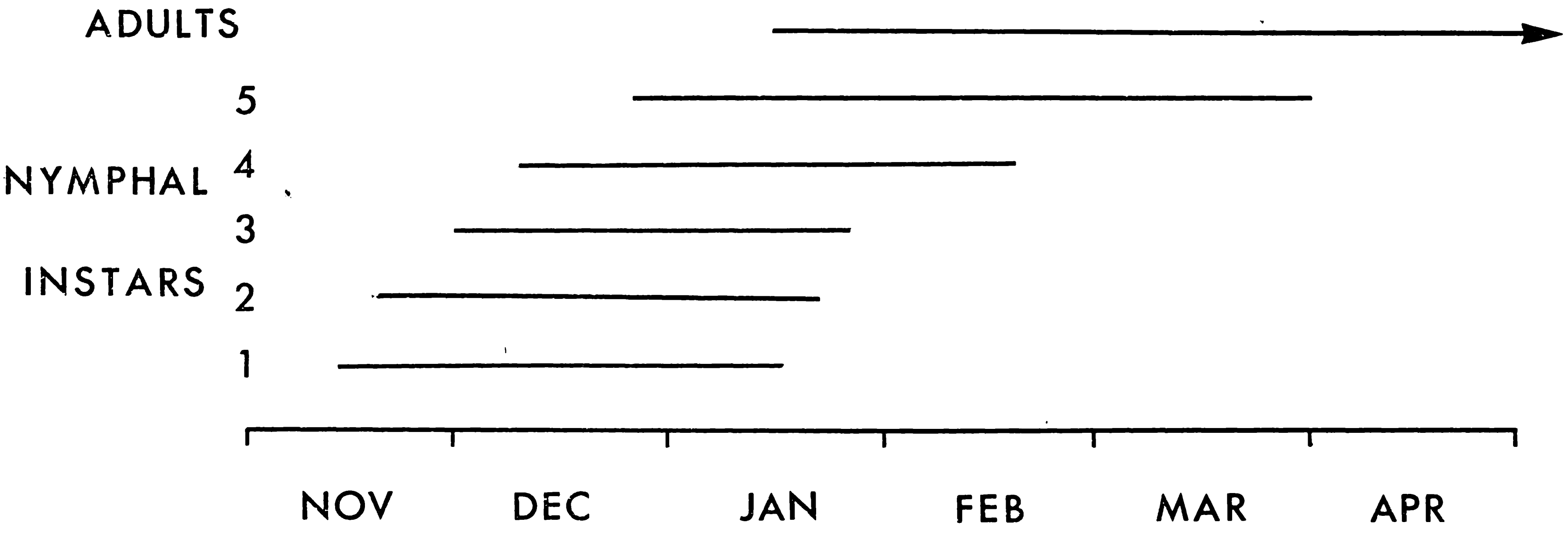
2.47 *S. australis* has been studied in detail by Cumber (1966, 1967) and Siew (1960). Cumber (1966) studies factors affecting the population levels of the species in New Zealand. This was undertaken to provide information about the biology of the species in this country prior to searching for parasites and predators in Australia (Cumber, 1967). Small numbers of a scelionid (Hymenoptera) egg parasite and two chrysopid (Neuroptera) species which prey on the eggs were released at the Bay of Islands, but there is at present no evidence of establishment of any of these species (R. Hill, pers. comm.). Siew's (1960) thesis covers various aspects of the species' biology, e.g. population studies and anatomical/histological studies of internal organs. Marshall (1973) describes vesicular structures in the dendrites of the olfactory receptors of *Pyrops candelaria* L. (Homoptera: Fulgoriidae) and *S. australis*.

3.1 INTRODUCTION

In New Zealand *Scolypopa australis* has a strictly univoltine life cycle. The nymphs and adults are active in the warmer parts of the year, and winter is spent in diapause at the egg stage. In the Waikato, nymphs are usually abundant during November, December and January, while adults are most common in the months February, March and April. This information is summarised in Fig. 3.1. The periods of activity are, obviously, extended in the north and shortened in the south. Winter is passed in the egg stage, the embryo undergoing a diapause which is apparently obligatory throughout New Zealand, at least. This was the subject of a separate investigation (Chapter 4). Information on the phenology of *S. australis* in other parts of its range, particularly Australia, is lacking despite persistent search and enquiry (see Section 4.1).

The gross morphology and architecture of the shell were the subject of another investigation (Chapter 4).

Fig. 3.1 Periods of *S. australis* activity in the Waikato in the years 1976/77 and 1977/78.


ADULTS
5
NYMPHAL 4
3
INSTARS 2
1
NOV
DEC
JAN
FEB
MAR
APR

3.2 MATERIALS AND METHODS

Observations and collections of the different stages of *S. australis* were made at various localities in the Waikato region. Nymphs were collected with an aspirator, and adults were usually numerous enough to capture simply by brushing them into a wide-mouthed jar. Eggs were extracted from the plant material in which they had been laid by splitting the twig lengthwise with a scalpel, snapping it into several pieces, and collecting the eggs that fell out.

Measurements were made on various stages with an eyepiece micrometer fitted to an Olympus stereomicroscope, using appropriate magnifications. The error in this technique was estimated to be ±0.25 eyepiece units which corresponds to ±0.005-0.015mm, depending upon the magnifications used.

Because of the variability in the degree of curvature of the abdomen in the nymphal stages, the length of head and thorax along the dorsal mid-line is used as an indication of the total size of the insect. In a morphometric study of the nymphal stages (Chapter 6) it was found that the width of the post-clypeus at its widest point and the length of the proboscis were the most useful measurements in classifying the nymphal stages. These, therefore, are given.

As well as being examined with the light microscope, nymphs were also inspected with the scanning electron microscope. The material used for this was preserved in 95% ethanol, and so was not fixed or dehydrated in the customary way. The nymphs were simply taken through a graded absolute ethanol/absolute freon series to absolute freon and dried in a Polaron E 3000 critical point drying apparatus. Material was then coated with a 50nm layer of gold in a Polaron E 5000 diode sputter system and examined with a JEOL JSM-35 scanning electron microscope at 20 or 25 kV. An Asahi Pentax 35mm SLR camera mounted on the microscope was utilized in taking the photographs. The hardness of the cuticular exoskeleton prevented any apparent damage resulting from the lack of fixation and proper dehydration.

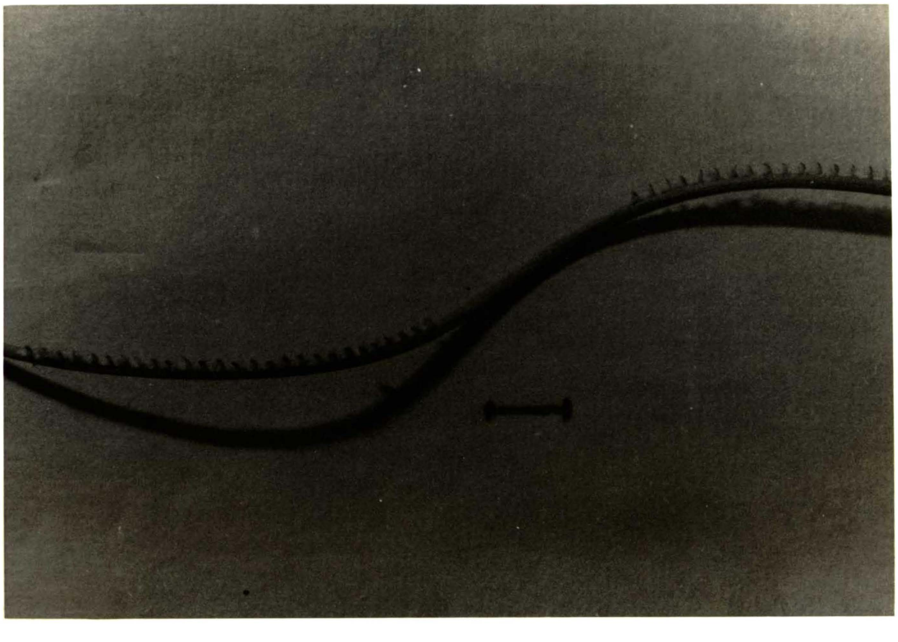
3.3 EGGS

Eggs are inserted mostly into dead, but also live, stems, tendrils, petioles etc. of a wide variety of plants. Requirements for suitable sites are not very stringent, and oviposition has also been observed in wooden gates, fence battens etc. The eggs are deposited in straight rows of varying numbers of eggs ($\bar{x} = 22$, $\sigma = 16$, $n = 990$), the rows running the length of the stem and there being up to five rows per circumference. Dead twigs are probably selected for their stability during the course of the egg's development, as growing twigs may subject eggs to pressures of up to 30 atmospheres (Hartley, 1965).

The ovipositor is pushed through the hard outer layer of the stem and the egg is placed in the pithy interior tissue, parallel to the surface with the cephalic or anterior end nearest the opening. As the ovipositor is withdrawn some plant fibres are drawn out, and these are left around the perimeter of the hole, appearing as a conspicuous white tuft of broken fibres (see Fig. 3.2). This occurs as an automatic consequence of the withdrawal of the ovipositor, and is not a "cap" of plant tissue "deliberately" constructed by the female.

Egg laying commences in late January. Winter is passed in the egg stage, development being arrested by diapause. Diapause in *S. australis* was the subject of a separate study (Chapter 4). The incubation period is not known, as individuals were not followed throughout the course of development. However, there is a great deal of variation in the time of hatching in the field (see Fig. 3.1).

Fig. 3.2 *Passiflora* tendril with oviposition scars. (Scale = 5mm)



3.4 NYMPHS

Nymphs begin to emerge in mid-November in the Waikato. First instar nymphs are active, and soon after emergence move from the previous season's growth to new leaves. This may be to fulfil nutritional requirements, as sap of growing leaves contains a greater variety and abundance of amino acids than leaves in an intermediate, fully-functioning condition (Mittler, 1953). Kennedy & Booth (1951) reported that certain leaf-feeding aphids, particularly *Aphis fabae* Scop., colonise growing leaves in preference to older ones. All stages of nymph exhibit this preference. *S. australis* nymphs are to be found feeding in many places, e.g. stems, tendrils, growing shoots etc. but mostly feed on the undersurface of young leaves. This is not primarily related to the leaf structure, as nymphs will still congregate beneath an inverted leaf (i.e. on the real upper surface), but is probably a reaction with protective and concealing functions.

Wax glands are present on the sternites of the eighth and ninth visible abdominal segments in all instars of *S. australis*. Wax glands are present in several orders of insects, and in Homoptera are most common in the Coccoidea, Aphidoidea and Fulgoroidea. Detailed studies have been made of wax glands in the Coccoidea by Matheson (1923) and Pollister (1937), and in Fulgoroidea by Šulc (1928, 1929). Maloeuf (1938) dealt with wax glands generally. The wax glands in *S. australis* were examined with the SEM (Fig. 3.3, 3.4), but no histological study of the structure of the glands was made. The peforated cuticular plates on the surface of the gland clusters indicate that the glands are of typical Fulgoroid structure (Pesson, 1951: 1437). The wax is produced by a mass of unicellular or multicellular glands, and its passage through the perforated plate differentiates it into many fine filaments. In *S. australis* these filaments radiate outwards in all directions, but particularly forwards because of the dorsal flexion of the abdomen. They may reach up to three or four times as long as the insect's body, although most are about twice the body length. The filaments detach very easily, but will reappear quite rapidly, attaining one body length in only 2-3 hr.

The function of these glands is rather enigmatic, and although some think that the wax is a type of excretion product which is a consequence of feeding exclusively on plant juices (Pollister, 1937), it is usually thought that the waxy filaments may serve a protective function (Lindsay, 1969).

To enable identification of each nymphal instar, scanning electron micrographs of each stage are included in this section (Fig. 3.7 - 3.11). Brief descriptions of some diagnostic characters are also given, including *average* values for some dimensions. These dimensions are defined in Section 6.2.

All instars

Head and mouthparts opisthorhynchous; rostrum reaching almost to hind coxae. Post-clypeus eliptico-ovoid, tricarinate, bearing pit-like sensory organs* all around the margin except along border with anteclypeus. Pronotum bearing a variable number of these sense organs. Mesonotum with two prominent, more or less longitudinal keels or ridges, and two sensory organs near lateral margin on each side. Metanotum with two longitudinal ridges parallel to the dorsal mid-line, but no sense organs. Abdomen soft, usually flexed ventrally through 90°-135°. Wax glands present on the sternum of the 8th and 9th visible

* Fig. 3.3, 3.4.

abdominal segments.

First instar

Length of head and thorax 0.65mm. Width of post-clypeus 0.31mm, length of rostrum 0.24mm. Insects mostly colourless. Ventral aspect of thorax basically triangular in shape, with metathorax considerably wider than the other segments. Pronotum with 5 sensory pits on each side.

Second instar

Length of head and thorax 0.91mm. Width of post-clypeus 0.43mm, length of rostrum 0.29mm. Colour patterns more developed on nota. Insect only slightly broader across the metanotum than the mesonotum. Small wing bud developing from mesothorax beneath the post-notal margin. 7 sensory pits on each side of the pronotum.

Third instar

Length of head and thorax 1.21mm. Width of post-clypeus 0.59mm, length of rostrum 0.39mm. Insect broader across mesonotum than metanotum. Post-notal margin of metathorax extending over abdomen. Meso- and metathoracic wing buds visible under repective nota. Insect creamy colour with brown colour pattern on nota. 11 sensory organs on each side of pronotum.

Fourth instar

Length of head and thorax 1.59mm. Width of post-clypeus 0.79mm, length of rostrum 0.51mm. Insect considerably broader across mesonotum than metanotum, and post-notal margin of the latter extending over the abdomen. Wing buds more developed and colour pattern conspciuous. Pronotum with 14 sensory organs on each side.

Fifth instar

Length of head and thorax 2.00mm. Width of post-clypeus 1.12mm, length of rostrum 0.64mm. Also with 14 sensory organs on each side of pronotum. Metanotum almost completely covered by post-notal lobe of mesonotum. Wing pads very well developed.

Fig. 3.3 Wax glands on the abdomen of *S. australis* nymph. (Scale =.5mm

Fig. 3.4 Wax glands on the abdomen of *S. australis* nymph.
(Scale = 0.1mm).

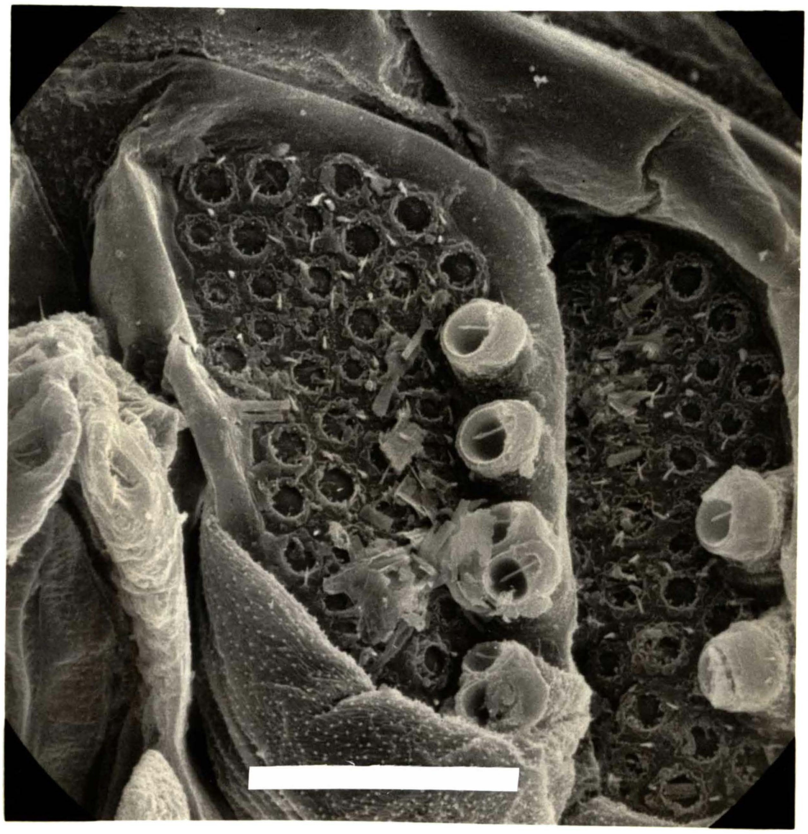
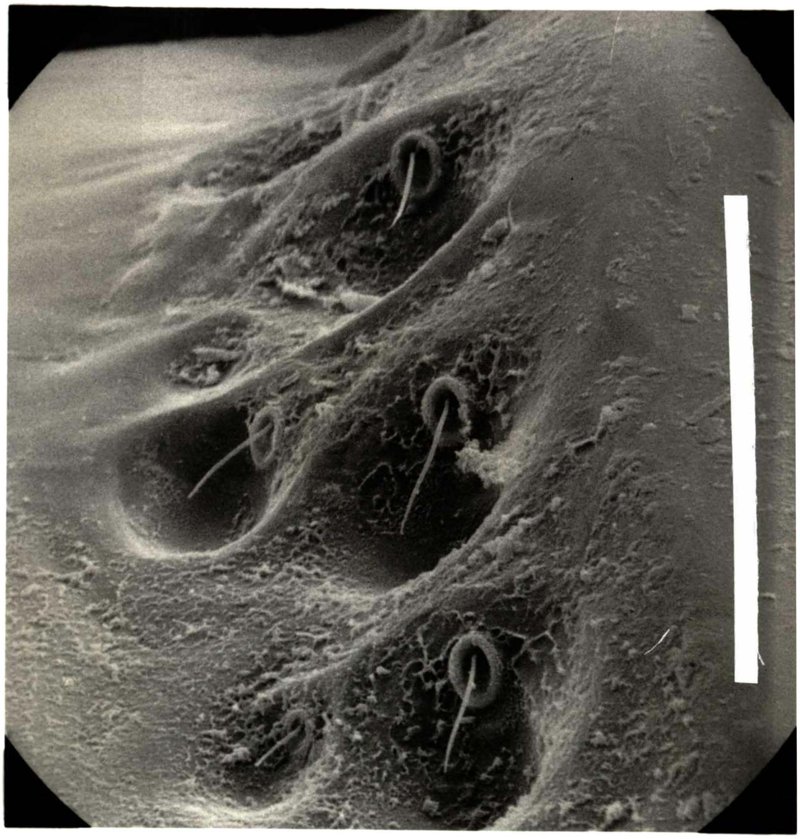


Fig. 3.5 Sensory pits on rim of post-clypeus. (Scale = 0.1mm).

Fig. 3.6 Detail of sensory pit. (Scale = 50μm)



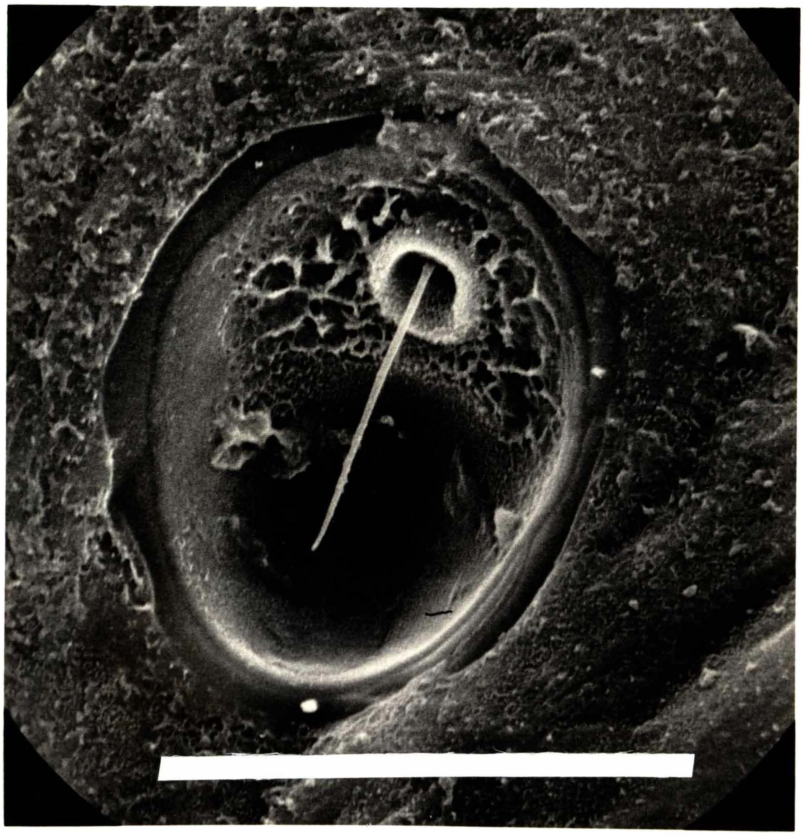


Fig. 3.7 First instar *S. australis* nymph. (Scale = 0.5mm).

Fig. 3.8 Second instar *S. australis* nymph. (Scale = 1mm).

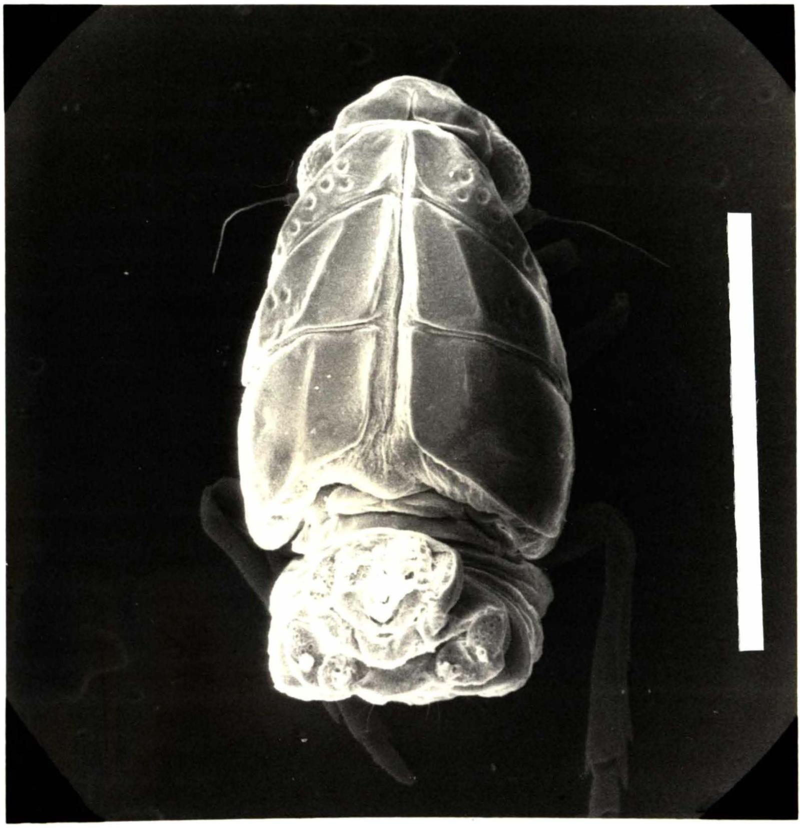


Fig. 3.9 Third instar *S. australis* nymph. (Scale = 1mm).

Fig. 3.10 Fourth instar *S. australis* nymph. (Scale = 1mm).

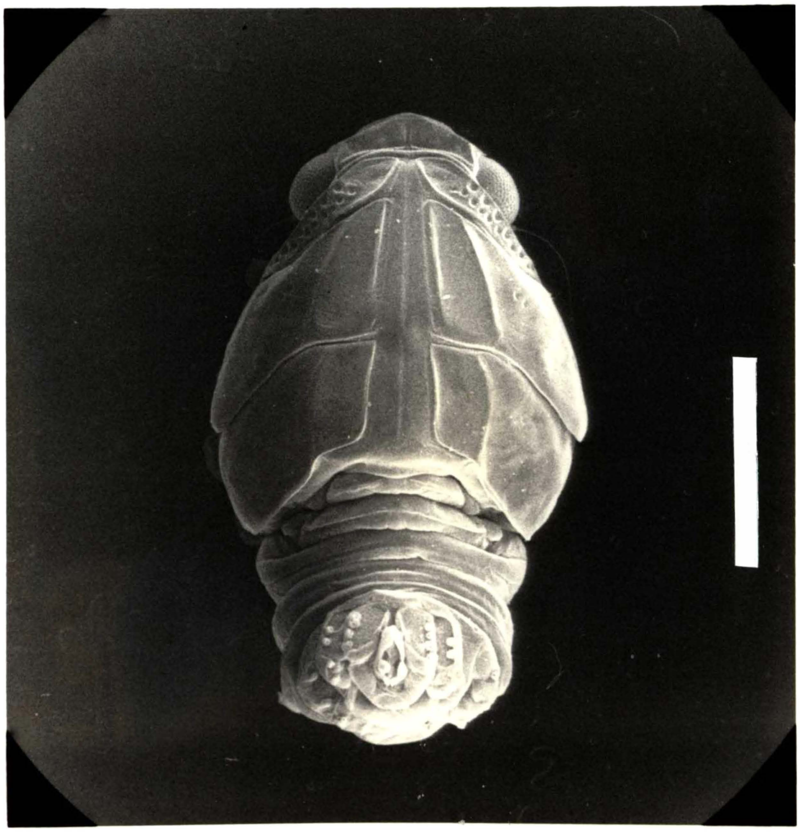
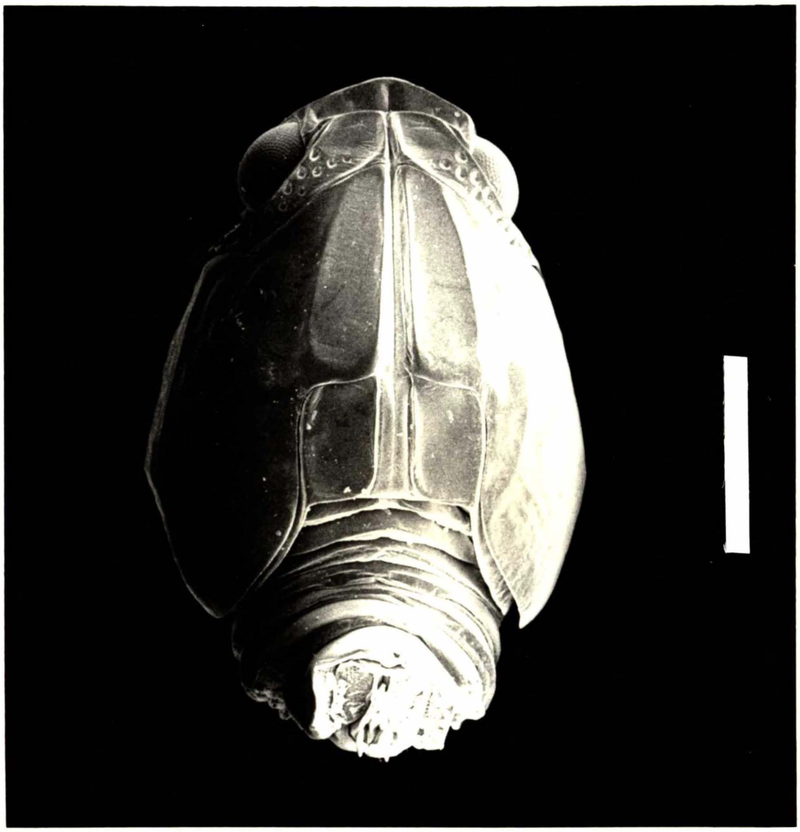


Fig. 3.11 Fifth instar *S. australis* nymph. (Scale = 1mm).



4.1 INTRODUCTION

Diapause has been defined by Harvey (1962) as "... a state of developmental arrest which persists even when environmental conditions are favourable for growth." Environmental conditions may function as a "trigger", but the final cause of arrested development is internal to the animal. Shelford (1929) suggested that the term "quiescence" be used in cases where development is stopped by unfavourable environmental conditions, but recommences as soon as conditions ameliorate. He also gave "diapause" its present meaning.

However, while this is the accepted terminology, there has been much debate in recent years on the subject. Mansingh (1971) proposed a new "physiological classification of dormancies in insects". Mansingh says: "The nature and extent of climatic variations are well distinguishable geographically, so should be the physiological adaptations required for survival in such areas. Recognition of such differences forms the basis for the proposed physiological classification of dormancies." However this classification has been rejected by Thiele (1973) who points out several cases of different dormancies operating in the same geographic location. In conclusion he states "The many different types of annual rhythmicity and dormancy even within one genus (*Pterostichus* (Coleoptera: Carabidae)) make it probable to assume a polyphyletic development of these adaptations to climates with severe winter conditions." Krysan *et. al.* (1977) also disagree with Mansingh on the basis of their studies of *Diabrotica virgifera* (Coleoptera: Chrysomelidae), a species whose egg diapause functions as an adaptation to both temperate and sub-tropical climates. *Scolypopa australis* appears to undergo an obligatory embryonic diapause throughout its New Zealand range (see below).

Müller (1970) proposed another new system where obligatory and facultative diapauses are roughly similar to "parapause" and "eudiapause". To avoid confusion, the term diapause will here be used in its customary sense (Harvey, 1962).

Diapause ensures that only a certain resistant stage of the insect's life cycle passes through unfavourable environmental conditions, and that development does not recommence prematurely. It occurs as an important adaptation in many species of insects, enabling them to persist in regions in which they might otherwise be killed by extremes of climate, or to maintain high numbers in an area which might only support a few. "Diapause may be of value to the species because it synchronizes the life-cycle with the weather and thereby ensures that the active stages of the life-cycle shall be present when there is an abundance of food and the weather favours rapid development and a high survival rate." (Andrewartha and Birch, 1954).

Differing theories of diapause are discussed in detail by Andrewartha (1952), Lees (1955, 1956, 1962), Hinton (1957), Howe (1967) and Tauber and Tauber (1976), and will only be mentioned briefly here. There are several main theories of diapause which are rejected by most workers on the grounds that they mistake the metabolic changes which must occur in the insect prior to diapause for the actual causes.

According to Roubaud (1922), diapause is initiated by a type of autointoxication (*asthenoboise*) when secretion of urates greatly exceeds disposal of waste products. Clear, experimental demonstration of this is lacking. Agrell (1951) suggests that the low respiratory quotient of diapausing lepidopteran pupae is caused by shortages of vitamins, thus inhibiting the Krebs cycle. However his initial assumptions and experimental results have been challenged (Schneiderman and Williams, 1953). Slifer's (1946, 1958) and Umeya's (1950) theory that dehydration initiates diapause is generally regarded as an example of effects being mistaken for causes.

The most widely-accepted theory of diapause is that it is under hormonal control. Larval and pupal diapause always begin at ecdysis, and result from the failure of the pro-thoracic ganglion to secrete ecdysone (Wigglesworth, 1948). In adult diapause, failure of the corpora allata to secrete corpus allatum hormone prevents maturation of the oocytes (Wigglesworth, 1936). Both these hormonal failures are due to the inactivity of the neurosecretory cells of the brain.

Diapause in eggs which have only just begun to develop must involve a different mechanism, because embryos do not possess an endocrine system. Fukuda (1951a, b) has determined the cause of embryonic diapause in the silkworm *Bombyx mori* (Lepidoptera: Bombycidae). The balance between concentrations of the "diapause factor", which is produced in the maternal sub-oesophageal ganglion, and the antagonistic hormone which is produced in the maternal corpora allata determines whether or not the egg will undergo diapause, and results in the different races of *B. mori*.

Embryonic diapause in *Orgyia antica* (Lepidoptera: Lymantriidae) is also induced by the product of the maternal sub-oesophageal ganglion .(Kind, 1972), and transplant of sub-oesophageal ganglia of many different insects into *B. mori* causes the production of diapausing eggs (Fukuda, 1951b; Hasegawa, 1952; Andrewartha *et. al.*, 1974). Diapausing eggs can be produced in *B. mori* by different cephalic organs of several insects (Takeda, 1977), suggesting that "... the substance(s) (associated) with the (diapause) hormone activity are ubiquitous in the cephalic organs of many insects."

Because of the difficulties in determining the causes of embryonic diapause not a great deal of work has been done on this subject, and it is quite possible that similar hormonal mechanisms will be elucidated in other species.

In most cases, the time spent in diapause is lessened if the egg is subjected to cold conditions for some time. This is achieved in natural conditions by passage through winter and is found in many temperature species, e.g. *Austroicetes* Acrididae (Andrewartha, 1943), *Spilosoma* Arctiidae (Baker, 1971), *Teleogryllus* Gryllidae (Browning 1952a, b, c; Hogan 1960a, b), *Ephippiger* Tettigonidae (Dean and Hartley 1977a, b), *Metatetranychus* (Acarina: Tetranychidae) (Lees, 1953), *Lymantria* Lymantriidae (Masaki, 1956), *Gryllus* Gryllidae (Rakshpal 1962a, b), *Leptophylemia* Muscidae (Way 1959, 1960) and *Myrmus* Coreidae (Woodward, 1952). The subject is briefly discussed by Roberts (1977).

Diapause in *Scolypopa australis* has been described as obligatory in New Zealand (Cumber, 1966). Cumber removed egg-containing material from several North Auckland field localities throughout autumn and winter and kept it at "normal laboratory temperatures", which presumably means that the material was not subjected to customary winter temperature conditions. No nymphs emerged from material thus collected before July, but material collected after that produced nymphs by August.

Information of the phenology of *S. australis* in Australia is sadly lacking. References in the Australian literature (e.g. Anon, 1973b; Froggatt, 1900 and Woodward *et. al.*, 1970) all fail to give details of the life history of the species.

In order to find out something of the life history of *S. australis* in Australia, and particularly to determine if a diapause is present, the author wrote to entomologists there. Information was received in reply on the localities from where *S. australis* has been collected, food plants, etc., but no details of species phenology were given. It is important to note that in Australia populations of *S. australis* do not reach the high densities that they do in New Zealand. Consequently the species is not considered a serious pest, and does not attract the same degree of attention as it does in this country. For instance, it is not regarded as a serious pest of passionfruit in Queensland (Murray, 1976). A list of localities from where *S. australis* has been reported in Australia can be found in Appendix 1.

The present series of results was designed to confirm Cumber's (1966) results in Waikato conditions, and to determine some parameters of the diapause under artificial conditions (e.g. duration, intensity, embryonic stage at which diapause intervenes, etc.).

4.2 MATERIALS AND METHODS

4.21 *Diapause under natural conditions*

Lengths of stems and tendrils containing *S. australis* eggs were collected from a row of raspberry (*Rubus idaeus* L.) and passionfruit (*Passiflora edulis*) plants, and placed in glass test tubes. Two such lengths were placed in each 19mm x 150mm glass test tube, which was stopped with 0.8mm mesh plastic gauze, held in place by a holed bark cork. This was done to prevent the escape of hatched nymphs, but at the same time to allow free passage of air.

28 tubes were filled and left outside in natural temperature conditions, but under a lean-to, to prevent collection of rain water in the tubes. Every fortnight from 1st April 1977 to 30th September 1977 inclusive, two tubes were removed and placed in constant temperature conditions, one tube being placed at 16 °C and the other at 22°C. They were examined weekly to determine numbers hatched.

4.22 *Diapause under artificial conditions*

Stems of the respberry plant (*Rubus idaeus*) containing *S. australis* eggs were collected from a row of plants growing against a garage wall. The material containing the eggs was mostly dead branches from the lower portion of the plant, up to a metre or so from the ground. Eggs were not found in green stems and leaves.

Two lengths of stem approximately 60-100mm long and containing approximately 100-200 eggs were placed in each 24mm x 150mm glass test tube. The tubes were stopped with 0.8mm mesh plastic gauze held in place with a bark cork. 352 such tubes were collected, and from counts made on a random selection of 28 of these, it is conservatively estimated that *in toto*, approximately 60,000 eggs were collected for this part of the experiment alone.

The eggs which were collected were subjected to various constant temperature conditions. This entailed a period of 0, 1, 2, 4, 6 or 8 weeks at 16°C or 22°C to simulate pre-diapause conditions. A period of 0, 2, 4, 6, 8 or 12 weeks at 3°C, 11°C or 16°C then followed, to enable diapause to be completed. Following this the tubes were kept at 16°C or 22°C, and examined weekly to determine numbers hatched. The temperature conditions are shown diagrammatically in Fig. 4.1. There are 352 combinations of temperature and time spent at each temperature, and one tube was subjected to each combination.

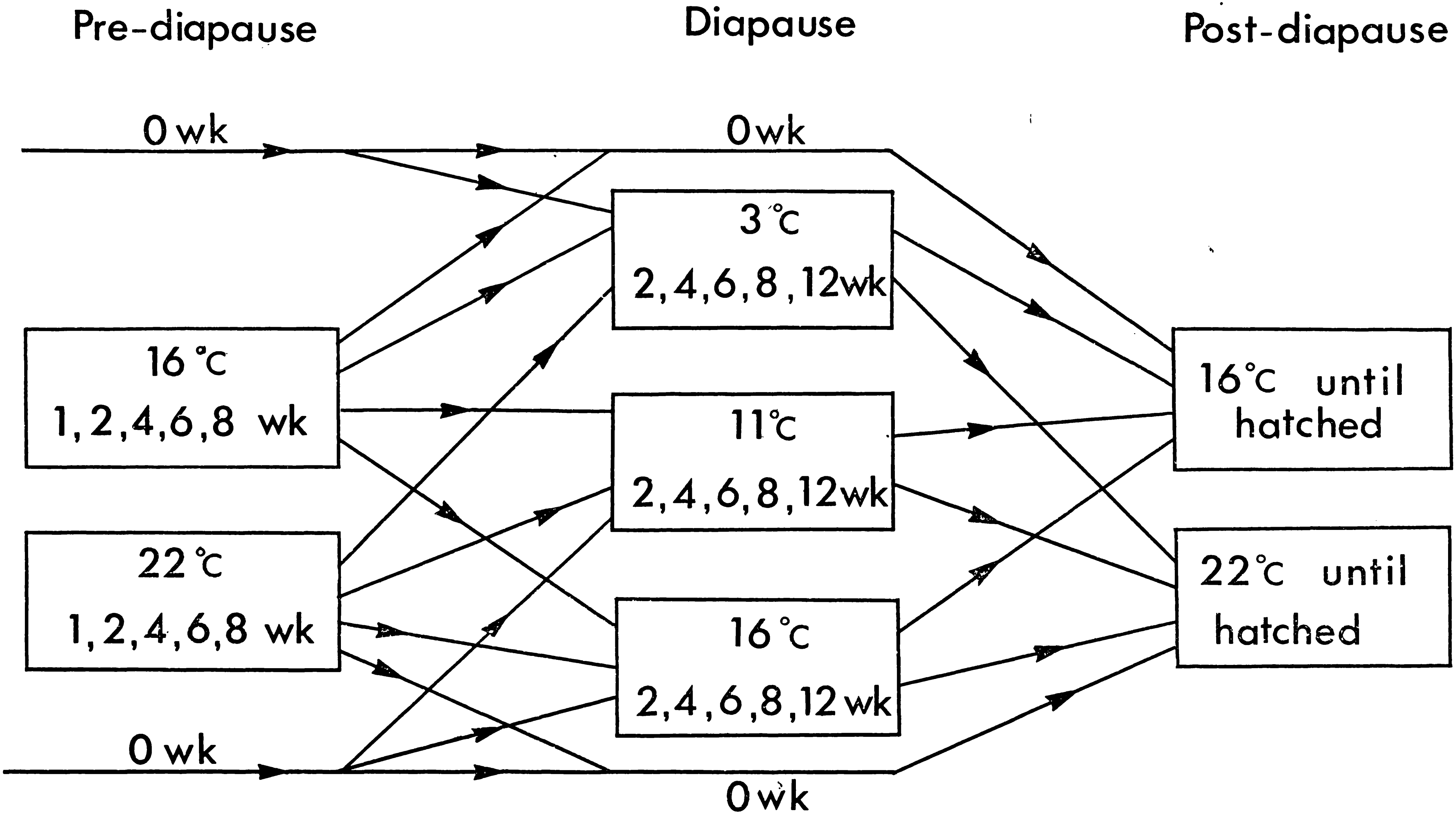
The temperatures were chosen so that natural Waikato conditions (Gerlach, 1974: 44) would be simulated, with considerable overlap both in temperature and duration. It was expected that some eggs would hatch and some would not, giving cut-off points for parameters of the diapause.

The temperature in the constant temperature rooms was measured with a thermohygrograph and found to vary only by about ± 0.5°C. The relative humidity was measured (at the end of the experiment) with a Telemechanics relative humidity meter. Conditions in the rooms are given in Table 4.1.

TABLE 4.1 Constant Temperature Environments Used for Diapause Experiments

Temperature	Facility	Relative Humidity	Photoperiod
3°C	constant temperature room	31%	L:D 0:24 hr
11°C	constant temperature room	56%	L:D 12:12 hr
16°C	B.O.D. cooled incubator	24%	L:D 0:24 hr
22°C	constant temperature room	45%	L:D 14:10hr

Fig. 4.1 Schematic diagram of the temperature regimes used in the diapause experiment (Section 3.22).


Pre-diapause
Diapause
Post-diapause
0 wk
0 wk
16 °C
1,2,4,6,8 wk
22 °C
1,2,4,6,8 wk
0 wk
3 °C
2,4,6,8,12wk
11°C
2,4,6,8,12wk
16 °C
2,4,6,8,12 wk
0 wk
16°C until hatched
22°C until hatched

4.3 RESULTS

1. No nymphs emerged from any material which spent the winter in constant temperature environments (Section 3.22). Some eggs were extracted from the plant matter in October, and immersed in 95% ethanol. This renders the chorion transparent, and any development is visible. No embryos could be seen in any of this material.

2. Eggs collected from various Hamilton field sites (other than from where the experimental material was collected) was examined at the same time. Discounting eggs that were already ruptured or shrivelled (which may have been damaged in the extraction process), 95% of the eggs contained a well-developed embryo. Segmentation, appendages, and eye spots could all be seen clearly.

3. Eggs from the experimental collection site that had been in a plant over the winter were examined in a similar fashion. Only 36% of the eggs contained developing embryos.

4. Some egg-containing plant material was kept under a lean-to (as described in Section 3.21). These eggs were subjected to ambient temperatures, but protected from rain. Only 11% of these eggs showed any development.

5. Tubes containing egg material were also placed in a garage in which they were slightly sheltered from ambient temperatures, but completely removed from moisture and light. None of these eggs developed.

4.4 DISCUSSION

The *S. australis* eggs at the experimental collection site had a much lower viability than those at other places, so that of the eggs subjected to artificial temperature regimes, many were not competent to develop.

One possible explanation for this is that either the adults or the eggs were exposed to chemicals which either induces partial sterility or had an ovicidal action. McIntyre and Mills (1975: 35) remark that "... insects that survive applications of insecticides may have reduced egg production, reduced fertility of eggs, and even complete sterility." The experimental material was collected from a suburban garden adjacent to two neighbouring properties and it is not possible to determine every chemical to which the insects were exposed. For instance, it is now known that Paraquat weed killer was applied to the immediate vicinity shortly before collection took place (unknown to the author!). This may have affected either the eggs or the adults.

Eggs which were sheltered from the rain (4) showed a further drop in viability, indicating that an artificial lowering of humidity at the egg's micro-environment may kill the egg. Under natural conditions, eggs deposited inside dead plant stems are somewhat insulated from the extremes of the physical environment, but may be reliant on periodic rain to maintain high humidity in the micro-environment of the egg (Southwood, 1956). The eggs kept in the garage (5) showed an even greater drop in viability than those simply kept out of the rain. The garage is completely enclosed and thus very dry, and this result would tend to confirm the observation that a high humidity is necessary for development of the egg.

In the field, oviposition occurs in stems that are near the ground amongst dense growth in sheltered, shady, and relatively humid environments. This has been particularly noted in the drier climates of Australia (M. Casimir, pers. comm.). With the benefit of hindsight it seems that humidity is one of the most crucial factors determining the survival of the developing egg. Although there is no hydropyle through which to take up free water (see Chapter 4), high humidity would be necessary to prevent dessication through the chorionic respiratory system.

It is not known whether or not photoperiod length plays any part in either initiating or terminating diapause in *S. australis*. Hinton (1953) remarks that "When a species diapauses in a late embryonic stage or as a definitive larva within the egg shell, determination of diapause may occur in the same generation. When, however, diapause occurs before development of the nervous system, the diapause is often (always?) maternally determined, as it is in the silkworm and in the mite, *Metatetranychus ulmi* Koch (Lees, 1953)." From field observations it is known that *S. australis* does diapause in a very early stage, and it would not, therefore, seem likely that the light regime in which the eggs were kept would have any effect on either the evocation or termination of diapause in this species.

Two other problems are worthy of mention. *S. australis* inhabits an environment in which temperatures normally fluctuate to some considerable degree. Constant temperatures therefore represent "unnatural" conditions, and although most diapause experiments are carried out in constant temperature environments, cases are known of cyclically fluctuating temperatures being necessary for survival of insects. Certainly the development of many insect species is retarded in comparison with those kept at oscillating temperatures (Cloudsley-Thompson, 1953). The study of insect development under oscillating temperatures is more difficult because of the numbers of parameters to decide upon. Variations are possible in minimum, maximum, and mean temperatures, time spent at minimum and maximum, rate of change between, etc. (Messenger and Flitters, 1959). The decision to employ constant-temperature conditions was also influenced by the range of facilities available.

The temperatures used were decided upon after consideration of Waikato climatic conditions (Gerlach, 1974: 44), but the decisions were largely based on guesswork. From his studies of egg and pupal development of *Spilosoma lubricipeda* (Lepidoptera: Arctiidae), Baker (1971) points out the many difficulties in relating development occuring in the fluctuating temperature conditions of natural environments to development/velocity curves determined in the laboratory under constant temperature conditions. In conclusion he states (p. 21): "It is not valid to sum temperatures on a linear basis and try to relate the result to a curvilinear function such as development (Richards and Suanraska, 1962). The same environmental conditions occuring at different times during the development cannot be given the same weight. This may apply throughout development if the hypothesis is correct that the various processes which together make up development respond to temperature in different ways." It cannot be known, therefore, what temperature conditions are required for development, simply by looking at climatic data for the area. Greater knowledge of the embryonic developmental processes of

S. australis, including developmental thresholds etc., must be obtained before much can be learned about the nature of the diapause. Certainly this is necessary before any forecasts can be made about development in the field. It was hoped that this experiment would provide much of this information.

4.5 SUMMARY

1. A large amount of plant matter containing *S. australis* eggs was collected and subjected to 352 different artificial temperature regimes, and varying degrees of "natural" environments.
2. No nymphs hatched from any of this material.
3. It is suggested that this was due in some measure to the unnaturally low humidity of the incubating chambers.
4. Various other possibly relevant factors are discussed; viz. defects in the population from which the eggs were collected, the photoperiod under which the eggs were incubated, and the degree of "naturality" of the artificial temperature conditions.

5.1 INTRODUCTION

Insects require a relatively large surface through which to absorb oxygen from the ambient environment. Because the oxygen molecule is larger than the water molecule, insects inhabiting dry environments are presented with the contrasting demands of absorbing oxygen, but at the same time conserving water. Hinton (1969) remarks that "dry environments present insect eggs, no less than other stages, with the contradictory demands already noted. The different types of chorionic respiratory systems that have been evolved in large measure reflect different solutions to the same problem: oxygen needs must be satisfied without losing too much water."

Although there are many differing solutions to this problem, the egg-shells of terrestrial insects possess many features in common. From the studies of many species, but in particular *Rhodnius prolixus* Stål (Heteroptera: Reduviidae) (Beament 1946a, b; 1947) and various Diptera (Hinton, 1967; Wigglesworth and Saltpeter, 1962), it is known that the majority of terrestrial eggs have meshworks in the chorion that hold a layer of gas. All such eggs also have aeropyles or holes connecting the gas-containing meshwork layer with the atmosphere. The interstices of the meshwork are, as would be expected, at least as wide as the mean free path of the respiratory gases (0.1nm for oxygen at 23°C). Gas exchange may also be achieved through the apparently solid chorion. In his study of the egg-shell of the wheat bulb fly *Leptohylemia coarctata* Fallén, Hinton (1962) states that the chorionin is made up of fibrils with interstices wide enough to permit gaseous exchange (in this case 2.0-2.5nm wide).

Since the chorion is laid down in the ovary, some provision is necessary to allow the subsequent entry of sperm. This takes the form of micropyles, which are canals passing through the chorion. They vary in number from one to several hundred, depending upon the type of insect.

Respiration systems in insect eggs have been reviewed by Hinton (1962a, 1969), Tuft (1950), and Wigglesworth and Beament (1950). The structure of the eggs, including the respiratory and micropylar systems, of Heteroptera has been reviewed by Southwood (1956) and Cobben (1968); and Cobben (1965) has also studied the respiratory and micropylar systems of the eggs of Homoptera.

In this study of the egg of *Scolypopa australis*, the aim was to describe the external morphology of the egg, and also to gain some insight into the nature of the aero- and micropylar system.

The structure of the chorion, and in particular the aeropylar and micropylar systems, has attracted a great deal of attention and has been studied in many different species, e.g. *Calliphora* Calliphoridae (Anderson, 1960), *Galleria* Galleriidae (Barbier and Chauvin, 1974), *Rhodnius* Reduviidae (Beament 1946a, b, 1947, 1948, 1949), *Metatetranychus* (Acarina: Tetranychidae) (Beament, 1951), *Tetrix* Tetrigidae (Hartley, 1962), *Deraeocoris* Miridae (Hartley, 1965), *Homorocoryphus* Tettigonidae (Hartley, 1971), Nepidae (Hinton, 1961), *Helopeltis* and other Miridae (Hinton, 1962b), *Leptohylemia* Muscidae (Hinton, 1962c), *Musca* Muscidae (Hinton, 1967), *Graphognathus* Curculionidae (Holdom, 1977), *Sphaerodema* Belostomatidae (Madhavan, 1974), *Chrysopa* Chrysopidae (Mazzini, 1970), *Hyalophora* Saturniidae (Smith *et. al.*, 1971), *Clitarchus* Phasmidae (Stringer, 1968), *Haematopinus* Haematopinidae (Hinton, 1977), *Lygocoris* Miridae

5.2 MATERIALS AND METHODS

5.21 *Scanning electron microscopy*

Plant material containing eggs was removed from the field in early autumn, approximately 1-2 months after oviposition. The eggs were extracted from the plant material (in this case raspberry canes) by splitting the stems lengthwise with a scalpel, snapping the twig in two, and simply collecting the eggs that fell out. These were then fixed overnight with 4% gluteraldehyde in phosphate buffer pH 7.2 at 4°C. The eggs were dehydrated in a graded ethanol series and infiltrated with Freon. Material was dried in a Polaron E 3000 critical-point drying apparatus and coated with a 50nm layer of gold in a Poloron E 5000 diode sputter system. Eggs were then examined in a JEOL JSM-35 scanning electron microscope at 25 kV. Photographs were taken with an Asahi Pentax 35mm SLR camera mounted on the microscope.

5.22 *Light microscopy*

At first, sectioning was attempted using the usual paraffin wax method (Eltringham, 1930). Cutting at thicknesses between 5µm and 15µm did not produce any useful results because of the hardness of the chorion and relative softness of the embedding medium. Stringer (1968, 1969), studying the eggs of the phasmid *Clitarchus hookeri* White, achieved only partial success using double embedding in celloidin and wax (Thomas, 1936), and was successful only with a complex technique using dioxan which was developed by Anderson (1964). It was therefore decided to use the epoxy resins employed. in cutting sections for transmission electron microscopy.

Epon 812 (Luft, 1961) was tried as the embedding medium, but did not produce satisfactory results. It is thought that this was due to incomplete penetration of the egg because of the high viscosity of the medium. Better results were obtained using Spurr's (1969) low-viscosity embedding medium.

The fixative used was gluteraldehyde 3%/formaldehyde 2% in Millonic's phosphate buffer pH 7.2 (see Appendix 2). Eggs that had been punctured with a fine entomological pin were fixed in this for 3 hours at 4°C, rinsed three times in the phosphate buffer (10 minutes per rinse), and post-fixed with osmium tetroxide 1% in phosphate buffer pH 7.2 for 1 hour. The material was dehydrated in an acetone series and embedded in standard Spurr's embedding medium (see Appendix 2).

Sections 1-2μm thick were cut with a glass knife on a Reikhert ultramicrotome, and stained using the methylene blue/basic fuchsin method developed by Aparicio and Marsden (1969). The staining procedure is as follows: 1% methylene blue in 1% borax (sodium tetraborate) for 15 seconds on a hot plate; wash in hot water; 2% basic fuchsin in distilled water 1-2 minutes at room temperature; wash, dry and mount in DPX. This technique gives a dichromatic section which is better than the monochromatic result achieved with stains such as toluidene blue.

Photographs were taken with a Nikon-F 35mm SLR camera mounted on a Reikhert Zetopan compound microscope, at a magnification of 1,000 times.

5.3 OBSERVATIONS

5.31 *Electron microscopy*

The egg of *S. australis* is a regular ovoid approximately 0.8mm long, and 0.4mm wide at the widest diameter (Fig. 5.1). In the anterior third or so of the egg, the surface is embossed with small tubercles (*Tuberkeln*: Cobben, 1965) (Fig. 5.2, 5.3) which reach their greatest height(about 3.5μm) towards the anterior pole (Fig. 5.4). The hexagonal imprints of the follicle cells can be clearly seen in the chorion of the egg, and are more or less regularly marked at each vertex by a tubercle (Fig. 5.5, 5.6). The anterior protruberence has been variously termed an aero-micropylar "process" (Southwood, 1956), or "cup" (Cobben, 1968 (*aufsatz*: Cobben, 1965)). In *S. australis* this structure is approximately 40μm across at the distal end, and reaches about 20-30μm from the surface of the egg. Examination of this structure clearly shows the central micropyle surrounded by spongy chorion material (Fig. 5.8, 5.9). The micropyle is a circular hole of approximately 2.2μm diameter.

The internal structure of the chorion can be seen where the eggs being examined have been torn (Fig. 5.10, 5.11). An open, meshwork layer occupies the interior third of the chorion, and the remaining portion appears to be more or less solid.

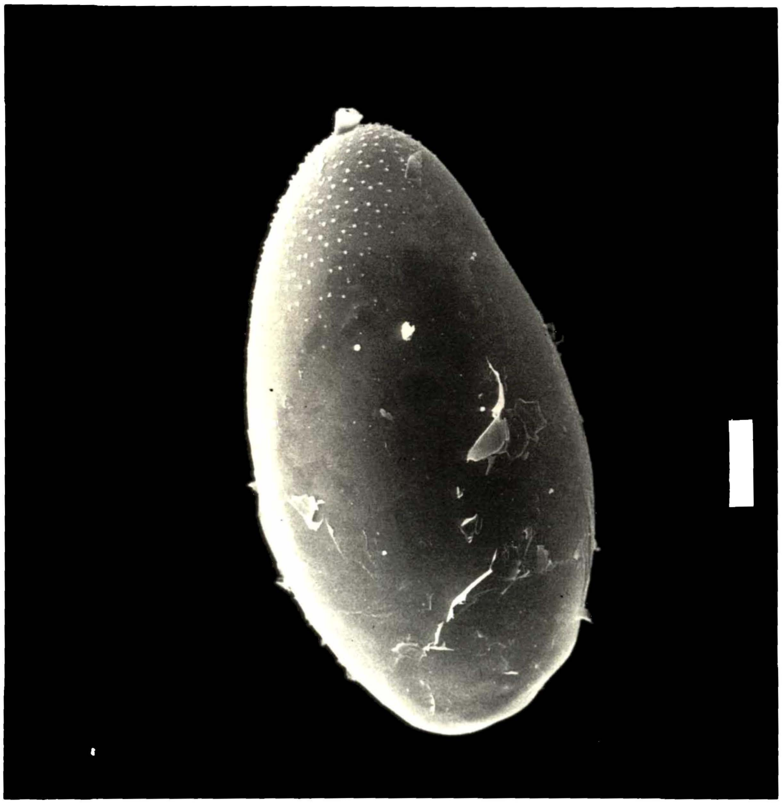
5.32 *Light microscopy*

The chorion of the eggs embedded and sectioned in Spurr's resin was usually torn away from the rest of the egg (Fig. 5.12). Closer examination of the chorion (Fig. 5.13, 5.14) confirms the existence of the inner meshwork layer and remaining solid portion seen with the SEM.

In most places, the vitelline membrane has been separated from the chorion (Fig. 5.15).

Fig. 5.1 *S. australis* egg. (Scale = 0.1mm).

Fig. 5.2 Tubercle on egg surface. (Scale = 1μm).



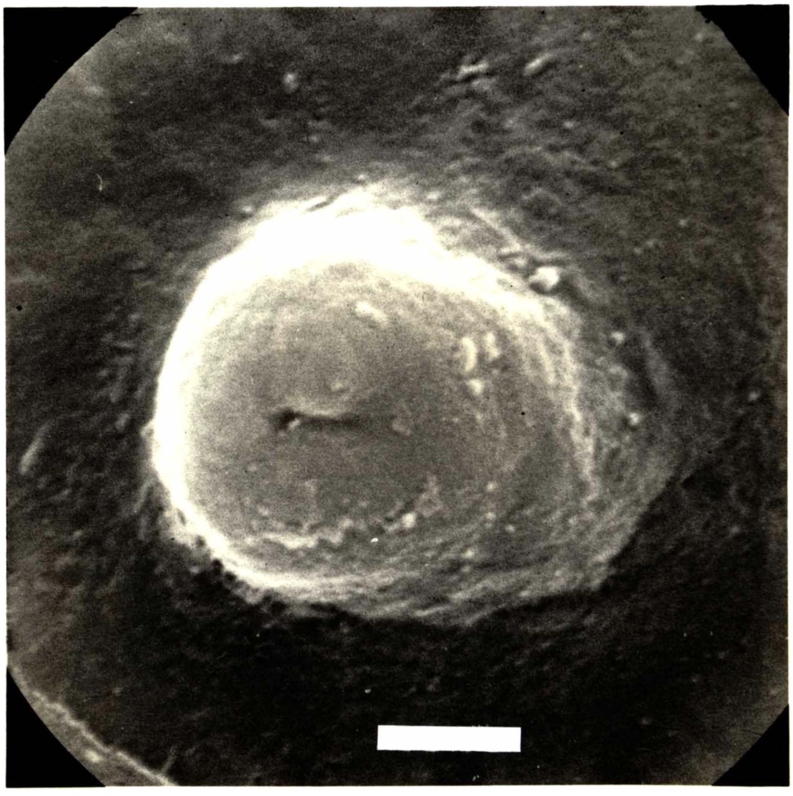
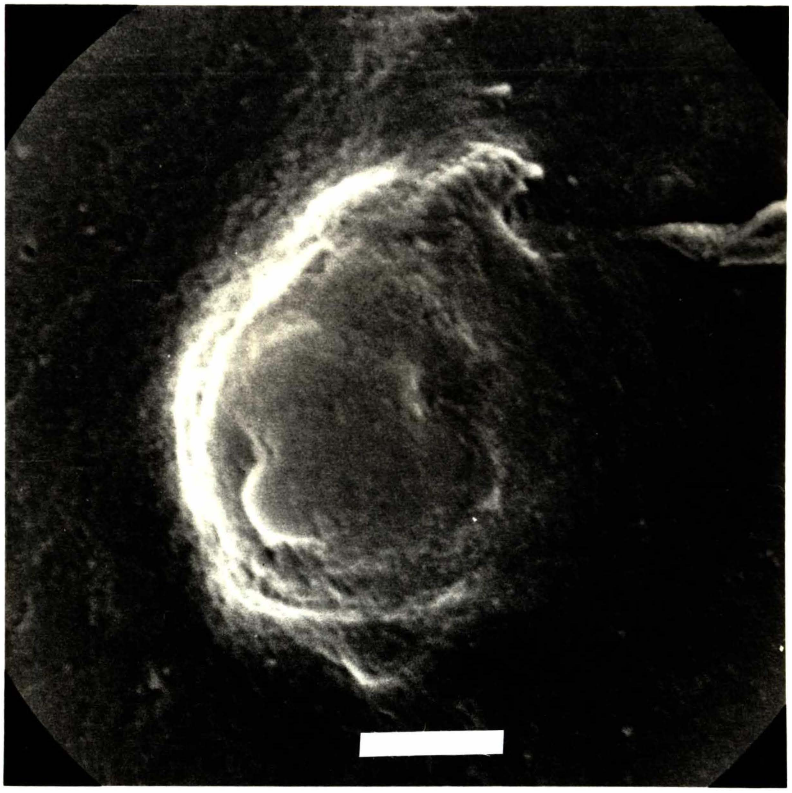


Fig. 5.3 Tubercle on egg surface. (Scale = 1μm).

Fig. 5.4 Anterior portion of egg, showing distribution of tubercles. (Scale = 0.1mm)



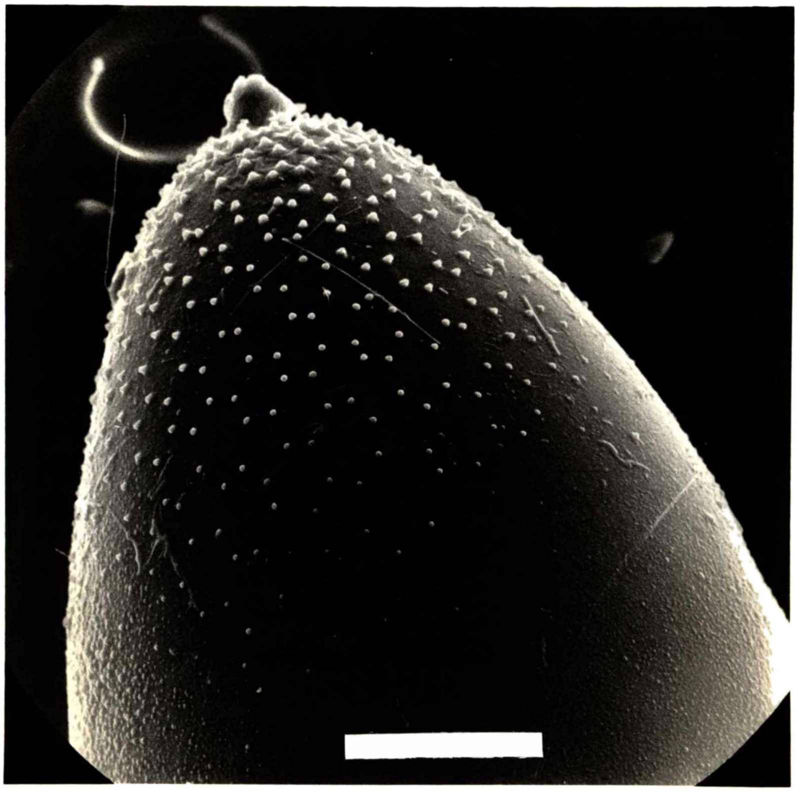
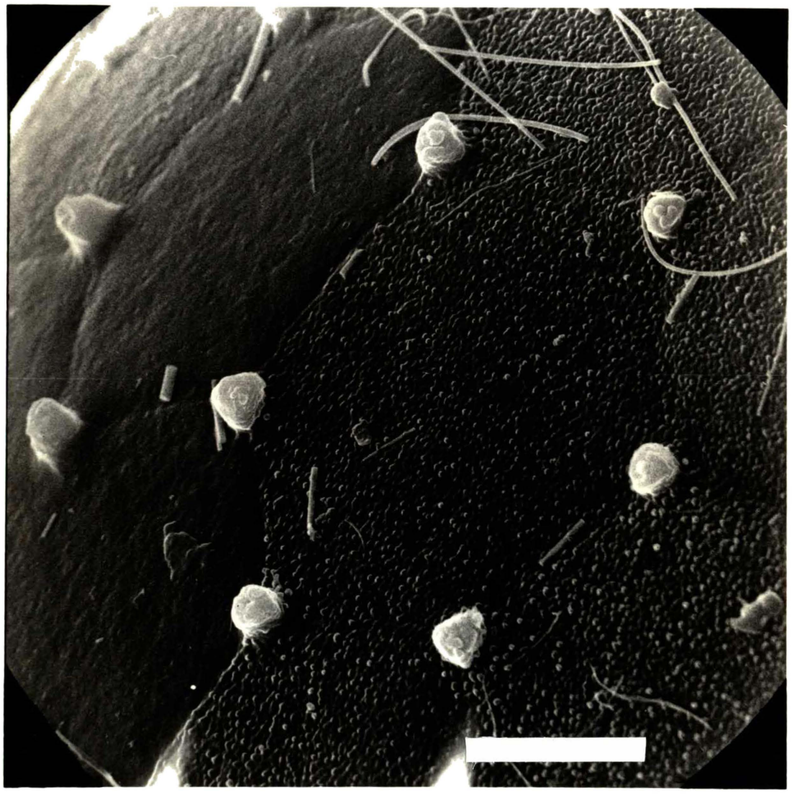


Fig. 5.5 Egg surface, looking towards anterior pole. Note tubercles marking vertices of the hexagons, and the comparison of smooth and rough surfaces. (Scale = 10µm

Fig. 5.6 Top layer of chorion peeling off. Tubercles still in hexagonal array. (Scale = 10µm



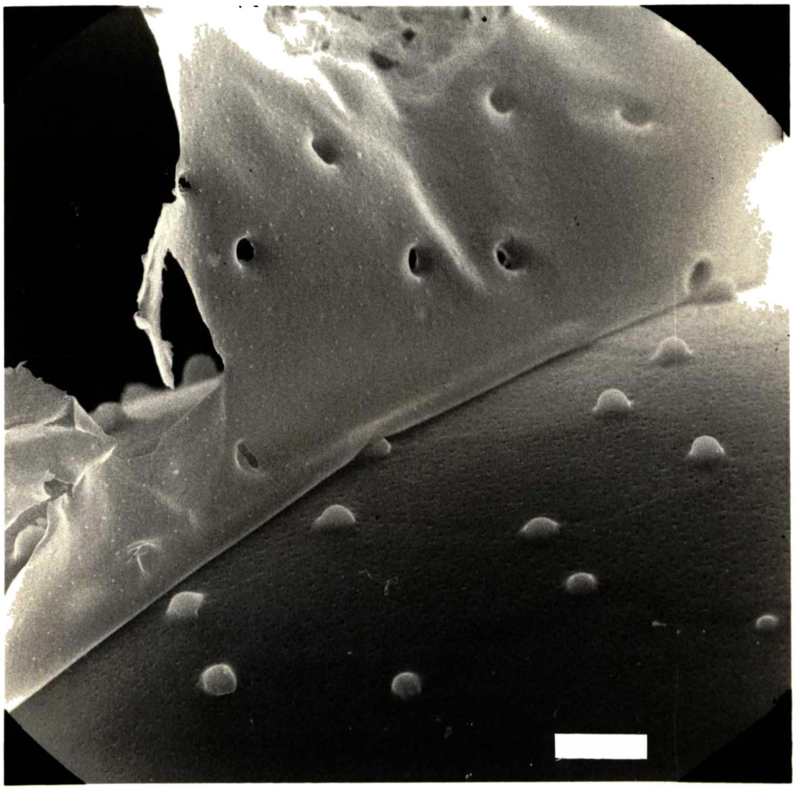
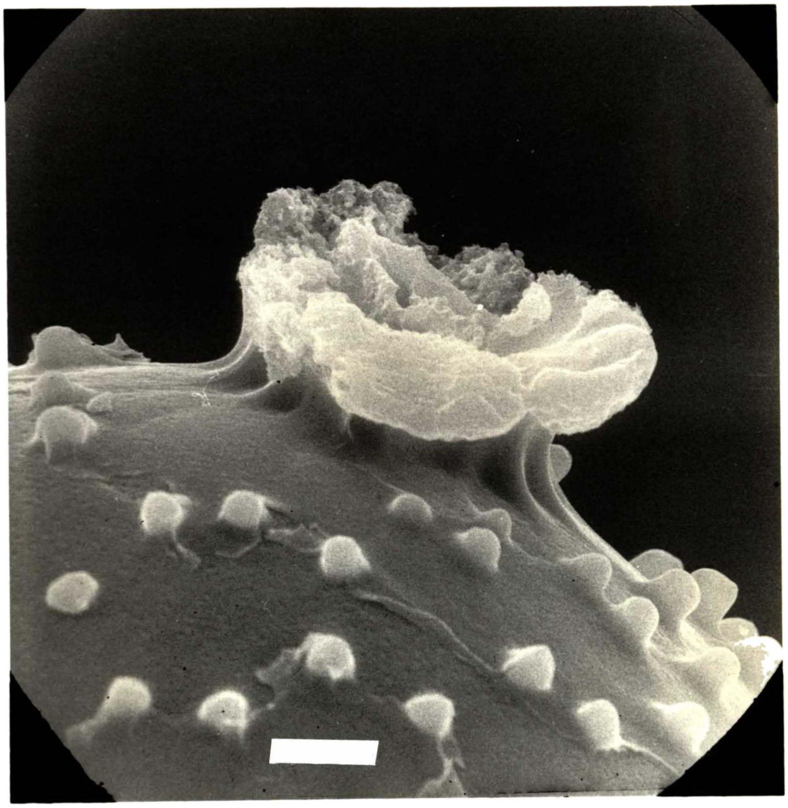


Fig. 5.7 Anterior micropylar process. (Scale = 10μm)

Fig. 5.8 Anterior view of aero-micropylar process, showing central micropyle surrounded by spongy chorion material. (Scale = 32 μm).



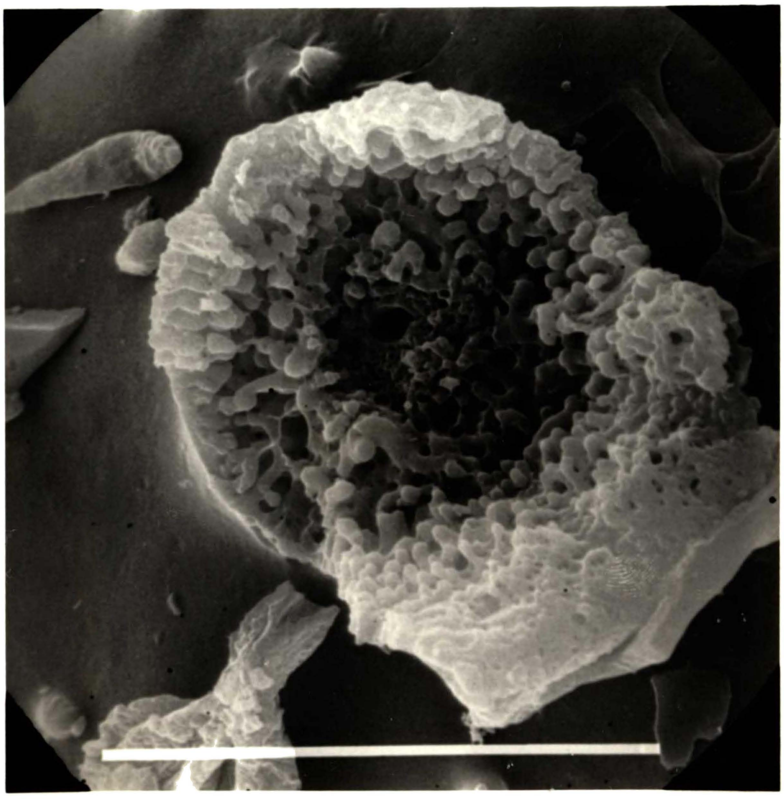


Fig. 5.9 Anterior view of aero-micropylar process, showing central micropyle surrounded by spongy chorion material. (Scale = 1µm).

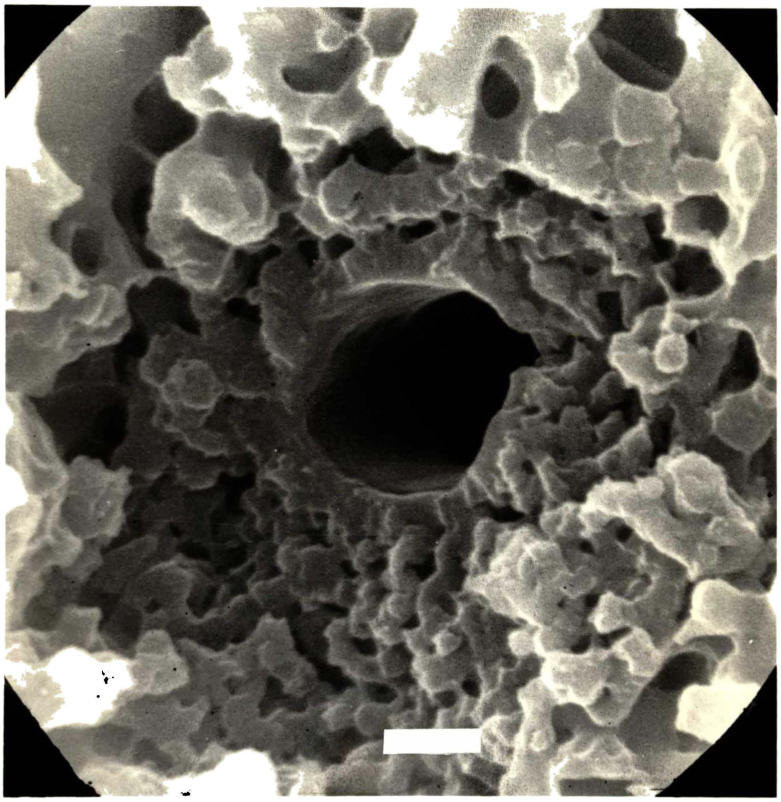


Fig. 5.10 Torn portion of the chorion, looking from the outside.

(Scale = 2μm)

Fig. 5.11 Torn portion of the chorion, looking from the inside.

(Scale = 1μm)

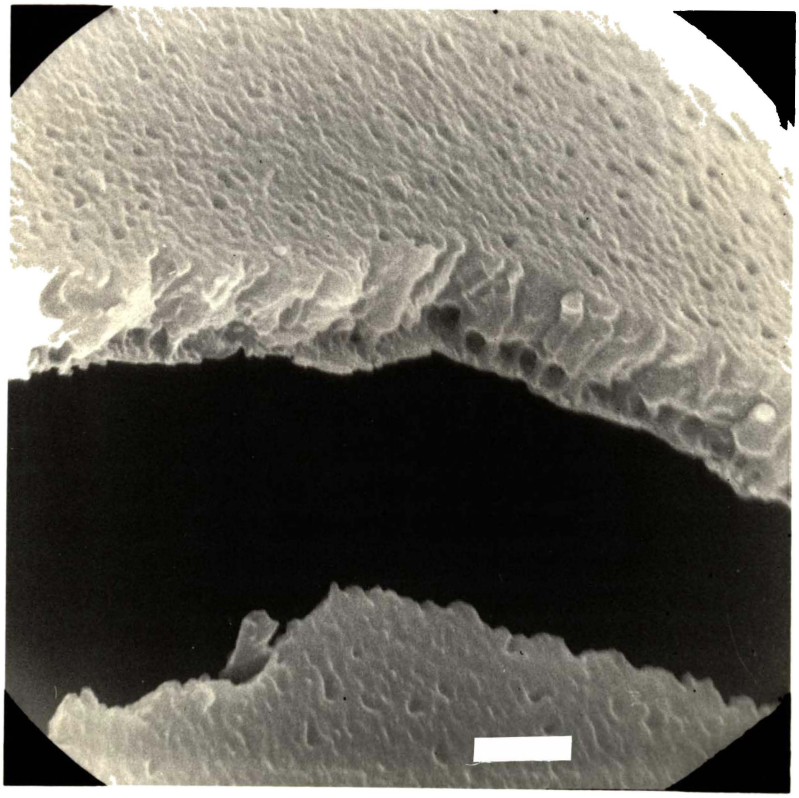
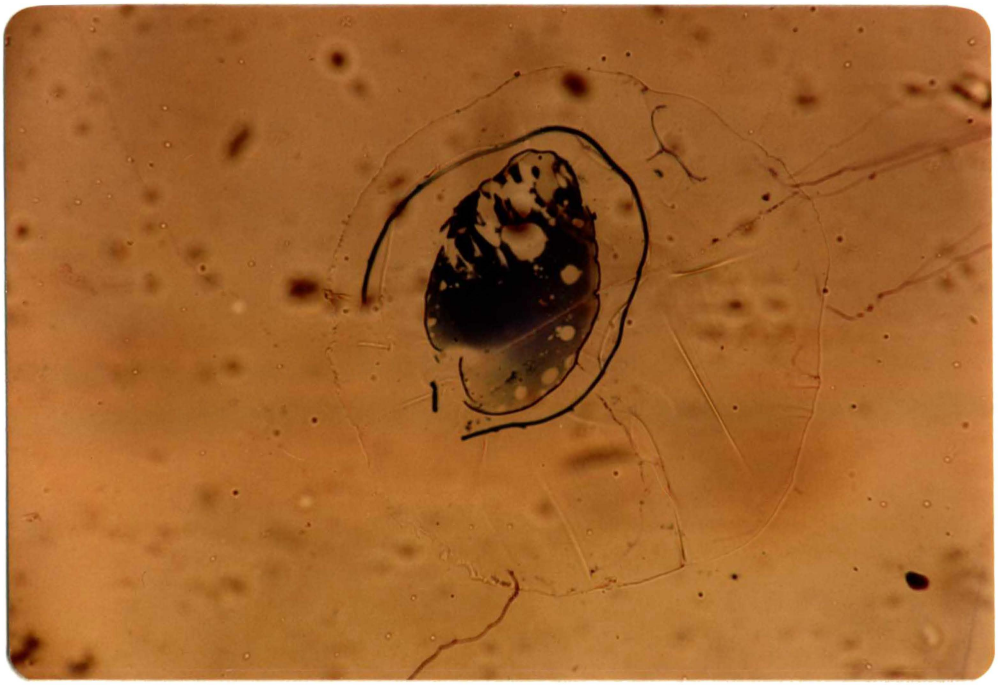


Fig. 5.12 Section of *S. australis* egg with chorion torn away from egg. 100 x

Fig. 5.13 Cross section of chorion, showing inner meshwork layer. 1,000 x.



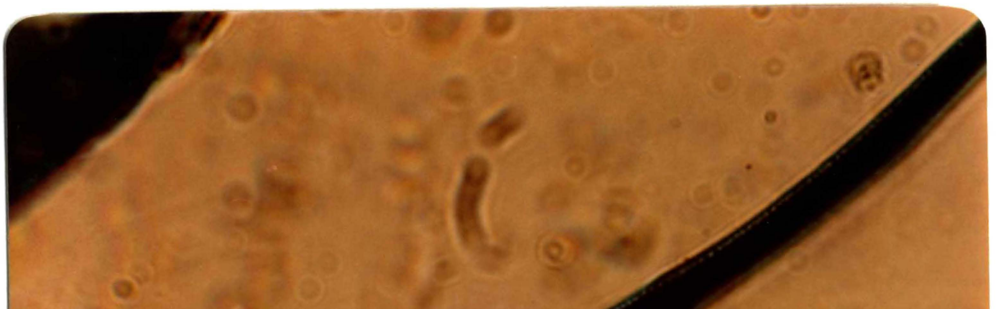
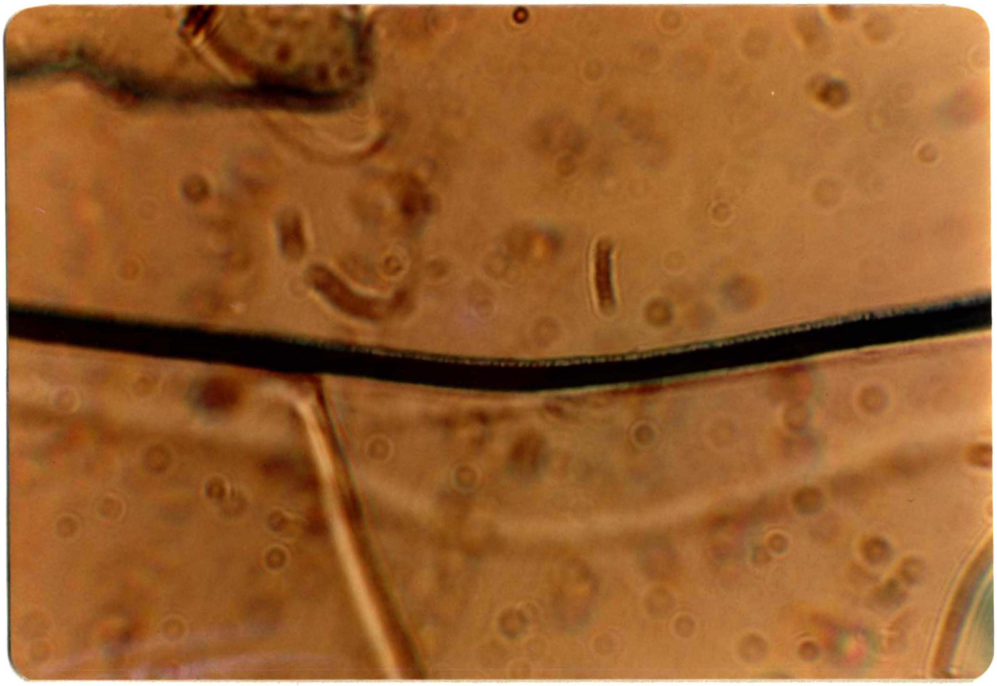
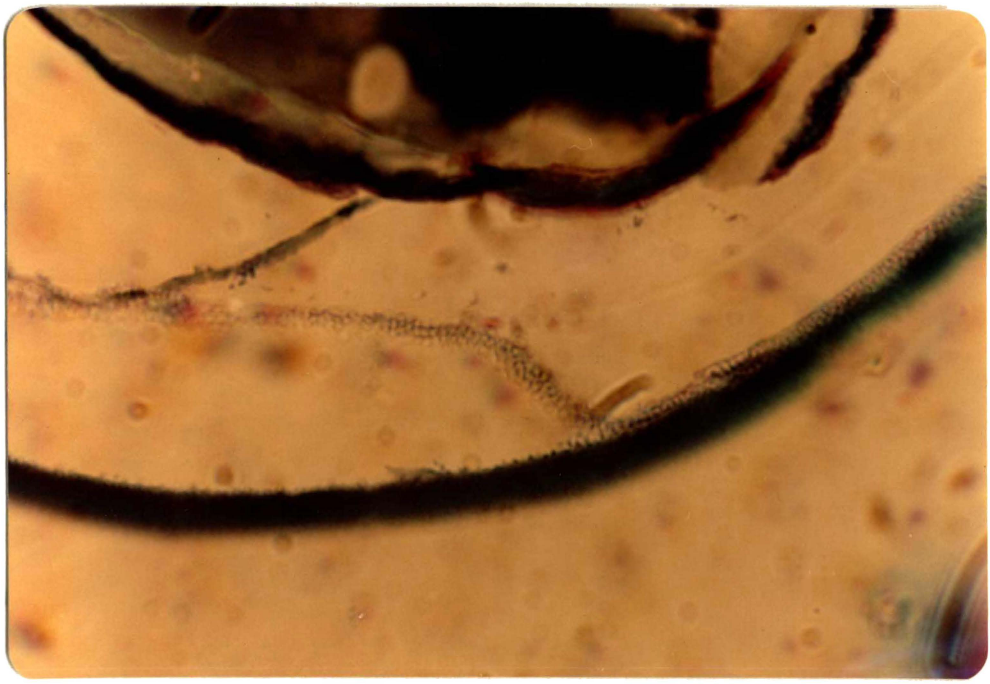


Fig. 5.14 Cross section of chorion, showing inner meshwork layer. 1,000 x.

Fig. 5.15 Vitelline membrane adhering in places to the chorion. The inner meshwork layer cannot be seen due to twisting of the section of chorion. 1,000 x.





5.4 DISCUSSION

The regular ovoid shape of the egg is typical of many Homoptera, the eggs of which are usually quite simple in form unlike in Heteroptera, where many elaborate structures are seen (Southwood, 1956). Hexagonal imprinting of the shape of the follicle cells is also a very common feature in insect eggs.

Conclusive proof of the aeropyle's connection with the interior meshwork layer is lacking from this study, however this is strongly suggested both by the evidence from this study and the literature. For instance, Cobben (1965) remarks that "Some fulgoromorph eggs have an anterior central prominence which outside the micropyle is usually surrounded by sponge-like chorion material, continuing all around the egg shell in a thin porous layer.... The structure resembles the aero-micropylar protruberences of pentatomorph bugs" (p. 42, translation).

It is thought that the tubercles do not contain aeropyles. Most appear solid (Fig. 5.3), although some appear as if they could contain an opening (Fig. 5.4). Cobben (1965: 21) says that in *Ricanula* sp (Ricaniidae) eggs scattered aeropyles are lacking, and the exterior openings of the respiratory system are contained in the circumspheral porous collar of the anterior process.

Many terrestrial insect eggs are submerged when it rains, and must therefore be adapted for both aquatic and terrestrial respiration, or else curtail metabolic activities when submerged. A number of terrestrial insect eggs that have been studied possess plastron-bearing structures, to permit gaseous exchange when submerged in water (Hinton, 1969). However these eggs are laid in places where prolonged flooding is possible or even frequent, and plastrons are generally not found in eggs that are laid in places that drain readily. *S. australis* eggs are laid mostly in vertical or near-vertical stems, which do not accumulate water during rainy periods. A plastron would not, therefore, be necessary, and no evidence of plastron-bearing structures can be seen in the electron micropyles.

There is no visible hydropyle through which water can be taken up. As mentioned above, *S. australis* is never exposed to free water and thus never absorbs water during development. Southwood (1956) categorizes oviposition sites into four classes, based on their relationship to the environment. Only eggs in or associated with living plant tissue absorb water, whereas *S. australis* eggs are laid in dead plant tissue.

No canals traversing the cut sections could be seen with the light microscope. The small holes in the outer surface of the chorion which were seen with the SEM (Fig. 5.10) may or may not connect with the inner meshwork layer. Further examination of sectional material using the transmission electron microscope would be necessary to settle this question. Lack of time and difficulties with the supply of chemicals prevented this from being carried out as part of this study.

5.5 SUMMARY

1. The egg of *S. australis* was examined with the scanning electron microscope and in section with the light microscope.
2. The egg is of typical fulgoromorph structure, being a regular ovoid in chape and bearing an anterior micropylar process.
3. The anterior micropylar process consists of a central micropyle surrounded by spongy chorion material.
4. There is no hydropyle, nor any evidence of plastron-bearing structures. Scattered aeropyles are probably not present.
5. The chorion in section is made up of one-third inner meshwork layer and two-thirds solid outer layer.

6.1 INTRODUCTION

Fully sclerotised insect cuticle does not expand, so growth of sclerotised parts of an insect body must occur stepwise, increases in size of an insect taking place only at each moult. Different parts of the body grow at different rates, this being due to variations in the hormonal control processes (Gould, 1966). The result of this is that each cuticular structure (leg, head, thorax etc.) has a rate of growth that is peculiar to itself.

When compared with the growth of the insect as a whole, a particular part of the body may change in size at a greater, lesser or equal rate (positive or negative allometry, isometry). Huxley and Teissier (1936) denoted this by the formula

$$y = bx^{\alpha}$$

where y is the part, x is the standard or whole, α is the growth rate of the part, and b is the initial growth index (a constant which represents the value of y when $x = 1$).

This means that the relationships between the sizes of different cuticular body parts of an insect should be unique (or reasonably so) for each stadium of its growth. This was first recognized by Dyar (1890), who studied head capsule widths of lepidopteran larvae and developed a general principle known as Dyar's Rule or Law. This states that "... the widths of the head of a larva in its successive stages follow a regular geometrical progression..." (Dyar, 1890: 420), i.e. can be described by the formula $y = bx^{\alpha}$ where α is a constant. Crosby (1973) pointed out that Dyar's Rule is predated by Brooks (1886), who developed a similar formula for larval stages of a stomatopod crustacean, but that this has been overlooked by most people because it was published in a relatively obscure journal. To conform to current usage, the term Dyar's Rule will be retained here.

Various extension of Dyar's Rule by Przibram and Megusar (1912), Richards (1949) and others led to many bivariate studies of allometric growth, particularly in identifying nymphal and larval stages (e.g. Cumber, 1952; Don 1963, 1967; Duarte, 1939; Matsuda, 1963 etc.). Similar simple techniques are used here, as the more modern multivariate analysis (e.g. Cuzin-Roudy and Laval, 1975; Blackith and Blackith, 1969; Blackith, Davies and May, 1963) entails complex computer techniques, and either collections of large number of data or less useful results when the number of data is small (Blackith and Reyment, 1971; Sprent, 1972).

Exopterygote insects such as Hemiptera exhibit hemimetabolous growth, i.e. there is a gradual and more or less constant change throughout the nymphal instars followed by a greater transition at the final ecdysis to the adult (Brown, 1977). Pesson (1951: 1493) observes the number of stadia in Homoptera varies between different species. The least, two, is found in the female Coccidae, and the most, seven, in Cicadidae. There are often four or five.

6.2 MATERIALS AND METHODS

The specimens used were collected with an aspirator from different Waikato field sites during the summers of 1976/77 and 1977/78, killed with trichloromethane (chloroform) vapour, and stored in 95% ethanol. Collections were made of as great a size range of nymphs as possible, to ensure that all instars were taken.

A total of 220 nymphs were collected, and measured with an eyepiece micrometer in an Olympus stereomicroscope at appropriate magnifications. The error using this technique was considered to be ± 0.25 eyepiece units, which corresponds to ± 0.005-0.015mm, depending upon the magnification used.

Eight body characteristics were measured. These are briefly described below, and illustrated in Fig. 6.1.

Definition of measurements:

1) *Width of post-clypeus* is the width of the post-clypeus at its widest point. The sclerite being measured was at first mistakenly identified by the author, and as Imms (1957: 421) remarks "... the frons and clypeus of many taxonomists are really the post and anteclypeus respectively."

2) *Distance from the dorsal mid-point of the post-clypeus to the posterio-lateral extremity of the nota* is a projection of that curved distance onto the flat surface of the eyepiece. In the first four instars, the tergum concerned is the metanotum, but in the last instar this is completely overlapped by the mesonotum.

3) *Length of proboscis* (or rostrum) is the distance from the distal end of the proboscis to the ventral edge of the ante-clypeus.

4) *Length of pronotum*
5) *Length of mesonotum*
6) *Length of metanotum*

These are the length of these terga along the dorsal midline.

7) *Distance from the cervix to the posterio-lateral extremity of the nota.* As in measurement 2, this involves the metanotum in the first four instars, and the mesonotum in the fifth. The term "cervix" is used *sensu* Crampton (1926).

8) *Length of tibia* includes the tibial spurs.

9) *Length of head and thorax* is the distance from the dorsal edge of the post-clypeus to the posterior margin of the metathorax, along the dorsal midline.

After 150 nymphs had been measured, it was decided not to continue with measurements 7, 8 and 9. This was done because measurement 7 was too similar to measurement 2 to be necessary, and because measurements 8 and 9 did not appear to be related to instar number in any significant way.

The growth ratio of a particular part at a moult can be represented by the formula

$$\frac{y_{n+1}}{y_n}$$

where y_{n+1} is the mean value of y in the n+1*th* stadium, and y is its value in the n*th* stadium.

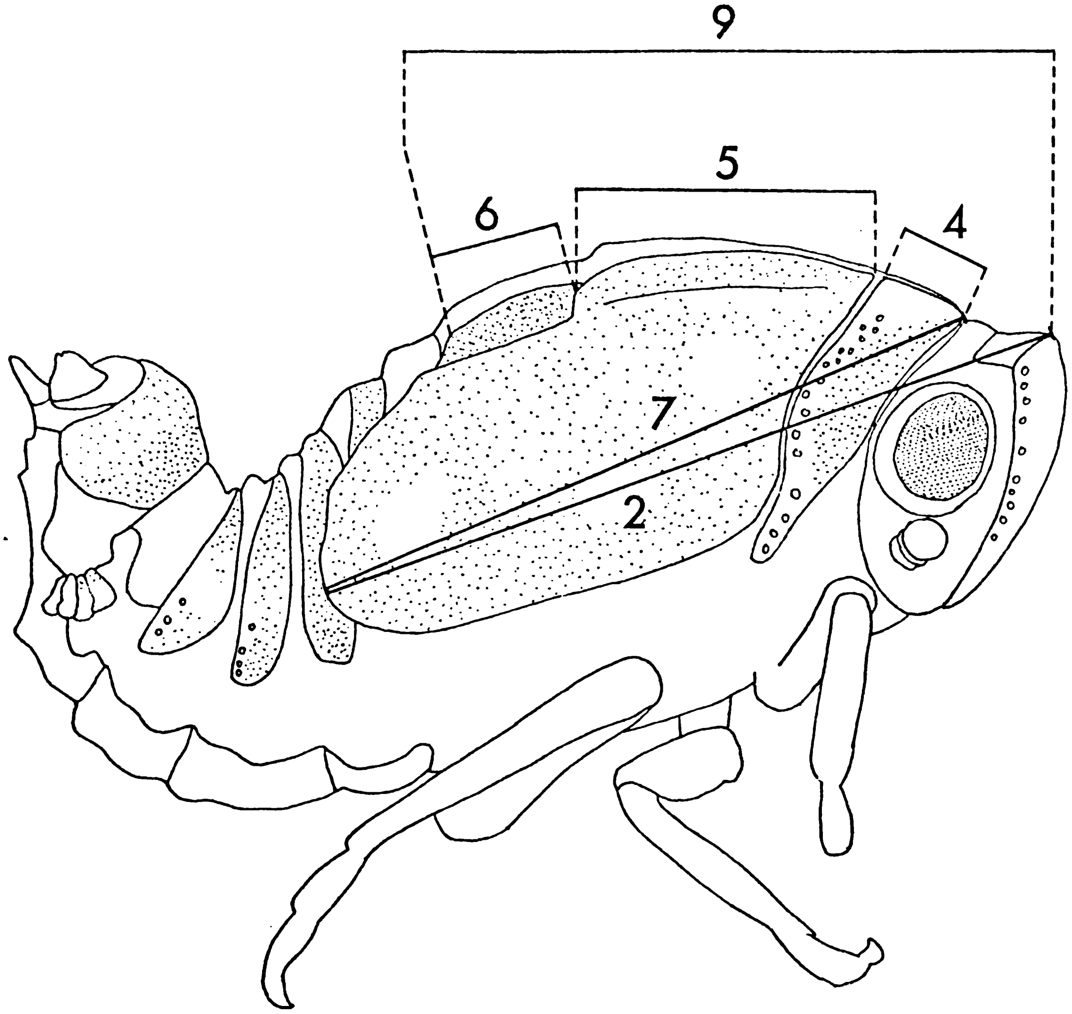
Przibram and Megusar (1912) concluded from their studies of *Sphodromantis bioculata* that at each moult the bodies and exuviae doubled their weight. This was considered to be the result of a doubling of cell numbers at each moult, which also caused the linear dimensions of sclerotised parts to increase at each moult by the cube root of two, or 1.26. Any growth ratios determined empirically to be greater than 1.26 were considered by Bodenheimer (1933) to be caused by hidden or "latent" divisions, which obscured the simple relationships determined by Przibram and Megusar but did not invalidate them.

In *S. australis*, a comparison was made of the progression series calculated according to Bodenheimer's indications, and the results determined experimentally. This was done by dividing the value of a measurement for the last instar by 1.26, dividing the result by 1.26, and so on until a quotient is obtained nearest to the value for the first instar.

A computer programme was run to see if any of the measurements, or combination of these, showed any degree of grouping into instars. The data (in millimetres) were fed in, any functions performed, and the results were scaled to fit a 1-100 array. The results were plotted on this array as a histogram, so that any clustering could be readily noticed. Combinations of measurements which were discretely grouped were then plotted by hand. For a fuller description of the programmes, see Appendix 3.

Fig. 6.1 Diagrammatic representation of measurements used (not to scale).

1. Width of post-clypeus
2. Distance from the dorsal mid-point of the post-clypeus to the posterio-lateral extremity of the nota
3. Length of proboscis
4. Legth of pronotum
5. Length of mesonotum
6. Length of metanotum


9
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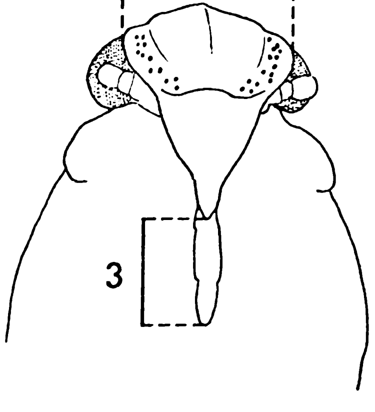
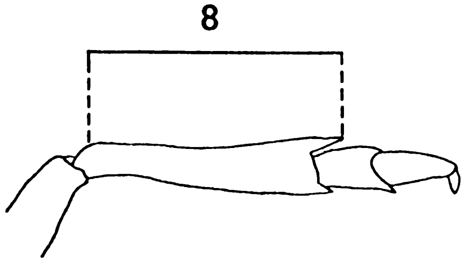
2


1
3


8

6.3 RESULTS

The results of the six measurements made on each insect are summarised in Table 6.1, and all data are listed in Appendix 4.

The width of the post-clypeus and length of the proboscis are the most important measurements for determining the number of nymphal instars, which are all quite discrete with respect to these measurements. For a brief description of each stage, see Section 3.4. Graphs of measurements 5 and 6, and 1 and 2 plotted against each other showed a high degree of discrete clumping, although not as good as Fig. 6.2.

Using the computer programme (BUGG), many other complex combinations of measurements were tested for clumping. Those which showed five reasonably distinct clumps, corresponding to the five nymphal instars include 1x9/7x8, 1x1/3, 1x1x8/9, 1x8x8/9, 2x7x9, 9x1x1/8, 1, 1x1x2/7, 7x1x1/9.

Growth ratios were calculated for all measurements at each moult and overall, and are shown in Table 6.2 and represented graphically in Figs. 6.3 and 6.4.

The progression series calculated from Przibram's hypothesis are compared with the actual data obtained, in Table 6.3. For measurements 1 and 2 the principle does not fit the data, but for measurements 3-6 a good degree of correlation is seen.

Table 6.1 Measurements of *S. australis* nymphs.

Table 6.2 Growth ratios of each measured part, at each moult and overall.

1. Width of post-clypeus
2. Distance from the dorsal mid-point of the post-clypeus to the posterio-lateral extremity of the nota
3. Length of proboscis
4. Legth of pronotum
5. Length of mesonotum
6. Length of metanotum

TABLE 6.1

Instar	Mean body measurement for each instar (mm).					
	1	2	3	4	5	6
1	0.31	0.75	0.24	0.11	0.19	0.17
2	0.43	1.04	0.29	0.13	0.29	0.26
3	0.59	1.55	0.39	0.15	0.46	0.36
4	0.79	2.00	0.51	0.21	0.62	0.44
5	1.12	2.82	0.64	0.27	0.93	0.54

TABLE 6.2

Moult	Growth ratio					
	1	2	3	4	5	6
1/2	1.39	1.39	1.21	1.18	1.53	1.53
2/3	1.37	1.49	1.34	1.15	1.59	1.38
3/4	1.34	1.29	1.31	1.40	1.35	1.22
4/5	1.42	1.41	1.25	1.29	1.50	1.23
Overall	1.38	1.40	1.28		1.49	

Fig. 6.2 Identification of nymphal instars by measurements of the width of the post-clypeus and the proboscis length.

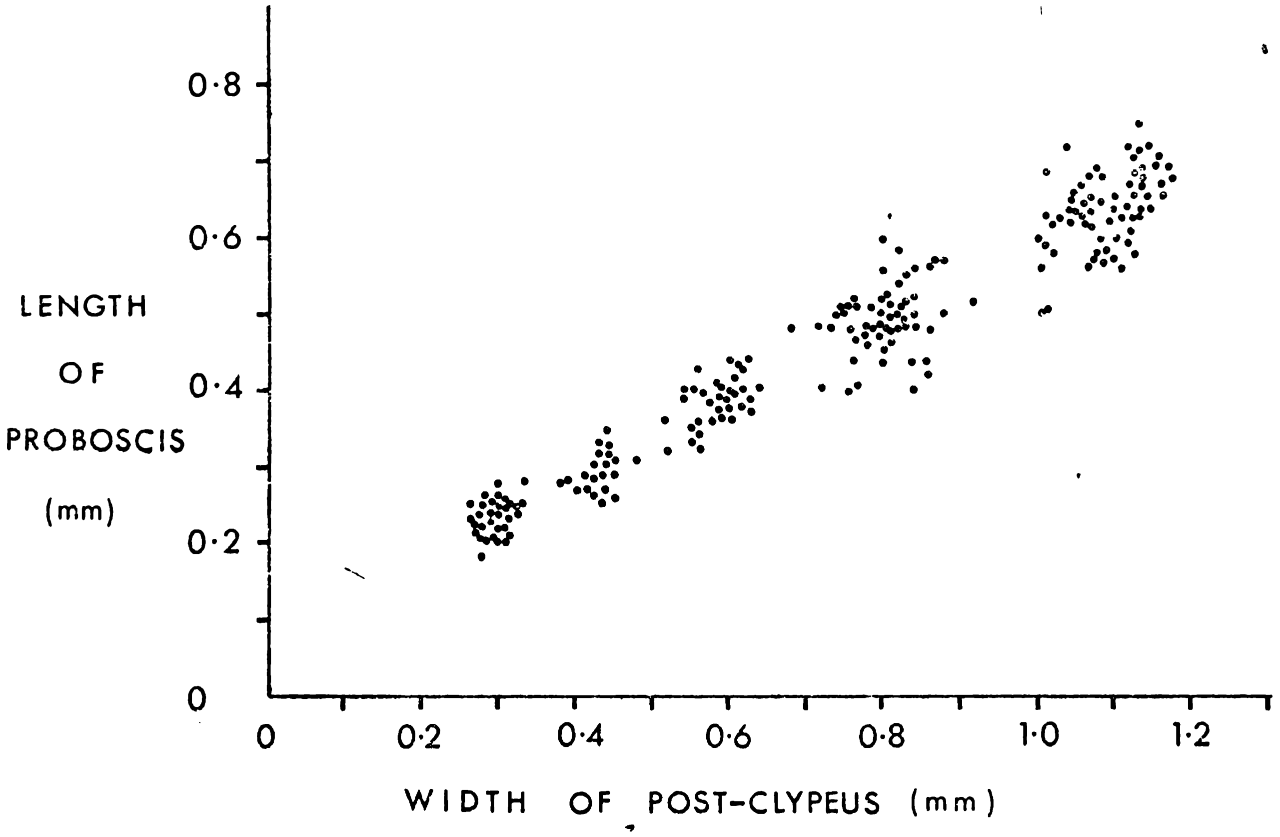

LENGTH OF PROBOSCIS (mm)
0·8
0·6
0·4
0·2
0
0
0·2
0·4
0·6
0·8
1·0
1·2
WIDTH OF POST-CLYPEUS (mm)

Fig. 6.3 Mean body measurements for each instar (arithmetic scale) and growth ratios.

1. Width of post-clypeus
2. Distance from the dorsal mid-point of the post-clypeus to the posterio-lateral extremity of the nota
3. Length of proboscis
4. Legth of pronotum
5. Length of mesonotum
6. Length of metanotum

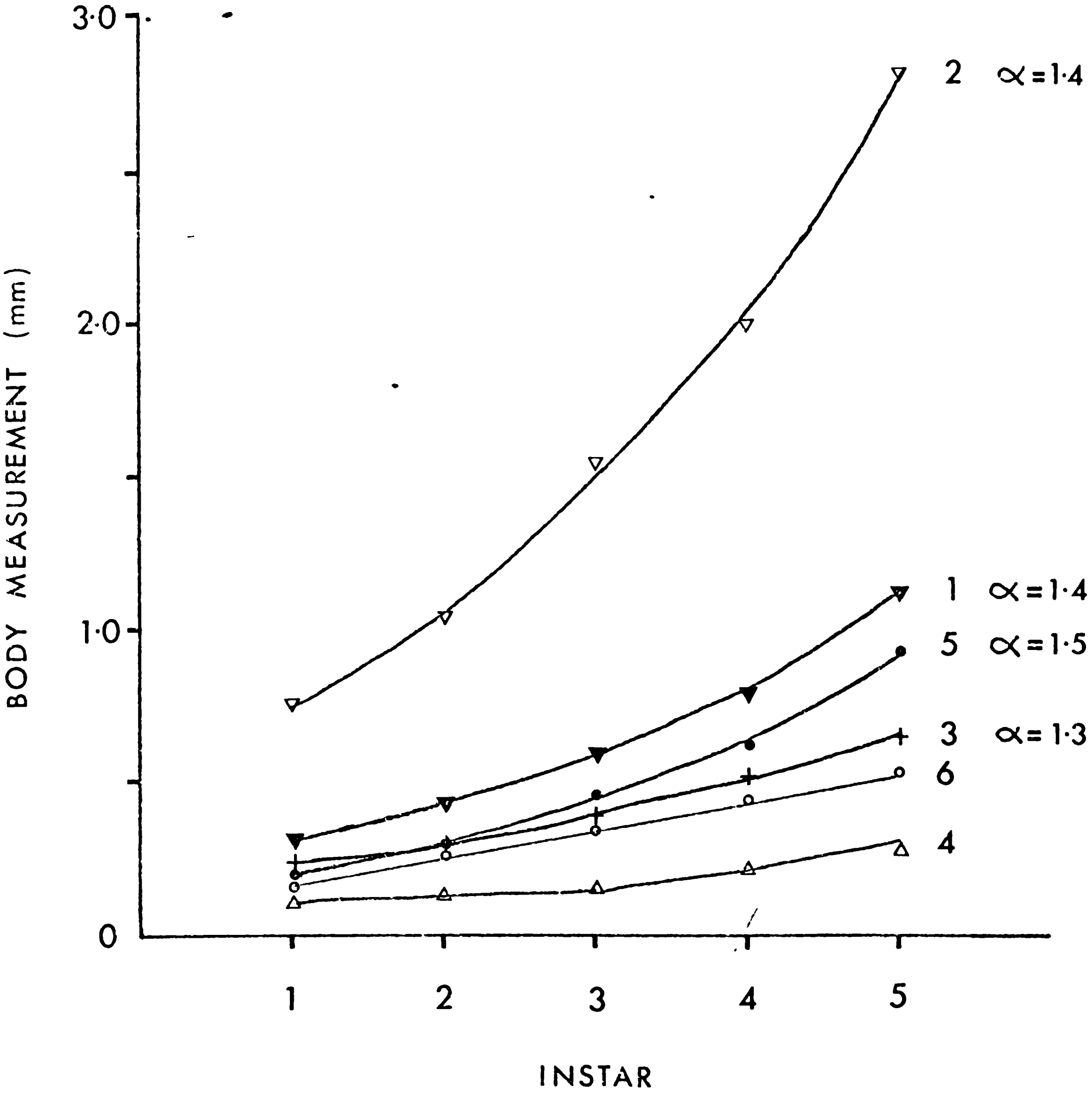

3·0
2·0
1·0
0
BODY MEASUREMENT (mm)
1
2
3
4
5
INSTAR
2 ∝=1·4
1 ∝=1·4
5 ∝=1·5
3 ∝=1·3
6
4

Fig. 6.4 Mean body measurements for each instar (logarithmic scale).

1. Width of post-clypeus
2. Distance from the dorsal mid-point of the post-clypeus to the posterio-lateral extremity of the nota
3. Length of proboscis
4. Legth of pronotum
5. Length of mesonotum
6. Length of metanotum

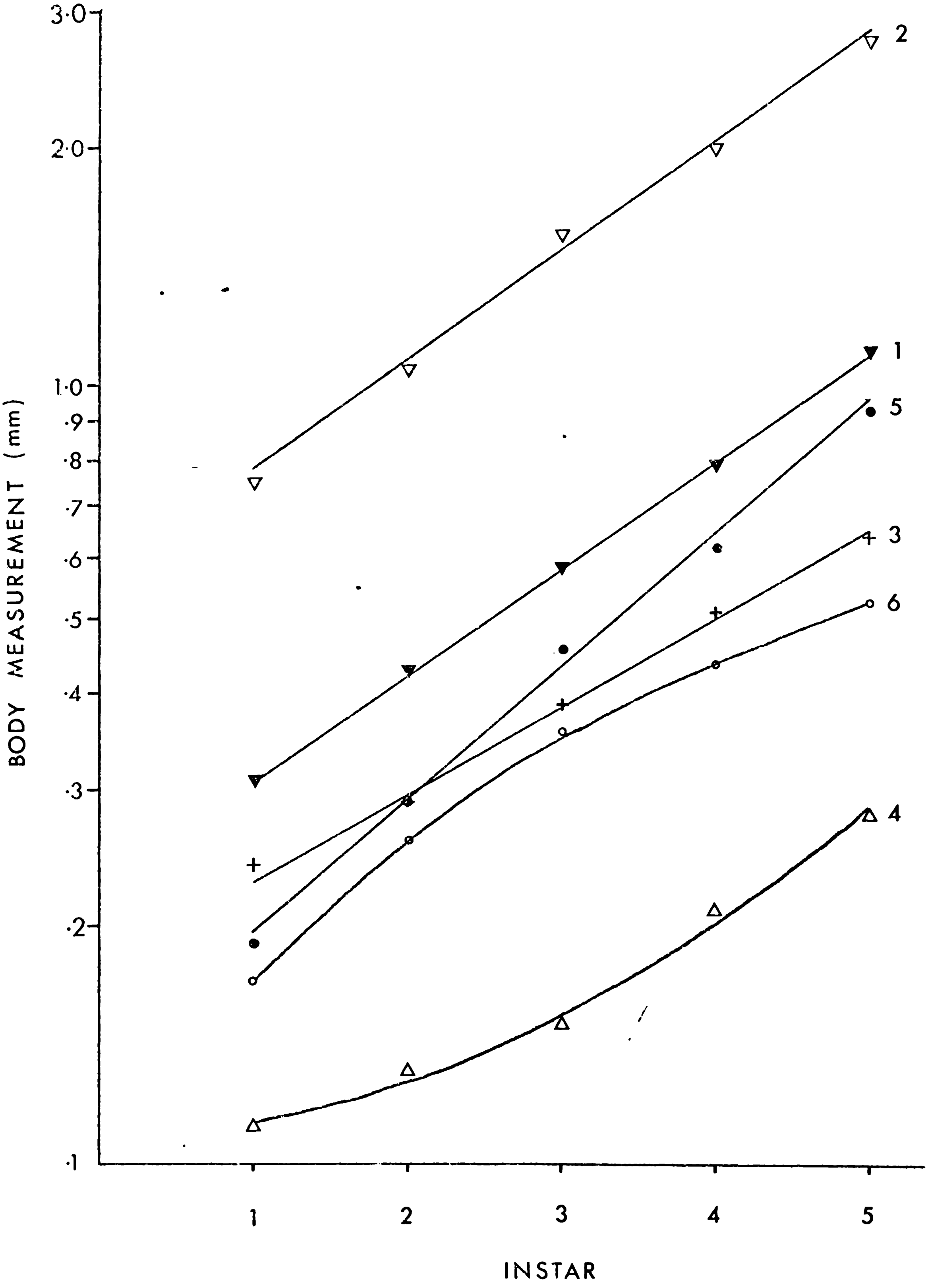

3·0
2·0
1·0
·9
·8
·7
·6
·5
·4
·3
·2
·1
BODY MEASUREMENT (mm)
1
2
3
4
5
INSTAR
2
1
5
3
6
4

TABLE 6.3: Application of Przibram's principle to the increase in size of the parts of *S. australis* nymphs.

A Actual measurements (mm).

C Calculated measurements, following Przibram's principle.

1. Width of post-clypeus
2. Distance from the dorsal mid-point of the post-clypeus to the posterio-lateral extremity of the nota
3. Length of proboscis
4. Legth of pronotum
5. Length of mesonotum
6. Length of metanotum

Instar	1		2		3		4		5		6	
	A	C	A	C	A	C	A	C	A	C	A	C
1	0.75	0.70	0.31	0.28	0.24	0.25	0.11	0.11	0.19	0.18	0.17	0.17
		0.89		0.35						0.23		0.21
2	1.04		0.43	0.44	0.29	0.32	0.13	0.14	0.29	0.29	0.26	0.27
		1.11								0.37		
3	1.55	1.40	0.59	0.56	0.39	0.40	0.15	0.17	0.46	0.47	0.34	0.34
		1.77										
4	2.00		0.79	0.71	0.51	0.51	0.21	0.21	0.62	0.59	0.44	0.43
		2.23		0.89						0.74		
5	2.82	-	1.12	-	0.64	-	0.27	-	0.93	-	0.54	-

6.4 DISCUSSION

Instars of *S. australis* have been separated morphometrically here on the basis of the width of the post-clypeus and the probiscis length. The width of the post-cypeus can be taken to be similar in growth characteristics to the width of the head capsule. This latter measurement is the sole basis of Cumber's (1952) morphometric identification of the nymphal stages of *Melampsalta cruentata* (Homoptera: Cicadidae). Matsuda (1963) also used head width, in conjunction with leg and antennal segments, in the study of relative growth in two species of *Orthotylus* (Heteroptera: Miridae). In identifying the nymphal stages of five species of Miridae (Heteroptera), Waloff and Southwood (1960) measured the rostrum length and the lengths of the first, second, third, and fourth antennal segments. Diagnosis of any immature insect of the five species could be achieved by reference to these measurements. Rodriguez and Maldonaldo (1974), in studying allometric growth in the mantid *Stagmatoptera biocellata,* measured head breadth, as well as the lengths of the prothorax and some leg segments.

The two body characteristics that were used in the diagnostic morphometric analysis of *S. australis* nymphal instars have been used for similar purposes in studies of other Hemiptera, and have been found by others to produce valid results.

Dyar (1890) found that a growth ratio of about 1:4 was common for the head capsules of lepidopteran larvae. The average value of 1:40 for the growth ratio of the post-cypeus confirms the application of

Dyar's Rule to this part in *S. australis*. Chapman (1967: 391) says that the growth ratios for different body parts of many insects are often about 1:4. This generality is valid for measurements 2, 3 and 5 also.

The decline of the growth ratio of the post-notal length throughout the insect's development illustrates a trend that is common in insect development. Duarte (1939: 448) found that the growth ratios of all of the parts (except the hind femur) that he measured in *Locusta migratoria migratorioides* declined throughout the instars. The greatest decline was in the length of the pronotum. No reason for this is suggested. The growth ratio of the mesonotum is the highest of any of the parts measured, and this results from the massive changes that occur in this segment with respect to the development of the tegmen and associated flight muscles. The metanotum, by comparison, develops at a much lesser rate, and the overall decline in value of its growth ratio may be to accommodate this relative change in importance of these two thoracic segments.

The irregular increase in the value of pronotum growth ratio is quite the opposite to that in *Locusta* (Duarte, *op. cit.*). It is surprising, and no immediate structural or functional reason for this change can be found.

The growth ratios determined for *S. australis* were worked out by examining many individuals. As Brown and Davies (1972) point out, different values may be obtained if individuals are measured throughout their development. Bliss and Beard (1954) showed that in *Oncopeltus fasciatus* this is due to slight changes in the part being measured (in this case the head capsule breadth).

The probiscis length, and the lengths of the three thoracic segments, show remarkable conformity to Przibram's principle, as modified by Bodenbeimer (1933). Insect tissues may grow by an increase in either cell numbers or cell size, or both (Chapman, 1967: 394). The close conformity of measurements 3-6 to the series predicted by Przibram's principle suggests that these tissues may grow chiefly by a doubling of cell numbers at each moult. There may be a different number of latent divisions in different parts of the insect (Duarte, 1939). There would seem to be none in the increase in length of the probiscis or pronotum, and three and one in the increase in lengths of the meso- and metanotum respectively. The hypothesis that this is what occurs in *S. australis* remains as such until such time as detailed cytological investigations are carried out.

However, the simple logic of Przibram's principle is not valid in all, or even most cases, because growth does not always occur by cell division alone. The width of the post-clypeus (1), and distance from the dorsal mid-point of the post-clypeus to the posterior extremity of the nota (2) are examples of measurements whose increase does not conform to Przibram's principle, presumably because of the reasons just mentioned.

6.5 SUMMARY

1. Measurements were made of six physical characteristics of 220 *S. australis* nymphs, viz. the width of the post-clypeus, the distance from the dorsal midpoint of the post-clypeus to the posterio-lateral extremity of the nota, the proboscis length, and the length of the pro-, meso-, and metanota.

2. Comparison of the proboscis length and width of the post-clypeus best shows the existence of five nymphal instars in *S. australis*.

3. Growth ratios are calculated for all dimensions overall and for each measurement. Four parts are found to increase with reasonable conformity to Dyar's Rule, and have growth ratios between 1:3 and 1:5.

4. The growth of the six measured parts is discussed in relation to Bodenheimer's modification of Przibram's rule, and this rule or principle is found to hold good for four parts.

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ADDENDA

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APPENDIX 1 AUSTRALIAN LOCALITIES FROM WHERE *SCOLYPOPA AUSTRALIS* HAS BEEN REPORTED

Queensland

Coolangatta, Brisbane, Redland Bay, Eagle Heights, Montville, Rita Island, Mt. Tambourine, Maleny, Imbil, Buderim, Bowen, Fletcher (near Stanthorpe), Maleny, Toowoomba, Bunya Mountains, Maryborough.

New South Wales

Sydney (various localities), Brookiana (East Dorrigo), Galston Gorge (Berowa), Trial Bay, Boogan River, Bowral, Armidale, Tenterfield.

Victoria

Melbourne.

Tasmania

Launceston (first recorded in February, 1975).

S. australis has not been reported from South Australia, Northern Territories or Western Australia.

In the states in which it is found, *S. australis* is reported from the coastal areas, and only rarely from the tableland areas. No locality given to the author was more than about 150 km inland, nor was any more than about 900m ASL. This may not reflect the species' true distribution however, because of its relative unimportance (discussed in Section 4.1). There is one anomalous record; from the

Bogan River which is on the western side of the Great Dividing Range in New South Wales. There is a specimen in the Australian Museum which was apparently collected there in 1935 (G. A. Holloway, pers. comm.).

The locality records range from Bowen, Queensland (20°S) to Launceston, Tasmania (41°25'S). The southern limit of distribution in New Zealand is at the same latitude as Launceston.

APPENDIX 2 MATERIALS USED IN MICROSCOPY (Section 5.22)

1) Millonic's phsophate buffer

1. 2.55% $NaH_2PO_4.2H_2O$
2. 2.52% NaOH

Adjust to pH 7.2

2) 3% gluteraldehyde/2% formaldehyde in phosphate buffer pH 7.2

1. 32 ml 2.55% $NaH_2PO_4.2H_2O$
2. 6 ml 25% gluteraldehyde
3. 2.5 ml 40% formaldehyde

Adjust to pH 7.2 with 2.52% NaOH. Dilute to 50ml with distilled water

3) 1% osmium tetroxide in phosphate buffer pH 7.2

1. 37 ml 2.55% $NaH_2PO_4.2H_2O$
2. 8 ml 2.52% NaOH
3. 5 ml 5.4% D+ glucose
4. 0.5g OsO_4

4) Spurr's embedding medium (Anon, 1973a)

1. 10.0g VCD resin (vinyl cyclohexene dioxide)
2. 6.0g DER 736 plasticiser (diglycidyl ether of polypropylene glycol)
3. 26.0 NSA hardener (nonenyl succinic anhydride)
4. 0.4 g DMAE accelerator (dimenthylamimoethanol)

APPENDIX 3 DESCRIPTION OF COMPUTER PROGRAMMES (BUGG) USED IN SECTION 5.2

The series of computer programmes were written in BASIC+ to run on a PDP 1170 under the RSIS operating system.

The first five programmes (BUGG1-BUGG5) read a sequential stream file from the disk which was originally loaded with cards. A series of up to eleven equations are tried on these data and the results stored in a virtual array on the disk. These results are scaled so that they are integers from 1 to 100 and the frequency of each integer in this range is calculated. The results are plotted on a histogram and stored in a sequential stream file called BUGG. OUT.

BUGG6 reads the virtual array file of equations made up in the earlier programmes. It rescales and plots a log/log or arithmetic graph of any two equation results selected interactively. The results are stored in s sequential file called GRAPH. OUT. The object of BUGG6 was to draw logarithmic or arithmetic graphs such as shown in Fig. 5.2, but this programme was not successful, and could not be "debugged" (!) in sufficient time for it to be useful.

APPENDIX 4 ACTUAL MEASUREMENTS OF *S. AUSTRALIS* NYMPHS (see Section 5)

First instar numphs (n = 37)

Measurements (mm). For a fuller description of these, see Section 5.2

1	2	3	4	5	6
0.30	1.03	0.20	0.13	0.19	0.13
0.30	1.81	0.20	0.09	0.20	0.18
0.40	0.76	0.20	0.13	0.21	0.24
0.33	0.80	0.25	0.10	0.20	0.20
0.30	0.79	0.21	0.13	0.20	0.21
0.30	0.76	0.24	0.08	0.20	0.20
0.30	0.77	0.25	0.13	0.23	0.20
0.28	0.76	0.25	0.13	0.19	0.18
0.30	0.76	0.20	0.11	0.21	0.18
0.28	0.76	0.28	0.10	0.20	0.15
0.29	0.76	0.23	0.11	0.20	0.13
0.30	0.79	0.23	0.12	0.19	0.16
0.30	0.76	0.26	0.10	0.18	0.18
0.28	0.64	0.21	0.06	0.13	0.10
0.30	0.68	0.28	0.10	0.16	0.15
0.30	0.76	0.23	0.11	0.20	0.14
0.30	0.65	0.25	0.10	0.13	0.15
0.26	0.68	0.25	0.10	0.18	0.15
0.31	0.84	0.25	0.15	0.23	0.19
0.30	0.65	0.25	0.09	0.15	0.16
0.30	0.69	0.21	0.09	0.16	0.15
0.30	0.64	0.24	0.09	0.13	0.13
0.30	0.74	0.25	0.10	0.18	0.15
0.31	0.63	0.25	0.10	0.20	0.15
0.33	0.63	0.25	0.09	0.15	0.15
0.30	0.68	0.23	0.08	0.15	0.15
0.28	0.84	0.23	0.09	0.20	0.20
0.30	0.68	0.23	0.08	0.18	0.14
0.30	0.68	0.23	0.10	0.18	0.15
0.30	0.72	0.20	0.13	0.18	0.15
0.28	0.65	0.20	0.09	0.13	0.15
0.30	0.73	0.23	0.13	0.15	0.16
0.33	0.84	0.28	0.10	0.20	0.20
0.30	0.68	0.23	0.08	0.15	0.15
0.33	0.84	0.24	0.10	0.21	0.18
0.30	0.73	0.25	0.08	0.18	0.15
0.30	0.76	0.23	0.10	0.20	0.15

Second instar nymphs (n = 21)

Measurements (mm)					
1	2	3	4	5	6
0.46	1.16	0.32	0.18	0.33	0.30
0.43	1.23	0.33	0.10	0.29	0.26
0.45	1.21	0.25	0.15	0.33	0.28
0.43	1.16	0.25	0.10	0.23	0.25
0.44	1.32	0.26	0.14	0.35	0.26
0.44	1.21	0.35	0.16	0.34	0.26
0.43	0.99	0.33	0.09	0.22	0.20
0.43	1.21	0.33	0.13	0.31	0.28
0.45	1.23	0.29	0.14	0.28	0.30
0.42	1.16	0.33	0.10	0.28	0.30
0.39	1.10	0.28	0.09	0.22	0.23
0.41	1.21	0.29	1.10	0.25	0.31
0.43	1.24	0.30	0.15	0.28	0.33
0.40	1.19	0.26	0.12	0.26	0.21
0.47	1.32	0.31	0.13	0.31	0.35
0.43	1.21	0.29	0.11	0.22	0.26
0.42	1.23	0.25	0.15	0.33	0.28
0.40	1.16	0.26	0.18	0.33	0.24
0.42	0.99	0.28	0.14	0.30	0.23
0.45	1.27	0.31	0.16	0.34	0.33
0.44	1.12	0.30	0.12	0.29	0.26

Third instar nymphs (n = 35)

Measurements (mm)

1	2	3	4	5	6
0.64	1.60	0.40	0.20	0.46	0.40
0.60	1.60	0.36	0.16	0.42	0.40
0.64	1.60	0.40	0.20	0.44	0.36
0.56	1.61	0.32	0.14	0.44	0.36
0.60	1.52	0.44	0.14	0.60	0.36
0.60	1.56	0.40	0.15	0.45	0.35
0.56	1.48	0.36	0.18	0.44	0.38
0.60	1.68	0.36	0.18	0.44	0.33
0.64	1.48	0.40	0.13	0.39	0.45
0.60	1.64	0.40	0.13	0.39	0.45
0.52	1.44	0.36	0.23	0.73	0.48
0.52	1.48	0.32	0.15	0.73	0.35
0.56	1.60	0.40	0.13	0.48	0.35
0.56	1.56	0.40	0.18	0.42	0.33
0.60	1.52	0.44	0.14	0.45	0.35
0.60	1.52	0.44	0.10	0.38	0.30
0.60	1.52	0.36	0.20	0.73	0.30
0.60	1.48	0.40	0.13	0.45	0.31
0.57	1.36	0.43	0.13	0.38	0.29
0.55	1.37	0.35	0.13	0.38	0.39
0.62	1.56	0.40	0.10	0.43	0.35
0.50	1.50	0.38	0.11	0.42	0.28
0.55	1.23	0.35	0.11	0.42	0.28
0.54	1.52	0.40	0.18	0.40	0.28
0.62	1.56	0.44	0.15	0.43	0.58
0.64	1.76	0.40	0.14	0.45	0.35
0.56	1.56	0.34	0.15	0.45	0.33
0.56	1.48	0.40	0.15	0.39	0.31
0.62	1.32	0.44	0.18	0.45	0.35
0.58	1.40	0.36	0.10	0.33	0.33
0.60	1.66	0.36	0.18	0.48	0.33
0.62	1.64	0.38	0.10	0.39	0.33
0.62	1.68	0.38	0.13	0.45	0.35
0.60	1.68	0.40	0.16	0.34	0.38

Fourth instar nymphs (n = 62)

Measurements (mm)

1	2	3	4	5	6
0.88	1.84	0.48	0.26	0.66	0.48
0.72	1.72	0.40	0.16	0.58	0.40
0.75	1.64	0.50	0.16	0.60	0.40
0.88	2.24	0.56	0.19	0.69	0.47
0.88	2.20	0.57	0.13	0.63	0.44
0.84	2.04	0.56	0.28	0.68	0.48
0.75	2.01	0.50	0.24	0.64	0.48
0.80	2.12	0.48	0.28	0.70	0.48
0.84	2.16	0.48	0.14	0.52	0.46
0.80	1.96	0.48	0.25	0.71	0.45
0.84	1.80	0.40	0.25	0.65	0.47
0.80	2.00	0.48	0.23	0.68	0.43
0.76	1.84	0.48	0.20	0.55	0.43
0.82	2.14	0.50	0.25	0.73	0.43
0.80	1.92	0.44	0.21	0.62	0.44
0.84	2.08	0.52	0.20	0.65	0.45
0.80	1.96	0.52	0.25	0.44	0.45
0.80	1.88	0.60	0.25	0.65	0.43
0.76	2.20	0.52	0.23	0.65	0.43
0.80	1.84	0.48	0.20	0.45	0.40
0.88	2.20	0.50	0.23	0.71	0.48
0.72	1.72	0.48	0.18	0.53	0.43
0.84	2.04	0.52	0.23	0.72	0.48
0.80	1.92	0.48	0.21	0.54	0.30
0.76	1.84	0.40	0.24	0.57	0.45
0.80	2.00	0.52	0.23	0.69	0.48
0.88	2.26	0.47	0.19	0.63	0.38
0.78	1.48	0.36	0.19	0.44	0.34
0.84	2.08	0.48	0.18	0.43	0.45
0.76	2.06	0.40	0.20	0.60	0.45
0.82	2.20	0.54	0.23	0.67	0.44
0.82	2.08	0.52	0.20	0.60	0.42
0.80	2.04	0.48	0.20	0.65	0.47
0.84	2.00	0.72	0.20	0.65	0.47
0.86	1.88	0.44	0.23	0.65	0.40
0.80	2.12	0.44	0.24	0.62	0.47
0.84	2.10	0.50	0.25	0.68	0.43
0.80	1.76	0.44	0.11	0.50	0.40
0.79	2.58	0.57	0.26	0.93	0.54
0.80	1.82	0.50	0.28	0.57	0.42
0.84	2.12	0.56	0.24	0.74	0.46
0.86	2.00	0.42	0.18	0.59	0.47
0.80	2.20	0.50	0.28	0.65	0.44
0.82	1.95	0.50	0.28	0.63	0.40
0.76	1.94	0.52	0.18	0.53	0.40
0.82	0.60	1.94	0.16	0.59	0.42

Fourth instar nymphs (Continued)

Measurements (mm)

1	2	3	4	5	6
0.82	0.50	2.20	0.20	0.69	0.43
0.75	0.50	2.20	0.24	0.62	0.50
0.72	1.88	0.48	0.18	0.60	0.40
0.80	1.88	0.48	0.18	0.58	0.45
0.78	1.48	0.48	0.20	0.60	0.45
1.08	2.60	0.60	0.24	0.92	0.52
1.00	2.52	0.60	0.24	0.94	0.52
1.00	2.52	0.56	0.24	0.92	0.46
1.06	2.56	0.56	0.24	0.88	0.52
0.92	2.32	0.52	0.24	0.92	0.50

Fifth instar nymphs

Measurements (mm)

1	2	3	4	5	6
1.07	2.89	0.63	0.31	1.32	0.60
1.19	3.14	0.75	0.28	1.07	0.57
1.01	2.89	0.69	0.35	1.07	0.50
1.07	2.58	0.63	0.25	1.01	0.50
1.01	2.52	0.50	0.19	0.95	0.50
1.07	2.58	0.63	0.28	0.98	0.54
1.07	2.83	0.69	0.22	1.04	0.57
1.12	3.14	0.69	0.28	0.88	0.52
1.07	2.89	0.63	0.32	1.02	0.46
1.07	2.77	0.94	0.30	0.98	0.56
1.13	2.83	0.63	0.32	1.06	0.52
1.07	2.58	0.57	0.20	0.86	0.52
1.13	3.02	0.88	0.31	0.01	0.60
1.13	3.08	0.69	0.34	1.12	0.60
1.01	2.89	0.63	0.28	1.04	0.52
1.13	2.26	0.69	0.28	1.08	0.52
1.01	2.58	0.50	0.20	0.82	0.52
1.07	2.83	0.63	0.32	1.04	0.56
1.14	3.25	0.82	0.20	1.00	0.60
1.07	2.77	0.63	0.38	1.00	0.52
1.13	2.77	0.69	0.28	1.00	0.56
1.13	2.83	0.69	0.32	1.06	0.46
1.13	2.96	0.63	0.26	1.00	0.60
1.07	2.70	0.63	0.26	0.98	0.58
1.13	2.96	0.63	0.28	1.10	0.60
1.13	3.05	0.63	0.28	1.04	0.60
1.07	2.89	0.64	0.28	0.98	0.54
1.13	2.99	0.68	0.28	1.02	0.58
1.07	2.93	0.66	0.24	0.84	0.54
1.01	2.74	0.63	0.28	0.88	0.57
1.15	2.93	0.64	0.32	1.06	0.50
1.13	2.74	0.63	0.28	0.97	0.54
1.07	2.83	0.69	0.28	0.96	0.52
1.07	2.64	0.69	0.24	0.88	0.52
1.16	2.89	0.69	0.30	1.04	0.60
1.07	2.64	0.66	0.30	1.00	0.50
1.13	2.86	0.63	0.34	1.04	0.54
1.01	2.52	0.63	0.26	0.92	0.54
1.13	2.20	0.44	0.24	0.71	0.45
1.07	2.70	0.57	0.26	1.00	0.52
1.10	2.64	0.57	0.24	0.88	0.54
1.10	2.52	0.57	0.20	0.84	0.52
1.10	3.24	0.63	0.32	1.16	0.56
1.16	3.11	0.66	0.28	0.96	0.60
1.10	2.99	0.63	0.18	0.76	0.52

Fifth instar nymphs (Continued)

Measurements (mm)

1	2	3	4	5	6
1.13	2.89	0.66	0.32	1.00	0.50
1.10	2.77	0.66	0.32	1.06	0.56
1.13	2.89	0.66	0.32	1.04	0.54
1.13	2.83	0.75	0.32	1.04	0.56
1.08	2.60	0.68	0.28	1.04	0.52
1.12	2.68	0.64	0.32	1.06	0.48
1.12	2.68	0.60	0.32	1.04	0.48
1.12	2.80	0.60	0.36	1.08	0.48
1.12	2.72	0.72	0.32	1.04	0.48
1.10	2.72	0.60	0.28	1.00	0.54
1.04	2.56	0.72	0.32	0.98	0.50
1.04	2.52	0.64	0.24	0.88	0.52
1.00	2.40	0.60	0.22	0.80	0.46
1.08	2.60	0.56	0.20	1.00	0.54
1.10	2.68	0.56	0.28	1.04	0.40
1.04	2.40	0.72	0.30	0.96	0.38
1.02	2.48	0.48	0.28	0.98	0.42
1.00	2.48	0.51	0.34	1.00	0.42
1.12	2.68	0.58	0.28	1.04	0.52
1.12	2.68	0.72	0.20	0.88	0.52