THE POSTEMBRYONIC DEVELOPMENT OF *ATRACTOMORPHA SINENSIS* BOLIVAR WITH PARTICULAR REFERENCE TO THE PHALLIC STRUCTURES (ORTHOPTERA : ACRIDOIDEA : PYRGOMORPHIDAE)

by

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POSTEMBRYONIC DEVELOPMENT OF *ATRACTOMORPHA SINENSIS* (ORTHOPTERA : PYRGOMORPHIDAE)

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ABSTRACT

M.Sc. SAI-KEUNG LEE Entomology

THE POSTEMBRYONIC DEVELOPMENT OF *ATRACTOMORPHA SINENSIS* BOLIVAR WITH PARTICULAR REFERENCE TO THE PHALLIC STRUCTURES (ORTHOPTERA : ACRIDOIDEA : PYRGOMORPHIDAE)

A culture of *A. sinensis*, obtained from the island of Oahu, Hawaiian Islands, was reared in the Department of Entomology, McGill University. The life-history of the species was studied and it was found that there were six nymphal instars in the male and seven in the female. A key to the instars of both sexes is given. This is based on the degree of development of the wing-pads, antennal segments, the metathoracic femur and the pronotum. The development of the subgenital plate, the paraprocts, and the upper and lower vulvulae are also important in the differentiation of the instars.

A study of the postembryonic development of the phallic complex showed these to originate from a pair of rudimentary penial bodies lying above the ninth abdominal sternum.

Phallic complexes from adults of different ages indicated that sclerotization of the phallic structures continues after the attainment of adulthood.

SOMMAIRE

M.Sc. SAI-KEUNG LEE Entomologie

LE DEVELOPPEMENT POST-EMBRYONNAIRE, PARTICULIEREMENT DU COMPLEXE PHALLIQUE, CHEZ *ATRACTOMORPHA SINENSIS* (ORTHOPTERES : ACRIDOIDES : PYRGOMORPHIDES)

Une culture d'*A. sinensis*, obtenue de l'île Oahu (îles Hawaii), a été élevée au Département d'Entomologie de l'Université McGill. Notre étude du développement de cette espèce a démontré la présence de six stades larvaires chez le mâle et de sept chez la femelle. Une clé d'identification des larves des deux sexes est donnée à partir de critères tels que le degré de développement des "plaques ailaires," des segments des antennes, du fémur métathoracique et de la cuirasse. Le développement de la plaque sous-génitale, des "paraproctes" et des valvules supérieures et inférieures se sont aussi révélés très importants dans la différenciation des stades larvaires.

Une étude du développement post-embryonnaire du complexe phallique a démontré que celui-ci est originaire d'une paire de corps péniles situés au-dessus du neuvième sternite abdominal.

L'observation du complexe phallique chez des adultes d'ages variés a révélé que la sclérotisation des structures phalliques se poursuivait au cours de la vie adulte.

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I. INTRODUCTION

The present study was stimulated by the fact that, although much reliance for taxonomic purposes is placed upon the form of the phallic structures of grasshoppers, considerable variation in these may occur within species, and that it has been suggested that some of this variation may result from continued development subsequent to the attainment of adulthood. Evidence for this is provided by two genera of Pyrgomorphidae: namely, *Atractomorpha* Saussure and *Desmopterella* Ramme (Kevan and Chen 1969; Kevan 1970, 1972). The primary object of the study was to test this hypothesis, using a representative species of a genus in which circumstantial evidence had already suggested its validity.

The grasshopper chosen for this study, *Atractomorpha sinensis* Bolivar, is common over a great part of China including eastern Inner Mongolia, Hong Kong and Taiwan. It also occurs in northernmost Indochina and in the southern Ryu Kyu Islands and has been introduced into some of the mid-Pacific islands, notably the Hawaiian chain (Kevan and Chen 1969), whence came the culture used in the present study. The species is frequently found in rice paddy and in vegetable fields and plots, in which it is often considered to be a pest. It is

sometimes used as food for caged song-birds and is featured in several famous Chinese paintings from the early 13th century A.D. onward.

Other members of the genus *Atractomorpha* are widely distributed throughout much of the Eastern Hemisphere (particularly in the tropical, subtropical and southern regions), some being of limited economic importance (Kevan and Chen 1969; Kevan 1970, 1971a, 1971b). They do not, however, occur in Europe and they are absent from the Americas, (Kevan, 1960).

Developmental studies on the phallic and other copulatory structures of grasshoppers in general have been few, and nothing of significance has been published on Pyrgomorphidae, so that the objective of this study was broadened in order to obtain a better understanding of the postembryonic development stages of the pyrgomorphid male terminalia, in addition to tracing the development of the phallic structures after the insect reached the adult stage. Embryonic development and the ultimate origin of the phallic structures, however, are not considered.

Incorporated into this study is a section on the previously undescribed immature stages of *Atractomorpha sinensis*. This is important for the recognition of the different immature stages of the insect and for distinguishing the sexes.

II. LITERATURE REVIEW

1. General adult morphology

Previous information on the morphology of the genus *Atractomorpha*, both external and internal, can be summarized very briefly. Apart from taxonomic works, notably those of Banerjee and Kevan (1960) and Kevan and Chen (1969), some of which include figures of the head and other external parts of the body, remarkably little of significance has been published considering the importance of the genus. Maki (1938) published a general account of the musculature; Knetsch (1939) referred to the tympanum; Laird (1943) described the testes; Slifer (1953) indicated "heat-sensitive" patches on the integument; and Ragge (1955) mentioned the wing venation. More recently, Banerjee and Kevan (1962) described the more notable features of the head capsule, pronotum, tympanum and some features of the external genitalia, and discussed the male and female reproductive systems. Phipps (1962) made brief references to the number of ovarioles. The names of the species studied by these various authors are omitted here as they have mostly been subject to change as a result of synonymy, as indicated by Kevan and Chen (1969).

The literature referring to concealed genitalic structures is reviewed in subsection 3.

2. General nymphal morphology

Apart from the occasional small figure of the entire nymph, e.g., by Fletcher (1917) who gives coloured illustrations of the nymphal stages of *Atractomorpha crenulata* (Fabricius), Agarwal (1955) was probably the first and virtually the only author to give even a brief account of the general nymphal morphology of *Atractomorpha*. No species was mentioned by Agarwal, although *A. crenulata* was referred to (D. K. McE. Kevan, personal communication). To date, there has been no published work aimed at the recognition of the sexes and the different nymphal instars of *Atractomorpha*, such as exist for several other species of grasshoppers.

Descriptions of nymphal instars of some other genera of Pyrgomorphidae are available. Quite a detailed illustrated account of the nymphal life of *Colemania sphenarioides* Bolivar is given by Coleman (1911). The species has five to six instars in both sexes. Fletcher (1914) illustrates the life history of the same species, as well as those of *Chrotogonus trachypterus trachypterus* (Blanchard) and *Poekilocerus pictus* (Fabricius). Drawings of each instar were also provided. Chesler (1938) indicates five instars for *Zonocerus elegans* (Thunberg.).

Poekilocerus pictus, *Phymateus aegrotus* (Gerstaecker), *Phymateus viridipes* Stal, *Chrotogonus robertsi* (Kirby) [= *Chrotogonus trachypterus trachypterus* (Blanchard)], *Aularches punctatus* (Drury) [= *Aularches miliaris* Linnaeus)] and *Poekilocerus bufonius* (Klug) have also been documented by Pruthi and Nigan (1939), Kevan (1949), De Lotto (1951), Latif and Haq (1951), Katiyar (1955) and Fishelson (1960), respectively. According to Kevan (1949) *Phymateus aegrotus* has five nymphal instars in the male and six in the female, although De Lotto (1951) found seven in each sex in a related species. Latif and Haq (1951) indicate that, in *Chrotogonus*, there are five to six moults in the male and six to seven moults in the female whose nymphal life, in consequence, is also longer than the male. There is thus no standard number of nymphal instars in the Pyrgomorphidae, as indicated in the summary by Ramsay (1964).

The postembryonic growth and changes of grasshoppers other than Pyrgomorphidae, particularly Old World species and especially locusts, have also been studied by a number of workers. Development of the nymphal stages has been described, for example, by Riley (1877) for *Melanoplus spretus* (Walsh); by Howard (1894) for *Schistocerca americana* (Drury); by Herrick and Hadley (1916) for *M. sanguipes* (Fabricius) and by Takahashi (1925) for *Pachytylus migratorioides* Reiche and Fairmaire [i.e., *Locusta migratoria migratorioides* (R. & F.)]. Studies on

specific parts of the external nymphal morphology have also been made. Nelsen (1931) indicated the importance of the terminal appendages in indicating differences between the sexes of nymphal Acrididae. Karandikar (1945), for example, also gives descriptions and figures of the development of terminal abdominal segments, pronotum and wing-pads of *Schistocerca gregaria* (Forskål), and Dirsh (1950) illustrates the differences between instars and sexes of *Locusta migratoria migratorioides* (R. & F.). Similar work has also been published by Burnett (1951) for *Nomadacris septemfasciata* (Serville) following earlier work by Nel (1929) on *Locustana pardalina* (Walker), Wilson (1941) on *Melanoplus marginatus* (Scudder), Shotwell (1941) on *M. bivittatus* (Say), and Kevan (1943) on *Schistocerca flavofasciata* (De Geer). A key to the immature stages of 21 species of *Melanoplus* was prepared by Handford (1946).

Roonwal (1952) and Katiyar (1953) studied the growth of individual parts in acridid nymphs, especially the antennal segments. The antenna increases in size not only by the addition of segments but also by their successive subdivisions, particularly of those of the basal half. The scape and pedicel, however, are not involved but become relatively more slender as the instars progress (Uvarov 1966). Guibord (1969) stressed the observation of Nelsen (1931) that the terminal appendages and the external genitalia are important in sex differentiation

and further pointed out that the ratio of the hind wing-pad length to the pronotal length is also useful in determining each nymphal stage.

In conclusion, it may be noted that Parker (1930), Shotwell (1930, 1941), Key (1936), Roonwal (1946), Burnett (1951) and Guibord (1969), among others, have reported the occurrence of nymphal instars additional to the usual number in some grasshoppers. In some species in which the female is much larger than the male (as it is in *Atractomorpha*) the former may have an additional instar to compensate for the size difference (Kevan 1943, 1949; Latif and Haq 1951), but this is by no means universal and extra instars may occur in either sex without reference to size.

3. Genitalic morphology

The morphology of the genitalic structures in grasshoppers has been discussed in detail by various authors such as Chopard (1920), Walker (1922), Snodgrass (1935), especially in the male (Roberts 1941; Dirsh 1956). The extensive literature on the subject is reviewed for both sexes by Kevan, Akbar and Chang (1969) with particular reference to Pyrgomorphidae, so that further discussion of the literature up to that time is unnecessary.

It may, however, be mentioned that the first description of the phallic structures of *Atractomorpha sinensis* (as *A.ambigua* Bolivar) is given by Roberts (1941). Dirsh (1956) illustrates certain of the phallic structures of *Atractomorpha crenulata* (Fabricius). Subsequently a few taxonomic publications have provided figures of phallic structures of the genus. In a preliminary revision of the genus, Banerjee and Kevan (1960) give sketches of the epiphallus of *A. aberrans* Karsch and *"A. brevicornis* (Thunberg)" [= *A. lata* (Motschoulsky)]; that of *A. crenulata* is illustrated by Kevan (1961). The male and female genitalia are briefly discussed by Banerjee and Kevan (1962). Kevan and Chen (1969) recognized the importance of the epiphallus, ectophallus and endophallus in distinguishing species. The last authors give comprehensive figures of the various concealed genitalic (including female) structures showing their variation, possibly due to an incomplete sclerotization. The most recent illustration of the genitalic apparatus of *Atractomorpha* is indicated in sketches of *A. crenulata* by Kevan and Tandon (1971). Kevan, Akbar and Chang (1969) provide complete generalized descriptions of, and detailed terminology for, the phallic and female structures of Pyrgomorphidae in general and which are applicable to *Atractomorpha sinensis*.

None of the above workers has attempted a study of the postembryonic development of the phallic structures. Nothing has been published on this aspect of any species of *Atractomorpha* or, to my knowledge, of any other genus of Pyrgomorphidae. Indeed, developmental studies on the genitalic structures of acridoid insects in general are very few, and such studies as do exist either do not refer to the phallic structures or are concerned almost entirely with embryonic development (which is not considered here). Nel (1929) described the nymphal development of the female reproductive organs (the external genitalia) including the development of the genital ducts and accessory organs in the pyrgomorphid *Colemania sphenarioides* Bolivar and the acridid *Locustana pardalina* (Walker). Probably the first author to have worked on the development of phallic structures in Acridoidea was Nelsen (1931), who claimed that the sexes of *Melanoplus differentialis* (Uhler) can be differentiated even before the insect hatches from the egg. He also claimed that the tenth pair of male embryonic appendages eventually forms the rudiments of the "penis," i.e., phallic structures.

Accounts of the embryonic development of the acridid phallus in relation to its form in the adult stage, are given by Else (1934) and Roonwal (1937). According to Else, the embryonic appendages of the tenth abdominal segment of the male

Melanoplus differentialis eventually form the complex phallic organ of the adult. These include the endophallus, ectophallus and epiphallus.

An origin of the acridid phallus of *Locusta migratoria migratorioides* from appendage rudiments is described also by Roonwal (1937) who claimed that the appendages of both the tenth and the ninth segments are involved.

Snodgrass (1937) and Qadri (1940), in their studies on the development of the genitalia, also refer to the "abdominal appendages" or "phallic lobes." Else (1934), in his study on *Melanoplus differentialis*, receives support from their observations and conclusions. The origin of the phallic complex, however, has not yet been determined in respect of which specific abdominal appendages are involved although it is generally agreed that the phallic complex develops from the "embryonic abdominal appendages."

III. MATERIALS AND METHODS

1. Source of material

The material used in the present study was obtained exclusively from a culture of *Atractomorpha sinensis* reared in the McGill University Department of Entomology. It originated from the progeny of a few field-collected specimens from a pineapple field a few kilometers northwest of Aiea, in the south of the island of Oahu, Hawaiian Islands, July, 1968. The original specimens were collected and identified by Dr. D. K. McE. Kevan.

2. Rearing

Pairs of *Atractomorpha sinensis* were placed in wooden cages basically similar to those described by Hunter-Jones (1961). The cages measured 35 x 36 cm. at the base and were 49 cm. high, having a screened floor, placed at 13 cm. from the true floor (Figure 1). A screened air vent was present high on one side. A 25-watt incandescent light-bulb placed on the hind wall provided light and heat and was operated by a time-switch set at a 14-hour photophase. The front wall was of glass. A 15 x 15 cm. door was set in the solid removable top.

The grasshoppers were fed on lettuce. When the females were ready to lay eggs, the screened floor of the cage was replaced by a wooden floor on which were two flower pots of sterilized moistened sand (Figure 2) which provided oviposition sites. Pots in which eggs had been laid were removed and replaced by fresh ones. The former were placed in an incubator at a temperature of 26 ± 2°C. for approximately three to four weeks. The humidity of the incubator was kept constant at approximately 80 per cent R.H. Relative humidity was controlled by means of a jar of water from which protruded strips of filter-paper to facilitate evaporation. No further treatment was necessary and the young hatched with little mortality, usually after about three weeks.

Batches of newly hatched nymphs were placed together for a few days in glass rearing jars having wire-mesh, screw-top lids (Figure 3) before they were sexed and transferred to individual jars as it was found that the immediate handling of the newly hatched nymphs could prove fatal to them (Kevan 1943). Each jar was labelled with dates of oviposition,of hatching and of attaining successive nymphal stages. Each jar contained a piece of twig to provide a foothold for moulting.

The jars were placed in an incubator at a temperature of 26 ± 2°C. and a photophase of 14 hours and the nymphs were fed regularly with lettuce. Water was sprayed on the lettuce as required, to keep the food moist and fresh.

The individual jars were checked each day for exuviae and the main characteristics of each instar were observed and noted. The exuviae were removed as soon as they were cast to prevent their being eaten. A complete record of the number of eggs laid, hatching dates, duration of each instar and the numbers of males and females was kept as rearing progressed.

3. Methods of study

The first batch of nymphs obtained was studied in order to determine the main characteristics differentiating each instar and the means of separating the males from the females. Observations were made using a Wild M 5 stereomicroscope. Each first-instar individual was placed in a small 10-gram vial and immobilized with a wad of cotton to facilitate study of various characters. The features studied were: the antennae, the wing-pads, the pronotum and the terminal abdominal appendages. Use of any kind of anaesthetic was avoided to insure maximum survival of numbers of specimens for further study.

After examination, each individual was returned to its individual jar and reared to maturity. The sex determination was checked as development proceeded. In large, later instars, the terminal abdominal appendages are distinctly different in the two sexes, but this is less readily observed in young individuals. Using the terminal abdominal structures, an accuracy of 100 per cent. in sexing the young was attained.

The number of instars present was counted by preserving the exuviae, removed immediately, from each individual rearing jar, the development of the different characters was studied immediately after moulting, from the first instar to the adult stage. The sexes were kept separate except when required for breeding purposes.

Specimens of different instars were fixed in Bouin's fluid or preserved in sweet-pickle fluid. The latter was made up as follows: distilled water 80 : cane-sugar 10 : formalin (40% formaldehyde) 5 : glacial acetic acid 3, parts by volume, to which was added a few drops of detergent (Teepol 401, Wood Co.). This is a good preservative for orthopteroid insects and prevents specimens from shrinking. It was found to be good for keeping specimens for morphological studies. The formula was recommended by Dr. V. R. Vickery.

Drawings were made from "sweet-pickled" specimens by using a Wild M 5 stereomicroscope equipped with a Wild M 5 drawing tube. Specimens fixed in Bouin's fluid were used for sectioning. Both cross- and longitudinal sections were made of each nymphal instar and of adult males.

Adult males were pickled at 0, 7, 14, 21 days after the final moult as well as in "old age" (up to 32 days) in order to study any changes in the phallic complex in the adult. Disscetion and examination were undertaken, as convenient, at varying periods after pickling.

To remove the phallic complex, the epiproct was raised and the subgenital plate lowered. The pallium was then slit and the phallic complex extracted by means of a fine needle. The removed complex was then immersed in a warm 10 per cent. potassium hydroxide solution for about ten minutes, after which it was washed with cold water. The phallic complex was then examined on a cavity slide in glycerol under a stereoscopic binocular microscope. The epiphallus, ectophallus and the endophallus were carefully dissected apart and drawn. All were drawn from the dorsal aspect. A lateral view of endophallus was also drawn.

For sectioning, abdomens (from the sixth segment rearwards) were embedded in paraffin and serial sections were made using a rotary microtome (Microtome 820' Fischer Co.). Sections were stained with Mallory Triple Stain (Humason 1967). This staining technique gave a good differentiation of the chitinous phallic structures and the tissues of other organs present. The mounting fluid used was "Permount" (SO-P-15 Fischer Co.). The slides were studied by using both Wild M 5 stereomicroscope and Wild M 11 compound microscope. The sections were photographed as appropriate to show the development of the phallic structures.

Many structures were investigated in determining the sex and in distinguishing the various stages of the nymphs, but only some of them were found to be of particular value. These

were: the pronotum, the wing-pad, the metathoracic femur, the male subgenital plate and the number of antennal segments. Measurements of these structures were made for the various instars. The pronotum was measured along the median carina, as shown in Figure 4. In the instars which had wing-pads pointing downwards, the wing-pads were measured as shown in Figure 6. Figure 7 indicates the method of measurement of upwardly pointing hind wing-pads, i.e., from the upper end of the meta-pleural sulcus, where the hind wing-pad originates, to the apical margin of the wing-pad.

4. Photography

Specimens to be photographed were killed using chloroform. They were placed in a jar with the vapour for as short a time as possible so as to prevent any colour change. Immediately after killing, the specimens were laid out in the desired position for photographing. The various instars, except the first, were photographed using an Asahi-Pentax SP camera equipped with a close-up lens. Owing to its very small size, the first instar and detail of its structure were photographed through a Wild M 5 stereoscopic microscope equipped with an MK 4 camera and an MEL 13 control unit. Specimens on slides were photographed by means of a Microflex AFMB automatic unit attached to a Nikon compound microscope Model FUC-KE.

IV. DESCRIPTIVE TERMINOLOGY

The terminology for the phallic structures used throughout the present text is that of Kevan, Akbar and Chang (1969) which is but slightly modified from that of Kevan and Akbar (1964) and the same as that used by Kevan and Chen (1969) for *Atractomorpha*. This has also been adopted by subsequent authors such as Key (1972), and there is no cause to elaborate on this here. The abbreviations used in the illustrations are explained on page 153.

V. RESULTS AND OBSERVATIONS

1. Life history of *Atractomorpha sinensis*

Although the primary object of this study was the investigation of the postembryonic development of the phallic structures of *A. sinensis*, it was necessary, as a background, to investigate the general features of the life history of the species, this information being unavailable from other sources.

a. Adult and copulation

Under laboratory conditions (26 ± 2°C. *ca.* 80% R.H. and a 14-hour photophase) the males were observed to reach maturity earlier than the females by a matter of three to four days. The first copulation by males occurred at an average of 10 days after the final moult. The process of copulation lasted from three to four hours. The males as well as the females were found to copulate at irregular intervals after the first occasion, but less frequently in the older adults (32 days or more after first copulation). Copulation, in the females, occurred both before and after oviposition. The mean duration of the adult stage from the time of the final moult until death was 55 days for the male and 62 days for the female (Table I).

b. Oviposition

Eggs were first laid by females on an average of 8.4 days after first copulation. Females were observed to oviposit more than once, up to three times during their lives. The eggs were deposited in pods of 15-23, with a mean of 18 eggs per pod. These figures are based upon numbers of nymphs hatching and assumed zero mortality of the eggs. The numbers of eggs were not counted directly as there was insufficient material available to permit this, but there was little evidence of any egg mortality under laboratory conditions.

c. Immature stages

Under laboratory conditions (26 ± 2°C. *ca.* 80% R.H. and a 14-hour photophase) the following details of the life history of the immature stages were observed.

The eggs usually hatched after two to three weeks of incubation. On the basis of 228 observations, the maximum period between oviposition and hatching was not more than 28 days, the minimum not less than 17 days and the statistical mean 21.4 days. The time between the emergence of the first and the last nymphs from any one egg pod did not exceed 24 hours. There seemed to be no significant difference in the time of hatching between the males and females. Any "vermiform" larval stage that may have occurred was not observed. The nymphs were seen to jump and to hold onto the side of the rearing jar as soon as they hatched.

Altogether there were six male and seven female nymphal instars. No deviations from these numbers was observed. Figures 8-14 illustrate the male nymphs of each instar and Figures 15-22 the female nymphs. The rate of development varied somewhat between individuals and between different instars, with slightly longer mean duration in the later instars, except the seventh instar of the female (Table II). The mean interval between hatching and final moult ~~to adult~~ was 56.2 days in the male and 59.6 days in the female.

2. Nymphal morphology

In the course of nymphal development, several external features underwent notable changes: the antenna, the pronotum, the wing-pads, the metathoracic femur and the abdominal terminalia. Size differences alone are not reliable in separating instars as the females gradually become much larger than the males. A brief outline of the general modifications in structure for each instar, common to both males and females, is given below. Changes in the abdominal terminalia will be mentioned later (Section 5).

a. Antennae

In addition to an overall increase in antennal length (Table III), the number of antennal segments was found to be useful in distinguishing between the various instars. The

antenna consists of three parts: a membranous base or scape, a cylindrical, round and rather short pedicel, and a flagellum consisting of a number of segments which increased in successive instars owing to division of the primary segments. Sometimes, the dividing sutures were obscure and sometimes there was coalescence of segments, so that the numbers in different instars varied, but in general, the number of segments was fairly constant for each instar. In succeeding nymphal instars (based on 228 individuals) the numbers of antennal segments were: 8; 8; 10; 13; 14; and 14-15 for males; and 8; 8; 10; 12; 14; 14; 14-15 for females. The antennal character (Figures 23 to 30) was used with discretion and in conjunction with the other features in distinguishing between instars.

b. Pronotum

There was a striking increase of the length of the pronotum (Figure 4) in successive instars. There were also some structural differences (Figures 31 to 37). Table III gives the measurements of the pronotal length for males and females. These are important in the identification of the instars once the sex has been determined.

c. Wing-pad development

The wings originate as downward projections of the meso- and metanotum. This is evident even in the first instar

(Figure 38). In succeeding instars, the wing-pads grow downwards and backwards (Figures 39, 40, 42). In the third instar, however, the wing-pads start to move upwards and this becomes pronounced in the male fourth (Figure 41) and female fifth instars. These instars are similar except that the female is larger. In the fifth and sixth instars of the male (sixth and seventh of female), the growth of the wing-pads is mainly by elongation posteriorly (Figures 43 and 44). The form and length of the wing-pads were found to be important in separating the instars. Table III shows the differences in the lengths of the hind wing-pads for the different nymphal instars of both sexes.

d. The methathoracic femur

Shotwell (1941) and Guibord (1969) showed that the length of the metathoracic femur was important and reliable in recognization of the different instars in certain Acrididae. In *A. sinensis* there was also gradual increase in length of the metathoracic femur. Table III shows differences in the lengths of the hind femur for the various male and female instars.

e. Sex differentiation

It was found possible to sex the instars as early as the first instar. This was important because only the males were of immediate significance to the main object of the present study. Sex differentiation was mainly based on the development

of the subgenital plate in the males and the ovipositor in the females, and to a lesser extent on the cerci and the overall size. A detailed description of the development of the external genitalia is given in section 5. The differences in successive nymphal instars are illustrated for each sex in Figures 45 to 57.

3. Key to nymphal instars of *Atractomorpha sinensis*

The following key is based on examination of 40 specimens.

1. Wing-pads pointing downwards or downwards and backwards (Figures 6, 38-40, 42); antennal segments 12 or less . . 2
- Wing-pads pointing upwards and backwards (Figures 7, 41, 43, 44); antennal segments 13 or more 5

2. Wing-pads directed downwards, without obvious traces of venation (Figures 6, 38, 39); antennal segments not more than 8; length of metathoracic femur less than 3.7 mm. . 3
- Wing-pads directed somewhat backwards with obvious traces of venation (Figures 40, 42); antennal segments 10-12; length of metathoracic femur more than 4 mm. . . . 4

3. Wing-pads very small, 0.2-0.28 mm.; length of metathoracic femur 2.0-2.68 mm. . . . . First instar*

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*Unless sex is specified, both sexes are included.

- Wing-pads clearly discernible, 0.32-0.5 mm.; length of metathoracic femur 2.68-3.68 mm. . . . . Second instar

4. Hind wing-pads blunt, with indistinct venation, not more than 0.68 (0.41-0.68) mm. (Figure 40); length of metathoracic femur less than 5.5 (4.23-5.33) mm.; antennal segments 10 (8 and 9 indistinct). . . . . Third instar

- Hind wing-pads pointed, with venation pronounced, at least 0.68 (0.68-0.8) mm. (Figure 42); antennal segments 11-12; length of metathoracic femur at least 5.5 (5.5-5.6) mm. . . . . Fourth instar female

5. Antennal length less than 5 mm., number of segments 13-14 (12-13 individual segments short, 11th and 12th indistinct); wing-pads shorter, triangular, pointing more upwards than backwards, 1.5-2.56 mm. (Figures 41, 43); length of metathoracic femur 6.0-7.5 mm. . . . . Fourth instar male or Fifth instar female

- Antennal length more than 5 mm., number of segments 13 or more (individual segments longer, all distinct); wing-pads more elongated, pointing more directly backwards, over 3 mm. (Figures 43, 44), length of metathoracic femur more than 7.5 mm. 6

6. Number of antennal segments 13 or 14; wing-pads not swollen, shorter, 4.58-4.28 mm. (Figure 43); metathoracic femur 7.5-8.8 mm. .Fifth instar male or Sixth instar female

- Number of antennal segments 14 or 15; wing-pads swollen, longer, 4.6-5.84 mm. (Figure 44); metathoracic femur 8.16-10.32 mm. Sixth instar male or Seventh instar female

4. The adult genitalia

a. The external genitalia

These, by convention, are recognized as comprising the terminal abdominal segments and the associated visible appendages. They are very similar in all species of *Atractomorpha* and of a generally unspecialised acridoid form, as indicated by Kevan and Chen (1969). In the male, the chief features, for reference purposes, are: the epiproct, representing the eleventh abdominal tergum, which is triangular in shape; the paraprocts, one on either side of the epiproct; the cerci which are short, conical and unspecialised; and the subgenital plate lying beyond the ninth sternum and curving upwards to conceal the phallic structures. In the female the epiproct and paraprocts are rather similar to those of the male, but of slightly different shape, the cerci are shorter, and the subgenital plate is flatter, terminating in a median point (the egg guide) lying posteriorly between the bases of the ventral of the three pairs of projecting appendages which form the ovipositor. None of these structures calls for special comment as their general nature is similar to that of other Acridoidea (*cf* Snodgrass 1935).

b. The phallic structures

These constitute the concealed copulatory apparatus of the male, sometimes called the internal genitalia. The phallic structures (or "phallic complex" of some authors) have been described in general terms for the Acridoidea, with special reference to the Pyrgomorphidae by Kevan, Akbar and Chang (1969), and are illustrated for *Atractomorpha* (and particularly *A. sinensis*) by various authors, but particularly by Kevan and Chen (1969). There is thus no need for a full description here.

The "phallic complex" is composed of three main sclerotized parts:

(i) the epiphallus (Figure 78), moderately strongly sclerotized and lying dorsally; in *Atractomorpha* it is of a peculiar anchor-like shape;

(ii) the ectophallus (Figure 79), capsule-like, less strongly sclerotized, connected to the epiphallus by a membrane and having a basal fold which covers the endophallus (iii);

(iii) the endophallus (Figures 80, 81), valve-like, very strongly sclerotized structure lying within the ectophallus.

5. Development of the male external genitalia

The following is an account of the development of the ninth abdominal sternum, the subgenital plate and the other

abdominal terminalia, from the first instar to the adult. The other abdominal segments appeared quite uniform in development.

In the first instar male, the ninth sternum was longer and wider than the sterna of the other abdominal segments (Figure 45). This difference became more pronounced in the second instar in which the rudimentary subgenital plate also became longer, extending somewhat dorsad at the apex, but remaining united with the ninth sternum (Figure 46). The lateral margins of the proximal portion of the subgenital plate also became bowed as they extended dorsad and the transverse groove separating the subgenital plate from the ninth sternum became weaker but remained rather more distinct laterally. The apex of the subgenital plate became more obtuse, and the paraprocts became more concealed by it. The epiproct increased in size and length. At the same time the cerci increased in length and became somewhat broader at the base in the ventral view.

During the third and fourth instars, the subgenital plate became increasingly more hood-like, the ninth sternum at the same time becoming broader. The groove separating the subgenital plate from the ninth sternum also became more widely obliterated medially. The other terminalia continued to grow at the same time (Figures 47, 49).

The most drastic change occurred during the fifth and sixth nymphal instars, the subgenital plate becoming more like that of the adult (Figures 51, 53), its dorso-caudad growth forming a hood terminating the abdomen and enclosing the phallic complex, which by this time had developed more fully (see section 6). In ventral view, the epiproct could also be seen projecting to a considerable extent beyond the subgenital plate. The cerci became more acutely pointed as compared with early instars. The paraprocts and epiproct changed little except in size and length.

In the adult, the subgenital plate completely obscured the paraprocts and epiproct when viewed ventrally. The transverse groove between subgenital plate and ninth sternum remained distinct laterally but completely obliterated ventrally (Figure 56).

Table III indicates the increase in length of the subgenital plate throughout the development.

6. Development of the phallic structures

In the first instar, there were two pairs of dark-staining areas present in the position of the ninth abdominal sternum. These may be clearly seen in cross- and longitudinal sections (Figures 58-60). They lay ventrally and close to the wall of the ninth abdominal sternum and presumably represented the

rudimentary genital apparatus. Forming part of these dark-staining areas, in the anterior part of the ninth segment, was a pair of pouch-like structures, the ampullae (AMP), or rudimentary accessory glands. Between the ampullae was a hollow structure, the rudimentary ejaculatory duct (EJD). Sections through the distal end of the ninth sternum revealed the rudimentary penial body (RPE), consisting of two masses of cells lying close to the ampullae.

In the second instar (Figures 61-63), little change took place in the rudimentary copulatory structures. The ampullae became larger and extended laterally (Figure 61). The ejaculatory duct became more tube-like and increased in diameter. The rudimentary penial body also increased in size. The membrane of the genital sinus (MGE) became very distinct, enveloping the other structures mentioned.

During the third instar, the left and right ampullae began to coalesce, forming a conjoint mass instead of two separate ones. The rudimentary vasa deferentia (VD) also began to appear dorsolaterally as projections on either side of the ampullae (Figure 64). Cell masses also began to migrate from the ampullae to begin the formation of the accessory glands. The penial body further increased in size with hollowing at the centres of the two parts. Cells also began to congregate along the inner side of the rudimentary penial body (Figure 65).

These probably represented the rudimentary aedeagal sclerites. The rudimentary penial body and the ampullae remained in intimate contact (Figure 66). The pallium (PA), in the meantime, became well formed, and the ejaculatory duct became very distinct (Figure 64).

The most evident development in the fourth instar was the appearance of small tubules, the accessory glands, derived from the ampullae, and the distinct differentiation of the vasa deferentia on either side (Figure 67). In the proximal end of the ninth segment, the base of the rudimentary penial body became much enlarged and cells started to migrate ventrally to form a sheath of cells surrounding the rest of the penial body (Figure 68), and which apparently represented the future ectophallus (RE). In the disal end of the ninth segment, the rudimentary penial body remained as two pouches of cells (Figure 69). The rudimentary aedeagal sclerites were more distinct here. Thus it was in the fourth instar that the phallic complex started to take shape, although virtually no sclerotization had occurred at this stage.

The most marked development of the nymphal phallic complex occurred in the fifth and sixth instars when the phallic structures began to take on something approaching the adult form (Figures 71 and 72), especially so in the sixth instar (Figures 73, 74 and 75). The epiphallus became

differentiated with some degree of sclerotization (Figures 72 and 75, EP). The capsule-like ectophallus also became distinct (Figures 71 and 73, EC). At the proximal end of the segment, a pair of ring-like structures began to appear on either side of the ejaculatory duct, the endophallic apodemes(Figures 71 and 73, EA). These arose as two separate plates and never quite fused with each other. Above the aedeagal sclerites(AS) was a sac-like structure, the spermatophore sac (Figure 74, SS). Sclerotization of the parts became quite pronounced in the sixth instar. Endophallic muscle cells also began to appear from the ectophallic walls to the endophallus (Figure 75, MUS). The accessory glands (ACG) became convoluted in the fifth and sixth instars. Figures 76 and 77 show transverse and longitudinal sections of the phallic complex of an adult male for comparison with the nymphal instars.

7. Development of the phallic structures after maturity

The phallic structures (Figures 78-81) were extracted from adult specimens of various ages: just matured (i.e., on the day of the final moult), at seven, fourteen and twenty-one days subsequent to the final moult, and old males which had become adult at least 32 days previously. Altogether, 25 specimens were examined, five individuals for each age class.

The examination of the phallic structures obtained from these specimens, dissected at different stages of maturity, showed that development of the phallic structures continued after the adult state was attained. The most prominent difference between a young and an old adult was the degree of sclerotization of these structures. Evidence from the nymphs had shown that some, but not much, sclerotization of the phallic structures had already begun by the time that an individual first matured (i.e., before the final moult). Sclerotization progressed thereafter in all parts of the phallic complex (Figures 78-81), but there was no general increase in size.

a. Epiphallus (Figure 78)

Sclerotization was very light in the freshly matured adult and became progressively heavier with age, particularly in marginal regions. In the freshly matured specimens the whole structure appeared almost transparent except at the projections of the lophi (L), but became more and more transluscent or opaque with age. The bridge of the epiphallus (B) was wider in young than in old adults. In the newly matured individuals, the appendices (A) were slender and club-shape, but in old adults they became robust and more rod-shaped. In the old adult, the lateral plates (LP) of the epiphallus became broad

and fused medially, whereas in young individuals they were very widely separated and virtually lacking. The whole epiphallus became more and more robust as the insect aged, the progressive change being quite even.

b. Ectophallus (Figure 79)

In comparison with those of the epiphallus, the structural changes in the ectophallus were of lesser magnitude. Most of the changes took place in the cingulum region. As a result of increasing sclerotization, the basal emargination (BE), initially deep, became progressively shallower, while the basal thickening (BC) and suprazygoma (SZ) became more and more distinct, forming a triangular plate-like structure. At the same time, the apodemal plates of the cingulum (AC) became relatively less extensive, while the central membrane (CM) became slightly more triangular. Some increase in the supra-rami (SR) also occurred.

c. Endophallus (Figures 80, 81)

Considerable progressive change took place in this structure as seen in lateral view (Figure 81), though relatively little in the dorsal view (Figure 80). The aedeagal valve (AV) was comparatively slender and more acute in the young adult but became more robust and blunter in older

individuals. No appreciable change was observed in the spermatophore sac (SS). The most obvious differences between the young and the old adults were the enlargement and increased sclerotization of the endophallic apodemes (EA) and an increase in robustness and curvature of the rami of the aedeagal sclerites (AS) in older individuals. In the younger males, the aedeagal sclerites were lighter, more flexible and less curved than in older specimens. The increase in curvature of the aedeagal sclerites with age seemed to be due to additional sclerotization ventrally. The distance between the endophallic apodemes also decreased somewhat with age (Figure 80).

VI. DISCUSSION AND CONCLUSION

1. The nymphs of *Atractomorpha sinensis*

From the present study, it was found that there were six nymphal instars in the males and seven in the females of this species. This contrasts to five instars (in the females) indicated for *A. crenulata* by Fletcher (1917). Extra nymphal instars in Acrididae have been reported by several workers (e.g., Parker 1930; Roonwal 1946; Shotwell 1941; Guibord 1969), but not usually as a regular feature of the life history. However, in some Acridoidea (including some Pyrgomorphidae) a normal difference has been reported in the number of instars as between males and females in species in which the two sexes differ appreciably in size (Kevan 1943, 1949). This does not appear to be a universal rule, but probably the additional instar in the female of *A. sinensis* is (at least under the laboratory conditions provided in the present study) explainable on account of its larger size than in the males.

Throughout the nymphal stadia, there were a few structures that changed considerably from instar to instar, and these characters were found to be useful in separating the different instars. These were degree of development of wing-pads, the length of the antennae and the number of antennal segments, and the length of the metathoracic femur. In this respect,

A. sinensis is similar to other Acridoidea (Coleman 1911; Key 1936; Pruthi 1939; Karandikar 1945; Burnett 1951; Katiyar 1955, 1957).

Sexing of even the youngest nymphs was found to be possible on account of the differences in the terminal abdominal segments between male and female. The differences became progressively more marked in later instars. This confirms the report of Nelsen (1931), that sexing of young acridoids is possible as early as the late revolution period of the embryo (i.e., the period just prior to hatching) and agrees with findings of other authors for other acridoids (Dirsh 1950; Guibord 1969).

2. Development of the genitalia

The post-embryonic development of the external genitalia principally takes the form of a relative increase in size of the ninth abdominal sternum and the subgenital plate. The sulcus separating the two, believed by Else (1934) to be the point of fusion of the embryonic appendages of the ninth and tenth abdominal segments, becomes less and less marked as development proceeds. The enlargement of the hood-like subgenital plate reveals a corresponding growth of the concealed rudimentary copulatory apparatus.

The phallic structures originate as a pair of rudimentary lobes. The origin of these lobes in Acrididae has been interpreted in different ways. Crampton (1920) and Walker (1922) regarded the rudiments as the endopodites (limb bases) of the ninth abdominal appendages. This has not, however, been widely accepted. Else (1934) believed that the copulatory apparatus derived from the embryonic appendages of the tenth abdominal segment, but, although Snodgress (1937) agreed with Else, Roonwall (1937) claimed that appendages of both ninth and tenth segments were involved in the formation of the structure. Since the embryonic stages were not considered in this study, it is impossible to indicate which is the most probable hypothesis.

According to Wheeler (1893), in males of the tettigonioid orthopteran, *Conocephalus*, the ampullae (the rudimentary accessory glands) withdraw and disappear during the nymphal development. This is, however, not true of *A.sinensis*, in which they continue to grow in the vicinity of the median line, taking a position along either side of the distal position of the ejaculatory duct. However, as *A. sinensis* is an acridoid, and hence only very distantly related to *Conocephalus*, there is no valid reason to contradict Wheeler's contention in respect of the latter insect.

Roonwall (1937) believed that the coelomic pouches in *Locusta* form the ampullae, and this is probably correct on morphological grounds. The present study seems to agree with Roonwall that the accessory glands originate from the ampullae and, thus, that they are of coelomic origin.

It is interesting to note that the endophallus is the last of the phallic structures to be differentiated from the penial rudiments. The development of the aedeagal sclerites in *Atractomorpha* seems to differ from that of Acrididae, as Snodgrass (1937) indicates for *Dissosteria carolina* (Linnaeus) that, in that family, they originate as a single pair of sclerites and not initially as two pairs which later become fused.

The suggestion (Kevan and Chen 1969; Kevan 1970a, 1972) that development of the phallic structures may continue after maturity, at least in some Pyrgomorphidae (*Desmopterella* and *Atractomorpha*), has been found to be true for *A. sinensis*. This occurs mainly as a progressive sclerotization resulting in an increase of strength and rigidity of the phallic complex, with, in some instances, significant changes in the appearance of the component parts. There seems to be a relationship between the degree of sclerotization of the phallus and the time of copulation. Usually copulation does not occur until 10 days after the insect has matured. From the phallic

structures observed it may be deduced that before this, they may be too slender and their sclerotization too light. It is not until about 40 days after maturity that they become fully sclerotized, by which time they exhibit less flexibility, and possibly decline in efficiency as an intromittant organ. The change is especially obvious in the lateral aspect of the aedeagal sclerites (AS) which become heavier and more curved as the insect ages.

In view of the emphasis placed upon phallic characters in the systematics of Acridoidea, and indeed of most other insects, it is essential that taxonomists, before they place too much reliance on relatively minor differences in phallic characters, should bear in mind that such changes as are herein described, can occur. Although the variations in the phallic complex of a single individual may be less spectacular than the seasonal differences reported by Müller (1957) for the homopteran genus *Euscelis*, the need for caution is stressed. Just how widespread or significant throughout the Acridoidea are changes in the phallic structures such as those described here, is, as yet, undetermined, but the fact that such changes can continue over several weeks, in one, and almost certainly two, genera at least, leads one to be somewhat suspicious of the recognition of new species based upon minor differences in phallic characters where an insufficiently long series has been examined.

T A B L E S

TABLE I. Adult life history of *Atractomorpha sinensis* at 26±°C *ca* 80% R.H. and 14-hour photophase

	Number of individuals observed	Days		$\bar{X}$
		Maximum	Minimum	
1st copulation ♂ after final moult	81	14	9	10.7
1st copulation ♀ after final moult	110	17	12	14.2
1st oviposition after copulation	109	12	6	8.4
Longevity of ♂	80	61	30	55.1
Longevity of ♀	109	70	28	62.4

TABLE II. Nymphal life of *Atractomorpha sinensis* at 26±°C., *ca.* 80% R.H. and a 14-hour photophase

Instars	Number of individuals observed	Days		$\bar{X}$
		Maximum	Minimum	
I ♂	18	10	6	9.0
♀	17	9	7	8.3
II ♂	18	11	9	10.4
♀	20	9	7	8.2
III ♂	20	11	6	9.7
♀	17	11	8	10.1
IV ♂	14	12	8	10.2
♀	16	8	5	6.1
V ♂	18	12	10	11.2
♀	20	11	9	10.5
VI ♂	16	13	10	11.7
♀	14	14	12	13.1
VII ♀	20	10	7	9.4
Total I-VI ♂	24	62*	52*	56.2*
Total I-VII ♀	18	70*	55*	59.6*

*These are not the sums of the columns but are totals for individual insects.

TABLE III. Measurements (in mm.) of the length of antenna, pronotum, hind wing-pad, metathoracic femur and male subgenital plate, for different nymphas instars of *Atractomorpha sinensis*. (based on means for 40 specimens for each instar)

Instar	Antenna	Pronotum*	Hind-wing pad*	Metathoracic femur*	♂ Subgenital plate
I ♂	1.64	0.88	0.28	2.68	0.08
♀	1.60	0.80	0.28	2.80	
II ♂	2.04	1.20	0.32	3.28	0.16
♀	2.10	1.34	0.30	3.50	
III ♂	2.83	1.83	0.41	4.52	0.20
♀	2.90	1.80	0.44	4.58	
IV ♂	4.16	2.91	2.08	6.41	0.41
♀	3.36	2.56	0.80	5.60	
V ♂	5.41	3.83	4.58	7.58	0.54
♀	4.40	3.76	2.56	7.20	
VI ♂	5.67	4.00	5.00	8.27	0.66
♀	5.04	4.86	5.28	8.80	
VII ♀	5.60	5.20	5.84	10.30	

*Measured as indicated in Figures 4-7.

F I G U R E S

Figure 1. Rearing cage with screened false floor.

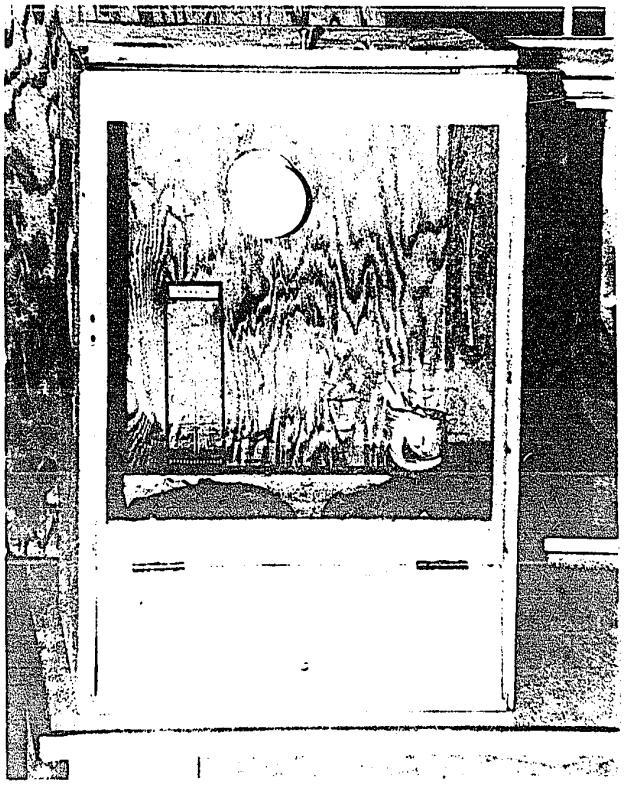


fig.1

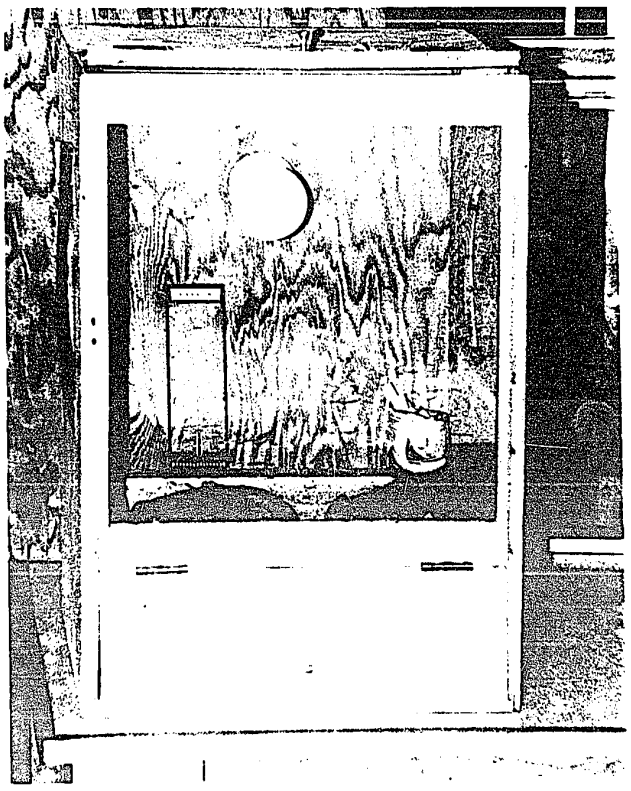


fig.1

Figure 2. Rearing cage with wooden floor and sand pots for oviposition.

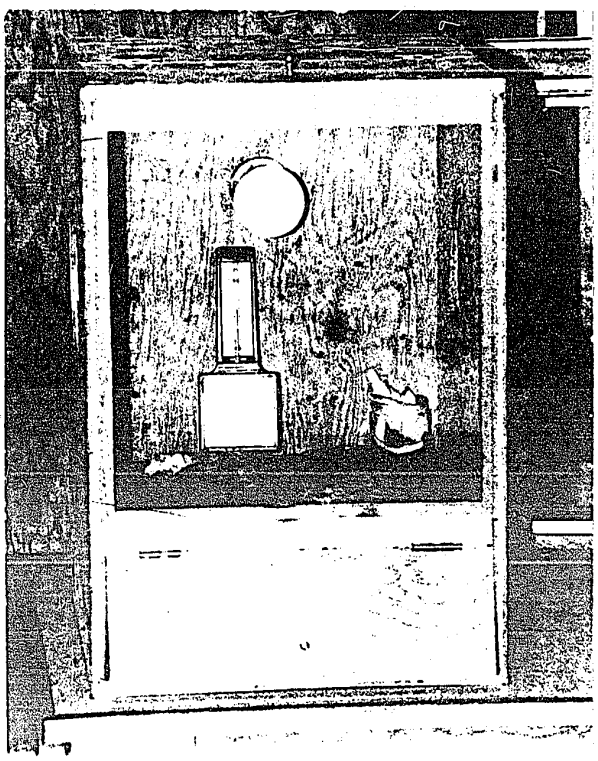


fig.2

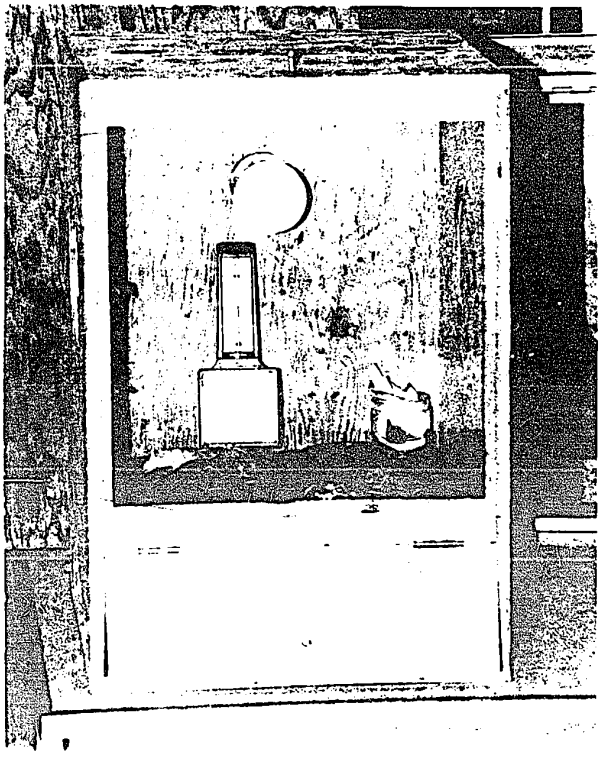


fig.2

Figure 3. Glass rearing jar with wire-mesh screw-top lid.

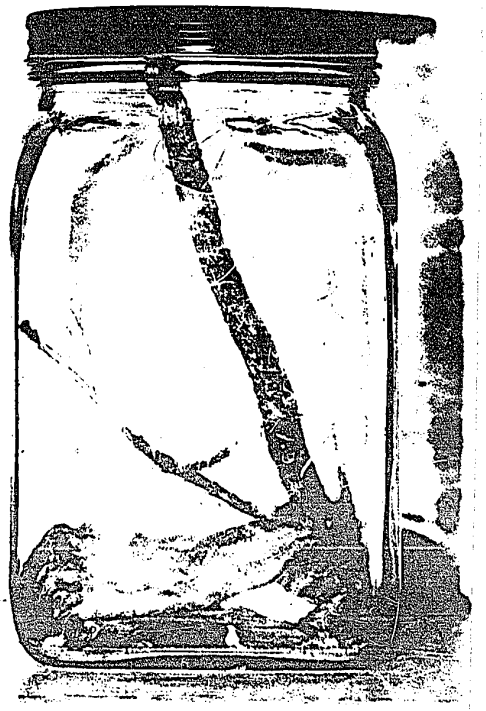


fig.3

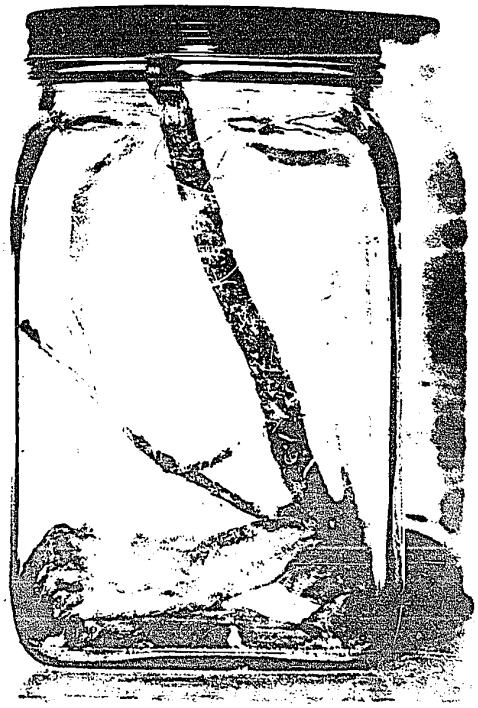


fig.3

Figure 4. Measurement of pronotum length (P.L.).

Figure 5. Measurement of metathoracic femur length (M.F.L.).

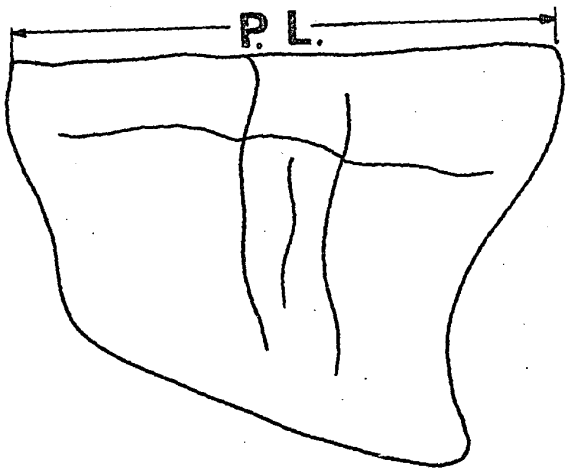


fig.4

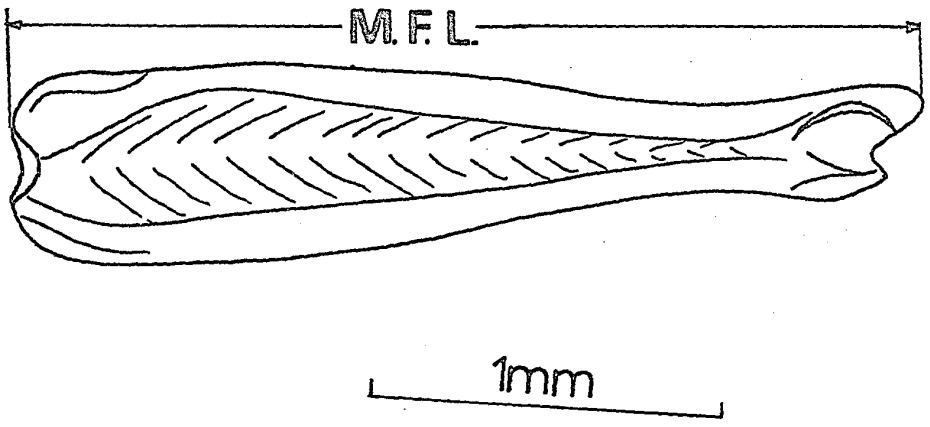


fig.5

Figure 6. Measurement of hind wing-pad length (H.W.P.L.) in the instars where wing-pads point downwards.

Figure 7. Measurement of hind wing-pad length (H.W.P.L.) where the wing-pads point upwards and backward.

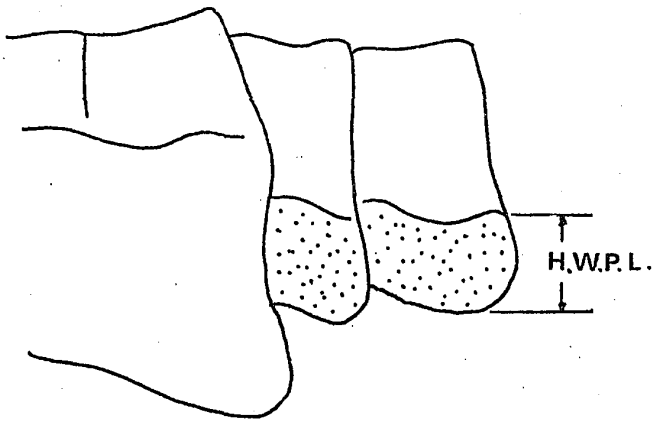


fig.6

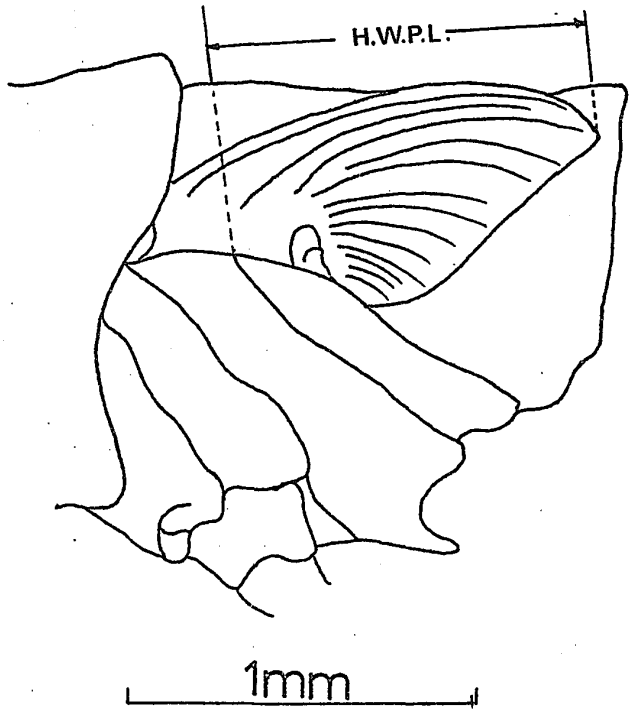


fig.7

Figure 8. *Atractomorpha sinensis*, male, first instar, lateral view. (12 X)

Figure 9. *A. sinensis*, male, second instar, lateral view. (4 X)

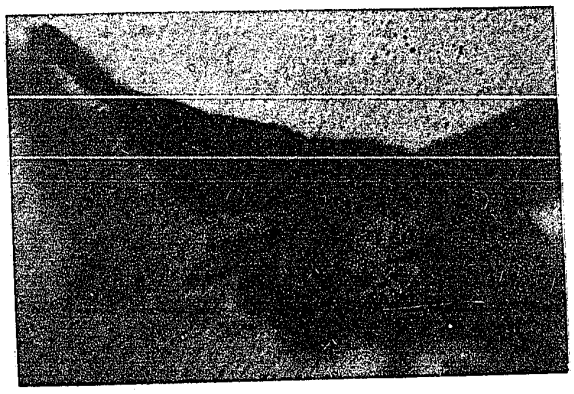


fig.8

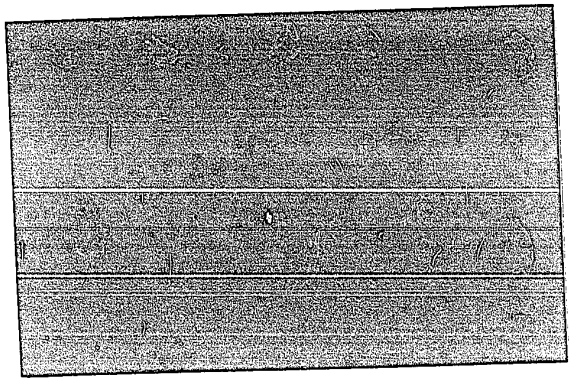


fig.9

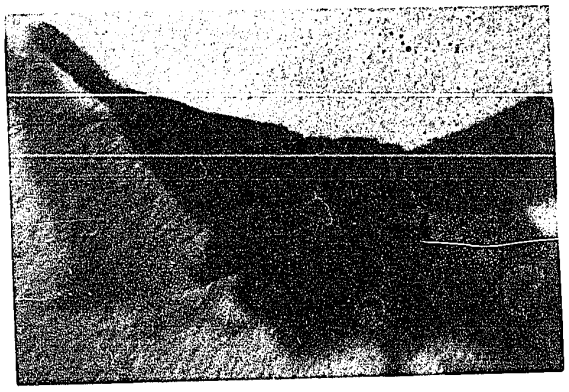


fig. 8

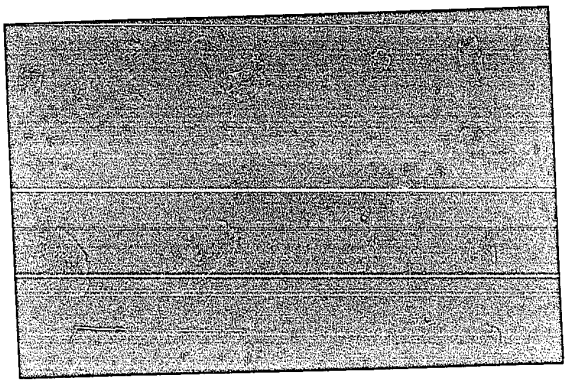


fig. 9

Figure 10. *A. sinensis*, male, third instar, lateral view. (6 X)

Figure 11. *A. sinensis*, male, fourth instar, lateral view. (3 X)

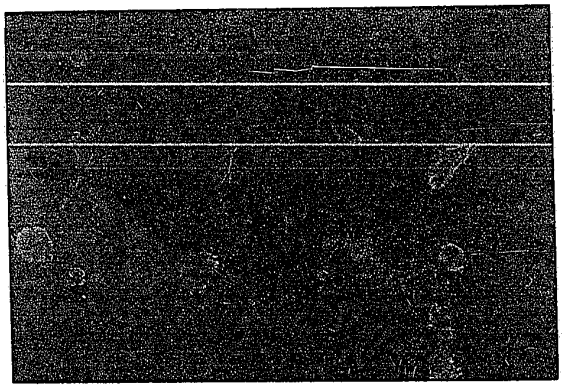


fig.10

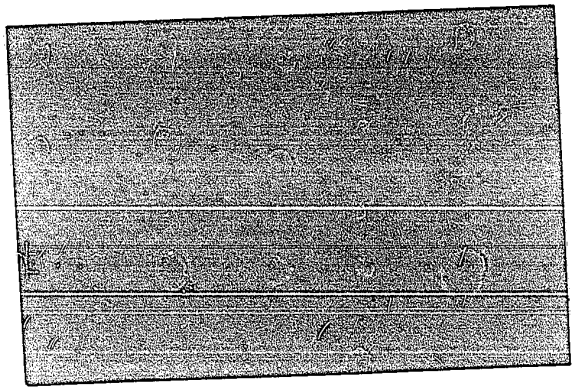


fig.11

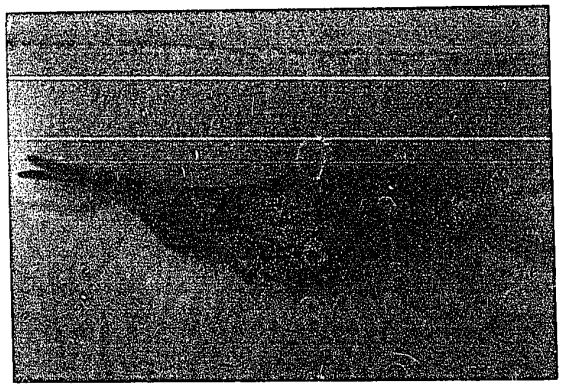


fig.10

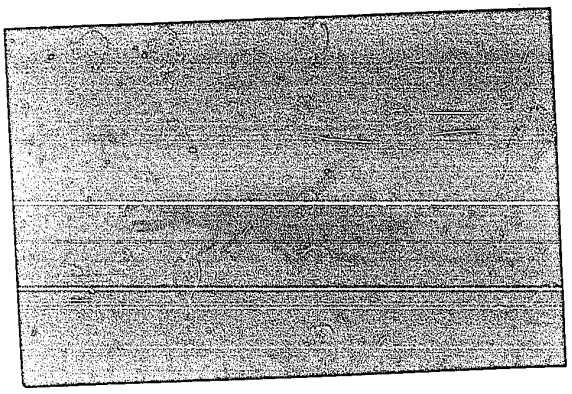


fig.11

Figure 12. *A. sinensis*, male, fifth instar, lateral view. (3 X)

Figure 13. *A. sinensis*, male sixth instar, lateral view. (2 X)

Figure 14. *A. sinensis*, adult male, lateral view. (2 X)

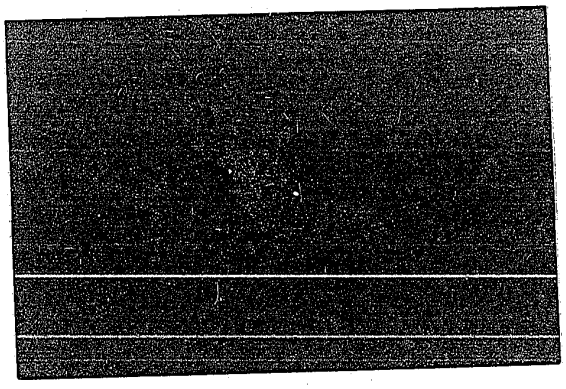


fig.12

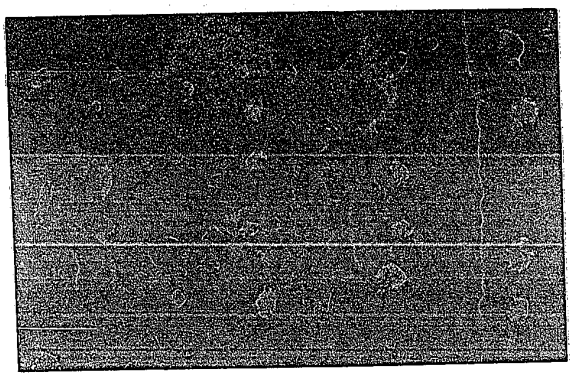


fig.13

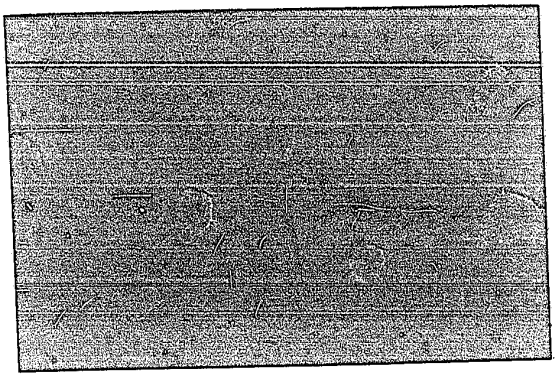


fig.14

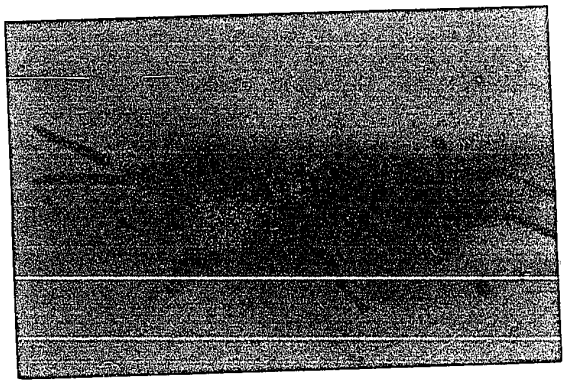


fig.12

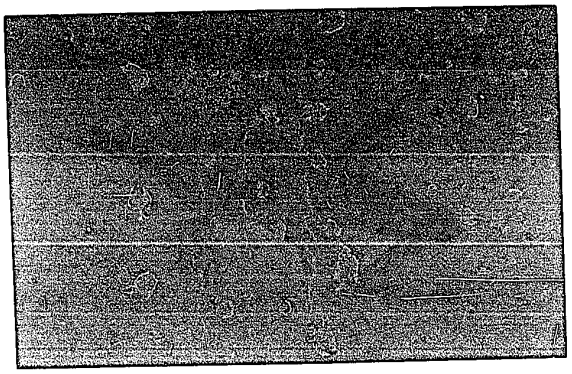


fig.13

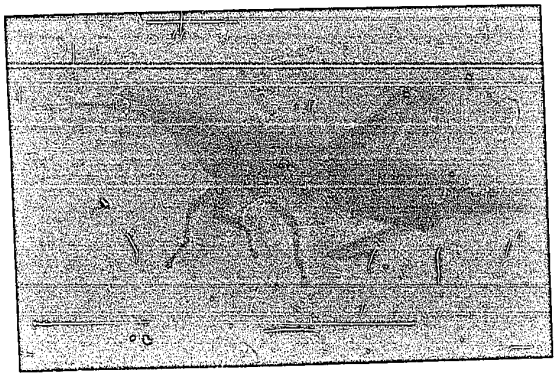


fig.14

Figure 15. *A. sinensis*, female, first instar, lateral view. (10 X)

Figure 16. *A. sinensis*, female, second instar, lateral view. (10 X)

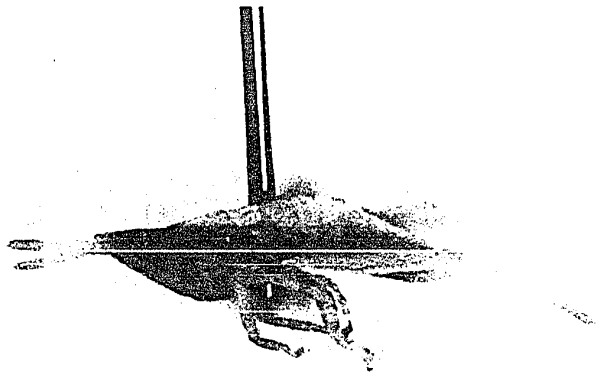


fig.15

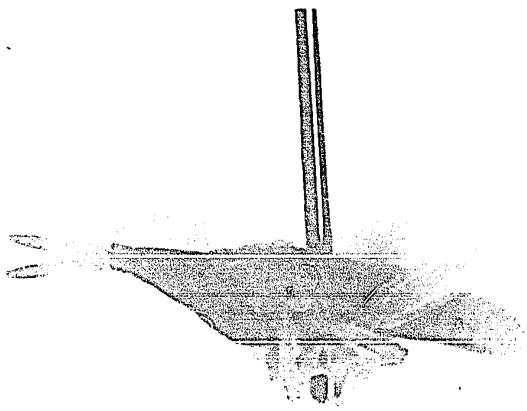


fig.16

Figure 17. *A. sinensis*, female, third instar, lateral view. (10 X)

Figure 18. *A. sinensis*, female, fourth instar, lateral view. (9 X)

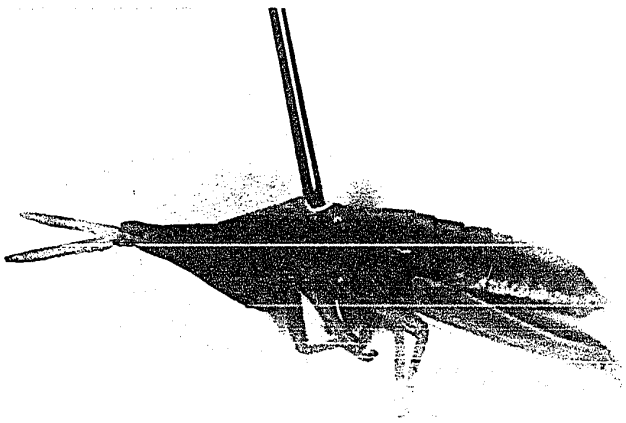


fig.17

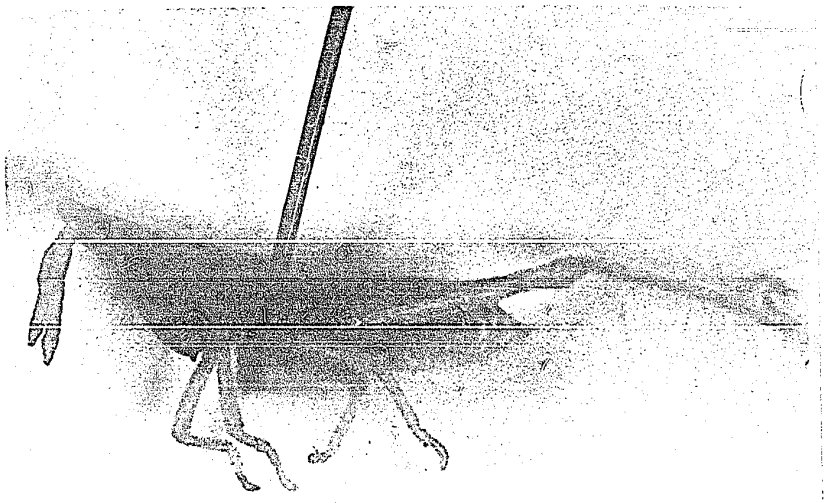


fig.18

Figure 19. *A. sinensis*, female, fifth instar, lateral view (9 X)

Figure 20. *A. sinensis*, female, sixth instar, lateral view. (5 X)

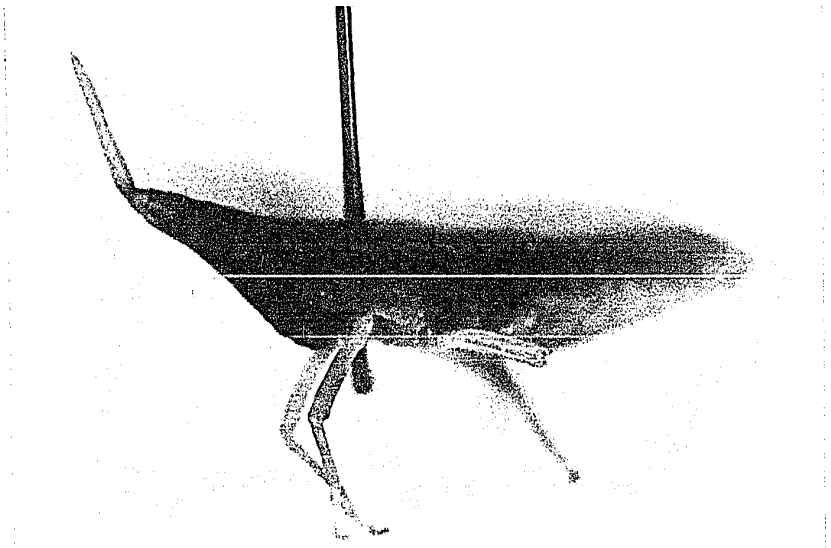


fig.19

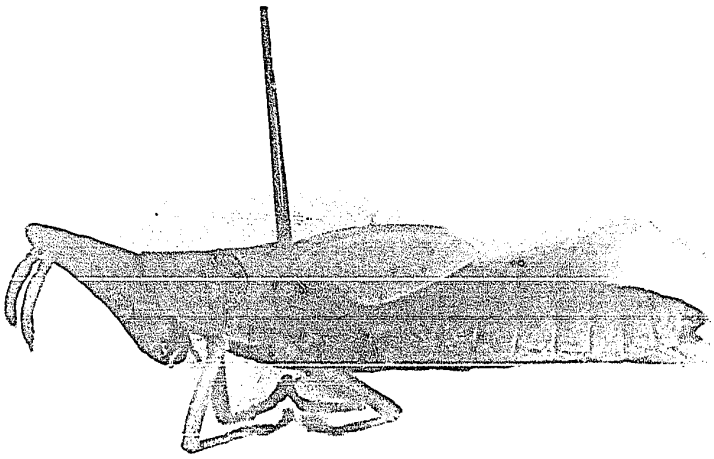


fig.20

Figure 21. *A.sinensis*, female, seventh instar, lateral view. (4 X)

Figure 22. *A. sinensis*, adult female, lateral view. (4 X)

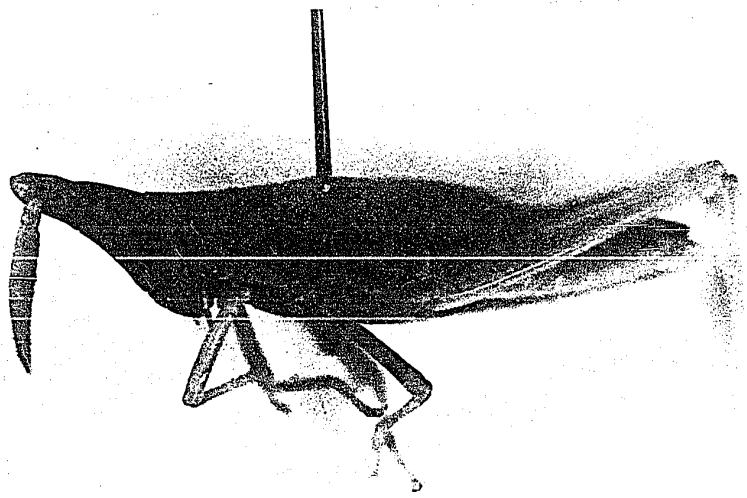


fig.21

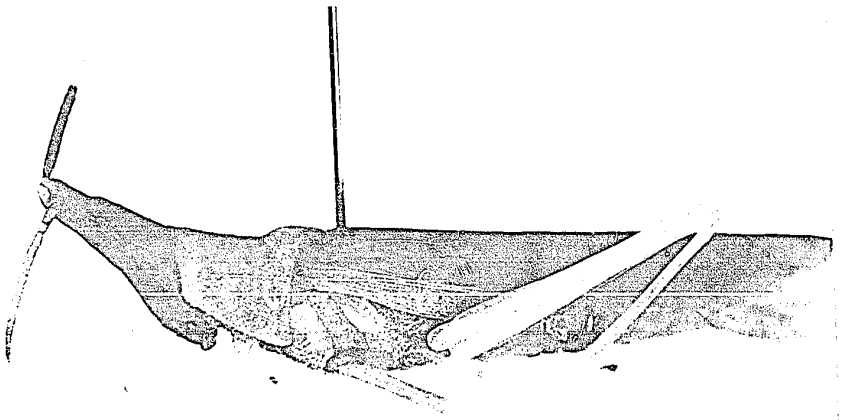


fig.22

Figures 23-25. *A. sinensis*, left antennae.

23. male, first instar
24. male, second instar
25. male, third instar

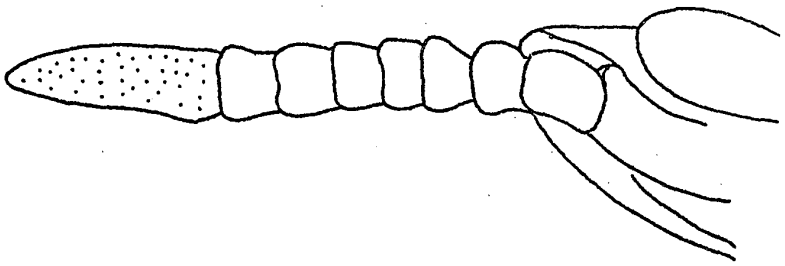


fig.23

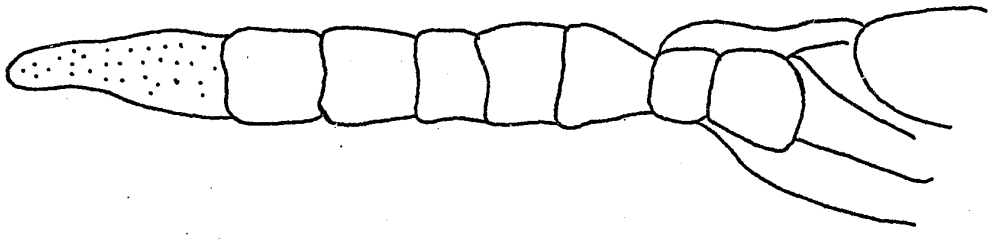


fig.24

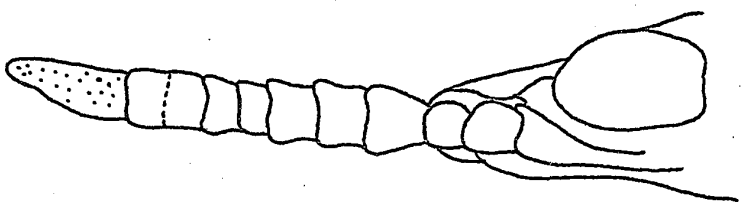
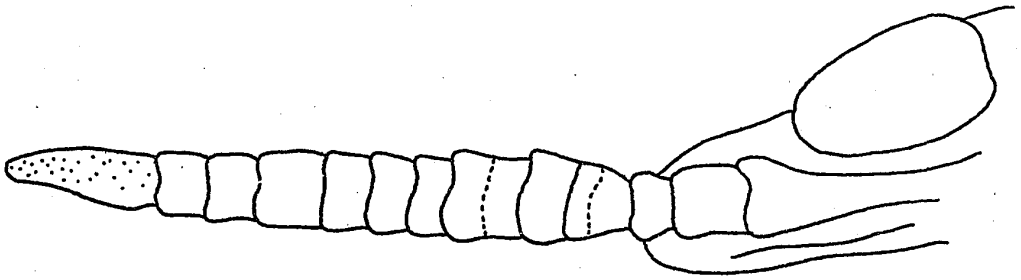


fig.25

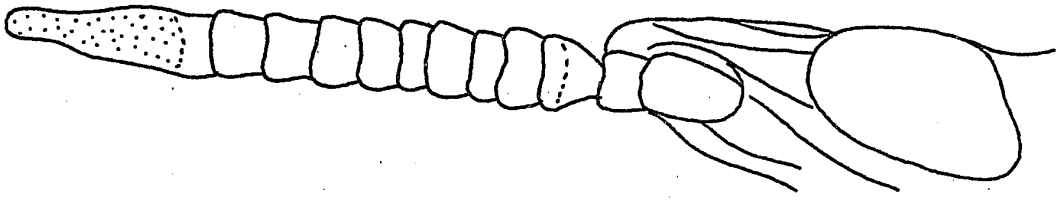
Figures 26-28. *A. sinensis*, left antennae.

26. male, fourth instar
27. female, fourth instar
28. male, fifth instar



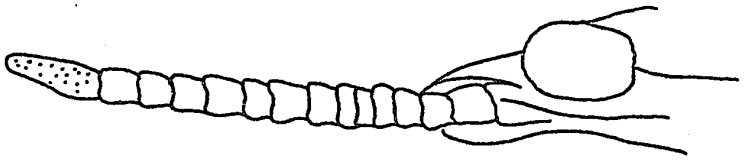
1mm

fig.26



1mm

fig.27



1mm

fig.28

Figures 29-30. *A. sinensis*, left antennae.

29. male, sixth instar

30. male, adult

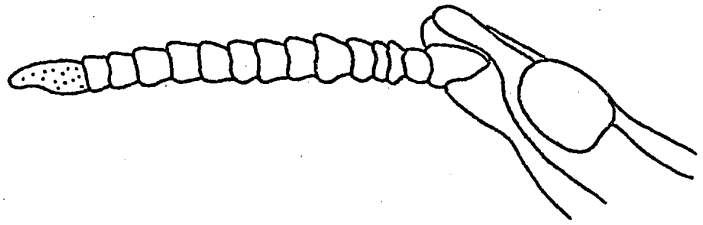


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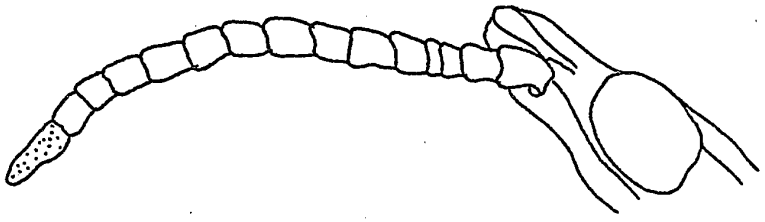
fig. 29



1mm

fig. 30

Figures 31-32. *A. sinensis*, male pronotum, lateral and dorsal.

31. first instar

32. second instar

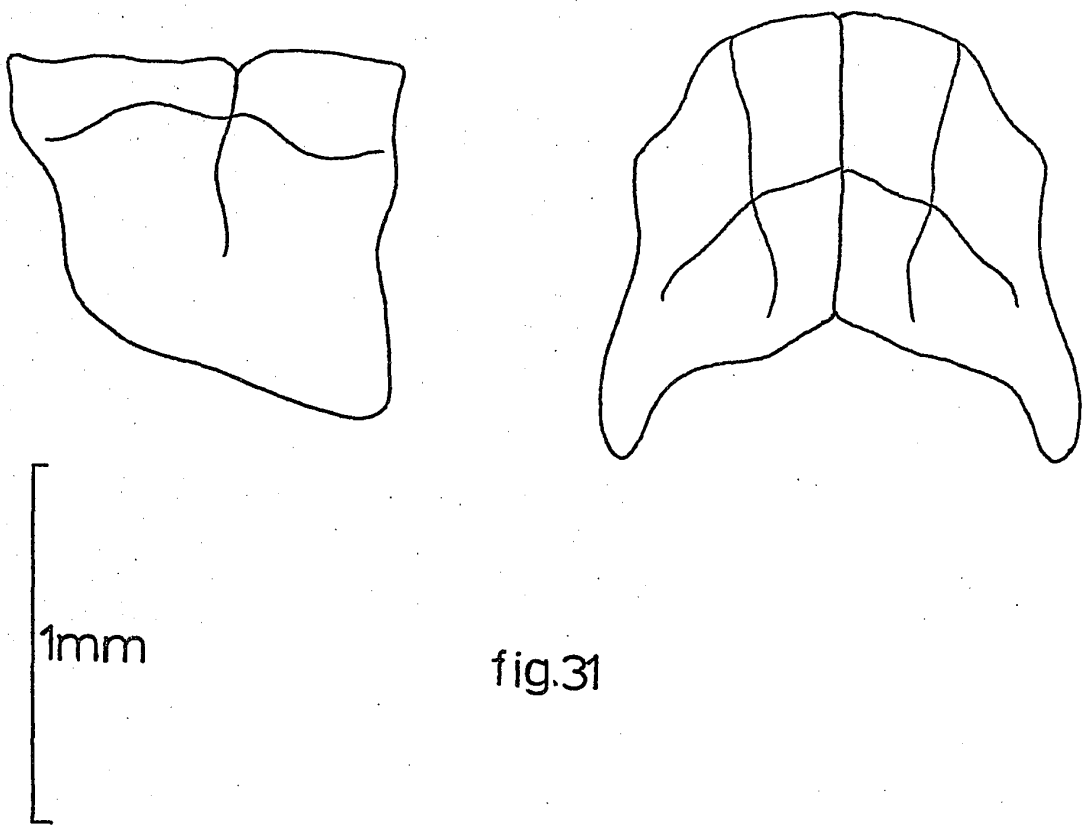


fig.31

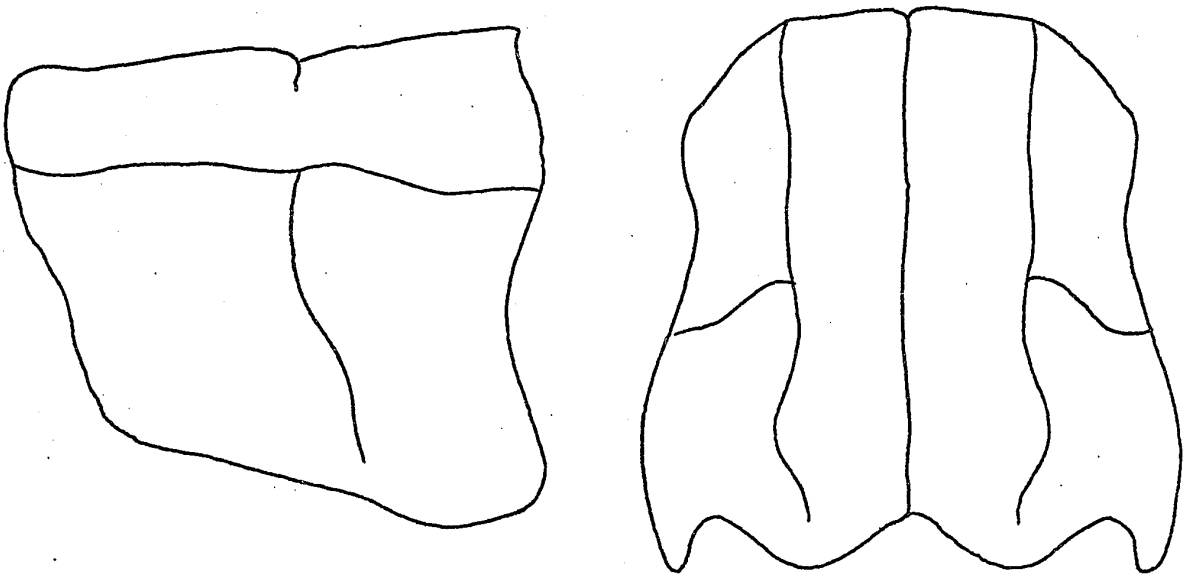


fig.32

Figure 33. *A. sinensis*, male pronotum, lateral and dorsal, third instar.

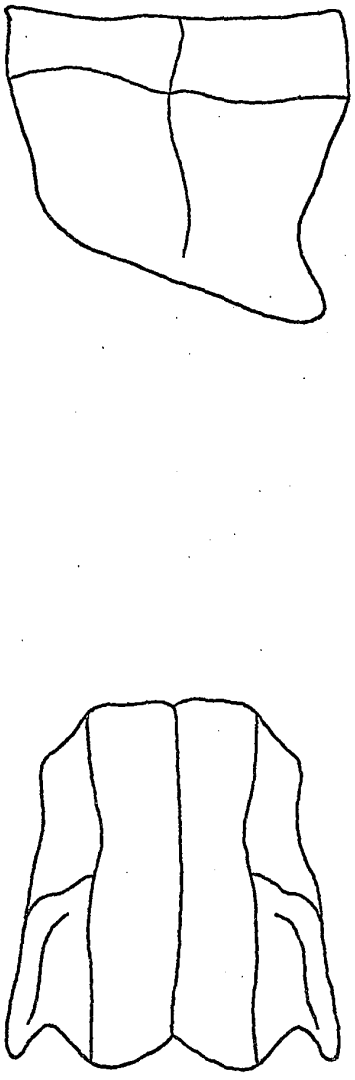


fig.33

Figure 34. *A. sinensis*, male pronotum, lateral and dorsal, fourth instar.

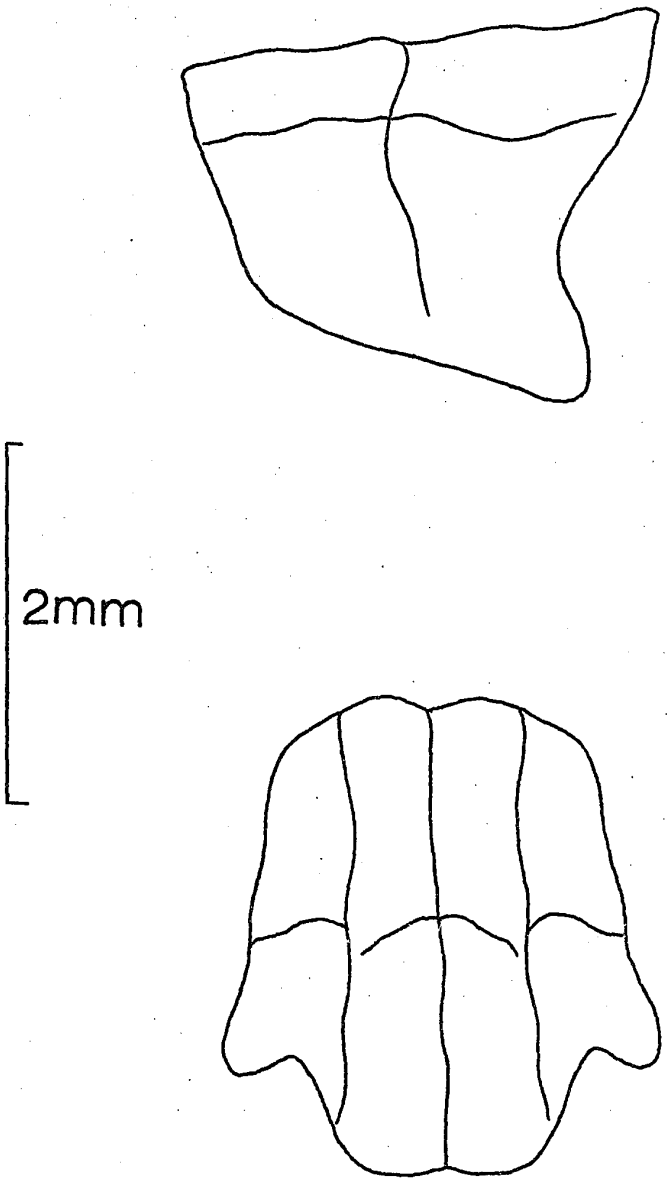


fig.34

Figure 35. *A. sinensis*, female pronotum, lateral and dorsal, fourth instar.

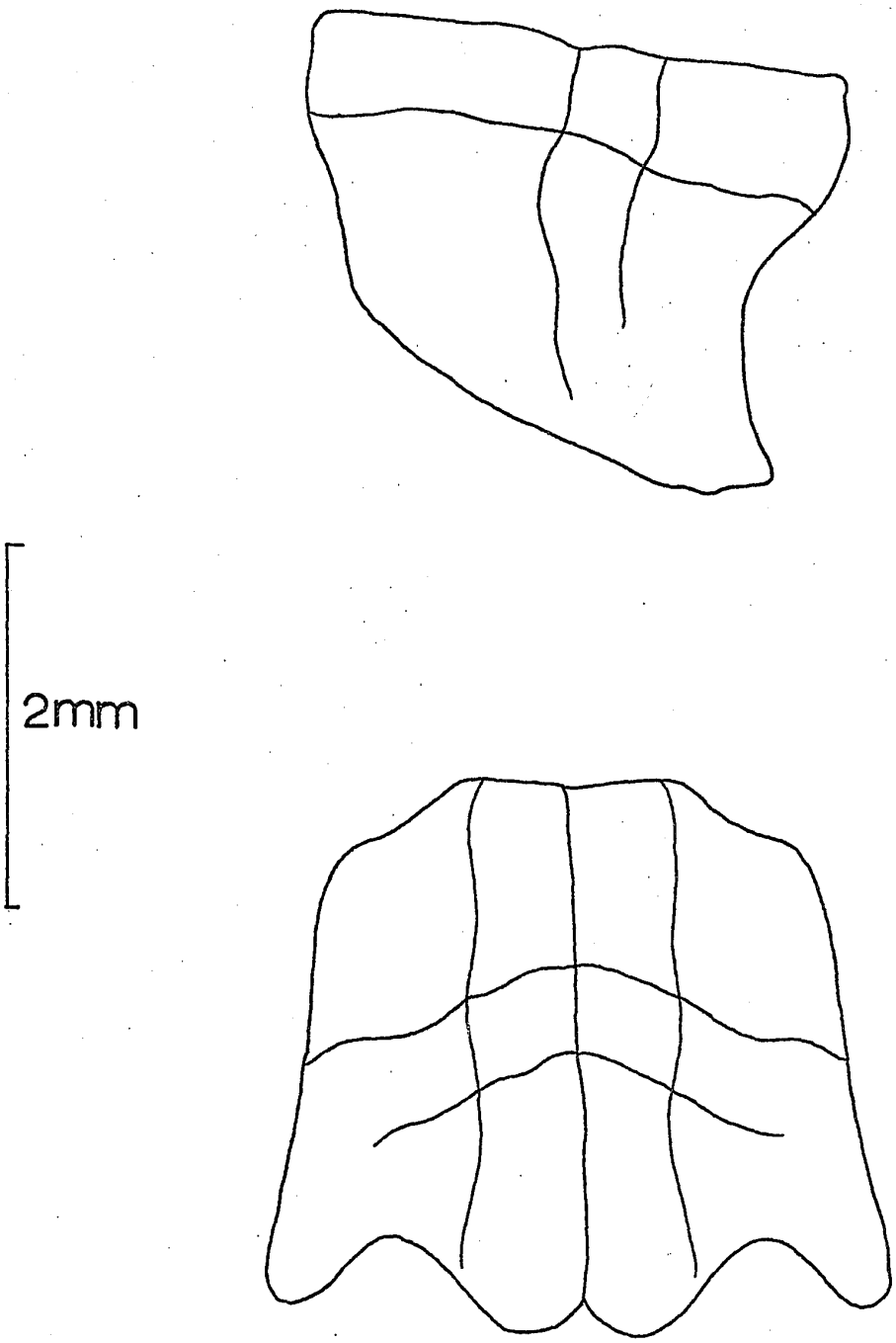


fig.35

Figure 36. *A. sinensis*, male pronotum, lateral and dorsal, fifth instar.

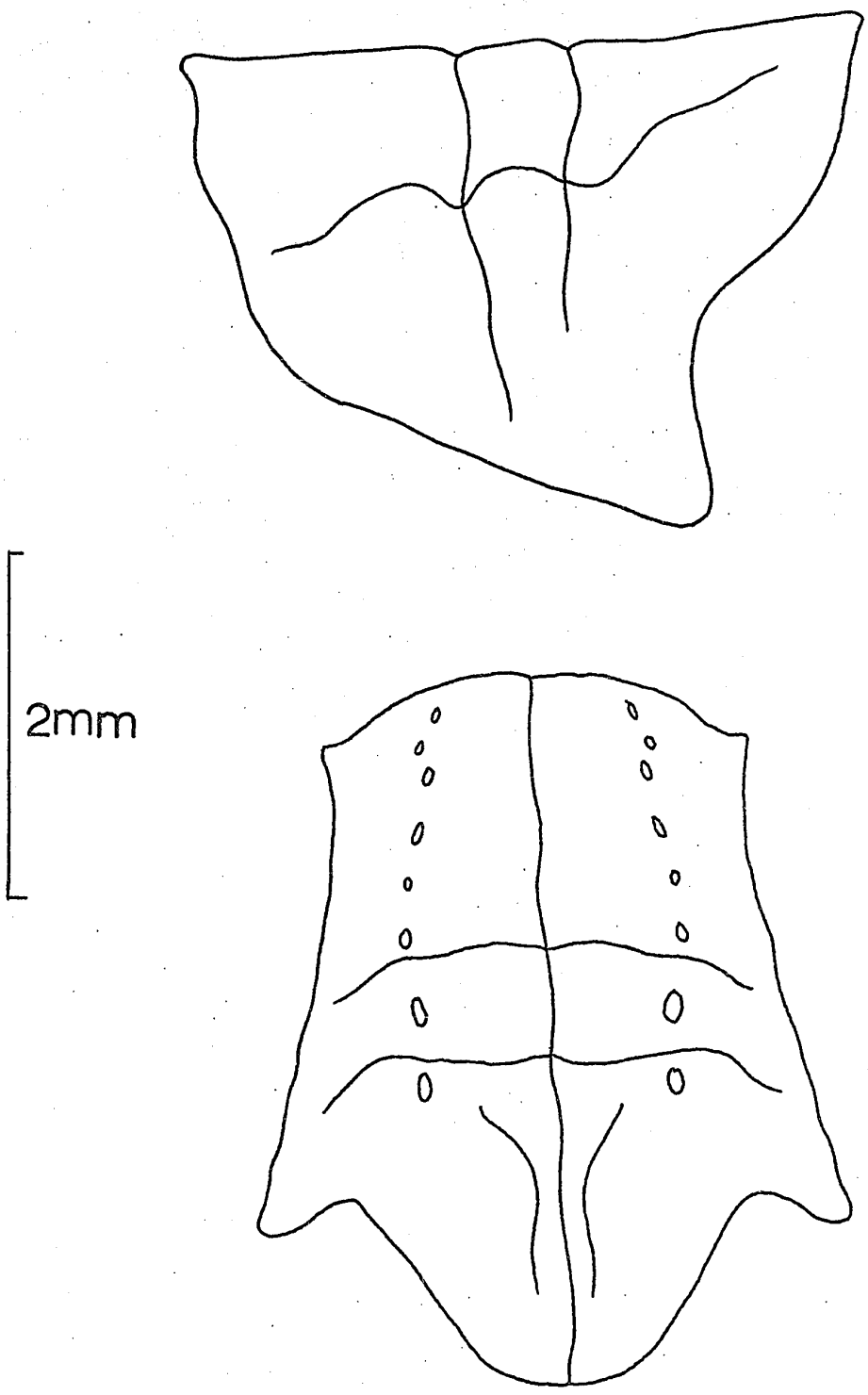


fig. 36

Figure 37. *A. sinensis*, male pronotum, lateral and dorsal, sixth instar.

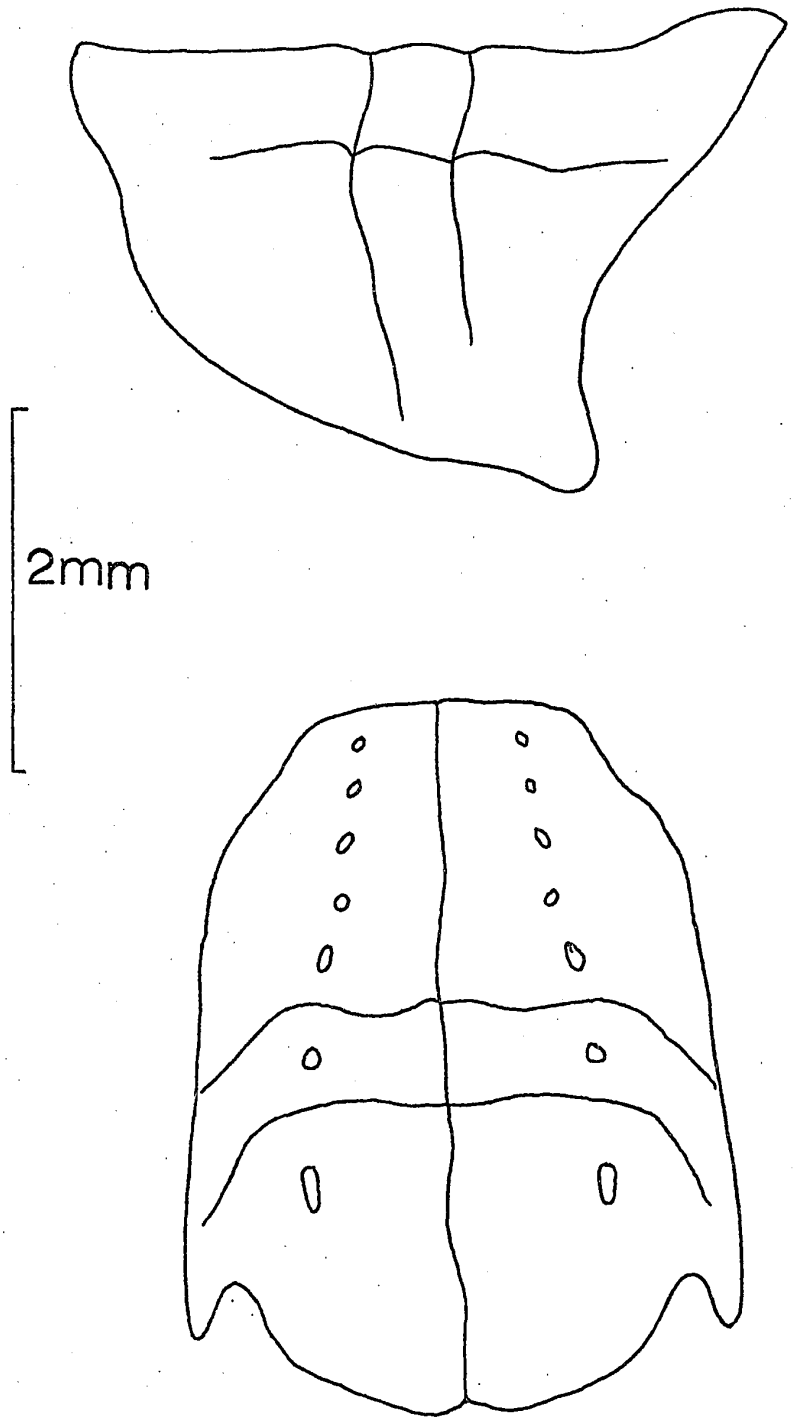


fig.37

Figures 38 and 39. *A. sinensis*, male wing-pads, lateral.

38. first instar
39. second instar

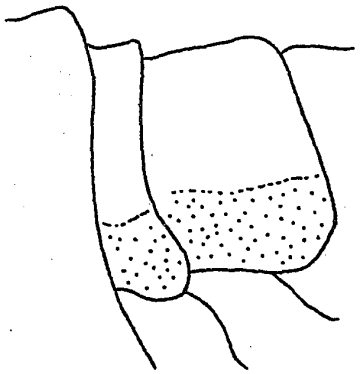


fig.38

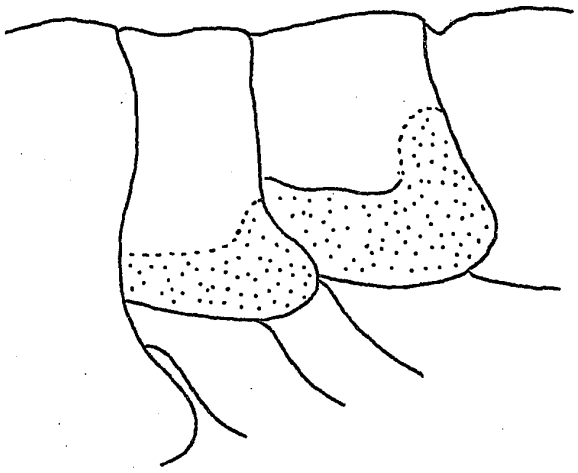


fig.39

1mm

Figures 40-41. *A. sinensis*, wing-pads, lateral.

40. male, third instar
41. female, fourth instar

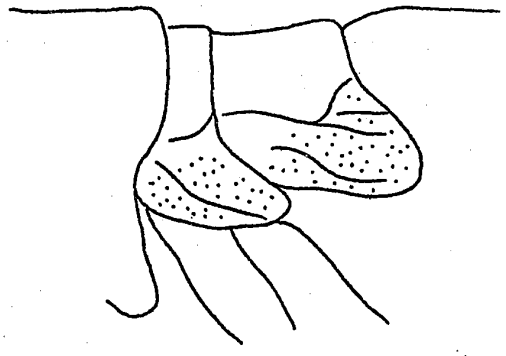


fig.40

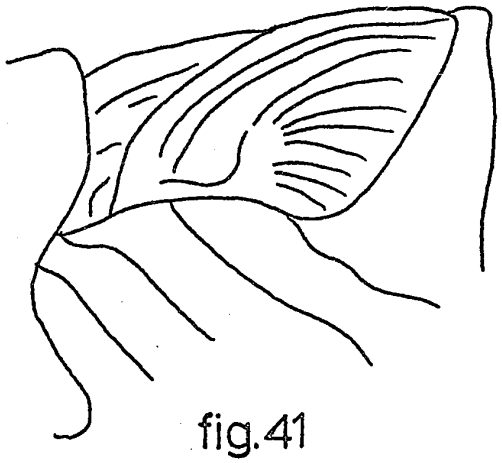
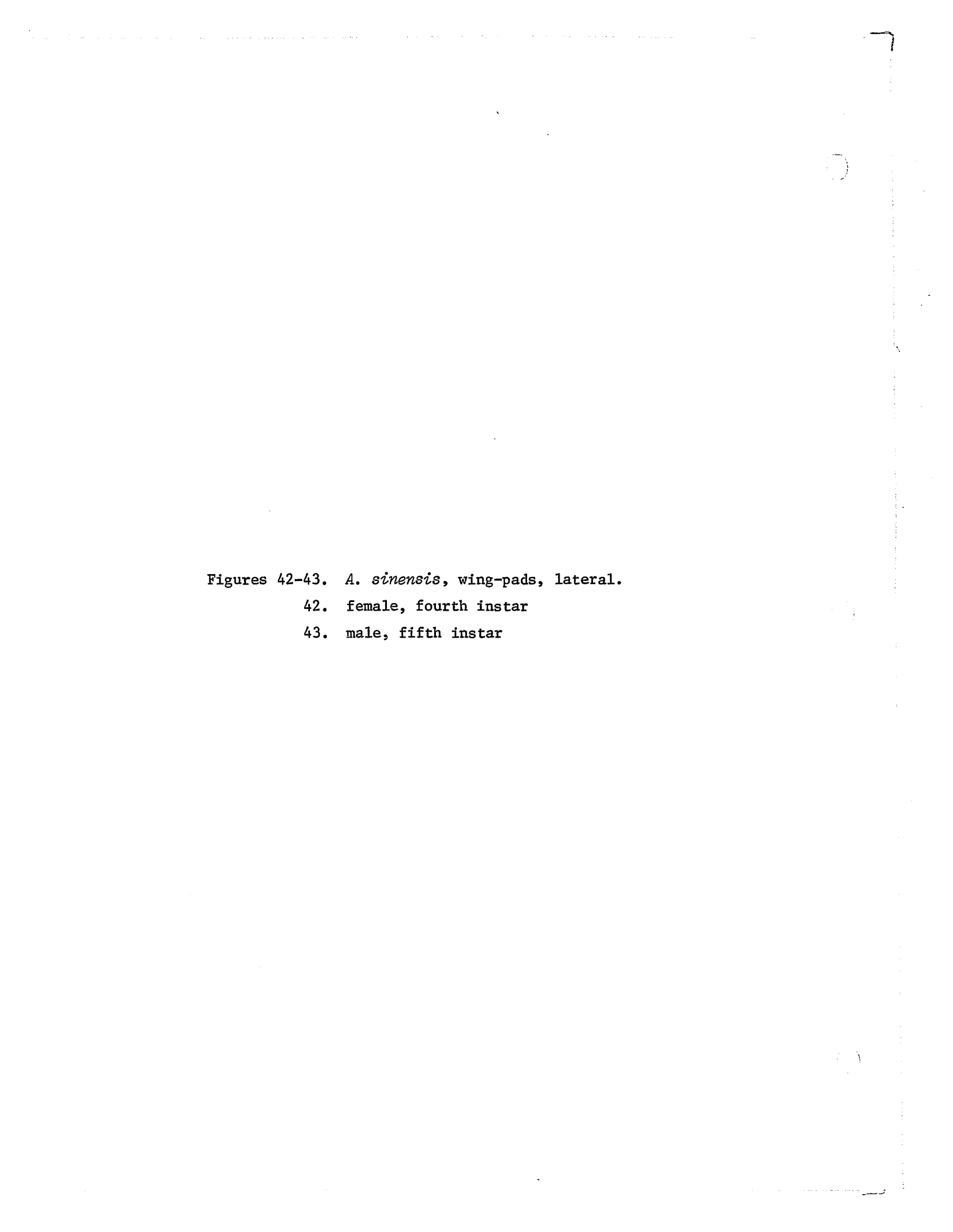


fig.41

1mm



Figures 42-43. *A. sinensis*, wing-pads, lateral.

42. female, fourth instar

43. male, fifth instar

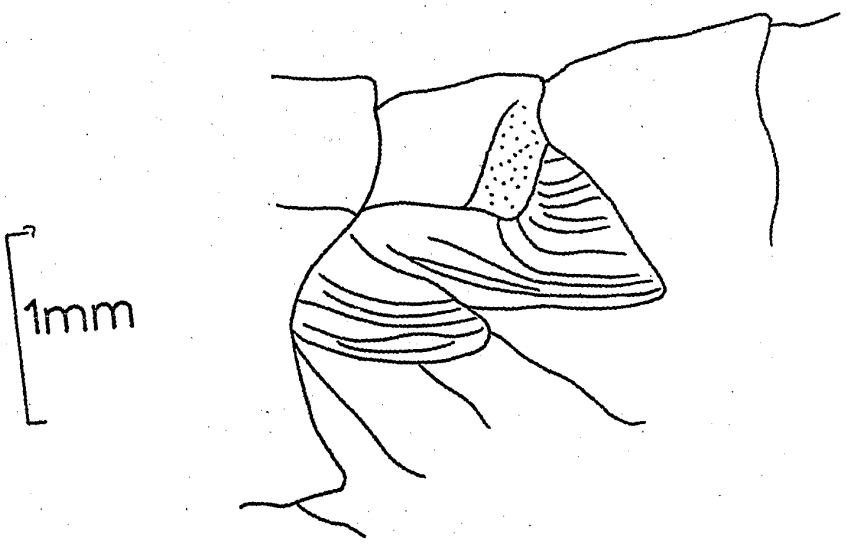


fig.42

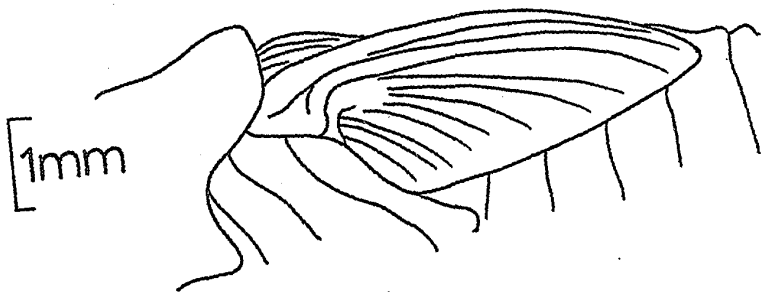
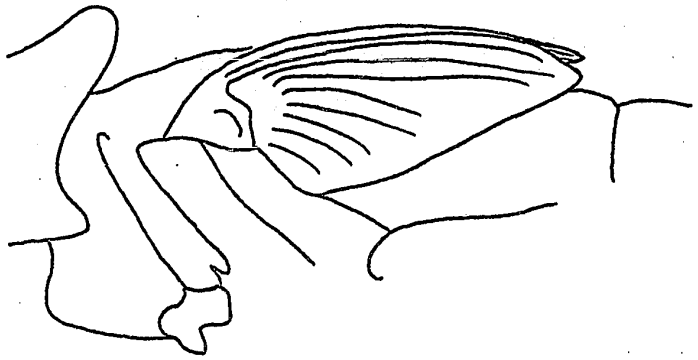


fig.43

Figure 44. *A. sinensis*, male hind wing-pad, lateral, sixth instar.



1mm

fig.44

Figure 45. Ventral view of male and female genital appendages, first instar nymph of *A. sinensis*.

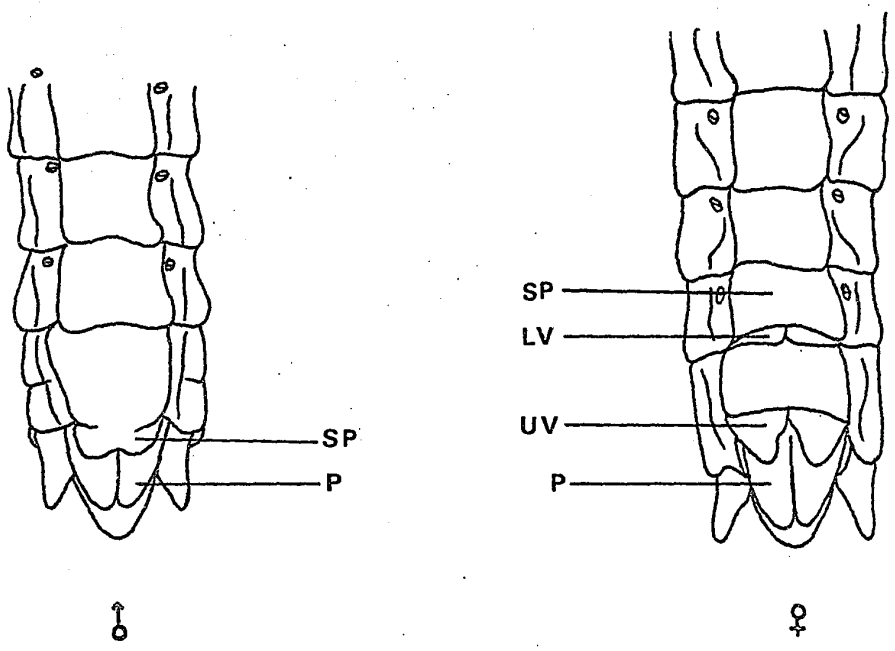


fig. 45

Figure 46. Ventral view of male and female genital appendages, second instar nymph of *A. sinensis*.

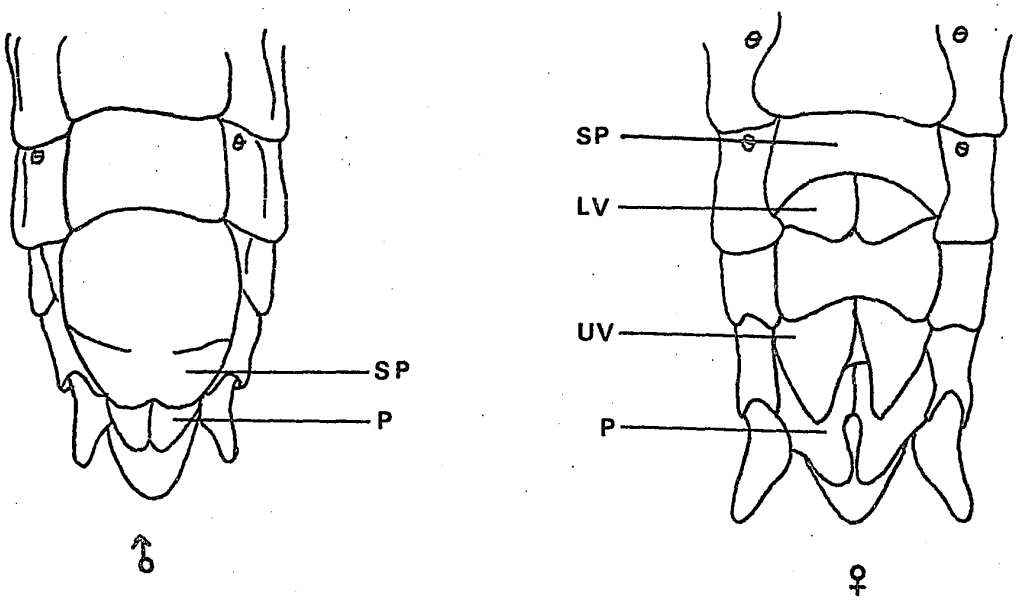


fig.46

Figure 47. Ventral view of male genital appendages, third instar nymph of *A. sinensis*.

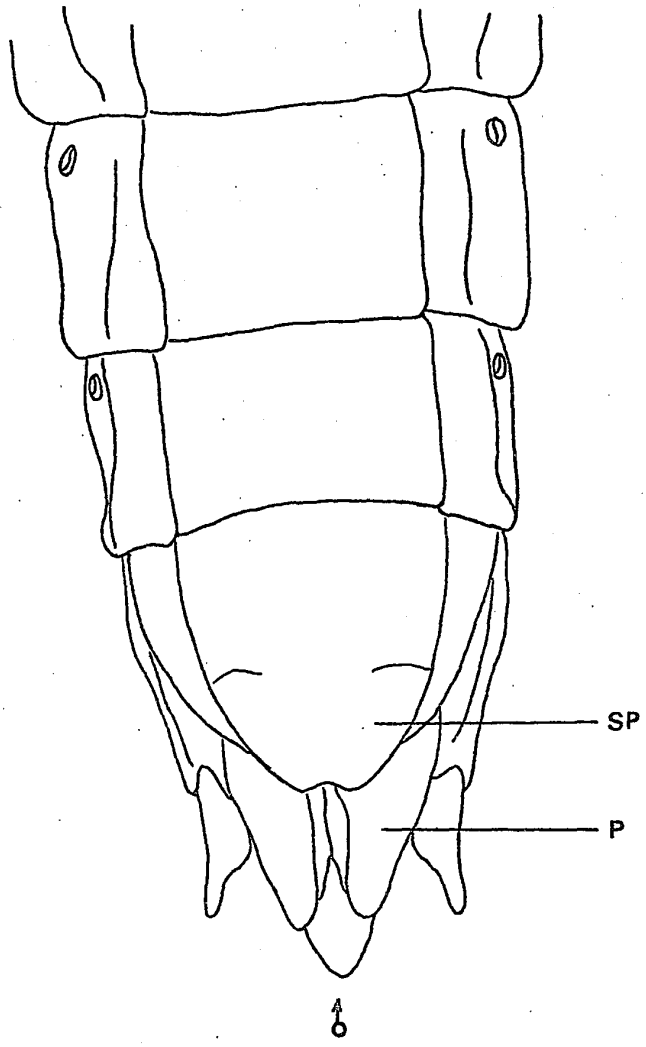
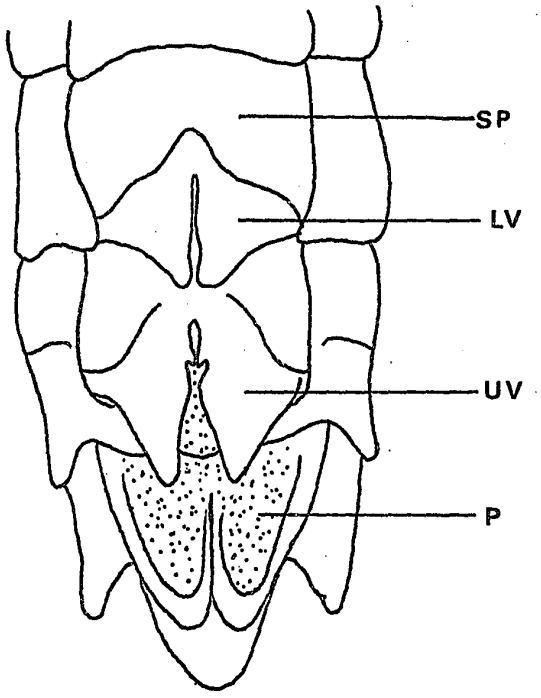


fig.47

Figure 48. Ventral view of female genital appendages, third instar nymph of *A. sinensis*.



1mm

fig.48

Figure 49. Ventral view of male genital appendages, fourth instar nymph of *A sinensis*.

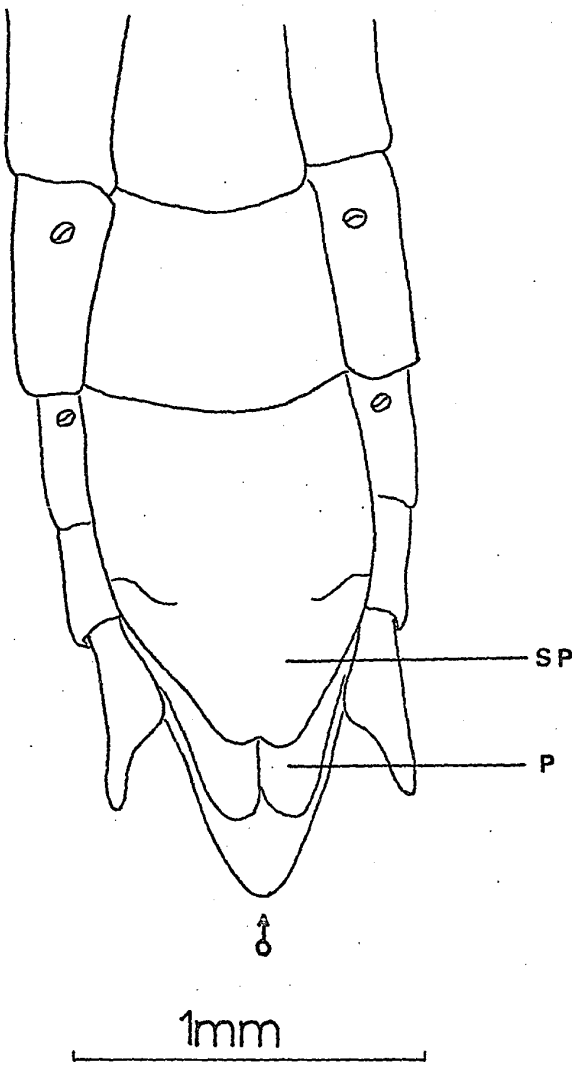
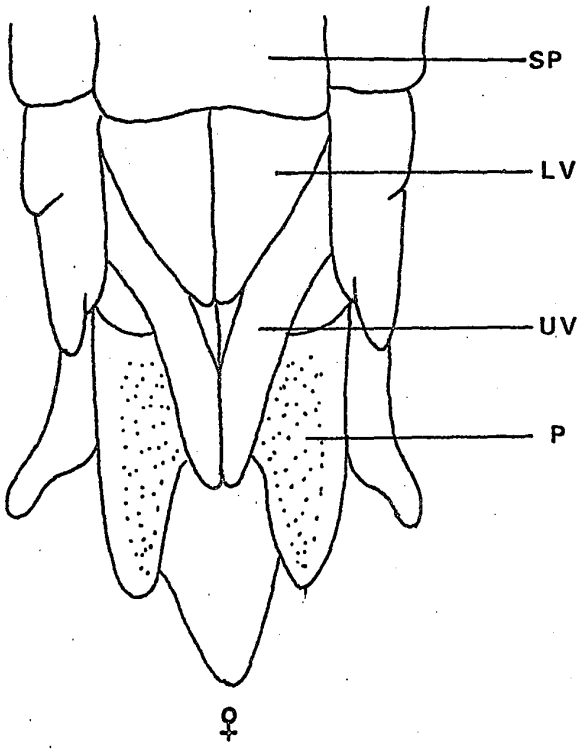


fig.49

Figure 50. Ventral view of female genital appendages, fourth instar of *A. sinensis*.



1mm

fig.50

Figure 51. Ventral view of male genital appendages, fifth instar nymph of *A. sinensis*.

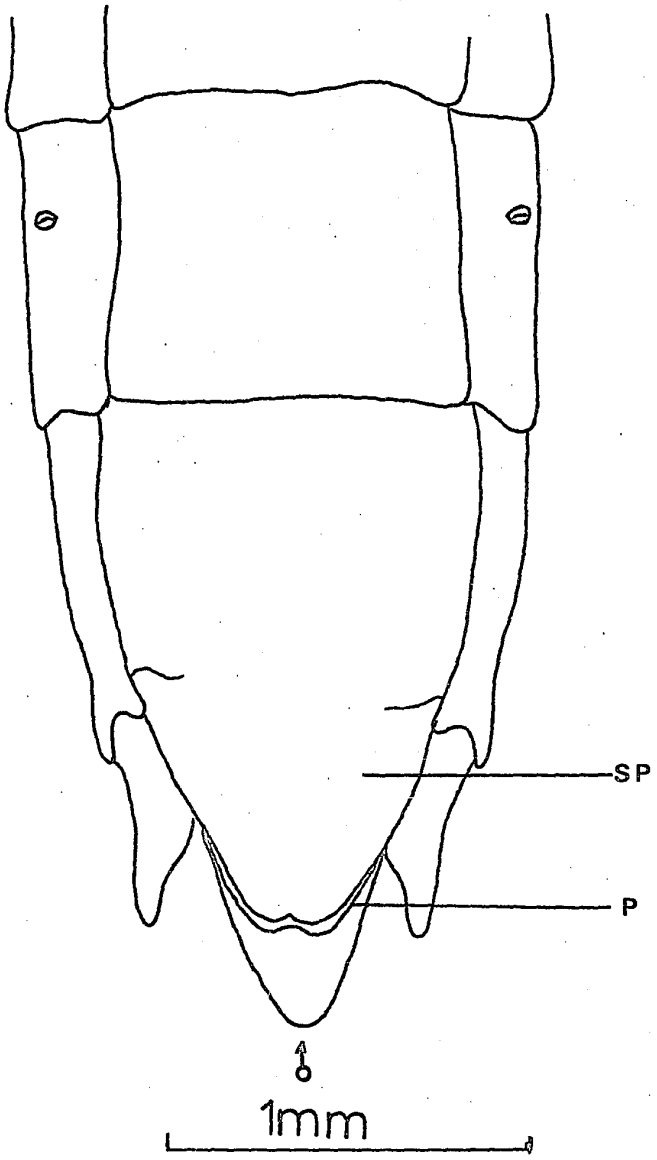


fig.51

Figure 52. Ventral view of female genital appendages, fifth instar nymph of *A. sinensis*.

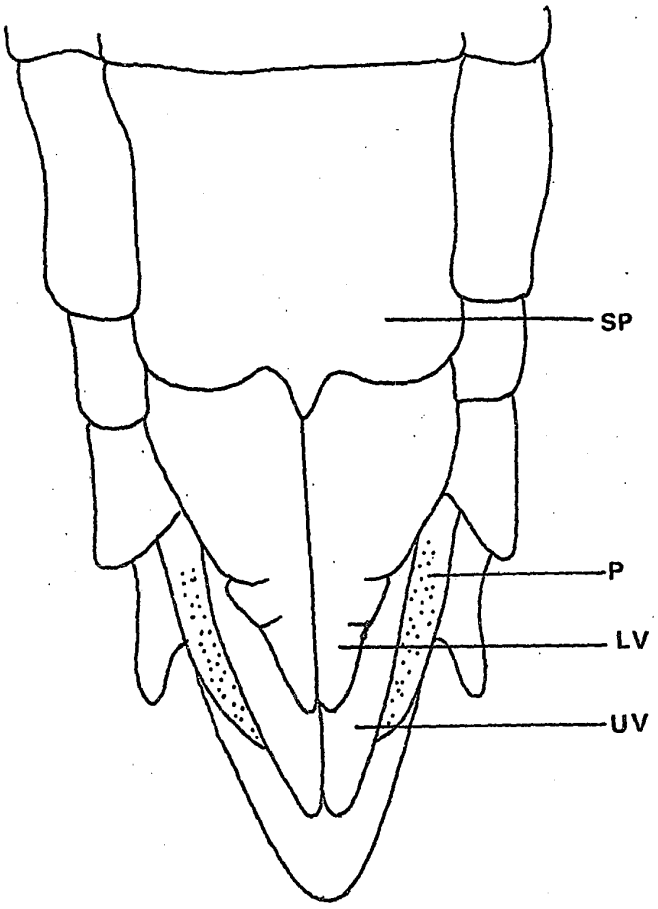


fig.52

Figure 53. Ventral view of male genital appendages, sixth instar nymph of *A. sinensis*.

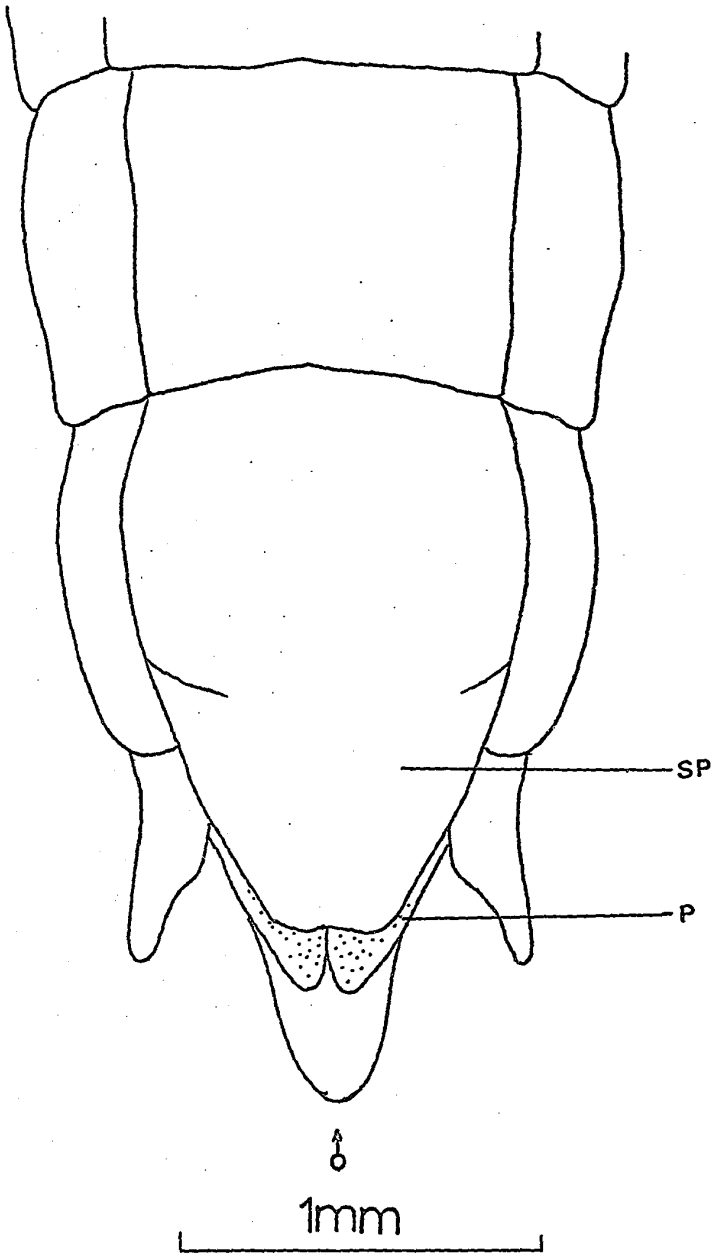


fig. 53

Figure 54. Ventral view of female genital appendages, sixth instar nymph of *A. sinensis*.

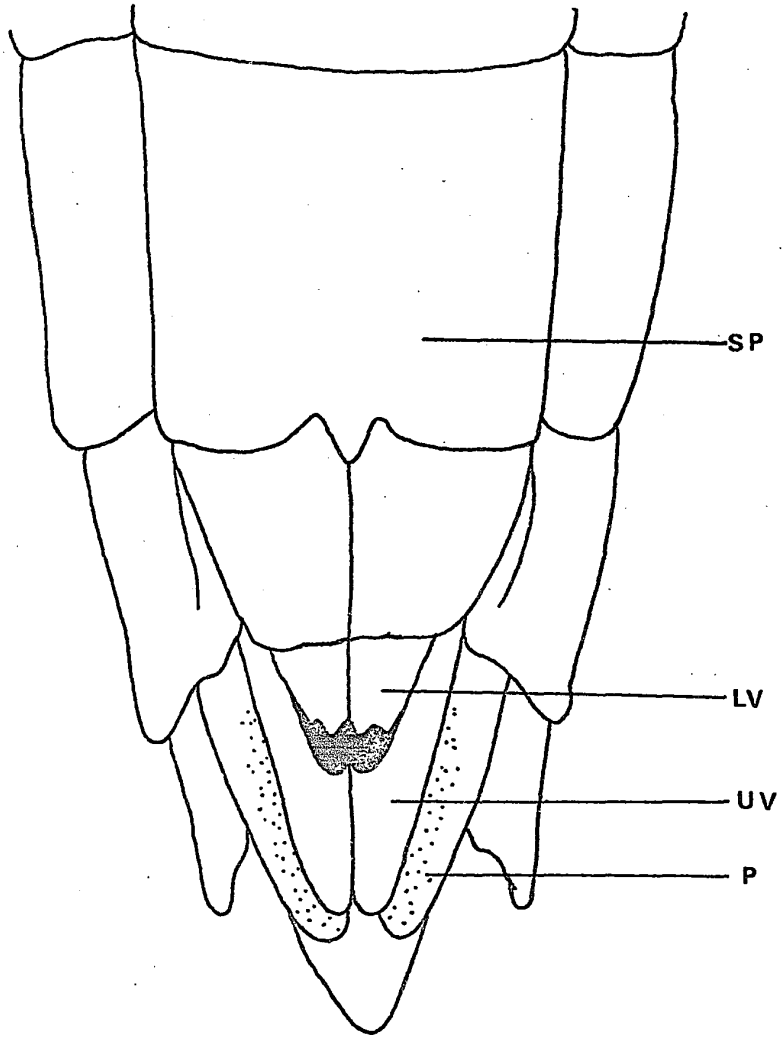


fig.54

Figure 55. Ventral view of female genital appendages, seventh instar nymph of *A. sinensis*.

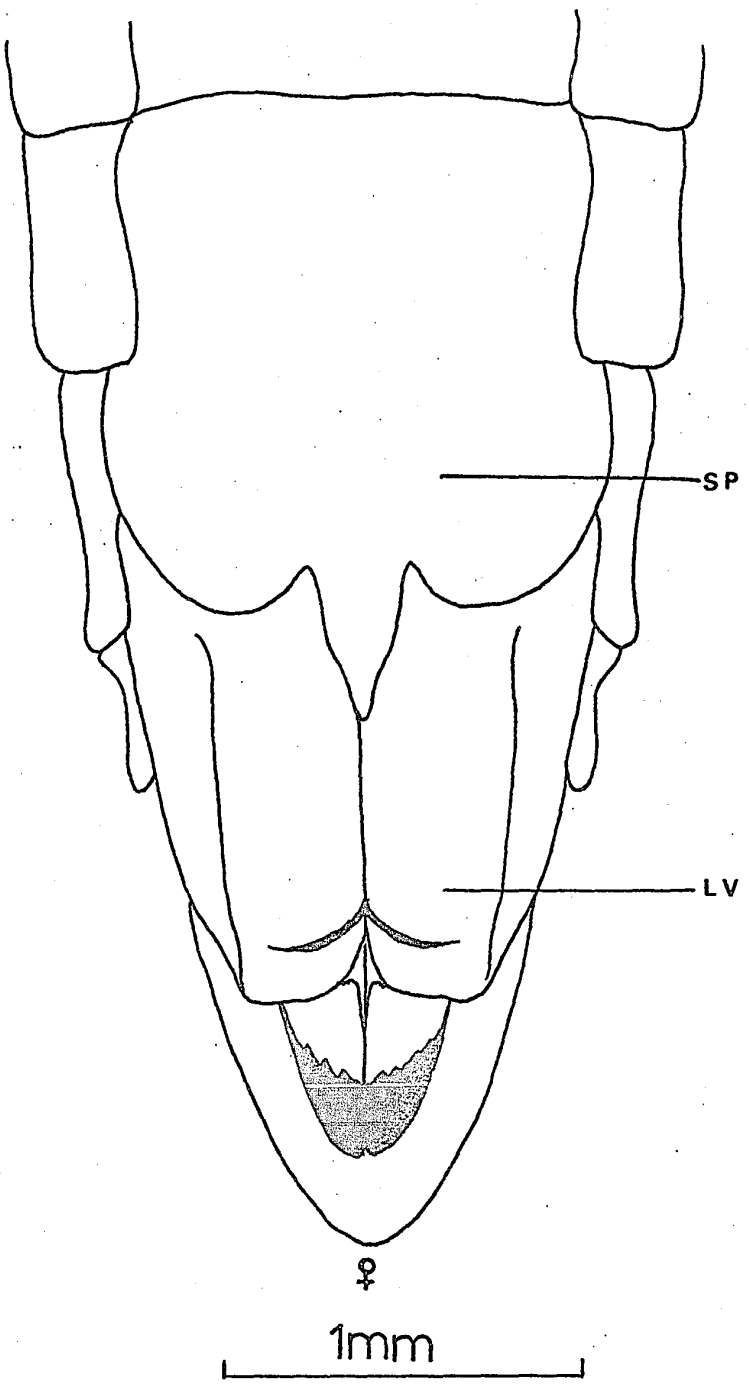
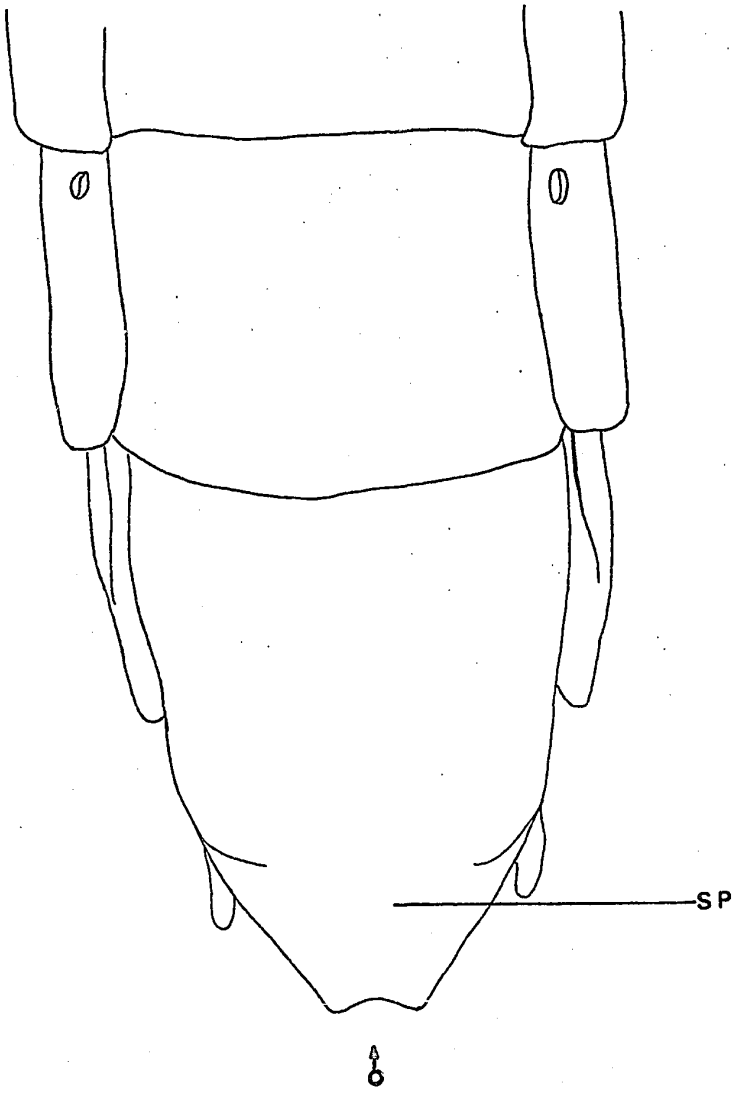


fig. 55

Figure 56. Ventral view of adult male genital appendages of *A. sinensis*.



1mm

fig.56

Figure 57. Ventral view of adult female genital appendages of *A. sinensis*.

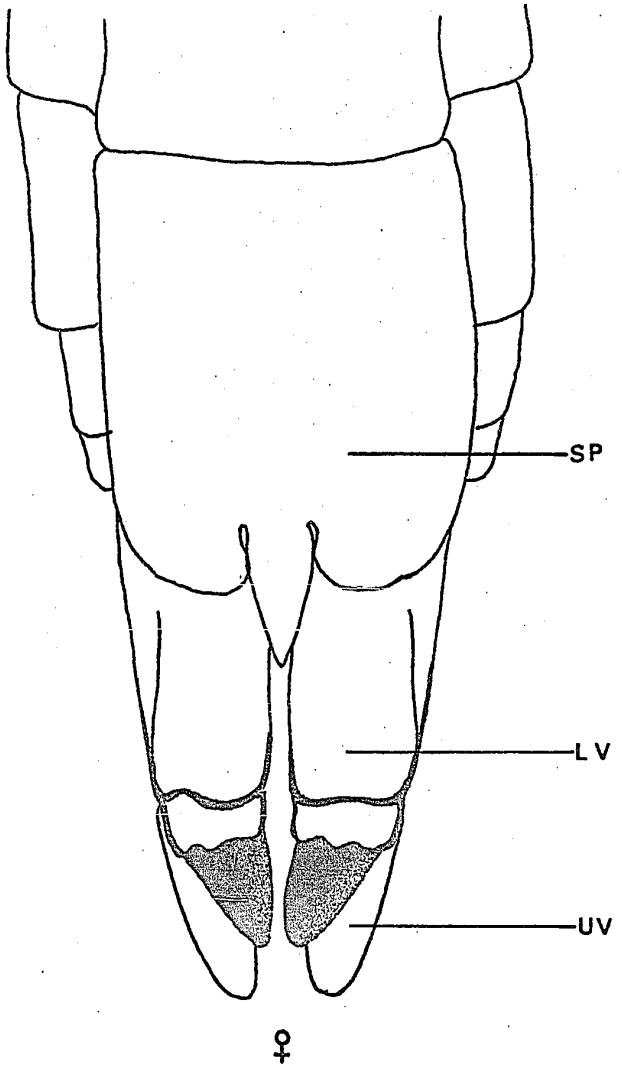


fig.57

Figure 58. T. S. of abdomen at cephalic portion of rudimentary penial body during first instar.

Figure 59. T. S. of abdomen at distal portion of rudimentary penial body during first instar.

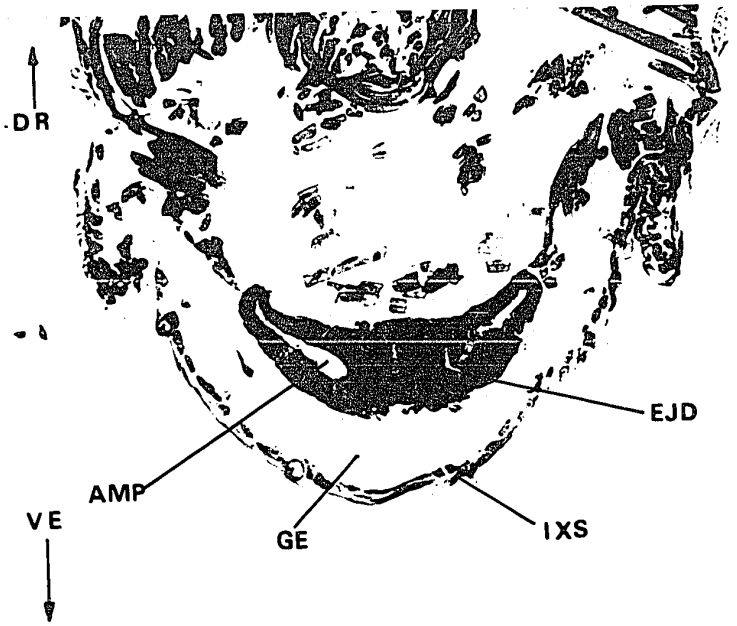


fig.58

0.2 mm

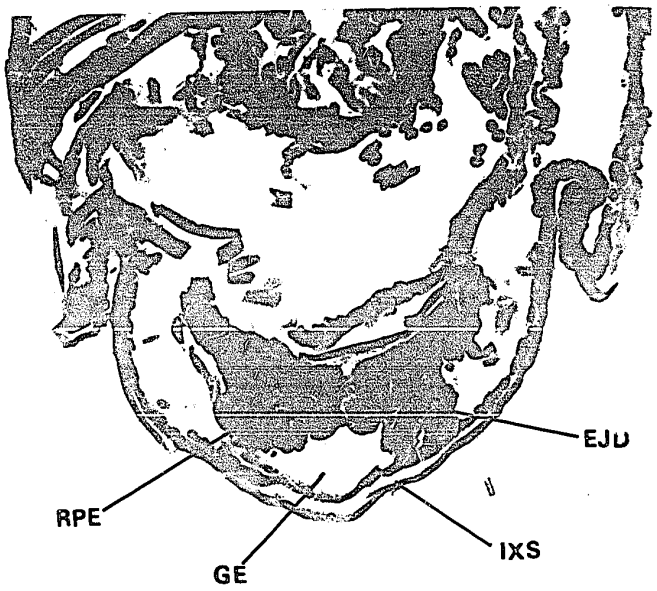


fig.59

Figure 60. L. S. of abdomen showing rudimentary accessory gland and penial body, first instar.

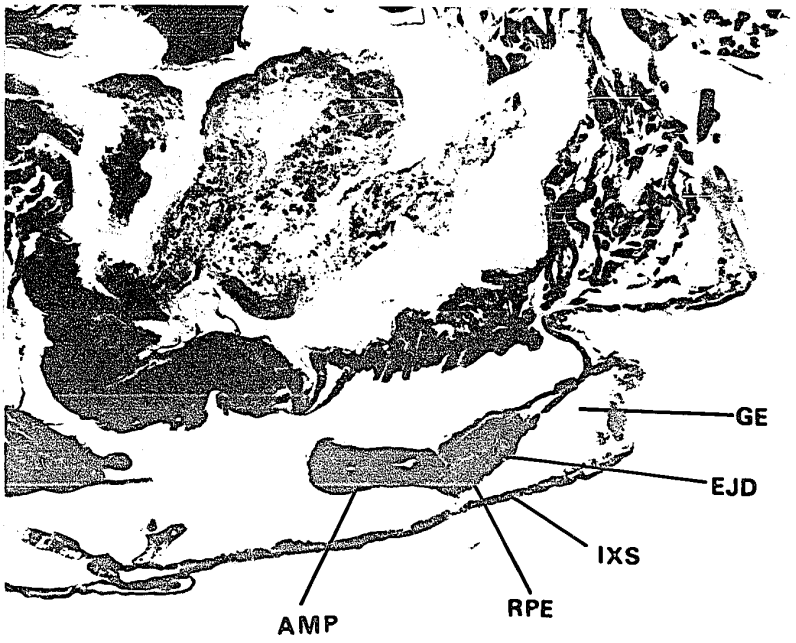


fig.60

0.2mm

Figure 61. T. S. of abdomen at cephalic portion of rudimentary penial body during second instar.

Figure 62. T. S. of abdomen at distal portion of rudimentary penial body during second instar.

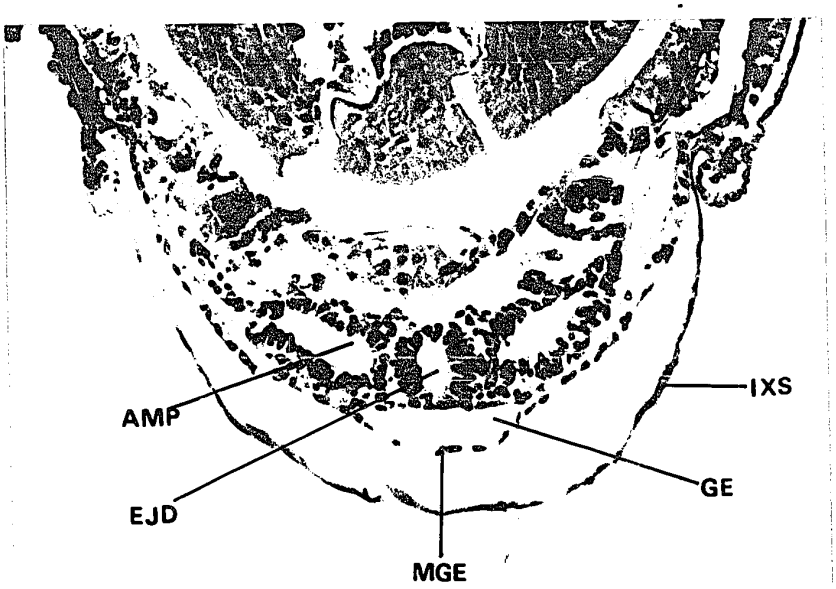


fig.61

0.2mm

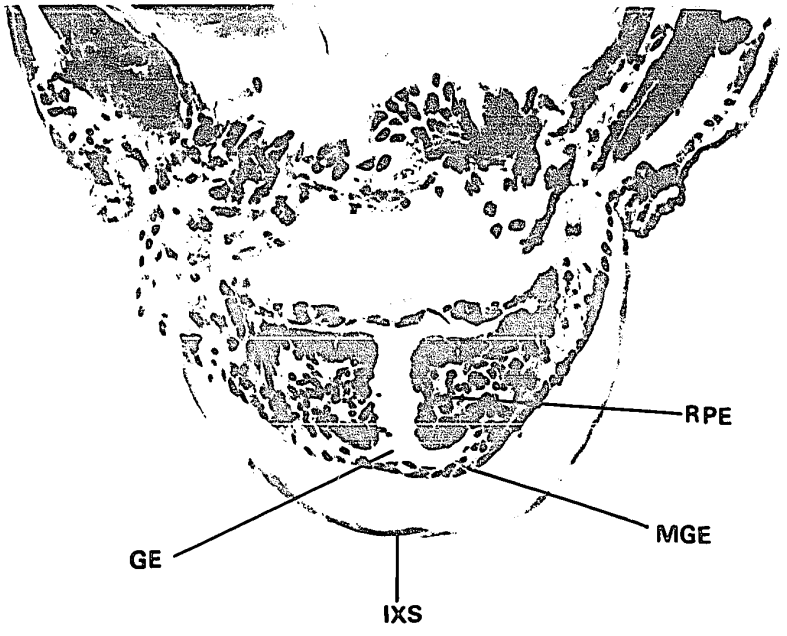


fig.62

Figure 63. L. S. of abdomen showing rudimentary accessory gland and penial body, second instar.

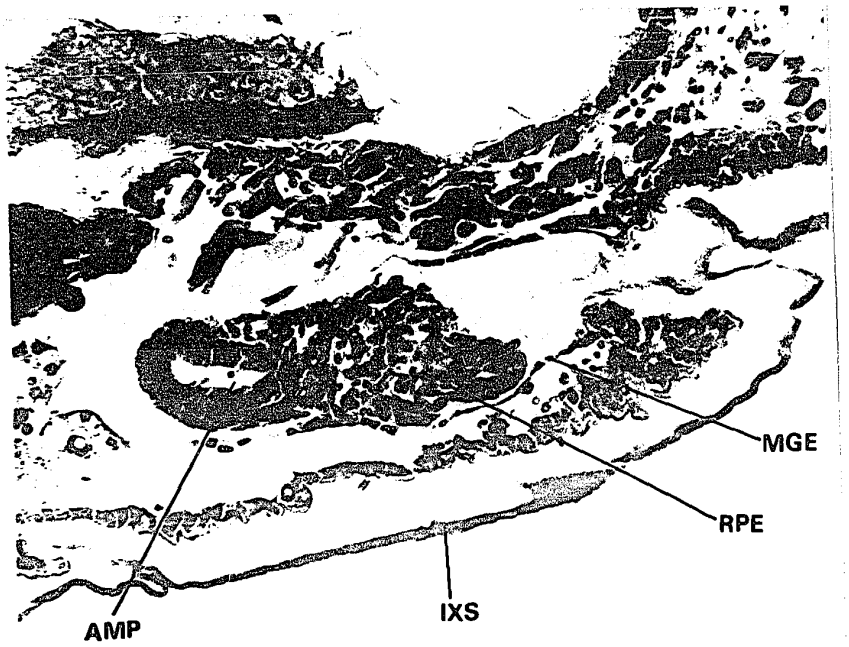


fig.63

0.2mm

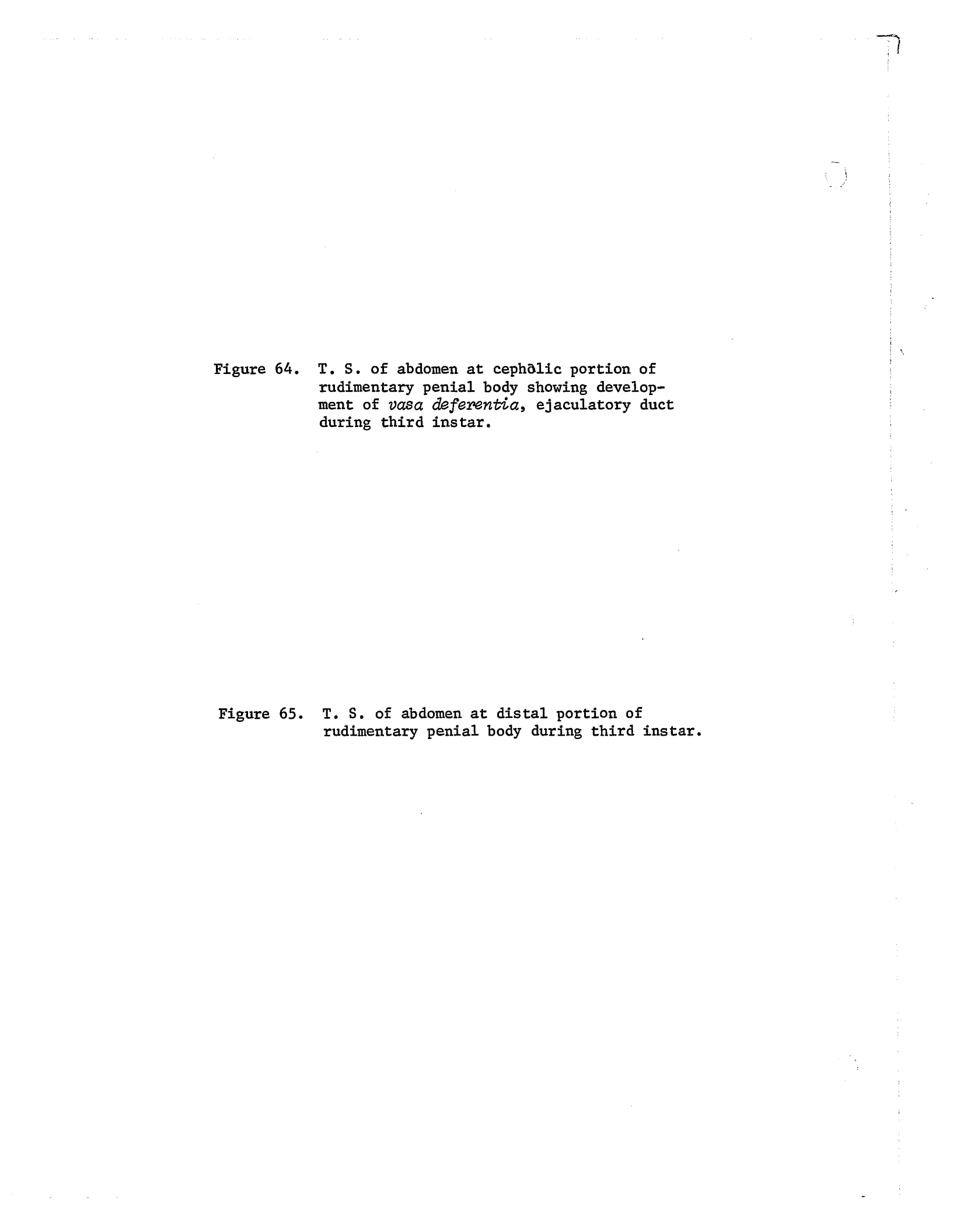


Figure 64. T. S. of abdomen at cephalic portion of rudimentary penial body showing development of *vasa deferentia*, ejaculatory duct during third instar.

Figure 65. T. S. of abdomen at distal portion of rudimentary penial body during third instar.

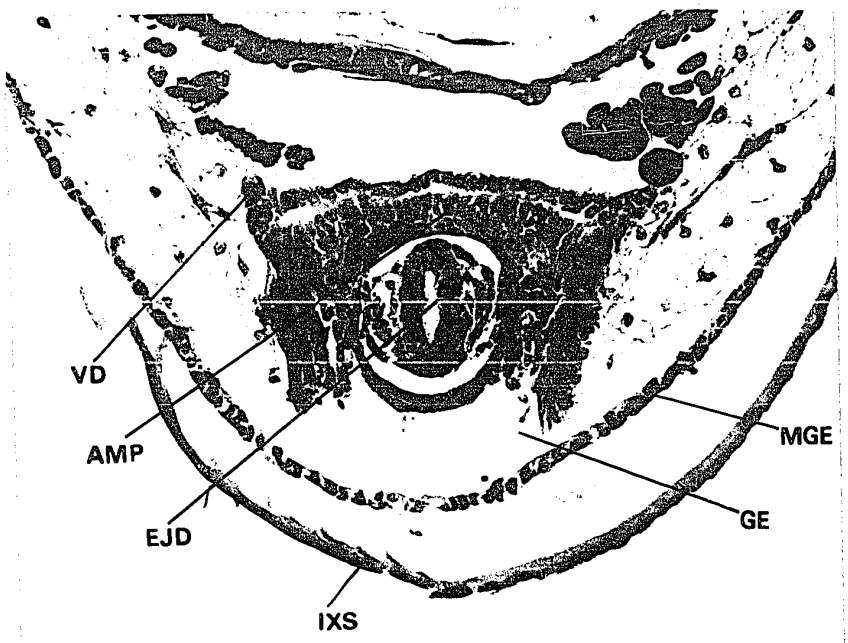


fig.64

0.2mm

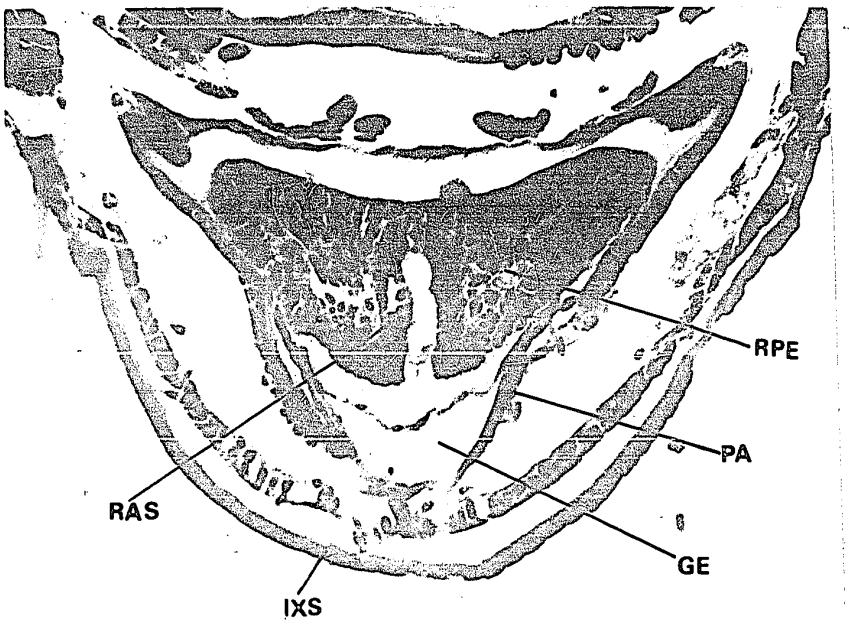


fig.65

Figure 66. L. S. of abdomen showing development of rudimentary accessory glands and penial body, third instar.

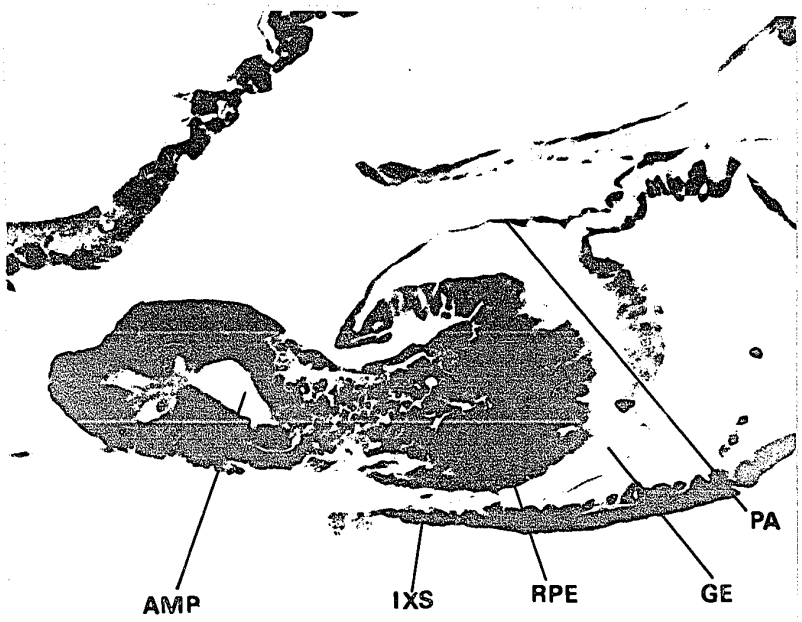


fig.66

0.2mm

Figure 67. T. S. of abdomen at cephalic portion of rudimentary penial body showing development of accessory glands and *vasa deferentia* during fourth instar.

Figure 68. T. S. of abdomen at cephalic portion of rudimentary penial body showing development of epiphallus, ectophallus and endophallus, during fourth instar.

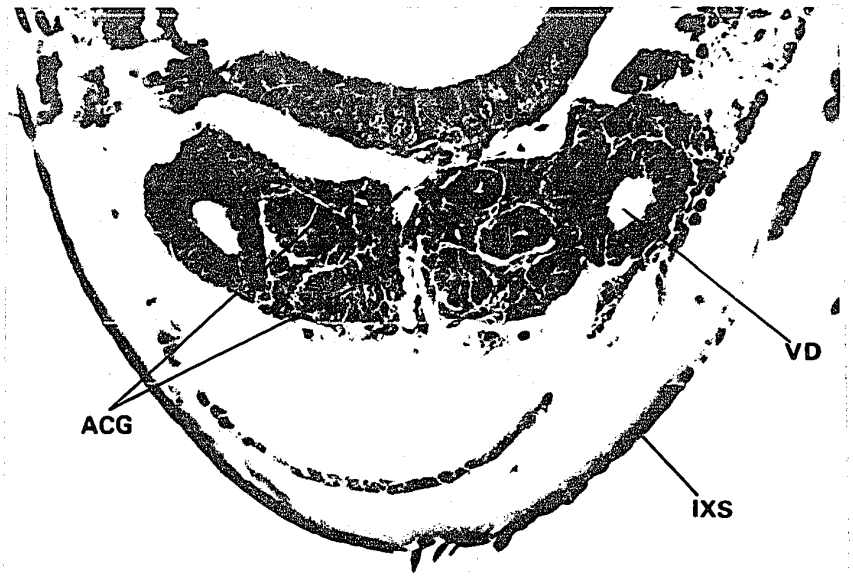


fig.67

0.2mm

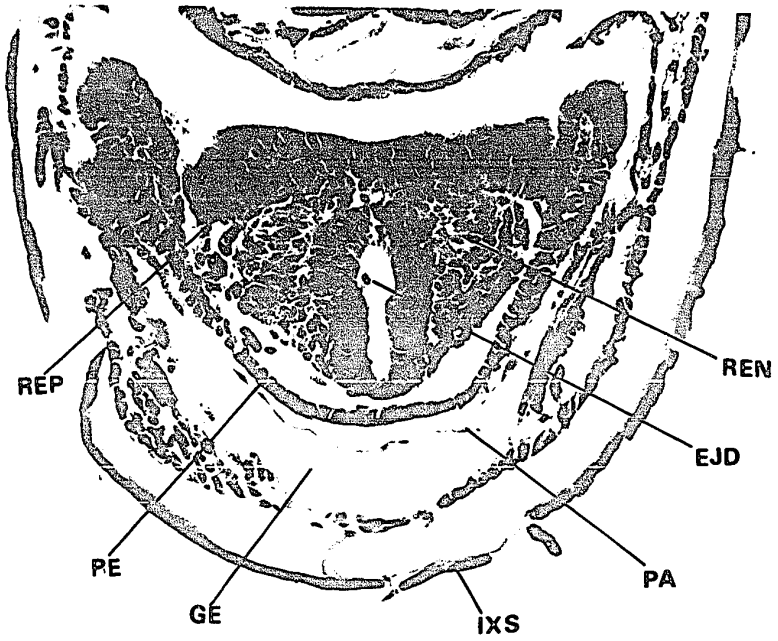


fig.68

Figure 69. T. S. of abdomen at distal portion of rudimentary penial body showing development of aedeagal sclerites during fourth instar.

Figure 70. L. S. of abdomen showing development of the phallic structures during fourth instar.

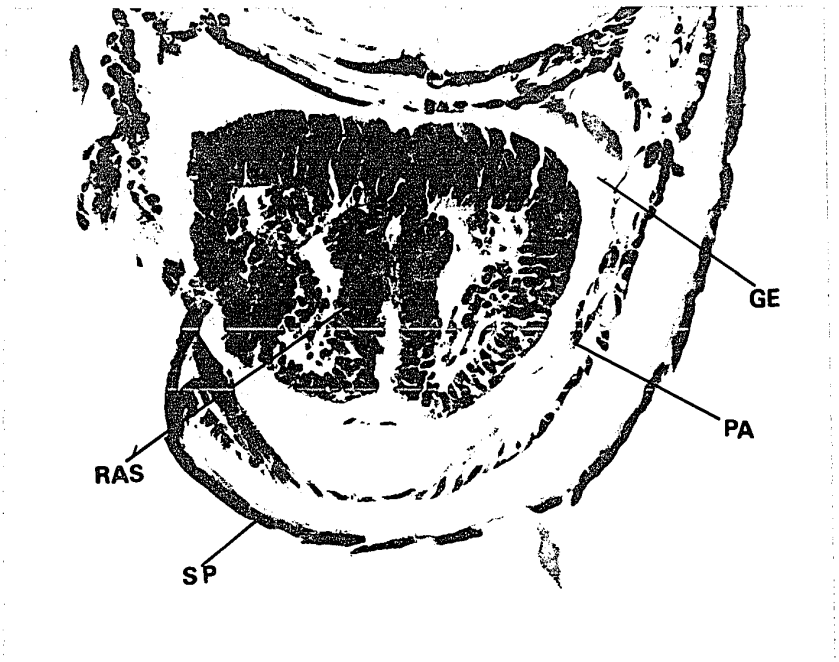


fig.69 0.2mm

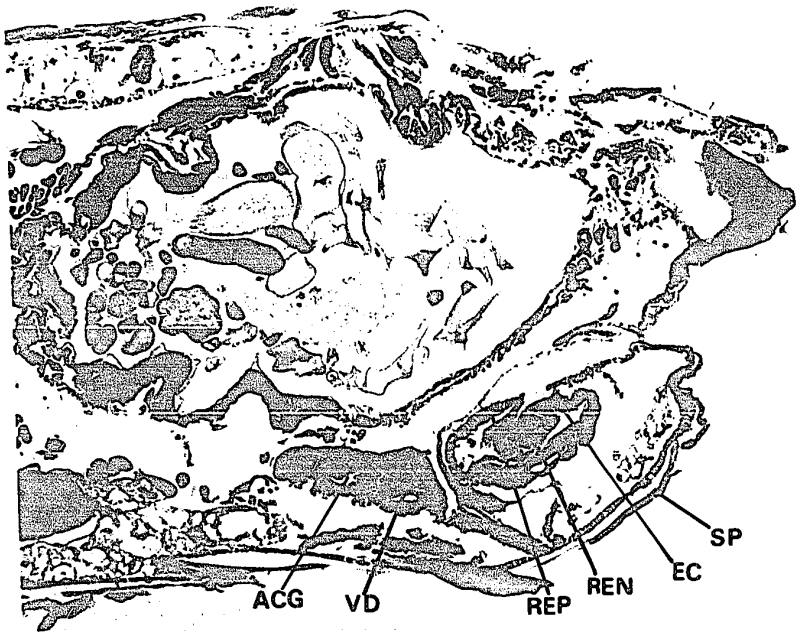


fig.70 0.2mm

Figure 71. T. S. of end of abdomen, showing development of the phallic structures during fifth instars.

Figure 72. L. S. of abdomen showing development of the phallic structures during fifth instar.

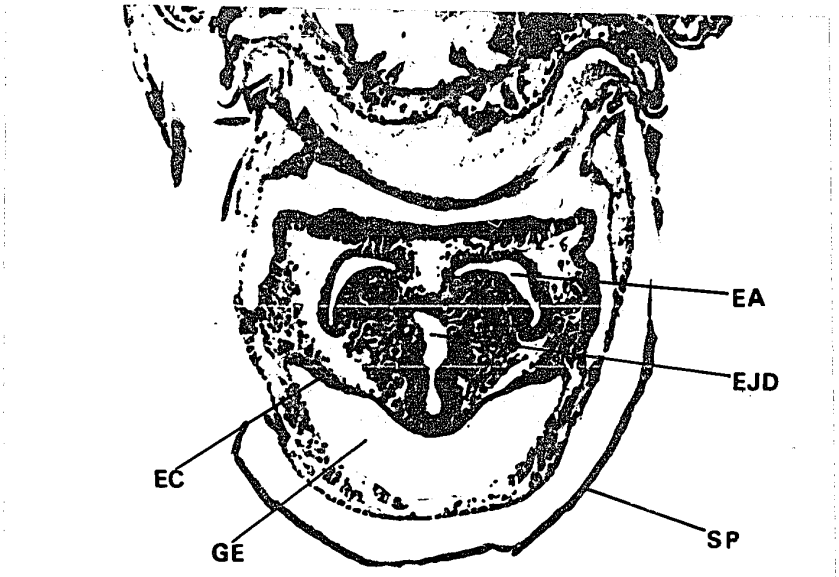


fig.71

0.2mm

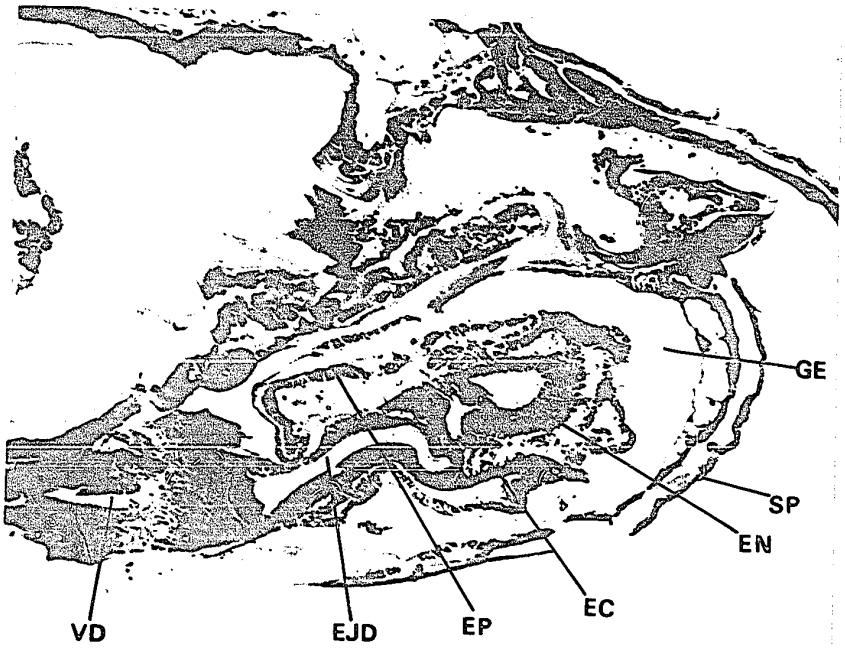


fig.72

Figure 73. T. S. of end of abdomen showing development of the phallic structures during sixth instar.

Figure 74. T. S. of end of abdomen showing development of the spermatophore sac and aedeagal sclerites during sixth instar.

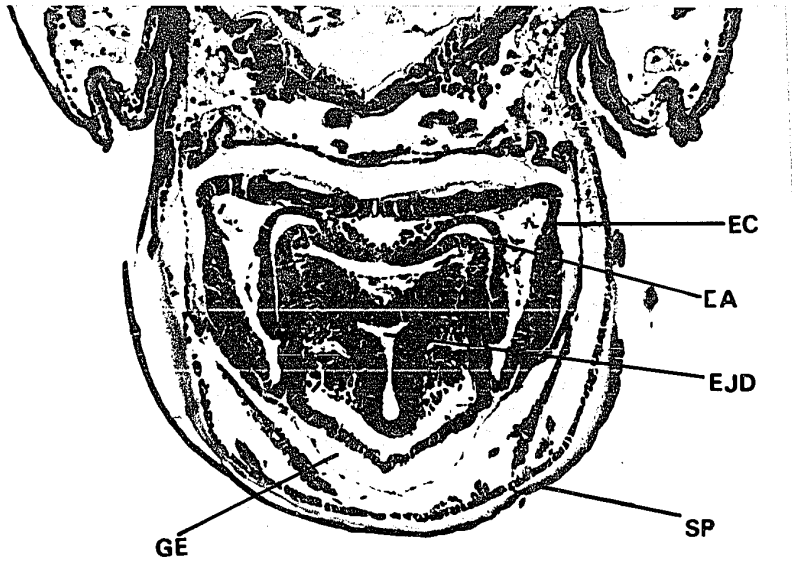


fig.73

0.2mm

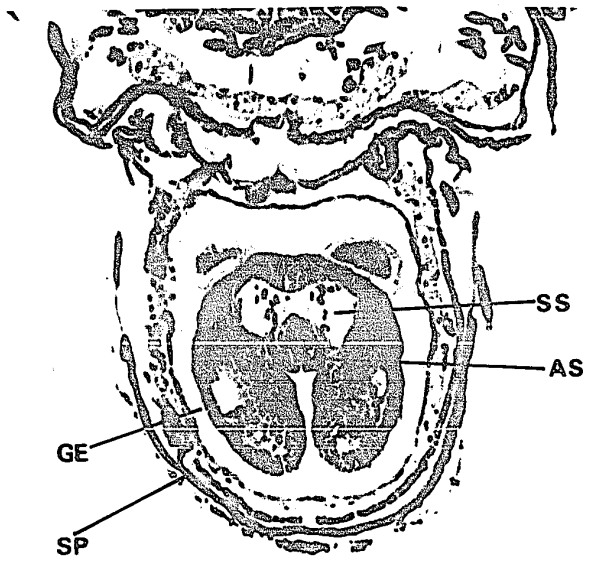


fig.74

Figure 75. L. S. of abdomen showing development of phallic structures during the sixth instar.

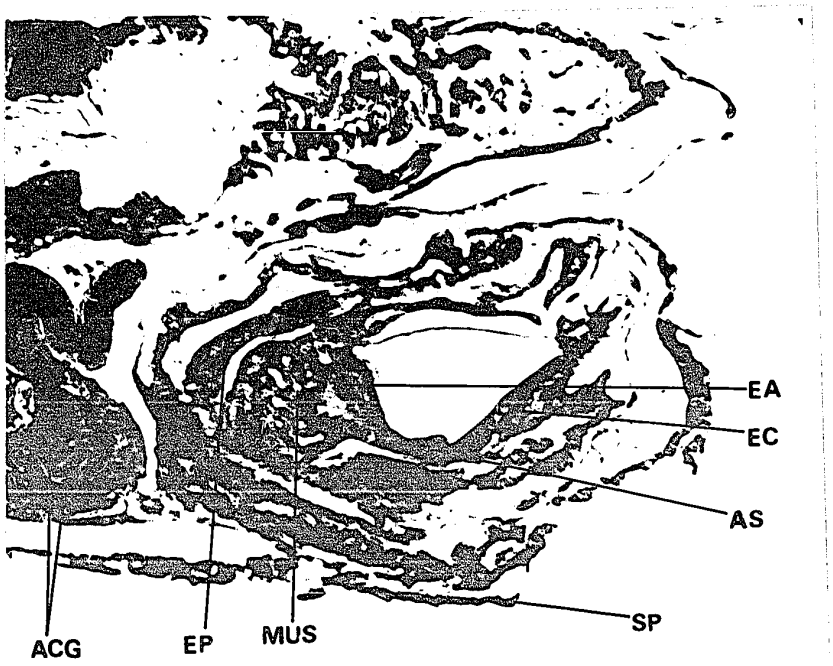


fig.75

0.2mm

Figure 76. T. S. of end of abdomen showing different parts of the phallic complex in adult male.

Figure 77. L. S. of abdomen showing different parts of the phallic complex in adult male.

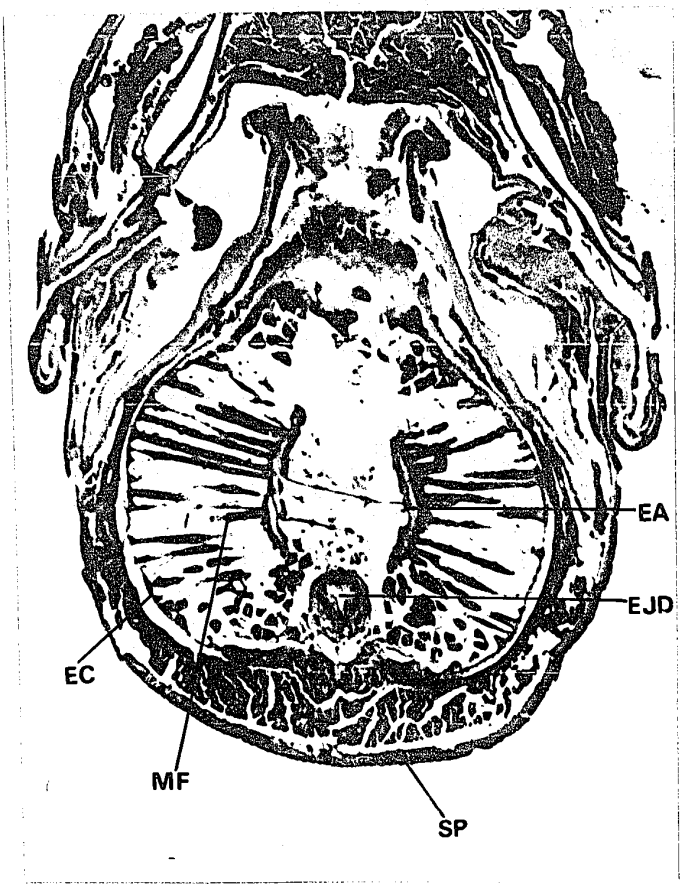


fig.76

0.2mm

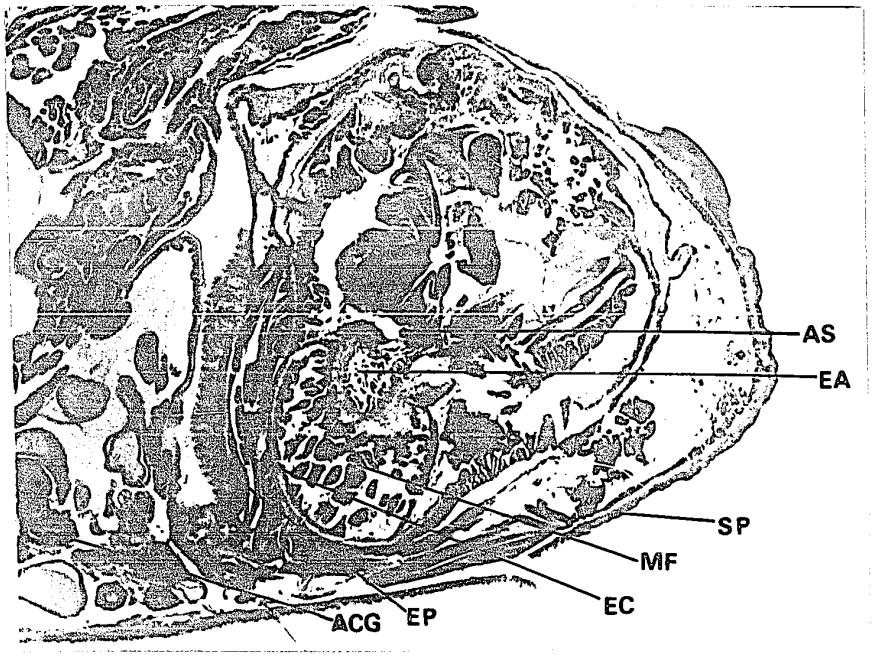


fig.77

Figure 78. Epiphalli of *A. sinensis*, dorsal, showing progressive sclerotization.

a. of just matured adult
b. 7 days after maturity
c. 14 days after maturity
d. 21 days after maturity
e. 32 days after maturity

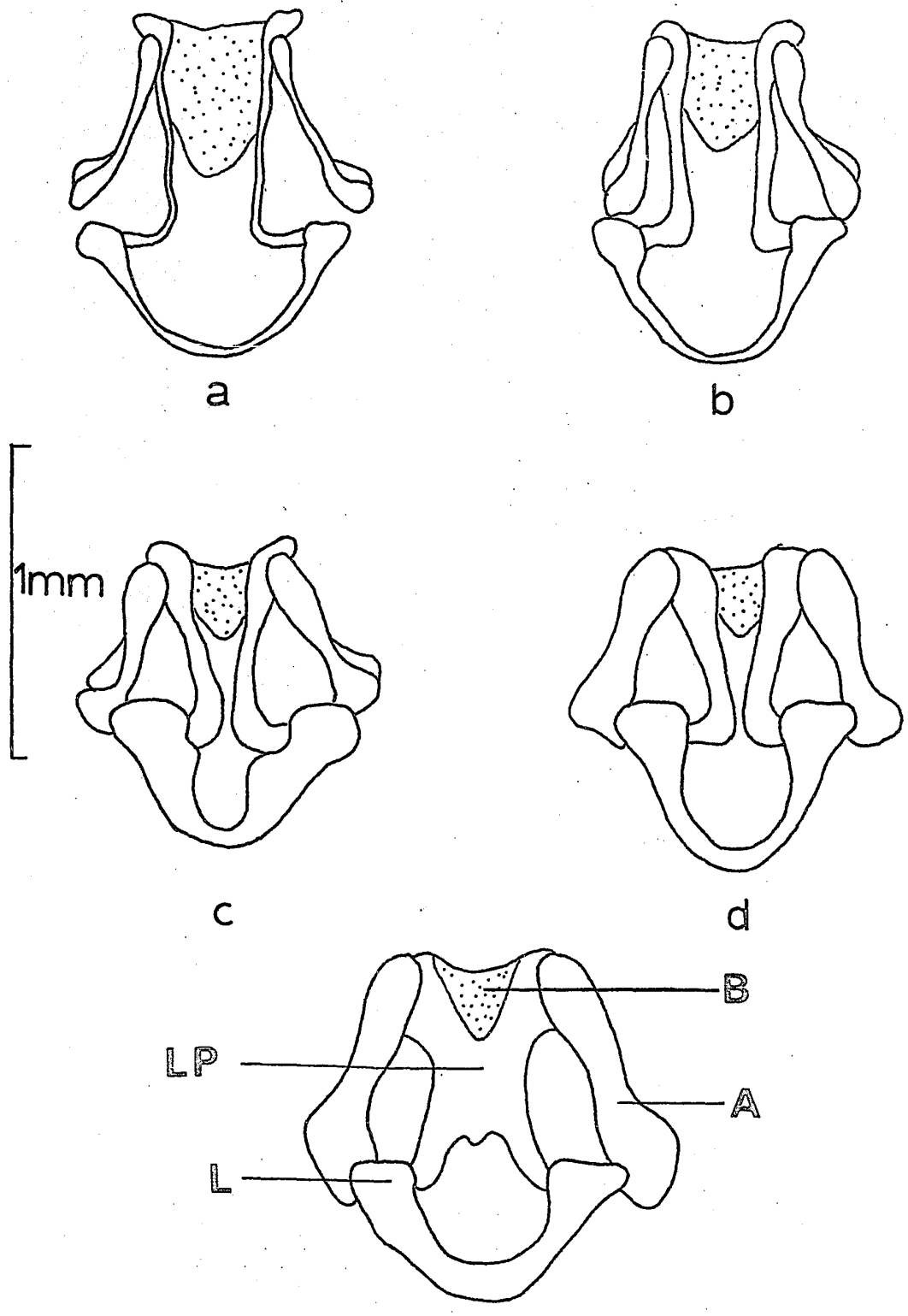


fig. 78

Figure 79. Ectophalli of *A. sinensis*, dorsal, showing progressive sclerotization.

a-e. as in Figure 78.

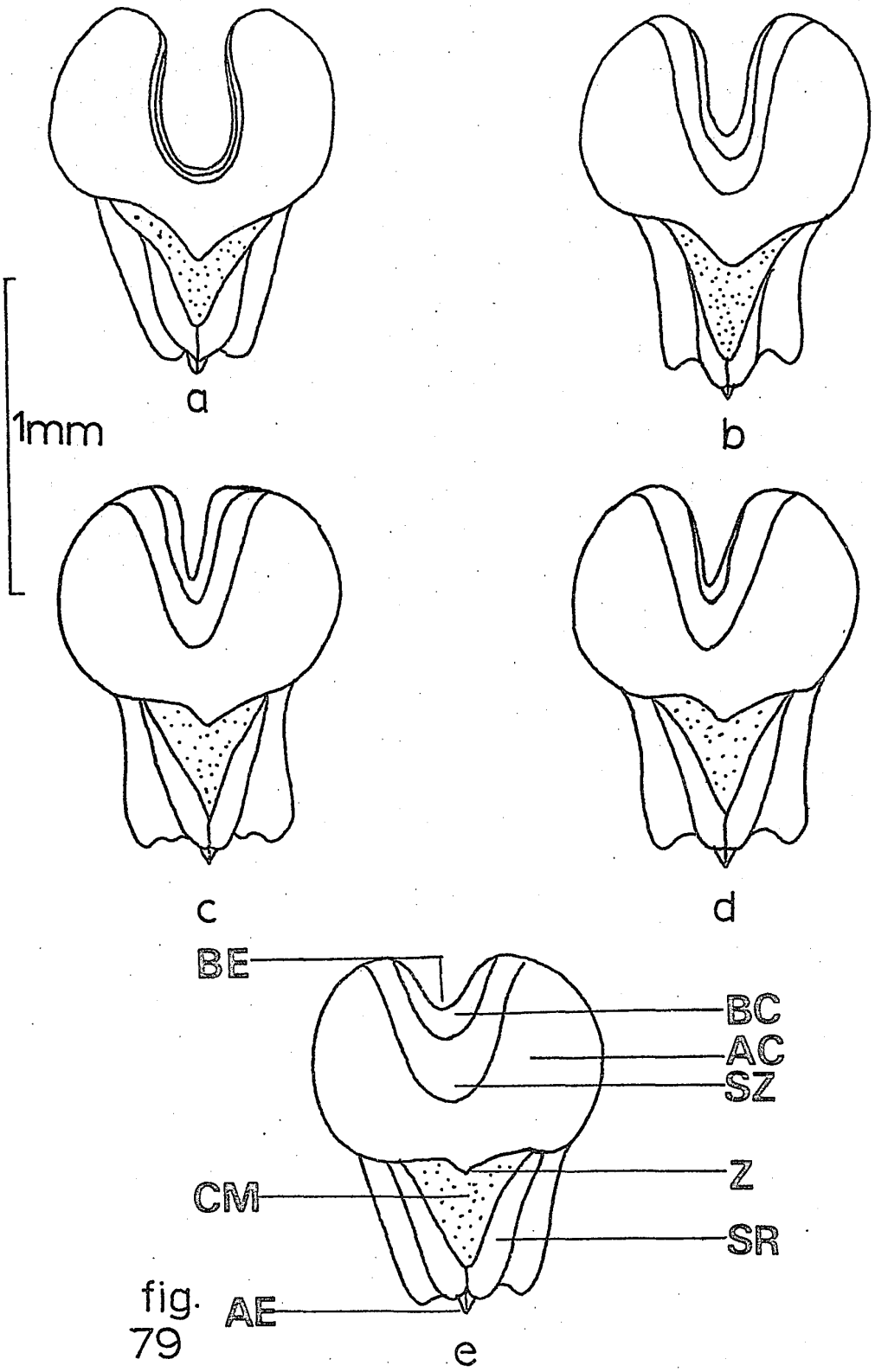


fig. 79

Figure 80. Endophalli of *A. sinensis*, dorsal, showing progressive sclerotization.

a-e. as in Figure 78.

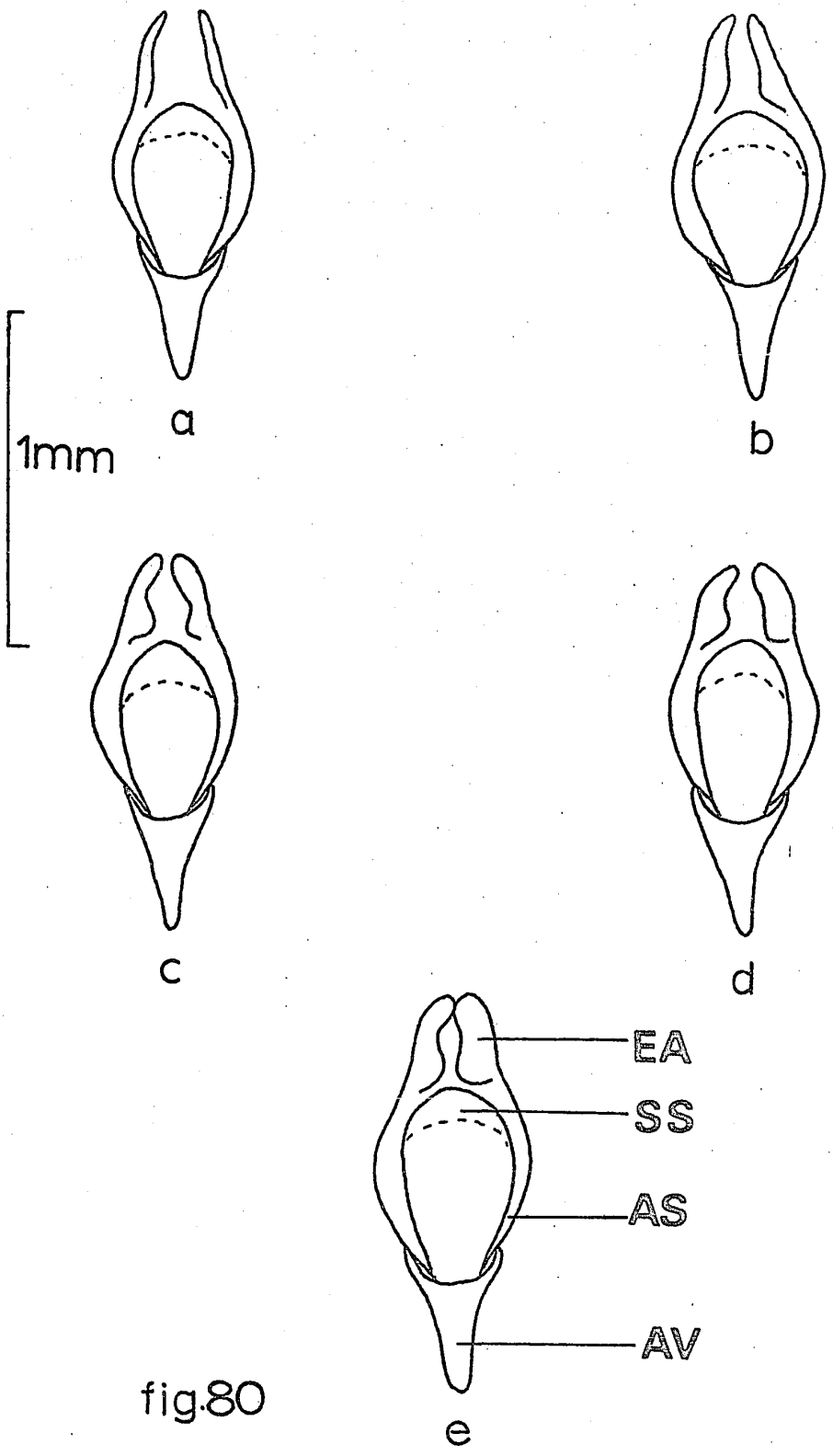


fig.80

Figure 81. Endophalli of *A. sinensis*, lateral, showing progressive sclerotization.

a-e. as in Figure 78.

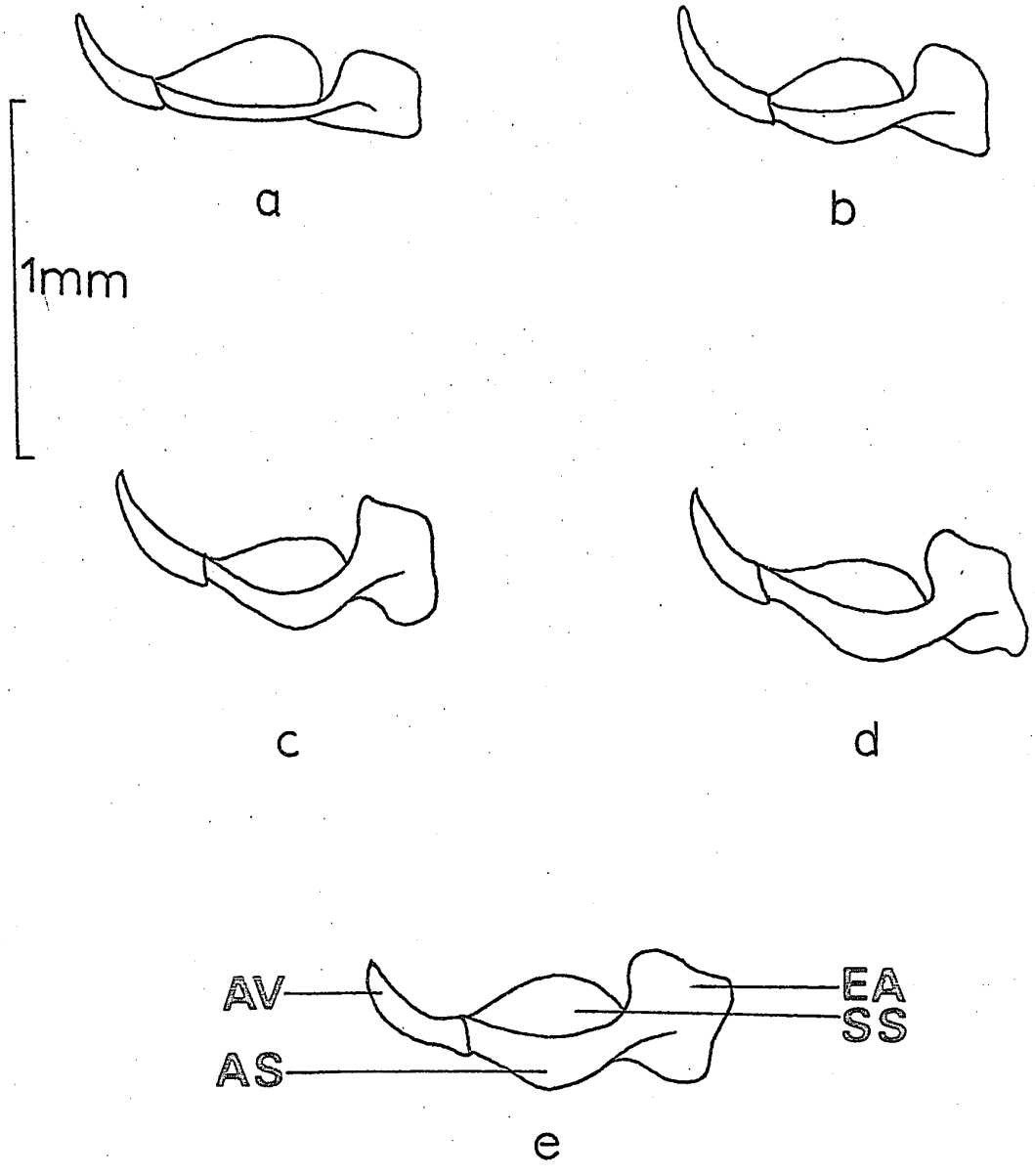


fig.81

LIST OF ABBREVIATIONS

A	Appendices of epiphallus
ACG	Accessory glands
AE	Aedeagus
AL	Apodemal plates of cingulum
AMP	Ampulla
AS	Aedeagal sclerite
AV	Aedeagal valve
B	Bridge of the epiphallus
BC	Basal thickening of cingulum
BE	Basal emargination
CM	Central membrane of cingulum
DR	Dorsal
EC	Ectophallus
EA	Endophallic apodeme
EJD	Ejaculatory duct
EN	Endophallus
EP	Epiphallus
GE	Genital sinus
IXS	9th abdominal sternum
L	Lophus
LP	Lateral plates of epiphallus
LV	Lower valves of ovipositor
MGE	Membrane of genital sinus
MF	Muscle fibre
MUS	Muscle cells
P	Paraproct
PA	Pallium
RAS	Rudimentary aedeagal sclerite
RE	Rudimentary glands
REN	Rudimentary endophallus
REP	Rudimentary epiphallus
RPE	Rudimentary penial body

SP	Subgenital plate
SR	Supraramus
SS	Spermatophore sac
SZ	Suprazygomal plate
UV	Aedeagal valve
VD	*Vasa deferentia*
VE	Ventral
Z	Zygoma

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